Landscape pattern and blister rust infection in whitebark pine (*Pinus albicaulis*) at alpine treeline, Northern Rocky Mountains, U.S.A.

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ABSTRACT

Whitebark pine (*Pinus albicaulis*) is a foundation and keystone species at alpine treelines of the northern Rocky Mountains and is threatened by the fungus white pine blister rust (*Cronartium ribicola*). This disease affects all five-needled white pines, but has caused particularly widespread mortality in whitebark pine. Objectives of this research were: 1) to characterize the landscape structure of the treeline study sites at Divide Mountain in Glacier National Park and at Wyoming Creek in the Beartooth Mountains of Montana using landscape metrics and fieldwork; 2) to determine the frequency of blister rust infection of whitebark pine trees and determine if landscape pattern is correlated with higher infection rates; and 3) to characterize the climate at alpine treeline. I used both field surveys and subsequent statistical analysis to meet these objectives. Field data collection included detailed surveys of blister rust infection of treeline whitebark pine and characterization of landscape cover type in a combined total of 60 quadrats, positioned at the study sites using a random sampling scheme stratified by aspect. Landscape analysis of metrics such as patch area, proximity and contagion were generated in FRAGSTATS software and ArcGIS. Spearman's rank correlation analysis found significant correlations between tree island patch size, patch perimeter, and percent of landscape and blister rust infection intensity at both study sites. These findings support previous research involving the relationship between patch area and blister rust

infection rates and contribute to the field of landscape ecology by understanding what other landscape metrics are significant in invasive disease infection patterns.

Dedication

For my family, who always support me.

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(*I took all photos in this document during fieldwork in July 2010*)

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Chapter 1. Introduction

Invasive pathogens are organisms that cause plant diseases that are non native and have been introduced, often accidentally, into an ecosystem. Presently, invasive pathogens affect many species worldwide, altering ecosystems by reducing or eliminating the species affected by the disease, and causing cascading effects that impact many other species. In the Northern Rocky Mountains, white pine blister rust (*Cronartium ribicola*) is infecting and causing widespread mortality in whitebark pine (*Pinus albicaulis*). Whitebark pine is a foundation and keystone species in the alpine treeline ecotone and subalpine ecosystems of the Rocky Mountains from northern Colorado, USA at the southern extent, through central Alberta and British Columbia, Canada, at the northern extent (Critchfield and Little, 1966). Researchers now understand that the loss of this species will likely impact ecosystem stability (Farnes, 1990; Tomback, et al., 2001; Ellison et al., 2005; Tomback and Resler, 2007).

The field of landscape pathology can help our understanding of how invasive pathogens may influence ecosystems, specifically in the context of landscape pattern. Landscape pathology is the integration of landscape ecology and pathology of forest species. Landscape pathology suggests that disease spread is influenced by landscape configuration of plants, such as their contagion or their patchiness (Holdenrieder et al., 2004; Plantegenest et al., 2007).

This research analyzed vegetation patterns, specifically patch size, connectivity, and other landscape metrics of trees and tree islands to determine if a relationship exists between vegetation pattern and blister rust infection in whitebark pine at treeline. The goal was to understand the relationship between disease manifestations and treeline vegetation pattern, as opposed to the relationship between infection and alternate host distribution. The specific objectives of this study were to: 1) characterize the landscape structure of the treeline study sites using landscape metrics and fieldwork; 2) determine the frequency of white pine blister rust infection of whitebark pine trees in the study areas and if landscape pattern is correlated with higher infection rates; and 3) characterize the microclimate at alpine treeline by aspect.

This study contributes to the research of landscape ecology and the field of landscape pathology. Determining how landscape characteristics may affect blister rust disease incidence will contribute to our knowledge of landscape pathology and is the basic significance of this research. The applied significance of my research will be to help determine the future spread of blister rust or other invasive pathogens, based on the influence of landscape metrics. By determining the relationship between alpine treeline vegetation pattern and blister rust infection, the results may help researchers determine if and how landscape structure influences other invasive species affecting other ecosystems, and how this will affect the treeline ecosystem as climate changes and whitebark pine mortality increases. This research will also be beneficial to park administrators and managers by providing more information on the factors that influence disease incidence, such as information on specific patch characteristics that may have higher rates of infection, and differences in microclimate between upper and lower treeline that may influence the disease. Ideally, this research will contribute to the management of blister rust and protecting the whitebark pine communities affected by this disease.

Chapter 2. Literature Review

The purpose of this literature review is to place my research into a conceptual framework. First, the work will be placed into a broader geographic context; specifically, I will address theory from the field of landscape ecology with specific emphasis on pattern and process relationships. Next, I will examine literature on the alpine treeline ecotone and the important processes that influence treeline vegetation pattern such as wind, snow, and geomorphic processes. The concept of foundation and keystone species is also pertinent to understanding the importance of whitebark pine trees, and ultimately, vegetation pattern at alpine treelines of the northern Rocky Mountains. Research on invasive species and their effect on pattern and process is examined as well as a detailed outline of white pine blister rust to understand the disease. Finally, the field of landscape pathology is evaluated to identify the gaps in the literature of research conducted on the influences of landscape in disease transport vectors, and what further research needs to be conducted that can contribute to the field of landscape pathology and fill in the gaps in research.

BROADER GEOGRAPHICAL CONTEXT

Because of their inherent spatial characteristics and their impact on the distribution of other species, invasive species are receiving increasing attention in the field of geography. Cowell and Parker (2004) addressed four fundamental themes in biogeography that apply to this subject: spatial pattern and process, landscape change, human modification of biotic communities, and linking physical and biological systems. Spatial pattern and process is the influence that biological, physical and cultural processes have on the spatial distributions of plants and animals. This theme is extremely important in assessing the pattern of vegetation on the landscape and the relationship landscape pattern may have on the process of blister rust infection of whitebark pine trees. Landscape change is occurring as a result of whitebark pine tree mortality. Since whitebark pine trees provide important ecosystem services, loss of the species is likely to alter ecosystem processes (Malanson et al., 2007; Tomback and Resler, 2007).

Human modification of biotic communities, as described by Cowell and Parker, are defined as the influences humans have on ecosystems through increased development. This theme is also highly relevant to this study because white pine blister rust was accidentally introduced to western North America in 1921 when a landowner imported eastern white pine seedlings from Europe, where the rust originated (McDonald and Hoff, 2001). Cowell and Parker (2004) also addresses linkages between physical and biotic systems. The whitebark pine ecosystem in the alpine environment is a prime example of the link between physical processes and biotic systems. Climate variables such as high winds and snow patterns as well as decreased soil nutrients affect the growth of alpine species like whitebark pine and influence pattern and process (Malanson and Butler, 1994; Holtmeier and Broll, 2005; Hiemstra et al., 2006).

Finally, the concept of spatial scale also percolates into all geographic research because there is no favored scale for spatial research—it must be determined by the problem being observed (Schumm, 1991). In landscape ecology studies, scale can vary depending on the landscape and species being examined and what the researcher is trying to observe (Levin, 1992).

LANDSCAPE ECOLOGY

The field of landscape ecology focuses on spatial patterns and processes on the landscape such as disturbance, energy flow, nutrients, and spatial heterogeneity (Urban et al., 1987; Forman, 1983; Risser et al., 1984). Turner et al. (2001) defines landscape ecology as a field that "emphasizes the interaction between the spatial pattern and ecological process, that is, the cause and consequences of spatial heterogeneity across a range of scales" (p. 2). The general definition of a landscape is an area that is spatially heterogeneous in at least one factor of interest (ibid.).

