

Understanding disturbance, facilitation, and competition for conservation of whitebark pine in the Canadian Rockies

by

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Abstract

Understanding forest resilience to novel disturbances and how tree interactions will be affected by global change is critical for predicting future forest composition. The widespread decline of the endangered whitebark pine (*Pinus albicaulis*) in the Canadian Rockies due to non-native white pine blister rust (*Cronartium ribicola*) and native mountain pine beetle (*Dendroctonus ponderosae*) and *Ips* sp. permitted examination of interactions between disturbances and tree responses in high-elevation forests. Disturbance severity was high with 20-90% whitebark pine mortality over 50 years in 16 stands. Basal annual increment (BAI) of whitebark pines prior to mortality from mountain pine beetles declined 46%, but only by 25% for those subsequently killed by blister rust and *Ips* sp.. Climate-growth relationships suggest blister rust increased sensitivity of whitebark pines to variation in summer precipitation, reducing resistance to beetles. The mortality of whitebark pine was used as an *in-situ* experiment simulating neighbour removal to test the stress-gradient hypothesis of tree interactions. Facilitation intensity, determined by comparing subalpine fir (*Abies lasiocarpa*) regeneration around live, top-killed, or dead adult whitebark pines, increased with elevation but depended on benefactor size and neighbourhood density. Large-diameter, top-killed whitebark pines were more facilitative than live trees, indicating thresholds in benefactor size, below which live, healthy trees were facilitators and above which they were competitors. Size thresholds were also found in interactions between adult trees where competition intensity increased between trees of greater diameter differences as indicated in BAI releases of subalpine fir after the death of neighbouring trees. Conversely, the importance of competition relative to other factors influencing growth increased between trees more similar in size and with abiotic stress. My results refine the stress-gradient hypothesis by demonstrating hierarchical influences on tree interactions. The predominant release from competition doubled subalpine fir's BAI from the landscape average pre-disturbances compensating for the decline predicted by climate-growth relationships. Lack of regeneration and growth release in surviving whitebark pines and an abrupt shift in key variables suggest a regime shift to fir dominance and whitebark pine extirpation. Whitebark pine resilience was higher at sites of low abiotic stress and disturbance severity, relationships useful for conservation.

Preface

This dissertation presents research conducted by Carmen Wong in collaboration with her supervisor, Dr. Lori Daniels. Carmen Wong was the primary investigator and responsible for the design of the research and the collection, analysis and interpretation of the data. Dr. Lori Daniels and Dr. Valerie LeMay provided analytical support and timely reviews throughout the research and the preparation of this dissertation.

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Working on whitebark pine, a species on precipitous decline, has heightened my sensitivity to our impact on the earth. This species is in decline because of our carelessness in how we transported nursery plants from one continent to another. The potential disappearance of whitebark pine from our high-elevation forests should be an admonition for us to walk with care and evaluate our impact on the world.

Dedication

This is dedicated to my Grandma, who wanted to go on in school but couldn't.

I wish I had the chance to celebrate this with you.

Chapter 1: Introduction

Almost every whitebark pine (*Pinus albicaulis*) tree in high-elevation forests of Waterton Lakes National Park, Alberta, Canada, has died because of attacks by the introduced species, white pine blister rust (*Cronartium ribicola*), the native mountain pine beetle (*Dendroctonus ponderosae*) or various *Ips* species of bark beetles. The few trees that remain alive are largely affected by blister rust. However, further north in Jasper National Park and Willmore Wilderness Park, Alberta, there are more live and healthy trees than dead trees in high-elevation forests (Figures 1 and Figure 2). At lower elevations in these northern locations in Alberta, an ongoing outbreak of mountain pine beetle has caused mortality of lodgepole pine (*Pinus contorta*) in thousands of hectares since 2005, and these beetles began to be observed in 2007 at higher elevations in subalpine forests containing whitebark pine (Dr. Joyce Gould, Alberta Parks Division Science Coordinator, pers. comm., 2007). The condition of subalpine forests in Waterton Lakes National Park presents a foreshadowing of what to expect in these whitebark pine forests perhaps 30 years from now assuming the mountain pine beetle outbreak concurs with blister rust. In this dissertation, I examined the response of trees in subalpine forests to the cumulative disturbance of bark beetles and blister rust, first at a stand and then at a tree level in Waterton Lakes National Park. The study results provided the basis of my discussion on how these disturbance events will affect the resilience of whitebark pine populations across the Canadian Rockies.

Whitebark pine has been described as a foundation or keystone species in subalpine forests (Tomback and Kendall 2001, Ellison et al. 2005). It has a close association with the Clark's nutcracker (*Nucifraga columbiana*), since this bird species opens its cones and disperses the unwinged seeds (Tomback 1982). Also, the fat- and protein-rich seeds are linked to the reproductive success of grizzly bears (*Ursus arctus*). In poor seed years, grizzlies seek foods at lower elevations and rates of human-bear conflicts and bear mortality is two to three times higher than in good seed years (Mattson et al. 1992). Unfortunately, whitebark pine is in severe decline throughout its range in western Canada and the United States (Campbell and Antos 2000, Kendall and Keane 2001, Zeglen 2002, Smith et al. 2008, Tomback et al. 2011). Cone yields have been reduced by outbreaks of mountain pine beetle that kill mature trees and by the widespread infection of cone-bearing branches by the introduced blister rust (Kendall and Keane 2001). Poor regeneration has also been attributed to blister rust and also to fire exclusion causing successional replacement of whitebark pine by more shade-tolerant species (Keane et al. 1990). Decline of this species could mean significant changes to the structure and composition of these ecosystems and to populations of Clark's nutcracker and grizzly bears (Tomback and Kendall 2001). In fact, in September 2009, the attempt to delist grizzly bears in the Yellowstone National Park area as a threatened species under the United States' Endangered Species Act was overturned partly because of the ongoing decline of whitebark pine. In 2010, whitebark pine was designated as federally endangered in Canada and is soon to be listed under the Species at Risk Act (Committee on the Status of Endangered Wildlife in Canada 2010).

Conservation of whitebark pine requires understanding every step involved in recruiting new trees to forests, beginning with producing healthy cone crops, caching of seeds by nutcrackers, successfully establishing seedlings, and, finally, transitioning to mature trees (Figure 3). By opening the canopy and exposing mineral soil, fire has

been thought to be key for creating attractive conditions for caching of seed by Clark's nutcrackers and thus enabling whitebark pine regeneration (Tomback 1982, Keane et al. 1990, Tomback et al. 2001). Fire regimes are highly variable across the range of whitebark pine but are predominantly of mixed-severity (Campbell et al. 2011). Whitebark pine forests can be influenced by varying combinations of low-severity fires and high-severity fires with mean fire return intervals ranging from 13 to 400 years. However, as more of the range of whitebark pine has received research, mounting evidence suggests that there are several successional trajectories for maintaining whitebark pine in the canopy and not all depend on fire, particularly where fire return intervals are long (Campbell and Antos 2003, Moody 2006, Larson et al. 2009, Campbell et al. 2011). This evidence includes observations of: 1) whitebark pine trees in the understory and overstory of late-seral stands (Campbell and Antos 2003); 2) positive correlations between whitebark pine regeneration and mortality of whitebark pine from mountain pine beetle (Larson and Kipfmüller 2010); 3) some unburned sites with more whitebark pine regeneration than recently burned sites (Moody 2006); and 4) whitebark pine stands with very little evidence of fire (this study). Central to the question of how to conserve whitebark pine is an understanding how whitebark pine was historically maintained on the landscape and how novel disturbance regimes are changing those processes.

In my research, I used annual tree growth, specifically, annual rings, to examine two key drivers behind the composition and structure of whitebark pine forests: disturbances and tree-to-tree interactions. Although my research is centered on whitebark pine, the ecological topics studied are more universal and of critical current interest, particularly: 1) resilience of ecosystems to novel disturbance regimes (Darling and Côté 2008, Thrush et al. 2009, van Nes and Scheffer 2009); and 2) plant-to-plant interactions and the stress-gradient hypothesis (original by Bertness and Callaway 1994; recent work featured in an issue of *Journal of Ecology* in 2009, see also review by Callaway 2007, Brooker et al. 2008, Maestre et al. 2009).

With the introduction of the non-native blister rust to North America in the early 1900s, the co-occurrence of mountain pine beetle, *Ips* sp. and blister rust is a novel disturbance regime for subalpine forests containing whitebark pine. Understanding how disturbance agents interact among themselves and whether a forest can recover to pre-disturbance conditions are key questions given the potential for extraordinary mortality of whitebark pine (Paine et al. 1998, Buma and Wessman 2011). Each of these disturbance agents depends on a *Pinus* host to complete its life cycle. Blister rust is specific to five-needled pines and the mountain pine beetles primarily attack lodgepole pine or whitebark pine to lay eggs although can use other species of *Pinus* as various *Ips* beetles do. When all three disturbance agents concur, there are several possibilities for interactions (Darling and Côté 2008): they can act synergistically, such that one agent weakens a tree and thus lowers the physiological thresholds that traditionally hold back another agent (e.g., blister rust can cause moisture stress in a tree, lowering resistance to mountain pine beetle; Six and Adams 2007), they can compete for the same hosts, such that one agent eliminates the presence of the other, or they can operate independently and be driven by other bottom-up controls and cause additive mortality.

The key to understanding disturbance agents and interactions is identifying drivers of the severity of each disturbance agent. Although all three disturbance agents rely on a pine host, in Chapter 2, I explored whether there are bottom-up controls, such as local topographic features, that are important and distinct between blister rust,

mountain pine beetle and *Ips* sp. which control the severity of disturbance in Waterton Lakes National Park in a predictable manner. I also tested whether these three disturbance agents acted independently or synergistically and examined the role of climate.

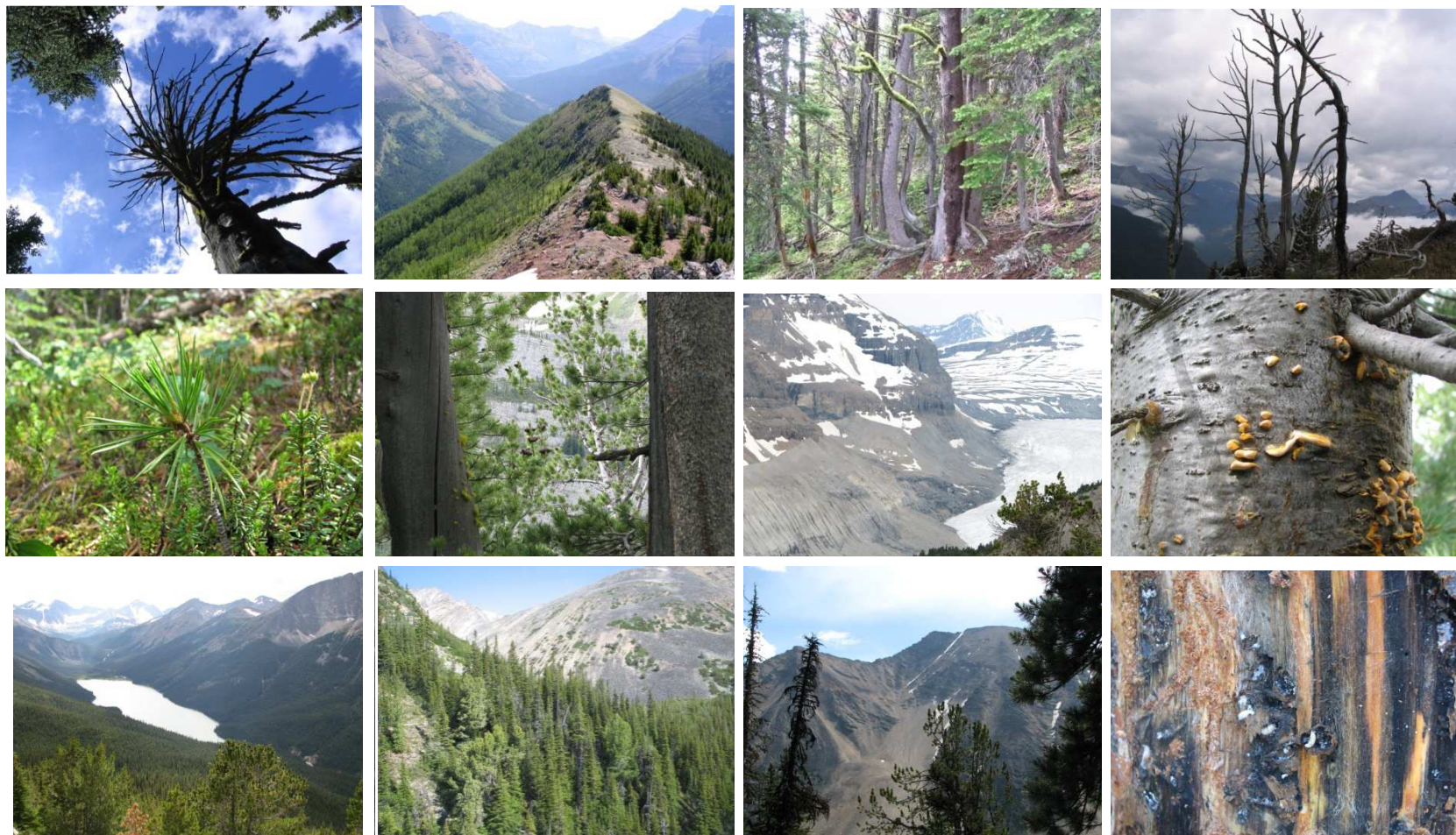
In Chapter 3, I used evidence in trends in tree regeneration and radial growth to determine whether whitebark pine forests are resilient to this “triple whammy” of disturbances. Ecological resilience has been defined as the capacity of an ecosystem to absorb disturbance or stress and undergo change while maintaining its essential identity, functions, structures, and feedbacks (Holling 1973). In whitebark pine forests, low resilience could result in a shift to another stable state where whitebark pine is extirpated and the more shade-tolerant, late-seral species, subalpine fir (*Abies lasiocarpa*) dominates the canopy. I quantified resilience based on the ability to recover to pre-disturbance conditions (i.e., subalpine forests with some whitebark pine component), which is often termed engineering resilience (Pimm 1991) that can be considered an indicator of the more difficult to measure ecological resilience (van Nes and Scheffer 2009). I then tested whether there is a relationship between resilience and disturbance severity and abiotic stress. These questions have been asked of many different ecosystems, including: subalpine forests (Buma and Wessman 2011), boreal forests (Rydgren et al. 2004, Johnstone et al. 2010), intertidal zones (Allison 2004, Harley and Paine 2009), experimentally manipulated salt marshes (Slocum and Mendelssohn 2008) and model simulations of arid ecosystems (Dakos et al. 2011). Conclusions on whether resilience can be predicted from disturbance severity and abiotic stress have varied. This is likely due to the gradient of disturbance and abiotic stress studied relative to the importance of the diversity and composition of the communities prior to disturbance (Brulheide and Luginbühl 2009).

In Chapters 4 and 5, I examined plant interactions in subalpine forests containing whitebark pine. The balance between facilitative (positive) and competitive (negative) interactions among plants plays an important role in structuring plant communities, including subalpine forests containing whitebark pine (Callaway and Walker 1997). The stress-gradient hypothesis predicts that the importance of facilitation increases along gradients of increasing abiotic stress while the importance of competition decreases (Bertness and Callaway 1994). This is an extension of the influential work by Grime (1977) which predicts that plant competition should increase with site productivity. However, both field experiments and meta-analyses suggest there are circumstances where the predictions of the stress-gradient hypothesis do not hold (Maestre et al. 2005, Lortie and Callaway 2006, Maestre et al. 2006). Natural disturbances and the life stages of interacting species may influence the stress-gradient relationship (Callaway and Walker 1997, Liancourt et al. 2005, Brooker et al. 2006). Because most studies have been short-term experimental manipulations and limited by only examining two points at the extremes of stress gradients (Lortie 2010, Malkinson and Tielborger 2010), the relationship between plant interactions and abiotic stress remains unclear in many plant communities. I used the widespread mortality of whitebark pine from mountain pine beetle and white pine blister rust in Waterton Lakes National Park as an *in-situ* experiment to simulate neighbour removal (*sensu* Callaway 1998) across a large landscape. In Chapter 4, I compared counts of whitebark pine and subalpine regeneration around live versus dead adult whitebark pine trees to determine whether live whitebark pine trees facilitate tree regeneration in a predictable way with the conditions of the benefactor, neighbourhood and stand. In Chapter 5, I examined the response in radial growth of adult subalpine fir trees to the death of their adult

whitebark pine neighbour using the same hierarchical framework. Note that in both chapters I call the adult whitebark pine trees, focal trees, but in Chapter 4, the term includes live and dead trees and in Chapter 5, the term only refers to dead trees.

This dissertation is structured in the following manner. This chapter provides the context and rationale for the questions asked and researched in the following four data chapters. Chapters 2 to 5 are data chapters addressing the research questions outlined above. Note that the number of stands sampled differs between the chapters because the presence of snow in one stand prevented measurement of tree regeneration. Chapter 6 presents the conclusions from Chapters 2 to 5 in light of current research, and discusses their limitations and implications for the conservation of whitebark pine in the Canadian Rockies.

Figure 1. Subalpine forests with whitebark pine in Waterton Lakes National Park (top row), Jasper National Park (middle) and in Willmore Wilderness Park (bottom).



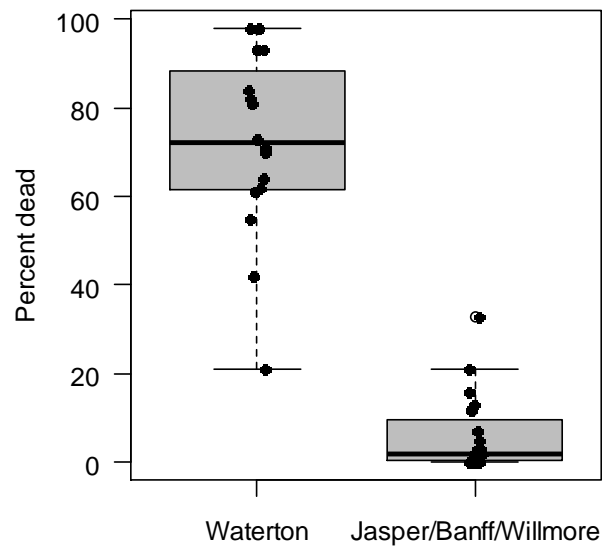
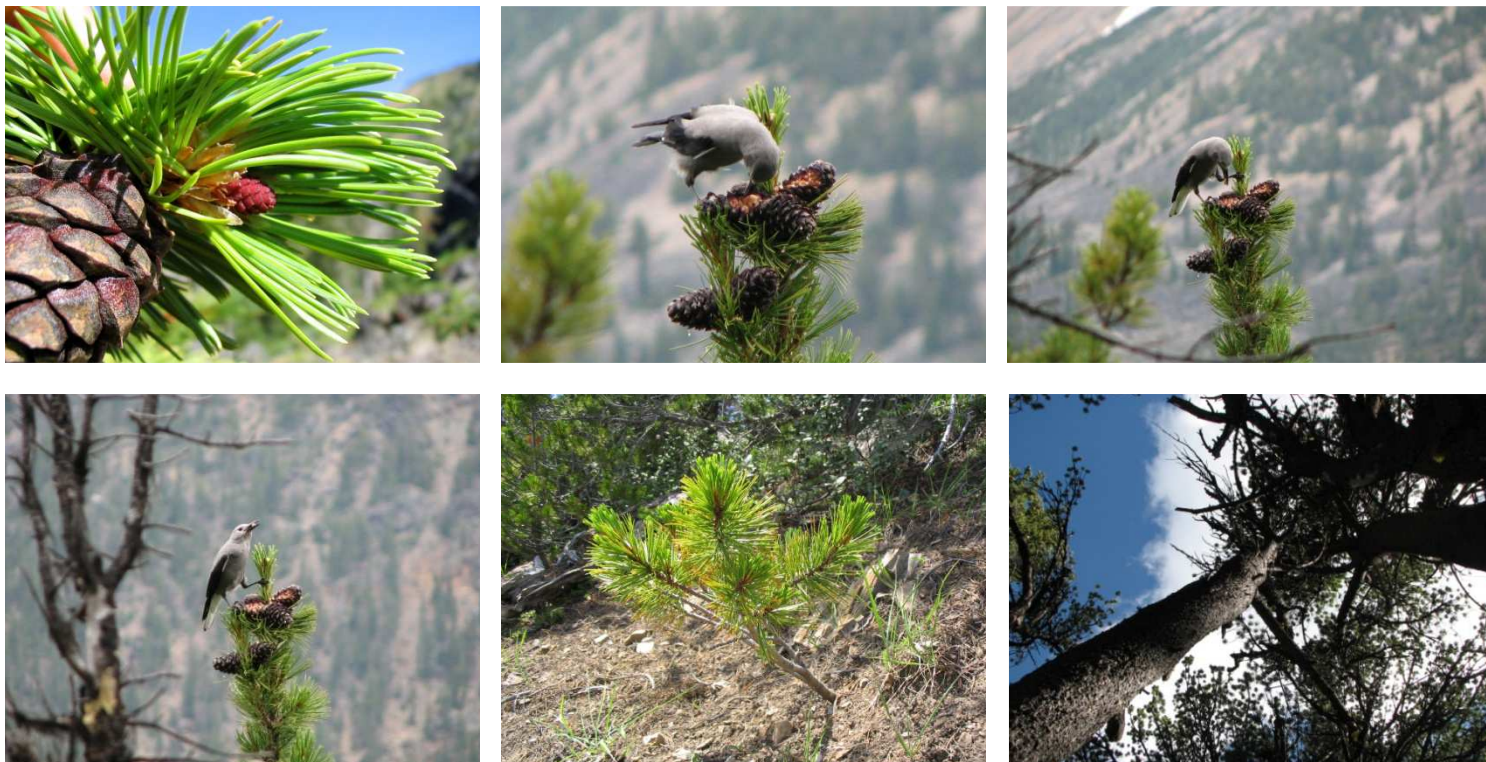


Figure 2. Stand-level mortality for whitebark pine trees in protected areas in the southern (Waterton Lakes National Park, Canada, n=16 stands) and northern Canadian Rockies (Jasper and Banff National Parks and Willmore Wilderness Park, n=19 stands). The box indicates the interquartile range, the solid line in the box indicates the median and the whiskers extend to 1.5 times the interquartile range. Dots indicate stands and are offset to prevent overlap for presentation purposes.

Figure 3. Whitebark pine from seed to tree with the distribution by the Clark's nutcracker.



Chapter 2: Bottom-up controls and interactions among blister rust and two bark beetles in whitebark pine forests

2.1 Introduction

Variation in disturbance severity creates a complex pattern of forest structure across landscapes. The spatial and temporal variation in the structural legacies resulting from disturbances have important ecological consequences in terms of fuels or hosts available for subsequent disturbances and seed sources available for subsequent forest trajectories. While the drivers of disturbance severity are well studied for forest fires, less is known about the drivers of the severity of forest diseases and insects at the landscape level, particularly when they concur and possibly interact (Turner 2010). Disturbance severity measures the degree to which pre-disturbance forests have been impacted by the disturbance and is often confused with disturbance intensity, which is the physical force of the event per unit area per time (Pickett and White 1985). In subalpine forests containing whitebark pine (*Pinus albicaulis*) and subalpine fir (*Abies lasiocarpa*), the disturbance regime of white pine blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*) and species of *Ips* bark beetles combines three disturbance agents which target whitebark pine, but not subalpine fir, and operate on different time scales and attack different demographic stages of the population. In this chapter, I use disturbed forests containing whitebark pine to infer the drivers of disturbance severity and interactions between disturbances.

Natural disturbance regimes are bounded by top-down controls acting at broad spatial scales, such as climate, and bottom-up controls acting at local spatial scales, such as local topography or forest composition and structure (Lertzman and Fall 1998, Peters et al. 2011). For example, as a top-down control for fire regimes, multi-decadal variability in sea surface temperatures in the Pacific and Atlantic Oceans can synchronize droughts and thus fires in western North America (Kitzberger et al. 2007). In contrast, local topography, such as small changes in aspect, can act as a bottom-up control on fire severity by influencing the moisture content and the continuity of fuels (Heyerdahl et al. 2001). Top-down and bottom-up controls which drive a forest disease or insect from endemic levels to an outbreak have been well described at the tree level. Predators are considered top-down and tree resistance is a bottom-up control (e.g., Raffa et al. 2005). At the landscape level, similar to fire regimes, top-down controls on the occurrence and severity of outbreaks are climatic. Precipitation has been linked to outbreaks of *Dothistroma* needle blight (Woods et al. 2005), warmer temperatures are conducive to univoltine life-cycles and winter survival of mountain pine beetles (Bentz et al. 2011) and drought has been associated with outbreaks of mountain pine and *Ips* bark beetles (Raffa et al. 2008). However, within a region and within an outbreak, the spatial variation is driven by factors other than climate such as forest composition and topography. Identifying specific bottom-up controls on the disturbance severity of blister rust and bark beetles when they concur can improve our ability to predict whitebark pine mortality. This is crucial for management activities aimed at

conserving whitebark pine which is considered a keystone species (Tomback and Kendall 2001) and has been designated as an Endangered Species in Canada (Committee on the Status of Endangered Wildlife in Canada 2010).

The contemporary disturbance regime in most subalpine forests containing whitebark pine is comprised of white pine blister rust and mountain pine beetle (Campbell et al. 2011). In this chapter, I do not consider fire because of the lack of evidence of frequent fire in stands containing whitebark pine in my study area (generally very old stands with no fire-scarred trees). White pine blister rust (hereafter “blister rust”), a non-native fungal disease introduced to North America in the early 1900s, is specific to five-needled pines and dependent on alternate hosts of *Ribes* sp. and *Castilleja* sp. (McDonald and Hoff 2001). Whitebark pine trees are directly killed or suffer top-kill typically from the girdling of the stem either directly by the disease or by rodents feeding on the spermagonial exudate (Smith et al. 2008). Blister rust can remain active in a stand for decades, affecting saplings to mature trees and causing varying levels of mortality (Campbell and Antos 2000, Smith et al. 2008). Mountain pine beetles are found at endemic levels in forests containing whitebark pine and at lower elevations in lodgepole pine (*Pinus contorta* var. *latifolia*) forests, but populations can build to an outbreak causing high levels of mortality over a few years. Mountain pine beetles favour large whitebark pines with bark and phloem thick enough to protect broods over the winter (Perkins and Roberts 2003). Unlike blister rust, death of a tree by mountain pine beetle is relatively quick once a tree is attacked (Safranyik and Carroll 2006). Outbreaks of mountain pine beetle in lodgepole pine forests are often preceded or followed by species of *Ips* bark beetles, such as the pine engraver (*I. pini*), which target stressed trees and/or smaller trees than those favoured by mountain pine beetle (Safranyik and Carroll 2006). While outbreaks of *Ips* species have not been widely reported in whitebark pine forests, preliminary observations of whitebark pine mortality from *Ips* species in the study area indicates that *Ips* sp. can also be a major disturbance. Combined, blister rust, mountain pine beetle and *Ips* sp. can cause mortality in almost all of the life-stages of a whitebark pine population.

When disturbances from blister rust and mountain pine beetle are examined separately, the influence of bottom-up controls on severity has been observed. Because both species target *Pinus*, one obvious candidate for a control is the density of host species in a stand. The probability of mortality from mountain pine beetle was higher in stands with relatively more, large whitebark pine trees growing in clumps than in stands with smaller, single trees in a study by Perkins and Roberts (2003). For blister rust, the configuration of hosts in a stand might be more important. Campbell and Antos (2000) found that mortality from blister rust was higher in relatively open stands than in closed stands hypothesizing that it was easier for airborne spores to spread and land on the alternate host, *Ribes* shrubs. Topographical features such as elevation, slope and aspect may modulate the bottom-up control of forest composition on disturbance severity. For example, the incidence of blister rust was found to increase with increasing summer moisture (Smith and Hoffman 2001, White et al. 2002) and decreasing elevations (Kearns and Jacobi 2007) because blister rust depends on cool, moist conditions for spore production (Van Arsdell et al. 1956). For mountain pine beetle, the severity decreases in colder environments because cold temperatures reduce beetle survival over winter and maintain a semivoltine life cycle (Shore et al. 2000, Logan and Powell 2001).

Understanding bottom-up controls is important for trying to predict when changes in the drivers of disturbance severity may push the system outside the range of natural variability (Peters et al. 2011). One such change may be the introduction of a new disturbance agent, such as blister rust, and subsequent interactions between disturbances.

When blister rust, mountain pine beetle and *Ips* sp. concur, the question is whether the bottom-up controls of each agent act as they do when the agent operates in isolation, or, whether the interactions between disturbances override the historic bottom-up controls on disturbance severity outlined in the previous paragraph. The legacies of fire or a bark beetle outbreak have been found to override the bottom-up controls of topography on subsequent fire in subalpine forests. For example, the severity of a fire after multiple disturbances was best predicted by, in decreasing order of importance, stand structure, composition, previous fires, elevation, slope, severity of previous beetle outbreaks and then aspect (Bigler et al. 2005). Previous fires decreased the severity of the next fire by shifting vegetation to a less flammability fuel type and also reduced the severity of subsequent beetle outbreak. Likewise, the severity of fire after a wind event in subalpine forests increased with windthrow severity with the effects of elevation as a secondary predictor (Kulakowski and Veblen 2007). In contrast, the odds of a stand burning in the Yellowstone fires of 1988 were significantly increased by previous mortality from mountain pine beetle, but this was minor relative to the influence of drought and aspect (Lynch et al. 2006).

I examined relationships between disturbance severity and bottom-up controls in forests containing whitebark pine in the Canadian Rockies which were affected by an outbreak of mountain pine beetle during 1977-1984, in addition to blister rust and *Ips* sp. I asked: 1) Which bottom-up controls explained the severity of each disturbance agent? 2) Did one disturbance agent enable another disturbance agent? Or did climatic stress on whitebark pine enable certain disturbance agents?

For the first question, I tested the influence of the same bottom-up controls on the severity of blister rust, mountain pine beetle and *Ips* sp. However, I hypothesized that each disturbance agent will be driven by a different combination of forest composition and topographic controls even though each relies on a *Pinus* host to reproduce (Table 1). For the second question, I expected blister rust infection to increase susceptibility to mountain pine beetle and *Ips* sp. (Six and Adams 2007). At the stand level, mortality as measured by the density of dead whitebark pine killed by both mountain pine beetle and *Ips* sp. should increase with the severity of blister rust because it weakens tree resistance. At the tree level, the radial growth of whitebark pine trees prior to attack by mountain pine beetle or *Ips* sp. should show a marked decline due to die-back caused by blister rust. Alternately, if climatic stress due to drought played a role, the radial growth of attacked whitebark pine should have declined with decreasing spring or summer precipitation.

2.2 Methods

2.2.1 Study area

The study area was in Waterton Lakes National Park, Alberta, Canada (49° 2' N, 113° 57' W; Figure 4). In the Park, whitebark pine is found over 3775 ha of the upper elevations (1600 to 2000 m) of subalpine forests, most commonly associated with subalpine fir but also with Engelmann spruce (*Picea engelmannii*) or lodgepole pine at lower elevations (Achuff et al. 2002). High levels of mortality of whitebark pine from blister rust and mountain pine beetle have been recorded during monitoring by Parks Canada (Smith et al. 2008). Blister rust infection of limber pine (*Pinus flexilis*) was first observed in the Park in the 1958 (Department of Forestry Canada 1963) and early in 1939 in the adjacent Glacier National Park in Montana, U.S. (McDonald and Hoff 2001). In 1977, a

mountain pine beetle outbreak spread into the Park from adjacent areas in Montana, United States (Watt 1981). The outbreak ended around 1984 in the Park, affecting 1835 ha dominated by either lodgepole or whitebark pine (Hawkes et al. 2004).

2.2.2 Sampling

I sampled 16 stands containing whitebark pine below treeline (Table 2). Stands were selected using a geographic information system (GIS) analysis of an existing vegetation inventory of the Park. Forested polygons were examined for where whitebark pine formed more than 10% of the canopy, were larger than one hectare and were accessible by foot. Furthermore, to ensure my sampling covered a wide range of environmental conditions, the stands suitable for sampling were stratified as being on either warm (91°- 270°) or cool (270°- 90°) aspects. Because the majority of stands were on warm aspects (76%), 12 stands were randomly selected from the warm stratum and four from the cool stratum.

