Population Structure and Biophysical Density Correlates of Whitebark Pine (*Pinus albicaulis*) at Two Treelines in the Northern Rocky Mountains

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ABSTRACT

This study analyzes the structure and biophysical correlates of density of two whitebark pine (*Pinus albicaulis*) populations in the northern Rocky Mountains. Whitebark pine is a keystone species and an important component of treeline ecosystem dynamics; however, subalpine populations have declined nearly rangewide in recent decades. Though declines in subalpine forests have been well documented in the literature, few studies have assessed population structure and habitat requirements at treeline. Various disturbances have combined to impact whitebark pine populations across its range, but the primary threat at treeline sites in the northern Rocky Mountains is white pine blister rust, caused by the exotic fungal pathogen *Cronartium ribicola*. In this study, I aim to: 1) assess population structure and regeneration within two geographically different treelines experiencing contrasting levels of infection, and 2) examine associations among several biophysical variables and whitebark pine density to better understand treeline habitat variability and regeneration patterns. I used density-diameter curves and non-parametric Kruskal-Wallis tests to compare population structure between sites, and developed generalized linear mixed models to assess correlations between whitebark pine density and biophysical site variables. The results demonstrate that despite very different ecosystems and blister rust infection rates, our two study sites have similar population structure. Our model results highlight marked differences between populations in terms of biophysical correlates of density. While correlations are similar within site, seedlings and saplings have stronger correlations with biophysical variables than established trees.

Dedication

To my family, for providing me with every opportunity to succeed.

To Brooke, for keeping me grounded (and well-fed) during my time as a graduate student.

Acknowledgements

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Attribution

Though there are co-authors on the manuscript included in this thesis, I led the collection of data for this project, performed all analysis and interpretation, and independently wrote this document. Lynn M. Resler is the principal investigator in the broader project that includes this thesis work, and provided guidance that has shaped the nature of this project. Emily Smith-McKenna is a collaborator on the project that has provided valuable input shaping the project, and has shared data that has allowed me to expand the scope and analysis I could perform on this work.

Chapter 1: Introduction and Hypotheses

1.1 Introduction

Whitebark pine (*Pinus albicaulis*) is a keystone and foundation species in high elevation forests of the western United States and Canada. This pine species has experienced dramatic declines throughout much of its range, due primarily to white pine blister rust caused by the introduced fungal pathogen *Cronartium ribicola*, the native mountain pine beetle (*Dendroctonus ponderosae*), and fire suppression (Kendall and Keane, 2001; Tomback and Aschuff, 2010). Though moderate levels of disturbance are beneficial at an eco-system level in the maintenance of diversity and ecosystem stability (White, 1979; Huston, 1979), the severeity of these disturbances could be too great for whitebark pine populations to withstand. Diminished presence of this species could impact ecosystem stability through a reduction in the many ecosystem services it provides, creating cascading ecological effects (Tomback et al., 2001; Ellison et al., 2005, Tomback and Resler, 2007).

The predominant driver of whitebark pine decline at alpine treeline in the northern Rocky Mountians is blister rust. Regeneration and recruitment will be key steps in whitebark pine's persistence on the landscape and developing blister rust resistance (Larson and Kipfmueller, 2010). However, most studies that have examined whitebark pine population structure and regeneration have focused on subalpine forests and recently burned areas (e.g. Tomback et al., 1993; Tomback et al., 1995; Larson and Kipfmueller, 2010); only one has considered treelines specifically (Mellmann-Brown, 2005). A more thorough understanding of how these threats affect high elevation whitebark pine populations would help guide future work examining potential consequences for treeline ecosystems, especially in the context of climate change.

Due to its important role in high elevation forests, whitebark pine conservation efforts have become increasingly common. Understanding the relationship between whitebark pine and its environment is necessary for the success of any management plans (Weaver, 2001). However, most work shaping the assessment of whitebark pine habitat has focused on subalpine forest, and presents varying requirements based on site characteristics (see Arno, 2001). Despite this variability, guidelines for planting rust-resistant whitebark pine, one of the most successful conservation practices, are fairly uniform in identifying suitable locations (McCaughey, 2009).

Figure 1.1: Range of whitebark pine (*Pinus albicaulis*) across the western United States and Canada, with our two study areas marked by plus signs. This map was created using data provided by Little (1971). Note that while the distribution appears continuous throughout the northern extent of its range, this species is restricted to high elevation sites across this area.

This study assesses the current state of regeneration and population structure within whitebark pine stands characterized by high and low blister rust. Our two study sites (Fig 1.1), Divide Mountain and Parker Ridge, are located within areas that differ notably in their infection rates; the area surrounding Divide Mountain in Glacier National Park and the Blackfeet Reservation area, Montana, experiences very high infection rates (~73%), while northern Banff National Park in Alberta, where Parker Ridge is situated, has relatively low infection rates (~16%) (Smith et al., 2008). In addition to assessing the structure of these populations, we aim to better understand the habitat associated with regeneration and establishment. We accomplish this latter goal by analyzing several key biophysical site variables to determine whether they are significantly associated with whitebark pine density. We compare differences in these associations between our study sites and life stages to assess habitat variability. The assessment of these variables will help to better understand the specific types of habitats supporting whitebark pine regeneration and establishment at treeline, and can inform conservation efforts. Specifically, the objectives of this research are to:

1. Document and compare patterns in whitebark pine population structures at sites with high and low blister rust infection;

2. Document the relative frequencies of whitebark regeneration and established trees within sampling plots, and determine if frequencies differ between sites;

3. Quantify nine biophysical site variables regarding characteristics such as topography and moisture availability for each study site, and determine whether any variables are associated with the density of regeneration and/or established whitebark pine;

4. Compare any important biophysical variables found through objective three between sites and life stages to understand habitat variability.

Presently, there is a knowledge gap regarding potential consequences of whitebark pine population decline, especially at treeline. Tomback and Resler (2007) hypothesize that treeline forest composition will become more homogeneous, and that the loss of this pioneering species may limit treeline response to climate change. Whitebark pine is an important species in the facilitation of tree recruitment and initiation of tree islands in the alpine treeline ecotone (ATE) (Callaway, 1998; Resler and Tomback, 2008). If whitebark pine is limited in this role, other species may take its place to some degree, but there is the potential for drastic change at many treelines. Therefore, severe blister rust infection that limits whitebark pine's functional role at treeline constitutes a heterogeneous local disturbance that may alter the structure and function of current and future treelines.

More broadly, this project will contribute to a growing body of research that examines the consequences of the loss of keystone and foundation tree species. The loss of these important species can affect fundamental ecosystem processes, producing cascading effects on the whole ecosystem (Ellison et al., 2005). A more complete understanding of whitebark pine population structure will help identify areas where ecosystem-level change may occur.

This work constitutes an important first step in understanding treeline population dynamics in the presence of blister rust infection, and will guide work examining the potential consequences of declining whitebark pine in this ecosystem. Moreover, the results of this research will provide valuable baseline data on treeline populations, and is likely to be useful to forest managers in conservation planning. Conservation strategies for preserving whitebark pine in the presence of blister rust include controlled burns, tending of regenerated stands, management of blister rust alternate hosts (*Ribes spp.)*, chemical control of blister rust, and

planting rust-resistant whitebark pine (Hoff et al., 2001). This work could help forest managers better answer the question, "where should we focus conservation efforts in order to preserve whitebark pine's role as a keystone species?"

1.2 Hypotheses

The following research questions and hypotheses will guide this document in meeting the objectives of this research (as stated on page 3):

Research question 1 and null hypothesis 1 address objective 1 through an inventory of whitebark pine at our sites, and a comparison of density-diameter curves based on the proportion of each population within different size classes.

Research Question 1: Do the two sites (with comparatively high and low blister rust infection) differ in terms of the proportion of the populations within each size class?

$H_0 1$: There is no variation in population structure between the two study sites, so density-diameter curves will exhibit a similar shape.

Research question 2 and null hypothesis 2 address objective 2 by comparing the relative frequencies of regeneration classes, as well as established trees, within sampling plots between our study sites.

Research Question 2: Does the relative frequency of regeneration classes or established whitebark pine trees differ between sites?

$H_0 2$: There are no significant differences between sites in the relative frequencies of regeneration or established trees within sampling plots.

Research question 3 and null hypothesis 3 address objective 3 by using generalized linear mixed models to identify statistically significant associations among several biophysical site variables and the density of whitebark pine regeneration and established trees.

Research question 3: Are there significant associations between surveyed biophysical site variables and the density of whitebark pine regeneration or established trees, and if so, what are the statistical correlates?

$H_0 3$: Whitebark pine density exhibits no significant association with sampled biophysical site variables.

Research question 4 and null hypothesis 4 address objective 4 by comparing the equation coefficients and P-values of any significant associations found while addressing objective 3.

Research question 4: Do the biophysical variables that are associated with higher density of whitebark pine vary with life stage and/or site?

H_04: If any statistically significant associations between whitebark pine density and biophysical

variables exist, they will be the same across life stages and sites.

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Chapter 2: Literature Review

2.1 Whitebark Pine Distribution and Ecosystems

The distribution of whitebark pine extends throughout the Rocky Mountains, Columbia Mountains, Interior Plateau, Cascade Mountains, and the Coast Mountains of the western United States and Canada (McCaughey and Schmidt, 1990; Ogilvie, 1990; Weaver, 1990). In the coastal states and provinces, whitebark pine extends from British Columbia (~55°N Latitude) through the Sierra Nevadas (~36°N Latitude), and in the Rocky Mountains from Alberta to the Wind River Range in western Wyoming (Arno and Hoff, 1989; McCaughey and Schmidt, 1990).

