Vegetation community characteristics and dendrochronology of whitebark pine (*Pinus albicaulis*) in the southern Coast Mountains, British Columbia

by

Kimberly Carlson
B.Sc., The College of Idaho, 2008

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Supervisory Committee

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Abstract

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Whitebark pine (*Pinus albicaulis*) is an endangered keystone tree species growing at the highest elevations in the mountain ranges of western North America. Across its range, whitebark pine is faced with a number of threats including fire suppression, mountain pine beetle, white pine blister rust, and climate change. Climate change is perhaps the greatest threat facing the species, yet it is the least understood. Most studies rely on model predictions and only look at the impacts on whitebark pine itself, not taking into consideration the other bird, mammal, and plant communities that are associated with it. In order to assess the potential effects of climate change on whitebark pine communities in the southern Coast Mountains of British Columbia, this thesis examined the vegetation associations and climate controls currently shaping the communities. My results showed that whitebark pine is growing in the open away from other subalpine tree species. This suggests that whitebark pine is not facilitating other subalpine tree species, contrary to what has been shown in the Rocky Mountains. Evidence of a distinct suite of understory vegetation associated with whitebark pine is weak and inconclusive. Differences in understory vegetation appear to be mainly due to site differences in climate, soils, and topography. Age distributions constructed from tree cores revealed that whitebark pine decline at lower elevation sites may be due to successional advancement to subalpine fir, and subalpine fir is currently encroaching into higher elevation sites. A dendrochronological assessment revealed that winter conditions, including snowpack, temperature, and the Aleutian Low Pressure Index (ALPI) were the most limiting to whitebark pine growth at high-elevation sites, but biotic factors including disease and competition appear to be more important than climate in determining annual ring growth at lower elevation sites. Bootstrapped correlations between annual ring widths and snowpack records showed that tree responses to fluctuating snowpack have changed over time. For most of the 20th century, low snowpack periods were associated with greater annual growth. Since around 1970, when the snowpack levels dropped below anything previously recorded for the area, annual tree growth has been reduced. It appears that these high elevation tree species require a balance between too much snow (shorter growing season) and too little snow (reduced protection from harsh winter conditions). Climate change models for the area predict drastically reduced snowpack in the coming decades. If snowpack continues to drop, as it has since 1970, it will likely lead to severe impacts on whitebark pine growth in the southern Coast Mountains.

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"But when the tree line is passed...the last tree seen is the whitebark pine. Ancient patriarchs, long dead, mark some ridges. For decades on end they stand erect even after life has passed. The live ones are bent, gnarled and dwarfed. Snow is not off these ridges for more than three months each year. Winters are severe, and the icy blasts that whirl across these mountains are great levelers. Only the whitebark pine survives, the one tree of our western mountains that seems to thrive on adversity."

William Douglas, 1960

Chapter 1: General Introduction

Natural History of Whitebark Pine

Whitebark pine (*Pinus albicaulis* Engelm.) is an early successional species that grows in high-elevation, cold, windy, and snowy areas with weakly developed soils. It is found in the Coast Ranges of British Columbia, the Cascade Range of Washington and Oregon, the Sierra Nevada Range of northern Nevada and California, and the Rocky Mountains from Alberta south to Wyoming. It is often the only tree species able to grow in these harsh conditions; therefore, it is considered a keystone species due to its importance as a source of food and shelter for wildlife species, including Clark's Nutcrackers (*Nucifraga columbiana* Wilson), grizzly bears (*Ursus arctos horriblilis* Ord), red squirrels (*Tamiasciurus* Trouessart spp.), Stellar's Jays (*Cyanocitta stellari* Gmelin), ravens (*Corvus* corax Linnaeus), chickadees (*Poecile* Kaup spp.), and other small birds and mammals (Hutchins and Lanner, 1982; Tomback, 1982; Lanner, 1996; Mattson and Reinhart, 1997). The relationship between whitebark pine and Clark's Nutcrackers is especially strong. Whitebark pine seeds are the nutcrackers' main food source and they create large caches of the seeds underground. Any cached seeds they do not eat later germinate (Tomback 1982). The two species have co-evolved to the point that nutcracker caching is the only reliable mechanism of germination and establishment for whitebark pine in its natural setting (Hutchins and Lanner, 1982; Lanner, 1996).

In addition to being a keystone species, whitebark pine has also been called a foundation species (Ellison et al., 2005). A foundation species is defined as a single species that shapes the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes (Dayton, 1972). At high elevations the presence of whitebark pine facilitates the growth of another subalpine tree species, subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall) in the Rocky Mountains (Callaway, 1998). It is also often the first tree species to colonize high-elevation sites, and once it becomes established it mitigates severe climate conditions so that less tolerant species including subalpine fir, limber pine (*Pinus flexilis* E. James), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) can also become established, forming tree islands (Resler and Tomback, 2008). Furthermore, whitebark pine collects and shades windblown snow, delaying snowmelt in the spring. This helps prevent erosion due to flooding and provides a reliable source of water over longer time periods to lower elevation sites (Arno and Hoff, 1989; Ellison et al., 2005).

Threats to Whitebark Pine

Whitebark pine is currently facing a number of threats across its range. These threats include fire exclusion and suppression, mountain pine beetle outbreaks, white pine blister rust infections, and climate change. The severity of these threats varies across the range of whitebark pine; different factors may be of greater importance in certain areas, and virtually nonexistent in others (see references below).

Fire Suppression

High-elevation whitebark pine communities have a natural fire return interval of approximately 50-300 years. As an early successional species, whitebark pine depends on this natural fire cycle to maintain its presence in the subalpine zone (Keane et al., 1990). Where fire exclusion and suppression are applied, whitebark pine is replaced by more shade-tolerant and less fire-resistant species such as subalpine fir and Engelmann spruce (Tomback et al., 1995; Callaway, 1998; Murray et al., 2000). Ultimately, this successional advancement can lead to widespread senescence and mortality of whitebark pine. Areas in western North America that were once a mosaic of whitebark pine communities at different seral stages are now dominated solely by subalpine fir (Murray et al., 2000). Besides this direct effect, older populations of whitebark pine are more vulnerable to blister rust infection and mountain pine beetle infestation. Older stands also have fewer suitable openings for nutcracker caching and seedling growth, and increased fuel loads leading to a greater frequency of high-intensity fires, creating a positive feedback mechanism that accelerates loss of whitebark pine cover (Arno and Hoff, 1989; Tomback et al., 1995; Lenihan et al., 2003).

Mountain Pine Beetle

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks are a natural part of forest dynamics in western North America and have caused periodic widespread mortality in both lodgepole pine and whitebark pine across the west from 1910 until the 1930s, and again from the 1970s to the 1990s in Idaho and Montana (Perkins and Swetnam, 1996; Murray et al., 2000).Mountain pine beetles are most commonly found in lodgepole pine (*Pinus contorta* Douglas ex Loudon) forests. However, during heavy infestations, or when whitebark pine stand characteristics are favorable to these beetles, they can move into adjacent whitebark pine forests (Arno and Hoff, 1989). Mountain pine beetles attack large, mature whitebark pine, primarily killing healthy trees that have inner bark that is thick enough to support the larvae (Perkins and Swetnam, 1996; Perkins and Roberts, 2003). This means that it is the larger, older trees that are hit the hardest. Since these trees produce most of the whitebark pine cones, heavy mountain pine beetle infestations can significantly diminish seed production (Keane et al., 1990). Mountain pine beetle outbreaks most commonly occur in southern portions of whitebark pine's range, especially in Idaho and Montana (Perkins and Swetnam, 1996; Murray et al., 2000), and are relatively rare in the northern portions of the species range in British Columbia (Campbell and Antos, 2000; Zeglen, 2002).

Major imbalances arise when the synchrony between the pest and host is disrupted (Logan et al., 2003). Fire suppression can increase the chance of beetle infestation because as forests increase in density, trees will become stressed from competition with subalpine fir and other late successional species and become more susceptible to mountain pine beetle outbreaks (Keane et al., 1990). Blister rust infestation can also increase the chance of beetle infestation. Trees infected with blister rust are preferentially selected by attacking beetles (Logan et al., 2010). Global climate warming will also likely affect the frequency and intensity of infestation. It has been shown that mountain pine beetles have altered their life cycles so that it is completed in just one year in response to warmer temperatures (Logan and Powell, 2001). This allows mountain pine beetles to reach much greater abundances (Logan et al., 2003), and will probably also increase spillover of outbreaks from lodgepole pine to whitebark pine, as the beetles search for a suitable food source. Mountain pine beetle outbreaks are already being reported farther north in British Columbia than have previously occurred (Logan et al., 2003). A recent study found that whitebark pine, as a naïve host, has weakly coevolved defenses to mountain pine beetle compared to lodgepole pine, the historical host (Raffa et al., 2013).

White Pine Blister Rust

The introduced white pine blister rust (*Cronartium ribicola* J. C. Fisch.) is a stem rust that infects five-needled white pines, including whitebark pine. The rust enters the pine through the needle stomata, grows into the branches and stems, erupts as spore-producing cankers that kill the branches, and eventually kills the tree itself (Patton and Johnson, 1970). Thus, white pine blister rust not only kills the trees it infects, it also effectively ends regeneration by killing the branches where cone production occurs (Tomback et al., 1995; McKinney and Tomback, 2007). Blister rust depends on currants (*Ribes* L. spp.) as an alternate host for its life cycle. Consequently, it is more prevalent in whitebark pine stands that occur where adequate moisture allows currants to grow (Arno and Hoff, 1989; Campbell and Antos, 2000). Unlike mountain pine beetle, blister rust infects all age classes of whitebark pine, not just the larger diameter classes (Arno and Hoff, 1989).

Estimates of white pine blister rust infection rates vary across whitebark pine's range. In northern Idaho, an estimated 29 percent of all new whitebark pine regeneration was infected with blister rust (Tomback et al., 1995). In the northern Rocky Mountains along the Idaho/Montana border, approximately 34 percent of all whitebark pine were infected (Resler and Tomback, 2008). In British Columbia, where the climate is generally cooler and moister (and thus more favorable to the fungus), one study estimated that 27 percent of all whitebark pine sampled was infected with blister rust (Campbell and Antos, 2000). A later study that encompassed many more stands found that the infection rate in British Columbia might actually be as high as 38 percent (Zeglen, 2002). The highest estimates come from the northern Rocky Mountains at the United States/Canada border, where 73 percent of all whitebark pine were infected with white pine blister rust (Smith et al., 2008). Most of these infections will become lethal, and in re-sampled stands in Waterton Lakes National Park, mortality increased 5 percent per year since the mid-1990s, all due to blister rust (Smith et al., 2008). Despite these high infection rates, there is some hope for whitebark pine. Early on, it was noted that even in the most severely infected stands, some trees had survived, or even completely escaped, blister rust infection. These individuals have some genetic resistance to blister rust, and efforts are currently underway to cultivate resistant seedlings in greenhouses and plant them in natural habitats (Arno and Hoff, 1989; Sniezko et al., 2011).

Climate Change

The impacts of global climate warming on whitebark pine distribution are inadequately studied and thus, poorly understood, especially in relation to the other threats facing the species. Because whitebark pine tends to grow in very open stands above the closed-canopy treeline, it is often excluded from climate change and treeline studies. Thus, future estimates of whitebark pine distributions in relation to climate warming are limited almost exclusively to model predictions and the specific climate factors controlling whitebark pine growth remain unknown. The studies have all investigated different portions of the species' range, but all the models show a decline in whitebark pine habitat and/or population size (see references below). For example, a study utilizing paleoecological records and General Circulation Models (GCMs) to estimate climate change patterns in Yellowstone National Park found that under warmer and drier conditions, there was a 90 percent decrease in available habitat for whitebark pine, and under warmer and wetter conditions, even the remaining subalpine environment became unsuitable for whitebark pine, and it became locally extinct (Romme and Turner, 1991). A more recent study modeling climate change at regional to landscape levels in Yellowstone National Park found that many high-elevation habitats were eliminated from the region, and whitebark pine was the most affected of all the conifers studied (Bartlein et al., 1997).

Increased temperatures are also expected to drive range restrictions at the northern limit of this species, despite the possibility for new habitat as temperature isolines move north. A study utilizing an ecosystem-based climate envelope modeling approach predicted that whitebark pine will lose habitat faster than it will gain new habitat, and its frequencies will decline rapidly at its current elevations (Hamann and Wang, 2006). The study predicted a 98 percent reduction in whitebark pine frequency in British Columbia by the year 2085, due to increased temperatures and increased precipitation alone. A more recent study by Wang et al. (2012a), looking at ecosystem distributions in British Columbia, estimated that alpine habitat would be reduced up to 81 percent by the 2080s, with little to no corresponding gain in new habitat.

None of these models incorporated fire suppression dynamics, mountain pine beetle outbreaks, white pine blister rust infection rates, or any of the other threats facing whitebark pine throughout its range. Taking these factors into consideration, population decreases and habitat losses will likely be even more severe than what is reported in these studies. Local extirpations are likely imminent in areas facing high instances of successional advancement, mountain pine beetle, and/or white pine blister rust (Campbell and Antos, 2000; Zeglen, 2002).

Research Questions

As the rapid decline of the tree became evident across its range over the past two decades, studies of whitebark pine increased and the species was listed as an Endangered Species in Canada in 2010 (COSEWIC, 2010). However, whitebark pine communities growing in the Coast Ranges of British Columbia remain largely unstudied. The southern Coast Mountains of British Columbia are an ideal study area for another reason. The area represents a transition between the mild, moist Maritime climate to the west and the cold, dry Continental climate to the east. This range of climatic conditions over a relatively small geographic area can serve as an analog to anthropogenic climate change, which is perhaps the greatest and least understood threat facing the species. In my MSc. research I ask the following three questions: (1) What are the spatial associations between whitebark pine and other subalpine tree species (almost exclusively subalpine fir in this area) in the southern Coast Mountains? (2) Is whitebark pine associated with different understory plant species than subalpine fir? (3) How has whitebark pine in the southern Coast Mountains responded to past variations in climate? This research is vital to our understanding of the basic vegetation composition and climate controls in whitebark pine communities in the southern Coast Mountains of British Columbia. Before we can understand the ability of these whitebark pine communities to respond to future climate change and the other threats facing it, we must first understand the biotic and abiotic controls that are currently shaping these communities, and have shaped them in the past.

Chapter 2: Tree spatial patterns and understory vegetation in whitebark pine communities of the southern Coast Mountains

Introduction

The bird and mammal communities associated with whitebark pine are well-studied and tight connections between them have been demonstrated (see Hutchins and Lanner, 1982; Tomback, 1982; Mattson and Reinhart, 1997). However, less is known about the plant communities associated with whitebark pine. If tight connections exist between whitebark pine and the understory vegetation, it will have serious implications for the future of these communities since climate change will not affect whitebark pine alone. In fact, it has been demonstrated that plant interactions are extremely important in determining the impacts of climate change (Graham and Grimm, 1990; Huntley, 1991), though they are often overlooked in favor of abiotic factors (Klanderud, 2005), and interdependence in plant communities is likely much more prevalent than current theories explain (Callaway, 1997).

Many plant interactions can be described by one of three theoretical models, first proposed by Connell and Slayter (1977) to explain the mechanisms of succession. The three models are inhibition, tolerance, and facilitation. In the inhibition model, one plant species secures space and/or resources, inhibiting the growth or colonization of other plant species (i.e. competition). The tolerance model assumes that modifications made by one species of plant neither increase nor decrease the growth and recruitment of other plant species. The facilitation model illustrates positive interactions, in which one plant species alters the environment so that it is more suitable for a different plant species.

These models have been taken from plant succession and applied to plant interactions, in general (see, for example, Callaway, 1998).

Facilitation is a widespread phenomenon among plants, occurring generally in harsher conditions such as those in deserts and alpine environments, and across all functional groups (Callaway, 1995). Positive interactions can influence seedling recruitment and species distributions (Callaway, 1992; Callaway, 1998; Maher et al., 2005), affect successional outcomes (Walker and Chapin, 1986; Berkowitz et al., 1995), ameliorate physical stress (heat/desiccation, low nutrient levels, osmotic stress, soil oxygen, soil moisture, disturbance, etc.; McClaran and Bartolome, 1989; Bertness and Shumway, 1993), increase productivity (Frost and McDougald, 1989; Callaway et al., 1991; Belsky, 1994; Lane et al., 2000) and reduce consumer pressure (Dullinger et al., 2005). Despite the important role of facilitation in community ecology, competition-centric explanations of community structure are more common (Bertness and Callaway, 1994). In reality, competition and facilitation likely operate simultaneously in a given plant community, and the overall outcome is the cumulative effect of multiple, complex interactions (Hunter and Aarssen, 1988; Callaway, 1995; Callaway and Walker, 1997; Holmgren et al., 1997; Starzomski et al., 2010).

Growing evidence suggests that competition and facilitation shift in importance as abiotic conditions change (Walker and Chapin, 1986; Bertness and Shumway, 1993; Callaway, 1998; Sthultz et al., 2007). When relatively benign abiotic conditions permit rapid resource acquisition, competition will be predominant (Bertness and Shumway, 1993). If severe abiotic conditions restrict resource acquisition, amelioration of the severe stress by a neighbor may be more likely to favor growth than competition with the neighbor would be to reduce growth (Bertness, 1991b). Bertness and Callaway (1994) hypothesized that competition and facilitation may vary inversely along gradients of abiotic stress. They predicted that facilitation would be common in communities with high abiotic stress. However, in communities where the physical habitat is relatively benign, facilitation would be rare, and competition would be the dominant force. This "stress-gradient hypothesis" was later revised to take into account life history traits (i.e. relative tolerance to stress and competitive ability) and the characteristics of the stress factor (resource vs. non-resource), so as to give a more accurate measurement of the general frequency of the shifts in interactions and not just how "common" they are (Maestre et al., 2009).

There have been a handful of tests on the effects of stress on the balance between competition and facilitation in plant communities, and the results have varied. Seedlings had increased survival under shrubs on hotter, drier slopes than on cooler, moister sites in the matorral vegetation of Chile (Fuentes et al., 1984). Similar results were seen in the coastal sand-dunes of the Netherlands, where seedling survival was higher under thickets than in the open (De Jong and Klinkhamer, 1988a). In the lower Sierra Nevada foothills of central California, tree canopy shading significantly increased grass productivity in years of below normal precipitation (Frost and McDougald, 1989). In a similar study, there was no evidence of competition between savannah trees and grasses at a low-rainfall site in Kenya, but competition was apparent at a nearby high-rainfall site (Belsky, 1994). The first direct test of the stress-gradient hypothesis (Bertness and Callaway, 1994) demonstrated that the effects of bunchgrasses on the bladderpod *Lesquerella carinata* Rollins in western Montana were competitive at a wet site in a wet year, but were facilitative at a dry site in a dry year (Greenlee and Callaway, 1996). Another study showed competition between tree species at low elevations, but facilitation at high elevations in the subalpine forests of western Montana (Callaway 1998). In global experiments of alpine and subalpine communities utilizing neighbor removal, competition was predominant in the lower stress, low-elevation sites and facilitation was predominant in the higher stress, high-elevation sites (Choler et al., 2001; Callaway et al., 2002). However, another study designed to test the stress-gradient hypothesis found that drought did not strengthen the positive or negative interactions between the forb *Cryptantha flava* (A. Nelson) Payson and the associated shrubs in eastern Utah (Casper, 1996).

The stress-gradient hypothesis has been widely demonstrated spatially over elevation gradients (see Callaway, 1998; Choler et al., 2001; Callaway et al., 2002) and temporally during years of drought (Belsky, 1994; Greenlee and Callaway, 1996), but evidence for the existence of a spatial stress-gradient along a precipitation gradient is scarce and indirect. In a precipitation stress-gradient, the limiting resource would be water availability. Drier sites would be considered more stressful for the vegetation growing there due to factors including reduced soil moisture and increased drought stress, whereas wetter sites would be considered less stressful because the vegetation growing there would always have sufficient water available. In a study from central California, grass biomass was found to be lower under tree canopy at high rainfall sites, but was higher under tree canopy at low rainfall sites (McClaran and Bartolome, 1989). In another study, grass leaf area and canopy height were found to increase with increasing rainfall along a broad precipitation gradient in the central grassland region of the United

States, suggesting increased competition for light in areas of high precipitation (Lane et al., 2000). Neither study was designed to directly test for varying competition and facilitation along a precipitation gradient, and the existence of a precipitation stress-gradient remains unknown.

My research investigated the spatial patterns and community composition within whitebark pine communities growing in the southern Coast Mountains of British Columbia. This study had two objectives. Firstly, to determine if competition and facilitation in whitebark pine communities vary inversely over a range of climatic conditions. The area of study covers a transition zone from a maritime climate in the west to a continental climate in the east. I hypothesized that competition between whitebark pine and subalpine fir would be more prevalent in the wetter, lower stress sites, which would be reflected by greater spacing between trees, but facilitation would be more common in the drier, higher stress sites, which would be reflected by closer spacing between trees. Secondly, I wished to determine if whitebark pine is associated with a different suite of plant species than subalpine fir (the dominant subalpine species in these sites). I hypothesized that whitebark pine, as a high-elevation keystone and foundation species, would be associated with particular plant species that are not associated with subalpine fir. Studying plant interactions over a range of climatic conditions can act as an analog for anthropogenic climate change by showing how plant communities currently differ at wetter or drier sites within a region. This will have the added benefit of supplying managers with an indication of how natural whitebark pine communities in the southern Coast Mountains will respond to anthropogenic climate change, as opposed to the mainly model predictions that are available now.

Methods

Study Area

Field work was conducted at four sites in the southern Coast Mountains of British Columbia (Figure 2.1) during July and August of 2011 and 2012. A particularly large snowpack prior to (and during) the 2011 field season led to a much shorter than normal timeframe in which to collect data, so each site was revisited in July and August of 2012. The area of study covers the transition from the coastal maritime climate to the interior continental climate. The western end of the study area, Pemberton, BC (50.317^{o}N, 122.797^{o}W) receives an annual average precipitation of 955 mm. Lillooet (50.686^{o}N, 121.936^{o}W), at the drier, eastern end of the study area, receives an annual average precipitation of only 330 mm (Environment Canada, 2012).

Due to the patchy distribution of whitebark pine, a randomized design was not feasible. Therefore, study sites were chosen solely by where healthy, mature stands of whitebark pine occur. Personal communication with fellow whitebark pine researchers and people familiar with the area supplied a number of potential sites (pers. comm. with Sierra Curtis-McLane, whitebark pine researcher; Carmen Wong, whitebark pine researcher; Scott Aitken, avalanche technician; John Tisdale, BC Parks; Yvonne Patterson, grizzly bear researcher), which were visited during the 2011 field season. A number of these sites were unsuitable for my study for various reasons including poor tree health, too few trees, dominance by krummholz trees, or location within Provincial Park boundaries. In the end 4 sites were chosen and revisited during the 2012 field season.

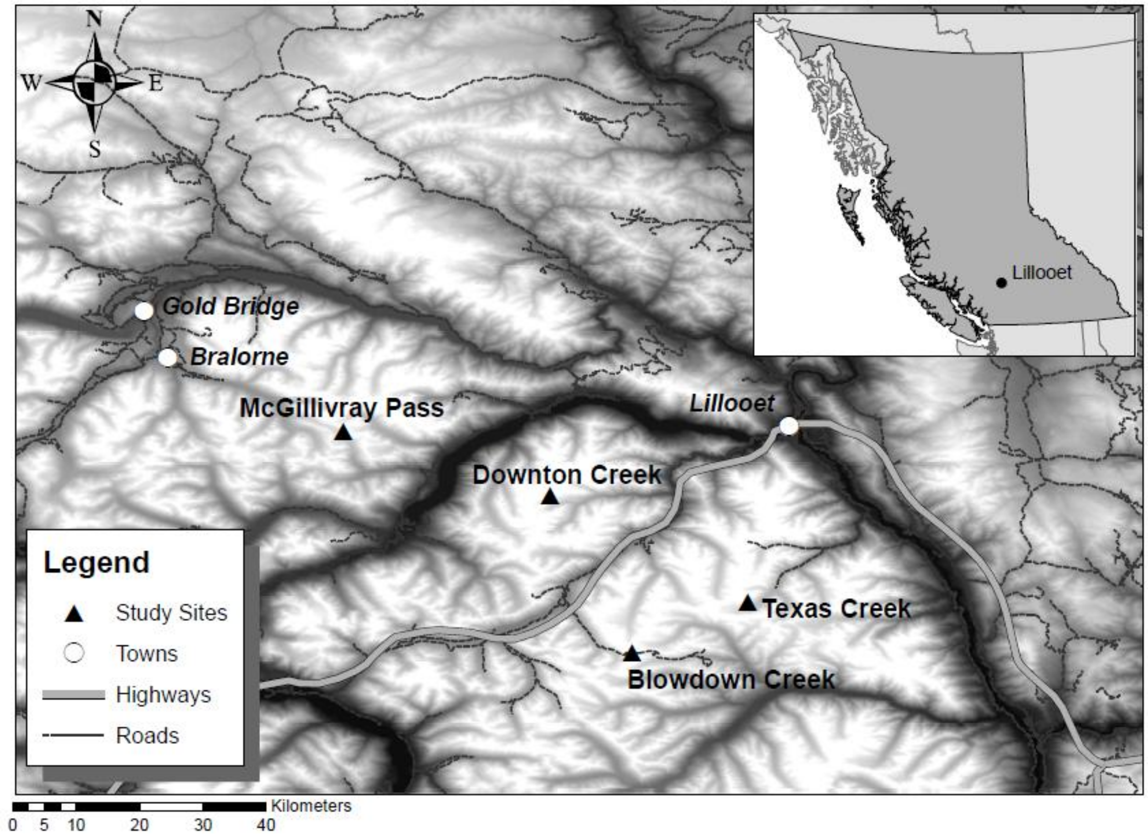

Figure 2.1**.** Location of the four high-elevation, open canopy study sites in the southern Coast Mountains of British Columbia. Lighter areas are mountain tops and darker areas are rivers and valley bottoms. Inset map shows the location of Lillooet in British Columbia.