Pattern and process are the foundation of the study of landscape ecology, but what generates pattern and process on the landscape? Pattern is often caused by abiotic factors like climate or landforms. Additionally, biotic factors such as competition, predation, and the concept of keystone species also influence the creation of pattern on the landscape (Turner, 2005). Some other processes that influence pattern formation include disturbance, succession and anthropogenic influence on the landscape (ibid.).

The concept of scale, both spatial and temporal, is important in landscape ecology, as each individual organism experiences the environment on a species-specific range of scales, which is important for describing the spatial and temporal pattern and dynamics of populations (Levin, 1992). How a landscape is quantified is also important in describing the patterns observed. Landscape metrics can be used to describe the composition and configuration of the landscape such as patch density, contagion, and proximity, but these metrics are sensitive to grain size and extent (Wickham and Ritters, 1995; Turner, 2005). The resolution of the aerial or satellite images can produce different descriptions of pattern. The relationship between pattern and process is the focus of the field of landscape ecology and further research of other landscapes will contribute to theoretical advances in the field and build upon previous studies on how the influence of the two concepts creates landscape. Pattern and process in landscape ecology is evidenced at the alpine treeline, in the vegetation patterns observed, and the physical and biotic processes that cause it.

THE ALPINE TREELINE ECOTONE: PATTERN AND PROCESS

The alpine treeline ecotone (ATE) is a transitional environment, representing the boundary between subalpine trees and tundra. Typically, alpine treelines represent climatic thresholds, where trees can no longer grow due to the colder-on-average temperatures of the tundra environment above timberline (Holtmeier, 2009). However, treeline position can also be influenced by other factors such as geomorphic processes, wind, and soil conditions (Malanson et al., 2007). The ATE falls under the 'landscape ecotone' concept as described by Gosz (1993), where the interactions of weather, topography and soil influence the transition between the two biomes. Because the transition between subalpine forest and tundra vegetation may be gradual, the alpine treeline is really a zone rather than a line as the name suggests (Arno and Hammerly, 1984; Walsh et al., 1992). Research on the ATE is important because of its ecological importance and as a potential front for vegetation response to climate change (Fagre, 2009).

Vegetation pattern at treeline is both a product of both processes that influence the establishment and growth of plant species at the ATE, and processes that are influenced by growth and establishment of trees and numerous other biotic and abiotic factors

(Malanson et al., 2007). Research by Marr (1977) on tree island formation indicates that trees become dwarfed and contorted and create ‘islands’ in a matrix of herbaceous and dwarf shrub vegetation due to the harsh conditions at that altitude. Whitebark pine has been found to be the primary colonizing species in tree island formation in Glacier National Park, more often than other conifer species at the alpine treeline ecotone (Resler and Tomback, 2008). Other research has been conducted on the positive feedback effects that these tree islands have on species establishment (Marr, 1977; Benedict, 1984; Bekker, 2005). The establishing tree provides wind protection as well as increases snow collection and aids in soil development at the patch microsite (Malanson, 1997; Callaway et al., 2002).

Additional research on the effects of snow on tree establishment suggests that tree islands create a collection area leeward for snow to be deposited. Snow provides seedlings with protection from winter wind and low temperatures as well as affect winter soil temperatures, and provides moisture through melting in warmer months (Walsh et al., 1994; Hiemstra et al., 2006). Researchers have also observed negative feedback effects of tree island formation from dense canopies shading the soil and decreasing the temperature on the windward side where the vegetation begins to die over time as new species establish in the leeward side of the wind (Marr, 1977; Benedict, 1984). Research by Marr (1977) on tree island formation also included observations of movement of islands across the landscape. He found evidence of live branches connected to dead branches leeward of the patch. Benedict (1984) determined rates of migration by dating the debris of wood fragments found in the trail leeward of the present island.

Many alpine treeline sites in the northern Rocky Mountains east of the Continental Divide exist in a periglacial climate with a freeze-thaw cycle that generates geomorphic processes such as solifluction, soil creep, landslides and erosion by wind and water (Butler and Walsh, 1994). These processes have created a post-glacial landscape characterized by terrace risers and treads, boulders, and topographic hollows (Resler, 2006). These geomorphic features aid in pattern formation by providing shelter for seedling establishment. Resler et al. (2005) found a significant spatial association at the alpine treeline between conifer growth and shelter sites including terrace risers, boulders and combinations of both features. Another geomorphic process observed by Butler et al. (2004) that creates a site suitable for seedling establishment is turf exfoliation. These geomorphic features, along with established vegetation, generate the protected sites needed to create the patches found at the alpine treeline. Where the prevailing wind is unidirectional, patches tend to grow parallel with wind direction, with windward to leeward establishment of seedlings (Bekker, 2005). Tree island patches tend to be triangular shaped rather than linear when trees establish in the lee of a feature where winds are inconsistent (Resler, 2006). While physical and biotic processes are extremely influential in pattern formation at the alpine treeline, the concepts of foundation and keystone species influence pattern and process among species, particularly when invasive species contribute.

FOUNDATION AND KEYSTONE SPECIES: PATTERN AND PROCESS

Foundation and keystone species are important to landscape pattern and process because they provide stability for biotic and abiotic factors in ecosystem processes, such as climate amelioration in alpine environments. Foundation species are defined as locally abundant and common within the ecosystem and therefore have a significant influence on other species by providing shelter or altering microclimates and soil characteristics of the ecosystem (Ellison et al., 2005). Keystone species are different from foundation species in that they are not usually as abundant as a foundation species, but in most circumstances, they play a greater role in the dynamics of an ecosystem and its stability. For example, research by Paine (1969) found that removing a predator species of starfish from an intertidal ecosystem allowed the prey species of mussel to thrive and outcompete 23 other species and to dominate the rock surfaces. Paine's research coined the term 'keystone species'. As he stated, "the species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the keystone of the community's structure, and the integrity of the community and its unaltered persistence through time…are determined by their activities and abundances" (Paine 1969, p. 92). Holling (1992) also hypothesized that ecosystems are controlled by a number of key plant, animal, and abiotic processes that structure the landscape at different scales.

Whitebark pine (*Pinus albicaulis*) has been found to be a foundation and keystone species in the alpine treeline ecotone of the northern Rocky Mountains (Tomback et al., 2001; Ellison et al., 2005). Whitebark pine trees facilitate community development by mitigating the harsh conditions and favoring the growth of shade-tolerant competitors (Callaway, 1998). They are also important for stabilizing soil, reducing erosion, and regulating the rate of snowmelt (Farnes, 1990; Tomback et al., 2001). Loss of whitebark pine due to blister rust infection can alter many ecosystem services such as avalanche control and local hydrology, as well as the potential response of the ecosystem to climate change (Resler and Tomback, 2008). Invasive species are a threat to foundation and keystone species and the feedback effects they have on ecosystems and landscape ecology.

INVASIVE SPECIES AND THEIR EFFECT ON PATTERN AND PROCESS

Numerous researchers have studied the influence of invasive species on ecosystems and the negative effects they impose. In North America, forest composition and stand dynamics have been altered by invasive diseases such as chestnut blight (*Cryphonectria parasitica*), Dutch elm disease (*Ophiostoma ulmi* and *Ophiostoma novo-ulmi*), and sudden oak death (*Phytophthora ramorum*) (Haugen, 1998; Paillet, 2002; Meentemeyer, 2004). However, these invasive diseases have affected trees in subalpine forests. Researchers have found that the introduction of non-native species can affect ecosystems at multiple spatial scales through the local and regional extinction of native species (Mack et al., 2000). Research by Crowl et al. (2008) suggests that it is important to monitor exotic species from broad scales to fine scales in order to determine exotic species invasion success, influenced by transport vectors, local environmental conditions, and population and community ecology.