Throughout this range, whitebark pine occupies cold, high-mountain environments with heavy snowfall, short growing seasons, and strong winds (McCaughey and Schmidt, 1990; Weaver, 1990). Though harsh, these zones are still generally moist, however whitebark pine is often absent from the most mesic sites across its range (Arno and Hoff, 1989). In moist ranges, such as the coastal ranges of British Columbia, whitebark pine is found primarily on comparatively dry, warm sites. However, in more arid ranges, it prefers cool, moist sites (Arno and Hoff, 1989). Thin-soiled, steep slopes that have been glacially scoured, as well as moraine and landslide deposits, are prime habitat for this species (Hansen-Bristow et al., 1990).

Whitebark pine is the only stone pine in North America. Stone pines have five needles per fascicle and large, wingless seeds that are dispersed by nutcrackers. Clark's nutcracker (*Nucifraga columbiana*) is the mechanism of dispersal for whitebark pine (Tomback, 1978; McCaughey and Schmidt, 2001).

In subalpine forests, whitebark pine exists primarily as a seral species where it establishes early in post-fire succession. In the upper subalpine zones and at treeline, whitebark pine is often the climax species (Arno, 2001), because it is a hardy species that is more tolerant of the extreme

climatic conditions than most associated conifers (Tomback, 1986). However, on sites that are

capable of supporting shade tolerant species, whitebark pine exists as the co-climax species. In

these sites, associated species are unable to grow vigorously enough to replace whitebark pine

(Arno, 2001). North of 50°N latitude, whitebark pine becomes a minor component of treeline

forests, but even at higher latitudes, it is still an important species (Arno and Hoff, 1989;

Tomback and Resler, 2007).

Studies have identified whitebark pine as both a foundation and keystone species

throughout its range (Ellison et al., 2005; Resler and Tomback, 2008). Foundation species are

prominent members of an ecological community that affect ecosystem processes, stability and

biodiversity (Soule et al., 2003). A keystone species plays the same role, but is further defined

by having a more important impact on an ecosystem than would be obvious based on its

abundance within that ecosystem (Krebs, 2001; Soule et al., 2003).

Flora and fauna in subalpine and treeline ecosystems rely on the many ecological goods

and services provided by whitebark pine. Its establishment facilitates further tree recruitment

(Callaway, 1998), and it provides a food source for many granivorous birds and animals,

including grizzly bears (*Ursus arctos*) and red squirrels (*Tamiasciurus hudsonicus*) (Mattson et

al., 2001). Moreover, whitebark pine stands are important to humans because its cover at high

elevations slows snowmelt, regulating downstream hydrology (Tomback et al., 2001b).

2.2 Regeneration in the Alpine Treeline Ecotone

Ecotones are transitional areas between biomes. The ATE, or treeline, is the transitional

area between subalpine forest and alpine tundra, and represents the upper altitudinal boundary of

tree growth. Treelines experience a broad range of extreme conditions, often over relatively

short periods of time and space, making growing conditions difficult for trees (Körner, 2003). These environments experience a wide range of temperatures on both daily and annual scales. Though climate data is limited at treeline, weather stations at Divide Mountain in Glacier National Park recorded a range in temperatures from -1.7 C to 22.6 C over a three-month period in the summer of 2010 (Franklin, 2011). Strong, persistent winds, with speeds that can damage or limit tree growth are common at treeline (Malanson et al., 2007). Even in summer, winds can exceed 75mph (L.M. Resler, *unpublished data*). Additionally, snowpack and cold conditions can extend into the summer months, creating a short growing season.

Natural regeneration of forests refers to forest renewal through the establishment of young trees, and is a critical step for the continued success of any tree species. Regneration at treeline is primarily accomplished through seed-produced or vegetative reproduction. Whitebark pine reproduces solely through the production of seeds. Many associated conifers, such as Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*), are able to do both, but often rely on vegetative reproduction at treeline. Trees that can reproduce through vegetative reproduction, also known as layering, are at a comparable advantage at treeline because this process is not dependent on the availability of seeds (Holtmeier, 2009). One factor complicating seed-based reproduction in the ATE is that, in general, these trees do not produce viable seeds in abundance (Tranquillini, 1979). As a result, regeneration depends on seed dispersal from more productive source areas in the subalpine forest. The manner of dispersal varies by species, but the primary agents are either wind (for *Abies* spp., *Picea* spp., and some *Pinus* spp.) or birds (for *Pinus albicaulis*) (Young and Young, 1992). The mechanism of dispersal has important consequences in determining spatial patterns of germination across the ecotone.

Whitebark pine is a coevolved mutualist with Clark's nutcracker, and is solely dependent

on the nutcracker for seed dispersal (Tomback, 1982). This unique bird can carry up to 150 seeds within its sublingual pouch, and has been documented carrying seeds more than 12 kilometers from where they were harvested (Tomback, 1982; Tomback et al., 1995). Nutcrackers cache seeds in open sites near landmarks (e.g., trees, rocks) that can serve as shelter for seedlings. The caches contain an average of 3-5 seeds (range 1-15) that are buried 1-3 cm deep, and serve as a food source for the bird throughout the winter and early spring (Hutchins and Lanner, 1982; Tomback, 1982). However, nutcrackers only consume about 55% of cached seeds, leaving unretrieved seeds to germinate (Tomback, 1982; Tomback and Linhart, 1990).

Once seeds are produced and dispersed from the subalpine to the upper extents of the ecotone, establishment is dependent upon the seed reaching an amenable with accessible soil and protection from harsh conditions that allows for germination and growth (Malanson et al., 2009). An amenable site has accessible soil and protection from harsh environmental conditions. Accessible soil is necessary for germination, as the seed's radicle must be able to reach soil to become established. Surface boulders (Resler, 2006) and vegetation (Seastedt, 2001), by impeding wind flow, may encourage eolian deposition, improving soil conditions for germination. In some environments, the bases of terrace risers, created through solifluction, experience turf exfoliation that exposes a small amount of fine-grained soil favorable for seed germination (Butler et al., 2004). Animals also play a role in creating favorable sites for seed germination through digging and exposing soil, but animals are also responsible for most seed predation at treeline (Butler, 1995; Malanson et al., 2007). Whitebark pine seeds have an advantage in reaching soil because nutcrackers bury seeds, while most associated conifers are wind dispersed.

In order to grow, a seedling must maintain a positive carbon balance, which can result

from a cumulative effect of favorable soil and microclimatic conditions (Malanson et al., 2009). Macroclimate provides for the general set of conditions at a site, and its modification by endogenous site characteristics, such as topography and existing vegetation, produces a microclimate that may be more favorable for growth. The physiology of a given tree species determines the suitability of the microclimate and soil, and as a result, the net carbon balance of a seedling at that site (Malanson et al., 2009). Therefore, the likelihood of seed-based regeneration within the ATE is a function not only of seed dispersal, but also reaching a site with microclimatic and soil conditions that are favorable for that species.

Microclimatic amelioration is often necessary for tree establishment in stressful environments, such as treeline (Spittlehouse and Stathers, 1990). Shelter, including site topography, presence of existing vegetation, or surface geomorphic features, may create microclimates favorable for seedling establishment and survival (Germino and Smith, 1999; Germino et al., 2002; Butler et al., 2004; Resler et al., 2005; Resler, 2006). In winter, shelter leads to snow accumulation and burial of seedlings, protecting them from desiccation and physical damage from abrasion by wind-blown snow and ice (Hadley, 1983). During the summer, shelter reduces sun exposure, insulates soil and provides longer-lasting soil moisture by regulating snowmelt (Germino et al., 2002; Resler et al., 2005).

Availability of suitable sites for seedling establishment increases the likelihood that a seed that reaches treeline and germinates, will continue to grow. Here again, whitebark pine regeneration is aided by Clark's nutcracker because they prefer to cache seeds near objects that serve as landmarks for orientation and that are also favorable for seedling germination and establishment (Tomback, 1978). The nutcracker's choice of caching sites is partially responsible for whitebark pine's success as a colonizer above treeline (Vander Wall, 1988).

Even within sheltered microsites, the environmental conditions at treeline cause high mortality rates in tree seedlings, sometimes more than 90% within the first year (Smith et al., 2003). With seedling mortality already very high, any threat that further hampers regeneration can have serious consequences for that species within the ATE. Although whitebark pine seedling mortality is also very high, their hardiness allows seedlings to be relatively more successful in establishment. For example, whitebark pine can grow at higher elevations than many associated conifers (Tomback, 1986; Tomback et al., 2001a)., and can also establish in the most exposed sites more often than Engelmann spruce (*Picea engelmannii*) or subalpine fire (*Abies lasiocarpa*) (Maher and Germino, 2006).

Though whitebark pine's hardiness affords it an advantage in initial establishment, species that can regenerate through layering are at a comparative advantage, as layering can occur in environmental conditions that would limit the production of viable seeds. Layering is common in many conifer species found in the Rocky Mountains, including Engelmann spruce and subalpine fir, and to a lesser degree, larch species (*Larix* spp.) (Holtmeier, 2009). Once these species become established at treeline, it is likely that they will regenerate through layering. Although larch, such as the subalpine larch (*Larix lyallii*), are hardy species that can colonize favorable sites within the ATE, subalpine fir and Engelmann spruce may be more dependent on established trees that provide shelter for their initial establishment at treeline.

Since whitebark pine depends on seed-based regeneration, the presence of this species in treeline communities is more vulnerable to factors that lower seed production. The threats ounlined in section 2.5 constitute mechanisms through which whitebark pine regeneration at treeline may be affected because of the potential for reduced seed production and juvenile recruitment. Although associated tree species are not as vulnerable to diminished seed

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production, their presence within the ATE may be affected by the diminished facilitative role of whitebark pine that may result from its decline.

