2010

Burn severity and whitebark pine (Pinus albicaulis) regeneration in the North Cascades

Stephanie A. (Stephanie Annie) McDowell
Western Washington University

Recommended Citation

McDowell, Stephanie A. (Stephanie Annie), "Burn severity and whitebark pine (Pinus albicaulis) regeneration in the North Cascades" (2010). *WWU Graduate School Collection*. 37.
https://cedar.wwu.edu/wwuet/37

BURN SEVERITY AND WHITEBARK PINE (*PINUS ALBICAULIS)* REGENERATION IN THE NORTH CASCADES

By

Stephanie A. McDowell

Accepted in Partial Completion
Of the Requirements for the Degree
Master of Science

Moheb A. Ghali, Dean of the Graduate School

ADVISORY COMMITTEE

Chair, Dr. Peter Homann

Dr. Regina Rochefort

Dr. John McLaughlin

MASTER'S THESIS

BURN SEVERITY AND WHITEBARK PINE (*PINUS ALBICAULIS)* REGENERATION IN THE NORTH CASCADES

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
Stephanie A. McDowell
February 2010

ABSTRACT

Whitebark pine (*Pinus albicaulis,* Engelm.) is a long-lived and slow-growing high elevation tree and a key part of subalpine communities in the North Cascades, Washington State. Whitebark pine populations in Washington are declining because of an exotic fungus, white pine blister rust (*Cronartium ribicola*), and successional replacement due to fire exclusion. An increase in whitebark pine seedling density could help restore populations and accelerate the process of natural selection towards rust resistance. Where whitebark pine is fire-dependent, fire exclusion has impeded whitebark pine regeneration. The relationship between whitebark pine regeneration and burn severity was studied in the subalpine and timberline ecotone in the North Cascades in 2005. Whitebark pine regeneration data were collected eleven years after two 1994 fires, the Boulder Creek Fire in the North Cascades National Park and in the Tyee Complex Fire in the Wenatchee National Forest. A comprehensive model of the ecological factors related to post-fire whitebark pine seedling presence and density was created showing how whitebark pine regeneration may be related to many characteristics of the environment, pre-fire forest, burn severity, and post-fire condition. Whitebark pine seedling presence and density models were compared using Akaike information criterion. Leading models for explaining variability in seedling presence on the Boulder Creek site included total overstory cover and burn severity factors, where areas with greater canopy cover and moderate burn severity had the greatest probability of seedling presence. At the Tyee Mountain site, the top models for explaining variability in seedling presence were overstory whitebark pine cover, char depth and soil organic matter. The probability of seedling presence increased as char depth increased and soil organic matter decreased. The variability of whitebark pine seedling densities was best explained by the distance to the edge of the burn, with seedling densities increasing with greater distance

into the core burn area. Allowing moderate severity fires to burn in large areas may create more opportunities for natural whitebark pine regeneration.

ACKNOWLEDGEMENTS

I thank the directors and members of the Whitebark Pine Ecosystem Foundation for providing essential information on all issues revolving around the decline and subsequent restoration efforts of whitebark pine. Tyler Creech collected a large share of the field data, and I am indebted to him for his stamina and persistence. I thank the North Cascades National Park and Wenatchee National Forest for permitting this research to be conducted on their property. I thank Dr. Regina Rochefort of the National Parks for the suggestion and manifestation of this endeavor, and for providing insight and counsel. I thank Dr. Peter Homann and Dr. John McLaughlin for their patient support and invaluable guidance. Special thanks to: Huxley College of the Environment notably, Nancy Bonnickson, Dianne Peterson, and Sally Elmore for field and laboratory equipment and continuing encouragement.

Table of Contents

List of Figures and Tables

INTRODUCTION

Whitebark pine (*Pinus albicaulis*, Eng.) is a long-lived and slow-growing tree and an integral part of subalpine communities throughout its range. The range of Whitebark pine extends through the Rocky Mountains from the Peace River in Northern British Columbia to Wyoming. It also grows high in the British Columbia's Coastal Mountains through the Cascades to California's Sierra Nevada Mountains in the south.

Cascadian whitebark pine populations have been declining over the past 50 years due to mountain pine beetle (*Dendroctonus ponderosae*) epidemics and an exotic fungus, white pine blister rust (*Cronartium ribicola*)(Kendall and Keane, 2001). In the Rocky Mountains, the decline of whitebark pine populations has also been attributed to successional replacement due to fire exclusion (Arno, 1986). White pine blister rust can kill 97% to 99% of infected trees, and of the 23 diseases and harmful insects that parasitize whitebark pine, white pine blister rust is the most damaging (Hoff and Hagle, 1990). In a study in Montana and Idaho, mountain pine beetles were more likely to successfully attack whitebark pine trees with white pine blister rust (Six and Adams, 2007). White pine blister rust therefore causes both direct and indirect impacts.

Kendall and Keane (2001) found whitebark pine trees infected with white pine blister rust in the North Cascades of Washington. In a study of whitebark pine stands in the North Cascades and Mt. Rainier National Parks from 1994 to 1999, white pine blister rust was found in every stand, with 31% of mature whitebark pines dead and 22% infected (Rochefort, 2008). Rates of blister rust infection decreased from north to south in the Cascade Range.

Understanding the natural regeneration process for whitebark pine is essential for effective whitebark pine restoration. An increase in whitebark pine seedling regeneration could accelerate the process of natural selection towards blister rust resistance. Fires are known to recycle accumulated biomass and macronutrients, rejuvenate vegetation, and conserve diversity (Agee, 1993); furthermore, fire may create re-establishment opportunities for whitebark pine by removing shade tolerant species such as subalpine fir. Managers outside of the North Cascades have considered stand-replacing fires vital to the creation of habitat suitable for successful whitebark pine regeneration. For example, the Caribou-Targhee National Forest is planning prescribed fires on roughly 718 acres to reduce encroaching shade tolerant stands and encourage natural regeneration of whitebark pine and aspen (Reese, 2004).

Tomback *et al*. (2001) examined the relationship between whitebark pine regeneration in three burn severity classes (unburned, moderate, and severe) among two moisture regimes (moist and dry) in the Greater Yellowstone Ecosystem. No significant difference between burned and unburned treatments was found (Tomback *et al.,* 2001). Moist sites in moderate and severe burns consistently had the highest seedling densities and greatest seedling mortality; whereas dry and burned sites had the least amount of regeneration and the highest seedling survival (Tomback *et al.*, 2001). This presents an interesting challenge, since sites beneficial to seedling establishment are unfavorable for seedling survival and vice versa.

Post-fire whitebark pine seedling recruitment, along with noble fir (*Abies procera*) and Pacific silver fir (*A. amabilis*), was observed on Mount Adams, Washington (Hoffman, 1917). The assumption that fire in the North Cascades creates conditions where whitebark pine thrives needs to be evaluated and investigated. Furthermore, if fire can have a positive effect on the regeneration of whitebark pine communities, then exactly what degree of burn severity creates the greatest opportunity for seedling establishment? Moreover, is the effect of fire different on moist and dry sites?

This research is designed to establish the relationship of post-fire whitebark pine regeneration in the North Cascades to burn severity and moisture regimes. This study examined whitebark pine regeneration at two sites in the North Cascades where wildfires had occurred 11 years previously. The objectives of this study were to determine:

- The relation of seedling presence to burn severity and moisture
- The importance of burn severity and moisture vs. other factors on seedling presence and density

This North Cascade study complements the much more extensive Rocky-Mountain research of post-fire whitebark pine regeneration. Cascadian whitebark pine forests have more conifer species, a maritime climate, and comprise less contiguous stands than Rocky Mountain whitebark pine populations. Forest managers in the Rocky Mountains have prioritized whitebark pine restoration efforts to areas with dominant, seral whitebark pine habitat.

Management activities include mechanically altering the forest stands, replanting rust-resistant seedlings, allowing natural burns, and introducing prescribed burns. This study examines the most favorable sites for natural whitebark pine regeneration and accordingly rust-resistant seedling planting in the North Cascades.

BACKGROUND

Geographic Distribution and Ecological Niche

Whitebark pine occurs only in western North America in discontinuous communities. There are two main sub-regions, the Rocky Mountains and the western coastal mountain ranges. The western sub-region extends from California's Sierra Nevada Mountains above 3600 m elevation to British Columbia's Coastal Mountains above 900 m elevation. The sub-regions are connected through southern British Columbia and northeastern Washington (McCaughey and Schmidt, 2001).

In the North Cascade Mountains of Washington State, whitebark pine trees are typically found above 1600 m, growing upright below the tree-line and in a krummholz (German for twisted branch) form above the tree-line. The tree-line in the North Cascades varies from approximately 1950 m to 2100 m in the North Cascades (Douglas and Bliss, 1977). Because whitebark pine is moderately shade intolerant, it is considered early seral on more favorable, wetter subalpine sites, including those at timberline (Arno and Huff, 1989). Alternatively, whitebark pine is considered a climax species on cold, dry rocky outcrops where it often exhibits the krummholz form. The shrub-like appearance of whitebark pine above the tree-line provides snow-fencing, important in preserving snow-pack in the mountains throughout the spring and early summer (Arno and Hoff, 1989).

In high elevation habitats, temperature, wind, and snow pack determine how well trees grow. The limber and waving branches of mature whitebark pine trees ease the mechanical stress from wind and thwart heavy snow pack. Snow pack is an important environmental factor in subalpine areas because it reduces the growing season, and more trees are typically found in areas that inhibit snow accumulation such as hummocks and steep south facing slopes (Mellmann-Brown, 2007). Tree islands (mosaic clusters of trees) form in high elevation areas because the trees shelter one another from extreme temperatures, wind, and snow (Mellmann-Brown, 2007).

White pine blister rust *(Cronartium ribicola)* was introduced to the West Coast of North America in 1910 through infected eastern white pines from France. The rust quickly spread through and weakened the five-needle pine populations. The five-needle pine species in the Pacific Northwest are *P. monticola* (western white pine), *P. lambertiana* (sugar pine), and *P. albicaulis* (whitebark pine); however, sugar pine does not occur in the study area. Recently, the disease was found for the first time on a bristlecone pine, *P. aristata.* By 1923, blister rust had spread throughout the entire range of western white pine (*Pinus monticola*) (Hoff and Hagle, 1990). The Pacific Northwest has an excellent climate for white pine blister rust because the rust requires humid, cool conditions for spore production and dissemination. Blister rust spores are very hardy and their spores can travel 300 miles annually when cool and moist conditions extend throughout late summer and early fall (Hoff and Hagle, 1990).

Whitebark pine branches die after becoming girdled by a blister rust canker; subsequently branch cankers greatly reduce cone production. Ultimately, branch cankers spread up the branch onto the main tree bole. Field surveys in the North Cascades National Park, documented that mature whitebark pine in 1999 had 23.8% mortality and 38.4% of whitebark pine were infected with blister rust and 23.8% had died from the rust (Rochefort, 2008).

Whitebark pine is a valuable resource for wildlife. In the Rocky Mountains, whitebark pine seeds can be over 50 percent of grizzly bears’ (*Ursus arctos horribilis*) diet during part of the year (Mattson *et al.,* 2001). The seeds are rich in dietary fat, with 30 to 50 percent fat content. Dietary fat is easily converted into adipose tissue, of which female grizzly bears need a large reserve to hibernate and support lactation (Hellgren, 1998). Grizzly bear populations in the lower 48 states were federally listed as Threatened in 1967. Other mammals and birds also forage on whitebark pine nuts, which are nutritional resources and the biggest seeds in the subalpine zone (Tomback and Kendall, 2001). The animals that feed on whitebark pine seeds include Clark's nutcracker (*Nucifraga columbiana*), American red squirrel *(Tamiasciurus hudsonicus),* black bear *(Ursus americanus),* chipmunk *(Tamias minimus),* common raven *(Corvus corax),* Stellar's jay *(Cyanocitta stelleri),* and pine grosbeak *(Pinicola enucleator)* (Tomback *et al*., 2001).

Regeneration

Whitebark pine has three strategies for exploiting favorable conditions: a canopy seed bank, an advanced seedling bank, and a subterranean seed bank. A canopy seed bank strategy is a long-lived over-story that produces seed. Whitebark pine trees typically start producing cones when 50 years old and reach peak cone production at 80 years, which continues for the next 200 to 300 years. Another strategy is to have an advanced seedling bank which can survive for many years, suppressed under an overstory canopy. Finally, whitebark pine employs a subterranean seed bank strategy, initiated by nutcrackers, that encourages seedlings to germinate in seedling clumps (Tomback, 2001).

Whitebark pine has indehiscent cones and seeds are dispersed by Clark’s nutcracker (*Nucifraga columbiana* Wilson) for its regeneration. Clark's nutcracker and the red squirrel harvest about 99% of the seeds in the Rocky Mountains (Lanner, 1986). Red squirrels store whitebark pine cones in middens, which are excavated by grizzly bears for the seeds (Lanner, 1986).

During summertime in the Rocky Mountains, Clark's nutcrackers disperse whitebark pine seeds up to 22 km away from the source, with a mean distance of 4 km (Tomback, 2001). A single nutcracker can carry up to 120 seeds in a sublingual pouch, and over one summer disperses up to 100,000 seeds (Lanner, 1986). Nutcrackers plant one to fifteen seeds (mean of 3.7) in subterranean caches in rocky soil at a depth of 1 to 3 cm (mean of 2).

Goheen *et al.* (2002) studied whitebark pine communities in the Umpqua National Forest in Oregon. They found that Clark's nutcrackers cache seeds in various sites, including loose gravelly soil and forest litter; at the base of trees, rocks, and logs; among roots; under rocky rubble; and in holes in trunks or bark of trees (Goheen *et al.,* 2002). Clark's nutcrackers retrieve many of their seeds, consuming up to 10,000 seeds per adult and 5,000 seeds per offspring (Goheen *et al.*, 2002). Caching sites have been observed across a wide range of elevations, in burns, harvested areas, forest openings, along lake shores, meadow edges, and on cliffs (Goheen *et al.,* 2002).

Whitebark pine seeds exhibit a pattern of delayed germination that can work to their advantage on dry rocky slopes with unpredictable weather (Tomback, 2001). Viable seeds stashed in subterranean caches can lie dormant for up to 8 years until favorable conditions exist for germination. Mellmann-Brown (2007) found higher germination was positively correlated to higher maximum July surface temperatures and late snow melt.

In the Beartooth Plateau in Montana and Wyoming, whitebark pine regeneration was more successful in areas with longer snow cover, downwind of tree groups or in depressions (Mellmann-Brown, 2007). High survival rates correlated with the presence of shade and shallow organic layers, and heat-scorch damage was considered to be a principal cause of mortality during the first growing season (Mellmann-Brown, 2007).

Fire and Regeneration

McCaughey and Schmidt (1990) examined the microsite influences on whitebark pine seedling establishment in the Gallatin National Forest in Montana. Seedling germination and success was monitored after hand-sowing whitebark pine seeds with combinations of three shade levels, two sowing depths, four predator exclusion levels, and three seedbed types (mineral, litter, and burned soil). All surface-sown seeds not protected from predators were lost and assumed to be consumed by foragers (McCaughey, 1990). Heat-scorching seedling mortality was higher on non-shaded than on partially-shaded sites; in addition, mineral soil plots had the greater whitebark pine seedling densities than litter and burned soil (McCaughey, 1990). Izlar (2007) found a negative correlation between direct sun and whitebark pine seedling survival in plantings. Whitebark pine seedling survival was greatest in areas with more microsite features such as rocks, woody debris, and stumps (Izlar, 2007).

On moist, favorable sites, fire disturbance has been regarded as essential to the upkeep of whitebark pine, where it would otherwise be replaced by shade tolerant species (Arno and Peterson, 1983). This assumption was further examined by Campbell and Antos (2003), who studied chronosequences in stands dominated by whitebark pine in the southern British Columbia. They found that whitebark pine is not completely replaced by shade-tolerant species, and as a stress-tolerator, it can grow slowly and persist under adverse conditions. Furthermore, whitebark seedling recruitment occurs in stands of all ages, but seedlings are least likely to survive in late seral stands (Campbell and Antos, 2003). The lower survival rate of seedlings in late seral stands could be attributed to a greater light requirement than established whitebark pine trees. Severe stand-replacing fires could initiate seedling establishment, which is three times more successful in early seral post-fire than in mid and late seral stands (Campbell and Antos, 2003).