The shrubby growth form of whitebark pine trees creates a large surface area, and large infection target for spores. Because spores require cool temperatures and high humidity, Campbell and Antos (2000) have suggested that the spread of the fungus may be limited in cold, dry environments, like the alpine treeline ecotone. However, Resler and Tomback (2008) found substantial rates of white pine blister rust infection in whitebark pine trees at the alpine treeline at Divide Peak and Lee Ridge study sites in GNP, where the conditions are cold and dry. They found a significant correlation between number of blister rust cankers and number of whitebark pine trees per sampling transect. Resler and Tomback (ibid.) also found evidence of infection on solitary trees which could potentially initiate tree islands, suggesting that the whitebark pine tree's role as a keystone species is at risk. Further research of vegetation patterns and blister rust infection at the alpine treeline is needed to establish a correlation between patch size and infection rates. White pine blister rust is the most significant invasive pathogen affecting whitebark pine trees at the alpine treeline and throughout the Rocky Mountains.

WHITE PINE BLSTER RUST: LIFE CYCLES AND THE ROLE OF CLIMATE

McDonald and Hoff (2001) outlined the complex life cycle of white pine blister rust (*Cronartium ribicola),* the pathogen that causes blister rust infection in five-needled white pines. The life cycle consists of five spore types, two hosted by pine species and three hosted by *Ribes* species. Aeciospores are produced in the blister like cankers (aecia) on living bark tissue of the tree. They can remain viable for weeks and travel long distances by wind, up to 500 meters. The aeciospores land on the bottom side of *Ribes* leaves and germinate into colonies of horseshoe shaped structures (uredinia) where urediniospores develop. These spores multiply on same or nearby bushes during summer in cool, wet periods with 100% relative humidity. The cool nights of August initiate the production of teliospores within the uredinia. In mid-late summer, teliospores develop into a barrel shaped spores and occur in multiple layers that form a structure called a telial column. The germination trigger of teliospores occurs with near 100% relative humidity for a period of 6-8 hours in late summer to early fall. When these conditions occur, each individual teliospore produces four basidiospores and each telial column produces ~6,000 basidiospores in a 20-48 hour time frame. The basidiospores are thin walled and fragile and require constant high humidity to survive and remain viable. These windborne spores travel short distances, usually less than 300 meters, to the needles of pine species where they infect through the stomata of the needle. The infection of the needle grows down to the stem of the tree where rust mycelia grows in the tissue of the branch and produces a canker. Cankers produce fusiform swelling of the branches and pycniospores that breed with neighboring infections that create new generations of aeciospores, thus completing the life cycle. The rust causes the loss of cone-bearing branches years before the tree dies, resulting in a decrease in seed production (McDonald and Hoff, 2001; McKinney and Tomback, 2007). McDonald et al. (2006) also suggested that sickletop lousewort (*Pedicularis racemosa*) and scarlet Indian paintbrush (*Castilleja mintata*) serve as alternate hosts as well, though the *Ribes* genus is more common.

LANDSCAPE PATHOLOGY

The field of landscape pathology acknowledges that landscape characteristics and pattern can influence, and be influenced by, patterns of disease development (Holdenrieder et al., 2004). Generally, habitat fragmentation is a detrimental process in the context of conservation because it increases the chance of extinction in isolated patches, but as far as management of a pathogen is concerned, fragmentation can aid in limiting the pathogen's influence on the landscape (ibid). In the case of blister rust, there is a high genetic differentiation between western and eastern American populations, explained by a large-scale barrier to gene flow in the Great Plains (Hamelin, 2000). Landscape structure and scale are important foundations to landscape pathology and has been the basis for landscape pathology research. Condenso and Meentemeyer (2007) found correlations between broadening scales, from plot scale to landscape scale, and higher rates of infection of sudden oak death (caused by pathogen *Phytophthora ramorum*) in contiguous forest than in plot level observations on bay laurel species.

Landscape pattern may be an important factor in blister rust infection of whitebark pine trees. Resler and Tomback (2008) found a significant correlation between length of the tree island and incidence of blister rust at the sites in their study. Trees that were a component of a tree island, and therefore part of a larger patch, had higher averages of active and inactive cankers than trees that were solitary, which indicates that patch size is an important landscape metric in blister rust incidence. From the research of Resler and Tomback (2008), questions arise regarding landscape pathology and blister rust infection in whitebark pine trees. There is need for further research to ascertain what specific characteristics of landscape pattern correlate with blister rust infection incidence and to understand how underlying mechanisms, such as climate and spore dispersal, may impact blister rust incidence in tree islands and solitary trees. Since blister rust spores are transmitted by wind, there is a possibility that larger tree islands have a higher chance of infection than solitary trees because they have a higher surface area; an answer to this question requires further research.

Landscape pathology best describes the integration of landscape ecology and plant pathogen research, though there are similar terms such as landscape epidemiology that have the same spatial framework, but research different forms of disease. Plantegenest et al. (2007) used the term, ‘landscape epidemiology’ to describe the application of the concepts of landscape ecology to the study of pathogen dynamics at the landscape scale when observing agricultural pests and diseases. Other researchers that focus on the influence of landscape on vector-borne diseases that affect animal or human health, use terms such as spatial epidemiology, ecological epidemiology, and landscape epidemiology (Ostfeld et al., 2005; Graham et al., 2004; Reisen, 2010). Though the focus of these studies is vector-borne diseases, the foundations of landscape ecology in pattern and process have been used to analyze the metrics that transport diseases. Epidemiological models that take into effect the influence of landscape geometry and pattern have been used by some researchers to determine the spatial extent of a disturbance that may not necessarily be disease (O’Neill et al., 1992). While there is some inconsistency in the research foci of studies in landscape epidemiology (i.e. human, animal, or vegetation studies), the unifying factor of every study is to describe landscape patterns that determine the spatial extent of pests, pathogens, or other disturbances in question.

Chapter 3. Methods

The goal of this research was to better understand the relationship between landscape pattern and white pine blister rust infection at alpine treeline. A secondary goal was to understand the climate conditions during the three month germination period of the blister rust life cycle. To obtain these goals we set three main objectives: 1) to characterize the landscape structure of the treeline study sites at Divide Mountain in Glacier National Park and at Wyoming Creek in the Beartooth Mountains of Montana using landscape metrics and fieldwork; 2) to determine the frequency of white pine blister rust infection of whitebark pine trees and determine if landscape pattern is correlated with higher infection rates; and 3) to characterize the climate at alpine treeline. To fulfill these objectives, a combination of fieldwork and statistical analysis was completed.

STUDY AREA

Fieldwork for this project was conducted in two northern Rocky Mountain locations in Montana in July 2010 (Figure 3.1). The first is situated east of the Continental Divide, on the eastern slope of Divide Mountain (48° 39’ 55.47” N, 113° 24’ 3.37” W; 2,462m elevation; Figure 3.2) which lies on the border between Glacier National Park and Blackfeet Indian Reservation in Montana. The second site is near Wyoming Creek (45° 1’ 17.02” N, 109° 23’ 59.42” W; 3,003m elevation; Figure 3.3) in the Greater Yellowstone Ecosystem on the Beartooth Plateau of northern Wyoming and southern Montana.

