The regeneration niche of whitebark pine: key to restoring a species

by

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Abstract

Understanding the regeneration stage of any species is key to determining the processes that lead to population persistence and structure, community development, and succession. In the case of the endangered whitebark pine (*Pinus albicaulis*), knowledge of regeneration processes will be important for developing approaches for recovery and restoration of the species. I investigated biophysical drivers of whitebark pine seedling presence, abundance, and growth in the northern Alberta Rocky Mountains where mortality from white pine blister rust (caused by the fungus *Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*) remains low and whitebark pine regeneration is poorly studied. Transects were established in different mesohabitats (community type and elevation) to determine how these factors influence whitebark pine regeneration. Mesohabitat-scale conditions and seedling density along each transect were measured and microsites with and without whitebark pine seedlings were characterized along each transect. The height, age and health of each whitebark pine seedling found in each microsite was recorded and a subset of seedlings was destructively sampled in order to analyze annual growth and release.

In forest mesohabitats canopy gaps at microsite scales favored occurrence, growth rate and growth release. However, at the mesohabitat scale seedling abundance was positively related to canopy cover. Whitebark pine seedlings in open habitats below treeline were negatively associated with cover of rock, graminoids and seedlings of other tree species, grew fastest at intermediate values of temperature and dryness, and exhibited release in microsites with little other understory cover. These results suggest that at the northern portion of its range, whitebark pine grows best in conditions that limit competitors but still allow for sufficient growth. This contrasted with the situation in alpine and treeline mesohabitats, where increased growth rates, growth release and seedling presence were associated with warmer microsites that had higher vegetation cover. Seedling density in both open and treeline environments was highest along southwest facing slopes. That release and general success of seedlings was better in canopy gaps supports the use of restoration activities such as thinning overstory trees and planting in open mesohabitats or microsites. As the regeneration niche of whitebark pine differed among mesohabitats and biophysical drivers of success differed among presence, abundance and growth of whitebark pine, I suggest that it is critically important to consider the mesohabitat and all factors of regeneration success when restoring whitebark pine.

Dedication

I lift my eyes up to the mountains –

where does my help come from?

My help comes from the Lord,

the Maker of heaven and earth.

Psalm 121: 1-2

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Table of Contents

List of Tables

Improvements in complexity parameter are in the fourth column; in brackets are the number of observations missed if that variable is used. Refer to Table 2.1 for explanation of abbreviations.

Appendix 2 – Table 3: Primary and alternate splits at each node for the seedling density regression trees in **A**) forest mesohabitat (Figure 2.5) and **B**) open mesohabitat (Figure 2.9); **C**) treeline mesohabitats (2.13); and **D**) alpine mesohabitats (2.14). Improvements in complexity parameter are in the fourth column; in brackets is the number of observations missed if that variable is used. Refer to Table 2.1 for explanation of abbreviations.

Appendix 2 – Table 4: Primary and alternate splits at each node driving release in **A**) forest mesohabitat (Figure 3.9), **B**) open mesohabitat (Figure 3.10) and **C**) alpine-treeline ecotone (ATE) mesohabitats (Figure 3.11). Improvements in complexity parameter are in the fourth column; in brackets is the number of observations missed if that variable is used. Refer to Table 2.1 for explanation of abbreviations.

Appendix 3 – Table 1: Plant species associated with vegetation groups, as determined using the average linkage method based on Euclidean distances. Species associated with each discrete vegetation group for each mesohabitat. Species associated with each group are listed in descending order based on the strength of association with that group. n = number of plots in the dataset for that plant group. Refer to Appendix 3 – Table 2 for an explanation of the species codes.

Appendix 3 – Table 2: List of species found in 5% or greater of microsite plots for any mesohabitat. Corresponding code for abbreviation found in Appendix 3 – Table 1.

List of Figures

numbers is the total number of replicates (seedlings) at that node. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 4. Unexplained error was 0.478. Only primary splits with a complexity parameter of 0.07 or greater are shown.

Figure 3.11: Results of regression tree analysis showing the drivers of whitebark pine seedling release in forest mesohabitats. Numbers underneath each node represent the ratio of suppressed to released seedlings; a split to the right represents increased seedling release while a split left is towards increased seedling suppression. The sum of both numbers is the total number of replicates (seedlings) at that node. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 4. Unexplained error was 0.231. Only primary splits with a complexity parameter of 0.04 or greater are shown.

Figure 3.12: Relationship between ring width and annual height growth for seedlings from all mesohabitats and of all release categories. Pearson's correlation coefficient was 0.687 (p-value<0.001).

Appendix 1 – Figure 1: Location of study area. Left box indicates study area location in relation to overall whitebark pine distribution (Whitebark Pine Ecosystem Foundation 2014). Top and bottom right boxes represent Willmore Wilderness Park and Jasper National Park study areas respectively. Characterization of the regeneration niche of whitebark pine (Chapter 2) took place at all sites as indicated by black and red dots while investigation into growth release of whitebark pine seedlings (Chapter 3) only occurred at sites designated by black dots.

CHAPTER 1: General introduction

1.1. Background biology

The summer of 2013 will forever be remembered as the summer of hiking, helicopters and mountains. As a result of my field research, I had the opportunity to hike approximately 100km in Jasper National Park and spend 17 nights straight camping above the treeline in Willmore Wilderness Park. Near the top of every mountain were majestic, battle worn, and wonderful whitebark pine. Whitebark pine make up a significant portion of the subalpine region of Jasper and adjacent Willmore but it might not be long before the trees that welcomed us to the heights of Roche Bonhomme and Verdant Creek join the ghost forests that have become prominent in Waterton Lakes and Glacier National Parks. Disease and infection have leveled the species in the core of its range and it seems as though it is only a matter of time before wide-scale mortality works its way north. I've committed to join the ranks of those committed to saving whitebark pine in part because of its ecological role, but also due to the grandeur of those individuals gracing the slopes that I traversed regularly during the summer of 2013. This thesis will explore the biophysical drivers of seedling regeneration in the hopes that we can inform restoration planning for the species here in Alberta.

Whitebark pine (*Pinus albicaulis* Engelm.) is a charismatic, long-lived subalpine tree species found in western North America (Tomback et al 2001b). On the western portion of its range whitebark pine is distributed along the Coastal Mountains from northern British Columbia to southeastern California. The eastern part of its range is along the Rocky Mountains just south of McBride, British Columbia to northeastern Nevada (McCaughey and Schmidt 2001). Taxonomically, whitebark pine is in the family Pinaceae, genus *Pinus*, subgenus *Strobus*, section *Strobus* and subsection *Cembrae* (McCaughey and Schmidt 2001). Characteristics of whitebark pine that are shared by *Cembrae* pines are: five needles per fascicle, indehiscent cones that remain mostly closed at maturity and are dispersed by birds of the genus *Nucifraga* (McCaughey and Schmidt 2001). Whitebark pine has a broad ecological niche that allows it to exist in different successional stages in several different community types, depending on site conditions and disturbance regime (Arno and Hoff 1989, Arno 2001). These include: climax (upright as well as treeline krummholz) in the coldest and driest subalpine zone; co-climax in sites capable of supporting shade-tolerant species such as subalpine fir and Engelmann spruce but in which conditions are too harsh for them to become dominant; and seral where conditions favor stronger competitors but disturbance events allow whitebark to inhabit open territory.

Whitebark pine is considered a keystone species (Ellison et al. 2005), one that plays a much more important role than its abundance would suggest (Paine 1969). It is an important food source for a host of subalpine and alpine animals due to the high fat and caloric content of its seeds (Lanner 1982). Squirrels, rodents, jays, finches, chickadees, nutcrackers have all been found to feed on whitebark pine seeds in the fall (Hutchins and Lanner 1982). Whitebark pine is also an important pre-hibernation food-source for black bears and grizzly bears (Mattson and Reinhart 1997). In fact, during mast years, grizzly and human encounters are reduced and grizzly reproductive success significantly increases (Mattson et al 1992). Whitebark pine plays an important role in regulating erosion and spring run-off as it is one of the few species capable of colonizing cold and dry subalpine terrain (Weaver 2001). By colonizing harsh and newly disturbed landscapes it is able to facilitate the colonization of shade-tolerant, less hardy species (Callaway 1998, Choler et al 2001). This facilitative effect has been observed recently in Montana and Canada where whitebark pine has shown a prominent role in treeline development and advancement (Resler and Tomback 2008, Tomback et al 2014).

As stated previously, whitebark pine cones are partially indehiscent and do not employ wind or gravity to disperse their seeds (Lanner 1982). Rather, they rely on an avian disperser, the Clark's nutcracker (*Nucifraga columbiana*) for seed dispersal (Tomback 1982, Lanner 1982). Nutcrackers predominantly harvest seeds in late August and September after seeds are mature (Tomback 1978). They will then cache the seeds in quantities that exceed their metabolic requirements (Tomback 1982, Lanner and Hutchins 1982). Cache sites are typically located within 31km of harvest sites and are often placed within the bird's ~400ha home range (Lorenz et al 2011). While whitebark pine seed may be cached in locations where establishment is impossible such as within trees, the sheer amount of seed cached results in some seed being placed in favorable microsites (Lorenz et al 2011). It is through this process with the coevolved Clark's nutracker that whitebark pine is able to establish in harsh open areas in the subalpine and quickly inhabit disturbed space in lower subalpine and montane regions (Tomback 2001). While whitebark pine is entirely dependent on the Clark's nutcracker for seed dispersal, Clark's nutcracker is much more of a generalist - able to feed on other conifers as well as berries and insects (Tomback and Linhart 1990). While the mutualism with Clark's nutcracker has been effective for dispersing whitebark pine seed, optimal foraging theory suggests that in the event of whitebark pine decline, Clark's nutcracker may move on to other food sources (Pyke 1984). Indeed recent research has suggested this very effect (McKinney et al 2009, Barringer et al 2012).

1.2. Limiting factors

Several limiting factors have resulted in population decline and fragmentation of whitebark pine throughout its range. First and foremost of these is an introduced fungus, *Cronartium ribicola* J. C. Fisch., which causes the disease known as white pine blister rust (WPBR) (Tomback and Achuff 2010). *Cronartium ribicola* was introduced to western North America from Eurasia via timber shipments on the west coast in the 1900's (Geils et al 2010). Since then it has spread to all but one of the five-needled pines in the west, causing significant declines in each (McDonald and Hoff 2001). *Cronartium ribicola* is an airborne pathogen that infects whitebark pine trees, saplings and seedling through the needles. Rust mycelia grow down through the phloem of the tree and cause annual eruptions in apparently healthy tissue in what are known as cankers. Erupting cankers ultimately girdle the branch or stem where WPBR is present, which kills the tree above the infection, causing top-kill, branch death or the death of the tree depending on the location of infection. These erupting cankers produce aeciospores that may travel up to 1200 km and transmit the fungus to alternate hosts which include predominantly *Ribes,* as well as *Castilleja* and *Pedicularis* species (Geils et al 2010). Repeated asexual reproduction during the uredinial stage on the alternate hosts eventually leads to the production of telia in late summer/fall when sexual reproduction takes place and produces haploid basidiospores. Basidiopsores travel up to 1-2 km and cause new infections in whitebark pine. WPBR has been observed in nearly all known whitebark pine populations in Canada (Smith et al 2008). Overall, the incidence of WPBR has slowly increased throughout Canada from 37% in 2003/04 to 44% in 2009 while WPBR induced mortality has increased from 18% to 28% (Smith et al 2013).

Mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) is a native insect of forests in western North America where outbreaks occur episodically (Logan et al 2010). Whitebark pine has also been exposed periodically to MPB outbreaks (Larson 2011) and these episodes were considered one of the primary disturbance agents of whitebark pine in some parts of its range (Arno 1986, Perkins and Roberts 2003). Whitebark pine lacks initial and induced chemical defenses to MPB, as well as some of the physical defenses possessed by lodgepole pine (Raffa et al 2013); in the past the unfavorable climatic conditions of subalpine environments has likely prevented outbreak levels of MPB in whitebark pine stands (Amman 1973). However, human-induced climate change has caused MPB range expansion east of the continental divide in the northern Canadian Rockies and into subalpine populations of whitebark pine where unprecedented infestation levels of MPB have occurred (Logan et al 2010). Mortality due to mountain pine beetle has been detected in whitebark pine stands throughout the United States and Canada and has caused serious decline in some regions. For example, large numbers of whitebark pine trees have been killed in Yellowstone National Park (Logan et al 2010), while surveys in northern Idaho have shown mortality rates from MPB ranging between 16 and 90% (Gibson et al 2008)..

Altered successional dynamics of communities in which whitebark pine plays a seral role has also been implicated in the decline of whitebark pine (Tomback and Achuff 2010). Whitebark pine is able to establish in disturbed sites via the dispersal of seed by Clark's nutcracker (Tomback 1982, Lanner 1982) and this may allow it to arrive at a site and regenerate more quickly than wind dispersed species such as Engelmann spruce (*Picea engelmannii* Parry ex Engelmann) and subalpine fir (*Abies lasciocarpa* Nuttal) (Tomback and Linhart 1990). In the absence of disturbance, however, shade-tolerant conifers eventually replace whitebark pine on productive sites in the subalpine zone (Arno and Hoff 1989, Campbell and Antos 2003). Fire frequency has declined in the mountain parks as a result of climate change and/or fire suppression which has been practiced in many of the mountain parks of western North America over the last 50 years (Arno 2001). As such, in regions where whitebark pine depends on fire, available habitat for whitebark pine has been limited (Tomback and Achuff 2010).

Whitebark pine was listed under the *Wildlife Act* as 'Endangered' in Alberta in 2008 in Canada under the *Species at Risk Act* in 2012 (Alberta Whitebark and Limber Pine Recovery Team 2014) and is now a candidate for federal listing in the US (US Fish and Wildlife Service 2014). Whitebark pine is declining throughout its range and is vulnerable to extirpation in many areas. Researchers fear that whitebark pine has already entered into the spiral of extinction (Tomback and Kendall 2001). However, given the long-lived nature of whitebark pine, if decisive and effective action is taken now, we may be able to prevent the loss of this charismatic, keystone species.

1.3. Restoration of whitebark pine

Under the Canadian *Species at Risk Act* we are required to prevent threatened and endangered species from becoming extinct and to provide for the recovery of species that have been extirpated, endangered or threatened due to human activity. Whitebark pine is endangered in Canada and Alberta, due to the impact of white pine blister rust, and further confounded by mountain pine beetle, human-induced climate change, and changing forest successional dynamics associated with changes to fire frequency in the lower subalpine zone where whitebark pine historically has played a seral role.

Current restoration plans for whitebark pine all include an enhancement of the regenerative process (Aubry et al 2008, Keane and Parsons 2010, Schwandt et al 2010, Keane et al 2012, Alberta Whitebark and Limber Pine Recover Team 2014). Specific actions may include thinning competing tree species, identifying traits of blister rust resistance in cone-bearing trees in the hopes of developing blister rust resistant seedlings, and imitating natural disturbance regimes such as fire that help perpetuate whitebark pine on the landscape. Each of these steps in restoring whitebark pine communities comes with the caveat that the biophysical drivers of successful whitebark pine regeneration are understood, not only for whitebark pine in general, but also on a region-by-region basis. Since whitebark pine is found in a number of different community types and across a broad geographical range it is important that the biophysical drivers of regeneration are known for each region (Larson and Kipfmueller 2012).

One investigation that may be useful in the restoration of whitebark pine is an examination of the difference between whitebark's fundamental and realized niche (*sensu* Hutchinson 1957). Many species occupy different habitat in the presence of competition (realized niche) than they would if that competition was removed (fundamental niche). Whitebark pine is known to have a broad fundamental niche that is reduced due to competition with such species as Engelmann spruce and subalpine fir, which tend to outcompete whitebark pine in mesic habitats (Arno 2001, Weaver 2001). Differences in the regeneration niche (Grubb 1977) have likely allowed these species to coexist but it is clear that both fir and spruce have a detrimental effect on whitebark pine's ability to regenerate (Larson and Kipfmueller 2010). Research has shown that the largest whitebark pines have the greatest reproductive capacity (largest cone crop) (Weaver and Forcella 1986, McCaughey et al 2009). More productive moderate habitats with longer growing seasons may have the highest propensity for producing large whitebark pine if it is able to escape the competitive understory (Arno and Hoff 1989, Arno 2001, Moody 2006). Further research is required on the conditions that allow whitebark to thrive in productive habitat of the lower subalpine zone.

1.4. Whitebark pine and disturbance

Although whitebark pine regeneration seems to be facilitated by the presence of open areas it is clear that the species does not necessarily rely on disturbance for its persistance. Whitebark pine for example, exists in several community types as a climax species where it is self-replacing (Arno and Hoff 1989). In addition, continuous whitebark pine recruitment occurs in all community types including (if at low levels) in late successional stands dominated by subalpine fir and Engelmann spruce (Campbell and Antos 2003). However, in many instances, whitebark pine clearly benefits from fire disturbance (Tomback et al 2001a, Arno 2001, Tomback and Achuff 2010). In fact, most restoration plans for the species include prescribed burning or include a let burn policy (Aubry et al 2008, Keane and Parsons 2010, Tomback and Achuff 2010, Keane et al 2012). Whitebark pine is often able to reach open areas first due to the caching behavior of Clark's nutcracker (Tomback and Linhart 1990). In these areas, if whitebark pine is established first, it can grow at the same rate as its primary competitors and be first to the canopy. Further, such areas are often too dry and windswept for its primary competitors, subalpine fir and Engelmann spruce (Tomback et al 2001).

It is important that I understand the specific benefits and drawbacks of using fire to promote whitebark pine seedling establishment. Fire is inherently dangerous and can lead to ecosystem change, property damage, and loss of life. Fire can also result in the mortality of mature whitebark pine trees, eliminating the seed source needed for future regeneration. Recent restoration trials performed by Keane and Parsons (2010) showed that mature whitebark pine mortality equaled that of subalpine fir and suggested that whitebark pine may not be as resistant to fire as previously thought (Ryan and Reinhardt 1988). In addition, several studies have observed mature subalpine fir that was older than whitebark pine growing in the same stand (Daniels et al 2006, Wong 2012) showing that whitebark pine may not be the first to colonize post-disturbance.

1.5. Biophysical drivers of the regeneration process for whitebark pine.

Whitebark pine trees are situated in lower to upper subalpine ecosystems over an incredibly wide geographic range and as such appear to be adapted to a number of different environmental conditions that might impact their growth. In order for regeneration to be considered successful a seed must be planted by a Clark's nutcracker, that seed must germinate and then survive and grow. Various biophysical processes affect each stage of regeneration differently.

The first limitation to successful regeneration is seed availability. Much of the research done on whitebark regeneration has focused on seedling abundance which is impacted by seed availability (Moody 2006, McKinney and Tomback 2009, Larson and Kipfmueller 2010, Barringer et al 2012). At a broad scale, proximity to seed source, size of seed source and cone production all affect seedling abundance. It has been suggested that a threshold of roughly 500-1000 cones/ha is required before sufficient seed escape occurs to promote regeneration (McKinney et al. 2009, Barringer et al 2012). If whitebark pine cone production falls below this threshold the likelihood of visitation by Clark's nutcrackers is reduced and the probability of seedling establishment is subsequently diminished. Whitebark pine trees with the largest crowns produce the largest cone crops (Weaver and Forcella 1986). Identifying conditions that lead to not only increased density of mature whitebark pine but also increased crown size would be important for developing approaches to ensure that sufficient cone production is reached.

Seed dispersal occurs solely via Clark's nutcrackers (Tomback 1982). Nutcrackers disperse mature seeds in late summer/early fall in levels above their caloric requirements (Tomback 1982, Lanner 1982) and seed cached in favorable microsites has a chance at germination if the nutcrackers or other secondary predators (such as chipmunks, squirrels and mice) do not retrieve it. Cache selection of nutcrackers is quite varied. Lorenz et al (2011) found on sites in eastern Washington, 98% of harvested seed was cached within a ~400ha home range and frequently in locations where germination was impossible. However, Tomback (1978) reported different caching behavior in eastern California. She noted several instances of “convergent caching” where multiple nutcracker cached on south/southwest facing slopes and found that preferred microsites were tree bases, open pumice/mineral soil and the base of rocks while wet or damp soil and the sites with grass were avoided. No research has been conducted on Clark’s nutcracker caching behavior anywhere throughout the Canadian Rockies and knowledge of their behavior at the peripheries of its northern range is limited.

A further limitation to seed availability is cache pilferage by secondary seed predators such as rodents. Rodents remove up to 50 percent of seed cached by nutcrackers (Pansing 2014) and this limits seed availability for germination, particularly when seed production is low (Calviño-Cancela 2007). Stand conditions influencing the level of post-dispersal predation in whitebark pine are not well understood.

The third hurdle for regeneration is seed germination. Germination of whitebark pine is controlled by several factors. Firstly, whitebark pine must go through an extensive cold stratification period which helps break down its tough seed coat and overcome several physiological barriers (McCaughey et al 2001). While soil moisture in subalpine environments is rarely limiting (Weaver 2001, Körner 2003), surface moisture availability appears to greatly influence germination. Several studies have shown an increased abundance of young seedlings in more moist sites (McCaughey and Weaver 1990, Tomback et al 1993, Tomback 2001, Moody 2006). Tomback et al (1993) related years of high episodic seedling recruitment in burned stands to years of elevated spring precipitation levels. In the alpine-treeline ecotone (ATE), whitebark pine is predominantly found in areas with longer snow cover, which in turn have higher soil moisture (Mellman-Brown 2005). Temperature also appears to have an effect on seedling germination. In general, successful germination appears to occur more frequently on warmer sites as long as there is sufficient moisture (McCaughey and Weaver 1990, Moody 2006, Larson and Kipmeuller 2010).

The fourth and final growth stage in the recruitment process is the seedling stage, or the transition from seedling to sapling. Characterization of the regeneration niche of whitebark pine needs to be done within the context of its environment. As mentioned previously, whitebark pine can be found in many different community types along an elevation gradient (Arno 2001) and different biophysical variables limit regeneration success depending on the specific site conditions. Indeed whitebark pine seedlings shift from being facilitated by nearby vegetation at high elevations to being negatively affected by competing vegetation at lower elevations (Callaway 1998). For this reason, at the upper elevational limit of whitebark's distribution, environmental stressors such as wind-induced moisture stress and length of growing season need to be considered, while in more moderate lower subalpine zones, competition appears to be the predominant factor in whitebark pine seedling success (Weaver 2001).

Recruitment of seedlings can occur in all forest stages. However, research shows that seedlings are unable to compete in dense, late seral stands (Campbell and Antos 2003, Moody 2006, McCaughey et al 2009, Larson and Kipfmueller 2010). Whitebark pine is considered moderately shade tolerant (Arno and Hoff 1989) but if it is growing lower in the canopy of later successional stands it may not acquire sufficient photosynthetic active radiation. Whitebark pine may escape from heavy competition by occupying more open harsh environments where other competing conifers struggle to survive (Maher et al 2005). These include upper-elevational forests as well as dry, open sites below treeline that are opened due to disturbance. In these locations whitebark pine outcompetes other conifer species but can still suffer from overexposure. Heat scorching of young whitebark pine seedlings can lead directly to mortality (McCaughey and Weaver 1990, Tomback 2001, Moody 2006, Larson and Kipfmeuller 2010). Tomback et al (2001) reported high mortality rates in moist burned sites where a heavy duff layer contributed to very high soil temperatures. Larson and Kipfmueller (2010) found that while seedling germination rates were high in warm sites, cooler sites led to more seedlings surviving to the sapling stage; this suggested a trade-off between germination and seedling survivorship where germination increases on warmer sites but emerging seedlings are more susceptible to heat scorching.

In open as well as alpine/treeline environment, whitebark pine seedlings can benefit from the presence of other vegetation or objects that help to alleviate water stress induced by wind. Izlar (2007) reported increased survival for seedlings planted in protected microsites compared to those without protection. This was particularly true for small seedlings. Tomback et al (1993) found that 81% of seedlings growing in post-burn transects were within 15cm of objects such as downed trees and rocks. Maher et al (2005) and Mellman-Brown (2005) both found that whitebark pine survivorship is significantly increased when in proximity to tree islands or other vegetation at treeline. Whitebark pine is an important tree island initiator (Resler and Tomback 2008, Tomback et al 2014), but whitebark pine seedlings that initiate tree islands seem to benefit initially from rocks found on their windward side.

1.6. Growth rate and release

Whitebark pine seedling growth rate varies with biotic and abiotic conditions. Poor growth is likely a better indicator of unfavorable conditions than absence of whitebark pine since absence may be a facet of caching behavior of Clark's nutcrackers. Weaver et al (1974) found that dominant whitebark pine trees had grown ~6 cm/year until they reached a height of 3 m after about 100 years. However, they did not mention microsite conditions leading to this growth. Perkins (2004) found greater growth rates in burned stands, attributing this to more open conditions. However Moody (2006) found the greatest growth rates occurred on mesic and submesic stands. Campbell and Antos (2003) found patterns of whitebark pine growth rates to be unpredictable; growth was rapid in some areas but slow in others. Eventual growth to the canopy, however, was similar to that of subalpine fir and Engelmann spruce. Weaver (2001) attributed much of the growth of whitebark pine trees to length of growing season. The most effective means of successfully restoring whitebark pine populations may be targeted planting of white pine blister rust resistant seedlings in environments that promote rapid growth of whitebark pine seedlings.

Height growth of plant species is often dependent on appropriate below ground growth and these growth responses to adequate below ground resources are well documented (Canhamm et al 1996, Poorter and Nagel 2000). Mycorrhizal associations are important for the retrieval of below-ground nutrients (Read and Perez-Moreno 2003). In whitebark pine. Mycorrhizae native to whitebark pine systems have been discovered and improve seedling survival in greenhouse trials (Cripps and Grimme 2011, Cripps and Antibus 2011) but more work needs be done to understand the effect below ground associations and growth have on height growth for whitebark pine.

Nearby vegetation, be it trees, shrubs, or even herbs, may initially facilitate survival of conifer seedlings (Callaway 1998). However this relationship soon becomes competitive as the benefits of water retention and protection from extreme temperatures and herbivores are soon supplanted by diminished availability of light and nutrients. Growth release can occur if overstory trees die, creating a canopy gap, or if the conifer seedling outgrows understory vegetation and “escapes” the competitive effects (Grubb 1976). Very little research has been done on releases in small whitebark pine seedlings. Campbell and Antos (2003) showed saplings and small trees appeared able to survive periods of long suppression and to show release growth. However, Keane et al (2007) found that while larger trees had the ability to release when competitive nearby trees were removed, that ability diminished in smaller trees. Annual whorls on many seedlings in Willmore Wilderness Park seem to suggest that seedlings will often tolerate many years of poor vertical growth before releasing (J Gould, personal observation, September 30, 2012). The ability to quickly reach the overstory is important for the maintenance of whitebark pine in areas where whitebark pine occupies a seral niche. Understanding the growth releases of whitebark pine seedlings may be critical in suggesting ways to assist whitebark pine in remaining in these productive environments. In addition, knowledge about the timing of releases may give further insight into the size of seedling that is best planted in various habitats.

1.7. Research summary and objectives

I studied patterns of regeneration in whitebark pine near the northern limits of its distribution in Willmore Wilderness Park and Jasper National Park, Alberta, Canada. The overarching objective of the research was to inform restoration planning for the species, particularly in Alberta.

In chapter 2 I investigate the drivers of presence and absence, density and growth of whitebark pine as all three aspects of regeneration paint a picture of mesohabitats and microsite environments that lead to increased regenerative success. My specific research objectives were to:

1. Characterize the biophysical conditions that determine whitebark pine seedling presence and absence, density, and growth and determine how these differ among community types and along elevation gradients;
2. Determine if and under which environmental conditions disturbance would benefit seeding establishment and seedling growth

I predicted that in forest mesohabitats whitebark pine seedlings will be excluded in very dense canopies and understories. In moderately dense forest environments growth rates will be suppressed while the highest growth rates would be observed in canopy gaps. Finally, I expected whitebark pine performance to be poorest in stands where subalpine fir and Engelmann spruce dominate.

Growth and density were expected to be highest in open habitats below treeline (due to reduced competition but moderate environment). I predicted that seedlings in open environments would prefer to co-occur with other vegetation (as germination is facilitated by water availability and shrubs and other herbs help to retain water but this trend will decrease as seedlings grow larger).

In alpine and treeline environments I predicted that seedlings would be very dependent on nearby objects and vegetation for survival. I hypothesized that regeneration success in both alpine and treeline environments will occur more frequently in close proximity to shelter such as vegetation or rocks in the windward direction.

In chapter 3 I investigate the biophysical drivers of whitebark pine seedling growth release. Specifically, my research objectives were to:

1. Determine if growth release occurs in whitebark pine seedlings at the north and east edge of its range;
2. If so, determine under what conditions and at what size and age growth release occurs; and
3. Determine how the environmental conditions contribute to growth release

I predicted that seedlings would release earlier and more frequently in openings compared to forest mesohabitats (due to the large effect of light availability on release). In alpine and treeline environments, I predicted that growth would be more erratic than in forest and open habitats (as seedlings may release initially but become inhibited by wind as they grow larger). I also predicted that released seedlings in open and forest mesohabitats would typically occur with dense understory vegetation while seedlings in treeline and alpine would be unaffected by the presence of understory vegetation.

CHAPTER 2: Factors influencing whitebark pine regeneration

2.1. Abstract

Understanding the recruitment stage of any species is key in determining the processes that lead to population persistence and structure, community development, and succession. In the case of the endangered whitebark pine, knowledge of regeneration processes will be important for developing approaches to successfully restore the species. Regeneration processes and stand dynamics of whitebark pine vary across its geographic range; thus information from different regions is needed to fill all of the information gaps. In particular, research in areas where mortality has not yet led to reduced or altered regeneration processes will be important for understanding regeneration processes in unimpaired ecosystems and may provide input into recovery of impaired ecosystems. I investigated biophysical associates of whitebark pine seedling presence, growth rate, and abundance in the northern Albertan Rocky Mountains (Canada) where mortality from white pine blister rust and mountain pine beetle remain low and where whitebark pine regeneration is poorly studied. My overarching goal was to inform recovery efforts and restoration planning for the species, particularly in Alberta, and to aid in defining critical habitat as required under *Species at Risk* legislation. I established regeneration transects in different mesohabitats (community type and elevation) to determine how these factors influence whitebark pine regeneration. In order to determine drivers of seedling abundance I measured mesohabitat-scale variables and recorded seedling density along

each transect. Along these same transects in order to determine factors of whitebark pine presence and growth rate I characterized the biophysical environment in microsite plots with and without whitebark pine seedlings and recorded the height, age and health of each whitebark pine seedling found in “occupied” plots.

In forest mesohabitats I observed a dichotomy of scale with regards to the effect of canopy cover on whitebark pine seedling success. At the microsite scale whitebark pine seedlings most often occurred in canopy gaps with diverse understory communities and availability of bare mineral soil. Seedling growth rate was highest in canopy gaps. At the mesohabitat scale seedling abundance was greatest along transects with higher (> 32%) average canopy cover. Whitebark pine seedlings in open habitats below treeline were negatively associated with cover of rock, graminoids and seedlings of other tree species and grew fastest at intermediate values of mean annual temperature, slope and terrain dryness. This suggests that at the northern portion of its range whitebark pine does best in conditions that limit competitors but are not so harsh as to severely hamper growth and survival. This contrasted with the situation in alpine and treeline environments, where increased growth rates and seedling presence were associated with microsites that had higher vegetation cover and were warmer. Seedling density in both open and treeline environments was highest along southwest facing slopes suggesting that climatic factors such as warmer temperatures and early snow melt contribute to germination and survival of seedlings or increased caching by Clark’s nutcrackers. The regeneration niche of whitebark pine differed among mesohabitats, for this reason I suggest that it is critically important to consider the mesohabitat as well as the microsite when planning for recovery or restoration of whitebark pine.

2.2. Introduction

Whitebark pine is a hardy subalpine conifer species occurring throughout the Rocky and Coastal Mountain Ranges of western North America from British Columbia and Alberta in the north to California and Nevada in the south (McCaughey and Schmidt 2001). In harsh, open areas it outcompetes other conifer species and occurs as a climax species in cold, dry upper subalpine environments (Arno and Hoff 1989). It also grows well in more moderate, resource abundant habitats in the lower subalpine but is not as shade tolerant as competing species such as subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). Whitebark pine relies on the Clark's nutcracker (*Nucifraga columbiana*) to disperse its seed (Tomback 1982). Nutcrackers disperse seed extensively throughout the subalpine and alpine as long as sufficient seed is produced to attract nutcrackers to whitebark pine stands (McKinney et al 2009, Barringer et al 2012).

Whitebark pine has been severely impacted in the core of its range by an introduced fungus *Cronartium ribicola* (J.C. Fisch) that causes white pine blister rust as well as unprecedented levels of mountain pine beetle (*Dendroctonus ponderosae)* (Tomback and Achuff 2010). The loss of this keystone species (Ellison et al 2005) may have profound ecological effects because of the multiple crucial roles it plays, including: an important food source for many birds and rodents (Hutchins and Lanner 1982); a pre-hibernation food source for black bear and grizzly bear (Mattson and Reinhart 1997); colonizing dry, cold, windswept slopes and facilitating the growth of less hardy, more shade tolerant species (Callaway 1998); and stabilizing subalpine soil, reducing erosion, and regulating winter run-off (Weaver 2001). Efforts to restore the endangered whitebark pine (*Pinus albicaulis*) are ongoing throughout its range (Tomback and Achuff 2010). These efforts are being planned on a region-by-region basis (Aubrey et al 2008, Keane et al 2012) in part due to its large geographic range which makes research findings from one area difficult to apply to others (Larson and Kipfmueller 2012). Specific restoration and recovery actions include thinning competing tree species, developing and planting blister rust resistant seedlings, and imitating natural disturbance regimes such as fire that help perpetuate whitebark pine in the lower subalpine (Schwandt et al 2010). Each of these actions requires that the regeneration niche of whitebark pine is understood. Indeed, most recovery plans for the species suggest research be conducted on the regeneration niche of whitebark pine (Aubrey et al 2008, Schwandt et al 2010, Alberta Whitebark and Limber Pine Recovery Team 2014).