In each stand, I sampled at four to six points. Before entering the field, the coordinates of the first point were selected close to the center of the stand using a GIS to avoid sampling at altitudinal treeline. The subsequent sample points were established at distances randomly selected between 40 and 100 m along a bearing parallel with the slope contour. For each stand, net solar radiation was modelled from digital elevation models using the GIS-based solar radiation model, ArcView Solar Analyst (Fu and Rich 1999) to account for the influences of the viewshed, surface orientation, elevation, and atmospheric conditions (D. Zell, GIS specialist, Parks Canada, unpublished data). The raster values were averaged over each stand for January and June to represent relative winter and summer net solar radiation.

At each sample point, I recorded the elevation and slope angle and for other measurements established three nested, circular plots. The radius of the smallest plot was 3.99 m. For dense stands (> 4,000 trees/ha), the radii of the medium and large plots were 5.66 and 8 m; for less dense stands, the radii were 8 and 12.66 m. In the small radius plots, I visually estimated the percent cover of area which was not vegetated but was rock, scree or soil; indicative of poorly developed soils. In the medium radius plot, the species and diameter at breast height (1.3m, DBH) of all live and dead trees taller than 1.3 m with a DBH larger than 4 cm were recorded. In the large radius plots, only live and dead trees with a DBH equal or larger than 15 cm and were not whitebark pine were measured. Estimates of the density and basal area per hectare of live and dead stems for each tree species were determined from the medium and large fixed-area plots.

Because the density of mature whitebark pine was sparse relative to subalpine fir and could be highly variable both within and between stands, estimates of stand-level whitebark pine density based on fixed-area plots could have low precision (Pielou 1977). Therefore, I used distance sampling. Although distance sampling has been criticized for producing biased estimates of densities when populations do not have a random spatial pattern (Pielou 1977), simulation tests suggest methods that use distances to at least the third closest individual from a random point perform well (Engeman et al. 1994). Distance sampling also guarantees a minimum number of whitebark pine trees at each sample point independent of density. I used the distance to the fourth tree (Pollard 1971) to estimate the densities of large (DBH \geq 15 cm) live and dead whitebark pine trees. I put greater effort into obtaining accurate estimates of whitebark pines with a DBH \geq 15 cm, because medium-sized trees from 4 to 15 cm DBH were relatively scarce (e.g., six stands had no dead whitebark pines in this size class). At each sample point (*i*) and

for each category of whitebark pine (large live trees, large dead trees), I estimated the average density or stems per ha (SPH) per stand (j):

$$[1] \quad \overline{SPH}_j = \frac{1}{m} \sum_{i=1}^m \frac{n_i}{A_i} \quad \text{where} \quad A_i = \left(\frac{n_i}{n_i - 1} \right) \frac{\pi}{10,000} (R_{ni}^2)$$

and where m is the number of sample points in a stand, n_i is the number of individuals measured around each point, and A_i is the area in hectares sampled around each point. Area was corrected for the expected radius under a Poisson distribution using $(n - 1)/n$ and R_{ni} , the distance in metres to the fourth closest individual to point i (Moore 1954, Eberhart 1967). The maximum distance searched was 30 m from each sample point. For 22% and 3% of sample points for live and dead trees, respectively, a fourth individual was not found within 30m and estimates of average stand density were corrected for this maximum search distance by substituting 30 m as R_{ni} in Eq. [1]. Less than half of whitebark pine trees (44%) grew in clumps of more than one stem (median: two stems, maximum: five stems). Because it was difficult to distinguish whether these clumps were individual trees or the same tree with multiple stems, I considered these to be one tree. For trees with multiple stems, the stem that was most dominant in the canopy was measured.

The potential cause of death for the four closest whitebark pines to a sample point was determined from evidence on the stem. I identified the likely beetle species based on the following characteristics of egg and larval galleries in the subcortical tissue: J-shaped galleries were indicative of mountain pine beetle, star-shaped galleries emanating from one nuptial chamber indicated *Ips pini*, and curved galleries with fine saw-toothed edges indicated *I. integer* (Furniss and Carolin 1977). Each whitebark pine tree was also examined for signs of blister rust, such as dead tops, branch and stem cankers and evidence of squirrel feeding on the phloem and spermatogonial exudate (Tomback et al. 2004). Because these symptoms of blister rust are not evident on the stem for long once the tree dies, I suspected blister rust as the cause of death for dead trees with no beetle evidence along their entire stem which died after 1940 (the year blister rust was observed nearby in Montana). When estimating the density of a particular subset of trees, for example, the density of trees killed by mountain pine beetle, Eq [1] remained the same. However, n_i in Eq.[1] was reduced to the number of trees with that characteristic.

2.2.3 Differentiating bottom-up controls on disturbance severity

I identified which bottom-up controls best explained the variability in disturbance severity (stems/ha of dead whitebark pine $DBH \geq 15$ cm) using an information-theoretic approach (Burnham and Anderson 1998). I used the density of dead trees and not the proportion which were dead to define disturbance severity. Note that candidate models for explaining the variability in disturbance severity included the density of all whitebark pine trees to account for different pre-disturbance densities of whitebark pine. Bottom-up controls were variables representing either forest composition or topography (Table 1). I developed a set of candidate models using a subset of variables describing topography, another subset of variables associated with forest composition and a third subset comprised of a combination of topographic and forest composition variables. All variables were calculated as averages over all points in each stand ($j=16$). Candidate models used primarily variables that were significantly correlated to the density of dead whitebark pine determined from Spearman rank correlations (Zar 1999, $\alpha = 0.05$, Table 3). Models

also were parsimonious, met the assumptions of linear regression and had no highly correlated explanatory variables to avoid models where the significance of one variable depended on the presence of another (collinearity). Three linear models were fit using `lm` function in the R Base package v.2.11.1 (R Development Core Team 2010) to predict the average j th stand density of dead whitebark pine ($\text{DBH} \geq 15 \text{ cm}$) killed by mountain pine beetle (u), likely blister rust (v), or *Ips* sp. (w) or all agents collectively (z):

$$[2] \quad u_j \text{ or } v_j \text{ or } w_j \text{ or } z_j = \beta_0 + \beta_1 x_{j1} + \beta_2 x_{j2} + \beta_3 x_{j3} + \varepsilon_j$$

where β_0 is the intercept and β_1 to β_3 are the coefficients associated with variables x_1 to x_3 from the list in Table 1. Note that the response variable was the cumulative density of dead whitebark pine due to each disturbance agent as recorded at the time of sampling and was square root transformed.

Since all models met the regression assumptions, the least squares solution is also the maximum likelihood solution. Therefore, I evaluated models using the Akaike's information criterion adjusted for a small sample size, AIC_c (Burnham and Anderson 1998). I included interactions between variables in Table 1 only if they reduced the AIC_c . I then quantified the empirical support for each model (i.e., quantifying support for different bottom-up controls on whitebark pine mortality) using Akaike weights (w) where models with high support had higher w (Burnham and Anderson 1998).

2.2.4 Death dates and radial growth of whitebark pine

To examine whether one disturbance agent enabled another and the role of climate, I reconstructed the distributions of the years of deaths and chronologies of basal area increment of live and dead whitebark pine trees using crossdated increment cores. I took increment cores from each of the four dead whitebark pines sampled at every point ($n=290$). I cored the stem parallel to the slope contour in locations where the outer rings were best preserved, i.e., those with solid outer wood and bark or with mountain pine beetle galleries which indicated the presence of the subcortical region. In efforts to obtain the most recent outer ring, I was able to obtain cores where the outer ring was thought to be well preserved in 74% of the trees and quality cores from both sides of the stem on 55% of the trees. Ring widths of well-sanded cores were measured to the nearest 0.01mm using a Velmex sliding stage interfaced with a computer. I estimated the death date of each whitebark pine by crossdating each ring-width series with a master chronology of ring-widths using the program COFECHA (Grissino-Mayer 2001). The median difference between pairs of cores from the same dead tree was 4 years (average = 12) possibly due to cambial dieback, wind erosion or decay occurring at asymmetrical rates around the stem. There were 57 trees that had mountain pine beetle galleries with outside dates of death prior to 1977 when the last outbreak started according to independent records. The median difference between 1977 and the death dates of these trees was 6 years (average = 13), which suggests a low level of decay. Therefore, to account for the level of uncertainty in the death dates, I examined distributions of death dates using 10-year classes (Wong and Lertzman 2000).

To develop chronologies of growth from each crossdated ring-width series, I calculated the annual basal area increment to remove the progressive decline in ring width due to the increase in circumference as a tree grows. I did not detrend each series to remove an age-related growth decline for three reasons: 1) most trees were old (274 ± 84 ; average \pm std. dev.) and I was examining recent growth since 1940; 2) in the presence of disturbance there is no clear model for detrending; and 3) I was looking for sudden changes in tree growth (Biondi and Qeadan 2008).

However, for subsequent analysis with climate I normalized each time series into a dimensionless index (BAI) by dividing annual increments of basal area by the average increment for each tree. I developed four Park-wide chronologies for whitebark pine (one for live trees, trees killed by mountain pine beetle, trees with *Ips* sp. evidence, and trees suspected to have been killed by blister rust) with a Tukey's biweight mean to reduce the effect of outliers (Cook and Kairiukstis 1990). Each chronology contained trees from all 16 stands and had more than nine trees for any year and was created using the dendrochronology program library in R (dplR; Bunn 2008).

I examined interactions between the three disturbance agents by: 1) Spearman rank correlations between the severity of one agent to another; 2) two-sample Kolmogorov Smirnov tests for comparing the distribution of death dates of whitebark pine between agents; and 3) correlations between the four chronologies of BAI with climate. I correlated BAI in the live whitebark pine chronology up to 1950 prior to the disturbances with 36 climatic variables: the average monthly temperatures from April of the year prior to tree-ring formation to September of the year current to ring formation. Temperature and precipitation records came from a weather station in Lethbridge (~100 km away, 49.63° N, 112.80° W) which had complete records from 1903 to 1986 for temperature and 1903 to 2004 for precipitation (Adjusted and Homogenized Canadian Climate Data; Mekis and Vincent 2011). I tested for a non-zero Pearson correlation by randomly arranging the sample data using 1000 bootstrapped samples, obtaining the 2.5 and 97.5 quantiles of the 1000 estimates, and seeing if the observed correlation was outside of these limits using DendroClim2002 (Biondi and Waikul 2004). For the climatic variables significantly correlated with whitebark pine growth, I tested for significant trends over time using the Mann-Kendall test.

2.3 Results

2.3.1 Disturbance severity varied with agent and location

Most (72%) large whitebark pine trees in the Park were dead (Table 2). Although evidence of mortality likely from blister rust or mountain pine beetle was observed in all the sampled stands, the percent of mortality caused by each was highly variable (Table 2, Figure 5). On average, 44% of dead whitebark pine had no evidence of mountain pine beetle or *Ips* sp. and were considered to have died from blister rust, 32% had egg galleries characteristic of mountain pine beetle, and 27% of the dead whitebark pine showed only evidence of *Ips pini* or *I. integer*.

Live, large whitebark pine formed a minor component of individual stands ($28 \pm 20\%$ (average \pm one standard deviation), Table 2). Although these trees were alive, most were in poor health; 12% had active sporulation of blister rust and 65% were reproductively dead because of dead tops resulting from blister rust. Smaller, live whitebark pine trees ($4 \leq \text{DBH} < 15$ cm) were also scarce (48 ± 61 trees/ha).

Cumulatively, most of the mortality of whitebark pine occurred over a relatively short period of time (interquartile range of 17 years between 1966 and 1983, Figure 6). Mortality from mountain pine beetle was more episodic than that from blister rust or *Ips* sp.. This was indicated by the shorter interquartile ranges between death dates for trees killed by mountain pine beetle than blister rust or *Ips* sp. (11 versus 24 or 18 years respectively) and significantly lower variance between blister rust and mountain pine beetle ($F = 1.64$, numerator $\text{df}_{\text{blister rust}} = 130$, denominator $\text{df}_{\text{mountain pine beetle}} = 87$, $p\text{-value} = 0.014$). Mortality from all disturbance agents was higher than the

estimated background rate of mortality of whitebark pine prior to 1940 due to senescence – the mortality rate due to blister rust over 60 years was about 11 times that of the background rate (Figure 6).

2.3.2 Different models explained severity of different disturbances

The variability in disturbance severity could be explained by different models for each disturbance agent. While I cannot directly conclude the causal mechanism behind each type of mortality, there were clear predictors of disturbance severity, distinct for each disturbance agent, from the set of models that I tested. The severity of blister rust was higher in stands which had relatively low solar radiation in the summer: the best model out of 12 candidates had one explanatory variable, the average solar radiation in July (Akaike weight of 0.406, Table 4, Figure 7). The severity of mountain pine beetle increased with increasing elevation and proportion of ground vegetated (Akaike weight of 0.460, variance inflation factor = 1.003; Table 4, Figure 7). For mortality from *Ips* sp., there were two possible models. The best model had an Akaike weight of only 0.325 and included the density of whitebark pine as an explanatory variable (Table 4). The severity of mortality caused by *Ips* sp. increased with the density of all whitebark pine. The next best model included the addition of solar radiation in July (Akaike weight of 0.214, variance inflation factors of 1.000, Table 16). The severity of mortality caused by *Ips* sp. was also higher in stands which had relatively high solar radiation in the summer. No model adequately predicted cumulative mortality from all three agents.

2.3.3 Disturbance interactions and decline in BAI before death

There was evidence of interactions among disturbances from the analysis of the dates of death and chronologies of radial growth but not from the correlations of the three disturbance agents. Mortality by mountain pine beetle was not correlated to mortality likely caused by blister rust or *Ips* sp.. Mortality by *Ips* sp. was not correlated to mortality likely caused by blister rust. This analysis was confounded by not being able to distinguish between trees which may have been affected by blister rust in addition to another agent. However, the distributions of death dates significantly differed between whitebark pine killed by mountain pine beetle and blister rust (two-sample Kolmogorov Smirnov test, $D = 0.30$, $p\text{-value} = 0.00014$) and *Ips* sp. ($D = 0.41$, $p\text{-value} = 4.17\text{e-}06$). In particular, the peak of mortality from *Ips* sp. lagged that from mountain pine beetle suggesting a secondary role for *Ips* sp. (Figure 6). The distribution of death dates from *Ips* sp. and blister rust did not significantly differ ($D = 0.14$, $p\text{-value} = 0.31$; Figure 6), suggesting that they may have acted at the same time.

BAI of whitebark pine trees began to decline around 1950; evident in both live trees and those subsequently killed (Figure 8). By 1980, there was a significant decline in growth (all chronologies had significant ($p < 0.05$) values of Mann-Kendall's tau). I suggest that the decline was primarily due to infection by blister rust and partly enabled by a change in the climatic drivers of BAI which may also be linked to blister rust. Blister rust was first observed in the Park in 1958 (Department of Forestry Canada 1963) and negatively impacts the radial growth of infected trees. Blister rust could also explain the decline of live trees because most were unhealthy with dead tops and/or had active infection by blister rust at the time of sampling. Live trees did somewhat recover in the following decades which could be a response to the release of resources as neighbours died or to a change in the climatic drivers as outlined below.

From 1903 to 1950, the BAI of live whitebark pine trees was positively correlated to average temperatures in May in both the year prior and the year current to ring formation and to average precipitation in January and March

in the year of ring formation (Pearson correlation coefficients (r) = 0.420, 0.391, 0.351, 0.440, respectively). Between 1950 and 1980, neither May temperature nor January or March precipitation significantly changed (Mann-Kendall's tau = 0.111, 0.065, -0.03; p = 0.401, 0.622, 0.812, respectively). The only climatic variable which significantly declined between 1950 and 1980 was June precipitation (tau = -0.297, p = 0.022). After 1950 and up until 1980, BAI of live trees and those eventually killed by blister rust and *Ips* sp. were positively correlated to average precipitation in June in the year of ring formation (r = 0.545, 0.554, 0.527, respectively; Figure 8) in addition to February precipitation. The switch after 1950 to June precipitation being a driver of BAI in all whitebark pine trees but those eventually killed by mountain pine beetle is notable in Figure 8.

2.4 Discussion

2.4.1 Disturbance interactions

A “triple whammy” of disturbances, which included blister rust, mountain pine beetle and *Ips* sp., formed a distinct disturbance event in the subalpine forests of Waterton Lakes National Park. Cumulatively, the event was specific to *Pinus*, widespread, long in duration (at least 50 years) and of mixed severity (range of 20 to 90% mortality of whitebark pine). Blister rust and mountain pine beetle have co-occurred in other forests containing whitebark pine in British Columbia, Idaho, Montana and Wyoming (Campbell and Antos 2000, Perkins and Roberts 2003, Six and Adams 2007, Logan et al. 2010). To the best of my knowledge, this is the first time *Ips* sp. have been reported as a significant disturbance in forests containing whitebark pine. Although *Ips* sp. are traditionally thought of as only locally eruptive, other *Ips* species have recently proven capable of widespread mortality. For example, *Ips confusus* caused over 1.5 million ha of mortality of pinyon pine (*Pinus edulis*) and juniper species woodlands in southwestern United States in 2003 (Raffa et al. 2008). Similar disturbances when multiple agents concur are found in other forest types when bark beetles, disease, and/or defoliating insects coincide (e.g., in interior Douglas-fir (*Pseudotsuga menziesii*) forests with western spruce budworm (*Choristoneura occidentalis*) and Douglas-fir bark beetle (*Dendroctonus pseudotsugae*); Hadley and Veblen 1993). I discuss further the inferred bottom-up controls to this distinct disturbance event in the Park, the role of climate and disturbance interactions and implications for conserving whitebark pine.

2.4.2 Bottom-up controls: forest composition and local topography

Local topography acting as a bottom-up control even in the presence of interactions between the disturbance agents was a key result. A fairly large proportion of the variation in mountain pine beetle severity (Adj. R^2 = 0.43) was explained by bottom-up controls of local topography (elevation) and forest composition (percent cover of non-vegetated ground). The amount of solar radiation received in a stand in the summer explained a smaller proportion of the variation in blister rust severity (Adj. R^2 = 0.27). The absence of host density in models for explaining the severity of mountain pine beetle and blister rust disturbances implies that the prime bottom-up control on disturbance severity was not the density of hosts but site conditions which reduced trees' resistance to beetle attack or were favourable for spore development. The severity of mountain pine beetle is predicted to be lower on sites with higher percent cover of rock or soil. This could be because stands with low cover of understory plants tend to be on steep slopes (highly correlated) and represent sites too cold or unproductive where whitebark pine is not dense enough for mountain pine beetle to be successful. The severity of mountain pine beetle is also predicted to

increase with elevation which contradicts results found by others (Shore et al. 2000, Logan and Powell 2001) but may reflect the density of hosts in this case. For blister rust, cool temperatures and moisture in the form of rain, dew or high humidity are required for basidiospores to develop on *Ribes*, survive dispersal by wind to five-needled pines and then germinate in the late summer (Van Arsdell et al. 1956). This supports the relationship I found where blister rust mortality was higher in stands which received relatively low amounts of summer solar radiation. The lack of a relationship between blister rust and the density of hosts, combined with positive relationships with summer moisture, has also been found in whitebark pine forests in Idaho and Wyoming (Smith and Hoffman 2001). Nearby to my study area in Montana, U.S., a higher incidence of blister rust infection on whitebark pine trees was found in moister sites (Smith et al. 2011).

While the severity of disturbance by *Ips* sp. increased with the total density of host species, topography was also influential. I found that *Ips*-caused mortality increased with increasing solar radiation, implying warmer or drier conditions facilitated *Ips* sp.. Elsewhere outbreaks of other *Ips* species, such as *I. pini* and *I. confusus*, have been observed after droughts (Safranyik and Carroll 2006).

2.4.3 Interactions among disturbances and with climate

I propose that the introduction of blister rust altered the expected relationship between precipitation and whitebark pine growth. The stress then caused by blister rust and/or summer drought reduced the capacity of trees to resist bark beetle attack, amplifying the mountain pine beetle outbreak at elevations traditionally considered too cold for beetle development.

Prior to 1950, whitebark pine growth was positively correlated with precipitation in the winter where deeper snow packs increase soil moisture at the beginning of the growing season. The lack of relationship with June precipitation prior to 1950 is notable because the region experienced one of the most severe summer droughts at low elevations between 1917 and 1941 (Watson and Luckman 2004, Pederson et al. 2006) and yet whitebark pine trees did not appear affected (Figure 8). It is possible that warmer temperatures which are associated with drier periods caused favourable growing conditions at high elevations (Kipfmüller 2008). After 1950, precipitation in June in the year of ring formation was highly and positively correlated to the growth of all whitebark pine trees, except those eventually killed by mountain pine beetle. What could have caused this change in climate-growth relations specific to a subset of trees? I propose that the introduction of blister rust to the Park was earlier than the first recorded observation in 1958 because blister rust was observed on whitebark pine earlier in 1939 in Glacier National Park, Montana which borders the Park (McDonald and Hoff 2001). Because blister rust reduces sapwood moisture and negatively affects water relations within a tree (Six and Adams 2007), infection could have heightened the sensitivity of whitebark pine trees to summer moisture. June precipitation significantly declined between 1950 and 1980, although there were relatively wet periods in the 1970s and from the 1990s to present.

Whitebark pine trees which were killed by mountain pine beetle were stressed as shown by the decline in BAI for at least 20 to 30 years prior to their death. This reduced the capacity of trees to resist beetle attack, ultimately reducing the threshold number of beetles necessary for a successful mass attack. Indeed, the BAI of trees prior to being killed by mountain pine beetle declined the greatest (46%) from 1950 to 1980 relative to the decline of live trees (9%) and trees killed by the other two agents (~25%). There is evidence from other studies that mountain pine beetles preferentially attack whitebark pine trees which have more severe blister rust (Six and Adams 2007,

Bockino 2008). The decrease in June precipitation could have also directly affected the dynamics of the outbreak. Drought stress in the spring or summer has been linked to the eruption of mountain pine beetle outbreaks in lodgepole pine forests (Safranyik and Carroll 2006, Raffa et al. 2008) and spruce bark beetle (*Dendroctonus rufipennis*) outbreaks in southern Alaska (Sherrif et al. 2011). Droughts are usually accompanied by higher temperatures which can accelerate the life cycle of a bark beetle because the rate of moving between developmental stages are temperature dependent (Bentz et al. 2010).

The introduction of blister rust and the heightened sensitivity of infected whitebark pine trees to summer moisture may have also permitted novel dynamics of *Ips* sp.. *Ips* sp. are traditionally considered secondary bark beetles, arriving after another disturbance agent or climate have stressed trees (Furniss and Carolin 1977). *I. pini* beetles have been observed to kill large numbers of pine trees one to three years following the collapse of mountain pine beetle outbreaks (Safranyik and Carroll 2006). *Ips* host trees usually have smaller diameters than trees attacked by mountain pine beetle (Safranyik and Carroll 2006). Indeed, I observed that the peak mortality from *Ips* sp. lagged that from mountain pine beetle (Figure 6) and that trees killed by *Ips* sp. were on average significantly smaller than those killed by mountain pine beetle (two sample t-test: $t = -8.830$, $df = 206$, $p < 0.0001$). However, it also appeared that *Ips* sp. was able to build in numbers and operate independently of mountain pine beetles as shown by very few trees had both mountain pine beetle and *Ips* sp. galleries. This may have been possible through trees' resistance being lowered by blister rust and/or summer drought. Indeed, the growth of trees prior to being killed by *Ips* sp. and their dates of death were highly correlated to those killed by blister rust. However, the novel dynamics of *Ips* sp. is not simply of working hand in hand with blister rust. Different bottom-up controls suggest partial independence from blister rust - the influence of summer solar radiation on *Ips* sp. was positive and that on blister rust was negative (Table 3). The dual ability of *Ips* sp., to be a follower or an independent cause of mortality, likely made it difficult to model mortality based on the bottom-up controls I examined.

2.4.4 Conclusions

Although the combination of the three disturbance agents is a novel disturbance to whitebark pine forests, traditional bottom-up controls on disturbance severity of forest composition and topography, similar to those found by other research that addressed each disturbance in isolation, remained in place for each agent. In particular, having a bottom-up control of local topography means that even in the face of climate change and introduction of new disturbances, disturbance severity remains somewhat predictable. To help the restoration of the endangered whitebark pine, I recommend that the bottom-up controls identified in my work be used to map the potential susceptibility of stands containing whitebark pine to blister rust, mountain pine beetle and *Ips* sp.. Valued whitebark pine stands with predicted high susceptibility should be prioritized for protection from mountain pine beetle using the inhibitory pheromone, verbenone (Bentz et al. 2005). I expect additional mortality from other disturbances such as blister rust and *Ips* sp. and the probability of these two types of mortality may be predicted from the level of net solar radiation received by a stand.

My work presents another example in which bark beetle eruptions have been amplified with the anthropogenic introduction of a new disturbance agent, blister rust (Raffa et al. 2008). Infection by blister rust stressed whitebark pine trees, leading to heightened sensitivity to summer moisture. Combined, these factors may explain why recent outbreaks of mountain pine beetle caused so much mortality at elevations typically thought to be too cold for beetle

development and why *Ips* sp. was able to cause widespread mortality although it has not been reported as a major disturbance agent in whitebark pine forests previously (Logan et al. 2003, Logan et al. 2010). Waterton Lakes National Park presents an example of where complex interactions between disturbance agents and climate created an unprecedented triple whammy disturbance in whitebark pine forests.

Table 1. Candidates for explanatory variables for linear models attempted to assess relationships between disturbance severity and characteristics of topography and forest composition. All values were averaged over the points sampled in each stand.

Type	Variable name	Description
Topography	Elevation	Elevation (meters above sea level)
	Slope	Slope (radians)
	Jan_mean	Modelled average solar radiation during January (WH/m^2)
	July_mean	Modelled average solar radiation during July (WH/m^2)
Stand composition	Total_pine	Density of all live and dead whitebark pine $\text{DBH} \geq 15$ cm as an estimate of pre-disturbance stand composition of whitebark pine (trees/ha)
	Live_pine	Density of live whitebark pine $\text{DBH} \geq 15$ cm
	Nonveg	Percent cover that is rock, scree or soil and is not vegetated; indicative of poorly developed soils

Table 2. Characteristics of sampled stands in Waterton Lakes National Park. Locations are in UTM, NAD83, Zone 11 except for Stands 3, 7, 10, and 16, Zone 12.

Stand	Name	Easting	Northing	Number of plots	Elevation (m)	Slope (degrees)	July solar radiation (Wh/m ²)	% cover not vegetated	Density of dead pine (stems/ha)	% of dead pine from MPB ¹	Density of live pine ² (stems/ha)	% of pine alive
1	Bauerman	708842	5445349	5	2066	39	201,429	39	107	42	45	30
2	Castle Divide	708309	5448788	5	2032	28	200,437	26	152	16	95	39
3	Coppermine	283498	5445471	3	2043	43	182,316	13	156	24	30	16
4	South Avion Ridge	709508	5449065	4	2124	36	189,363	14	305	54	74	19
5	Little Cirque Basin	717303	5434859	5	2006	36	175,777	17	76	22	107	58
6	Rowe Lakes	714135	5438529	4	2249	31	203,729	18	101	55	22	18
7	Buchanon North	281777	5438341	3	2011	48	171,286	68	198	0	112	36
8	Upper Lone	710656	5442860	5	2114	42	204,367	33	117	36	97	45
9	Blakiston Mid	713526	5444699	5	1812	31	192,569	43	53	1	195	79
10	Crypt Lake	292256	5431849	5	1948	6	186,479	5	54	73	2	3
11	Glendowne	716304	5447969	6	1913	19	190,519	16	226	22	93	29
12	Lower Lone	709061	5442244	6	2124	13	200,633	3	197	68	120	38
13	Toe of Anderson	715522	5446139	5	1931	24	168,181	3	135	52	10	7
14	Tamarack	711316	5439307	5	2056	27	180,417	5	195	11	72	27
15	Blakiston Junction	708693	5444486	6	1887	25	195,709	3	201	32	16	7
16	Carthew Alderson	283413	5436453	6	1855	24	181,314	0	202	0 ³	5	2

¹ Percent all dead whitebark pine killed by mountain pine beetle (MPB)

² ≥ 15 cm dbh

³ Observed evidence of mountain pine beetle at one location in the stand, but did not form the sampled trees.

Table 3. Spearman's rank correlation coefficients between live and dead whitebark pine stand density and various topography and forest composition variables (n=16 stands). Dead_rust, Dead_Ips, Dead_MPB and Dead_pine represent density of whitebark pine killed by blister rust, *Ips* sp., mountain pine beetle and all agents respectively. Numbers in bold indicate correlations that were significantly different from 0 when $\alpha = 0.05$.

Variable	Live_pine	Dead_rust	Dead_Ips	Dead_MPB	Dead_pine
Elevation	0.162	-0.443	0.314	0.437	0.004
Slope	0.357	0.019	0.275	-0.285	-0.113
Jan_mean	0.203	-0.406	0.409	0.364	-0.174
July_mean	0.168	-0.606	0.405	0.381	-0.168
Nonveg	0.561	-0.278	0.327	-0.323	-0.415
Total_pine	0.609	0.282	0.490	0.068	0.674
Live_pine		-0.174	0.456	-0.191	-0.065
Dead_rust			-0.381	-0.324	0.535
Dead_Ips				0.398	0.330
Dead_MPB					0.235

Table 4. Best linear models for estimating the stand density of whitebark pine killed by blister rust, mountain pine beetle or *Ips* sp. (n = 16 stands). β_0 is the intercept and β_1 to β_3 are coefficients for explanatory variables in Eq. [2] (standard errors in brackets). Fir_sph is square root transformed for modelling mortality from mountain pine beetle. Adj. R^2 = adjusted R^2 , K = number of model parameters including one for σ^2 , AICc = Akaike's information criterion for small samples, and w = Akaike weight relative to the other 17 models (see Table 16 in Appendix).

Response variable	Explanatory variables	β_0	β_1	β_2	Adj. R^2	K	AICc	w
Blister rust	$\beta_0 + \beta_1 \text{July_mean}$	39.457 (12.498)	$-1.685 \cdot 10^{-4}$ ($6.600 \cdot 10^{-5}$)		0.269	3	38.811	0.406
Mountain pine beetle	$\beta_0 + \beta_1 \text{Elevation} + \beta_2 \text{Nonveg}$	-25.940 (12.392)	0.017 (0.006)	-0.096 0.038	0.427	4	38.598	0.460
<i>Ips</i> sp.	$\beta_0 + \beta_1 \text{Total_pine}$	0.648 (2.331)	0.022 (0.010)		0.216	3	40.960	0.325

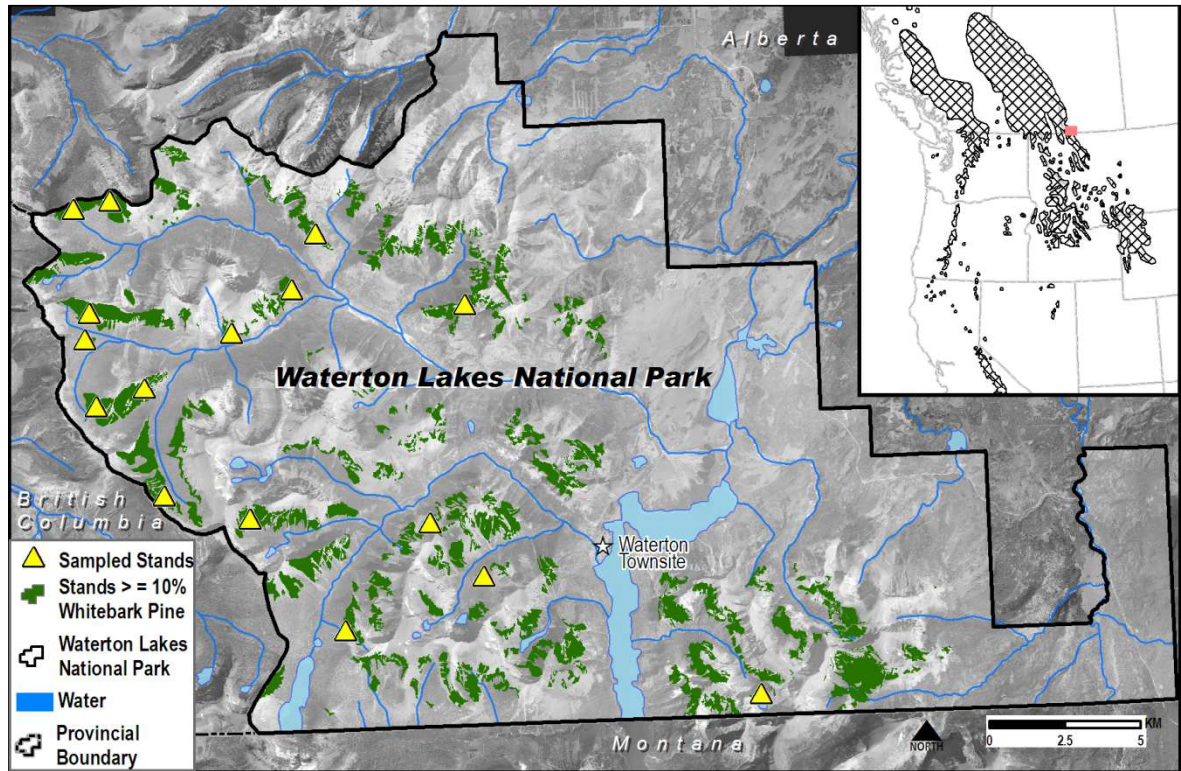


Figure 4. The locations of the 16 stands sampled in Waterton Lakes National Park, Alberta, Canada (51, 000 ha; the inset shows the location of the park (pink) relative to the range of whitebark pine in North America (hatched)).