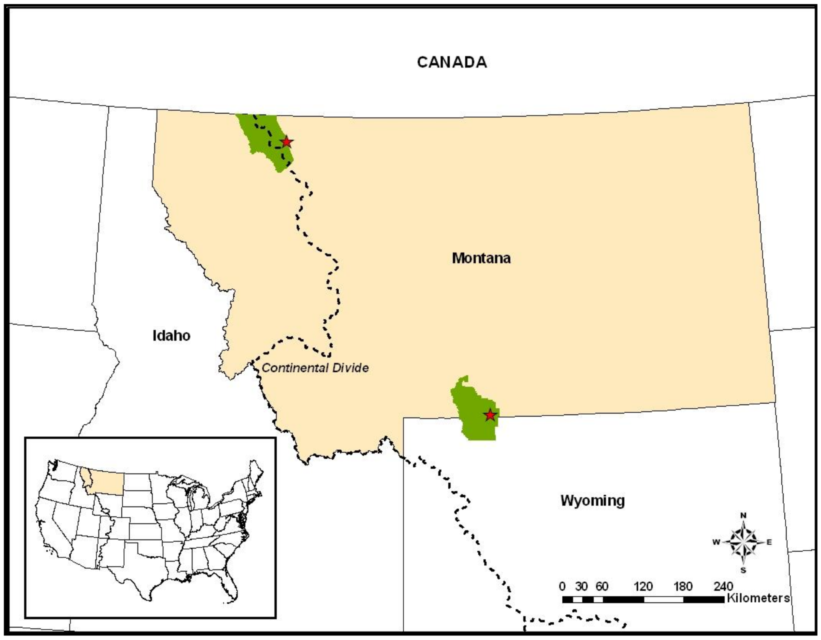


Figure 3.1: Map of Montana and study areas

The treeline in both study sites is climatically developed, meaning that temperature, moisture and wind are major determinants of treeline position (Holtmeier, 2009). At both Divide Mountain and the Beartooth study sites, whitebark pine is an important component of the heterogeneous subalpine and treeline vegetation pattern and often exists as tree islands. These tree islands are the focus of my landscape analysis and can range in size from a few centimeters in width (for a single seedling) to hundreds of meters (for clusters of many individuals and species).

DIVIDE MOUNTAIN

Glacier National Park covers an area of 462,500 hectares and straddles the western Continental Divide. Divide Mountain is on the border of the EPA Level III ecoregions “Northern Rockies” and “Canadian Rockies” (Omernik, 1987). The eastern slopes of the Rocky Mountains are characterized by climates that are drier, windier and cooler than the western slopes (Elias, 1996). In addition to whitebark pine, other alpine treeline species include lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and the occasional alpine larch (*Larix lyallii*) and Douglas-fir (*Pseudotsuga menziesii*). Shrubs and alpine forbs, grasses, sedges and rushes are prevalent and intermixed with trees at the alpine treeline (Dutton and Marrett, 1997). Animal species found in the alpine treeline environment include mammal species that rely on whitebark pine seed as a food source, such as grizzly bears (*Ursus arctos horribilis*), black bears (*Ursus americanus*), and red squirrels (*Tamiasciurus hudsonicus*) (Mattson et al. 2001). The bird species, Clark’s nutcracker (*Nucifraga Columbiana*), is the primary species for whitebark pine seed distribution throughout the alpine treeline (Tomback, 2001).

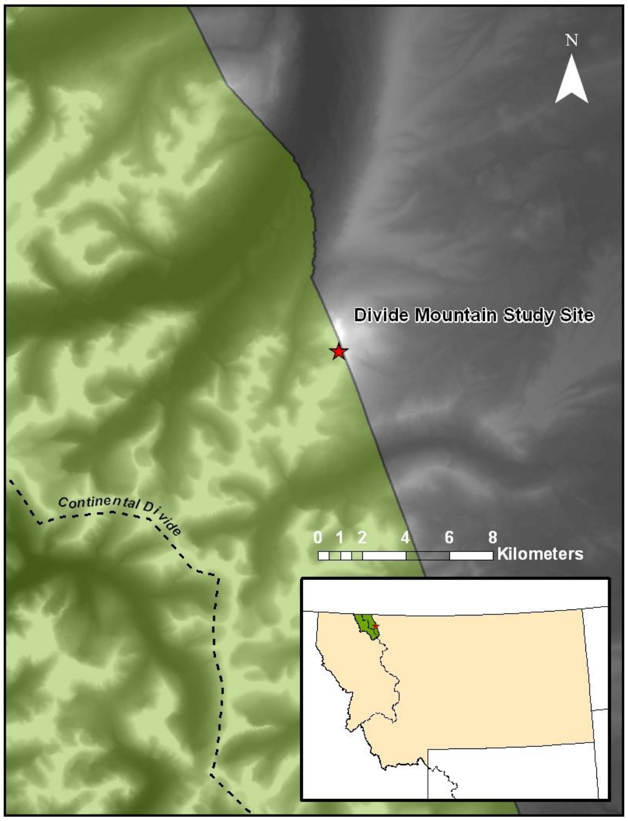


Figure 3.2: Map of Divide Mountain on the border of Glacier National Park

The eastern slopes of Glacier National Park are characterized by a continental climate with an annual average precipitation of 58.5 cm. Average January maximum temperatures on the eastern slopes are approximately -3°C and average minimum temperatures are approximately -14°C. July average maximum temperatures are around 24.5°C and average minimum temperatures are around 7°C. These temperature and precipitation averages are for the town of Saint Mary, just north of Divide Mountain, which stands at an elevation of about 1,367 meters. Prevailing winds of the region are westerly, with local topographic modification of wind direction and speed (Finklin, 1986).

Although the glaciers of Glacier National Park are rapidly retreating, prominent glacial landscape features such as steep-walled U-shaped valleys, cirques, horns, moraines and finger lakes characterize most of the park (Elias, 1996). Divide Mountain, located on the eastern edge of the Lewis Overthrust, is characterized by the Altyn limestone formation, formed during a shallow, warm sea environment during the mesoproterozoic era (Raup et al., 1983). Soils found in the alpine treeline ecotone are primarily “ice patterned soils” and “alpine meadow limestone soils”, as characterized by Dutton and Marrett (1997). Ice-patterned soils occur on upper mountain slopes and mountaintops, with parent materials of residuum and colluvium that has been exposed to intense frost action. Alpine meadow limestone soils are soils with parent material of limestone residuum and colluvium and a surface layer of volcanic ash-rich wind deposits.

WYOMING CREEK

The Wyoming Creek study site is located just outside of the Absaroka-Beartooth Wilderness, an established protected land comprised of three National Forests, including Custer National Forest where Wyoming Creek is located. Wyoming Creek is part of the Line Creek Plateau Research Natural Area, established to protect the biodiversity of alpine plant communities (Shelly, 2003). Wyoming Creek is found in the “Middle Rockies” ecoregion as described by Omernik (1987). Wyoming Creek, like other alpine areas of the Rocky Mountains, has a rich biodiversity of animal species which includes mammal species such as grizzly bears (*Ursus arctos horribilis*), black bears (*Ursus americanus*), mountain goats (*Oreamnos americanus*), and elk (*Cervus Canadensis*)

(Pattie and Verbeek, 1967). The range of the Clark's nutcracker also stretches down throughout the Beartooth Mountains.