Regeneration of whitebark pine has been studied with regards to the following factors: seedling recruitment and abundance in different environments and in areas with different disturbance histories (Campbell and Antos 2003, Moody 2006, Larson 2010 and Kipfmueller); effects of vegetation and microsite on survival in alpine-treeline environments (Maher et al 2005, Mellman-Brown 2005, Maher and Germino 2006); timing of germination after fire (Tomback et al 2001a); survival and growth of planted seedlings in different microsites (Izlar 2007); and abundance, growth and survival as affected by microsite conditions in post-fire plots (Tomback et al 1993). The majority of these investigations focused on one or two aspects of regeneration in the core of its range. There is a dearth of research at the northern edge of whitebark pine distribution where environmental factors limiting whitebark pine may differ. Filling this void is important for informing provincial and federal recovery plans for whitebark pine and defining critical habitat under the *Species at Risk Act* (SARA). Further, white pine blister rust infection remains low in northern Alberta (Smith et al 2008, Smith et al 2013) and thus interactions between whitebark pine and the Clark's nutcracker have not yet been severely impacted. Research in this area can therefore provide insight into regeneration processes in unimpaired ecosystems. Finally, populations at the northern edge of the range may be important for survival and adaption to climate change (McLane and Aitken 2012).

In this study I characterized the biophysical associates of whitebark pine regeneration at the northern edge of its distribution in Alberta. I examined environmental factors affecting presence and absence, growth and abundance of whitebark pine since all three characteristics are important to regenerative success. The overarching goal of the research was to inform recovery of the species, particularly in Alberta. Specific research objectives were to:

1. Characterize the biophysical conditions that determine whitebark pine seedling presence and absence, density, and growth and determine how these differ among community types and along elevation gradients
2. Determine if and under which environmental conditions disturbance such as fire would benefit seeding establishment and growth.

2.3. Methods

2.3.1. Site Selection

Whitebark pine transects were established by Alberta Parks and Alberta Sustainable Resource Development in 2006 and 2008 in Willmore Wilderness Park and by Parks Canada in Jasper National Park in 2003 to evaluate health of populations. These sites were selected as representative of the whitebark pine populations in the area and used here to simplify the site selection procedure, to facilitate future collaboration between university and parks research, and to link levels of white pine blister rust infection to future work. At the macrotopographic scale, Willmore and Jasper are both in the eastern shadow of the Continental Divide and have similar climatic conditions. Sites in Willmore occured between 53.778566°N 119.716731°W and 53.449737°N 119.178122°W with an elevation range of 1584-2200m, while our Jasper sites lie between 53.033953°N 118.148226°W and 52.463574°N 117.421878°W with an elevation range of 1610-2263m (Appendix 1 – Figure 1, Table 1). One of the biggest differences between whitebark pine populations in Willmore and Jasper appears to be white pine blister rust infection rates with 5% and 25% infection levels, respectively (Smith et al 2008). These sites represent a range of topographic variation, biotic diversity, and abiotic conditions which allowed us to compare the effects of the biophysical characteristics on regeneration densities and characteristics. Sixteen out of a possible 18 sites were sampled in Willmore and 13 of a possible 14 sites were sampled in Jasper. The unsampled sites were omitted due to difficulty in access.

2.3.2. Mesohabitat Characterization

In order to examine how regeneration changes with respect to community type and abiotic environment, I sampled the previously-established whitebark pine transects and at up to three new transects in different mesohabitats at each study site. Mesohabitats were characterized by vegetation type, slope, elevation and topography. Sample mesohabitats included: 1) mixed conifer or pure whitebark pine forest (hereafter referred to as forest); 2) open canopied areas below treeline (hereafter referred to as open); 3) treeline where conditions were much more open and tree growth tended to be more horizontal but not yet krummholz (hereafter referred to as treeline); and 4) alpine habitats at least 5m above tree islands but within close proximity to a whitebark pine seed source (hereafter referred to as alpine). In three locations I was also able to include a recently burned area as a mesohabitat. An example of a typical site layout is shown in Figure 2.1.

In each mesohabitat for each study site, transects - ideally 100m long - were established within a relatively homogenous area representative of the mesohabitat. In the case where less than 100m of relatively homogenous habitat was available I used 60 or 80m transects or two shorter transects. The forest transect was selected using the same starting point as the formerly-established health transects. Open, treeline and alpine transects were selected based on a brief exploration of the site and were most often located in the first appropriate location that contained at least some whitebark pine seedlings. For these transects, the start point was randomly selected from a choice of four points that all allowed us to stay within homogenous habitat.

For each transect I measured: slope, aspect, soil pH, and a qualitative description of soil moisture regime, nutrient regime, and topographic position (e.g., crest, upper slope, midslope, depression and toe). Slope was measured with a clinometer. Aspect was defined as the predominant slope direction and was measured with a compass. Aspect was later converted to heat load index by changing aspect in degrees to a linear value from 0-1 and transforming the data so that the warmest aspect (SSW or 225°) equaled 1 and the coolest aspect (NNE or 45°) equaled 0 (Beers et al 1996 in Moody 2006). Soil pH was measured using a soil pH kit in the field, taking care to only measure mineral soil and not the organic layer. Slope, aspect, and soil pH were all measured at the transect start point. Moisture regime, nutrient regime and topographic position were designated using the BC Ministry of Forests Field Manual for Describing Terrestrial Ecosystems. This manual uses a broad filter approach to characterize these variables. In order to determine the minimum forest age and successional stage I cored up to three overstory trees of each species randomly along forest transects (Fritts and Swetnam 1989) and considered the age of the oldest individual to be the minimum age of the stand. Tree cores were mounted and sanded using successively finer sandpaper until all rings were clearly visible. Tree rings were measured by scanning each core with a high definition scanner (Epson Perfection V750 PRO) and using digital imaging software CooRecorder (ver. 7.8, Cybis Elektronik and Data AB, Mousseau et al 2012). For each transect I also calculated stand density (total and by each overstory tree species), average understory vegetation cover, and average availability of different substrates (e.g., bare mineral soil) by taking the average from the microsite plots (procedure below) for a given transect. Mean annual temperature and precipitation for each transect were retrieved using a climate model developed by Hamann et al (2013).

To quantify seedling density, I recorded the number of seedlings within a 4m swath (2 m to either side) along the entire transect. Due to the caching behavior of Clark's nutcracker, whitebark pine seedlings often grow together as clumps, particularly when small (McCaughey et al 2001). This poses a difficulty when it comes to classifying individual seedlings. Each stem was treated as a separate individual whether in a clump or not. I ensured stems were separate at the root collar before they were counted as separate individuals. For each seedling I recorded size class [small (0-0.5m height), large (0.51-1.3m height)], health class [healthy (H), chlorotic (C), active blister rust canker (AC), inactive blister rust canker (IC)] and clump size (number of stems).

2.3.3. Microsite Characterization

In order to examine the associates of presence/absence and growth rate of whitebark pine, each transect was divided into five 20m segments. Within each segment I compared biophysical characteristics in one microsite plot (1x1m) containing a whitebark pine seedling (hereafter referred to as occupied plots) and one microsite plot without that was at least 2m away from a whitebark seedling (procedure modified from Purdy et al. 2002). In order to ensure our selection of microsite plots was random, I sampled the occupied plot closest to the start point for each segment and then randomly selected an unoccupied plot within the segment using a random number generator. In the case that the random number generator did not lead us to a site that met our selection criteria (see above) I selected a new random number. If after three unsuccessful attempts to randomly select an unoccupied plot I actively sought out an unoccupied plot within that segment along the transect.

Biophysical characteristics that I sampled in each microsite plot included: organic layer depth, litter depth, canopy cover, tree basal area and percent cover for ground cover types (see below) and for vascular plants to species. Organic layer depth was measured by digging a small hole in the center of each plot and measuring the depth to mineral soil. Litter depth was measured at center of the plot and included all non-decomposed dead organic material. Percent canopy cover was determined using a convex spherical densiometer (average of four readings, one in each of the four cardinal directions). Basal area was measured using a prism (Basal Area Factor 4) from the centre of each plot. Visual estimates of percent cover (within 1%) were made for each vascular plant species as well as for seven ground cover types (these include moss, lichen, rock, mineral soil, litter, downed woody material and cryptogamic crust).

For each seedling (in occupied plots) I recorded height, age, substrate it was found on (mineral soil, organic soil, rock, and wood), microtopographic position (lower slope, midslope, upper slope, depression, crest, level, and toe; BC Ministry of Forests Field Guide to Terrestrial Ecosystems) and whether it was found in a clump or as a single individual. Height was measured using a ruler from ground level to the terminal bud at the point farthest from the stem base. Age was estimated in the field using whorl counts. I destructively sampled a subset of seedlings in order to validate this aging procedure (as well as to analyze growth release; see chapter 3). Seedling growth rate was determined for every seedling found in each occupied plot by dividing height by age. Average growth rate per plot was calculated for plots with more than one seedling.

2.3.4. Motion camera analysis

Motion cameras were placed along eight transects in order to examine anecdotal evidence of how depth of snowpack and timing of snowmelt differ between mesohabitats and contribute to seedling occurrence as well as to record animal activity in whitebark pine habitat. Motion cameras were placed at three different sites, 08WBL07, 08WBL02 and 06WBL05 and were located at the forest, open and treeline mesohabitats, forest, open and alpine mesohabitats, and forest and open mesohabitats at each site respectively. The locations of each transect with a motion camera can be found in Appendix 1 – Table 3.

2.3.5. Data Analyses

The data collected can be grouped into predictor and response variables. The response variables were presence/absence of seedlings, seedling growth rate, and seedling density. Predictor variables included every measured biophysical variable. Variable names used in analysis and their corresponding names used in the figures are reported in Table 2.1 while transects characterized for each study site are reported in Appendix 1 - Table 1.

To examine variation in plant community and biophysical conditions between occupied and unoccupied plots within each mesohabitat type I used unconstrained ordination (non-linear multi-dimensional scaling; NMDS) using the vegan package (ver. 2.2) (Oksanen et al 2014) of the R statistical language (R Core Team 2013). I included all of the abiotic variables measured at the microplot scale as well as total percent cover for combined functional groups (explained below). Mesohabitat variables passively overlain on the NMDS based on their correlation with microplot variables in an indirect gradient analysis. The iteration with the lowest stress value after 20 iterations was used in each analysis. In plotting the results of NMDS I used symbols to distinguish occupied and unoccupied plots and varied symbol size to reflect whitebark growth rate. I analyzed each mesohabitat separately due to the large amount of variation between each mesohabitat and our interest in seeing how the predominant factors of regeneration change depending on mesohabitat.

I used regression trees using the mvpart package (ver. 1.6) (Therneau and Atkinson 2014) of the R statistical language (R Core Team 2013) to determine which biophysical variables were most strongly influencing seedling presence/absence and growth rate at the microsite scale and seedling density at the mesohabitat scale. For the analyses of presence/absence I used every environmental variable recorded at the microsite scale, while for growth rate I used the microsite scale variables as well as the variables collected at the mesohabitat scale. In order to incorporate the influence of plant community in the regression trees I completed an analysis to define vegetation types. Agglomerative cluster analysis based on Euclidean distance measures was conducted using the vegan package (ver.2.2) (Oksanen et al 2014) of the R statistical language (R Core Team 2013) to define five vegetation types within each mesohabitat; subsequently each microsite plot was assigned to one of those vegetation types (Appendix 3). I also summed percent cover of species by functional group as follows: trees (total cover of all tree species for individuals >1.4m in height in microsite plot), seedlings (all conifer species other than whitebark pine <1.4m in height), graminoids (grass, sedge and rush species), forbs (herbaceous broadleaf vascular species), prostrate shrubs (woody vascular species <5cm in height), and upright shrubs (woody vascular species >5cm height). These plant community variables were included with the environmental variables as predictor variables in the analysis. Seedling growth rate was square root transformed to improve normality and decrease the effect that outliers had in the regression tree analysis. Seedling density was transformed (log base two) to improve normality and decrease the effect that outliers had on the regression trees. Seedling growth rate and density were analyzed as quantitative response variables while presence/absence was analyzed as a categorical variable.

2.4. Results

2.4.1. Forested mesohabitat

In the unconstrained ordination of biophysical data from the microsite plots in the forest mesohabitat there was no apparent separation between occupied and unoccupied plots (Figure 2.2); however, there did appear to be some clustering towards the higher end on axis 2 for occupied plots in which whitebark pine seedling growth rate was relatively high. Microsites with higher overall growth rates were associated with: higher slope and elevation (at the mesohabitat scale), and with greater cover of rock and bare mineral soil, but lower canopy cover and basal area.

Whitebark pine seedling presence in forest mesohabitats was driven primarily by vegetation (Figure 2.3; Table 2.2). The highest occupancy occurred in microsite plots with higher cover of bare mineral soil while the lowest occupancy occurred in plots with little bare mineral soil and low species richness. The first split demonstrated the importance of bare mineral soil in determining whitebark pine seedling presence. Microsites with greater than 2.5% bare mineral soil cover favored whitebark presence with 76% of such plots containing seedlings, while microsites with less than 2.5% bare mineral soil had 45% occupancy. For sites with < 2.5% bare mineral soil, microsites with lower species richness had lower whitebark pine presence. Microsites with < 2.5 species had 26% occupancy compared to 49% for their counterparts. The third split in the regression tree, which followed the branch with higher species richness, demonstrated the negative effect of grass cover on whitebark pine seedling presence. Graminoid cover > 2.5% resulted in an occupied microsite 27% of the time while sites with < 2.5% graminoid cover were occupied 53% of the time. High cover of forbs also led to increased presence of whitebark pine as demonstrated by the fourth split. Greater than 4.5% cover of forbs led to 65% occupancy while lower forb cover resulted in 48% occupancy. The final split in the regression tree shows the potential importance of prostrate shrubs in assisting whitebark pine survival and occupancy. Sites with greater than 8.5% total cover of prostrate shrubs had 58% whitebark pine seedling occupancy while sites with less than 8.5% cover had 38% occupancy.

There are several potential meaningful alternate splits throughout the regression tree shown in Figure 2.3 (Appendix 2 – Table 1A). The first few alternate splits show the negative influence of dense overstory and understory cover and higher cover of decayed woody material on whitebark pine occurrence. Alternate splits further along the tree suggest that some level of understory vegetation cover may be beneficial to whitebark pine occurrence or at the very least indicate sites where whitebark pine seedlings can survive.

There was a much stronger effect of overstory variables on whitebark pine growth rate than I saw for presence/absence in forested mesohabitats (Figure 2.3 versus 2.4; Table 2.2). The regression tree results showed that whitebark pine seedlings grew best in very open sites with few trees in close proximity and most slowly in sites with many trees. These sites also happened to have lower cover of understory vegetation. The first split in the regression shows whitebark pine seedlings grew faster in sites associated with a low total basal area. Microsites with less than 10 m^2/ha basal area had seedling growth rates of 1.63 cm/year while seedlings in more densely treed areas grew at an average of 1.07 cm/year. The second split for sites with lower basal area further demonstrates the benefit of growing in more open environments. Sites with > versus < 2.45% canopy cover had average growth rates of 1.47 versus 2.96 cm/year, respectively. In the sites with the higher tree basal area, seedlings in plots with higher vegetation cover grew better. Seedling in microsite plots with less than 15.1% vegetation cover grew on average 0.60 cm/year while sites with more cover grew 1.16 cm/year. The next split for these sites with higher vegetation cover was due to slope; there were two microsite plots that had > 51° slopes that had seedlings growing rapidly (3.02cm/year versus 1.12 cm/year for plots to the other side of the split). The final split for these plots with < 51° slope showed that seedlings in plots with higher cover of prostrate shrubs grew slower. Sites with > versus < 8.1% cover of prostrate shrubs had average growth rates of 0.890 versus 1.32 cm/year, respectively.

Factors associated with increased whitebark pine seedling density in forested mesohabitats differed from those observed for occupancy and growth rate at the microsite scale (Figure 2.5; Table 2.2). While canopy cover had a negative effect on growth rate and presence, canopy had a positive effect on seedling density. Transects with the highest overall seedling density were found on sites with greater moisture regimes and higher canopy and understory vegetation cover. The first split in this regression separate transects with higher canopy cover, which had higher average density of whitebark pine seedlings. Transects with an average canopy cover of < versus > 32% had an average seedling density of 335 seedlings/ha compared to 1076 seedlings/ha, respectively. For sites with lower canopy cover, transects with higher average cover of bare mineral soil had a lower average seedling density. Forest transects with an average of > versus < 5.7% bare mineral soil in the microsite plots had an average of 129 seedlings/ha and 513 seedlings/ha respectively. Drier sites with higher canopy cover tended to support more seedlings. A moisture regime of greater than 3.5 (i.e., mesic and wetter) resulted in an average seedling density of 373 seedlings/ha while a moisture regime of less than 3.5 (i.e., submesic and drier) resulted in 1355 seedlings/ha. The final split on the right of the regression tree, which was on the branch for the drier transects, shows that drier, more closed canopied sites with higher average vegetation cover, tended to also support more whitebark pine seedlings. In this case, an average vegetation cover of < versus > 29.5% resulted in a seedling density of 646 seedlings/ha and 1761 seedlings/ha respectively.

2.4.2. Open mesohabitat

Ordination results for biophysical variables in open mesohabitats (Figure 2.6) showed that, as for the forest mesohabitat, there was little separation between occupied and unoccupied plots. However seedlings found in sites with higher cover of ground shrubs, as well as higher elevation and warmer slopes did seem to grow somewhat better than those found in more mesic, denser canopied areas.

In open mesohabitats, occupied plots were characterized by lower cover of rock, graminoids, conifer seedlings, saplings and trees (Figure 2.7; Table 2.3). Rock cover had the greatest effect on presence/absence of whitebark pine. Microsites with > versus < 62.5% rock cover contained whitebark pine seedlings 17% and 53% of the time respectively. In sites with lower cover of rock, graminoid cover appeared to limit the occurrence of whitebark pine seedlings (similar to the trend observed in forested mesohabitats in Figure 2.3). In open microsites with greater than 7.5% graminoid cover I saw 20% presence of whitebark seedlings, while occurrence increased to 57% with less graminoid cover. Low cover of subalpine fir and Engelmann spruce seedlings further improved whitebark occurrence. Sites with greater than 13% seedling cover (not including whitebark pine) had 33% occupancy, while sites with less seedling cover had 63% whitebark pine seedling occupancy. The final split denoted whitebark pine seedlings clustering away from dense tree cover. I had six unoccupied plots and no occupied plots with > 42.5% tree cover while 65% of plots were occupied with < 42.5% tree cover.

Whitebark pine seedlings in open mesohabitats grew best in sites with an intermediate mean annual temperature (MAT) and little bare mineral soil, and worst in warm sites or cold sites with steep slopes (Figure 2.8; Table 2.3). MAT was the most influential on growth rate. Seedlings in sites with a MAT between -0.45 and -0.25°C, greater than -0.25°C and less than -0.45°C grew an average of 2.38 cm/year, 1.06 cm/year and 1.37 cm/year respectively. For the colder sites (left side of second split) seedlings on transects with a slope of > versus < 37.5° were growing at an average rate of 0.99 cm/year and 1.57 cm/year, respectively. The final split in the regression tree shows that for sites with an intermediate MAT, higher cover of bare mineral soil was associated with slower seedling growth. Two microsite plots with greater than 34.5% bare mineral soil cover had seedlings growing at an average rate of 0.76 cm/year while seedlings at sites with less than 34.5% bare mineral soil cover grew at 2.69 cm/year.

Seedling density in open mesohabitats was affected predominantly by aspect (as transformed into Heat Load Index (HLI); 0=NE and 1 = SW) as well as presence of rock (Figure 2.9; Table 2.3) with the importance of vegetation indicated in the alternate splits (Appendix 2 – Table 3B). The highest density of seedlings was found along transects with high HLI (i.e., warmer SW aspects) while the sites with lowest seedling density were rocky transects on cooler aspects. HLI was very important in determining whitebark pine seedling density in open habitats. Sites with a HLI > versus < 0.9178 had on average 3392 seedlings/ha and 728 seedlings/ha, respectively. For sites with cooler aspects, higher rock cover appeared to further reduce seedling density. Sites with an average of < versus > 47.5% rock cover had an average of 972 seedlings/ha versus 274 seedlings/ha, respectively. It is important to note that vegetation cover was an important alternate split at both nodes in the regression tree in Figure 2.9 (Appendix 2 – Table 3B). In both cases, transects with higher average vegetation cover had higher average seedling densities.

2.4.3. Treeline mesohabitat

Results of the ordination analysis for microsites in treeline mesohabitats (Figure 2.10) demonstrates that there was little difference in general between occupied and unoccupied plots. In addition, slower and faster growing seedlings were found under a wide variety of conditions.

For treeline mesohabitats, a minimum amount of understory vegetative cover increased whitebark pine presence, while increased canopy cover reduced whitebark pine presence (Figure 2.11; Table 2.4). Vegetation cover was the most influential in determining occurrence. Total vegetation cover of > versus < 10.5% resulted in 54% and 13% whitebark pine seedling occupancy, respectively. The second split shows that, similar to forest mesohabitats, high canopy cover is detrimental for seedling presence. Canopy cover > versus < 67.5% canopy cover resulted in 0% and 58% occupancy of whitebark pine seedlings, respectively.

Biophysical drivers of growth rate in treeline mesohabitats demonstrate some interesting similarities and differences to other mesohabitats (Figure 2.12; Table 2.4). Similar to growth rate in open environments, MAT appeared to be the most important determinant with faster growth on warm sites and poorer growth rates on cold rocky slopes. Sites with higher cover of prostrate and upright shrubs also had rapidly growing seedlings (contrary to forest mesohabitats where higher cover of prostrate shrubs was associated with suppressed seedlings). The first split demonstrates warmer MAT benefited the growth rate of whitebark pine seedlings. MAT of > versus < 0.75°C resulted in growth rates of 3.10 cm/year and 1.37 cm/year respectively. Increased presence of rock in cold environments also reduced whitebark pine seedling growth rate.

Sites with > versus < 4.5% rock cover experienced an average growth rate of 1.23 cm/year and 1.72 cm/year respectively. Presence of prostrate shrubs in colder microsites with little rock cover increased growth rates, while sites with > and < 5% prostrate shrub cover had an average growth rate of 2.17 cm/year and 1.03 cm/year, respectively. The final split in this regression related to upright shrub cover. Occupied microsites with < 3.5% cover of upright shrubs had whitebark pine seedlings growing at 1.80 cm/year, less than half that of their counterparts which grew at 3.76 cm/year.

Seedling density in treeline mesohabitats was greatest along transects that received high mean annual precipitation (MAP) with increased overall species richness and lowest in habitats with low MAP (Figure 2.13; Table 2.4). Other variables linked to higher average density included higher average understory vegetation cover, sites with warmer aspects and sites with cooler MAT (Appendix 2 – Table 3C). Sites that received a MAP of < versus > 867 mm/year had an average seedling density of 173 seedlings/ha and 1504 seedlings/ha, respectively. The second split in the regression tree demonstrated sites supporting a more diverse plant community also tended to support a greater density of seedlings. Transects with an average species richness of less than 4.85 species/microsite plot had an average seedling density of 468 seedlings/ha while sites with greater than 4.85 species/microsite plot had an average seedling density of 2787 seedlings/ha.

2.4.4. Alpine mesohabitat

Both occupied and unoccupied microsites in alpine mesohabitats were associated with many variables as shown in the unconstrained ordination in Figure 2.14. There is little evidence for association of occupied microsites or sites that exhibit poor or good growth with particular variables. However, unoccupied microsite plots were associated with higher rock cover.

The presence of nearby vegetation was the predominant driver for presence and absence in alpine mesohabitats (Figure 2.15; Table 2.5). However species richness also influenced occupancy and rock cover was frequently shown to be an alternate split associated with reduced whitebark pine presence (Appendix 2 – Table 1D). Litter cover had the greatest influence on whitebark pine occurrence in alpine mesohabitats. Microsites with > versus < 0.1cm of litter depth demonstrated 69% and 37% occupancy respectively. For microsites with litter, the absence of krummholz trees appeared to further benefit whitebark pine seedling presence. Sites with < versus > 5.5% krummholz tree cover had 76% and 0% occupancy of whitebark pine respectively. On the left side of the regression tree, sites with no litter and little other vegetation cover were mostly too harsh for whitebark pine seedlings. Sites with < versus > 4.7% vegetation cover had 11% compared to 43% occurrence. Species rich sites in the alpine also did not favor whitebark pine presence. Sites with > 5 species exhibited 33% occupancy while sites with < 5 species showed 63% occupancy. The final two splits on the left of the regression tree demonstrate that whitebark pine had the highest occupancy with intermediate values of vegetation cover. Microsites with vegetation cover between 22.3 and 40.4% had 82% occupancy while sites with > 40.4% and sites with < 22.3% vegetation cover experienced 13% and 30% occurrence, respectively.

In alpine mesohabitats, sites with low cover of rock and lichen supported the most rapidly growing seedlings, while for microsite plots with higher rock cover, seedlings grew best with very low graminoid cover, greater litter depth and along transects with cooler aspects. The slowest growth was in microsite plots with higher graminoid cover and lower forb cover (Figure 2.16; Table 2.5). Rock cover was the most influential variable on growth. Seedlings at sites with < versus > 0.5% rock cover grew at a rate of 2.52 cm/year and 1.30 cm/year, respectively. Seedlings at the few sites that had essentially no rock cover (on the right side of the regression tree) grew best in locations with lower lichen cover. Lichen cover > versus < 4% resulted in seedling growth of 1.40 cm/year and 4.36 cm/year, respectively. For alpine microsite plots with higher rock cover, seedlings grew slower when graminoid cover was higher. Seedlings found in microsite plots with < versus > 0.8% graminoid cover grew 1.59 cm/year and 0.97 cm/year, respectively. Those seedlings competing with graminoid species were further affected by forb cover as evidenced by the third split on the left. Plots with > versus < 8.6% forb cover had seedlings growing at an average rate of 1.50 cm/year and 0.76 cm/year, respectively. Seedlings in plots with low graminoid cover benefitted from the presence of an established litter layer. Seedlings with litter depth of > 0.1 cm grew 2.34 cm/year while those without an established litter layer grew 1.33 cm/year. Finally, for microsite plots with higher litter depth, seedlings grew worst on warm SW aspects. Seedlings found growing on an aspect with an heat load index (HLI) of > versus < 0.929 grew at an average rate of 1.34 cm/year and 3.33 cm/year, respectively.

Seedling density in alpine mesohabitats was driven by substrate conditions (Fig. 2.16, Table 2.5). The lowest average density was on transects with low average litter cover while the highest seedling abundance was on sites with higher average litter, some available bare mineral soil and an intermediate amount of rock cover. Transects with an average litter depth of < versus > 0.55 cm had an average seedling density of 102 seedlings/ha and 638 seedlings/ha, respectively. Next, the presence of at least some bare mineral soil had a positive effect on seedling density. Transects with an average of < versus > 0.44% bare mineral soil had 202 seedlings/ha compared to 897 seedlings/ha respectively. An intermediate amount of rock cover in microsites within alpine transects was beneficial for seedling density. With average rock cover of < 20.35%, 20.35 - 42.25%, and > 42.25% seedling densities were 260 seedlings/ha, 2856 seedlings/ha and 735 seedlings/ha, respectively.

2.4.5. Burned mesohabitat

The burned mesohabitat was not quantitatively analyzed due to poor replication and problems with all three sampled transects. Analysis of seedling ages from the Greenhock burn site in Jasper National Park using tree rings indicated that many of the seedlings selected from that transect were older than the burn itself, suggesting that much of the understory had not burned in that location. The two other burn transects occurred along the same 10-year-old burn in Willmore Wilderness Park. Extensive searching revealed only two seedlings in a 0.1ha area at our first site and only five seedlings in a 0.1ha area at our second site.

2.4.6. Seedling population structure and infection

In each mesohabitat, seedlings in the smaller size class (< 0.5 m) far outnumbered seedlings in the larger size class (0.5 – 1.4 m) (Figure 2.18). Seedlings less than 0.5m in height made up over 70% of the seedlings found at each mesohabitat. Seedlings in forest mesohabitats were somewhat less likely to be found in clumps compared to other mesohabitats; seedlings in the forest transect were found in clumps 53% and 56% of the time for small and large seedlings respectively. Small seedlings were found in clumps 70%, 68% and 70% of the time for open, treeline and alpine mesohabitats, respectively. This ratio was similar in larger seedlings for treeline (60%) and alpine (70%) transects while in the open mesohabitat the percentage of larger seedlings found as clumps dropped (to 59%) compared to the smaller seedlings. Open mesohabitats also had the greatest proportion of seedlings found in the smaller size class with over 85% in size class 1 compared to 73%, 83% and 72% for forest, treeline and alpine mesohabitats respectively.

Larger seedlings were much more likely to be infected by white pine blister rust than smaller seedlings and this was true across all mesohabitats (Figure 2.19). Mean infection rate for small and large seedlings, respectively, in forest was 1.4% and 5.5%, in open was 0.8% and 5.5%, in treeline was 0.5% and 12.0% and in alpine was 1.2% and 4.0%. Overall infection rates increased from 0.9% to 6.2% for small to large seedlings. Alpine and treeline mesohabitats had much higher proportions of large unhealthy seedlings than forest and open mesohabitats. Unhealthy seedlings made up 16.7% and 19.5% for alpine and treeline, respectively, compared to 4.6% and 4.4% for forest and open mesohabitats, respectively.

The majority of seedlings found in occupied plots were less than 20 years old (Figure 2.20). Seedlings aged 1-10 years and 11-20 years made up 36% and 34% of the total number of seedlings found respectively. Seedlings 21-30 years old were found 16% of the time, while 7% were 31-40, 4% were 41-50, 2% were 51-60 and the remaining 1% of seedlings were found to be older than 60.

The aging method of whitebark pine seedlings in the field was validated via destructive sampling of a subset of whitebark pine seedlings found in occupied microsites and subsequent dendrochronological analysis. Ring counts at the base of 90 seedlings had a correlation of 0.79 (Figure 2.21) with field counts of whorls and revealed on average, approximately two additional years of growth. The average absolute difference between the two counts was 6.11 years of growth.

2.4.7. Motion camera investigation

I was unable to examine differences in depth of snowpack between the eight transects that received motion cameras. In every case the camera was eventually buried by snow during the winter and the height of the camera was not recorded prior to placement or upon retrieval. I was able to record the timing of snow melt accurately at four transects and estimate the timing at three others at which the camera had been repositioned due to animal activity. One camera was unusable. A large snowfall on October 31st covered the ground at all seven camera locations and snowpack was held at each site until the spring.

The timing of snowmelt varied between camera locations (Table 2.6). At two sites 06WBL05 and 08WBL07, snowmelt occurred at the open transects earlier than at other mesohabitats. Snowmelt occurred at site 06WBL05 on May 31st and June 11th for open and forest mesohabitats, respectively and at 08WBL07 on May 24th, June 11th and June 14th for open, forest and treeline mesohabitats, respectively. Snowmelt occurred at the open mesohabitat at site 08WBL02 on June 18th but I was unable to determine snowmelt dates for the alpine and forest transects at this site. Clark's nutcracker caching and retrieval events were recorded at the open mesohabitat of 08WBL07 on September 29th, 2013 and May 27th, 2014 respectively. This is the only location where nutcracker activity was recorded via motion cameras.

2.5. Discussion

2.5.1. Forested mesohabitat

Whitebark pine seedling establishment and growth at the microsite scale occurred in canopy gaps and was associated with dense understory vegetation while at the mesohabitat scale, increased canopy cover resulted in greater seedling densities. Specifically, occurrence at the microsite scale in forest mesohabitats was positively associated with bare mineral soil, plant communities with increased species richness, forb and prostrate shrub cover. Seedling density was positively influenced by canopy and vegetation cover and negatively associated with bare mineral soil and moisture.

Whitebark pine growth was positively affected by vegetation cover but negatively impacted by tree basal area, canopy cover and prostrate shrub cover.

In forest mesohabitats canopy gaps were associated with increased growth rate and occurrence of whitebark pine seedlings at the microsite scale. Whitebark pine is known to be moderately shade intolerant (Arno and Hoff 1989) and shade limitation to whitebark pine growth and survival is well documented in the literature (Campbell and Antos 2003, Keane et al 2007, Izlar 2007, McCaughey et al 2009, Larson and Kipfmueller 2010). While not a primary driver of seedling occurrence, whitebark pine was negatively associated with high canopy cover (Appendix 2 – Table 1A) and all variables that were positively associated with whitebark pine occurrence (bare mineral soil cover, species richness, forb cover, prostrate shrub cover) are associated with more open environments.

The fact that canopy gaps in forest environments benefitted seedling presence and growth at the microsite scale is not surprising; what is surprising is the positive association of understory vegetation cover with increased growth rate and seedling occurrence at both mesohabitat and microsite scales. Out of all understory plant community variables, only graminoid cover had any negative influence on whitebark pine occurrence. Increased vegetation cover is associated with canopy gaps (Anderson et al 1969) and this may have played a role in this positive association; however, it is significant that whitebark pine seedlings do not appear to be negatively affected by competition from dense understory plant communities. Weaver (2001) suggested that the lower elevational boundary of whitebark pine may be set by the zone of tolerance of competing species and whitebark pine is able to grow well in lower elevational conditions when that competition is removed. In addition Moody (2006) found that the best growing conditions for whitebark pine occurred in these less harsh, lower-subalpine environments. It is in locations where whitebark pine occupies a seral role that it might be the most productive if it is capable of escaping competition and more fully occupying its fundamental niche (Arno 2001). Forest environments with species-rich prostrate shrub and forb communities might be excellent places to target for canopy thinning or planting of whitebark pine seedlings.