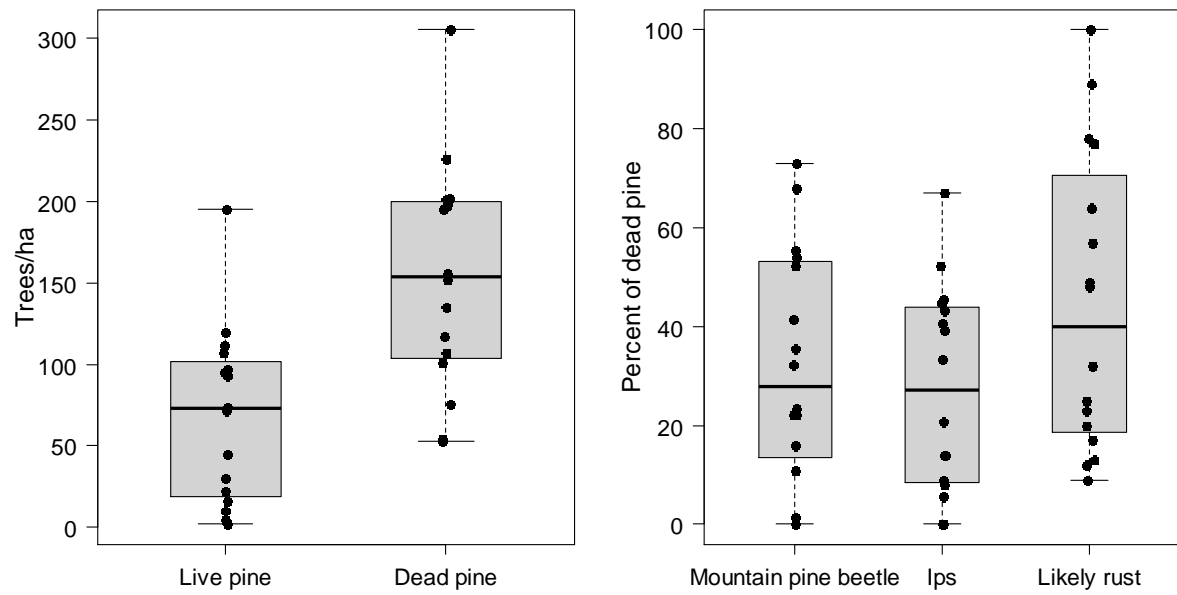


Figure 5. Boxplots of the stand density of live and dead whitebark pine trees (left) and the proportion of dead whitebark pine trees with evidence of mountain pine beetle, *Ips* species or blister rust (right) in Waterton Lakes National Park. The box indicates the interquartile range, the solid line in the box indicates the median and the whiskers extend to 1.5 times the interquartile range. Dots indicate average values for each stand.

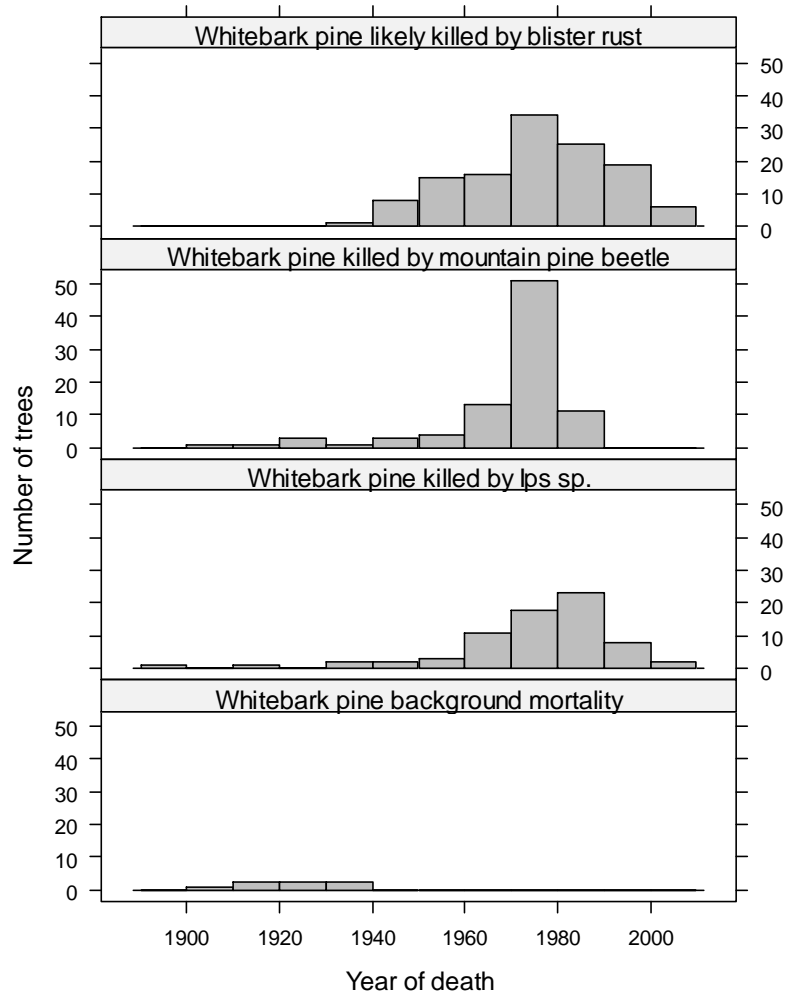


Figure 6. Distributions of the year of death of whitebark pine trees killed by the three disturbance agents and those killed by unknown causes of death prior to the introduction of blister rust in the area ~1940.

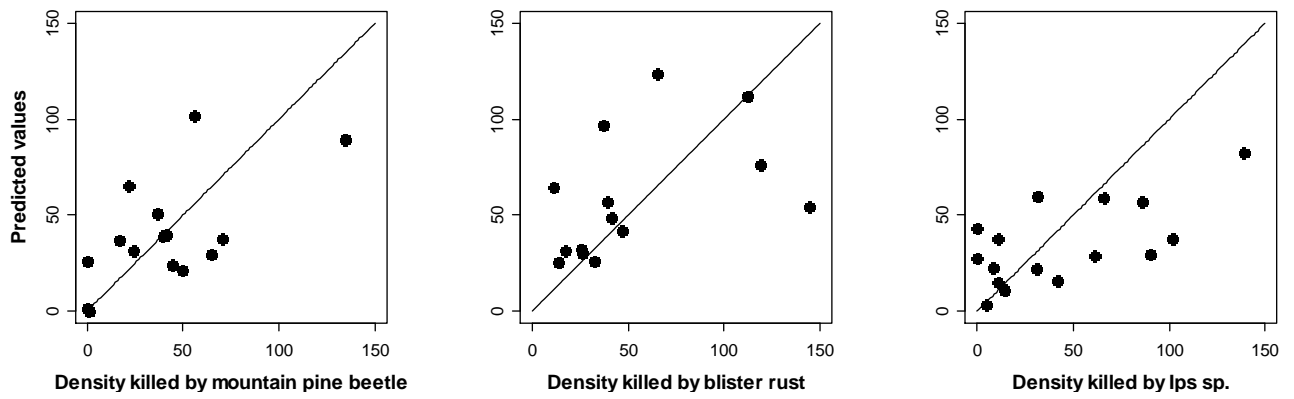


Figure 7. Observed versus predicted whitebark pine mortality from the three disturbance agents, lines indicate 1:1 relationship. Predicted values are from models in Table 4.

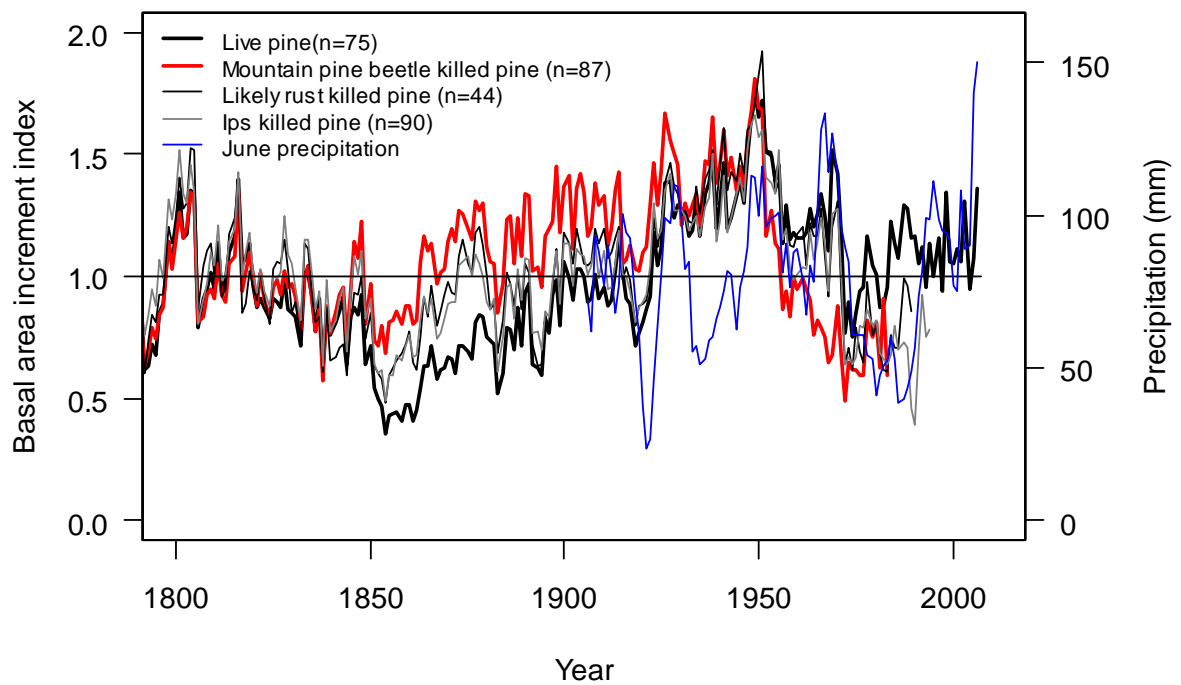


Figure 8. In 1950 the beginning of a marked decline in the growth of whitebark pine trees prior to being killed by mountain pine beetle is evident and in the other chronologies, a positive correlation with June precipitation until ~1980. Each chronology is normalized where $y=1$ represents the average basal area increment. Sample depth given in the legend was that at 1900 and all chronologies end when the sample depth decreased to nine trees. Total precipitation in June is from station records in Lethbridge, Alberta and is plotted as a five-year moving average.

Chapter 3: High disturbance severity and site stress lowers whitebark pine resilience

3.1 Introduction

Certain forest diseases and insects have recently occurred with unprecedented severity and extent enabled by climate change (Dale et al. 2001, Raffa et al. 2008, Bentz et al. 2010, Sturrock et al. 2011). The spread of non-native pathogens to North American forests from other continents has also resulted in novel disturbance regimes (Chapter 2). Whether forests are resilient to these recent outbreaks, which are outside their range of the natural variability (Raffa et al. 2008), is unknown. In this study, I determine how regeneration and surviving trees in subalpine forests of the Rocky Mountains in southern Alberta, Canada containing whitebark pine (*Pinus albicaulis*) respond to the interactions of three pine-specific disturbances, one of which is non-native. Because whitebark pine is designated Endangered in Canada due to extensive decline throughout its range (Committee on the Status of Endangered Wildlife in Canada 2010), I then examine whether the cumulative impact exceeds whitebark pine's resilience to disturbance.

Ecological resilience is the capacity of an ecosystem to absorb disturbance or stress and undergo change while maintaining its essential identity, functions, structures, and feedbacks (Holling 1973, Peterson et al. 1998). Ecosystems can shift from one stable state to another, triggered by a combination of gradual changes in drivers and disturbance that forces the ecosystem to cross a threshold (Scheffer and Carpenter 2003). High ecological resilience prevents such regime shifts. However, resilience is challenged when novel disturbance regimes create conditions for which tree species are not adapted (Buma and Wessman 2011). In forests, there are examples where multiple disturbances in quick succession have led to the failure of tree regeneration and a shift to grassland, parkland, or dominance by deciduous trees (Payette and Delwaide 2003, Johnstone et al. 2010, Buma and Wessman 2011).

Changes in ecological regimes are difficult to predict as is measuring ecological resilience (Thrush et al. 2009). Inferring a regime shift requires several lines of evidence including: a slowing down in the recovery after a disturbance (van Nes and Scheffer 2009); increased variance or an abrupt shift in a driving variable or system behaviour over time (Carpenter and Brock 2006); trends of decreasing abundance of a key species; and, changes in recruitment and juvenile mortality (Thrush et al. 2009). The response in subalpine trees to a change in disturbance regime, both in terms of regeneration and growth of surviving trees, is expected to be complex. The cumulative disturbance varies in severity across the landscape and regeneration and growth can be affected by the level of abiotic stress at a particular site. High levels of abiotic stress for subalpine trees is caused by extremely low temperatures causing photo-inhibition, poor soils causing moisture or nutrient limitation, and wind desiccation and abrasion (Callaway 1998, Germino and Smith 1999, Maher et al. 2005, Baumeister and Callaway 2006). Spatial

and temporal variation in disturbance severity and abiotic stress can lead to different successional pathways in different locations on the landscape (Shenoy et al. 2011). If the rate of recovery to conditions prior to the disturbance (also termed engineering resilience) is an indicator of ecological resilience (van Nes and Scheffer 2009), then ecological resilience on the landscape should be predictable from pre-disturbance condition, disturbance severity and level of abiotic stress at a site (Rydgren et al. 2004, Bruelheide and Luginbühl 2009). For example, in boreal forests of Yukon, recruitment of trees after a high-severity fire illustrated that sites experiencing greater abiotic stress showed the lowest resilience to disturbance (Johnstone et al. 2010) and, in salt marshes of Mississippi River Delta, more stressed locations also recovered more slowly from experimental herbicide disturbances (Slocum and Mendelssohn 2008).

It has been suggested that forests containing whitebark pine are undergoing a regime shift in which whitebark pine may be extirpated and replaced by late-seral tree species and that these forests will be unable to recover from this change (Keane et al. 1990, Logan et al. 2010). This has been attributed to a marked change in the natural disturbance regime in which the non-native white pine blister rust (*Cronartium ribicola*, hereafter termed “blister rust”) has been introduced, fires have been excluded and warmer temperatures and drier growing seasons have facilitated the population growth of mountain pine bark beetles (*Dendroctonus ponderosae*), resulting in increased mortality and reduced reproductive capacity of mature whitebark pine trees (Logan and Powell 2001, Raffa et al. 2008, Logan et al. 2010). The axiom that this shift in disturbance regime leads to an unrecoverable shift to late-seral species remains untested, particularly where fires were historically infrequent. While mountain pine beetle is generally considered detrimental because it kills mature whitebark pine trees, gaps created in the canopy also offer opportunity for whitebark pine regeneration (Larson and Kipfmüller 2010). It is possible that there is a threshold at which cumulative mortality of whitebark pine from the contemporary disturbances of mountain pine beetle and blister rust represents either an opportunity or a net loss to whitebark pine recruitment. Below this threshold, mortality of adults and infection of saplings by blister rust would be low enough that the release of resources would represent a regeneration opportunity for whitebark pine. Above this threshold, high mortality of adults, reducing the seed source, and high infection of saplings by blister rust would represent a net loss.

The contemporary disturbance regime in subalpine forests with whitebark pine contains disturbance agents which operate on different time scales and affect different demographic stages of the population (Chapter 2). In this chapter I do not consider fire because of the lack of evidence of frequent fire in stands containing whitebark pine in my study area which generally are very old stands with no fire-scarred trees. Blister rust is a fungal disease specific to five-needled pines introduced to North America in the early 1900s (McDonald and Hoff 2001). Once infected by blister rust, a tree dies slowly as the disease girdles the stem. Often the top half or more of the tree is killed, leaving the lower stem and branches alive. Unfortunately for whitebark pine, cones are produced only on the top few branches, meaning that top-killed trees, although alive, are reproductively dead. Blister rust can remain active in a stand for decades, affecting saplings to mature trees and causing varying levels of mortality (Campbell and Antos 2000, Smith et al. 2008). Mountain pine beetles are found at endemic levels in whitebark pine forests and at lower elevations in lodgepole pine (*Pinus contorta* var. *latifolia*) forests, but populations can build to an outbreak causing high levels of mortality over a few years. Mountain pine beetles favour large whitebark pine trees with phloem

thick enough to protect broods over the winter (Perkins and Roberts 2003). Unlike blister rust, death of a tree by mountain pine beetle is relatively quick once a tree is attacked (Safranyik and Carroll 2006). Outbreaks of mountain pine beetle in lodgepole pine forests are often preceded or followed by *Ips* sp. bark beetles, such as the pine engraver (*I. pini*), which target stressed and/or smaller trees than those favoured by mountain pine beetle (Safranyik and Carroll 2006). Combined, blister rust, mountain pine beetle and *Ips* sp. can cause mortality in almost all of the life-stages of a whitebark pine population (Chapter 2).

The response of whitebark pine forests to the cumulative disturbance of blister rust and bark beetles is not well understood. Variation in disturbance severity will create gaps of various sizes in the canopy, thereby freeing up resources (Pickett and White 1985). This disturbance may trigger additional regeneration and/or enable trees in the understory to release as has been found in lodgepole pine forests after mountain pine beetle outbreaks (Romme et al. 1986, Dordel et al. 2008, Axelson et al. 2010). Whitebark pine is thought to establish best after a fire (Keane 2001, Tomback et al. 2001); however, it can tolerate shade and regenerate under a range of light conditions in the understory of mature forests (Campbell and Antos 2003, Moody 2006). The late-seral species, subalpine fir (*Abies lasiocarpa*) is very shade tolerant but also responds to gaps in the forest canopy (Coates 2000). It is inhibited by low temperatures more than whitebark pine (Arno and Hoff 1989, Germino et al. 2002). Unlike subalpine fir, the seed of whitebark pine cannot be dispersed by wind, but rather depends on the caching behaviour of the bird, Clark's nutcracker (*Nucifraga columbiana*). This means that the regeneration response of whitebark pine to disturbance gaps can be limited when the mortality of the local seed source is too high (McKinney et al. 2009). Thus, while increasing disturbance severity may increase the opportunity for regeneration of both species, successful establishment of subalpine fir may be limited on more abiotically stressful sites and that of whitebark pine regeneration may be limited by seed availability.

There are several possible models for predicting the response of regeneration after the cumulative disturbance of blister rust and bark beetles in whitebark pine forests. I hypothesize that disturbance severity will be a strong predictor; however, the relationship between regeneration and disturbance severity can be confounded by other factors. For example, in lodgepole pine forests after a mountain pine beetle outbreak, browsing by ungulates on seedlings confounded the relationship between regeneration and disturbance severity (Dordel et al. 2008). In whitebark pine forests, blister rust may play a similar modifying role, although the dynamics of blister rust itself, may be affected by disturbance severity and the associated change in humidity at the microsite (Van Arsdell et al. 1956). Thus, I compare the support for a model for predicting regeneration density from disturbance severity with various other models which include explanatory variables of local topography, seed source and site conditions, and interspecific interactions such as facilitation/competition with other seedlings, shrubs or herbaceous plants (Table 5).

The responses in surviving trees in whitebark pine forests after the cumulative disturbance of blister rust and mountain pine beetle will likely follow those observed in lodgepole pine forests after a mountain pine beetle outbreak. It is expected that surviving trees in the canopy and understory will accelerate in growth and that there will be a shift to late-seral, non-host tree species in the canopy (Hawkes et al. 2004, Axelson et al. 2009). Growth releases of 20 to 70% in canopy trees and 60 to 260% in understory trees have also been observed after a mountain

pine beetle outbreak in lodgepole pine forests, likely in response to the increase in availability of light and other resources (Romme et al. 1986). However, the latter may not be maintained, since gaps in the canopy from the mortality of mature trees may also trigger the regeneration of early-seral species and subsequent dominance of these species in the canopy (Dordel et al. 2008, Axelson et al. 2010). Thus, the rate of a shift to late-seral species will depend on how strongly the regeneration of whitebark pine and the rate of infection by blister rust are related to disturbance severity.

In the Rocky Mountains of southern Alberta, Canada, the interactions of blister rust, mountain pine beetle and *Ips* sp. formed a distinct disturbance event in the subalpine forests of Waterton Lakes National Park. Cumulatively, the event was host-specific, widespread, long in duration (at least 50 years) and of mixed severity (range of 20 to 90% mortality of whitebark pine; Chapter 2). I sampled 15 randomly selected stands containing whitebark pine and subalpine fir approximately 30 years after the mountain pine beetle outbreak in Waterton Lakes National Park and asked: 1) Does the cumulative disturbance create or dampen opportunity for tree regeneration? Does it increase the incidence of blister rust on whitebark pine regeneration? 2) How did mature subalpine fir and surviving whitebark pine predating the disturbances respond to the cumulative disturbance? and 3) Can I predict the ecological resilience of whitebark pine from disturbance severity and level of abiotic stress?

3.2 Methods

3.2.1 Study area

The study area was in Waterton Lakes National Park, Alberta (49° 2' N, 113° 57' W; Figure 9). In the Park, whitebark pine is found over 3775 ha of the upper elevations (1600 to 2000 m) of subalpine forests in one of four plant communities: 1) subalpine fir and bear grass (*Xerophyllum tenax* (Pursh) Nutt.); 2) subalpine fir, Hitchcock's woodrush (*Luzula hitchcockii* Hämet-Ahti) and low bilberry (*Vaccinium myrtillus* L.); 3) Engelmann spruce (*Picea engelmanni* Parry ex Englem.), false azalea (*Menziesia ferruginea* Sm.); common juniper (*Juniperus communis* L.) and white-flowered rhododendron (*Rhododendron albiflorum* Hook.); and 4) common juniper, soapberry, (*Shepherdia canadensis* (L.) Nutt.) and kinnickinnick (*Arctostaphylos uva-ursi* (L.) Spreng.) (Achuff et al. 2002). High levels of mortality of whitebark pine from blister rust and mountain pine beetle have been recorded during monitoring by Parks Canada (Smith et al. 2008). Limber pine (*Pinus flexilis*) infected by blister rust were first observed in the Park in the 1958 (Department of Forestry Canada 1963). In 1977, a mountain pine beetle outbreak spread into the Park from adjacent areas in Montana, US (Watt 1981). The outbreak ended around 1984, affecting 1835 ha of forests dominated by either lodgepole or whitebark pine (Hawkes et al. 2004).

3.2.2 Sampling

I sampled 15 stands (average = 31 ha) containing whitebark pine below treeline. Stands were selected using a geographic information system (GIS) analysis of an existing vegetation inventory of the Park interpreted from aerial photographs. Stands were randomly selected from a population of forested polygons where whitebark pine formed more than 10% of the canopy, were larger than one hectare and accessible by foot. To ensure the sampling covered a wide range of environmental conditions, the population of stands was stratified as either predominantly

on warm (91°- 270°) or cool (270°- 90°) aspects. Most of the whitebark pine stands were on warm aspects (76%); 12 stands were randomly selected from this stratum and three stands from the cool stratum.

In each stand, I sampled at four to six points. Before entering the field, the coordinates of the first point were selected close to the center of the stand using a GIS to avoid sampling at treeline. The subsequent sampling points were established at distances randomly selected between 40 and 100 m along a bearing parallel with the slope contour. For each stand, net solar radiation was modelled for each month from digital elevation models using the GIS-based solar radiation model, ArcView Solar Analyst (Fu and Rich 1999) to account for the influences of the sun's position, viewshed, surface orientation, elevation, and atmospheric conditions (D. Zell, GIS specialist, Parks Canada, unpublished data). The raster values were averaged over each stand and I used the averages for the months of January and June in further analyses.

At each sampling point, I established three nested, circular plots. The radius of the smallest plot was 3.99 m. For dense stands (> 4,000 trees/ha), the radii of the medium and large plots were 5.66 and 8 m; for less dense stands, the radii were 8 and 12.66 m. For the small radius plots, I recorded the elevation and slope angle. I also visually estimated the percent cover of shrubs, herbs, lichen, moss and non-vegetated area and averaged a visual estimate of the percent of canopy closure from four locations approximating the four cardinal directions from the sampling point. I recorded subalpine fir and whitebark pine regeneration as the number of germinants, seedlings and saplings which were less < 4 cm diameter at breast height (1.3 m above ground; DBH). To estimate the dates of establishment of subalpine fir regeneration, I systematically sampled subalpine fir to obtain cross-sections of five trees in each of the three height classes at the first sampling point in each stand (n=191). For small germinants where a cross-section was not possible, I collected the entire seedling. To limit impact on whitebark pine recruitment, I only destructively sampled whitebark pine regeneration that was infected with blister rust (n=62). In the medium radius plots, the species and DBH of all trees taller than 1.3 m and larger than 4 cm DBH were recorded (n=1326). In the large radius plots, only trees with a DBH equal or larger than 15 cm were measured (n=958). Estimates of the density and basal area per hectare for each tree species were determined from these fixed-area plots.

Because the density of mature whitebark pine was sparse relative to subalpine fir and could be highly variable within and among stands, estimates of whitebark pine density based on fixed-area plots could have low precision (Pielou 1977). Therefore, I estimated the average stand density of whitebark pine using distance sampling. Although distance sampling has been criticized for producing biased estimates of densities when populations do not have a random spatial pattern (Pielou 1977), simulation tests suggest methods that use distances to at least the third closest individual from a random point perform well when trees are spatially aggregated (Engeman et al. 1994) as can be the case in whitebark pine forests. Distance sampling also guarantees a minimum number of measured whitebark pine trees at each sample point regardless of density. I used the distance to the fourth tree (Pollard 1971) to estimate the densities of two categories of whitebark pines: large (DBH \geq 15 cm) live trees and large dead trees. I put more effort into obtaining accurate estimates of whitebark pines with a DBH \geq 15 cm, because medium sized trees from 4 to 15 cm DBH were relatively scarce. At each sample point (*i*) and for each category of whitebark pine, I estimated the average density or stems per ha (SPH) per stand (*j*) using Eq. [1] in

Chapter 2 where m_j is the number of sampled points (i) in a stand (j), n is the number of trees measured around each point ($n = 4$), and A_{ij} is the area in hectares sampled around each point based on the distance (i.e., radius, R_{ij}) to the fourth closest tree. Area was corrected for the expected radius under a Poisson distribution using $(n - 1)/n$ (Moore 1954, Eberhart 1967). The maximum distance searched was 30m from each sample point. For 22% and 3% of sample points for live and dead trees, respectively, a fourth individual was not found within 30m and estimates of average stand density were corrected for this maximum search distance by substituting 30m as R_{ij} in Eq. [2]. Less than half of whitebark pine trees (44%) grew in clumps of more than one stem (median: two stems, maximum: five stems). Because it was difficult to distinguish whether these clumps were individual trees or the same tree with multiple stems, I considered these to be one tree. For trees with multiple stems, the stem that was most dominant in the canopy and closest to the sample point was measured.

The potential cause of death for the four closest whitebark pines to a sampling point was determined from evidence on the stem. The likely beetle species was based on characteristics of egg and larval galleries in the subcortical region (Furniss and Carolin 1977) and signs of blister rust included dead tops, branch and stem cankers and evidence of red squirrel (*Tamiasciurus hudsonicus*) feeding on the phloem and spermagonial exudate (Tomback et al. 2004). Because these symptoms of rust are not evident on the stem long after a tree dies, I suspected rust as the cause of death on dead trees with no beetle evidence. When estimating the density of a particular subset of trees, for example, the density of trees killed by mountain pine beetle, Eq [2] remained the same. However, n in Eq.[1] was reduced to the number of trees (maximum of four) with that characteristic.

3.2.3 Death dates and radial growth

To estimate the death date and growth of whitebark pine, I took increment cores from each of the four dead whitebark pines sampled at every point ($n=290$). I cored the stem parallel to the slope in locations where the outer rings were best preserved, meaning those with solid outer wood and bark or with bark beetle galleries which indicated that the subcortical tissue was present. I was able to obtain cores where the outer ring was thought to be well preserved in 74% of the trees and high-quality cores from both sides of the stem on an average of 55% of the trees. To examine growth responses of subalpine fir, I extracted increment cores from one small ($4 \leq \text{DBH} < 15$ cm) and one large ($\text{DBH} \geq 15$ cm) tree randomly selected within a 2 m radius of the targeted whitebark pine tree. To increase the probability of selecting a large tree, the third tree was randomly selected from those within a variable radius plot (i.e., trees selected with probability proportional to DBH) around the dead whitebark pine using a prism of basal area factor 2.0 m²/ha.

3.2.4 Determining the role of disturbance severity in regeneration dynamics

I determined whether the variability in disturbance severity could explain the variability in the regeneration density better than variables representing influences of local topography, seed source or interspecific interactions. I used an information-theoretic approach to attribute support to models representing various hypotheses outlined in Table 5. I substituted candidate explanatory variables associated with the hypotheses in Table 5 for x_1 to x_3 in the following generalized linear mixed-effects model:

$$[3] \quad w_{ij} \text{ or } y_{ij} \text{ or } z_{ij} = g^{-1}(u_{ij}) * f(p_{ij}) + \varepsilon_{ij} \text{ where } g(u_{ij}) = \beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \beta_3 x_{3j} + \varepsilon_j$$

where the density of subalpine fir regeneration (w_{ij}), total whitebark pine regeneration (y_{ij}) or whitebark pine regeneration infected by blister rust (z_{ij}) is that in plot (i) in stand (j). All were modelled as negative binomial distribution with the log-link function $g(u_{ij})$ (whitebark pine mean: 478 trees/ha, variance: 656,781; subalpine fir mean: 4121, variance: 1,2163,313). Because zeros formed 4% and 24% of subalpine fir and whitebark pine regeneration counts respectively and could be due to both true zeros and observation error, I also modelled a constant probability for zero-inflation with the logit-link function $f(p_{ij}) = (1 - \exp^v / (1 + \exp^v))$. Between-stand and within-stand variances were partly explained by the fixed-effects part of the model (i.e., coefficients β_1 to β_3 associated with explanatory variables x_1 to x_3), and the remaining residual between-stand variance and within-stand variances (i.e., random-effects) are represented by ε_j and ε_{ij} respectively.

For a reasonable number of candidate models, I limited explanatory variables to those which had relatively high Spearman's correlation coefficients with tree regeneration (this was set as > 0.150 for subalpine fir and > 0.350 with whitebark pine regeneration). I also restricted models to three explanatory variables for parsimony except where interactions or quadratic terms improved the Akaike's information criterion adjusted for a small sample size (AIC_c). I included quadratic terms for elevation for subalpine fir regeneration and disturbance severity for whitebark pine regeneration because I hypothesized that there were thresholds to the response of regeneration to these variables. The correction factor for small sample sizes for AIC_c was based on the number of plots and the number of estimated parameters (k), including the fixed-effects parameters, two error terms and a zero-inflation factor. For subalpine fir, four plots where regeneration densities exceeded 20,000 trees/ha were excluded because they were five times greater than the overall average (subalpine fir: $i=67$ plots, $j=14$ stands). For whitebark pine, four plots exceeding 5000 trees/ha in one stand, which was 15 times larger than the overall average and suspected to be due to a recent surface fire, were excluded ($i=68$ plots, $j=14$ stands). Model coefficients were estimated using maximum likelihood methods with the `glmmadmb` function from the package `glmmADMB` (version 0.6.3; Skaug et al. 2011) in the R language and environment (v.2.11.1, R Development Core Team 2010). I used the associated Akaike weights to quantify the relative support for each hypothesis (Burnham and Anderson 1998).