In the northern Cascades, whitebark pine is associated with Engelmann spruce *(Picea engelmannii)*, subalpine fir *(Abies lasiocarpa)*, lodgepole pine *(Pinus contorta murrayana)*, and subalpine larch *(Larix lyalli)*. One considerable disadvantage that whitebark pine has after a fire is the lack of serotinous cones, which open after being heated in a severe fire. After a severe stand-replacing fire, whitebark seedlings compete with serotinous cone producing species such as lodgepole pine. Antos and Campbell (2003) found substantial mortality in the initial post-fire whitebark pine seedlings where lodgepole pine is abundant.

Buffo (2003), in his senior thesis, described subalpine forests with a focus on whitebark pine trees in the North Cascades. Buffo anticipated comparing burned and unburned areas within the North Cascades Boulder Creek fire area nine years after the fire for whitebark pine regeneration densities, but found an insufficient number of small trees in the burned zone of his study area. He observed fewer tree species with increased elevation, slow tree recruitment in burned areas, and whitebark pine dominance restricted to the rockiest areas.

Chappell and Agee (1996) conducted a study to determine the relationship between fire severity and tree seedling establishment. The study focused on recent natural burns in Shasta red fir (*Abies magnifica var. shastensis)* stands exploring the relationships between landscape composition, fire history, and seeding establishment. Variations in fire severity were measured by basal area mortality and were found to play a significant role in post-fire stand structure, successional pathways, and species composition. Shasta red fir seedling densities were greatest in low and moderate severity burns.

Fire in North Cascades

Fire has been recognized as a prime regulator of forest dynamics in the Pacific Northwest for at least 10,000 years in the Cascades, a claim validated by charcoal in sediments in lake cores collected throughout the Oregon Cascades (Long *et al.*, 1998). Fire intensities, and consequently burn severities, vary depending on biological and geospatial controls, mainly topographic position and fuel loading. Fire intensity is a measure of the rate of energy released from organic matter, which includes both radiant and convectional heat. Burn severity is a measure of the loss of organic matter from the physical combustion process. The magnitude of heat that is produced as a fire burns, or fire intensity, is correlated to burn severity, which is a measure of environmental change on a landscape scale. The relationship between whitebark regeneration and burn severity has not been established in the North Cascades. Relative to other factors that influence seedling regeneration, burn severity may be the most important (Campbell and Antos, 2003).

The North Cascades has seen an increase of shade-tolerant species relative to shade-intolerant species since the 1920's (Siderius and Murray, 2005). Increasing fire may perhaps lead to less post-fire shade, promoting facilitating the establishment of shade-intolerant species rather than shade-tolerant species. The topographic variability in the whitebark pine zone creates mixed severity fires; however, an increasing fuel load supports increasing fire intensity. Siderius and Murray (2005) reported that roughly half of the most recent fires in the North Cascades were of high severity.

A fire regime with fewer burns and greater burn severity may not be beneficial for whitebark pine communities on the North Cascades. Although high severity fires kill mature trees, they also create more open canopies for seedlings to develop. This study is designed to help understand the response that whitebark pine regeneration has in altered fire regimes. Altered fire regimes can influence the occurrences and magnitude of burn severities (Agee, 1993).

Problem Statement and Study Approach

The information presented above indicates multiple relations may exist between whitebark pine regeneration, fire, and environmental variables. A theoretical conceptual model shows interaction between the pre-fire forest structure and the burn severity, which together create a post-fire condition in which seedlings become established (Fig 1). Therefore, whitebark pine regeneration may be related to many readily measurable characteristics of the environment, pre-fire forest, burn, and post-fire condition; furthermore, the potential relationships could have different pathways on moist and dry sites.

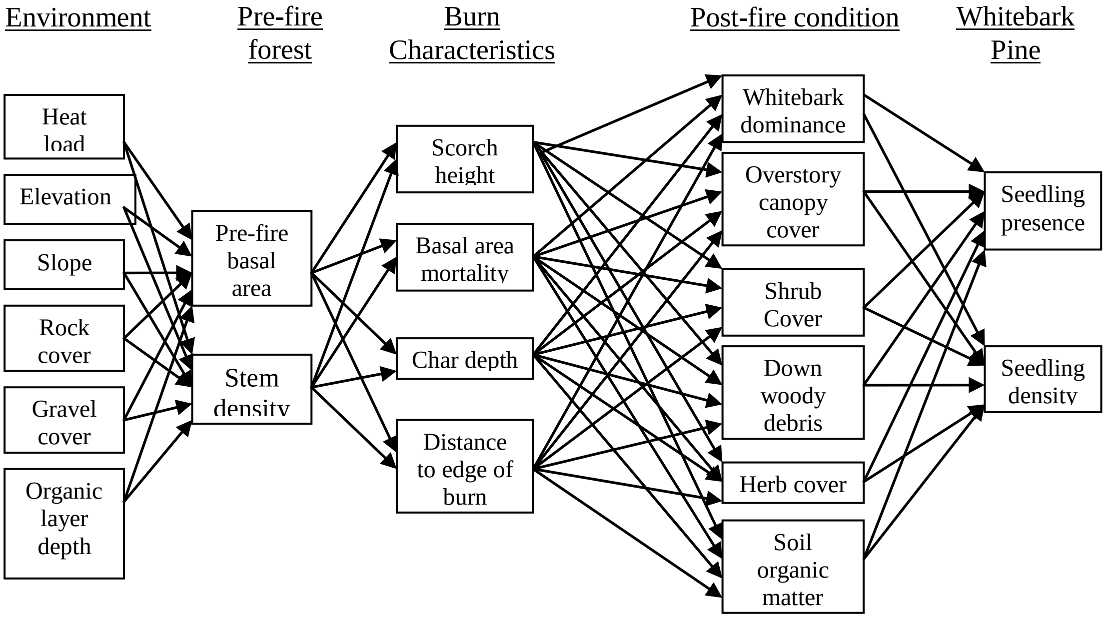

Figure 1. Conceptual model of relationships among measureable characteristics and whitebark pine seedling presence and density.

This study examined whitebark pine regeneration at two sites in the North Cascades where wildfires had occurred 11 years previously. The objectives of this study were to determine

- The relation of seedling presence to burn severity and moisture
- The importance of burn severity and moisture vs. other factors on seedling presence and density

Each objective was addressed with a set of specific questions (Table 1), and each question was answered by a statistical test applicable to the type and distribution of the data. The environmental, pre-fire forest, burn, and post-fire characteristics were measured as continuous variables. The seedling presence was a dichotomous variable. The seedling density was a discrete variable approximated by the Poisson distribution.

Table 1. Specific study questions and statistical tools used to address objectives

Objective 1. Relation of seedling presence to burn severity and moisture		
1.1	Do pre-fire conditions vary among burn severities?	Cluster Analysis
1.2	Does seedling presence differ among burn severities?	Chi squared test of independence
1.3	Does the relation between seedling presence and moisture differ among burn severities?	Chi squared test of independence
Objective 2. Importance of burn severity and moisture vs. other factors on seedling presence and density		
2.1	What is the relation among environmental, burn severity, and forest characteristics?	Kendall's tau correlation
2.2	Which variables explain seedling presence best?	Logistic regression, multi-model comparison
2.3	Which variables explain seedling density?	Poisson regression, multi-model comparison

In the explanation of seedling density and abundance by logistic and Poisson regression analyses, the statistical multi-model approach was used. The parameters for each statistical model (Table 2) were chosen based on their theoretic ability to limit or promote germination and survival of whitebark pine seedlings. Whitebark pine regeneration may be related to many characteristics of the environment, pre-fire forest, burn severity, and post-fire condition.

Table 2. Parameters contained in each statistical model for explaining the presence and abundance of whitebark pine seedlings.

Explanatory Models for Variability in Seedling Presence and Density	
Null	
1.	Constant
Environment	
2.	Rock cover + gravel cover
3.	Elevation + Slope
4.	Heat load + organic layer depth
Burn characteristics	
5a.	Char depth
5b.	Char depth * Moisture
6a.	Distance to edge of burn
6b.	Distance to edge of burn * Moisture
7a.	Scorch height
7b.	Scorch height * Moisture
7c.	Scorch height (quadratic)
8a.	Basal area mortality
8b.	Basal area mortality * Moisture
8c.	Basal area mortality (quadratic)
Post-fire conditions	
9a.	Whitebark pine cover
9b.	Whitebark pine cover * Moisture
10a.	Overstory cover
10b.	Overstory cover * Moisture
11a.	Shrub cover
11b.	Shrub cover * Moisture
12a.	Down woody debris
12b.	Down woody debris * Moisture
13a.	Soil organic matter
13b.	Soil organic matter * Moisture
14a.	Herb cover
14b.	Herb cover * Moisture

These characteristics could affect regeneration differently in moist and dry areas; therefore, moisture regime is examined as an indicator variable for all models with burn or post-fire parameters.

Model 1 has no parameters and assumes seedling distributions are due to chance. Alternatively, the environmental niche for whitebark regeneration could be restricted to the rockiest and most gravelly environments (model 2) or steep, high elevation zones (model 3).

Dark charred material and organic layers create a warming effect by absorbing incoming solar radiation and converting it to heat. Heat generation can be beneficial for seedlings in a subalpine environment with a short growing season, but too much heat can lead to heat scorch which is a very limiting factor for seedling survival (McCaughey, 1990). If heat generation is a limiting factor by creating scorching conditions for seedlings or by melting snow earlier in the growing season, then increased organic layer depth and heat load (model 4), increased char depth (model 5), and increased soil organic matter (model 13) may be detrimental to whitebark pine seedlings due to heat scorch mortality. If whitebark pine seedling survival is limited by competition by more rapidly growing trees, then whitebark pine seedling densities will decline as soil organic matter and soil moisture increase in tandem, because mesic soils rich in organic matter support rapid growth of species that outgrow whitebark pine. Decreasing partial shade created by overstory trees (model 10), shrub (model 11), or downed woody debris cover (model 12) may create openings to allow more sunlight to reach the seedbed, therefore increasing seedling presence and abundance.

Burn severity, the measure of the ecological impact of fire, is simultaneously created by past conditions and creating future conditions. Basal area mortality (model 8) and scorch height (model 7) are the model parameters that characterize the magnitude of burn severity. Burn severity is also examined as a second level polynomial to ensure that the pattern of seedling distribution is most accurately modeled. Areas of high burn severity may provide conditions that allow too much heat at the seedling level due to high amounts of incoming solar radiation with low shade cover and high incidence of dark materials at the surface; conversely, unburned areas may not allow enough incoming sunlight to allow whitebark pine seedlings to thrive.

To understand seedling distributions, it is important to recall the seed dispersal mechanics of the whitebark pine. Clark’s nutcrackers can distribute whitebark seeds deep into burned areas; farther than the winged seeds of competing tree species can travel (Tomback *et al*., 2001).A subterranean seed bank strategy can work well after a stand replacing fire exposes new ground for nutcrackers to cache seeds. A deficiency in seed availability may be the limiting factor for whitebark pine seedling presence and abundance; therefore, seedling presence and abundance may increase with an increase in living whitebark pine overstory (model 9) cover and a decrease in the distance to the edge of the burn (model 6) .

METHODS

Study Sites

The study sites are in two 1994 wildfire locations, the Boulder Creek and Tyee Complex fires, which overlap large whitebark pine populations (Figure 2). These sites were chosen because they have the large stands of whitebark pine and the high concentrations of Clack's nutcrackers. Clark's nutcrackers are responsible for dispersing the seeds of whitebark pines into burned and unburned areas.

The first site is in the Boulder Creek Burn in the North Cascades National Park near Lake Juanita and six kilometers east of the town of Stehekin, Washington (Figure 2). Lightning strikes initiated the fire on July 24, 1994, and it continued to burn until snowfall in October. Roughly 1,000 hectares burned in a mosaic pattern, with a full spectrum of fire intensities, including unburned areas.

The Boulder Creek study site is situated between 1700 m and 2200 m elevation, covers 523 hectares, and extends up to 150 m outside of the burn boundary. The area is dominated by subalpine fir and mountain hemlock and the last stand-replacing fire in Boulder Creek area was approximately 1840, although there is fire-scar evidence from 1864 and 1893 (Siderius and Murray, 2005). The mean fire return interval at Boulder Creek is 27 years (Siderius and Murray, 2005). According to the Western Regional Climate Center (WRCC) data station in nearby Stehekin which has been collecting climate data since 1905, the mean annual precipitation in is 34.04 inches.

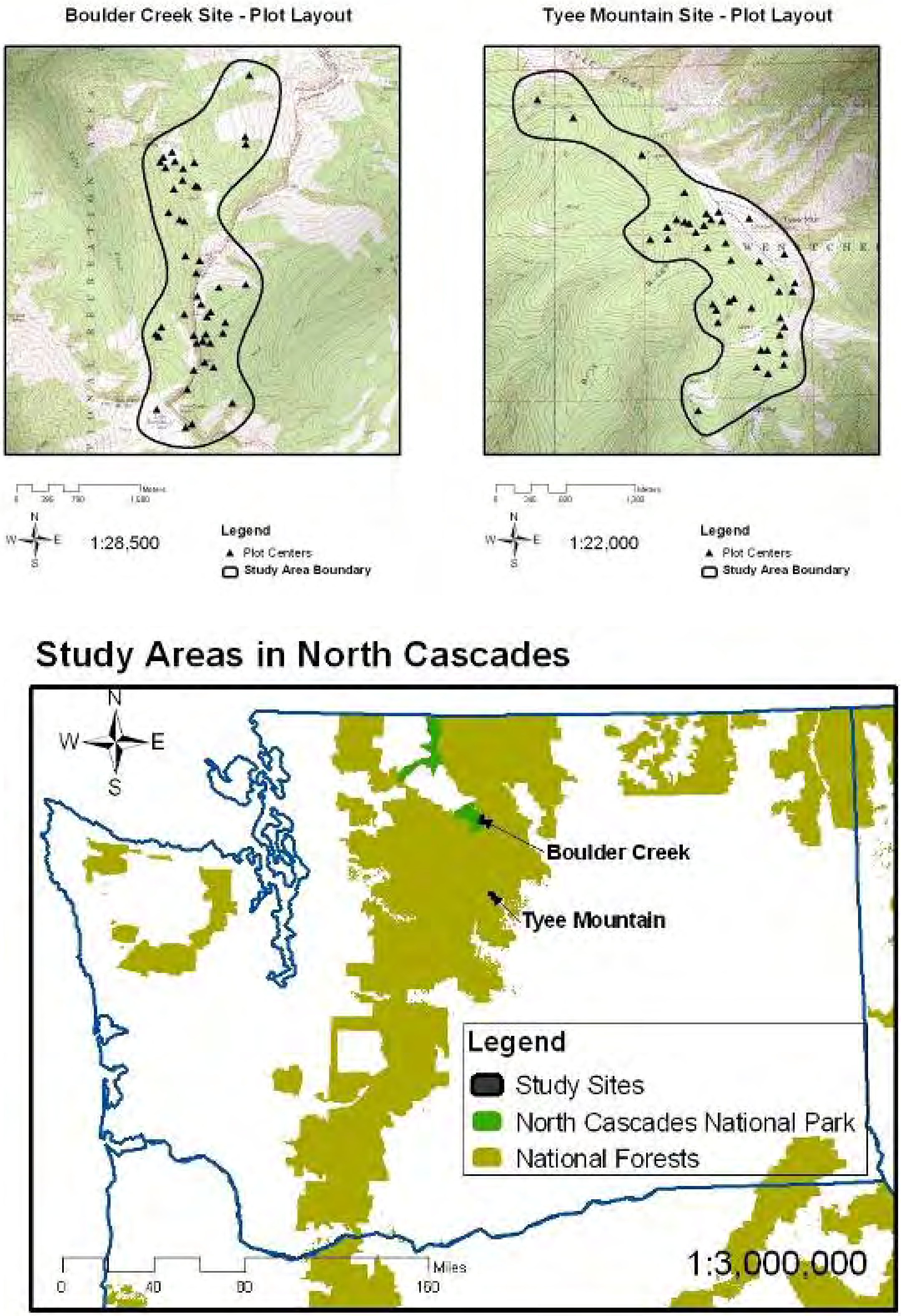

Figure 2. The two study sites are located within the subalpine zone in the North Cascades.

The second site is on Tyee Ridge in the Wenatchee National Forest, near the Tyee Mountain Lookout. The Tyee Mountain study site is situated between 1660 m and 2050 m elevation, covers 566 hectares, and extends up to 150 m outside of the boundary of the Tyee Complex Fire. Unlike the Boulder Creek site, the Tyee Mountain area is dominated by subalpine fir, lodgepole pine trees, and a greater Douglas fir component.