2.3 Defining and Measuring Regeneration

Many studies have measured tree regeneration with widely varying methodologies. Trees often grow in dwarf, krummholz and other atypical forms above treeline, so traditional forestry methods that rely on record diameter at breast height (DBH)-based, density-diameter curves are inappropriate at many treelines; even though regeneration may be occurring, many trees never grow tall enough to record DBH

The most common method of recording regeneration at treeline is by measuring the density of seedlings and saplings. This method has been used successfully in many study areas, including high-elevation forests in the Rocky Mountains (Tomback et al., 1995; Mellmann-Brown, 2005; Larson and Kipfmueller, 2010), but authors often use different definitions of seedlings and saplings in their studies. Height is commonly used to define seedlings and saplings versus mature trees. In a study of post-fire whitebark pine regeneration, Tomback et al. (1995) defined seedlings and saplings as any tree less than breast height, 137 cm. In a study of whitebark pine regeneration at treeline on the Beartooth plateau, Mellmann-Brown (2005) assessed regenerative success by the density of juvenile trees; juvenile trees were classified as any tree under 150 cm. Larson and Kipfmueller (2010) also used measures of seedling and sapling density to assess whitebark pine regeneration in several upper subalpine forest zones near treeline across Montana, Idaho, and Oregon. In their study, the definitions of saplings and seedlings were based on tree diameter at ground level and at breast height. The authors defined a seedling as any tree measuring less than 2 cm in diameter at ground level, and a sapling measures

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greater than two cm at ground level, but less than five cm in diameter at breast height. Because of the atypical growth forms common within the ATE, size-based definitions of seedlings and saplings may be inappropriate for measuring treeline regeneration.

An alternate method used to classify trees as seedlings or saplings is based on age. In their study on *Pinus uncinata* at treeline in the Catalan Pyrenees, Ninot et al. (2008) sampled only small trees (< 50 cm) along their transects. The authors aged small trees by counting whorls of branches or the scars they create. More precise dating was done on a subset of sampled trees by examining cross-sections of root and stem tissue. The authors assessed regeneration by looking at seedling and sapling (any small tree less than 10 years old) density between plots and across the ecotone. Field-based age assessment in this study produced an average dating error of 3.1 years for trees aged using both methods. In other studies examining regeneration patterns at treeline, Battlori et al. (2010) and Batllori and Rodriguez (2008) aged small trees by counting terminal bud scars along the main stem of the seedling or sapling. Although these methods avoid the problems associated with classifying seedlings and sapling based on height or DBH, this strategy is more labor intensive, and can cause high levels of error.

2.4 Competition and Facilitation on Environmental Gradients

Interactions among plants are important in determining the success of any tree species. The net effect of neighboring vegetation on a seedling can fall on a continuum between facilitation, where the neighboring vegetation improves growing conditions for the seedling, and competition, where the presence of neighboring vegetation is detrimental to the germination and growth of seedlings. Neighboring vegetation may simultaneously exert both facilitative and competitive effects, so the net effect of these interaction in based on multiple, complex

interactions (Callaway, 1995).

Competition is the struggle for a plant to preempt resources that are necessary for growth. A traditional view in ecology regarded the presence of neighboring vegetation to be unfavorable because of resource-limiting interspecific competition. Within the last few decades, however, studies have found that the facilitative interactions between vegetation become more important with increasing abiotic stress (Bertness and Callaway, 1994). In extreme environments, harsh conditions may restrict a plant's ability to acquire and utilize necessary resources, and amelioration of environmental conditions by neighboring plants can favor growth to a greater degree than competition restricts growth.

Though sheltered sites offer some competitive disadvantages (such as cooler nights and greater competition for water) unsheltered seedlings experienced much higher transpirational stress. Germino et al. (2002) found that combinations of high sunlight, low temperature and/or water stress were important factors in causing mortality at treeline. So despite some competitive disadvantages of sheltered sites, transpirational stress was more detrimental to seedling survival than lowered water supply resulting from competition. At treeline, competition still exists among species, but the sheltering effect of neighboring vegetation can improve conditions and prevent mortality.

In the subalpine vegetation zone, environmental conditions pose less of a limitation on growth than at treeline, so the importance of the facilitative interactions among plants decreases (Choler et al., 2001). Since conditions in subalpine forests are not as stressful as at treeline, protection from harsh environmental conditions is less important, and the presence of neighboring vegetation is detrimental to seedling growth because competition becomes more important in defining the relationship between plants (Callaway et al., 2002).

The nature of plant interactions can also vary based on life-stage of participants. Life-stage may affect the net relationship between vegetation because trees are most vulnerable in their early years. Neighboring vegetation that positively influences the growth of a seedling by providing shelter may hinder growth at a later stage through resource competition (Callaway and Walker, 1997). Once a tree becomes established, the benefits of neighboring vegetation are somewhat less important, and the former beneficiary of the relationship becomes a significant competitor, and competitive interactions may come to dominate the interaction. The conditions within the ATE are so harsh, however, that this trend based on life-stage may not always hold true, and even mature trees may benefit from neighboring vegetation. For example, Callaway (1998) found that the growth rates of mature subalpine fir (*Abies lasiocarpa*) within the ATE dropped 24% when neighboring whitebark pine trees died.

The interactions highlighted in this section help to explain whitebark pine's role in community dynamics at treeline. More broadly, these interactions play an important role in determining regenerative success of tree species within the subalpine and above treeline. Since whitebark pine is a poor competitor, it is often outcompeted by more shade-tolerant competitors. In dry, cold, and windy sites, however, whitebark pine's hardiness allow it to establish in these environments more often then associated conifers (Minore, 1979).

Within the subalpine zone, where competition is more intense, whitebark pine is often fire dependent, and establishes early in post-fire succession (Arno, 2001). Although whitebark pine persists in these environments, its presence diminishes as it is replaced by more shade-tolerant competitors, often subalpine fir and Engelmann spruce, until the community is renewed by fire every 50-400 years (Arno, 1980; Romme, 1982; Keane et al., 1990; Barrett, 1994). Depending on its successional stage within the subalpine, the competitive pressure exerted by

other tree species may decrease whitebark pine regeneration due to decreased presence and seed production.

At treeline, whitebark pine's hardiness allows for its continued presence and influence on vegetation dynamics. Whitebark pine's ability to become established in more exposed sites more often than other common conifer species allows it to be more capable of colonizing open meadows within the ATE. This relatively high success as a colonizer at treeline make whitebark pine an important species in community development because its initial establishment allows it to serve as shelter, creating a facilitative on other tree species. At treeline, less-hardy tree species are often found preferentially around whitebark pine (Callaway and Walker, 1997; Callaway, 1998; Maher and Germino, 2006).

The process of whitebark pine establishment and its recruitment of other conifers can lead to the development of tree islands above treeline (Bekker, 2005; Resler et al., 2005; Resler and Tomback, 2008). In some cases, this can lead to advancement of subalpine forests (Bekker, 2005). Although the results of this process vary by site, these studies demonstrate the importance of whitebark pine in treeline vegetation dynamics. Moreover, these interactions play an important role in determining regenerative success of tree species within the subalpine and across the ATE, and must be taken into consideration when studying regeneration.

Whitebark pine is not the only species capable of providing these facilitative effects, but in many locations, it is the best equipped to initiate this process. Lowered whitebark pine regeneration may therefore reduce the number of sites available for tree establishment due to loss of its facilitative effects. The loss of this keystone species may lead to altered community structure and disruption of treeline vegetation dynamics.

2.5 Threats to Whitebark Pine and Pine Regeneration

Many whitebark pine populations have experienced a dramatic decline in recent decades,which have typically been attributed to three major disturbance agents: white pine blister rust, mountain pine beetle, and successional replacement as a result of fire suppression. Currently in northern Montana and southern Alberta, blister rust is the disturbance agent that causes the highest mortality rates of whitebark pine.

Cronartium ribicola is an introduced fungal pathogen that causes the disease white pine blister rust (WPBR) in five-needle pines in North America, among which whitebark pine is particularly vulnerable (McDonald and Hoff, 2001). *C. ribicola* was accidentally introduced to western North America in 1910 (Hoff and Hagle, 1990). Blister rust spores enter host pine trees through the stomata in the needles of five-needle pines (Kendall and Keane, 2001). Blister rust mycelia (the thread-like vegetative part of the fungus) then grow down through the cambium of branches and the trunk. After several years, mycelia growth produces cankers that damage the living cambium and girdle that particular branch; this process can kill the tree depending on the location of infection (Kendall and Keane, 2001). Regardless of tree mortality, blister rust often kills mature, cone-bearing branches, thereby decreasing seed production and lowering the quantity of seeds available for dispersal (McDonald and Hoff, 2001).

Mountain pine beetle (MPB) has also contributed to whitebark pine population decline. MPB is a native species that has caused sporadic oubreaks, but the detrimental effect of beetles on whitebark pine has recently increased, probably due to increased beetle occurrence resulting from warming climate (Raffa et al., 2008). Mountain pine beetle preferentially attack large, mature whitebark pines that are responsible for seed production (Kendall and Keane, 2001), and their mortality can further reduce seed production. Blister rust and mountain pine beetle can also

act in concert to exacerbate decline. For example, Six and Adams (2007) found that whitebark pine trees that were damaged by white pine blister rust were significantly more likely to be attacked by mountain pine beetle.

The third major cause of whitebark pine decline is fire suppression. Fire opens sites within the subalpine suitable for seed caching by Clark's nutcracker (Tomback et al., 1993; Tomback et al., 1995). Also, whitebark pine can often be outcompeted in less-harsh environments that experience higher levels of competition because of its shade intolerance (Minore, 1979). Fires can clear out competitors, and encourage whitebark pine regeneration in these environments. Without fire, natural regeneration is less likely to occur, leading to whitebark pine stands growing older and more vulnerable to other threats, while being replaced more shade-tolerant trees (Kendall and Keane, 2001). As a result, prolonged fire suppression in important seed source areas can further limit seed production.

Whitebark pine seeds are an important food source for many species of wildlife. As a result, many seeds are subject to predation before they can germinate and become established. For example, red squirrels can consume as much as 80 percent of the cone crop in a given year (Hutchins and Lanner, 1982). While seed production can be lowered by blister rust and MPB damage, seed predators are left unaffected in the short term, leading to an increase in the percentage of seeds that are consumed (McKinney and Tomback, 2007). When this happens, there simply may not be enough cones produced so that sufficient seeds are available to be dispersed after seed predation.