3.2.5 Timing of regeneration

I examined how the timing of regeneration corresponded with the timing of mortality. I estimated the death date of each whitebark pine by crossdating each ring-width series with a master chronology of ring-widths. To do so, I counted well-sanded cores under a stereomicroscope. Ring widths of all cores were measured to the nearest 0.01mm using a Velmex sliding stage interfaced with a computer. I created a master chronology of ring-widths for each stand using the program COFECHA (Grissino-Mayer 2001). The median difference between pairs of cores from the same dead tree was 4 years (average = 12) and could have been due to cambial dieback, wind erosion or decay occurring at asymmetrical rates around the stem. There were 57 trees that had mountain pine beetle galleries with outside dates of death prior to 1977 when the last outbreak started according to independent records. The median difference between 1977 and the death dates of these trees was 6 years (average = 13), which suggests a low

level of outer-ring decay. Therefore, to account for the level of uncertainty in the death dates, I examined distributions of death dates using 10-year classes.

To estimate years of establishment for subalpine and whitebark pine regeneration, I counted well-sanded cross sections under a stereomicroscope. Because of the short time series, I did not crossdate seedlings but instead accounted for missing rings by counting two radii, the longest and an adjacent one separated by 45 degrees on half of the samples (the difference between radii averaged two years for subalpine fir and one year for whitebark pine). For seedlings that were too small to examine a cross section, I counted terminal bud scars along the stem (10% of samples).

I inferred how the timing of whitebark pine mortality may influence the timing of subalpine fir establishment by first visually inspecting histograms of death dates of whitebark pine versus establishment dates of subalpine fir. I determined whether regeneration was continuous or episodic based on the distribution of establishment dates and whether it occurred prior or after peak mortality in each stand. The year associated with the 25th quartile of dates of whitebark pine mortality in each stand was identified. I calculated the difference between the number of subalpine fir seedlings which established within 25 years before and after this date. I tested whether the mean difference across the stands was zero using the Wilcoxon signed rank test. I did not do the same analysis for whitebark pine regeneration because my sampling was limited by conservation concerns and thus biased towards saplings that were dead or infected with blister rust.

3.2.6 Determining the response of mature subalpine fir to disturbance

I determined whether there was a response in the growth of mature subalpine fir and surviving whitebark pine to the cumulative mortality of whitebark pine. Mature trees were those larger than 4 cm DBH and established before 1960. To develop chronologies of growth, I calculated the annual basal area increment for each crossdated ring-width series. I then normalized each time series into a dimensionless index (BAI) by dividing annual increments of basal area by the average increment for each tree using the dendrochronology program library in R (dplR package Version: 1.3.8; Bunn 2008). I did not detrend each series to remove an age-related growth trend for three reasons: 1) most trees were old (subalpine fir: 180 ± 58 years, pine: 274 ± 84 ; average \pm std. dev.) and I was examining recent growth since 1940; 2) in the presence of disturbance there is no clear model for detrending (e.g., most subalpine fir exhibited an increase, not a decrease, in growth with age); and, 3) I was looking for sudden changes in tree growth (Biondi and Qeadan 2008). I developed a Park-wide chronology of BAI for subalpine fir and four chronologies for whitebark pine (one for live trees, trees killed by mountain pine beetle, trees with *Ips* sp. evidence, and trees suspected to have been killed by blister rust) using a Tukey's biweight mean to reduce the effect of outliers (Cook and Kairiukstis 1990). Each chronology contained trees from all 16 stands and had more than eight trees for any year.

I identified abrupt shifts in the growth of surviving subalpine fir and whitebark pine using piecewise regression. I fitted segmented linear models for the chronologies of BAI versus year and searched for a breakpoint in the model between the years 1940 and 1990 that minimized the residual standard error using R software

(Crawley 2007; version 2.8.1). To avoid discontinuities in the model, the predicted value was constrained to be equal for both segments at the breakpoint.

I examined how climate was related to subalpine fir growth prior to the disturbances. I correlated the Park-wide chronology of subalpine fir BAI with 36 climatic variables: the average monthly temperatures or total precipitation from April of the year prior to tree-ring formation to September of the year current with ring formation. Temperature and precipitation records came from a weather station in Lethbridge (~100 km away, 49.63° N, 112.80 °W) which had complete records from 1903 to 2004 (Adjusted and Homogenized Canadian Climate Data; Mekis and Vincent 2011). To avoid the potential response in growth due to the disturbance event, I truncated the data so that the last year used in the correlation was 1950. I calculated the Pearson correlation coefficient for BAI and each of the 36 climatic variables. I tested for a non-zero correlation by randomly arranging the sample data using 1000 bootstrapped samples, obtaining the 2.5 and 97.5 quantiles of the 1000 estimates, and seeing if the observed correlation was outside of these limits using DendroClim2002 (Biondi and Waikul 2004).

I examined whether the year of any identified abrupt shifts in subalpine fir growth corresponded to the peak period of cumulative whitebark pine mortality and/or shifts in climatic variables. I determined the peak period of cumulative whitebark pine mortality as the interquartile range of death dates. For those climatic variables that were deemed significantly correlated to subalpine fir BAI, I tested for significant temporal trends and shifts using linear regression and/or piecewise regression over the entire instrumental record.

3.2.7 Assessing resilience

I quantified the resilience, or the potential recovery, of whitebark pine at each sample point as the ratio of the density of healthy whitebark pine regeneration and mature trees to the density of mature whitebark pine trees prior to disturbance. I reconstructed the historical density by summing that of live and dead mature trees. For analyses, I added one to this ratio and then took the natural log. Stands were considered resilient if this index was greater than 0.694, meaning that the density of healthy regeneration and trees was equal or more than that in the mature canopy prior to disturbance. Because the rate of mortality of regeneration and trees in the understory was not known, I also recalculated the resilience index assuming 10% or 20% mortality will occur before these trees reach the canopy. I then evaluated the influence of disturbance severity and stress (using topographic surrogates of elevation, slope and average solar radiation in January and July as modelled from a digital elevation model) on the resilience of whitebark pine using a linear model fitted using multiple linear regression in R (base package Version 2.11.1).

3.3 Results

3.3.1 Regeneration: few pine, many fir and both relatively old

The density of whitebark pine regeneration was highly variable between stands from no regeneration in one stand to a maximum of 7659 seedlings per hectare in another. Whitebark pine regeneration (966 ± 1919 trees /ha, average \pm one standard deviation) was sparse relative to subalpine fir regeneration (5238 ± 4282 trees/ha) and the regeneration density of these two species was not correlated (Spearman's $\rho=0.13$, $p=0.64$). Eleven percent of

whitebark pine regeneration had some damage attributable to blister rust. Both whitebark pine (81 ± 65 years) and subalpine fir regeneration (65 ± 64 years) were relatively old and established in every decade since 1850 (Figure 10). Only 22% of subalpine fir established after 1977, the recorded onset of the mountain pine beetle outbreak. This indicates that most of the subalpine fir regeneration was not triggered by this outbreak. Only 6% of the sampled whitebark pine regeneration established after the outbreak but this sample was limited to seedlings infected by blister rust and may not reflect the healthy population.

3.3.2 Disturbance severity partly explained regeneration

Most large whitebark pine trees in the Park were dead (72%, range 20-90%, Chapter 2). On average, 44% of dead whitebark pine had no insect evidence and were considered to have died from blister rust, 32% had egg galleries characteristic of mountain pine beetle, and 27% of the dead whitebark pine showed only evidence of the bark beetles, *Ips* sp (Chapter 2). The variability in disturbance severity explained some of the variability in regeneration density for both species; however, the best models also included elevation (Table 6 and Table 7). Either an indirect outcome of disturbance severity, the density of live mature whitebark pine, or a direct outcome of disturbance severity, the density of dead whitebark pine killed by blister rust and *Ips* sp. were present in the top models for subalpine fir and whitebark pine regeneration (Akaike weights = 0.597, 0.250; Table 6, Table 7). Subalpine fir regeneration increased with the severity of cumulative disturbance by blister rust and *Ips* sp. to the whitebark pine overstory until a certain elevational threshold (Figure 11a). Subalpine fir regeneration also decreased with increasing density of mature whitebark pine. Whitebark pine regeneration first decreased and then increased with the severity of disturbance by blister rust once a certain threshold of disturbance severity was exceeded (Figure 11c). This threshold decreased as elevation increased. Models for predicting whitebark pine regeneration were relatively weak. Model [1] with elevation and the density of live whitebark pine was not clearly better than Model [5] with elevation and the quadratic term of density of whitebark pine killed by blister rust (Akaike weights of 0.248 versus 0.244). Seed source, as represented by the amount of mature conspecific trees and as hypothesized in Table 5, was important for whitebark pine models but not for subalpine fir. Interspecific interactions between seedlings and shrubs/herbs were not important for explaining either subalpine fir or whitebark pine regeneration.

In contrast, the incidence of whitebark pine regeneration infected by blister rust reflected site conditions and not disturbance severity (top Akaike weight 0.451; Table 7). Infected whitebark pine regeneration increased with the percent cover of non-vegetated area and with subalpine fir basal area (Slopes (standard error): 0.013 (0.008); 0.034 (0.013)).

Although disturbance severity explained some of the variability in regeneration density, the dates of regeneration of subalpine fir in all stands, except Stands 7 and 14, were continuous rather than episodic (Figure 10 and Figure 12). All stands except Stand 7 had relatively old subalpine fir regeneration that established before the reconstructed whitebark pine mortality. There was no significant difference in the number of subalpine fir which regenerated 25 years prior versus after the death of whitebark pine (Wilcoxon test: $V=40$, $p=0.987$, 15 stands).

3.3.3 Mature subalpine fir grew faster after disturbance

The high level of whitebark pine mortality appeared to affect the growth of already established subalpine fir but not surviving whitebark pine (Figure 13). Since 1750, the annual basal area increment of subalpine fir gradually increased until 1969 when the rate of increase became 10 times greater (Figure 13). This increase was present in both overstory and understory subalpine fir and subalpine fir older than 1900 and younger than 1900 (not shown). I found that the best model for piecewise regression between time and BAI for all subalpine fir had a significant break at 1969 (Figure 13; residual standard error = 0.15, Adj. R^2 =0.94, $p < 0.001$, $df=251$; year< 1969: $BAI = -7.96 + 0.0045 \text{ year}$; year> 1969: $BAI = -95.71 + 0.047 \text{ year}$). There was some ambiguity around the year at which the breakpoint occurred because the residual standard error was low for alternate breakpoints fit for years between 1969 to 1977 (0.149 to 0.153). The shift in subalpine fir growth that occurred between 1969 and 1977 was within the period of time between 1966 and 1983 when 50% of the pine died and included 1977, the median of death dates. I did not find a significant breakpoint in the BAI of surviving whitebark pine between 1940 and 1990.

The distinct increase in the growth of subalpine fir after 1969 was not due to climate. Although I found significant climate-growth correlations, none of the climatic variables exhibited a shift which could support the abrupt increase in subalpine fir growth. Between 1903 and 1950, BAI was significantly and positively correlated to the average temperatures in May (Pearson correlation coefficient=0.239) in the year prior to ring formation and in July (Pearson correlation coefficient=0.274) and September (0.259) in the year current to ring formation. BAI was also significantly and positively correlated to total precipitation in January (0.317) and March (0.366) in the year current to ring formation from 1903 to 1950. None of the temperature variables shifted abruptly around 1969, nor did any have strong linear relationships with time (Adj. R^2 values: -0.007 to 0.05). Precipitation in January and March did significantly shift in 1971 and 1967 respectively from increasing to decreasing over time (Figure 13). However, because precipitation in January and March were positively correlated to BAI prior to 1971, this shift to drier winters does not support the abrupt increase in subalpine fir growth.

3.3.4 Resilience

Live, large whitebark pine formed a minor component of individual stands ($28 \pm 20\%$). Although these trees were alive, most were in poor health; 12% had active sporulation of blister rust and 65% were reproductively dead because of dead tops resulting from blister rust. Smaller, live pine trees ($4 \leq \text{DBH} < 15 \text{ cm}$) were also scarce ($48 \pm 61 \text{ trees/ha}$). Resilience of whitebark pine varied greatly across the landscape (Figure 14). Whitebark pine were not resilient at 57% of the sample points at the time of sampling (median index of resilience =0.496). At the stand level, whitebark pine were not resilient in 47% of the stands at the time of sampling (median index of resilience =0.721). Average resilience at the stand level was positively explained by average solar radiation in January (Adj. $R^2 = 0.336$, $F_{1,13}=8.074$, $p=0.014$) and elevation (Adj. $R^2 = 0.222$, $F_{1,13}=4.989$, $p=0.044$; Figure 14) but was not related to slope or solar radiation in July. Resilience was also related to the severity of blister rust (Adj. $R^2 = 0.296$, $F_{1,13}=6.892$, $p=0.021$) but not to the severity of cumulative disturbances.

3.4 Discussion

3.4.1 Regeneration response to disturbance

I made three key observations about the response of subalpine fir and whitebark pine regeneration to the blister rust and bark beetle disturbances in Waterton Lakes National Park. First, while multiple factors influenced tree regeneration in these subalpine forests, cumulative disturbance to mature whitebark pine in the forest canopy by blister rust and *Ips* sp. played a role. I had hypothesized that disturbance severity would be a strong predictor; however, models with solely disturbance severity as an explanatory variable were poor, indicating that regeneration response is complex and conditional on other factors. For subalpine fir, regeneration increased with increasing severity of blister rust and *Ips* sp.; however, regeneration decreased with increasing elevation after 2100m, likely because sites above this threshold were too abiotically stressful for seedling survival (Figure 11a; Johnson et al. 2004). For whitebark pine, low- to moderate-severity blister rust dampened regeneration possibly because the release of resources from the death of mature whitebark pine was small relative to the impacts of blister rust directly on whitebark pine seedlings. However, when mortality of mature whitebark pine was high, the release of resources was likely enough to create an opportunity for whitebark pine to regenerate. In addition, the opening of the canopy likely decreased humidity enough to make it inhospitable for spores of blister rust to develop and survive (Van Arsdell et al. 1956). The availability of seed source obviously limits whitebark pine regeneration which was not captured by this model. Equally supported by the data was another model which included the density of live mature whitebark pine and elevation (Table 7). The lack of strong support for any particular model for predicting whitebark pine regeneration may reflect an incomplete record of the density of whitebark pine regeneration because I did not count dead whitebark pine seedlings or it may reflect the absence of modelling the import and caching of seed by Clark's nutcracker.

Second, the type of disturbance was important. Models which included either the mortality from mountain pine beetle or the cumulative mortality from all three types of disturbances were not well supported for predicting subalpine fir or whitebark pine regeneration. Others have suggested that when fires are infrequent, mountain pine beetle, by creating gaps and opportunities for regeneration, plays an important role in self-perpetuation of whitebark pine forests (Larson and Kipfmüller 2010) and lodgepole pine forests (Stuart et al. 1989, Axelson et al. 2010). Prior to the introduction of blister rust to North America, mountain pine beetle may have played this role in the study area, especially because most stands were old and lacked fire-scarred trees. Aside from the 1970s outbreak, I have evidence from good quality increment cores of mortality in the late 1920s (two stands) and late 1950s (four stands) due to mountain pine beetle. However, in the presence of blister rust, my results do not support the hypothesis that mountain pine beetle is the sole mechanism triggering regeneration of either subalpine fir or whitebark pine. Additionally, although the scant evidence of fire in my study area suggests it was infrequent, it could have historically played a role in triggering regeneration in the one stand omitted in the regression analyses because of high whitebark pine regeneration values. In this stand, all the whitebark pine in the overstory predated 1700 but a crossdated fire scar indicated a fire burned in 1834. A low-severity fire could have burned since then because the average date of establishment of subalpine fir and whitebark pine regeneration was ~1950.

I present a conceptual model relating disturbance severity to the amount of subalpine fir and whitebark pine regeneration after a mountain pine beetle outbreak with and without the cumulative disturbance of blister rust in Figure 15. Because subalpine fir is relatively more shade tolerant than whitebark pine (Alexander et al. 1990), it could regenerate better than whitebark pine where disturbances were small and low-severity, such as small gaps in the canopy caused by an endemic mountain pine beetle attacks. Subalpine fir would only respond up until a certain level of disturbance. After disturbances of very high severity, regeneration may be limited by seed availability, low-temperatures and/or poor seedbeds. This type of threshold has been observed in experimental trials where subalpine fir naturally regenerated 10 times more in small gaps than in clearcuts (Eastham and Jull 1999). In the absence of blister rust, the amount of whitebark pine seedlings would increase with disturbance severity until a threshold where disturbances of very high severity eliminate viable seed sources. In the presence of blister rust, while gaps are being created by mortality of mature whitebark pines by mountain pine beetle, blister rust and *Ips* sp., blister rust is subsequently killing whitebark pine seedlings and saplings and reducing competition with subalpine fir regeneration. While there may be some positive response of whitebark pine regeneration at relatively high levels of blister rust, overall, the introduction of blister rust dampens whitebark pine regeneration and possibly accelerates the response of subalpine fir regeneration. The introduction of blister rust, thus, shifts succession after mountain pine beetle to dominance by subalpine fir.

Finally, while disturbance by blister rust and *Ips* sp. may trigger some new regeneration, particularly of subalpine fir, the regeneration of whitebark pine and subalpine fir can occur in these stands without high-severity disturbance. There was no distinct post-disturbance cohort because regeneration of both species also occurred well before the peak of whitebark pine mortality in 1977 (median date). Furthermore, because “seedlings” are relatively old, the lag time for establishment is long in subalpine forests.

3.4.2 Evidence of regime shift and low resilience

Since the triple whammy of disturbances, the species composition of stands has shifted from a state in which whitebark pine formed approximately 40% of stand basal area (22% of stand density) to the current state in which whitebark pine forms less than 14% (8% of stand density). There is little indication that whitebark pine will be able to regain its previous proportion of stand composition based on the following observations: 1) resilience of whitebark pine was quantified to be low; 2) blister rust was observed on whitebark pine regeneration in almost every stand; and 3) the growth of surviving whitebark pine did not respond to the triple whammy of disturbances. In contrast, regeneration was dominated by subalpine fir and there was a pronounced growth release in subalpine fir trees in the understory and overstory, both further accelerating the dominance of subalpine fir in the canopy.

These observations provide evidence that a shift to an alternate stable state, in which whitebark pine is extirpated and subalpine fir dominates the canopy, is occurring. The first two observations illustrate that there is a slowing down in the recovery of whitebark pine to the mountain pine beetle outbreak. While mountain pine beetles were a natural disturbance in the past, the additional effects of blister rust and *Ips* sp. are decreasing the abundance of seed-bearers and blister rust is increasing juvenile mortality. Successive disturbances and their interactions have dampened tree regeneration enough to cause a shift to alternate stable states in other forests. Buma and Wessman (2011) found that structural legacies from a windthrow event in a subalpine forest furthered the distance to seed

bearers and increased the residence time of a subsequent fire and the likelihood that seed banks were destroyed. This slowing in recovery has been found in other systems just before catastrophic change (e.g., the collapse of arid shrub-dominated ecosystems to desert; Dakos et al. 2011).

The third observation on the response in radial growth to cumulative disturbance to the canopy suggests that there has been an abrupt switch in the driving variables of the system. The death of whitebark pine reduced competition for limited resources and increased the growth of subalpine fir. The average BAI of mature subalpine fir of the last 30 years is 100% more than the average growth between 1945 and 1975. This growth response was notable as it overrode the expected decline in growth in response to decreasing precipitation in January and March (Figure 13). Prior to disturbance, the growth of subalpine fir was positively correlated to winter precipitation. However, after disturbance, the correlation became significantly negative (-0.432 and -0.256 for January and March precipitation respectively). Thus, the climate-growth relationship for subalpine fir appears to have been decoupled by the triple whammy of disturbances. This switch amplifies the shift to domination by subalpine fir in these forests.

Resilience of whitebark pine to the triple whammy of disturbances was, on average, low; however, there were locations on the landscape considered resilient. I found that resilience of whitebark pine increased with decreasing severity of blister rust and with decreasing abiotic stress at a site. Buma and Wessman (2011) also found that the dampening effects of fire on tree regeneration in subalpine forests increased with the severity of prior wind disturbance and then with elevation or slope. This relationship between resilience and disturbance intensity has been demonstrated in other systems such as boreal forests (Rydgren et al. 2004) and intertidal macroalgal communities (Allison 2004). The relationship between resilience and level of abiotic stress at a site has also been found in boreal forests of Yukon (Johnstone et al. 2010).

In the future, it is possible that additional seedlings of whitebark pine will be recruited in the Park, thus increasing the potential resilience of whitebark pine. However, McKinney et al. (2009) estimated that stands of whitebark pine need to produce ~1000 cones/ha to be attractive to Clark's nutcrackers to elicit seed dispersal and that this level of cone production may be met when the basal area of healthy whitebark pine exceeds 5.0 m²/ha. Even based on the most optimistic estimate, which assumes that all live whitebark pine were healthy, nine out of the 16 stands I sampled in the Park did not meet this threshold. The real situation is likely worse than this optimistic estimate because the landscape average of basal area of live whitebark pines (4.8 m²/ha) was below the threshold of 5.0 m²/ha and 67% of live trees had dead tops meaning they were reproductively dead. The low abundance of live mature trees and regeneration, plus the impact of blister rust, may mean that whitebark pine might disappear completely in the Park without active planting of rust-resistant seedlings.

3.4.3 Recommendations for whitebark pine's future

Whitebark pine is considered a foundation or keystone species in subalpine forests (Tomback and Kendall 2001, Ellison et al. 2005). The triple whammy of coinciding host-specific disturbances has profoundly changed the composition of the subalpine forests in Waterton Lakes National Park. My results, 30 years after a mountain pine beetle outbreak, are dire forebodings for other whitebark pine forests where blister rust, mountain pine beetle and

Ips sp. may concur. I provide three recommendations based on my work to help the restoration of the endangered whitebark pine after a mountain pine beetle outbreak. First, because cumulative disturbance severity can partially explain the variation in whitebark pine regeneration, the severity of mortality during the outbreak should be mapped using aerial surveys in the year following the outbreak. Second, although the density of surviving whitebark pine trees is positively associated with successful whitebark pine regeneration, there are potential confounding influences from blister rust. Moreover, I should expect an increase in subalpine fir regeneration and the growth of mature subalpine fir particularly to prolonged disturbance. Thus, the regeneration response of whitebark pine and subalpine fir should be monitored after an outbreak in a sample of stands representing a gradient in disturbance severity. Planting of rust-resistant whitebark pine should be targeted in stands of very high mortality where live, healthy whitebark pines are less than 5m²/ha. Third, the relationship that I found between the resilience of whitebark pine, severity of blister rust and solar radiation in January as modelled from a digital elevation model can be used to map the resilience of whitebark pine across landscapes and prioritize planting activities. These recommendations offer hope for increasing the resilience of whitebark pine to multiple, concurrent disturbances.

Table 5. Hypotheses and accompanying set of candidate explanatory variables for models used to explain the variation in subalpine fir (Fir_regen) and whitebark pine (Pine_regen) regeneration densities (trees/ha). Spearman's rank correlation coefficients (rho) in bold are significantly different from zero, $\alpha = 0.05$, $i = 67$ plots.

Hypothesized influences on regeneration	Spatial scale	Explanatory Variables	Subalpine fir rho	Whitebark pine rho	Infected whitebark pine rho
Local topography: Subalpine fir regeneration decreases whereas whitebark pine regeneration increases with increasing elevation, slope and solar radiation.	Stand-level	Elevation (metres, logarithmic transformed)	0.158	0.455	0.169
		Slope (radians)	-0.086	0.409	0.465
		Jan_mean (Modelled solar radiation, monthly mean; WH/m ²)	0.043	0.460	0.311
Disturbance severity: Regeneration density increases with increasing mortality (disturbance) of the forest canopy. Whitebark pine will be limited by surviving level of seed source.	Point-level	Live_pine	-0.350	0.483	0.377
		Dead_pine (Density all dead whitebark pine DBH ≥ 15 cm)	0.370	-0.169	-0.113
		Dead_beetle (Density whitebark pine DBH ≥ 15 cm killed by mountain pine beetle)	0.109	0.107	-0.138
		Dead_lps (Density whitebark pine DBH ≥ 15 cm killed by <i>lps</i> sp.)	0.107	0.381	0.353
		Dead_rust (Density of whitebark pine DBH ≥ 15 cm likely killed by blister rust)	0.149	-0.444	-0.162
		Dead_rust_lps (Dead_lps + Dead_none)	0.273	-0.189	0.061
Seed source and site conditions: Regeneration density increases with increasing density/basal area of mature trees. For whitebark pine, opportunities increase with increasing mineral soil exposure.	Point-level	Live_pine (Density live whitebark pine DBH ≥ 15 cm; trees /ha)	-0.350	0.483	0.377
		Nonveg (Percent cover of non-vegetated area)	-0.268	0.480	0.420
		Fir_ba (Basal area live subalpine fir DBH ≥ 4 cm; m ² /ha)	0.387	-0.474	-0.234
Interspecific interactions: Regeneration increases 1) if facilitated by other seedlings, shrubs or herbs, or 2) if seedlings are better competitors.	Point-level	Fir_regen	n/a	-0.045	0.072
		Pine_regen	-0.050	n/a	0.391
		Shrub (Percent cover)	0.043	-0.292	-0.229
		Herb (Percent cover)	-0.075	0.139	0.059

Table 6. Summary of generalized linear mixed-effects models for the plot-level density of subalpine fir regeneration (i= 67 plots, k = 14 stands). Shaded models indicate the best models based on Akaike weights (w). Explanatory variables are described in Table 5. K is the number of model parameters plus one for zero-inflation parameter, AICc is the Akaike's information criterion for small samples and diff is the difference from the minimum AICc.

No.	Model	k	AICc	diff	w
1	Elevation + Elevation ² + Mineral	7	1225.558	11.148	0.002
2	Elevation + Elevation ² + Fir_ba	7	1224.816	10.406	0.003
3	Elevation + Elevation ² + Dead_pine	7	1222.782	8.372	0.009
4	Elevation + Elevation ² + Live_pine	7	1216.160	1.750	0.249
5	Elevation + Elevation ² + Dead_rust_IPS	7	1224.788	10.378	0.003
6	Elevation + Elevation ² + Live_pine* Dead_rust_IPS	9	1214.410	0.000	0.597
7	Mineral+ Fir_ba	6	1226.894	12.484	0.001
8	Mineral+Dead_pine	6	1223.968	9.558	0.005
9	Mineral + Live_pine	6	1222.330	7.920	0.011
10	Mineral + Dead_rust	6	1225.958	11.548	0.002
11	Fir_ba+Dead_pine	6	1222.034	7.624	0.013
12	Fir_ba+ Live_pine	6	1220.864	6.454	0.024
13	Fir_ba + Dead_rust_IPS	6	1225.174	10.764	0.003
14	Dead_pine+ Live_pine	6	1220.038	5.628	0.036
15	Dead_pine + dead_rust	6	1224.984	10.574	0.003
16	Live_pine+ Dead_rust_IPS	6	1219.888	5.478	0.039

Table 7. Summary of generalized linear mixed-effects models for predicting the plot-level density of whitebark pine regeneration ($i=68$ plots, $j = 14$ stands). Shaded models indicate the best models based on Akaike weights (w). Explanatory variables are described in Table 5. K is the number of model parameters plus one for zero-inflation parameter, AICc is the Akaike's information criterion for small samples and diff is the difference from the minimum AICc.

			Total whitebark pine regeneration			Blister rust infected whitebark pine regeneration		
No.	Model	k	AICc	diff	w	AICc	diff	w
1	Elevation + Live_pine	6	744.113	0.000	0.248	284.467	5.062	0.036
2	Elevation + Nonveg	6	746.369	2.256	0.080	284.321	4.916	0.039
3	Elevation + Fir_ba	6	746.343	2.230	0.081	282.191	2.786	0.112
4	Elevation + Dead_IPS + Dead_IPS ²	7	748.409	4.296	0.029	329.897	50.492	0.000
5	Elevation + Dead_rust + Dead_rust ²	7	744.143	0.030	0.244	475.445	196.040	0.000
6	Jan_mean + Live_pine	6	748.183	4.070	0.032	388.599	109.194	0.000
7	Jan_mean+ Nonveg	6	750.459	6.346	0.010	283.291	3.886	0.065
8	Jan_mean + Fir_ba	6	750.437	6.324	0.010	282.111	2.706	0.116
9	Jan_mean+ Dead_IPS + Dead_IPS ²	7	750.509	6.396	0.010	333.537	54.132	0.000
10	Jan_mean + Dead_rust + Dead_rust ²	7	747.113	3.000	0.055	474.459	195.054	0.000
11	Live_pine+ Nonveg	6	748.865	4.752	0.023	285.227	5.822	0.025
12	Live_pine + Fir_ba	6	747.767	3.654	0.040	281.913	2.508	0.129
13	Live_pine+ Dead_IPS + Dead_IPS ²	7	752.325	8.212	0.004	317.439	38.034	0.000
14	Live_pine + Dead_rust + Dead_rust ²	7	747.715	3.602	0.041	385.497	106.092	0.000
15	Nonveg + Fir_ba	6	750.711	6.598	0.009	279.405	0.000	0.451
16	Nonveg+ Dead_IPS + Dead_IPS ²	7	752.549	8.436	0.004	334.851	55.446	0.000
17	Nonveg+ Dead_rust + Dead_rust ²	7	748.151	4.038	0.033	475.709	196.304	0.000
18	Dead_IPS + Dead_rust + Dead_rust ²	7	747.511	3.398	0.045	284.881	5.476	0.029

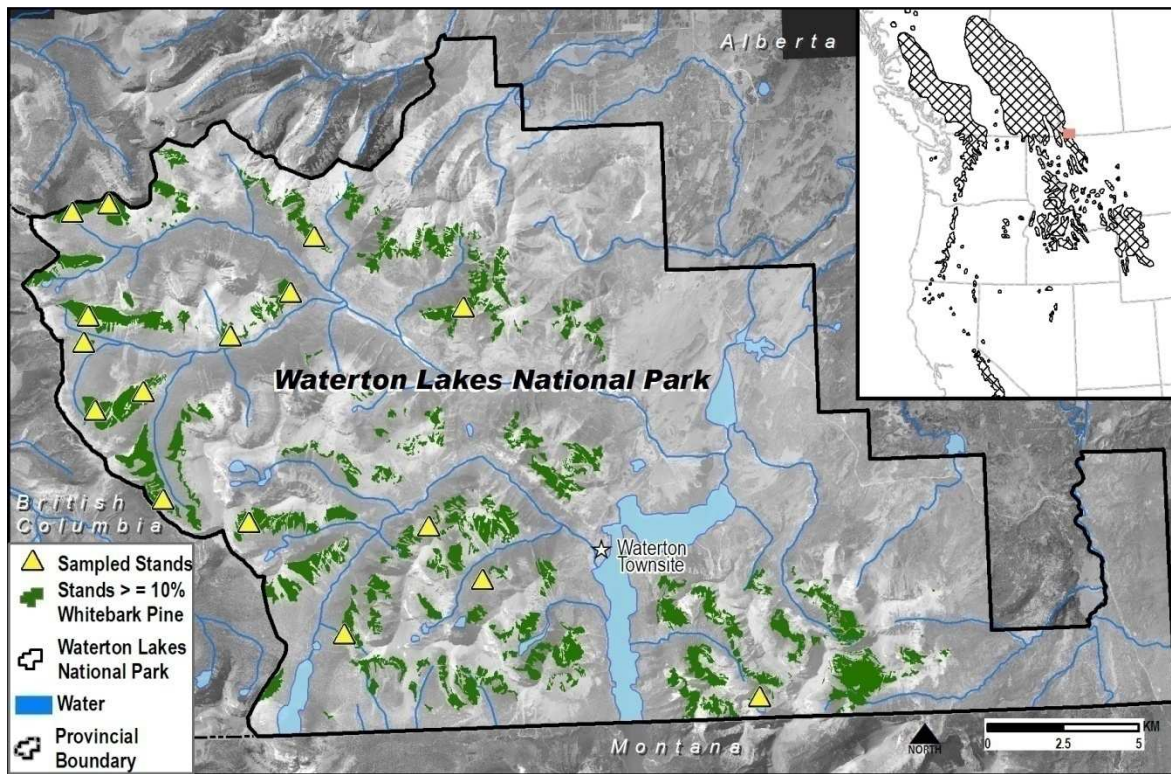


Figure 9. The locations of the 15 stands sampled in Waterton Lakes National Park, Alberta, Canada (51, 000 ha; the inset shows the location of the park (pink) relative to the range of whitebark pine in North America (hatched)). Photographs of Stands 6 (left, dead trees are whitebark pines) and 11 (right) illustrate the range of conditions found in the Park.