At each site a mixed stand was chosen (whitebark pine with other subalpine species: subalpine fir and occasionally Engelmann spruce) for sampling. All four stands were open canopy forests at approximately 2000-2100 m elevation. Mean annual precipitation and mean annual temperature for each site were determined using the 1961-1990 climate normals from the ClimateWNA model (Wang et al. 2012b). Aspect, elevation, and slope of each stand were recorded onsite (Table 2.1).

Table 2.1. Study site locations and characteristics. Mean annual precipitation (MAP) and mean annual temperature (MAT) come from the ClimateWNA 1961-1990 climate normals. Data for Lillooet, BC is from Environment Canada 1971-2000 climate normals (1961-1990 climate normals are not available for Lillooet).

Site	Location	MAP (mm)	MAT(^{o}C)	Elevation (m)	Aspect (^{o})	Slope (%)
Lillooet, BC	50.6864^{o}N, 121.9364^{o}W	330	9.2	250	--	--
Blowdown Pass	50.3656^{o}N, 122.1591^{o}W	1672	0.2	2105	202	70
Downton Creek	50.5881^{o}N, 122.2749^{o}W	1125	-0.4	2104	194	50
McGillivray Pass	50.6796^{o}N, 122.5681^{o}W	1167	0.3	1963	200	75
Texas Creek	50.4358^{o}N, 121.9950^{o}W	1297	-0.2	2115	158	60

Tree Community Spatial Patterns

To quantify the spatial patterns of trees in each stand, I used the point-centered quarter method (Cottam et al., 1953; Cottam and Curtis, 1956). This method was chosen because a previous study had found that new trees often grew on the leeward side of already established trees (usually whitebark pine) in the Rocky Mountains (Resler and Tomback, 2008), and I wanted to see if the same pattern occurred in the Coast Mountains. Seven healthy, upright whitebark pine trees from each stand were selected for center points using random bearings and paces generated from a random number table. The area around these trees was divided into four quadrants along the four cardinal directions. In each quadrant, the distance from the center tree to the nearest non-whitebark pine tree species (almost always subalpine fir, but occasionally Engelmann spruce; “interspecific”) was recorded. The process was repeated, measuring the distances from 7 whitebark center trees to the nearest whitebark pine in each quadrant, and the distances from 7 subalpine fir center trees to the nearest subalpine fir in each quadrant (“intraspecific”). Subalpine fir center trees were chosen using different sets of random bearings and paces, which meant that they were not necessarily the same ones used for the interspecific portion. To establish “controls” 7 random points were placed on the ground instead of at a tree. These locations were determined by additional random bearings and paces. The distances from these 7 randomly generated center points to the nearest tree in each quadrant were also measured (“control”). Trees with a multi-stem growth form (which is common in whitebark pine) were treated as single trees, and the largest diameter stem was used for purposes of measuring distances. A total of 112 distances were recorded at each stand (7 center points x 4 quadrants x 4 “treatments”: interspecific, whitebark intraspecific, subalpine intraspecific, control).

In addition to measuring the distances to trees in each quadrant, each of the trees used in the point-centered quarter method at each stand also had their diameter at breast height (dbh), height, and reproductive output measured. Diameters were measured using logger’s tape and heights were measured using a Nikon Forestry 550 hypsometer. Reproductive output was determined by counting the number of cones per tree. The largest stem from any multi-stem whitebark pine cluster was used to measure dbh and collect a core, but the entire tree cluster was used to determine the reproductive output. Due to the timing of the field season, cones were not yet ripe at the time of sampling and could not be collected.

To determine stand age structures and produce tree ring chronologies for each site (Chapter 3), all trees used in the point-centered quarter method were also cored. One core per tree was taken at breast height using a 5.2 mm Hagloff increment borer. Cores were stored in drinking straws and allowed to dry before being processed in the lab. See Chapter 3 for more details on dendrochronological procedures.

Understory Vegetation

At each stand, understory vegetation was sampled under five mature whitebark pine trees and under five mature subalpine fir trees. I used targeted sampling to select the trees for this portion of the sampling because I wanted to use only trees that did not have canopies that overlapped with other trees. Four transects were set up at each tree, extending from the trunk of the tree out towards the canopy edge in each of the four cardinal directions. On each transect, a 1 m^2 frame was placed every meter, starting directly adjacent to the tree trunk and extending 3 m away from the tree. The distance of 3 m was chosen because a pilot study during the 2011 field season revealed that differences in understory vegetation were most apparent directly beneath a tree's canopy and quickly became less evident away from the tree canopy in the open. The trees at these sites are relatively small and their canopies often extend only about 1-2 m from their trunks. Measuring the vegetation every meter for three consecutive meters allowed me to capture the abrupt change that occurred from under the canopy into the open environment.

In each quadrant the percent cover of all species falling within each frame was visually estimated, including shrub or tree canopy cover over the plot. Trees falling within plots were categorized by their height. Seedlings (up to 15 cm tall) were considered ground cover, saplings (15-199 cm tall) were considered mid-canopy, and trees (2 m tall or more) were considered canopy (PPS Arctic Group, 2008). Ground cover was also recorded (i.e. bare ground, litter, rock, wood, moss, and lichen). Percent cover was always measured by the same person to increase consistency and reduce error. The order of site visitation followed snowmelt timing, so that all sites were in roughly the same stage of phenology during sampling. All of the vegetation data were collected in the 2012 field season.

Statistical Analysis

To test for differences in neighbor distances between trees I used a nested ANOVA design with two factor levels: “site” and “species” (whitebark-whitebark, subalpine-subalpine, whitebark-subalpine, control). Quadrant distances from each site were pooled and tested the same way. Tukey HSD tests were used to test for post hoc mean differences. The distance data were noticeably left-skewed (more shorter distances than longer distances), so data were square root transformed prior to analyses. All tests were carried out using R software version 2.13.2 (R Development Core Team, 2011).

Differences in understory vegetation were tested using non-metric multidimensional scaling (nMDS) and two-way nested analysis of similarities (ANOSIM; factors: “site” and “species”). Non-metric multidimensional scaling used 50 random restarts and a minimum stress of 0.01 with Kruskal fit scheme 1. Prior to analyses, data were square root transformed and Bray-Curtis similarities between samples were calculated. Following analyses, similarity percentages (SIMPER) were used to determine which species most influenced the observed patterns. An initial run revealed that site differences in ground cover (i.e. % bare ground, % rock, % wood, % moss, % lichen, % litter) and canopy variables (i.e. cover from trees greater than 2 m tall) were heavily influencing the observed vegetation differences. Since I was most interested in the differences in vegetation growing beneath each tree species, I removed these variables from further analyses in order to downplay the site differences and highlight the species differences. “Mid-canopy” variables (i.e. tree saplings 15-199 cm tall) consisted almost entirely of subalpine fir saplings (there was only one instance of whitebark pine mid-canopy cover). An initial SIMPER revealed that the mid-canopy cover was overwhelming the vegetation differences because their percent cover was so much higher than what was observed for a typical forb or grass. Because of this, the mid-canopy variables were also removed from further analysis. A separate nMDS analysis was run on all abiotic variables (ground cover, mid-canopy and canopy cover) to distinguish differences between sites and canopy species. All analyses were performed using Primer version 6.1.13 (PRIMER-E, 2009). Differences between important canopy and ground cover variables were examined using Mann-Whitney U-tests in R (R Development Core Team, 2011).

A species abundance curve of the plot data revealed that there were a large number of species that only occurred in a small number of plots (Figure 2.2). The species were ranked according to how many of the 480 total plots they were found in, and then subdivided into categories based on the trajectory of the resulting curve. The 40 species that occurred in fewer than 12 plots were considered “rare,” the 50 species that occurred in fewer than 85 plots were considered “sub-dominant,” and the 20 species that occurred in 85 plots or more were considered "dominant" (Appendix I). To determine what effect, if any, the large number of rare species had in driving the vegetation patterns observed, separate nMDS, ANOSIM, and SIMPER analyses were run on the vegetation data with the 40 "rare" species removed.

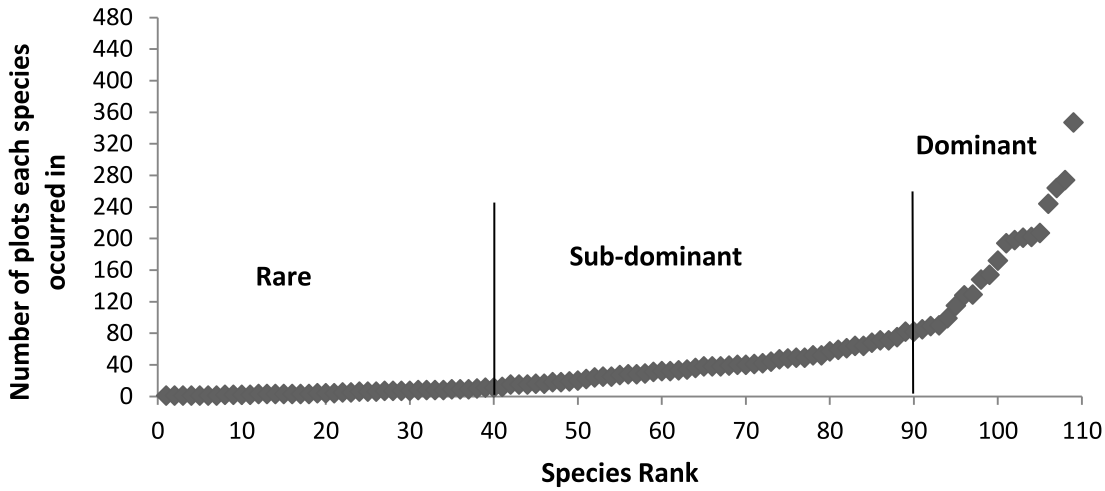

Figure 2.2. Species abundance curve created from vegetation plot data. Species are ranked by how many of the 480 total plots they appeared in and then subdivided into categories based on the trajectory of the curve. The 40 species occurring in fewer than 12 plots are considered rare. The 50 species occurring in fewer than 85 plots are considered sub-dominant. The 20 species occurring in 85 or more plots are considered dominant.

Results

Tree Community Spatial Patterns

Tree spacing differed significantly, both among sites (ANOVA; n=28, df=3, F= 12.1931, p<<0.001) and species (n=28, df=3, F=58.9879, p<<0.001), as well as the site:species interaction (df=9, F=2.5347, p=0.007677). Post hoc Tukey HSD tests revealed that the distances between trees, over all categories, were significantly larger at both Texas Creek and McGillivray Pass and significantly lower at Downton Creek and

Blowdown Pass (Figure 2.3). The distances between trees were not significantly different between Texas Creek and McGillivray Pass or between Downton Creek and Blowdown Pass.

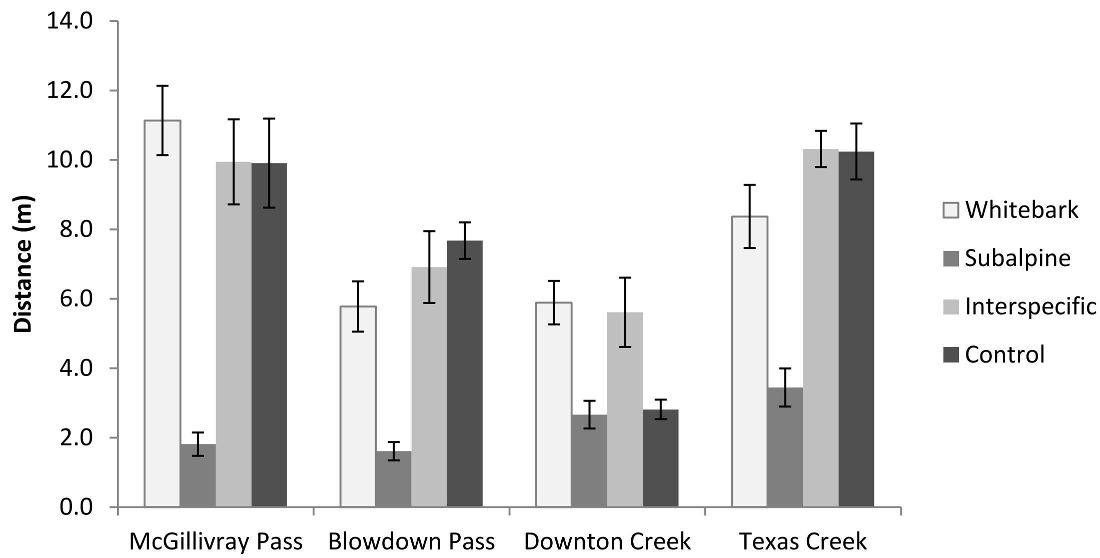

Figure 2.3. Distance between center point trees and their nearest neighbors pooled over all quadrants. “Whitebark” and “Subalpine” refer to the distance from a center tree of that species to its nearest intraspecific neighbors. “Interspecific” refers to the distance between a center whitebark pine and the nearest subalpine fir and “Control” refers to the distance between a random non-tree center point and the nearest subalpine fir. Error bars are ±1 standard error of the mean.

At the species level, the Tukey HSD tests revealed that distances between whitebark pine and other whitebark pine did not differ significantly from the distances between whitebark pine and subalpine fir (interspecific) or the distances between random points and subalpine fir (control). However, the distances between subalpine fir and other subalpine fir were significantly shorter than the whitebark pine distances, the interspecific distances, and the control distances (Figure 2.3). This pattern was observed at three of the four sites, even though the overall spacing between trees varied by site. The only exception to the pattern was at Downton Creek, where the mean intraspecific subalpine fir distance did not differ from the mean control distance, but were almost significantly smaller than the mean intraspecific whitebark distance (p=0.052) and the mean interspecific distance (p=0.052).

The dbh, height, and number of cones per tree varied per site as well (Table 2.2). Dbh was greater in whitebark pine than in subalpine fir. The trees with the greatest dbh for both species occurred at McGillivray Pass and the trees with the smallest dbh for both species occurred at Blowdown Pass. In general, subalpine fir were taller than the whitebark pine at each site, other than at Texas Creek, where the whitebark pine were slightly taller than the subalpine fir. There were substantially fewer cones per tree in whitebark pine than in subalpine fir at each site. The whitebark pine at McGillivray Pass had virtually no cones for the 2012 season. The other three sites all averaged 3 cones per tree. The subalpine fir at Texas Creek and Downton Creek averaged the fewest cones per tree (10 and 11, respectively). The subalpine fir at McGillivray Pass averaged the most cones per tree, with 38.

Table 2.2. Average dbh, height, and number of cones per tree for each species at each site. Numbers are mean±SD.

	Downton Creek		**Blowdown Pass**		**McGillivray Pass**		**Texas Creek**	
	Whitebark pine	Subalpine fir	Whitebark pine	Subalpine fir	Whitebark pine	Subalpine fir	Whitebark pine	Subalpine fir
dbh (cm)	16.1±9.4	13.5±10.1	11.3±5.8	9.3±3.2	19.2±11.3	15.4±7.1	17.9±8.9	11.4±5.9
Height (m)	5.1±2.2	6.5±2.9	4.5±2.0	4.9±1.5	5.5±2.8	7.0±3.6	5.2±2.2	4.8±1.9
No. cones	3±6	11±13	3±4	23±31	0±1	38±36	3±5	10±11

When distances were pooled by quadrant across all sites, there were no significant differences between the distances between center trees and their nearest neighbors in any of the quadrants (ANOVA; n=28, df=3, F=1.5307, p=0.2059; Figure 2.4). The pooled dbh, height, and number of cones per tree did not vary by quadrant either (Table 2.3). The center trees for both species had greater dbh, were taller, and had more cones than any of the quadrant trees, but this is an artifact of the sampling, since trees deemed to be the most visually mature were targeted for use as center trees.

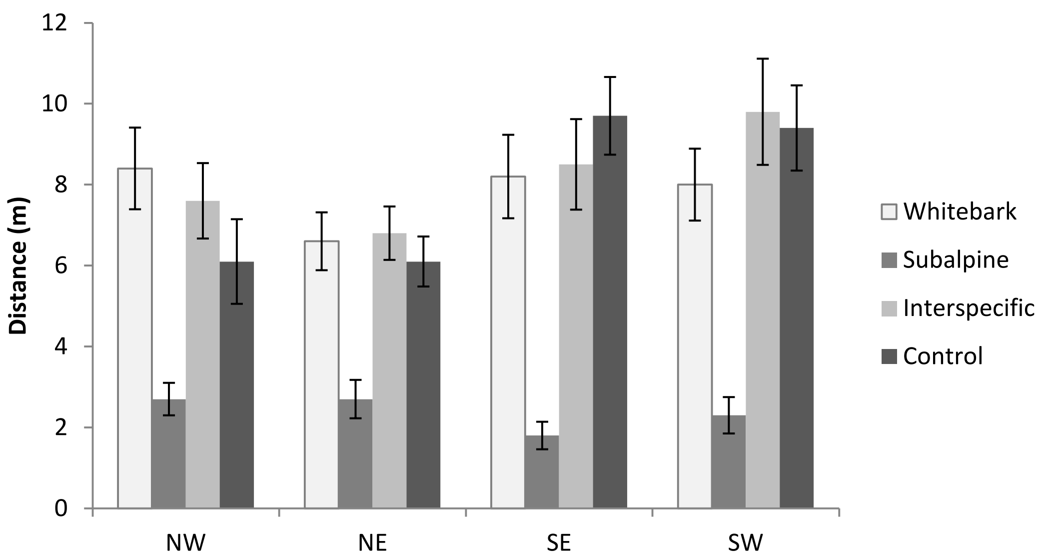

Figure 2.4. Distances between trees pooled by quadrant across all sites revealed no directional patterns in the spacing of nearest neighbors around center trees for any of the categories. “Whitebark” and “Subalpine” refer to the distance from a center tree of that species and its nearest intraspecific neighbors. “Interspecific” refers to the distance between a center whitebark pine and the nearest subalpine fir and “Control” refers to the distance between a random center point and the nearest subalpine fir. Error bars are ±1 standard error of the mean.

Table 2.3. Quadrant differences in the average dbh, height, and number of cones per tree for all sites pooled. Numbers are mean±SD.

	Whitebark pine					Subalpine fir				
	NW	NE	SE	SW	Center	NW	NE	SE	SW	Center
dbh (cm)	13.0±8.0	16.8±11.8	14.3±9.4	17.0±9.2	19.5±7.5	11.6±8.2	9.2±5.9	13.2±8.1	11.4±5.2	16.7±6.7
Height (m)	4.2±2.3	5.0±2.7	4.7±2.3	5.1±2.2	6.2±1.7	5.4±3.4	4.9±2.8	5.7±2.4	5.8±2.3	7.2±2.3
No. cones	2±3	3±7	2±4	1±1	5±5	16±30	12±16	14±17	25±34	37±29

Understory Vegetation

Understory vegetation differed significantly at each site (two-way nested ANOSIM; global R=0.833, p=0.01; Figure 2.5). The understory vegetation was also statistically different beneath each tree species (R=0.128, p=0.001); however, the observed global R value was very low and may have been the result of the large sample size (Clarke and Warwick, 2001). The vegetation growing beneath whitebark pine and subalpine fir did not differ in any of the plots, either adjacent to the trunks (plot 1: R=0.035, p=0.004, Note: low global R value), or more than one meter away from the tree trunk (plot 2: R=0.015, p=0.056; plot 3: R=0.011, p=0.079). When the “rare” species were removed the results of the ANOSIM were virtually the same at the site (R=0.833, p=0.01) and species level (R=0.127, p=0.001), suggesting that the rare species are not driving the observed patterns between each canopy species at each site.

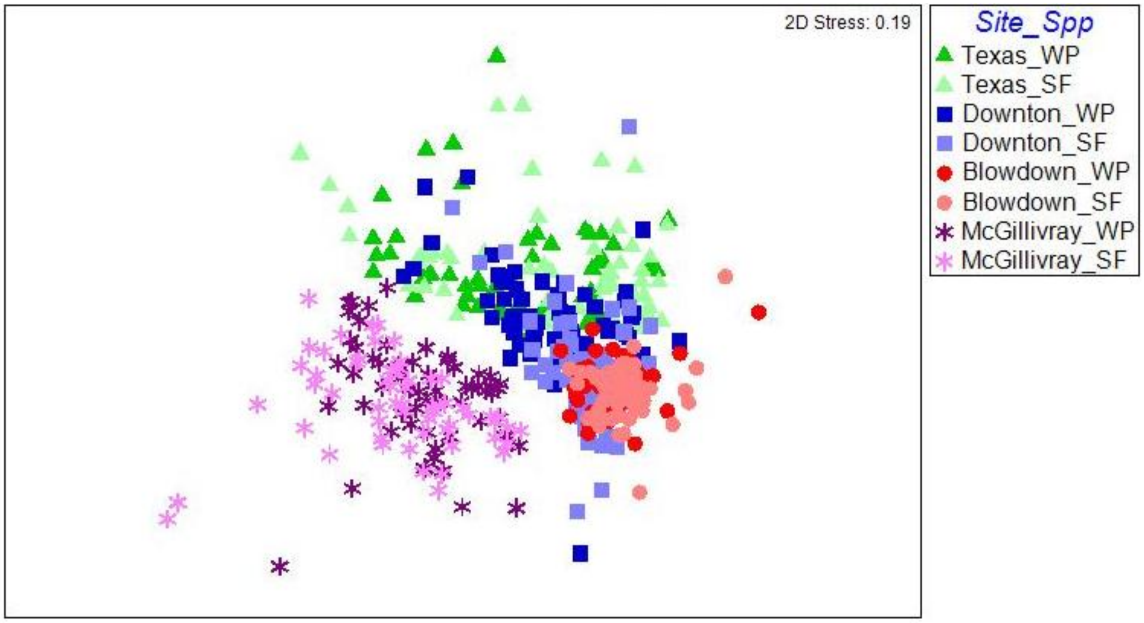

Figure 2.5. nMDS of vegetation plots across all sites. Each point represents one 1 m^2 plot and points are grouped based on similarities in the vegetation they contained. ANOSIM revealed significant differences in the vegetation at each site (R=0.833, p=0.01), but vegetation beneath each canopy species showed only weak evidence of differentiation (R=0.128, p=0.001).

The SIMPER results also showed that the dominant species contributed most to the observed similarities between all of the vegetation plots at both the site and species level (Appendix II). At the site level, differences in the cover of *Phlox diffusa* Benth., *Epilobium angustifolium* L., and *Artemisia norvegica* Fr. contributed the most to the differences in understory vegetation observed between Blowdown Pass, Downton Creek, and Texas Creek. However, the greater abundance of species like *Thalictrum occidentale* A. Gray and *Viola glabella* Nutt. at McGillivray Pass contributed the most to the observed differences in understory vegetation between McGillivray Pass and the other three sites (Appendix II).

At the species level, the number of species contributing to the observed differences between the vegetation associated with whitebark pine and subalpine fir at each site was generally high. A range of 25-29 species accounted for 90% of the dissimilarities between whitebark pine and subalpine fir understory vegetation at all sites. The top ten understory species that most contributed to the dissimilarities between whitebark pine and subalpine fir at each site are shown in Table 2.4.

Table 2.4. SIMPER results showing the top ten understory species that contributed to the dissimilarities observed between whitebark pine plant communities and subalpine fir plant communities at each site. Cumulative contributing percentage is the cumulative percentage of each understory species' contribution to the observed dissimilarities.