While increased canopy cover in forest mesohabitats was negatively associated with occurrence and growth of whitebark pine seedlings at the microsite scale, it was positively associated with seedling density at the mesohabitat scale. This dichotomy is likely a result of nutcracker caching behavior at the stand scale. McKinney and Tomback (2009) as well as Barringer et al (2012) showed that frequency of Clark's nutcracker visitations and likelihood of seed dispersal was directly related to cone production and seed source size. Moody (2006) too found that the best predictors of seedling density were seed source size and distance to seed source. Since all of the forest transects occurred within stands of mature whitebark pine, increased canopy cover most likely means more mature whitebark pine trees and increased cone production. The dichotomy of scale observed with canopy cover also occurred with regards to bare mineral soil cover. Bare mineral soil was positively associated with seedling presence at the microsite scale but negatively associated with seedling density at the mesohabitat scale in more open areas of the forests. Mineral soil is known to be an important substrate for whitebark pine seedling occurrence (McCaughey and Weaver 1990) although increased abundance of bare mineral soil may indicate very dry, open conditions where soil moisture may be insufficient for germination or early seedling survival. Recovery efforts aimed at developing canopy gaps or more bare mineral soil availability need to ensure that the whitebark pine seed source is unaffected and that extensive patches of bare mineral soil are not created.

2.5.2. Open mesohabitat

Whitebark pine occurrence and growth at the microsite scale in open mesohabitats was negatively associated with conditions that limit nutrient availability and positively associated with conditions that may limit competitors. Specifically, seedling occurrence was negatively associated with cover of rock, graminoids, other tree seedlings and trees. Growth was greatest at intermediate mean annual temperatures and reduced on steep slopes and microsites with high proportions of bare mineral soil. Seedling density at the mesohabitat scale was highest on southwest facing slopes and lowest on rocky, north facing slopes.

Rock cover limited whitebark pine occurrence at the microsite and mesohabitat scale. Interestingly, protection from rock has shown to increase whitebark pine seedling survival and can alleviate harsh environmental conditions (Tomback et al 1993, Izlar 2007, McCaughey et al 2009). However, this likely requires that other requirements for growing conditions are met. Microsites with high rock cover likely have limited soil development and thus poor conditions for establishment and low availability of nutrients and water. In addition, shifting of rocks due to subalpine freeze-thaw cycles (Körner 2003) can damage small seedlings. Moody (2006) found that prevalence of rock was one of the main drivers of reduced seedling density. Open environments are often said to favor whitebark pine occurrence (Arno 2001, Tomback and Achuff 2010), but the prevalence of rocky substrates should be considered before environmental conditions are altered to create canopy gaps.

In forest environments, occurrence was often associated with vegetation cover, while in open mesohabitats avoidance of competing species such as graminoids and other conifer seedlings was more prevalent. The negative association with graminoid cover may reflect competitive effect of graminoids (Tomback et al 1993, McCaughey et al 2009), nutcracker caching preferences (Tomback 1978) or a combination of both. Much literature has described the poor competitive ability of whitebark pine (Campbell and Antos 2003, Weaver 2001) and the negative impact of other conifer species on whitebark pine survival (Izlar 2007, McCaughey et al 2009, Larson and Kipfmueller 2010) and as such the impact of other conifer seedlings and tree cover on whitebark pine occurrence was unsurprising. Whitebark pine seedling avoidance of other conifer species may reflect the influence of mean annual temperature (MAT) on growth rate. In open sites, seedlings grew fastest in sites with intermediate MAT. This may represent conditions where growing season is long enough to facilitate growth of whitebark pine, but not long enough for competing species (Weaver 2001).

Southwest facing slopes (HLI~1) typically experienced the highest seedling density, with more than four times as many seedlings/ha as transects situated on cooler aspects. Southwest facing slopes experience the earliest snowmelt and likely experience warmer temperatures overall which has been shown to impact abundance (Moody 2006, Tomback et al 2001, Larson and Kipfmueller 2010) however early snowmelt may also influence nutcracker behavior. While nutcrackers often prefer to cache within forested sites where there is greater protection from predation (Lorenz et al 2011), nutcrackers may display “convergent caching behavior” on sites where the combination of aspect and slope is such that snow is readily blown off or melts quickly in the spring so the Clark’s nutcrackers have a readily available food source in the spring (Tomback 1978, Tomback 1982). Open sites on southwest facing slopes will be the first to experience spring/summer snowmelt and thus are the first to be accessible to Clark’s nutcrackers. This is corroborated by the fact that our motion camera data show multiple Clark’s nutcracker caching events occurred only on the open southwest-facing slope. Convergent caching has been observed at the southern edge of Clark’s nutcracker range (Tomback 1978) and in the core of its range (Hutchins and Lanner 1982), while Willmore Wilderness and Jasper National Parks are near the northern edge of the range for the bird. Further research on Clark’s nutcracker behavior at the periphery of its distribution should be conducted to confirm whether convergent caching is common. If so, southwest facing slopes in close proximity to an abundant seed source would be excellent targets for prescribed fire or partial harvesting of competing species.

2.5.3. Treeline mesohabitat

Correlates of growth rate and occurrence for whitebark pine seedlings in treeline mesohabitats contrasted with those in open and forest mesohabitats in that they reflected amelioration of harsh treeline conditions or indicated less harsh conditions overall. However, there was also evidence that too much competition or cover can hinder success.

Specifically, seedling occurrence at the microsite scale was positively associated with understory vegetation cover but negatively associated with canopy cover. Growth rate was positively associated with mean annual temperature (MAT), prostrate shrub cover and upright shrub cover and negatively associated with rock cover. Seedling density was the highest on transects with higher mean annual precipitation (MAP) and with increased species richness.

Avoidance of harsh climatic conditions is very important in facilitating seedling success in treeline mesohabitats. This held true for all of our response variables as vegetation cover was positively associated with occurrence at the microsite scale; MAT, prostrate and upright shrub cover were associated with higher growth rates; and MAP and species richness were associated with increased seedling density. Increased vegetation cover had the strongest association with increased occurrence at the microsite scale. Maher and Germino (2006) showed that vegetation cover facilitated conifer seedling survival in alpine-treeline conditions in Wyoming U.S.A. Our results are similar and support the theory of shifting the balance between competitive interactions to facilitative as you increase elevation (Callaway 1998). Prostrate and upright shrub cover, as well as MAT, was associated with increased growth rate. That MAT was associated with increased growth rate is unsurprising. At treeline I are likely above the zone of tolerance for many of whitebark pine’s primary competitors and the length of the growing season correlates strongly with growth rate (Weaver 2001). Ground cover (prostrate) shrubs have been shown to reduce fluctuations in ground temperatures, reducing scorching in the summer and overcooling in the winter (Körner 2003) while upright shrubs likely indicate less harsh treeline conditions overall. Treeline transects with greater MAP were associated with an eight fold increase in seedling density compared to sites with low MAP. Moisture is important for germination and young seedling survival (Tomback et al 1993, Tomback et al 2001, McCaughey et al 2009) and at treeline increased snowpack can increase the length of growing season by insulating the soil and protecting from late frosts that prolong bud-break in seedlings (Körner 2003, Mellman-Brown 2005).

Similar to conditions in forest and open mesohabitats, both increased rock cover and increased canopy cover reduced seedling success in treeline mesohabitats. In their study on microsite effects on seedling survival in alpine-treeline conditions in Wyoming U.S.A, Maher and Germino (2006) found that trees and herb cover had an additive effect on survival and Resler and Tomback (2008) found that singular krummholz trees in alpine and treeline environments were instrumental in providing shelter for seedlings in Northern Montana, U.S.A. However, in my investigation vegetation cover was clearly associated with whitebark pine presence while increased canopy cover was detrimental. Nutcrackers will cache seed at the base of trees (Tomback 1978, Lorenz et al 2011) and the fact that I had no occupied plots under heavy canopy cover suggests that whitebark pine cannot establish in close proximity to trees in northern Alberta. While rock can be important in creating microsites for seedlings and facilitating survival (Izlar 2007, Resler and Tomback 2008), once again it is associated with poor growth. This may due to the fact that rock here is acting as a substrate rather than a windbreak. High rock content as a substrate is associated with xeric conditions and poor nutrient availability.

2.5.4. Alpine mesohabitat

Seedling success in alpine mesohabitats was associated with similar conditions to those that factored in success in treeline mesohabitats with more of an emphasis on plant community. Specifically presence at the microsite scale was positively associated with litter depth and intermediate levels of vegetation cover and negatively associated with tree cover and species rich understory communities. Increased growth rate was associated with litter depth and forb cover while decreased growth rate occurred at sites with increased rock, graminoid and lichen cover as well as on southwest facing slopes.

Certain levels of vegetation and litter were positively associated with whitebark pine seedling occurrence and growth; however, high levels of vegetation, cover of some functional groups (namely grasses and trees), and species-rich understory communities were associated with reduced occurrence and growth. Litter accumulation occurs gradually in the alpine and is facilitated by the presence of vegetation (Körner 2003). Microsites that have litter have had vegetation, likely have a bit of a soil base and are capable of supporting plant life. While increased litter accumulation potentially means increased presence of surrounding vegetation, which did reduce whitebark pine occurrence in alpine mesohabitats, the absence of litter likely indicates conditions that are difficult for growth and survival. Tree cover and species rich communities were associated with reduced whitebark pine occurrence at the microsite scale while graminoid cover was associated with reduced growth rate. Negative affects of tree cover (in this case krummholz) and graminoid cover are not surprising and have been discussed above. The negative association of species richness with whitebark pine seedling occurrence was surprising as species richness was positively associated with occurrence at the microsite scale in forest mesohabitats and at the mesohabitat scale in treeline environments. This may make more sense in light of increased species richness being associated with increased vegetation and potentially graminoid cover. In alpine environments nutrient availability is likely more limiting than in treeline and, in particular, in forest mesohabitats. In addition, alpine plants are typically perennial species that develop extensive rooting systems in comparison to their above ground size. Therefore, high levels of above ground vegetation cover in the alpine may be indicative of a very competitive below ground environment.

2.4.5. Burned mesohabitat

My ability to statistically examine associates of whitebark pine seedling regeneration in burned mesohabitats was limited by poor replication and a lack of regeneration in two of the burn transects. However, the lack of regeneration in the burn in Willmore Wilderness Park is concerning as both of my transects were situated in close proximity to productive seed sources. Most restoration plans for whitebark pine call for prescribed burning or allowing natural burns to occur (Aubry et al 2008, Keane and Parsons 2010, Tomback and Achuff 2010, Keane et al 2012). Further and more extensive research should take place in burned areas in close proximity to whitebark pine seed sources.

2.4.6. Seedling population structure and infection

Seedlings in forested mesohabitats were the least likely to be found in clumps in comparison to open, treeline and alpine mesohabitats. This likely indicates a shift from competitive to facilitative interactions between the different mesohabitats (Callaway 1998). In open, treeline and alpine mesohabitats the facilitative effect of mutual shelter may outweigh the negative aspects of within-clump competition, while in forests which are more sheltered and where seedlings likely suffer from limited light availability there would be negative effects of within-clump competition. Open transects had the smallest proportion of large seedlings compared to the other three mesohabitats. This may be due increased heat causing increased germination success but also increased mortality or could indicate that seedling release is occurring more frequently in open mesohabitats and therefore whitebark pine seedlings in open mesohabitats spend less time in the larger seedling class size (i.e., they are growing above our maximum size cut-off).

Several studies have reported higher infection levels for larger whitebark pine seedlings and for seedlings in more exposed habitat (Tomback et al 1995, Moody 2006, Resler and Tomback 2008). My results support the former on size of seedlings but are unable to support the latter on exposed habitat. I found in all mesohabitats that white pine blister rust infection levels were higher in larger seedlings while infection rates did not differ between mesohabitats. This investigation did not look at mortality over time and it is possible that small seedlings with blister rust die before they can be observed with the disease. Unhealthy seedlings were most prevalent in alpine and treeline conditions. This is likely a result of the greater propensity for whitebark pine seedlings to undergo physical damage in these environments (Körner 2003).

2.4.7. Motion camera investigation

The timing of snowmelt varied between mesohabitats at different locations. In two sites where motion cameras were placed, snowmelt occurred much earlier in the open mesohabitats in comparison to the forest mesohabitat (site 06WBL05) and in comparison to the forest and treeline mesohabitats (site 08WBL07). Interestingly, it was at these two transects where whitebark pine seedling abundance was the highest in comparison to the other transects included in this particular investigation. While this can only be an anecdotal observation as our sample size is low, we can hypothesize that earlier spring melt in open environments contributes to increased growing season length, thus improving seedling germination and survival. Alternatively, we could hypothesize that Clark's nutcrackers are caching seed in locations where they will be able to retrieve them at an earlier date. Clark's nutcracker caching and retrieval events were recorded at the open mesohabitat in site 08WBL07.

2.6. Conclusions

There were several environmental variables that appeared to have a relatively consistent effect in all mesohabitats. First of all, the negative association of increasing rock cover with seedling success was nearly universal in all mesohabitats and for all three response variables. Secondly, graminoid cover had a negative impact on seedling success in three out of the four mesohabitats. Finally, a minimum amount of understory plant cover was positively associated with occurrence and growth in nearly all of our mesohabitats. In forest mesohabitats, increased vegetation cover was likely a response to decreased canopy cover while in other mesohabitats vegetation perhaps played a more facilitative role; the fact that the positive association of some vegetation cover outweighed any negative impact of too much cover is significant.

I had evidence to suggest convergent nutcracker caching may be occurring in both treeline and open mesohabitats at the northeast periphery of the range of whitebark pine. The frequency with which nutcrackers participate in this behavior is unclear. Little research has been done on nutcracker behavior and ecology at the northern limit of its range. However convergent caching makes intuitive sense, as slopes that are empty of snow would be critical sources of food for birds returning in the spring. If this is the case, use of prescribed fire or even prescribed logging on landscape features that are southwest facing and within close proximity of large whitebark pine cone crops may be an excellent way to promote regeneration in this region.

There was a shift from competitive to facilitative processes from the forest to treeline to alpine mesohabitats. In forest mesohabitats, the strongest association with regards to occurrence and growth was a negative association with canopy cover. In treeline and alpine conditions, variables that indicated alleviated environmental conditions became more influential. This lends support to the theory of Callaway (1998) that interspecific facilitative interactions become more important than competitive as environmental conditions become harsher.

It is important to analyze multiple aspects of regeneration when determining conditions conducive to success. Most studies performed previously have focused on abundance (Moody 2006, Larson and Kipfmueller 2010) and/or survival (Tomback et al

1995, Tomback et al 2001a, Mellman-Brown 2005, Izlar 2007) and there is only one known study that has looked at differences between occupied and unoccupied microsites (Tomback et al 1993). I found that the factors of regeneration success differed between occurrence and growth and at different scales (microsite to mesohabitat). Information on drivers of growth rate, occurrence at the microsite scale and seedling density is needed in order to gain the understanding needed for restoration and recovery.

Whitebark pine seedlings were increasingly likely to be affected by white pine blister rust as they became larger. This does not bode well for the continuing survival of whitebark pine in mountain ecosystems if increased regeneration success leads to increased likelihood of with white pine blister rust infection. Even if we had complete knowledge of the regeneration niche of whitebark pine and knew with certainty how to facilitate high levels of regeneration, white pine blister rust will most likely reduce the effectiveness of our efforts.

2.7. Tables

Table 2.1: Predictor variables used in ordination and regression tree analyses and the scale (mesosite or microsite) at which they were sampled. Also provided are the units or scale used in collection of the data for each variable. Abbreviations in the first column are used in figures and in Appendices 2 and 3.

Variable	Explanation	Units/Scale	Level
ELEV_M	Elevation	m	Mesosite
HLI	Heat load index	0-1	Mesosite
MAP	Mean annual precipitation	mm/year	Mesosite
MAT	Mean annual temperature	°C	Mesosite
MESOPOS	Mesotopographic position	NA	Mesosite
MIN_AGE	Minimum age of stand based on oldest tree cored	Years	Mesosite
MR_SCALE	Moisture regime	0-5*	Mesosite
NR_SCALE	Nutrient regime	0-5*	Mesosite
PH	pH of mineral soil		Mesosite
SLOPE	Slope	°	Mesosite
RICHNESS	Species richness	Species/m^2	Microsite
BA_ABBI	Basal area of mature *Abies lasiocarpa*	m^2/ha	Microsite
BA_PIAL	Basal area of mature *Pinus albicaulis*	m^2/ha	Microsite
BA_PICO	Basal area of mature *Pinus contorta*	m^2/ha	Microsite
BA_PIEN	Basal area of mature *Pinus engelmannii*	m^2/ha	Microsite
BA_TOT	Total basal area of trees	m^2/ha	Microsite
BARE	Bare mineral soil cover	%	Microsite
CAN_COV	Canopy cover	%	Microsite
FORBS	Total cover of forbs	%	Microsite
PR_SHRUB	Total cover of prostrate shrubs (< 5cm)	%	Microsite
GRAMS	Total cover of all graminoid species	%	Microsite
LICHEN	Lichen cover	%	Microsite
LITDEP	Litter depth at plot center	cm	Microsite
LITTER	Litter cover	%	Microsite
MICROPOS	Microtopographic position	NA	Microsite
MOSS	Moss cover	%	Microsite
ORGDEP	Depth of organic matter depth	cm	Microsite
PLANTGROUP	Vegetation group as determined by cluster analysis	1-5	Microsite
ROCK	Rock cover	%	Microsite
SEEDLING	Total seedling cover (not including *Pinus albicaulis*)	%	Microsite
TREE	Total tree cover in understory plot	%	Microsite
UP_SHRUB	Total cover of erect shrubs (>5cm height)	%	Microsite
VEGCOVER	Sum of understory vegetation cover (all species)	%	Microsite
WOOD	Downed and decayed woody material cover	%	Microsite

*As found in the Field Manual for Describing Terrestrial Ecosystems (BC Ministry of Forests 1998)

Table 2.2: Factors positively and negatively associated with whitebark pine seedling occurrence, growth rate and density in the forest mesohabitat. Values above which the effect was observed are listed with each factor. Factors are listed in order of importance as observed in regression trees in Figures 2.3-2.5.

Response	Positive	Negative
Occurrence	1. Mineral soil cover: ≥ 2.5% 2. Species richness: ≥ 2.5 spp/plot 3. Forb cover: ≥ 4.1%	1. Graminoid cover: ≥ 2.6%
Growth Rate	1. Vegetation cover: ≥ 15.1% 2. Slope: ≥ 51°	1. Basal area: > 10 m^2/ha 2. Canopy cover: ≥ 2.45% 3. Prostrate shrub cover: ≥ 8.1%
Density	1. Canopy cover: ≥ 32% 2. Moisture regime: submesic or dryer 3. Vegetation cover: ≥ 29.49%	1. Mineral soil cover: ≥ 5.7%

Table 2.3: Factors positively and negatively associated with whitebark pine seedling occurrence, growth rate and density in the open mesohabitat. Values above which the effect was observed are listed with each factor. Factors are listed in order of importance as observed in regression trees in Figures 2.7-2.9.

Response	Positive	Negative
Occurrence		1. Rock cover: ≥ 62.5% 2. Graminoid cover: ≥ 7.5% 3. Seedling cover: ≥ 13% 4. Tree cover: ≥ 42.5%
Growth Rate	1. Mean annual temperature: -0.45°C to -0.25°C	1. Slope: ≥ 37.5° 2. Mineral soil cover: ≥ 34.5%
Density	1. Heat load index: ≥ 0.918	1. Rock cover: ≥ 47.5%

Table 2.4: Factors positively and negatively associated with whitebark pine seedling occurrence, growth rate and density in the treeline mesohabitat. Values above which the effect was observed are listed with each factor. Factors are listed in order of importance as observed in regression trees in Figures 2.11-2.13.

Response	Positive	Negative
Occurrence	1. Vegetation cover: ≥ 10.8%	1. Canopy cover: ≥ 67.05%
Growth Rate	1. Mean annual temperature: ≥ -0.75°C 2. Prostrate shrub cover: ≥ 5% 3. Upright shrub cover: ≥ 3.5%	1. Rock cover: ≥ 4.5%
Density	1. Mean annual precipitation: ≥ 867 mm/year 2. Species richness: ≥ 4.85 spp/plot	

Table 2.5: Factors positively and negatively associated with whitebark pine seedling occurrence, growth rate and density in the alpine mesohabitat. Values above which the effect was observed are listed with each factor. Factors are listed in order of importance as observed in regression trees in Figures 2.15-2.17.

Response	Positive	Negative
Occurrence	1. Litter depth: ≥ 0.1 cm 2. Vegetation cover: 22.3 – 40.4%	1. Tree cover: ≥ 5.5% 2. Species richness: ≥ 4.5 spp/plot
Growth Rate	1. Forb cover: ≥ 8.6% 2. Litter depth: ≥ 0.1 cm	1. Rock cover: ≥ 0.5% 2. Lichen cover: ≥ 4% 3. Graminoid cover: ≥ 0.8% 4. Heat load index: ≥ 0.929
Density	1. Litter cover: ≥ 0.55% 2. Mineral soil cover: 0.44% 3. Rock cover: 20.35 – 42.25%	

Table 2.6: Mesohabitat, aspect, slope, elevation, snowmelt date and seedling density at motion camera locations.

Site	Mesohabitat	Aspect (°)	Slope (°)	Elevation (m)	Snowmelt date	Seedling density (stems/ha)
06WBL05	Forest	343	2	1591	June 11	250
06WBL05	Open	343	4	1584	May 31	1625
08WBL02	Forest	107	34	1931	*	75
08WBL02	Open	121	6	1897	June 18	5
08WBL02	Alpine	5	160	2066	*	225
08WBL07	Forest	163	37	1896	June 11**	1000
08WBL07	Open***	224	11	1937	May 24	9125
08WBL07	Treeline	215	32	1996	June 14	1925

* Unable to record snowmelt date due to camera difficulties

** Camera position altered; snowmelt date estimated based on new area

*** Nutcracker activity observed at this site

2.8. Figures

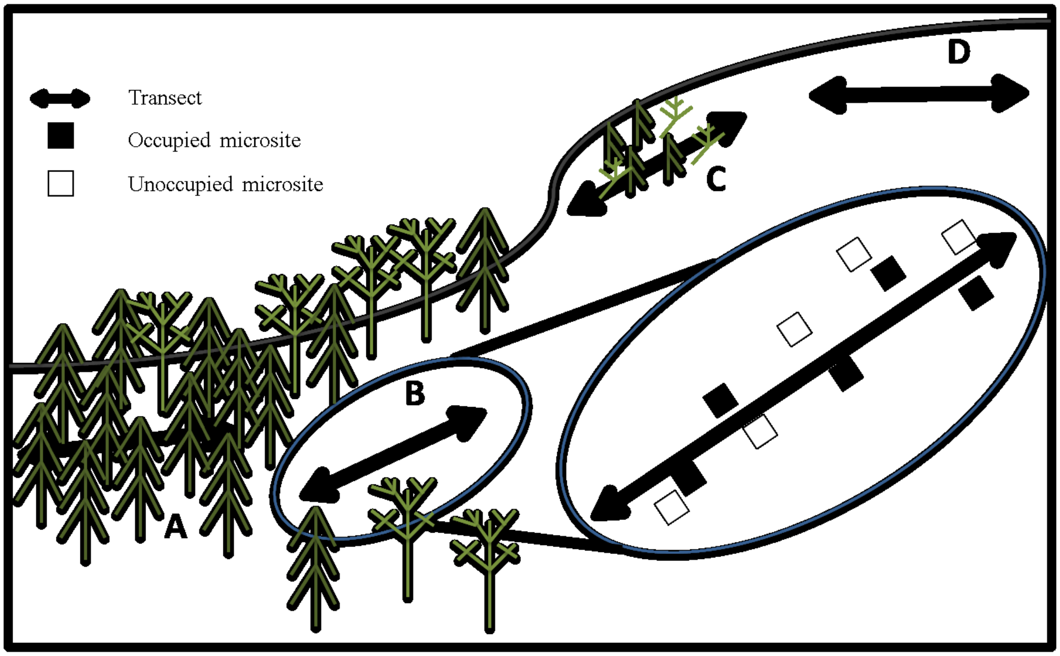

Figure 2.1: Simplified example of sampling design at a study site including the four typical mesohabitats sampled: A) forest; B) open; C) treeline; D) alpine. The open mesohabitat has been enlarged to demonstrate placement of occupied and unoccupied microsite plots, represented by open and closed squares respectively.

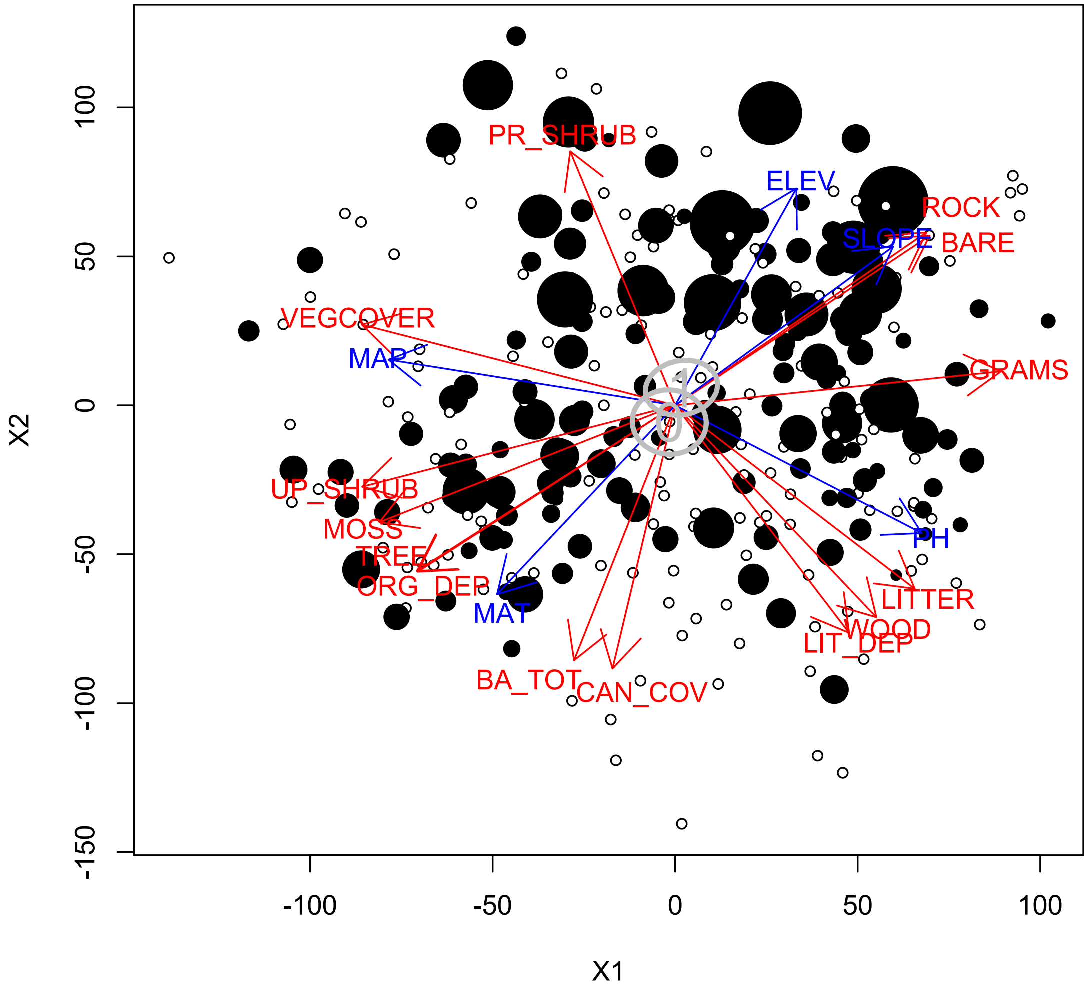

Figure 2.2: Results of NMDS ordination for the forest mesohabitat. NMDS was based on biophysical variables taken at the microsite scale (red vectors); variables measured at the mesohabitat scale (blue vectors) were passively overlain on the ordination. Abbreviations in this figure are defined in Table 2.1. Points represent microsite plots; filled and open points representing occupied and unoccupied plots, respectively. The size of each point for the occupied plots reflects the average growth rate of seedlings. Ellipses are the 95% standard error around the mean position for occupied and unoccupied plots denoted by 1 and 0 respectively. The cut off for display of vectors was $|r| > 0.25$; minimum stress was 0.245 after 10 iterations; variation accounted for was 0.751.

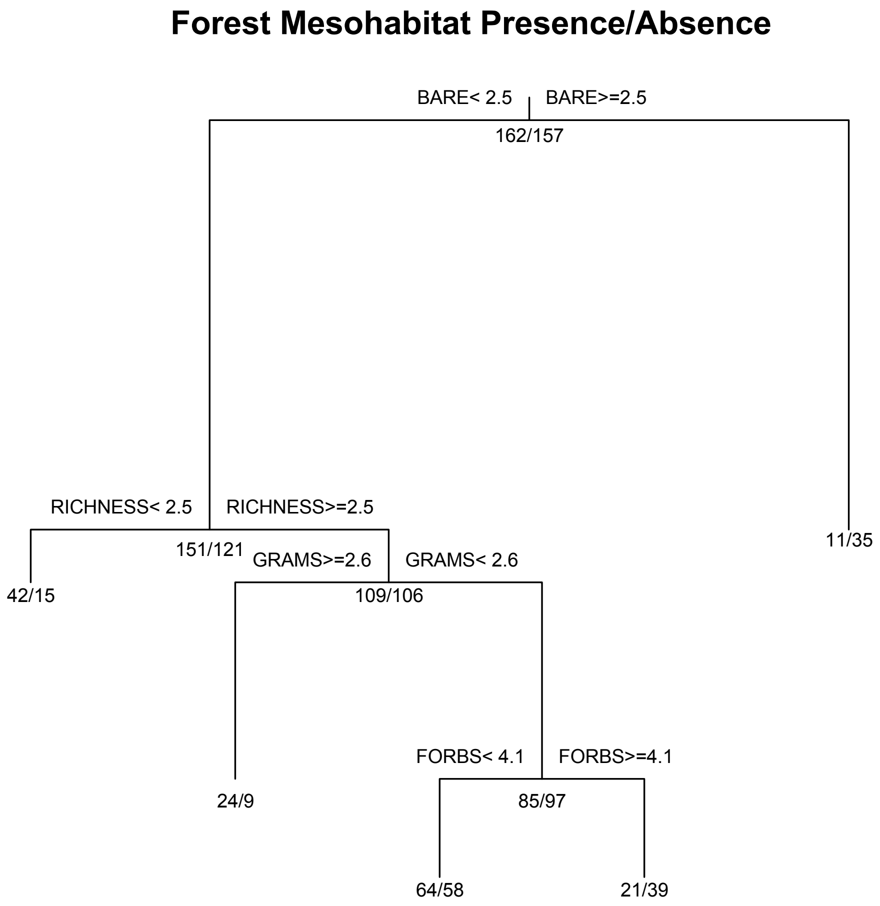

Figure 2.3: Results of regression tree analysis showing the drivers of whitebark pine seedling presence for the forest mesohabitat. Numbers beneath each node represent the ratio of unoccupied to occupied plots; a split to the right represents higher whitebark pine presence while a split left is towards lower whitebark presence. The sum of both numbers is the total number of replicates (microsite plots) at that node. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 1. Unexplained error was 0.669. Only primary splits with a complexity parameter of 0.037 or greater are shown.

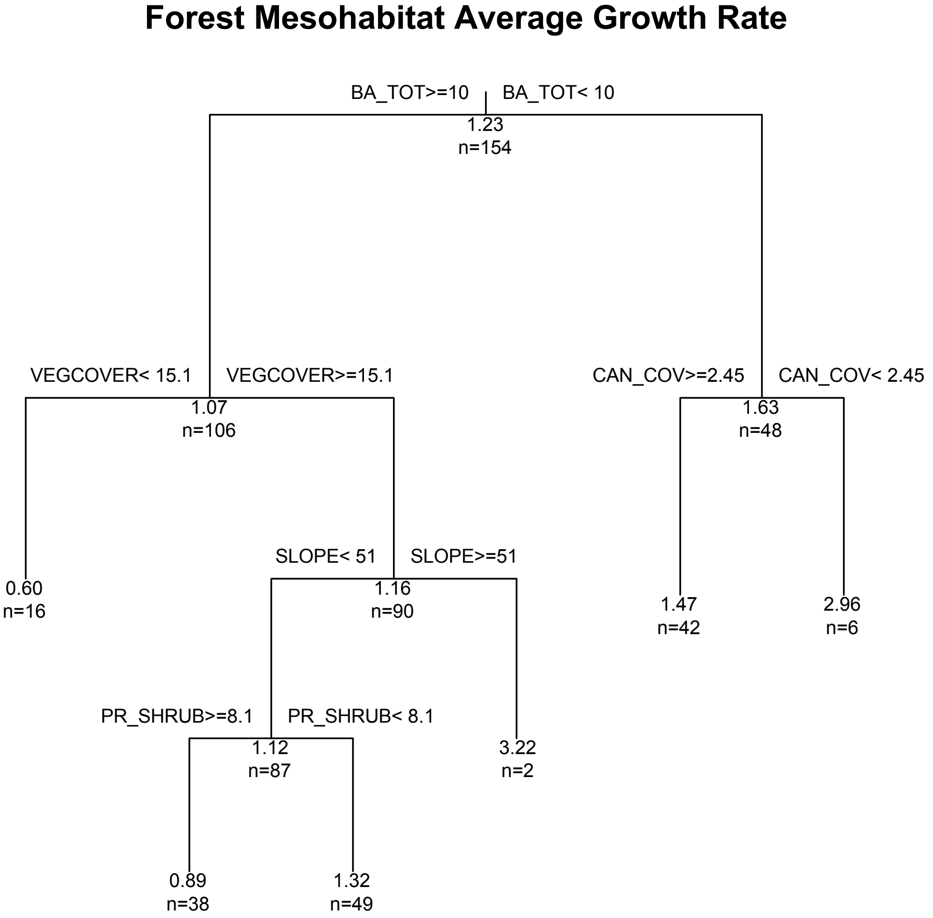

Figure 2.4: Results of regression tree analysis showing the drivers of whitebark pine seedling growth rate in forest mesohabitats. Underneath each node is the average growth rate (cm/year) for n=the number of occupied microsite plots; a split right represents increased average growth rate while a split left represents decreased growth rate. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 2. Regression tree is based on square root transformed average growth rates. Unexplained error was 0.678. Only primary splits with a complexity parameter of 0.04 or greater are shown.