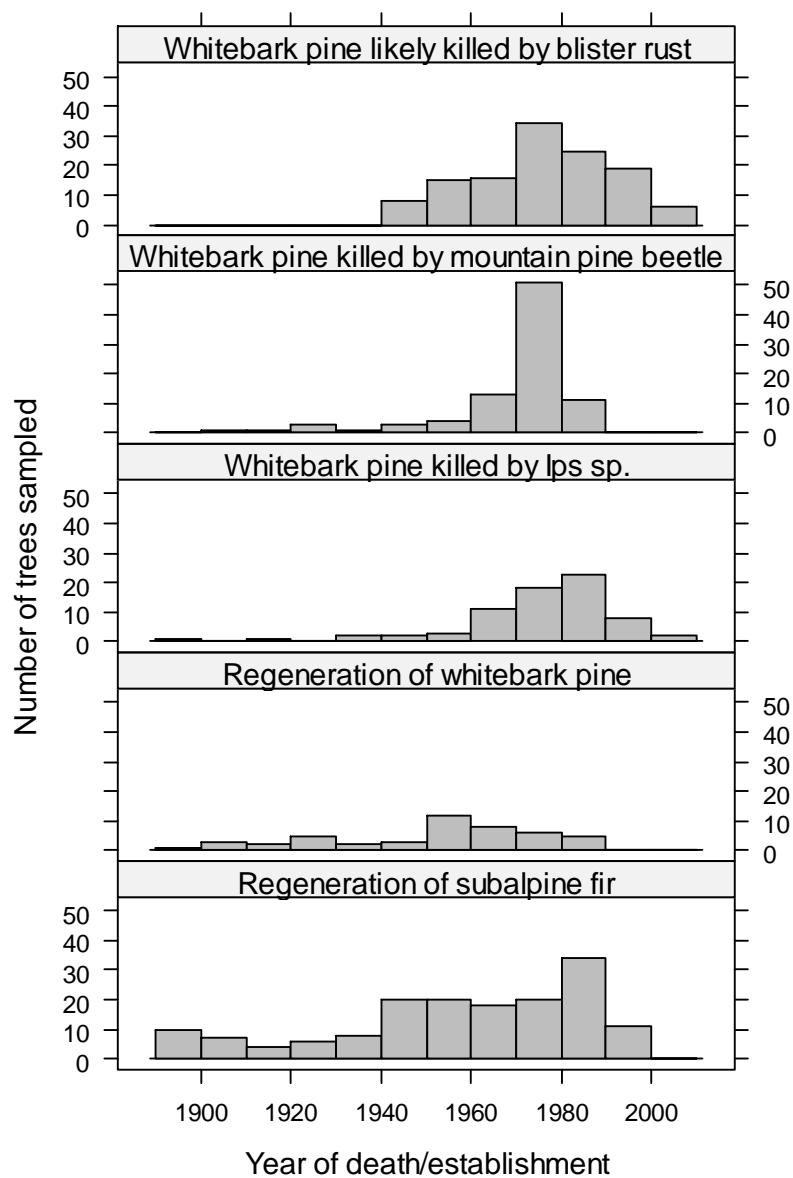


Figure 10. Distributions of dates of the outer most ring of dead whitebark pine killed by three disturbance agents along with dates of establishment of whitebark pine and subalpine fir regeneration. Years on the x-axis indicate upper date for date-class

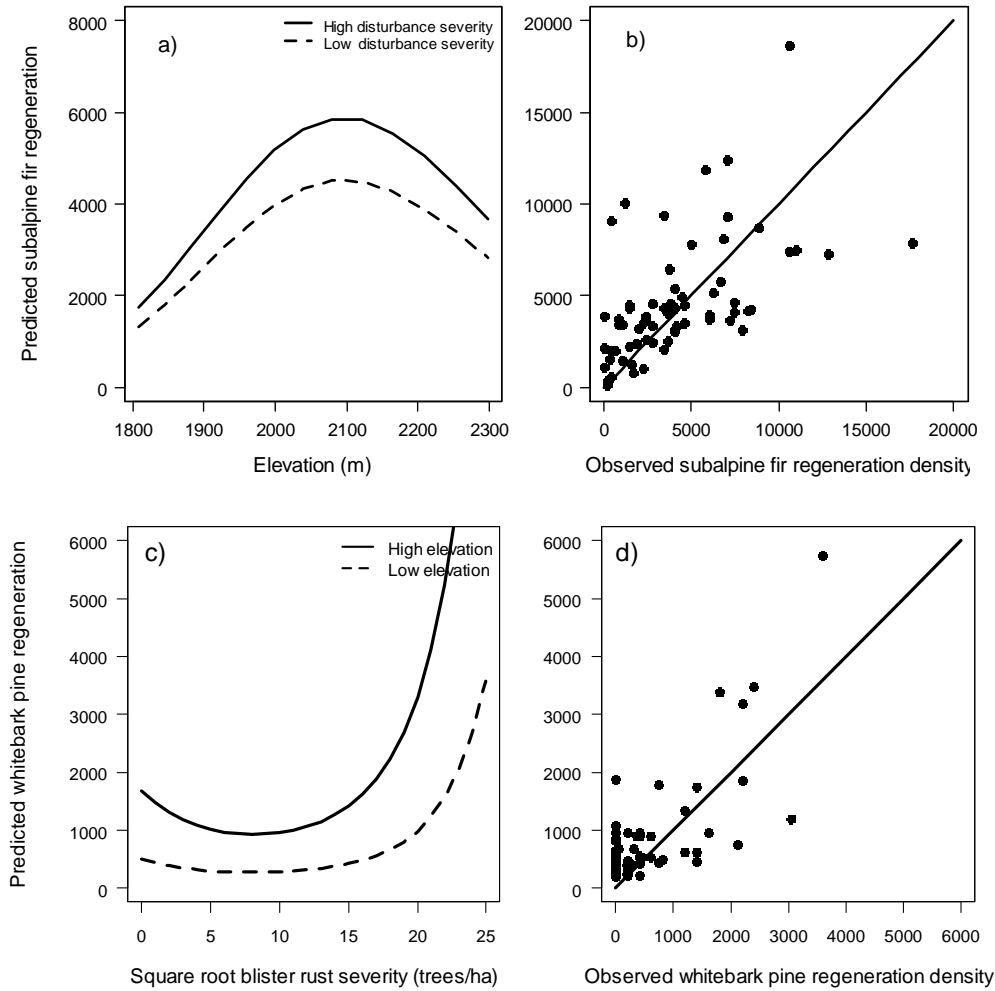


Figure 11. a) Subalpine fir regeneration (trees/ha) increases with the severity of cumulative disturbance by blister rust and *Ips* sp. to whitebark pine overstory until a certain elevational threshold (using fixed coefficients from Model [6] in Table 6 where density of live whitebark pine was kept at the average of observed values and low and high disturbance severity are the 25th and 75th quartile of observed values). b & d) Observed versus conditional predicted densities (trees/ha) from best models with variation around 1:1 lines indicating unexplained variability in subalpine fir regeneration and whitebark pine regeneration. c) At relatively high levels of mortality from blister rust of whitebark pine in the overstory, whitebark pine regeneration increases (using fixed coefficients from Model [5] in Table 7 where low and high elevation are the 25th and 75th quartile of observed values).

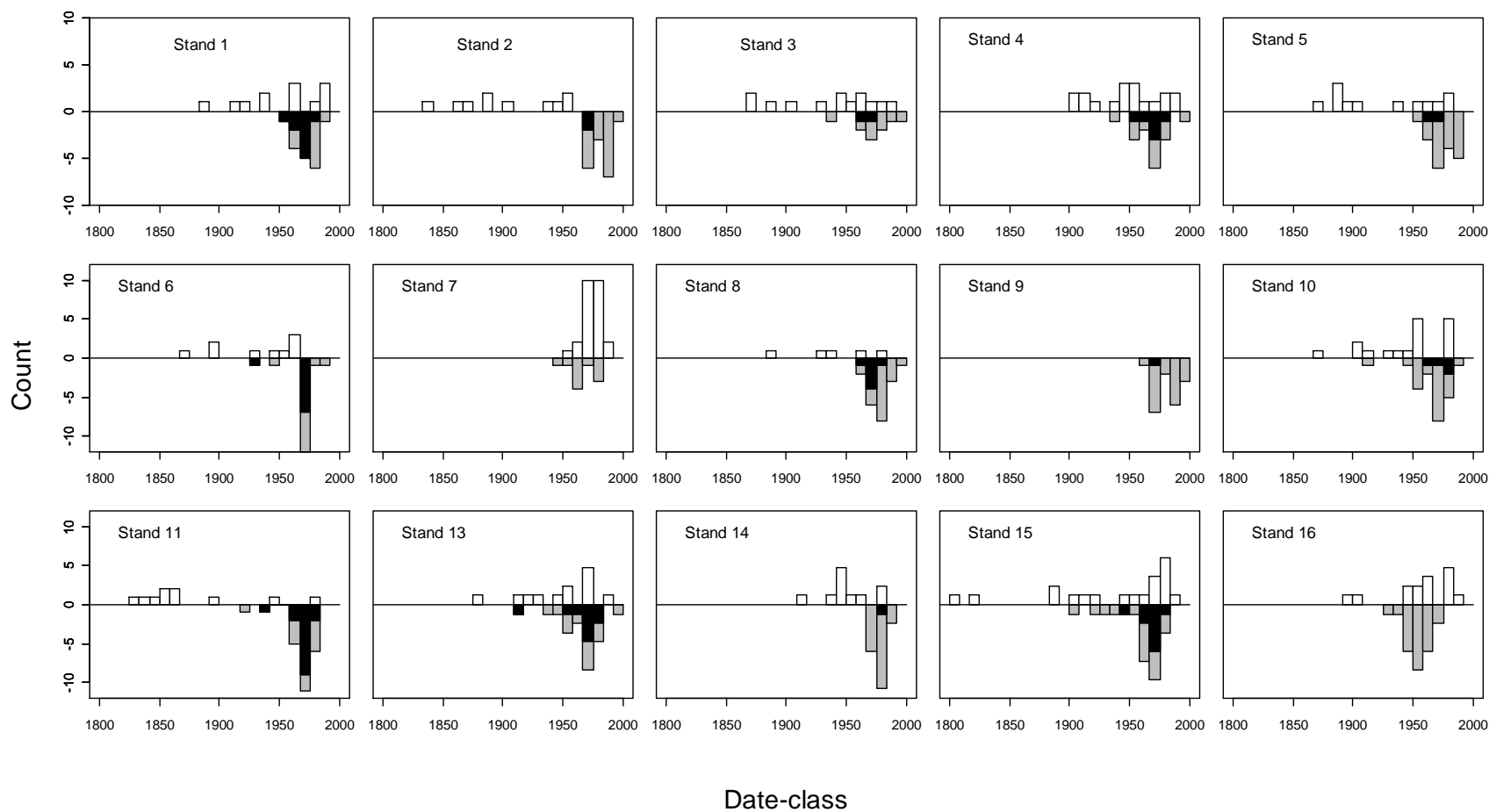


Figure 12. Distribution of estimated dates of death of whitebark pine (shown as negative values) from mountain pine beetle (black) and from other agents of mortality (grey) with dates of establishment of subalpine fir (white, positive values) in each stand. Note that subalpine fir seedlings were observed in Stand 9 but were sparse enough to not be encountered in plots.

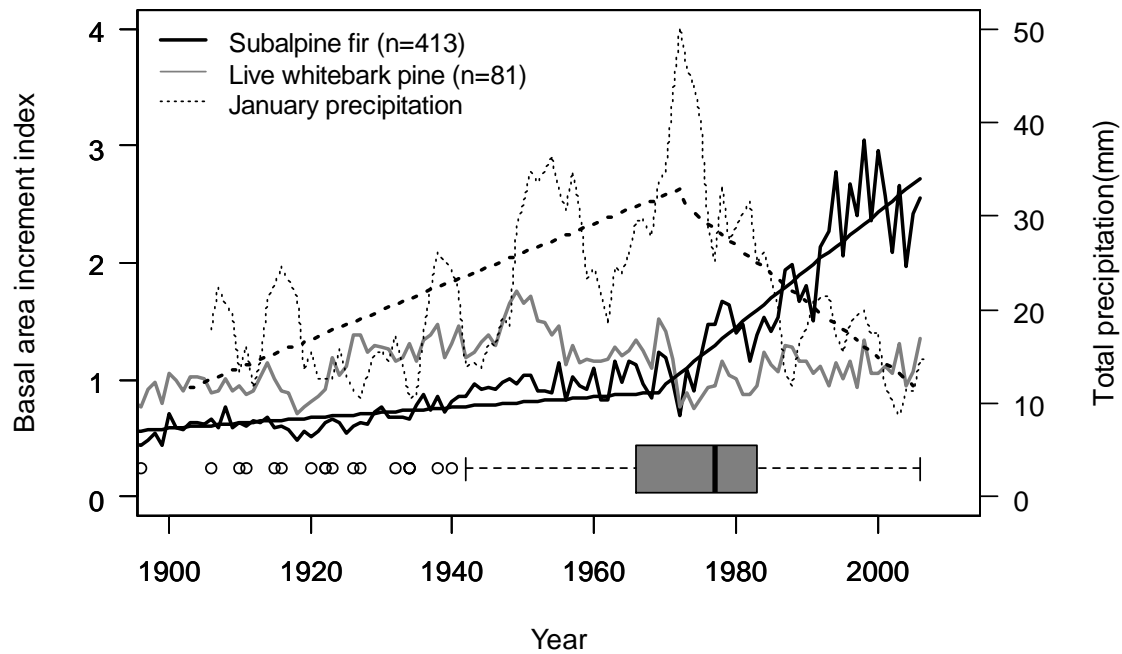


Figure 13. Comparison of whitebark pine and subalpine fir growth relative to the cumulative mortality of whitebark pine (boxplot of 290 trees) and trends in January precipitation during the 20th century. Each growth chronology was normalized where $y=1$ represents the average basal area increment. Sample depth given in the legend was that for 1900 and both chronologies end when the sample depth decreases to nine trees. Total precipitation in January was from station records in Lethbridge, Alberta and was plotted as a five-year moving average. The heavy black lines show the piecewise linear models with a breakpoint at 1969 for subalpine fir growth (solid) and a breakpoint at 1971 for precipitation in January (dotted). The box indicates the interquartile range of estimated death dates of whitebark pine trees, the solid line in the box indicates the median and the whiskers extend to 1.5 times the interquartile range.

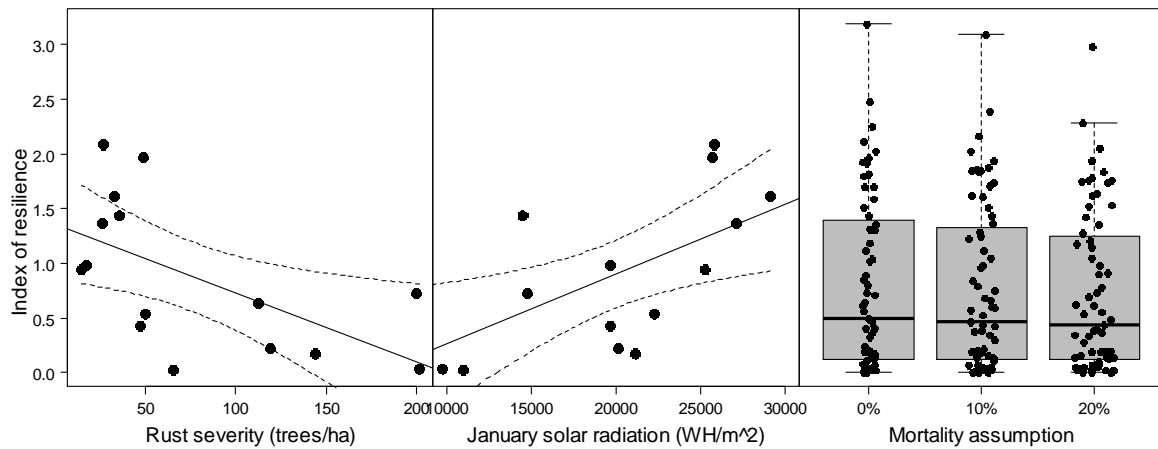


Figure 14. Resilience of whitebark pine increases with warmer sites and decreases with increasing disturbance from blister rust. Left and mid: Linear regressions of the average resilience versus solar radiation in January and severity of blister rust at the stand-level with 95% confidence limits around the predicted values as dotted lines ($j=15$ stands). Right: Boxplots of index values of whitebark pine resilience assuming 0, 10 and 20% mortality of whitebark pine regeneration and trees in the understory ($m=67$ sample points). Resilience is defined as the natural log of one plus the ratio of the density of healthy whitebark pine regeneration and mature trees to the density of mature whitebark pine trees prior to disturbance. Stands were considered resilient if this index was greater than 0.694; i.e., the density of healthy regeneration and trees was equal or more than that in the mature canopy prior to disturbance.

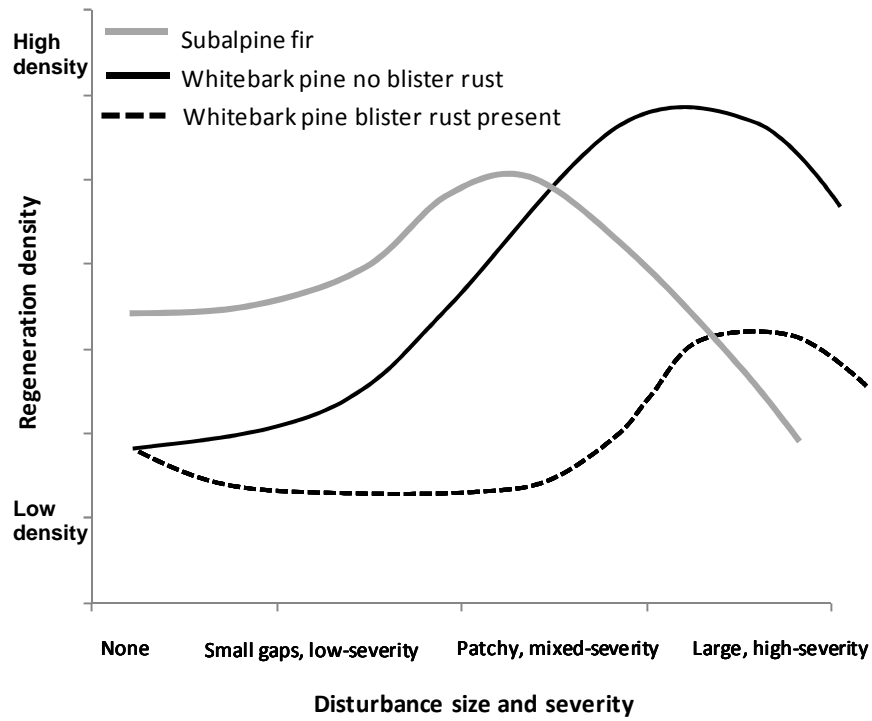


Figure 15. Conceptual model relating the response in subalpine fir and whitebark pine regeneration to disturbance size and severity which varies with the presence of blister rust.

Chapter 4: Facilitators versus competitors: size, density, and stress thresholds in subalpine forests

4.1 Introduction

Shifts from net facilitative to competitive interactions have been observed at the plant level, particularly for young plants as they outgrow their older and larger neighbouring nurse plants (Miriti 2006, Sthultz et al. 2007). Shifts from net facilitative to competitive interactions have also been observed at the stand level along environmental gradients from high to low stress and is known as the stress-gradient hypothesis (Bertness and Callaway 1994); this shift in plant interactions along a stress gradient can be affected by the density of plants in the neighbourhood (Canham et al. 2006, Fajardo and McIntire 2010). Together, these observations suggest hierarchical influences on plant interactions at the plant, neighbourhood and site levels. However, incorporating these hierarchical influences to predict net interactions among plants has received little attention. This knowledge gap likely exists because many studies have used experiments with limited ranges of treatments, small spatial scales and smaller plants to study plant interactions. As a result, incorporating influences operating at multiple spatial scales, and in particular, a complete stress gradient, has been difficult (Lortie 2010). In this study, I used the natural death of whitebark pine (*Pinus albicaulis*) in subalpine forests as a surrogate for experimental removal (*sensu* Callaway 1998) to model this hierarchical process of influences on plant interactions. Specifically, I examined whether the condition (alive versus dead) of whitebark pine trees, a pioneer species capable of establishing on harsh sites (Tomback and Kendall 2001), facilitated or inhibited the establishment of seedlings and saplings of whitebark pine and a late-seral species, subalpine fir (*Abies lasiocarpa*), across a range of stands using information across spatial scales.

Mature trees in subalpine forests, such as the whitebark pine trees in my study, can facilitate the germination, survival and growth of smaller trees beneath their crowns by providing shade and moderating extreme temperatures to prevent moisture stress and photoinhibition and by leeward shelter from wind desiccation and abrasion (Callaway 1998, Germino and Smith 1999, Maher et al. 2005, Baumeister and Callaway 2006). In contrast to open areas, mature trees contribute litter and retain the snowpack which prevents soils from freezing during the winter, both of which increase soil nutrients below the canopy (Van Miegroet et al. 2000). Mature trees can also be a source of beneficial ectomycorrhizal fungi (Hasselquist et al. 2005, Cripps and Antibus 2010). These mechanisms enhance the survival and growth of seedlings and saplings, resulting in higher regeneration success near mature trees than in openings close to the altitudinal treeline (Callaway 1998, Maher et al. 2005). At the same time, mature trees can inhibit the survival and growth of small trees by competing for available nutrients and water and by intercepting sunlight (Canham et al. 2006). Whether the net interaction between large, live trees and smaller trees is facilitative, competitive or neutral is conditional on several factors including the sizes of the two interacting plants, the neighbourhood density of trees and stand conditions related to the level of stress.

The net competitive effect of a tree on the growth of a neighbouring tree has long been assumed and demonstrated to vary as a direct function of the size of the neighbours (e.g., Bella 1971, Weiner 1984, Canham et al. 2006). It is reasonable to assume the same relationships for facilitative effects of larger plants on tree seedlings. For example, seedlings are initially facilitated by larger trees (Kellman and Kading 1992, Eränen and Kozlov 2008), shrubs (Rousset and Lepart 2000, Sthultz et al. 2007) and even herbs (Simard et al. 2006) until these seedlings reach a threshold size when the benefits provided (e.g., shade, moisture retention, protection from herbivores) are outweighed by competition for light, moisture and nutrients. Increased density of trees in the neighbourhood is traditionally thought to increase competition through additional pressure on resources (Weiner 1984, Canham et al. 2006). However, depending on the size of trees in question, there are potential benefits. Fajardo and McIntire (2010) found that the density of conspecific trees facilitated seedlings growing in stressful open spaces. Facilitation could dominate plant-to-plant interactions where there is a large difference in plant sizes, whereas competition could be more important between plants of similar size (Callaway and Walker 1997, Eränen and Kozlov 2008).

The stress-gradient hypothesis predicts that the importance of facilitation increases along gradients of increasing abiotic stress while the importance of competition decreases (Bertness and Callaway 1994). Callaway and Walker (1997) incorporated the effects of benefactor size and neighbourhood density by predicting that, under harsh conditions, increasing benefactor size or density increases the relative strength of facilitation. Under low stress, increased benefactor size or density was thought to increase the relative strength of competition. Callaway and Walker (1997) showed that the densities of subalpine fir seedlings, saplings and mature trees did not increase with the area of the canopy of individual whitebark pines at low stress sites but did show a positive relationship with canopy area at high stress sites. This effect also has been demonstrated with the size of beneficiaries in arid woodlands (Sthultz et al. 2007). The survival of juvenile pinyon pine trees (*Pinus edulis*) of all sizes was facilitated by shrubs at high-stress sites but, in contrast, only small seedlings were facilitated by shrubs at low-stress sites. Both examples support parts of the stress-gradient hypothesis, but the effects of benefactor/beneficiary size have not been tested over varying neighbourhood densities nor over an entire stress gradient. In other ecosystems, field experiments and meta-analyses suggest there are circumstances in which the stress-gradient hypothesis does not apply (Maestre et al. 2005, Lortie and Callaway 2006, Maestre et al. 2006).

When do the benefits of a live large tree on neighbouring regenerating trees outweigh its competitive costs? How do neighbourhood density of large trees and stand-level stress affect this size-interaction relationship and the thresholds distinguishing facilitative from competitive interactions? In this study, I used generalized linear mixed-effects models to predict counts of subalpine fir and whitebark pine regeneration in the vicinity of large whitebark pine trees, hereafter termed “focal trees”. I expected no relationship between regeneration counts and the sizes of neighbouring dead focal trees. I expected the regeneration counts to increase with the sizes of live focal trees because of the increasing benefits of larger canopies in stressful conditions in subalpine forests. Counts of regeneration around unhealthy but live focal trees were expected to be intermediate between those around live versus dead focal trees. Further, given that the size-relationship around dead focal trees is neutral, then the point at which regeneration under live focal trees equals that for dead focal trees is the size threshold for competition

(below the threshold) versus facilitation (above the threshold). Because whitebark pine is more resistant than subalpine fir of low temperature-photoinhibition (Maher et al. 2005), I expected that facilitation of whitebark pine regeneration by focal trees would not be as evident as that for subalpine fir. Finally, I hypothesized that the density of large trees in the neighbourhood of the focal tree could facilitate or compete with tree regeneration, depending on stress levels.

4.2 Methods

4.2.1 Sampling

The study area was in the upper elevations (1600 to 2250m) of subalpine forests containing whitebark pine and subalpine fir in Waterton Lakes National Park, Alberta, Canada (49° 2' N, 113° 57' W). Over the last 50 years mountain pine beetle (*Dendroctonus ponderosae*), species of *Ips* bark beetles and white pine blister rust (*Cronartium ribicola*) cumulatively caused the widespread mortality of whitebark pine of mixed-severity (range of 20 to 90% of whitebark pine density, Chapter 1). To ensure the sampling covered a wide range of environmental conditions and yet avoid subjectively defining a stress gradient for immature trees, I stratified stands containing at least 10% whitebark pine into either warm or cool aspects using a geographic information system (GIS) analysis of an existing vegetation inventory of the Park prior to sampling. Fourteen stands were sampled using proportional allocation by area, resulting in 11 stands from the warm aspects and three from cool aspects.

Four to six sampling points were randomly located 40-100 metres apart in each stand. At each point, I identified and measured the distance to the four closest live and the four closest dead whitebark pine trees with diameter at breast height (DBH; 1.3 m above ground) ≥ 15 cm (i.e., focal trees, $n=445$). If focal trees occurred in clumps of multiple stems, I considered each clump to be one tree with subsequent measurements based on the stem that dominated the canopy within the clump. Within a radius of 2 m around each focal whitebark pine, I counted the number of whitebark pine and subalpine fir seedlings and saplings (DBH < 4 cm). A radius of 2 m conservatively sampled the direct zone of influence of the canopy of mature whitebark pines since crown widths were often more than this distance.

Variables that could explain net tree-to-regeneration interactions were measured at three spatial scales, tree, neighbourhood and stand, centred on the focal whitebark pines (Table 8). For each tree, I measured the DBH. For focal trees, I estimated the year of establishment (live and dead focal trees), and the year of death (dead focal trees) based on two increment cores per tree taken at right angles, on average 34 cm above ground. Each ring-width series was cross-dated using a master chronology for each stand. The condition of each focal tree was also classified as: Condition 1: live; Condition 2: live but dead tops from top-kill by blister rust; Condition 3: died within the last 20 years; or Condition 4: died between 21-40 years ago. I used two categories of dead trees because the influence of a dead tree on soil moisture and nutrients decreases with time (Facelli and Brock 2000). I also only used dead focal trees that died less than 40 years ago because I wanted to avoid long times since death where other trees might establish and grow into medium-sized trees which influences regeneration dynamics. Determining

whether regeneration counts differed with the condition of the focal trees was critical for interpreting tree-regeneration interactions and is described further on.

To measure the level of competition or facilitation from other trees in the neighbourhood of the focal trees, I recorded the density of live, mature (DBH > 4 cm) trees within a 2 m radius of the focal tree. I also measured the basal area per ha of all live trees around each focal tree using a variable radius plot and basal area factor 2.0 m²/ha (i.e., each tree was selected for inclusion with a probability proportional to size, and, therefore, each selected tree represented a constant 2.0 m²/ha).

Although stress is a composite of environmental factors limiting plant germination and success, these factors are difficult to measure and often surrogates are used, such as elevation (Callaway 1998), overall plant productivity (Lortie and Turkington 2008) or abiotic or biotic disturbance (Kawai and Tokeshi 2007, Smit et al. 2007). In this study, I measured several surrogates for stress (Table 8) because stress gradients for subalpine fir and whitebark pine regeneration were not known *a priori*. At each sample point, I recorded the elevation and slope angle. I also established three nested, circular plots. The radius of the smallest plot was 3.99 m. For dense stands (> 4,000 trees/ha), the radii of the medium and large plots were 5.66 and 8 m; for less dense stands, the radii were 8 and 12.66 m. In the small-radius plots, I visually estimated the percent cover of bare ground (i.e., an inverse of vegetation productivity and indicative of poorly developed soils with low nutrient and water retention levels) and layering by subalpine fir (i.e., a growth form more commonly occurring in harsh growing conditions). In the medium-radius plots, the species and DBH of each live tree where DBH was between 4 and 15 cm were recorded. In the large-radius plots, large, live trees with DBH values ≥15 cm were measured. Total basal area per ha was calculated for each sample point using medium-radius and small-radius plots, and averaged over all points in a stand to obtain stand-level average basal areas per ha. Stand subalpine fir basal area was used as an index of productivity. As an index of disturbance severity to the forest canopy due to whitebark pine mortality from blister rust, mountain pine beetle and *Ips* sp., the density of dead whitebark pine was estimated using the 4-n distance method at each sample point (Pollard 1971). Further to field measurements for surrogates of stress, the amount of net solar radiation incoming to each stand for January and June was modelled from digital elevation models using the GIS-based model, ArcView Solar Analyst (Fu and Rich 1999), to account for viewshed, surface orientation, elevation and atmospheric conditions (D. Zell, Parks Canada, unpublished data).

4.2.2 Analyses

To evaluate the relative importance of tree-, neighbourhood- and stand-level variables, I built four generalized linear mixed-effects models to predict counts of subalpine fir regeneration (y_{ij}) and whitebark pine regeneration (z_{ij}) around the focal trees (i) in each stand (j) (Table 9). For each species, a negative binomial distribution with the log-link function $g(u_{ij})$ was used (whitebark pine mean: 1.286, variance: 5.743; subalpine fir mean: 5.046, 17.880). Because zeros formed 18% and 59% of subalpine fir and whitebark pine regeneration counts, respectively, and could be due to both true zeros and observation error, I also included a constant probability for zero-inflation in the models. For model building, I commenced with explanatory variables representing tree-level influences on regeneration survival and establishment and then incrementally included variables influential at the neighbourhood and stand levels to evaluate their relative importance (Table 9). Specifically, I started with the size (DBH) of the

focal trees in Model [1], and then tested for improvements using likelihood ratio tests by adding the following variables: the condition of the focal trees and interactions with DBH in Model [2]; the density of trees $DBH \geq 4$ cm and the presence of bear grass (*Xerophyllum tenax*) in the neighbourhood of the focal trees in Model [3]; stand-level surrogates for stress in Model [4]; and the age of the stand (average age of focal trees) in Model [5]. This order of variables allowed me to evaluate the hypothesis that factors which influence regeneration processes are hierarchical in importance beginning at the tree level and decreasing in strength to the stand level. Also, to avoid including very highly correlated explanatory variables that can cause instability in parameter estimates, I excluded seedling density and total live basal area in the neighbourhood.