Site	Understory Species	Average % Cover per plot under Whitebark pine	Average % Cover per plot under Subalpine fir	Cumulative Contributing Percentage (%)
Texas Creek	*Phlox diffusa*	1.37	1.23	6.79
	Thalictrum occidentalis	1.34	0.54	13.50
	Lupinus arcticus	1.21	0.92	19.72
	Epilobium angusitfolium	0.73	0.77	24.97
	Arnica cordifolia	0.58	0.50	29.79
	Poa cusickii spp. pallida	0.99	0.54	34.58
	Vaccinium scoparium	0	1.03	39.36
	Arenaria capillaris	0.88	0.68	43.94
	Senecio integerrimus	0.63	0.76	48.25
	Erigeron peregrinus	0.64	0.69	52.45
Downton Creek	*Phlox diffusa*	2.13	2.96	7.19
	Artemisia norvegica	0.71	2.07	14.23
	Epilobium angustifolium	1.75	0.68	20.52
	Juniperus communis	1.27	0.72	26.53
	Fragaria virginiana	1.34	0.44	31.68
	Vaccinium caespitosum	0	1.19	36.48
	Solidago multiradiata	0.81	0.94	41.01
	Arctostaphylos uva-ursi	1.14	0.16	45.24
	Erigeron peregrinus	0.5	1.03	49.12
	Arenaria capillaris	0.9	0.95	52.77
Blowdown Pass	*Vacciniuim membranaceum*	0.75	0.92	7.08
	Artemisia norvegica	1.94	2.26	13.75
	Phlox diffusa	2.68	2.43	20.26
	Erigeron peregrinus	1.08	0.88	26.01
	Arnica mollis	0.97	1.05	31.36
	Lupinus arcticus	0.92	0.15	36.59
	Anemone occidentalis	0.28	0.85	41.74
	Silene douglasii	1.06	0.82	46.61
	Carex rossii	0.85	1.07	51.46
	Senecio integerrimus	0.74	1.12	56.03
McGillivray Pass	*Thalictrum occidentalis*	2.73	2.45	9.04
	Viola glabella	1.10	1.81	15.80
	Lupinus arcticus	1.84	1.32	22.54
	Aquilegia formosa	1.22	0.82	27.71
	Artemisia norvegica	1.13	0.99	32.85
	Heracleum maculatum	1.00	1.11	37.91
	Aster foliaceous	1.32	1.70	42.96
	Epilobium angustifolium	1.35	1.00	47.92
	Phlox diffusa	1.11	0.74	52.72
	Silene douglasii	1.08	1.25	57.33

The species contributing most to the observed differences in community composition between each tree species were separated into two groups based on whether their average abundance was greater beneath whitebark pine or beneath subalpine fir (Table 2.5). Of all the species with greater abundances beneath whitebark pine, none were present at all four sites. *Epilobium angustifolium*, *Poa cusickii* Vasey (two varieties), *Lupinus arcticus* S. Watson, and *Trisetum spicatum* (L.) K. Richt. all had relatively high abundances beneath whitebark pine at three of the four sites. *Arnica parryii* A. Gray, *Aster modestus* Lindl., *Achillea millefolium* L., *Cerastium arvense* L., *Frageria virginiana* Duchesne, *Arctostaphylos uva-ursi* (L.) Spreng., and *Solidago multiradiata* Aiton all had relatively higher abundances under whitebark pine at two of the four sites. *Thalictrum occidentale* and *Phlox diffusa* had higher abundances under whitebark pine at two sites, but had higher abundance under subalpine fir at another site. None of the species with the higher relative abundances beneath subalpine fir from the SIMPER analysis were common at all four sites, or at three of the four sites. *Valeriana sitchensis* Bong., *Arnica mollis* Hook., and *Anemone occidentalis* S. Watson all had higher relative abundances under subalpine fir than under whitebark pine at two of the four sites. *Artemisia norvegica*, *Arenaria capillaris* Poir., and *Castilleja miniata* Douglas ex Hook. had higher cover beneath subalpine fir at two sites, but were higher under whitebark pine at another site.

Table 2.5. Species more often associated with either whitebark pine or subalpine fir at each site based on their relative average abundances from the SIMPER analysis. Only species that were more abundant beneath one of the tree species at more than one site are included. Numbers are the number of sites at which the species was more common under one tree, followed by the sites in parentheses. B=Blowdown Pass, D= Downton Creek, M=McGillivray Pass, and T=Texas Creek.

	More Frequent beneath:	
Species:	Subalpine fir	Whitebark pine
Achillea millefolium		2 (D, T)
Anemone occidentalis	2 (B, D)	
Arctostaphylos uva-ursi		2 (D, T)
Arenaria capillaris	2 (B, D)	1 (T)
Arnica mollis	2 (B, D)	
Arnica parryi		2 (M, T)
Artemisia norvegica	2 (B, D)	1 (M)
Aster modestus		2 (M, T)
Castilleja miniata	2 (B, M)	1 (T)
Cerastium arvense		2 (D, T)
Epilobium angustifolium		3 (D, M, T)
Fragaria virginiana		2 (D, T)
Lupinus arcticus		3 (B, M, T)
Phlox diffusa	1 (D)	2 (M, T)
Poa cusickii		3 (B, M, T)
Solidago multiradiata		2 (B, D)
Thalictrum occidentale	1 (M)	2 (D, T)
Trisetum spicatum		3 (B, D, T)
Valeriana sitchensis	2 (D, M)	

When the vegetation was analyzed by quadrant or by transect at each site, the ANOSIM revealed no significant patterns across all sites or between all whitebark pine and all subalpine fir. However, there were some statistically significant differences between the quadrants and transects at certain sites or with either whitebark pine or subalpine fir (Table 2.6). At Blowdown Pass beneath whitebark pine, quadrant 1 (adjacent to tree trunk) had significantly different vegetation than quadrant 3 (furthest from tree; R=0.076, p=0.015). At Downton Creek beneath whitebark pine, quadrant 1 was also significantly different than the vegetation in quadrant 3 (R=0.069, p=0.026). In addition, beneath whitebark pine, the vegetation differed significantly on the east and west transects ($R=0.092$, $p=0.038$) and the south and west transects ($R=0.09$, $p=0.03$). At McGillivray Pass, the vegetation differed significantly between the north and south transects beneath whitebark pine ($R=0.186$, $p=0.006$). Beneath subalpine fir the vegetation differed significantly between the north and south transects ($R=0.411$, $p=0.001$), the east and south transects ($R=0.232$, $p=0.003$), and the south and west transects ($R=0.327$, $p=0.002$). At Texas Creek, the vegetation in quadrant 1 differed significantly from the vegetation in quadrant 3 beneath subalpine fir ($R=0.082$, $p=0.031$). Again, nearly all of these differences showed low global R values, suggesting the statistical significance may be the result of the large sample size and not true differentiation in the vegetation communities (Clarke and Warwick, 2001).

Table 2.6. ANOSIM results revealed that there were no overall patterns in the vegetation in each quadrant (1=adjacent to tree trunk, 3=furthest from tree trunk) and transect (N=North, E=East, S=South, W=West) between the two different tree species at each site, and with all sites pooled. Any statistically significant (p<0.05) pairwise comparisons are also listed. * =p<0.05, ** =p<0.01, *** =p<0.001.

Site	Variable	Whitebark pine	Subalpine fir
Blowdown Pass	Transect	R=-0.016, p=0.737	R=0.02, p=0.158
	Quadrant	R=0.023, p=0.151	R=-0.021, p=0.853
		1,3 R=0.076, p=0.015*	
Downton Creek	Transect	R=0.033, p=0088	R=-0.02, p=0.823
		E,W R=0.092, p=0.038* S,W R=0.09, p=0.03*	
	Quad	R=0.022, p=0.153	R=0.011, p=0.273
		1,3 R=0.069, p=0.026*	
McGillivray Pass	Transect	R=0.05, p=0.04*	R=0.155, p=0.001**
		N,S R=0.186, p=0.006**	N,S R=0.411, p=0.001*** E,S R=0.232, p=0.003** S,W R=0.327, p=0.002**
	Quad	R=0.011, p=0.282	R=-0.028, p=0.913
Texas Creek	Transect	R=0.024, p=0.174	R=-0.015, p=0.678
	Quad	R=-0.013, p=0.699	R=0.011, p=0.27
			1,3 R=0.082, p=0.031*
All Sites	Transect	R=-0.002, p=0.592	R=0.008, p=0.131
			N,S R=0.025, p=0.035* S,W R=0.025, p=0.031*
	Quad	R=0.011, p=0.049*	R=0.001, p=0.381
		1,3 R=0.035, p=0.005**	

There was little evidence to support site and species differences in the cover of the abiotic variables (ANOSIM; site: $R=0.189$, $p=0.001$; species: $R=0.058$, $p=0.001$). Despite the statistical significance, the low global R values again suggest that the groupings are essentially indistinguishable (Clarke and Warwick, 2001). There was a significant difference between the abiotic variables and the distance from the tree, as measured by the quadrant number ($R=0.272$, $p=0.001$). In all cases, the SIMPER revealed the differences were due mainly to canopy cover and litter. Canopy cover and litter were greatest in the plots adjacent to the trees, and lessened further away from the trunk. The Mann-Whitney U-tests of the differences between the canopy cover of each species revealed that the canopy cover of whitebark pine did not differ from the canopy cover of subalpine fir over plot 1 (adjacent to the trunk; $n=80$, $W=3356$, $p=0.5951$), but whitebark pine had significantly greater canopy cover than subalpine fir moving away from the tree trunk (plot 2: $n=80$, $W=1973.5$, $p<<0.001$; plot 3: $n=80$, $W=2618$, $p<<0.001$; Figure 2.6). Litter did not differ between the species in any of the plots (plot 1: $n=80$, $W=3055.5$, $p=0.623$; plot 2: $n=80$, $W=3175.5$, $p=0.935$; plot 3: $n=80$, $W=3474.5$, $p=0.350$).

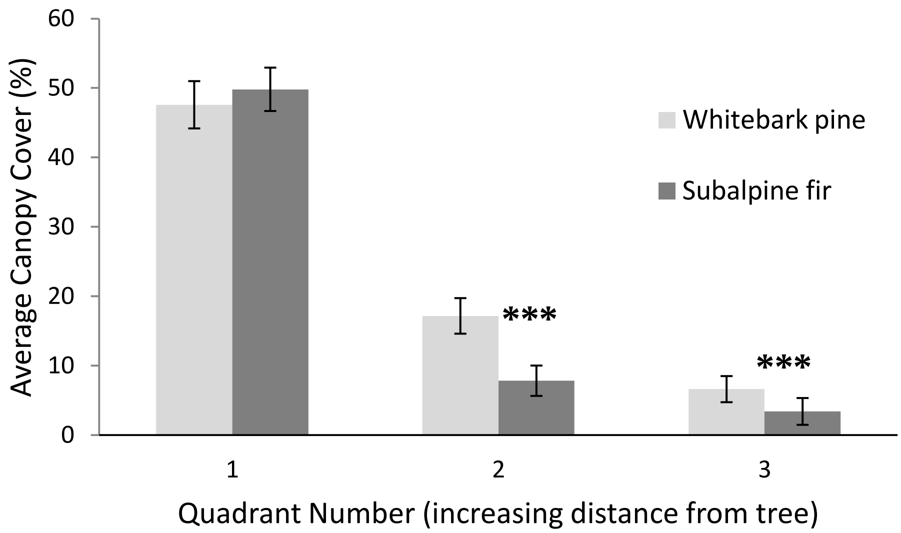

Figure 2.6. Average percent cover of the tree canopy over each quadrant. The canopy cover of each species did not differ over quadrant 1 (directly adjacent to the trunk; Mann Whitney, p=0.5951), but did differ over quadrant 2 (1 m from trunk; p<<0.001) and quadrant 3 (2 m from trunk; p<<0.001). Error bars are ±1 standard error of the mean.

Discussion

Tree Community Spatial Patterns

My results provide no evidence that whitebark pine is facilitating subalpine fir in the southern Coast Mountains, contrary to the strong facilitative effect of whitebark pine on subalpine fir seen in the Rocky Mountains (Callaway, 1998; Resler and Tomback, 2008). The distances between whitebark pine and subalpine fir, and between whitebark pine and other whitebark pine, did not differ from the control distances, suggesting whitebark pine has no effect—facilitative or competitive—on other subalpine trees in the Coast Mountains. The absence of facilitation observed for the whitebark pine in this study, when such a strong facilitative effect has been observed in other studies, could be due to the study area. In the study by Callaway (1998), the strong facilitative effect of whitebark pine on subalpine fir was attributed to a high-stress environment (i.e. temperature extremes, low soil moisture). The Coast Mountains receive much higher annual precipitation and have a milder climate than the Rocky Mountains. It is possible that the conditions in the southern Coast Mountains never become stressful enough to make it beneficial for whitebark pine and subalpine fir to grow closely together, compared to the conditions at the eastern end of whitebark pine distribution in the Rocky Mountains. Also, whitebark pine is only a minor constituent in open timberline habitats in the Coast Mountains compared to its relative abundance in the Rocky Mountains (Arno and Weaver, 1990), which could contribute to it playing a lesser role in treeline dynamics.

The subalpine fir in my sites are growing together in tight clumps of "tree islands." Close distances between trees could provide evidence of facilitation (Callaway, 1998), or it may simply reflect dispersal patterns. The only reliable mechanism for the establishment of whitebark pine is the germination of seeds cached by Clark's Nutcrackers, and the birds often cache the seeds in the open away from other trees (Hutchins and Lanner, 1982; Tomback, 1982). Subalpine fir seeds, on the other hand, are passively dispersed by gravity or wind. This could lead to increased establishment of fir seedlings beneath or near the parent tree, which could also explain the clusters of fir trees I observed. However, dispersal patterns still cannot explain why the whitebark pine in my study area are not growing in tree islands with subalpine fir, as has been shown in the Rocky Mountains. Other possibilities for the observed tree spatial patterns could simply include environmental heterogeneity and microsite conditions in the stands, including the amount and distribution of rocks or soil conditions favorable to seedling germination and establishment (Holtmeier and Broll, 2005).

The only site where subalpine fir was not distinctly clustered was Downton Creek. At Downton Creek the subalpine fir distances did not differ from the control distances, and were only marginally different from the intraspecific whitebark distances or the interspecific distances. This suggests a more uniform spacing of all trees throughout the stand than what was observed at the other three sites. Downton Creek also had some unique site features that could explain the difference in the tree spatial patterns. The stand was bordered below by a wet meadow and above by an old rock slide. Both features may have limited tree establishment to a smaller area and caused the trees to grow more uniformly spaced than what was seen at the other three sites.

One of my original hypotheses was that the spacing of trees would vary over a precipitation gradient, with trees growing closer together (facilitation) at the drier, more stressful sites, and trees growing further apart (competition) at the wetter, less stressful sites. The driest site, Downton Creek, did have the most tightly spaced trees; however, the tree spacing at Downton Creek did not differ significantly from the spacing of the trees at Blowdown Pass, the wettest site. The intermediate sites, McGillivray Pass and Texas Creek, had significantly larger distance between trees, so the amount of precipitation a site receives seems to have no effect on the tree spatial patterns observed at each site. None of the environmental factors collected (aspect, slope, elevation, stand age) and none of the climate variables from ClimateWNA (mean annual precipitation, mean annual temperature, precipitation as snow, etc.) can account for the observed pattern. It could be that my sites do not vary enough with respect to their annual precipitation. The driest and wettest sites differ by about 500 mm of annual precipitation. I originally planned to sample trees at additional sites growing under even wetter conditions west of the study area, but the larger-than-normal snowpack meant that these sites were under snow and inaccessible even in late August. Perhaps if I could have extended the precipitation gradient, a clearer pattern in the spacing of the trees would have emerged. It could also be that in the Coast Mountains, where precipitation is not limiting to tree growth (See Chapter 3), even the driest sites are still wet enough to not be "stressful" for the trees, and the spatial patterns observed are due to some other factor not measured in this study.

No significant patterns were found in the distance between center trees and their nearest neighbors for either species, across all sites. A previous study had shown that new trees often grew on the leeward side of already established trees (usually whitebark pine) in the Rocky Mountains (Resler and Tomback, 2008), but since the whitebark pine in my study are not growing closely to other trees, it makes sense that there would be no directional patterns in the spacing of their nearest neighbors. Although the subalpine fir in my study area do grow closely together, there were no significant directional patterns in the spacing around them either. Trees in tree islands benefit from attenuation of intense solar radiation, thermal radiation loss, reduced water loss, reduced wind scouring and altered snow deposition (Callaway, 1995; Maher et al., 2005), so it seems likely that the subalpine fir in the tree clusters are benefitting in some way from their proximity to other subalpine fir—just not in a directional pattern. Or perhaps the lack of directional patterns is simply due to passive seed dispersal and the microsite conditions around subalpine fir center trees.

Site differences in tree size are likely related to stand age. The smallest whitebark pine and subalpine fir both occurred at Blowdown Pass, which were the youngest trees, and the largest whitebark pine and subalpine fir trees occurred at McGillivray Pass, which were the oldest trees (see Chapter 3). Despite their young age, the subalpine fir at Blowdown Pass had a high number of cones per tree, suggesting that Blowdown Pass is a very productive site for subalpine fir. Site differences in subalpine fir stand productivity are likely due to factors including stand density, stand age, or climate. The lower number of subalpine fir cones at Downton Creek could be due to the closer spacing of the trees at that site. Stand density has been shown to affect cone production for other tree species, with fewer cones produced in denser stands (Krannits and Duralia, 2004). The low number of cones per tree at Texas Creek could be due to the young age of the trees (see Chapter 3). Low productivity at Downton Creek and Texas Creek could also be related to harsh conditions since they are the two coldest sites, with mean annual temperatures below 0^{o}C. Studies on several different species have shown that warm temperatures are required to produce large cone crops (Grace et al., 2002; Camarero and Gutiérrez, 2004; Krannits and Duralia, 2004).

The number of whitebark pine cones for the 2012 season was very low across all sites, particularly at McGillivray Pass (Table 2.2). Whitebark pine has extreme annual variation in cone production (McKinney and Tomback, 2007) and produces mast cone crops every 2-5 years (McCaughey and Schmidt, 1990; Tomback et al., 2001b). In 2011, the whitebark pine in the Coast Mountains produced a large number of cones (Yvonne Patterson, personal communication), so it is likely the 2012 season was between masts.

Even so, the low number of cones at McGillivray Pass suggests that the trees may have declining health, despite their large size and circumference.

The lack of any significant patterns in the height, dbh, and number of cones in the quadrant trees surrounding the center suggests that the center trees are not affecting the growth or productivity of the trees surrounding them in a directional way. A study of treeline dynamics in Austria found that pine cover did not impair the fecundity of spruce or larch growing near them (Dullinger et al., 2005).

Understory Vegetation

Significant differences in community composition at each site are likely related to variation in soils, topography, or climate. The Coast Mountains have granitic bedrock (Ogilvie, 1990; Ministry of Environment, Lands and Parks, 1999); however the soils at each site are very different (Baldwin-Corriveau, 2012). To the extent possible, I controlled the elevation and aspect at each site to be within about a 150 m elevation range and a 50^{o} aspect range. However, even small changes in elevation and aspect can lead to significant changes in vegetation in these sites (Baldwin-Corriveau, 2012). Each of the sites has a unique climate as well. The mean annual precipitation between the wettest site and the driest site differs by over 500 mm. When combined with the mean annual temperature, these differences likely have profound effects on the vegetation communities present. A cold, dry site like Downton Creek can be expected to host a different array of species than a mild, wet site like Blowdown Pass. Of all the sites, the vegetation at McGillivray Pass was the most different from the other three sites (Appendix II). McGillivray Pass is the most northern and western geographically of the sites, and it historically experiences a warm/dry climate combination that is not experienced at the other three sites. The trees at McGillivray Pass were also the oldest of the sites I sampled and forest age can influence the chemical and structural properties of the soil, and thus, the vegetation (Barbier et al., 2008).

Studies of plant communities associated with whitebark pine have been virtually non-existent across the entire species' range, especially in the Coast Ranges of British Columbia. Two previous studies had shown that whitebark pine most commonly grew with *Shepherdia canadensis* (L.) Nutt., *Potentilla fruticosa* L., *Arctostaphylos uva-ursi*, and *Vaccinium scoparium* Leiberg ex Coville in the Coast Mountains (Ogilvie, 1990; McCaughey and Schmidt, 1990), but neither of these studies looked specifically at associated understory vegetation. Of these species, only *Potentilla fruticosa* was not present in my sampling areas; however, *Shepherdia canadensis* and *Vaccinium scoparium* were each only present at one of the four sites. Despite the relatively small geographic area encompassed by my study sites, only fifteen understory species were present at all four sites, again highlighting the importance of site characteristics in determining vegetation communities.

My results provide limited evidence that whitebark pine supports a different community of undercanopy vegetation than subalpine fir. The plants more commonly associated with whitebark pine generally grow in drier, less shaded conditions. Of the species more common beneath whitebark pine, *Epilobium angustifolium*, *Lupinus arcticus*, *Trisetum spicatum*, *Achillea millefolium*, and *Arctostaphylos uva-ursi* all have intermediate shade tolerance, while *Aster modestus* and *Solidago multiradiata* are considered shade intolerant (USDA, 2013). *Epilobium angustifolium*, *Lupinus arcticus*, and *Solidago multiradiata* have low drought tolerance. *Trisetum spicatum*, *Achillea millefolium*, and *Aster modestus* have medium drought tolerance. *Arctostahpylos uva-ursi* has high drought tolerance (USDA, 2013). Information about the specific tolerances of *Poa cusickii*, *Arnica parryi*, *Cerastium arvense*, and *Fragaria virginiana* are not available, but they all generally grow in dry to moist meadows, rocky areas, or open forests (UBC, 2013). *Arctostaphylos uva-ursi* is considered an indicator species meaning its presence indicates particular environmental conditions, including certain soil or rock types (Klinka et al., 1989). *Arctostaphylos uva-ursi* commonly grows on nitrogen-poor soils and is an indicator of moisture-deficient sites (UBC, 2013), which suggests that the soils beneath whitebark pine may be dry and low in nitrogen. However, *Arctostaphylos uva-ursi* was only commonly associated with whitebark pine at two of the four sites, so this might point to site-level differences in soil properties, rather than a species-level difference.

The plants found more commonly beneath subalpine fir generally grow in moister, shaded habitats. *Arnica mollis* has intermediate shade tolerance and high moisture-use (USDA, 2013). *Anemone occidentalis* and *Valeriana sitchensis* commonly grow in moist to mesic meadows, rocky slopes, or open forests (UBC, 2013). *Valeriana sitchensis* is also considered an indicator species. It commonly grows on nitrogen-rich, water-collecting sites (UBC, 2013), which suggests the soil below subalpine fir is moist and high in nitrogen. Like *Arctostaphylos uva-ursi*, *Valeriana sitchensis* was only commonly associated with subalpine fir at two of the four sites, so it is hard to separate between site effects and possible species effects.

Even if the understory communities growing beneath each tree species do not truly differ, the presence of the indicator species suggests that the abiotic conditions experienced by the plants growing beneath each tree species might differ. A review of the effect of tree species on the vegetation that grows beneath them found that trees influence understory vegetation through a variety of mechanisms including light, soil water, soil nutrients, litter, and phytotoxic compounds (Barbier et al., 2008). The availability and nature of these resources can be tied to canopy species-specific differences including canopy height and composition (Azeria et al., 2011), canopy transmittance levels (Barbier et al., 2008), canopy branching patterns (Legates et al., 2011), water uptake by roots (Barbier et al., 2008), and needle litter chemistry (von Rudloff, 1975; Binkley and Giardina, 1998; Finzi et al., 1998a; Finzi et al., 1998b; Hickey et al., 2001; Kokaly et al., 2003; Prescott et al., 2004; Prescott and Vesterdal, 2005; Barbier et al., 2008).

If the light and/or soil properties do differ beneath whitebark pine and subalpine fir and the understory vegetation does not differ, it would suggest that the species making up the communities are able to grow under a wide variety of conditions. This would provide evidence that the plant communities in the southern Coast Mountains may be more resilient to climate change than previously thought, even if whitebark pine is not. This is supported by a study of the alpine meadow vegetation adjacent to my study sites, which also suggested the communities might have a wide tolerance for changes in climate (Baldwin-Corriveau, 2012).

Conclusion

The results of the tree nearest neighbor analysis reveal that whitebark pine in the southern Coast Mountains is not playing a facilitating role to other subalpine tree species, as has been seen in the Rocky Mountains (Callaway, 1998; Resler and Tomback, 2008). Rather, mature whitebark pine trees are growing on their own, away from other whitebark pine and subalpine fir trees. However, mature subalpine fir are growing in clusters and may be facilitating other subalpine fir in tree islands within these same stands. The results of the understory vegetation sampling show that site characteristics are driving the main patterns in the understory vegetation. Evidence of differences in the understory vegetation beneath whitebark pine and subalpine fir is weak, but the prevalence of different indicator species beneath each tree species suggest that the soils beneath whitebark pine may have lower soil moisture and lower nitrogen content and the soils beneath subalpine fir may have higher soil moisture and higher nitrogen content.