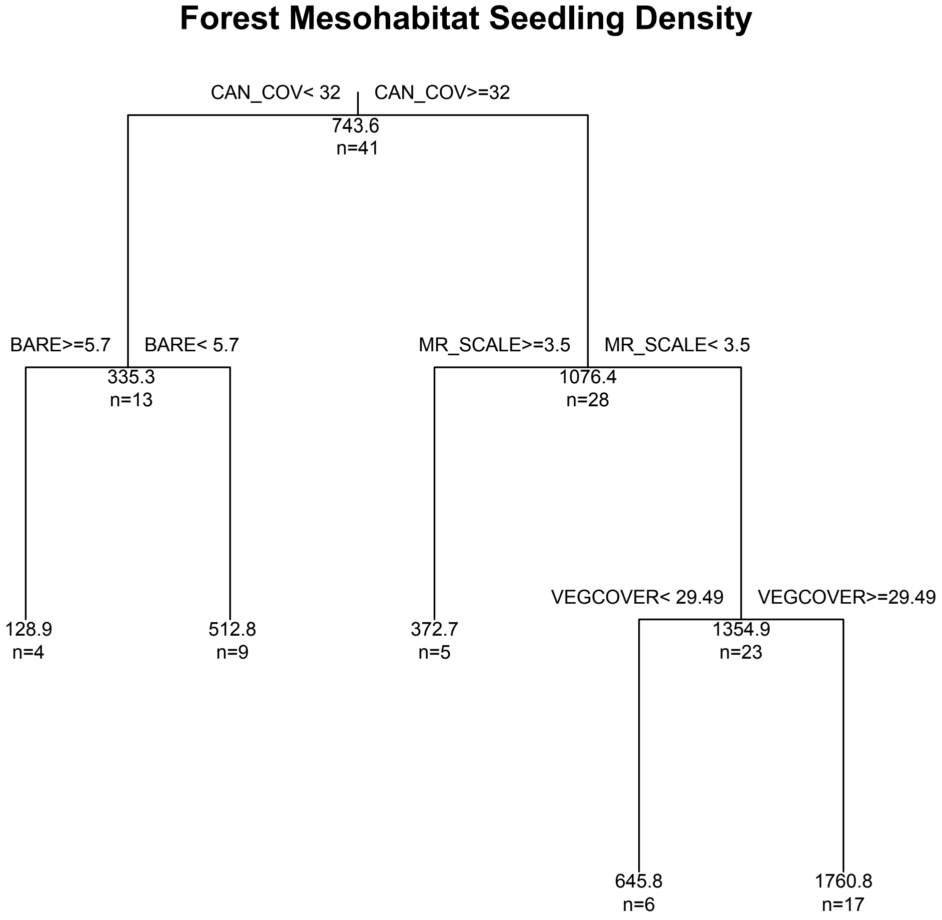

Figure 2.5. Results of regression tree analysis for drivers of whitebark pine seedling density at the transect scale in forest mesohabitats. The first number underneath each node is the average seedling density (seedlings/ha); n=the number of transects at each node; a split to the right represents increased average seedling density while a split left represents decreased density. Regression tree is based on $\log_2$ transformed average seedling density Alternate splits for each node are shown in Appendix 2 – Table 3. Unexplained error was 0.317. Only primary splits with a complexity parameter of 0.1 or greater are shown.

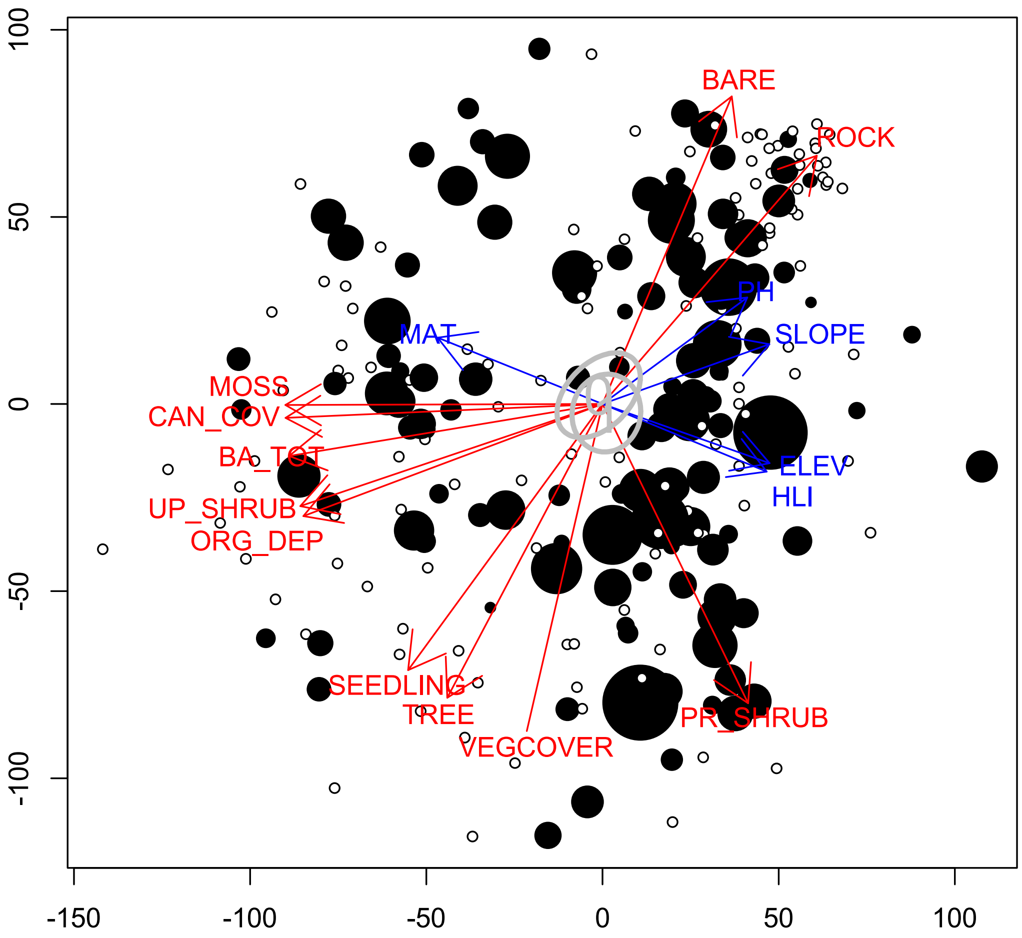

Figure 2.6. Results of NMDS ordination for the open mesohabitat. NMDS was based on biophysical variables taken at the microsite scale (red vectors); variables measured at the mesohabitat scale (blue vectors) were passively overlain on the ordination. Abbreviations in this figure are defined in Table 2.1. Points represent microsite plots; filled and open points representing occupied and unoccupied plots, respectively. The size of each point for the occupied plots reflects the average growth rate of seedlings. Ellipses are the 95% standard error around the mean position for occupied and unoccupied plots denoted by 1 and 0 respectively. The cut off for display of vectors was $|r| > 0.25$; minimum stress was 0.211 after 10 iterations; variation accounted for was 0.830.

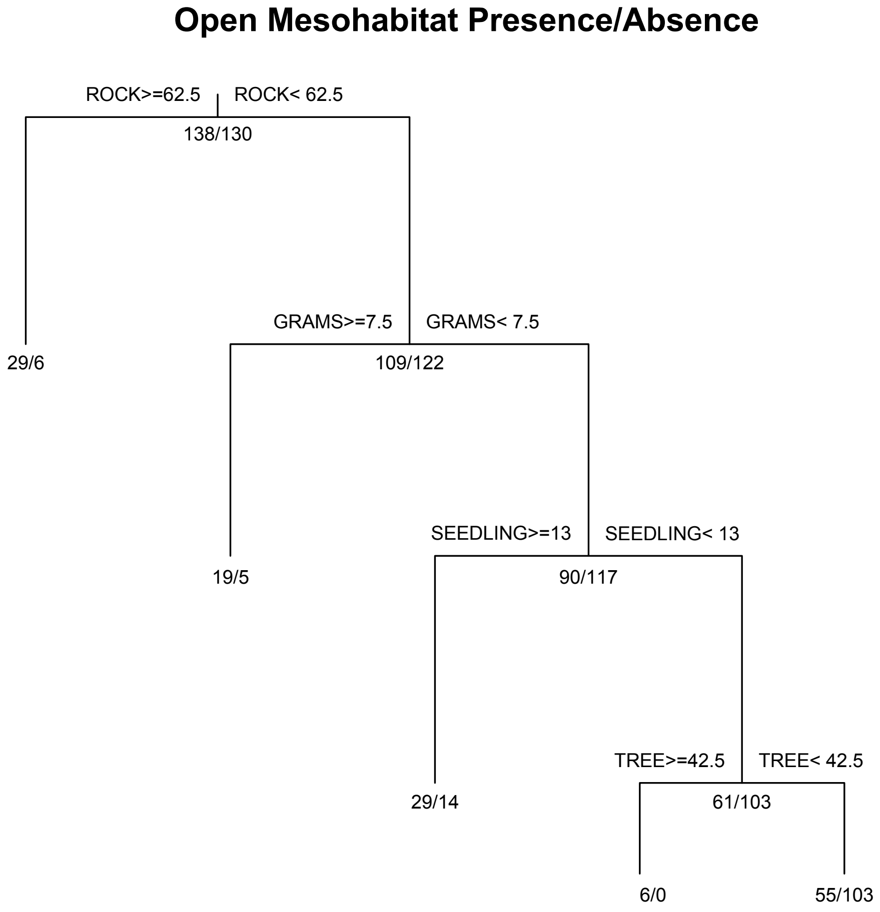

Figure 2.7: Results of regression tree analysis showing the drivers of whitebark pine seedling presence for the open mesohabitat. Numbers beneath each node represent the ratio of unoccupied to occupied plots; a split to the right represents higher whitebark pine presence while a split left is towards lower whitebark presence. The sum of both numbers is the total number of replicates (microsite plots) at that node. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 1. Unexplained error was 0.615. Only primary splits with a complexity parameter of 0.04 or greater are shown.

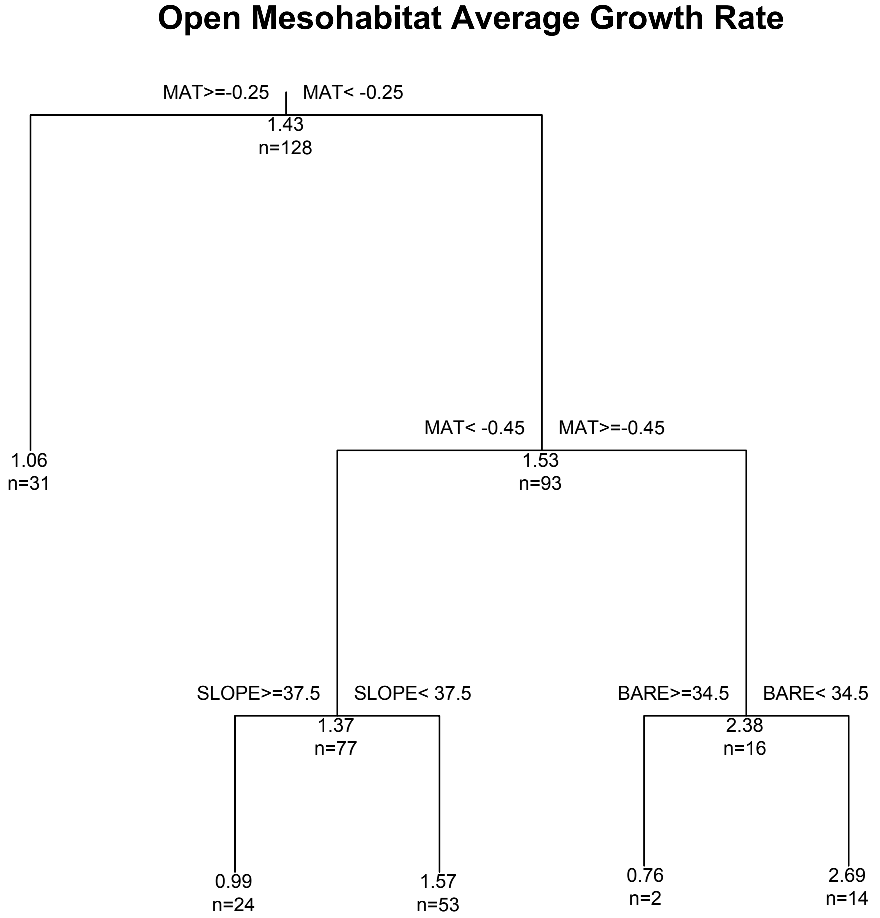

Figure 2.8: Results of regression tree analysis showing the drivers of whitebark pine seedling growth rate in open mesohabitats. Underneath each node is the average growth rate (cm/year) for n=the number of occupied microsite plots; a split right represents increased average growth rate while a split left represents decreased growth rate. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 2. Regression tree is based on square root transformed average growth rates. Unexplained error was 0.609. Only primary splits with a complexity parameter of 0.05 or greater are shown.

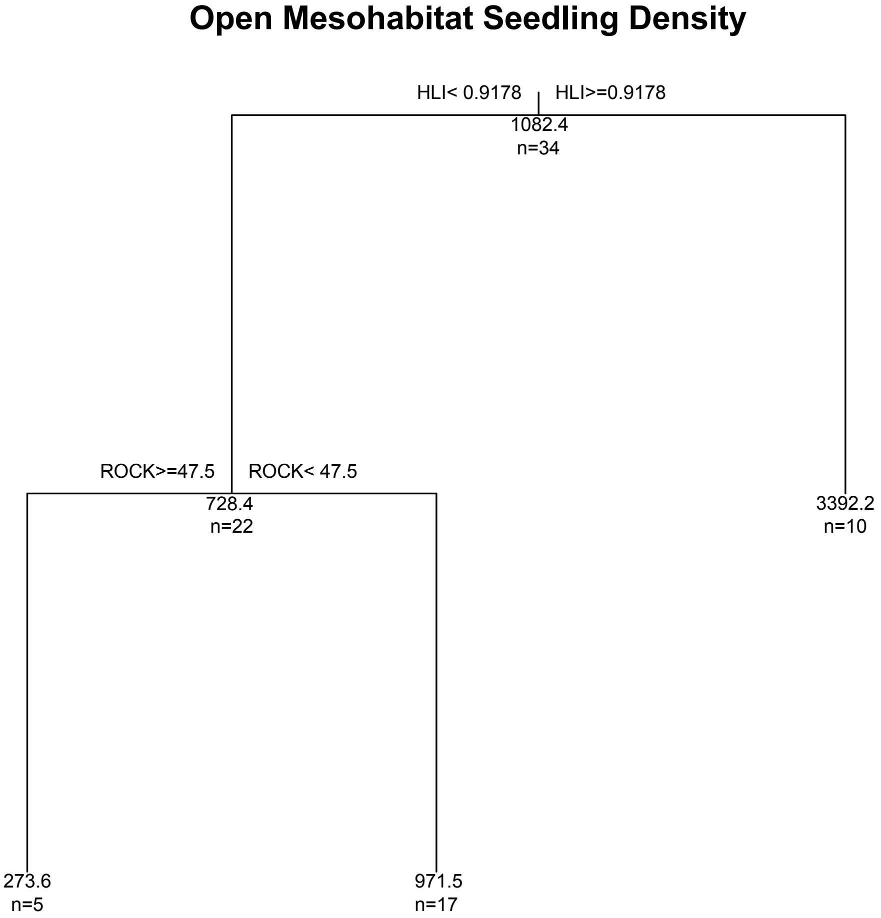

Figure 2.9. Results of regression tree analysis for drivers of whitebark pine seedling density at the transect scale in open mesohabitats. The first number underneath each node is the average seedling density (seedlings/ha); n=the number of transects at each node; a split to the right represents increased average seedling density while a split left represents decreased density. Regression tree is based on $\log_2$ transformed average seedling density Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 3. Unexplained error was 0.323. Only primary splits with a complexity parameter of 0.07 or greater are shown.

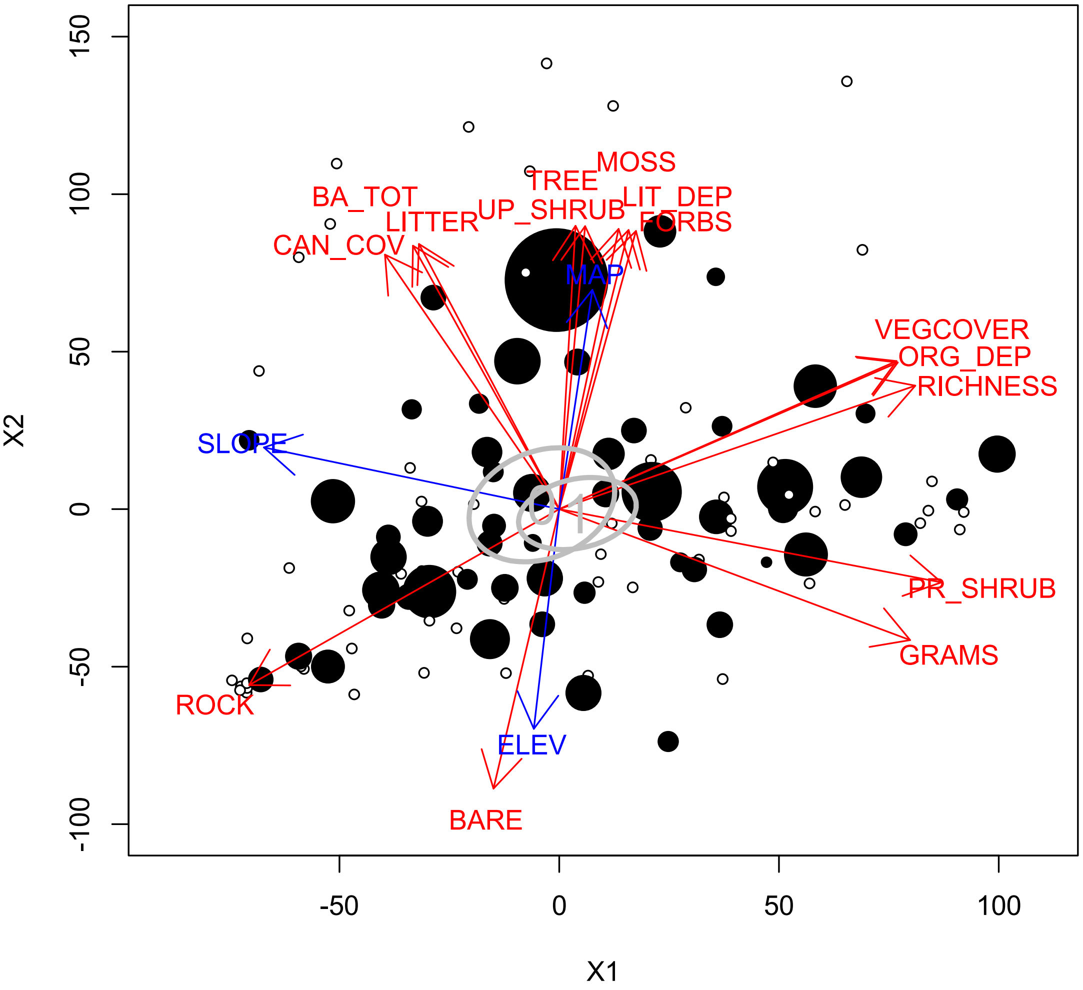

Figure 2.10: Results of NMDS ordination for the treeline mesohabitat. NMDS was based on biophysical variables taken at the microsite scale (red vectors); variables measured at the mesohabitat scale (blue vectors) were passively overlain on the ordination. Abbreviations in this figure are defined in Table 2.1. Points represent microsite plots; filled and open points representing occupied and unoccupied plots, respectively. The size of each point for the occupied plots reflects the average growth rate of seedlings. Ellipses are the 95% standard error around the mean position for occupied and unoccupied plots denoted by 1 and 0 respectively. The cut off for display of vectors was $|r| > 0.25$; minimum stress was 0.185 after 10 iterations; variation accounted for was 0.883.

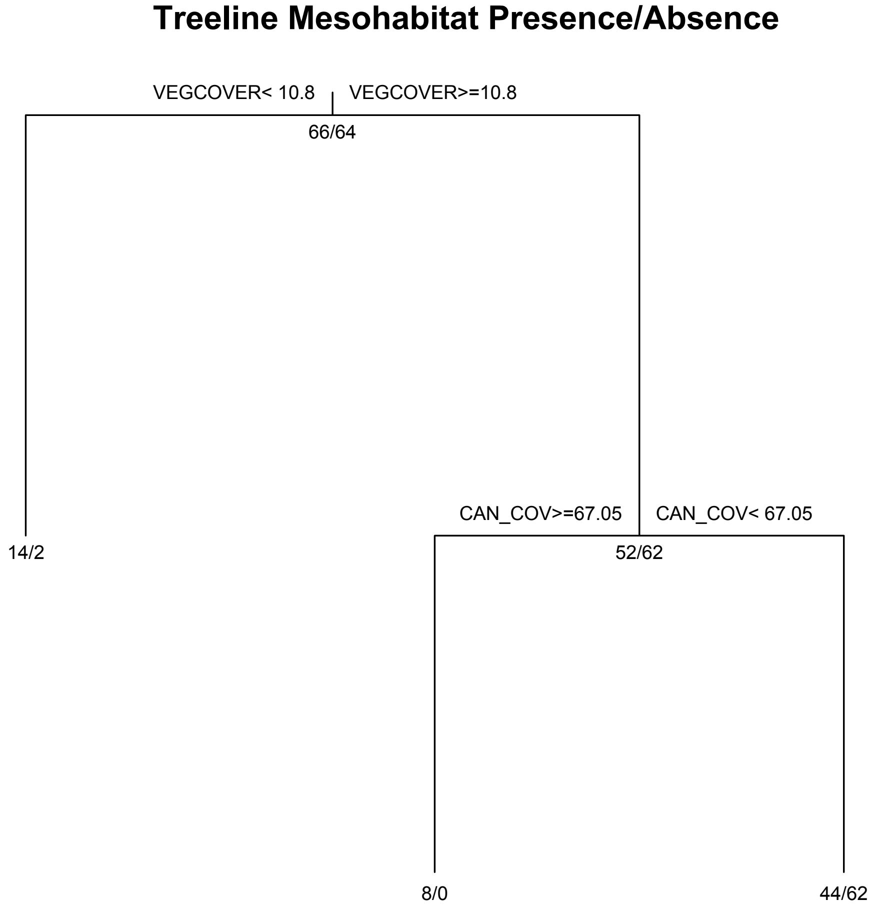

Figure 2.11: Results of regression tree analysis showing the drivers of whitebark pine seedling presence for the treeline mesohabitat. Numbers beneath each node represent the ratio of unoccupied to occupied plots; a split to the right represents higher whitebark pine presence while a split left is towards lower whitebark presence. The sum of both numbers is the total number of replicates (microsite plots) at that node. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 1. Unexplained error was 0.734. Only primary splits with a complexity parameter of 0.06 or greater are shown

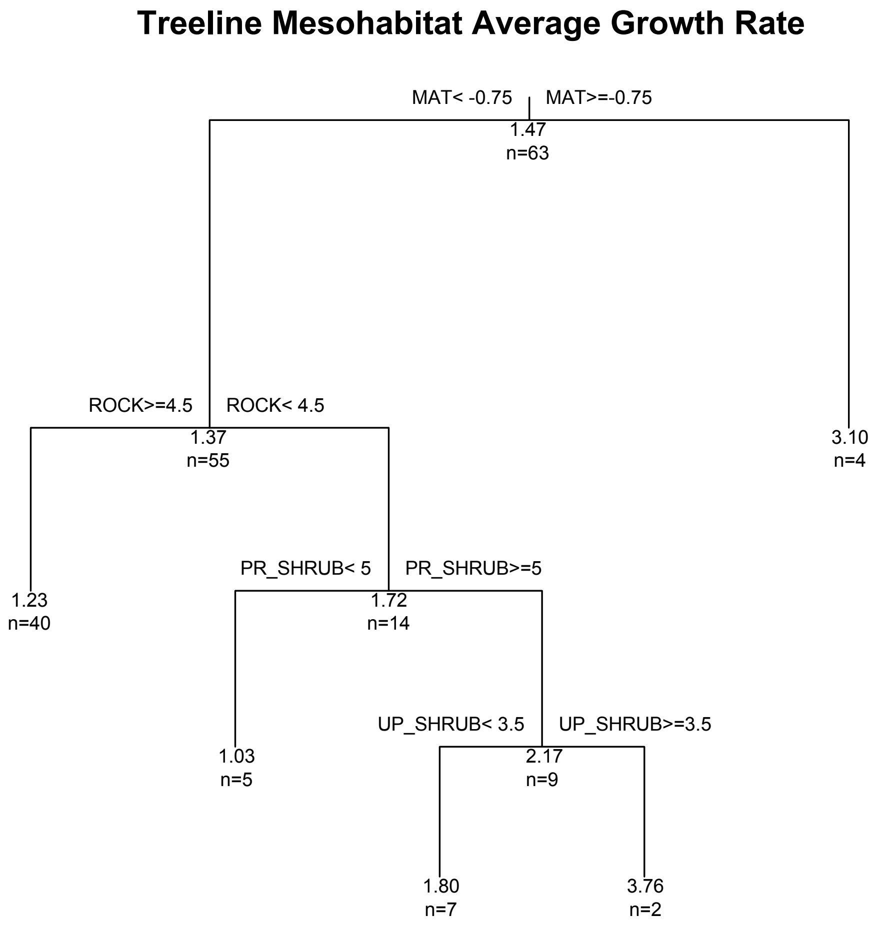

Figure 2.12: Results of regression tree analysis showing the drivers of whitebark pine seedling growth rate in treeline mesohabitats. Underneath each node is the average growth rate (cm/year) for n=the number of occupied microsite plots; a split right represents increased average growth rate while a split left represents decreased growth rate. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 2. Regression tree is based on square root transformed average growth rates. Unexplained error was 0.594. Only primary splits with a complexity parameter of 0.04 or greater are shown.

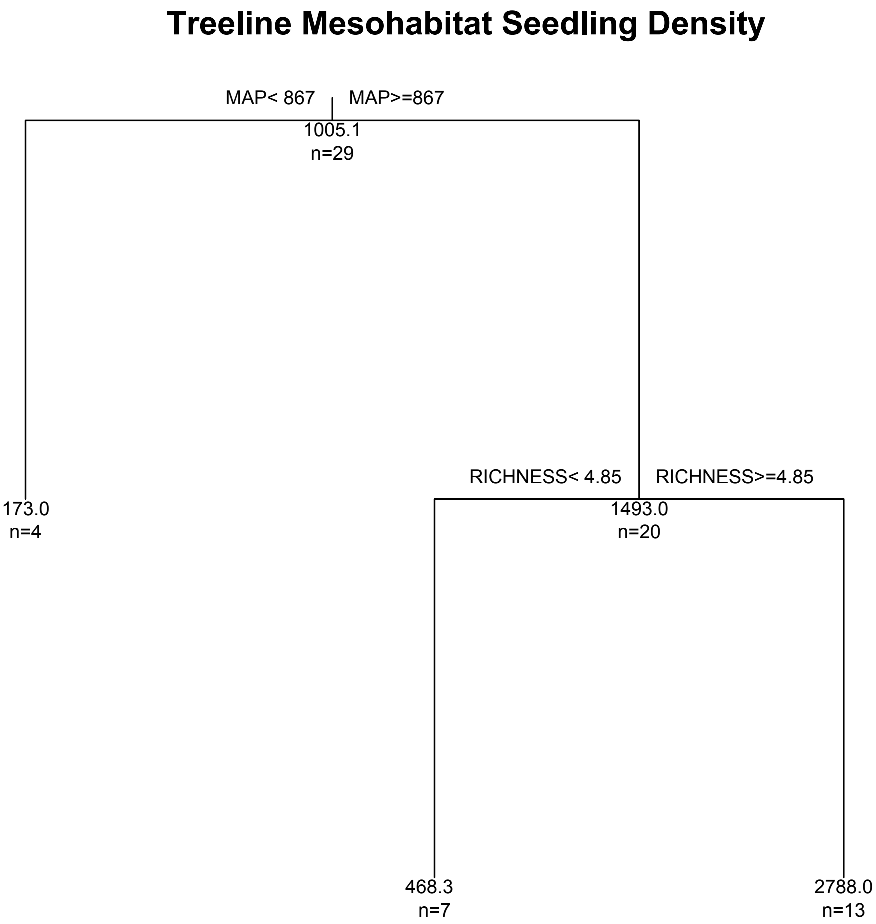

Figure 2.13. Results of regression tree analysis for drivers of whitebark pine seedling density at the transect scale in forest mesohabitats. The first number underneath each node is the average seedling density (seedlings/ha); n=the number of transects at each node; a split to the right represents increased average seedling density while a split left represents decreased density. Regression tree is based on $\log_2$ transformed average seedling density. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 3. Unexplained error was 0.260. Only primary splits with a complexity parameter of 0.08 or greater are shown.

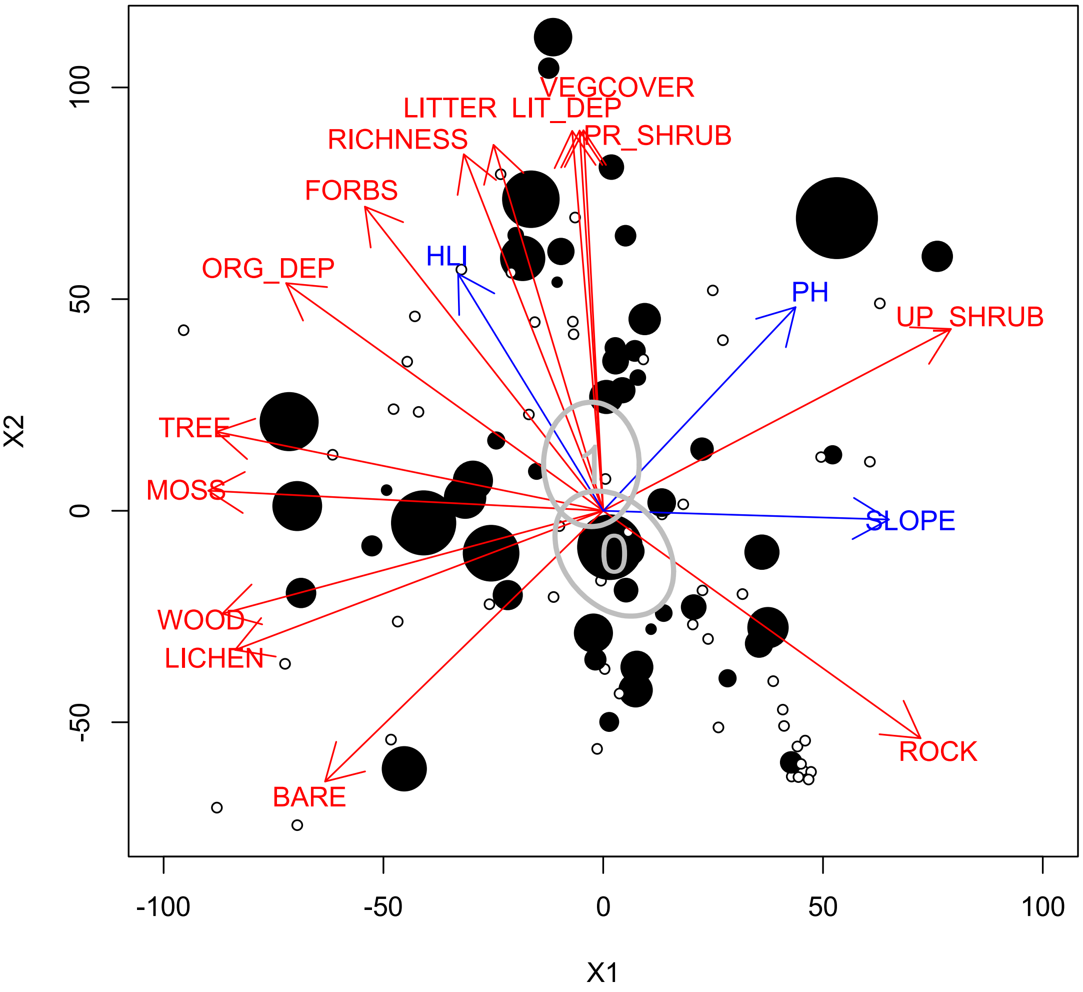

Figure 2.14: Results of NMDS ordination for the alpine mesohabitat. NMDS was based on biophysical variables taken at the microsite scale (red vectors); variables measured at the mesohabitat scale (blue vectors) were passively overlain on the ordination. Abbreviations in this figure are defined in Table 2.1. Points represent microsite plots; filled and open points representing occupied and unoccupied plots, respectively. The size of each point for the occupied plots reflects the average growth rate of seedlings. Ellipses are the 95% standard error around the mean position for occupied and unoccupied plots denoted by 1 and 0 respectively. The cut off for display of vectors was $|r| > 0.25$; minimum stress was 0.171 after 10 iterations; variation accounted for was 0.887.

