POST-FIRE REGENERATION AND SURVIVAL OF WHITEBARK PINE (*Pinus albicaulis* Engelm.)

by

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Abstract

The recruitment trends of whitebark pine (*Pinus albicaulis* Engel.) were investigated in 18 recently burned stands in the Canadian Rockies and the North Cascades. Whitebark pine recruitment in recently burned stands (fires < 60 years prior) was compared to that on paired control stands (no recent fire) to determine if fire was necessary for successful recruitment. Recruitment in recently burned stands was compared with ecological and seed source variables. Along a chronosequence, whitebark pine recruitment was compared with precipitation and with Pacific Decadal Oscillation (PDO). Field sampling consisted of systematic plots established in sampling grids in both burned and control stands. In each plot ecological data was collected as was data regarding whitebark pine age, height, and disease status. Recent fire was not found to be a requirement for recruitment. Both distance to and size of seed source were important predictors of whitebark pine recruitment. Whitebark pine regeneration densities were low on warm steep rocky sites. High whitebark pine recruitment on cooler aspects suggested that whitebark pine could establish on cooler sites when competition was removed by fire. Most stands were composed of mixed conifers, but only lodgepole pine appeared to limit the growth of whitebark pine. Whitebark pine recruitment was episodic on all stands, and recruitment years were correlated among many stands separated by large distances. Episodic recruitment may be due to more than cone masting as recruitment in several stands was also correlated with growing season precipitation and positive PDO values, which may increase the length of growing season. A logistic regression model suggested that infection by white pine blister rust is most likely on older seedlings. The percentage of whitebark pine trees infected by white pine blister rust on a site increased with time since fire. Prescribed fires and wildfires should address retention of whitebark pine seed trees on site. Fires that remove competition from mesic-submesic stands may result in the most rapid recruitment of whitebark pine. With the exception of stands heavily stocked with lodgepole pine, all recently burned stands in this study would benefit from increased stocking of whitebark pine by planting.

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Acknowledgments

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Chapter 1. Whitebark Pine Regeneration and Survival

1.1 Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) is the only North American stone pine, a group of bird-dispersed pines characterized by indehiscent cones and large wingless seeds (Bruederle et al. 1998). The stone pines are of the subsection *Cembrae*, a group which globally contains five species that rely on members of the nutcracker genus (*Nucifraga*) for seed dispersal. The Clark's nutcracker (*Nucifraga columbiana* Wilson) is responsible for the dispersal of whitebark pine seeds. Whitebark pine coevolved with and formed a mutualistic relationship with the Clark's nutcracker. The nutcracker disperses pine seeds by burying them in small caches for retrieval during times of low food availability. Forgotten caches may germinate new trees. The distribution of whitebark pine across the landscape is almost exclusively due to the caching behaviour of the Clark's nutcracker (Hutchins and Lanner, 1982).

Whitebark pine was first described by Engelmann in 1863 as growing at high elevations from central B.C. to the Sierra Nevada, the Ruby Mountains of Nevada, to Northwestern Wyoming (Critchfield and Little 1966, McCaughey and Schmidt 2001) (Figure 1.1). In Canada, whitebark pine grows in the Rocky and Columbia Mountains to north of McBride; at scattered locales through the interior plateau; in the Cascade Mountains; and from the southern Coast Mountains northward to Smithers (Ogilvie 1990). In the U.S. portion of its range whitebark pine forms extensive stands, whereas in the majority of its Canadian range it is a minor component of subalpine forests (Arno and Hoff 1990).

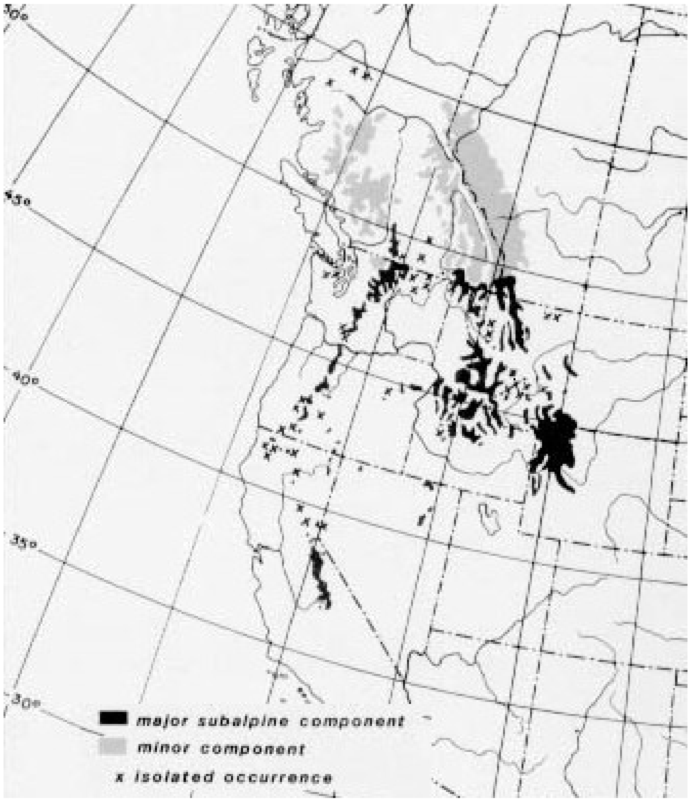

Figure 1.1 Range map of whitebark pine (Arno and Hoff 1990).

Ecological site requirements for whitebark pine are confused by the nutcracker mediated distribution of seed. Whitebark pine is most common on southern aspect slopes and ridgetops with direct exposure to wind and sun; however, the largest and best formed whitebark pine are typically found on the northern aspect slopes (Arno and Hoff 1990). In B.C. whitebark pine is an indicator of alpine tundra and boreal climate types; moderately dry to fresh soil moisture regimes; and nitrogen medium soils (Klinka et al. 1989). It typically grows as a treeline species, but can grow as much as 700 m below treeline and 300 m above treeline in krummholz form (Ogilvie 1990). Although it is restricted to high mountain environments, the diversity of these different environments is considerable (Ogilvie 1990).

Whitebark pine functions as a keystone species in high elevation stands because it pioneers otherwise inhospitable stands and its seeds provide a valuable food source to numerous species of wildlife (Tomback and Kendall 2001). Once established, whitebark pine may moderate the harsh local environment and facilitate the growth of competing species (Callaway 1998, Tomback and Kendall 2001). Whitebark pine may also prolong snowpack, modifying the local soil moisture and runoff regimes (Farnes 1990).

The large nutritious seeds of whitebark pine serve as an important food source for many species of wildlife. Under controlled conditions, rodents ate or removed nearly all sown whitebark pine seeds (Hutchins 1990). Red squirrels are known to hoard cones into middens for future consumption. In the Greater Yellowstone Ecosystem these middens are regularly raided by Grizzly bears as an important food source. Poor cone crops are associated with increased bear mortalities and conflicts with humans as bears move to lower elevations in search of other food sources (Mattson et al. 1992).

Years of poor cone production are common in whitebark pine forests. Whitebark pine produces mast cone crops every 3 to 5 years with little production in between (Morgan and Bunting 1992). During years of poor cone production, Clark's nutcrackers have been known to disperse from their normal range. During a poor cone crop in Southern Alberta, nutcrackers traveled as far as 300 km to the Cypress Hills in search of food (Fisher 1979, Fisher and Myres 1979, Wilson and Stuart-Smith, 2002). Cone masting varies geographically (McCaughey and Tomback 2001), and the masting interval in the northern populations of whitebark pine is poorly studied. The instability caused by episodic cone production may be exacerbated by the slow maturation rate of whitebark pine. Female cones are not produced until trees are twenty to thirty years old and not in great quantity until trees are sixty to eighty years old (Day 1967; Krugman and Jenkinson 1974; McCaughey and Tomback 2001).

1.2 Disturbance Agents

Natural disturbance agents, such as disease, insects and fire, each play an important role in altering whitebark pine ecosystems (Arno 2001). However, the disturbance regimes that govern whitebark pine ecosystems have been greatly modified in recent time. White pine blister rust which aggressively attacks and kills five needle pines including whitebark pine, has been introduced into North America (McDonald and Hoff et al. 2001); mountain pine beetle (*Dendroctonus ponderosae* Hopkins) populations have expanded to epidemic proportions (B.C. Ministry of Forests 2005); and the fire regime that is important in stand maintenance and initiation has been altered due to fire suppression policies (Keane 2001).

1.2.1 White Pine Blister Rust

The greatest threat facing whitebark pine is white pine blister rust (Murray 2005), an introduced disease caused by the fungus *Cronartium ribicola* (J.C. Fisch). White pine blister rust was introduced into western North America in 1910, on a shipment of *Pinus strobus* L. seedlings imported to Vancouver, B.C. from France. It was not identified in B.C. until 1921, largely due to personnel being distracted by the war effort (Gussow 1923). Since the fungus originated in Asia, North American five-needled pines have little genetic resistance to it and have readily succumbed to its effects.

Like other rusts, white pine blister rust exhibits a complex life cycle that involves several spore stages requiring different host and alternate host species. In B.C. and Alberta, the five needled pines *P. albicaulis*, *P. flexilis,* and *P. monticola* serve as hosts, and *Ribes* spp. (currants and gooseberries) act as alternate hosts. Recent studies have found that *Pedicularis* spp. and *Castilleja* spp. may also serve as alternate hosts (Tomback et al. 2005).

The life cycle of white pine blister rust involves five spore stages, two on the pine host and three on the *Ribes* alternate host. On infected whitebark pine the spermatia stage serves to exchange genetic material, which is transferred by insects attracted to the sweet liquid produced in this stage. One year later, aeciospores are formed, and may travel as far as 1300 km to infect *Ribes* plants (Edmonds et al. 2000). Infected *Ribes* plants host the urediniospore, teliospore, and basidiospore stages. Urediniospores are dispersed to other *Ribes* plants, but only basidiospores are dispersed to pine hosts. Though short lived and sensitive to UV radiation, basidiospores are capable of traveling several kilometers to a suitable pine host.

When basidiospores land on the needles of a pine host, they germinate under moist and cool conditions, and enter the needle through the stomata. Infected needles may display yellowing at the infection site. The hyphae then move from the needle to colonize the phloem of the branches and stem. Cankers begin to develop at these sites and eventually kill the tree or branch above the infected site. Smaller trees are readily killed by a single stem canker. Large trees are usually killed slowly due to crown dieback, but the fungus often kills the cone-bearing branches first, greatly reducing reproductive potential (Arno and Hoff 1990, Keane and Arno 1993).

The decline of whitebark pine due to blister rust has been well documented. In B.C., Zeglen (2002) found 30% of the trees were infected, with 9% already dead from blister rust and only 50% classified as uninfected. Also in B.C., Campbell and Antos (2000) suspected infection rates as high as 44% on the live cohort, and found 21% of the population dead likely due to blister rust. Province wide, a gradient of infection was observed with the highest rates found in the Rocky Mountains, declining towards the western portions (Zeglen, 2002). Stuart-Smith (1998) found infection rates as high as 76% in the southern Canadian Rockies, with infection rates declining with increasing latitudes (Wilson and Stuart-Smith 2002).

1.2.2 Mountain Pine Beetle

Mountain pine beetle epidemics have frequently impacted stands of mature whitebark pine (Ciesla and Furniss 1975; Furniss and Carolin 1977; Campbell and Antos 2000). Typically, mountain pine beetle has spread from lower elevation lodgepole pine (*Pinus contorta var. latifolia* Engelm.) forests into higher elevation whitebark pine forests. However, whitebark pine stands have been infested in the absence of lodgepole pine (Bartos and Gibson 1990). Recent work has shown that mountain pine beetle may spread down slope from whitebark pine stands to infest lodgepole pine stands (S. Kegley, Personal Communication). Although mountain pine beetle is a natural insect pest of whitebark pine, the recent epidemic is believed to be largest in B.C.'s history (B.C. Ministry of Forests 2005) resulting in the potential for far greater impacts than previous outbreaks.

1.2.3 Fire

Whitebark pine is believed to benefit from both stand maintaining and stand initiating fire. Its high resistance to fire when compared with other site associates (Morgan and Bunting 1990) as well as its potential for long distance seed dispersal (Tomback et al. 1990) make whitebark pine well suited to a range of fire regimes (Arno and Hoff 1990; Morgan et al. 1994; Keane 2001). Whitebark pine cones are not serotinous; rather, the openings created by fire are preferred seed caching areas for the Clark's nutcracker (Tomback 1986, Tomback and Linhart 1990).

Fire Regimes

Low severity surface fires that primarily consume understory vegetation, including whitebark pine regeneration, serve to maintain whitebark pine stands. Surface fires may prove lethal to mature Engelmann spruce (*Picea engelmanii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) due to their low branching habit, shallow roots, and thin bark; while mature whitebark pine is typically able to survive such fires due to its thicker bark, thinner crown and deeper roots (Arno and Hoff 1990, Keane 2001). In Wyoming, fire scarred whitebark pine were found in the majority of stands sampled (Morgan and Bunting 1990). Stand maintaining surface fires often result in open parkland stands dominated by whitebark pine (Arno 1986).

Following periods of extended drought, high severity stand replacing fires may occur at the landscape level converting large tracts of forest back to an early successional state. It is under these conditions that the Clark's nutcracker provides whitebark pine with a clear recruitment advantage when compared with its wind disseminated counterparts. Nutcrackers tend to cache most seeds adjacent to parent trees, but high densities may be found up to 2 km from parent trees, and dispersal distances up to 22 km have been recorded (Vander Wall and Balda 1977; Tomback 1978; Tomback et al. 1990). Recruitment of wind dispersed species is usually dependent on the availability of local seed sources and not long distance dispersal of seeds (Clements 1910; Lotan 1976; Turner et al. 1999). The seed dispersal pattern of most wind dispersed conifers generally follows a negative exponential pattern with most seeds falling within 50m of the parent tree with few traveling beyond 250m (McCaughey et al. 1986; Tomback et al. 1990). Lodgepole pine's serotinous cones may release millions of seeds/ha following fire (Lotan and Jensen 1970), but the effective stocking distance from the seed source is typically less than 100 m (Fowells 1965; Archibald 1989; Turner et al. 1999).

A mixed severity fire regime which results in a variable pattern of burn severity and a mixture of burned and unburned stands is common in whitebark pine habitat. The interruption of fuels by topographic features such as scree slopes, rock outcrops and alpine tundra contributes to a heterogeneous fire pattern in high elevation forests (Hawkes et al. 1997**).** Mixed severity fires typically kill a smaller proportion of fire resistant than non-resistant species, including whitebark pine (Keane and Arno 1993). The openings created by mixed severity burns provide important caching habitat for the Clark's nutcracker (Hutchins and Lanner 1982; Tomback et al. 1990; Norment 1991; Hesburg et al. 1999; Keane and Arno 2001)**.**

Fire Suppression

Fire severity regime is inversely related to fire frequency. Ecosystems maintained by low severity regimes have frequent fires (5 to 30 years); mixed severity regimes have fires occurring at 30 to 100 year intervals; and stands maintained by high severity regimes experience stand replacing fire at intervals of one to several hundred years (Arno et al. 2000). Since fire suppression has not been in effect for the time scale at which high severity fire events occur, mixed and low severity fire regimes have been most affected by fire suppression policies. Fire suppression has increased the time between fires in low and mixed severity regimes, resulting in an increased fuels buildup and a greater chance of high severity fire when the stands do burn (Pengelly and White 1998). In Glacier National Park, MT, fire suppression has been very effective in suppressing fire in ecosystems characterized by a mixed severity regime, but less effective in areas characterized by a stand replacing regime (Barrett et al. 1991; Arno et al. 2000).

Fire frequency distributions in Yoho National Park (Tymstra 1991), Kootenay National Park (Masters 1990), and the Kananaskis watershed (Johnson and Larsen 1991) have remained unchanged by fire suppression (Weir et al. 1995). However, fire suppression has reduced the total area burned in the southern Canadian Rocky Mountains (Pengelly and White 1998). Suppressed fires in the Canadian Rockies typically occurred under conditions where they would not likely spread, whereas large wildfires occurred under extreme fire conditions where suppression activities were largely ineffective (Weir et al. 1995). In the southern Canadian Rockies, 95% of the total area burned in the last three decades is attributed to only 3% of the fires (Johnson and Wowchuk 1993, Weir et al. 1995). When fires were easily suppressed and only a small area burned, changes in slope, aspect, elevation and vegetation type had a significant impact on fire behavior (Alexander and McAlpine 1987, Weir et al. 1995). Changes in aspect, elevation and vegetation type had little influence on fire behavior under extreme conditions (Anderson 1968; Alexander et al. 1983; Nimchuk 1983; Janz and Nimchuk 1985; Street 1985; Flannigan and Harrington 1988; Fryer and Johnson 1988; Weir et al. 1995).

In Jasper National Park, the introduction of fire suppression policies in 1913 resulted in a lengthening of the mean fire return interval and an increase in mature forest area coverage (Tande 1979). In Kootenay National Park, the fire cycle lengthened after1788, and again after 1928; however, these changes are respectively attributed to the little ice age and a period of higher precipitation, and not due to fire suppression activities (Masters 1990). Although fire weather conditions in Banff National Park were comparable in the decades preceding fire suppression as in those following (Balling et al. 1992; Fuenekes and Van Wagner 1995; Luckman and Seed 1995), a much greater area burned prior to suppression activities (Pengelly and White 1998). Studies have found that the low proportion of area burned by fire in the Canadian Rockies over the last five to seven decades is unprecedented over the previous four or five centuries (Pengelly and White 1998).

In the U.S., fire suppression has allowed for seral replacement of whitebark pine by more shade tolerant, less fire resistant species such as Engelmann spruce and subalpine fir (Keane 2001). A reduction in the area burned has reduced the opportunity for successful whitebark pine regeneration (Morgan and Bunting 1990). In the Selway-Bitterroot Wilderness of Montana and Idaho, the area of whitebark pine habitat burned annually decreased by half since the introduction of fire suppression practices (Brown et al. 1994).

1.3 Restoration

The recent declines in whitebark pine populations attributed to the impacts of white pine blister rust, mountain pine beetle, and fire suppression have resulted in a need for restoration treatments (Tomback 2001). Genetic studies and seedling trials are ongoing to isolate genetic resistance to white pine blister rust (McDonald et al. 2001). Verbenone treatments have been applied in several areas to protect large, potentially blister rust resistant, trees from beetle attack (Perkins 2005). Within Canada, prescribed fire for whitebark pine restoration has been applied on Helen Ridge in Banff National Park and is slated for further application in Waterton Lakes and Yoho National Parks (Wilson and Stuart-Smith 2002).

Prescribed fire has been applied as a means of restoring whitebark pine habitat in the Rocky Mountain areas of the U.S., and a large body of literature supports more extensive application of prescribed fire as a whitebark pine restoration tool (eg. Arno and Hoff 1990; Morgan and Bunting 1990; Morgan et al. 1994; Peterson 1996; Murray et al. 2000; Keane 2001; Keane and Arno 2001). However, in Canada relatively little has been published regarding the application of prescribed fire for whitebark pine restoration. The whitebark pine conservation plan for Parks Canada outlines a need for prescribed fire (Wilson and Stuart-Smith 2002). Stuart-Smith (1998) found continuous regeneration on several stands, and recommended that fire be applied in the Canadian Rockies based on the potential for increased regeneration. However, Campbell (1998) found little evidence that fire suppression has been a major threat to whitebark pine in B.C.

The management plan for Banff National Park targets maintenance of 50% of the long-term area burned through prescribed and lightning caused fire (Parks Canada 1997). However, to date the burn program has underemphasized upper subalpine areas which would burn in the summer months (White et al. 2005). The fire management plan for Manning Provincial Park recommends prescribed burning on stands where fire suppression has impacted ecosystem health, altered structure and function, or has moved conditions beyond the range of historic variability (Blackwell and Coulthard 2001).

1.4 Regeneration Research

Given the altered disturbance regimes which are negatively impacting whitebark pine populations, relatively few studies have addressed natural regeneration trends to assist in selecting sites that would best respond to restoration treatments. Although it is well established that fire plays an important role in the establishment and maintenance of many whitebark pine stands, we know relatively little about the early seral pathways following fire leading to whitebark pine stand development. Increasing our knowledge of these early seral pathways is imperative if we are to make informed decisions regarding the application of prescribed fire in restoring this vital species.

The whitebark pine conservation plan for the Canadian Rocky Mountain National Parks identifies prescribed burning as one of seven approaches to whitebark pine conservation (Wilson and Stuart-Smith 2002); and in Manning Park, B.C. Parks is adopting prescribed fire as a means of vegetation and habitat enhancement (Blackwell and Coulthard 2001). In support of aiding in the decision making process when applying prescribed fire, the general objectives of the present study are:

1) To determine whether regeneration density is greater in recently burned or older burned stands;

2) To determine the most suitable conditions for whitebark pine regeneration following fire; and

3) To determine the factors influencing the rates of seedling recruitment and infection by whitepine blister rust in recently burned areas.

Chapter 2. Factors Influencing Whitebark Pine Seedling Establishment

2.1 Introduction

Whitebark pine occurs on a wide range of sites as a direct result of seed caching by the Clark's nutcracker (Hutchins and Lanner 1982); resulting in a highly variable seral role between sites. It may be climax on cold high elevation stands that exclude other species or it may be seral on sites that are capable of supporting other, typically shade tolerant, tree species (Arno 2001). Where whitebark pine is early seral, fire is important in creating suitable microsites for regeneration, primarily because whitebark pine is outcompeted by shade tolerant conifer species in late seral stands (Keane 2001). Campbell and Antos (2003) found that in B.C. whitebark pine declined in abundance in late seral stands, but they found no evidence that it would be completely replaced by late seral species.

Regeneration of whitebark pine is slow and complex, even on sites ideal for tree growth. Open areas are preferred caching locations for Clark's nutcrackers (Hutchins and Lanner 1982), but many other factors are also critical in facilitating successful recruitment of whitebark pine to a site. Identifying sites best suited for regeneration is confounded by cone cycles, variable dormancy, seed herbivory and seedling mortality.

Clark's nutcrackers may travel great distances and against prevailing winds to cache whitebark pine seeds (Tomback 1994). In Idaho, regeneration density decreased with increasing distance from the seed source to about 2 km, and occurred at lower densities for at least 3.5 km from the seed source (Tomback 1994). Long distance dispersal provides whitebark pine with a recruitment advantage against its wind dispersed competitors, whose seeds rarely travel beyond 250 m (McCaughey et al. 1986, Tomback et al. 1990).

Nutcracker caching of seed often results in the multi-stemmed form, characteristic of whitebark pine. Although a certain percentage of clumping is attributed to basal branching or mechanical damage (Weaver and Jacobs 1990), a high percentage is attributed to the germination of multi-seed nutcracker caches (Hutchins and Lanner 1982). A study in Montana attributed a greater number of stems per seedling cluster to more favourable site conditions permitting seed higher germination, and potentially to increased distance from seed source which may be attributed to Clark's nutcracker's investing more effort by caching more seeds in more costly seed caches (Tomback et al. 1993).

In the U.S., factors having the greatest effect on seedling survival have been insolation, drought, animals, and white pine blister rust (McCaughey and Weaver 1990). Insolation damage, caused by scorching of the stem at ground level, usually occurred in early to mid summer; whereas drought mortality has been greatest in mid to late summer when soil moisture levels are lowest (McCaughey and Weaver 1990). Animal caused mortality was caused by burial, uprooting or nipping by pocket gophers (*Thomomys talpoides*) (McCaughey and Schmidt 1990). White pine blister rust infects increasingly more seedlings as they grow taller and become larger targets for basidiospores (Tomback et al. 1995).

Fire suppression has limited both the initiation of new stands of whitebark pine, and our potential to study how high elevation ecosystems respond to fire. Several studies have retrospectively examined post-fire dynamics through stand reconstruction techniques (eg. Morgan and Bunting 1990; Murray et al. 2000; Campbell and Antos 2003); but until recently, few studies had examined early post-fire dynamics of whitebark pine stands (eg. Tomback et al. 2001; Perkins 2004). The few studies that have examined early post-fire dynamics occurred in the U.S., where whitebark pine forms extensive stands and is often a major component of subalpine forests. In its northern range in Alberta and B.C. whitebark pine is sparsely distributed and is usually only a minor component of subalpine forests (Arno and Hoff 1990). The differences in whitebark pine stand density coupled with inherent ecological differences associated with increasing latitude such as length of growing season and regional climate, restricts the application of findings from U.S. studies to Canadian populations of whitebark pine.

Studies examining seedling recruitment have reported conflicting site requirements. This is likely due to the caching behaviour of the Clark's nutcracker which is almost solely responsible for the distribution of whitebark pine across the landscape (Hutchins and Lanner, 1982). Whitebark pine is most common on southern aspects and ridgetops with direct exposure to wind and sun; however, the largest and best formed whitebark pines are typically found on the northern aspects (Arno and Hoff 1990). In Yellowstone, regeneration density following fire was greatest on moist sites, but dry sites had higher rates of seedling survival (Tomback et al. 2001). Several studies have cited a nutcracker caching preference for warm aspect slopes (Vander Wall and Balda 1977, Tomback 1978), while others have identified more mesic sites as ideal for whitebark pine regeneration (Tomback et al. 1990, Tomback et al. 2001).

Given the conflicting site requirements of whitebark pine regeneration and its unique seral role, it is difficult to devise a conservation strategy that maximizes regeneration recruitment. Accordingly, the main objective of this chapter is to identify factors that are most closely related to the recruitment and growth of whitebark pine in recently burned stands.

2.2 Study Areas

The study areas were distributed between the Rocky Mountains and North Cascades (Figure 2.1). Four of the sampling sites were in E.C. Manning Provincial Park located in the North Cascades. In the Rocky Mountains, four sites were located in Kootenay National Park; two were in Yoho National Park; three were in Banff National Park; and four were in Jasper National Park.

The land base of the B.C. Provincial Parks is classified using the Biogeoclimatic Ecosystem Classification (BEC) system (Pojar et al. 1987), whereas the National Parks land base is classified using the Ecological Land Classification (ELC) system of Parks

Canada (Holland 1976, Walker et al. 1978). Ecologically, the study areas in the provincial parks and protected areas of the North Cascades were classified as occurring within the ESSFmw and ESSFdc BEC subzones. Although neither Parks Canada nor the Province of Alberta employs the BEC system, the northern portion of the Rockies study area is likely in the ESSFmm, ESSFmmp subzones. The Southern Rockies study area is likely in the ESSFdk, ESSFwc, ESSFdc, and ESSFwm subzones. Within the ELC classification, sites are further classified; for the purpose of this study, Ecoregion and Vegetation type (Vegtype) were the two site classifiers used to identify candidate study sites. Study sites were located in the Upper Subalpine and Lower Subalpine Ecoregions; and in or directly adjacent to the C15, C21, O4, or O13 Vegtypes, as these Vegtypes were characterized by the presence of whitebark pine.