The reduced seed availability can disrupt the mutualism between whitebark pine and Clark's nutcrackers. In early summer, Clark's nutcracker forages among trees and assesses cone development. If they sense that sufficient seeds will be produced, they settle in this area, and

disperse seeds later in summer by creating seed caches; if they sense a shortage, they will emigrate to other areas and not revisit the site (Vander Wall, 1988). McKinney and Tomback (2007) and McKinney et al. (2009) found that sites severely affected by blister rust did not have sufficient reproductive ability to meet a minimum cone production threshold, and Clark's nutcrackers visited these sites less frequently. As a result, whitebark pine regeneration within at treeline may be further hampered by reduced seed distribution to these areas as a result of lowered nutcracker presence in seed source areas.

Clark's nutcracker can carry whitebark pine seeds as far as 12.5 km from seed source to cache site, but the majority of seeds are cached within a few hundred meters of their source (Tomback, 1978; Hutchins and Lanner, 1982). Nutcrackers typically only carry seeds long distances to carry them to lower-elevation communal storage areas. For example, a study in Grand Teton National Park found that Nutcrackers cached their harvested seeds either within 100 m of source trees in temporary caches, which may or may not be moved later to more permanent caches in cliff faces several kilometers away (Hutchins and Lanner, 1982). Since most long-distance dispersal is down slope to large, communal caches, the seeds that are dispersed to treelines are likely to be locally sourced, so regeneration within the ATE may reflect declines within the associated subalpine area that limit seed production and dispersal.

Beyond lowered seed production and dispersal, blister rust can affect whitebark pine regeneration by preventing juvenile recruitment. In the cases where sufficient seeds are produced, dispersed to treeline, and germinate, whitebark pine seedlings that become infected with blister rust typically die within three years after developing cankers (Hoff and Hagle, 1990). Contrary to the long-standing thought that the harsh conditions at treeline limited blister rust infection, Resler and Tomback (2008) found treeline blister rust infection to be quite common.

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Chapter 3: Manuscript

Population Structure and Biophysical Density Correlates of Whitebark Pine

(*Pinus albicaulis*) at Two Treelines in the Northern Rocky Mountains

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Abstract

Whitebark pine (*Pinus albicaulis*) is a keystone treeline species throughout the Rocky Mountains. Subalpine populations have experienced severe declines in recent decades; with white pine blister rust playing a major role. Declines in subalpine populations are well documented, few studies have assessed the population structure and regeneration of treeline whitebark pine populations. Our objective was to document regeneration patterns in areas with high and low blister rust infection by (1) documenting and comparing the relative frequency of regeneration and established whitebark pine, and (2) to determine the relationship between biophysical variables and density of regeneration and established whitebark pine at each site to better understand habitat variability between two treeline study sites in the northern Rocky Mountains. We used density-diameter curves and Kruskal-Wallis tests to compare population structures. To assess biophysical correlates of density, we created generalized linear models. Our results indicate that both populations have similar structures, but our site with high blister rust infection had a low proportion of early regeneration. We found pronounced variability in the biophysical variables associated with whitebark pine density. This variability reflects the importance of site-specific factors in defining optimum whitebark pine habitat, and should be a consideration in future management decisions.

Introduction

Whitebark pine (*Pinus albicaulis*) is an ecologically important treeline species in high elevation forests of the western United States and Canada (Tomback, 1978). In coastal states and provinces, whitebark pine's range extends from the Sierra Nevadas (~36°N latitude) in California through British Columbia; in the interior Rocky Mountains, its range extends from the Wind River Range in Wyoming through Alberta (~55°N latitude). The large, wingless seeds of whitebark pine are primarily dispersed by Clark's nutcracker (*Columbiana nucifraga*), and serve as an important food source for many granivorous birds and mammals that overlap in distribution, including black bears (*Ursus americanus*) grizzly bears (*Ursus arctos horribilis*), and red squirrels (*Tamiasciurus hudsonicus*) (Tomback, 1978; Hutchins and Lanner, 1982; Kendall, 1983).

Whitebark pine is a hardy species (Arno and Hoff, 1989), and its establishment at treeline facilitates community development by mitigating harsh conditions, and allowing more shade tolerant competitors to establish (Callaway, 1998). For example, tree islands were initiated in the lee of whitebark pine more than any other tree species at several alpine treeline ecotones on the eastern Rocky Mountain Front in Glacier National Park and the Blackfeet Nation (Resler 2004, Resler and Tomback (2008). At these same sites, approximately two-thirds of solitary trees were whitebark pine, thereby representing an important driver of spatial pattern.

Despite these benefits, subalpine whitebark pine populations have declined nearly range-wide over recent decades, primarily in response to to white pine blister rust (caused by the fungal pathogen *Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, and successional replacement associated with fire suppression (Kendall and Keane, 2001; Tomback and Achuff, 2010). Whitebark pine has been classified as both a foundation and keystone species, and its decline could have drastic consequences on the high elevation western forests

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where it occurs (Ellison et al., 2005; Resler and Tomback, 2007).

Treeline environments experience a wide range of temperatures on both daily and annual time scales, as well as strong, persistent wind, which make growing conditions poor for most plants (Malanson et al., 2007). Even in sheltered microsites, first-year conifer seedling mortality can exceed 90% (Smith et al., 2003) indicating that despite its hardiness, whitebark pine seedling mortality is still high. Unlike most associated treeline conifer species that reproduce by layering, whitebark pine regenerates through the dispersal, germination, and establishment of seeds. Conditions at treeline prohibit development of sufficient seeds, so its regeneration relies on seed production and dispersal from subalpine forests (Tranquillini, 1979); any disturbance that reduces seed production and dispersal has the potential to drastically limit treeline regeneration. Limited presence of whitebark pine would also reduce the ecosystem services it provides (Tomback and Resler, 2007).

Though there are numerous threats across its range, blister rust infection appears to be the primary cause of whitebark pine mortality at treelines in the northern Rocky Mountains. Blister rust was introduced to the United States from Eurasia in 1910, and though all five-needle pines are vulnerable, whitebark pine is particularly susceptible (Hoff and Hagle, 1990). Airborne blister rust spores enter host trees through needle stomata, and its mycelia grow down through the cambium of infected branches, producing cankers after several years. This process damages the cambium, and eventually kills the infected branch. Blister rust frequently kills cone-bearing branches years before tree mortality, reducing seed production (McDonald and Hoff, 2001). Seed production can be so diminished in heavily infected areas that these stands are not visited as frequently by Clark's nutcracker, limiting seed dispersal (McKinney and Tomback, 2007; McKinney et al., 2009), further limiting regeneration. Blister rust also hinders juvenile

recruitment, as saplings nearly always die within three years of infection (Hoff and Hagle, 1990).

Contrary to the long-standing belief that harsh conditions limited infection at treeline, Resler and Tomback (2008) found blister rust to be present in these environments, noting that almost one-quarter of krummholz whitebark pine sampled in Glacier National Park had at least one active or inactive canker. While blister rust is the primary threat at treeline in the Rocky Mountains, our sites (Fig. 1.1) have experienced drastically different levels of infection, with the Glacier and Waterton Lakes area characterized by some of the highest whitebark pine infection rates (~73%), while northern Banff National Park in Alberta has some of the lowest rates (~16%) within the continental range (Smith et al., 2008).

To persist on the landscape, long-term genetic adaptation that increases rust resistance will be necessary, and natural regeneration and recruitment constitute important steps in that process (Larson and Kipfmueller, 2010). To this point, most whitebark pine regeneration studies have been conducted in the subalpine, with an emphasis on recently burned areas (Tomback et al., 1993; Tomback et al., 1995; Tomback et al., 2001; Larson and Kipfmueller, 2010). An assessment of treeline whitebark pine population regeneration and habitat variability is necessary to better understand the status of these stands, as well as focus conservation efforts. The specific goal of this study is to assess regeneration patterns at two very different treeline locations, each chrazterized by different levels of blister rust infection, by (1) documenting and comparing the density and relative frequency of regeneration and established whitebark pine at each site, and (2) assessing the relationship between several biophysical variables (Table 1) and the density of regeneration and established whitebark pine at each study site for the purpose of exploring the variability in site characteristics associated with regeneration and establishment.

Study Areas

In northwest Montana, we conducted fieldwork on Divide Mountain (48.67° N, 113.40° W; 2,462 m elevation), located on border between Glacier National Park and the Blackfeet Nation, east of the Continental Divide. In Alberta, we sampled at Parker Ridge (52.180° N, 117.10° W; 2,221 m) in northern Banff National Park, approximately 470 km northwest of Divide Mountain.

Divide Mountain

Divide Mountain lies east of the Continental Divide where climates are drier, cooler, and in general, more windy than west of the Divide (Finklin, 1986). The parent material is Altyn limestone (Raup et al., 1983), and soils are characterized as "ice-patterened" soils with colluvium and residuum parent material that has been exposed to intense frost action (Dutton and Marrett, 1997). Prevailing winds are from the west, and wind speeds increase with elevation (Finklin, 1986). Much of the site is characterized by linear patterned ground, creating microtopographic relief that can offer shelter for conifer establishment (Resler et al., 2005). Additional climatic and topographic factors for both sites are summarized in Table 2.

Common tree species include whitebark pine (*Pinus albicaulis*), Engelmann spruce (*Picea englemannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and less often, douglas-fir (*Pseudotsuga menziesii*). Juniper (*Juniperus communis*) and willow (*Salix spp.*) are common shrubs throughout the site, and groundcover species include bearberry (*Arctostophylos uva-ursi*), white dryas (*Dryas octepetala*), cinquefoils (*Potentilla spp.*), and lupines (*Lupinus spp.*)

The treeline ecotone on the northern face of Divide Mountain has gently sloping terrain with large islands of trees interspersed with dense, herbaceous vegetation. Towards the south,

the terrain becomes more complex with numerous gullies and ridges. This region becomes more rocky and steep, and includes numerous, smaller patches of trees. The complex terrain, as well as Divide Mountain itself, creates numerous sheltered coves that often contain large upright and/or flagged trees. Though much of the treeline appears to be climatically controlled, some steep, unstable slopes suppress treeline in spots.