The Tyee Complex fire was ignited by lightning on July 24, 1994 and burned until it was considered controlled 33 days later. Tyee Ridge, which overlaps the study site, endured a stand-replacing fire in approximately 1880, has fire scar evidence from 1915, and has a mean fire return interval of 57 years (Siderius and Murray, 2005). The mean annual precipitation is 26.31 inches, six miles to the southeast at the nearest WRCC data station in Plain, Washington.

Data Collection

Plot Establishment and Classification

An ArcGIS polygon, furnished in April 2005 by the GIS specialist, Natalya Antonova, at the North Cascades National Park, delineates the boundary of the Boulder Creek Burn. The study area boundary extends 50 meters beyond the burn boundary to encompass the adjacent unburned areas. The Tyee Mountain site was delineated on location. MS Excel generated two hundred random plot locations as UTM coordinates (NAD27 map datum) within the boundary of each study site. The potential plot locations were used if they were accessible by foot without need of climbing gear.

At each site, an attempt was made to establish study plots using a stratified random sampling method. Potential plots were established until at least seven plots were chosen for each combination of three burn severity and two moisture classifications. However, fewer than seven moderate burn severity plots were established in moist sites, due to availability.

Plot centers were located in the field within 10 meters estimated horizontal error using a handheld GPS device (Magellan 300), map and compass. Fire severity classes were defined by basal area mortality and scorch height (Table 3). Moist and dry sites were determined by the plant composition found on the site (Table 4). One positive point was given for each wet site indicator and one negative point was given for each dry site indicator plant. Points were tallied and the positive or negative value of the sum determined the moist or dry status, respectively.

Table 3. Burn severity classes are determined by the magnitude of the mortality and scorch heights on overstory trees.

	Burn Severity Class	Basal area mortality	Scorch height
I.	Unburned	0%	0 m
II.	Moderate	<60%	< 6 m
III.	Severe	>60%	>6 m

Table 4. The distinction between "Dry" (more xeric) and "Moist" (more mesic) treatments, a relative comparison, is based on whether or not moist-site and dry-site plant indicators are present. This list is comprised of common species found in high elevation areas in the North Cascades.

Moisture regime	Indicator plant	Common name
Moist site	*Alnus sinuata*	Sitka alder
	Arnica latifolia	Mountain Arnica
	Galium boreale	Northern Bedstraw
	Heracleum lanatum	Cow parsnip
	Luzula hitchcockii	Small flowered wood-rush
	Picea engelmannii	Engelmann spruce
	Ribes lucustre	Black gooseberry
	Sambucus racemosa	Red elderberry
	Senecio triangularus	Arrow-leaved groundsel
	Valeriana sitchensis	Sitka valerian
	Veratrum virde	Indian hellebore
Dry site	*Arctostaphylos uva-ursi*	Kinnikinnick
	Carex geyeri	Sedge
	Festuca idahoensis	Idaho fescue
	Heurchera cylindrica	Alumroot
	Juniperus communis	Common juniper
	Pachistima myrsinites	Mountain boxwood
	Penstimon fructicosus	Beard-tongue
	Saxifraga bronchialis	Spotted saxifrage

Environmental, Burn, and Vegetation Data

Minimal impact field methods were used to ensure that this project preserved and protected the Forest and Park's natural, cultural, and social resources. Whitebark pine seedlings were sporadic throughout the study areas, requiring sample plot areas covering 500 m^2 with five 10 m^2 nested subplots (Figure 3).

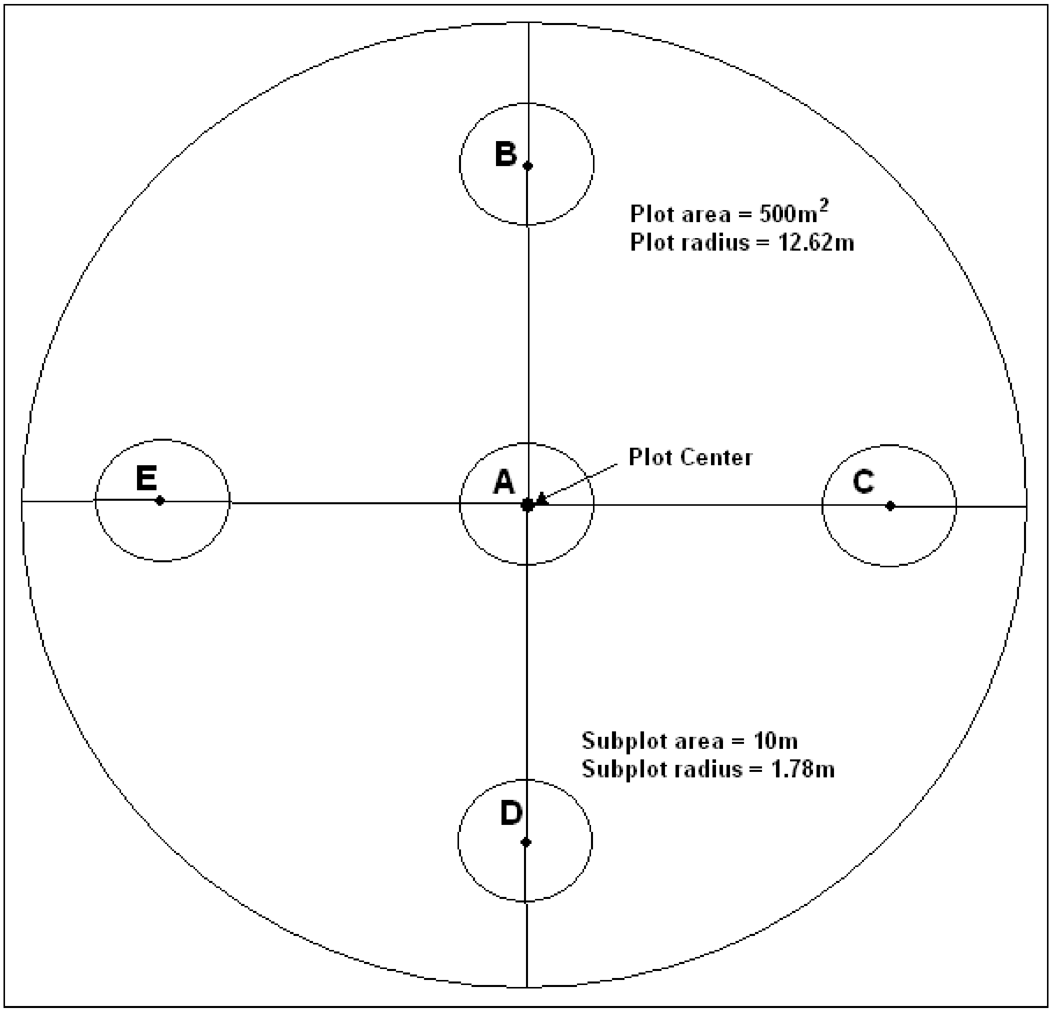

Figure 3. Each study plot had five nested subplots with one at plot center and four in each cardinal direction.

The following observations were made on the plots:

500 m^2 plot data: Over-story canopy cover (%) per species, scorch height (m) on overstory trees, slope (%), aspect (degrees), elevation (m), distance to edge of burn (m), live and fire-killed tree basal area (m^2) for all species.

10 m^2 subplot data: char depth (cm), soil organic matter (%), surface rock cover (%), surface gravel cover (%), shrub cover (%), herb cover (%), down woody debris cover (%), and seedling and sapling data for all species.

Seedling and sapling data: species, age (years), basal diameter (cm), height (cm), nearest neighbor distance (cm), and disease incidence. Seedlings are defined as less than 147 cm in height; whereas, saplings are greater than 147 cm in height and less than 10 cm diameter at breast height (dbh).

Char depth was measured as distance from surface to the base of charred material. Organic layer depth was measured from the top of the litter layer to the boundary between the organic horizon and mineral soil. Char depth and organic layer depth were measured at the soil core location (see *Soil measurements* below).

Plot aspect was measured by standing at plot center and recording the predominant aspect in degrees, 0° to 360°. If aspect varied gradually across the plot, an average aspect was recorded. If the plot fell on or straddled a canyon bottom or narrow ridge top, the aspect of the ridgeline or canyon bottom was recorded.

For correlation analysis, the relative heat load was determined by the aspect of each plot. Aspects were transformed trigonometrically into a Heat Load Index (HLI) value using a function that provided a maximum value (+1) for SW aspects (225°) and minimum value (0) for NE aspects (45°). Hand-held clinometers were used to measure percent slope to the plot boundary along the predominant aspect. Elevation was determined by a handheld GPS device (Magellan).

Canopy cover, which is a measure of intercepted sunlight, was assessed with an ocular estimate per species. Tree seedling and sapling ages were determined by counting annual whorls and bud scale scars.

Soil Measurements

Cylindrical soil core samples 4 cm in diameter and 16 cm deep (200 cm^2) were obtained as near to subplot centers as possible, avoiding areas too rocky to sample. Soil cores included the organic horizon and mineral soil. Previous to drying, individual subplot soil sample weights (w_{tot}) were recorded, then sub-sampled and amalgamated into a single composite sample per plot. From the composited soil sample, two 10-mL portions were collected and dried for a minimum of one hour at 110°C in crucibles, and moist (w_m) and dry (w_d) soil weights were recorded. Bulk density was calculated by averaging the total sample weights, multiplying by a ratio of dry/moist soil weights, and dividing volume (200 mL).

$$\text{Bulk density} = [(wtot\ g * wd\ g) / (wm\ g * 200\ mL)]$$

The crucibles were then covered and placed in a muffle furnace at 450°C for 12 hours, and ash weights (w_a) were recorded. Soil organic matter was taken to be loss on ignition (LOI), which was calculated as

$$\text{Soil organic matter} = LOI = [(wd\ g - wa\ g) / (wd\ g)] * 100\%$$

Statistical Analysis

Statistical analyses were carried out for each site separately.

Cluster Analysis

It is important to consider first the assumption that the study plots are comparable between burn severity classes, especially because this study is observational. Multiple environmental factors with significant heterogeneity between burn severity classes could confound the results, making it impossible to distinguish environmental effects from fire effects. If the three burn severity classes are from significantly differing ecological regions, then a clustering analysis would be able to group them based on their environmental attributes.

An assessment of the site characteristics was made to see if study plots significantly differ between burn severity categories. To test for continuity, a non-metric conceptual clustering package, RIFFLE, was used with the program R, developed by Geoffrey and Robin Matthews at Western Washington University. Nonmetric conceptual clustering is a multivariate analysis method based on the iterative process of separating data into clusters based on their attributes. The clusterings are optimized based on their ability to accurately explain variability in the data (Matthews, 1995). RIFFLE produces Proportional Reduction in Error terms (PRE scores), which can be averaged to create a measure of nonmetric fitness. A cluster analysis was performed three times on all variables that are presumed unchanged after a wildfire: pre-fire basal area, elevation, slope, heat load, rock cover, gravel cover, and organic layer depth.

First, RIFFLE clustered the data set into three groups. Then, the relationship between cluster classifications and burn severity classes was evaluated with a chi-squared test with a significance level (α) set at 0.05. Next, the variables were re-sampled randomly to generate a new randomized data set. The new randomized data set had the same dimensions as the original data set, with the same number of entries and range of values.

An identical cluster analysis was performed three times on the randomized data set. The non-metric fitness terms from the randomized and original data sets was compared with a one-way ANOVA, with a significance level (α) set at 0.05. If the data do not cluster significantly into burn severity categories and the non-metric fitness terms are not significantly different than those generated by the randomized data set, then the environmental and pre-fire conditions do not vary significantly between burn-severity categories.

Tests of Independence

The relation of seedling presence to burn severity and moisture was determined by tests of independence using chi-square analysis. To test if seedling presence was independent of burn severity and moisture, a partial independence test (Zar 1999, p. 512) was conducted on a 2 x 3 x 2 contingency table containing the number of plots occurring in each combination of 2 levels of presence (present or absent), 3 levels of burn severity class, and 2 levels of moisture class (Zar 1999, p. 512). When the null hypothesis of independence was rejected ($P<0.05$), the data were subdivided (Zar 1999, p. 466) to test if seedling presence was independent of burn severity, independent of moisture, and independent of moisture within each burn severity class. In these tests, the rejection of the null hypothesis of independence at $P < 0.05$ indicated burn severity or moisture affected seedling presence.

Correlations

Environmental and pre-fire variables, burn characteristics, and post-fire conditions were potential explanatory variables of seedling presence and density. The relationships among these variables were determined with Kendall's rank correlation. The correlations were considered significant at $P < 0.05$.

Logistic and Poisson Regression of Zero-Inflated Data

Whitebark pine seedlings occurred on less than half of the study plots, producing a zero-inflated data set. Consequently, in developing the regression relationships of seedling presence and density, a two-step process method was adopted to compensate for the high number of zeroes.

The first step consisted of a multivariate logistic regression on the presence/absence of whitebark pine seedlings. Multiple models that had a broad range of explanatory variables were assessed (Table 2). The Akaike information criterion (AIC) was used to select leading models. To avoid a bias due to small sample size (sample size/ number of parameters < 40), a corrected Akaike information criterion (AIC_c) was used (Burnham and Anderson, 2002). The AIC_c is

$$AICc = 2k - 2 \ln L + (2*K*(K+1))/ (n-K-1)$$

where k is the number of parameters, and L is the likelihood function. When selecting models based on AIC_c, the balance of model fitness is measured against the model complexity. Low AIC_c values indicate models have more empirical support. AIC_c values are re-scaled to the lowest AIC_c value of zero where

$$\Delta AIC_{c\,i} = AIC_{c\,i} - \min (AIC_c).$$

The top model has an $\Delta\ \mathrm{AIC}_{c\ i}$ score of zero; and models with an $\Delta\ \mathrm{AIC}_{c\ i}$ value less than two are in the confidence set.

The second step was a multivariate Poisson regression on the density of whitebark pine seedlings. Whitebark pine seedling count data fit the Poisson distribution, which is a discrete probability distribution. The Poisson distribution is characterized by having only zero and positive integers and by the mean being equal to the variance. This analysis was carried out only on the study plots with whitebark pine seedling presence. Individual models were compared using Akaike information criterion selection method.

To incorporate model selection uncertainty, conclusions from model selection were based on a confidence set of models. Akaike weights were used to determine confidence sets and include those models with AIC_c values that were within 2 units of the lowest AIC_c ($\Delta\mathrm{AIC}_{c\ i} < 2$).

Global Model Fitness

The overall fit of a global model, including all variables, was considered for each study site. The overall fit was determined by a goodness of fit statistic using the Hosmer-Lemeshow statistic for each global model. The evaluation of global model fitness was assessed using the Hosmer-Lemeshow (2000) fitness test because it is designed to categorize continuous variables for a chi-squared analysis. The Hosmer-Lemeshow test is performed by dividing the predicted probabilities into groups based on percentile ranks and then calculating a Pearson chi-square, comparing the predicted to the observed frequencies. Lower values and non-significance indicate good global model fitness.

RESULTS

Relation of Seedling Presence to Burn Severity and Moisture Classes

Boulder Creek Burn Site

A total of 48 study plots were measured in the North Cascades National Park at the Boulder Creek Burn site. The spatial extent of moderately burned areas was lacking in the Boulder Creek Burn site. In particular, moist and moderately burned areas were less extensive, which is reflected in the number of sites measured (Table 5).

Table 5. Number of study plots at the Boulder Creek site within each burn severity and moisture classification cell.

	Unburned	Moderately Burned	Severely Burned
Moist	9	4	9
Dry	9	8	9

Cluster analysis indicated burn-severity categories did not vary significantly in their environmental and pre-fire conditions, which included pre-fire basal area, elevation, slope, heat load, rock and gravel cover, and organic layer depth (Table 6). For each run of the RIFFLE cluster analysis the Chi-square analysis did not produce any statistically significant probabilities, where $P < 0.05$. Additionally, the average Percent Reduction in Error (PRE) scores from the randomized data was not significantly different from the non-randomized data PRE scores.

Table 6. The outcome of each run of the RIFFLE cluster analysis for the Boulder Creek site is shown here with Chi-square values and their associated p-values and the averaged Percent Reduction in Error (PRE) scores.

Boulder Creek Site		Chi-squared	df	P	Average PRE score
Non-randomized data					
	run 1	3.50	4	0.48	0.35
	run 2	2.17	4	0.71	0.32
	run 3	4.86	4	0.30	0.30
Randomized data					
	run 1	5.33	4	0.25	0.32
	run 2	1.83	4	0.77	0.31
	run 3	2.17	4	0.71	0.28

Whitebark pine seedlings were found on 14 of the 48 study plots at the Boulder Creek site. Seedling presence means at least one seedling was found on at least one of the five 10-m^2 subplots. Seedling density ranged from 0 to 800 per ha, with an average of 73 per hectare. Seedling clump sizes ranged from one to eleven seedlings, with an average size of 2.26 seedlings.