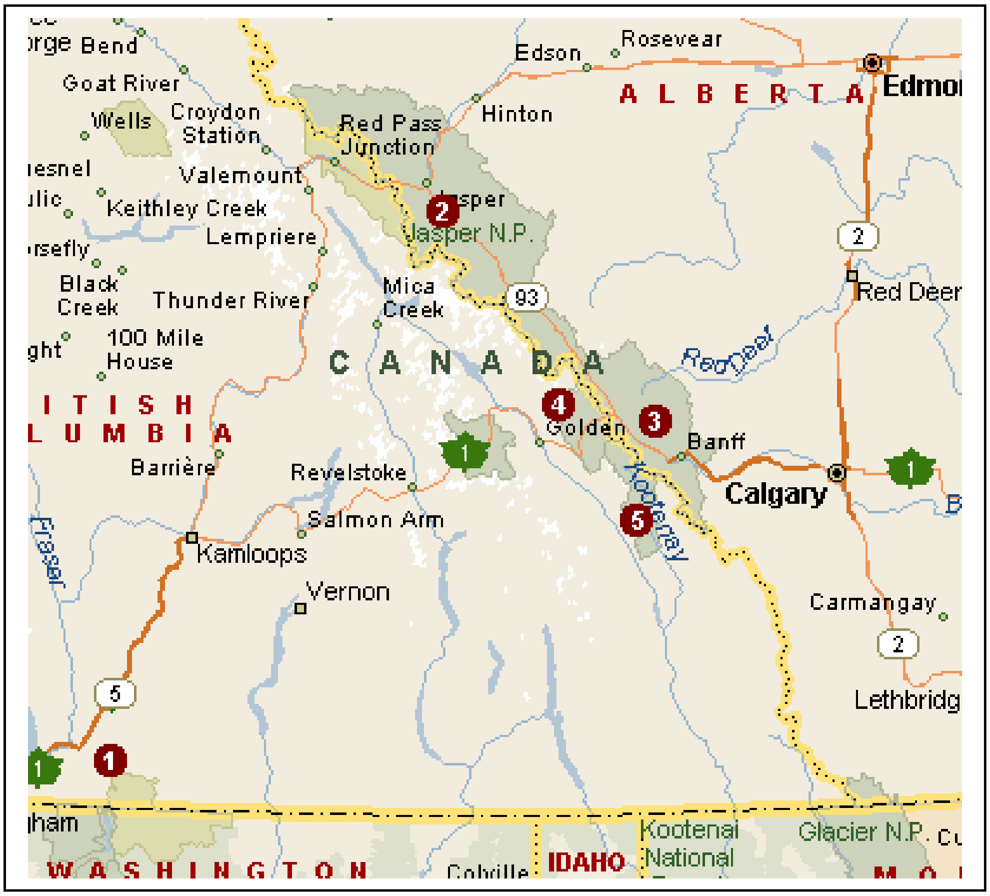

Figure 2.1 Map showing locations of study areas in parks 1) E.C. Manning Provincial Park, 2) Jasper National Park, 3) Banff National Park, 4) Yoho National Park, and 5) Kootenay National Park.

Both the Rocky Mountain and North Cascade study areas are characterized by mountainous terrain. The Rocky Mountains were formed primarily by thrust faulted and folded sedimentary layers (Price and Mountjoy 1970, Holland et al. 1982). The landforms in the North Cascades are composed of a combination of volcanic and sedimentary rock. The Rockies experienced major glaciation during the Pleistocene era and smaller glaciations during the more recent Holocene era. The North Cascades were glaciated several times during the Pleistocene, most recently by the Fraser Glaciation which ended 11,000 years B.P. at the beginning of the Holocene era (Ryder and Clague 1989, Hamilton et al. 2003).

Soils supporting subalpine whitebark pine are typically young and underdeveloped. Lithic Regosols, Dystric and Eutric Brunisols, and Orthic Humo-Ferric Podzols are the most common soils at subalpine whitebark pine sites (Canadian Society of Soil Science 1976; Canadian Soil Survey Committee 1978; Clayton et al. 1977; Ogilvie 1990). Organic layers are often thin or absent. Parent materials range from calcareous to non-calcareous. Soil forming processes of the subalpine are typically glacial, fluvial, glacial fluvial and colluvial action (Walker et al. 1984). The soil moisture regimes of whitebark pine stands range from xeric to mesic (Ogilvie 1990).

Sampling sites varied ecologically. Mean slope inclination ranged from 38% to 73%, and moisture regimes ranged from xeric to mesic (Table 2.1). Sampling sites were established on both warm and cool aspects. In addition to whitebark pine, forest cover consisted of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and subalpine larch (*Larix lyalli*). Common shrub species were *Juniperus communis, Menziesia ferruginea, Vaccinium scoparium, and Arctostaphylos uva-ursi*. Herb cover was dominated by *Epilobium angustifolium, Arnica cordifolia*, and *Valeriana sitchensis*.

Table 2.1 Characteristics of sampling sites in the North Cascades and Rocky Mountains. Sites represent recently burned and control stands; time since fire is for the recently burned stands.

Number	**Site**	**Time Since Fire (years)**	**Park**	**Sampling Year**	**Northing**	**Easting**	**Elevation (m)**	**Slope (%)**	**Aspect (degrees)**	Moisture Regime
1	Red Mountain (RM)	~60	Manning	2005	5434635	648811	1907	53	185	**submesic**
2	Heather Trail (HT)	49	Manning	2004	5448177	660668	1982	43	182	**submesic**
3	Silverdaisy (SD)	44	Manning	2005	5447849	642928	1925	54	225	**subxeric**
4	Skyline Trail (SL)	11	Manning	2005	5434797	637026	1856	66	171	**subxeric-xeric**
5	Hawk Creek (HC)	2	Kootenay	2005	5662646	568399	1774	49	180	**subxeric**
6	Honeymoon Pass (HP)	2	Kootenay	2005	5655592	573514	2109	64	288	**subxeric**
7	Stanley Glacier (SG-T)*	2	Kootenay	2005	5672567	565298	1873	53	268	**subxeric**
8	Stanley Glacier (SG)*	37	Kootenay	2005	5672451	565367	1899	59	252	**subxeric**
9	Assiniboine Slide (AS)	21	Kootenay	2005	5650467	571121	1870	62	82	**submesic**
10	Parker Ridge (PR)	~54	Banff	2005	5780296	494714	1761	55	137	**subxeric -xeric**
11	Arnica Lake (AL)	37	Banff	2005	5676113	569546	1930	38	348	**mesic**
12	Spray Lake (SP)	4	Banff	2005	5637552	610382	1934	43	131	**subxeric**
13	Amiskwi W (AM)	34	Yoho	2005	5716330	523959	2016	46	249	**submesic**
14	Amiskwi E (AP)	34	Yoho	2005	5715989	523246	2040	38	108	**submesic**
15	Whistler (WH)	33	Jasper	2005	5852477	425763	1866	52	109	**subxeric**
16	Old Man (OM)	20	Jasper	2005	5865690	433952	1810	63	229	**subxeric**
17	Medicine Lake (ML)	8	Jasper	2004	5857545	448678	1682	73	209	**subxeric -xeric**
18	Moab (MO)	5	Jasper	2005	5836450	433554	1955	55	85	**Submesic**

Climate patterns varied among study sites. The nearest meteorological weather station to the Manning Park sites was at Allison Pass (elevation 1340 m), where between 1974 and 1989, the mean annual temperature was 1.9°C, with mean annual highs and lows of 7.3°C and -3.5°C, respectively. Mean annual precipitation was 1095 mm, with 356 mm of rain and 675 cm of snow. In the Rocky Mountains, weather stations at Marmot Basin (2072 m) and Lake Louise (1529 m) were used for reference. At Marmot Basin, the mean annual temperature between 1996 and 2003 was -0.4°C, with mean annual highs and lows of 3.9°C and -4.6°C, respectively. Mean annual precipitation was 991 mm, with 342 mm of rain and 515 cm of snow. At Lake Louise, the mean annual temperature between 1965 and 2002 was -0.3°C, with mean annual highs and lows of 7.2°C and -7.7°C, respectively. Mean annual precipitation was 645 mm, with 264 mm of rain and 379 cm of snow.

2.3 Methods

Site Selection

Study stands were located by identifying recent high elevation burned stands from geographic information system (GIS) layers in national parks and from air photos in Manning Park. A GIS query on the Parks Canada database was performed to identify burned areas that were located near potential stands of whitebark pine based on ELC parameters. The age of each recently burned site was obtained from the ELC database in the National Parks and from the B.C. Ministry of Forests Protection Branch database for Manning Park. The ages of the Parker Ridge and Red Mountain burns were estimated based on the age of local trees. However, a certain amount of error is likely associated with these ages due to the slow recruitment of trees at these high elevations.

Whitebark pine regeneration was sampled at seventeen paired sites composed of recently burned – older burned stands in B.C. and Alberta. Two burns were sampled at the Stanley Glacier site, one which burned in 1968 (SG) and another which burned in 2003. The 1968 burned stand served as the control for the 2003 stand, and both stands were assessed as recently burned stands in the analysis. Recent burns ranged from two to sixty years post-fire.

At each site, plots were established within a recently burned stand and in a nearby paired control stand which had not burned recently. The control stands were ideally ecologically comparable to the recently burned stand, and contained a large component of whitebark pine; however, in many cases the stands differed ecologically, and whitebark pine was only a minor component of the stand. In each burned and control stand, twenty plots were systematically established from a random starting point. Plots were established at 25 m intervals in a sampling grid of 4 plots x 5 plots. In some stands the shape of the study area or local topography resulted in the plot layout being altered. In one control stand only eight plots were established due to extensive fire damage to all remaining forest. Basic plot design was adapted from those described in the Whitebark Pine Conservation Plan for the Canadian Rocky Mountain National Parks (Wilson and Stuart-Smith 2002). Two plot types and sizes were established at each location; a 5.6 m radius ecological/stand structure plot and an 11.3 m radius whitebark pine inventory plot, both using the same plot centre. The larger plot size for whitebark pine was used only during the 2005 field season; thus all whitebark pine sampled during the 2004 field season were within the smaller 5.6 m radius plot.

Ecological and Stand Structure Sampling

Environmental data collected in each 5.6 m radius plot included slope, aspect, elevation, latitude, longitude, meso-slope position, ground cover, and moisture regime. Elevation, latitude, and longitude were each measured using a Garmin 12 XL hand held GPS unit. Ground cover was determined by conducting a floristic survey and estimating the percent cover of each species. Trees other than whitebark pine were categorized by species and then tallied by diameter classes within height classes.

Since many stands occurred at the upper margins of the Engelmann Spruce – Subalpine Fir (ESSF) biogeoclimatic zone, many stands occurred outside of the range of the BEC classification system and could not be classed to site series. Therefore, stands were classed by moisture regime based on the vegetation present, slope position, slope, aspect, coarse fragment content, and comparisons with other stands, but were not classed to site series.

Vegetation and ground cover data were collected using the line intercept method. Four 5.64 m survey lines radiated out from the plot center along the contour and along the fall line of the slope. Vegetation cover of canopy ($\geq$10m), tall shrub (2-9.9 m), shrub (woody vegetation < 2 m) and herb (herbaceous species) intercepting the lines were estimated visually. Ground cover categories were bedrock, rock, bryophytes, mineral soil, organic soil, and decayed wood.

Whitebark Pine Sampling

Within each 11.3 m radius plot (5.6 m radius during the 2004 field season), all whitebark pine were sampled. Each tree had its height and diameter at breast height (DBH) measured and was assessed for dominance class and health status. The age of whitebark pine regeneration was determined by counting terminal bud scars or annual branch whorls on the main stem; counting annual rings on trees large enough to have increment cores taken; and destructive sampling on several trees to confirm the validity of the methods used. Dominance classes were - dominant, co-dominant, intermediate, or suppressed, based on the exposure to sunlight and apparent growth rate regardless of tree size. Dominant and co-dominant trees had captured their local site, regardless of the height of surrounding canopy trees; thus, regeneration growing in a canopy gap was classed as dominant or co-dominant if the gap was large enough to permit full sun and the tree displayed signs of vigorous growth.

Nutcracker caches often result in seedling clusters when more than one seed germinates. The size and frequency of seedling clusters may be a surrogate for seed germination or seedling survival as nutcrackers typically make multi-seed caches. Larger or more frequent clusters may indicate that a greater number of seeds germinated or seedling survival was greater. However, it cannot be assumed outright that a larger number of clusters is due exclusively to more than one seed germinating as basal branching may account for a large percentage of clusters (Weaver and Jacobs 1990). The angle of tree cluster branching was used to determine if a cluster was of seed or basal branching origin as tree clusters originating from basal branching typically display obtuse branching, whereas tree clusters originating from multiple seeds typically display acute branching (Jacobs and Weaver 1990). When clusters containing suspected branch originating stems were encountered, the stem was traced back to the point of germination to determine if the origin was branching or seed. Only stems originating from seed were counted as individual trees. While this method may not have eliminated all branch originating clusters, it likely increased the ability to count seed origin stems without tracing back each individual stem or conducting genetic analysis.

Whitebark pine seed availability is affected by a number of factors, and no standard techniques of seed source quantification have been developed. Seed sources were surveyed as major or minor; major seed sources occurred when whitebark pine formed a leading component of local forests, minor seed sources occurred as scattered individuals across the landscape. The distance to seed source, size of seed source and density of seed source were determined using several methods. Distance to seed source was determined by GPS, visual estimates, GIS, or from topographic maps. Size of seed source was determined from GIS layers or from visual estimates in the field. Density of major seed sources was usually determined from inventories completed where possible. In those cases where the seed source could not be inventoried, estimates were made by visual assessment.

2.4 Statistical Analysis

To identify what factors were most closely related to the recruitment and growth of whitebark pine, a multi-tiered approach was used. First, it was determined whether stands differed ecologically; second, recruitment in recently burned stands was compared with that in control forests to determine if burning facilitated whitebark pine recruitment; next the relationships between seed sources and recruitment were examined; and fourth, stands that differed ecologically but were somewhat homogeneous in terms of seed availability were examined. Tree growth and the presence of seedling clusters, used as a surrogate for multiple seed germination, were also compared between ecologically differing stands.

2.4.1 Site Characteristics

To assess whether stands differed ecologically, I used Canonical Correspondence Analysis (CCA) to relate physical characteristics to the understory species cover present at each study stand. For this analysis, understory plant species cover was compared with site descriptors of slope, aspect, Site Severity Index (SSI), elevation, soil moisture regime, ground cover of rock, mineral soil, organic soil (forest floor or Ah), latitude and longitude.

Aspect values in degrees were not suitable for analysis as, for example, 360° is closer to 1° than to 350°. Therefore, aspects were transformed into heat load and site severity indexes (SSI). Aspect values were rescaled along the northeast- southwest line with transformed values ranging from zero to one with one being the warmest aspect (southwest) and zero being the coldest aspect (northeast). Site severity index (SSI) is a measure combining slope and aspect, to provide an estimate of moisture and solar insolation (Beers et al. 1966). Measures for SSI range between -2 and +2, with steep southwest slopes scoring highest and steep northeast slopes the lowest.

Heat load (McCune and Keon 2002) is defined as:

$$\text{Heat load index} = \frac{1 - \cos(\theta - 45)}{2}$$

Site severity index (SSI) (Beers et al. 1966) is defined as:

$$\text{SSI} = [\sin(\text{aspect in degrees} + 225)](\%\ \text{slope}/45)$$

2.4.2 Comparison of Recently Burned and Control Stands

To determine if whitebark pine establishment was greater on recently burned or control stands, I compared the density of regeneration present on the recently burned stands with the density of regeneration originating within the same time period on the corresponding control stands. I used the non-parametric Wilcoxon signed rank test to compare each paired site. A non-parametric test was required because the tree density did not display a normal distribution. Since regeneration on control stands may not necessarily recruit to taller height classes, I plotted the height class distributions for all whitebark pine trees on each control site. Height classes were 1 m wide with the class number indicating the upper limit of the class.

2.4.3 Factors Affecting Whitebark Pine Recruitment on Recently Burned Stands

To compare whitebark pine recruitment between stands that burned at different times, I normalized the recruitment at each site to recruitment density per year. Although this approach better permits comparisons between different aged burns, the annual reproductive output of whitebark pine is highly variable due to the cyclical nature of cone production. Recruitment density per mast year may be a more informative dependant variable when assessing factors influencing recruitment.

Seed Source

Linear regression analysis was used to determine if annual recruitment densities were related to the seed source variables of size (ha) or density (stems/ha of seed trees). All variables were $\log_{(10)}$ transformed to establish a better linear relationship between the annual recruitment density and seed source variables. A nonlinear model was fit to the regression of recruitment density and distance to seed source.

Influence of ecological factors on whitebark pine establishment

Ecological parameters and species response curves rarely form linear relationships; this is particularly so for whitebark pine, whose distribution across the landscape may be more related to Clark's nutcracker behaviour than to ecological factors. By square-root transforming the response data, I was able to establish linear relationships in the data set. Using multiple regression, I compared the dependent variable [square root(stems/ha/year)] with the independent variables - slope, transformed aspect, elevation, SSI, and percent cover of rock, mineral soil, organic soil (Ah and forest floor), and vegetation cover. Since no regeneration was found at any site that burned since 2001, I did not include the Hawk Creek, Honeymoon Pass, Stanley Glacier (SG-T) or Spray Lake recently burned stands in the analysis.

Using the insolation values generated by integrating the Parks Canada Digital Elevation Model (DEM) with Solar Analyst (Fu and Rich 2000), I used Spearman's rank correlation to test whether regeneration density for the Rocky Mountain National Park locations was correlated with insolation values. To determine insolation values, the DEM model accounts for latitude, slope, aspect, and local topography to determine the solar radiation inputs to a given site in watts per m^2. Since a DEM did not exist for the North Cascade stands, only Rocky Mountain stands were used for this analysis.

To assess if seedling cluster characteristics differed between stands, I compared both the proportion of the population occurring in clusters and the mean size of clusters using the non-parametric Kruskall-Wallis one-way ANOVA. I further examined the seedling clustering tendencies using Spearman's rank correlation to test the presence and size of seedling clusters against latitude, longitude, soil moisture regime, aspect, and seed source descriptors.

The suitability of stands for tree growth was examined using linear regression to compare $\log_{10}$(height) to $\log_{10}$(age). Age and height data were $\log_{10}$ transformed to equalize the variance within the datasets. Four stands representative of xeric, sub-xeric, submesic and mesic moisture regimes were used in the analysis.

2.4.4 Analysis Software

Statistical analyses were performed using several software programs. Ordination was performed using PC-Ord (McCune and Mefford 1999). Non-parametric tests and linear regression were conducted using XLstat 2006 (Addinsoft, New York, U.S.A.). Nonlinear regression was performed using CurveExpert 1.38 (Hyams 1995).

2.5 Results

2.5.1 Site Characteristics

The ordination of sites based on environmental variables was significant ($P < 0.05$ – Monte Carlo randomized test), indicating that the site characteristics measured allow discrimination between the study stands. The first two canonical axes together explained 29.2% of the variance, the addition of a third axis increased the total variance explained to 41.4%. The environmental variables and intra-set correlations are shown in Table 2.2; the final scores for the species variables are shown in Table 2.3. The graph using the first two axes (Figure 2.2) shows the dispersed distribution of stands across environmental gradients.

The first canonical axis was negatively correlated with organic soil, soil moisture, and elevation, and positively correlated with rock cover and latitude. The second axis was negatively correlated with soil moisture and latitude; and positively correlated with aspect. Site severity index and mineral soil were not strongly correlated with any of the first three axes. The clustering of the North Cascade study stands in the upper left corner is due to the lower latitude and southern aspect of the stands.

Table 2.2 Results of the Canonical Correspondence Analysis relating ten environmental variables to understory vegetation cover on high elevation burns in the Rocky Mountains and the North Cascades correlation coefficients are given for the first three canonical axes.

Variable	Axis 1	Axis 2	Axis 3
Eigenvalue	0.736	0.583	0.550
Cumulative % explained	16.3	29.2	41.4
Pearson Correlations spp.-env.	0.995	0.989	0.954
Intraset Correlations of Environmental Variables			
SSI	0.088	0.295	-0.360
Mineral Soil	0.239	0.165	-0.263
Organic Soil	-0.494	0.201	0.550
Soil Moisture	-0.525	-0.505	0.261
Elevation	-0.531	-0.058	0.535
Slope	0.123	0.016	-0.632
Aspect	-0.067	0.566	-0.390
Rock Cover	0.467	-0.097	-0.615
Latitude	0.495	-0.466	-0.241
Longitude	-0.319	0.361	0.416

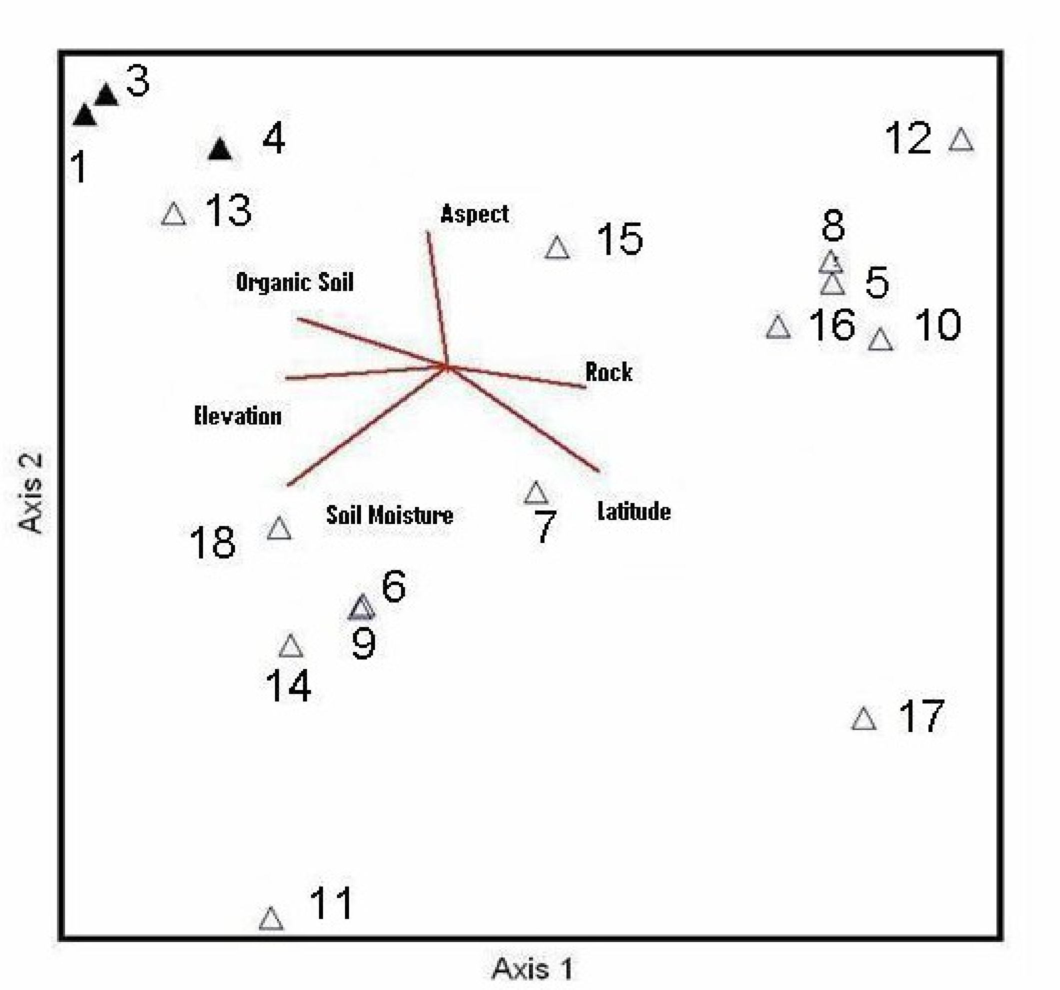

Figure 2.2 Ordination of the first two axes of the Canonical Correspondence Analysis (CCA). Stands indicated by Δ were located in the Rocky Mountains; stands indicated by ▲ were located in the North Cascades. The numbers correspond with stand numbers given in Table 1.1.

Table 2.3 Species scores on three axes for the Canonical Correspondence Analysis.

Species	Axis 1	Axis 2	Axis 3	Species	Axis 1	Axis 2	Axis 3
Achillea millefolium	0.462	0.507	-0.768	*Orthilia secunda*	-0.494	-0.051	0.395
Agoseris aurantiaca	1.174	0.100	-1.612	*Paxistima myrsinites*	-1.239	1.294	-0.166
Amelanchier alnifolia	1.353	0.307	-1.372	*Pedicularis racemosa*	1.103	0.282	1.900
Alnus crispa	0.577	0.684	-0.369	*Penstemon fruticosus*	-0.940	0.886	-0.248
Anaphalis margaritacea	-0.966	0.629	0.152	*Phlox diffusa*	-1.185	1.093	-0.559
Anemone multifida	-0.053	0.353	0.741	*Phyllodoce empetriformus*	-0.061	0.605	-0.174
Antennaria alpina	1.562	0.085	-1.589	*Poa* spp.	1.667	0.917	2.299
Antennaria spp.	0.330	0.139	-0.396	*Populus balsamifera*	1.057	-0.014	-1.432
Aquilegia formosa	0.322	-0.378	0.270	*Populus tremuloides*	1.522	0.118	-1.534
Arenaria capillaris	-0.959	1.054	-0.970	*Potentilla fruiticosa*	1.407	0.353	0.318
Arctostaphylos uva-ursi	1.335	-0.029	-1.424	*Rhododendron albiflorum*	-0.574	-1.180	0.394
Arnica cordifolia	0.003	-0.856	0.175	*Ribes* spp.	-0.363	-0.098	-0.074
Arnica mollis	-1.046	1.312	-0.176	*Rosa* spp.	1.060	0.100	-0.271
Aster spp.	0.961	0.167	0.177	*Rubus idaeus*	1.140	-1.762	-2.455
Betula glandulosa	1.562	0.085	-1.589	*Rubus parviflorus*	-0.164	-1.231	0.778
Campanula rotundifolia	1.005	-0.050	-0.736	*Salix arctica*	-0.661	-1.062	0.608
Carex spp.	1.335	-1.585	-2.535	*Salix* spp.	0.169	-0.106	-0.414
Cassiope mertensiana	-0.383	-0.541	0.400	*Sambucus racemosa*	-0.283	-1.040	0.514
Castilleja miniata	0.470	0.078	0.298	*Sedum* sp.	-0.634	1.063	-0.794
Cirsium sp.	1.234	0.808	0.951	*Senecio integerrimus*	-0.457	0.859	0.493
Cornus canadensis	0.067	-0.096	-0.084	*Senecio streptanthifolius*	1.219	0.213	-1.273
Dryas drummondii	1.562	0.085	-1.589	*Sherperdia canadensis*	1.196	0.374	-0.240
Empetrum nigrum	-0.359	-0.637	0.168	*Solidago multiradiata*	0.865	0.377	-0.547
Epilobium angustifolium	-0.248	-0.652	0.010	*Sorbus sitchensis*	-0.610	-0.326	-0.133
Erigeron peregrinus	0.307	0.460	-0.968	*Spirea betulifolia*	0.932	0.134	0.375
Erythronium grandiflorun	-0.427	0.626	0.537	*Stenanthium occidentale*	1.352	-0.479	-1.880
Fragaria virginiana	0.366	-0.027	0.017	*Thalictrum occidentale*	0.468	0.327	0.149
Gentianella amarella	1.174	0.100	-1.612	*Vaccinium ovalifolium*	-0.395	-1.294	0.831
Juniperis communis	1.054	0.263	-1.078	*Vaccinium membranaceum*	-0.889	0.176	0.021
Lathyrus nevadensis	1.669	0.945	2.261	*Vaccinium scoparium*	-0.985	0.828	-0.187
Ledum glandulosum	-0.660	-2.388	0.902	*Vaccinium* spp.	-0.561	-1.793	0.830
Linnaea borealis	1.221	0.566	-0.043	*Valeriana sitchensis*	-0.760	-0.095	-0.014
Lomatium sp.	-0.903	1.066	-1.519	*Veratrum viride*	-0.729	-0.361	0.295
Luetkea pectinata	-1.123	0.894	-0.082	*Viola orbiculata*	0.095	-0.140	0.156
Lupinus sp.	-1.178	1.116	-0.557	*Zigadenus elegans*	1.149	0.467	0.454
Menziesia ferruginea	-0.342	-1.649	0.810				

2.5.2 Comparison of Recently Burned and Control Stands

The comparison of recently burned and control stands produced mixed results. Though not all comparisons produced statistically significant differences, seven stands had higher regeneration on recently burned plots, three stands had higher regeneration on the control plots and one site had equal amounts of regeneration on both the recently burned and control plots (Table 2.4). Significantly greater regeneration occurred in burned stands at the Arnica Lake and Amiskwi Pass (W) sites; and significantly greater regeneration occurred in control stands at the Silverdaisy and Parker Ridge sites. The greatest net increase in regeneration on burned stands was at the Arnica Lake site which had nearly four times the regeneration of the adjacent control site (Table 2.4). The greatest post-fire recruitment was observed on mesic – submesic stands, and some xeric – subxeric stands had greater recruitment in the control forests. On the xeric – subxeric Parker Ridge site, regeneration was over 5 times greater in the control site than on the burned site.

Table 2.4 Comparison of regeneration densities between burned and control pairs using the Wilcoxon signed rank test. P values and differences in bold are statistically significant ($P < 0.05$).