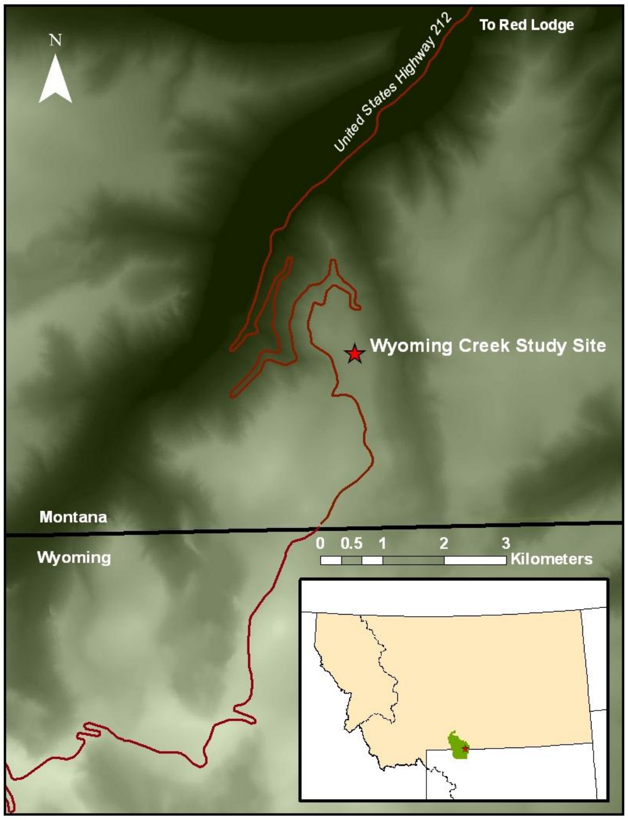


Figure 3.3: Map of Wyoming Creek just off of US highway 212

The climate of the Beartooth Mountains is continental, with hot, dry summers and cold, wet winters (WRCC, 2011). Daily summer temperatures of the Yellowstone/Beartooth region average around 25°C in daytime and may fall below freezing at higher elevations at night time (NPS, 2011). Average winter temperatures range between -17°C and -6°C in the daytime and subzero temperatures are common at night in the winter months (ibid.).

The Beartooth Mountains are primarily uplifted Precambrian granite and gneiss, flanked by sedimentary rocks (Hughes, 1933). Large, treeless plateaus are common in the Beartooth Mountains, with elevation averages around 10,000 ft. The soils of the Beartooth Mountains are primarily Orthents or Entisols— dry soils that lack pedogenic horizons due to steep slopes and highly resistant parent materials (Soil Survey Staff, NRCS, 2011).

FIELD DATA COLLECTION

For the purpose of characterizing the landscape structure of the treeline study sites (Objective 1) and to characterize blister rust infection intensity (Objective 2) I recorded vegetation composition of tree islands at treeline and recorded blister rust infection of whitebark pine by aspect. Furthermore, I geolocated tree island boundaries and individual conifers using a hand-held Trimble XT GPS. Finally, in order to meet Objective 3 (to characterize study site climate) I assembled weather stations with the field team that recorded weather conditions throughout a three month period. This three month period is a significant stage in the lifecycle of blister rust, where germination of teliospores and basidiospores occurs.

Prior to fieldwork, maps of the study area were downloaded into a GIS. These maps included imagery, topographic maps, and aspect maps. I used these maps to develop a proportional, stratified random sampling scheme of the study area; the number of plots placed in each aspect (NW, NE, SW, SE) was proportional to the percent of area of our study area represented in each aspect class. The decision to use a stratified sampling scheme was based on previous research that found aspect to have a significant influence in blister rust infection rates (Smith et al., 2011).

Vegetation Sampling

I sampled 30 quadrats each at the Divide Mountain and Wyoming Creek study sites for a total of 60 sampling quadrats. Quadrats were located by aspect, measured by a hand compass, and quadrat centroids were determined using a blind toss of a transect pin. The quadrat boundaries were then measured out in each direction to create a 15x15 meter quadrat in the downslope direction. Once the quadrat boundaries were set, red flags were used to mark locations of whitebark pines and yellow flags were used to mark the presence of other conifer species. A red and yellow flag marked tree islands with both whitebark pine and other conifer species. Trees were considered part of a tree island if more than one tree created a contiguous patch of vegetation. Once the trees were flagged, GPS points for any individual conifer type other than whitebark pine were geolocated using a Trimble GeoXT GPS with species type recorded in the data dictionary.

Determination of positions of individual whitebark pine trees, whitebark pine within tree islands, and other conifer species, was important for characterizing landscape pattern and the importance of whitebark pine at treeline. Locations of individual whitebark pine trees and whitebark pine trees growing in tree islands were geolocated using a GPS and assigned a unique ID. Using data sheets compiled before entering the field (Appendix A), multiple variables were recorded for every whitebark pine. Length, width and height in meters were recorded for every individual whitebark pine and for every tree island. If a tree was growing in the lee of a shelter on the landscape, we recorded the shelter type, rock, topographic depression, other, or no shelter. If the tree was protected by vegetation such as willow (*Salix*), the shelter type was classified as “other”. In the lee of such shelters, microclimate conditions of alpine treeline may be ameliorated and thus provide suitable establishment sites for whitebark pine and other trees (Resler et al., 2005).

Whitebark pine trees may grow in clusters due the seed caching habits of the Clark’s nutcracker. Therefore, when counting whitebark pine trees, I took into account if the tree was a cluster of multiple stems or a single stem. A cluster is defined as multiple stems within 10-20cm of each other. When seeds are in close proximity to others, they were likely amassed in a single caching event. Clusters were taken into consideration to reduce potential of over counting trees, since the whitebark pine stems will grow outward from a collection of seeds into a single cluster (Tomback, 2001).

Each canker found on whitebark pine trees was counted, and characterized as potential, active, or inactive, following guidelines established by Hoff (1992). Blister rust cankers were classified as potential cankers if the branch showed signs of fusiform swelling, but without obvious aecial sacs present on the branch (Figure 3.4a). Cankers were considered “active” if the sporulating cankers were breaking through the bark in distinctive orange sacs (Figure 3.4b). Finally, inactive cankers were identified by the presence of dead, cracked bark and swollen stems – testament to locations where formerly active cankers girdled the branch (Figure 3.4c).

Whitebark pine often grows as part of tree islands at the study sites. For each tree island in the study plots, length, width and height of the tallest conifer were recorded.

Shelter type was recorded along with starting conifer species, as whitebark pine has been shown to be significant in tree island initiation (Resler et al., 2005). The boundaries of tree islands were traced using a GPS for subsequent landscape analysis. If the tree island did not include whitebark pine, the same information was recorded as it is important in describing the landscape pattern. This sampling method was replicated for all quadrats.

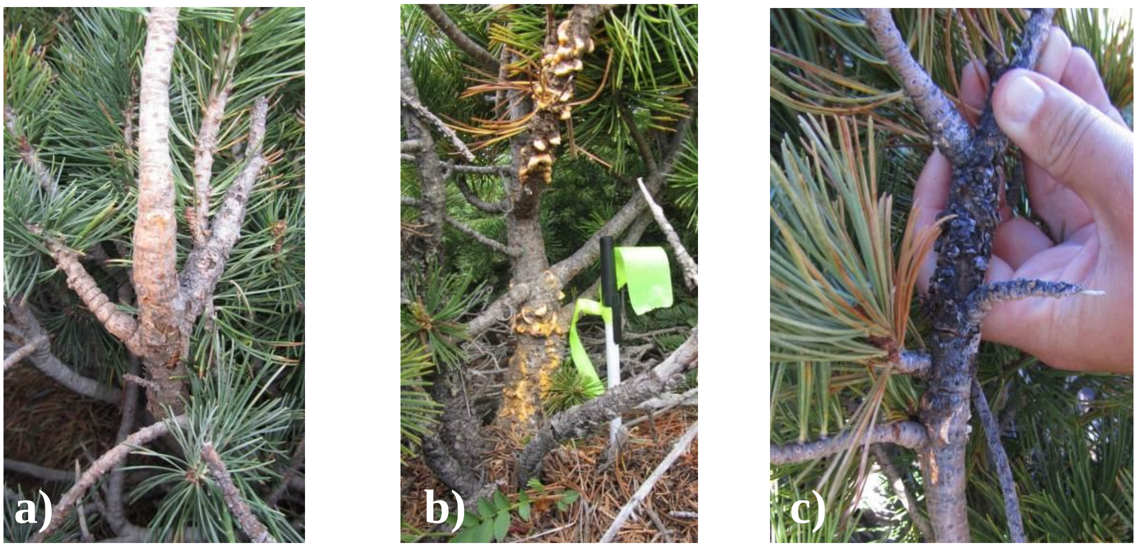


Figure 3.4: (a) Fusiform swelling on the bark indicating a potential canker; (b) two active cankers, one on the main stem and one on the branch; (c) dead, cracked bark indicating an inactive canker with an active canker below the inactive canker on branch