Seedling presence is not independent of burn severity and moisture conditions; it depends on the interaction of conditions (Table 7). There was greater presence on dry-moderate sites than other combinations as indicated by the large individual chi-square value (8.13) for that combination.

Table 7. The results from a test of independence on the relationship between whitebark pine seedling presence and combinations of moisture and burn severity classes.

Burn Severity	MOIST		DRY		
	Present	Absent	Present	Absent	Total
Unburned	2 *(2.62)*	7 *(6.38)*	2 *(2.62)*	7 *(6.38)*	18
Moderate	2 *(1.17)*	2 *(2.83)*	6 *(2.33)*	2 *(5.67)*	12
Severe	1 *(2.62)*	8 *(6.38)*	1 *(2.62)*	8 *(6.38)*	18
Total	22		26		N=48
		$\chi^2_{0.05,4} = 9.488$		$\chi^2_{calc} =$ 12.23	p<0.001

Tyee Mountain Burn Site

A total of 43 study plots were measured at the Tyee Mountain Burn site (Table 8). Similar to Boulder Creek, the moderately burned areas were also less frequent at the Tyee Mountain site.

Table 8. Number of study plots at the Tyee Mountain site within each burn severity and moisture classification cell.

	Unburned	Moderately Burned	Severely Burned
Moist	8	7	7
Dry	8	6	7

Burn-severity categories did not vary significantly in environmental and pre-fire conditions, which include pre-fire basal area, elevation, slope, heat load, rock and gravel cover, and organic layer depth. The RIFFLE cluster analyses did not show any statistically significant probabilities ($p \leq 0.05$) with a Chi-squared analysis. Additionally, the average Percent Reduction in Error (PRE) scores from the randomized data was not significantly different from the non-randomized data PRE scores (Table 9).

Table 9. The outcome of each run of the RIFFLE cluster analysis for the Tyee Mountain site is shown here with Chi-square values and their associated p-values and the averaged Percent Reduction in Error (PRE score).

Tyee Mountain Site		Chi-squared	df	P	Average PRE score
Non-randomized data					
	run 1	7.94	4	0.09	0.36
	run 2	8.55	4	0.07	0.32
	run 3	7.94	4	0.09	0.36
Randomized data					
	run 1	8.38	4	0.08	0.32
	run 2	8.94	4	0.06	0.28
	run 3	1.32	4	0.86	0.30

Whitebark pine seedlings were present on 22 of the 43 study plots. Seedling density ranged from 0 to 500 per ha, with an average of 112 per hectare. Seedling clump sizes ranged from one to eleven seedlings, with an average 2.74 seedlings. Seedling presence was independent of burn severity class and moisture class (Table 10).

Table 10. Number of Tyee Mountain study plots in which whitebark pine seedlings were either present or absent for every combination of burn severity and moisture class.

Burn Severity	MOIST		DRY		
	Present	Absent	Present	Absent	Total
Unburned	5 *(4.09)*	3 *(3.91)*	4 *(4.09)*	4 *(3.91)*	16
Moderate	4 *(3.58)*	3 *(3.42)*	3 *(3.07)*	3 *(2.93)*	13
Severe	3 *(3.58)*	4 *(3.42)*	3 *(3.58)*	4 *(3.42)*	14
Total	22		21		43
		$\chi^2_{0.05,4} = 9.488$		$\chi^2_{calc} = 0.96$	0.95>p>0.90

Relations among Potential Explanatory Variables

Boulder Creek Site Variable Correlations

Areas with greater pre-fire forest stocking also had deeper organic layers, less rock and gravel cover, and greater burn severity (Figure 4). The three measures of burn severity -- scorch height, basal area mortality, and char depth -- were strongly correlated to one another. Areas farther from the edge of and deeper into the core of the burn had greater pre-fire stocking, soil organic matter, and down woody debris. All three measures of burn severity were negatively associated with both total overstory canopy cover and overstory whitebark pine coverage. On the contrary, down woody debris, herb cover, and soil organic matter were all positively associated with burn severity measures. Heat load, elevation, and slope were not strongly correlated to any pre-fire forest conditions.

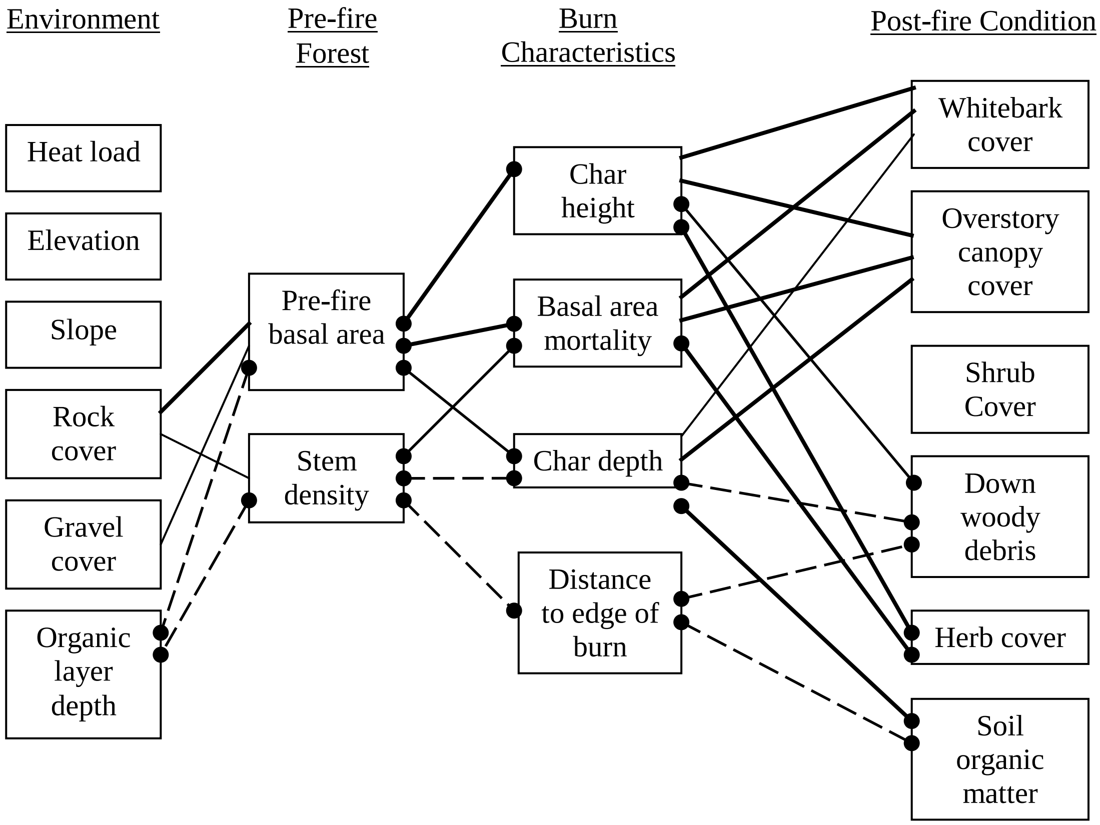

Figure 4. This ecological model shows only the significant correlations between potential explanatory variables at the Boulder Creek site. Linkages represent correlations between variables and the line thickness represents the statistical significance of the relationship. Dashed lines [- - - - - - -] signify p-values less than 0.10; medium weight lines [______] signify p-values less than 0. 05; and thick lines [━━━━] signify p-values less than 0.01. Lines without arrowheads [______] illustrate a negative correlation; whereas, lines with circular arrowheads [●———●] illustrate positive correlations.

Tyee Mountain Variable Correlations

The Tyee Mountain site shared several associations with Boulder Creek (Figure 5). For example, greater pre-fire forest stocking was negatively related to rock cover and positively related to organic layer depth and distance to the edge of the burn. Burn severity was also negatively associated with total canopy cover at Tyee Mountain. Additionally, areas with greater char depth had a larger percent of soil organic matter and more down woody debris cover.

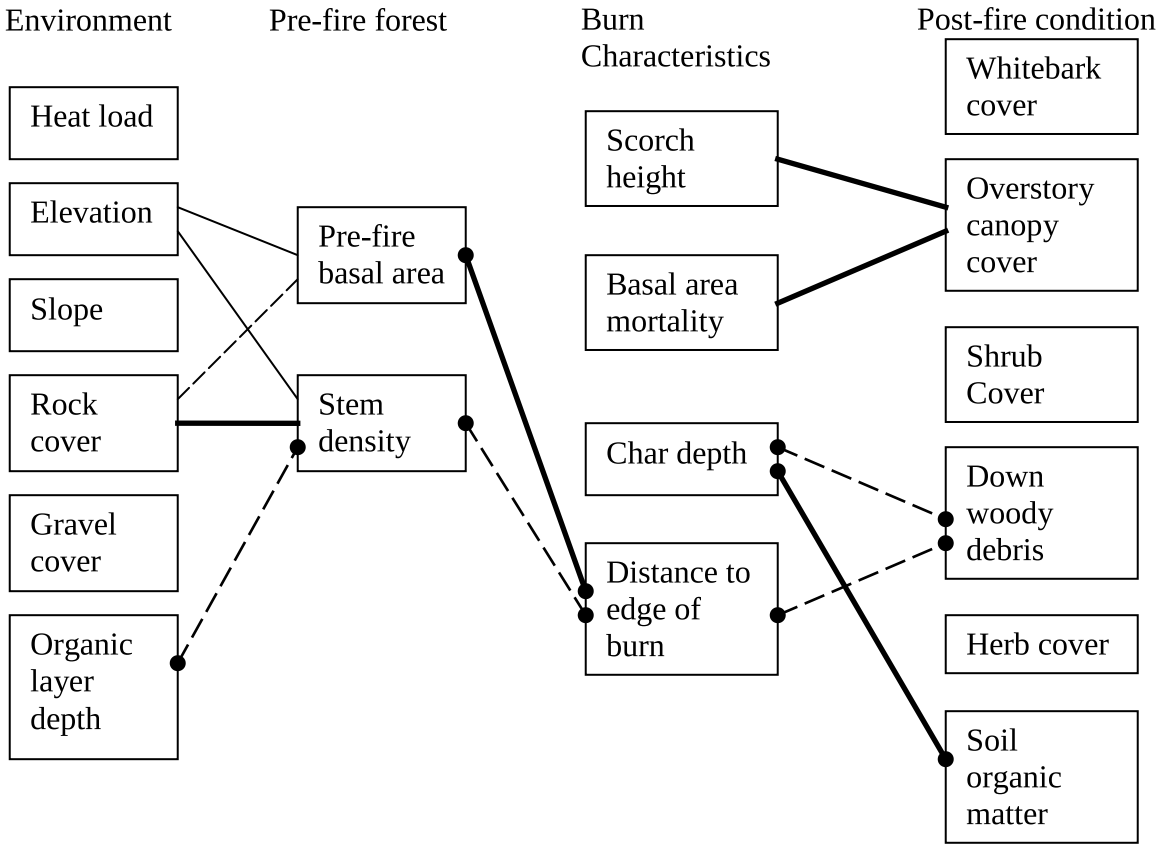

Figure 5. This ecological model shows only the significant correlations between potential explanatory variables at the Tyee Mountain site. Linkages represent correlations between variables and the line thickness represents the statistical significance of the relationship. Dashed lines [- - - - - - -] signify p-values less than 0.10; medium weight lines [_______] signify p-values less than 0. 05; and thick lines [━━━━━] signify p-values less than 0.01. Lines without arrowheads [_______] illustrate a negative correlation; whereas, lines with circular arrowheads [●———●] illustrate positive correlations.

Unique to the Tyee Mountain site is the negative relationship between elevation and pre-fire forest stocking. Both study sites showed no significant relationship between burn severity and shrub cover; however, shrub cover was significantly correlated to less rock cover and lower elevations at Tyee Mountain and increasing slope at Boulder Creek.

Models for Explaining Seedling Presence and Density at Boulder Creek

Logistic Regression for Seedling Presence

Four models were included in the confidence set for explaining seedling presence (Table 11). It is improbable that models outside of the confidence set (Appendix Table A-1) are supported by the data collected from the Boulder Creek site. The Akaike weight of each model is the weight of the evidence for the model being the best model in the candidate set; accordingly, a weight of 0.20 for the whitebark pine overstory model equates to 20% likelihood for that model to be the best model in the candidate set. There are better chances (24 % or 22%) that basal area mortality or scorch height (quadratic), provide the best explanation of variation in seedling presence by information-theoretic criterion.

Table 11. Coefficients for the logistic regression models§ in the confidence set (Δ AICc i <2) for the Boulder Creek dataset (n = 48). The estimated number of parameters and Δ AIC values are reported with all model results in Appendix A.

Model	Explanatory Variable	Coefficient (1 SE)§	$AIC_{c\ i}$	AIC_c $weight_i$
8c. Basal area mortality (quadratic)	Intercept	-1.206 (0.54)	54.07	0.24
	Basal area mortality	0.098 (0.04)		
	(Basal area mortality) ^{2}	-0.001 (0.00)		
7c. Scorch height (quadratic)	Intercept	-0.893 (0.49)	54.21	0.22
	Scorch height	0.921 (0.48)		
	(Scorch height) ^{2}	-0.154 (0.08)		
9a. Whitebark pine overstory cover	Intercept	-1.630 (0.46)	54.46	0.20
	Whitebark pine cover	0.216 (0.09)		
10b. Overstory cover *Moisture	Intercept (dry)	-2.503 (0.96)	54.80	0.17
	Overstory cover (dry)	0.109 (0.04)		
	Intercept (moist)	-1.894 (2.27)		
	Over story cover (moist)	0.025 (0.09)		

§ Models have the structure: $\log [P(seedlings)/ P(no\ seedlings)] = b_0 + b_1X_1 +\ldots+ b_pX_p$

Figure 6 illustrates the negative quadratic probability distribution for seedling presence with respect to basal area mortality (model 8c). The probability of seedling presence reaches a maximum of 0.72 when basal area mortality is at 44.4%, and drops to less than 0.10 at 100% and 0.23 at 0% basal area mortality. The probability of seedling presence with moderate mortality is up to three times greater than low mortality.

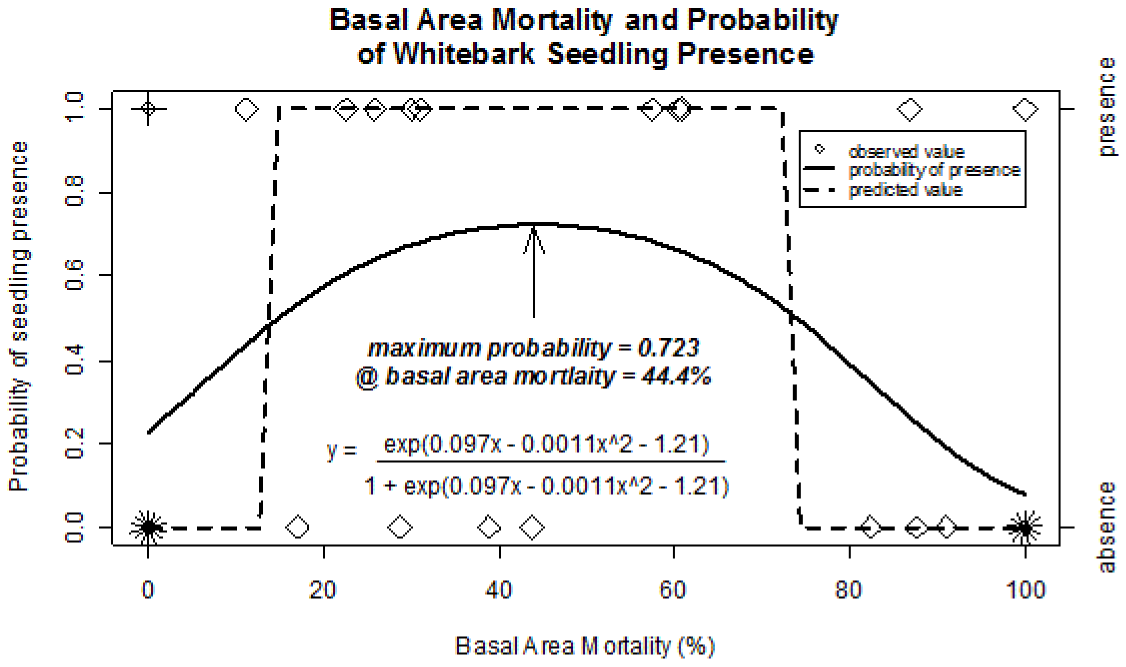

Figure 6. Basal area mortality has a negative quadratic relationship with the probability of whitebark pine seedling presence at the Boulder Creek site. Observed values are represented by diamonds for single points and “sunflowers” for multiple points with each ray representing an observation. The dashed line represents predicted values.