Parker Ridge

Parker Ridge extends eastward from Mount Athabasca, and is characterized by gently sloping terrain to the north and south giving way to a steep rock face on the east extending down to the Icefields Parkway. Parker Ridge is a morainal landscape dominated by brunisolic soils, with less-developed regosolic soils at the western end, closer to the Colubmia Icefield (Walker et al., 1976). Parker Ridge has calcareous parent material with medium texture, and is primarily well drained to moderately well drained. However, the northeast end of Parker Ridge contains some poorly drained areas with gleysolic soils developing from prolonged water saturation (Walker et al., 1976; Stonehouse, 1998). The cold climate appears to encourage active periglacial influence on the site, resulting in miniature striped patterned ground at treeline and tundra locations.

Above 50º N, whitebark pine is a minor component of high-elevation forests (Arno and Hoff, 1989). As such, whitebark pine presence was sparser at Parker Ridge than at Divide Mountain. Common tree species include Engelmann spruce and subalpine fir, and lodgepole pine (*Pinus contorta*) becomes more abundant in lower subalpine forests. Willow (*Salix spp.*) occurs on moist sites across the ecotone. Common ground-cover species include four-angled mountain-heather (*Cassiope tetragona*), everlasting (*Anaphalis margaritacea*), cinquefoils

(*Potentilla spp.*), and moss campion (*Silene acaulis*).

The treeline ecotone on Parker Ridge is characterized by a gradual transition from closed forest to tundra, with dense forests of fir, spruce and pine to the south, and fir and spruce to the north, giving way to patches of tree islands, and eventually to tundra vegetation and rock and snow at the highest points. The steeper eastern end is more abrupt, with dense fir and spruce in subalpine forest below a large rockface, and scattered tree islands above.

Methods

Field and GIS Methods

We conducted fieldwork in July of 2010 and 2011. Prior to fieldwork, we examined aerial photography to identify potential sampling areas. Sampling plot placement was stratified by aspect, with a random pin toss determining plot centroids. Based on this centroid, we delineated fixed-area, square sampling plots with sides measuring 15m. We took care to represent the range of topographic conditions (e.g., slope, elevation) within each study area, with the exception of locations limited by dangerous topography and rock fall potential. We sampled within 28 plots across the alpine treeline ecotone at Divide Mountain and 20 at our Parker Ridge site. For each plot, we recorded aspect and slope using a compass and clinometer, and elevation and coordinates using a Trimble GeoXT GPS unit. We inventoried all trees within the plots, recorded locations for all individual trees, and delineated all tree islands using the GPS. We also recorded diameter at ground level (DGL) for all whitebark pine to develop density-diameter curves and quantify regeneration. Size-based measurements have been frequently used to assess regeneration and stand structure in whitebark pine research (e.g. Tomback et al., 1995; Zeglen, 2002; Smith et al., 2008). Diameter at breast height (DBH) is used more commonly in density-diameter curves, but DGL has previously been used at treeline (Miller and Cummins, 1982).

where trees exhibit stunted, atypical and krummholz growth. The protected status of our study sites precluded the collection of tree ring cores.

Given the high degree of local variability in the condition of whitebark pine stands, we established several plots in adjacent subalpine forests to corroborate the results of previous field studies (Smith et al., 2008). Hutchins (1982) suggested that Clark's nutcracker caches many seeds within 100m of where they are harvested (Hutchins, 1982), so we chose to place subalpine plots within 100m of the uppermost limit of subalpine forest. Within this buffer, we randomly placed three 15m by 15m plots across the major aspect classes (NE, SE, SW, and NW) of subalpine forest for each study site. In these plots, we measured species composition, and recorded height and DGL for all whitebark pine seedlings and saplings. For all whitebark pine at least 1.5m tall, we measured DBH. We also surveyed whether each whitebark pine was infected with blister rust infection, and estimated canopy kill, if applicable.

For each treeline plot, we created sub-meter DEM surface models to characterize biophysical variables at a fine scale. The first step to develop these models was to slowly traverse each plot while recording GPS points at a constant height. In traversing the plot, we gave special attention to any prominent changes in the surface, including breaklines, ridges, depressions, etc. In the lab, we differentially corrected all GPS points, and interpolated a surface for each plot following methods described by Smith et al. (2011).

High levels of sunlight and water stress are common causes of mortality, especially among seedlings at treeline (Germino et al., 2002), so our assessment of biophysical site characteristics focused on variables that reflect insolation and moisture. In ArcMap 10 (ESRI, 2011), we used our surface DEMs to calculate curvature and potential incoming solar radiation surfaces. Curvature surfaces help determine whether the surface of the plot is relatively flat, or if

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it is primarily convex or concave. Concave surfaces may retain snowpack longer, and/or accumulate moisture compared to convex plots, and represent more mesic plots. Potential solar radiation estimates the amount of insolation in units of watt hours/m^2 reaching a plot throughout a calendar year, and plots with comparatively high insolation are warmer and drier.

The amount of upslope contributing area can affect moisture available within a given area, as areas with very small upslope areas, such as ridges, are typically drier than valley bottoms that drain a large area. Flow accumulation calculates the number of cells in a raster that drain through a given cell, so cells with higher values have larger upslope contributing area. We downloaded the highest resolution DEMs available for each study area to calculate flow accumulation values for each sampling plot. For the Divide Mountain study site, we downloaded 10m resolution DEMs from USGS Seamless Data Warehouse (http://seamless.usgs.gov), and 23m resolution DEMs from GeoBase (http://www.geobase.ca/geobase/en/index.html) for the Parker Ridge site. We constructed separate models for each site, avoiding direct quantitative comparisons between sites, and preventing potential problems associated with the discrepancy between the two DEM resolutions. The zonal statistics tool extracted the mean values for all DEM-derived biophysical variables for each plot, and these values are were used as predictor variables in our models.

Since whitebark pine seeds are often cached within 100 meters of where they are foraged (Hutchins, 1982), we hypothesized that distance to each plot from the closest subalpine seed source may affect the quantity of seeds each plot receives. High, isolated plots may not receive a sufficient number of cached seeds for ample regeneration. In ArcMap, we delineated the closest subalpine forest, and then used a spatial join to calculate the distance from each treeline plot to the subalpine.

Vegetation, including herbaceous cover, trees, and tree islands can act as shelter and have a positive effect on seedling establishment at treeline (Maher et al., 2005; Maher and Germino, 2006), so we quantified several variables relating to vegetation cover. Using ArcGIS, we delineated tree islands, and then calculated percent of each plot that was covered by tree islands. Additionally, we tallied the number of non-whitebark pine trees within each sampling plot, and included this number in our models.

Statistical Analysis

Density-diameter curves characterized whitebark pine stand structure. Since whitebark pine is less prominent in high-elevation forests north of 50° latitude, we divided all counts by the total number of whitebark pine sampled at each site, giving us a proportional value for whitebark pine within each size class. To compare regeneration density between sites, we categorized all young trees as either seedlings or saplings with definitions adapted from Larson and Kipfmueller (2010). Seedlings were defined as any whitebark pine stem having a DGL under 20mm, while saplings had a DGL between 20mm and 29.9mm. We considered small and large seedlings (0-9.9mm and 10-19.9mm) separately for comparing relative frequencies. We used Kruskal-Wallis non-parametric tests to compare proportional values for whitebark pine occurrence in three 10mm size classes (0-9.9mm, 10-19.9mm, and 20-29.9mm), as well as all established whitebark pine with a DGL of 30mm or greater. We chose a non-parametric test because we had a small sample sizes (20 for Parker Ridge, 25 for Divide Mountain), and the distributions of relative frequency values were non-normal.

We assessed the relationships between biophysical variables and whitebark pine density using generalized linear models (GLM) because they are more appropriate than traditional linear regression options for assessing non-normal response variables with a poisson distribution

(Nelder and Wedderburn, 1972). To avoid pseudoreplication due to spatial autocorrelation among sampling plots (Hurlbert, 1984), as well as to account for unmeasured variation among sampling units, we were interested in including sampling plots as a random effect. For each study site, we constructed separate models for total regeneration (DGL 0-29.9mm) and established trees (DGL 30mm+). We developed both generalized linear models and generalized linear mixed models (GLMM) with the random effect set as the plot for both dependent variables and sites, and tested the significance of the random effect using log likelihood ratio tests. In all cases, the inclusion of random effects produced significantly different models, so we chose to use GLMMs of the poisson family, fit with the Laplace approximation following stemps outlined in Bolker et al. (2009). The large values calculated from the ArcGIS solar radiation tool caused false convergence errors in the generalized linear models, so we transformed these values using a linear rescale to a range of zero to one. Additionally, we square root transformed flow accumulation values for the Glacier site due to an extreme outlier.

In addition to the variables outlined above, we included elevation and slope in our models. Elevation is a common component of habitat description, and can be a proxy for temperature. Slope can be an important influence on habitat in two ways. First, our study areas are characterized by steep topography, and steep slopes may be more prone to landslide disturbances, limiting tree establishment. Slope is also a component of many moisture indices (Parker, 1982; Iverson et al., 1997), with flatter surfaces generally being more mesic.

For all pairs of predictor variables, scatterplots and correlation values helped determine if multicollinearity existed among pairs of independent variables. Based on this information, we excluded elevation from Parker Ridge models. All remaining independent variables were included in our model, and we used backward and forward stepwise regression to eliminate

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insignificant variables. We stopped and accepted our final model when we reached the lowest

Bayesian Information Criterion (BIC). BIC evaluates how well the independent variables

explain the dependent variable, and is often used for model selection. BIC is similar to the more

commonly used Akaike Information Criterion (AIC); the main difference is the inclusion of n in

the BIC equation, producing a greater penalty term for the total number of variables (Zucchini,

2000).