Chapter 3: Factors limiting the annual growth of whitebark pine and subalpine fir in the southern Coast Mountains

Introduction

Anthropogenic climate warming is currently expected to increase average annual global temperatures at a rate of 0.2^{o}C per decade (IPCC, 2007), and its potential effects on ecosystems, communities, and species is a hot topic in current scientific research. Studies suggest that high-elevation ecosystems may be particularly vulnerable to climate change (Pauli et al., 1996; Diaz et al., 2003; Grabherr et al., 2010). Many of the studies investigating the effects of climate change in high-elevation ecosystems focus on the elevational limit of trees, or the treeline. These studies typically investigate two aspects of treeline dynamics: tree physiology and shifts in elevation, both of which are expected to change with increased temperature (see references below).

A review of the impacts of climate change on treeline concluded that there are three aspects of environmental change that trees respond to: (1) increasing temperature, (2) rising concentration of carbon dioxide, and (3) increasing deposition of nitrogen (Grace et al., 2002). Since high-altitude treelines are thought to be most limited by temperature (Luckman, 1993; Grace et al., 2002; Lloyd and Fastie, 2002), this is the factor most often studied. It is expected that annual tree growth will increase as temperatures rise and growing seasons lengthen due to global climate change. This phenomenon has been illustrated in several studies using tree cores. Annual tree ring widths declined during periods that coincided with northern hemisphere cooling in the areas adjacent to Banff and Jasper National Parks in Alberta, Canada (Lloyd, 1993).

Another study showed that annual tree ring width of treeline trees growing at three sites in Alaska were positively correlated with summer temperatures, but were also often correlated with growing season precipitation (Lloyd and Fastie, 2002). In fact, temperature-induced drought stress (i.e. an increase in temperature without an increase in precipitation) can have a significant negative effect on some tree species' radial growth (Wilmking et al., 2004). It has also been suggested that winter conditions (as opposed to summer conditions) may have the strongest influence on tree growth in subarctic and subalpine regions (Gamache and Payette, 2004). Either way, trees growing at treeline are likely to respond differently to warming temperatures depending on local site characteristics (Holtmeier and Broll, 2005).

In addition to the physiological effects of climate change, studies across taxa suggest that increased temperatures will also influence recruitment, with ecosystems and species distributions shifting to higher elevations and latitudes (e.g. Pauli et al., 1996; Parmesan and Yohe, 2003; Hickling et al., 2006). Recent evidence suggests that this is already occurring. Ranges across several taxonomic groups have shifted poleward 6.1 kilometers per decade and upward 6.1 meters per decade in response to warming temperatures (Parmesan and Yohe, 2003). A recent review of treeline movement in response to climate warming found that treelines had advanced in 52 percent of the studies examined, while the rest remained stable (Harsch et al., 2009). Again, local factors play a crucial role in whether or not treelines will advance, remain stable, or even retreat (Holtmeier and Broll, 2005; Lloyd, 2005; Payette, 2007). For example, in southern Siberia, forest area increased and shifted upward 63 m in elevation (Kharuk et al., 2010). However, in Glacier National Park, Montana and in the Spanish Pyrenees, an increase in the size and density of treeline trees was observed, but not an increase in the maximum elevation (Klasner and Fagre, 2002; Camarero and Gutierrez, 2004). Land use change can sometimes even override treeline responses to climate change. Diminished grazing in the mountains of central Norway was found to be a more important factor in treeline position than global climate change (Hofgaard, 1997).

Dendrochronology studies in the Pacific Northwest USA and adjacent Canada show the importance of both summer and winter climate variables. A study of subalpine fir just west of my study area in Garibaldi Provincial Park, British Columbia showed that ring widths were positively correlated with summer temperature and the Pacific Decadal Oscillation (PDO), but negatively correlated with winter precipitation and spring snowpack (Koch et al., 2004). Another study of subalpine fir in Mt. Rainier National Park, Washington showed that rings were positively correlated with May and June precipitation and July temperature (Rochefort and Peterson, 1996). Two studies of subalpine fir in the Cascade and Olympic Ranges of Washington and Oregon found that climatic variables associated with winter snowpack were the best predictors of annual ring widths. Summer temperature was also positively correlated with annual growth at the wettest sites (Ettl and Peterson, 1995a; Peterson et al., 2002). A study utilizing the tree rings of subalpine fir and whitebark pine in central British Columbia revealed that both species growth was correlated with PDO (Starheim et al., 2013). Another study in the Mt. Waddington area of British Columbia using both whitebark pine and subalpine fir found that whitebark pine annual growth was positively correlated with summer temperature and negatively correlated with previous November temperature. Subalpine fir was positively correlated with July temperature and negatively correlated with previous summer temperature and April 1 snowpack (Laroque and Smith, 2005). A study of whitebark pine in the southeastern Canadian Rockies revealed that the correlations with annual growth were dominated by negative correlations with temperature, particularly for the spring and summer months (Youngblut and Luckman, 2012).

My research investigated the stand structures of whitebark pine and subalpine fir and the climate factors limiting their annual growth in both open canopy, high elevation sites and closed canopy, lower elevation sites in the southern Coast Mountains of British Columbia. I had two objectives. First, I wanted to compare the differences in ages and age distributions of both species at different elevations. I hypothesized that whitebark pine, as an early successional species, would be much older than subalpine fir, a late successional species, across all sites. Second, I wanted to determine which climate variables were most limiting to each species' growth at both high and low elevation sites. I hypothesized that climate would play a lesser role in the closed canopy, lower elevation sites due to competition between individuals, resulting from the close spacing of trees. However, in the open canopy, high elevation sites, I hypothesized climate variables relating to growing season temperature and winter snow depths would strongly contribute to annual tree growth due to the trees' location at their altitudinal limit. Since 1948, the mean annual temperature in the southern British Columbia mountain ranges has increased 1.7^{o}C and the mean winter temperature has increased 3.0^{o}C (Environment Canada, 2013). Studying the dendrochronology of each species will provide valuable information about how subalpine trees in the southern Coast Mountains have responded to this past climate variability and which climate factors are most limiting to their growth. This information is crucial for predicting how they will respond to future anthropogenic warming, especially whitebark pine, which has largely been ignored in tree ring studies.

Methods

Field Methods

To construct tree-ring chronologies, tree cores were collected from whitebark pine and subalpine fir at six sites in the southern Coast Mountains of British Columbia during July and August of 2012 (Figure 3.1). Cores were collected at each of the four high-elevation, open canopy sites described in detail in Chapter 2. Two lower elevation/closed canopy sites were also sampled (Table 3.1). Due to the patchy distribution of whitebark pine in this area, I could not necessarily select sites based on the normal principles of dendrochronology (i.e. selection of sites that are limited by the climate factor of interest; Fritts, 1976). I had to choose sites based solely on where whitebark grew. However, at each of my high elevation sites, whitebark pine and subalpine fir were growing on steep slopes at their altitudinal limit, suggesting that their rings would display maximum sensitivity to climate (Fritts, 1976).

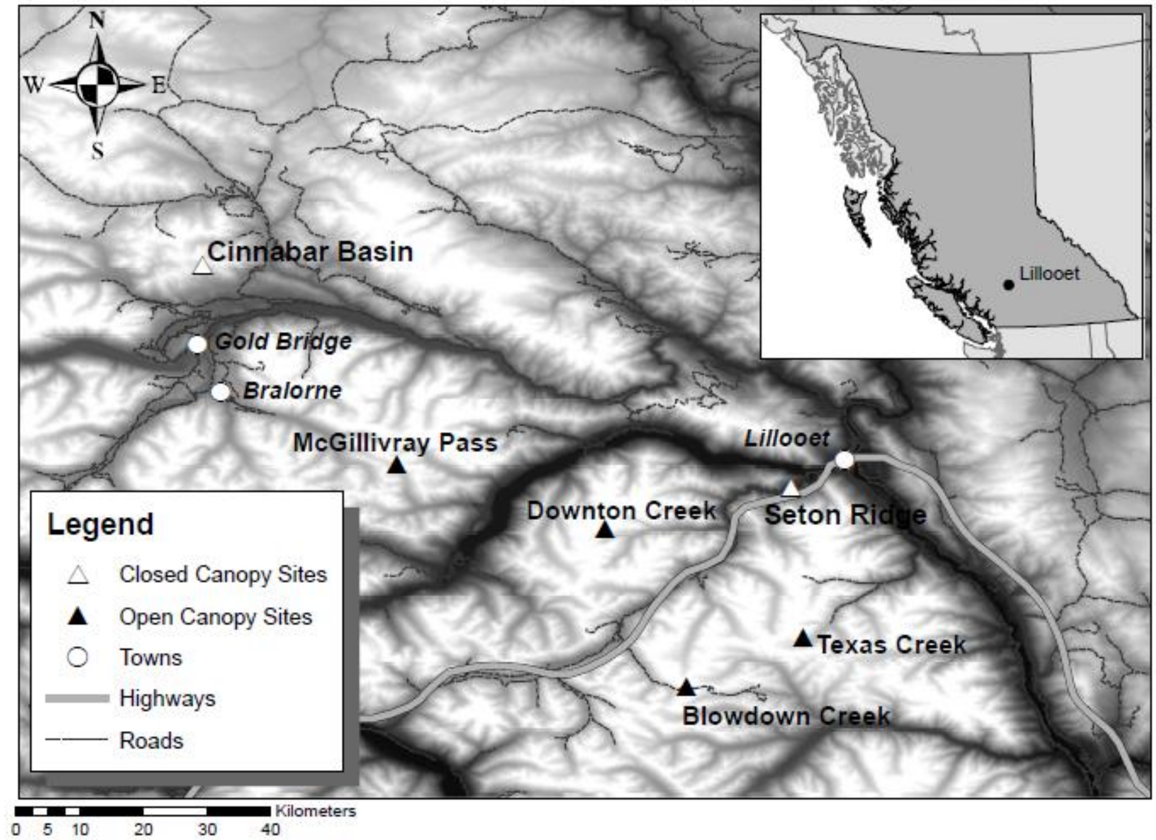

Figure 3.1. Location of the 6 study sites in the southern Coast Range of British Columbia. The dendrochronological study utilized the same 4 higher elevation, open canopy sites described in Chapter 2 and 2 lower elevation, closed canopy sites. Lighter areas of the map are mountain tops and darker areas are rivers and valley bottoms. Inset map shows the location of Lillooet in British Columbia.

At each site a 2 m wide belt transect of variable length was extended upslope from the base of each stand. Each subalpine fir or whitebark pine encountered along the transect was cored at breast height and its height, dbh, and number of cones were recorded. Cores were collected in this manner until the total cores collected per site was brought up to at least 50 subalpine fir and at least 25 whitebark pine. For each of the four high elevation sites, I already had anywhere from 23-35 cores per species from the tree community spatial patterns analysis (See Chapter 2). Thus the transect length and number of transects needed varied by site. Cores from each tree along the belt transect were taken at breast height, just like the trees used in the tree community spatial pattern analysis (Chapter 2), so that cores collected from either method would be comparable and chronologies could be constructed. All sites but one required only a single long transect to collect all of the needed cores. The shape of the stand at Downton Creek required three shorter elevational transects, all starting from the same baseline. At each site, cores were taken from 1-2 larger diameter trees at slightly lower elevations to ensure that older trees at each site were represented in the sampling. A total of 455 cores were collected. All cores were stored in plastic drinking straws and allowed to dry before being processed in the lab (Stokes and Smiley, 1964).

Table 3.1. Study site locations and characteristics. Mean annual precipitation (MAP) and mean annual temperature (MAT) come from the ClimateWNA 1961-1990 climate normals. Data for Lillooet, BC is from Environment Canada 1971-2000 climate normals (1961-1990 climate normals are not available for Lillooet).The first four sites are the high elevation, open canopy high elevation sites from Chapter 2. The bottom two sites are the lower elevation, closed canopy sites added in Chapter 3.

Site	Location	MAP (mm)	MAT(°C)	Elevation (m)	Aspect (°)	Slope (%)
Lillooet, BC	50.6864°N, 121.9364°W	330	9.2	250	--	--
Blowdown Pass	50.3656°N, 122.1591°W	1672	0.2	2105	202	70
Downton Creek	50.5881°N, 122.2749°W	1125	-0.4	2104	194	50
McGillivray Pass	50.6796°N, 122.5681°W	1167	0.3	1963	200	75
Texas Creek	50.4358°N, 121.9950°W	1297	-0.2	2115	158	60
Seton Ridge	50.6461°N, 122.2749°W	479	0.4	1771	148	60
Cinnabar Basin	50.9609°N, 122.8417°W	893	0.6	1842	162	5

Lab Methods

Dried cores were mounted on slotted boards and progressively sanded to a 600-grit finish using a belt sander. Ring widths were measured to 0.01 mm using a Velmex measuring system and MeasureJ2X software (v4.2, 2010). The relative average ages of whitebark pine and subalpine fir at each site were compared using a two-way ANOVA. (Because tree cores were taken at breast height and not at ground level the number of rings represents a relative age. The actual ages of the trees are approximately 20-30 years older, based on height-diameter comparisons.) In addition, I compared the age distributions of each species at each site using Kolmogorov-Smirnov tests. All statistical tests were carried out using R statistical software (R Development Core Team, 2011).

Cross-dating of site-specific chronologies was completed with the aid of the COFECHA program (Holmes et al., 1986). Cross-dating correlations were calculated over 50 year intervals with a 25-year lag and were considered statistically significant at the 0.01 level (Grissino-Mayer, 2001). Individual series that were not significantly correlated to their site-specific master chronologies were omitted to ensure the maximum common climate signal. All but two of the chronologies exhibited a significant common signal (Table 3.2). The ring widths for both lower elevation/closed canopy whitebark chronologies (Seton Ridge and Cinnabar Basin) showed no apparent pattern, and I was not able to cross-date them. They were omitted from further analysis.

Table 3.2. Chronology statistics. The whitebark pine series from Seton Ridge and Cinnabar Basin did not cross-date and were not included in any further analyses.

Site	Species	Number of cores	Start Date	Interseries correlation	Mean Sensitivity	Auto-correlation
Blowdown Pass	Whitebark pine	23	1928	0.501	0.283	0.734
	Subalpine fir	43	1917	0.467	0.302	0.585
Downton Creek	Whitebark pine	21	1902	0.511	0.248	0.738
	Subalpine fir	37	1785	0.529	0.262	0.639
McGillivray Pass	Whitebark pine	15	1841	0.496	0.234	0.765
	Subalpine fir	37	1799	0.510	0.260	0.665
Texas Creek	Whitebark pine	22	1871	0.530	0.281	0.676
	Subalpine fir	33	1902	0.569	0.327	0.523
Seton Ridge	Subalpine fir	15	1859	0.458	0.225	0.646
Cinnabar Basin	Subalpine fir	28	1827	0.480	0.233	0.619

The remaining chronologies were standardized using ARSTAN (Holmes et al., 1986). Typically at this point, tree ring series are detrended to remove the influence of growth trends from the climate signal (Fritts, 1976); however, the vast majority of the individual series did not display the typical negative exponential pattern of ring widths, so I did not detrend them. The series were simply standardized using a horizontal line through the mean. Both standardized and residual chronologies were produced, due to the relatively high first order autocorrelation for each chronology (Table 3.2). The expressed population signal (EPS) was calculated for each chronology to detect where decreasing sample size had a significant effect on the observed ring-width variation (Wigley et al., 1984).

Historical climate data, including monthly and annual rainfall, snowfall, and temperature from the Lillooet weather station, were accessed online (Environment Canada, 2012). The Lillooet station was the nearest weather station to most of the sites and also had the longest and most complete climate record compared to other weather stations in the area. However, large sections of data were missing from the 1940s, 1950s, and 1960s for some of the climate variables, especially temperature. Therefore, I also used gridded climate data for each site from the Centre for Environmental Data Archival (University of East Anglia Climatic Research Unit, 2008), which produces datasets of month-by-month climate variation over the past century, calculated on 0.5 x 0.5 degree grids based on archived monthly mean temperatures provided by over 4000 weather stations worldwide. Correlations between the weather station data and the gridded data showed a very strong match ($R \sim 0.95$).

In addition to the weather station and gridded climate data I also gathered data from several climate indices known to affect the climate of the Pacific Northwest USA and adjacent Canada (Table 3.3). Monthly mean records for the Southern Oscillation Index (SOI) and the Niño Region 3.4 sea surface temperature (SST) indices were retrieved from the Australian Bureau of Meteorology (ABM, 2012) and the National Center for Atmospheric Research (NCAR, 2012) websites. The SOI and SST both describe variability in the El Niño Southern Oscillation (ENSO). Monthly mean records for the Pacific Decadal Oscillation (PDO) were accessed from the Joint Institute for the Study of the Atmosphere and Ocean (JISAO, 2012) website. Annual records for the Aleutian Low Pressure Index (ALPI) were accessed from the Fisheries and Oceans Canada (DFO, 2012) website. The ALPI measures the relative intensity of the Aleutian

Low pressure system of the North Pacific for December through March (Beamish et al., 1997). Annual summer reconstructions of the Palmer Drought Severity Index (PDSI; Cook et al., 1999) were accessed for 52.5^{o}N, 122.5^{o}W (the grid point nearest all sites) from the National Oceanic and Atmospheric Administration (NOAA, 2012) website.

Table 3.3. List of all climate variables used in the correlation analysis.

Climate Variable	Source	Length of Record
Snowpack	Lillooet Weather Station, Environment Canada	1917-2001
Temperature	Gridded Climate Data, University of East Anglia	1901-2009
Precipitation	Gridded Climate Data, University of East Anglia	1901-2009
Aleutian Low Pressure Index (ALPI)	Fisheries and Oceans Canada	1900-2008
Pacific Decadal Oscillation (PDO)	Institute for the Study of the Atmosphere and Ocean	1900-2012
Palmer Drought Severity Index (PDSI)	National Oceanic and Atmospheric Administration	1900-1990
Sea Surface Temperature (SST)	National Center for Atmospheric Research	1950-1999
Southern Oscillation Index (SOI)	Australian Bureau of Meteorology	1876-2012

Pearson correlation coefficients were calculated between both the standardized and residual chronologies and the climate data. Due to the high number of correlations run (10 chronologies x 66 climate variables), spurious correlations are highly probable. To reduce the chance of spurious correlations I only used correlation coefficients above or below the 0.35/-0.35 level (Fritts, 1976), and I only included a correlation coefficient if it was significant for more than one chronology. As a final precaution, the R program bootRes, which utilizes moving correlation or response windows, was used to visualize how the correlations changed over time. Only the correlation coefficients that did not change greatly over time were considered significant. When two or more consecutive months were shown to correlate significantly, the data were averaged into 3-month seasons and correlations re-run. Winter consisted of December-February, spring consisted of March-May, summer consisted of June-August, and fall consisted of September-November. All analyses were carried out using R statistical software (R Development Core Team, 2011).

Results

Tree Age

The relative ages of the trees cored differed significantly by site (ANOVA: $F=47.519$, $p<<0.001$) and between the two tree species ($F=44.402$, $p<<0.001$). However, post hoc Tukey HSD tests revealed that the species' ages only differed significantly at Seton Ridge and Cinnabar Basin, the two lower elevation closed canopy sites (Figure 3.2). At both low elevation sites, the whitebark pine were significantly older than the subalpine fir, while at the four higher elevation, open canopy sites, whitebark pine and subalpine fir ages did not differ.

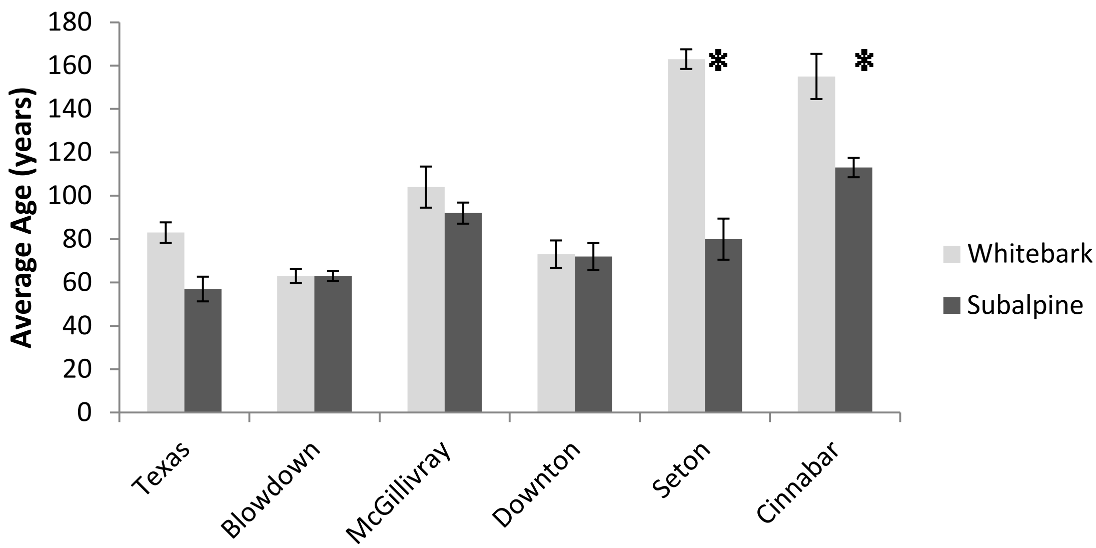

Figure 3.2. Relative ages of trees by site. Whitebark pine were significantly older than subalpine fir at both lower elevation, closed canopy sites (Seton Ridge and Cinnabar Basin, $p<0.05$), but there was no significant difference in the tree ages at any of the high elevation, open canopy sites. Error bars are ±1 standard error of the mean.

The age distribution of whitebark pine differed from that of subalpine fir at Texas Creek (Kolmogorov-Smirnov test: $D=0.5587$, $p<<0.001$), Cinnabar Basin ($D=0.5133$, $p=0.0004$), and Seton Ridge ($D=0.8303$, $p<<0.001$). The age distributions did not differ between the two species at Downton Creek ($D=0.1941$, $p=0.407$), Blowdown Pass ($D=0.1204$, $p=0.952$), or McGillivray Pass ($D=0.2185$, $p=0.388$). In the cases where the age distributions did differ, the whitebark pine had a much greater proportion of older trees, while the subalpine fir had a much greater proportion of younger trees. The difference in the average age and the distribution of age classes between the two species was most pronounced at Seton Ridge, which has the lowest elevation of the 6 sites (1771 m). It is important to note that the two lowest elevation sites are also the two driest sites, which may be confounding the effects of elevation in some of the results.

It appears that the whitebark pine was originally present at each low elevation site approximately 200 years ago (one 330 year old whitebark pine from Cinnabar Basin suggests it was present even before then) and is now in decline, with virtually no regeneration for the past 60-80 years. There is evidence that whitebark pine was present at two of the high elevation sites (McGillivray Pass and Downton Creek) about that same time, but it was absent from the two highest elevation sites (Blowdown Pass and Texas Creek) until approximately 60 years later (Figure 3.3). Subalpine fir, on the other hand, first moved into the lower elevation sites decades after whitebark pine, and has had near-continuous recruitment since then. At the high elevation sites, the oldest subalpine fir and whitebark pine trees indicate that both species arrived at each site at approximately the same time.