Site	**Time Since Fire* (Years)**	**Whitebark Pine Regeneration Density Recently Burned (stems/ha)**	**Whitebark Pine* Regeneration Density Control (stems/ha)**	**Difference**
Red Mountain	~60	5	0	+ burned
Heather Trail	49	13	46	+ control
Skyline Trail	11	5	4	+ burned
Silverdaisy	44	104	371	**+ control**
Hawk Creek	2	0	0	**-**
Honeymoon Pass	2	0	0	**-**
Stanley Glacier	2	0	0	**-**
Assiniboine Slide	21	116	89	+ burned
Parker Ridge	~54	105	615	**+ control**
Arnica Lake	37	406	110	**+ burned**
Spray Lake	4	0	0	
Amiskwi –W	35	25	0	**+ burned**
Amiskwi –E	35	16	0	+ burned
Whistler	33	0	0	-
Old Man	20	0	0	-
Medicine Lake	8	1	1	**-**
Moab	5	36	0	+ burned

Whitebark Pine Height Class Distribution in Control Plots

The height class distributions for the Parker Ridge (PR) and the Silverdaisy (SD) control stands, which had higher recruitment than their paired burned stands, are shown in Figure 2.3. The Parker Ridge control stand had very high densities of regeneration with nearly 600 stems/ha in the 1 m height class, and the next largest height class being the 4 m height class with 10 stems/ha. Recruitment patterns in the Silverdaisy control stand were also weighted heavily to the 1 m height class with 202 stems/ha, although the 2 m and 3 m height classes had 155 stems/ha and 20 stems/ha; respectively.

The height classes for the control stands at the Arnica Lake (AL) and Amiskwi Pass (AM) sites, which had significantly higher recruitment in the recently burned stands, are shown in Figure 2.4. The 1 m height class was most common in the Arnica Lake stand at 83 stems/ha, followed by the 3 m height class at 18 stems/ha. The Amiskwi Pass stand had very poor recruitment at less than 4 stems/ha, all in the 1 m height class. The height class distributions for all control stands are shown in Appendix A.

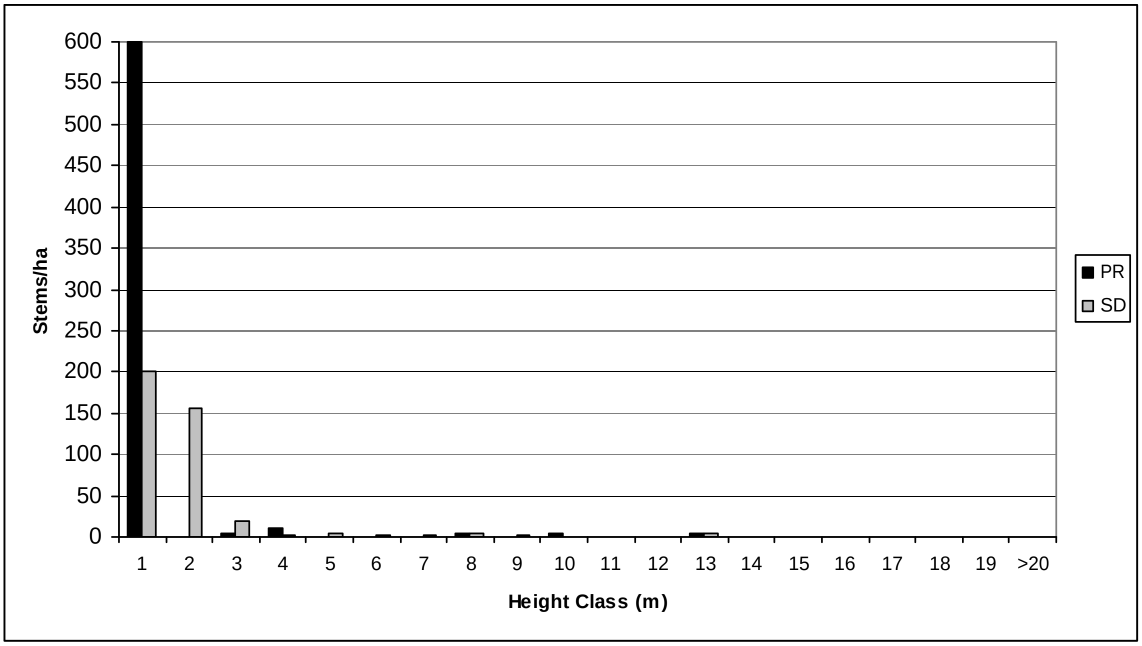

Figure 2.3 Height class (m) distribution of whitebark pine at the Silverdaisy and Parker Ridge control plots.

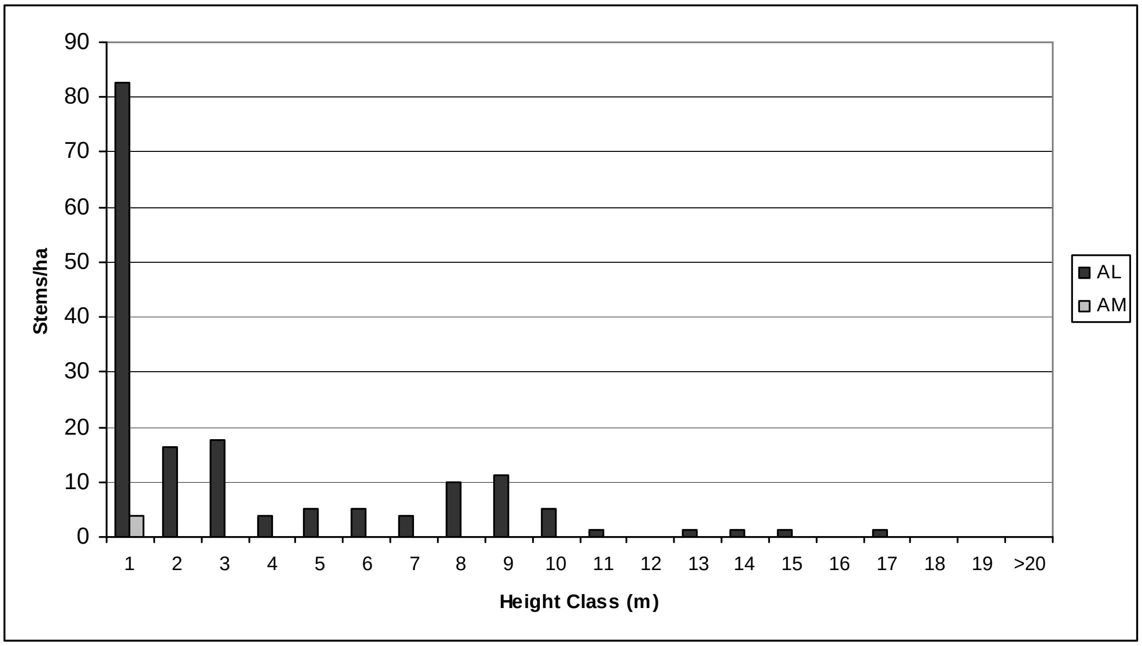

Figure 2.4 Height class (m) distribution of whitebark pine at the Arnica Lake (AL) and Amiskwi Pass (AM) control plots.

2.5.3 Factors Affecting Whitebark Pine Recruitment on Recently Burned Stands

Conifer Species on Recently Burned Stands

Lodgepole pine had the greatest density of all tree species in xeric-subxeric stands (mean of 1989 stems/ha) (Figure 2.5). Engelmann spruce had the greatest density in mesic and submesic stands at 225 stems/ha; it also exceeded whitebark pine density in xeric and subxeric stands. All tree species displayed patchy distributions both within and among burned stands as shown by the wide standard deviations displayed in Figure 2.5.

Seed Source Factors

Seed source factors were important predictors of whitebark pine regeneration. The linear regression of recruitment rate to size of seed source was significant ($R^2 = 0.56$, $P < 0.05$) (Figure 2.6); the linear relationship with seed source density was significant , but not as strong ($R^2 = 0.50$, $P < 0.05$) (Figure 2.7). Recruitment rate as a function of distance to seed source was best fit with a hyperbolic function ($R^2 = 0.58$, $P < 0.05$) (Figure 2.8).

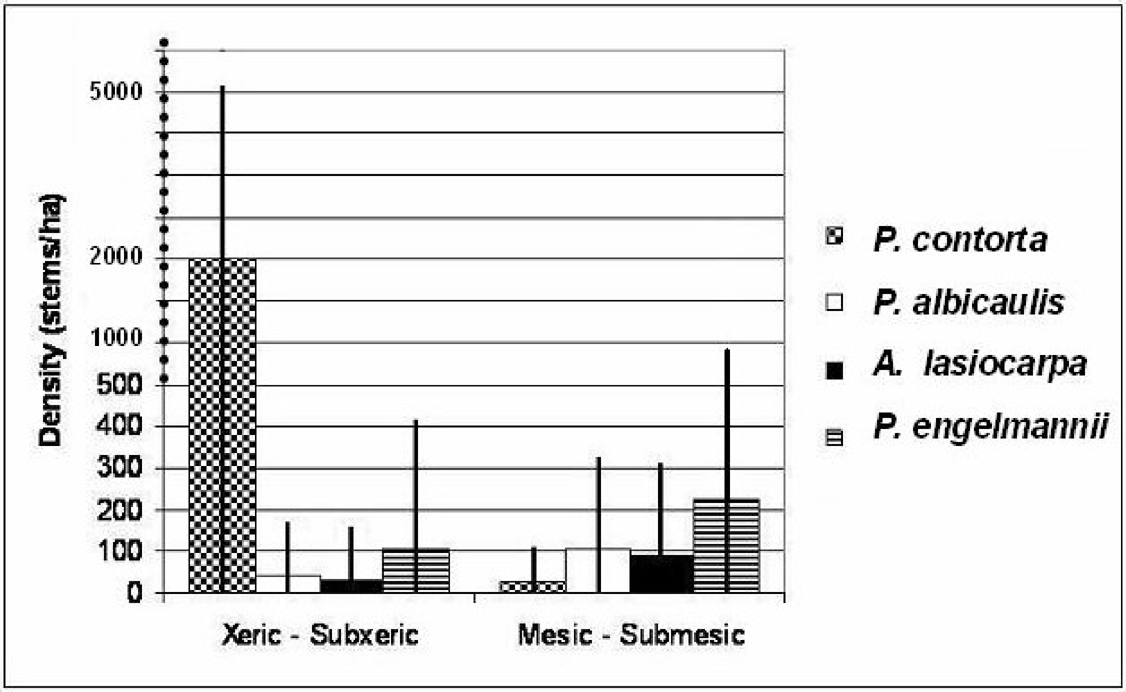

Figure 2.5 Mean densities of conifer species on xeric-subxeric stands and mesic-submesic recently burned stands. Error bars displayed show one standard deviation about the mean.

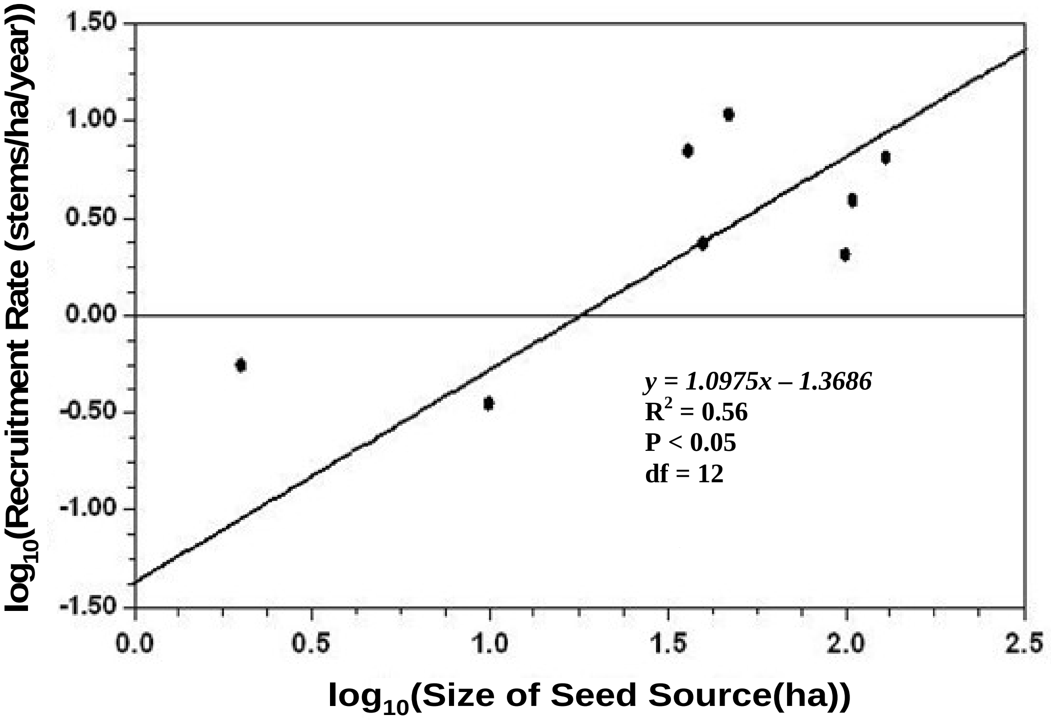

Figure 2.6 Regression of recruitment rate versus size of seed source for recently burned stands.

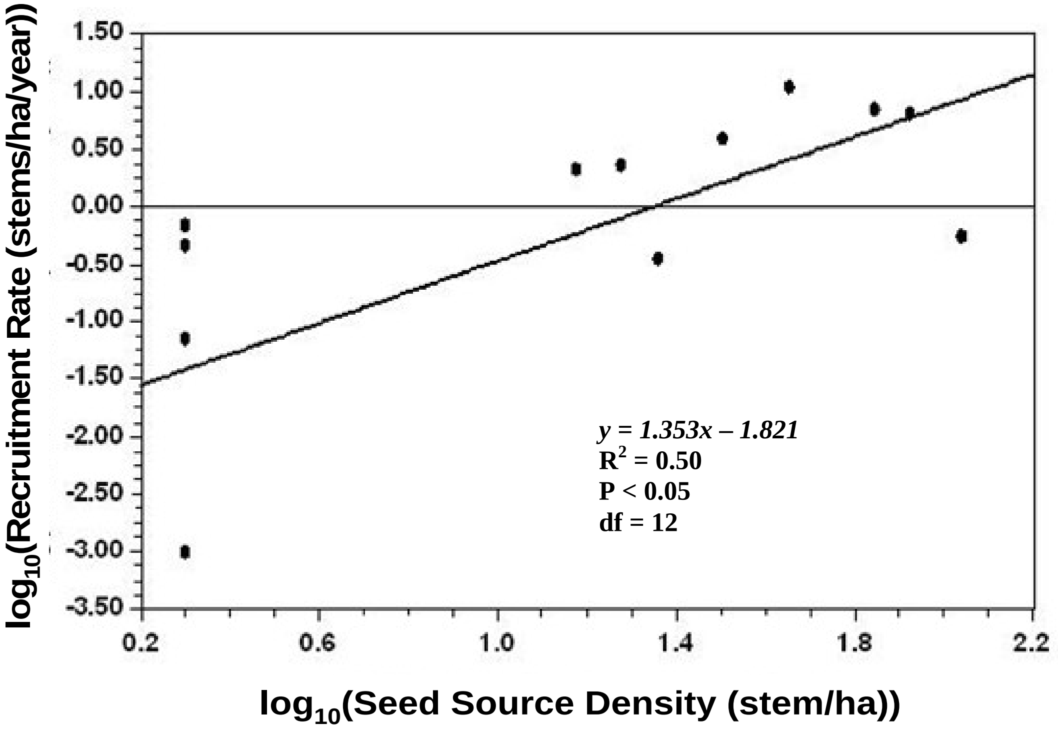

Figure 2.7 Regression of recruitment rate versus seed source density for recently burned stands.

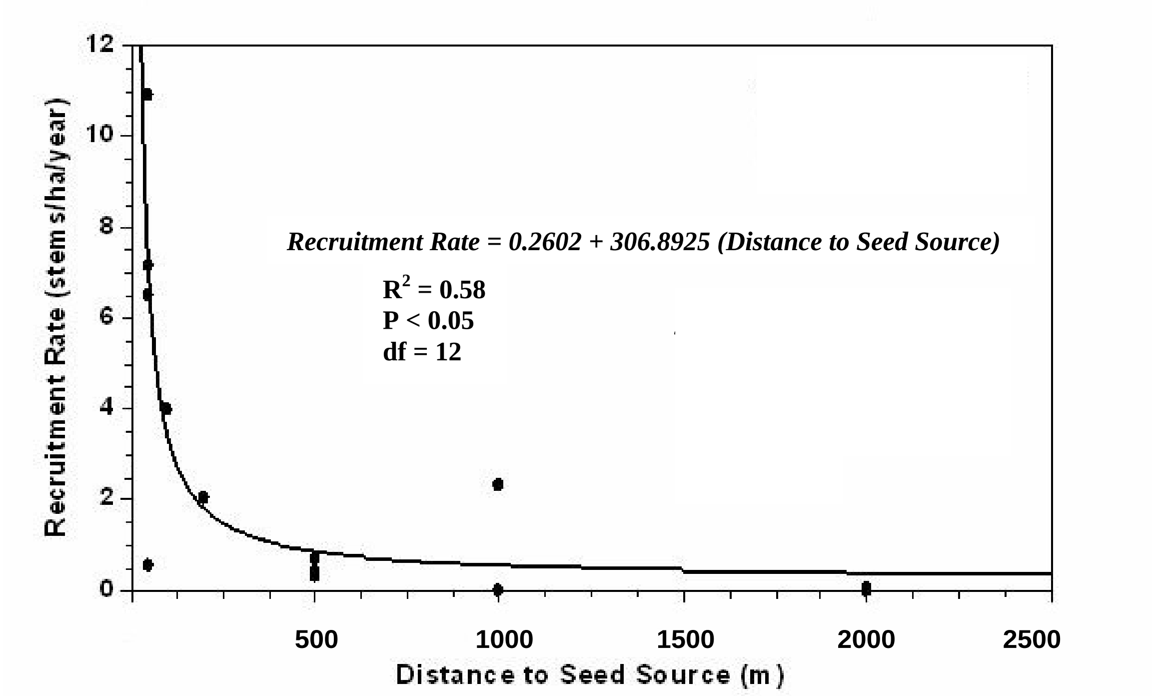

Figure 2.8 Regression of recruitment rate versus distance to seed source for recently burned stands.

The influence of ecological factors on whitebark pine establishment

Following the analysis of the seed source parameters, I eliminated stands with seed sources <2 ha in area and greater than 1000 m from the sampling site in order to reduce the effects of seed source factors on the analysis of ecological factors. This reduced the dataset to the Arnica Lake, Assiniboine Slide, Moab, Parker Ridge, Silverdaisy, Stanley Glacier, and Medicine Lake stands.

The best linear model for the recruitment of whitebark pine was: √Recruitment Rate = 3.225 – 0.0004(slope)(rock) – 1.124(aspect) ($R^2 = 0.87$; $P < 0.05$, d.f. = 7). Site severity index, elevation, bedrock, mineral soil, organic soil, decaying wood, and vegetation cover did not appear to be important in predicting the occurrence of whitebark pine regeneration. The mean values of each variable used in the regression are shown in Table 2.5**.**

Table 2.5 Mean values of site factors included in the multiple linear regression of recruitment rate in recently burned stands. Site abbreviations are given in Table 1.

	AL	AS	MO	PR	SD	SG	SL	ML
Site Severity Index	-0.46	-0.99	-0.87	0.04	1.19	1.15	0.8	1.53
Elevation (m)	1930	1870	1955	1761	1925	1899	1856	1682
Slope (%)	38	62	55	55	54	59	66	73
Transformed Aspect	0.23	0.13	0.16	0.51	0.99	0.93	0.78	0.97
Rock Cover (%)	8	12	9	60	13	21	47	56
Bedrock Cover (%)	7	1	3	1	1	5	6	7
Mineral Soil (%)	1	4	1	5	16	6	2	17
Organic Soil (%)	67	74	80	34	65	68	47	19
Decaying Wood (%)	7	2	3	0.5	5	3	2	2
Understory Vegetation Cover (%)	37	37	53	40	60	20	19	19
Stems/ha/year	11	6.5	7.2	2.1	2.4	4.0	0.4	0.6

Insolation

Recruitment rate was generally not related to monthly insolation values over the growing season (Figure 2.9). Recruitment showed a negative relationship with insolation values in all months, but significant correlations were only found in February (Spearman's rho = -0.88, $P < 0.05$), March (Spearman's rho = -0.94, $P < 0.05$), September (Spearman’s rho = -0.94, $P < 0.05$), and October (Spearman’s rho = -0.94, $P < 0.05$). The highest insolation values occurred in June during the longest days of the year.

Seedling Clusters

Whitebark pine regeneration occurred in clusters in ten of the twelve stands that had seedlings (Table 2.6). Red Mountain and Medicine Lake lacked whitebark pine clusters, whereas 91% of the trees at the Arnica Lake site were in clusters. On stands with clusters, the size of cluster did not differ (Kruskal-Wallis one-way ANOVA, $H=8.45$, $P>0.05$, d.f. = 9). The proportion of the whitebark pine population occurring in clusters differed between stands (Kruskal-Wallis one-way ANOVA, $H=105.2$, $P<0.05$, d.f. = 11). Significant correlations were found between cluster occurrence and several site characteristics, although all correlations were weak (Table 2.7). Cluster occurrence was positively correlated with soil moisture and size and density of seed source, and negatively correlated with distance from seed source. Clustering was also negatively correlated with warmer aspects. No correlation was found between changes in latitude or longitude. The Arnica Lake, Moab, and Skyline stands had the greatest proportion of whitebark pine in clusters. However, the latter two stands had very little regeneration.

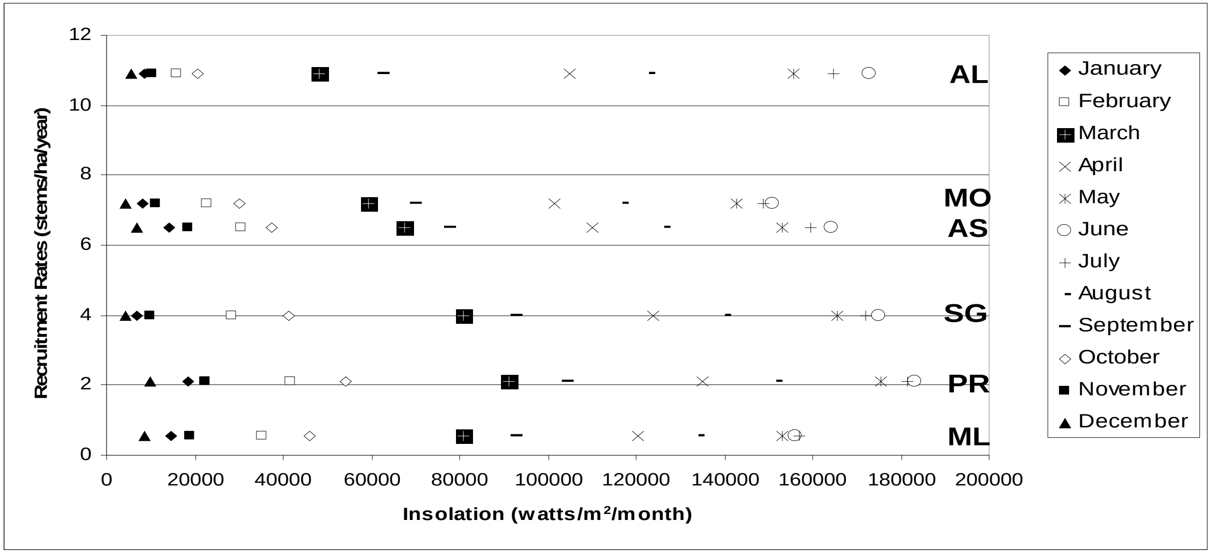

Figure 2.9 Whitebark pine recruitment per year in recently burned stands compared with monthly insolation values (watts/m^2/month) at the Rocky Mountain study stands. Stand location is indicated by letters on the right side of the figure.

Table 2.6 Summary of whitebark pine clusters in each recently burned stand.

Site	**Number of whitebark pine trees**	**Number of clusters**	**Proportion of whitebark pine in clusters**	**Mean cluster size**
Red Mountain	3	0	0.00	0.0
Heather Trail	15	3	0.73	3.7
Silverdaisy	83	18	0.77	3.6
Skyline	3	1	1.00	3.0
Hawk Creek	0	0	0.00	0.0
Honeymoon Pass	0	0	0.00	0.0
Stanley Glacier	118	24	0.86	4.3
Assiniboine Slide	93	21	0.80	3.5
Parker Ridge	23	3	0.52	3.0
Arnica Lake	325	77	0.91	3.8
Spray Lake	0	0	0.00	0.0
Amiskwi – W	20	3	0.45	3.0
Amiskwi – E	13	2	0.38	2.5
Whistler	0	0	0.00	0.0
Old Man	0	0	0.00	0.0
Medicine Lake	1	0	0.00	0.0
Moab	29	5	0.97	5.6

Table 2.7 Correlations of cluster occurrence and cluster size with ecological and seed availability factors in recently burned stands.

	Proportion of Pa in Clusters		**Cluster Size**	
Factor	**Spearman's rho**	**P**	**Spearman's rho**	**P**
Moisture Regime	0.202	**0.002**	0.171	**0.008**
Distance to Seed Source	-0.274	**0.000**	-0.256	**0.000**
Seed Source Density	0.266	**0.000**	0.250	**0.000**
Seed Source Area (ha)	0.449	**0.000**	0.438	**0.000**
Aspect	-0.140	**0.031**	-0.119	0.065
Latitude	-0.074	0.255	-0.073	0.264
Longitude	0.099	0.130	0.096	0.142

Whitebark Pine Height Growth

The rate of height growth decreased in the order – mesic > submesic > subxeric (Table 2.8, Figure 2.10). Age explained between 18 and 74% of the variation in height growth.

Table 2.8 Regression models for $\log_{10}$(age) – $\log_{10}$(height) of whitebark pine regeneration in recently burned stands on a range of moisture regimes.

Site	Moisture	Model	R^2	P
Arnica Lake (AL)	mesic	$\text{Log}_{10}(\text{height}) = 2.77\log_{10}(\text{age})-1.39$	0.74	0.00
Assiniboine Slide (AS)	submesic	$\text{Log}_{10}(\text{height}) = 2.72\log_{10}(\text{age})-1.44$	0.37	0.00
Silverdaisy (SD)	subxeric	$\text{Log}_{10}(\text{height}) = 1.68\log_{10}(\text{age})-0.29$	0.40	0.00
Stanley Glacier (SG)	subxeric	$\text{Log}_{10}(\text{height}) = 1.51\log_{10}(\text{age})-0.4$	0.18	0.00

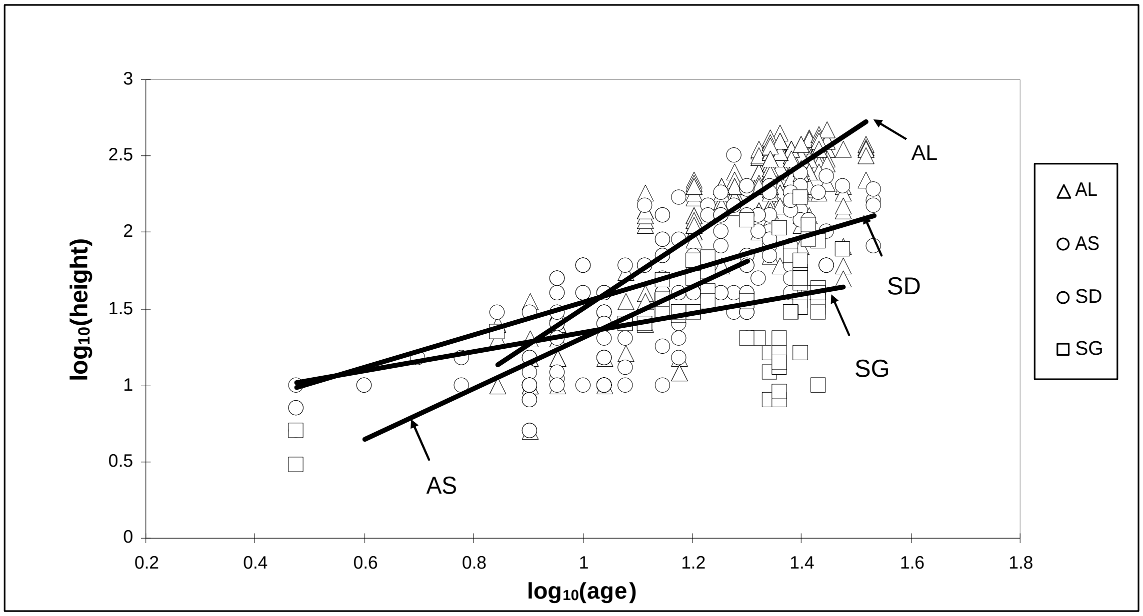

Figure 2.10 Scatterplot showing the relationships of whitebark pine height growth at Arnica Lake, Assiniboine slide, Silverdaisy, and Stanley Glacier stands to tree age.