The negative quadratic equation generated by the scorch height model (Figure 7) paints a similar picture as the quadratic basal area mortality model; the probability of seedling presence is greatest when burn severity is moderate. Scorch height ranged from zero to 22 meters at the Boulder Creek site, but the maximum probability of seedling presence at 0.62 corresponds to a scorch height of nearly three meters. The probability drops sharply to zero when scorch height reaches nine meters. Areas without scorch marks on overstory trees have roughly half of the maximum probability of seedling presence.

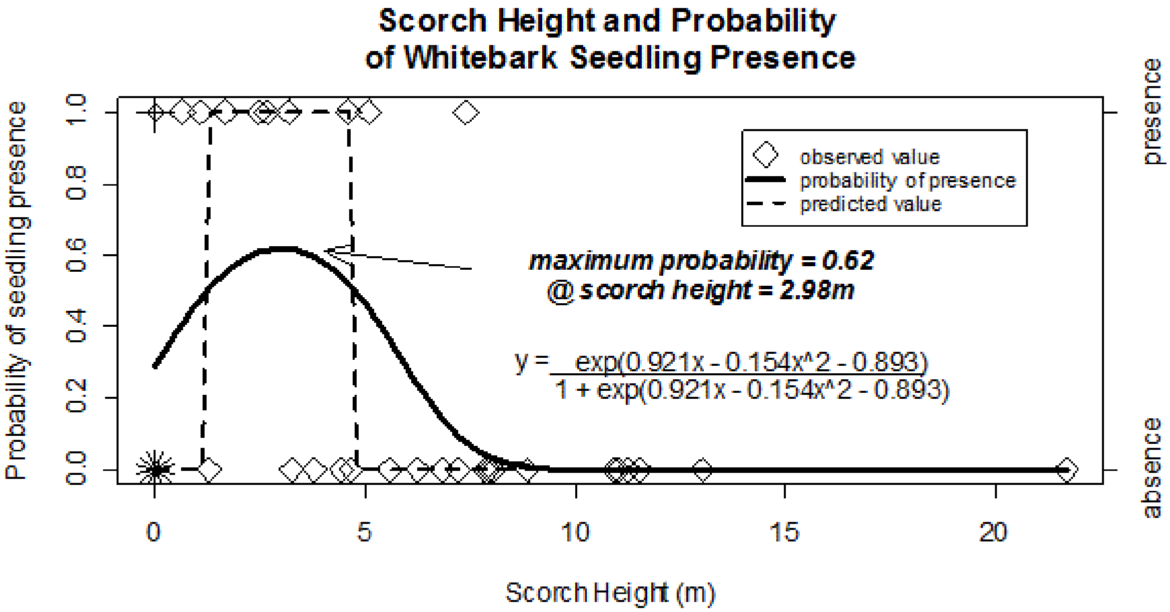

Figure 7. Scorch height (quadratic) on overstory trees and the probability of whitebark pine seedling presence at the Boulder Creek site. Observed values are represented by diamonds for single points and "sunflowers" for multiple points with each ray representing an observation.

The overstory whitebark pine model shows a positive relationship between the probability of seedling presence and overstory whitebark pine cover (Figure 8). The maximum overstory cover of whitebark pine at Boulder Creek was 15%, where probability of seedling presence reaches 0.83. When whitebark pine cover is near its midrange at 10%, a one percent increase in whitebark pine cover corresponds to a five percent increase in the probability of seedling presence. Additionally, the probability is 0.5 when whitebark pine cover is 7.6%.

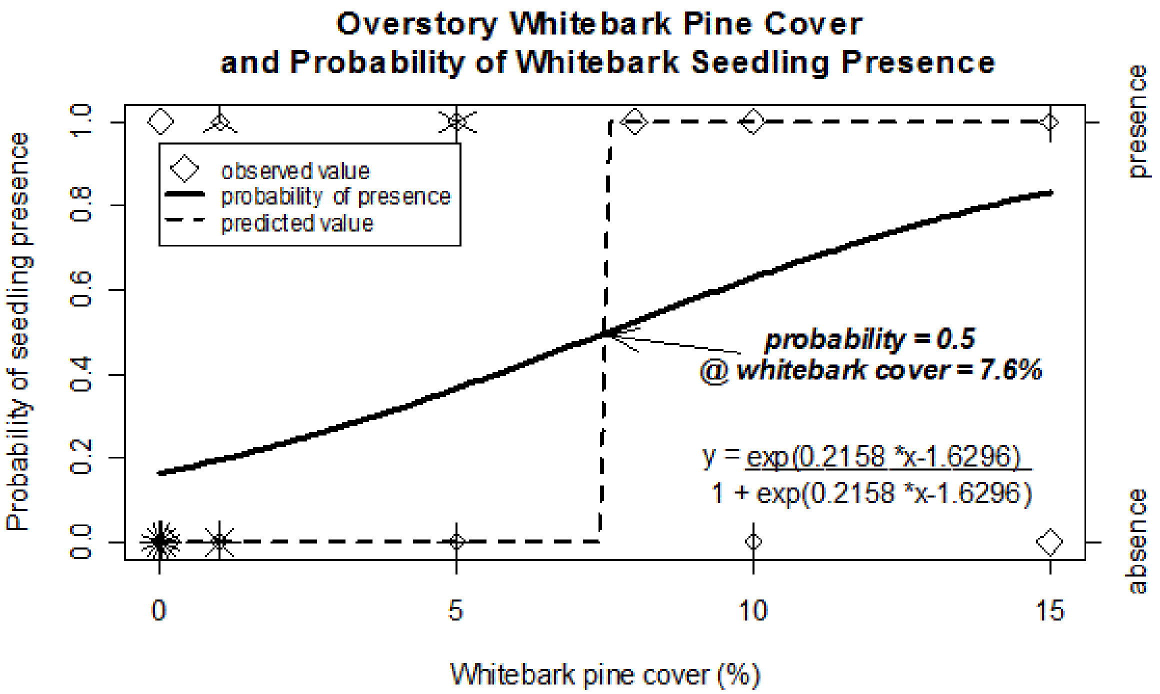

Figure 8. Whitebark pine overstory cover and the probability of whitebark pine seedling presence for the Boulder Creek site. Observed values are represented by diamonds for single points and "sunflowers" for multiple points with each ray representing an observation. The dashed line represents predicted values.

The final model in the confidence set for Boulder Creek contains an interaction term, where the change in response with overstory cover depends on available moisture. Areas with less moisture availability respond more sharply to increased overstory cover than areas with higher moisture availability (Figure 9). For dry plots, the chance of seedling presence is above 50% when overstory canopy cover is above 23%. In the response curve for moist plots, the probability of seedling presence never exceeds 50%.

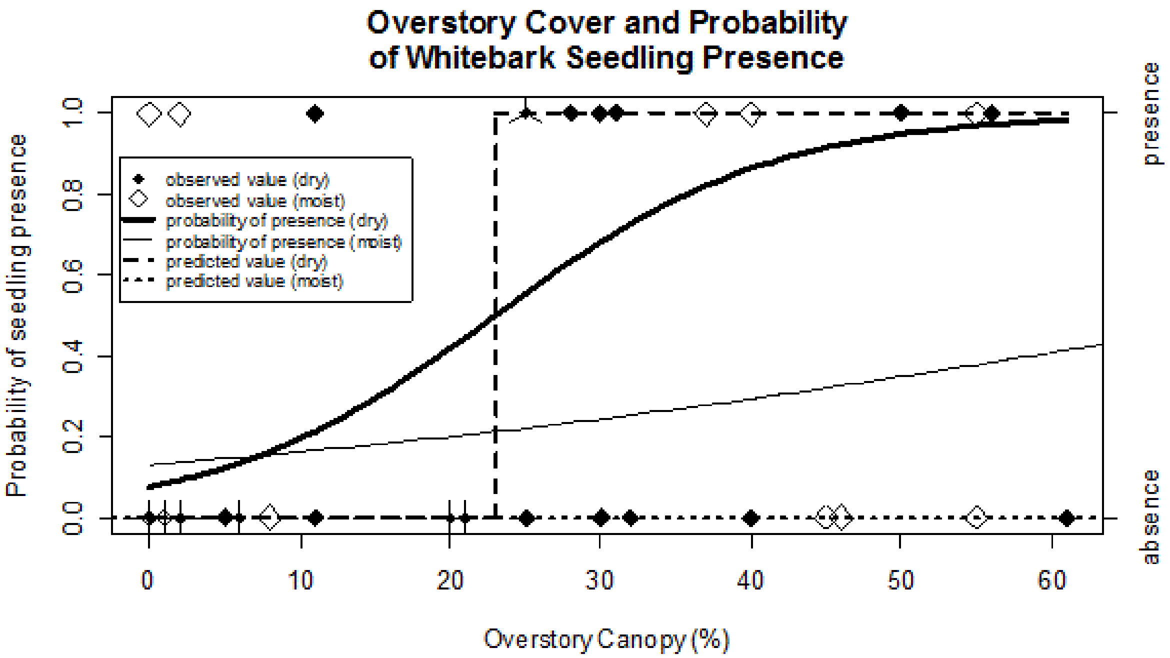

Figure 9. Total overstory cover and the probability of whitebark pine seedling presence for the Boulder Creek site. Observed values are represented by diamonds for single points and “sunflowers” for multiple points with each ray representing an observation.

Poisson Regression for Seedling Density – Presence Data Subset

There are four other models that are included in the confidence set (Table 12). In accordance with the logistic regression results, seedling densities were greatest at moderate basal area mortality, and least when nearing zero or 100% basal area mortality (Figure 10).

Table 12. Coefficients for the Poisson regression models in the confidence set for the Boulder Creek seedling presence data subset (n = 14). The estimated number of parameters and Δ AIC values are reported with all model results in Appendix A**.**

Model	Explanatory Variable	Coefficient (1 SE)	$AIC_{c\ i}$	AIC_c $weight_i$
8c. Basal area mortality (quadratic)	Intercept	0.333 (0.37)	56.34	0.07
	Basal area mortality	0.041 (0.02)		
	(Basal area mortality) ^{2}	-0.0004 (0.0002)		
13a. Soil organic matter	Intercept	1.978 (0.62)	54.46	0.18
	Soil organic matter	-0.107 (0.06)		
12a. Down woody debris	Intercept	1.308 (0.28)	54.62	0.19
	Down woody debris	-0.050 (0.03)		
14a. Herb cover	Intercept	1.121 (0.25)	55.08	0.14
	Herb cover	-0.016 (0.01)		

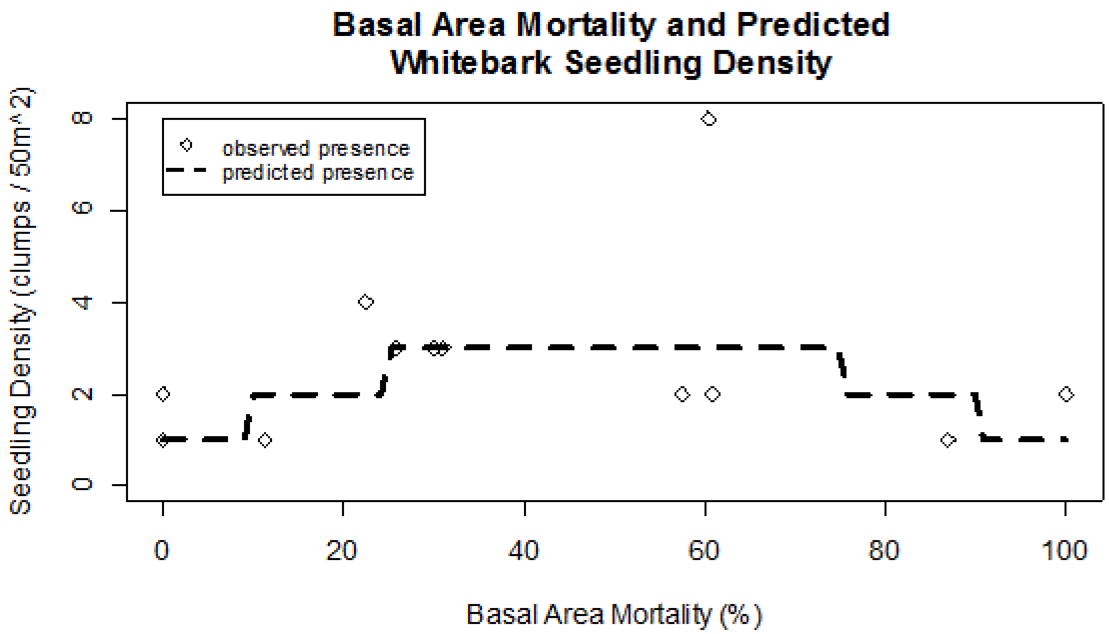

Figure 10. For the Boulder Creek site, observed whitebark pine seedling densities are highest when basal area mortality is roughly between 40 and 60%. Observed values are represented by diamonds and the dashed line represents the predicted value for seedlings.

Down woody debris cover, herb cover, and soil organic matter all show negative relationships with observed seedling clump densities. Counts follow a Poisson distribution, therefore the predicted probabilities of whitebark pine seedlings are expressed using the following formula:

$$P(Y_i = y) = \frac{e^{-\mu_i}\mu_i^{y}}{y!}$$

Each of the three models in the confidence set estimates three seedling clumps at the minimum values and one seedling clump at maximum values (Figures 11, 12, and 13).

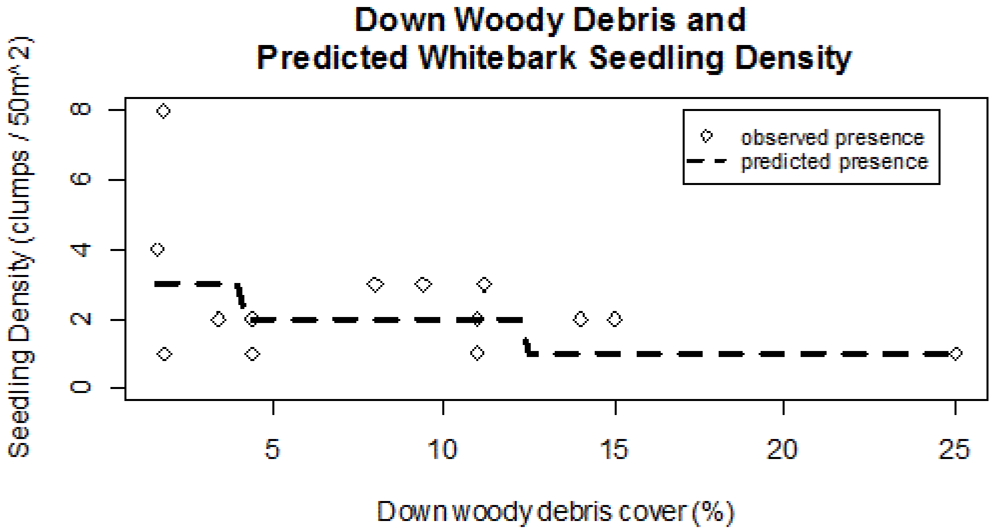

Figure 11. Predicted whitebark pine seedling densities (number of seedling clumps per $50m^2$) decrease with down woody debris for the Boulder Creek site. Observed values are represented by diamonds and the dashed line represents the predicted value for seedlings.