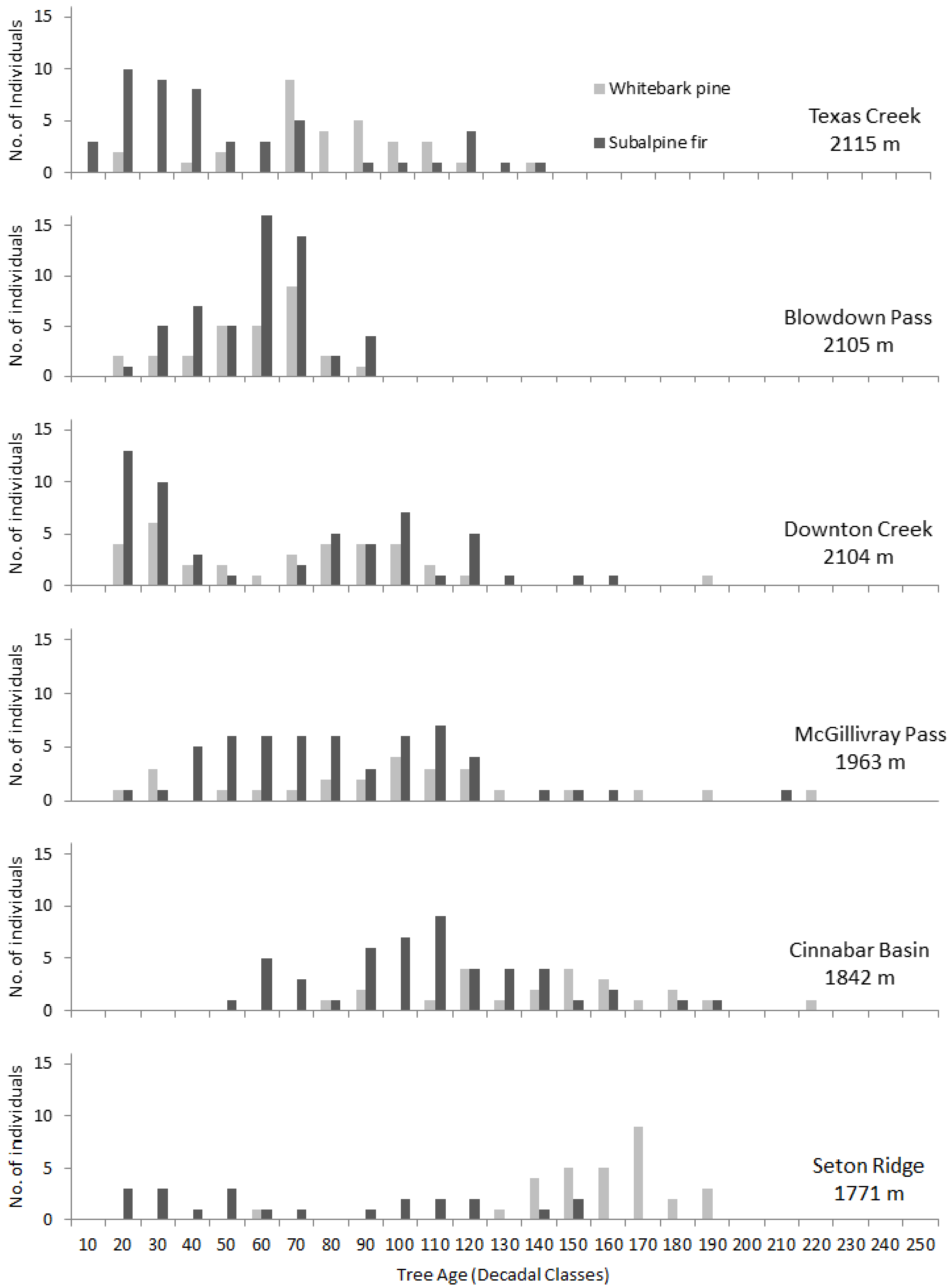

Figure 3.3. Age distributions of whitebark pine and subalpine fir at each site, divided into 10-year classes. One 330-year old whitebark pine at Cinnabar Basin was an outlier and is not shown on this graph. Sites are arranged in order of decreasing elevation to illustrate the shift from distinct age distributions between the species at lower elevations to more uniform age distributions at higher elevations. The highest elevation site, Texas Creek, was an exception where the age distributions did differ.

Chronology Statistics

A total of 10 chronologies were produced. The two longest chronologies came from the subalpine fir at Downton Creek (228 years) and McGillivray Pass (214 years). The two shortest chronologies were both of the chronologies from Blowdown Pass. The Blowdown Pass subalpine fir chronology spanned 96 years and the Blowdown Pass whitebark pine chronology spanned 85 years (Table 3.2). The subalpine fir chronologies were longer than the whitebark pine chronologies at Blowdown Pass, Downton Creek, and McGillivray Pass, but the whitebark pine chronology was longer than the subalpine fir chronology at Texas Creek. The whitebark pine chronologies from the two lower elevation sites (Seton Ridge and Cinnabar Basin) showed very low interseries correlation and I was not able to produce chronologies from them.

Mean sensitivity of each chronology ranged from 0.234 (McGillivray Pass) to 0.283 (Blowdown Pass) for whitebark pine and from 0.260 (McGillivray Pass) to 0.327 (Texas Creek) for subalpine fir in the open canopy, higher elevation sites (Table 3.2). The mean sensitivity was higher for subalpine fir than for whitebark pine at the four sites with whitebark pine chronologies. The mean sensitivity for the subalpine fir at the lower elevation, closed canopy sites (Seton Ridge: 0.225 and Cinnabar Basin: 0.233) was lower than that observed for either species at the higher elevation, open canopy sites. First order autocorrelation between the ring widths ranged from 0.676 (Texas Creek) to 0.765 (McGillivray Pass) for whitebark pine, and from 0.523 (Texas Creek) to 0.665 (McGillivray Pass) for subalpine fir. Autocorrelation was higher in whitebark pine than in subalpine fir at each of the four higher elevation, closed canopy sites. At the site level, autocorrelation for both species was lowest at Texas Creek, followed by Blowdown Pass, Downton Creek, and McGillivray Pass. Autocorrelation for the two lower elevation, closed canopy subalpine fir chronologies fell around the middle of the range for the species (Seton Ridge: 0.646 and Cinnabar Basin: 0.619).

Correlations with Climate Data

The correlation analysis showed that a number of climate variables and climate indices displayed strong correlations with a number of the chronologies (Table 3.4; see Appendix III for all correlation coefficients). Correlation coefficients were greater for the residual chronologies than the standardized chronologies, so I used only the results for the residual chronologies in the final results. Of the climate variables, snowpack and temperature had the strongest correlations with the most chronologies. None of the precipitation variables were correlated with any of the chronologies. Total snowpack (previous year September through current year August) showed a strong negative correlation with 5 of the 10 chronologies (4/4 whitebark pine chronologies and 1/6 subalpine fir chronologies). For temperature, previous fall temperature (September-November) and current winter temperature (December-February) produced the highest correlations. Previous fall temperature was positively associated with 4 of the 10 chronologies (1/4 whitebark pine chronologies and 3/6 subalpine fir chronologies). Current winter temperature was positively associated with 5 of the 10 chronologies (4/4 whitebark pine chronologies and 1/6 subalpine fir chronologies).

Table 3.4. Correlations between climate variables and tree ring chronologies with coefficients above or below 0.35/-0.35. All results shown are significant at the 0.05 level. +/- denote positive or negative correlations. Lowercase seasons are from the year previous to ring growth (lagged relationship). Uppercase seasons are from the same year as ring growth. “Total” refers to the total snowpack (previous September through current August) prior to ring growth. WBP= Whitebark pine. SF= Subalpine fir.

		Blowdown		**Downton**		**McGillivray**		**Texas**		**Seton**	**Cinnabar**
		WBP	SF	WBP	SF	WBP	SF	WBP	SF	SF	SF
Snowpack	Total	-0.42		-0.40		-0.48		-0.45	-0.36		
Temp	spring		0.36								
	summer										
	fall				0.44		0.36	0.38	0.35		
	WINTER	0.50	0.38	0.42		0.37		0.35			
	SPRING										
	SUMMER										
	FALL										
PDO	spring										
	summer										
	fall						0.36				
	WINTER			0.36		0.41	0.37				
	SPRING										
	SUMMER										
	FALL										
SST	spring										
	summer					0.38		0.41	0.41		
	fall					0.40		0.43	0.39		
	WINTER					0.37		0.39	0.40		
	SPRING								0.37		
	SUMMER										
	FALL										
ALPI	Annual	0.37		0.40				0.35			

Of the climate indices, the SST, PDO, and ALPI had the strongest correlations with the most chronologies (Table 3.3). The SOI and PDSI showed no strong correlations with any of the chronologies. The strongest SST correlations were limited to three chronologies at two sites: the McGillivray Pass whitebark, the Texas Creek whitebark, and the Texas Creek subalpine fir. Previous summer SST, previous fall SST, and current winter SST were all positively correlated with these 3 chronologies. Current year spring SST was positively correlated with only the subalpine fir chronology at Texas Creek.

Similarly, the strongest PDO correlations were limited to only three chronologies at two sites: the Downton Creek whitebark pine, the McGillivray Pass whitebark pine, and the McGillivray Pass subalpine fir. Each of these chronologies was strongly positively correlated with current winter PDO. Only the McGillivray Pass subalpine fir chronology was strongly positively correlated with previous fall PDO. Unlike the SST and PDO, the ALPI is an annual index calculated only over the period December-March. The ALPI was positively correlated with 3 of the 4 whitebark pine chronologies, but was not correlated with any of the subalpine fir chronologies.

Each of the chronologies had significant correlations with at least a few climate variables or climate indices, except for Seton Ridge and Cinnabar Basin, the two lower elevation, closed canopy sites (Table 3.4). Despite successfully cross-dating and having a significant interseries correlation, these chronologies did not show significant correlations with any of the seasonal climate variables or climate indices examined. Other than Seton Ridge and Cinnabar Basin, the subalpine fir chronologies for Downton Creek and Blowdown Pass showed the fewest significant correlations. The whitebark pine and subalpine fir chronologies for Texas Creek and the whitebark pine chronology for McGillivray Pass had the most significant correlations.

The climate variables that were correlated with more than one chronology seemed to fall into two categories: those that were species-specific and those that were site-specific (Figure 3.4). Correlations with the Aleutian Low Pressure Index (ALPI) displayed a strong difference between the two species, with whitebark pine showing greater growth than subalpine fir at all the high-elevation sites when the ALPI was greater. Similarly, whitebark pine also showed more severely reduced growth than subalpine fir when total snowpack was higher and greater increased growth than subalpine fir when winter temperatures were higher at each of the high elevation sites. In contrast, the correlations with PDO and SST appeared to be more site-specific than species-specific. Both species of trees at McGillivray Pass showed the strongest responses to winter PDO, while both Texas Creek chronologies and the McGillivray Pass whitebark pine chronology showed the strongest responses to SST. The correlations with previous fall temperature were much less clear, with no apparent site or species patterns.

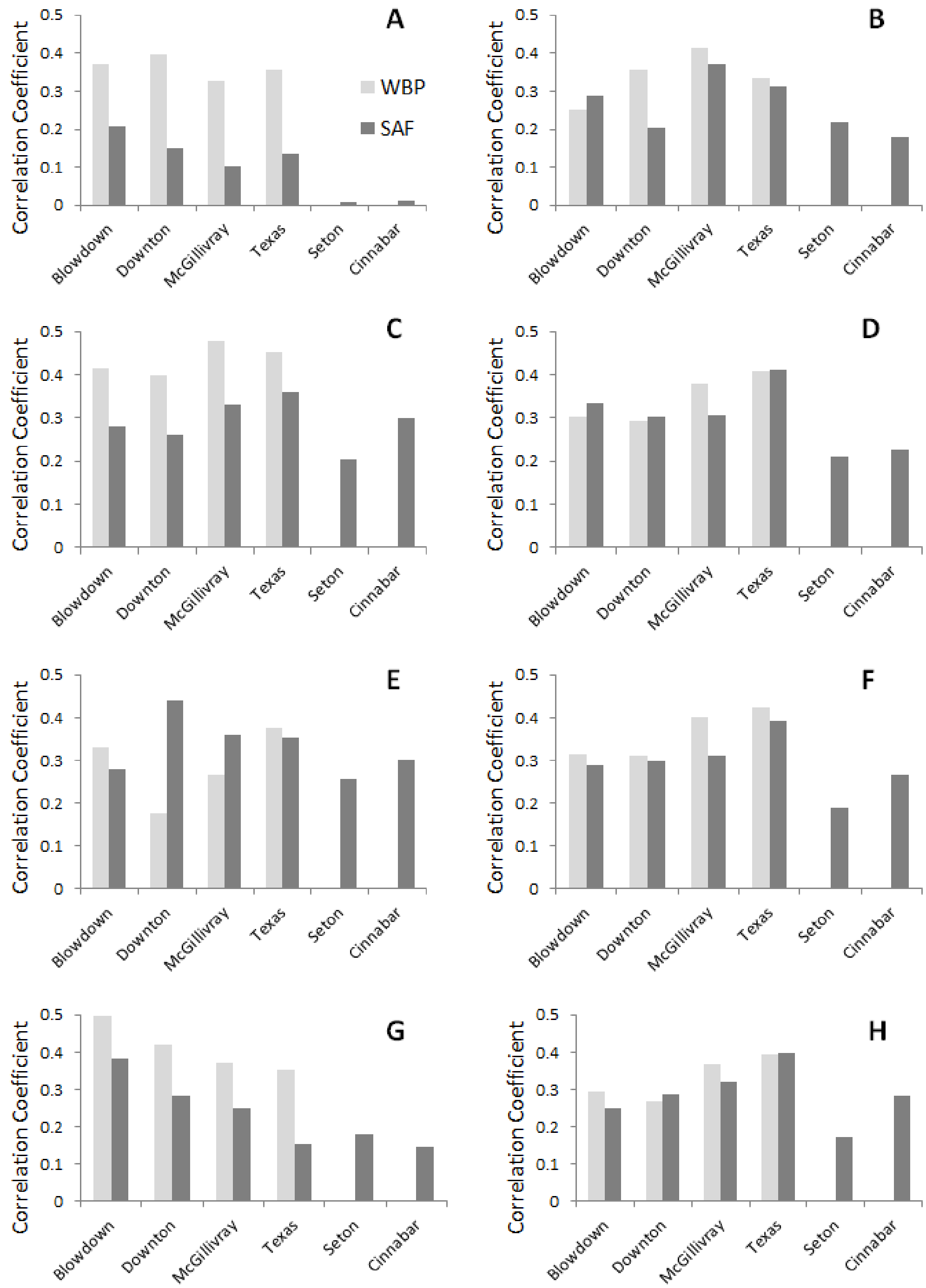

Figure 3.4. Magnitude of correlation coefficients for the climate variables that strongly correlated with more than one chronology: (A) Aleutian Low Pressure Index (ALPI), (B) Winter Pacific Decadal Oscillation (PDO), (C) Total snowpack (correlation coefficients are the absolute values since the correlation was negative), (D) Previous summer Sea Surface Temperature (SST), (E) Previous fall temperature, (F) Previous fall SST, (G) Winter temperature, and (H) Winter SST. Climate variables in the left column show a more species-specific pattern. Climate variables in the right column show a more site-specific pattern. WBP=Whitebark pine. SAF=Subalpine fir.

Expressed Population Signal (EPS)

An EPS value of 0.85 is typically used as a cut-off value to determine at which point in a chronology the strength of the common variance signal becomes unreliable due to decreasing sample size (Wigley et al., 1984). The EPS values I calculated from my chronologies were generally low and fell below the 0.85 level very early in the chronology, even in the most recent years which are made up of the maximum number of cores. In addition, the EPS values fluctuated widely over time (Table 3.5). I investigated the low EPS values (see Discussion); however, it is important to note that I had significant interseries correlations for each of my chronologies and large sample sizes (ranging from n=15 to n=43), so I felt justified in carrying out the correlations with the climate variables, despite the low EPS values.

Table 3.5. Expressed population signal (EPS) calculated over 10 year windows for each chronology. Boldface indicates values over 0.85. WBP=Whitebark pine. SF=Subalpine fir.

	Blowdown		Downton		McGillivray		Texas		Seton	Cinnabar
Year	WBP	SF	WBP	SF	WBP	SF	WBP	SF	SF	SF
1860	--	--	--	--	--	--	--	--	--	0.3883
1870	--	--	--	--	--	0.8399	--	--	--	0.6392
1880	--	--	--	--	0.6426	0.5994	--	--	0.4792	0.7485
1890	--	--	--	--	0.4999	0.7256	--	--	0.0688	0.6679
1900	--	--	--	0.2352	0.7527	0.494	0.6817	--	0.6397	0.5228
1910	--	--	--	0.2767	**0.8885**	0.489	0.5159	--	0.7566	0.802
1920	--	--	--	0.8198	**0.8703**	0.6444	**0.8608**	--	**0.8518**	0.8053
1930	--	--	0.5747	0.542	**0.8608**	0.7226	0.8048	--	0.543	0.8332
1940	**0.9349**	0.4199	0.7809	0.7482	**0.8646**	**0.8977**	**0.9189**	--	0.7728	**0.8875**
1950	**0.8529**	**0.9504**	**0.8771**	0.8278	**0.9648**	**0.9315**	**0.9356**	0.8166	**0.8545**	**0.9247**
1960	0.643	0.8424	0.7628	0.8183	0.7778	**0.8878**	**0.8871**	0.4215	**0.8598**	**0.8969**
1970	**0.931**	**0.9244**	0.8497	**0.8758**	0.8322	**0.927**	0.8033	0.793	0.8346	**0.9257**
1980	**0.8899**	**0.9637**	0.8393	**0.8742**	**0.8908**	**0.9263**	**0.8564**	**0.9177**	0.8296	**0.9324**
1990	**0.9562**	**0.9714**	**0.9373**	**0.9124**	**0.8873**	**0.9458**	**0.9544**	**0.9228**	**0.9182**	**0.9113**
2000	**0.8902**	**0.9186**	**0.8667**	**0.8812**	0.6601	**0.9471**	0.8381	**0.8774**	0.8247	**0.8932**

Discussion

Tree Age

Age distributions show evidence of senescent whitebark pine populations (greater proportion of older trees) at lower elevations and an expanding subalpine fir population at higher elevations (greater proportion of younger trees; Harcombe, 1987). Most studies of mixed whitebark pine/subalpine fir stands have found that whitebark pine is significantly older than subalpine fir, suggesting that subalpine fir moves into pure whitebark pine stands from lower elevations (Morgan and Bunting, 1990). In the lower elevation stands, where successional advancement to subalpine fir occurred decades earlier, whitebark pine has seen virtually no regeneration. At the high elevation sites, whitebark pine has shown recent regeneration, but it was generally less than what had been seen in previous decades. In contrast, the subalpine fir populations in some of these sites are expanding, with most regeneration occurring in the last few decades. This provides evidence that subalpine fir encroachment into previously pure whitebark pine stands may limit whitebark pine recruitment. As subalpine fir further expands into the high elevation sites, whitebark pine recruitment may be suppressed, as has already occurred at the lower elevation sites. This could severely limit whitebark pine's ability to migrate upward as temperatures increase.

The fact that the species' ages do differ at lower elevations, but not at higher elevations suggests that whitebark pine may have a narrower limit of climatic tolerance than subalpine fir, which has led to it migrating upward more slowly than subalpine fir as temperatures warm. This is reflected by a gradual shift from separate distributions for each species at the lower elevation sites, to a single distribution for both species at the higher elevation sites (Figure 3.3).

It is possible that there were much older whitebark pine at each site at one time that have since died, or were merely missed during my sampling. The age distributions for Downton Creek and McGillivray Pass show some evidence of this, with a few individuals decades older than the main distribution of tree ages (Figure 3.3). It is unlikely that they were missed, since all of these stands were very small and I targeted mature trees for my center trees, but older dead trees are certainly a possibility. Blister rust has killed whitebark pine in areas of the southern Coast Mountains (Campbell and Antos, 2000; Zeglen 2002). The stands I worked in appeared to be very healthy with no widespread mortality; however, I did not core any of the dead trees, so there is no way to tell if they established long before the live whitebark pine on site. The narrow range of ages for both whitebark pine and subalpine fir at Blowdown Pass suggest another possibility: disturbance. It is possible that some major event wiped all the species out at one time and they have been recolonizing since. In this part of the Coast Mountains, forest fires are not common. A more likely culprit would be an avalanche or rockslide. There is evidence of rockslides near the stand at Blowdown Pass and avalanches occur frequently—an exceptionally large one blocked the access road to the site in 2011.

Chronology Statistics

Subalpine fir is commonly used in dendrochronological studies of subalpine ecosystems because their annual growth rings tend to have high mean sensitivities and relatively low autocorrelation (Zhang et al., 1999; Laroque & Smith, 2005). Whitebark pine is less commonly used because their rings can be highly autocorrelated and have low mean sensitivities (Laroque & Smith, 2005; Youngblut & Luckman, 2012). While the mean sensitivities of the rings in my whitebark pine chronologies were lower than those of the subalpine fir chronologies, they were higher than those reported for other studies. A study of whitebark pine in the southeastern Canadian Rockies reported mean sensitivities of approximately 0.15 (Youngblut & Luckman, 2012), and a study in south-central Idaho reported a mean sensitivities ranging from 0.12-0.17 (Perkins & Swetnam, 1996). Two studies in western British Columbia, closer to my study area, reported slightly higher mean sensitivities of 0.184 and 0.202 (Laroque & Smith, 2005; Starheim et al., 2013). These values are still below the average mean sensitivity I observed in the annual rings of the whitebark chronologies of my four high-elevation sites. This could be a result of elevation and/or annual precipitation differences. Trees growing at dry, lower elevation sites can display smaller variations in annual ring width (Ettl & Peterson, 1995a; Peterson et al., 2002). This phenomenon was observed between the subalpine fir chronologies of Seton Ridge and Cinnabar Basin. These two lowest elevation sites (which also happened to be the two driest sites) had lower mean sensitivities than any of the chronologies.

Another explanation for the higher whitebark pine annual ring mean sensitivities could be due to tree health. Across much of its range whitebark pine is not in optimal health due to white pine blister rust infection and mountain pine beetle infestation, which can have a significant impact on its annual ring growth (Laroque & Smith, 2005). The whitebark pine trees at my high elevation sites were generally in very good health, and it is likely that more of the annual ring variability is due to climate than individual tree responses to disease or infestation. Tree health could also explain, in part, why the whitebark pine from my two lower elevation sites did not cross date. The whitebark pine at these two sites were not in as good condition, particularly at Seton Ridge, where the majority of the trees were dead or dying.

Correlations with Climate Data

My findings support the view that winter conditions are playing a bigger role in tree growth than previously thought (Gamache and Payette, 2004; Kharuk et al., 2010). Nearly all of the significant correlations with climate variables occurred with current winter conditions, and occasionally previous fall conditions. Snowpack, winter temperature, winter PDO, winter SST, and ALPI (which is measured over the winter months) produced the strongest correlations with the most chronologies in my study. Other than positive correlations between the previous summer SST and three chronologies, strong positive correlations with summer variables were absent.

Trees at high elevations have a very limited growing season, between perhaps June and September (Fritts, 1966), so the strong correlations between ring widths and fall or winter conditions are occurring through indirect means, likely fluctuations in snowpack. In mountains in a maritime climate, tree growth and regeneration depend on the length of the snow-free season (Holtmeier and Broll, 2005). In my study, snowpack produced the most strongly negative correlations for the most chronologies. In large snowpack years, the trees produce narrow rings because the snow persists longer into the summer and the growing season is shortened (Rochefort et al., 1994). Conversely, when snowpack is lower, the growing season for the trees will be longer, leading to wider annual rings. Many factors determine snowpack depth including temperature and the storm patterns, influenced at interannual and decadal scales by large-scale weather patterns including ENSO (as measured by SST), PDO, and ALPI. Warm winter temperatures yield reduced snowpack as more precipitation would fall as rain instead of snow, and snow already in place could begin to melt sooner. Positive values for each of the climate indices are associated with warm, dry winter conditions (reduced snowpack) in the Pacific Northwest (Shabbar and Khandekar, 1996; Shabbar et al., 1997; Beamish et al., 1997; Mantua and Hare, 2002). In my study, positive correlations were observed between winter temperature and ring widths, and between each of the climate indices and ring widths, suggesting again that reduced snowpack is favorable to tree growth at these high-elevation sites.

Lower elevation sites showed a smaller role for climate in determining annual tree growth. Despite cross-dating well, the subalpine fir chronologies for the two lower elevation, closed-canopy sites (Seton Ridge and Cinnabar Basin) exhibited no strong correlations (above or below 0.35/-0.35) with any of the climate variables and the whitebark pine chronologies did not cross-date at all. Since these two stands were within closed canopy forest it is more likely that biotic factors such as competition are playing the biggest role in tree growth (Callaway, 1998). Trees growing at or above treeline are growing at their ecological limit and are most sensitive to fluctuations in the climate (Fritts, 1976), which is illustrated by the number of strong correlations to climate variables that occurred for my high-elevation, open-canopy chronologies. Abiotic conditions are more important to these trees than biotic conditions are.

Whitebark pine showed a stronger response to winter temperature, snowpack, and the ALPI than subalpine fir at all high elevation sites. The difference was most pronounced in the ALPI correlations. The location and intensity of the Aleutian low-pressure center (as measured by the ALPI), largely determines the nature of the winter climate system in the Pacific Northwest. When the pressure system is large, storms move into British Columbia from the southwest, instead of in a more westerly manner, bringing warmer air and less snow (Overland et al., 1999). The greater effect of the Aleutian Low, winter temperature, and snowpack on whitebark pine than on subalpine fir could be due to some difference in whitebark pine's physiology, perhaps relating to the species drought or shade tolerance, that makes it more susceptible to winter conditions. The difference could also be due to the spacing of the trees I observed in these stands (see Chapter 2). The spatial pattern of tree establishment can determine the upper tree line sensitivity to climate (Elliott, 2011). The whitebark pine in these stands are growing in the open away from other trees. As such, they are receiving the full brunt of winter storms and the resulting snowpack. The subalpine fir, which are growing close together, may be better able to tolerate the harsh winter conditions. Trees growing in tree islands are protected from wind and cold temperatures, and have reduced snowpack around them (Callaway, 1995; Maher et al., 2005), which could lead to a longer growing season than is experienced by the whitebark pine at the same sites.