2.6 Discussion

2.6.1 Source of Potential Errors

The potential sources of sampling error in this study were due to sample plot size, techniques used to quantify seed sources, tree aging techniques, the distribution of burns across the landscape, and poor pairing of burn and control stands. Whitebark pine is a species which grows in a clumped distribution across the landscape. During the first sampling season, a 5.64 m radius plot was used, which resulted in a very low number of whitebark pine being sampled; in the second sampling season, the plot radius was increased to 11.28 m in an attempt to increase the number of trees sampled. Random or systematic sampling using small fixed radius plots are not the most suitable methods for sampling a rare species with a clumped distribution such as whitebark pine; transects which cover a large area or very large plots are preferred sampling methods.

In quantifying the size of, density of, and distance to, seed sources, empirical measurements were taken where possible, otherwise values were derived from estimates in the field, from maps or from GIS layers. Further, given the long distance dispersal activities of Clark's nutcrackers, it is possible that regeneration did not originate from the nearby seed source. As well, other seed sources may have been located near study stands, but were not detected in the field.

The method used to determine the age of regeneration was subject to errors. Annual whorls used to determine age may be miscounted due to the presence of false whorls (Figure 2.11). The accuracy of the aging method was confirmed by destructive sampling of several trees for age confirmation, and by using the technique on trees of known age being grown at the University of British Columbia. Confounding this aging technique is the ability of whitebark pine to grow in a suppressed state ($\leq$0.25mm/year) (Campbell and Antos 2003); and the possibility of growth years missing due to persistent snowpack late into the growing season. Accuracy is likely greatest on young trees with vigorous growth and less accurate on older and suppressed trees.

The conclusions reached in this study are based exclusively on the characteristics of the stands surveyed. A large number of other potential site types exist, such as those with mesic conditions on gentle aspects, but these were not sampled due to limitations imposed by selecting only stands which had recently burned. Fire suppression limited the number of older recently burned stands (~> 30 years old), which, given the low recruitment of whitebark pine, are more informative for trend analysis than are many of the younger burns (< 20 years old) surveyed in this study.

Figure 2.11 Whorls used to determine tree age showing annual whorl and false whorl.

In comparing recently burned stands with older burned control stands, errors were present in that paired stands likely differed in ecological conditions. When assessing wildfires it is difficult to accurately establish adjacent paired stands as fire behaviour often changes with changing vegetation and ecological conditions. The stands in this study were paired as closely as locally available stands permitted; however, better pairings may have been made by studying stands following a more controlled prescribed fire situation or by expanding the pairings to include comparable sites located elsewhere on the landscape.

2.6.2 Site Characteristics

The ordination of stands suggested that the more important site factors related to the abundance of herbaceous and shrub species were soil moisture and the amount of organic soil present. The latitudinal gradient was marginally more important than the longitudinal gradient in influencing plant communities. This greater importance along the latitudinal gradient despite the wide separation longitudinally in stands between the Rockies and North Cascades is likely because the study stands in Manning Park were located in a zone characterized by interior species. High elevation species characteristic of more westerly maritime climates, such as mountain hemlock, were not found in any of the study stands. Thus although the Manning Park stands were located significantly further west, they were probably more floristically similar to Rocky Mountain stands than to nearby stands located several kilometers to the west of Manning Park. The large number of stands located along the latitudinal gradient effectively captured the transition in species composition due to reduced length of growing season and adaptations to the differing regional climates. Species associations of significance were the presence of *Gentianella amarella* exclusively in Jasper plots; the absence of *Sheperdia canadensis* from Manning Park plots; the very high abundance of *Menziesia ferruginea* at several of the Banff stands; and the singular presence of *Thuja plicata* in one of the Parker Ridge control plots in northern Banff National Park. *Thuja plicata* is more characteristic of Columbian forests, but has been reported in the headwaters of the Alexandra River in Banff National Park and the Fortress Pass area of Jasper National Park (Gadd 1995).

The importance of elevation as a variable was interesting in that all plots existed near the treeline and had similar species. It is possible that the abundance of a few species such as *Rubus idaeus* on the lower stands, and the greater abundance of *Cassiope mertensiana* and *Phyllodoce empetriformis* at the higher stands, contributed to elevation being a significant factor. The range in elevation of study stands from a maximum of 2109 m in Kootenay National Park to a minimum of 1682 m in Jasper National Park is indicative of the shift in treeline with latitude as the lowest site containing whitebark pine was also the furthest north. Little change in treeline elevation was noted between the North Cascades and the southern Canadian Rocky Mountains. Stuart-Smith (1998) found a distinct decrease in the elevation of whitebark pine stands north of the Columbia Ice Fields. Although the lowest site was north of the ice fields, other stands north of this point had elevations similar to more southerly stands. Treeline elevation depends partly on local topography and climate, but more importantly on regional climate arising from latitudinal location (Arno and Hammerly 1984, Stuart-Smith 1998).

2.6.3 Comparison of Recently Burned and Control Plots

The comparison of recently burned and control stands found that burning often increased seedling recruitment although not consistently. At several locations, higher recruitment was present in control stands, although whitebark pine was not necessarily a self replacing species in these stands. Other studies have also found that in some stands fire is not a necessity for seedling recruitment (Campbell 1998, Stuart-Smith 1998, Perkins 2001, Perkins 2004); however, fires have generally been found to have a positive effect on recruitment (Perkins 2004). An increase in recruitment following fire has important conservation implications, as it would help to maintain more, potentially blister rust resistant, genotypes on the landscape (Krakowski et al. 2003).

The higher recruitment in the control stands at the Heather Trail, Silverdaisy, and Parker Ridge sites does not necessarily suggest that whitebark pine plays a climax role in these stands. Based on the height class distribution in each of these stands, only in the Heather Trail control stand is whitebark pine self replacing; it may have limited self replacing ability in the Silverdaisy control stand; and it is not presently self replacing in the Parker Ridge control stand. Although the latter stand had the highest seedling density of all burned or unburned stands, most seedlings were suppressed under a closed lodgepole pine forest. Although suppressed whitebark pine may release over time, conservation concerns dictate that seedlings with a high potential to grow to reproductive size are more important than those whose future is uncertain. Likewise, greater recruitment in recently burned stands did not always indicate that whitebark pine in paired control forests was not self replacing. The Assiniboine Slide, Arnica Lake, Moab and Skyline control stands each displayed a potential to be self replacing, but had higher whitebark pine recruitment in the paired burn stands. Further, recruitment within the control forests represents only a portion of the reproductive output produced by the mature trees present. It is unclear whether the increased recruitment in burned stands outweighs the foregone reproductive output lost to seed trees killed by fire, as seeds may be dispersed out of mature closed canopy stands to nearby open areas. On stands with individuals phenotypically resistant to blister rust, fire should be limited or suppressed until cones can be collected (Krakowski et al. 2003).

Although seedling density may not always increase following fire, Perkins (2004) found greater seedling growth rates in burned stands. She attributed higher growth rates to an increase in NO_3^- and a potential increase in available P following fire. Phosphorous is important for early root development in whitebark pine seedlings (Perkins 2004) and inadequate root formation has been identified as a cause of seedling mortality (McCaughey and Schmidt 1990).

2.6.4 Factors Affecting Whitebark Pine Recruitment on Recently Burned Stands

Seed Source

Distance, size and density of the seed source were associated with whitebark pine recruitment. Stands adjacent to large seed sources showed higher recruitment rates than stands with distant or low density seed sources. Regardless of ecological conditions, proximity to a seed source is a basic requirement for adequate stocking following fire. The relationship between regeneration density and distance to seed source followed a negative exponential curve, with stands directly adjacent to seed sources exhibiting the greatest recruitment. This pattern is comparable to that found in other studies (Tomback et al. 1990, Tomback 1994). Perhaps too much emphasis has been placed on the long distance seed dispersal abilities of the Clark's nutcracker (Vander Wall and Balda 1977; Hutchins 1990), and not enough about the more likely shorter distance dispersal tendencies. Tomback et al. (1990) noted that nutcrackers buried greater densities of seeds adjacent to parent trees. Restoration recommendations derived from a genetic structure study state that "canopy openings should be in close proximity to seed-producing trees for successful regeneration via nutcrackers" (Richardson et al. 2002b).

The establishment of disjunct populations resulting from long distance dispersal by Clark's nutcrackers may be the most common form of population expansion in whitebark pine. The present distribution of whitebark pine is attributed to successive avian founder events from glacial refugia in the southern Canadian Rockies and northern U.S. (Richardson et al. 2002a, Krakowski et al. 2003). Based on the relationship of seedling establishment and distance to seed source, long distance dispersal is a slow means by which whitebark pine establishes new populations. Over time, individual trees may be added to these populations by additional long distance dispersal events; or when the founding trees reach maturity, a large number of their seeds are likely to be cached locally (Figure 2.12). On sites where long distance dispersal from numerous seed sources overlap, the low recruitment densities may be increased via seed inputs from multiple sources. The stand composition created by multiple long distance caches of varying relatedness may result in different mating opportunities within the same area including selfing, consanguineous mating, and outcrossing (Krakowski et al. 2003). Despite the potential genetic bottleneck caused by limited genetic diversity entering the new populations, genetic diversity observed in the Canadian Rockies suggests that gene flow by nutcrackers and wind dispersed pollen has been high enough to counter the effects of isolation (Stuart-Smith 1998). Further, lethal and detrimental genes may have been eliminated from the population, resulting in a species that is not adversely affected by inbreeding (Hoff et al. 1994), although several studies have speculated that blister rust may select against homozygous genotypes (Stuart-Smith 1998, Krakowski et al. 2003).

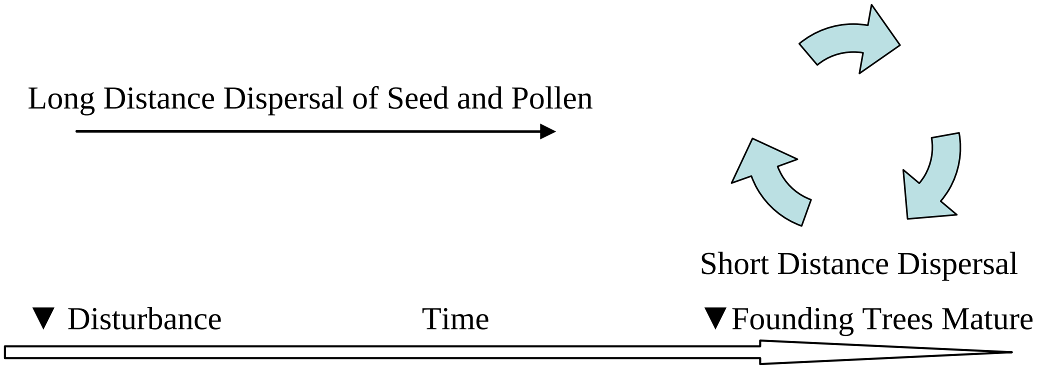

Figure 2.12 Schematic of tree recruitment from long distance dispersal. Width of dispersal arrow indicates relative volume of seed inputs.

Size and density of seed source contributed to the success of whitebark pine recruitment to a site. A combination of these variables may be important in total seed output, particularly during mast years. Another wind pollinated pine, *Pinus sylvestris*, experienced poor pollination in stands less than 2 ha in size (Sarva 1962, Weaver and Forcella 1985). In their study of cone production, Weaver and Forcella (1985) found that stand size was a major factor during mast years but not during non-mast years; indicating that the masting effect may be reduced in stands with small seed sources. They also found stand size and canopy cover, two variables easily measured from air photos, to be the best predictors of cone production.

The establishment of regeneration in recently burned areas may be restricted if seed sources are limited by blister rust damage (Campbell and Antos 2000). If seed production declines, recruitment patterns may mimic those associated with low density seed sources which will result in poor recruitment. This may result in more stands being dominated by other species and possibly converting to meadow, conspecific stands of lodgepole pine, or being dominated by Engelmann spruce or subalpine fir in early seral situations.

Influence of ecological factors on whitebark pine establishment

The lack of association between whitebark pine recruitment and many site variables is indicative of the wide ecological amplitude of this tree species. The tree was observed growing on sites ranging from cliffs throughout its range to boggy stands in Jasper National Park. Although elevation, bedrock and decaying wood were not important variables in selecting the best stands for regeneration in this study, they were important determinants of groups within the whitebark pine alliance in Alberta (Timoney 1999).

The significance of steep rock and aspect as significant variables in the regression model highlights sites poorly suited to tree establishment and a likely division of sites by aspect into those best suited to seed caching and those best suited to tree growth. The negative regression coefficient associated with interaction of slope inclination and rock cover is indicative of the poor suitability of steep rocky sites for whitebark pine establishment. Only the Arnica Lake site had a slope of less than 40%, and of the remaining steep sites, the Parker Ridge, Medicine Lake and Skyline Trail sites were each characterized as being both steep and rocky. Whitebark pine grew best on the gentler sloped site, and poorest on sites that were both steep and rocky. Whitebark pine commonly grows on sites with a high proportion of colluvial material (Timoney 1999). Steep rocky sites exhibit xeric moisture conditions with poor soil development, which limits the establishment of trees. In addition to poor soil moisture and nutrient conditions, rocky sites may also limit tree establishment by the downslope movement of rocks and cobbles which may cause mechanical damage to seedlings, saplings and trees. Although these sites are poorly suited to tree establishment, hardy species such as whitebark pine commonly establish on them, although other sites sampled in this study were more conducive to whitebark pine establishment.

Sites presumably best suited to seed cache recovery by Clark's nutcrackers were not necessarily best suited to tree recruitment. The slightly negative correlation of tree recruitment with warmer aspects may indicate that cooler aspects are more conducive to recruitment despite the fact that a disproportionate number of seeds may be cached on warm-dry aspects. This identifies a probable ecological separation in stands - those suited to tree establishment and growth, and those favoured for seed caching by the Clark's nutcracker. In this study the stands best suited to tree growth were on cool aspects, which had mesic-submesic soil moisture regimes. However, warm aspect stands on gentle slopes exhibiting mesis to submesic moisture conditions may be equally as well suited, but limitations imposed by the distribution of historic fires on the landscape limited the sampling of these stands. Whitebark pine establishes on hygrotopes ranging from very xeric to mesic, with the latter being best suited to tree growth (Krajina et al. 1982).

A study of the distribution of whitebark pine in western Canada found that typical habitats were ridge crests and steep southwest aspect slopes which receive high wind exposure and accordingly little snow cover (Ogilvie 1990). Based on the abundance of whitebark pine in stands with these characteristics, the location of mature whitebark pine stands is directly influenced by climatic factors resulting from geologic and topographic features (Stuart-Smith 1998). However, in the present study, cool aspect sites were best suited to early seral establishment of whitebark pine. These conditions for establishment are comparable to those found in work done in the U.S. (Tomback et al. 2001).

Whitebark pine displays different successional roles on different sites (Arno 2001). It is outcompeted by shade tolerant subalpine fir, Engelmann spruce, and mountain hemlock (*Tsuga mertensiana*) (Minore 1979); but is often able to coexist indefinitely with lodgepole pine, subalpine larch, and Douglas-fir. The shade tolerant species are also more common on mesic sites; whereas the latter grouping is characteristic of poorer and drier growing conditions, and is characterized by more open crowns. Weaver (2001) considered whitebark pine to have a broad fundamental niche, but a narrow realized niche due to competition. When competition is excluded, whitebark pine often expands its range, covering more of its physiological niche (Arno 2001, Weaver 2001). Elimination of competition through fire is a likely explanation for the success of whitebark pine on the mesic and submesic burned stands in the present study.

Clark’s nutcracker cache recovery behaviour may also contribute to increased recruitment on cooler sites. Warmer sites are usually snow free earlier, so nutcracker foraging may be concentrated in these areas. In laboratory studies, nutcrackers recovered caches in order of increasing costs (Bednekoff and Balda 1997), which in the natural setting may be associated with greater amounts of snow on cooler sites. Hutchins and Lanner (1982) observed nutcrackers making short distant seed caches near a seed source, then, following the complete removal of the cone crop, re-caching seeds to more distant secondary caches at a cliff site. The authors identified this behaviour as maximizing the number of seeds cached per individual. When cones were present, short distant flights to cache sites allowed for the greatest number of caching flights. When all cones were removed, the cached seeds were recovered and transported to sites better suited to cache recovery. Thus the same bird may cache seeds on both mesic and xeric sites; but is more likely to recover seeds from the xeric caches due to lower costs of recovery. Poor germination due to a lack of moisture on dry sites may be amplified by seed predation, as un-germinated seeds are more likely to be found over time by nutcrackers or rodents.

Although cooler aspects were the most suitable for whitebark pine establishment, the cool aspect stands in this study were still exposed to winds and insolation due to slope inclination, meso-slope position and valley orientation. In other studies, a lack of whitebark pine on sheltered north aspects has been attributed to fungal diseases associated with a prolonged snow pack, as well as competition from subalpine fir (Campbell 1998). No snow related fungal diseases were noted as a cause of mortality in this study. Snow creep is an important cause of whitebark pine seedling mortality (Keane Pers. comm.). The Red Mountain and Heather Trail stands in Manning Park may have had reduced recruitment due to snow creep. Both stands were located on warm aspects, but the North Cascades experience very high snow accumulations and the study stands were sheltered from prevailing winds by nearby ridges.

High snow accumulation may be more limiting to whitebark pine than the limitations imposed by xeric site conditions, as suggested by the presence of whitebark pine on cliffs and talus slopes and the absence of whitebark pine on sheltered sites. This may in part explain why whitebark pine is better known as a warm aspect species. Geologic features may also explain why whitebark pine is not widespread on cooler aspects. The dip of the bedrock in the front ranges of the Rocky mountains results in long smooth slopes on the southwest aspects and steep broken northeast aspects (Holland et al. 1982). Thus, cool aspect sites suited to early seral recruitment of whitebark pine may not be as common as warmer aspect sites, and steep rocky sites, which are poor for tree growth, may be more common on northeast aspects.

The negative correlation of recruitment rate with insolation value was statistically significant only during non-growing season months. This may indicate that cold stratification is more complete on these sites; that low insolation allows cooler sites to retain higher moisture levels through snowpack retention and lower evapotranspiration rates; that snowpack on cooler sites protects seeds from seed cache recovery; or likely a combination of these factors. During the growing season, insolation values on the Arnica Lake site, which had the greatest recruitment rate, increased to levels comparable to those on southerly aspects, but by September declined to levels comparable to other cooler aspect sites. Though reductions in insolation occurred late in the growing season, this trend may allow a balance between adequate amounts of solar inputs with the moderating effects of reductions in these inputs shortly after moisture deficits and summer drought effects have accumulated in August. Two major causes of seedling mortality are insolation and drought (McCaughey and Weaver 1990). Insolation damage is greatest earlier in the season during the longest days, with drought occurring later in the season as moisture deficits accumulate (McCaughey and Weaver 1990). On limber pine (*Pinus flexilis*) stands in Colorado, succession rates were negatively correlated with solar radiation (Donnegan and Rebertus 1999). Higher succession rates were attributed to high mortality of pioneer limber pine coupled with high recruitment of competing species 200 years post-fire, while on xeric stands with greater solar inputs, succession was stable or slowly increasing 300 years post fire. If succession rates show comparable trends in whitebark pine stands, the negative effects of fire suppression are likely present sooner on stands with lower insolation.

The comparisons of recruitment with insolation values were limited by the relatively low number of study stands spread out along a large latitudinal gradient. However, the results do indicate the potential utility of DEM models in predicting suitable sites for whitebark pine recruitment. To determine the utility of the insolation model values, a study of stands located at approximately the same latitude and covering a wide range of ecological conditions would likely reveal the full utility of the model.

Seedling Clusters

The proportion of the population occurring in clusters was greater in mesic - submesic stands on cooler aspects, while the size of seedling clusters was greater in mesic stands, further supporting greater germination and survival in cool moist stands. Although some of the differences in cluster occurrence could be attributed to nutcracker caching habits, other studies have also found greater clustering tendencies on cool moist stands (Tomback et al. 1990, Tomback et al. 2001). Smaller seedling clusters on warmer-drier aspects were attributed to higher intra-cluster competition for moisture (Tomback et al. 2001).

Breaking dormancy by exposure to cold is a requirement for germination of whitebark pine seeds (McCaughey and Tomback 2001). Reported stratification periods required by whitebark pine range from one month (Jacobs and Weaver 1990), to long (several months) or compound (multiple stratifications) (Pitel and Wang 1980, 1990, Leadem 1986, Burr et al. 2000, Tomback et al. 2001). The short stratification period (one month) is believed to be an adaptation preventing fall germination, but allowing for very early spring germination (Jacobs and Weaver 1990). Long or compound stratification periods may be due to underdeveloped embryos. Long stratification periods were found to reduce the temperature threshold for seed germination and root growth (Jacobs and Weaver 1990). Regardless of the requirements to break dormancy, cooler stands can provide long, compound or short stratification requirements while not compromising germination potential.

Germinating seeds indicate the presence of a seed cache to nutcrackers. Vander Wall and Hutchins (1983) found that 20% of caches recovered by adult nutcrackers were located by this technique, and all caches located by juvenile birds were found in this manner. Vander Wall and Hutchins (1983) also postulated that the duration over which germinating seeds are edible is only about 2-3 days post germination. This suggests that if germination of all seeds occurred simultaneously, higher intra-cluster recruitment could be expected than with staggered germination which would betray the presence of the seed cache, allowing non germinating seeds to be consumed.

Tree Growth

The presence of other conifer species regenerating in all stands is typical of the mixed species forests in which whitebark pine occurs. Only lodgepole pine appeared to limit whitebark pine recruitment at the early seral stage, as it quickly captured the site at the Stanley Glacier, Old Man and Whistler stands. In the lodgepole pine dominated stands, whitebark pine regeneration was found only at the Stanley Glacier site, where it was suppressed under the canopy of lodgepole pine. This is common in early seral stands, as lodgepole pine coexists with, and often competes with, whitebark pine for early successional dominance (Campbell and Antos 2000). Suppressed whitebark pine may release under canopy gaps after 150 years (Campbell and Antos 2003). It is possible that the recent widespread mountain pine beetle infestation may kill many of the canopy forming lodgepole pine, releasing the understory whitebark pine. Both the amount and age of lodgepole pine present in the pre-fire stand are important, as lodgepole pine grows at a much faster rate than does whitebark pine (Campbell and Antos 2003). In stands where whitebark pine competes with lodgepole pine, fire suppression may favour whitebark pine or other conifer species over lodgepole pine following disturbance if the forest composition shifts to late seral species prior to disturbance. The distribution of whitebark pine in the Rockies may be limited by successive fires that favor the regeneration of lodgepole pine (Day 1967, Timoney 1999).

The greater growth rate observed on mesic and sub-mesic stands is significant for conservation purposes as cone production is positively correlated with crown size (Weaver and Forcella 1985), and trees with greater growth rates may develop large crowns sooner, resulting in a reduction in time to reach full reproductive output. On more than half of the area in the U.S. where whitebark pine forms erect cone bearing trees, it is seral (Pfister et al. 1977, Steele et al. 1981, Steele et al. 1983, Arno 1986). The stands where whitebark pine is seral tend to be more moist and productive than stands where it is climax (Arno 1986).

I did not determine height-age relationships for the other conifer species present, so, with the exception of lodgepole pine leading stands, it is difficult to accurately assess if the present composition will be maintained as the forest matures. However, a comparison of Site Index equations and curves for B.C. (Hegyi et al. 1979) showed that on comparable stands whitebark pine should compete well with *Abies* spp. and *Picea* spp. This underscores the importance of early seral site conditions to whitebark pine which allow it to compete with shade tolerant species in stands where conditions are conducive to tree growth, as it ultimately may be replaced by the more shade tolerant species which have a greater self replacing ability.

Whitebark pine has been identified as not being as shade tolerant as subalpine fir or Engelmann spruce, but more tolerant than lodgepole pine (Arno and Hoff 1990). However, site factors may affect the shade tolerance of whitebark pine. In the Mountain Hemlock zone of B.C., whitebark pine was identified as shade tolerant on very dry sites, but these sites rarely supported enough tree cover to make shade a limiting factor (Krajina 1969). A later study found it to have low shade tolerance on very xeric to xeric sites (Krajina et al. 1982). In Alberta, whitebark pine was identified as competing successfully in heavy shade and competition (Day 1967, Timoney 1999). Whitebark pine has been rated as very intolerant of shade (Baker 1949), to intolerant, to intermediate tolerance of shade and competition (Arno and Weaver 1990, Day 1967, McCaughey and Schmidt 1990, Pfister et al. 1977, Steele et al. 1983, Arno and Hoff 1990).

The recruitment of conifer competition appeared to be limited by seed source. Poor recruitment of all tree species was observed in the Amiskwi Pass (2 stands), Heather Trail and Red Mountain burns decades following large scale stand replacing fire. The latter two stands have largely converted to meadow environments with scattered tree islands. All three stands were previously covered with forest cover as indicated by the number of standing and fallen snags remaining on site.

2.7 Summary and Conclusions

Fire was found to usually increase the recruitment of whitebark pine regeneration, but was not always a requirement. Several control forests had higher recruitment than their paired burn stands, but this did not necessarily mean that control forest had self-replacing potential as recruitment to taller height classes appeared unlikely. Conversely, greater recruitment on burned stands was not necessarily indicative of poor self replacing potential in the paired control. In many control stands the resulting regeneration was suppressed in the understory.

In predicting recruitment success, location near a large, well stocked seed source was a minimum requirement for reliable recruitment of whitebark pine to a site. Despite the known abilities of Clark's nutcrackers to transport seeds long distances, short distance seed dispersal appears to be more likely. In addition to proximity to a seed source, several other ecological site variables were also important in facilitating whitebark pine recruitment.

Whitebark pine occurred on a wide range of sites on all aspects. Aspect and the combination of slope and rock cover were the most important site variables affecting tree recruitment. Recruitment was positively correlated with cool aspects and negatively correlated with steep rocky stands. Other site variables such as bedrock, organic soil, mineral soil, elevation, vegetation cover, site severity index, decayed wood, and moisture regime were not important variables in predicting the success of whitebark pine recruitment to a site.

The increased recruitment on cooler aspects is contrary to the seed caching habits of Clark’s nutcrackers reported in other studies. On cooler aspects whitebark pine grew in greater densities and at greater rates than on warmer sites. The greatest recruitment occurred on sites that exhibited high but not prolonged insolation inputs over the growing season. This likely maximized productivity, but minimized the risk of drought. In cool aspect stands whitebark pine is an early successional species as more shade tolerant, conifer species also grew at higher densities when compared with drier stands. However, the greater growth rate of whitebark pine on cooler sites may reduce the time before large seed crops are produced by shortening the time required to develop a large full crown.

Although whitebark pine may be outcompeted by other conifer species in late seral situations, most of these other species coexisted or were less abundant in early seral situations. In early seral situations, only lodgepole pine regeneration limited the ability of whitebark pine to establish on drier sites. In suitable habitat whitebark pine did not coexist with lodgepole pine when whitebark pine seed sources were distant. In stands with adjacent whitebark pine seed sources, the two species coexisted, with lodgepole pine forming the dominant canopy layer and whitebark pine forming the suppressed layer.