For each model predicting counts of regeneration, coefficients were estimated using maximum likelihood methods with the `glmmadmb` function from the package `glmmADMB` (version 0.6.3; Skaug et al. 2011) in the R language and environment (v.2.11.1, R Development Core Team 2010). Because the models are nested reflecting the hypothesized hierarchy of influences on tree interactions, I used likelihood ratio tests to test the significance of adding variables to Model [1] (Zuur et al. 2009). The degrees of freedom were estimated from the stand-level (fixed) effects because I kept the random effects the same for each model. I also examined goodness of fit and evaluated whether models met assumptions using residual plots. Initially, residual plots showed that very high counts of subalpine fir regeneration were poorly estimated. Therefore, dataset was truncated to counts of regeneration < 30 (98% of records) for subalpine fir models only.

The best-supported model was used to depict how interactions between focal trees and regenerating trees changed along gradients of benefactor size, neighbourhood density and stand-level stress. I used the difference between predicted counts of regeneration around live focal trees (Condition 1) versus long-dead focal trees (Condition 4) to determine whether net facilitation or competition was occurring. Where differences are positive, growing around live focal trees is beneficial (net facilitation); whereas, where differences are negative, growing without the influence of live focal trees is better (net competition). I assessed how these interactions might change with the health of the focal trees and whether tree interactions extend beyond the death of the focal trees by also comparing predicted values of regeneration around focal trees of Conditions 2 (unhealthy but alive) and 3 (recently dead) with those around long-dead focal trees of Condition 4.

4.3 Results

For subalpine fir regeneration, the sequential fitting of Models [1] through [5] and the significant improvement of each upon its predecessor (Table 10) illustrated three results. First, it showed that live focal trees were influencing subalpine fir regeneration differently than dead focal trees because the addition of the variable of focal tree condition and its interaction with DBH in Model [2] significantly improved Model [1]. Second, this influence was affected by the levels of competition/facilitation in the neighbourhood as represented by the density of mature trees because its addition in Model [3] significantly improved upon Model [2]. Third, elevation of the stand when included in Model [4] significantly improved upon Model [3]. Other surrogates for stress at the stand level and the age of the stand in Model [5] did not significantly improve Model [4].

For the final model for predicting subalpine fir regeneration, Model [4], the interaction term between DBH and Condition was significant (likelihood ratio between Model [4] and a model where the interaction term was removed = 7.86, $df=3$, $p=0.049$). The size of long dead focal trees (Condition 4) did not affect the number of regeneration subalpine fir in its vicinity (confidence interval of slope with DBH included zero; Table 11). In contrast, the size of focal trees of the three other conditions did affect interactions with regenerating subalpine fir (Figure 16). Facilitation decreased with the increasing diameter of healthy, live focal trees (Condition 1) whereas the inverse occurred for unhealthy (Condition 2) or recently dead focal trees (Condition 3). This was not an artefact of trees with dead tops being larger than healthy trees (2-sample t-test = -0.3461, $p=0.730$, $df=161$). Asymptotic thresholds in DBH occurred at which there were no interactions between focal trees and subalpine fir regeneration— e.g., predicted differences from Condition 4 trees were zero at ~40 cm DBH for live, healthy focal trees (Figure 16).

The size and condition of the focal tree affected the relationship of tree interactions with neighbourhood density and elevation. Facilitation increased with increasing neighbourhood density if focal trees were live (Condition 1) and relatively small; whereas the same relationship only occurred for larger focal trees if focal trees were alive but with dead tops (Condition 2) (Figure 17). Facilitation increased with increasing elevation if focal trees were live (Condition 1) and 30 cm in DBH or smaller (Figure 17c). At larger diameters, neutral or competitive interactions increased with increasing elevation. In contrast, for focal trees with dead tops, facilitative interactions increased with elevation and tree size. These results collectively indicate that there were size thresholds distinguishing between facilitative and competitive interactions depending on the condition of the focal trees, neighbourhood density and elevation.

In contrast to subalpine fir regeneration, the size and the condition of focal whitebark pines were not significant explanatory variables in models to predict whitebark pine regeneration. There was no benefit or cost to regenerating whitebark pine to be near a live focal tree when compared to a dead focal tree (Table 10). Location of whitebark pine seedlings likely reflects site selection for seed caches by Clark's nutcracker. The only significant explanatory variables were the density of neighbouring mature subalpine fir and elevation. Whitebark pine regeneration significantly decreased with increasing neighbourhood density and decreasing elevation. Further, for predicting whitebark pine regeneration, Model [4] was not improved by including stand age.

4.4 Discussion

My results add to the growing body of refinements of the original stress-gradient hypothesis, by demonstrating that plant-to-plant interactions: 1) are conditional on benefactor size and health, and beneficiary species; 2) occur at local as well as larger spatial scales and these larger scales are important; and 3) are potentially nonlinear relationships. I discuss each of these main observations further.

I demonstrated that smaller live focal trees were more facilitative than larger live trees of subalpine fir regeneration at high stress as represented by high elevations (Figure 16). This result does not support Callaway and Walker's (1997) conceptual model which predicted that facilitation would increase in intensity with the size of the benefactor in abiotically stressful environments. I did find that facilitation increased with the size of focal trees of

Conditions 2 and 3 with increasing stress (Figure 16b). Focal trees of these conditions were either alive with dead tops or recently dead. This difference between focal trees which were healthy and those which were top-killed or dead suggests a size threshold which indicates whether focal trees were facilitators or competitors. When trees were top-killed, the competitive costs of large tree canopies on seedlings were removed and other characteristics related to tree size became more important. Subalpine fir seedlings benefit from protective tree cover because exposure to sunlight in combination with cold temperatures can increase photoinhibition (Germino and Smith 1999). Tree cover decreases solar radiation and increases minimum daily temperatures because the warming of the canopy during the day enhances longwave irradiance to the ground at night (Maher et al. 2005). However, at some size of tree canopy, shade can limit the height growth of regenerating trees (Canham et al. 2006) and increase snow interception such that seedlings beneath the canopy are not protected from desiccating winds nor freezing soils (Rocheffort et al. 1994, Varhola et al. 2010). Top-killed trees can still benefit seedlings by increasing snow accumulation, providing shelter from the wind or underground benefits such ectomycorrhizal infection of seedling roots or nutrient accumulation and these benefits can increase with tree size (Facelli and Brock 2000). At some point, there is a trade-off where the canopy of a live focal tree becomes too large and the costs of shading or snow interception outweighs the benefits of protection against low-temperature photoinhibition. Using Figure 16b, a DBH of ~ 30 cm was the size threshold where this occurs for these study data.

In other ecosystems, competition, not facilitation, at the very extremes of stress gradients have been observed (Maestre et al. 2009) and thought to reflect competition for very scarce resources. Maestre et al. (2009) proposed that predictions of the stress-gradient hypothesis could be improved by classifying the life history of interacting plants as either competitive or stress tolerant. Competitive interactions at the extremes of a stress gradient where a resource is lacking could be explained by the interacting species having similar competitive or stress-tolerant life histories. I further suggest that when conspecifics are involved or where there are plants which have a range of sizes, that interactions can be predicted by size thresholds in benefactors.

Few studies of plant facilitation have incorporate spatial scale into their design (Brooker et al. 2008). By solely examining plant-to-plant interactions without considering the effects at the neighbourhood or site level, the interpretation of how important plant interactions are relative to other factors affecting plant growth may be biased (Lortie et al. 2005). For example, Tewksbury and Lloyd (2001) found that the facilitative effects of a tree on diversity of understory plants in the Sonoran Desert were only evident when topographic effects on water availability were controlled. By using a hierarchical approach to modelling, I demonstrated that individual focal trees, in combination with factors operating at large spatial scales, facilitated subalpine fir regeneration. Neighbourhood density was positively related to subalpine fir regeneration, suggesting either facilitative interactions with the neighbourhood such as canopy protection from low-temperature photoinhibition or the availability of seeds and suitable site conditions. In contrast, for whitebark pine regeneration I found little evidence for facilitative interaction with the focal tree relative to the influences of neighbourhood density and elevation.

The original form of the stress-gradient hypothesis assumed linear and monotonic change of net interaction intensity along a stress gradient (Bertness and Callaway 1994). Malkinson and Tielborger (2010) argue that physiological responses of plants to changes along stress gradients are not linear and this should translate into non-

linear functions for describing plant interactions along stress gradients. The majority of field studies testing the stress-gradient hypothesis have sampled only contrasting low- versus high-stress positions along a gradient and can not specify the shape of the interaction function over the entire gradient (exceptions: Foster 1999, Kikvidze et al. 2005, Kawai and Tokeshi 2007, Smit et al. 2007). My study design permitted me to model a range of stress conditions. I did not test different non-linear models but the modelled exponential relationship via a log-link illustrated that there are asymptotic thresholds for plant interactions influenced by tree size, neighbourhood tree density and elevation.

I did not subjectively select a single stress gradient *a priori*, for two reasons. First, I assumed that the multiple gradients of stress on plant survival and growth as identified by others (e.g., Elmendorf and Moore 2007) would apply to whitebark pine and subalpine fir regeneration. Second, prior to sampling, I did not know the distribution of whitebark pine stands, the range of stressors or their relative influence. Elevation was significant in the models for predicting both subalpine fir and whitebark pine regeneration. Elevation has been used by other plant interaction studies as an index of stress (e.g., Callaway et al. 2002, Stultz et al. 2007, Lortie and Turkington 2008), including research on interactions between whitebark pine and subalpine fir trees (Callaway 1998). In subalpine forests, higher elevations are associated with greater stress caused by lower mean annual temperatures, shallower soils, poorer water retention, higher wind speeds and blowing snow and ice relative to lower elevations (Callaway 1998, Xu et al. 2004).

Because of the landscape scale, large sample size and random selection of stands and trees in my study, my results present strong evidence for the conditionality of the stress-gradient hypothesis. While research has demonstrated that facilitative benefits increase with the size of benefactors (e.g., Kellman and Kading 1992, Facelli and Brock 2000, Tewksbury and Lloyd 2001), to the best of my knowledge, this is the first time the relationship between benefactor size and plant interactions has been empirically modelled over a stress gradient with the influence of neighbourhoods. However, the choice of using a landscape scale and random selection of study sites meant that I forewent other more intensive measurements which could help elucidate mechanisms. For example, my results suggest that recently dead focal trees (Condition 3) influence subalpine fir regeneration similar to live focal trees with dead tops. Without more research, I cannot distinguish between whether this reflects a long residence time of soil nutrients under trees or whether this was an artefact of a small sample size ($i=42$) for focal trees of Condition 3. Further, unexplained variation remains in the models (e.g., inability to predict high densities of subalpine fir regeneration) which might be mitigated by including variables which better represent mechanisms of facilitation, such as canopy size.

Whitebark pine is labelled a keystone species in subalpine forests (Tomback and Kendall 2001). In this study, I presented evidence that living mature whitebark pines facilitate regenerating subalpine fir, conditional on the size and health of the benefactor, neighbourhood density and the level of stress at a site. The size threshold of benefactors has particular implications for predicting the response of subalpine forests containing whitebark pine to outbreaks of mountain pine bark beetle which preferentially attack larger pine trees (Logan et al. 2010). In the study area, if large whitebark pine trees are killed, net interactions with regenerating subalpine fir will shift from competitive to facilitative. The presence of size and stress thresholds which dictate whether competition versus

facilitation prevail suggest that subalpine forests could exhibit tipping-point behaviour towards ecosystem reorganization (Scheffer et al. 2001). Mortality of large whitebark pine from subalpine forests due to blister rust and bark beetles as observed in my study area and many other locations such as the Greater Yellowstone area, U.S. (Logan et al. 2010), means rates of recruitment of subalpine fir seedlings to saplings to understory trees may increase due to increased net facilitation, while recruitment of whitebark pine will be impacted by the loss of seed sources. Without mature whitebark pine present, recruitment of regenerating whitebark pine will be jeopardized and subalpine forests will shift towards dominance by subalpine fir.

Table 8. Explanatory variables considered for the models and their correlations with counts of subalpine fir and whitebark pine regeneration around focal whitebark pines (n=445). Significant ($\alpha=0.05$) Spearman rank correlation coefficients (rho) are highlighted in bold.

Variable	Description	Range of values	Sub-alpine fir rho	Whitebark pine rho
Tree level: Variables of focal whitebark pines				
DBH	DBH (cm)	8 - 63	0.027	0.004
Condition	Class variable indicating whether focal tree was, 1: live, 2: live with dead top, 3: dead within the last 20 years, 4: dead between 21-40 years ago.	n/a	n/a	n/a
Neighbourhood level: Variables of competition or facilitation from neighbouring plants				
Local_ba	Total live basal area (m ² /ha) in the neighbourhood of focal whitebark pine estimated with variable radius plots	0 - 60	0.217	0.009
Density	Count of all live trees DBH \geq 4 cm in 2 m radius of focal whitebark pine	0 - 10	0.340	-0.239
Density_pine	Count of all live whitebark pine DBH \geq 4 cm in 2 m radius of focal whitebark pine	0 - 2	-0.003	0.034
Xero	Binomial variable indicating presence or absence of <i>Xerophyllum tenax</i>	n/a	n/a	n/a
Seed_fir	Count of seedlings of subalpine fir regeneration DBH < 4 cm in 2 m radius of focal whitebark pine	0-36	n/a	0.160
Seed_pine	Count of seedlings of whitebark pine regeneration DBH < 4 cm in 2 m radius of focal whitebark pine	0-14	0.160	n/a
Stand level: Variables of abiotic stress at the stand-level				
Elevation	Elevation (m)	1812 - 2249	0.175	0.345
Slope	Slope (degrees)	13 - 48	0.046	0.244
Jan_insol	Net solar radiation in January (Wh/m ²)	8,566 – 29,083	0.027	0.162
July_insol	Net solar radiation in July (Wh/m ²)	168,181 – 204,367	0.003	0.175
Nonveg	Percent cover that is rock, scree or soil and is not vegetated; indicative of poorly developed soils	3 - 68	-0.174	0.134
Layer	Percent cover that is subalpine fir layering, indicative of stressful conditions for subalpine fir	0 - 11	0.024	0.220
Stand_fir_ba	Basal area (m ² /ha) of live subalpine fir DBH \geq 4 cm	0.75 – 40.27	0.267	-0.302
Density_dead	Index of disturbance; density of all dead whitebark pine (trees/ha)	53-305	0.179	-0.017
Successional stage				
Stand_age	Average age of whitebark pine in stand (yrs.)	162- 346	0.106	0.044

Table 9. Models tested to predict the counts of subalpine fir and whitebark pine regeneration around focal whitebark pine trees, i in stand, j , where explanatory variables for *Neighbourhood* and *Stress* are taken from Table 8 and between-stand variance is represented by ε_j , and within-stand variance is represented by ε_{ij} . Both were modelled as a negative binomial distribution with the log-link function $g(u_{ij})$ and logit-link function $f(p_{ij}) = (1 - \exp^v / (1 + \exp^v))$ to model zero-inflation.

Subalpine fir: $y_{ij} = g^{-1}(u_{ij}) * f(p_{ij}) + \varepsilon_{ij}$ $i = 436, j = 14$ stands	
Whitebark pine regeneration: $z_{ij} = g^{-1}(u_{ij}) * f(p_{ij}) + \varepsilon_{ij}$ $i = 445, j = 14$ stands	
1	$g(u_{ij}) = \beta_0 + \beta_1 DBH_{ij} + \varepsilon_j$
2	$g(u_{ij}) = \beta_0 + \beta_1 DBH_{ij} + \beta_2 (Condition_{ij} = 1) + \beta_3 (Condition_{ij} = 2) + \beta_4 (Condition_{ij} = 3) + \beta_5 (Condition_{ij} = 4)$ $+ \beta_6 ((Condition_{ij} = 1) * DBH_{1ij}) + \beta_7 ((Condition_{ij} = 2) * DBH_{1ij}) + \beta_8 ((Condition_{ij} = 3) * DBH_{1ij})$ $+ \beta_9 ((Condition_{ij} = 4) * DBH_{1ij}) + \varepsilon_j$
3	$g(u_{ij}) = \beta_0 + \beta_1 DBH_{ij} + \beta_2 (Condition_{ij} = 1) + \beta_3 (Condition_{ij} = 2) + \beta_4 (Condition_{ij} = 3) + \beta_5 (Condition_{ij} = 4)$ $+ \beta_6 ((Condition_{ij} = 1) * DBH_{1ij}) + \beta_7 ((Condition_{ij} = 2) * DBH_{1ij}) + \beta_8 ((Condition_{ij} = 3) * DBH_{1ij})$ $+ \beta_9 ((Condition_{ij} = 4) * DBH_{1ij}) + \beta_{10} Neighbourhood_{ij} + \varepsilon_j$
4	$g(u_{ij}) = \beta_0 + \beta_1 DBH_{ij} + \beta_2 (Condition_{ij} = 1) + \beta_3 (Condition_{ij} = 2) + \beta_4 (Condition_{ij} = 3) + \beta_5 (Condition_{ij} = 4)$ $+ \beta_6 ((Condition_{ij} = 1) * DBH_{1ij}) + \beta_7 ((Condition_{ij} = 2) * DBH_{1ij}) + \beta_8 ((Condition_{ij} = 3) * DBH_{1ij})$ $+ \beta_9 ((Condition_{ij} = 4) * DBH_{1ij}) + \beta_{10} Neighbourhood_{ij} + \beta_{11} Stress_j + \varepsilon_j$
5	$g(u_{ij}) = \beta_0 + \beta_1 DBH_{ij} + \beta_2 (Condition_{ij} = 1) + \beta_3 (Condition_{ij} = 2) + \beta_4 (Condition_{ij} = 3) + \beta_5 (Condition_{ij} = 4)$ $+ \beta_6 ((Condition_{ij} = 1) * DBH_{1ij}) + \beta_7 ((Condition_{ij} = 2) * DBH_{1ij}) + \beta_8 ((Condition_{ij} = 3) * DBH_{1ij})$ $+ \beta_9 ((Condition_{ij} = 4) * DBH_{1ij}) + \beta_{10} Neighbourhood_{ij} + \beta_{11} Stress_j + \beta_{12} Stand_age_j + \varepsilon_j$

Table 10. Evidence that predictions of density of subalpine fir regeneration but not whitebark pine by Model [1] was significantly improved by adding explanatory variables related to the condition of the focal whitebark pines, as well as the neighbourhood and stand-level stress. P-values result from likelihood (logL) ratio tests with the model on the row above. Bold values were significantly different ($\alpha=0.05$). K is the number of estimated parameters.

	Model	k	Subalpine fir logL	Subalpine fir logL ratio (df) p-value	Whitebark pine logL	Whitebark pine logL ratio (df) p-value
1	<i>DBH</i>	5	1230.500		-571.498	
2	<i>DBH + Condition + Condition*DBH</i>	11	-1222.920	15.160 (6) 0.019	-569.548	3.900 (6) 0.690
3	<i>DBH + Condition + Condition*DBH +Density</i>	12	-1219.380	7.080 (1) 0.008	-562.262	14.572 (1) 0.0001
4	<i>DBH + Condition + Condition*DBH +Density + Elevation</i>	13	-1217.270	4.220 (1) 0.040	-559.136	6.252 (1) 0.012
5	<i>DBH + Condition + Condition*DBH +Density + Elevation +Stand_age</i>	14	-1216.300	1.94 (1) 0.164	-558.383	1.506 0.220

Table 11. Estimated coefficients for Model 4 in Table 10 for predicting subalpine fir regeneration around focal trees where Condition 1 was considered level 1 of the categorical variable and * is significant at $\alpha=0.05$.

Coefficient	Estimate	Standard Error	P-value
β_0	-5.533	3.627	0.127
β_1	-0.018	0.013	0.188
β_3	-0.994	0.376	0.008*
β_4	-0.985	0.482	0.041*
β_5	-0.512	0.383	0.181
β_7	0.031	0.015	0.034*
β_8	0.034	0.019	0.073
β_9	0.010	0.015	0.500
β_{10}	0.058	0.022	0.009*
β_{11}	0.004	0.002	0.030*

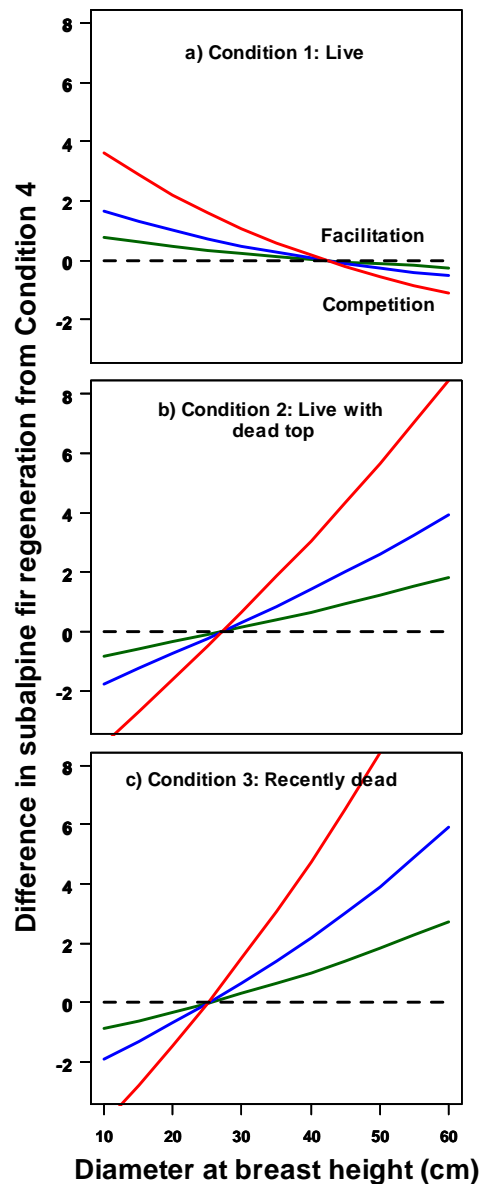


Figure 16. If alive and healthy, smaller focal whitebark pine trees are better facilitators than larger focal trees, particularly at high elevations. The opposite is true if they are alive but with dead tops or recently dead. Differences are between the predicted counts of subalpine fir regeneration around focal whitebark pines of Conditions 1 (live), 2 (live with dead top), 3 (recently dead) versus dead focal whitebark pines of Condition 4. Where differences in predicted counts are positive, growing around focal whitebark pines of Conditions 1, 2 or 3 is beneficial (net facilitation). Where differences are negative, growing without the influence of focal trees of Conditions 1, 2 or 3 is better (net competition). Predicted counts are from Model [4] where the neighbourhood density of subalpine fir trees was 796 trees/ha. Green, blue and red lines indicate differences predicted at low, moderate and high elevation (minimum, average and maximum observed values).

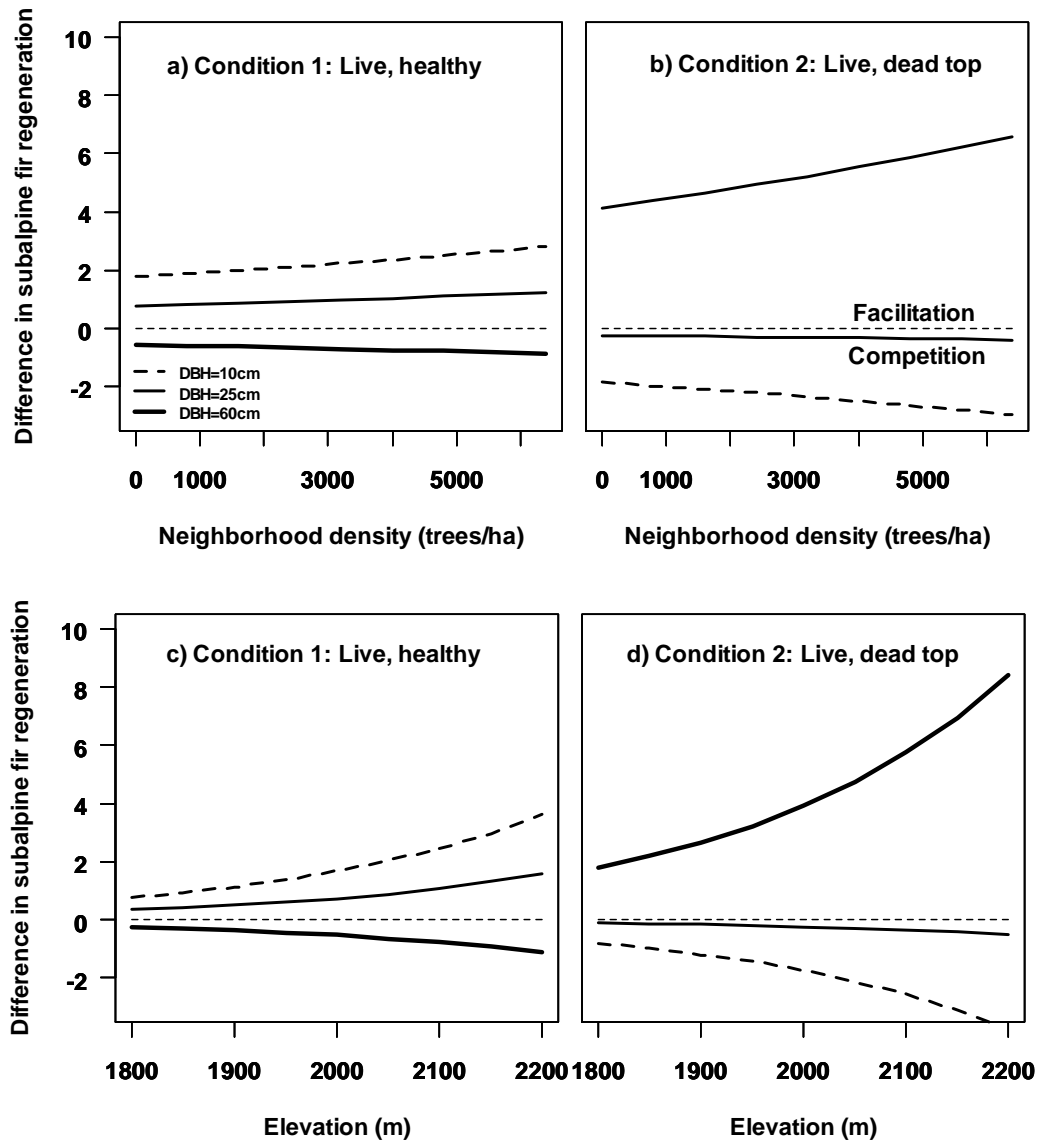


Figure 17. Interactions between focal whitebark pine trees and subalpine fir regeneration generally become more facilitative with the increasing elevation and neighbourhood density depending on the size and condition of focal trees. Differences are between the predicted counts of subalpine fir regeneration from Model [4] for live focal whitebark pines of the conditions indicated versus dead focal whitebark pines of Condition 4. The elevation for Figures 2a and 2b and the density of neighbouring trees for Figures 2c and 2d were kept at the average of observed values.

Chapter 5: Size then climatic stress: hierarchical influences on adult tree interactions

5.1 Introduction

The original stress-gradient hypothesis predicts that facilitative interactions between plants should increase with increasing abiotic stress (Bertness and Callaway 1994). Recent refinements to the hypothesis suggest that interactions depend on the type of stress and the relative competitiveness or stress-tolerance of interacting plants (Maestre et al. 2009). Stress and resulting limitations to growth can be caused by a shortage of a resource like water or variations in a non-resource like temperature or soil quality (Maestre et al. 2009). Some stresses are directly controlled by climate. Evidence of interannual variation in precipitation (e.g., Greenlee and Callaway 1996, Kitzberger et al. 2000, Tielborger and Kadmon 2000, Sthultz et al. 2007) and temperature (Bertness and Ewanchuk 2002, Callaway et al. 2002) causing switches between facilitation and competition have been found. Interactions also depend on the size (Chapter 4; Callaway and Walker 1997), life stage (Miriti 2006, Lortie and Turkington 2008), and life strategies (competitive versus stress-tolerant; Maestre et al. 2009) of interacting plants and neighbourhood density (Canham et al. 2006, Kunstler et al. 2011, McIntire and Fajardo 2011). This suggests that multiple gradients of abiotic stress and other influences exist, varying in time and space, and could affect plant interactions in opposing directions. This makes predictions of the intensity and importance of tree interactions challenging. Identifying a hierarchy of influences on plant interactions would be a useful addition to the stress-gradient hypothesis, but such hierarchies are rarely demonstrated. This gap exists because it is difficult to test plant interactions over multiple gradients of factors, particularly since most plant studies have been based on short-term experiments. In this study, I treated the natural death of whitebark pine (*Pinus albicaulis*) in high-elevation forests like an experimental removal (*sensu* Callaway 1998) and examined the radial growth response of subalpine fir (*Abies lasiocarpa*), a late-seral and shade-tolerant tree species (Sala et al. 2001) over 10 years. I examined the relative importance of temporal variation in precipitation and temperature versus tree-, neighbourhood- and stand-level factors in explaining the variation in the intensity (absolute magnitude and direction) and importance (impact relative to other factors; Welden and Slauson 1986) of competition and facilitation between trees across a landscape.

In the last decade, evidence of variations in plant interactions due to interannual variation in precipitation and temperature has increased, but equivocal support for the stress-gradient hypothesis remains. Facilitation during stressful climatic periods and competition during non-stressful periods has been observed. Greenlee and Callaway (1996) found that during a wet year, grasses competed with herb seedlings, but during a dry year, grasses facilitated the survival of herb seedlings in a grassland in Montana, U.S.. Competition between grass and shrub seedlings increased with increasing spring precipitation on south-facing slopes, but no relationship was found on north slopes in open steppe ecosystems in central Spain (Soliveres et al. 2010). Additionally, multiple shifts between facilitation and competition were observed throughout the life stages of the shrub. Facilitative interactions

of tree seedlings by shrubs have also been observed to increase during seasonal dry periods in dry woodlands in southwestern United States (Sthultz et al. 2007). These observations can be explained by the shade and moisture retention provided by the benefactor during dry years compensating for the cost of shading on the growth of the beneficiary which is expressed during wet years. In contrast, Tielborger and Kadmon (2000) found that during a wet year, Negev desert shrubs had a neutral effect or facilitated the fitness of understory plants through possible nutrient accumulation but, during a dry year, the shrubs inhibited understory plants by intercepting rainfall. In northern Patagonia, facilitation of tree seedlings by shrubs through shading did not occur during at levels of extreme drought stress but only during moderately dry periods (Kitzberger et al. 2000). Maestre and Cortina (2004) also found facilitation of shrub seedlings by tussock grass (*Stipa tenacissima*) prevailed at intermediate levels of rainfall, but that net competition dominated at both extremes of the precipitation gradient. The revised stress-gradient hypothesis attempts to reconcile these results by distinguishing between the type of stress (resource versus non-resource) and also the life history of the interacting plants (Maestre et al. 2009).

Most research on the relationship between plant interactions and gradients of abiotic stress has been conducted on herbaceous plants, shrubs or juvenile trees. In general, facilitation is more likely to be found when a beneficiary is small/young and a benefactor is large/old (Miriti 2006). However, my work in Chapter 4 demonstrated that there are diameter thresholds in adult trees below which they facilitate tree seedlings and above which the costs of larger canopies to seedlings in terms of shading and precipitation interception become apparent. By extension, differences in the size of adult trees could affect the intensity of their interactions along a stress gradient. In dry Mediterranean forests, Gomez-Aparicio et al. (2011) demonstrated that the intensity of competition of 15 tree species decreased with the increasing abiotic stress due to precipitation and that trees of the smallest diameters were most impacted by neighbourhood competition. Coomes and Allen (2007) concluded that the intensity of competition for light decreased but competition for nutrients increased with increasing elevation in mountain beech (*Nothofagus solandri* var. *cliffortioides*) in New Zealand. Competition for light affected the growth of only small trees whereas competition for nutrients affected the growth of trees of all sizes. Kunstler et al. (2011) report decreasing importance of competition with increasing abiotic stress, but no relationship for interaction intensity for adult trees of 16 species across a wide gradient of growing degree days and a water availability index in France. They found much higher importance values of competition for shade-intolerant species versus shade tolerant species. In contrast to these competitive interactions, Callaway (1998) reported facilitation of the radial growth of adult subalpine fir by adult whitebark pine trees in subalpine fir forests in the southern Rocky Mountains in Montana, U.S.. However, he only found evidence of facilitation at one of two sites and his dendrochronological analyses made numerous assumptions which may not be valid (e.g., he examined growth response in subalpine fir trees 40 years after the death of whitebark pine trees using only measurements from the first and last years). It remains unclear how the relative size of trees may affect tree-tree interactions and whether facilitation between adult trees exists and the stress-gradient hypothesis holds.