Both tree species were more strongly affected by PDO and SST at certain sites. Winter PDO was most strongly positively correlated with both McGillivray Pass chronologies and the whitebark pine chronology from Downton Creek. Again, snowpack appears to be an important factor. The stands at McGillivray Pass and Downton Creek are both on similar south-southwest aspects and receive equivalent annual precipitation as snow according to ClimateWNA. Western aspects typically receive less snowfall than eastern aspects during winter (Golding, 1974) and trees at sites with similar precipitation characteristics often show similar correlations between annual ring growth (Ettl and Peterson, 1995a; Peterson et al., 2002). Only the subalpine fir chronology at Downton Creek correlating with winter PDO (instead of both chronologies, as occurred at McGillivray Pass) could again be due to tree spacing (see Chapter 2). The trees at Downton Pass are more closely spaced than at McGillivray Pass. Thus, they are generally more protected and may be less affected by winter conditions.

Site differences in tree spacing could explain the strong positive correlations of previous summer, fall, and current winter SST with both Texas Creek Chronologies and the McGillivray Pass whitebark chronology. Both McGillivray Pass and Texas Creek had greater distances between trees than Blowdown Pass or Downton Creek (see Chapter 2). Since the trees at these two sites are growing further apart they would be less protected and more vulnerable to changing weather conditions. Previous summer and fall SST conditions appear to be just as important to tree growth as winter SST conditions at these sites. Typical El Niño and La Niña events (extreme high and low phases of ENSO, respectively) tend to develop during the summer to early autumn, mature during the winter, and terminate the following spring (Shabbar et al., 1997), whereas PDO and Aleutian Low are more commonly associated with just the winter months (Mantua and Hare, 2002; Beamish et al., 1997; Overland et al., 1999).

EPS and Snowpack

The low EPS values I observed were surprising since my interseries correlations were high. The EPS is determined by the number of cores, the common variance of the chronology, and the method of standardization used (Briffa, 1984; Wigley et al., 1984). Briffa (1984) recommends no fewer than 5 cores should be used for constructing chronologies, while Wigley et al. (1984) and Cook and Kairiukstis (1990) show that as few as 4 trees can potentially be used for climate reconstructions. My sample sizes were larger than this. Even my chronologies constructed from the fewest number of cores (N=15) were above this level, and the rest of my chronologies had sample sizes greater than 20 (Table 3.2), so sample size is not likely contributing to the low EPS observed. Likewise, the interseries correlations calculated for each chronology were all above 0.45, suggesting that a lack of common variance in the chronology is not an issue. For my method of standardization I used a horizontal line through the mean, which is one of the most conservative forms of standardization and is likely not leading to the low EPS values observed.

The fact that my observed EPS values fluctuated widely through time suggests that the strength of the factors influencing tree growth is changing over time as well (Bethany Coulthard, personal communication). The bootstrapped correlation values calculated from bootRes showed that the strength of the chronology correlation with snowpack changed over time (Appendix IV). This illustrates the control that the variation in snowpack has on the strength of the correlation between snow and ring widths from year to year. This variation over time can explain the generally low and fluctuating EPS values observed in this study.

Across the chronologies for all sites and species, two general patterns emerged in the comparison of the correlation coefficients with the snowpack data. For low snowpack months (November and February), weak correlation coefficients (weakly positive, zero, or weakly negative, depending on chronology) were associated with low monthly snowfall over time. During periods of high snow, the correlation coefficients become more strongly negative. For high snowpack months (December and especially January), the same general pattern occurred until around 1970. At this point, correlation coefficients became strongly negative even though the average snow decreased, opposite to the pattern observed for November and February snow, and that observed earlier in the December and January correlations. Sometime around 1970, the average annual snowpack started declining to values below anything seen since 1917 (when snowpack records began for Lillooet; Figure 3.5). Since December and January contribute the most to the annual snowpack in this area (Figure 3.5), declining snow in these months leads to a diminished annual snowpack. The results of my correlations with climate variables (see previous section) suggest that snowpack is the most significant limiting factor to annual tree growth in the southern Coast Mountains. This suggests that lower snowpack should benefit trees, but only to a point. When the snowpack falls below a certain level, like that observed since around 1970, it is actually leading to reduced tree growth (as evidenced by the strong negative correlation coefficients).

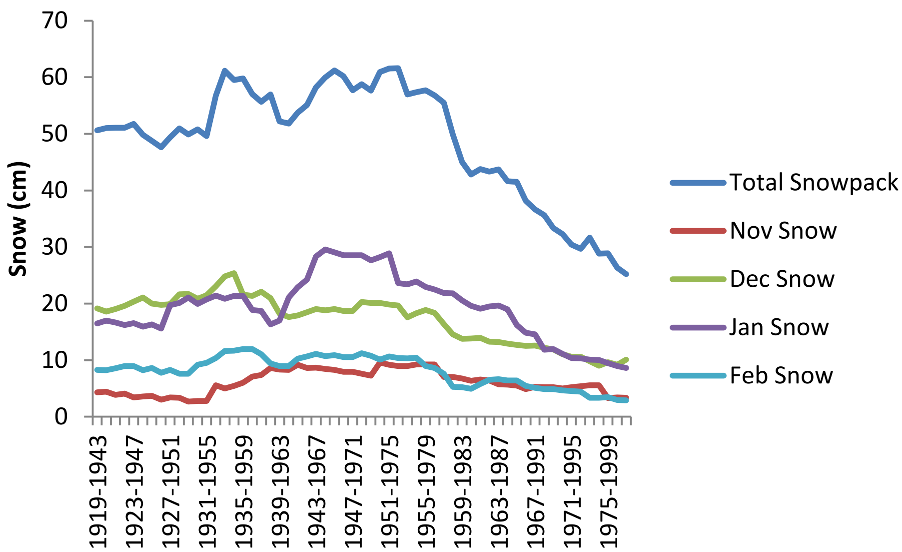

Figure 3.5. Twenty-five year running average of the monthly snowfall and total annual snowpack at Lillooet, BC since records began. Around 1970, total snowpack declines sharply to values well below anything seen in the twentieth century.

This shift in the trees' annual growth response could be due to drought stress (Wilmking et al., 2004). Lower annual snowpack means less meltwater and lower soil moisture during the growing season. However, there was no evidence of negative effects of high temperature or low precipitation on annual tree growth in any of the correlations I ran, and the PDSI (a drought index) was not strongly correlated with any of my chronologies. Another possible mechanism is through snow protection of the trees in the winter. Snowpack can insulate vegetation from extreme temperatures and protect it from scouring winds during the winter months (Kharuk et al., 2010). If snowpack is much reduced, trees (especially the smallest ones) would be subjected to harsh conditions throughout the winter (McLane and Aitken, 2012), which could leave them stressed and diminish their annual growth later in the season.

Conclusion

Differences in the age distributions of each species suggest that whitebark pine senescence at lower elevation sites may be due to successional advancement to subalpine fir. As subalpine fir encroaches into higher elevations, it may limit whitebark pine regeneration, which could reduce the species' ability to migrate in the face of climate change. Results of the dendrochronological study show that winter conditions, especially snowpack, are the most limiting to the annual growth of both tree species in the high-elevation stands. Interannual and interdecadal warm/dry climate patterns associated with the ALPI, ENSO and PDO enhance annual tree growth. Whitebark pine annual growth is more strongly affected by winter temperature, snowpack, and ALPI than subalpine fir growth across all high elevation sites included in the study. In the lower elevation, closed-canopy stands, biotic factors like competition and disease were likely more important than climate in determining annual tree ring growth for individuals of both species. The bootstrapped climate correlations revealed that changing snow cover levels over time limit annual tree growth in different ways. Prior to 1970, large December and January snowpack was strongly negatively correlated to annual growth and low December and January snowpack was correlated with increased annual growth. After about 1970, when annual snowpack in the area began dropping below levels ever recorded, annual tree growth became strongly negatively correlated to reduced snowpack, suggesting that subalpine trees require a balance between too much snow (short growing season) and too little snow (damage from freezing and wind scouring).

Chapter 4: General Discussion

Summary of Results

My results highlight the importance of both biotic and abiotic factors in the whitebark pine communities of the southern Coast Mountains of British Columbia. The results of the tree community spatial pattern study (Chapter 2) show that whitebark pine in this area are not facilitating the recruitment of other subalpine tree species, as has been seen in the Rocky Mountains (Callaway, 1998; Resler and Tomback, 2008). Nevertheless, mature subalpine fir may be facilitating the establishment of other subalpine fir in tree islands in these same stands. The results of the understory vegetation sampling show that differences in vegetation communities are due mainly to site characteristics. Evidence of distinct understory communities beneath whitebark pine and subalpine fir was weak. The results of the age distribution comparisons (Chapter 3) show that whitebark pine senescence at lower elevations may be due to successional advancement to subalpine fir. Subalpine fir is currently expanding in some of the high elevation sites, which could reduce whitebark pine recruitment at these sites in the future.

Abiotic factors are important in these stands as well. Results of the dendrochronological study (Chapter 3) show that winter conditions, including temperature and snowpack, are the most limiting to the annual growth of both tree species in the high-elevation stands. The Aleutian Low Pressure system, and to a lesser extent ENSO and PDO, are influencing annual tree growth over interannual, interdecadal, and even multidecadal scales through improved growth during warmer and drier climate cycles. The investigation into my low and fluctuating EPS values led to the discovery of the importance of changing snow cover levels on annual tree growth. However, in the lower elevation, closed-canopy stands, biotic factors like competition and disease were more important than climate in determining annual tree ring growth.

The Future of Whitebark Pine

My results provide valuable information for the conservation of whitebark pine in an understudied part of its range, the southern Coast Mountains. Overall, the populations of whitebark pine growing at the high elevation sites were in very good condition, with no major widespread mortality. It appears that these trees have largely escaped blister rust infections, which suggests they may have some genetic resistance to the fungus (Arno and Hoff, 1989). This would make them ideal candidates for seed collection and propagation in nurseries, which can then be replanted in parts of whitebark pine's range that have experienced greater mortality. At the lower elevation sites in my study area, the whitebark pine are in poor health and my age structure results show virtually no regeneration of the species for many decades, likely due to successional advancement and increased competition with subalpine fir. As subalpine fir encroaches into the high elevation sites, whitebark pine regeneration there may be reduced as well. Measures may need to be taken to prevent the loss of valuable seed resources and the overall good health of the whitebark pine growing in these high elevation sites.

The results of my dendrochronological study supply important information on how whitebark pine communities may respond to future anthropogenic climate change in the southern Coast Mountains. Three different General Circulation Models (GCMs) applied to western North America predict warmer and wetter conditions in the coming decades (Wang et al., 2012b). My results suggest that, at least initially, warmer temperatures are likely to benefit whitebark pine by reducing snowpack and lengthening the growing season. Currently, all six sites have mean annual temperatures around 0^{o}C. Even the most conservative model shows increases in temperature of 2-3^{o}C by the 2080s, and the least conservative model shows increases of 5-6^{o}C by the 2080s. Changes of that magnitude in such a short time will likely have consequences for subalpine trees and the understory plant communities.

Wetter conditions may be of even more concern. Demographic, dendroecological, and physiological data indicate that changes in the distribution and abundance of subalpine tree species in western North America in a warmer climate will depend just as much, if not more, on precipitation patterns as on temperature (Peterson, 1998). In moist areas, whitebark pine is most abundant on warm, dry exposures (Arno and Hoff, 1989) and its abundance diminishes as precipitation and humidity increase at more northerly latitudes (Tomback et al., 2011). In the Coast Mountains, whitebark pine is already only a minor component of subalpine forests due to the wet maritime climate (Arno and Weaver, 1990; Tomback et al., 2011). Increasingly wet conditions in the Coast Mountains could lead to the extirpation of the species entirely.

It is not only increased precipitation that needs to be taken into account, but the nature of the precipitation. My results suggest that whether the precipitation falls as rain or snow will have different impacts on whitebark pine. The three models described by Wang et al. (2012b) show increased total precipitation, but drastically reduced snowpack by the 2080s. This suggests that a greater portion of the winter precipitation will fall as rain rather than snow as winter temperatures rise above freezing. My results suggest that snowpack is the most limiting factor to tree growth in the Coast Mountains, especially to whitebark pine. Reduced snowpack could initially favor whitebark pine growth, as growing seasons are lengthened. However, the results of my EPS investigation revealed that reduced December and January snowpack since 1970 (Figure 3.5) is correlated with increasingly reduced annual tree growth (Appendix IV). It seems that there is a balance between too much snowpack and not enough in these high elevation environments. Too much snowpack limits tree growth through a shortened growing season. Too little snowpack limits tree growth through the loss of protection from freezing and wind scouring during the winter (McLane and Aitken, 2012). Snowpack in the Coast Mountains has been falling steadily since about 1970. If it drops even more in the coming decades, it will likely lead to severe impacts on whitebark pine growth and reproduction in the southern Coast Mountains.

In the face of changing climate there are three scenarios for tree populations: (1) persistence through adaptation, (2) persistence through migration, or (3) extirpation (Aitken et al., 2008). Whitebark pine is a very long-lived species, commonly living up to 1000 years, and sometimes beyond (Perkins and Swetnam, 1996; Smith et al., 2008). Current evidence indicates that long-lived species will be poor adaptors in the face of rapidly changing climate because their generation time will likely be too long for climate-related traits to develop at a sufficient rate (Romme and Turner, 1991; Krakowski et al., 2003; Aitken et al., 2008). Because whitebark pine is so long-lived, mature trees could persist for decades after the climate becomes unsuitable for the regeneration of their offspring. These populations may appear to be stable, but any disturbance (such as a high-intensity forest fire, pine beetle outbreak, blister rust infection, etc.) could completely wipe them out (Romme and Turner, 1991).

In the case of whitebark pine, the species is already at a further disadvantage. Several studies have shown that whitebark pine's genetic variability is very low at all scales, ranging from small groups of trees to the entire species' range (Furnier et al., 1987; Jorgenson and Hamrick, 1997; Rogers et al., 1999; Richardson et al., 2002a; Krakowski et al., 2003). This is due mostly to the patchy nature of the whitebark pine distribution. Many populations are small and geographically isolated meaning that pollen—which is the primary means of gene flow (Richardson et al., 2002a)—plays only a small role in increasing genetic diversity, and there is pronounced inbreeding within populations (Krakowski et al., 2003). A general pattern of reduced genetic variability at tree species' northern boundaries (Davis and Shaw, 2001) could complicate matters further. Krummholz whitebark pine has been found to have more genetic variability than upright whitebark pine tree clumps, suggesting that krummholz whitebark pine may have the genetic potential to respond to favorable shifts in climate (Rogers et al., 1999). However, krummholz whitebark pine has also been found to have higher levels of blister rust infection and mortality (Resler and Tomback, 2008), so the point may be moot.

Dispersal to more suitable climatic conditions is another possibility for the persistence of whitebark pine, but a whole new suite of factors can limit dispersal ability, including dispersal distance and degree of range fragmentation (Aitken et al., 2008). Two factors relating to the very nature of whitebark pine's life history and biogeography will hamper its ability to migrate northward and upward in response to warming temperatures. The first factor is that whitebark pine is co-evolved with Clark's Nutcrackers (Hutchins and Lanner, 1982; Tomback, 1982), and dispersal and caching of whitebark pine seeds by nutcrackers is the only natural mechanism by which whitebark pine can migrate (Furnier et al, 1987; Krakowski et al., 2003). Current estimates of the migration rates necessary for tree species to keep up with shifting temperature isolines were in excess of 1000 meters per year (Malcolm et al., 2002). In contrast, nutcrackers tend to cache seeds close to the trees from which they collect them (Richardson et al., 2002b), although a maximum caching distance of 22 kilometers was recorded for a nutcracker caching piñon pine seeds in Arizona (Vander Wall and Balda, 1977). Evidence suggests that co-evolved species will not respond in the same way to climate change, resulting in increasingly negative asynchronies between them (Parmesan, 2006). Migration of co-evolved communities will be limited by the slowest species, and could result in drastically different community composition and function (Malcolm et al., 2002).

Even if nutcracker caching was able to keep up with the pace of climate warming, another factor comes into play: the highly fragmented nature of whitebark pine distribution. There are often large areas of unsuitable habitat between populations of whitebark pine that already impose a significant barrier to nutcracker seed dispersal (Richardson et al., 2002b). As a subalpine species, whitebark pine is already near the altitudinal limit on mountains, and opportunities for upward migration will be fewer and fewer if climate continues to warm. To further complicate matters, whitebark pine exhibit a delay in seed germination of 1-3 years. Whitebark pine appear to only reproduce and recruit when conditions are suitable, meaning that regeneration of the species is infrequent and very unpredictable (Tomback et al., 2001b). My results suggest that whitebark pine recruitment may be limited by subalpine fir encroachment. This, in conjunction with mortality from mountain pine beetle outbreaks and blister rust infections, may severely depress seed production (Tomback et al., 1995; McKinney and Tomback, 2007). The net effect is that whitebark pine will likely have limited dispersal ability (Krakowski et al., 2003) and may fail to arrive to take advantage of the newly appropriate climatic conditions at higher altitudes (where available) and latitudes.

Extirpation

All of the available literature on whitebark pine focuses on different aspects of the species, but there is a consensus on one point: the outlook for the species is dire and getting worse. The reduction or loss of whitebark pine would have important impacts on the composition of wildlife and plants, and on the function of the high-elevation communities it inhabits. As mentioned previously, whitebark pine is a keystone species and many different animals and plants depend on its presence. If whitebark pine populations and cone crops are severely reduced, population reductions for several bird and mammal species, especially red squirrels, Clark's Nutcrackers, and grizzly bears would also be expected (Hutchins and Lanner, 1982; Tomback, 1982; Keane et al., 1990). Some of the species that rely on whitebark pine, such as grizzly bears, are themselves keystone species with a whole different suite of species that rely on them (Tardiff and Stanford, 1998). Thus, the loss of whitebark pine would have cascading effects in the ecosystem beyond just the species that directly rely on them for food and shelter (Ellison et al., 2005). In addition, when whitebark pine seeds are scarce, grizzly bears tend to spend more time in the vicinity of roads and town sites, as they search for alternate food sources (Mattson and Reinhart, 1997). This could lead to increased instances of human-grizzly contact, which is generally not favorable for either species.

The poor condition of current whitebark pine stands, in addition to the species' low ability to adapt and disperse naturally in the face of rapid anthropogenic climate warming, means that extirpation is very likely without some sort of human involvement. Populations at the greatest risk of mortality from blister rust (i.e. Canada/United States border) should be targeted for rust-resistant seed collection, propagation, and planting, and natural fire intervals should be allowed to return—or artificially maintained through prescribed burning—where human activities are not at risk (Keane et al., 1990; Krakowski et al., 2003). Silvicultural thinning may be a good option for those areas that cannot be easily or safely burned (Keane et al., 2007). Facilitated migration, a controversial method in which seedlings are planted several hundred kilometers north of their current range to mitigate climate change, may become necessary if this species is to survive into the future (Krakowski et al., 2003; Aitken et al., 2008).

Research Challenges

One of the biggest challenges of working in the mountains is a very short time frame in which to conduct fieldwork. Snowmelt in the Coast Ranges typically occurs from mid-June to early July, but when a larger-than-normal snowpack occurs snowmelt date can be pushed back even farther. I happened to conduct my MSc. fieldwork during two big snowpack years in the Coast Mountains. A La Niña weather pattern combined with cool spring temperatures prior to the 2011 season led to an especially large snowpack. Snowpack in the South Coast region of British Columbia was 281% of normal on June 1, 2011 and snowmelt was delayed by 3-4 weeks (Ministry of Forests, Lands, and Natural Resource Operations, 2011). This led to an extremely short field season in which I essentially only scouted potential locations for whitebark pine and collected some preliminary data. Sites I had planned to visit on the west side of the Coast Mountain Divide near Whistler, BC remained under snow the entire season.

The 2012 field season was only slightly better. June 1, 2012 snowpack was 153% of normal, and snowmelt was delayed by 2-3 weeks due to cool, wet spring conditions in the South Coast region (Ministry of Forests, Lands, and Natural Resource Operations, 2012). This led to another short field season in which to collect the remainder of my data. Thus, my biggest research challenge was balancing the amount of data I could collect with the amount of time and resources I had. I made the decision to sacrifice collecting certain data (soil samples, extra tree cores, visiting extra sites, etc.) in order to increase my sample sizes at the 6 sites I had visited during the 2011 field season. Because of this, I am only able to hypothesize about certain outcomes of my research (i.e. abiotic differences experienced by the understory vegetation beneath whitebark pine and subalpine fir).

Future Directions

As with any research, this project raises some interesting questions. Some of these are:

(1) Why isn't subalpine fir growing in tree islands around whitebark pine in the southern Coast Mountains? This is the predominant pattern in mixed high-elevation stands in the Rocky Mountains. Why doesn't it occur here?

(2) Do the growing conditions experienced by the vegetation beneath whitebark pine and subalpine fir differ? This would involve measuring canopy height of each species, collecting and analyzing soil and litter samples from beneath each species, and assessing the light levels beneath each species' canopy.

(3) Is whitebark pine and subalpine fir establishment tied to the same climate variables as their annual growth? To determine this, cores would need to be taken at the base of trees to determine their exact ages. Peaks in establishment could then be correlated to the same climate variables used in this study.

(4) What do tree spatial patterns and understory vegetation look like in mixed whitebark pine/subalpine fir stands in the wettest parts of its range, west of the study area? Is the annual growth of these stands correlated to the same climate variables? Answering these questions would have big implications for how these communities may respond to the predicted future wetter climate.

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Supporting Information

Appendix I—Complete Species List

Rare	
DRBO	*Draba borealis*
PHSE	*Phacelia sericea*
SAXI	*Saxifraga* spp.
FORB3	Unknown forb
VIAD	*Viola adunca*
CIED	*Cirsium edule*
MITR	*Mitella trifida*
FORB1	Unknown forb
CRAT	*Crepis atrabarba*
ARLA	*Arnica latifolia*
SARI	*Salix richardsonii*
CRFR	*Crystopsis fragilis*
LUAR2	*Luzula arcuata*
MIPE	*Mitella petandra*
FORB2	Unknown forb
PERA	*Pedicularis racemosa*
SANI	*Salix niphoclada*
PIAL_COVER	*Pinus albicaulis* (whitebark pine tree cover over subalpine fir)
JUPA	*Juncus parryii*
POPRAL	*Poa pratensis* ssp. *alpigena*
SOSC	*Sorbus scopulina*
SIHY	*Sitanion hystrix*
POWH	*Poa wheeleri*
CACALA	*Calamagrostis canadensis* var. *langsdorfii*
SEDI	*Sedum divergens*
SHCA	*Sherperdia canadensis*
POPU	*Polemonium pulcherillum*
PHAL	*Phleum alpinum*
CAHO	*Carex hoodii*
TACE	*Taraxacum ceratophorum*
EPLA	*Epilobium lactiflorum*
SABR	*Saxifraga bronchialis*
HALY	*Happlopappus lyallii*
VEVI	*Veratrum viride*

ARDR	*Arabis drummondii*
LUSP	*Luzula spicata*
PHEM	*Phyllodoce empetriformis*
PHGL	*Phyllodoce glanduliflora*
HIGR	*Hieracium gracile*
MYLA	*Myosotis laxa*

Sub-dominant

POFL	*Potentilla flabellifolia*
BRSI	*Bromus sitchensis*
PIAL	*Pinus albicaulis* (seedlings)
LUHI	*Luzula hitchcockii*
SETR	*Senecio triangularis*
VACC	*Vaccinium* spp.
SAOC	*Saxifraga occidentalis*
BRVU	*Bromus vulgaris*
ABLA	*Abies lasiocarpa* (seedlings)
FESTU	*Festuca* spp.
CASP	*Carex spectabilis*
VACA	*Vaccinium caespitosum*
ERUM	*Eriogonum umbellatum*
VASC	*Vaccinium scoparium*
LUCA	*Luzula campestris*
POAL	*Poa alpina*
DAIN	*Danthonia intermedia*
CIHO	*Cirsium hookerianum*
CAPH	*Carex phaeocephala*
AGGL	*Agoseris glauca*
VASI	*Valeriana sitchensis*
CEAR	*Cerastium arvense*
SIPR	*Sibbaldia procumbens*
ARCO	*Arnica cordifolia*
GEAM	*Gentianella amarella*
ASMO	*Aster modestus*
PIAL_MID	*Pinus albicaulis* (saplings)
LICO	*Lilium columbianum*
DEME	*Delphinium menziesii*
MESU	*Melica subulata*
VAME	*Vaccinium membranaceum*
ARUV	*Arctostaphylos uva-ursi*
PEPR	*Penstemon procerus*
ANOC	*Anemone occidentalis*
CLLA	*Claytonia lanceolata*

CAMI	*Castilleja miniata*
PEBR	*Pedicularis bracteosa*
AQFO	*Aquilegia formosa*
HEMA	*Heracleum maculatum*
AGAU	*Agoseris aurantiaca*
ELGL	*Elymus glaucus*
ARPA	*Arnica parryii*
ERGR	*Erythronium grandiflorum*
MAST	*Maianthemum stellatum*
ANMI	*Antennaria microphylla*
JUCO	*Juniperus communis*
ABLA_MID	*Abies lasiocarpa* (saplings)
POCUEP	*Poa cusickii* ssp. *epilis*
POCUPA	*Poa cusickii* spp. *pallida*
VIGL	*Viola glabella*

Dominant

SOMU	*Solidago multiradiata*
SELA	*Sedum lanceolatum*
ASFO	*Aster foliaceous*
FRVI	*Fragaria virginiana*
POCUPU	*Poa cusickii* spp. *purpurescens*
ARMO	*Arnica mollis*
CARO	*Carex rossii*
PODI	*Potentilla diversifolia*
SEIN	*Senecio integerrimus*
LUAR	*Lupinus arcticus*
ACMI	*Achillea millefolium*
EPAN	*Epilobium angustifolium*
THOC	*Thalictrum occidentalis*
TRSP	*Trisetum spicatum*
ERPE	*Erigeron peregrinus*
ARNO	*Artemisia norvegica*
SIDO	*Silene douglasii*
ARCA	*Arenaria capillaris*
PHDI	*Phlox diffusa*

Appendix II—SIMPER Results

SIMPER results showing the percentage contributions (up to 90%) of each species to the overall pattern observed between sites and between whitebark pine and subalpine fir at each site. Av.Abund is the average abundance of each species. Av.Diss is the average dissimilarity of each species' abundance under the two different tree species. Diss/SD is the average dissimilarity (previous column) divided by the standard deviation of each dissimilarity across all pairs of samples. Contrib% is the percentage each species contributed to the observed dissimilarity between whitebark pine and subalpine fir communities. Cum.% is the cumulative percentage of each species' contributions to the dissimilarities between the two tree species. WP=Whitebark pine. SF=Subalpine fir. A complete list of plant codes is available in Appendix I.