Whitebark pine occurred more frequently in seedling cluster on cooler aspects. The greater occurrence of whitebark pine in larger and more abundant clusters in these stands may be due to several factors such as higher germination rates due to better cold stratification; improved moisture conditions resulting in greater germination and survival; lower seed depredation by Clark’s nutcrackers due to increased foraging costs; or a reduction in seedling mortality due to the moderating of drought and insolation factors.

Chapter 3. Chronology of Whitebark Pine Recruitment and Infection by White Pine Blister Rust

3.1 Introduction

The future of whitebark pine is considered to be threatened by a number of factors including white pine blister rust (*Cronartium ribicola*) and fire suppression which allows for seral replacement by more shade tolerant species. Prescribed fire has been used as a means of restoring whitebark pine by killing competing tree species and creating suitable microsites for Clark's nutcracker to cache seeds. This technique has been used in Canada's National Parks and in many protected areas in the U.S. The natural regeneration process following fire may facilitate selection of blister rust resistant individuals (Hoff unpublished, Tomback et al. 1995). In areas with heavy infection by white pine blister rust, most new seed will likely be produced by surviving individuals with some mechanism of rust resistance.

Reproduction in whitebark pine does not occur every year as cone production is cyclical with mast years separated by years of little or no cone production (Morgan and Bunting 1992). Numerous theories exist as to why plants have adopted masting as a reproductive strategy (Kelly 1994). One theory states that in animal dispersed species, a higher proportion of seeds are cached during mast years, as species that forage on seeds and species that both forage and cache seeds are quickly satiated and more of the seed crop is available exclusively for caching (Vander Wall 2002). Also, repeated large crops would increase populations of seed predators. A higher number of seeds cached equates to a higher number which could germinate if forgotten, which often corresponds to episodes of high recruitment following mast years. A demographic analysis of mature whitebark pine stands in the Canadian Rockies found that recruitment was episodic in some stands but continuous in others (Stuart-Smith 1998). This may suggest that masting or site factors limit establishment in some stands while in other stands recruitment is constant over time due to unknown factors.

Whitebark pine seeds exhibit variable dormancy, with seeds from the same cohort germinating asynchronously, typically between one to four years post dispersal (McCaughey 1993). This asynchronous germination allows whitebark pine to form a soil seed bank following years of high cone production. Asynchronous germination and the creation of a soil seed bank is believed to be an adaptation linked to the episodic production of seeds to equalize germination rates over time; to ensure that some seeds germinate under favourable moisture conditions; and to ensure the availability of seeds for consumption by nutcrackers following years of cone failure (Lanner and Gilbert 1994).

For seeds that do germinate, production is limited by three factors: growing season length (Weaver 1994; Kajimoto 1994); temperature (Kokorian and Nazarod 1995); and moisture (Perkins and Swetnam 1996). Climate variability linked to the winter Pacific Decadal Oscillation (PDO) was found to be an important factor governing growing season length and the establishment of other high elevation conifer species in the U.S. Pacific Northwest as positive PDO values were associated with lower snow packs (Peterson and Peterson 2001, Peterson et al. 2002).

Recent declines in whitebark pine populations due to white pine blister rust are a great conservation concern. White pine blister rust is an introduced disease caused by the fungus *Cronartium ribicola.* The fungus attacks 5-needled pines, with whitebark pine being particularly susceptible, resulting in widespread decline. In order to complete its life cycle, blister rust requires *Ribes, Pedicularis, or Castilleja* species as alternate hosts; passing from pine to the alternate host, then back to pine. The basidiospores which are dispersed from the alternate host infect increasingly more seedlings as they grow taller and become larger targets for basidiospores (Tomback et al. 1995).

Given the episodic tree recruitment observed in demographic studies and the increasing impacts of white pine blister rust on regeneration over time, the objectives of this chapter are to identify the recruitment rate of regeneration into recently burned areas; to determine what climate variables influence episodic recruitment; and to determine if white pine blister rust impacts increase with time since fire in the North Cascade Mountains of B.C. and the southern Canadian Rocky Mountains.

3.2 Study Areas

Whitebark pine regeneration was sampled at seventeen post fire stands in B.C. and Alberta. The stands ranged from two to sixty years post-fire. The study areas were distributed between the Rocky Mountains and North Cascades (Figure 2.1). Four of the sampling stands were in E.C. Manning Provincial Park located in the North Cascades. In the Rocky Mountains, four stands were located in Kootenay National Park; two were in Yoho National Park; three were in Banff National Park; and four were in Jasper National Park.

The land base of the B.C. Provincial Parks is classified using the Biogeoclimatic Ecosystem Classification (BEC) (Krajina 1959) system, whereas the National Parks land base is classified using the Ecological Land Classification (ELC) system. Ecologically, the study areas in the Provincial Parks and protected areas of the North Cascades were classified as occurring within the ESSFmw and ESSFdc subzones. Although neither Parks Canada nor the Province of Alberta employs the BEC system, the northern portion of the Rockies study area is likely in the ESSFmm and ESSFmmp subzones. The Southern Rockies study area is likely in the ESSFdk, ESSFwc, ESSFdc, and ESSFwm subzones. Within the ELC classification, Ecoregion and Vegetation type (Vegtype) were the two site classifiers used to identify candidate study stands. Study stands were located in the Upper Subalpine and Lower Subalpine Ecoregions; and in or directly adjacent to the C15, C21, O4, or O13 Vegtypes, as these Vegtypes were characterized by the presence of whitebark pine.

Both the Rocky Mountain and North Cascade study areas are characterized by mountainous terrain. The Rocky Mountains were formed primarily by thrust faulted and folded sedimentary layers (Price and Mountjoy 1970, Holland et al. 1982). The landforms in the North Cascades are composed of a combination of volcanic and sedimentary rock. The Rockies experienced major glaciation during the Pleistocene era and smaller glaciations during the more recent Holocene era. The North Cascades were glaciated several times during the Pleistocene, most recently by the Fraser Glaciation which ended 11,000 years B.P. at the beginning of the Holocene era (Ryder and Clague 1989, Hamilton et al. 2003).

Soils supporting subalpine whitebark pine are typically young and underdeveloped. Lithic Regosols, Dystric and Eutric Brunisols, and Orthic Humo-Ferric Podzols are the most common soils at subalpine whitebark pine stands (Canadian Society of Soil Science 1976; Canadian Soil Survey Committee 1978; Clayton et al. 1977; Ogilvie 1990). Organic layers are often thin or absent. Parent materials range from calcareous to non-calcareous. Soil forming processes of the subalpine are typically glacial, fluvial, glacial fluvial and colluvial action (Walker et al. 1984). The soil moisture regimes of whitebark pine stands range from xeric to mesic (Ogilvie 1990).

Sampling stands varied ecologically. Mean slope inclination ranged from 38% to 73%, and moisture regimes ranged from xeric to mesic (Table 1). Plots were established on both warm and cool aspects. In addition to whitebark pine, forest cover consisted of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and subalpine larch (*Larix lyalli*). Common shrub species were *Juniperus communis, Menziesia ferruginea, Vaccinium scoparium*, and *Arctostaphylos uva-ursi*. Herb cover was dominated by *Epilobium angustifolium*, *Arnica cordifolia*, and *Valeriana sitchensis*.

Climate patterns varied among study sites. The nearest meteorological weather station to the Manning Park sites was at Allison Pass (elevation 1340 m), where between 1974 and 1989, the mean annual temperature was 1.9°C, with mean annual highs and lows of 7.3°C and -3.5°C, respectively. Mean annual precipitation was 1095 mm, with 356 mm of rain and 675 cm of snow. In the Rocky Mountains, weather stations at Marmot Basin (2072 m) and Lake Louise (1529 m) were used for reference. At Marmot Basin, the mean annual temperature between 1996 and 2003 was -0.4°C, with mean annual highs and lows of 3.9°C and -4.6°C, respectively. Mean annual precipitation was

991 mm, with 342 mm of rain and 515 cm of snow. At Lake Louise, the mean annual temperature between 1965 and 2002 was -0.3°C, with mean annual highs and lows of 7.2°C and -7.7°C, respectively. Mean annual precipitation was 645 mm, with 264 mm of rain and 379 cm of snow. In addition to these weather stations, data was also used from Environment Canada meteorological stations at Hope Slide (674 m) and Kootenay Crossing (1170 m) to compare with recruitment patterns. The Hope Slide station was used as it had data over a longer time frame (1975 – 2002); and the Kootenay Crossing station was used as it was located near three of the Kootenay National Park study sites and had long term data (1965-2002). Snow water equivalent data was obtained from the B.C. Ministry of Environment snow survey data. Snow water equivalents were obtained for Floe Lake located at 2090 m elevation in Kootenay National Park and Blackwall Peak located at 1940 m elevation in Manning Provincial Park.

3.3 Methods

Site Selection

Study stands were located by identifying high elevation burn stands from GIS layers in the national parks or from air photos in Manning Park. A GIS query on the Parks Canada database was performed to identify burned areas that were located near potential stands of whitebark pine based on ELC parameters.

In each recently burned stand, twenty plots were systematically established from a random starting point. Plots were established at 25 m intervals in a rectangular sampling grid of 4 plots x 5 plots. On some stands the shape of the study area or local topography resulted in the plot layout being altered.

Whitebark Pine Sampling

Whitebark pine trees were sampled within a 5.6 m radius plot in 2004 and a larger 11.3 m radius plot in 2005. Each whitebark pine tree occurring in the plot area had its height and diameter at breast height (DBH) measured and was assessed for its dominance and health status. The age of whitebark pine regeneration was determined by counting terminal bud scars or annual branch whorls on the main stem. Dominance classes were dominant, co-dominant, intermediate, or suppressed, based on the exposure to sunlight and apparent growth rate regardless of tree size. Dominant and co-dominant trees had captured their local site, regardless of the height of surrounding canopy trees. Thus, regeneration growing in a canopy gap was classed as dominant if the gap was large enough to permit full sun and the tree displayed outward signs of vigorous growth.

Whitebark pine were classified as healthy, sick or dead. Trees were classified as sick based on the presence of white pine blister rust. Trees declining due to environmental conditions were not classified as sick. Dead trees with cankers were classified as dead due to blister rust; dead trees without cankers were classified as dead unknown.

At the Arnica Lake, Assiniboine Slide and Stanley Glacier stands in the Rocky Mountains, and the Silverdaisy, Red Mountain and Heather Trail stands in Manning Park, the regeneration density of whitebark pine each year was compared with precipitation amounts in spring (May + June), summer (July + August), total growing season, total growing season from the year prior to germination and total growing season from the year following germination. Regeneration was compared with precipitation data at these stands only, because the selected stands had long-term regeneration data and the weather stations had long-term precipitation data. Many other weather stations existed throughout the study areas, but no others were found that had long-term, consistent precipitation data.

Winter PDO values were obtained from the Climate Impacts Group at the University of Washington. I compared the year of whitebark pine establishment with PDO values and with spring snow water equivalents (May 1) for the year of establishment. I compared these values for each site, for the total recruitment on all stands, for xeric – subxeric stands, and for mesic-submesic stands.

3.4 Statistical Analysis

3.4.1 Recruitment Trends of Whitebark Pine on Recently Burned Stands

I used the non-parametric Spearman's rank correlation test to examine recruitment against time since fire and recruitment among different stands to determine if recruitment is constant over time and if recruitment events occur independently on different stands. Recruitment rate between stands grouped by moisture regime was compared using the non-parametric Mann-whitney test.

Climate Variables

Using the precipitation data for Kootenay National Park and Manning Park, I compared recruitment in six stands with the precipitation variables using the Spearman's Rank Correlation test. I also used the Spearman's Rank Correlation test to compare recruitment with PDO values and snow water equivalents.

3.4.2 White Pine Blister Rust Infection of Regeneration on Recently Burned Stands

At the stand level, I used non-linear regression to test whether the level of blister rust infection was related to time since fire. The infection of individuals by white pine blister rust was tested using stepwise logistic regression. The dependent variable of rust infection was tested against the independent variables tree age, tree height, latitude, and longitude.

3.4.3 Analysis Software

Statistical analyses were performed using several software programs. Non-parametric tests were performed using Graphpad 4.0 for Windows (Graphpad Software, San Diego, California). Linear and logistic regression were done using Statgraphics Centurion XV Version 15.0 (Statpoint Inc. 2006).

3.5 Results

3.5.1 Recruitment Trends of Whitebark Pine on Recently Burned Stands

The rate of recruitment following fire was typically low. Spearman's rank correlation for recruitment and time since fire was significant only when recent burns were included in the analysis, which weighted the analysis to recent burns with low regeneration (Spearman's rho = 0.68; $P<0.05$). However, when burns which occurred since 2001 were removed from the analysis, recruitment was not significantly correlated with time since fire (Spearman's rho = 0.42; $P > 0.05$).

Stands located near seed sources had greater whitebark pine recruitment than did stands requiring long distance seed inputs. Red Mountain did not have recruitment until 35 years post fire, and the Whistler and Old Man stands had no whitebark pine several decades following fire. Aside from these three stands and stands burned within the last four years, all other stands had regeneration within 15 years of fire. Mesic – submesic stands showed higher rates of recruitment than did xeric – subxeric stands (Mann-Whitney $P < 0.05$). (Figure 3.1). This comparison was not significant when the Arnica Lake stand was removed; however, it was left in for the comparison as it was not statistically different than several other stands (SG,AS), in the study (Dunn's $P<0.01$).

Three stands that burned since 1994 had recruitment. Recruitment on the Moab site exceeded the recruitment of the other two stands by a factor of seven, despite only burning 5-years prior to this survey (Figure 3.2). The Moab site recruitment was 36 stems/ha compared with 5 stems/ha at Medicine Lake and 4 stems/ha in the Skyline recently burned plots. On stands burned prior to 1985 (Figure 3.3), recruitment over the past ten years was greatest in the Assiniboine slide plots (50 stems/ha) followed by Arnica Lake (35 stems/ha).

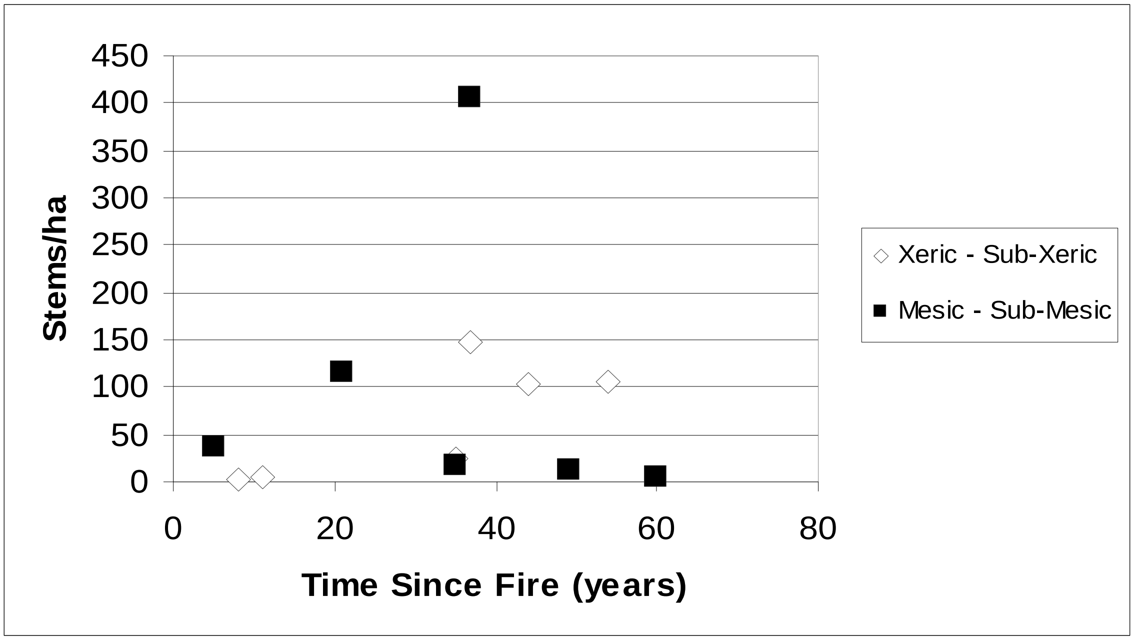

Figure 3.1 Regeneration density of whitebark pine in xeric-subxeric stands and mesic – submesic stands burned at different times.

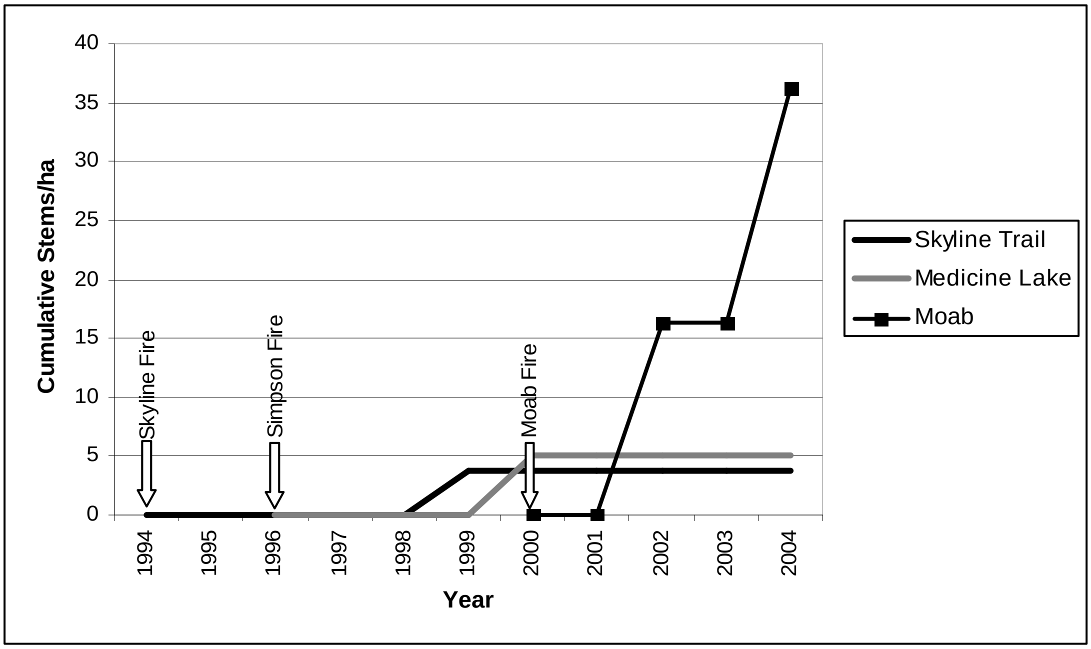

Figure 3.2 Whitebark pine recruitment trends in recently burned stands. The Medicine Lake site was located within the Simpson fire.

Recruitment showed similar trends across the entire study area as illustrated by five stands (Figure 3.3). Recruitment peaked in the early 1980's and then again to a lesser extent in the early 1990's. The Arnica Lake and Stanley Glacier stands were about

10 km apart, with the Parker Ridge site located approximately 150 km north; the Assiniboine slide site located approximately 50 km south, and the Silverdaisy site located about 450 km west. Recruitment at the Stanley Glacier site was correlated with that of all other stands except the Assiniboine Slide, which was not correlated with any other stands (Table 3.1). Recruitment in the Arnica Lake, Stanley Glacier and Silverdaisy stands was significantly correlated. The greatest correlation was between the Stanley Glacier and Arnica Lake stands, which were also the two stands in closest proximity.

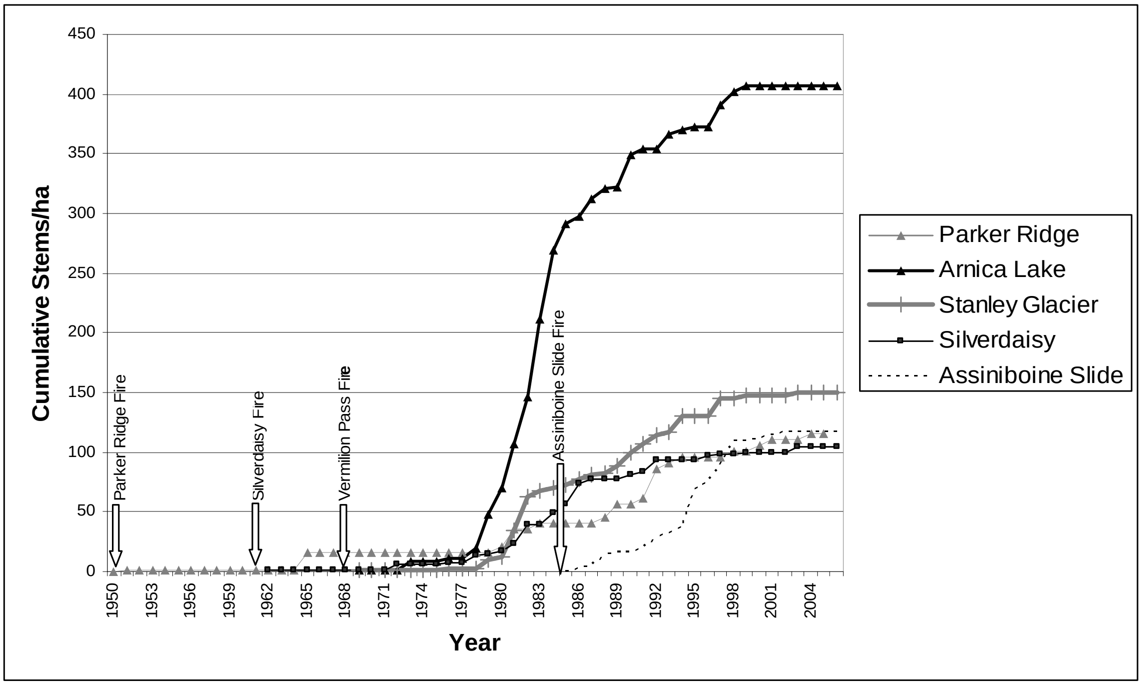

Figure 3.3 Whitebark pine recruitment trends in stands burned prior to 1985. The Arnica Lake and Stanley Glacier stands were located within the Vermilion Pass fire area.

Table 3.1 Spearman’s correlation coefficients of whitebark pine recruitment in stands which burned prior to 1985. Significant correlations (Bonferroni’s multiple comparison adjusted P<0.008) are shown in bold.

Recently Burned Site	PR	AL	SG	SD	AS	RM	HT
Parker Ridge	**1**						
Arnica Lake	0.18	**1**					
Stanley Glacier	**0.35**	**0.66**	**1**				
Silverdaisy	0.07	**0.41**	**0.53**	**1**			
Assiniboine Slide	-0.11	0.12	0.08	-0.18	**1**		
Red Mountain	0.17	0.11	0.12	0.01	0.01	**1**	
Heather Trail	-0.17	-0.04	0.08	-0.02	-0.03	**0.34**	**1**

Recruitment and Climate Patterns

Recruitment showed weak associations with precipitation patterns (Figures 3.4 - 3.5, Table 3.2). In the Rocky Mountains near the Kootenay Crossing weather station, recruitment was significantly correlated with growing season precipitation in the Stanley Glacier burn plots (Spearman's rho = 0.49, P <0.01); and with summer precipitation in the Arnica Lake burn plots (Spearman's rho = 0.52, P < 0.01). Recruitment in the Assiniboine slide burn plots was not significantly correlated with either spring or summer precipitation.

In Manning Park, recruitment in the Red Mountain burn plots was correlated with summer precipitation (Spearman's rho = 0.42, P < 0.01); and recruitment in the Heather Trail burn plots was correlated with total growing season precipitation (Spearman's rho = 0.38, P <.01). Recruitment in the Silverdaisy burn plots was correlated with precipitation amounts in the growing season following that in which seed germinated (Table 3.2).

Table 3.2. Spearman's correlation coefficients for tree recruitment and precipitation. Significant correlations (Bonferroni's multiple comparison adjusted P<0.01) are shown in bold.

Period of Precipitation	Arnica Lake	Stanley Glacier	Assiniboine Slide	Silverdaisy	Red Mountain	Heather Trail
Spring	0.04	0.38	0.25	0.15	0.36	0.39
Summer	**0.52**	0.31	0.20	0.15	**0.42**	0.32
Growing Season	0.31	**0.49**	0.31	0.14	0.44	**0.38**
Previous Growing Season	0.35	0.19	0.37	0.11	0.05	-0.04
Following Growing Season	0.25	0.29	0.34	**0.41**	0.01	-0.06

Correlations between the PDO Index and whitebark pine recruitment in each stand were significant only at the Arnica Lake recently burned stand (Spearman's rho = 0.38; P < 0.05) (Figure 3.6). However, significant correlations were found when whitebark pine stands were grouped by moisture classes into xeric-subxeric stands (Spearman's rho = 0.38; P < 0.05) and mesic – submesic stands (Spearman's rho = 0.34;

P = 0.04). Snow water equivalents for May 1 were significantly negatively correlated with annual PDO values (Spearman's rho = -0.62; P < 0.05). However, snow water equivalents were not correlated with whitebark pine recruitment on any site.

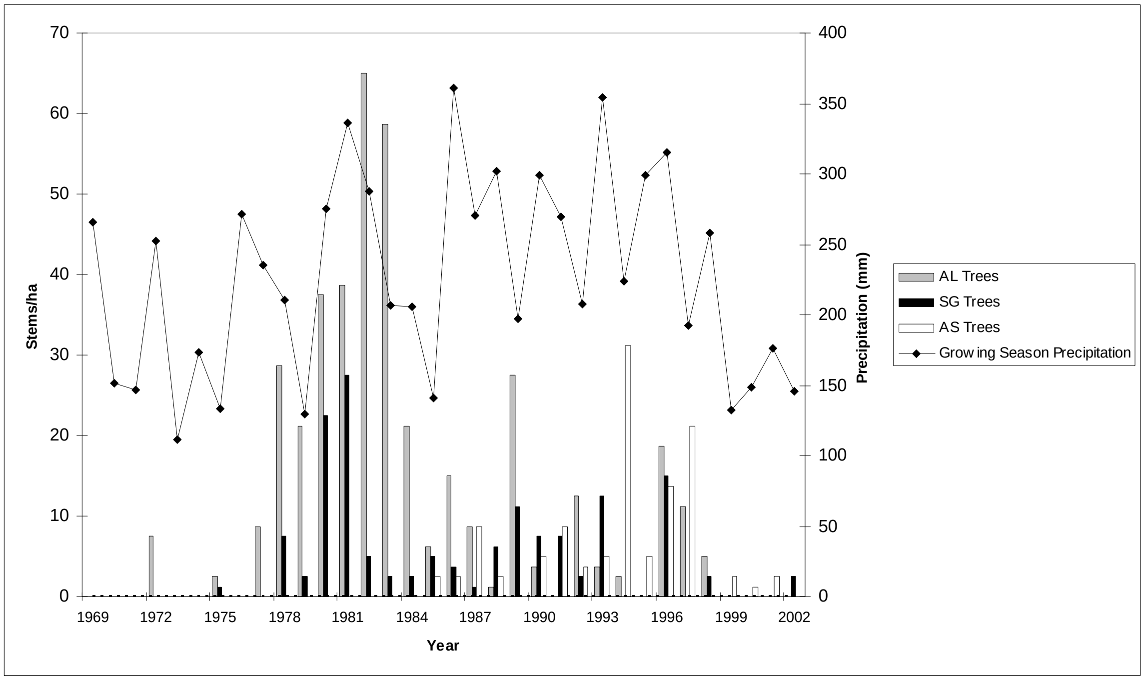

Figure 3.4 Whitebark pine recruitment in the Arnica Lake (AL), Stanley Glacier (SG) and Assiniboine Slide (AS) burn plots in relation to growing season precipitation.