The revised stress-gradient hypothesis posed by Maestre et al. (2009) attempts to accommodate these various discordant results by proposing that the importance of competition versus facilitation depends on whether the stress is caused by a resource versus a non-resource and whether life histories of the benefactor and beneficiary are stress-

tolerant versus competitive (following the CSR classification of Grime 1977). Because trees cover a wide range of sizes, it is possible that larger trees are more stress-tolerant than smaller trees. The revised hypothesis predicts that when the benefactor is stress-tolerant and the beneficiary is competitive and where the resource such as water is abundant, there would be little interaction because the benefactor is not a good competitor. At intermediate levels of water availability, facilitation would prevail because of the effects of shading and reduced evapotranspiration near the benefactor. At high stress caused by drought, competition would increase because the water consumption of the benefactor would outweigh its benefits to the beneficiary. If abiotic stress is caused by a non-resource such as temperature, facilitation will be more important at high levels of stress. If the beneficiary is relatively more stress-tolerant than competitive, then competition would dominate during a drought and less facilitation would be expected at high levels of stress from a non-resource. Maestre et al. (2009) hypothesized various predictions for a matrix of scenarios; however, no evidence was found in the literature on quantifying the relative importance of life histories versus different abiotic stresses in determining the magnitude and direction of plants interactions. In other words, is there a hierarchy of influences on plant interactions? In order to understand how environmental change will affect the composition of plant communities it is critical to quantify the relative importance of climatic stress on determining plant interactions (Brooker 2006).

Here, I used linear mixed-effects models to examine support for the refined stress-gradient hypothesis (Maestre et al. 2009) and test the hypothesis that factors which influence the response in radial growth of subalpine fir after the natural death of neighbouring large whitebark pine trees (hereafter termed “focal trees”) are hierarchical in importance beginning with tree-level factors and decreasing in strength to those operating at the regional level. This hierarchy included the natural variation in the size differential and distance between interacting trees, the tree density and basal area in the neighbourhood, abiotic stress at the stand level and regional climatic stress. I randomly selected stands across a large landscape and systematically selected focal trees within it to avoid sampling subjectively chosen pairs of plants along preconceived stress gradients based on incomplete knowledge of stressors. Because I sampled focal trees dying in many different years, I was able to compare tree interactions over a range of climatic conditions. I expected that the intensity and importance of interactions between focal and subalpine fir trees to be negatively related to the relative size of subalpine fir trees and to the distance between interacting trees. Following Maestre et al. (2009), the importance of competition is hypothesized to increase with abiotic and climatic stress if it affects water availability; otherwise, facilitation is expected to dominate. I also hypothesized that the density of trees in the neighbourhood could facilitate subalpine fir trees at stands of high abiotic stress, whereas, at low levels, competition would dominate.

5.2 Methods

5.2.1 Sampling

I studied 15 randomly selected stands from the upper elevations (1600 to 2250m) of subalpine forests containing whitebark pine and subalpine fir in the Rocky Mountains in Waterton Lakes National Park, Alberta, Canada (49° 2' N, 113° 57' W). Disturbances over the last 50 years by white pine blister rust (*Cronartium ribicola*; hereafter “blister rust”), mountain pine beetle (*Dendroctonus ponderosae*) and species of *Ips* bark beetles

cumulatively caused the mortality of whitebark pine which was widespread and of mixed-severity (range of 20 to 90% of whitebark pine density, Chapter 2). To ensure my sampling covered a wide range of environmental conditions and yet avoid subjectively defining a stress gradient for immature trees, I stratified stands containing at least 10% whitebark pine into either warm or cool aspects using a geographic information system (GIS) analysis of an existing vegetation inventory of the Park prior to sampling. Stands were sampled using proportional allocation by area, resulting in 11 stands from the warm aspects and four from cool aspects.

Four to six sampling points were randomly located 40-100 metres apart in each stand. Before entering the field, the coordinates of the first point were selected close to the center of the stand using a GIS to avoid transitions from forest to alpine tundra at treeline. At each point, I identified and measured the distance to the four closest dead whitebark pine trees with diameter at breast height (DBH; 1.3 m above ground) ≥ 15 cm (i.e., focal trees). At 11 points I could not find a fourth focal tree with DBH ≥ 15 cm so I sampled trees DBH ≥ 10 cm. If focal trees occurred in clumps of multiple stems, I considered each clump to be one tree with subsequent measurements based on the stem which dominated the canopy within the clump. To examine growth responses of subalpine fir to the death of the focal whitebark pine trees, I randomly selected one small (DBH 4-15 cm) and one large (DBH >15 cm) subalpine fir tree within a 2 m radius of each focal tree. To increase the probability of selecting a large subalpine fir, a third tree was selected within a variable radius plot using a basal area factor 2.0 m²/ha (i.e., each tree was selected for inclusion with a probability proportional to size resulting in each sampled tree representing a constant basal area per ha), but within 4 m maximum distance from the focal tree. I had wanted two subalpine fir trees of different sizes for each focal tree, but this was not possible to achieve for most (70%) focal trees because many focal trees only had one neighbour or crossdating of some ring-width series was not possible. Increment cores were taken from each of the focal whitebark pine and the selected subalpine fir trees. For each species independently, each ring-width series was cross-dated using a master chronology for each stand and the software COFECHA (Grissino-Mayer 2001). To increase accuracy of identifying the year of death (hereafter termed “death date”), I took two increment cores per focal tree in locations on the stem where the outer rings were best preserved, meaning those with solid outer wood and bark or with bark beetle galleries which indicated that the subcortical tissue was present. I only used focal trees in subsequent analyses if the ring-width series could be crossdated and the outer ring was thought to be well preserved (74% of the trees) or high-quality cores from both sides of the stem were obtained (55% of the trees), which yielded 184 focal whitebark pine. The median difference in death dates between pairs of cores from the same focal tree was 4 years and could have been due to cambial dieback, wind erosion or decay occurring at asymmetrical rates around the stem. Where the two increment cores yielded different dates of death, I used the most recent year.

Variables that might explain the variation in the intensity and importance of interactions between subalpine fir and focal trees were measured at four spatial scales: tree, neighbourhood, stand and region (Table 12). At the tree level, I measured the DBH and the distance between interacting trees. To measure the level of competition or facilitation from other trees in the neighbourhood of the focal trees, I recorded the density of mature (DBH > 4 cm), live trees within a 2 m radius of the focal tree and measured the total basal area per ha of live trees using variable radius plots with basal area factor 2.0 m²/ha.

I measured several surrogates for stress at the stand level (Table 12) because stress gradients for subalpine fir were not known *a priori*. At each sample point, I recorded the elevation and slope angle and established three nested, circular plots. The radius of the smallest plot was 3.99 m. For dense stands (> 4,000 trees/ha), the radii of the medium and large plots were 5.66 and 8 m; for less dense stands, the radii were 8 and 12.66 m. In the small-radius plots, I visually estimated the percent cover of bare ground (i.e., an inverse of vegetation productivity and indicative of poorly developed soils with low nutrient and water retention levels) and layering by subalpine fir (i.e., a growth form more commonly occurring in harsh growing conditions). In the medium-radius plots, the species and DBH of each live tree where DBH was between 4 and 15 cm were recorded. In the large-radius plots, large, live trees with DBH values ≥ 15 cm were measured. Stand averages for subalpine fir basal area (used as an index of productivity) were estimated by averaging values from fixed-area plots. As an index of disturbance severity to the forest canopy due to whitebark pine mortality from blister rust, mountain pine beetle and *Ips* sp., the density of dead whitebark pine was estimated using the 4-n distance method at each sample point (Pollard 1971). Also, the average net solar radiation incoming to each stand for January and June was modelled from digital elevation models using the GIS-based model, ArcView Solar Analyst (Fu and Rich 1999), to account for viewshed, surface orientation, elevation and atmospheric conditions (D. Zell, Parks Canada, unpublished data).

I included regional climatic stress by calculating ratios of temperature and moisture for the 5-year period before the death of each focal tree relative to the long-term averages based on the 30-year prior period. In particular, I calculated these ratios for average monthly temperature, *Stress_temp*, and for total monthly precipitation, *Stress_ppt*, where ratios less than 1.0 indicated that the 5-year period was cooler or drier than average (i.e., higher climatic stress). To account for the effect of climate on the growth response of the subalpine fir trees, I also included concurrent average monthly temperatures and total monthly precipitation values defined as climatic measures corresponding to each year following focal tree death (*Temp*, *Ppt*). Records of the average monthly temperatures were from a weather station in Pincher Creek (~45 km away, 49.52° N, 113.98° W) and those of the total monthly precipitation were from Lethbridge, Alberta (~100 km away, 49.63° N, 112.80° W; Adjusted and Homogenized Canadian Climate Data; Mekis and Vincent 2011).

5.2.2 Analyses

To assess the growth of subalpine fir trees before and after the death of their neighbouring focal trees, I first converted tree-ring widths into basal area increments (BAI) to reduce the circumference effect (the decrease in ring widths due to the geometrical constraints of adding annual increments of wood to an expanding surface; Biondi and Qeadan 2008). I did not detrend BAI for age-dependent growth because the curvilinear age effect on BAI was considered minimal given the slow-growing nature of subalpine fir in these high-elevation forests. Furthermore, I was only examining a relatively short time period of 10 years after the death of the focal trees.

I calculated the relative interaction index, RII (Armas et al. 2004), as a metric of the intensity of interactions between subalpine fir and focal whitebark pine trees, defined as:

$$[4] \ RII_{ijkl} = \frac{N_{imp_{ijkl}}}{BAI_{pre_{jkl}} + BAI_{post_{ijkl}}}$$

where $N_{imp_{ijkl}} = BAI_{pre_{jkl}} - BAI_{post_{ijkl}}$,

$BAI_{pre_{ijkl}}$ is the average BAI of a subalpine fir tree j of the five years prior to the death of its neighbouring focal whitebark pine tree in neighbourhood k of stand l , and $BAI_{post_{ijkl}}$ is the BAI of subalpine fir tree j in neighbourhood k and stand l at year i up to 10 years after the death of a focal tree. I considered five years prior an adequate reflection of growth prior to the death of whitebark pine because growth in this time period (mean = 1.663; sd=1.957) did not significantly differ from that 6-10 years prior (mean= 1.483 (sd= 1.711); Wilcoxon test: W= 19417, p=0.276, j=192). If $N_{imp_{ijkl}}$ is negative, resulting in a negative RII_{ijkl} , then the subalpine fir tree is growing better after the death of the focal tree which indicates that the interaction between the two trees was competitive. If $N_{imp_{ijkl}}$ is positive, resulting in a positive RII_{ijkl} , then the death of the focal tree results in slower growth of the subalpine fir tree and the interaction between the two trees prior to the death of the focal tree was facilitative.

I calculated the importance index, I_{imp} as a metric of how the magnitude of the growth response for each year i since the death of the focal tree compares to the optimum growth recorded for subalpine fir in stand (Seifan et al. 2010):

$$[5] \ I_{imp_{ijkl}} = \frac{N_{imp_{ijkl}}}{|N_{imp_{ijkl}}| + |E_{imp_{ijkl}}|}$$

where $E_{imp_{ijkl}} = BAI_{post_{ijkl}} - \max_BAI_l$,

$$I_{imp_{ijkl}} = 0 \text{ if } |N_{imp_{ijkl}}| + |E_{imp_{ijkl}}| = 0,$$

$N_{imp_{ijkl}}$ is the influence of the neighbouring focal tree on subalpine fir growth, and $E_{imp_{ijkl}}$ is the relative influence of other environmental factors such as site productivity affecting optimum growth, \max_BAI_l , of the subalpine fir tree. Seifan et al. (2010) acknowledged that the true value of optimum growth is difficult to determine and suggested that when doing neighbour-removal experiments, the maximum observed growth in the absence of neighbours could be used as a proxy measure of optimal growth. For this study, I defined \max_BAI_l as the maximum value found over all sampled subalpine fir trees in stand l over the 10 year period. Thus, \max_BAI_l is considered to reflect the maximum growth possible under the levels of abiotic stress and climatic conditions during the 10 years after potential competing trees were “removed”. Similar to RII, I_{imp} values are limited to values between -1 and 1 and are positive when facilitation dominates, negative when competition prevails and zero when there are no interactions.

To evaluate the relative importance of tree-, neighbourhood-, stand- and regional-level explanatory variables on tree interactions (Table 12), I built linear mixed-effects models to predict RII and I_{imp} , for each subalpine fir tree for each year after the death of the focal tree up to year 10:

$$[6] \quad RII_{ijkl} \text{ or } I_{impijkl} = \beta_0 + \beta_1 Year_{ijkl} + f_1(Tree_{jkl}) + f_2(Neighborhood_{kl}) + f_3(Stand)_l \\ + f_4(Climatic_stress)_{jkl} + f_5(Concurrent_climate_{ijkl}) + \varepsilon_l + \varepsilon_{kl} + \varepsilon_{jkl} + \varepsilon_{ijkl}$$

where f_1 to f_5 are linear functions of tree, neighbourhood, stand, relative climate, and concurrent climate variables, respectively (Table 12). Between-stand, between-neighbourhoods and within-tree variances were partly explained by the fixed-effects part of the model (i.e., years-since-death and f_1 to f_5) and the remaining residual variances were represented by error terms, ε_l , ε_{kl} , ε_{jkl} , and ε_{ijkl} respectively. Within tree correlations over time were modelled using AR(1) as the residual correlation structure.

In model building, I commenced with years-since-death, and then sequentially added explanatory variables measured at the tree, neighbourhood, and stand, before adding in climatic variables (termed regional level in this paper). This order of variable inclusion allowed me to evaluate the hypothesis that factors which influence the response in radial growth of subalpine fir trees are hierarchical in importance beginning with tree-level factors and decreasing in strength to those operating at the regional level. Because the models are nested reflecting the hypothesized hierarchy of influences on tree interactions, I used likelihood ratio tests to determine whether the subsequent addition of each explanatory variable significantly improved upon previous models. Explanatory variables were only retained in the model if their inclusion improved the model. I also tested whether including quadratic terms of the climatic variables, interaction terms between climatic variables, the diameter differential and distance between interacting trees improved the models. Also, to avoid including very highly correlated explanatory variables which can cause instability in parameter estimates, I excluded total live basal area in the neighbourhood in lieu of neighbourhood density. Model coefficients and random effects were estimated using maximum likelihood methods in the lme function from the package nlme (version 3.1-96; Pinheiro et al. 2009) in the R language and environment (v.2.11.1, R Development Core Team 2010). Once the best supported model was determined for predicting RII and I_{imp} , I removed each explanatory variable from this full model and used the likelihood ratio between the full and nested model to determine the relative importance of each variable.

5.3 Results

Competition dominated interactions between focal and subalpine fir trees prior to the death of focal trees as indicated by the negative values of the overall median RII (Figure 18). However, 36% of subalpine fir trees decreased in BAI within five years of the death of the focal tree, meaning these interactions between subalpine fir and focal trees were of net facilitation (positive RII; Figure 18).

Variation in the intensity of interactions (RII) was best explained by the years-since-death of the focal tree, the diameter ratio between interacting trees and two concurrent climatic variables. Variables representing abiotic or climatic stress were not significant. The intensity of competition significantly increased (i.e., RII values decreased)

with the years-since-death of the focal tree (likelihood ratio from comparing full model with nested model: 48.960, $df=1$, $p\text{-value} < 0.0001$). The model with years-since-death (Model 1 in Table 13) was significantly improved by the addition of the ratio of subalpine fir DBH to that of the focal tree (Model 2 in Table 13). Model 2 was not improved by the density or basal area of trees in the neighbourhood (density: $\log L = 0.417$, $df=1$, $p=0.518$) nor by any stand-level variables representative of abiotic stress. Including concurrent total precipitation in the spring in Model 3 and then concurrent average temperature in September in Model 4, resulted in significant improvements (Table 15). Quadratic terms of the climatic variables and interaction terms between climatic variables did not further improve the final model, Model 4. The relative importance of variables in the final model was years-since-death, followed by concurrent average temperature in September, the concurrent total spring precipitation and the ratio of subalpine fir DBH to that of the focal tree (likelihood ratios from comparing full model with nested model: 48.960, 42.681, 11.315, 7.519; Table 13).

Predicted values of RII were negative when subalpine fir trees were smaller than focal trees under average climatic conditions after the death of the focal tree (Figure 19). This indicated that competition dominated the interactions between small subalpine fir trees and large focal trees and subalpine fir trees were subsequently releasing in growth. If the climate after the death of the focal tree was cool in September or dry in spring, the growth response of subalpine fir trees was dampened (Figure 19). In contrast, if climate was warm in September or wet in spring, this growth response was enhanced. The intensity of competition and, thus, the growth release decreased when interacting trees were more similar in size. When subalpine fir trees were larger than the focal tree, the predicted relationship with RII reached an asymptote close to zero indicating neutral interactions. The predicted RII values for these trees could be positive but this only occurred when Septembers were cold and dampening BAI_{post} and would not indicate facilitation of large subalpine fir trees by smaller focal trees.

The importance of competition relative to other factors affecting the growth of a subalpine fir tree was low (average $I_{imp} = -0.078$ ten years after the death of focal pine, Figure 18). The importance of competition did significantly increase (i.e., I_{imp} values decreased) with the years-since-death of the focal tree (likelihood ratio from comparing full model, Model 9, with nested model: 21.159, $df=1$, $p\text{-value} < 0.0001$). The best model for explaining the variation in I_{imp} over 10 years included the years-since-death of the focal tree, the diameter ratio between interacting trees and relative and concurrent climatic variables. Model 5 in Table 14 was significantly improved by the addition of the ratio of subalpine fir DBH to that of the focal tree, but not by the distance between trees. Model 6 was not improved by density or basal area of trees in the neighbourhood (density: $\log L = 0.929$, $df=1$, $p\text{-value} = 0.335$) nor by any stand-level variables representative of abiotic stress. Climatic stress of relative annual precipitation and two concurrent climatic variables did significantly improve Model 6 (Table 14). Quadratic terms of the climatic variables and interaction terms between climatic variables did not further improve the final model, Model 9. The most important variable explaining the variation in I_{imp} was years-since-death, followed by concurrent average temperature in September, then concurrent total precipitation in March, size ratio between interacting trees, and then the relative total annual precipitation (significant likelihood ratios from comparing full model with nested model: 21.176, 18.252, 13.269, 9.701, 4.215).

In contrast to the intensity of competition, the importance of competition relative to other factors was low for small subalpine fir trees but increased as subalpine fir trees were similar or larger in size to the focal trees (Figure 20a). The importance of competition also increased in years that were relatively dry (climatically stressful; Figure 20). When it was a relatively wet year, facilitative interactions became more important for small subalpine fir trees next to large focal trees. This suggests tree-tree interactions were not important influences on the growth of small subalpine fir trees, unless it was a relatively wet year, when being next to a large focal tree was beneficial. Other influences may include cool Septembers which dampen the response in BAI after the death of the focal tree (Figure 20d).

5.4 Discussion

I have multi-year and landscape-wide evidence that the intensity of interactions (RII) between adult trees was influenced primarily by the relative size of trees and not by abiotic or climatic stress. The importance of competition relative to other factors affecting tree growth (I_{imp}) was also influenced by the relative size of trees and increased with climatic stress. The patterns I found provide support for: 1) some predictions of the revised stress-gradient hypothesis (Maestre et al. 2009); and 2) a hierarchy of influences on plant interactions.

5.4.1 Revised stress-gradient hypothesis

I did find evidence of facilitation in adult trees (positive RII values in Figure 18), but no evidence that it increased with abiotic stress as predicted by the original stress-gradient hypothesis (Bertness and Callaway 1994). Subalpine fir trees were obviously sensitive to fluctuations in precipitation and temperature as indicated by concurrent climatic variables being the strongest predictor of RII by affecting the BAI in subalpine fir trees after the death of the focal trees. However, focal trees may not be able to mitigate water availability or cold temperatures for adult subalpine fir trees, unlike the increased facilitation of subalpine fir regeneration by focal trees with increasing elevation that I documented in Chapter 4. Facilitation has been found to be more frequent for juvenile plants than adults (Miriti 2006, Sthultz et al. 2007) and switches from competition to facilitation with increasing abiotic stress have yet to be demonstrated for adult trees. Facilitation of adult trees by adult trees may occur because of some other stress gradients, such as gradients in soil nutrient, not represented by my surrogate variables. Of other studies of adult trees which examined for facilitation, none found evidence of facilitation between adult trees but suggest they may not have observed it because they were either not sampling at the extremes of a stress gradient (Kunstler et al. 2011) or because it may only be apparent in root growth if competition for nutrients, not light, increases with abiotic stress (Coomes and Allen 2007).

The revised stress-gradient hypothesis by Maestre et al. (2009) predicts that when the life histories of a benefactor and beneficiary are stress-tolerant and competitive, respectively, high abiotic stress caused by a resource shortage like water, will increase the importance of competition. I found that the importance of competition between whitebark pine (stress-tolerant) and subalpine fir (competitive) trees increased with the climatic stress of decreasing total annual precipitation (Figure 20b). In high-elevation forests, it appears that when water is not limiting, interactions between adult trees relative to other factors are unimportant influences on tree growth. This is

likely because these high-elevation forests are relatively stressful environments with harsh climate and poor soils which are more important in dictating tree growth than competition when water is not limiting. In Mediterranean forests, the importance of competition between adult trees also increased as precipitation decreased (Gomez-Aparicio et al. 2011). Subalpine forests are not often considered water limited in the same vein as Mediterranean forests; however, the diffusion coefficient for water vapour increases substantially with decreasing pressure at higher altitudes, leading to transpiration rates typical of much warmer climates (Smith and Geller 1981). Subalpine fir, a shade-tolerant species, is less drought tolerant than whitebark pine, a shade-intolerant species (Knapp and Smith 1981, Sala et al. 2001, Niinemets and Valladares 2006). These two observations mean that high-elevation forests can be sensitive to water stress. There is evidence during the Holocene that drought stress and historically warmer conditions caused a decline in treeline elevation in the Sierra Nevada mountains, U.S. (Lloyd and Graumlich 1997). More recently, in the Rocky Mountains in Colorado, U.S., increased mortality of subalpine fir was linked to increasing occurrence of late-season drought (Bigler et al. 2007). Together, my results and Gomez-Aparicio et al. (2011) support the prediction that the importance of competition increases as resources become scarce for adult trees. It is not unusual for relationships between interaction intensity and abiotic stress not to match those between interaction importance and abiotic stress (Welden and Slauson 1986). Like Kunstler et al. (2011) who examined interactions between 16 trees species in France, I only found a significant relationship between stress and the importance of adult tree interactions but not with interaction intensity.

In contrast to the predictions of Maestre et al. (2009), I did not find a humped-back shaped relationship between interaction importance, I_{imp} , and relative total annual precipitation where facilitation becomes important at intermediate levels of water availability (i.e., quadratic terms were not significant in Model 9). I did find that at low stress, when it was a wetter than average year, that neutral interactions became important. It is possible that in this system, facilitation is relatively unimportant at all levels of climatic stress except when subalpine fir trees are very small.

5.4.2 Hierarchy of influences on tree interactions

I found a hierarchy in variables which could explain the variation in RII and I_{imp} where the size differential between interacting trees was the most influential variable. Climatic stress, whether the year was dry relative to the 30-year average, was a secondary influence for I_{imp} . Note that concurrent climatic variables were actually the most important variables in the models but affected the growth of subalpine fir trees after the death of the focal tree and, thus, were additive to the growth response caused by the death of the focal tree. If I had excluded concurrent climatic variables, relative climatic stress would have been a significant variable in the final model to predict RII. This points to the hierarchical nature of influences on tree growth and that year-to-year variation in fall temperatures can completely override the influences of tree interactions on radial growth. It was challenging to separate climatic variation into that which causes “regular” year-to-year variation in the widths of tree rings versus variation that represents a climatic stress to a tree. I did so by including both concurrent and relative climatic variables in the models. It would have been more ideal to remove the climatic signal from the ring-width series with a simple, universal model; however, shifts in the climate-growth relationships for subalpine fir as described in the previous chapters would have made this difficult.

The intensity of competition (i.e., the magnitude of growth release after the death of focal trees) was highest for subalpine fir trees which were smaller than the focal trees likely because of the negative effects of shading on growth. Others have also found that smaller trees are more sensitive than larger trees to tree competition from the neighbourhood (Coates et al. 2009, Gomez-Aparicio et al. 2011). Competition is thought to be for light when trees are small and switch to being for below-ground resources as a tree matures (Coomes and Allen 2007). The size range of subalpine fir trees that I sampled likely straddles the differentiation between competitive and stress-tolerant life histories described by Maestre et al. (2009). Small subalpine fir trees are likely more competitive but less stress-tolerant than large subalpine fir trees and this difference makes relative size an important variable in predicting RII and I_{imp} .

Much effort in the forestry literature has been on calculating indices of neighbourhood competition (e.g., Bella 1971, Lorimer 1983, Uriarte et al. 2004, Canham et al. 2006). However, I found that the influences of the density or basal area of other trees in the neighbourhood did not significantly predict the growth response of subalpine fir after the death of the focal tree. There are three reasons why neighbourhood-level competition may not have been important in predicting the intensity of tree interactions in my study. 1) The high-elevation forests I studied are relatively stressful environments and open (e.g., average percent canopy cover was 18%) in comparison to productive forests at lower elevations, so that classic density-dependent competition may not be influential in these systems. 2) The size differential between subalpine fir and focal trees that I used has proven to be a mediocre index of neighbourhood competition in other studies (Bella 1971, Biging and Dobbertin 1992) and may have captured neighbourhood competition adequately in my study. Relative to other tree species, subalpine fir has been found to be disproportionately sensitive to the presence of very large neighbours (Coates et al. 2009). 3) A larger search radius combined with a more sophisticated index which accounts for the diameter, distance and species-specific competitive ability of neighbouring trees (e.g., that in Canham et al. 2006) may have better described neighbourhood competition. As well, I modelled only 10 years after the death of the focal tree but the resulting growth releases could last more than 20 years (Stan and Daniels 2010). It is possible that neighbourhood competition becomes more important for predicting the long-term growth response to the death of the focal tree as trees grow and zones of resource use overlap.

Identifying a hierarchy of explanatory factors on tree interactions offers a useful framework for designing studies to test the stress-gradient hypothesis. Even with recent revisions (Maestre et al. 2009, Holmgren and Scheffer 2010), the stress-gradient hypothesis remains without a context grounded in spatial and temporal scales. I first recommend dividing hypothesized influences on plant interactions based on spatial and temporal scales – e.g., fine- versus coarse-grain factors and factors which change annually or seasonally versus those which are slow changing. Studies can be designed which attempt to address a range of spatial and temporal scales by choosing influences from each level to examine and include in the experimental design. This hierarchy of influences emphasizes that annual climatic variation must be accounted in any multi-year study of plant interactions. Annual variation in climate is currently absent in most of the neighbourhood modelling efforts quantifying the effects of tree competition on adult tree growth. Generally, other studies of competition in adult trees have assumed that

climate has remained the same between the two years of measurement and that each species responds the same to year-to-year climatic variation (e.g., Coomes and Allen 2007, Coates et al. 2009).

5.4.3 Change in high-elevation forests and tree interactions

High-elevation forests containing whitebark pine are undergoing two broad scale changes. First, the widespread decline of whitebark pine from blister rust, mountain pine beetle and *Ips* sp. has lowered its resilience (Chapter 3) and, thus, its ability to retain its presence in the canopy. My results indicate that the absence of adult whitebark pine trees will decrease the competition pressure on smaller subalpine fir trees and cause a subsequent growth release. In Waterton Lakes National Park, where on average 70% of the whitebark pine have died, the growth release has been significant (Figure 13 in Chapter 3). However, the magnitude of the growth release will be dampened if springs are dry and/or falls are cool. While some subalpine fir trees were facilitated by whitebark pine trees, the negative effects of the death of whitebark pine on the growth of subalpine fir will decrease over time. For subalpine fir trees similar in size to whitebark pine, there will be little impact of the decline of whitebark pine because interactions were close to neutral. Because the landscape average of RII was negative, the projected response to the widespread decline in whitebark pine is a release in the growth of smaller subalpine fir trees which will accelerate the dominance of subalpine fir in these forests. How long the growth release will last and at what intensity remains a research question to explore.

High-elevation forests grow in harsh environmental conditions which can be amplified by small shifts in precipitation or temperature caused by climate change (Lloyd and Graumlich 1997). Water availability during the summer is affected in part by the spring snowpack. In the Canadian Rockies, the water content in the spring snowpack has declined between 20-40% since 1950 and most locations have declined in snowfall since 1950 (Mote et al. 2005). Although projections of changes in summer precipitation are uncertain, if summer drought increases, it would amplify the decline in soil moisture caused by the declines in spring snowpack. I demonstrated that the relative importance of competition between adult subalpine fir and whitebark pine trees increased as the total annual precipitation decreased. This important relationship between tree interactions and climate is currently missing from studies using climate envelope models to predict how tree distributions will change with climate (e.g., Schrag et al. 2008). The widespread decline of whitebark pine means that the bulk of future tree-tree interactions of subalpine fir will be with unhealthy whitebark pine, other subalpine fir or with Engelmann spruce (*Picea engelmannii*) trees. Relationships between these tree interactions and the temporal variation in climate are unknown but are important to define in order to predict the future composition of high-elevation forests.

Table 12. Explanatory variables considered for explaining variation in intensity (RII) and importance (I_{imp}) indices of interactions between subalpine fir trees and focal whitebark pine trees.

Variable	Description	Range of values
Tree level		
Year	Years-since-death of focal tree	1-10
DBH_ratio	Ratio of subalpine fir DBH to focal tree DBH (natural log)	0.07- 2.02
Dist	Distance from focal tree to subalpine fir (m)	0.22 – 4.00
Neighbourhood level: Variables competition/facilitation from other trees		
BA	Total live basal area in neighbourhood of focal tree (m ² /ha)	0 - 52.60
Density	Density of live trees DBH >4 cm in 2 m radius of focal tree (trees/ha)	0 - 8758
Stand level: Variables of abiotic stress		
Elev	Elevation (m)	1855 - 2249
Slope	Slope (degrees)	6 - 48
Jan_insol	Net solar radiation in January (Wh/m ²)	8,566 – 29,083
July_insol	Net solar radiation in July (Wh/m ²)	168,181- 204,367
Nonveg	Percent cover that is rock, scree or soil and is not vegetated, indicative of poorly developed soils	0.33 - 68.33
Layer	Percent cover that is subalpine fir layering, indicative of stressful conditions for subalpine fir	0.00 - 11.25
D_density	Index of disturbance; density of all dead whitebark pine (trees/ha)	54 - 305
Stand_fir_ba	Basal area (m ² /ha) of live subalpine fir DBH ≥ 4 cm	3.99 - 40.27
Regional level: Climatic variables		
Stress_ppt	Climatic stress (relative precipitation/temperature): Ratio of total monthly precipitation (mm) or average monthly temperature (°C) five years prior to the death of focal tree to the 30-year average prior to the death. Values < 1 indicate cooler/drier (i.e., stressful) conditions than average. Only significant in models are reported on right.	Ratio_total_ppt:
Stress_temp		0.80-1.2
Ppt	Concurrent precipitation/temperature: Monthly total precipitation or monthly average temperature for year <i>i</i> after death of focal tree.	September_temp:
Temp		5.6 -16.1
		March_ppt: 2.4 - 87.3 Spring_ppt: 35-250

Table 13. Evidence that the index of interaction intensity (RII) between subalpine fir and whitebark pine trees was best predicted by climatic variables and the ratio of DBH of interacting trees ($j=184$ trees, $l=15$ stands, 1809 observations). P-values result from likelihood ratio (logL) tests with the model on the row above.

#	Model	df	AIC	logL ratio p-value
1	Year	7	-879.504	
2	Year + DBH_ratio	8	-884.647	7.143 0.008
3	Year + DBH_ratio+ Spring_ppt	9	-893.056	10.409 0.001
4	Year + DBH_ratio+ Spring_ppt + September_temp	10	-933.736	42.681 <.0001

Table 14. Evidence that the importance (I_{imp}) of interactions between subalpine fir and whitebark pine trees relative to other factors affecting radial growth were best predicted by climatic variables and the size differential between interacting trees ($j=184$ trees, $l=15$ stands, 1809 observations). P-values result from likelihood ratio tests with the model on the row above.