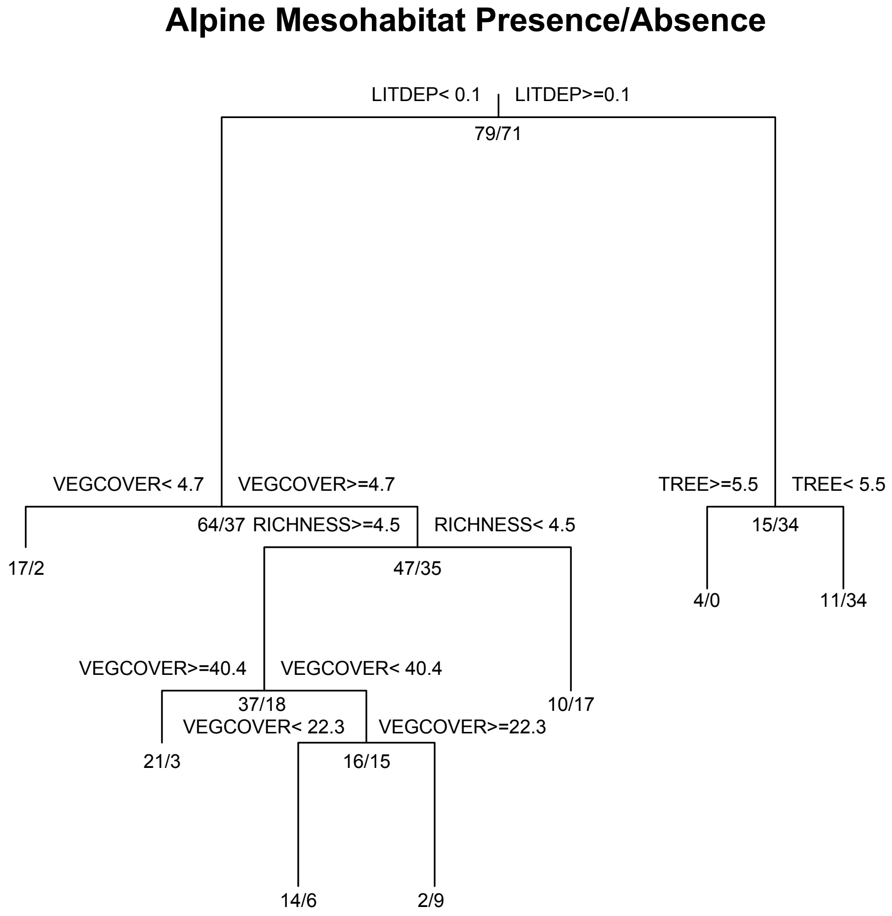

Figure 2.15: Results of regression tree analysis showing the drivers of whitebark pine seedling presence for the alpine mesohabitat. Numbers beneath each node represent the ratio of unoccupied to occupied plots; a split to the right represents higher whitebark pine presence while a split left is towards lower whitebark presence. The sum of both numbers is the total number of replicates (microsite plots) at that node. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 1. Unexplained error was 0.479. Only primary splits with a complexity parameter of 0.04 or greater are shown.

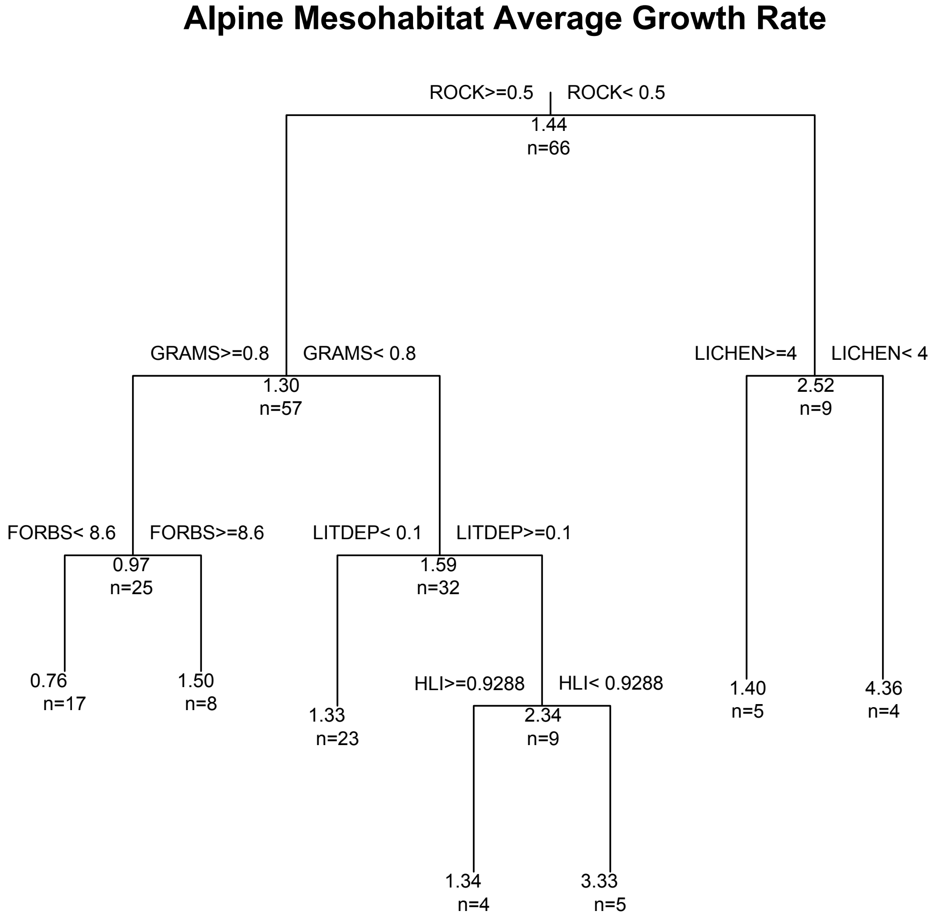

Figure 2.16: Results of regression tree analysis showing the drivers of whitebark pine seedling growth rate in alpine mesohabitats. Underneath each node is the average growth rate (cm/year) for n=the number of occupied microsite plots; a split right represents increased average growth rate while a split left represents decreased growth rate. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 2. Regression tree is based on square root transformed average growth rates. Unexplained error was 0.343. Only primary splits with a complexity parameter of 0.05 or greater are shown.

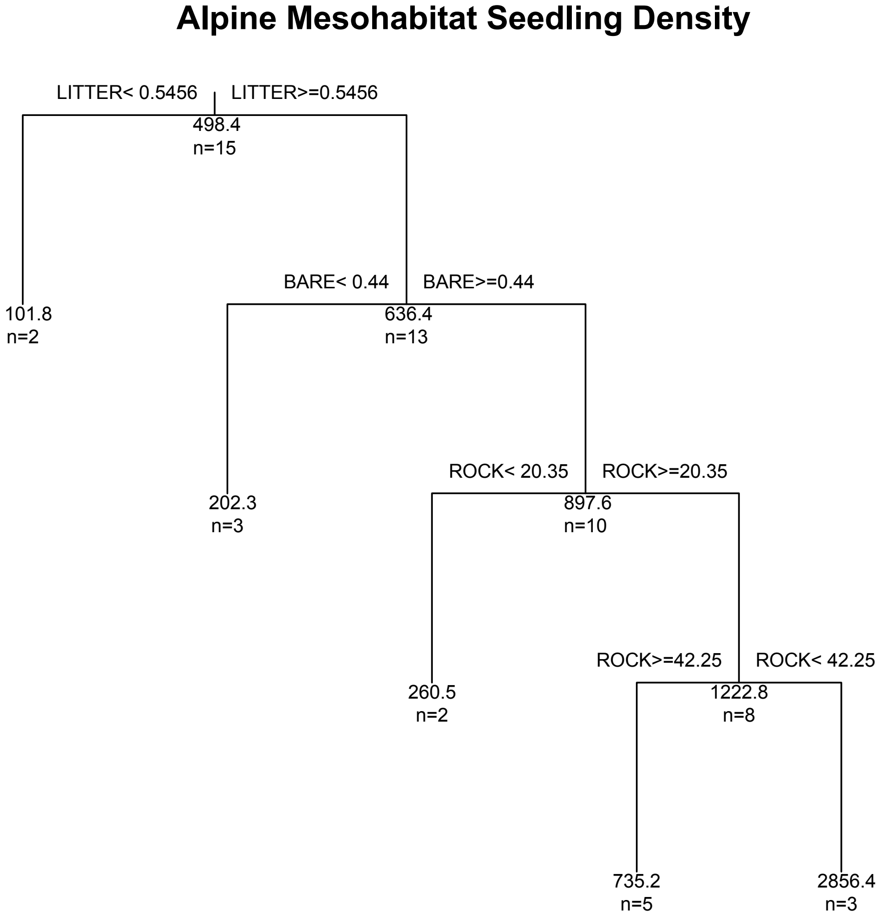

Figure 2.17: Results of regression tree analysis for drivers of whitebark pine seedling density at the transect scale in alpine mesohabitats. The first number underneath each node is the average seedling density (seedlings/ha); n=the number of transects at each node; a split to the right represents increased average seedling density while a split left represents decreased density. Regression tree is based on $\log_2$ transformed average seedling density. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 3. Unexplained error was 0.163. Only primary splits with a complexity parameter of 0.04 or greater are shown.

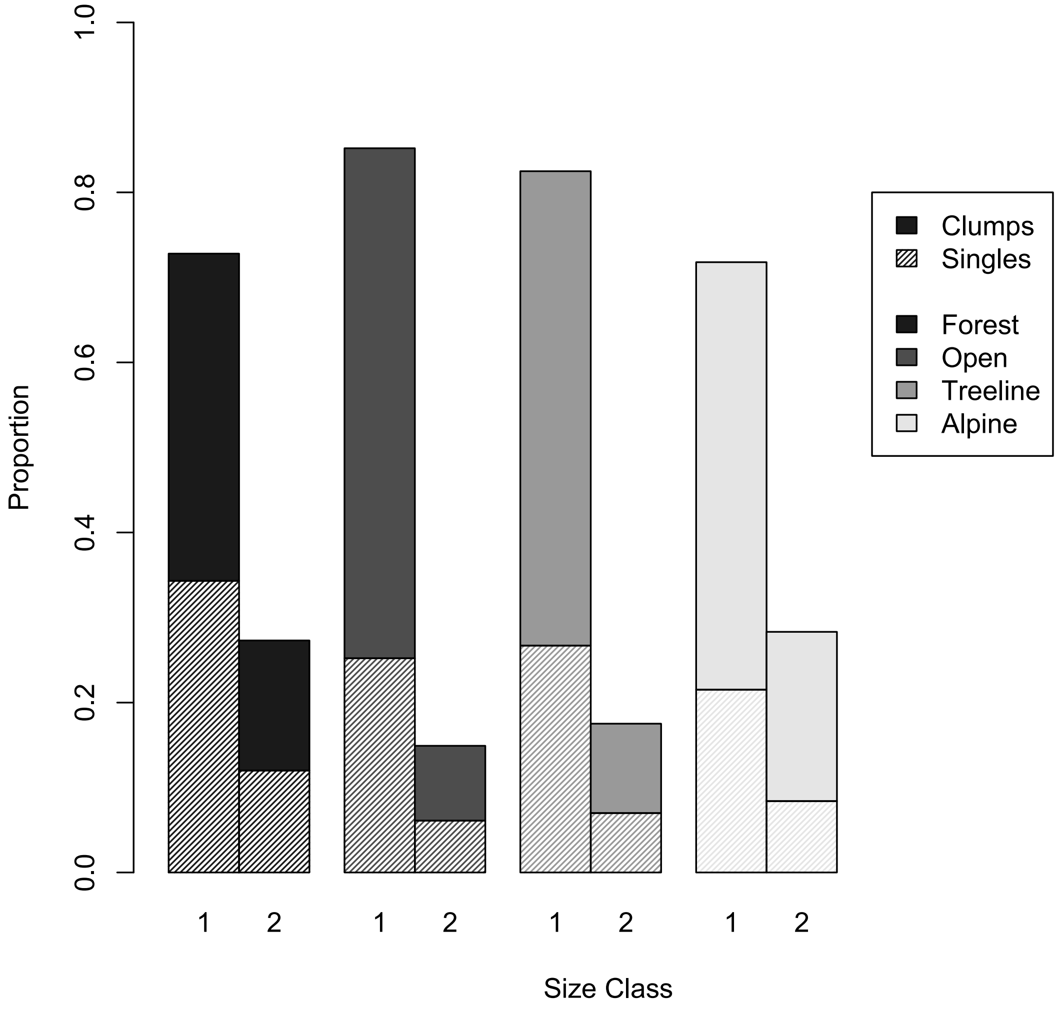

Figure 2.18: Bar plot showing proportion of seedlings in each mesohabitat found as singles, or clumps as well as in the two size classes; 1) 0 – 0.5m and 2) 0.5 – 1.4m. Proportions are of the total number of seedlings found at that particular mesohabitat.

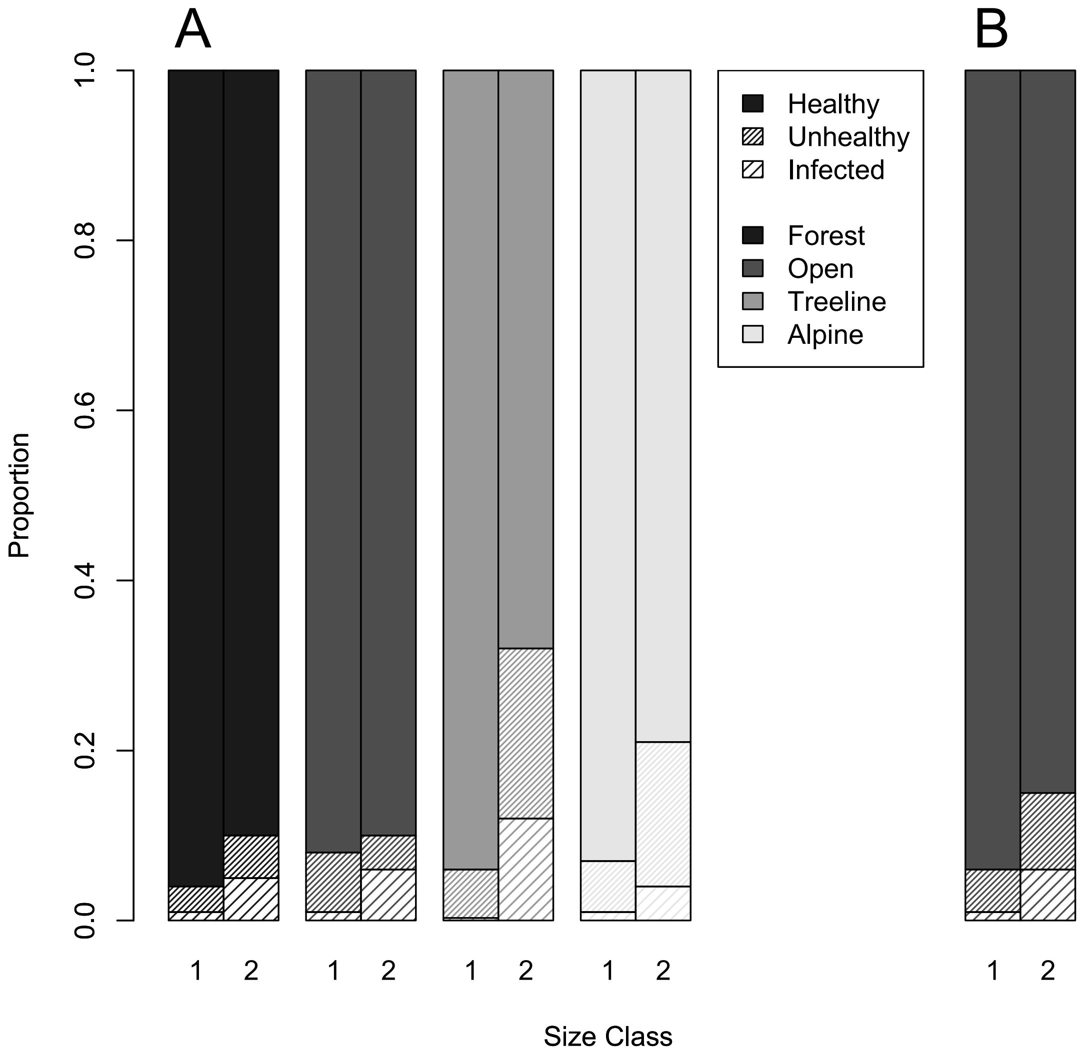

Figure 2.19: Bar plot showing proportions of seedlings found as healthy, unhealthy and infected for size class 1) 0 – 0.5m and 2) 0.5-1.4m in (A) mesohabitat: and B) for all mesohabitats combined. Proportions are calculated based on total number of seedlings of the specified size class and mesohabitat.

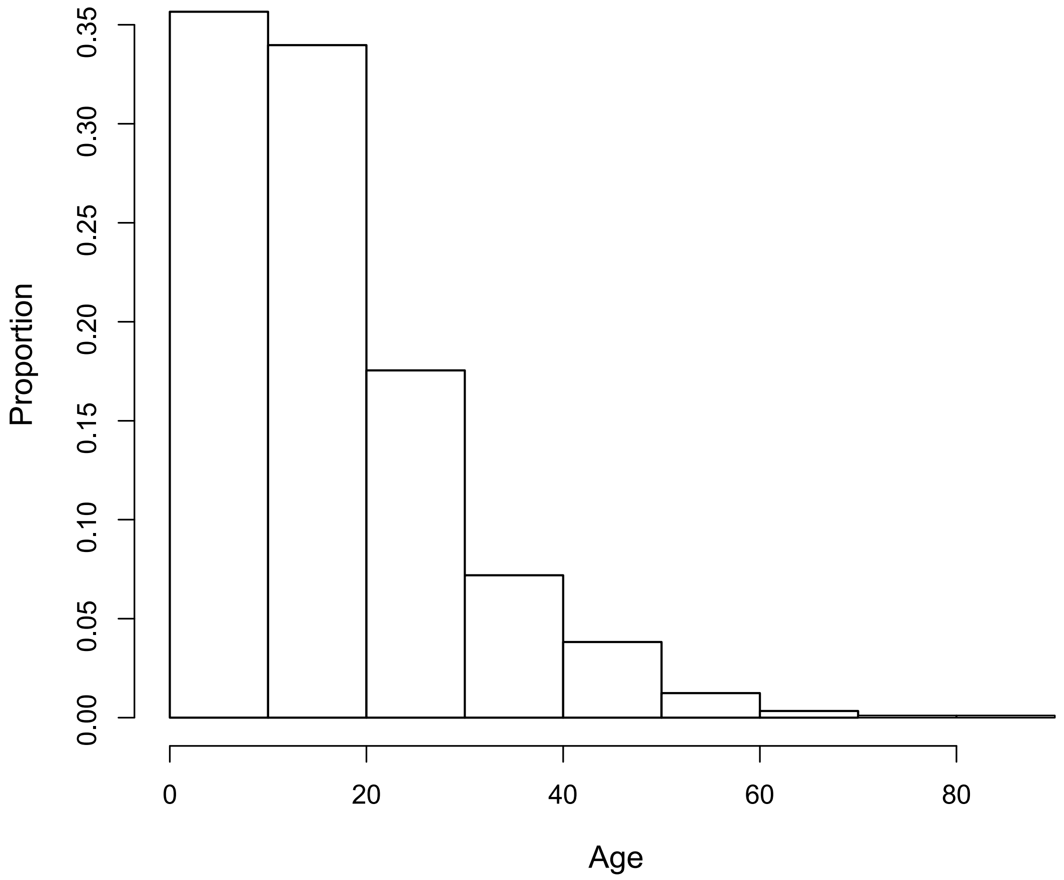

Figure 2.20: Histogram of whitebark pine seedling ages for all seedlings found in occupied plots in all mesohabitats. Each bar represents the proportion of total seedlings made up by the respective ten-year age classes.

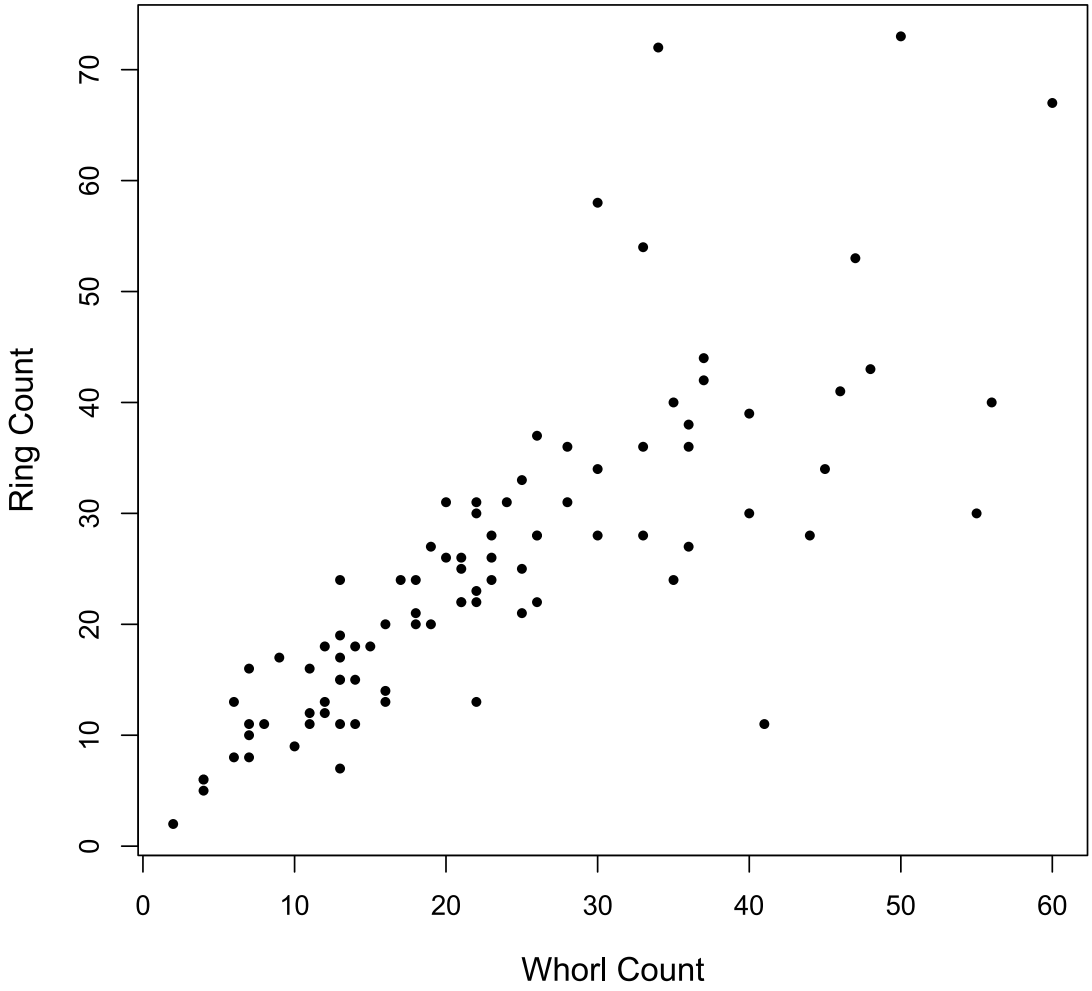

Figure 2.21: Age based on in-field whorl count versus ring count using dendrochronology. Pearson correlation between the two aging techniques was 0.79.

CHAPTER 3: Factors influencing whitebark pine seedling release

3.1. Abstract

Efforts to restore populations of endangered whitebark pine ecosystems are ongoing throughout the species' range. Introducing white pine blister rust resistant seedlings and promoting natural regeneration of whitebark pine will be important approaches, but it will take time for the regenerating cohort to replace the mature individuals lost to white pine blister rust or other causes of mortality such as mountain pine beetle. Understanding factors associated with released growth of seedlings can inform approaches to reduce the time for seedlings to reach reproductive maturity. Release growth in whitebark pine seedlings has been poorly studied and it is even unknown whether whitebark pine seedlings even have the ability to release following long periods of suppression. I investigated microsite drivers of seedling release at the northern extent of the species' range in Alberta. I destructively sampled a subset of whitebark pine seedlings found in 1x1 microsite plots in several different mesohabitats. I measured stem growth whorls and annual rings to quantify yearly height and diameter growth, respectively and to determine whether release events occurred. I compared surrounding microsite conditions of released and suppressed seedlings in different mesohabitats and compared the height prior to release to the current height of suppressed seedlings for each mesohabitat. The results showed that whitebark pine seedlings have

the capacity to release and that overstory conditions affect rates of release. Only 16.7% of seedlings in forest mesohabitats exhibited release conditions compared to 43.8% and 40.5% for those in open and alpine-treeline mesohabitats respectively. Furthermore, forest seedlings were much taller at the time they released; 18.6cm compared to 10.6 and 8.7cm for open and alpine-treeline seedlings, respectively. Seedlings that released in forest environments were found in significantly more open microsites. These results support the use of overstory thinning and planting in open mesohabitats for restoration. Further research investigating long-term survival of released seedlings in open mesohabitats should be conducted to determine the longer term-outlook for released seedlings.

3.2. Introduction

Whitebark pine, the charismatic, keystone, long-lived, food-providing, five-needled subalpine tree, is currently in decline throughout its range (Tomback and Achuff 2010). The combination of an introduced fungus, *Cronartium ribicola*, which leads to a debilitating disease called white-pine blister rust (McDonald and Hoff 2001, Smith et al 2013, Geils et al 2010), increased mountain pine beetle numbers (*Dendroctonus ponderosae,* Logan et al 2010), and successional displacement due to increased fire return intervals in the lower subalpine (Murray et al 2000, Arno 2001) has resulted in whitebark pine being placed on the endangered species list in Canada and Alberta and a recommendation for a federal listing is in place in the United States of America (Tomback and Acuff 2010).

Research is currently underway developing and outplanting white pine blister rust resistant whitebark pine seedlings (Sniezko et al 2014). Outplanting of rust-resistant seedlings will likely be one of the primary means of overcoming the impact of blister rust infection on populations of this species (Schoettle and Sniezko 2007, Schwandt et al 2010). Programs for developing rust resistance in whitebark pine have been ongoing for many years in Washington, Oregon and Idaho **(**Sniezko et al 2014**)** and a program for blister rust screening has commenced in southern British Columbia **(**Murray 2012). A secondary method for increasing blister rust resistance in healthy whitebark pine populations would be to simply increase the amount of regeneration occurring in these populations (Schoettle and Sniezko 2007). Since white pine blister rust rapidly removes seedlings without genetic resistance to the rust, increasing the seedling cohort would increase the possibility of some naturally-resistant individuals joining the population. Unfortunately, whitebark pine is a slow-growing species, averaging 6 cm per year in the best of circumstances (Weaver and Dale 1974) and does not typically reach reproductive maturity until 50 years of age (McCaughey and Schmidt 1990). In scenarios where rust resistant seedlings are planted, or where seedling populations are large enough to lead to natural resistance developing, it will take time for seedlings to grow and replace the ecosystem functions lost due to mortality of mature whitebark pine (Schoettle and Sniezko 2007). In cases where growth is suppressed or mechanical damage occurs, reproductive maturity and sufficient size to fulfill important ecosystem functions might not be reached for a very long time, if at all (McCaughey and Schmidt 1990). Any means of decreasing the time to reproductive maturity for whitebark pine should be explored and applied.

Other restorative actions being considered for whitebark pine populations include emulating natural disturbance patterns that promote the establishment of whitebark pine seedlings and thinning competing species to allow existing regeneration to grow to canopy height (Aubrey et al 2008, Keane and Parsons 2010, Schwandt et al 2010, Keane et al 2012). However, both methods of restoration have several major unknowns. Emulating natural disturbances, such as fire, is inherently risky and would likely only be a viable option in lower subalpine zones with a large nearby whitebark cone crop (Tomback et al 1995). With regards to thinning competing overstory species, some research has been done on changes in growth rate for saplings and mature trees (Keane et al 2007. Wong 2012), but little research has been conducted on understory and overstory conditions that allow whitebark pine seedlings to release and advance towards reproductive maturity. Both emulation of natural fire regimes and thinning are expensive, particularly in remote regions, and benefit to whitebark pine is not guaranteed.

Release has been defined in many different ways depending on the objectives and/or field of research of the investigation (Copenheaver and Abrams 2003). Growth release in seedlings has been studied with regards to forestry applications (Kneeshaw et al 2002, Thiffault 2013) and as a means of inferring disturbance frequency or gap dynamics in old growth forests (Lorimer and Frelich 1989, Gray and Spies 1997, Stan and Daniels 2010, Brienen et al 2010). Seedlings respond to changes in resource availability (such as light) with a change in growth (Grubb 1977). An understanding of the conditions leading to growth releases can help shed light on the physiological requirements of seedlings and a clear understanding of the timing of release can enhance our knowledge of seedling growth more than overall growth rate, since seedlings that have recently released may show poor overall growth rate.

There is little current literature on the factors associated with growth release in whitebark pine seedlings. Whitebark pine are described as moderately shade intolerant (Arno and Hoff 1989) and it is likely that increasing exposure to light could result in growth release, as has been observed in many other conifer species (Oliver and Dolph 1992, Wright et al 2000, Stan and Daniels 2010). Other factors such as competition with understory species (Gray and Spies 1997) and edaphic controls (Macdonald and Yin 1999, Purdy et al 2002) on release have also been observed for other conifer species, but thus far no research has addressed changing growth rates in whitebark pine seedling cohorts. Understanding factors driving successful regeneration of whitebark pine is critical for successful restoration of this keystone species (McCaughey and Tomback 2001, Aubrey et al 2008, Keane and Parsons 2010, Keane et al 2012, Alberta Whitebark and Limber Pine Recovery Team 2014). Growth release of whitebark pine seedlings has yet to be documented in the literature but recently whitebark pine seedlings in Willmore Wilderness Park were observed to be exhibiting rapid height growth following what appeared to be long periods of suppression (J Gould, personal communication, August 30, 2012). Understanding the drivers of such growth releases in whitebark pine seedlings will contribute to the overall knowledge of the regeneration stage of whitebark pine and help land managers understand the potential effectiveness of restoration activities such as thinning the overstory, planting seedlings of a certain size or planting in certain microsites. In addition, investigating growth releases via annual vertical whorls is seldom performed and knowledge of how annual height growth is correlated to ring widths will be helpful for further research in this area.

Here I investigated microsite associates of growth release in whitebark pine. The specific objectives of my research were to:

1. Identify whether growth release is occurring in whitebark pine seedlings, and if so determine whether seedlings are releasing at different heights and if this differs among mesohabitats;
2. Examine microsite drivers that facilitate seedling release; in particular, determine the relative importance of the understory and overstory environment for release; and
3. Assess whether annual height growth is correlated with radial growth in order to assist future research in this area.

I predict that growth release in forest mesohabitats will be positively associated with canopy gaps while growth release in treeline and open mesohabitats will reflect microsite conditions that protect seedlings from solar insolation and wind desiccation. Suppression will be observed most frequently and maintained for the longest time for seedlings in forest mesohabitats.

3.3. Methods

3.3.1. Site selection

Research on the determinants of growth release in whitebark pine seedlings took place in the lower subalpine to alpine ecotones of Jasper National Park and Willmore Wilderness Park in the Canadian Rockies. Sites were chosen based on established whitebark pine health transects by Parks Canada and Alberta Parks and included a thorough representation of the whitebark pine populations in this area. In Willmore, sites occurred between 53.778566°N 119.716731°W and 53.449737°N 119.178122°W with an elevation range of 1584-2200m, while the Jasper sites were situated between 53.033953°N 118.148226°W and 11U 52.463574°N 117.421878°W with an elevation range of 1610-2263m (Appendix 1 – Figure 1). All together seven sites in Willmore and eleven sites in Jasper were sampled (Appendix 2 – Table 2). This was a subsample of the sites used to investigate characteristics of seedling density, presence and absence, and growth rate (Chapter Two) based on seedling densities within separate mesohabitats (procedure below).

3.3.2. Mesohabitat and microsite characterization

In order to determine how seedling release differs among plant communities and abiotic conditions, several mesohabitats were sampled at each site. These included: 1) mixed conifer or pure whitebark pine forest (hereafter referred to as forest); 2) open canopied areas below treeline (hereafter referred to as open); 3) treeline where conditions were much more open and tree growth tended to be more horizontal but not yet krummholz (hereafter referred to as treeline); and 4) alpine habitats at least 5m above tree islands but within close proximity to a whitebark pine seed source (hereafter referred to as alpine). Due to our seedling sampling regime (described below), there were relatively few replicates of the treeline and alpine mesohabitats. These two habitats were therefor combined into one category hereafter referred to as the alpine – treeline ecotone (ATE).

Linear transects – mostly 100m long – established within relatively homogeneous conditions representative of the mesohabitat were used to characterize each mesohabitat. Transects were broken up into 20m segments; at the first whitebark pine seedling within 1 m of the transect a 1m x 1m microsite plot was established (the "occupied" microsite plot in Chapter 2); one microsite plot per segment, up to five per transect was established.

Larger scale environmental variables measured for each transect included: slope, aspect, soil pH, moisture regime, nutrient regime, mesotopographic position (such as crest, upper slope, midslope, depression and toe) and minimum forest age. Biophysical variables measured in each microsite plot included: organic layer depth, litter depth, canopy cover, tree basal area, and percent cover for ground cover types (moss, lichen, rock, mineral soil, litter and cryptogammic crust) and for all vascular plants to species. I then summed percent cover of all species (total understory vegetation cover) and by functional group as follows: trees (total cover of individuals of all tree species >1.4m in height found in microsite plot), seedlings (all conifer species other than whitebark pine <1.4m in height), graminoids (grass, sedge and rush species), forbs (broadleaf, herbaceous vascular species), prostrate shrubs (<5cm in height), and upright shrubs (>5cm height). Details on the recording of mesohabitat and microsite variables can be found in Chapter Two of this thesis.

3.3.3. Seedling selection

In order to determine annual growth rates and calculate the change in those rates over time, seedlings were destructively sampled and analyzed within the lab (done under the authority of Alberta Tourism, Parks and Recreation permit number 13-073). I used population-based sampling to ensure that the destructive sampling conducted did not result in undue harm to current whitebark pine populations. During the mesohabitat characterization of each transect (Chapter Two), the number of seedlings within 2m of either side of the transect line was counted. On this basis, I set a criteria that no more than 10% of the seedlings located along a transect would be destructively sampled up to a maximum of five seedlings per transect. In the event that 50 or more seedlings were found along a transect, the focal seedling located in the occupied microsite plot was removed for later analysis. If fewer than 50 seedlings were counted along each transect only a subsample of seedlings was taken (for example, if 40-49 seedlings were found, focal seedlings in segments 1-4 were destructively sampled; if 30-39, focal seedlings in segments 1-3 were sampled). If the focal seedling in a microsite plot was a clump of seedlings, the largest seedling in the clump was removed. For each seedling I recorded height, age, clump size and health (categories were: healthy (H), infected with *Cronartium ribicola* (I) and uninfected but unhealthy (U)). Seedlings were cut at ground level using pruning shears. Height was measured from the ground to the terminal bud of the tallest seedling leader and age was determined by counting annual growth whorls along the stem.