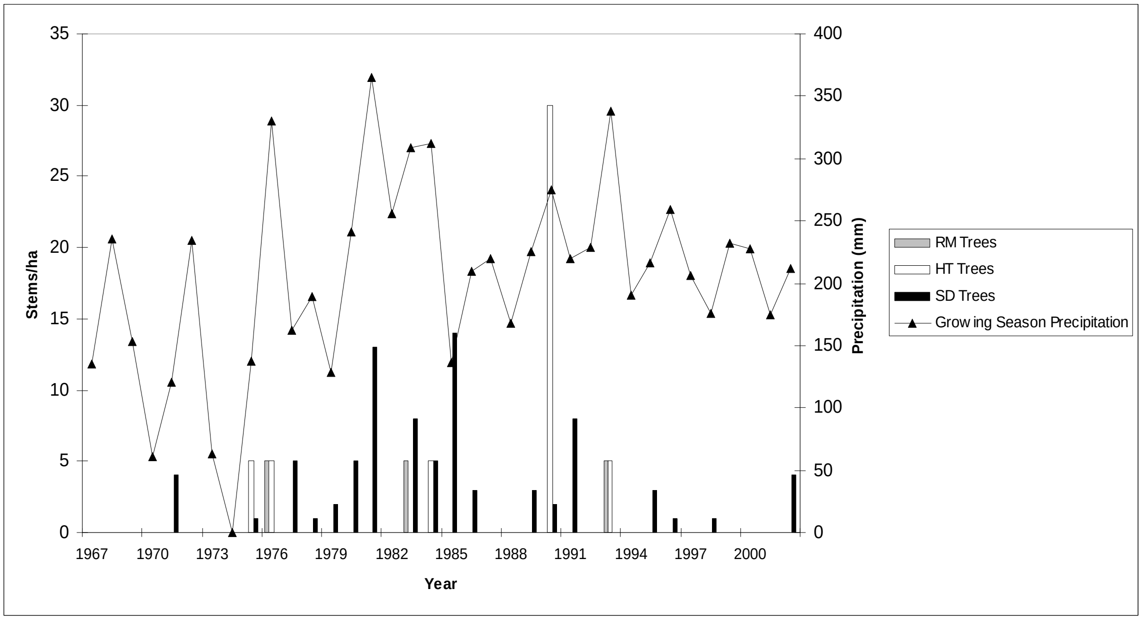

Figure 3.5 Whitebark pine recruitment in the Red Mountain (RM), Heather Trail (HT) and Silverdaisy (SD) burn plots in relation to growing season precipitation.

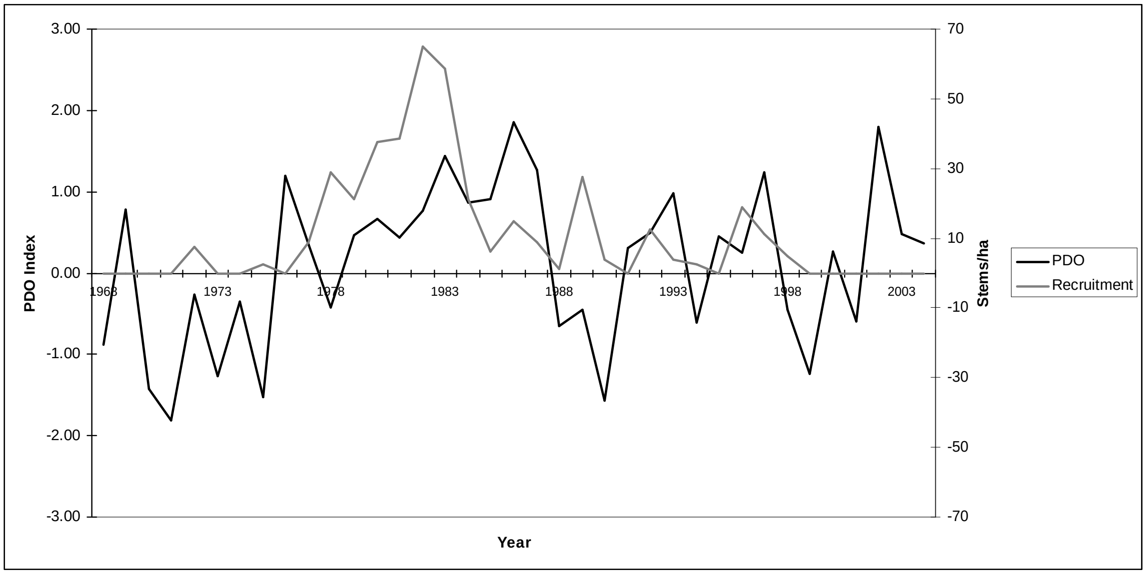

Figure 3.6 Whitebark pine recruitment on the Arnica Lake recently burned stands and winter PDO Index values.

3.5.2 White Pine Blister Rust Infection of Regeneration in Recently Burned Stands

White pine blister rust was present in all stands, with the exception of the Red Mountain recently burned stand in Manning Park and the Amiskwi Pass control stands (AM and AP) in Yoho National Park, each of which had very small sample sizes (Figure 3.7). The Heather Trail site in Manning Park had the highest infection rates, with 67% of the trees in the control stand and 60% of trees in the recently burned stand infected. On sites where whitebark pine was present in both recently burned and control plots, the greatest difference was on Parker Ridge where the recently burned stand had 56% infected and the control stand had only 5% infected. In Manning Park, 42% of the infected whitebark pine were dead due to blister rust, which accounted for 19% of the sampled population (Figure 3.8). In the Rocky Mountain National Parks these numbers were lower, with only 3% of the total regeneration dead due to blister rust in Yoho and Banff, and 5% and 6% dead in Jasper and Kootenay, respectively.

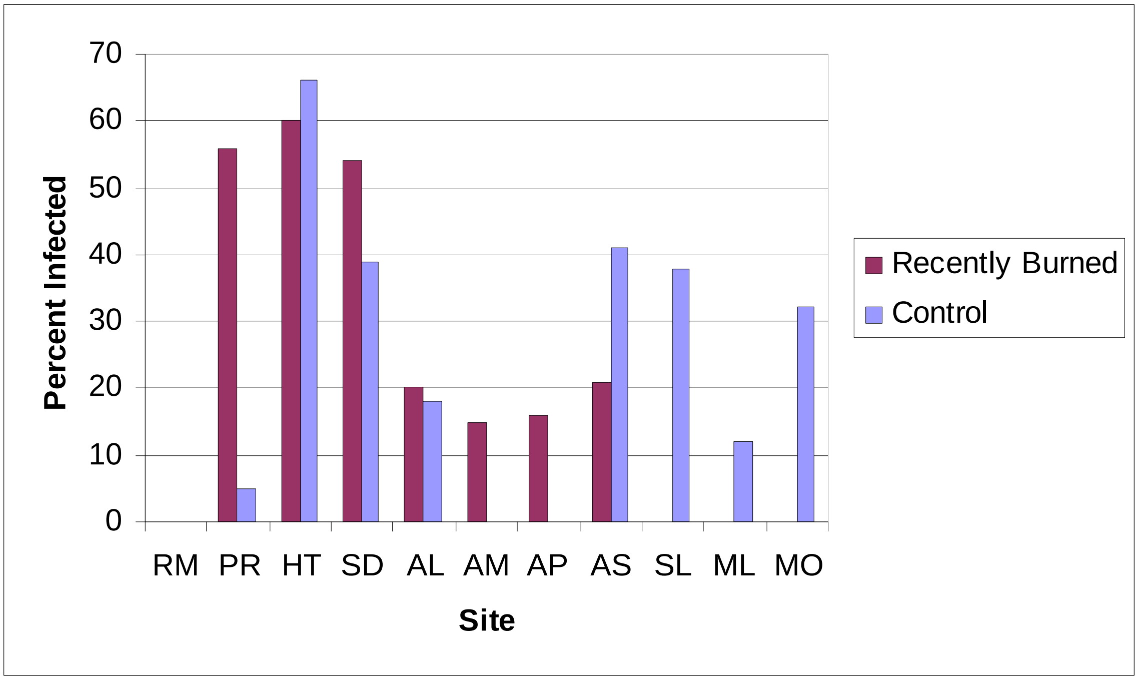

Figure 3.7 Percentage of whitebark pine infected by white pine blister rust on recently burned and paired control plots.

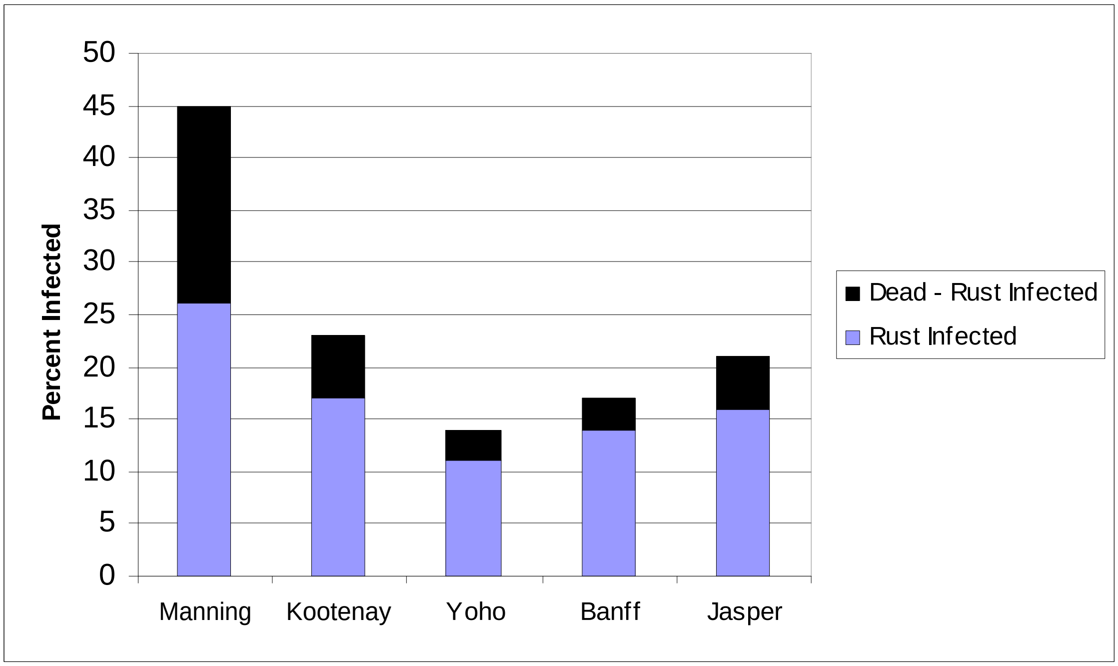

Figure 3.8 Percent infection by white pine blister rust of whitebark pine observed in live and dead cohorts for each Park.

Infection of seedlings by white pine blister rust increased over time. No stands younger than 11 years post-fire had infected seedlings present. The regression of percent infected with time since fire was significant ($R^2 = 0.76$, $P < 0.05$) (Figure 3.9). Only recently burned stands with whitebark pine regeneration were included, as stands with no regeneration would not contribute to the model. The Red Mountain and Amiskwi Pass stands (AP, AM) stands were also omitted due to very small sample sizes. Despite small sample sizes, recently burned stands with whitebark pine regeneration were used in the model as they likely reflect the true trends of low initial infection rates.

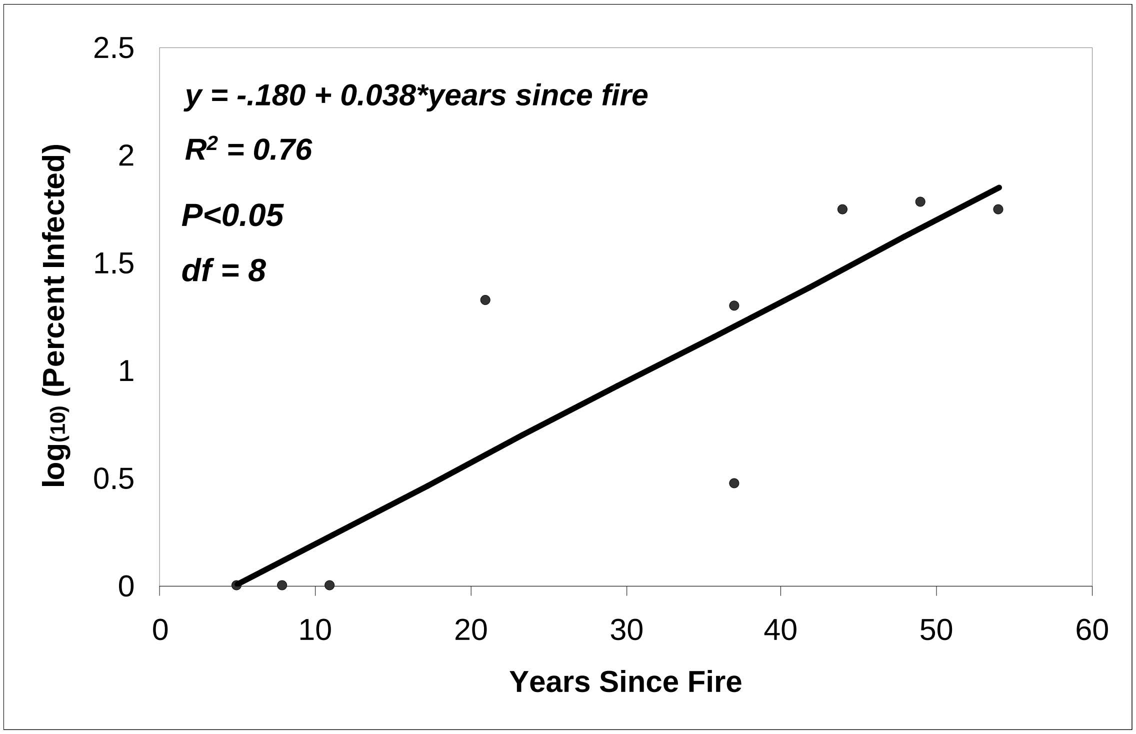

Figure 3.9. Percent (log10) of whitebark pine regeneration infected with white pine blister rust in recently burned stands.

The best logistic regression model relating percent of blister rust infection on individual trees used tree age as the only independent variable (Figure 3.10). The best equation was Probability of Blister Rust Infection = exp(-2.56826 + 0.0646372*age)/(1+exp(-2.56826 + 0.0646372*age)) (Chi-square $P < 0.01$, d.f. = 1). Height and geographic location were not significant variables in predicting blister rust infection (Figures 3.11 and 3.8, respectively).

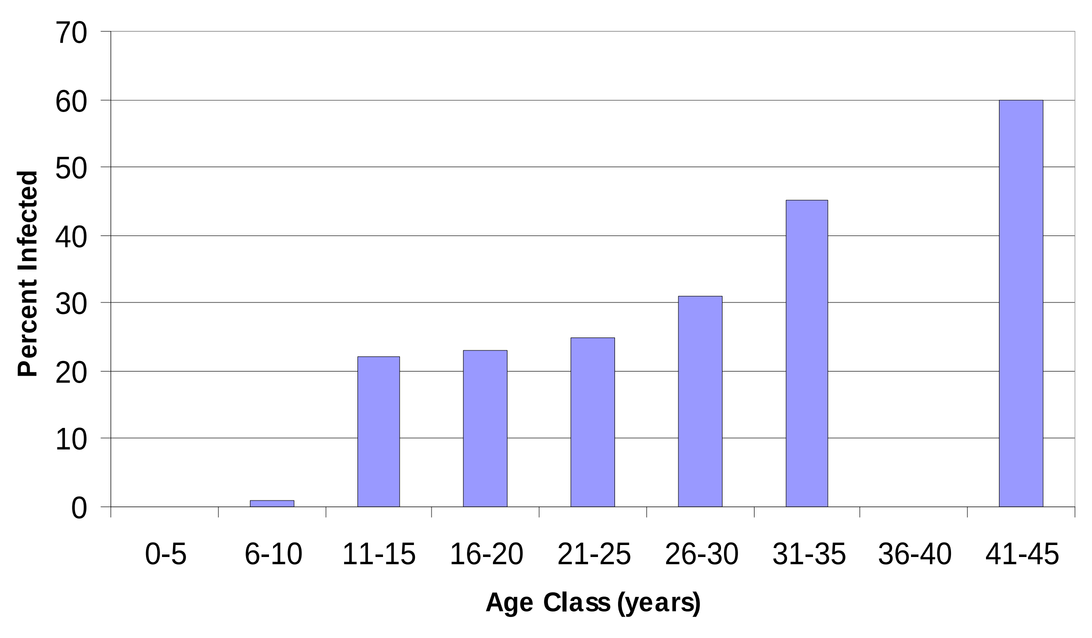

Figure 3.10 Distribution of infection by white pine blister rust across age classes.

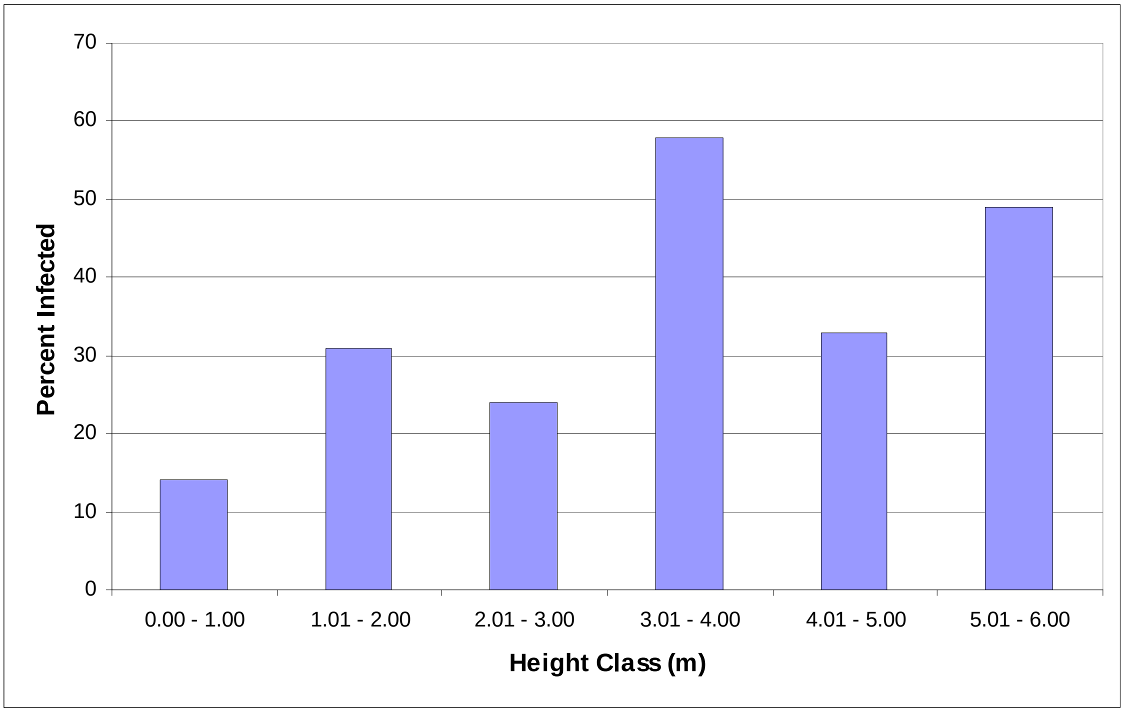

Figure 3.11 Distribution of infection by white pine blister rust across height classes.

3.6 Discussion

3.6.1 Source of Potential Errors

The method used to determine the age of regeneration was subject to errors. Annual whorls used to determine age may be miscounted due to the presence of false whorls. The accuracy of the aging method was confirmed by destructive sampling of several trees for age confirmation; and by using the technique on trees of known age being grown at the University of B.C. Confounding this aging technique is the ability of whitebark pine to grow in a suppressed state ($\leq$0.25mm/year) (Campbell and Antos 2003), and the possibility of growth years missing due to persistent snowpack late into the growing season. Accuracy is likely greatest on young trees with vigorous growth and less accurate on older and suppressed trees. Although this source of error limits the full interpretation of the observed chronosequence relationships, plausible explanations are provided which provide theoretical explanations for the patterns observed. Only through regular monitoring of recruitment trends in permanent plots can the factors that temporally affect recruitment be fully assessed.

The level of white pine blister rust infections was likely underestimated as trees were classed as infected based only on the presence of cankers or fruiting bodies. Discoloured needles may also indicate early infection, but this symptom was not used as an indicator of infection as needles may discolour for a variety of reasons such as age or moisture stress. Further, on mature trees cankers may not have been visible from the ground, even when viewed through binoculars.

3.6.2 Recruitment Trends of Whitebark Pine in Recently Burned Stands

The generally low recruitment rate of regeneration observed in most stands is due to several factors. First, depending on the fire severity, any soil seed bank may have been destroyed by the fire and will only be replaced following years of mast cone production; second, adequate moisture needs to be present for seed germination and seedling establishment; and third, the length of growing season each year is not necessarily sufficient to support the establishment of whitebark pine regeneration. Following the Yellowstone fires of 1988, regeneration was not observed in the area until 1991, due to the destruction of the pre-fire seed bank by fire and the variable dormancy inherent in the newly created seed bank (Tomback et al. 2001). On Mount Henderson near Yellowstone National Park, once a seed bank had been established, seeds germinated in 4 out of 5 years (Tomback et al. 2001). Periods of high recruitment such as this were observed on most stands in this study, but these episodes were also followed or preceded by extended periods of no recruitment.

Stands with large geographic separation showed comparable recruitment patterns, possibly attributed to comparable climate patterns; to masting over a large geographic area; or likely a combination of the two factors. Recruitment peaked in all stands in the early 1980's. During this period, moisture levels were high near both the Rocky Mountain and North Cascade stands, and PDO values were positive resulting in longer growing seasons, but an excess of seeds must have also been available near each site.

Synchronous mast seed crops in the genus *Pinus* have been shown to extend up to 2500 kilometers (Koenig and Knops 1998). The lack of correlation between recruitment on the Assiniboine slide and other stands may be attributed to differing masting cycles between stands in recent time; differing conditions suitable for germination and establishment; or differing levels of seed predation between stands. Although synchronous masting may cover large areas, it is highly variable across those areas. Weaver and Forcella (1985) found cone yields varied between trees and stands in a region.

The initial recruitment lag observed in most stands in the first few years following fire may be related to the growth of adjacent herb and shrub cover. McCaughey and Weaver (1990) found that plots with 25% shade exhibited the best seed emergence compared with 0 or 50% shade. They speculated that too much sun or too much shade may be detrimental. Thus, the development of an adequate shading layer in the form of herb or shrubs may facilitate the emergence of germinants. On some stands an adequate level of shade may be present immediately following fire due to the flush of herbaceous growth; on other stands adequate shade may take significantly longer to develop.

The comparison of stands burned since 1994 supports the findings from Chapter 2, as the Moab site had 7 times the recruitment density of either the Medicine Lake or Skyline stands. The Moab site was located on a cool aspect and the latter two stands were located on steep, rocky, warm aspect sites. The long-term comparison of older burns is also consistent with the findings in Chapter 2, as many stands showed gains in recruitment densities over the same time periods, but gains were greater in cool aspect stands.

In several stands, whitebark pine recruitment showed correlations with periods of high precipitation. This is likely the result of suitable conditions allowing more seeds to germinate, when both a high number of seeds and adequate moisture conditions were present. In a seed planting experiment, higher recruitment occurred during a year of high growing season precipitation (Perkins 2004). Whitebark pine displays variable dormancy, an adaptation which may improve germination by allowing the accumulation of a seed bank and spreading germination over time, increasing the odds that suitable conditions may be present for germination (Lanner and Gilbert 1994). In species that form seed banks, recruitment improves when favourable conditions arise, particularly adequate moisture (Krugmann et al. 1974, Tomback et al. 2001).

High precipitation did not always result in high recruitment, indicating that either seed was not available for germination, or germinating seeds experienced high mortality. Seed availability may be a limiting factor, either due to infrequent masting or high seed predation. Cone masting patterns may be difficult to observe in recruitment patterns due to variable dormancy and seedling mortality. Tomback et al. (2001) found regeneration was best correlated with cone production two years previously. Good cone production years are often followed by years of poor production (Weaver and Forcella, 1985). When seeds are produced in great abundance during a mast year, species that consume seeds are easily satiated; however, species that both consume and cache seeds continue to cache long after they are satiated, resulting in a larger proportion of seeds being cached in mast years (Vander Wall 2002).

Years of high recruitment and moisture followed by years of low moisture may have reduced the total number of seedlings establishing successfully. The effects of a mast year on recruitment potential may be negated by seedling mortality attributed to drought (Vander Wall 2002). The age demographic snapshot in the present study does not provide enough detail to determine if some years of high germination were followed by high mortality or if the patterns of episodic establishment shown here are reflective of true germination patterns. In the U.S., adequate moisture was more important for seed germination than for one year seedling survival (Tomback et al. 2001).

At the Silverdaisy and Assiniboine Slide recently burned plots, regeneration was poorly correlated with precipitation in the year of seedling establishment. This may be due to a combination of factors. At the Silverdaisy site, which burned in 1961, this may be due to sampling error when determining seedling age as recruitment was positively correlated with precipitation in the years following seed germination. This correlation with precipitation in the second year may indicate that moisture levels were sufficient in the first year for germination, but the high precipitation in the second year allowed for good seedling development and establishment.

A lack of correlation between recruitment and moisture in the Assiniboine Slide recently burned plots may also be due to the lack of large mast seed crops since the site burned in 1984. The largest recruitment episodes in nearby stands occurred pre-1984. Thus, poor correlations at this site may be due to poor seed crops in the years since fire, so that occurrence of a large seed crop has not been synchronized with adequate moisture to produce a large recruitment peak. Further, given the cool aspect of this site, it is likely that moisture has been less limiting than on warmer sites.

In Manning Park, the near synchronous recruitment events on Red Mountain and along the Heather Trail, are indicative of the serendipitous relationship between ideal site conditions and available seed required for seedling recruitment. The recruitment occurred during a period of high growing season precipitation, and seed was present on both stands, despite the fact that both stands required long distance seed dispersal. These long distance dispersal events may occur due to more than just chance. During mast years, seed dispersal distance may increase. The distance Jeffrey and sugar pine seeds were cached by rodents was found to increase by up to 28.6% in mast years (Vander Wall 2002). Although Clark's nutcrackers are the primary disperser of whitebark pine seeds, if flying effort increased proportionately, long distance dispersal would be more likely during mast years.

Winter PDO affects the recruitment of whitebark pine as periods of positive PDO are associated with lower snowpack resulting in an earlier spring and a longer growing season (Selkowitz et al. 2002). PDO likely had a greater influence on recruitment in the Arnica Lake recently burned stand as it was on a cool aspect where growing season length is limited, and other site variables such as available moisture may not be as great a limiting factor as in warmer, drier stands. Spring moisture was not correlated with recruitment on this site, and the correlation of recruitment with summer precipitation is possibly coincidental and not indicative of a causal relationship. However, the high insolation values associated with this site (Figure 2.9), indicate that moisture may be limiting during portions of the growing season, and summer precipitation may alleviate any deficits. On moist stands, shallow snowpack associated with positive PDO Index values were found to result in greater growing season length and increased growth of mountain hemlock (Peterson and Peterson 2001) and subalpine fir (Peterson et al. 2002). This also suggests that on mesic stands, causes of seedling mortality in years of short growing seasons are likely due to inadequate time for the development of photosynthetic area and root systems prior to winter dormancy.

The poor correlations between PDO and recruitment in other stands may indicate that growing season length is less important in these stands. However, when stands were grouped by moisture class or as a single unit, significant correlations were present; indicating that to some extent, growing season length may be important on both cool and warm sites. Low seed availability and poor moisture availability may obscure correlations with PDO in individual stands. The effect of PDO presents a dilemma on sites which are limited by both length of growing season and availability of moisture. Although positive PDO increases the growing season length, the reduced snowpack may introduce moisture limitations earlier in the season. On dry sites, factors that delay snowmelt and reduce the summer soil moisture deficit are favourable for growth (Peterson et al. 2002). The poor correlation between recruitment and PDO in the recently burned submesic Moab and Assiniboine slide stands may be attributed to the short time period sampled as no long-term PDO positive or negative periods have been present since the stands burned.

The lack of correlation between May snow cover and recruitment but correlations between PDO and both whitebark recruitment and May snow cover, indicates that to some extent snow cover likely affects recruitment, although the relationship is not clearly positive or negative. Years of high snowpack positively affect recruitment by providing higher levels of soil moisture, and by allowing the accumulation of a seed bank by protecting the seeds from being recovered by Clark's nutcrackers. On whitebark pine sites, stored soil water from melting snow and spring runoff is the main source of water during the summer; subsoils may remain moist, but on windswept stands, surface soils on certain aspects may dry (Tomback et al. 2001). Conversely, during years of lower snowpack, growing season length is increased; however, so too is the period of foraging by Clark's nutcrackers on both warm and cool aspects. In Wyoming, caches were recovered from windswept south aspect slopes year-round; however, caches were removed from northeast facing slopes and from under forest canopies only from June – August, due to longer lasting snow cover (Vander Wall and Hutchins 1983, Hutchins 1990). Cache recovery is limited by the rate at which Clark's nutcrackers can forage, thus those seeds cached on moist sites suitable for germination may germinate before Clark's nutcrackers can recover the cache.