Site Differences

Groups Texas & Downton

Average dissimilarity = 81.46

	Group Texas	Group Downton				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
PHDI	1.3	2.54	5.97	1.28	7.33	7.33
EPAN	0.75	1.21	4.3	0.99	5.28	12.61
ARNO	0	1.39	4.26	1.05	5.24	17.84
JUCO	0.38	1	3.58	0.65	4.39	22.24
THOC	0.94	0.45	3.26	0.89	4.01	26.24
LUAR	1.06	0	3.1	0.9	3.81	30.05
ARCA	0.78	0.93	3.04	1.07	3.73	33.78
FRVI	0.21	0.89	2.97	0.77	3.65	37.43
ERPE	0.67	0.76	2.89	0.96	3.55	40.98
SOMU	0.05	0.88	2.69	0.77	3.3	44.28
POCUEP	0	0.75	2.48	0.9	3.04	47.32
SIDO	0.28	0.81	2.46	1.03	3.02	50.34
POCUPA	0.76	0	2.38	0.86	2.93	53.27
ARUV	0.21	0.65	2.34	0.53	2.87	56.14
ACMI	0.37	0.69	2.22	0.99	2.73	58.87
TRSP	0.25	0.69	2.14	1.07	2.62	61.5
SEIN	0.69	0.06	2.06	0.75	2.53	64.03
ARCO	0.54	0	1.82	0.48	2.23	66.26
VACA	0	0.59	1.77	0.46	2.18	68.44
VASC	0.51	0	1.72	0.43	2.11	70.55
PODI	0.32	0.39	1.66	0.81	2.04	72.58
ERGR	0.27	0.23	1.28	0.59	1.57	74.15
CARO	0.11	0.33	1.26	0.57	1.55	75.7
ARPA	0.4	0	1.21	0.53	1.49	77.19

VACC	0.3	0	0.98	0.35	1.2	78.39
ANOC	0	0.3	0.9	0.35	1.1	79.49
PHGL	0	0.24	0.88	0.24	1.08	80.57
PHEM	0	0.29	0.88	0.25	1.08	81.66
DAIN	0	0.3	0.86	0.42	1.06	82.71
VASI	0.08	0.22	0.85	0.31	1.04	83.75
ARMO	0	0.25	0.79	0.49	0.97	84.72
ASMO	0.26	0	0.78	0.31	0.95	85.67
DEME	0.27	0	0.77	0.56	0.95	86.62
CAMI	0.25	0.01	0.74	0.5	0.91	87.54
CLLA	0.22	0.01	0.7	0.61	0.86	88.39
ANMI	0.06	0.18	0.67	0.48	0.83	89.22
CASP	0	0.22	0.65	0.44	0.8	90.01

Groups Texas & Blowdown
Average dissimilarity = 81.42

	Group Texas	Group Blowdown				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
ARNO	0	2.1	7.1	1.84	8.71	8.71
PHDI	1.3	2.55	5.85	1.25	7.18	15.89
LUAR	1.06	0.53	3.78	0.99	4.65	20.54
ARMO	0	1.01	3.46	1.1	4.25	24.79
ARCA	0.78	1.3	3.44	1.26	4.23	29.02
ERPE	0.67	0.98	3.3	1.07	4.06	33.07
CARO	0.11	0.96	3.23	1.16	3.97	37.04
SEIN	0.69	0.93	3.17	1.24	3.9	40.94
THOC	0.94	0	2.98	0.78	3.66	44.6
VAME	0	0.83	2.9	0.63	3.56	48.17
SIDO	0.28	0.94	2.87	1.18	3.52	51.69
EPAN	0.75	0.04	2.54	0.69	3.12	54.81
POCUPA	0.76	0	2.43	0.9	2.98	57.79
POCUPU	0	0.64	2.19	0.96	2.69	60.48
ARCO	0.54	0.02	1.88	0.5	2.31	62.79
ANOC	0	0.57	1.78	0.52	2.19	64.98
VASC	0.51	0	1.75	0.45	2.15	67.13
JUCO	0.38	0.2	1.74	0.38	2.14	69.27
PODI	0.32	0.38	1.7	0.86	2.08	71.35
PEPR	0.02	0.43	1.41	0.54	1.73	73.08
ACMI	0.37	0.1	1.23	0.75	1.52	74.59
ARPA	0.4	0	1.23	0.55	1.52	76.11
TRSP	0.25	0.17	1.03	0.71	1.26	77.37
LUHI	0.13	0.13	1.01	0.27	1.24	78.61

VACC	0.3	0	1	0.36	1.23	79.83
CAMI	0.25	0.08	0.95	0.54	1.17	81
PEBR	0.17	0.13	0.86	0.43	1.06	82.06
FRVI	0.21	0.1	0.85	0.55	1.04	83.1
ERGR	0.27	0.03	0.82	0.54	1.01	84.11
ASMO	0.26	0	0.79	0.32	0.97	85.09
DEME	0.27	0	0.79	0.57	0.97	86.06
SOMU	0.05	0.22	0.75	0.41	0.92	86.98
SIPR	0	0.24	0.75	0.5	0.92	87.9
SELA	0.04	0.21	0.74	0.66	0.91	88.81
CLLA	0.22	0.01	0.72	0.62	0.88	89.69
ANMI	0.06	0.17	0.71	0.55	0.87	90.56

Groups Downton & Blowdown
Average dissimilarity = 70.43

	Group Downton	Group Blowdown				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
ARNO	1.39	2.1	4.44	1.27	6.31	6.31
PHDI	2.54	2.55	4.13	1.12	5.86	12.16
EPAN	1.21	0.04	3.44	0.93	4.88	17.05
JUCO	1	0.2	2.97	0.58	4.22	21.27
ERPE	0.76	0.98	2.8	1.16	3.97	25.24
ARMO	0.25	1.01	2.75	1.1	3.91	29.15
CARO	0.33	0.96	2.7	1.19	3.84	32.99
SEIN	0.06	0.93	2.63	1.28	3.73	36.72
FRVI	0.89	0.1	2.57	0.79	3.65	40.37
SOMU	0.88	0.22	2.52	0.85	3.57	43.94
ARCA	0.93	1.3	2.51	1.14	3.56	47.5
VAME	0	0.83	2.48	0.64	3.52	51.02
SIDO	0.81	0.94	2.4	1.17	3.4	54.42
POCUEP	0.75	0	2.15	1.02	3.05	57.47
ANOC	0.3	0.57	2.07	0.63	2.93	60.41
ACMI	0.69	0.1	1.91	1.06	2.71	63.11
POCUPU	0	0.64	1.87	0.99	2.65	65.77
TRSP	0.69	0.17	1.81	1.14	2.57	68.34
ARUV	0.65	0	1.68	0.5	2.38	70.72
VACA	0.59	0	1.58	0.47	2.25	72.96
PODI	0.39	0.38	1.44	0.96	2.04	75.01
LUAR	0	0.53	1.42	0.46	2.01	77.02
PEPR	0.08	0.43	1.35	0.56	1.92	78.93
THOC	0.45	0	1.31	0.64	1.85	80.79
DAIN	0.3	0.04	0.85	0.46	1.21	82

ANMI	0.18	0.17	0.83	0.63	1.18	83.18
PHEM	0.29	0	0.79	0.26	1.11	84.3
PHGL	0.24	0	0.74	0.26	1.05	85.34
ERGR	0.23	0.03	0.7	0.42	1	86.34
SELA	0.06	0.21	0.7	0.67	0.99	87.33
SIPR	0.01	0.24	0.66	0.51	0.94	88.28
LUCA	0	0.21	0.59	0.47	0.83	89.11
CASP	0.22	0	0.58	0.44	0.82	89.93
VASI	0.22	0	0.57	0.27	0.82	90.75

Groups Texas & McGillivray
Average dissimilarity = 88.14

	Group Texas	Group McGillivray				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
THOC	0.94	2.59	7.37	1	8.37	8.37
VIGL	0	1.45	4.92	0.73	5.58	13.95
LUAR	1.06	1.58	4.76	1.14	5.4	19.35
PHDI	1.3	0.93	4.54	1.06	5.15	24.5
ASFO	0	1.51	4.21	1.24	4.77	29.27
EPAN	0.75	1.17	3.94	0.87	4.47	33.74
SIDO	0.28	1.16	3.08	1.04	3.49	37.23
AQFO	0	1.02	2.91	0.7	3.3	40.53
HEMA	0	1.05	2.88	0.72	3.27	43.8
ARNO	0	1.06	2.73	0.65	3.1	46.9
ASMO	0.26	0.72	2.43	0.52	2.75	49.66
POCUPA	0.76	0	2.3	0.82	2.62	52.27
ARCA	0.78	0	2.28	0.85	2.59	54.86
MAST	0	0.69	2.08	0.76	2.36	57.22
ELGL	0	0.71	2.05	0.77	2.32	59.54
ERPE	0.67	0.03	2.04	0.72	2.31	61.86
SEIN	0.69	0.01	1.95	0.71	2.22	64.07
ARPA	0.4	0.42	1.89	0.67	2.14	66.22
ARCO	0.54	0	1.76	0.46	2	68.21
VASC	0.51	0	1.66	0.42	1.88	70.1
CIHO	0	0.47	1.45	0.46	1.64	71.74
MESU	0	0.46	1.42	0.56	1.61	73.35
PEBR	0.17	0.41	1.41	0.53	1.6	74.95
JUCO	0.38	0.09	1.38	0.35	1.56	76.51
VASI	0.08	0.39	1.36	0.37	1.55	78.06
ACMI	0.37	0.14	1.23	0.73	1.4	79.45
LICO	0	0.45	1.22	0.62	1.38	80.84
VACC	0.3	0	0.95	0.34	1.07	81.91

PODI	0.32	0	0.94	0.51	1.06	82.97
CAMI	0.25	0.11	0.92	0.53	1.05	84.02
TRSP	0.25	0.12	0.86	0.64	0.97	84.99
ERGR	0.27	0.05	0.8	0.53	0.91	85.91
DEME	0.27	0	0.75	0.55	0.85	86.75
VEVI	0	0.2	0.68	0.24	0.77	87.52
CLLA	0.22	0	0.66	0.56	0.75	88.27
ARUV	0.21	0	0.63	0.22	0.72	88.99
AGAU	0.05	0.21	0.62	0.47	0.71	89.7
FRVI	0.21	0	0.59	0.44	0.67	90.37

Groups Downton & McGillivray
Average dissimilarity = 88.13

	Group Downton	Group McGillivray				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
THOC	0.45	2.59	6.54	1.1	7.42	7.42
PHDI	2.54	0.93	6.15	1.5	6.98	14.4
VIGL	0	1.45	4.12	0.83	4.68	19.08
ARNO	1.39	1.06	4.08	1.1	4.63	23.7
EPAN	1.21	1.17	3.69	1.04	4.19	27.9
ASFO	0	1.51	3.69	1.25	4.19	32.09
LUAR	0	1.58	3.67	0.9	4.16	36.25
SIDO	0.81	1.16	2.91	1.18	3.3	39.55
JUCO	1	0.09	2.63	0.55	2.98	42.53
AQFO	0	1.02	2.55	0.71	2.89	45.42
HEMA	0	1.05	2.53	0.72	2.87	48.29
ARCA	0.93	0	2.48	1.05	2.81	51.1
FRVI	0.89	0	2.4	0.72	2.72	53.82
SOMU	0.88	0.05	2.28	0.77	2.58	56.41
ERPE	0.76	0.03	2.07	0.85	2.34	58.75
POCUEP	0.75	0	2.04	0.92	2.32	61.07
ACMI	0.69	0.14	1.84	0.98	2.08	63.15
MAST	0	0.69	1.8	0.79	2.04	65.2
ELGL	0	0.71	1.79	0.77	2.03	67.23
TRSP	0.69	0.12	1.77	1.07	2.01	69.24
ASMO	0	0.72	1.67	0.43	1.9	71.14
ARUV	0.65	0	1.59	0.49	1.8	72.94
VACA	0.59	0	1.5	0.45	1.7	74.64
VASI	0.22	0.39	1.47	0.43	1.67	76.3
CIHO	0	0.47	1.25	0.47	1.41	77.72
MESU	0	0.46	1.23	0.56	1.39	79.11
LICO	0	0.45	1.08	0.62	1.22	80.33

PODI	0.39	0	1.01	0.7	1.15	81.48
PEBR	0.03	0.41	0.98	0.44	1.11	82.59
CARO	0.33	0.02	0.92	0.51	1.04	83.63
ARPA	0	0.42	0.92	0.43	1.04	84.67
ANOC	0.3	0	0.76	0.34	0.86	85.53
PHEM	0.29	0	0.74	0.25	0.84	86.37
DAIN	0.3	0	0.73	0.42	0.83	87.2
PHGL	0.24	0	0.71	0.24	0.8	88
ERGR	0.23	0.05	0.69	0.41	0.78	88.78
ARMO	0.25	0	0.66	0.5	0.74	89.53
VEVI	0	0.2	0.58	0.24	0.66	90.19

Groups Blowdown & McGillivray
Average dissimilarity = 89.51

	Group Blowdown	Group McGillivray				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
THOC	0	2.59	7.21	1.16	8.05	8.05
PHDI	2.55	0.93	6.43	1.67	7.19	15.24
ARNO	2.1	1.06	5.24	1.41	5.85	21.09
VIGL	0.01	1.45	4.17	0.87	4.66	25.75
LUAR	0.53	1.58	4.11	1	4.59	30.34
ASFO	0	1.51	3.77	1.29	4.21	34.56
ARCA	1.3	0	3.66	1.77	4.09	38.65
EPAN	0.04	1.17	3.17	0.97	3.55	42.19
SIDO	0.94	1.16	3.05	1.28	3.41	45.6
ARMO	1.01	0	2.86	1.09	3.19	48.79
ERPE	0.98	0.03	2.75	1.03	3.07	51.87
CARO	0.96	0.02	2.7	1.15	3.02	54.88
AQFO	0	1.02	2.6	0.73	2.9	57.79
HEMA	0	1.05	2.58	0.74	2.89	60.67
SEIN	0.93	0.01	2.57	1.24	2.88	63.55
VAME	0.83	0	2.39	0.62	2.67	66.22
MAST	0	0.69	1.84	0.81	2.05	68.27
ELGL	0	0.71	1.82	0.79	2.04	70.31
POCUPU	0.64	0.18	1.8	0.96	2.01	72.32
ASMO	0	0.72	1.71	0.43	1.91	74.23
ANOC	0.57	0	1.49	0.52	1.67	75.9
CIHO	0	0.47	1.27	0.48	1.42	77.32
MESU	0	0.46	1.25	0.57	1.4	78.72
PEBR	0.13	0.41	1.2	0.5	1.34	80.06
PEPR	0.43	0	1.15	0.52	1.29	81.35
LICO	0	0.45	1.1	0.63	1.23	82.57

VASI	0	0.39	1.06	0.35	1.18	83.75
PODI	0.38	0	1.05	0.74	1.17	84.92
ARPA	0	0.42	0.94	0.44	1.05	85.97
AGAU	0.19	0.21	0.85	0.64	0.95	86.92
JUCO	0.2	0.09	0.77	0.22	0.86	87.78
SELA	0.21	0.12	0.74	0.71	0.83	88.61
SOMU	0.22	0.05	0.64	0.38	0.72	89.33
SIPR	0.24	0	0.63	0.49	0.7	90.03

Canopy Species Differences

Groups Texas_WP & Texas_SF

Average dissimilarity = 77.31

	Texas_WP	Texas_SF				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
PHDI	1.37	1.23	5.25	1.14	6.79	6.79
THOC	1.34	0.54	5.19	0.99	6.71	13.5
LUAR	1.21	0.92	4.8	1.19	6.21	19.72
EPAN	0.73	0.77	4.06	0.94	5.25	24.97
ARCO	0.58	0.5	3.73	0.55	4.82	29.79
POCUPA	0.99	0.54	3.71	0.83	4.8	34.58
VASC	0	1.03	3.7	0.7	4.78	39.36
ARCA	0.88	0.68	3.54	1.07	4.58	43.94
SEIN	0.63	0.76	3.33	1	4.3	48.25
ERPE	0.64	0.69	3.24	0.93	4.2	52.45
JUCO	0.4	0.35	2.51	0.47	3.24	55.69
ARPA	0.5	0.31	2.36	0.73	3.05	58.74
VACC	0.49	0.1	2.33	0.49	3.01	61.75
ACMI	0.46	0.29	1.93	0.85	2.5	64.25
PODI	0.42	0.23	1.92	0.73	2.49	66.74
ASMO	0.33	0.2	1.77	0.44	2.28	69.02
SIDO	0.4	0.17	1.69	0.74	2.18	71.2
ARUV	0.43	0	1.67	0.33	2.16	73.37
DEME	0.39	0.14	1.58	0.75	2.04	75.41
TRSP	0.39	0.11	1.51	0.75	1.96	77.37
ERGR	0.31	0.22	1.49	0.69	1.93	79.29
CAMI	0.27	0.23	1.44	0.68	1.86	81.15
FRVI	0.26	0.15	1.27	0.62	1.64	82.79
CLLA	0.19	0.26	1.21	0.84	1.57	84.36
BRSI	0.24	0.12	1.15	0.49	1.49	85.85
LUHI	0.14	0.11	1.14	0.34	1.47	87.32
PEBR	0.16	0.18	1.09	0.45	1.41	88.74
AGGL	0.21	0.02	0.85	0.46	1.11	89.84

POAL	0.2	0.02	0.75	0.47	0.97	90.81

Groups Downton_WP & Downton_SF
Average dissimilarity = 68.04

	Downton_WP	Downton_SF				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
PHDI	2.13	2.96	4.89	1.16	7.19	7.19
ARNO	0.71	2.07	4.79	1.31	7.04	14.23
EPAN	1.75	0.68	4.28	1.25	6.29	20.52
JUCO	1.27	0.72	4.09	0.79	6.01	26.53
FRVI	1.34	0.44	3.5	1.04	5.15	31.68
VACA	0	1.19	3.27	0.73	4.8	36.48
SOMU	0.81	0.94	3.08	0.96	4.52	41.01
ARUV	1.14	0.16	2.88	0.75	4.23	45.24
ERPE	0.5	1.03	2.64	1.12	3.88	49.12
ARCA	0.9	0.95	2.49	1.14	3.65	52.77
SIDO	0.63	0.99	2.37	1.16	3.49	56.26
POCUEP	0.67	0.82	2.24	1.09	3.29	59.55
THOC	0.78	0.12	2.09	0.97	3.07	62.62
ACMI	0.87	0.51	2.03	1.15	2.99	65.61
TRSP	0.81	0.58	1.82	1.17	2.68	68.29
PHEM	0	0.58	1.62	0.37	2.38	70.67
ANOC	0.04	0.57	1.6	0.51	2.36	73.03
PHGL	0	0.48	1.56	0.37	2.29	75.31
CARO	0.24	0.42	1.53	0.71	2.25	77.56
PODI	0.28	0.51	1.5	0.98	2.21	79.77
DAIN	0.14	0.47	1.42	0.6	2.08	81.85
ERGR	0.08	0.39	1.24	0.58	1.82	83.68
ARMO	0.08	0.43	1.22	0.83	1.8	85.47
VASI	0.02	0.41	1.17	0.38	1.71	87.18
CASP	0.18	0.26	1	0.61	1.47	88.65
ANMI	0.19	0.16	0.81	0.58	1.18	89.83
CAPH	0.11	0.23	0.79	0.54	1.16	90.99

Groups Blowdown_WP & Blowdown_SF
Average dissimilarity = 51.88

	Blowdown_WP	Blowdown_SF				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
VAME	0.75	0.92	3.68	0.91	7.08	7.08
ARNO	1.94	2.26	3.46	1.15	6.66	13.75
PHDI	2.68	2.43	3.38	1.14	6.52	20.26

ERPE	1.08	0.88	2.98	1.22	5.74	26.01
ARMO	0.97	1.05	2.78	1.18	5.35	31.36
LUAR	0.92	0.15	2.71	0.69	5.23	36.59
ANOC	0.28	0.85	2.67	0.78	5.15	41.74
SIDO	1.06	0.82	2.53	1.26	4.87	46.61
CARO	0.85	1.07	2.52	1.21	4.85	51.46
SEIN	0.74	1.12	2.37	1.24	4.56	56.03
PEPR	0.67	0.19	2.1	0.79	4.05	60.08
ARCA	1.25	1.36	1.98	1.14	3.81	63.89
POCUPU	0.75	0.52	1.96	1.08	3.77	67.66
PODI	0.39	0.38	1.46	1	2.82	70.48
SIPR	0.32	0.16	1.12	0.72	2.16	72.64
SOMU	0.4	0.03	1.12	0.53	2.16	74.8
JUCO	0.12	0.29	1.1	0.27	2.12	76.92
LUCA	0.22	0.21	1.01	0.68	1.94	78.86
LUHI	0.26	0.01	0.95	0.25	1.83	80.69
AGAU	0.27	0.11	0.91	0.68	1.76	82.45
SELA	0.26	0.17	0.9	0.85	1.73	84.18
ANMI	0.21	0.14	0.85	0.68	1.64	85.82
ABLA	0.16	0.1	0.75	0.27	1.45	87.27
TRSP	0.17	0.17	0.75	0.68	1.44	88.71
PEBR	0.1	0.16	0.68	0.38	1.31	90.03

Groups McGillivray_WP & McGillivray_SF

Average dissimilarity = 69.57

	McGillivray_WP	McGillivray_SF				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
THOC	2.73	2.45	6.29	1.01	9.04	9.04
VIGL	1.1	1.81	4.7	1.02	6.76	15.8
LUAR	1.84	1.32	4.69	1.12	6.74	22.54
AQFO	1.22	0.82	3.6	0.94	5.17	27.71
ARNO	1.13	0.99	3.58	0.88	5.14	32.85
HEMA	1	1.11	3.53	0.97	5.07	37.91
ASFO	1.32	1.7	3.51	1.18	5.04	42.96
EPAN	1.35	1	3.45	1.04	4.96	47.92
PHDI	1.11	0.74	3.34	0.79	4.8	52.72
SIDO	1.08	1.25	3.21	1.17	4.61	57.33
ASMO	1.29	0.15	3.14	0.62	4.52	61.85
MAST	0.97	0.4	2.47	0.93	3.55	65.4
ELGL	0.87	0.55	2.36	0.95	3.39	68.79
CIHO	0.45	0.48	2.04	0.61	2.93	71.72
MESU	0.23	0.68	1.9	0.79	2.73	74.45

VASI	0.47	0.32	1.83	0.47	2.63	77.08
ARPA	0.53	0.3	1.59	0.62	2.29	79.37
LICO	0.44	0.46	1.59	0.84	2.28	81.65
PEBR	0.48	0.34	1.58	0.6	2.28	83.93
VEVI	0.26	0.15	1.07	0.34	1.54	85.47
AGAU	0.11	0.31	0.81	0.62	1.17	86.63
POCUPU	0.22	0.14	0.8	0.55	1.15	87.78
BRVU	0.14	0.22	0.73	0.5	1.05	88.83
SHCA	0	0.3	0.61	0.31	0.88	89.71
ACMI	0.24	0.05	0.6	0.56	0.86	90.57

Appendix III—All Correlation Coefficients

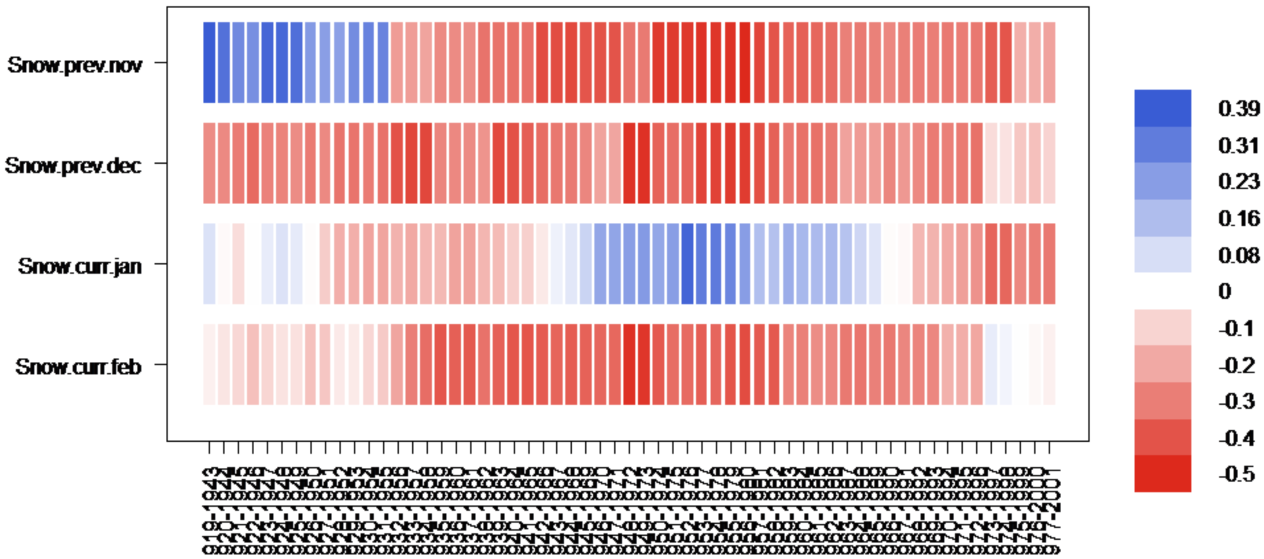
All correlation coefficients from the Pearson correlations between chronology ring widths and climate variables. Correlations above or below 0.35/-0.35 in **bold**. Lowercase seasons are from the previous year to ring growth. Uppercase seasons are from the current year of ring growth. Winter=December-February. Spring=March-May. Summer=June-August. Fall=September-November. Total snowpack refers to the October-April snowfall prior to ring growth. The ALPI is an annual index measured over the December-March period prior to ring growth. All correlations were done using the residual chronologies.