Results

We sampled 552 whitebark pine in our treeline plots at the Divide Mountain site and 252

at Parker Ridge. Average basal are in both subalpine and treeline plots was greater at Divide

Mountain (Table 3). Densities of both seedlings and saplings were also higher at Divide

Mountain (Table 3). As a percentage of total trees sampled, occurrence of seedlings and saplings

were comparable between the study sites. Seedlings accounted for 64.86% of all whitebark pine

trees at Divide Mountain and 73.82% at Parker Ridge, and saplings accounted for 11.96% and

5.82%, respectively. Blister rust infection rates and canopy kill were greater at Divide Mountain,

(Table 3). Though blister rust has been documented in northern Banff area (Smith et al., 2008),

we found no blister rust in the Parker Ridge plots.

Our density-diameter curves for both sites both exhibited a similar reverse-J shape (Fig

3.1). The curve for our Parker Ridge site had a steep drop between the first and second size

class. Divide Mountain had a low proportion of its population within the smallest size class, but

it exhibited only a small drop between the first and second size classes, indicating comparatively

higher recruitment.

Results of our Kruskal-Wallis tests to compare proportional whitebark pine occurrence

based on size category are listed in table four. Only the comparison for the 10-19.9 size class

was statistically significant ($H = -1.9$, $df = 1$, $P = 0.05$), with Divide Mountain plots having a higher proportion of the population within the 10-19.9 mm size class, representing older seedlings. Our model analysis revealed several significant associations, highlighting some marked differences in terms of biophysical variables associated with higher whitebark pine density between sites. Final model information is summarized in Table 5.

Discussion

The abundance and density of seedlings and saplings at both sites indicate that regeneration is not yet limited in either location, despite the presence of disturbance agents that damage and kill whitebark pine. Though blister rust infection rates and whitebark pine density differ between sites, both populations are similar in the percentage of population within each size class, with the exception of the smallest size class (0-9.9mm DGL). Our models revealed important differences in the biophysical variables correlated with whitebark pine density between sites. While regeneration and established trees have similar within-site correlations, seedlings and saplings have stronger correlations with the selected variables than established trees.

Regeneration and Population Structure

Whitebark pine trees sampled at the treeline ecotones of Divide Mountain and Parker Ridge had similar density-diameter curves, but the smallest size class (0-9.9mm DGL) exhibited notable differences in proportional membership between sites (Fig 3.1). The high proportion of seedlings and a lower density of established whitebark pine at Parker Ridge, the more northern site, suggest that these populations are characterized by high rates of seedling mortality. One

possible explanation is the active periglacial processes at Parker Ridge. Relict periglacial processes may encourage seedling establishment through turf exfoliation and the creation of topographic shelter (Butler et al., 2004), but active geomorphic processes can disturb small seedlings (Butler et al., 2007). If this population is characterized by high rates of seedling mortality while blister rust infection rates are low, the population is particularly susceptible given that any increase in infection could further limit whitebark pine establishment.

There are numerous possible explanations for the low percentage (34.6%) of Divide Mountain's population in the small size class. The severe blister rust in adjacent subalpine forests (~77% at Divide Mountain and ~73% in the greater Glacier ecosystem [Smith et al., 2008]) may be one cause of few seedlings, as a reduction in seed production would leave fewer available for dispersal to treeline (Tomback and Resler, 2007), but the low proportion may simply indicate a period of low germination and establishment, as regeneration at treeline can be episodic with favorable years (Holtmeier, 2009b). For example, negative pacific decadal oscillation (PDO) periods have been tied to seedling establishment pulses due to increased snowall (Alftine and Malanson, 2004). Additional cycles over varying time scales likely affect the favorability for seedling establishment, and could be another mechanism affecting the prorportion of each poupulation falling within the smallest size class. While there are relatively few small seedlings at Divide Mountain, this population exhibited only a small change to the second size class on the density-diameter curve compared to Parker Ridge. Moreover, the higher density of established whitebark pine at Divide Mountain suggests more success in establishment over the long term.

Results of our Kurskal-Wallis tests (Table 4) confirm that at the plot level, the two sites were similar in the proportion of each population within various size classes. The insigificant

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result for the 0-9.9mm size suggests that most plots from both Parker Ridge and Divide Mountain contain similar proportions of small seedlings, and that the notable differences at the population level result from several plots at Parker Ridge that contain many small seedlings. The only significant result was for the 10-19.9mm size class, indicating that Divide Mountain plots had proportionally more large seedlings. This difference is reflected in density-diameter curves for populations at each site, and supports the idea that seedlings are more successful in establishment at Divide Mountain despite very high blister rust infection rates.

Moderate levels of disturbance encourage for the maintancence of both stability and diversity in many ecosystems (White, 1979; Huston, 1979), and whitebark pine can decline when fire, a common disturbance in western forests, is suppressed (Arno, 1986). However, multiple high-intensity disturbances over short time periods can be very detrimental, and have lead to dramatic declines in this species. Though some research has found severe blister rust infection to limit whitebark pine regeneration (Tomback, 1995), we found no definitive evidence of limited regeneration at our sites. Population structures at both sites are quite similar and regeneration is common, but there may be a lag effect before severe blister rust infection is reflected at treeline. For example, subalpine whitebark pine stands in some nearby areas saw an increase in blister rust rates from 43% to 71%, and an increase in mortality from 26% to 61% between 1996 and 2004 (Smith et al., 2008), so the extreme infection and mortality may be a relatively recent occurrence, and treeline populations may not yet have adjusted to these declines.

Alternatively, whitebark pine regeneration at these treelines may still be limited by environmental variables more than seed availability, but there may be a threshold level of infection severity where diminished seed production and dispersal limit regeneration more than site factors, as Mckinney and others (2009) propose. Though regeneration is common, the

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maintenance of a healthy uneven age stand structure does not necessarily guarantee that blister rust has not already affected the overall density of whitebark pine at our sites. Based on our survey, blister rust is quite common at Divide Mountain, and infection and mortality can affect whitebark pine trees of any size. Larger whitebark pine may be more at risk for infection because they provide more surface area to catch airborne blister rust spores (Tomback et al., 1995; Resler and Tomback, 2008). As such, declines may be occurring across all size classes, but we cannot test this based solely on stand structure and regeneration density, as whitebark pine within all size classes may decline. Continued monitoring would help determine whether declines are occurring across all size groups, and whether the low percentage of seedlings at Divide Mountain was an episodic occurrence or an indication of suppressed regeneration.

Geographic Variability in Treeline Whitebark Pine Habitat

Our model results highlight variability between sites in biophysical variables associated with whitebark pine density. In the drier conditions of Divide Mountain, whitebark pine density is negatively associated with solar radiation and slope angle, and positively associated with tree island cover. These correlations suggest higher density of whitebark pine in relatively moist, sheltered sites. In the comparatively mesic environment of the Canadian Rockies, whitebark pine density on Parker Ridge is positively associated with solar radiation and negatively associated with flow accumulation, suggesting greater success in sunny, exposed plots with lower levels of water collection. These trends at treeline agree with habitat preferences described by Arno and Hoff (1989), who suggest that in moist mountain ranges, whitebark pine is found preferentially on warm, dry exposures, while in more arid mountain ranges, it is found in cooler, mesic sites.

Whitebark pine's increasing density in sunny, dry plots at Parker Ridge suggests that moisture availability is not an important limiting factor in determining optimum whitebark pine habitat at this site. Based on our experience and available aerial photography, Parker Ridge can stay partially snow covered into late summer, and many of our plots that were positioned down slope from snowpack likely received soil moisture throughout the summer. Conversely, most north-facing plots contained dense willow shrubs, indicative of moist soils. These plots may be too wet for whitebark pine, as the species is often absent on the most mesic sites across its range (Arno and Hoff, 1989). Large areas on Parker Ridge appeared to maintain snowpack year round, precluding growth, and areas with late snow release may have limited whitebark pine due to cooler soils that inhibit seed germination (McCaughey, 1990).

Warmer temperatures and higher levels of solar radiation due to Divide Mountain's more southerly location could make moisture availability more important in defining whitebark pine habitat at this site. While moist plots in close association with plenty of other trees may be atypical whitebark pine habitat, the generally dry conditions and extreme wind necessitate establishment in sheltered sites (Spittlehouse and Stathers, 1990). However, the positive association between density of established whitebark pine trees and convexity indicates that concave plots may not favor establishment, even though they are typically more mesic and sheltered. Despite these benefits, concave surfaces often lack drainage, have a higher probability of nocturnal temperature inversions, and retain snow cover late into summer, all of which can limit tree establishment (Wardle, 1968; Senn et al., 1994)

Sheltering effects play an important role in whitebark pine pattern at Divide Mountain as evidenced by the positive correlations we uncovered between whitebark pine density and tree island cover, as well as the density of other tree species. Shelter provided by tree islands and

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established trees can prevent seedling mortality by preventing ice particle abrasion and seedling breakage resulting from high winds, preventing wind desiccation, decreasing incoming solar radiation, and accumulating snow to provide soil moisture (Holtmeier, 2009a). Even after establishment, shelter from adjacent trees still improves growing conditions, as the removal of adjacent trees has been demonstrated to lower growth rates even among mature trees at harsh treeline sites (Choler et al., 2001). However, lowered soil temperature in shaded sites may be a limiting factor of pine seedling germination, establishment, and growth (Holtmeier, 2009a), so neighboring vegetation in plant communities simultaneously exert both facilitative and competitive effects (Callaway, 1995). The net effect of neighboring vegetation within a given treeline ranges across a continuum from strong, competitive effects in low-stress, mesic, sheltered sites to strong facilitative effects in high-stress, exposed sites (Callaway, 1995; Choler et al., 2001). The conditions faced at Divide Mountain may be more extreme than Parker Ridge from the point-of-view of whitebark pine establishment, likely making the sheltering effects of neighboring vegetation outweigh the effects of competition at Divide Mountain, while at Parker Ridge the competitive influences of adjacent trees may outweigh the facilitative effects.