3.3.4. Seedling analysis

In order to determine whether a seedling had released or not, the height growth represented by the distance between each annual growth whorl (referred hereafter as whorl) was measured, the age of the seedling based on whorl counts was subsequently verified by tree ring analysis and each whorl was then assigned to a particular age (and year). The length between whorls was measured with calipers to the nearest tenth of a mm. Measurements were made starting at the top of the seedling and the growth for each year was recorded. If the whorls became difficult to identify, the length from the nearest identifiable whorl to the root collar was measured. Then cross-sectional cuts of the stem ("cookies") were removed at the point at which whorls became hard to identify and at the root collar and prepared for dendrochronological analysis in order to verify whorl counting and determine the final age of the seedling. Seedling cookies were sanded with successively finer sandpaper until smooth and the rings were as clearly visible as possible. The rings were then counted using a dissecting microscope (10x magnification) while the radial width of each ring was measured by scanning each cookie with a high definition scanner (Epson Perfection V750 PRO) and then using the software package CooRecorder (ver. 7.8, Cybis Elektronik and Data AB, Mousseau et al 2012).

3.3.5. Release criteria

Growth releases have been defined in many different ways and used for many different purposes (Copenheaver and Abrams 2003, Black and Abrams 2003). In this investigation, seedlings were grouped into three different release categories: 1) seedlings were considered suppressed if annual height growth of the seedling never exceeded 15 mm/year and the seedling at no time experienced an obvious “release event”, which was defined as a doubling of growth above 10 mm/year which was subsequently maintained at that increased rate (Lorimer and Frelich 1989); 2) seedlings were considered released if the seedling experienced an obvious “release event” (as defined above); 3) seedlings were considered irregular if they had periods of high growth mixed with periods of poor growth. For each seedling in the “released” category, the year in which they released was identified and the height prior to release recorded.

In addition to assignment of seedlings to these release categories and determination of the year of release for the released seedlings, the average annual height growth from 2007-2012 was calculated for each seedling (hereafter referred to as recent growth). These years were used because there is a higher degree of certainty in the measurements for recent growth years and because there would be a higher degree of separation in recent growth versus overall growth between seedlings that have released and seedlings that are suppressed. The growth in 2013 was omitted as seedlings were collected during different times throughout June-August of 2013 and not all would have completed growth at the time of sampling.

3.3.6. Data analysis

All analyses were conducted using the statistical software R (R Core team 2013).

Analysis of variance (ANOVA) was used to determine whether there were significant differences (α=0.05) in recent growth between suppressed, irregular and released seedlings for each mesohabitat; recent growth of released seedlings among mesohabitats; mean canopy cover and understory cover (refer to Table 2.2 for definitions of canopy and understory cover) for released and suppressed seedlings in forest mesohabitats, and mean understory cover for released and suppressed seedlings in open and ATE mesohabitats; the mean height of released seedlings at the time of release among mesohabitats; and the mean height of released seedlings at the time of release versus the current mean height of suppressed seedlings for each mesohabitat. Tukey's HSD experiment-wise adjustment of α was used for any post hoc tests. I examined the linear relationship between current height and recent growth for each mesohabitat to determine whether recent growth for a given size differed between mesohabitats.

Regression trees were used to identify microsite and mesohabitat characteristics (Table 2.2) that were associated with a seedling being suppressed or released. Age was also included in order to determine whether release was occurring predictably within mesohabitats and to remove those seedlings that had not released simply due to their age.

Pearson correlation analysis was conducted to determine whether annual radial ring widths were correlated with annual height growth. I examined correlations between annual radial rings width and annual height growth for all years of all seedlings, all years for seedlings that had whorl counts that were validated (within 20%) by radial ring counts, and recent growth (2007-2012) for all seedlings.

3.4. Results

3.4.1. Release criteria

The release criteria used in this investigation led to three well defined groups of seedlings categorized as “released”, “suppressed” and “irregular”. Released seedlings were characterized by an obvious inflection point in their cumulative height curve at which point growth obviously doubled, while suppressed seedlings had steady growth that did not increase substantially over time (Figures 3.1, 3.2, 3.3). In forest mesohabitats eight seedlings (16.7% of the total for forest mesohabitats) were released while 26 seedlings (54.2%) were suppressed. In open mesohabitats 28 seedlings (43.8%) were released and 23 seedlings (35.9%) were suppressed. In alpine-treeline ecotone (ATE) mesohabitats 15 seedlings were released (40.5%) compared to 13 suppressed (35.1%).

Not surprisingly, average annual growth in the last six years was much higher in released seedlings than in suppressed seedlings (Figure 3.4). In forest mesohabitats the average recent growth of released seedlings was 3.25cm/year – 8.6 times that of suppressed seedlings. The average growth of released seedlings in open mesohabitats was 3.21cm/year which was 6.8 times that of suppressed seedlings. Finally, released seedlings in the ATE had an average recent growth rate of 2.83cm/year – 8.1 times that of suppressed seedlings.

3.4.2. Recent growth and release height

Average recent growth rates for released seedlings didn't differ significantly among mesohabitats (Fig. 3.4). However, recent growth for a given height of seedling was much greater in open and ATE mesohabitats than it was in forest mesohabitats (Figure 3.5); slopes (and standard errors) were 0.056 (0.0040), 0.058 (0.0057) and 0.038 (0.0037) respectively. This might be explained in part, by significantly lower release heights in open and ATE environments compared to the forest mesohabitat (Figure 3.6). In forest mesohabitats the height of seedlings at the time of release was 185.9mm, which was significantly greater than the release height in open mesohabitats (105.6mm) and ATE mesohabitats (86.9mm) (Fig. 3.6). The average height of released seedlings at the time of release was significantly different from the current height of suppressed seedlings in open and ATE but not in forest mesohabitats.

3.4.3. Microsite drivers of release

Simple univariate analyses of factors that might lead to suppression or growth release demonstrated that canopy cover and understory vegetative cover were significantly different in forest microsites with released seedlings compared to suppressed or irregular seedlings (Figure 3.7). Mean canopy cover for released seedlings in forest mesohabitats was 14.9% which was less than one third that of suppressed and irregular growing seedlings. In contrast, mean understory vegetative cover for released seedlings in forest mesohabitats was 62.6%, which was about twice that of suppressed and irregular seedlings (Fig. 3.7). There were no significant differences in mean understory vegetative cover between microsites with released, suppressed and irregular seedlings in open and

ATE mesohabitats; all values fell between 40 and 50% cover (Figure 3.8). Canopy cover values in open and ATE mesohabitats were not analyzed as both were near zero.

The regression tree constructed to examine factors associated with suppression versus release in forest mesohabitats (Figure 3.9) further supported the results of the univariate analyses. Canopy openings appear to be the most important determinant of seedling release in forest mesohabitats. Microsite plots with less than 10.4% canopy cover all had seedlings that had shown release. Secondarily, the results suggested that if the microsite is conducive to understory vegetation it was also conducive to seedling growth release. For microsites with greater than 10.8% canopy cover, 96% of seedlings found in plots with less than 68.2% understory vegetative cover were suppressed in contrast to the plots with > 68.3% cover, in which all seedlings were released. The vegetation that was primarily growing along with these released seedlings were upright and prostrate shrubs (Appendix2 Table 4A).

In contrast to the results for forest mesohabitats, understory cover did not govern suppression and release in open mesohabitats. Cover of rock was the most important factor related to release in open mesohabitats; microsite plots with > 22.5% rock cover had released seedlings 82% of the time. For plots with less rock cover, age was an important factor in seedling release. The majority of seedlings older than 32 years had released (83%) while the majority of those seedlings under the age of 32 had not yet released (61%). For seedlings less than 32 years old, there were two plots with litter depth > 1.75 cm that had two released seedlings while 71% of plots with lower litter depth had suppressed seedlings. Throughout the regression tree there were many alternate splits that appeared to be directly opposed to the splits found in forest mesohabitats

(Appendix 2 – Table 4B). In forest mesohabitats seedlings were releasing in locations with high vegetation cover made up of functional groups such as prostrate and upright shrubs, graminoids and forbs. In open mesohabitats all of these groups are negative influences on seedling release in the first two splits.

Seedling age was the most important factor determining release in the alpine-treeline ecotone mesohabitat (Fig. 3.11). No seedlings less than an average of 6.5 years showed release. For seedlings older than this it appeared as though protection from harsh conditions increased the probability of release. Specifically, plots with higher cover (>11.6%) of prostrate shrubs mostly had released seedlings (87 %). Vegetation cover in general was important in plots with lower cover of prostrate shrubs. For these plots, there were three plots with vegetation cover < 27.6% and all three had suppressed seedlings whereas in the three plots with > 27.6% vegetation cover two had released seedlings.

3.4.4. Correlation between diameter and height growth

Annual ring width and annual height growth were positively correlated ($r^2 = 0.687$). Recall that only those seedlings where the whorl count was well validated (within 20%) were used in this analysis and the most recent year of growth (2013) was removed, as the growing year was not yet complete. Certainty in ring and whorl measurements should be the highest in the most recent years of growth.; an analysis of the correlation between ring widths and the distance between whorls for only the most recent six years of growth showed a similar correlation ($r^2 = 0.681$).

3.5. Discussion

3.5.1. Growth release in whitebark pine seedlings

Growth releases have been defined in many different ways depending on the objectives and/or field of research of the investigation (Copenheaver and Abrams 2003). I defined growth release as a sustained doubling of growth above 10 mm/year. Figures 3.1-3.3 illustrate that this criteria results in a reasonably clear categorical distinction between released and suppressed individuals. Inflection points in released seedlings and reduced growth in suppressed seedlings seem to suggest that the criteria I used resulted in a good reflection of released and suppressed seedlings.

Prior to this study there was no published literature indicating whether or not whitebark pine seedlings have the ability to survive long periods of suppression yet still release upon an introduction to improved environmental conditions or resource availability (Keane et al 2007). Figures 3.1D, 3.2D and 3.3D all show the existence of individual seedlings that grew at less than 10 mm/ year for approximately 20 years before eventually releasing and growing well above 15 mm/year. This suggests that advanced regeneration may have the ability to release following long periods of suppression and that overstory thinning could be effective in promoting their growth. However, more direct research such as monitoring seedling release for a period of time or following an experimental reduction in canopy density is needed to further verify this and to determine the longer-term fate of released seedlings.

Recent growth of released seedlings was an average of 8.6, 6.8 and 8.1 times greater than their suppressed counterparts in forest, open and ATE mesohabitats, respectively. This reinforces the importance of determining how and why release occurs since developing approaches that can facilitate release growth could have important implications for growth of seedlings and development of mature whitebark pine stands. Released seedlings may be more likely to reach reproductive maturity and certainly more quickly than suppressed or irregular growing seedlings. By facilitating release growth in cohorts of seedlings that have been exposed to blister rust we could promote the establishment of blister rust resistant populations (Schoettle and Sniezko 2007). This may well generate a positive feedback loop of increasing genetic resistance to blister rust if blister rust resistant individuals reproduce and further distribute seedlings that have innate resistance to white pine blister rust.

3.5.2. Recent growth and release height

Seedlings in the alpine-treeline ecotone (ATE) and open mesohabitats were growing faster at given heights than seedlings in forest environments (Figure 3.5). In the subalpine zone, trees occur where soils are well developed and climate conditions allow for upright growth forms (Körner 2003). Access to below ground resources typically increases growth rates (Canhamm et al 1996, Poorter and Nagel 2000), particularly when light is available (Huante et al 1998, Barberis and Tanner 2005). Thus I expected that if light is available in forest environments, seedlings that have released would be growing faster there than in other mesohabitats because they would have access to the most nutrient rich and moisture abundant soils, but this wasn't the case. The pattern of growth in forest mesohabitats shows that even large, released seedlings are growing more slowly than released seedlings in open and ATE mesohabitats. Low replication (8 replicates) of released forest seedlings may have led to an inability to observe growth patterns. This low number of released seedlings, however, is likely reflective of the likelihood of release in the forest mesohabitat than a sampling artifact. In ATE and open habitats, released seedlings made up a much higher proportion of the total number of seedlings sampled than in forest mesohabitats; this suggests that release is simply much more likely in open and ATE.

The fact that height at the time of release in forest mesohabitats was much larger than in open and ATE mesohabitats (Figure 3.6) points to the importance of light availability in allowing for seedling release. Whitebark pine is moderately shade intolerant (Arno and Hoff 1989) and both open and ATE mesohabitats have much higher light availability than does the forest mesohabitat; this can help explain the earlier (shorter) release of seedlings in the former two mesohabitats. Even if overhead canopy cover in some microsite plots in the forest is comparable to that found in the two more open mesohabitats (open and ATE), forest areas are likely experiencing less total light because of shading from the sides or from more dense, taller understory cover. Understory vegetation cover was measured below 1.3m in height and no effort was to measure cover at other heights. It has been shown that when a resource is scarce, plants will devote more of their resources to tissues needed to acquire that resource (Canhamm et al 1996, Poorter and Nagel 2000). Thus, it is likely that seedlings in forest environments are allocating a greater proportion of resources to shoot growth, in which case the differences in height growth between forest and the two more open (open and ATE) mesohabitats is likely even more significant.

The fact that mean height of released seedlings at the time of release was greater than the mean height of suppressed seedlings at the time of sampling for all mesohabitats (though not significant in forest) supports the existence of size criteria at which release is possible. This may be significant for informing recovery activities in whitebark pine habitat such as overstory thinning. If a size threshold for release exists efforts should be made to ensure that advance regeneration is of appropriate size to utilize increased light availability.

Size, however is unlikely to be the sole factor regulating release growth. Below-ground development occurs alongside above-ground growth and microsite conditions will also impact a seedling's ability to reach a certain size. Shade intolerant seedlings that are held in a suppressed state for a long time are more likely to die than to release (Walters and Reich 1996, Kobe and Coates 1997). Further, mortality in open and ATE mesohabitats is more likely in microsites without sufficient protection in early seedling stages (Tomback et al 1993, Izlar 2007, Chapter 2). Rooting development is also important for long-term growth and survival and establishment of mycorrhizal relationships may initiate rapid growth (Read and Perez-Moreno 2003). Mycorrhizae native to whitebark pine systems have been discovered and found to improve seedling survival in greenhouse trials (Cripps and Grimme 2011, Cripps and Antibus 2011). This investigation did not look into below ground responses, nor did it examine mortality over time. Further work is needed to determine how the rooting structure of whitebark pine seedlings affects above ground growth release and how long whitebark pine seedlings could remain suppressed without mortality.

3.5.3. Microsite factors associated with release

The importance of light availability for release is repeatedly highlighted in our results. Released seedlings in forest mesohabitats were located in significantly more open microsites (Figure 3.7), canopy cover was the primary driver for release in forest mesohabitats (Figure 3.9) and, as previously mentioned, a far greater percentage of seedlings were found as released in open and ATE mesohabitats than in forest mesohabitats. For the majority of tree species, light availability is the primary determinant of growth release in forest environments (Oliver and Dolph 1992, Kneeshaw et al 2002, Barberis and Tanner 2005, Stan and Daniels 2010). Light availability is important for release in saplings and mature trees of whitebark pine (Keane et al 2007, Wong 2012) but ours is the first documentation of it as a driver of growth release in the seedling stage.

Interestingly, average understory vegetation cover was not different between microsites with released versus suppressed seedlings in open and ATE mesohabitats although it was greater for released seedlings in forest mesohabitats. This was initially surprising, as below-ground competition and light interception likely both negatively affect seedling vitality. However, this result can be explained by the fact that understory vegetation flourishes where the growing conditions are also favorable for whitebark pine seedlings, such as in canopy gaps in forested environments. Further, in open and ATE habitats understory vegetation cover results in protection from wind desiccation and high solar insolation, which may counter possible negative impacts of competition in these more open mesohabitats. More research investigating the effects of plant interactions on growth, release and survival by directly manipulating the surrounding plant community needs to be done.

Multivariate analysis of microsite drivers showed that differing affects of nearby vegetation are occurring in open and ATE mesohabitats. In open mesohabitats released seedlings were associated with more open, rocky terrain rather than with understory vegetation (Figure 3.10), while the opposite appeared to be the case in the ATE mesohabitats. Rock cover as a nurse object has been shown to be beneficial in other studies of microsite effects on whitebark pine survival and growth (Tomback et al 1993, Resler and Tomback 2008). Izlar (2007) found that in open areas, seedling growth was poorest when planted near snags, live trees or shrubs and best when planted near logs, downed trees or rocks. She attributed poor growth in those selected microsites to a potential competition effect of nearby vegetation. It was only in the open mesohabitat that I observed an apparent negative effect of adjacent vegetation on whitebark pine seedlings. In the ATE mesohabitat, release for seedlings over a certain age was associated with greater cover of prostrate shrubs and more vegetation cover in general. Prostrate shrubs in alpine environments help to hold moisture, dampen changes in soil temperature and alleviate wind speeds (Körner 2003). Outplanting of whitebark pine seedlings will need to consider both the mesohabitat and microsite type within it. In ATE mesohabitats, microsites with ground cover shrubs such as *Dryas octopetela* (L.)*, Vaccinium uliginosum* (L.) or *Cassiope tetragona* (L.) D. Don should be targeted while vegetation cover in general likely needs to be avoided in open mesohabitats. Unfortunately the distinction between open and ATE mesohabitats will occasionally become blurred, as open areas below treeline may be open due to alpine-like abiotic conditions. In this study I did not determine the cause of open areas below treeline; further investigation of this in future studies could provide better insight into the complex combined influence of mesohabitats and microsites within them.

Release of seedlings in ATE and open mesohabitats appeared to be much more predictable than release in forest mesohabitats. Age was a primary microsite driver of release in both ATE (Figure 3.11) and open (Figure 3.10) mesohabitats but not in forest (Figure 3.9). Further, the release height of seedlings in open and ATE mesohabitats was significantly greater than the current height of suppressed seedlings while this was not the case in forest mesohabitats. It may be that in forest mesohabitats, increased canopy cover prolongs suppression but higher soil nutrients and moisture and less desiccation from sun and wind allow seedlings to survive in a suppressed state for longer than in the other mesohabitats where light might be higher but these other conditions are less favourable.

Seedlings showing irregular growth were found in similar canopy conditions to suppressed seedlings. Irregular seedlings tend to be larger on average than the suppressed seedlings and have experienced episodic growth. This may be due to intermittent exposure to sunlight or short-term improvement in environmental conditions or availability of below-ground resources. Further research examining the causes of alternating patterns of growth release and suppression could provide further insight into how and why seedlings are releasing.

3.5.4. Correlation between diameter and height growth

The correlation between ring width growth and annual height growth (distance between whorls) was not as high (0.687), given that these two response variables should be influenced directly by the same biophysical factors. There are several possible reasons for the lower-than expected correlation. Cross validation of the ring measurements was not a priority of this investigation so little time was spent ensuring ring counts were perfect and techniques that such as cross-dating against master chronologies (Fritts and Swetnam 1989) were not utilized. Many samples had incredibly little height growth per year and many samples had incredibly faint, tight growth rings that made measuring difficult. However, when I reduced the data to only growth between the years of 2007-2012 (where you would expect the highest degree of accuracy) and to those samples where the age based on whorl counts was quite close to that using ring counts the age height correlation did not improve. This suggests that it is unlikely to be fully due to problems with the accuracy of measurements.

The lower-than expected correlation can be attributed to the effects of growth suppression. Whitebark pine seedlings appear able to survive even when they are putting on almost no growth in a given season and may be held suppressed for a few years without a long-term negative effect. In addition, harsh subalpine conditions may lead to radial growth with little height growth or vice versa. There is no record in the literature that I am aware of on the correlation between ring width and height growth for whitebark pine. Further analysis on this topic may allow researchers to be more certain of in-field aging techniques and lessen the need for destructive sampling of this endangered species in the future.

3.6. Conclusions

Growth release is occurring for whitebark pine seedlings. This is the first time that release has officially been documented for whitebark pine seedlings and will help to better inform restoration practices such as prescribed fire and canopy thinning.

Sunlight availability is paramount to release. Growth release is occurring more frequently and at lower heights for seedlings in open and ATE as opposed to forest mesohabitats and is only occurring in canopy gaps in forest environments. However microsite effects are still important in release and these differed between mesohabitats. Release occurred apart from competing vegetation in association with rock, and along with vegetation in ATE. Outplanting of whitebark pine seedlings should focus on open environments but ensure microsites appropriate for the mesohabitat are identified.

There are several recommendations for further research that arose from this study. Long term monitoring of released seedlings should commence to determine whether released growth rates are maintained and result in earlier reproductive maturity. More research is needed on the effects of understory cover on release. Released seedlings were associated with understory cover in forest and ATE mesohabitats but direct manipulation of the plant community will inform us whether this is an artifact of the greater environmental context or a facilitative effect of understory cover. Finally, investigation into the effects of below ground growth and mycorrhizal associations on growth release help to better understand this process and help inform planting and environmental manipulations that will better promote whitebark pine growth.

3.7: Figures

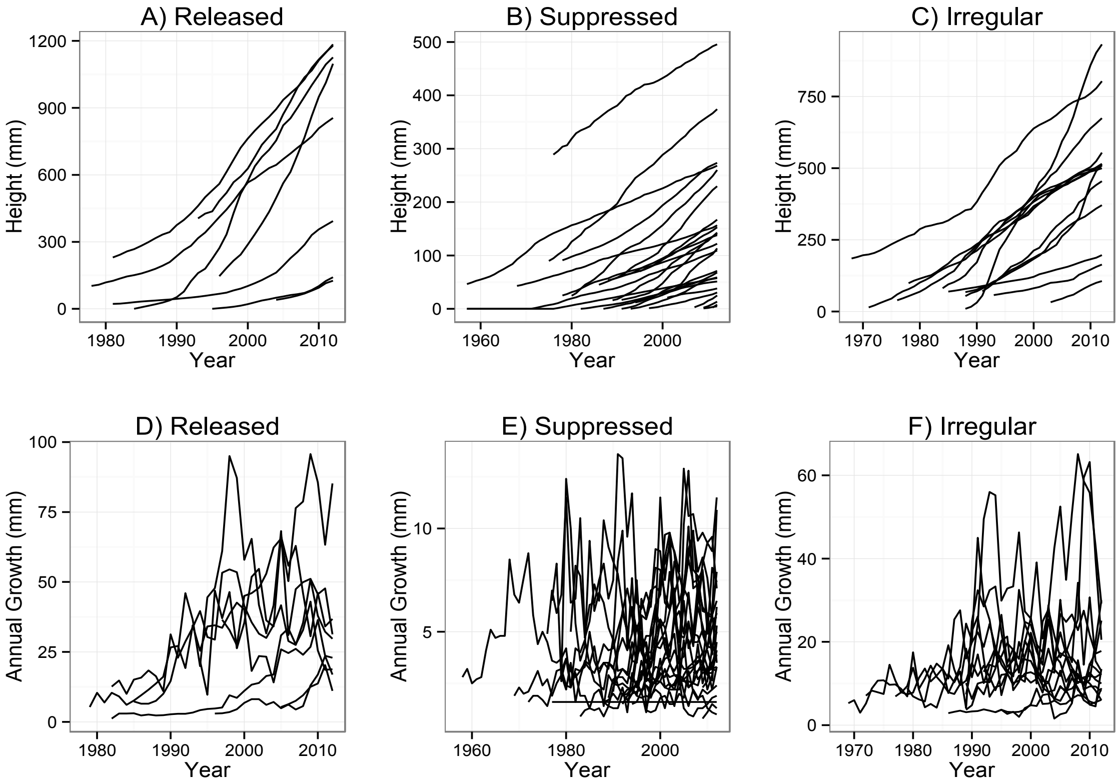

Figure 3.1: Cumulative and annual height growth in forest mesohabitats for whitebark pine seedlings that were categorized as released (A, D, n=8), suppressed (B, E; n=26), or irregular (C, F; n=14). Note differences in scale of y-axis.

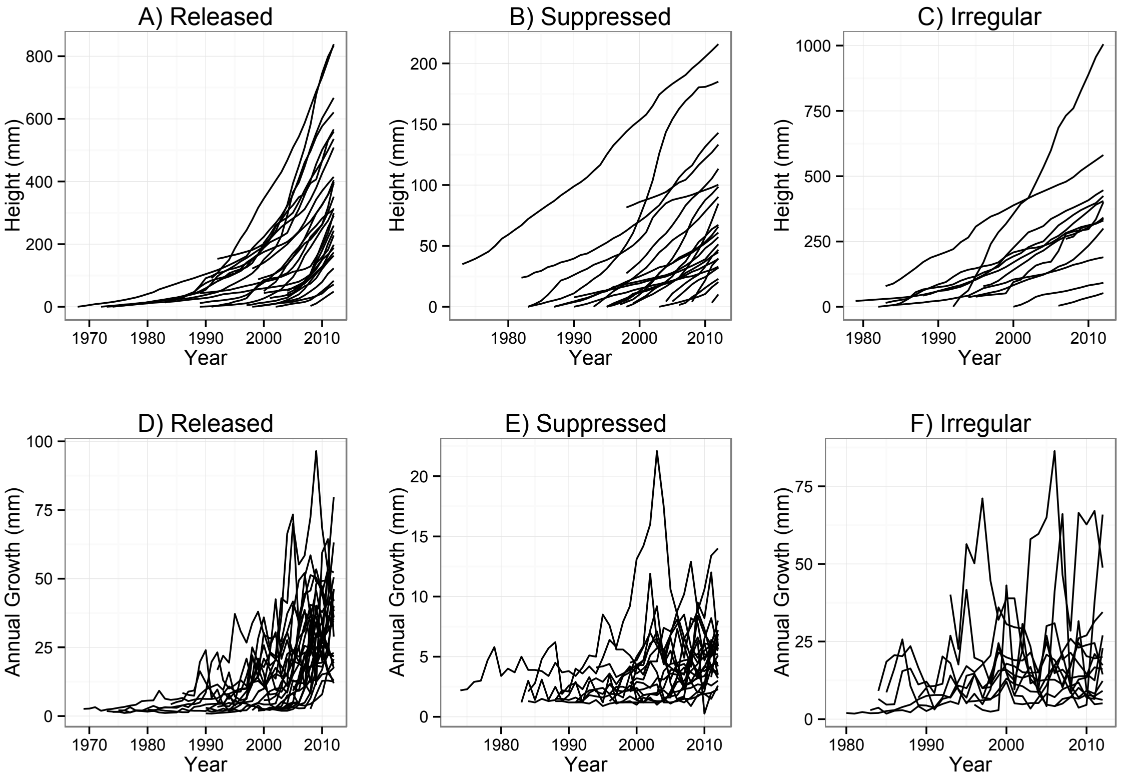

Figure 3.2: Cumulative and annual height growth in open mesohabitats for whitebark pine seedlings that were categorized as released (A, D, n=28), suppressed (B, E; n=23), or irregular (C, F; n=13). Note differences in scale of y-axis.

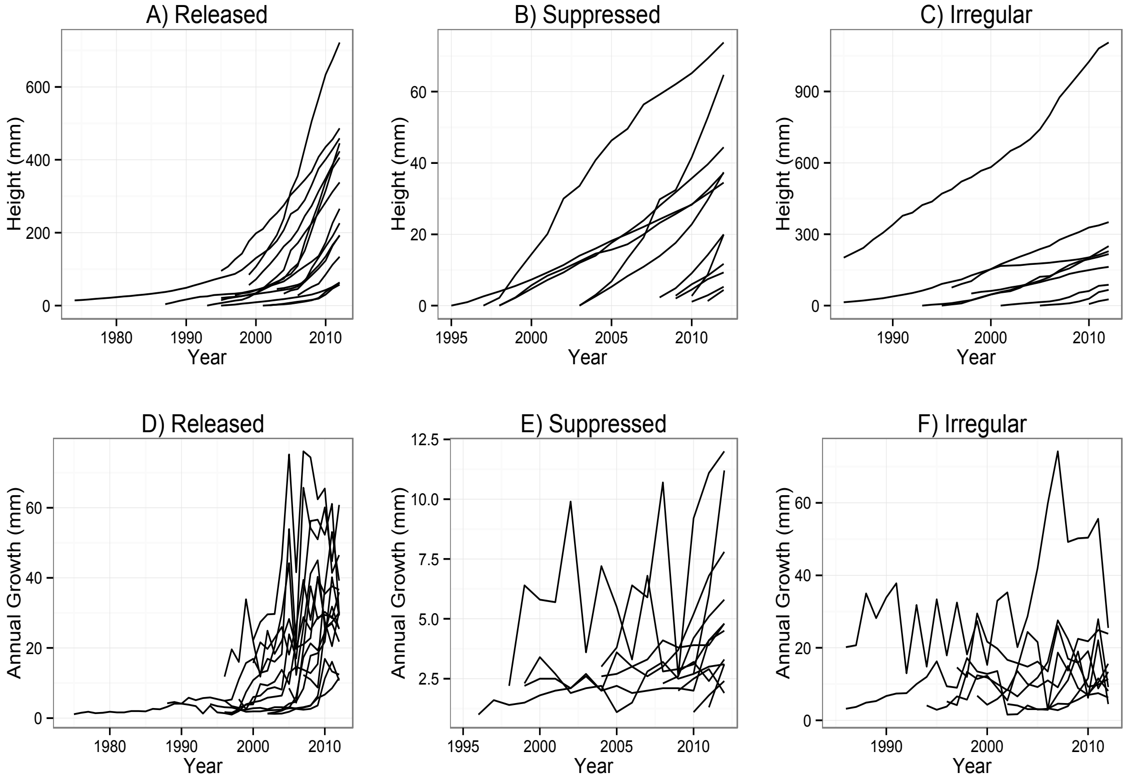

Figure 3.3: Cumulative and annual height growth in alpine-treeline ecotone (ATE) for whitebark pine seedlings that were categorized as released (A, D, n=15), suppressed (B, E; n=13), or irregular (C, F; n=13). Note differences in scale of y-axis.

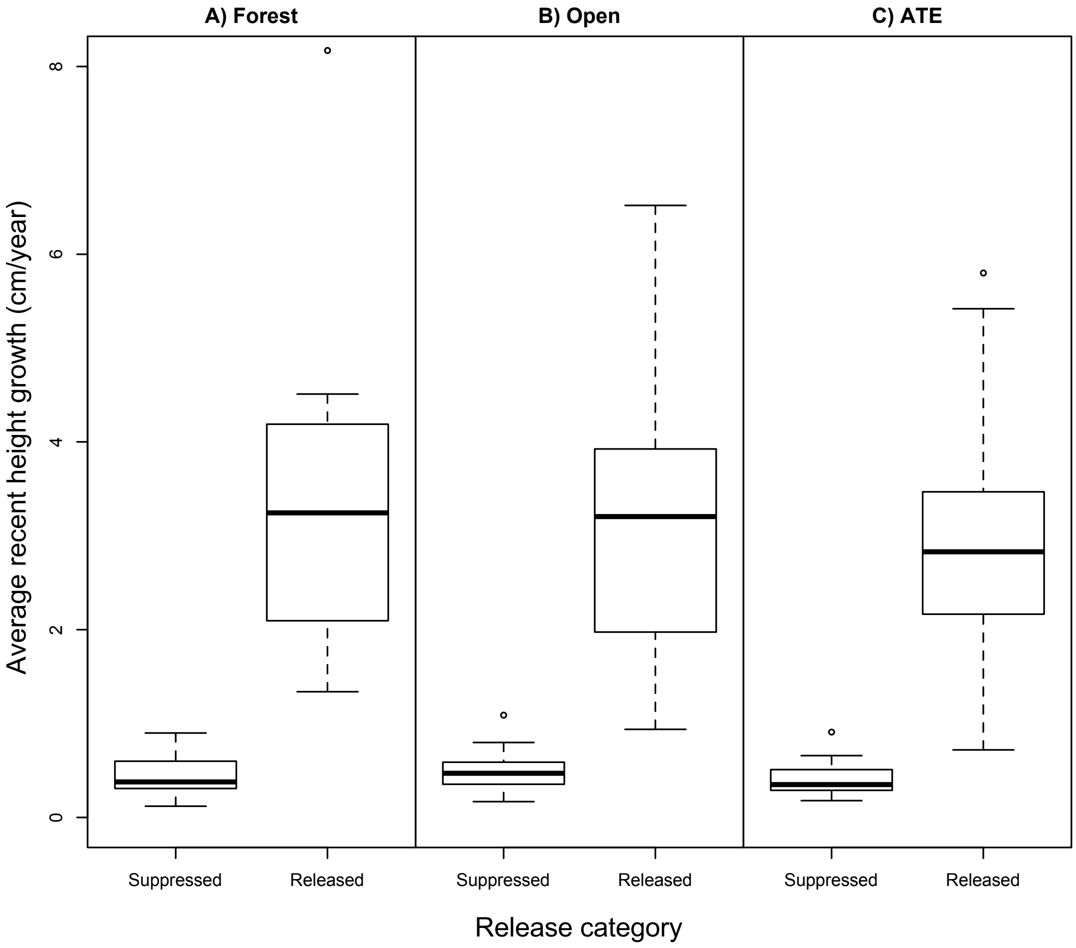

Figure 3.4: Average recent height growth (annual average for last six years (2007-2012)) for suppressed and released seedlings in A) forest; B) open; and C) alpine-treeline ecotone (ATE) mesohabitats. The bold line represents the group mean, boxes include the 25-75% range, whiskers are the 5th and 95th percentiles, and points are outside that range. For each mesohabitat, released seedlings exhibited significantly greater growth than suppressed at α=0.001 while for average annual growth of released seedlings there is no significant difference among mesohabitats.