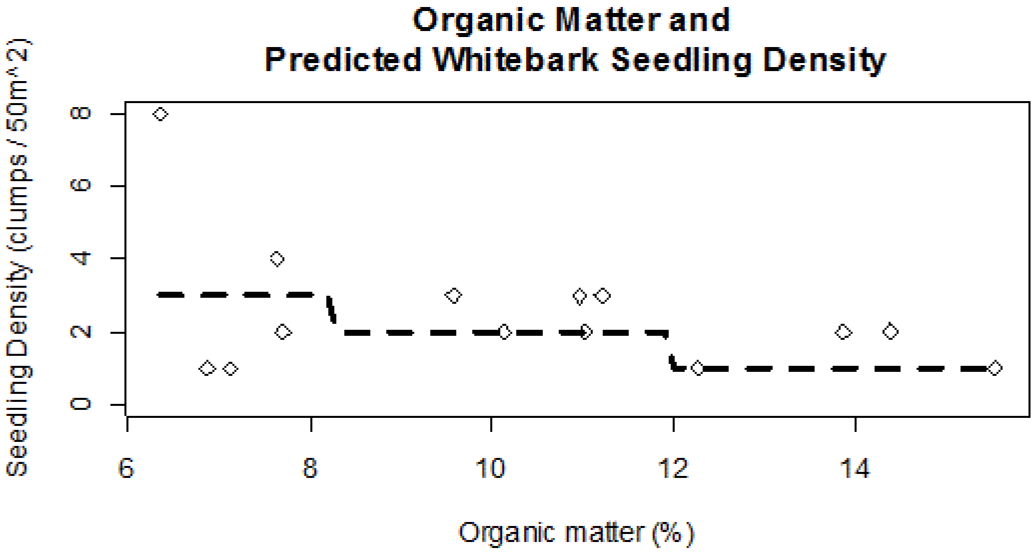

Figure 12. Predicted whitebark pine seedling densities decrease with increasing soil organic matter for the Boulder Creek site. Observed values are represented by diamonds and the dashed line represents the predicted value for seedlings.

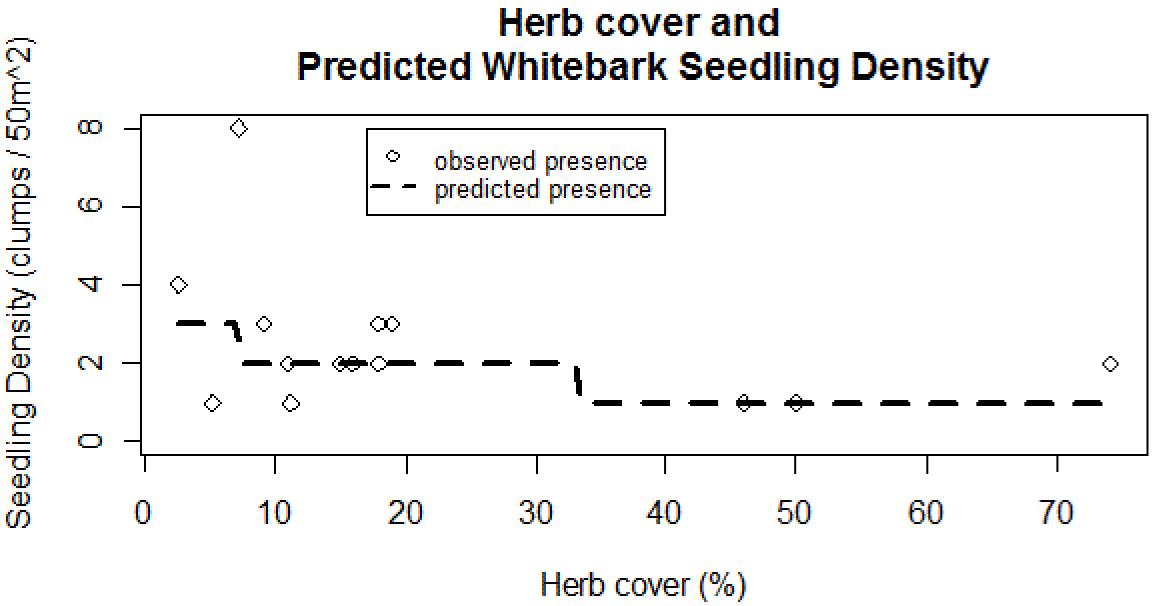

Figure 13. Predicted whitebark pine seedling densities decrease with higher ground cover of herbaceous at the Boulder Creek site. Observed values are represented by diamonds and the dashed line represents the predicted value for seedlings.

Models for Explaining Seedling Presence and Density at Tyee Mountain

Logistic Regression for Seedling Presence – Full Dataset

With 91% likelihood of the model being the best model in the candidate set, the soil organic matter (SOM) model with a moisture interaction term was clearly the best model by information-theoretic criterion for explaining variability in seedling presence at the Tyee Mountain site (Table 13). This model shows that the probability for seedling presence increases with SOM on dry plots and decreases with SOM on moist plots; however, the uncertainty of coefficient for SOM (moist) contains zero and does not contribute meaningful information to the model. The probability of seedling presence is above 50% when SOM is above 8.9% on dry sites (Figure 14).

Table 13. Coefficients for the explanatory models in the confidence set for the Tyee Mountain data set (n = 43). The estimated number of parameters and Δ AIC values are reported with all model results in Appendix B**.**

Explanatory Model	Explanatory Variable	Coefficient (1 SE)	$AIC_{c\ i}$	AIC_c $weight_i$
13b. Soil organic matter *Moisture	Intercept (dry)	-10.535 (4.81)	51.61	0.91
	Soil organic matter (dry)	1.244 (0.56)		
	Intercept (moist)	5.318 (10.82)		
	Soil organic matter (moist)	-0.585 (1.27)		

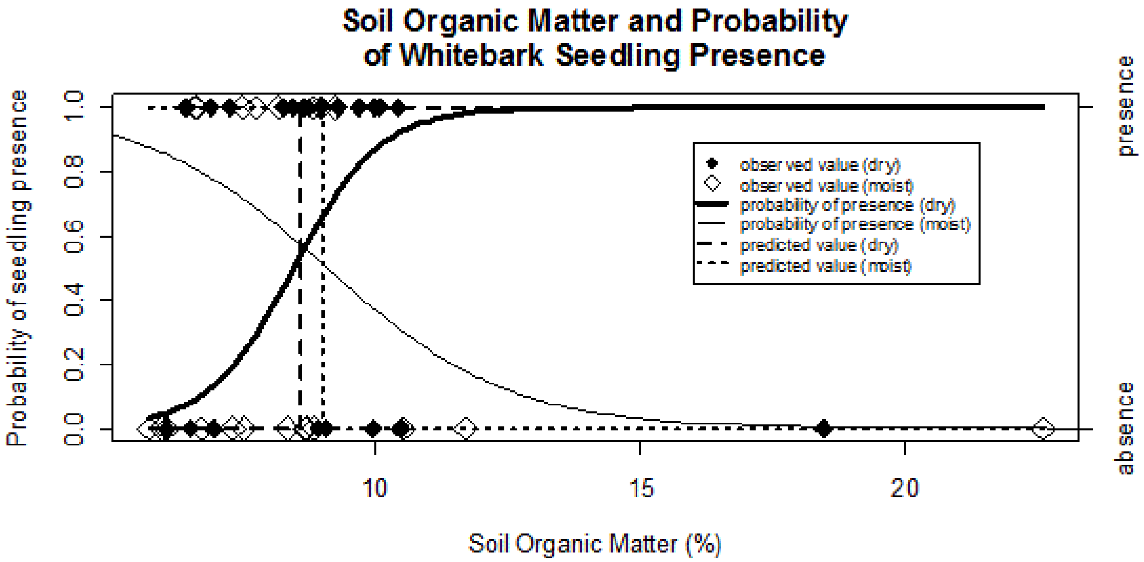

Figure 14. The probability of whitebark pine seedling presence increases with soil organic matter on dry plots at the Tyee Mountain site.

Poisson Regression for Seedling Density – Presence Data Subset

The Tyee Mountain data subset that includes only plots in which whitebark pine seedlings were present contained only one model in the confidence set (Table 14). The distance to the edge of the burn is positively related to the probability of seedling presence (Figure 15). Stated alternatively, a farther distance into the burned area is correlated to a greater density of whitebark pine seedlings. This model is strongly supported by the data, with a 61% likelihood of being the best model by information-theoretic criterion (Table B-2). The global model, using all variables in the candidate set, had an AIC value of 82.65.

Table 14. Coefficients for the Poisson regression models in the confidence set for the Tyee Mountain seedling presence data subset (n = 22). The estimated number of parameters and Δ AIC values are reported with all model results in Appendix B.

Explanatory Model	Explanatory Variable	Coefficient (1 SE)	$AIC_{c\ i}$	AIC_c $weight_i$
6b. Distance to edge of burn	Intercept	0.654 (0.162)	71.83	0.61
	Distance to edge of burn	0.003 (0.001)		

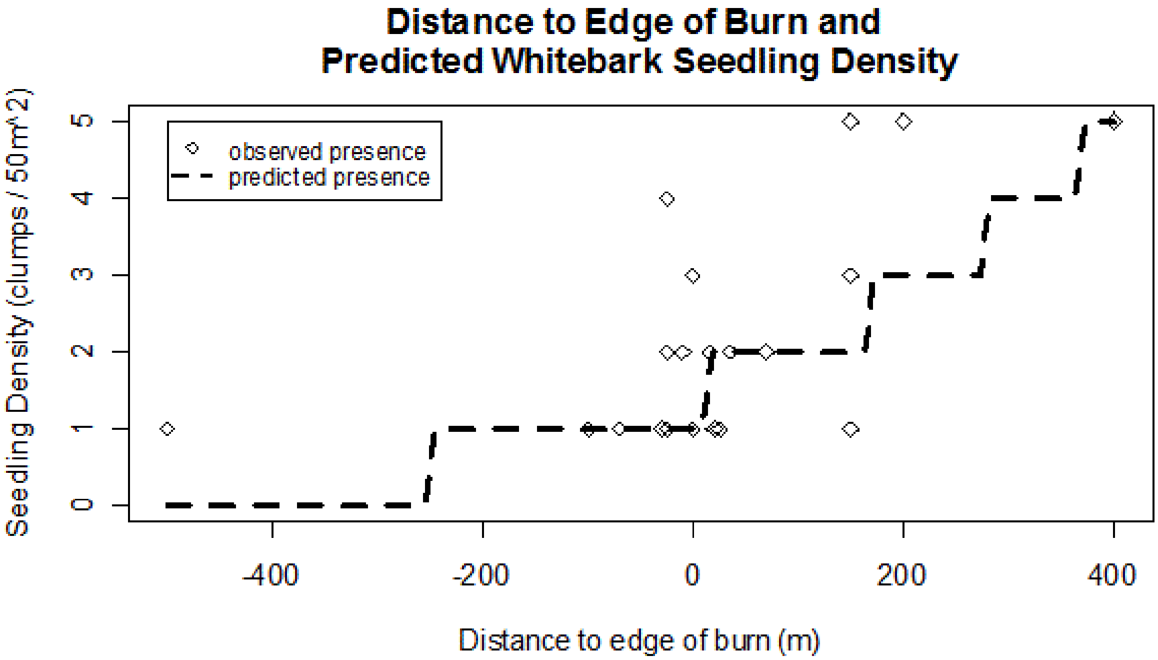

Figure 15. Predicted whitebark pine seedling densities (number of seedling clumps per $50m^2$) and distance to the edge of the burn. Observed values are represented by diamonds and the dashed line represents the predicted value for seedlings.

Global Model Fitness

The overall fit of a global model was considered for each study site. The overall fit was determined by a goodness of fit statistic using the Hosmer-Lemeshow statistic. Expected values were not significantly different from observed values (Table 15).

Table 15. The global model fitness statistics were low for each site, indicating a good fit to the data.

Study Site	Pearson χ^2	Degrees of Freedom	P-value
Boulder Creek	3.95	8	0.86
Tyee Mountain	5.94	8	0.65

DISCUSSION

The relation of whitebark pine seedling presence to burn severity and moisture was significant at the Boulder Creek site, and not an important factor at the Tyee Mountain site. Burn severity and moisture were very important relative to other factors on seedling presence and density at the Boulder Creek site, but not at the Tyee Mountain site. The study results substantiate my conceptual model that multiple relations exist between pre- and post-fire environmental variables, fire indicators, and whitebark pine regeneration in the North Cascades. The relations found in this study vary between the two study sites, and differ from other geographic locations examined by other researchers.

Variation in the North Cascades

Boulder Creek Site

Whitebark pine seedlings were present on 75% of the moderate severity–dry sites compared to less than 25% for most of the other combinations of burn severity and moisture regime. Because environmental and pre-fire conditions did not vary significantly between burn-severity categories, these results were due to the burn severity rather than other potentially confounding factors.

Basal area mortality, scorch height, overstory cover, and whitebark pine overstory cover best explained the variation in whitebark pine seedling presence at the Boulder Creek site (Table 16). Increasing burn severity and scorch height were positively correlated to seedling presence at low levels, and negatively associated with seedling presence at high levels. The negative quadratic response curves generated by basal area mortality and scorch height suggest that moderately burned areas promote successful whitebark pine regeneration. This is consistent with the observation that whitebark pine seedlings were present on 75% of the moderate severity–dry sites compared to lesser amounts on other sites. The results from the seedling-density analysis also support the assertion that moderate severity burns promote more whitebark pine regeneration (Table 14).

Table 16. Summary of relations of whitebark pine seedling presence and density to increased values of explanatory variables at two study sites in the North Cascades, Washington.

Explanatory Variable	***--------Boulder Creek-------***		***--------Tyee Mountain------***	
	Presence	***Density***	***Presence***	***Density***
Basal area mortality	Positive then negative	Positive then negative		
Scorch height	Positive then negative			
Whitebark pine overstory cover	Positive			
Total overstory cover	Positive			
Soil organic matter		Negative	Positive with low moisture	
Down woody debris		Negative		
Herb cover		Negative		
Distance to edge of burn				Positive

The positive relation of seedling presence to overstory cover (Table 16) may indicate better survival in partial shade. This would support the findings of Izlar (2007), who found a negative correlation between direct sun and whitebark pine seedling survival in plantings.

The negative relation of seedling presence to moisture availability may be indicative of whitebark pine's adaptation to withstanding extreme weather conditions found near the tree-line. As a poor competitor with other species in moist, preferable areas, whitebark pine can thrive in areas that are too high and too harsh for competitors.

Soil organic matter, downed woody debris, and herb cover explained the variability in seedling density best on all plots which had whitebark pine seedling presence (Table 16). The negative relation of seedling density to soil organic matter and herb cover may be indicative of whitebark pine's ability to survive in dry, rocky outcrops. The negative relation of seedlings to downed woody debris contradicts the findings of Izlar's study (2007) in which whitebark pine seedling survival was greatest in areas with more microsite features such as rocks, woody debris, and stumps. Length of growing season can be a limiting factor for tree seedling survival in subalpine systems (Agee, 1993). An increased downed woody debris component and increased herb cover can hold snow cover farther into the growing season by (Valendik *et al.*, 2006). McCaughey (1990) found greater densities of whitebark pine seedlings in study plots with bare soil, which supports the finding of a negative association between seedling establishment and ground cover.

These relations of seedling presence and density to multiple environmental factors build upon the complex relations among the environmental factors themselves. Areas with deeper organic layers before the fire also had greater stocking indicated by high basal area and stem density. Greater stocking led to greater burn severity and in turn increased levels of DWD, herb cover, and soil organic matter. Rock and gravel cover on dry sites was around twice the cover on moist sites. Moist, favorable areas have greater stocking and in turn greater burn severity, resulting in greater organic matter and herb coverage.

Burn severity was negatively associated with mature whitebark pine and overall canopy coverage, suggesting that greater severity burns might reduce mature, cone-producing whitebark pines. The reduction in overstory canopy cover could be attributed to a primary fire effect, in which the areas with the highest stem density were burned most completely.

Dry areas with lower pre-fire stocking retained higher post-fire whitebark pine cover and total overstory cover.

Tyee Mountain Site

Unlike the Boulder Creek site, whitebark pine seedling presence did not vary among burn severities at the Tyee Mountain site; furthermore, the relation between seedling presence and moisture did not differ among burn severities. Similar to the Boulder Creek site, the pre-fire conditions did not vary among burn severities at the Tyee Mountain study site.

Unlike the Boulder Creek site, whitebark pine seedling presence was not related to fire-severity indicators (Table 16). Moisture interacted with other variables on their effect on seedling presence (Table 16).

Soil organic matter was found to be an important factor for explaining variability in seedling presence at Tyee Mountain; whereas, at Boulder Creek, soil organic matter was only useful in explaining seedling densities. Tyee Mountain data suggest that soil organic matter is an interacting factor for explaining variability in seedling presence, being positively associated on dry sites with seedling presence and not a factor on moist sites (Table 16). The same interaction with moisture availability was true for downed woody debris, where more debris was beneficial on dry sites and not a factor on moist sites.

The interaction between soil organic matter and moisture could be attributed to the notion that the niche for whitebark pine is on the continuum between moist and dry sites, where seedlings have less competition for and an adequate supply of soil nutrients. Soil organic matter is seemingly beneficial for whitebark pine seedling on dry sites, which are possibly too harsh for competition.