3.6.3 White Pine Blister Rust Infection of Regeneration in Recently Burned Stands

Blister rust infection increased with time since fire and increases in tree age, suggesting that in open stands basidiospores will eventually come in contact with susceptible hosts. The age at time of infection could not be determined, only the age of currently infected individuals. Thus, it is unclear if age is a factor in susceptibility to infection, or if an expected proportion of the population becomes infected each year and infection levels are accumulating on the older cohorts. The significant relationship between age of regeneration and blister rust infection is consistent with other studies (Tomback et al. 1995, Campbell and Antos 2000) which also found height to be an additional factor in predicting blister rust infection. It was theorized that as trees grow larger, they form larger targets for basidiospores and have a correspondingly higher rate of infection (Tomback et al. 1995).

Following the initial lag attributed to the age or size of regeneration, the infection rate on recently burned plots displayed logistic growth over time to a high of 60% on the Heather Trail. This infection rate is similar to infection rates of several other mature stands such as the Heather Trail and Silverdaisy control stands in the North Cascades and the Assiniboine slide control stand in the Rocky Mountains. A survey of whitebark pine regeneration in B.C. found 85% of the trees to be free of blister rust (Zeglen 2002), which contrasts sharply with this study which found that only on burns less than 30 years old would that level of infection be present. This contrast in infection rates is attributed to the open grown nature of trees in the recently burned stands in this study, compared with the regeneration surveyed by Zeglen, which was a component of the mature forests being surveyed for blister rust impacts. The Parker Ridge burn, which had a 56% infection rate in the recently burned stand, only had a 6% infection rate in the paired control plots, where most regenerating whitebark pine trees were suppressed and < 1 m in height. Decreased infection of understory whitebark pine was correlated with increased canopy cover, due to airborne basidiospores being intercepted by the overstory canopy (Campbell and Antos 2000).

The lack of a relationship between blister rust infection and geographic location is inconsistent with other studies. Zeglen (2002) found poor but significant relationships between geographic location and rust infection, which indicated a west to east trend in declining tree health when data were pooled by mountain range. This trend is contrary to those observed in this study which found the greatest infection rate in the western region

(Manning Park), although the infection trends were not statistically significant. However, most data in this study were from regeneration, which limits the ability to compare between studies as tree age and height have been shown to be important determinants of rust infection.

Although sample sizes were quite small in most of the older burns, the maximum infection rate near 60% suggests that despite high infection rates on some stands, healthy individuals from high risk groups (taller and >10 years old) are still common. Prior to the introduction of blister rust, the level of resistance in the population was less than one percent (Hoff et al. 1994). If the level of resistance is increasing or is a more common trait in some populations, selection over time may return whitebark pine to former levels. On stands with lower resistance, however, management action may be required. Infection rates may not continue to increase on older burns due to recruitment compensating for mortality, saplings shielding seedlings from rust spores, and possibly rust resistant individuals becoming established and increasing in frequency in the population.

3.7 Conclusions

Recruitment following fire showed slow and episodic patterns. Cool stands had recruitment sooner after fire than did warmer stands. Episodic recruitment patterns extended over a wide geographic range, which was attributed to regional climate patterns and possibly to widespread cone masting. During years of high recruitment, cool aspects experienced greater recruitment than did warm aspects, and during years of low recruitment, little difference was present between stands. High recruitment episodes corresponded with periods of higher precipitation. However, periods of high precipitation occurred more frequently than did episodes of high recruitment, indicating that seed availability may be more limiting than suitable moisture conditions.

Positive Pacific Decadal Oscillation (PDO) winter index values were important in recruitment to mesic stands frequently limited by growing season length due to late snowpack. PDO values were less important in drier stands, indicating that length of growing season may be less limiting on these sites. Positive PDO values may not necessarily assist recruitment in drier stands, as increased growing season length is associated with lower soil moisture due to earlier snowmelt.

White pine blister rust infection rates increased with stand age and tree age in recently burned stands since older trees were more susceptible to blister rust, as they have spent more time exposed to basidiospores and are likely larger, forming a larger target for spores.

Chapter 4. Conclusions and Management Recommendations

4.1 Conclusions

The theory that burning will increase whitebark pine recruitment holds true on many sites. However, fire is not always required for recruitment. Recruitment occurred in all types of forested and burned stands. However, it is the recruitment to taller height classes, and ultimately to reproductive status, that is paramount when assessing the success of regeneration on a site. The greater likelihood of regeneration growing to maturity in open stands favours burning to promote recruitment. The increased regeneration promoted through burning is theorized to promote rust resistance by increasing the germination of seeds originating from rust resistant adults. However, rust infection was still common on older regeneration, and infection rates in older burns approximated that observed in nearby forests. Although burning may favour whitebark pine recruitment, the loss of seed trees to fire mortality must be considered against the potential recruitment gains. Whitebark pine may take decades to reproduce and recruitment to pre-fire densities may take equally as long. Dispersal of seed to burned stands greater than 1 km from seed sources was found to be unlikely, resulting in formerly forested stands converting to meadows.

It is apparent that the sites best suited to cache recovery by Clark's nutcracker are rarely the most suitable stands for tree growth. Even though all sites where whitebark pine occurred were characterized by harsh conditions, it still grew best on mesic - submesic stands moderated by greater moisture availability and lacking the damaging effects of excessive insolation and mechanical damage caused by rockfall or snowcreep. Mesic – submesic stands supported a greater density of shade tolerant conifer associates, but on subxeric stands lodgepole pine was found to outcompete whitebark pine in early seral situations.

Regardless of site conditions, recruitment events were primarily episodic in nature, with years of high recruitment followed by periods of low recruitment. Episodic recruitment events were probably the result of more than cone masting, as recruitment was correlated with high availability of soil moisture and longer growing seasons associated with positive PDO values. However, during this longer growing season, recruitment was more likely in mesic stands where available moisture could be fully utilized by germinants over the lengthened growing season. Very large recruitment episodes apparently have not occurred in any of the study stands in the past 20-years, indicating that seed availability may be declining or the ideal combination of available seed, moisture, and growing season length has not occurred for an extended period.

4.2 Management Recommendations

The management recommendations arising from this study address approaches to wildfires, selecting stands for prescribed burning, increasing recruitment through planting, and regeneration monitoring.

Wildfire

Recent large wildfires throughout the range of whitebark pine in B.C. and Alberta suggest that increased recruitment of whitebark pine may occur. Many of these fires burned stands well suited to nutcracker caching and conducive to whitebark pine growth. However, the potential loss of large seed sources destroyed by fire, increasing the distance to seed for most stands, may prevent these fires from promoting whitebark pine regeneration. The greatest utility of these fires may be the preparation of suitable seedbeds for restorative planting. Future fire suppression activities should attempt to leave a landscape which mimics mixed severity burns, resulting in a landscape characterized by competition free burned areas in close proximity to seed sources. Although allowing a fire to burn upslope to the alpine may be the easiest means of fire management, maintaining seed sources within the burn would greatly improve the likelihood of whitebark pine recruitment in the area. Therefore, it is suggested that some suppression activity be applied to subalpine forests containing whitebark pine, despite the fact that many of these sites border on alpine environments.

Prescribed Fire

When selecting stands for prescribed fire, managers should consider the following factors: 1) present stand composition; 2) location and condition of seed source; and 3) local site factors.

1) Present stand composition

Stands containing a high percentage of whitebark pine may be more valuable as a seed source for other stands than as a site for the application of prescribed fire. Given that whitebark pine may expand its distribution into competition free stands, managers should consider burning directly below or adjacent to existing stands of whitebark pine. This may result in high recruitment and growth rates as the lower elevation stands are likely better suited to tree growth and the nearby seed source will maximize recruitment. Whitebark pine in open canopied stands often displayed a self replacing potential and such stands should not be considered for prescribed burning. However, both open and closed stands that are not self replacing should be considered for treatments other than stand replacing burns, such as surface fires or mixed severity fires which retain seed trees on site. In mixed conifer stands, fires that kill Engelmann spruce and subalpine fir, but retain the more fire resistant whitebark pine on site are desired. Stands containing a high component of lodgepole pine should not be considered for prescribed fire. It is possible that the recent widespread mountain pine beetle infestation may kill many of the canopy forming lodgepole pine, releasing the understory of whitebark pine, which is too small at present to be attacked by the pine beetle. Burning beetle infested stands may reinitiate lodgepole pine dominance on a site and should be avoided if whitebark pine is coexisting in the stand.

2) Location and condition of seed source

Conducting a prescribed fire without ensuring the presence of a nearby seed source (<1000 m) is likely to result in very slow recruitment. Further, the presence of mature whitebark pine does not guarantee a seed source if the majority of cone bearing branches have been damaged by white pine blister rust. A healthy seed source may also indicate a greater potential for the recruitment of rust resistant individuals.

3) Local site factors

Stands should be selected based on the potential for whitebark pine growth. This can best be achieved by selecting stands with mesic soil moisture conditions which also have the potential for long growing seasons and a moderate amount of solar insolation. Although in this study these sites were on cool aspects, it is probable that mesic sites on gentle slopes and warm aspects may also prove to be ideal candidate sites. Xeric-subxeric stands are often understocked and can support additional recruitment without fire creating a new seedbed. Mesic-submesic stands located near seed sources should experience the greatest recruitment following fire. The slow recruitment of other tree and shrub species (except lodgepole pine) in high elevation stands should permit whitebark pine to establish on most stands before competing species.

Seed Collection and Planting

Recruitment episodes of whitebark pine appeared to be more limited by seed availability or growing season length than by available moisture conditions or availability of suitable seedbeds. Therefore, a seed collection and direct sowing program may be the most effective means by which to restore whitebark pine populations, as steps taken to ensure early germination may result in artificially lengthening the growing season. Seeds may be accumulated over time and planted during years with early snow melt. Such a program also has the advantage of selecting seeds from phenotypically rust resistant trees, possibly expediting the rate at which rust resistant trees are established across the landscape. The areas available for planting treatment are vast. Recent large wildfires have created an array of suitable treatment sites, and each burn surveyed in this study could support additional whitebark pine recruitment through planting. Mellmann-Brown (University of Colorado, Personal communication) recommends sowing seeds rather than planting seedlings as the harsh stands on which whitebark pine occurs are difficult for seedlings to establish.

Regeneration Monitoring

To further test the recruitment trends observed in this study, the establishment of permanent plots is recommended. Permanent plots were established as a part of this study in 6 stands in the Rocky Mountains and one stand in the North Cascades. Additional monitoring plots should be established to include a greater range of site conditions than is present in the current permanent sample plots. Re-measurement of the existing plots should be carried out at least every 5 years to allow for the incorporation of cone masting data with climate data to better understand how these variables interact to affect whitebark pine recruitment.

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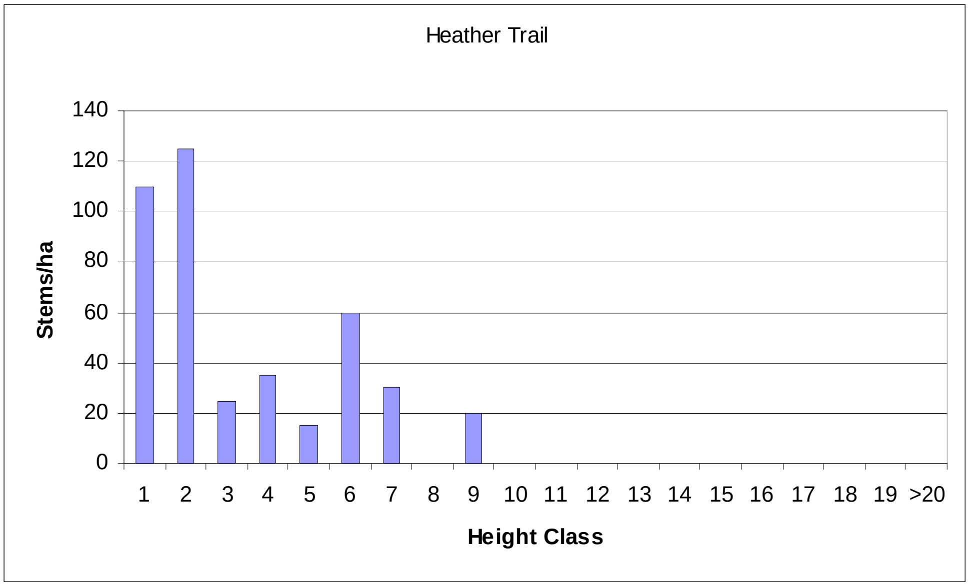
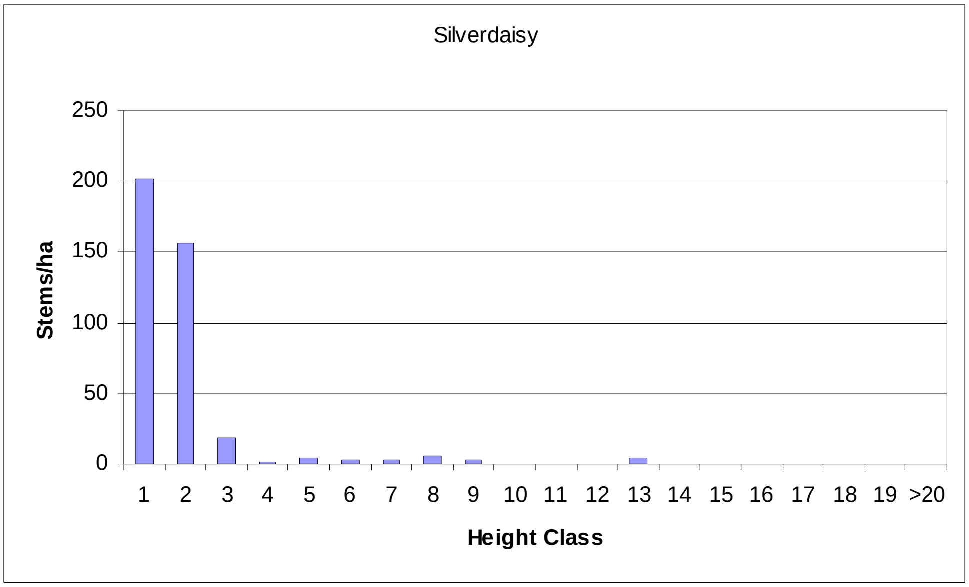
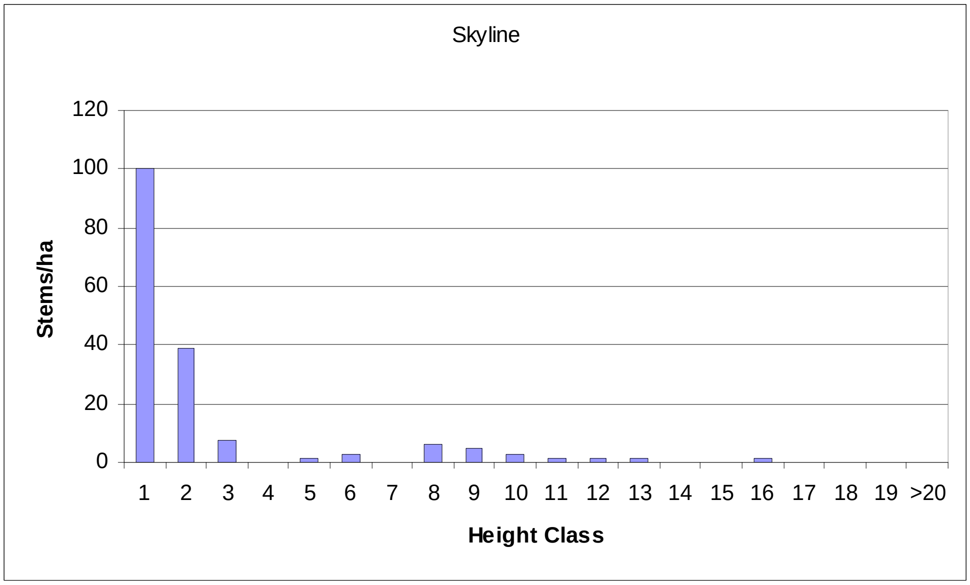
Appendix A – Height Class Distribution of Whitebark Pine in Control Stands



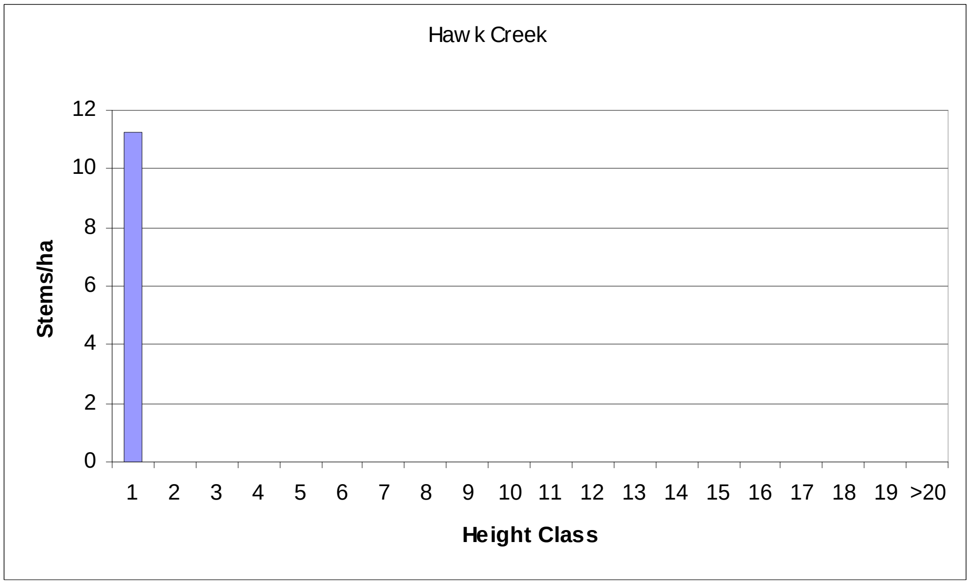
Height class distribution of whitebark pine in the Heather Trail control stand, Manning Park.



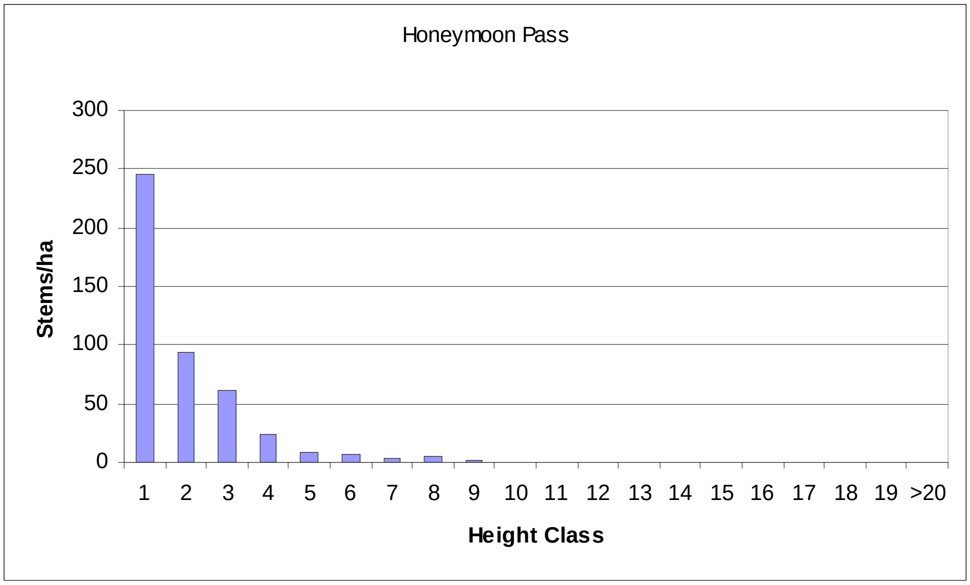
Height class distribution of whitebark pine in the Silverdaisy control stand, Manning Park.



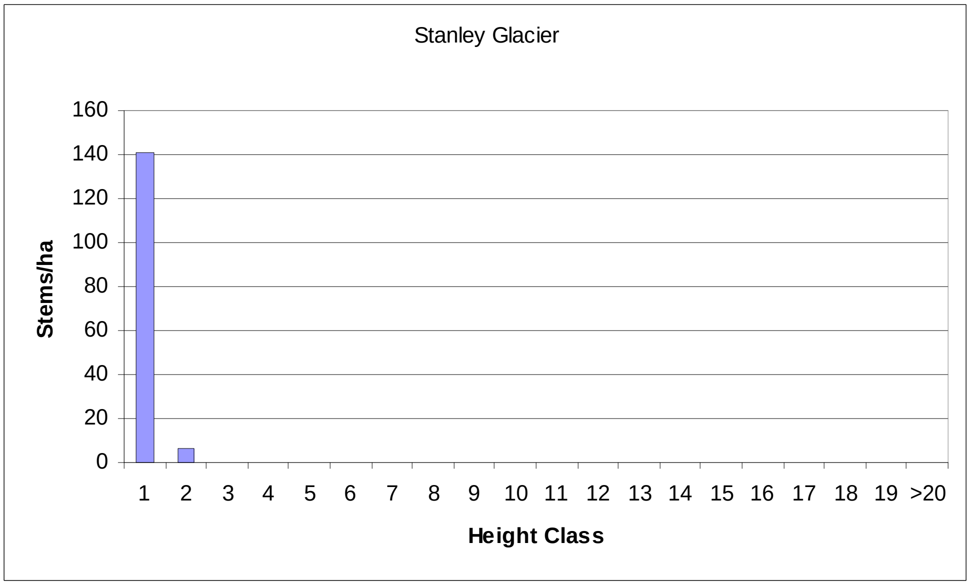
Height class distribution of whitebark pine in the Skyline Trail control stand, Manning Park.



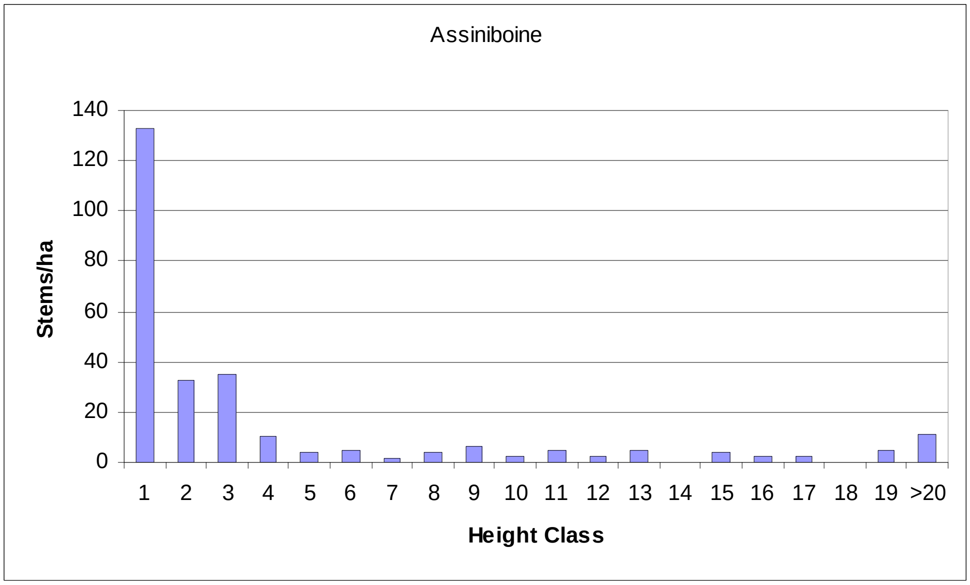
Height class distribution of whitebark pine in the Hawk Creek control stand, Kootenay National Park.



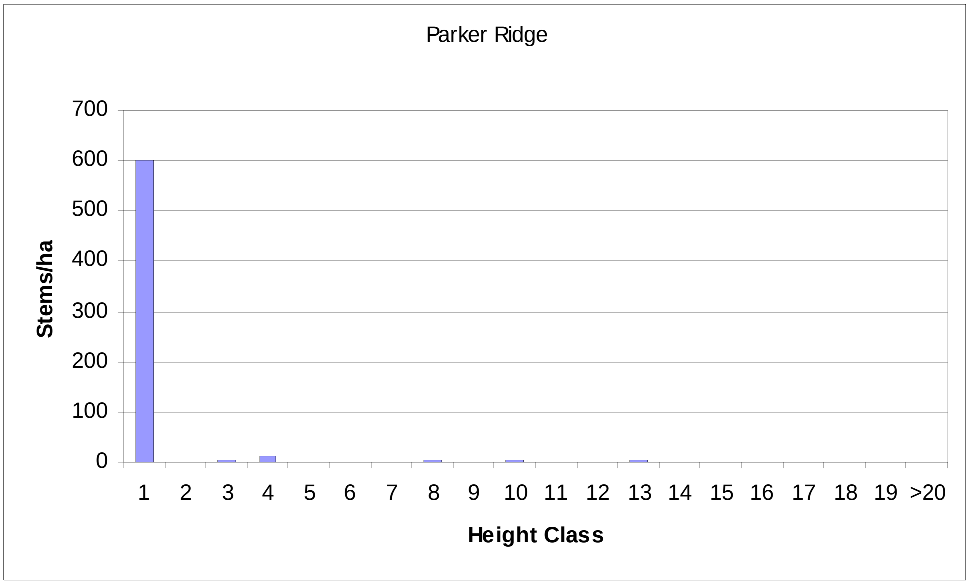
Height class distribution of whitebark pine in the Honeymoon Pass control stand, Kootenay National Park.



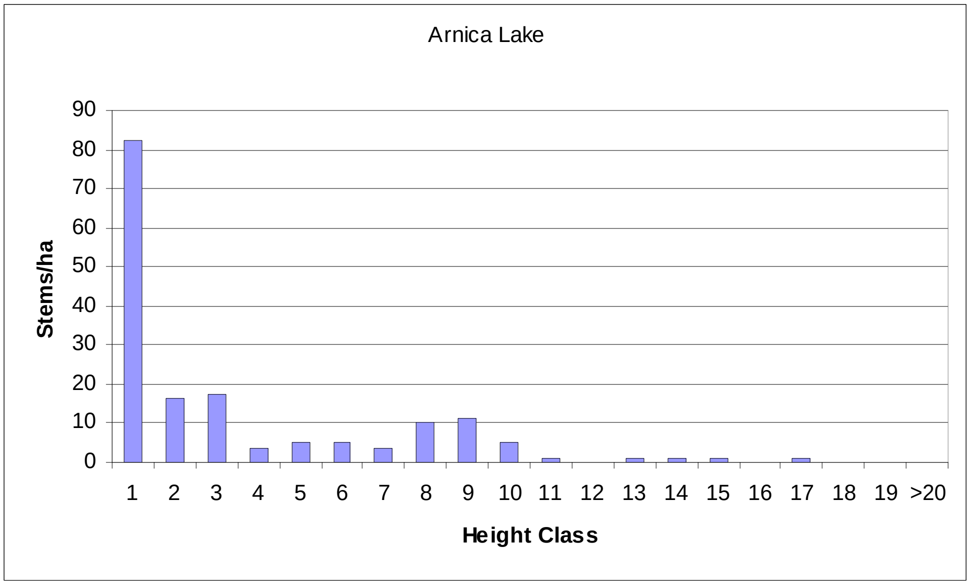
Height class distribution of whitebark pine in the Stanley Glacier control stand, Kootenay National Park.