#	Model	df	AIC	logL ratio p-value
5	Year	7	-1798.031	
6	Year + DBH_ratio	8	-1804.839	8.808 0.003
7	Year + DBH_ratio + Ratio_total_ppt	9	-1807.250	4.411 0.036
8	Year + DBH_ratio + Ratio_total_ppt + March_ppt	10	-1818.787	13.537 2e-04
9	Year + DBH_ratio + Ratio_total_ppt + March_ppt + September_temp	11	-1835.039	18.252 <.0001

Table 15. Estimated coefficients (standard error) for final models from Tables 13 and 14 for predicting RII and I_{imp} .

	Model	β_0	β_1	β_2	β_3	β_4	β_5
<i>RII</i>	Year + DBH_ratio+	0.114	-0.017	0.059	$2.371 \cdot 10^{-4}$	-0.012	
	Spring_ppt +	(0.038)	(0.002)	(0.021)	($7.035 \cdot 10^{-5}$)	(0.002)	
	September_temp						
	<i>p-values</i>	0.0001	0.0000	0.006	0.001	0.000	
<i>I_{imp}</i>	Year + DBH_ratio +	-0.266	-0.008	-0.056	0.251	0.0007	-0.006
	Ratio_total_ppt +	(0.117)	(0.002)	(0.016)	(0.117)	($1.880 \cdot 10^{-4}$)	(0.001)
	March_ppt +						
	September_temp						
	<i>p-values</i>	0.024	0.000	0.001	0.033	0.0003	0.000

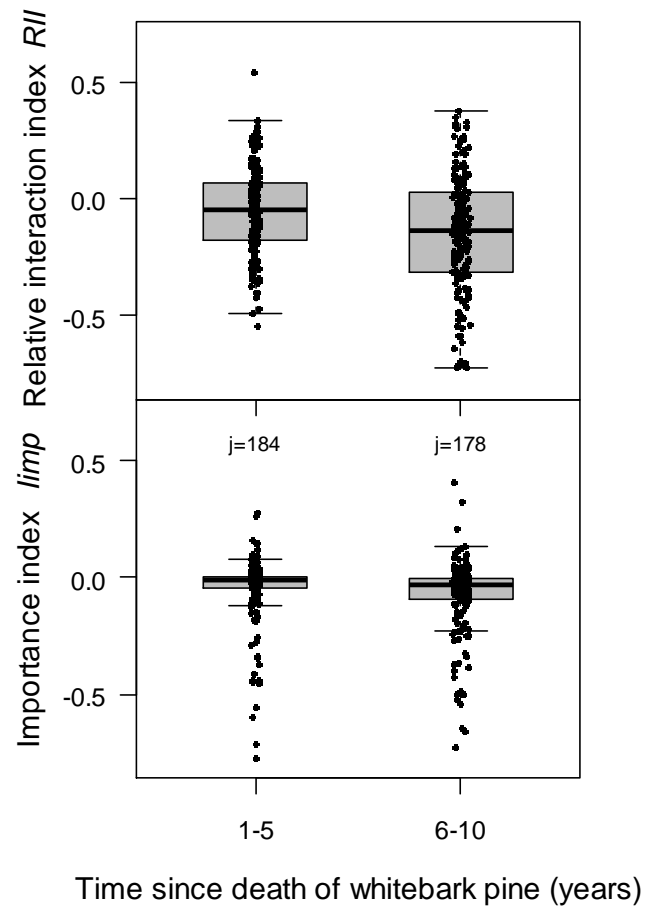


Figure 18. Competition dominated interactions between mature whitebark pine and subalpine fir trees (j). Negative values of RII and I_{imp} indicate when competition prevailed, positive values indicate when facilitation prevailed and zeros occurred when the net balance of the interaction was neutral. The box indicates the interquartile range of the data (RII and I_{imp} averaged for the time period), the solid line in the box indicates the median and the whiskers extend to 1.5 times the interquartile range.

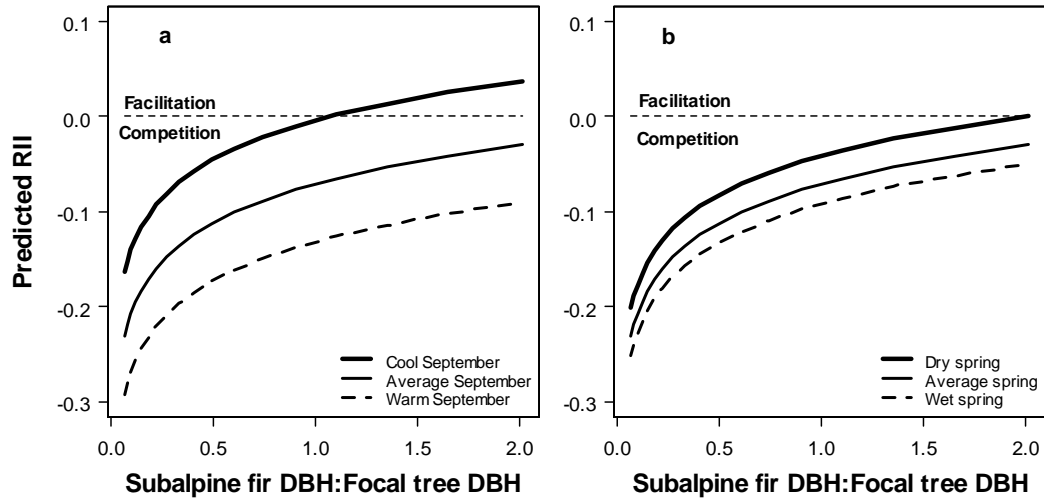


Figure 19. Relationships between the predicted intensity of interactions (RII) with the ratio of subalpine fir DBH to that of the focal tree and the influence of different climatic conditions on the growth response at year five after the death of the focal tree, BAI_{post} . The additive effects of concurrent climatic variables to the growth response caused by the death of the focal tree, a) September temperatures, and b) spring precipitation, were shown at their observed minimum, average and maximum values. Predicted values were from Model 4 in Table 13 where the other explanatory variables not shown were at their observed average values.

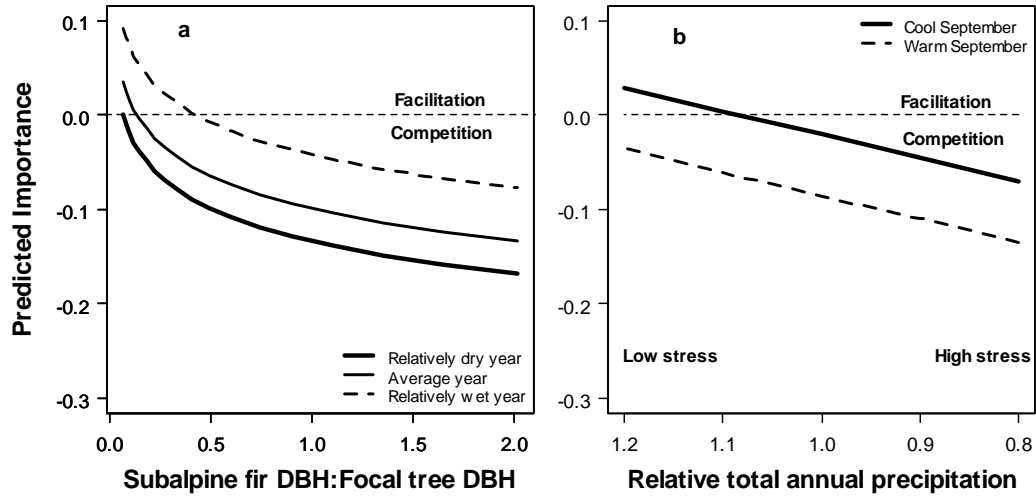


Figure 20. Relationships between the predicted importance of interactions (I_{imp}) with the ratio of subalpine fir DBH to that of the focal tree and the influence of an index of climatic stress (ratio of total annual precipitation to long-term average). If it was drier than average, competition was relatively more important. Predicted values were from Model 9 in Table 14 where the other explanatory variables not shown were at their observed average values (e.g., in b.) the DBH of subalpine fir was half that of the focal tree). The additive influence of the concurrent average temperature in September on BAI_{post} in b) was illustrated using the observed minimum and maximum values.

Chapter 6: Conclusions

6.1 Introduction

Understanding the resilience of ecosystems to novel disturbance regimes and how plant-plant interactions will be affected by global change is critical for predicting the future of forested ecosystems (Tylianakis et al. 2008, Thrush et al. 2009). In this dissertation I used the widespread decline of whitebark pine (*Pinus albicaulis*) as an opportunity to examine the dynamics and responses of high-elevations forests to the novel disturbance regime of the non-native white pine blister rust (*Cronartium ribicola*) when coupled with two native bark beetles. I also used the widespread mortality as an *in-situ* experiment to simulate neighbour removal (*sensu* Callaway 1998) and examined juvenile and adult tree interactions over multiple years and gradients of abiotic and climatic stress. In this chapter I summarize conclusions from this dissertation, their links to current research and the limitations of my work. The consideration of whitebark pine as a keystone species (Tomback and Kendall 2001) and its severe decline over the last few decades has led it to become the first tree species to be recommended for a federal listing in Canada as an endangered species (Committee on the Status of Endangered Wildlife in Canada 2010). In this chapter, I conclude by making recommendations for the conservation of whitebark pine and for future research.

6.2 Contributions to current research

6.2.1 A novel disturbance regime has decreased whitebark pine resilience

The introduction of non-native blister rust has profoundly changed high-elevation forests containing whitebark pine. Beyond the high mortality of whitebark pine trees which is visually obvious on the landscape, in Chapters 2 and 3 I found evidence of substantive changes to the mechanisms underpinning the dynamics of these high-elevation forests. Two of these changes involved switches in the relationships between climate and the radial growth of whitebark pine and subalpine fir (*Abies lasiocarpa*) trees. Prior to 1950 and the introduction of blister rust, whitebark pine growth was positively correlated with snowfall concurrent with ring formation, yet after 1950 was positively correlated to precipitation in June concurrent with ring formation. Because blister rust reduces sapwood moisture and negatively affects water relations within a tree (Six and Adams 2007), I proposed that infection may have heightened the sensitivity of whitebark pine trees to summer moisture. Thus, the introduction of blister rust could have decoupled the historical relationship between snowfall and whitebark pine growth and shifted it to be sensitive to summer precipitation. This switch could amplify the susceptibility of whitebark pine trees to attack by mountain pine beetle (*Dendroctonus ponderosae*) and *Ips* sp. (shown by beetle-killed trees having the greatest decline in BAI prior to death) resulting in the novel “triple whammy” of disturbances at elevations traditionally considered too cold for outbreak development. The death of whitebark pine from the triple whammy reduced competition for limited resources and increased the growth of subalpine fir. The average BAI of mature subalpine fir over the last 30 years was double the average growth between 1945 and 1975. This growth response was notable as it overrode the expected decline in growth in response to decreasing precipitation in January and

March as predicted from climate-growth relationships prior to rust. Thus, the climate-growth relationship for subalpine fir also appears to have been decoupled by the introduction of blister rust.

While mountain pine beetles were a natural disturbance in the past and may have triggered whitebark pine regeneration in my study area, the additional effects of blister rust and *Ips* sp. are decreasing the abundance of seed-bearers and blister rust is increasing the mortality of whitebark pine saplings. Furthermore, in Chapters 3 and 4, I found evidence to suggest that subalpine fir regeneration increases in response to disturbance to large whitebark pine trees and proposed that it is likely due to a release from light competition and facilitation of winter conditions by dead whitebark pine trees. The slowing down in the recovery of a keystone species (Thrush et al. 2009, van Nes and Scheffer 2009) and the abrupt shift in the driving variables of system behaviour (Edwards and Richardson 2004, Carpenter and Brock 2006), as evident in the shifts in climate-growth relationships, are convincing evidence that a regime shift is occurring. Combined, these changes have amplified the shift in the species composition of high-elevation forests to increasing dominance by subalpine fir and extirpation of whitebark pine, a keystone species. Resilience of whitebark pine to the triple whammy of disturbances was, on average, low; however, there were locations on the landscape considered resilient. In Chapter 3, I found that resilience of whitebark pine increased with decreasing severity of blister rust and with decreasing abiotic stress at a site. While the shift to subalpine fir and the loss of whitebark pine resilience has been anticipated by others (e.g., Keane 2001, Tomback and Kendall 2001), my work is the first to quantify changes in specific mechanisms maintaining whitebark pine trees in these high-elevation forests and is an important contribution to the resilience literature.

6.2.2 Refining the stress-gradient hypothesis

Most studies testing the stress-gradient hypothesis proposed by Bertness and Callaway (1994) used experimental removals or additions of herbs or shrubs to examine plant interactions on subjectively selected or created gradients of abiotic stress. These studies tended to examine pairs of plants over one to two growing seasons at only two sites which represent the low and high extremes of abiotic stress. These designs have been criticized for not being capable of detecting temporal variation in plant interactions, not sampling multiple points along the stress gradient, nor multiple abiotic stresses (Lortie 2010). Moreover, I argue that there was a propensity in these studies to subjectively select study sites which may result in biased conclusions in that there may be a tendency to perform experiments under conditions providing reasonable expectations of detecting statistically significant effects (Gurevitch and Hedges 1999). The experimental design is also unable to provide estimates of the natural occurrence of facilitation versus competition in plant communities across large landscapes or long time periods (Freckleton and Watkinson 2001). Quantifying the relative importance of competition or facilitation on the landscape is key for predicting impacts on plant communities from climate change (Brooker et al. 2005).

My work presented in Chapters 4 and 5 makes a key contribution to refining the stress-gradient hypothesis by designing a study which exceeded the spatial and temporal scale of previous stress-gradient experiments. I used the widespread mortality of whitebark pine as an *in-situ* experimental removal to examine both juvenile-adult and adult-adult tree interactions. Although the design originated from Callaway's work (1998), it improved upon his design by sampling more locations (n=14 randomly selected versus n=4 subjectively selected) and using crossdating to associate the death of whitebark pine to the response in subalpine fir growth and climatic variables

by exact dates. My design benefitted from random selection of stands from a large landscape which permitted the natural variation in tree size, neighbourhood tree density, climatic and abiotic stress to dictate the boundaries of the “experiment”. Others have also used a non-manipulative regression approach using plots from forest inventories but unlike mine, had to simulate the removal of neighbours by varying the density of neighbouring trees in their models (Coomes and Allen 2007, Gomez-Aparicio et al. 2011, Kunstler et al. 2011).

Because of the landscape scale, large sample size and random selection of stands and trees in my study, my results present strong evidence for the conditionality of the stress-gradient hypothesis. To the best of my knowledge, my work presented in Chapter 4 is the first time the relationship between benefactor size and plant interactions has been empirically modelled over a stress gradient with varying neighbourhood densities in a neighbour removal “experiment”. In general, facilitation of regenerating subalpine fir by adult whitebark pines increased with abiotic stress. However, there were clear thresholds in benefactor size, neighbourhood density and stress indicating a shift to competition or neutral interactions. For example, above a certain diameter, live whitebark pine trees inhibit subalpine regeneration likely by excessive shading or precipitation interception. In Chapter 5, these size thresholds to the intensity of interactions also existed between adult subalpine fir and whitebark pine trees. In this case, the thresholds were asymptotic and indicated where interactions shifted from competitive to neutral as interacting trees were more similar in size. The presence of size thresholds is interesting because they, not neighbourhood competition/facilitation nor abiotic or climatic stress, dictated the intensity or direction of the interaction between adult trees. The importance of competition between adult trees did increase in drier years, but again, the relative size of interacting trees was a more influential factor. This emphasizes that assessing for a hierarchy in the factors affecting plant interactions is critical and is an important addition to the current discussions around refining the stress-gradient hypothesis (Maestre et al. 2009).

6.3 Linking conclusions to conservation

Current conservation actions for whitebark pine include collecting and archiving seed in cold storage, planting of blister rust-resistant seedlings (Schoettle and Snieszko 2007), using verbenone to protect valuable seed source trees (Perkins 2010), using prescribed fire to restore fire where it has been excluded and was once frequent (Keane and Parsons 2010), thinning of competing vegetation (McCaughey et al. 2009), and assisted migration to locations thought to be climatically appropriate for whitebark pine in the future (McLane and Aitken in press). Results from my work in the proceeding chapters offer insights for guiding some of these management actions.

6.3.1 Plant whitebark pine seedlings where they best enhances resilience

Both the disturbance severity from and the resilience of whitebark pine to blister rust, mountain pine beetle, and *Ips* sp. can be predicted using explanatory variables identified in Chapters 2 and 3 and mapped by using values from digital elevation models and vegetation inventories in order to prioritize conservation actions. Because past attempts (Campbell and Antos 2000, White et al. 2002) have modelled each disturbance agent primarily in the absence of the others, my modelling of disturbance severity represents the first attempt appropriate for the contemporary disturbance regime in which all three disturbance agents concur. In Chapter 2, I identified specific

characteristics of both topography and forest composition which are bottom-up controls on the severity of these disturbance agents. These characteristics included for mountain pine beetle, percent cover of bare ground and elevation, for blister rust, net solar radiation in July, and for *Ips* sp., net solar radiation in July and total density of whitebark pine. In Chapter 3, I found that the resilience of whitebark pine was higher on sites with relatively high net solar radiation in January and low mortality in the overstory from blister rust. Net solar radiation can be modelled from a digital elevation model whereas the mortality of whitebark pine requires frequent aerial or ground surveys. Mapping variables capable of predicting disturbance severity and whitebark pine resilience, stands of potentially high severity and low resilience could be targeted for restoration whereas stands of high severity but high resilience would be second priority. For example, in stands where the severity of mountain pine beetle is predicted to be high, mature whitebark pine trees could be protected with verbenone in the face of an outbreak and whitebark pine seedlings could be planted before the outbreak impacts the density of living whitebark pine trees. In the absence of process-driven models capable of simulating the spread of blister rust across a landscape, the mapping I describe here, may represent the best available information for guiding effective planting of whitebark pine seedlings even though I cannot infer causality from the observed correlations.

6.3.2 To thin or not to thin?

To enhance the establishment whitebark pine seedlings, mechanically removing competing trees and understory vegetation have been suggested (McCaughey et al. 2009). I found no evidence to support removing subalpine fir regeneration, shrubs or herbs, such as bear grass (*Xerophyllum tenax*), would increase the density of whitebark pine regeneration. In my modelling efforts to predict densities of whitebark pine regeneration, I found that variation in neither the density of subalpine fir regeneration nor the percent cover of understory vegetation were significant predictors (Chapter 3). Other work has found that other trees and herbs can actually facilitate the survival and growth of whitebark pine seedlings (Maher et al. 2005). I did find that the incidence of blister rust on seedlings was higher where the basal area of subalpine fir was high. This may have resulted because of the inverse relationship found between blister rust severity and solar radiation (Chapter 2) and the association of subalpine fir with cooler sites. Alternately, it may suggest that removing subalpine fir regeneration can decrease the relative humidity enough to make it inhospitable for spores of blister rust to develop and survive (Van Arsdell et al. 1956). Further work such as removal trials are required to test these hypotheses.

I found that the average radial growth of adult subalpine fir trees increased 100% from growth prior to the mountain pine beetle outbreak in Waterton Lakes National Park (Figure 13). This is likely a release from competition with whitebark pine because I found: 1) no relationship to a shift in climatic drivers of the radial growth of subalpine fir, and 2) that the dominant direction of interactions between neighbouring adult subalpine fir and whitebark pine was competitive (Figure 18). I interpret this to support testing mechanical thinning of subalpine fir trees to enhance the growth of adult whitebark pine trees, with the following cautions:

1. My work only examined one side of the competitive relationship. The costs to whitebark pine of competition with subalpine fir are unknown. The tenet that removal of subalpine fir trees will increase the radial growth of whitebark pine needs to be confirmed by designing thinning treatments as an experiment. It should be noted that I did not observe a notable increase in radial growth in surviving whitebark pine to

the cumulative mortality of whitebark pine in Chapter 3. This suggests if whitebark pine trees are infected by blister rust, a growth response to thinning may not result. Testing the relationship with blister rust should also be incorporated in thinning trials.

2. Not every interaction between adult trees was competitive. I found strong relationships between the intensity of interactions and the size differential between trees. For example, if trees were of similar size, the intensity of interactions was close to null. This suggests that it would be most efficient to thin only subalpine fir trees which are much smaller in size than whitebark pine trees.

Prescribed fire has also been suggested for thinning competing vegetation (Keane and Parsons 2010). This assumes that fire was a historical part of the disturbance regime of whitebark pine stands and that fires have been excluded long enough to permit ingrowth of subalpine fir. I did not observe widespread historical evidence of fire in stands containing whitebark pine in Waterton Lakes National Park. In Waterton Lakes, I observed very few fire-scarred trees (2.3% of 1204 sampled whitebark pine) in only three stands: 4 (n=3), 8 (n=3) and 15 (n=17). Each fire-scarred tree only had one scar lobe visible. Few of the increment cores captured the tips of the scars so I was only able to date two fires: 1772 (Stand 15 in Table 2) and 1836 (Stand 4). In addition, I found no evidence of charred logs or snags. The long time-since-fire, the absence of trees with multiple fire scars from lower-severity fires and the relatively old age of subalpine fir regeneration (65 ± 64 years; average ± 1 std. dev.) indicates that fires were infrequent and of high severity in most of the stands. Thus, given infrequent fires, disturbance by mountain pine beetle and perhaps *Ips* sp., by creating gaps and opportunities for regeneration, clearly could play an important role in the ability of whitebark pine forests to self-perpetuate. Aside from the 1970s mountain pine beetle outbreak, I have evidence from good-quality increment cores of mortality in the late 1920s (2 stands) and late 1950s (4 stands) due to mountain pine beetle. Stand 10 had mortality from all three periods: 1920, 1950s and the 1970s outbreak. Outbreaks were also recorded in whitebark pine stands nearby in Montana between 1899 and 1909 (Hawkes et al. 2004) and in the 1930s in Kootenay National Park (Dykstra and Braumandl 2006) and central Idaho (Logan and Powell 2001). The role for mountain pine beetle in self-perpetuating whitebark pine forests has also been suggested for forests in Montana (Larson et al. 2009) and in lodgepole pine forests for triggering lodgepole pine regeneration where fire is absent (Stuart et al. 1989). However, in the presence of blister rust, my results do not support the hypothesis that mountain pine beetle is a reliable mechanism for currently triggering the regeneration of whitebark pine. Fire may have played a more important role in the three additional protected areas I sampled in the northern range of whitebark pine where 41% of the 17 sampled stands contained either fire-scarred trees or charred snags and logs.

Others have cautioned against the use of prescribed fire in whitebark pine stands, questioning whether fire suppression is causing declines ubiquitously in whitebark pine stands and that restoration of whitebark pine forests requires fire management (both prescribed and prevention) (Coop and Schoettle 2011, Larson and Kipfmüller in press). I believe I make a compelling argument that stands containing whitebark pine in Waterton Lakes National Park are not declining because fire exclusion is causing subalpine fir ingrowth but rather of the cumulative effects of the triple whammy disturbance. I further recommend avoiding prescribed fire and the risk of killing mature trees when seed sources for whitebark pine are close to their thresholds for attracting Clark's nutcrackers (*Nucifraga*

columbiana) for caching ($5\text{m}^2/\text{ha}$; McKinney et al. 2009). As I pointed out in Chapter 3, the landscape average for live whitebark pine is below this threshold in Waterton Lakes National Park ($4.8\text{m}^2/\text{ha}$). Furthermore, 60% of live whitebark pine trees were reproductively dead with top kill from blister rust. In the protected areas in the northern Canadian Rockies (Jasper, Banff and Willmore Wilderness), the status of whitebark pine is much better. I estimated that the average landscape basal area of live whitebark pine was above the threshold for Clark's nutcrackers at $8.9\text{m}^2/\text{ha}$ (std. dev. = $4.3\text{m}^2/\text{ha}$) and less of these stands were affected by blister rust, only 22% of live pine had dead tops ($n=19$ stands). If prescribed burns are planned in any of these protected areas or if wildfires at lower elevations spread and impact high-elevation forests, intensive planting and monitoring of whitebark pine seedlings should be conducted.

6.4 Limitations of present work

Whitebark pine grows in locations which are typically challenging to access. We spent four or five hours a day simply hiking to access the sample sites. Furthermore, dendrochronological work on ring-width series from high-elevation species is notoriously challenging to crossdate with a master chronology because of slow growth rates and high variability between sites (Kipfmüller and Salzer 2010). Often tree rings were only a cell wide, particularly in whitebark pine trees affected by blister rust. These challenges limited the sampling intensity at each site. Ideally, I would have liked to sample each location more intensively and in particular: 1) sample the age, height and radial growth of seedlings and saplings under live and dead whitebark pine to better examine the timing and the mechanisms of facilitation/competition by whitebark pine in Chapter 4; 2) sample the growth response of Engelmann spruce (*Picea engelmannii*) to the death of whitebark pine in Chapter 5, particularly because this is a common species further north in whitebark pine's range; and 3) sample the growth response of adult whitebark pine to the death of subalpine fir to test for asymmetric competition for Chapter 5.

In Chapter 5, non-linear models may better represent the relationships between various explanatory variables and the intensity and importance of competition/facilitation between adult trees. However, given the hierarchical nature of the data, and unknown size and climate-growth relationships for high-elevation trees, non-linear modelling was beyond the scope of this dissertation.

6.5 Directions for future research

This dissertation contains significant advancements to our knowledge on disturbance dynamics and tree interactions in high-elevation forests containing whitebark pine. Conclusions also highlight future research questions and these are discussed below.

6.5.1 Can we predict the amplification of other disturbances by blister rust?

The triple whammy of disturbances in Waterton Lakes National Park was years in the making. Blister rust severely stressed whitebark pine trees for 30 years, made them sensitive to fluctuations in summer precipitation and

caused up to 46% decline of pre-1950 growth before trees died from mountain pine beetle. Outbreaks of bark beetles in other locations have been amplified by changes in temperature or precipitation which have accelerated their life-cycles (Raffa et al. 2008, Bentz et al. 2010). New research questions about interactions between disturbances and with climate result from these observations. Can we identify the stress on whitebark pine by blister rust using declines in basal area increment (BAI) as an early detection method (Bigler and Bugmann 2004)? Does the decline in BAI occur earlier than the phenotypic display of rust? Can we confirm from other locations, that blister rust infection increases the sensitivity of whitebark pine to summer precipitation? Does blister rust increase the susceptibility of whitebark pine to attack by *Ips* sp. and mountain pine beetle? Are there thresholds in these relationships which indicate a tipping point in the behaviour of this system?

6.5.2 How does climatic variation affect interactions between adult whitebark pine trees and tree regeneration?

In Chapter 4, I demonstrated that adult whitebark pine trees facilitated the establishment of subalpine fir regeneration depending on the benefactor's size and condition, neighbourhood level of facilitation and level of disturbance. However, the intensity of facilitation or competition can depend on which metrics of fitness are used and temporal variation in climate (Tielborger and Kadmon 2000). Because I did not sample the radial growth of the regenerating trees, nor estimate their age, I was not able to determine how adult whitebark pine trees influenced the growth of regenerating trees and how interactions varied over time with climatic stress. This remains an important topic to examine in the face of climate change.

6.5.3 What are the mechanisms for the facilitation of subalpine fir seedlings and adult trees by adult whitebark pine trees?

I inferred that focal whitebark pine trees facilitated subalpine fir seedlings when the benefits provided by a canopy (protection from low-temperature photoinhibition, moisture retention) exceeded the cost of shading or interception of rain or snow by the canopy. Critical evidence for this inference was that the intensity of the interaction was demonstrated to be a function of the size and condition of the benefactor. For example, as benefactors increased in size, facilitation by live trees with top-kill was higher than for healthy live trees with a full canopy. Recently dead trees were also facilitators at large diameters and levels of high abiotic stress and I hypothesized that this was because their stems provided shelter against winter winds and increased snow accumulation. These inferred mechanisms need to be tested by comparing the light environment, snowpack depth and soil moisture and nutrients beneath the canopies of live, unhealthy and dead whitebark pine trees. Determining how environmental conditions change with the size of the canopy and the distance away from the benefactor tree is also an important gap in our understanding of how large trees modify their environments. Experimental manipulations of the environment around seedlings (e.g., artificial shading, watering, fertilizing) could also be used. For interactions between adult whitebark pine with adult subalpine fir trees, heightened competition for water during the summer needs to be confirmed. Studies of both seedlings and adult trees could be designed to test whether the humped-back shaped model of Holmgren et al. (2011) for predicting non-linear effects of shading holds in these high-elevation forests. Studies could also test Tilman's hypothesis (1982) which predicts that there is

a shift from above-ground competition to below-ground competition as environments become less productive or more stressful.

6.5.4 Can thinning enhance the growth of whitebark pine and resistance to blister rust?

My results presented evidence on thinning which conflicts with guidelines for planting whitebark pine (McCaughey et al. 2009). These guidelines recommend removing overstory trees within a 6-metre radius of planted seedlings to reduce competition and reducing understory vegetation to reduce competition for water and nutrients. While the guidelines do cite evidence for facilitation of whitebark pine seedlings by *Vaccinium scoparium*, the general premise is that all nearby trees and vegetation would inhibit whitebark pine seedlings. There has not been a formal test of whether or not thinning by mechanical means or by prescribed fire can increase: 1) the survival of planted seedlings, 2) the growth of established seedlings and saplings, 3) the growth of adult trees, and 4) the resistance of all life stages of whitebark pine to blister rust. I recommend that thinning be designed as experimental trials to assess these assumptions.

6.5.5 If whitebark pine is extirpated, how will remaining tree interactions vary with abiotic stress and life stage?

In Chapters 4 and 5 I focused on interactions between subalpine fir and whitebark pine. I was only able to examine these interactions in terms of the impact of whitebark pine on the growth of subalpine fir, leaving several questions about interactions with other species unanswered. How does subalpine fir interact with its conspecifics and other species? How do these interactions vary with abiotic and climatic stress? Understanding how tree interactions vary as the species composition in these high-elevation forests changes with the probable extirpation of whitebark is important for monitoring the general resilience of high-elevation forests.

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Appendix

Table 16. Linear models for estimating the stand density of whitebark pine killed by mountain pine beetle, blister rust or *Ips* sp. (n = 16 stands). Shading indicates the models with the strongest support based on w_i . Blanks indicate variables with no relationship with the response variables. K = number of model parameters plus 1 for σ^2 , Adj. R^2 = adjusted R^2 , AIC_c = Akaike's information criterion for small samples, Diff = difference in model's AIC_c from minimum AIC_c , w = Akaike weight.

Model	Explanatory variables	K	Mountain pine beetle (u_i)				Likely blister rust (v_i)				<i>Ips pini</i> or <i>I. integer</i> (z_i)			
			Adj. R^2	AIC_c	Diff	w	Adj. R^2	AIC_c	Diff	w	Adj. R^2	AIC_c	Diff	w
1	Elevation	3	0.202	41.446	2.848	0.110	0.061	42.810	3.999	0.060	0.020	44.522	3.563	0.054
2	July_mean	3	0.067	43.949	5.351	0.031	0.269	38.811	0.000	0.441	0.059	43.876	2.916	0.075
3	Slope	3	0.012	44.852	6.254	0.020	-0.055	44.682	5.871	0.023	0.016	44.588	3.628	0.053
4	Nonveg	3	0.165	42.178	3.580	0.076	-0.059	44.746	5.935	0.023	0.065	43.779	2.819	0.079
5	Elevation + July_mean	4	0.173	44.460	5.862	0.024	0.234	42.015	3.204	0.089	0.018	47.007	6.047	0.016
6	Slope + July_mean	4	0.065	46.423	7.825	0.009	0.219	42.328	3.517	0.076	-0.002	45.530	4.570	0.033
7	Slope + Elevation	4	0.354	40.513	1.915	0.175	0.050	45.453	6.642	0.016	0.105	47.341	6.381	0.013
8	Elevation + Nonveg	4	0.427	38.598	0.000	0.457	-0.002	46.307	7.496	0.010	0.079	45.980	5.020	0.026
9	Total_pine	3	-0.047	45.804	7.206	0.012	0.013	43.621	4.810	0.040	0.216	40.960	0.000	0.323
10	Live_pine	3	-0.057	45.947	7.349	0.012	-0.056	44.688	5.877	0.023	0.101	43.153	2.193	0.108
11	Total_pine + July_mean	4	0.019	47.204	8.606	0.006	0.307	40.408	1.597	0.198	0.292	41.779	0.819	0.214
12	Live_pine * Nonveg	5	0.399	42.459	3.861	0.066	-0.159	51.723	12.912	0.001	0.085	48.957	7.997	0.006