Higher soil organic matter and downed woody debris can increase the heat generation near the surface, which can be beneficial for seedlings in a subalpine environment with a short growing season; however, too much heat generation can lead to seedling mortality through heat scorching. Mellmann-Brown (2007) found high whitebark pine survival rates in the presence of shade and shallow organic layers, and also heat-scorch to be the primary cause of mortality while the seedlings were in their first growing season. Notably, whitebark pine seedlings were found only on sites with the percentage of soil organic matter between 7 and 11 percent. Soil organic matter levels at the site ranged between 0 and 24 percent.

The seedling density results show that seedling densities are positively correlated to the distance to the edge of the burn. This supports the conclusions of Tomback (2001) that Clark’s nutcrackers prefer to distribute seeds further into recently burned areas. The distance to the edge of the burn was significantly and positively correlated with pre-fire stocking, which was determined by stem densities and total basal area. However, the pre-fire stocking components were not tested against seedling presence or densities.

The different seedling–environmental relations at the Tyee Mountain and Boulder Creek sites may be attributed to many site differences. The two sites differed in tree composition and historic fire frequency, which could explain some of the variation between the sites. Tyee Mountain has experienced more frequent burns in the recent past than Boulder Creek; however, the mean fire return interval for Tyee Mountain (57 years) is greater than the mean fire return interval for Boulder Creek (27 years) (Siderius and Murray, 2005).

Another important difference is that the Tyee site had more lodgepole pine and fewer subalpine fir trees than the Boulder Creek site. Lodgepole pine has serotinous cones and has the ability to reproduce promptly following a burn. Campbell and Antos (2003) found considerable mortality in the initial post-fire whitebark pine seedlings where lodgepole pine is abundant. Therefore, soil organic matter may be a more important factor when lodgepole pine is present; conversely, burn severity and overstory cover may be the most important factors in areas dominated by subalpine fir.

Variation beyond the North Cascades

There were some similarities and differences between the results of this study and other studies in whitebark pine communities outside of the North Cascades. Tomback *et al*. (2001) examined the relationship between whitebark pine regeneration in distinct burn severity classes and among moist and dry areas in the Greater Yellowstone Ecosystem (GYE). The results of that study showed no significant difference in whitebark pine seedling presence between burned and unburned treatments (Tomback *et al.,* 2001). However, in the GYE moist sites in moderate and severe burns consistently had the highest seedling densities and greatest seedling mortality; whereas at the Boulder Creek site dry and burned sites had the least amount of regeneration (Tomback *et al.*, 2001). The moist and unburned sites in the GYE presumably were occupied by shade-tolerant species that could out-compete whitebark pine seedlings.

The findings of Campbell and Antos (2003) in southern British Columbia showed whitebark pine seedling establishment was more successful in post-fire than in unburned stands. Similarly, the pattern of seedling establishment at Boulder Creek was more successful in moderately burned stands than in unburned; however, in this study moderately burned stands also had more seedling presence than severely burned stands.

Recommendations for Management and Future Study

White pine blister rust was present in every whitebark pine stand in the on-going, long term monitoring program in the North Cascades National Park (Rochefort, 2008). The demise of whitebark pine in the subalpine ecotone in the North Cascades continues and may confront unexpected challenges with global climate change. Mature, cone-bearing whitebark pine trees, plagued by an exotic fungus, may hold the key to whitebark pine restoration. Providing conditions for increasing successful natural seedling regeneration could accelerate the process of natural selection towards blister rust resistance. Potential management strategies to maintain whitebark pine in the North Cascades are (i) protect mature whitebark pine, especially trees that seem rust-resistant, from severe burns by controlling pre-fire stand density, and (ii) allow large, moderate severity burns, natural and prescribed, to reduce partial overstory cover of shade-tolerant species.

Whitebark pine overstory cover was an important factor for explaining seedling presence at the Boulder Creek site. More information on the survivorship of mature whitebark pine trees, in the North Cascades and throughout its range, is needed to make sound management decisions regarding the re-introduction of fire. The lethal burning of mature and potentially disease-resistant would be counterproductive to whitebark pine restoration efforts.

For the purpose of identifying priority whitebark pine habitat for restoration in areas similar to the Tyee site, large contiguous blocks of forest would offer a greater core area in which seedling could establish. Moderation may be the best approach to prescribed burns or other approaches to landscape manipulation that are designed to increase whitebark pine regeneration in areas similar to the Boulder Creek. Burned areas with overstory mortality approaching 100 percent had few seedlings present and in low densities.

Mechanically altering over-stocked forest stands could improve the pre-fire condition, making the forest more conducive to a moderate severity burn. A stand density analysis would be helpful to assess ‘normal’ and critical stand densities in whitebark pine stands. Stocking levels above critical stand density may lead to fires, natural or prescribed, that are too severe to be favorable for natural whitebark pine regeneration. Stocking levels which constitute ‘normal’ and critical densities may differ by whitebark pine plant association types.

Soil organic matter was a key proponent explaining seedling distributions, with a positive association with seedling presence on dry sites and was not a factor on moist sites. This could be due to the fact that soil organic matter content contributes to nutrient holding capacity and overall soil color. The availability of primary soil nutrients, such as nitrogen, phosphorous, and potassium, may be key factors in explaining the variability of whitebark pine seedling presence. Relatively high levels of dissolved inorganic nitrogen and low levels of dissolved organic nitrogen are often found near the tree-line in subalpine systems, where primary productivity exceeds cellular respiration (Burns and Tonkin, 1982). The availability of nitrogen and other soil nutrients could be investigated further as a limiting factor for seedlings near the tree-line. Understanding nutrient cycling at the tree-line could assist in restoration efforts by identifying the optimum conditions for whitebark pine plantings.

Many of the variables in this study did not explain the variability in seedling presence or density at either study site. Rock and gravel cover, elevation, slope, aspect, shrub cover, and char depth were not useful explanatory variables in this study. The candidate set of models may include variables that are not very relevant to whitebark pine seedling density. Other variables that were not considered in this study such as interspecific competition and soil nutrient availability may further explain seedling distributions. Testing a large number of models can give rise to a leading explanatory model by chance. The leading models are well supported by the data nevertheless they are from large model candidate set relative to number of data points.

Researchers may generalize that whitebark pine seedlings regenerate more successfully in moderately burned areas. Yet generalizing this assumption to other settings, such as throughout the entire Cascades, may be making an unproductive oversight. The results could duly be applied in areas spatially limited to the North Cascades and similar in forest composition.

This study had common limitations associated with observational studies conducted in the field, such as the availability of seedlings, the variability of environmental factors among study plots, and the inaccessibility of the high elevation landscape. To overcome these limitations, a high number of study plots were installed and many environmental factors were recorded and analyzed while in the remote setting. Greater plot size might increase the likelihood of encountering the sparse whitebark pine seedlings in future studies.

CONCLUSION

To increase natural whitebark pine regeneration, managers should allow moderate severity fires to burn in large areas, cautiously leaving partial overstory cover, especially mature whitebark pine trees. This recommendation is supported by several observations from this study. Whitebark pine seedling presence and densities were greatest when fire-induced mortality was moderate and basal area mortality was between 40 and 60 percent. The probability of seedling presence was the lowest with the highest basal area mortality and scorch height without fail. Overstory cover was an important factor in explaining the variability in whitebark pine seedling presence. The relationship between overstory cover and seedling presence was positive on burned and unburned sites, and the effect of overstory cover varies by moisture availability, with a greater effect on dry sites than on moist sites. Whitebark pine seedlings were found more often on dry sites with relatively high levels of soil organic matter and on moist sites with relatively low levels of soil organic matter. Management strategies should concentrate on defining ‘normal’ and critical densities for whitebark pine communities, altering areas with critical densities thereby creating conditions for moderate severity burns, and allowing moderate severity burns, natural and prescribed, in areas with ‘normal’ densities. Further investigation into whitebark pine’s ability to tolerate fire and the roles of soil nutrient cycling, soil organic matter, and herb cover at the tree-line could provide insight into the requirements for successful whitebark pine restoration.

REFERENCES

Agee, J. 1993. Fire Ecology of the Pacific Northwest forests. Island Press, Washington, D.C. and Covelo, CA.

Arno, S. F. 1986. Whitebark pine cone crops: A diminishing source of wildlife food? *West. J. Appl. For*. Vol.1, p.92-94

Arno, S.F., and R.J. Hoff, 1989. Silvics of Whitebark Pine (P*inus albicaulis*). USDA Forest Service Technical Report, INT-253, 11 p.

Arno, S.F., and T.D. Peterson, 1983. Variation in estimates of fire intervals: a closer look at fire History on the Bitterroot National Forest. USDA Forest Service Res. Pap. INT-301

Buffo, M. 2004. Whitebark Pine (P*inus albicaulis*) in Subalpine Forest of the Cascade Range: a Case Study of Forest Structure with Management Recommendations. Senior Thesis, Bates College, Lewiston, Maine

Burnham, K. P. and D. R. Anderson, 2002. Model selection and multimodel inference: A practical information-theoretic approach. New York: Springer-Verlag.

Burns S. F., P. J. Tonkin, 1982. Soil-geomorphic models and the spatial distribution and development of alpine soils. In: Space and Time in Geomorphology. Thorn CE p. 25–44

Campbell, E. M., and J.A Antos,. 2003. Postfire succession in *Pinus Albicaulis –Abies Lasiocarpa* forests of Southern British Columbia. *Canadian Jounal of Botany*; Vol. 81, No. 4, p. 383-397

Chappell, C.B. and J.K. Agee, 1996. Fire Severity and Tree Seedling Establishment in *Abies magnifica* Forests, Southern Cascades, Oregon. *Ecol. Appl*., Vol. 6, No. 2, p. 628-640

Douglas, G. W. and L. C. Bliss. 1977. Alpine and high subalpine plant communities of the North Cascades region, Washington and British Columbia. *Ecological Monographs* Vol. 47, No.2, p. 113-150

Goheen E. M., D.J. Goheen, K. Marshall, R. S. Danchok, J. A. Petrick, and D. E. White, 2002. The Status of Whitebark Pine Along the Pacific Crest National Scenic Trail on the Umpqua National Forest. United States Department of Agriculture Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-530

Hellgren, E.C. 1998. Physiology of Hibernation in Bears. Ursus Vol.10, p. 467-477.

Hoff, R. and S. Hagle. 1990. Diseases of Whitebark Pine with Special Emphasis on White Pine Blister Rust. In Schmidt, W.C. and K. S. McDonald, compilers, Proceedings -

Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, 1989 March 29-31, Bozeman, MT; Ogden, UT: USDA, Forest Service, Intermountain Research Station, General Technical Report INT-270, June 1990.

Hofmann, J.V. 1917. Natural reproduction from seed stored in the forest floor. *Journal of Agricultural Research*. No. 11, p.1-26.

Hosmer, D.W., & Lemeshow, S. (2000). *Applied logistic regression (2nd Edition)*. New York: Wiley

Izlar, D.K. 2007. Assessment of Whitebark Pine Seedling Survival for Rocky Mountain Plantings. Senior Thesis, Humboldt State University, Arcata, California

Kendall, K. C. and R. E. Keane. 2001. Whitebark pine decline: Infection, Mortality, and Population Trends. Tomback, D.F., Stephen F. Arno, and Robert E. Keane, editors. Island Press, Washington, DC. p. 221-242

Long, C. J., Whitlock C., Bartlein P.J., and Millspaugh, S.H. 1998. A 9000-year fire history from the Oregon coast range, based on a high-resolution charcoal study. *Can J Forest Res* No. 28, 774–87

Matthews, G. 1995. Riffle Information Page. http://sanjuan.cs.wwu.edu/matthews/riffle

Mattson, D., K Kendall, D. and Reinhart, 2001. Whitebark Pine, grizzly bears, and red squirrels. In: Tomback, D., S. Arno, and R. Keane., editors. Whitebark Pine Communities. Washington: Island Press. p. 121-136

McCaughey, W. W., W. C. Schmidt, 1990. Autecology of whitebark pine. In: Schmidt, W. C. and K. J. McDonald, compilers. Proceedings-symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, Montana. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 85-96.

Mellmann-Brown, S. 2007.The regeneration of whitebark pine in the timberline ecotone of the Beartooth Plateau, Montana and Wyoming. URL: http://nbn-resolving.de/urn

Reese, J. B., 2004. Centennial Salvage Timber Sale; Caribou-Targhee National Forest, Fremont and Clark Counties, ID. Federal Register Vol. 69, No. 174, p. 54627-54629

Rochefort, R.M., 2008. The influence of white pine blister rust *(Cronartium ribicola)* on whitebark pine *(Pinus albicaulis)* in Mount Rainier National Park and North Cascades National Park Service Complex, Washington. *Natural Areas Journal.* Vol. 28, No. 3, p. 290-298

Siderius, J., Murray, M.P. 2005. Fire knowledge for managing Cascadian whitebark pine ecosystems. Final report to the Joint Fire Sciences Program, (#01B-3-3-26). 44 p.

Six, D.L. and J. Adams. 2007. White Pine Blister Rust Severity and Selection of Individual Whitebark Pine by the Mountain Pine Beetle (Coleoptera: Curculionidae, Scolytinae). *Journal of Entomological Science.* Vol. 32, No. 3, p. 345-353

Tomback, D.F., A.J. Anderies, K.S. Carsey, M.L. Powell, S. Mellmann-Brown. 2001. Delayed Seed Germination in Whitebark Pine and Regeneration Patterns Following the Yellowstone Fires. *Ecol.* Vol. 82, No. 9, p.2587-2600

Tomback, D.F., and K.C. Kendall. 2001 Biodiversity losses: the downward spiral, chapt. 12. In: Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, D.C. p. 243-262.

Valendik, E. N., Brissette, J. C., Kisilyakhov, Y. K., Lasko, R. J., Verkhovets, S. V., Eubanks, S. T., Kosov, I. V., and Lantukh, A. Y., 2006. An Experimental Burn to Restore a Moth-Killed Boreal Conifer Forest, Krasnoyarsk Region, Russia. *Mitigation and Adaptation Strategies for Global Change*. Vol. 11, No. 4, p.883-896

Zar, J. H., 1999. Biostatistical Analysis. Prentice Hall, New Jersey, 663 pp.

Appendix A. Predictive Models for the Boulder Creek Datasets.

A - 1. A comparison of the competing models for explaining variability in whitebark pine seedling presence on all study plots in the Boulder Creek site. Models included in the confidence set are in bold type.

Explanatory models	**K[1]**	**$AIC_{c\,i}$**	**Δ_ $AIC_{c\,i}$[2]**	**AIC_c weight$_i$[3]**
1. Constant	2	66.81	12.74	0.00
Environment				
2. Rock cover + gravel cover	4	64.03	9.96	0.00
3. Elevation + Slope	4	64.30	10.23	0.00
4. Heat load + organic layer depth	4	63.05	8.98	0.00
Burn characteristics				
5a. Char depth	3	60.43	6.36	0.01
5b. Char depth * Moisture	5	64.49	10.42	0.00
6a. Distance to edge of burn	3	61.57	7.50	0.01
6b. Distance to edge of burn * Moisture	5	65.24	11.17	0.00
7b. Scorch height * Moisture	3	63.09	9.02	0.00
7c. Scorch height (quadratic)	5	54.21	0.14	**0.22**
8a. Basal area mortality	4	64.31	10.24	0.00
8b. Basal area mortality * Moisture	3	65.19	11.12	0.00
8c. Basal area mortality (quadratic)	4	54.07	0.00	**0.24**
Post-fire conditions				
9a. Whitebark pine cover	3	54.46	0.39	**0.20**
9b. Whitebark pine cover * Moisture	5	58.95	4.88	0.02
10a. Overstory cover	3	56.17	2.10	0.08
10b. Overstory cover * Moisture	5	54.80	0.73	**0.17**
11a. Shrub cover	3	62.46	8.39	0.00
11b. Shrub cover * Moisture	5	66.40	12.33	0.00
12a. Downed woody debris	3	62.47	8.40	0.00
12b. Downed woody debris * Moisture	5	66.54	12.47	0.00
13a. Soil organic matter	3	62.39	8.32	0.00
13b. Soil organic matter * Moisture	5	66.51	12.44	0.00
14a. Herb cover	3	61.39	7.32	0.01
14b. Herb cover * Moisture	5	65.29	11.22	0.00

---

[1] K is the number of parameters used, an error term and slope intercept are counted as parameters.

[2] AIC values are commonly expressed as Δ_AIC's, which are the differences between each model's AIC value the lowest AIC value in the set. Subsequently, the best model has a Δ_AIC value of zero, and higher values indicate poorer models.

[3] The AIC weight of model j is equal to: exp(-0.5*Δ_$AIC_{,j}$)/(the sum of exp(-0.5*Δ_AIC) values for all the models fit to the data).