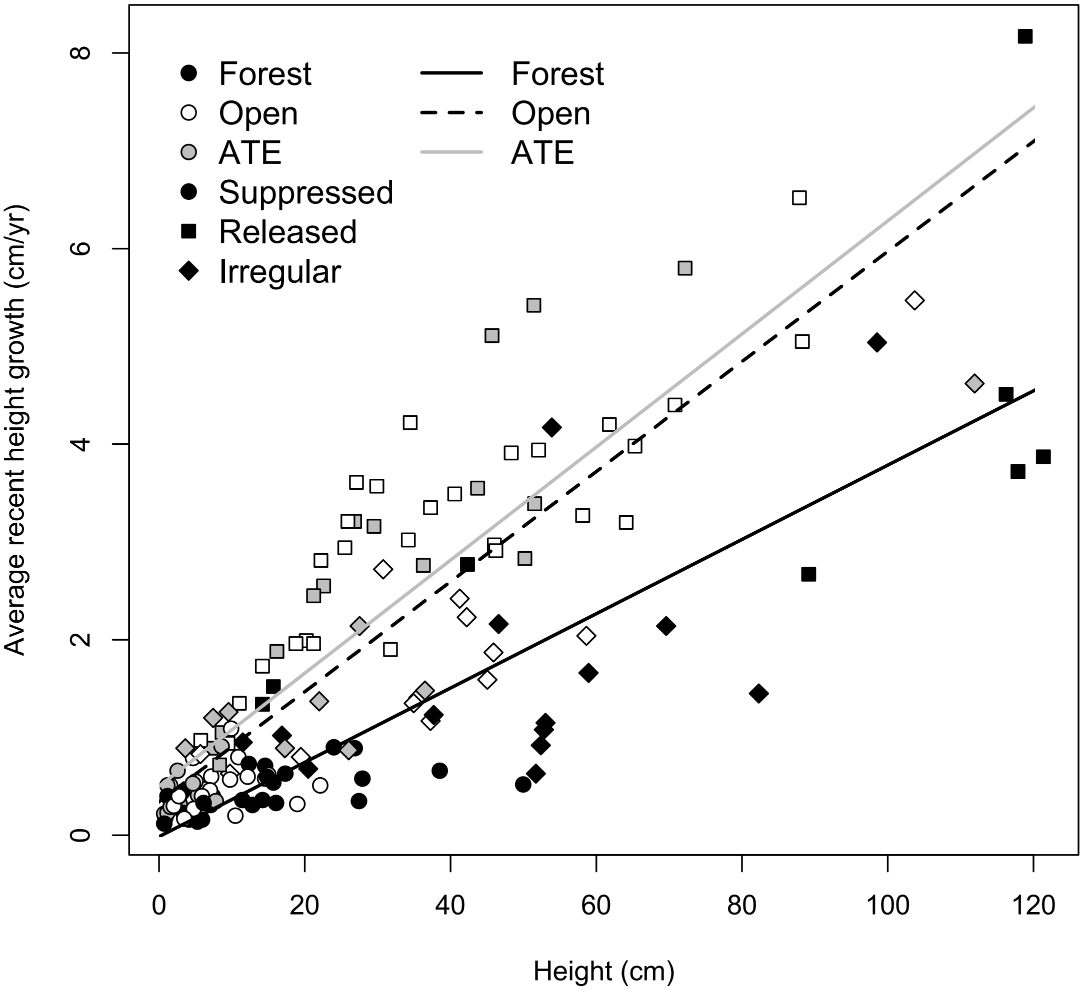

Figure 3.5: Linear relationship between recent height growth (annual average for last six years; 2007-2012) and current height for seedlings in forest, open and alpine-treeline ecotone (ATE) mesohabitats. Linear models are based on all seedlings in each mesohabitat.

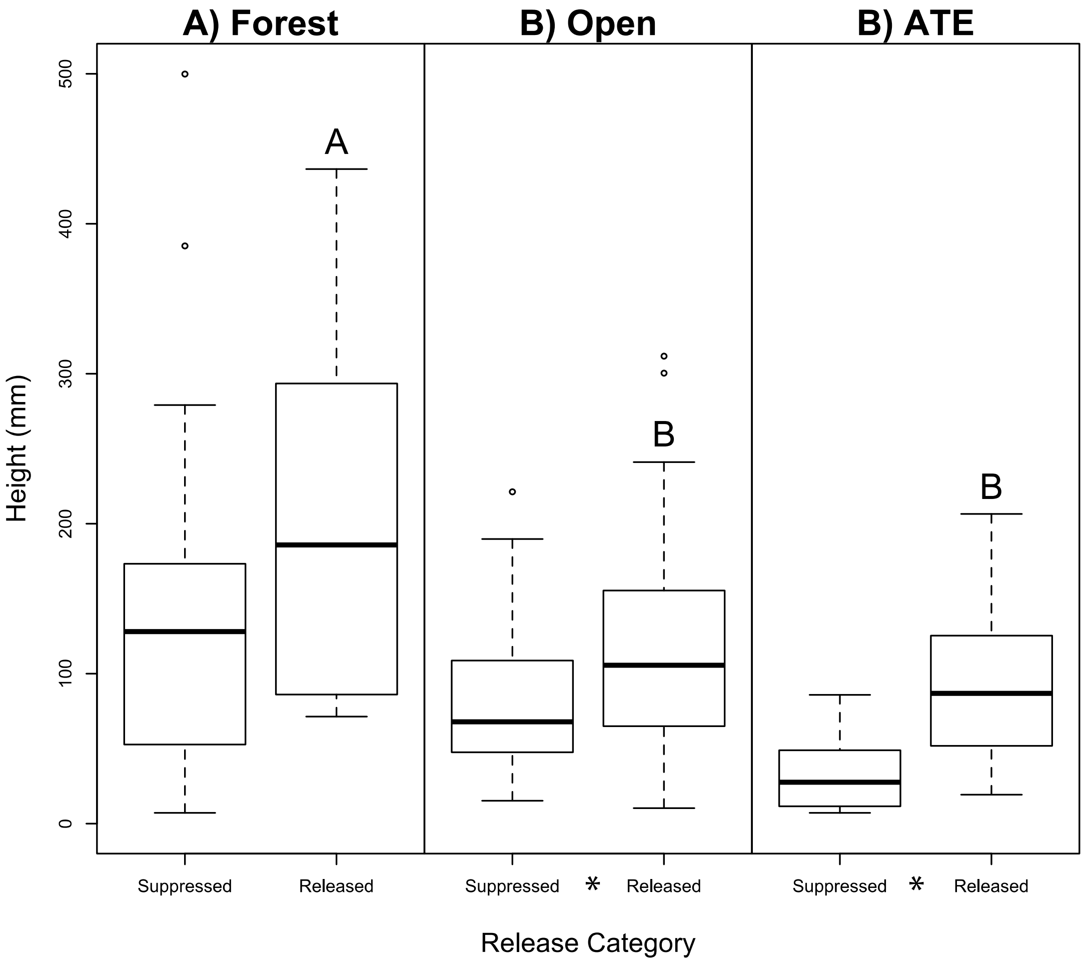

Figure 3.6: Comparison between the average height of released seedlings at the time of release to the current (2013) height of suppressed seedlings for each mesohabitat; *on the x axis labels indicates that the mean height of released seedlings was significantly greater than the current mean height of suppressed seedlings for that mesohabitat (at α=0.05). Different letters above the bar for released seedlings indicate significant differences among mesohabitats for the mean release height (Tukey HSD adjusted α=0.05) Refer to 3.4 for an explanation of box and whiskers.

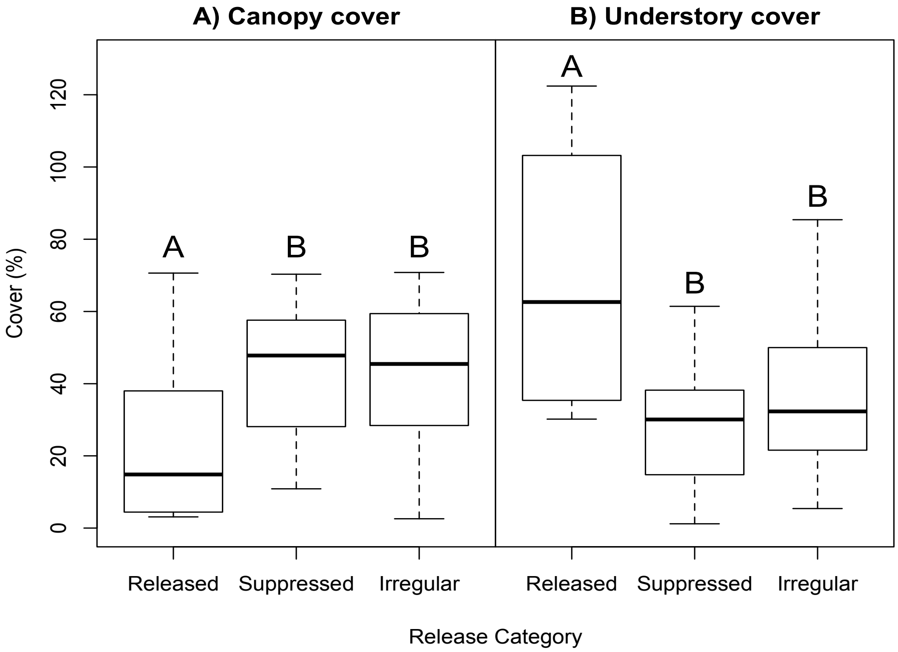

Figure 3.7: Average A) canopy and B) understory vegetative cover for released, suppressed and irregular whitebark pine seedlings in forest mesohabitats. Different letters for a given response variable indicate significant differences among seedling categories (Tukey HSD adjusted α=0.05). Refer to 3.4 for an explanation of box and whiskers.

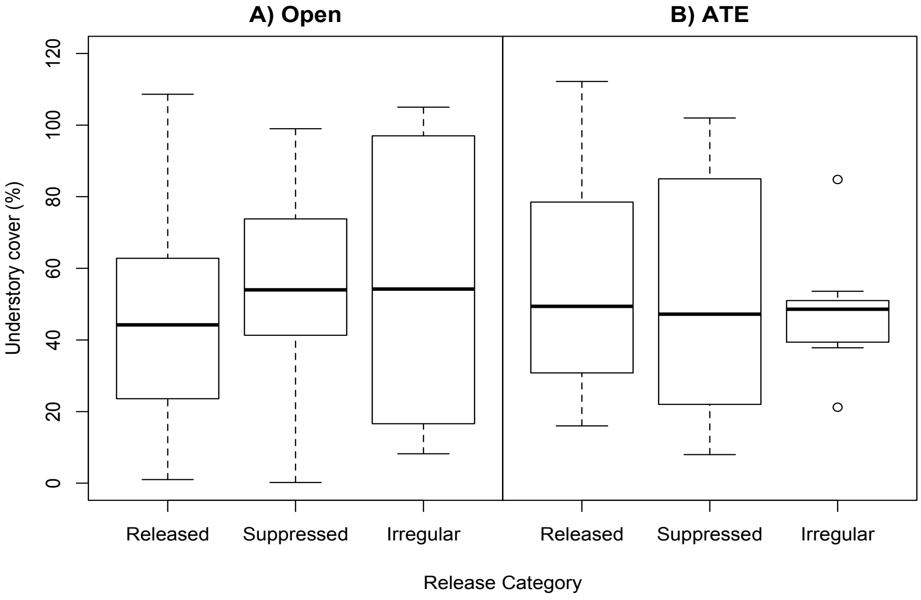

Figure 3.8: Average understory vegetative cover for released, suppressed and irregular seedlings in A) open and B) ATE mesohabitats; there were no significant differences among seedling release categories within each mesohabitat (Tukey HSD adjusted α=0.05) Refer to 3.4 for an explanation of box and whiskers.

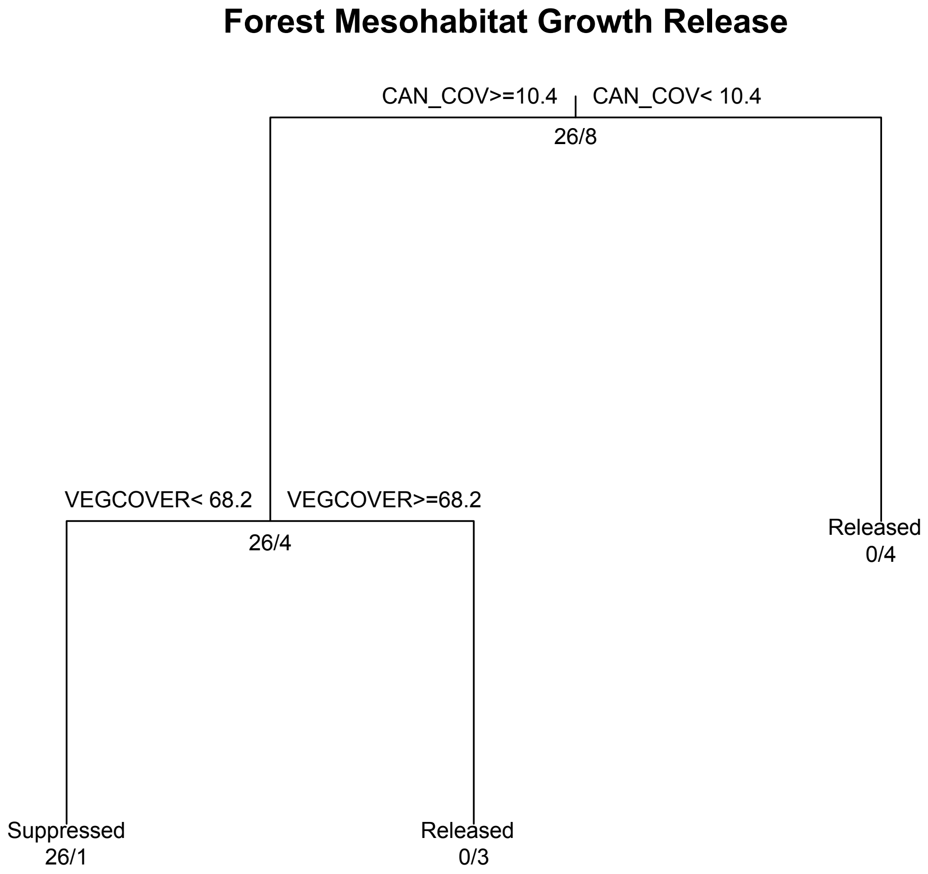

Figure 3.9: Results of regression tree analysis showing the drivers of whitebark pine seedling release in forest mesohabitats. Numbers underneath each node represent the ratio of suppressed to released seedlings; a split to the right represents increased seedling release while a split left is towards increased seedling suppression. The sum of both numbers is the total number of replicates (seedlings) at that node. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 4. Unexplained error was 0.125. Only primary splits with a complexity parameter of 0.10 or greater are shown.

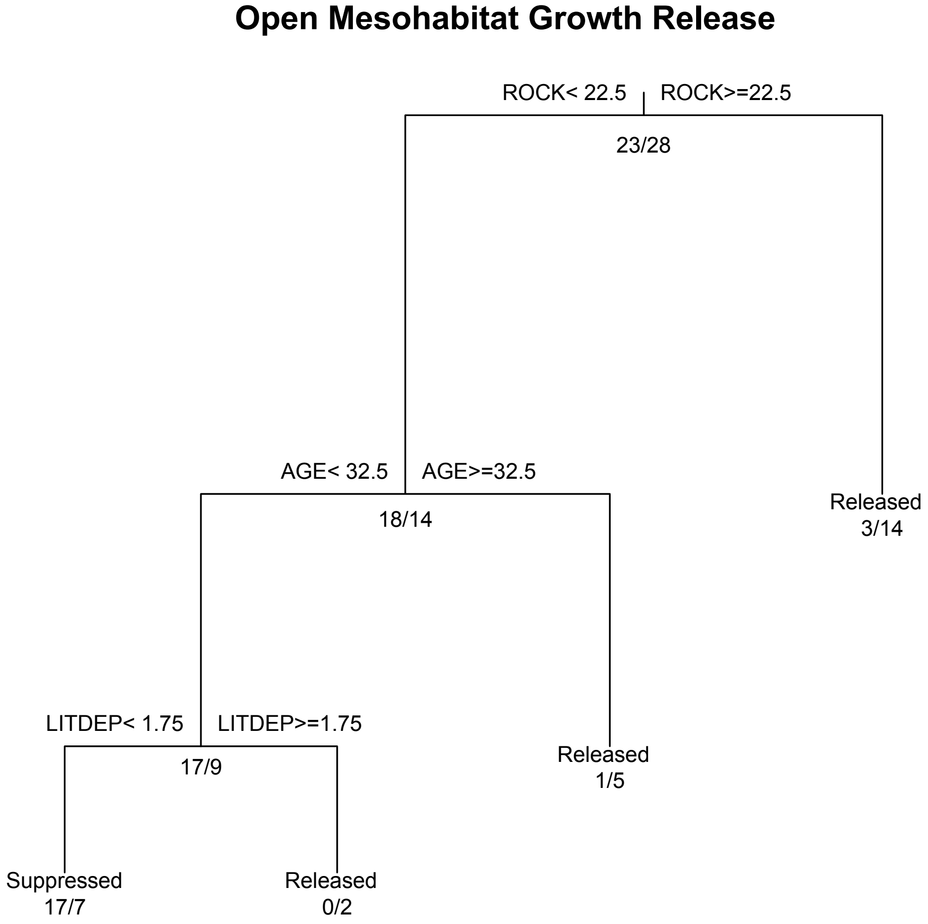

Figure 3.10: Results of regression tree analysis showing the drivers of whitebark pine seedling release in forest mesohabitats. Numbers underneath each node represent the ratio of suppressed to released seedlings; a split to the right represents increased seedling release while a split left is towards increased seedling suppression. The sum of both numbers is the total number of replicates (seedlings) at that node. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 4. Unexplained error was 0.478. Only primary splits with a complexity parameter of 0.07 or greater are shown.

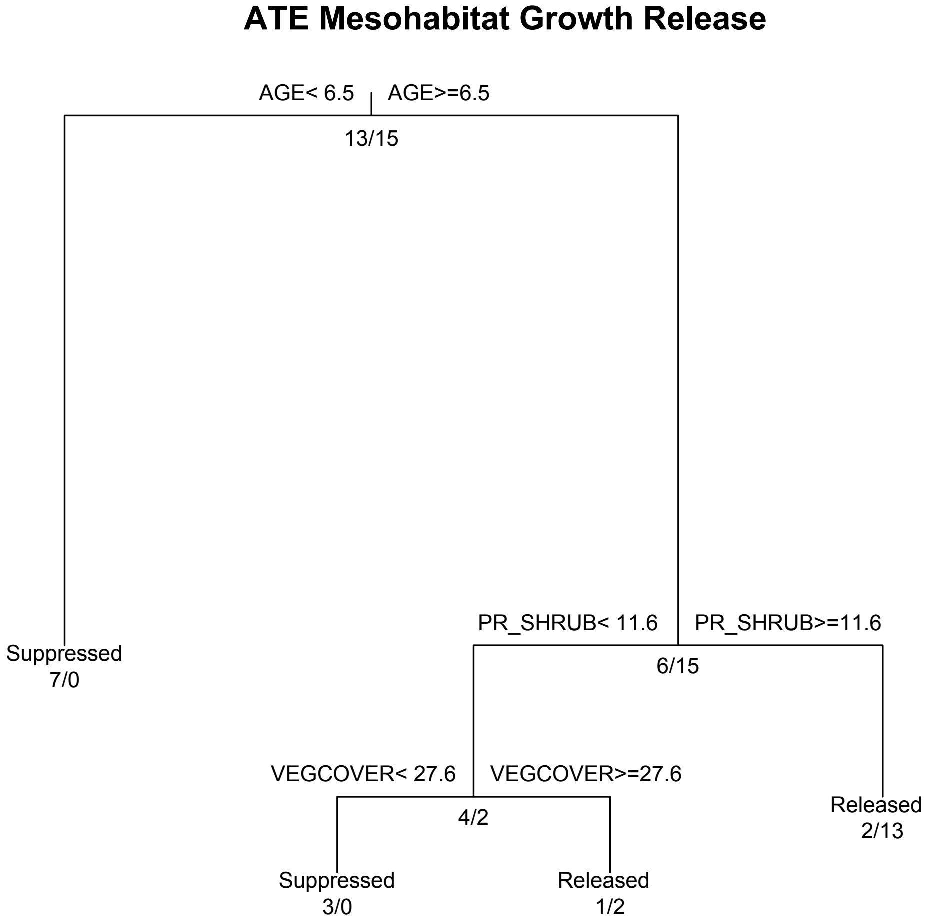

Figure 3.11: Results of regression tree analysis showing the drivers of whitebark pine seedling release in forest mesohabitats. Numbers underneath each node represent the ratio of suppressed to released seedlings; a split to the right represents increased seedling release while a split left is towards increased seedling suppression. The sum of both numbers is the total number of replicates (seedlings) at that node. Abbreviations are defined in Table 2.1. Alternate splits for each node are shown in Appendix 2 – Table 4. Unexplained error was 0.231. Only primary splits with a complexity parameter of 0.04 or greater are shown.

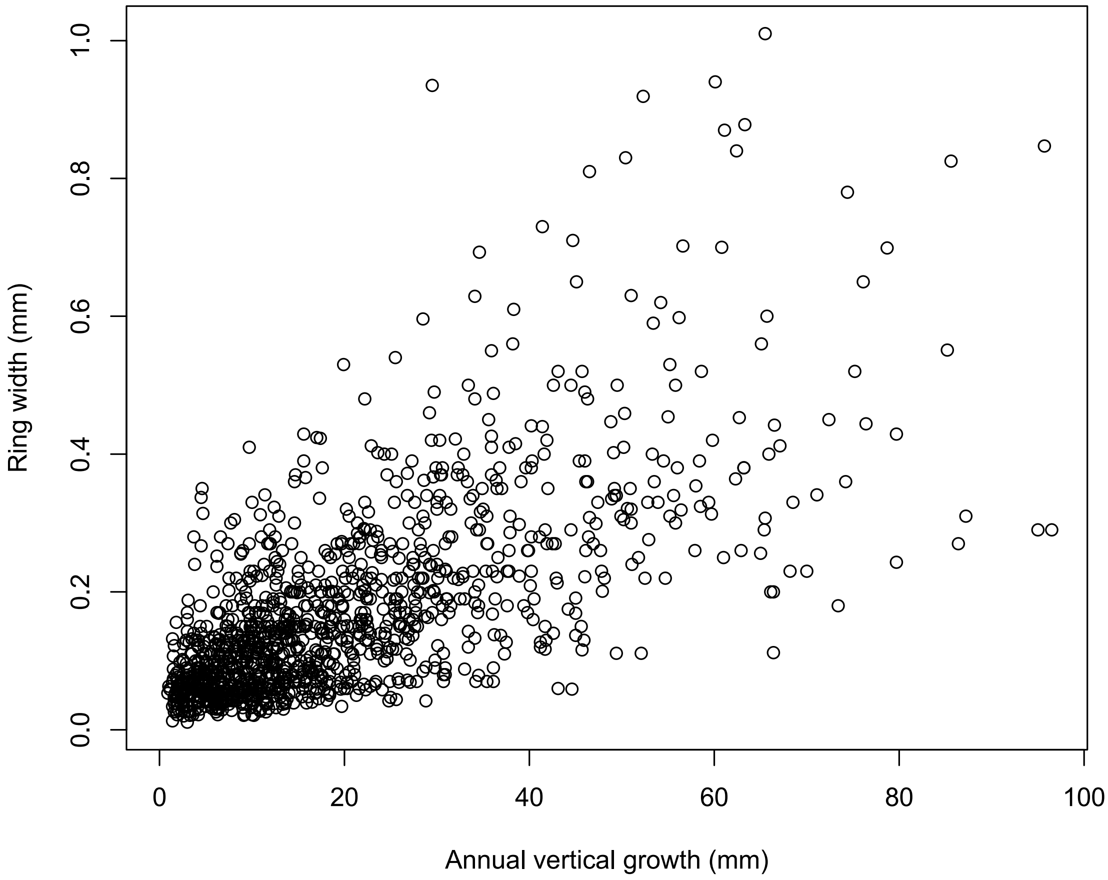

Figure 3.12: Relationship between ring width and annual height growth for seedlings from all mesohabitats and of all release categories. Pearson's correlation coefficient was 0.687 (p-value<0.001).

Chapter 4: Conclusions and Management Implications

4.1. Conclusions

The objectives of this investigation were to determine drivers of whitebark pine regeneration success in the northern Rockies of Alberta in order to assist in recovery planning and help to define critical habitat for the species. Understanding the regeneration niche of whitebark pine will help to inform restoration activities such as prescribed fire, canopy thinning, planting of disease resistant seedlings and direct efforts to locations that are crucial to the survival and recovery of the species.

A number of biophysical factors were identified that were positively associated with occurrence, growth and density of whitebark pine seedlings but these differed between the microsite and mesohabitat scale and also differed among mesohabitats. Overall these factors were indicative of a balance between conditions that favored establishment and survival while limiting competition. In forest mesohabitats canopy gaps favored occurrence and higher growth rate of whitebark pine seedlings at the microsite scale. However, at the mesohabitat scale seedling abundance was greatest along transects with higher canopy cover. Seedlings in the open mesohabitats were negatively associated with cover of rock, graminoids and seedlings of other tree species and grew fastest at intermediate values of temperature and dryness. Factors associated with seedling presence and growth rate in alpine and treeline mesohabitats differed from those in open mesohabitats in that there was a positive association with warmer microsites and higher vegetation cover. Seedling density in both open and treeline environments was highest along southwest facing slopes.

Growth release is occurring in whitebark pine seedlings and canopy cover influenced this. Release occurred in canopy gaps in forest mesohabitats and occurred much less frequently in the forest mesohabitat compared to open and alpine-treeline mesohabitats. In alpine-treeline mesohabitats release occurred in microsites with higher understory vegetation cover while microsites devoid of vegetation cover were associated with release in open habitats below treeline.

Factors influencing regeneration success mostly reflected light availability, competition and/or shelter. The importance of these three factors influencing successful establishment varied among mesohabitats. Light availability seems to be the predominant driver of success in forest mesohabitats while also influencing success in treeline environments. Shelter was important in open mesohabitats but association with graminoids, other seedlings and vegetation cover in general reduced occurrence and growth. This contrasted with the situation in forest, treeline and alpine mesohabitats where there was a positive association between occurrence and vegetation cover. However, it was difficult to determine whether this was a facilitative effect of vegetation cover or a reflection of microsite effects benefitting both whitebark pine and other plant species. In forest mesohabitats the latter is likely the case, while in the alpine-treeline ecotone it is likely a combination of both.

The negative effect of rock on occurrence and growth rate was nearly universal across all mesohabitats. This is surprising, as previous literature has recognized rock as having important sheltering effects on whitebark pine. It is important to differentiate between rock as a substrate, rock as an indicator of poor nutrient and moisture availability, and rock as a provider of shelter. The latter can grant benefits to whitebark pine survival provided the former two aren't factors. In the case of this study increased rock cover likely indicated poor overall growing conditions.

4.2. Implications for recovery and restoration

Recovery and restoration planning is ongoing throughout the range of whitebark pine. This investigation was targeted at informing and directing recovery activities, particularly in Alberta while also aiming to contribute to our knowledge of whitebark pine's regeneration niche which was identified as a priority under the *Alberta Whitebark Pine Recovery Plan* (Alberta Whitebark and Limber Pine Recovery Team 2014). This research provides insight into ideal microsites for the planting of seedlings and in this can help inform recovery activities that will increase regeneration abundance and growth. Further, the results will help to identify critical habitat that will be crucial for the future survival and success of the species.

Recovery actions for whitebark pine need to consider the mesohabitat as well microsite-scale environmental effects on growth rate and density when considering where to focus efforts. In this investigation the drivers of regeneration success varied with respect to type of mesohabitat, scale (mesohabitat versus microhabitat), and between growth rate and occurrence.

This investigation reports several findings that may inform larger scale recovery techniques. First, southwest facing slopes had the highest seedling densities in open mesohabitats and high seedling densities in treeline mesohabitats. Prescribed fire or targeted removal of competing tree species should occur on southwest facing slopes near well-stocked whitebark pine seed sources. Second, release of suppressed seedlings in forest mesohabitats, and increased success of seedlings in canopy gaps in general suggests canopy thinning could be effective for encouraging regeneration or release growth of whitebark pine seedlings in forest mesohabitats. However, this should never come at the expense of mature whitebark pine. Whitebark pine has the ability to be the most productive in environments where it gains a competitive advantage over competitors and fills its fundamental rather than its realized niche. The creation of large canopy gaps in productive lower subalpine environments or removal of understory competition in open mesohabitats likely have the greatest chance of resulting in long-term reproductive success.

This investigation highlighted several guidelines for the planting of whitebark pine seedlings. However, it is important to note that the development of white pine blister rust resistance is paramount to effectively implement long-term recovery of depleted whitebark pine populations. Planting of whitebark pine seedlings will likely be the most effective in open mesohabitats below treeline. In open habitats, light is available and will continue to be and the growing season is longer than in alpine and treeline environments. It would be important to avoid planting seedlings in rocky substrates; however, planting near rock could be beneficial because of the potential for provision of shelter if mineral soil and litter are present. Removal of or avoiding planting in areas with high cover of grasses or sedges is also important. In forest and treeline mesohabitats planting in canopy gaps and in alpine and treeline environments would help ensure microsite protection.

Informing whitebark pine critical habitat is important for the recovery of the species and will help to direct restoration activities and management practices. While regeneration is occurring in forest habitats, the most successful regeneration occurs in open areas outside of where mature whitebark pine occurs. Whitebark pine's future success likely depends on the conservation of these open areas with abundant regeneration. Unfortunately, open areas are often targeted for the development of roads, ski hills and trails. I suggest that minimal development occurs within open habitat near whitebark pine populations.

4.3. Future research

This investigation documented natural patterns of whitebark pine regeneration occurrence and growth. Studies involving direct manipulations of the seedling environment would further enhance our understanding of factors driving regeneration success at the northern limits of whitebark pine's range in Alberta. Specifically, future research should focus on the effect of competition on the growth of whitebark pine seedlings through a direct manipulation of the understory vegetation and testing whether the association of specific species of understory plants influences whitebark pine success.

This study incorporated several aspects of whitebark pine regeneration including occurrence at the microsite and mesohabitat scales as well as growth rate and release. Including the additional aspects of release growth allowed for better overall understanding of regeneration processes. In the future, research on whitebark pine regeneration throughout its range should make efforts to incorporate all aspects of regeneration rather than focusing on only one or two aspects. This study too, was somewhat limited in this regard as I was not able to gain knowledge of the long-term success of regeneration. Future research should monitor survival and growth of released seedlings as well as areas with high seedling density to determine conclusively whether increased regeneration success ultimately leads to a future increase in reproductive success.

Clark's nutcracker behavior has yet to be studied at the northern limits of distribution for it and whitebark pine. This study identified several potential avenues for future research that will help to inform our knowledge of behavior ecology of the bird as well as guide recovery actions for whitebark pine. Future research in this area should focus on whether convergent nutcracker caching is a frequent phenomenon at the northern limits of its range. This knowledge will allow us to facilitate nutcracker caching in habitat that will be beneficial to whitebark pine regeneration success.

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Appendix 1: Site locations and designations

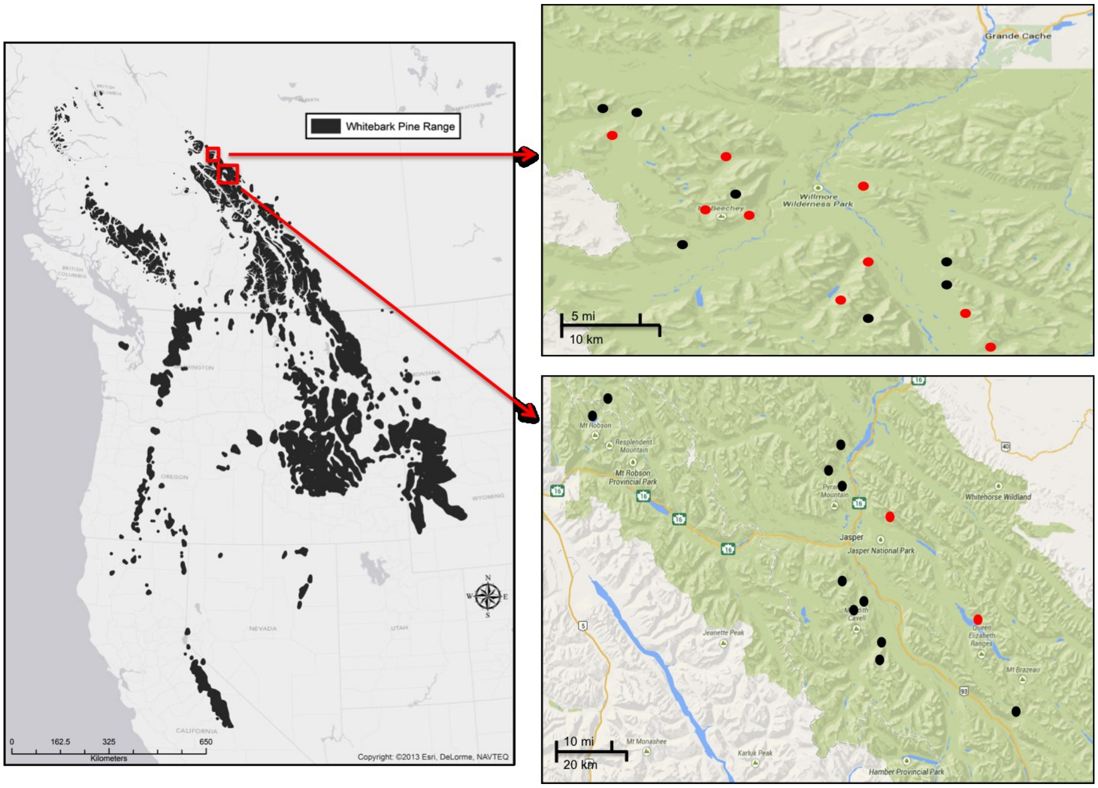

Figure 1: Location of study area. Left box indicates study area location in relation to overall whitebark pine distribution (Whitebark Pine Ecosystem Foundation 2014). Top and bottom right boxes represent Willmore Wilderness Park and Jasper National Park study areas respectively. Characterization of the regeneration niche of whitebark pine (Chapter 2) took place at all sites as indicated by black and red dots while investigation into growth release of whitebark pine seedlings (Chapter 3) only occurred at sites designated by black dots.