Characterizing Weather

The three month period during late summer and early fall is an important germination period for teliospores and basidiospores, which require high humidity to remain viable. These spores are dispersed by wind from *Ribes* to the needles of the whitebark pines (McDonald and Hoff, 2001). Two, 2-meter HOBO® weather stations were assembled at each alpine treeline study site, one on a southwest aspect and one on a northeast aspect at both locations (Figure 3.5). Each station was equipped with temperature and relative humidity sensors and an anemometer and weather vane for wind direction, wind speed, and gust speed. Data loggers on the weather stations recorded measurements every five minutes. The stations were recording for a three month period from July 12th and 17th for the Glacier stations and July 23rd for the Beartooth stations, until September 11th for the Glacier stations and September 14th for the Beartooth stations. The wind sensor on the station on the southwest aspect at Divide Mountain broke during high winds at 5:34am on August 27th, meaning data for wind speed, gust speed and direction could no longer be recorded. The weather data collected from these stations characterized the climate conditions for one growing season during the three month germination period for white pine blister rust.

Figure 3.5: Weather station on southwest aspect at Wyoming Creek

LANDSCAPE METRIC ANALYSIS

To fulfill objectives 1 and 2, I converted the quadrat data (originally collected in vector format) to a raster format for import into FRAGSTATS (v3; McGarigal et al., 2002), which uses raster layers to analyze landscape patterns. This method of vector to raster conversion was used as an alternative to the originally proposed methodology, which was to use 0.5 meter Quickbird® satellite imagery to classify tree, tundra, and rock class types at the study sites. Overall accuracy of the Quickbird imagery was below 50% for all classification methods used when compared to reference points collected from field observations, and therefore an alternate methodology was chosen.

FRAGSTATS analyzes raster imagery at the patch, class, and landscape levels to obtain landscape metric information of vegetation patterns. Patch-level metrics are calculated on every patch of a specific vegetation class. The program calculates class-level metrics on the entire class, for every class of vegetation in the imagery. Finally, landscape-level metrics are calculated on the entire landscape, with no delineation of vegetation classes.

Patch and landscape level analyses were important to summarize landscape pattern at treeline and to determine any relationships between landscape pattern and blister rust infection rates. I converted the vector data collected from the field for individual conifers and for tree island boundaries for every quadrat to raster with a cell size of 0.12 meters. This cell size was chosen based on the cell size that best represented the tree island or tree on the ground, and to avoid cells being disconnected and counted as multiple patches, as recommended by the FRAGSTATS user guidelines (McGarigal, et al., 2002). After conversion to a raster format, the raster layers for individual conifers and tree islands were reclassified to values of 0 and 1, where 0 represented non-tree and 1 represented tree classes. The raster layers for both individual conifers and tree island patches were then added together using raster calculator in ArcGIS 9.3.1 to create a single layer, and then reclassified a final time to get only values of 1 for tree pixels. This process was replicated for each of the 60 quadrats, 30 at the Divide Mountain site in Glacier National Park and 30 at the Wyoming Creek site in the Beartooth Mountains.

Once the raster layers were generated for each quadrat, I used FRAGSTATS to calculate patch contiguity, Euclidean nearest neighbor, and contagion. Due to the transformation of a vector point to a raster cell during conversion, some metrics were not accurately calculated in FRAGSTATS. To counter this inaccuracy, some metrics (patch area, patch perimeter, number of patches, and percent of landscape) were calculated from the field data using Excel following the same methods used in FRAGSTATS (Table 3.1).

Table 3.1: Summary of landscape metrics used and calculation methods

Metric	Definition and Calculation	Method
Patch Area	Measurement of patch area in square meters, calculated as length*width of individual whitebark and tree island dimensions recorded in the field; patch level metric.	Manual
Patch Perimeter	Measurement of patch perimeter in meters, calculated as 2*(length + width) of individual whitebark and tree island dimensions recorded in the field; approximation of perimeter at the patch level.	Manual
Number of Patches	Calculated by adding the total number of tree islands in the data sheets (individual and multi-tree patches) with the number of other individual non- whitebark conifer types from the shapefile of GPS conifer locations; quadrat level metric.	Manual
Percent of Landscape	Calculated from the sum of patch areas divided by quadrat area of 225m^2; quadrat level metric.	Manual
Contiguity Index	Assess the spatial connectedness, or contiguity, of cells within a grid-cell patch to provide an index of patch boundary configuration and thus patch shape; measured on a scale of 0-1 where 0 equals less connected and 1 equals most connected.	FRAGSTATS
Euclidean Nearest Neighbor	Simple measure of patch context and quantification of patch isolation; calculated using simple Euclidean geometry as the shortest straight-line distance between focal patch and its nearest neighbor; measured in meters.	FRAGSTATS
Contagion	Measure of patch aggregation on the landscape; measured on a scale of 0-100 where 0 equals maximally disaggregated patch types and 100 equals maximally aggregated, when the landscape consists of a single patch type; landscape level metric	FRAGSTATS

STATISTICAL ANALYSIS OF BLISTER RUST INTENSITY, LANDSCAPE PATTERN, AND CLIMATE CONDITIONS

Patch metrics and blister rust observations were summarized by quadrat at each study site to characterize the landscape at treeline using descriptive statistics. Data were analyzed using JMP version 8 (JMP, 2008). The data were not normally distributed, so a linear regression was not used in this analysis. Since the data did not meet the assumption of normality required for many parametric tests, nonparametric statistics were used. Spearman’s rank-order correlation coefficient analyses were used to determine if a correlation existed between each landscape metric and the dependent variable, canker density—our measure of blister rust infection. A Kruskal-Wallis one-way ANOVA was used to determine if slope aspect was a significant factor in landscape pattern development, as characterized by each landscape metric (patch area, patch perimeter, number of patches, percent of landscape, contiguity, Euclidean nearest neighbor, and contagion). Aspect was categorized by azimuthal degree into 4 categories: NW (271-360°), NE (1-90°), SE (91-180°) and SW (181-270°). A Puri and Sen nonparametric two-way ANOVA (Toothaker and Newman, 1994) determined if slope aspect, study site location (Divide Mountain or Wyoming Creek), and interactions between the two, were statistically related to blister rust infection intensity, represented by the canker density variable.

Weather data collected from the stations were summarized using descriptive statistics to portray climate patterns during the three month period that the stations were recording. The number of 6-8 hour periods with near 100% relative humidity was also determined from the data so that the conditions for teliospore germination and basidiospore production and viability could be quantified from observed data. Near 100% is somewhat arbitrary when quantifying data, so a threshold of greater than 90% for a minimum of 6-8 hours was used for this analysis (McDonald and Hoff, 2001).