A - 2. A comparison of the competing models for explaining whitebark pine seedling density on the study plots with seedling presence in the Boulder Creek site. Models included in the confidence set are in bold type.

Explanatory models	**K**	**AIC$_{c\ i}$**	**Δ_ AIC$_{c\ i}$**	**AIC$_c$ weight$_i$**
1. Constant	2	74.34	19.88	0.00
Environment				
2. Rock cover + gravel cover	4	58.54	4.08	0.02
3. Elevation + Slope	4	60.13	5.67	0.01
4. Heat load + organic layer depth	4	60.85	6.39	0.01
Burn characteristics				
5a. Char depth	3	57.45	2.99	0.04
5b. Char depth * Moisture	5	65.29	10.83	0.00
6a. Distance to edge of burn	3	57.28	2.82	0.05
6b. Distance to edge of burn * Moisture	5	65.21	10.75	0.00
7a. Scorch height	3	57.48	3.02	0.04
7b. Scorch height * Moisture	3	65.76	11.30	0.00
7c. Scorch height (quadratic)	5	58.64	4.18	0.02
8a. Basal area mortality	4	56.87	2.41	0.06
8b. Basal area mortality * Moisture	3	64.72	10.26	0.00
8c. Basal area mortality (quadratic)	4	56.34	1.88	**0.07**
Post-fire conditions				
9a. Whitebark pine cover	3	56.73	2.27	0.06
9b. Whitebark pine cover * Moisture	5	65.45	10.99	0.00
10a. Overstory cover	3	57.49	3.03	0.04
10b. Overstory cover * Moisture	5	65.59	11.13	0.00
11a. Shrub cover	3	57.34	2.88	0.05
11b. Shrub cover * Moisture	5	63.99	9.53	0.00
12a. Downed woody debris	3	54.62	0.16	**0.18**
12b. Downed woody debris * Moisture	5	62.64	8.18	0.00
13a. Soil organic matter	3	54.46	0.00	**0.19**
13b. Soil organic matter * Moisture	5	61.97	7.51	0.00
14a. Herb cover	3	55.08	0.62	**0.14**
14b. Herb cover * Moisture	5	63.44	8.98	0.00

Appendix B. Predictive Models for the Tyee Mountain Datasets.

B - 1. A comparison of the competing models for explaining whitebark pine seedling presence on all of the study plots in the Tyee Mountain site. Models included in the confidence set are in bold type.

Explanatory models	**K**	**AIC$_{c\ i}$**	**Δ_ AIC$_{c\ i}$**	**AIC$_c$ weight$_i$**
1. Constant	2	59.91	8.30	0.01
Environment				
2. Rock cover + gravel cover	4	64.80	13.19	0.00
3. Elevation + Slope	4	65.53	13.92	0.00
4. Heat load + organic layer depth	4	66.19	14.58	0.00
Burn characteristics				
5a. Char depth	3	62.17	10.56	0.00
5b. Char depth * Moisture	5	63.59	11.98	0.00
6a. Distance to edge of burn	3	64.20	12.59	0.00
6b. Distance to edge of burn * Moisture	5	68.23	16.62	0.00
7a. Scorch height	3	62.40	10.79	0.00
7b. Scorch height * Moisture	3	67.17	15.56	0.00
7c. Scorch height (quadratic)	5	62.97	11.35	0.00
8a. Basal area mortality	4	63.32	11.71	0.00
8b. Basal area mortality * Moisture	3	67.30	15.69	0.00
8c. Basal area mortality (quadratic)	4	64.91	13.30	0.00
Post-fire conditions				
9a. Whitebark pine cover	3	60.27	8.66	0.01
9b. Whitebark pine cover * Moisture	5	60.74	9.13	0.01
10a. Overstory cover	3	64.15	12.54	0.00
10b. Overstory cover * Moisture	5	66.69	15.08	0.00
11a. Shrub cover	3	63.93	12.32	0.00
11b. Shrub cover * Moisture	5	66.73	15.12	0.00
12a. Downed woody debris	3	63.79	12.18	0.00
12b. Downed woody debris * Moisture	5	60.48	8.87	0.01
13a. Soil organic matter	3	61.82	10.21	0.01
13b. Soil organic matter * Moisture	5	51.61	0.00	**0.91**
14a. Herb cover	3	63.44	11.82	0.00
14b. Herb cover * Moisture	5	68.28	16.67	0.00

B - 2. A comparison of the competing models for explaining whitebark pine seedling density on all plots in the Tyee Mountain site with seedling presence. Models included in the confidence set are in bold type.

Explanatory models	**K**	**AIC$_{c\ i}$**	**Δ_ AIC$_{c\ i}$**	**AIC$_{c}$ weight$_{i}$**
1. Constant	2	97.39	25.56	0.00
Environment				
2. Rock cover + gravel cover	4	78.30	6.47	0.02
3. Elevation + Slope	4	80.17	8.34	0.01
4. Heat load + organic layer depth	4	81.18	9.35	0.01
Burn characteristics				
5a. Char depth	3	79.20	7.37	0.02
5b. Char depth * Moisture	5	81.03	9.19	0.01
6a. Distance to edge of burn	3	71.83	0.00	**0.61**
6b. Distance to edge of burn * Moisture	5	78.04	6.21	0.03
7a. Scorch height	3	79.09	7.25	0.02
7b. Scorch height * Moisture	3	81.79	9.96	0.00
7c. Scorch height (quadratic)	5	79.68	7.84	0.01
8a. Basal area mortality	4	77.72	5.88	0.03
8b. Basal area mortality * Moisture	3	79.19	7.36	0.02
8c. Basal area mortality (quadratic)	4	78.76	6.92	0.02
Post-fire conditions				
9a. Whitebark pine cover	3	77.49	5.66	0.04
9b. Whitebark pine cover * Moisture	5	83.60	11.77	0.00
10a. Overstory cover	3	78.68	6.84	0.02
10b. Overstory cover * Moisture	5	80.11	8.28	0.01
11a. Shrub cover	3	78.73	6.90	0.02
11b. Shrub cover * Moisture	5	80.15	8.32	0.01
12a. Downed woody debris	3	79.19	7.35	0.02
12b. Downed woody debris * Moisture	5	85.27	13.44	0.00
13a. Soil organic matter	3	76.66	4.82	0.05
13b. Soil organic matter * Moisture	5	82.23	10.40	0.00
14a. Herb cover	3	77.52	5.69	0.04
14b. Herb cover * Moisture	5	83.51	11.68	0.00

Appendix C. Average Values for Explanatory Variables.

C - 1. The variables are by moisture class and the burned or unburned state. The p-values are from analyses of variance examining observed differences in burned vs. unburned and moist vs. dry plots, and the interaction between burn and moisture.

Explanatory Variables	Burned		Unburned		P		
	Moist	Dry	Moist	Dry	Interaction	Burn	Moisture
Boulder Creek Burn							
Heat load index	0.33	0.62	0.50	0.52	0.19	0.84	0.07**
Elevation (m)	6381	6557	6333	6648	0.40	0.91	0.006***
Slope (%)	49.7	62.6	51.9	56.0	0.48	0.63	0.11
Rock (%)	10.8	22.6	14.4	31.6	0.55	0.26	0.003***
Gravel (%)	4.6	6.6	1.0	6.8	0.24	0.27	0.03**
Basal area (cm^2)	16611	9528	10373	5443	0.69	0.09*	0.03**
WBP dom. (%)	6.1	18.6	7.5	35.1	0.33	0.32	0.02**
Overstory cover (%)	9.4	10.5	43.7	23.9	0.02**	3.9 e-6***	0.14
Shrub cover (%)	22.0	17.2	35.1	13.5	0.08*	0.33	0.02**
DWD cover (%)	11.4	10.3	8.3	3.6	0.40	0.03**	0.31
Herb cover (%)	31.0	21.6	24.4	28.4	0.25	0.90	0.44
Organic depth (cm)	5.24	4.91	6.2	3.14	0.03**	0.52	0.03**
Soil organic matter (%)	9.9	10.0	13.0	10.4	0.22	0.12	0.32
Scorch height (m)	8.5	4.8	0.0	0.0			0.18
Basal area mort. (%)	76.0	70.0	0.0	0.0			0.96
Char depth (cm)	1.50	1.19	0.0	0.0			0.72
Dist. to burn edge (m)	47	142	-112	-389			0.77
Tyee Complex Burn							
Heat load index	0.43	0.62	0.55	0.62	0.79	0.42	0.31
Elevation (m)	5852	6231	6130	6135	0.03**	0.31	0.007***
Slope (%)	39.8	38.2	30.5	41.7	0.12	0.48	0.44
Rock (%)	2.2	13.3	2.1	16.3	0.59	0.64	6.4e-5***
Gravel (%)	6.8	6.6	5.8	7.3	0.84	0.51	0.81
Basal area (cm^2)	17118	8127	10692	5267	0.47	0.08*	0.003***
WBP dominance (%)	4.4	44.1	15.6	36.0	0.30	0.83	0.001***
Cover (%)	29.7	17.5	46.6	22.9	0.31	0.08*	0.006
Shrub (%)	11.3	3.0	13.2	4.8	1.00	0.64	0.02**
DWD (%)	14.6	11.7	13.5	9.5	0.83	0.50	0.16
Herb (%)	33.7	38.9	37.3	37.5	0.70	0.85	0.57
Organic depth (cm)	3.20	2.27	7.44	2.24	0.06*	0.09*	0.03**
Soil organic matter (%)	7.8	7.9	12.2	10.3	0.05**	0.003***	0.22
Char depth (cm)	1.44	0.94	0.97	0.39			0.08*
Scorch height (m)	2.5	3.5	0.0	0.0			0.48
Basal area mort. (%)	60.3	69.7	0.0	0.0			0.70
Dist. to burn edge (m)	400	49	-107	-46			0.80

** p-values less than 0.05

*** p-values less than 0.01

Appendix D. Accuracy of explanatory models predicting seedling presence.

Site	**Data subset**	**Explanatory Model**	% of time model correctly predicted		
			presence	absence	Presence and absence
Boulder Creek	All (48)	Overstory cover * Moisture	64.3	82.4	77.1
		Whitebark pine overstory cover	28.6	91.2	72.9
		Scorch height (quadratic)	42.9	64.7	58.3
		Basal area mortality (quadratic)	50.0	88.2	77.1
	Burned (30)	Scorch height	70.0	90.0	83.3
		Overstory cover	70.0	80.0	80.0
	Unburned (18)	Overstory cover	100.0	75.0	77.8
Tyee Mountain	All (43)	Soil organic matter * Moisture	68.2	28.6	48.8
	Burned (27)	Soil organic matter * Moisture	69.2	42.9	55.6
		Downed woody debris * Moisture	76.9	35.7	55.6
	Unburned (16)	Soil organic matter	100.0	28.6	68.8

Appendix E. Matrices of Correlation Coefficients between Explanatory Variables[4]

	PIAL	STM	COV	BA	BAM	SCR	CD	ELV	SLP	HLI	RCK	GRV	OD	DWD	SHR	HRB	OM	DB
PIAL	1.00																	
STM	-0.04	1.00																
COV	**0.63**	-0.24	1.00															
BA	**-0.36**	**0.50**	**-0.30**	1.00														
BAM	**-0.62**	**0.33**	**-0.60**	**0.48**	1.00													
SCR	**-0.64**	0.12	**-0.53**	**0.41**	**0.64**	1.00												
CD	**-0.30**	0.24	**-0.36**	**0.28**	**0.40**	**0.41**	1.00											
ELV	**0.35**	-0.02	0.24	-0.11	-0.16	**-0.25**	-0.07	1.00										
SLP	0.11	0.07	-0.15	-0.12	-0.06	-0.15	-0.02	-0.01	1.00									
HLI	**0.41**	0.06	0.12	-0.20	-0.08	-0.16	0.04	0.25	0.16	1.00								
RCK	**0.32**	**-0.27**	0.18	**-0.59**	**-0.36**	**-0.33**	-0.17	0.13	**0.32**	**0.26**	1.00							
GRV	0.16	-0.07	-0.07	-0.28	-0.14	-0.22	-0.15	0.11	0.20	0.05	0.16	1.00						
OD	-0.04	0.24	-0.14	0.23	0.22	0.17	**0.47**	-0.06	0.03	0.03	-0.19	-0.09	1.00					
DWD	-0.20	0.21	**-0.33**	**0.33**	0.23	**0.26**	0.24	-0.19	0.05	-0.01	-0.21	-0.14	0.23	1.00				
SHR	0.12	-0.03	0.14	-0.04	-0.12	-0.13	-0.04	-0.20	**0.33**	0.16	0.08	-0.12	0.04	-0.01	1.00			
HRB	**-0.37**	0.09	-0.24	**0.36**	**0.39**	**0.35**	0.13	-0.04	**-0.29**	-0.22	**-0.62**	-0.10	0.08	0.14	-0.17	1.00		
OM	-0.07	-0.14	0.13	-0.05	0.00	0.00	0.04	0.03	-0.07	0.03	0.09	-0.22	-0.05	0.14	0.06	0.12	1.00	
DB	-0.08	0.23	-0.19	0.10	0.19	0.09	0.17	0.04	0.05	-0.02	0.00	0.10	0.24	0.25	-0.13	0.08	-0.02	1.00

E - 1. An empirical correlation matrix was constructed using Kendall's rank correlation method from the Boulder Creek Burn data set. Kendall's tau (τ) value represents the strength of the dependence between the eighteen explanatory variables used in the analyses. Bold type indicates a significant correlation ($P \leq 0.05$).

---

[4] PIAL = overstory whitebark pine cover
STM = stem density
COV = overstory cover
BA = total basal area
BAM = basal area mortality
RCK = rock cover
GRV= gravel cover
OD = organic depth
DWD = downed woody debris
CD = char depth
ELV = elevation
OM = organic matter
HLI = heat load index
HRB = herb cover
SLP = slope
SCR = scorch height
SHR = shrub cover

	PIAL	STM	COV	BA	BAM	SCR	CD	ELV	SLP	HLI	RCK	GRV	OD	DWD	SHR	HRB	OM	DB
PIAL	1.00																	
STM	-0.20	1.00																
COV	**0.27**	0.18	1.00															
BA	**-0.25**	**0.67**	0.12	1.00														
BAM	-0.12	-0.01	**-0.36**	0.11	1.00													
SCR	-0.14	-0.18	**-0.40**	-0.03	**0.62**	1.00												
CD	-0.05	0.22	-0.05	0.17	0.10	0.03	1.00											
ELV	**0.48**	**-0.31**	-0.06	**-0.29**	0.22	0.16	-0.01	1.00										
SLP	0.02	0.17	0.18	0.09	**-0.41**	**-0.35**	-0.21	-0.23	1.00									
HLI	0.19	-0.06	0.04	0.01	-0.05	-0.09	**-0.29**	0.17	0.18	1.00								
RCK	0.22	**-0.46**	-0.20	**-0.27**	0.04	0.13	**-0.35**	**0.35**	0.01	**0.33**	1.00							
GRV	0.08	-0.20	-0.18	-0.20	0.09	0.18	-0.11	0.19	-0.13	0.22	0.24	1.00						
OD	-0.08	**0.26**	-0.05	0.17	0.08	0.06	**0.55**	-0.07	-0.18	-0.17	**-0.32**	-0.15	1.00					
DWD	-0.14	-0.02	-0.01	-0.12	0.03	0.07	0.23	0.07	-0.02	-0.23	-0.13	-0.02	0.12	1.00				
SHR	**-0.45**	0.15	0.22	0.12	-0.19	-0.17	-0.04	**-0.46**	0.06	-0.09	**-0.26**	-0.06	-0.09	0.13	1.00			
HRB	0.03	-0.01	0.03	0.18	0.16	0.21	-0.10	0.06	-0.15	-0.03	0.18	-0.25	0.12	-0.24	-0.18	1.00		
OM	-0.03	0.10	0.16	0.15	-0.03	-0.08	0.17	0.04	-0.05	-0.18	0.09	-0.14	0.07	0.24	0.18	0.09	1.00	
DB	-0.18	**0.26**	0.02	**0.38**	0.21	0.14	0.17	-0.10	0.02	-0.03	-0.13	0.12	0.12	0.24	-0.03	0.03	0.02	1.00

E - 2. An empirical correlation matrix was constructed using Kendall's rank correlation method from the Tyee Mountain Burn data set. Kendall's tau (τ) value represents the strength of the dependence between the eighteen explanatory variables used in the analyses. Bold type indicates a significant correlation ($P \leq 0.05$).