Table 1: Location and designation of mesohabitats for each site. Secondary designations were used as a means of differentiating transects and not for analyses.

Park	Site	Primary mesohabitat	Secondary mesohabitat	Location of transect (latitude-longitude)
Willmore	06WBL01	Alpine	Alpine	53.5552°N 119.3654°W
Willmore	06WBL01	Alpine	Treeline	53.5557°N 119.3739°W
Willmore	06WBL01	Forest	Forest	53.5552°N 119.3736°W
Willmore	06WBL01	Treeline	Treeline	53.5559°N 119.3664°W
Willmore	06WBL02	Alpine	Alpine	53.5684°N 119.2318°W
Willmore	06WBL02	Forest	Open	53.5682°N 119.2337°W
Willmore	06WBL02	Forest	Treeline	53.5684°N 119.2338°W
Willmore	06WBL02	Open	Treeline	53.568°N 119.2328°W
Willmore	06WBL02	Treeline	Alpine	53.5687°N 119.2336°W
Willmore	06WBL03	Alpine	Alpine	53.5836°N 119.2035°W
Willmore	06WBL03	Alpine	Treeline	53.5842°N 119.2016°W
Willmore	06WBL03	Forest	Open	53.5836°N 119.2034°W
Willmore	06WBL03	Open	Open	53.5834°N 119.2035°W
Willmore	06WBL03	Treeline	Open	53.5847°N 119.2038°W
Willmore	06WBL03	Treeline	Treeline	53.584°N 119.2023°W
Willmore	06WBL04	Forest	Forest	53.7852°N 119.7529°W
Willmore	06WBL04	Forest	Open	53.7883°N 119.7572°W
Willmore	06WBL04	Open	Forest	53.7906°N 119.7556°W
Willmore	06WBL04	Treeline	Treeline	53.7871°N 119.7577°W
Willmore	06WBL05	Burn	Open	53.7778°N 119.7169°W
Willmore	06WBL05	Forest	Forest	53.7803°N 119.7168°W
Willmore	06WBL05	Forest	Open	53.7785°N 119.7164°W
Willmore	06WBL05	Open	Burn	53.7778°N 119.7165°W
Willmore	06WBL05	Open	Forest	53.7792°N 119.7159°W
Willmore	06WBL07	Alpine	Alpine	Not recorded
Willmore	06WBL07	Alpine	Treeline	53.8183°N 119.5976°W
Willmore	06WBL07	Open	Open	Not recorded
Willmore	06WBL08	Forest	Forest	53.68°N 119.3454°W
Willmore	06WBL09	Open	Treeline	Not recorded
Willmore	08WBL01	Alpine	Treeline	53.5155°N 119.3566°W
Willmore	08WBL01	Forest	Forest	53.5147°N 119.3535°W
Willmore	08WBL01	Open	Forest	53.5126°N 119.3489°W
Willmore	08WBL01	Open	Treeline	53.5154°N 119.3542°W
Willmore	08WBL02	Alpine	Alpine	53.5976°N 119.6693°W
Willmore	08WBL02	Forest	Forest	53.5972°N 119.6577°W
Willmore	08WBL02	Open	Forest	53.5973°N 119.6549°W
Willmore	08WBL02	Open	Open	53.5965°N 119.6546°W
Willmore	08WBL03	Forest	Forest	53.6365°N 119.6184°W
Willmore	08WBL03	Treeline	Treeline	53.6368°N 119.6169°W
Willmore	08WBL04	Alpine	Alpine	53.5217°N 119.3944°W
Willmore	08WBL04	Forest	Forest	53.5236°N 119.3972°W
Willmore	08WBL04	Open	Open	Not recorded
Willmore	08WBL04	Treeline	Treeline	53.5217°N 119.3939°W
Willmore	08WBL05	Alpine	Alpine	53.7097°N 119.6022°W
Willmore	08WBL05	Forest	Forest	53.7061°N 119.6007°W
Willmore	08WBL05	Open	Open	53.7067°N 119.6006°W
Willmore	08WBL06	Alpine	Alpine	53.7069°N 119.6007°W
Willmore	08WBL06	Burn	Open	53.7654°N 119.7364°W
Willmore	08WBL06	Forest	Open	53.7657°N 119.7368°W
Willmore	08WBL06	Forest	Treeline	53.7664°N 119.7384°W

Willmore	08WBL06	Open	Edge	53.7679°N 119.7324°W
Willmore	08WBL07	Alpine	Alpine	53.6633°N 119.5492°W
Willmore	08WBL07	Forest	Forest	53.6606°N 119.5555°W
Willmore	08WBL07	Open	Treeline	53.6612°N 119.5555°W
Willmore	08WBL07	Treeline	Treeline	53.665°N 119.5514°W
Willmore	08WBL08	Forest	Forest	53.6478°N 119.5315°W
Willmore	08WBL08	Open	Edge	53.6453°N 119.5316°W
Willmore	08WBL08	Open	Forest	53.6478°N 119.5308°W
Jasper	Adolphus	Alpine	Alpine	53.1798°N 119.0848°W
Jasper	Adolphus	Forest	Open	53.1817°N 119.0935°W
Jasper	Adolphus	Open	Forest	53.1832°N 119.1013°W
Jasper	Adolphus	Treeline	Treeline	53.1813°N 119.0876°W
Jasper	Bonhomme	Forest	Treeline	52.9339°N 117.9527°W
Jasper	Chetamon	Forest	Forest	53.034°N 118.1482°W
Jasper	Chetamon	Open	Open	53.034°N 118.1482°W
Jasper	Edith	Forest	Forest	52.699°N 118.0665°W
Jasper	Edith	Open	Edge	52.6958°N 118.0622°W
Jasper	Edith	Open	Treeline	52.6944°N 118.0685°W
Jasper	Endless	Forest	Forest	52.4634°N 117.4218°W
Jasper	Endless	Forest	Lodgepole	52.4584°N 117.4243°W
Jasper	Endless	Open	Open	52.4648°N 117.4217°W
Jasper	Endless	Treeline	Forest	52.4668°N 117.4175°W
Jasper	Fryatt	Forest	Treeline	52.6047°N 117.9249°W
Jasper	Fryatt	Open	Open	52.6043°N 117.9256°W
Jasper	Geraldine	Forest	Forest	52.6383°N 117.936°W
Jasper	Geraldine	Open	Open	52.6385°N 117.9355°W
Jasper	Greenhock	Burn	Burn	53.0993°N 118.0844°W
Jasper	Greenhock	Forest	Forest	53.0961°N 118.0827°W
Jasper	Greenhock	Open	Open	53.0965°N 118.0827°W
Jasper	Palisades	Forest	Forest	52.9828°N 118.1164°W
Jasper	Palisades	Open	Open	52.9828°N 118.1173°W
Jasper	Peveril	Forest	Forest	52.7521°N 118.1437°W
Jasper	Peveril	Open	Edge	52.7522°N 118.1439°W
Jasper	Peveril	Open	Open	52.7521°N 118.1437°W
Jasper	Peveril	Treeline	Treeline	52.7526°N 118.1441°W
Jasper	Samson	Forest	Forest	52.6919°N 117.5592°W
Jasper	Samson	Forest	Treeline	52.6925°N 117.5595°W
Jasper	Samson	Treeline	Open	52.6926°N 117.5591°W
Jasper	Toboggan	Alpine	Alpine	53.1677°N 119.1511°W
Jasper	Toboggan	Forest	Forest	53.1598°N 119.1607°W
Jasper	Toboggan	Open	Open	53.1635°N 119.1574°W
Jasper	Toboggan	Treeline	Forest	53.1635°N 119.1574°W
Jasper	Verdant	Alpine	Treeline	52.6729°N 118.1015°W
Jasper	Verdant	Forest	Forest	52.6727°N 118.108°W
Jasper	Verdant	Open	Open	52.6731°N 118.1051°W
Jasper	Verdant	Treeline	Treeline	52.6724°N 118.1039°W

Table 2: Location and number of seedlings removed (n) for each transect used in analysis of growth release in whitebark pine seedlings (Chapter 3).

Park	Site	Primary mesohabitat	Secondary mesohabitat	n	Location
Willmore	06WBL02	Alpine	Alpine	2	53.5684°N 119.2318°W
Willmore	06WBL02	Forest	Open	5	53.5682°N 119.2337°W
Willmore	06WBL02	Open	Treeline	5	53.568°N 119.2328°W
Willmore	06WBL02	Treeline	Alpine	5	53.5687°N 119.2336°W
Willmore	06WBL03	Forest	Open	5	53.5836°N 119.2034°W
Willmore	06WBL03	Open	Open	5	53.5834°N 119.2035°W
Willmore	06WBL03	Treeline	Open	5	53.5847°N 119.2038°W
Willmore	06WBL05	Forest	Forest	1	53.7803°N 119.7168°W
Willmore	06WBL05	Open	Burn	2	53.7778°N 119.7165°W
Willmore	06WBL05	Open	Forest	5	53.7792°N 119.7159°W
Willmore	08WBL01	Alpine	Treeline	2	53.5155°N 119.3566°W
Willmore	08WBL01	Open	Forest	1	53.5126°N 119.3489°W
Willmore	08WBL01	Open	Treeline	3	53.5154°N 119.3542°W
Willmore	08WBL02	Open	Forest	1	53.5973°N 119.6549°W
Willmore	08WBL06	Forest	Open	2	53.7657°N 119.7368°W
Willmore	08WBL06	Open	Edge	3	53.7679°N 119.7324°W
Willmore	08WBL07	Alpine	Alpine	2	53.6633°N 119.5492°W
Willmore	08WBL07	Forest	Forest	3	53.6606°N 119.5555°W
Willmore	08WBL07	Open	Treeline	5	53.6612°N 119.5555°W
Willmore	08WBL07	Treeline	Treeline	5	53.665°N 119.5514°W
Jasper	Adolphus	Forest	Open	5	53.1817°N 119.0935°W
Jasper	Adolphus	Open	Forest	3	53.1832°N 119.1013°W
Jasper	Adolphus	Treeline	Treeline	2	53.1813°N 119.0876°W
Jasper	Chetamon	Forest	Forest	5	53.034°N 118.1482°W
Jasper	Edith	Forest	Forest	5	52.699°N 118.0665°W
Jasper	Edith	Open	Edge	2	52.6958°N 118.0622°W
Jasper	Edith	Open	Treeline	5	52.6944°N 118.0685°W
Jasper	Endless	Forest	Forest	5	52.4634°N 117.4218°W
Jasper	Endless	Forest	Lodgepole	4	52.4584°N 117.4243°W
Jasper	Endless	Open	Open	2	52.4648°N 117.4217°W
Jasper	Endless	Treeline	Forest	2	52.4668°N 117.4175°W
Jasper	Fryatt	Open	Open	4	52.6043°N 117.9256°W
Jasper	Geraldine	Forest	Forest	2	52.6383°N 117.936°W
Jasper	Geraldine	Open	Open	1	52.6385°N 117.9355°W
Jasper	Greenhock	Burn	Burn	3	53.0993°N 118.0844°W
Jasper	Greenhock	Forest	Forest	2	53.0961°N 118.0827°W
Jasper	Greenhock	Open	Open	2	53.0965°N 118.0827°W
Jasper	Palisades	Forest	Forest	1	52.9828°N 118.1164°W
Jasper	Palisades	Open	Open	4	52.9828°N 118.1173°W
Jasper	Peveril	Open	Edge	4	52.7522°N 118.1439°W
Jasper	Toboggan	Alpine	Alpine	2	53.1677°N 119.1511°W
Jasper	Toboggan	Forest	Forest	5	53.1598°N 119.1607°W
Jasper	Toboggan	Open	Open	4	53.1635°N 119.1574°W
Jasper	Toboggan	Treeline	Forest	5	53.1635°N 119.1574°W
Jasper	Verdant	Alpine	Treeline	1	52.6729°N 118.1015°W
Jasper	Verdant	Forest	Forest	5	52.6727°N 118.108°W
Jasper	Verdant	Open	Open	5	52.6731°N 118.1051°W
Jasper	Verdant	Treeline	Treeline	5	52.6724°N 118.1039°W

Appendix 2: Regression tree alternate splits

Table 1: Primary and alternate splits at each node for the Regression Trees of whitebark pine presence in: **A**) forest mesohabitat (Figure 2.2); **B**) open mesohabitat (Figure 2.6); **C**) treeline mesohabitats; and **D**) alpine mesohabitats. Improvements in complexity parameter are in the fourth column; in brackets are the number of observations missed if that variable is used. Refer to Table 2.1 for explanation of abbreviations.

A) Forest

VARIABLE	SPLIT	IMPROVE
First node		
BARE	> 2.5	7.859 (1)
TREE	< 22.5	6.446 (0)
WOOD	< 2.5	5.419 (1)
CAN_COV	< 65.5	5.055 (0)
ALPHADIV	> 0.5	4.673 (0)
Second node		
ALPHADIV	> 2.5	4.761 (0)
TREE	< 26	3.748 (0)
WOOD	< 2.5	3.477 (0)
FORBS	> 28.5	3.14 (0)
CAN_COV	< 65.5	2.936 (0)
Third node		
GRAMS	< 2.5	3.784 (0)
FORBS	> 28.5	2.631 (0)
WOOD	< 37.5	2.489 (0)
VEGCOVER	> 23.5	2.103 (0)
LICHEN	> 37.5	2.095 (0)
Fourth node		
FORBS	> 4.5	2.33 (0)
WOOD	< 37.5	2.323 (0)
VEGCOVER	> 13.5	2.319 (0)
TREE	< 71	2.216 (0)
ALPHADIV	> 4.5	2.026 (0)
Fifth node		
PR_SHRUB	> 8.5	2.469 (0)
LITDEP	< 3.25	2.361 (1)
LICHEN	> 0.1	2.357 (0)
BA_TOT	< 11.5	2.146 (0)
WOOD	< 37.5	1.906 (0)

B) Open

VARIABLE	SPLIT	IMPROVE
First node		
ROCK	< 62.5	7.735 (2)
PR_SHRUB	> 0.1	6.36 (0)
GRAMS	< 6.5	4.149 (0)
TREE	< 42.5	3.383 (0)
VEGCOVER	> 6.5	2.913 (0)
Second node		
GRAMS	< 7.5	5.478 (0)
PR_SHRUB	> 0.1	4.714 (0)
TREE	< 42.5	4.027 (0)
SEEDLING	< 13	3.811 (0)
VEGCOVER	< 37.3	3.546 (0)
Third node		
SEEDLING	< 13	6.233 (0)
TREE	< 42.5	4.629 (0)
VEGCOVER	< 65.7	3.95 (0)
GRAMS	> 4.5	3.557 (0)
PR_SHRUB	> 0.1	3.42 (0)
Fourth node		
TREE	< 42.5	4.913 (0)
PR_SHRUB	> 0.1	2.369 (0)
GRAMS	> 4.5	2.023 (0)
MIN_AGE	> 316	1.929 (116)
CAN_COV	> 0.15	1.861 (1)

C) Treeline

VARIABLE	SPLIT	IMPROVE
First node		
VEGCOVER	> 10.5	4.923 (0)
LICHEN	> 0.1	3.826 (1)
CAN_COV	< 67.5	3.586 (0)
PR_SHRUB	> 5.5	3.036 (0)
ROCK	< 95.5	3.002 (1)
Second node		
CAN_COV	< 67.5	4.412 (0)
TREE	< 47.5	3.094 (0)
VEGCOVER	< 23.5	2.856 (0)
LITTER	< 52.5	2.417 (1)
ORGDEP	< 6.5	1.823 (0)

D) Alpine

VARIABLE	SPLIT	IMPROVE
First node		
LITDEP	> 0.1	7.079 (0)
VEGCOVER	> 4.7	4.825 (0)
LITTER	> 0.1	4.496 (0)
ROCK	< 72.5	4.483 (0)
PR_SHRUB	> 0.6	4.382 (0)
Second node		
VEGCOVER	> 4.7	3.19 (0)
LITTER	> 0.1	2.964 (0)
ROCK	< 96	2.652 (0)
PR_SHRUB	> 0.6	2.648 (0)
LICHEN	> 9	2.007 (0)
Third node		
TREE	< 5.5	4.194 (0)
VEGCOVER	< 30.8	3.673 (0)
MOSS	< 15	2.884 (1)
FORBS	< 25.8	2.721 (0)
ALPHADIV	< 7.5	2.569 (0)
Fourth node		
ALPHADIV	< 4.5	3.311 (0)
VEGCOVER	< 40.4	3.053 (0)
PR_SHRUB	> 70.2	2.046 (0)
TREE	< 25	1.94 (0)
FORBS	< 0.1	1.662 (0)
Fifth node		
VEGCOVER	< 40.4	3.484 (0)
LICHEN	> 9	2.624 (0)
ROCK	> 37.5	2.541 (0)
FORBS	> 27.9	1.879 (0)
ORGDEP	> 4.75	1.542 (0)
Sixth node		
VEGCOVER	> 22.3	3.811 (0)
LICHEN	> 7.5	2.773 (0)
ORGDEP	> 0.35	2.005 (0)
CAN_COV	> 3.25	1.77 (0)
UP_SHRUB	> 11.5	1.77 (0)

Table 2: Primary and alternate splits at each node for the growth rate regression trees in **A**) forest mesohabitat (Figure 2.3) and **B**) open mesohabitat (Figure 2.7). **C**) treeline mesohabitats; and **D**) alpine mesohabitats. Improvements in complexity parameter are in the fourth column; in brackets are the number of observations missed if that variable is used. Refer to Table 2.1 for explanation of abbreviations.

A) Forest

VARIABLE	SPLIT	IMPROVE
First node		
BA_TOT	< 10	0.096 (0)
CAN_COV	< 10.3	0.089 (0)
WOOD	< 0.1	0.086 (1)
FORBS	> 1.9	0.084 (0)
VEGCOVER	> 15.1	0.083 (0)
Second node		
VEGCOVER	> 15.1	0.115 (0)
SLOPE	> 51	0.11 (1)
FORBS	> 1.9	0.091 (0)
WOOD	< 0.1	0.077 (1)
UP_SHRUB	> 24.5	0.073 (0)
Third node		
CAN_COV	< 2.45	0.178 (0)
MOSS	< 1.5	0.113 (0)
LICHEN	< 13.5	0.098 (0)
HLI	< 0.38	0.087 (3)
FORBS	> 1.1	0.08 (0)
Fourth node		
SLOPE	> 51	0.12 (1)
VEGCOVER	< 17.5	0.076 (0)
BA_TOT	< 42	0.067 (0)
PR_SHRUB	< 4.5	0.065 (0)
Fifth node		
PR_SHRUB	< 8.1	0.12 (0)
VEGCOVER	< 17.5	0.096 (0)
FORBS	> 1.8	0.094 (0)
UP_SHRUB	> 24.5	0.08 (0)

B) Open

VARIABLE	SPLIT	IMPROVE
First node		
MAT	< -0.25	0.062 (4)
MAP	< 924	0.061 (4)
SLOPE	> 15	0.061 (3)
LITDEP	> 1.75	0.06 (0)
ROCK	< 82.5	0.043 (2)
Second node		
MAT	> -0.45	0.161 (0)
UP_SHRUB	> 26.5	0.11 (0)
MAP	< 927	0.101 (0)
BARE	< 4	0.088 (2)
LITDEP	> 2.25	0.063 (0)
Third node		
SLOPE	< 37.5	0.146 (0)
MAT	> -1.9	0.066 (0)
MAP	< 802	0.064 (0)
HLI	> 0.952	0.064 (0)
BARE	< 0.1	0.057 (2)
Fourth node		
BARE	< 34.5	0.482 (0)
SEEDLING	> 0.7	0.441 (0)
MR_SCALE	> 0.5	0.43 (0)
NR_SCALE	> 0.5	0.43 (0)
VEGCOVER	> 32.7	0.427 (0)

C) Treeline

VARIABLE	SPLIT	IMPROVE
First node		
MAT	> -0.75	0.162 (4)
HLI	< 0.022	0.151 (4)
LITDEP	> 4.25	0.139 (0)
CAN_COV	> 58.35	0.086 (0)
LICHEN	< 3.5	0.07 (1)
Second node		
ROCK	< 4.5	0.085 (1)
MAP	< 803.5	0.072 (0)
MAT	< -2.35	0.072 (0)
LICHEN	< 3.5	0.072 (1)
ALPHADIV	> 7.5	0.07 (0)
Third node		
PR_SHRUB	> 5	0.384 (0)
FORBS	< 3.2	0.361 (0)
ORGDEP	< 1.25	0.351 (0)
LITTER	< 4.5	0.295 (0)
MIN_AGE	> 108	0.284 (4)
Fourth node		
UP_SHRUB	> 3.5	0.637 (0)
FORBS	< 3.3	0.373 (0)
LITDEP	> 0.25	0.29 (0)
MOSS	< 4	0.286 (0)
GRAMS	< 1.5	0.251 (0)

D) Alpine

VARIABLE	SPLIT	IMPROVE
First node		
ROCK	< 0.5	0.146 (0)
LITTER	> 32.5	0.116 (0)
GRAMS	< 0.8	0.108 (0)
LITDEP	> 0.1	0.093 (0)
ALPHADIV	> 13.5	0.091 (0)
Second node		
GRAMS	< 0.8	0.16 (0)
FORBS	< 2.1	0.076 (0)
ALPHADIV	< 5.5	0.072 (0)
HLI	< 0.992	0.067 (4)
ROCK	< 37.5	0.064 (0)
Third node		
LICHEN	< 4	0.746 (0)
HLI	> 0.640	0.7 (1)
PR_SHRUB	< 25	0.628 (0)
PH	> 7.25	0.606 (0)
LITTER	> 7.5	0.511 (0)
Fourth node		
FORBS	> 8.6	0.386 (0)
ORGDEP	> 0.75	0.352 (0)
LICHEN	< 12.5	0.243 (0)
LITDEP	> 0.1	0.185 (0)
VEGCOVER	> 24.8	0.162 (0)
Fifth node		
LITDEP	> 0.1	0.235 (0)
PLANTGROUP	< 2.5	0.113 (0)
LITTER	> 6	0.104 (0)
FORBS	< 2.2	0.093 (0)
ROCK	< 37.5	0.088 (0)
Sixth node		
HLI	< 0.929	0.775 (0)
PH	< 6.75	0.75 (2)
MOSS	> 0.1	0.549 (0)
LITDEP	< 0.35	0.446 (0)
LICHEN	> 0.1	0.443 (0)

Table 3: Primary and alternate splits at each node for the seedling density regression trees in **A**) forest mesohabitat (Figure 2.4) and **B**) open mesohabitat (Figure 2.8); **C**) treeline mesohabitats; and **D**) alpine mesohabitats. Improvements in complexity parameter are in the fourth column; in brackets are the number of observations missed if that variable is used. Refer to Table 2.1 for explanation of abbreviations.

A) Forest

VARIABLE	SPLIT	IMPROVE
First node		
CAN_COV	> 32	0.288 (0)
ORGDEP	> 0.95	0.243 (0)
HLI	> 0.37	0.192 (1)
ALPHADIV	> 2.25	0.191 (0)
ROCK	< 29.97	0.172 (0)
Second node		
BARE	< 5.7	0.436 (0)
VEGCOVER	> 64.09	0.413 (0)
ORGDEP	> 0.95	0.381 (0)
LITTER	< 14.59	0.277 (0)
ROCK	< 9.6	0.252 (0)
Third node		
MR_SCALE	< 3.5	0.386 (0)
WOOD	< 4.33	0.304 (0)
CAN_COV	< 70.9	0.271 (0)
BA_TOT	< 3.95	0.265 (0)
MOSS	< 67.5	0.253 (0)
Fourth node		
VEGCOVER	> 29.49	0.466 (0)
BA_TOT	< 4.06	0.284 (0)
MAP	> 840	0.281 (2)
WOOD	< 3.73	0.277 (0)
MOSS	> 8.14	0.254 (0)

B) Open

VARIABLE	SPLIT	IMPROVE
First node		
HLI	> 0.92	0.373 (2)
VEGCOVER	> 41.29	0.233 (0)
WOOD	< 0.39	0.231 (0)
MAP	> 906.5	0.225 (1)
MAT	> -1.75	0.211 (1)
Second node		
ROCK	< 47.5	0.411 (0)
MOSS	> 0.07	0.348 (0)
VEGCOVER	> 16.2	0.348 (0)
WOOD	< 0.44	0.289 (0)
SLOPE	< 27.5	0.274 (0)

C) Treeline

VARIABLE	SPLIT	IMPROVE
First node		
MAP	> 867	0.321 (5)
MAT	> -1.95	0.262 (5)
ALPHADIV	> 2.7	0.215 (0)
ORGDEP	< 3.31	0.187 (0)
HLI	> 0.99	0.168 (3)
Second node		
ALPHADIV	> 4.85	0.58 (0)
VEGCOVER	> 26.15	0.428 (0)
HLI	> 0.92	0.427 (0)
MAT	> -1.85	0.32 (0)
ROCK	< 50.59	0.309 (0)

D) Alpine

VARIABLE	SPLIT	IMPROVE
First node		
LITTER	> 0.55	0.267 (0)
SLOPE	> 10.5	0.267 (1)
VEGCOVER	> 28.16	0.258 (0)
CAN_COV	> 1.35	0.205 (0)
MOSS	< 3.86	0.168 (0)
Second node		
BARE	> 0.44	0.351 (0)
LITTER	< 5.04	0.349 (0)
MAT	> -1.75	0.346 (3)
ROCK	> 20.35	0.318 (0)
ALPHADIV	< 7.88	0.243 (0)
Third node		
ROCK	> 20.35	0.42 (0)
ALPHADIV	< 7.88	0.376 (0)
HLI	< 1	0.344 (0)
WOOD	> 0.15	0.34 (0)
MAT	> -1.75	0.297 (2)
Fourth node		
ROCK	< 42.25	0.838 (0)
ALPHADIV	> 4.8	0.385 (0)
SLOPE	< 25.5	0.37 (0)
WOOD	> 0.1	0.341 (0)
HLI	> 0.7	0.256 (0)

Table 4: Primary and alternate splits at each node driving release in **A**) forest mesohabitat (Figure 3.9), **B**) open mesohabitat (Figure 3.10) and **C**) alpine-treeline ecotone (ATE) mesohabitats (Figure 3.11). Improvements in complexity parameter are in the fourth column; in brackets is the number of observations missed if that variable is used. Refer to Table 2.1 for explanation of abbreviations.

A) Forest

Variable	Split	Improve
First node		
CAN_COV	< 10.4	5.302 (0)
VEGCOVER	> 68.2	5.302 (0)
UP_SHRUB	> 24.5	5.302 (0)
GRAMS	> 0.7	2.711 (0)
BA_TOT	< 10	2.511 (0)
Second node		
VEGCOVER	> 68.2	5.007 (0)
UP_SHRUB	> 24.5	5.007 (0)
PR_SHRUB	> 44.1	3.219 (0)
ALPHADIV	> 6.5	1.6 (0)
FORBS	> 1	1.395 (0)

B) Open

Variable	Split	Improve
First node		
ROCK	> 22.5	3.309 (2)
BA_TOT	< 26	2.617 (0)
VEGCOVER	< 34.5	2.162 (0)
PR_SHRUB	< 21	1.95 (0)
GRAMS	< 4	1.922 (0)
Second node		
AGE	> 32.5	2.314 (0)
LITDEP	> 1.75	2.095 (0)
BA_TOT	< 26	1.75 (0)
CAN_COV	> 1.55	1.556 (0)
UP_SHRUB	< 0.6	1.373 (0)
Third node		
LITDEP	> 1.75	1.853 (0)
ORGDEP	> 8	1.761 (1)
GRAMS	< 0.1	1.521 (0)
PR_SHRUB	> 41.2	1.515 (0)
ALPHADIV	< 7.5	1.484 (0)

C) ATE

Variable	Split	Improve
First node		
AGE	> 6.5	5.357 (0)
PR_SHRUB	> 11.6	2.607 (0)
TREE	> 0.5	2.012 (0)
ALPHADIV	> 2.5	1.449 (0)
ROCK	> 0.5	1.449 (0)
Second node		
PR_SHRUB	> 11.6	2.438 (0)
ORGDEP	> 3.25	2.256 (0)
VEGCOVER	> 15.6	2.256 (0)
ROCK	> 37.5	1.714 (0)
GRAMS	> 2.1	1.071 (0)
Third node		
VEGCOVER	> 27.6	1.333 (0)
MOSS	> 4	1.333 (0)
UP_SHRUB	> 12	1.333 (0)
PR_SHRUB	> 2.5	1.333 (0)
FORBS	> 8.9	1.333 (0)

Appendix 3: Plant species list and groupings

Table 1: Plant species associated with vegetation groups, as determined using the average linkage method based on Euclidean distances. Species associated with each discrete vegetation group for each mesohabitat. Species associated with each group are listed in descending order based on the scores. n = number of plots in the dataset for that plant group. Refer to Table 2 in this appendix for explanation of the species codes.

A) FOREST					
GROUP	1	2	3	4	5
SPEC 1	JUNI_COM	EMPE_NIG	PIAL_TRE	DRYA_OCT	VACC_VIT
SPEC 2	LINN_BOR	ABBI_SEE	VACC_MEM	SOLI_MUL	ARTE_NOR
SPEC 3	PIEN_TRE	ABBI_TRE	PHYL_GLA	ELYM_TRA	SOLI_MUL
SPEC 4	SHEP_CAN	VACC_MEM	EMPE_NIG	CARE_SPP	ABBI_SAP
SPEC 5	ARCT_UVA	ABBI_SAP	ABBI_TRE	ZIGA_ELE	CARE_SPP
n	96	177	21	21	4
B) OPEN					
GROUP	1	2	3	4	5
SPEC 1	CARE_SPP	DRYA_OCT	ABBI_SEE	VACC_SCO	VACC_VIT
SPEC 2	ZIGA_ELE	ARCT_UVA	EMPE_NIG	RHOD_ALB	
SPEC 3	SOLI_MUL	PIEN_SEE	CASS_MER	CORN_CAN	
SPEC 4	DASI_FRU	JUNI_COM	VACC_MEM	ABBI_SEE	
SPEC 5	ANEM_PAR	ELYM_TRA	RHOD_ALB	CARE_SPP	
n	24	65	175	2	2
C) TREELINE					
GROUP	1	2	3	4	5
SPEC 1	CASS_MER	DRYA_OCT	DRYA_INT	CASS_TET	GRASS
SPEC 2	EMPE_NIG	ABBI_SAP	HEDY_BOR	DRYA_OCT	SALI_NIV
SPEC 3	ABBI_TRE	SALI_VES	CARE_SPP	VACC_VIT	
SPEC 4	ABBI_SEE	PHYL_GLA	ARCT_RUB	PIEN_SEE	
SPEC 5	JUNI_COM	ARCT_RUB	ARCT_UVA	ARCT_UVA	
n	66	49	9	5	1
D) ALPINE					
GROUP	1	2	3	4	5
SPEC 1	DRYA_OCT	PHYL_GLA	DRYA_INT	CASS_MER	PEDI_BRA
SPEC 2	EMPE_NIG	JUNI_COM	CARE_SPP	ANEM_OCC	PHLE_COM
SPEC 3	SALI_VES	CASS_MER	HEDY_BOR	ARTE_NOR	ERIG_PER
SPEC 4	VACC_ULI	LUZU_PAR	PIEN_SEE	VACC_CES	
SPEC 5	CASS_TET	CASS_TET	DRYA_OCT	SALI_ARC	
n	108	14	8	19	1

Table 2: List of species and corresponding code (Table 1 of this Appendix) found in 5% or greater of microsite plots for any mesohabitat.

Code	Species	Code	Species
PIAL_TRE	*Pinus albicaulis* Tree	HEDY_BOR	*Hedysarum borealis*
ABBI_SEE	*Abies lasiocarpa* seedling	JUNI_COM	*Juniperus communis*
ABBI_SAP	*Abies lasiocarpa* sapling	LUET_PEC	*Luetkea pectinata*
ABBI_TRE	*Abies lasiocarpa* tree	LUZU_PAR	*Luzula parviflora*
PIEN_SEE	*Picea engelmannii* seedling	LINN_BOR	*Linneus borrealis*
PIEN_TRE	*Picea engelmannii* tree	PEDI_BRA	*Pedicularis bracteosa*
ANEM_OCC	*Anemone occidentalis*	PHLE_ALP	*Phleum alpinum*
ANEM_PAR	*Anemone parviflora*	PHYL_EMP	*Phylodocea empetriformis*
ANTE_ALP	*Antenneria alpinus*	PHYL_GLA	*Phylodocea glandiflora*
ARCT_RUB	*Arctostaphylos rubra*	POLY_VIV	*Polygonum viviparum*
ARCT_UVA	*Arctostaphylos uva-ursi*	PYRO_ASA	*Pyrola asarifolia*
ARTE_NOR	*Artemesium norvegica*	RHOD_ALB	*Rhododendron albiflorum*
CARE_SPP	*Carex* species	RUBU_PED	*Rubus pedatus*
CASS_MER	*Cassiope mertensiana*	SALI_ARC	*Salix arctica*
CASS_TET	*Cassiope tetragona*	SALI_NIV	*Salix nivalis*
CORN_CAN	*Cornus canadensis*	SALI_VES	*Salix vestita*
DASI_FRU	*Dasiphora fruticosa*	SHEP_CAN	*Shepherdia canadensis*
DRYA_INT	*Dryas integrifolia*	SOLI_MUL	*Solidago multiradiata*
DRYA_OCT	*Dryas octopetela*	VACC_CES	*Vaccinium cespitosum*
ELYM_TRA	*Elymus trachycaulus*	VACC_MEM	*Vaccinium membranaceum*
EMPE_NIG	*Empetrum nigrum*	VACC_SCO	*Vaccinium scoparium*
EPIL_ANG	*Epilobium angustifolium*	VACC_ULI	*Vaccinium uliginosum*
ERIG_PER	*Erigeron peregrinus*	VACC_VIT	*Vaccinium vitis-idea*
GENT_PRO	*Gentianella propinqua*	ZIGA_ELE	*Zigadenus elegans*
GRASS	Vegetative grass		