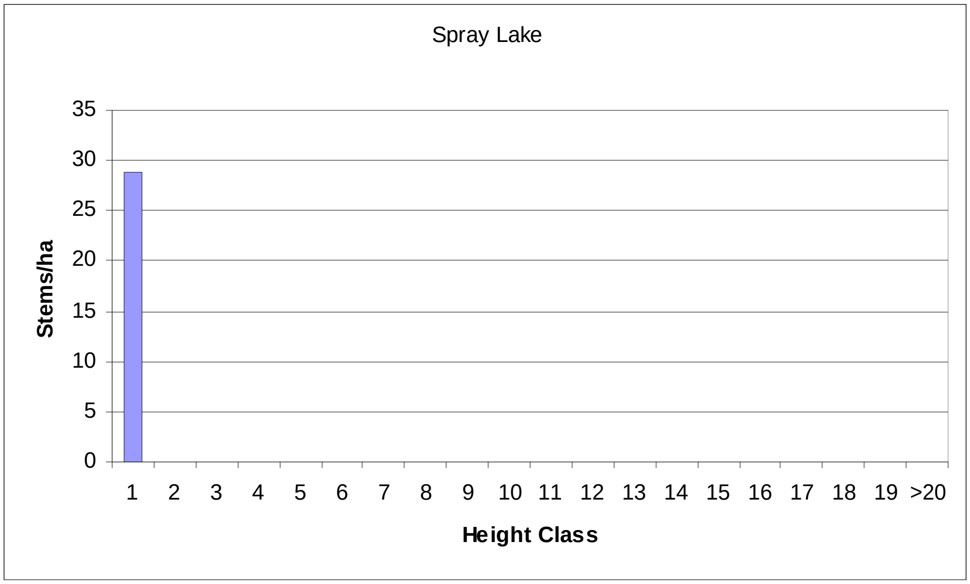
Height class distribution of whitebark pine in the Assiniboine Slide control stand, Kootenay National Park.



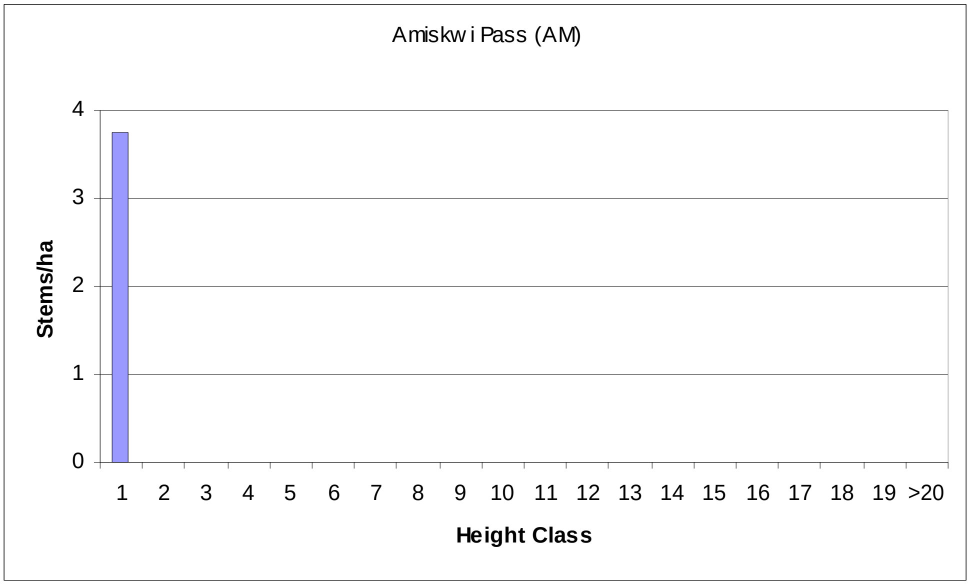
Height class distribution of whitebark pine in the Parker Ridge control stand, Banff National Park.



Height class distribution of whitebark pine in the Arnica Lake control stand, Banff National Park.

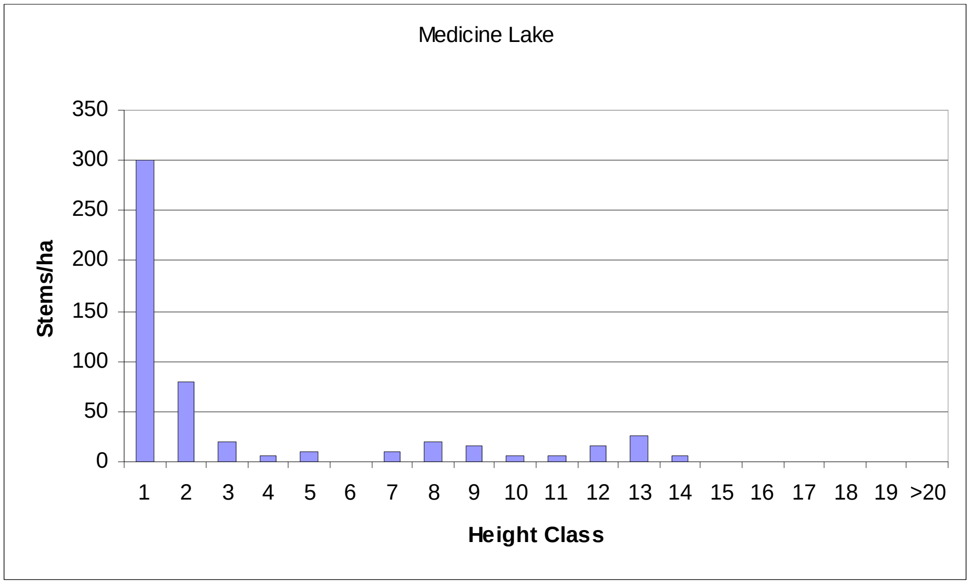


Height class distribution of whitebark pine in the Spray Lake control stand, Banff National Park.



Height class distribution of whitebark pine in the Amiskwi Pass (AM) control stand, Yoho National Park.

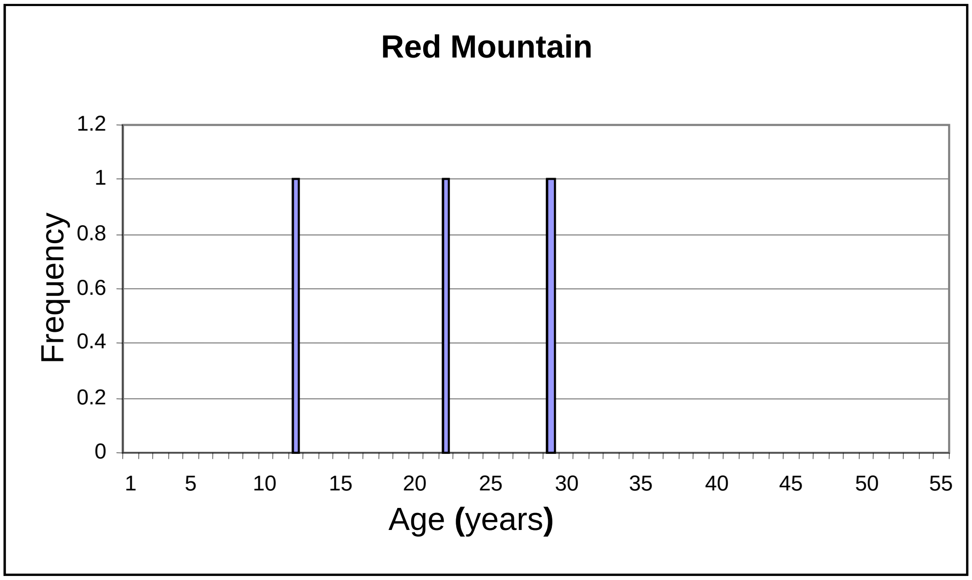
Height class distribution of whitebark pine in the Amiskwi Pass (AP) control stand, Yoho National Park.



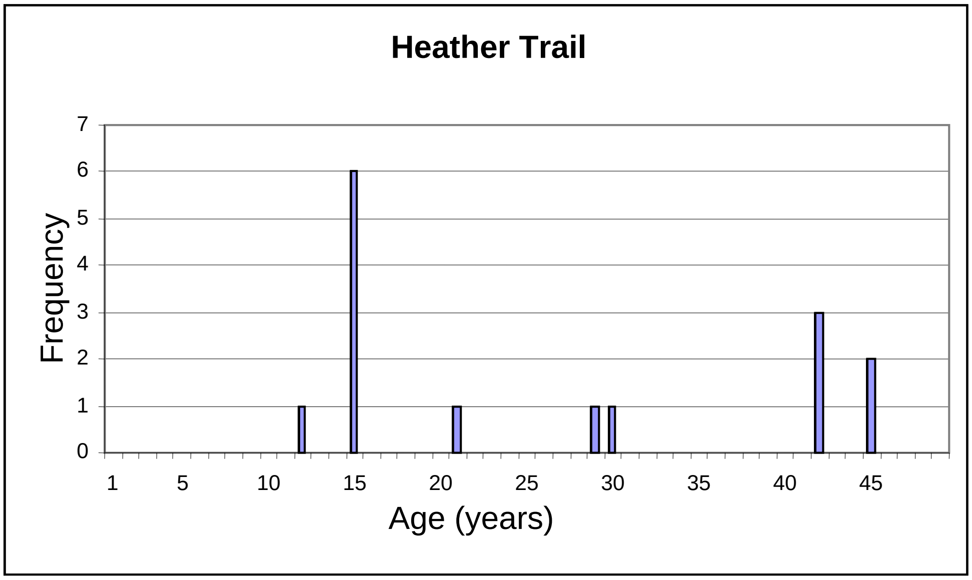
Height class distribution of whitebark pine in the Medicine Lake control stand, Jasper National Park.

Height class distribution of whitebark pine in the Moab control stand, Jasper National Park.

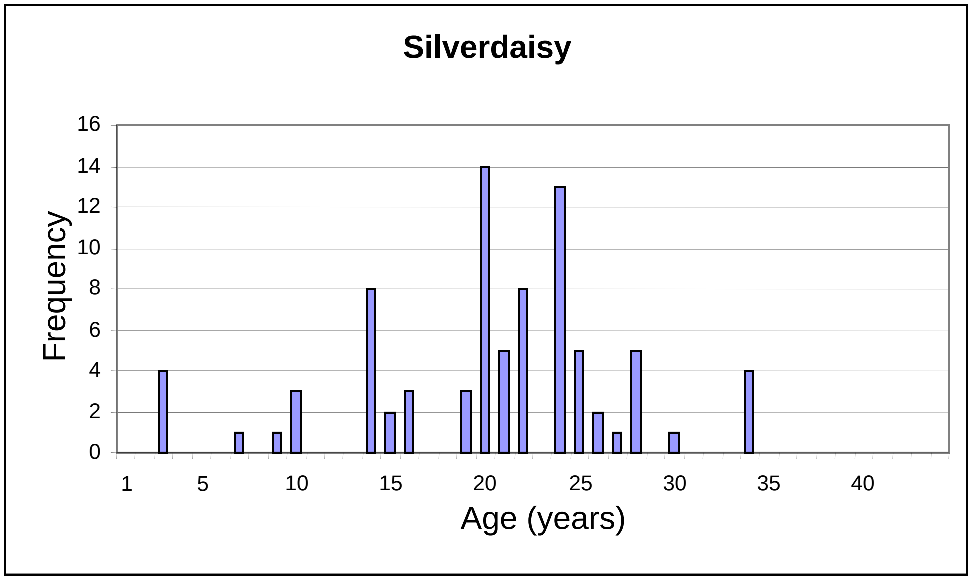
Appendix B – Age Class Distribution of Whitebark Pine in Recently Burned Stands



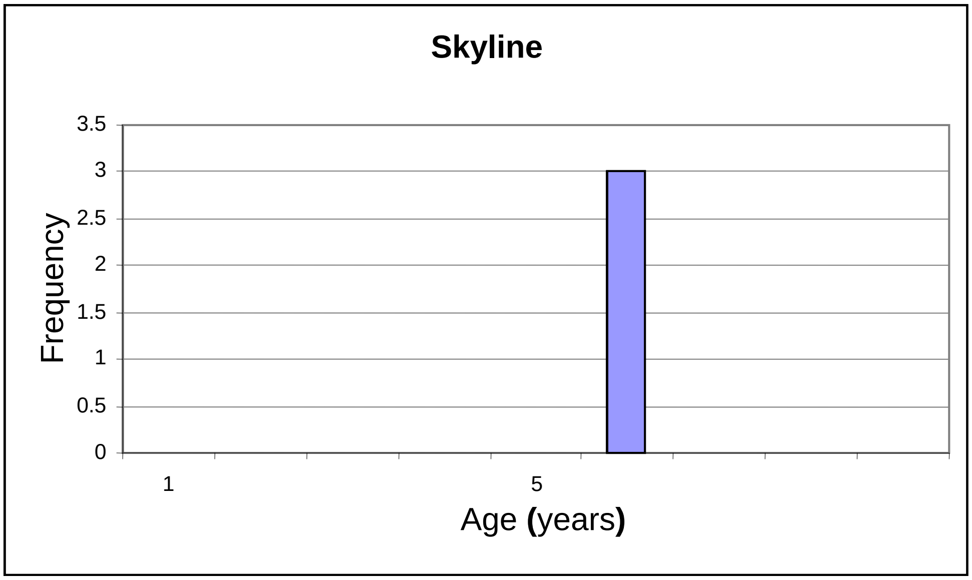
Age class distribution of whitebark pine in the Red Mountain recently burned stand, Manning Park.



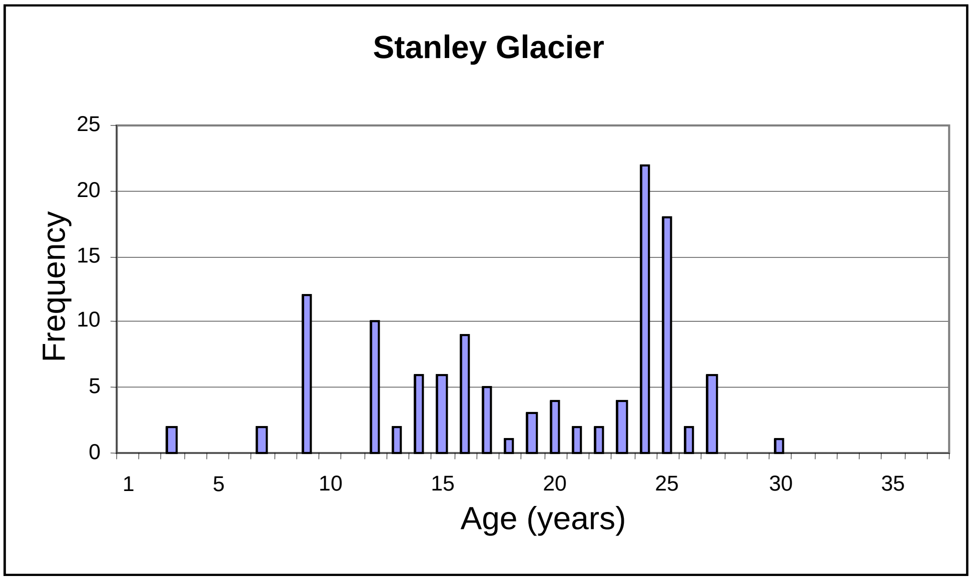
Age class distribution of whitebark pine in the Heather Trail recently burned stand, Manning Park.



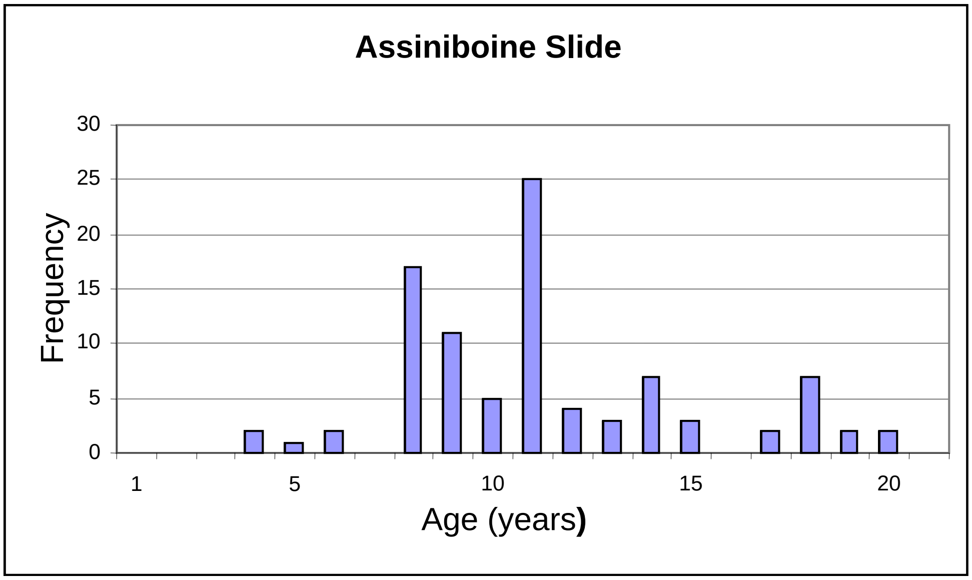
Age class distribution of whitebark pine in the Silverdaisy recently burned stand, Manning Park.



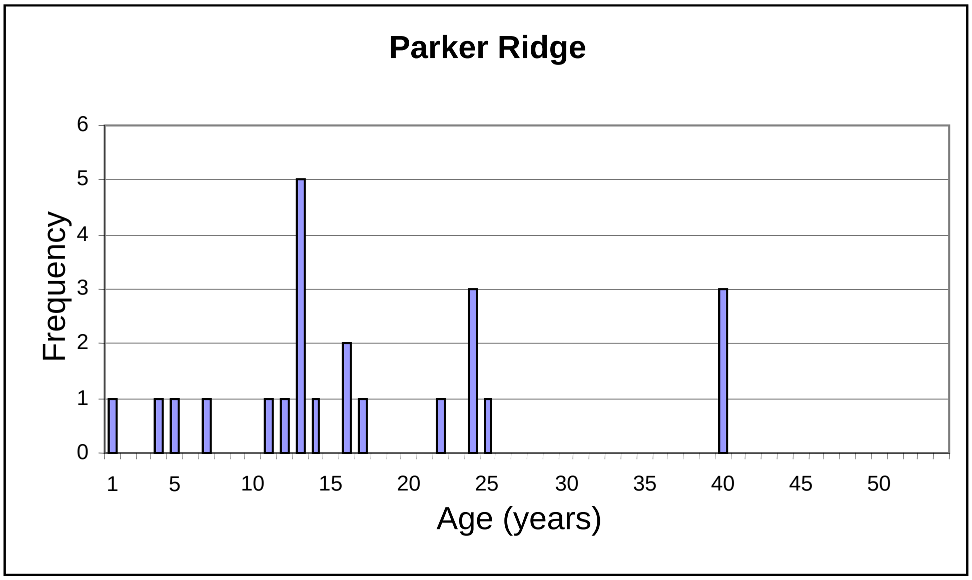
Age class distribution of whitebark pine in the Skyline Trail recently burned stand, Manning Park.



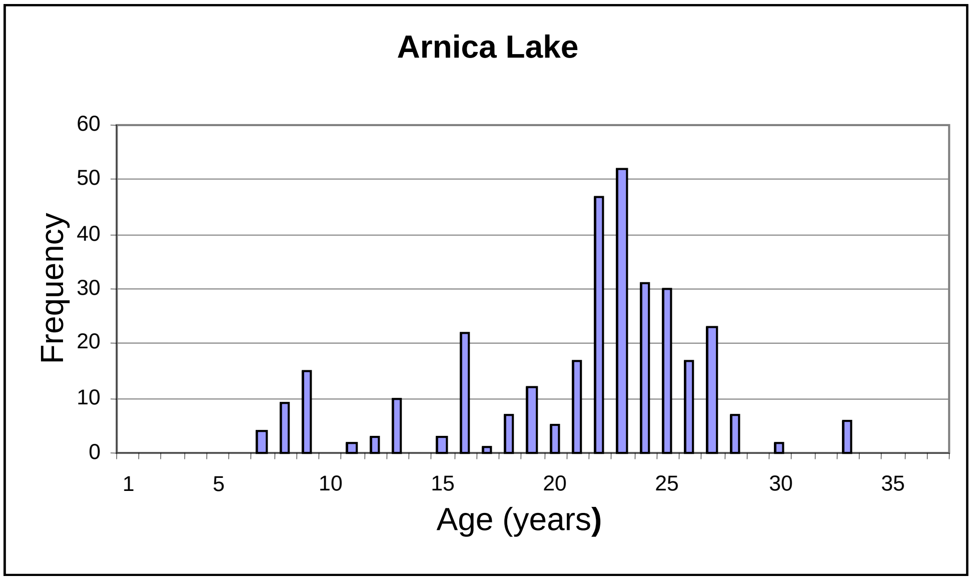
Age class distribution of whitebark pine in the Stanley Glacier recently burned stand, Kootenay National Park.



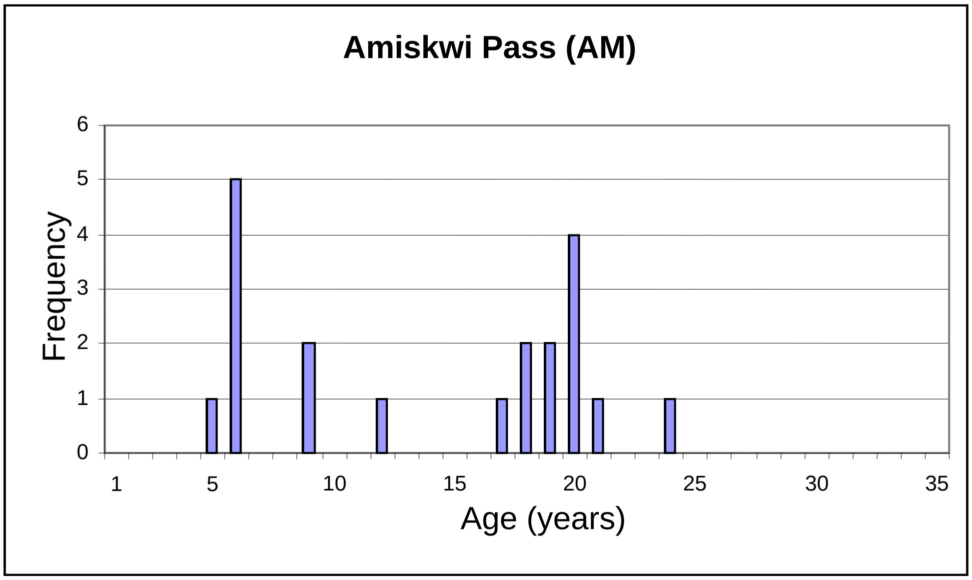
Age class distribution of whitebark pine in the Assiniboine Slide recently burned stand, Kootenay National Park.



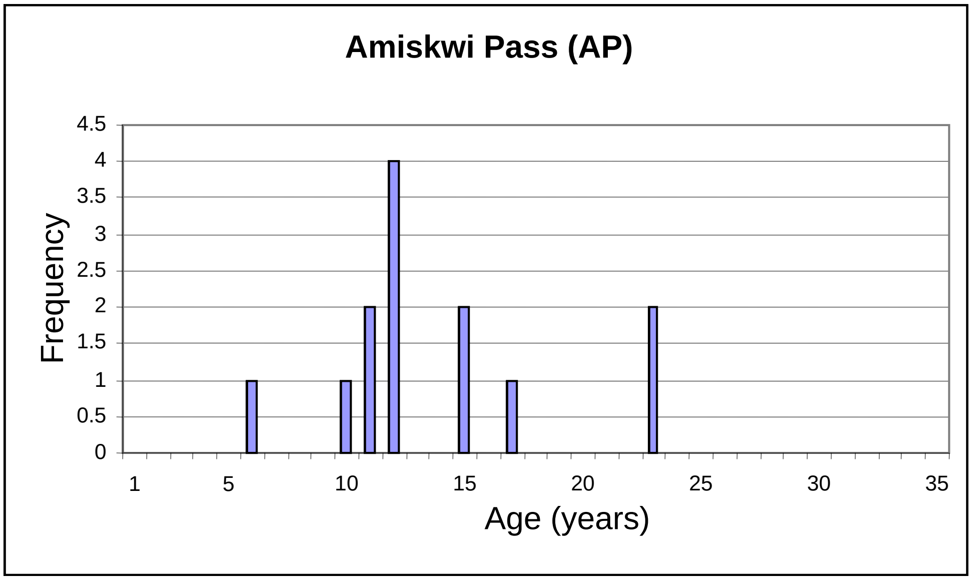
Age class distribution of whitebark pine in the Parker Ridge recently burned stand, Banff National Park.



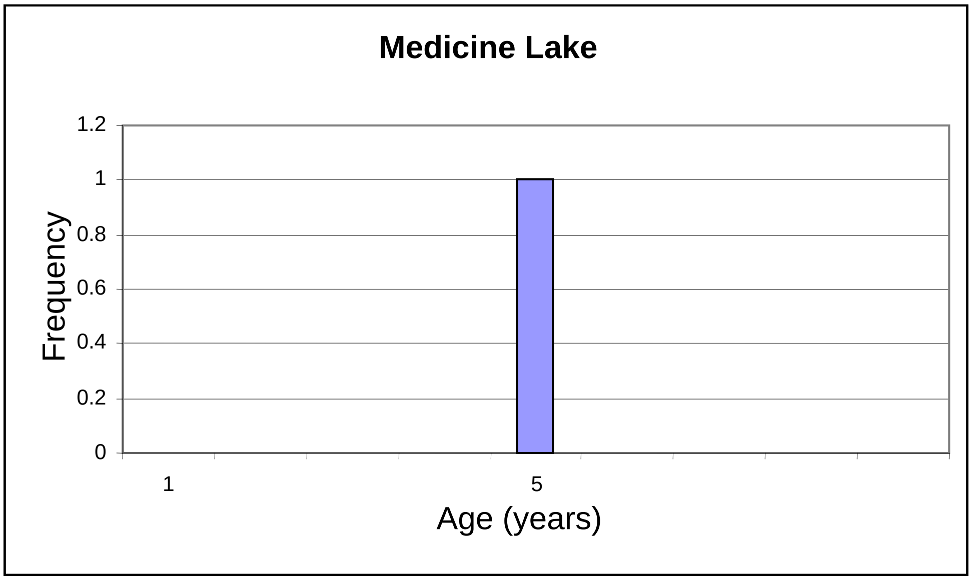
Age class distribution of whitebark pine in the Arnica Lake recently burned stand, Banff National Park.



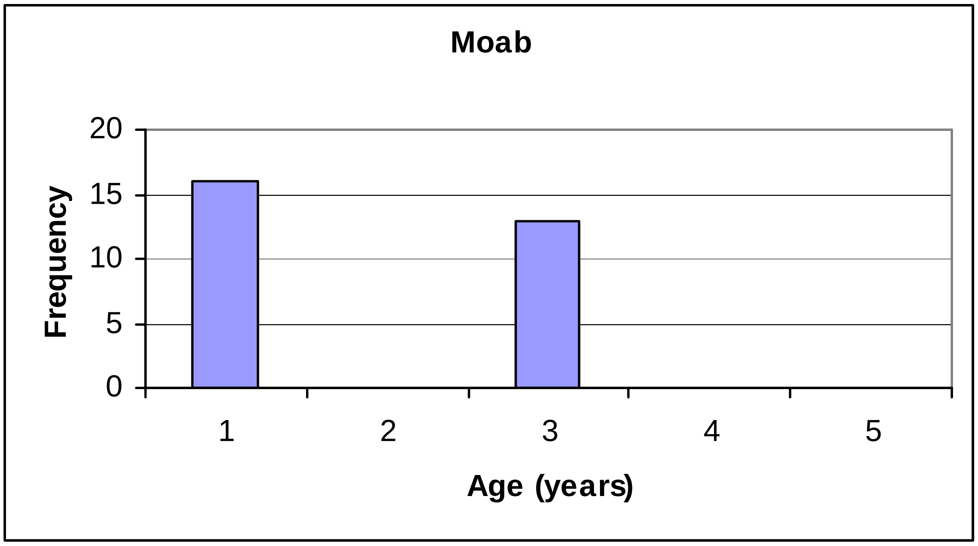
Age class distribution of whitebark pine in the Amiskwi Pass (AM) recently burned stand, Yoho National Park.



Age class distribution of whitebark pine in the Amiskwi Pass (AP) recently burned stand, Yoho National Park.



Age class distribution of whitebark pine in the Medicine Lake recently burned stand, Jasper National Park.



Age class distribution of whitebark pine in the Moab recently burned stand, Jasper National Park.