Increased competitive ability by whitebark pine at Divide Mountain may also contribute to its association with neighboring trees. Strong, persistant topographically funneled winds could explain the increased importance of shelter, as well as an increased competitive ability of whitebark pine. The primary competitors at Divide Mountain, subalpine fir and englemenn spruce, are very sensitive to dessication and wind damage (Mattson and Reinhart, 1990). While these species are similar to whitebark pine in their temperature limits, increasing wind at higher elevation (Finklin, 1986) could limit spruce and fir growth, giving whitebark pine a comparative advantage. Though Parker Ridge experiences colder temperatures, it does not appear to have the

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same level of topographically enhanced wind, allowing spruce and fir to be more competitive at treeline. The resulting competiaiton may be another reason for why densities of whitebark pine are lower at Parker Ridge.

Differences in model estimates and significance levels between size classes within each site indicate that there are also differences between life stages. Regeneration groups were each significantly associated with three variables, while the established tree classes each had only one significant association at the .05 level. Moreover, most model coefficients were more extreme for the regeneration class. Pre-establishment seedlings are within the most sensitive life stage for most trees (Smith et al., 2009), so the stronger associations reflect higher success in plots with specific variables favorable for whitebark pine. These strong associations as seedlings and saplings could act as constraints that define where whitebark pine populations can persist, and may be one reason for the similarities in associations across life stages. Though a biophysical variable may be less important to whitebark pine once it has become established, it may still show an association due to habitat preference as a seedling. In fact, conditions that favor germination do not necessarily favor growth (Larson and Kipfmueller, 2010), so experimental studies with plantings could be helpful in understanding important variables when germination is excluded. This is an important consideration from a management perspective, as the steps of caching and germination within the landscape are skipped when planting rust-resistant whitebark pine.

Implications

Choice of size classes for analysis is an important study design consideration that could affect the results in similar studies. . Here we classified seedlings and saplings into one group

termed "regeneration," as well as an established trees group with DGL greater than 30mm. Our approach of aggregating seedlings and saplings into a regeneration class prevents us from investigating how the associations may change in various stages of regeneration. Instead, our approach of designating all small whitebark pine as regeneration means that we examine the relationship between biophysical variables and nutcracker caching preferences, germination, and early growth. Future inventories that are more comprehensive could provide an opportunity to study the associations within smaller size classes, and would be an informative complement to the experimental studies mentioned above.

Broad-scale climatic influences that affect moisture availability appear to be an important control of the specific habitat occupied by whitebark pine across its range, as well as its interaction with other vegetation. For example, in wet areas such as the Cascades and Canadian Rockies, whitebark pine prefers excessively well-drained substrates (e.g. pumice in Cascades) that inhibit competitors, whereas in dry areas such as the central Rocky Mountains, well-drained substrates can exclude whitebark pine (Weaver, 2001). Our model results suggest that our study sites follow this pattern, and that broad-scale factors influence the correlates of whitebark pine density at each study site. While both sites receive similar levels of precipitation (Table 2), Parker Ridge experiences lower levels of solar radiation and lower temperatures due to its more northerly location (Table 2; Barry, 1992). Combined with the cooling effect and moisture supply of the nearby Colubmia Icefied, these factors make Parker Ridge a generally moist, cool site throughout the year. Given these initial conditions, plots that are relatively dry and warm are more favorable for whitebark pine, which is typical favorable habitat for the species in all but the driest regions (Arno and Hoff, 1989). The type of site favored by whitebark pine at Parker Ridge may be too xeric for establishment at Divide Mountain, and we instead see density increasing in

relatively mesic plots at Divide Mountain. Shifts in temperature or precipitation regimes with changing climate could adjust these broad-scale climates, leading to a shift in what constitutes favorable habitat at any given site, potentially adding increased pressure to migrate on a species that is already stressed in many cases.

Of available management strategies, planting rust-resistant whitebark pine is a costly but comparatively effective strategy for conservation of whitebark pine (Hoff et al., 2001; Schoettle and Sniezko, 2007). Recent research has suggested planting resistant whitebark in shaded areas with moist soils (McCaughey et al., 2009). Though this may be optimum habitat in most cases, especially in the relatively arid areas of Divide Mountain, we have found this may not always be optimal. In the mesic northerly extent of whitebark pine, shaded areas with moist soils may be more prohibitive to establishment. While whitebark pine populations near our study area in Banff National Park are of lower immediate concern due to low infection rates, any future conservation efforts in this area should take this into account. However, we do not advocate for a direct application of these site conditions to management plans. Instead, we wish to stress the importance of evaluating current stands of whitebark pine within priority conservation landscapes to understand optimum whitebark pine habitat on a site-by-site basis.

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Tables and Figures

Figure 3.1. Density-diameter curves for our two study sites, with the proportion of trees within each size class at that site on the y-axis, and our size classes on the x-axis. Figure 2 includes all sampled whitebark pine, and while the first size class differs notably, the curves follow a rough reverse-J shape.
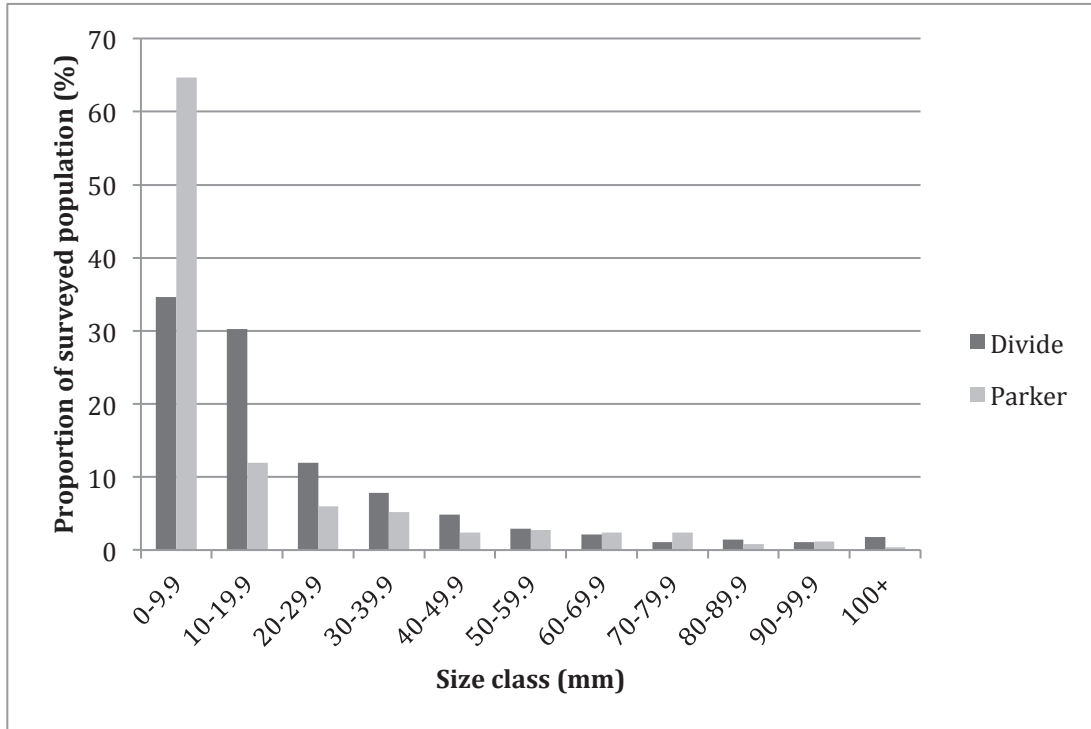
Table 1. Predictor variables (and abbreviations) used in our models, as well as range of variables for each study area.

Predictor Variables	Abbreviation	Divide Mountain	Parker Ridge
n	N/A	28	20
Elevation	elev	2097.24-2261.08m	2143.42-2284.60m
Slope Angle	slope	4-25°	1-28°
Curvature	curv	-8.24-8.06	-5.35-4.21
Potential Solar Radiation (watt hour/m^2)*	solar	692406.50-892607.56	647135.56-897198.63
Flow Accumulation (# cells)	flowacc	0-1210	1-98
Tree Island Percent Cover	ti	0-23.95	0-22.38
Distance to Subalpine (m)	dist	33.99-516.98	5.32-405.02
Number of non-whitebark pine trees	nonpial	0-19	0-36

* Due to the lage values causing false convergence errors for the modeling software selected, these values were rescaled to between 0 and 1 for each site, creating a relative potential solar radiation value.

Table 2. Range of elevation, slope, and climatic variables for our study site

	Divide Mountain	Parker Ridge
Elevation (m)	2097.24-2261.08m	2143.42-2284.60m
Slope Angle	4-25°	1-28°
Avg Jan Low	-11.7	-21.4
Avg Jan High	-0.5	-7.5
Avg July Low	7.6	3.9
Avg July High	25.9	20.1
Avg Precip	651mm	792mm

All temperatures are in Degrees Celsius. Parker Ridge data reported is from Columbia Icefields, AB (Walker and Holland, 1983). Divide mountain data reported from Saint Mary, MT and are provided by the Western Regional Climate Center (2011)

Table 3. Summary of whitebark pine and blister rust presence at Divide Mountain and Parker Ridge

		Divide Mountain	Parker Ridge
Subalpine Plots	BR* Infection	76.92%	0%
	Basal Area[+]	4.31±1.17 m^2 ha^{-1}	3.59±1.21 m^2 ha^{-1}
	Canopy Kill[+]	60.3±29.66%	0%
Treeline Plots	BR* Infection	24.09%	0%
	Basal Area[+]	0.89±1.26 m^2 ha^{-1}	0.33±0.32 m^2 ha^{-1}
	Seedling Density[+]	568.25±625.66	428.89±597.55
	Sapling Density[+]	104.76±124.08	33.33±45.31

*BR-Blister Rust.
+ Mean ± Standard Deviation

Table 4. Results of one-way Kruskal-Wallis tests of the relative frequencies of four size classes within plots at Divide Mountain and Parker Ridge

Size Class (mm)	Mean Rank Score		H	d.f.	P
	Parker	Divide			
0-9.9	24.80	24.29	0.1157	1	0.91
10-19.9	19.88	27.80	-1.9431	1	0.05
20-29.9	22.75	25.75	-0.7605	1	0.45
30+	25.65	23.68	0.4726	1	0.64

Table 5. Biophysical correlates of whitebark pine density at Parker Ridge and Divide Mountain. Model information is at the left hand side of each model, and all significant correlates are included and marked with significance levels in "P" column.