Chapter 4. Results

FIELD DATA RESULTS

Field data was collected at Divide Mountain between July 8th and July 18th 2010. Elevation of sampled quadrats ranged from 2097-2261m. The proportions of aspects of sampled quadrats were 12 northeast, 10 southeast, 4 southwest and 4 northwest (Table 4.2a). Sampling occurred at Wyoming Creek between July 20th and July 26th 2010. Elevation of sampled quadrats ranged from 2961-3029m. The proportions of aspects of the 30 quadrats sampled at this site resulted in 14 northeast, 8 southeast, 4 southwest and 4 northwest (Table 4.2b).

At Divide Mountain (DM), sampling in the 30 quadrats yielded a total of 585 whitebark pines, 268 of which were individual trees and 317 were found associated with the 86 sampled tree islands. Of the 585 whitebarks sampled, 138 showed signs of infection. There were a total of 505 cankers (potential, active and inactive) and 23.59% of whitebark pine was infected among all quadrats. Whitebark pine density, calculated as the total number of whitebark pine trees sampled at the site, divided by the total area of the sampling quadrats (6750 m^2), was 86.67 trees km^{-2}. Canker density, calculated has the number of cankers divided by the total number of whitebark averaged 0.86 cankers per tree (Tables 4.1, 4.2a, and 4.3a for summary statistics).

In the 30 quadrats sampled at Wyoming Creek (WC), 323 whitebark pines were sampled, 191 of which were individual trees and 137 associated with the 62 tree islands sampled at that site. Of the 328 whitebark pines sampled, 63 showed signs of infection. There were a total of 437 cankers and 19.21% of whitebark pine was infected among the quadrats. Whitebark pine density was 47.85 km^{-2} and canker density at Wyoming Creek averaged 1.33 cankers per tree (Tables 4.1, 4.2b, and 4.3b).

Table 4.1: Summary of field sampling results per study site

Samples	**Divide Mountain**	**Wyoming Creek**
No. Whitebark Pine (WBP)	585	328
No. Individual WBP Tree Islands (TIs)	268 (45.81%)	191 (58.23%)
No. WBP in Multi-tree TIs	317 (54.19%)	137 (41.77%)
No. Multi-tree TIs	86	62
No. Other Individual Conifer Sp.	153	59
No. WBP trees km^{-2}	86.67	47.85
Total No. Patches	507	312
No. Infected WBP	138 (23.59%)	63 (19.21%)
No. Cankers	505	437
Canker Density (No. Cankers/No. WBP)	0.86	1.33

Table 4.2: Description of quadrats at Divide Mountain (a) and Wyoming Creek (b)

(a)

Quad ID	**DM1**	**DM2**	**DM3**	**DM4**	**DM5**	**DM6**	**DM7**	**DM8**	**DM9**	**DM10**	**DM11**	**DM12**	**DM13**	**DM14**	**DM15**
Elevation (m)	2229	2214	2261	2245	2215	2210	2180	2176	2155	2156	2156	2187	2189	2097	2101
Slope (°)	7	25	15	17	14	13	6	8	4	4	15	20	18	8	10
Aspect	NE	E	NW	N	S	SE	E	N	S	E	SW	E	NE	NE	N
Number of Patches	14	28	6	25	22	29	12	47	4	10	3	10	20	2	38
Patch Area (m²)															
Range	0.003 - 109.474	0.01 - 42.90	0.46 - 8.31	0.008 - 124.89	0.006 - 35.26	0.013 - 80.56	0.03 - 5.95	0.005 - 129.16	0.001 - 14.04	0.04 - 3.60	0.005	0.003 - 9.60	0.001 - 4.08	0.290	0.001 - 56.65
Mean	16.795	5.691	4.383	21.436	4.377	6.540	1.391	3.545	7.020	0.855	0.005	2.518	0.440	0.290	2.414
S.D.	40.971	11.156	5.549	50.686	10.290	20.224	2.242	20.929	9.927	1.245	0.005	3.649	1.150	0.290	9.960
Quad ID	**DM16**	**DM17**	**DM18**	**DM19**	**DM20**	**DM21**	**DM22**	**DM23**	**DM24**	**DM25**	**DM26**	**DM27**	**DM28**	**DM29**	**DM30**
Elevation (m)	2197	2224	2221	2159	2158	2150	2203	2133	2205	2190	2254	2227	2163	2165	2171
Slope (°)	15	9	8	8	16	20	16	23	11	18	18	22	4	13	8
Aspect	SE	SW	SE	NW	S	E	E	NE	NE	N	SE	NE	SE	E	SE
Number of Patches	2	4	21	14	9	6	16	21	31	45	6	30	12	17	3
Patch Area (m²)															
Range	0.02 - 0.19	0.09 - 0.97	0.06 - 32.34	0.001 - 32.04	0.02 - 245.00	0.02 - 12.99	0.01 - 101.70	0.02 - 12.00	0.01 - 96.33	0.001 - 2.91	0.01 - 0.52	0.01 - 63.63	0.03 - 12.72	0.02 - 25.38	0.22 - 12.35
Mean	0.109	0.529	4.919	3.026	50.055	4.498	19.589	0.976	5.501	0.224	0.242	5.250	2.619	2.827	6.283
S.D.	0.121	0.617	9.307	9.155	108.981	4.946	38.490	3.167	19.250	0.559	0.193	16.074	4.042	6.553	8.580

(b)

Quad ID	**WC1**	**WC2**	**WC3**	**WC4**	**WC5**	**WC6**	**WC7**	**WC8**	**WC9**	**WC10**	**WC11**	**WC12**	**WC13**	**WC14**	**WC15**
Elevation (m)	2961	2993	2999	2995	3022	3023	3016	3012	3029	3029	3011	3001	3006	2990	3002
Slope (°)	8	9	4	6	13	18	8	3	5	4	10	3	2	10	3
Aspect	NW	NE	E	NE	NE	E	N	N	SE	SE	N	N	N	E	E
Number of Patches	4	8	3	4	19	8	4	21	4	14	12	10	7	15	13
Patch Area (m²)															
Range	0.79 - 37.20	0.01 - 90.30	0.29 - 7.56	5.13 - 102.38	0.001 - 5.62	1.18 - 19.80	0.539	0.81 - 21.15	3.98 - 12.60	0.01 - 7.06	0.34 - 15.70	0.02 - 119.85	0.88 - 13.20	0.004 - 9.86	1.22 - 5.90
Mean	11.047	12.022	3.136	41.475	1.049	7.426	0.539	8.182	7.195	2.161	4.432	17.461	4.851	2.182	4.156
S.D.	17.486	31.663	3.884	46.184	1.711	6.941	0.539	7.013	4.708	2.424	6.411	45.151	4.575	3.549	2.091
Quad ID	**WC16**	**WC17**	**WC18**	**WC19**	**WC20**	**WC21**	**WC22**	**WC23**	**WC24**	**WC25**	**WC26**	**WC27**	**WC28**	**WC29**	**WC30**
Elevation (m)	2994	2989	2982	2987	2971	2969	2964	2982	2976	2992	2994	2995	2981	2981	2969
Slope (°)	7	6	10	2	7	16	9	10	12	11	6	10	13	23	8
Aspect	NE	E	E	W	W	E	NW	NE	E	E	E	NE	S	SW	NE
Number of Patches	29	15	18	4	7	4	4	22	19	4	10	8	8	4	10
Patch Area (m²)															
Range	0.004 - 14.70	0.001 - 4.41	0.03 - 8.38	0.12 - 108.10	0.004 - 6.10	0.25 - 1.09	1.44 - 5.23	0.004 - 19.44	0.004 - 1.76	1.70 - 53.68	0.01 - 20.30	0.004 - 9.00	0.61 - 89.46	0.003 - 8.18	0.01 - 12.64
Mean	2.192	0.88	1.851	36.152	2.852	0.505	3.365	2.125	0.524	20.751	5.688	1.648	22.538	4.048	4.386
S.D.	4.004	1.95	2.427	50.819	2.775	0.393	2.159	4.748	0.688	23.956	6.331	3.004	33.996	3.35	4.912