		Blowdown		Downton		McGillivray		Texas		Seton	Cinnabar
		WBP	SF	WBP	SF	WBP	SF	WBP	SF	SF	SF
Snowpack	Total	**-0.42**	-0.28	**-0.40**	-0.26	**-0.48**	-0.33	**-0.45**	**-0.36**	-0.20	-0.30
Temp	spring	0.08	**0.36**	0.20	0.20	0.22	0.15	0.28	0.30	0.04	0.02
	summer	-0.02	0	0.03	-0.12	0.04	-0.19	0.01	-0.06	-0.27	-0.18
	fall	0.33	0.28	0.17	**0.44**	0.27	**0.36**	**0.38**	**0.35**	0.26	0.30
	WINTER	**0.50**	**0.38**	**0.42**	0.28	**0.37**	0.25	**0.35**	0.15	0.18	0.15
	SPRING	0.33	0.28	0.17	0.03	0.19	0.03	0.22	0.20	-0.03	-0.02
	SUMMER	0.32	0.30	0.27	0.28	0.27	0.25	0.27	0.16	-0.04	0.25
	FALL	0.03	0.09	0	0.11	0.12	0.07	0.09	0.01	-0.06	0.07
PDO	spring	-0.02	0.27	0.12	0.14	0.23	0.22	0.15	0.21	0.13	0.13
	summer	0.07	0.21	0.22	0.23	0.24	0.28	0.18	0.15	0.22	0.21
	fall	0.18	0.19	0.27	0.28	0.31	**0.36**	0.31	0.31	0.29	0.34
	WINTER	0.25	0.29	**0.36**	0.20	**0.41**	**0.37**	0.33	0.31	0.22	0.18
	SPRING	0.23	0.30	0.25	0.11	0.30	0.25	0.26	0.26	0.14	0.12
	SUMMER	0.25	0.17	0.25	0.05	0.32	0.20	0.25	0.28	0.16	0.12
	FALL	0.06	-0.02	0	-0.07	0.14	0.07	0.07	0.12	0.04	0
SST	spring	0.07	0.22	0.06	0.17	0.12	0.16	0.15	0.24	0.11	0.09
	summer	0.30	0.33	0.29	0.30	**0.38**	0.31	**0.41**	**0.41**	0.21	0.23
	fall	0.32	0.29	0.31	0.30	**0.40**	0.31	**0.43**	**0.39**	0.19	0.27
	WINTER	0.30	0.25	0.27	0.29	**0.37**	0.32	**0.39**	**0.40**	0.17	0.28
	SPRING	0.24	0.13	0.19	0.10	0.31	0.24	0.30	**0.37**	0.06	0.21
	SUMMER	0	-0.04	-0.04	-0.09	0.09	0.04	0.01	0.10	-0.10	0.07
	FALL	-0.04	-0.08	-0.06	-0.12	0.02	-0.03	-0.06	0.03	-0.12	0.02
ALPI	Annual	**0.37**	0.21	**0.40**	0.15	0.33	0.10	**0.35**	0.14	0.01	0.01

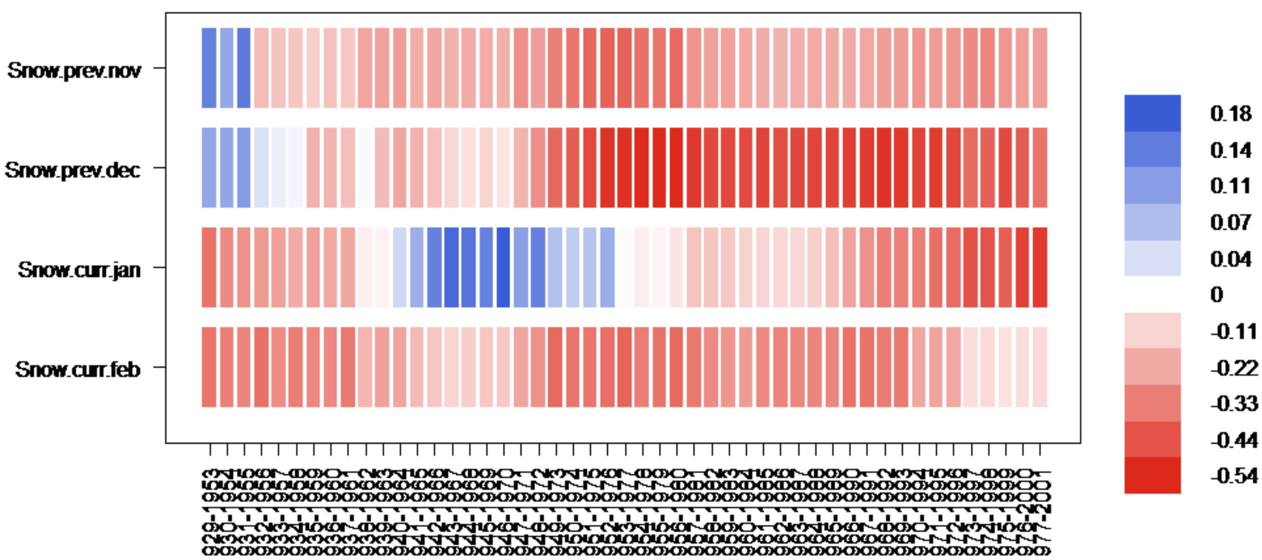
Appendix IV—Bootstrapped Correlations with Snowpack

Bootstrapped correlations with snow from the R program bootRes. The strength and direction (+/-) of the correlation change over time.

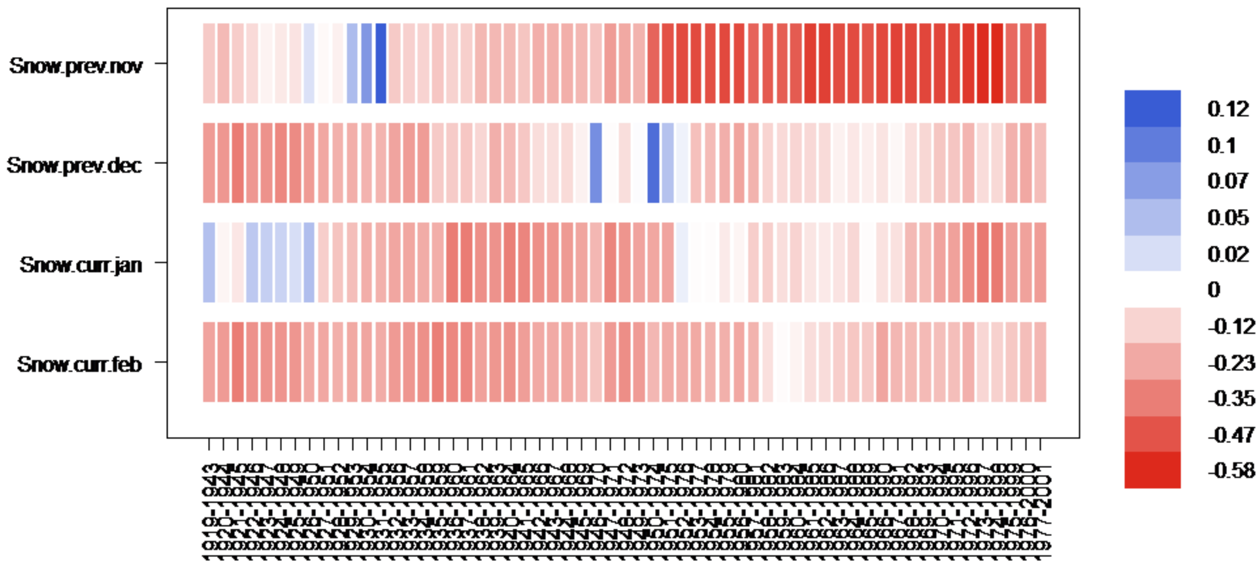
Blowdown Pass Subalpine Fir



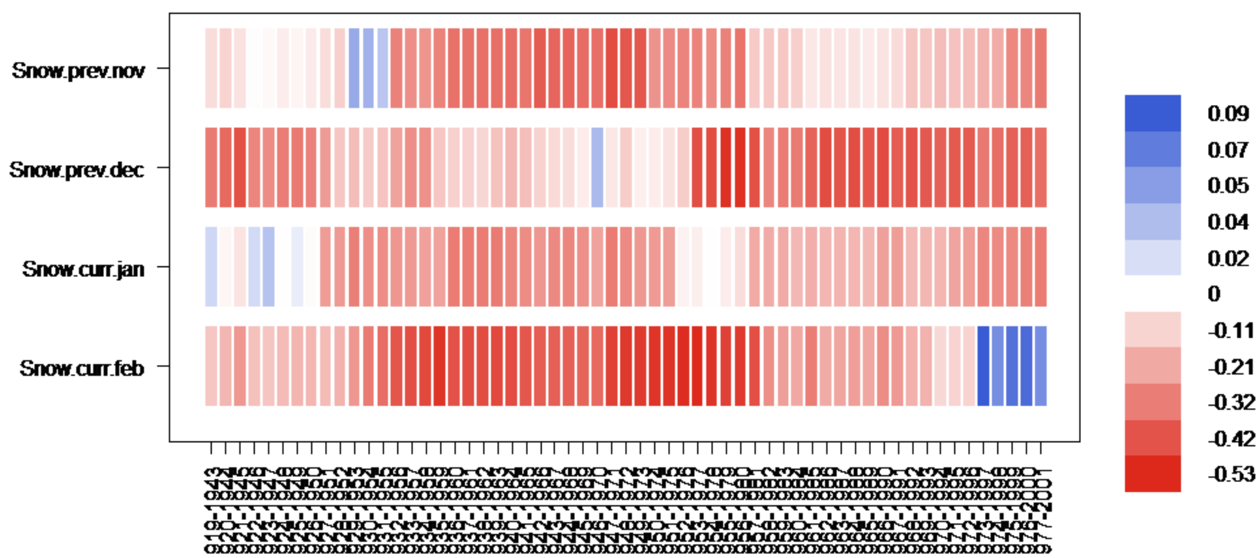
Blowdown Pass Whitebark Pine



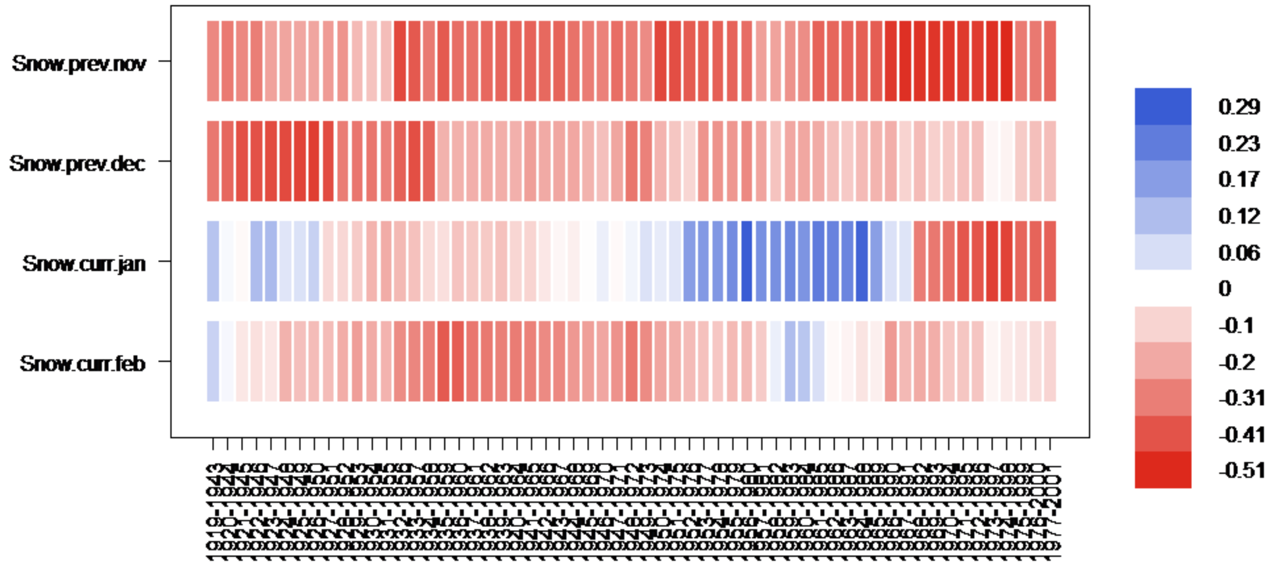
Texas Creek Subalpine Fir



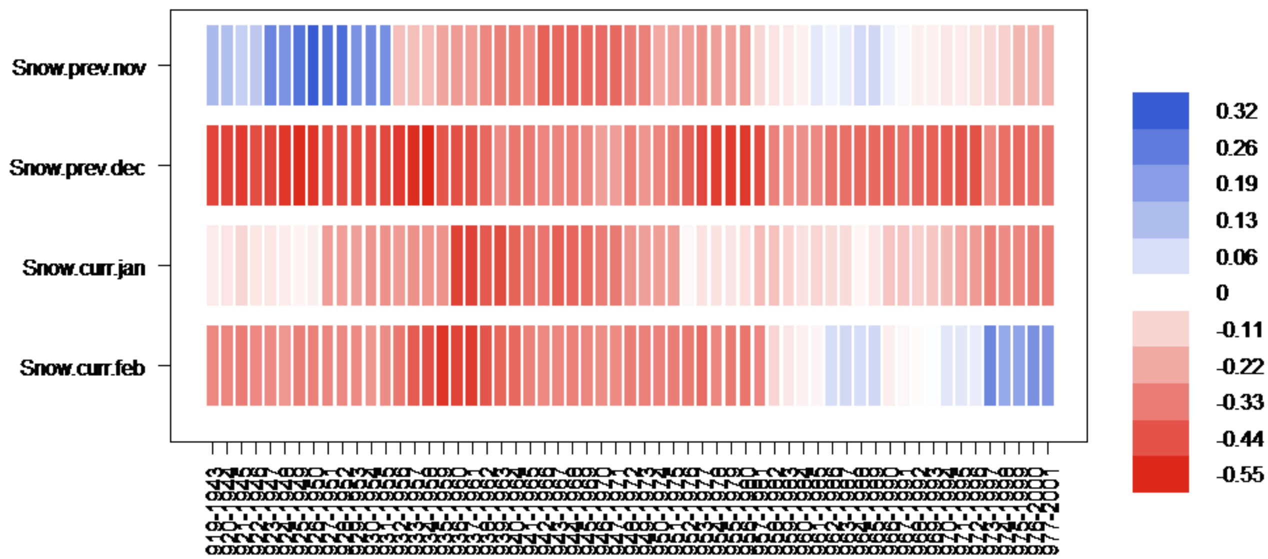
Texas Creek Whitebark Pine



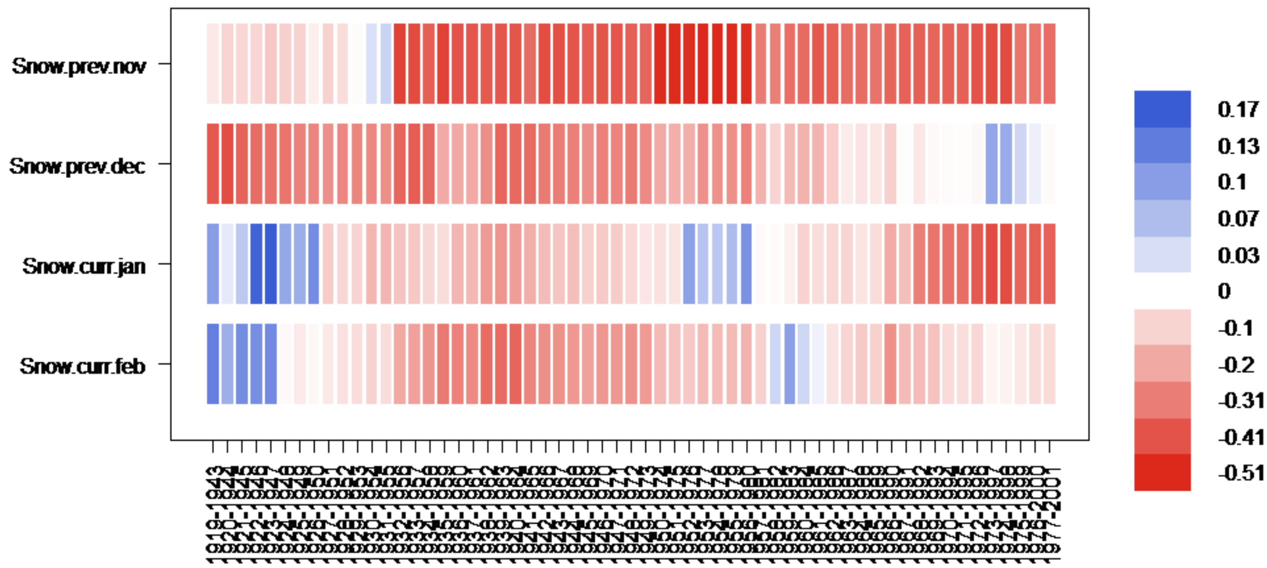
Downton Creek Subalpine Fir



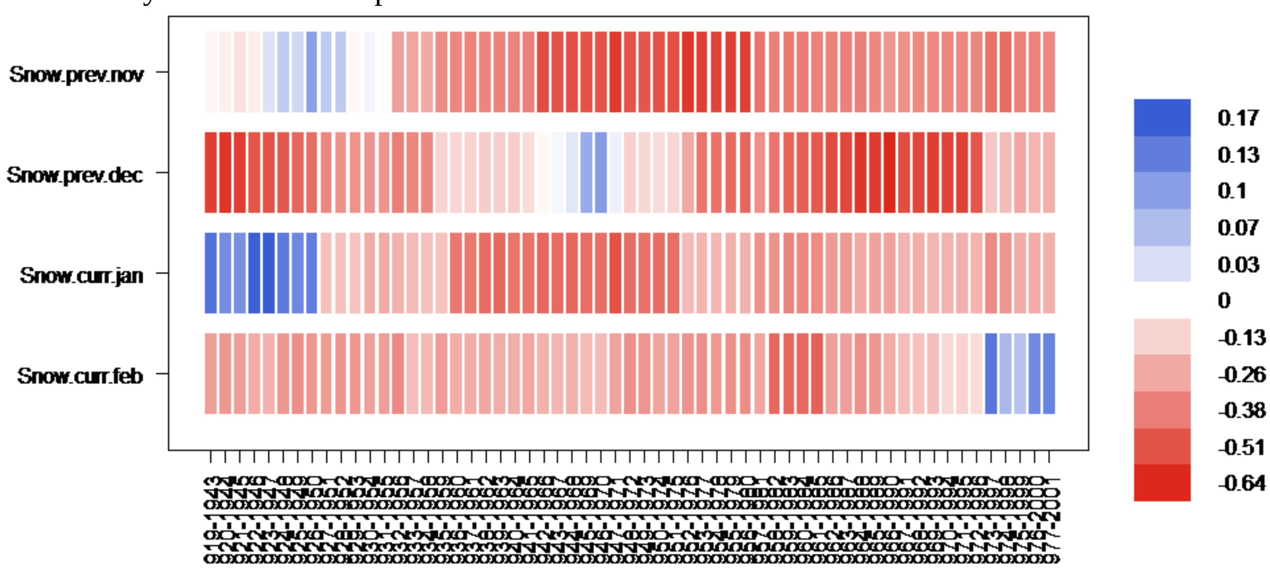
Downton Creek Whitebark Pine



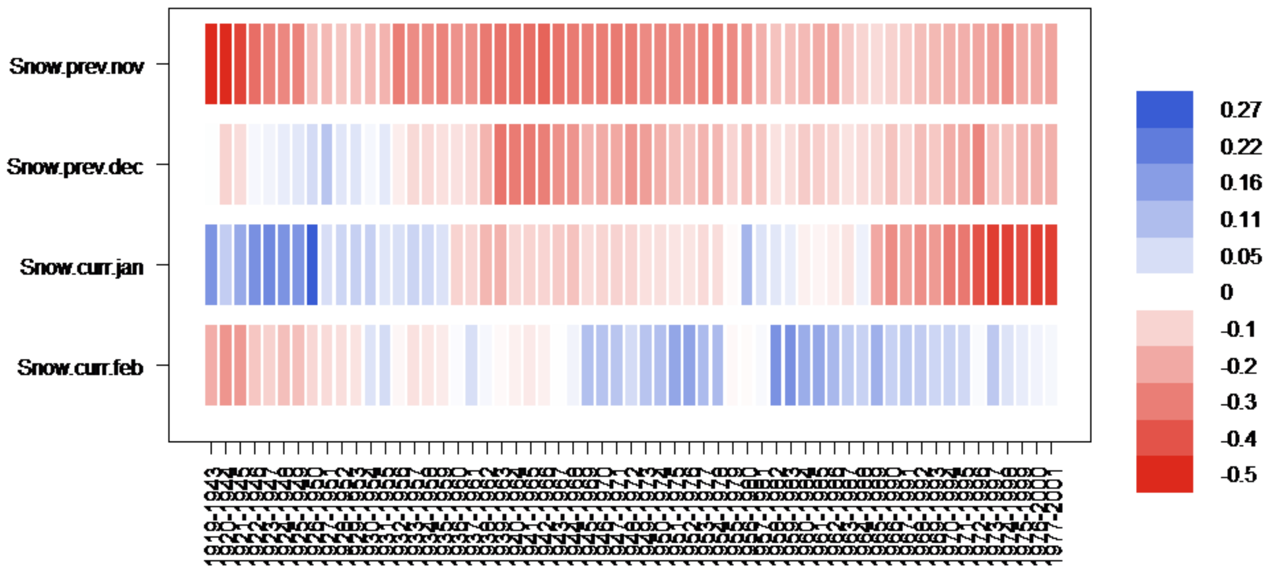
McGillivray Pass Subalpine fir



McGillivray Pass Whitebark pine



Seton Ridge Subalpine fir



Cinnabar Basin Subalpine Fir