Divide Mountain							Parker Ridge			
Regeneration Model		Variable	Estimate	Std. Error	Z	P	Regeneration Model		Variable	Estimate
BIC	91.71	(Intercept)	3.601	0.642	5.607	***	BIC	68.31	(Intercept)	3.373
logLik	-37.53	ti	0.09	0.019	4.203	***	logLik	-26.67	dist	-0.008
Deviance	75.05	slope	-0.069	0.029	-2.37	*	Deviance	53.34	flowacc	-0.079
		solar	-2.291	0.625	-3.667	***			solar	2.487
30mm+ Model		Variable	Estimate	Std. Error	Z	P	30mm+ Model		Variable	Estimate
BIC	84.22	(Intercept)	0.423	0.313	1.351	NS	BIC	27.23	(Intercept)	-0.077
logLik	-33.78	ti	0.065	0.026	2.501	*	logLik	-9.122	solar	1.476
Deviance	67.56	Curv+	0.077	0.047	1.649	^	Deviance	18.24		
		nonpial	0.071	0.041	1.743	^				

Significance: <0.1 (^), <0.05 (*), <0.01 (**), <0.001 (***), Not Significant (NS)
+ Curvature values are near zero for relatively flat surfaces, while concave surfaces are negatie and convex surfaces are positive.
Variables: ti-Tree island Perent Cover, slope-Slope Angle, solar-Relative Potential Solar Radiation, curv-Curvature, dist-Distance flowacc-Flow Accumulation, nonpial-Number of non-whitebark pine trees

Correlation Matrices for Predictor Variables at Divide Mountain and Parker Ridge. See Table 1 for abbreviation descriptions.

Parker Ridge

	slope	ti	dist	curv	nonpial	flowacc	solar	elev
slope	1.0000	-0.3065	0.1211	0.0037	-0.4482	-0.2497	-0.0343	0.3391
ti	-0.3065	1.0000	0.0018	0.0360	0.1230	-0.0768	-0.2340	-0.1852
dist	0.1211	0.0018	1.0000	-0.0648	-0.5235	-0.4539	0.1392	0.4177
curv	0.0037	0.0360	-0.0648	1.0000	0.5333	0.1411	-0.2846	-0.3509
nonpial	-0.4482	0.1230	-0.5235	0.5333	1.0000	0.3108	-0.2489	-0.5940
flowacc	-0.2497	-0.0768	-0.4539	0.1411	0.3108	1.0000	-0.4593	-0.6734
solar	-0.0343	-0.2340	0.1392	-0.2846	-0.2489	-0.4593	1.0000	**0.7666**
elev	0.3391	-0.1852	0.4177	-0.3509	-0.5940	-0.6734	**0.7666**	1.0000

Divide Mountain

	slope	ti	dist	curv	nonpial	flowacc*	elev	solar
slope	1.0000	0.1904	0.2037	-0.1040	0.3225	-0.1914	0.3736	-0.4834
ti	0.1904	1.0000	0.1430	-0.0972	0.4727	0.0820	0.2059	-0.2988
dist	0.2037	0.1430	1.0000	0.0892	0.1756	-0.1257	0.4827	0.1759
curv	-0.1040	-0.0972	0.0892	1.0000	-0.2501	-0.0729	-0.0176	0.4184
nonpial	0.3225	0.4727	0.1756	-0.2501	1.0000	-0.0570	0.4565	-0.5280
flowacc	-0.1914	0.0820	-0.1257	-0.0729	-0.0570	1.0000	-0.3200	0.0391
elev	0.3736	0.2059	0.4827	-0.0176	0.4565	-0.3200	1.0000	-0.0658
solar	-0.4834	-0.2988	0.1759	0.4184	-0.5280	0.0391	-0.0658	1.0000

*Correlations based on square-root transformed data

Appendix B

List of biophysical correlates and whitebark pine counts for Divide Mountain and Parker Ridge.
See Table 1 for abbreviation descriptions.

Divide Mountain

quad	Slope	ti	dist	curv	nonpial	flowacc	elev	solar	0-29.9mm DGL	30mm+ DGL
GlacQuad01	7	17.50	437.16	-0.3980	6	1.33	2229.40	0.7836	10	5
GlacQuad02	25	23.95	130.65	0.2338	4	66.33	2214.24	0.0000	28	1
GlacQuad03	15	2.84	227.06	-3.5870	4	0	2261.08	0.2206	2	0
GlacQuad04	17	11.41	236.53	-8.2423	19	1.5	2244.89	0.1128	23	7
GlacQuad05	14	14.68	516.98	-2.4006	5	18.5	2214.88	0.4750	20	9
GlacQuad06	13	10.94	334.32	8.0608	11	9	2209.60	0.3970	24	9
GlacQuad07	6	5.77	166.06	-0.8165	1	0	2180.44	0.5983	13	2
GlacQuad08	8	18.59	141.25	-4.1773	9	104	2176.21	0.3867	72	7
GlacQuad09	4	2.50	63.41	4.5278	2	1.33	2155.40	0.6931	7	10
GlacQuad10	4	2.36	35.51	-0.6516	3	1210.33	2155.70	0.6588	8	0
GlacQuad11	15	0.00	73.04	-0.8994	2	137	2155.81	0.6730	1	0
GlacQuad13	18	1.31	438.01	0.2976	8	73.33	2189.01	0.1299	8	9
GlacQuad14	8	0.00	160.31	-0.1167	1	0	2097.24	0.4619	1	0
GlacQuad15	10	16.95	163.89	-0.7355	3	466.5	2101.05	0.3722	45	4
GlacQuad16	15	0.00	342.50	-0.5879	0	12.75	2197.45	0.7759	2	0
GlacQuad17	9	0.00	411.17	1.6668	2	110.33	2223.76	1.0000	1	1
GlacQuad18	8	19.94	422.32	-3.6772	9	82.5	2221.22	0.7344	6	10
GlacQuad19	8	8.10	295.61	2.0366	2	21.67	2158.65	0.5997	19	2
GlacQuad20	16	10.12	238.14	-4.5214	4	100	2158.39	0.2773	3	8
GlacQuad21	20	7.17	211.93	-2.4471	0	2.33	2149.86	0.8002	2	8
GlacQuad22	16	17.28	379.96	5.5953	9	162	2203.13	0.8535	10	20
GlacQuad24	11	18.48	43.61	2.2671	6	0.33	2204.98	0.4475	31	24
GlacQuad25	18	3.64	80.09	-4.4243	11	4.5	2190.37	0.0743	36	3
GlacQuad26	18	0.00	371.52	4.8182	1	1.33	2254.05	0.9142	4	1
GlacQuad27	22	16.06	245.15	2.6087	13	0	2226.81	0.3502	21	8
GlacQuad28	4	2.74	33.99	0.7875	1	3.33	2163.45	0.8877	12	2
GlacQuad29	13	3.63	188.15	1.5948	1	5.67	2165.12	0.5303	14	8
GlacQuad30	8	3.93	183.11	2.6087	1	4.4	2170.75	0.8629	1	5

Parker Ridge

quad	slope	ti	dist	curv	nonpial	flowacc	elev	solar	0-29.9mm DGL	30mm+ DGL
Quad01PR	20	0.00	74.87	-5.3479	0	31	2263.46	0.8094	6	1
Quad02PR	20	7.68	405.02	4.2117	4	1	2208.21	0.2136	2	1
Quad03PR	8	5.38	386.97	-3.6912	4	15	2199.44	0.5239	0	1

Quad04PR	6	1.95	194.18	0.8441	8	98	2156.81	0.3585	0	2
Quad05PR	22	0.98	187.51	-4.6032	0	57.5	2154.88	0.0000	0	2
Quad06PR	20	13.89	172.16	0.0179	12	57	2152.22	0.0732	0	1
Quad07PR	28	0.00	256.54	-3.3978	0	3	2281.50	0.8699	5	2
Quad08PR	16	5.51	238.31	-1.7473	0	3	2279.28	0.9188	28	8
Quad09PR	13	3.61	295.72	-4.2876	2	2.5	2284.60	0.9069	20	2
Quad10PR	25	1.21	237.20	1.0190	6	30.5	2268.07	0.9736	16	4
Quad11PR	15	10.42	258.70	-0.4309	1	2	2283.66	0.9156	24	4
Quad12PR	15	2.64	154.87	-1.8993	0	25	2254.00	0.9685	46	4
Quad13HG	19	0.00	36.45	2.5453	18	40.5	2143.42	0.2057	3	0
Quad14HG	9	12.28	72.21	-3.4699	6	35	2187.35	0.2633	0	1
Quad15HG	20	0.00	229.11	-0.0014	3	30	2220.07	0.0722	1	0
Quad16HG	16	0.00	192.98	1.3024	23	30	2220.62	0.2970	0	1
Quad17HG	13	22.38	76.80	-0.1789	17	35	2187.42	0.2064	1	1
Quad18HG	1	3.14	5.32	1.3799	36	43	2144.35	0.7507	3	2
Quad22PR	8	14.54	307.66	-2.3667	10	17	2197.30	0.4630	13	3
Quad23PR	21	5.24	83.88	0.5705	12	20	2167.34	0.2522	40	4