Table 4.3: Characteristics of cankers by quadrat at Divide Mountain (a) and Wyoming Creek (b)

(a)

Quad ID	**DM1**	**DM2**	**DM3**	**DM4**	**DM5**	**DM6**	**DM7**	**DM8**	**DM9**	**DM10**	**DM11**	**DM12**	**DM13**	**DM14**	**DM15**
No. of Cankers	19	10	1	6	12	43	9	22	13	5	0	7	9	0	40
Canker Density (#cankers per #trees)	1.46	0.34	0.50	0.20	0.41	1.39	0.60	0.28	0.76	0.63	0.00	0.64	0.64	0.00	0.78
No. Infected Trees	1	2	1	4	4	11	3	12	4	3	0	3	3	0	8
No. of Whitebark	13	29	2	30	29	31	15	79	17	8	1	11	14	1	51
Percent Infected Trees	7.69	6.9	50	13.33	13.79	35.48	20	15.19	23.53	37.5	0	27.27	21.43	0	15.69
Quad ID	**DM16**	**DM17**	**DM18**	**DM19**	**DM20**	**DM21**	**DM22**	**DM23**	**DM24**	**DM25**	**DM26**	**DM27**	**DM28**	**DM29**	**DM30**
No. of Cankers	0	1	34	34	36	12	62	22	40	7	0	16	9	24	12
Canker Density (#cankers per #trees)	0.00	0.50	2.13	1.62	4.00	1.71	2.95	1.29	0.83	0.18	0.00	0.57	0.64	1.09	3.00
No. of Infected Trees	0	1	5	10	7	2	10	8	12	4	0	6	4	7	3
No. of Whitebark	2	2	16	21	9	7	21	17	48	38	5	28	14	22	4
Percent Infected Trees	0	50	31.25	47.62	77.78	28.57	47.62	47.06	25	10.53	0	21.43	28.57	31.82	75

(b)

Quad ID	**WC1**	**WC2**	**WC3**	**WC4**	**WC5**	**WC6**	**WC7**	**WC8**	**WC9**	**WC10**	**WC11**	**WC12**	**WC13**	**WC14**	**WC15**
No.of Cankers	0	4	20	80	5	13	0	0	14	3	2	3	0	0	0
Canker Density (#cankers per #trees)	0.00	0.33	6.67	5.71	0.28	1.44	0.00	0.00	2.80	0.19	0.20	0.09	0.00	0.00	0.00
No.of Infected Trees	0	3	1	9	1	3	0	0	3	2	1	2	0	0	0
No. of Whitebark	4	12	3	14	18	9	1	0	5	16	10	34	1	12	0
Percent Infected Trees	0.00	25.00	33.33	64.29	5.56	33.33	0.00	0.00	60.00	12.50	10.00	8.82	0.00	0.00	0.00
Quad ID	**WC16**	**WC17**	**WC18**	**WC19**	**WC20**	**WC21**	**WC22**	**WC23**	**WC24**	**WC25**	**WC26**	**WC27**	**WC28**	**WC29**	**WC30**
No. of Cankers	6	0	8	22	1	1	0	0	0	14	14	1	210	12	4
Canker Density (#cankers per #trees)	0.18	0.00	0.38	1.29	0.17	0.25	0.00	0.00	0.00	2.00	1.27	0.11	16.15	3.00	0.33
No. of Infected Trees	4	0	5	5	1	1	0	0	0	3	3	1	9	3	3
No. of Whitebark	33	14	21	17	6	4	4	17	17	7	11	9	13	4	12
Percent Infected Trees	12.12	0.00	23.81	29.41	16.67	25.00	0.00	0.00	0.00	42.86	27.27	11.11	69.23	75.00	25.00

Landscape metrics were summarized to understand vegetation pattern at both treeline sites. This data is important to compare the similarities and differences in pattern at both sites and what factors may be influencing the landscape (Table 4.4).

Table 4.4: Summary of landscape metric analysis

Landscape Metric	**Divide Mountain**	**Wyoming Creek**
Patch Area (m^2)		
Range*	0.001 - 245.00	0.001 - 119.85
Mean	4.76	5.65
S.D.	20.10	15.74
Patch Perimeter (m)		
Range*	0.08 - 84.00	0.08 - 45.20
Mean	4.17	6.21
S.D.	8.45	7.50
Number of Patches	507	312
Percent of Sampled Landscape	2.73	3.51
Patch Contiguity (0-1)		
Mean	0.27	0.29
Euclidian Nearest Neighbor (m)		
Range	0.25 - 11.33	0.27 - 11.35
Mean	1.28	1.91
S.D.	1.45	1.73
Contagion (0-100)		
Mean	85.68	87.81

**Minimum values represent calculation of seedling dimensions*

CORRELATION BETWEEN LANDSCAPE PATTERN AND BLISTER RUST INFECTION

I found that a significant, positive correlation existed between the patch area and blister rust canker density at both study sites (DM Spearman's r_s=0.59, $P<0.001$ and WC r_s=0.43, $P<0.05$). The patch perimeter metric was also significantly correlated with canker density at both study sites (DM $r_s=0.58$, $P<0.001$ and WC $r_s=0.43$, $P<0.05$) as well as the percent of landscape metric (DM $r_s=0.51$, $P<0.01$ and WC $r_s=0.43$, $P<0.05$). The only other landscape metric found to be significant at Divide Mountain was patch contiguity ($r_s=0.51$, $P<0.01$). At Wyoming Creek, the only landscape metric found to be significant was number of patches ($r_s= -0.41$, $P<0.05$). All other metrics were not significantly correlated with blister rust canker density.

To determine if landscape pattern was influenced by slope aspect, a Kruskal-Wallis one-way analysis of variance tested the relationship between quadrat aspect (factor with four categories: NW, NE, SE, and SW) each landscape metric (patch area, patch perimeter, number of patches, percent of landscape, contiguity, Euclidean nearest neighbor, and contagion). Results of the tests found that aspect is not significant in landscape pattern development, quantified by landscape metrics. Results of the Puri and Sen non-parametric, two-way ANOVA found that neither aspect, study site, nor the interaction of aspect and study site were significant in blister rust canker density at the $P<0.05$ level. However, study site (Puri and Sen test statistic= 3.16, df=1) and the interaction between study site and aspect (Puri and Sen test statistic= 6.92, df=3) were slightly significant at the $P<0.1$ level.

CLIMATE CONDITIONS AT ALPINE TREELINE

Descriptive statistics were used to summarize the climate conditions recorded by the weather stations at both study sites. The results reveal similarities in variables recorded on the same aspects and differences in the variables recorded between both study sites. The southwest aspects tend to have higher relative humidity and wind speed than the northeast aspects at both study sites (Table 4.5).

Analysis of hourly relative humidity averages found multiple periods of time at each weather station where there was at least 90% relative humidity for a minimum of six hours. In most cases, the same time periods and durations were recorded at both stations on opposing aspects, with the exception of the Divide northeast station that did not reach the RH threshold at the same time that the southwest station did (Table 4.6).

Table 4.5: Summary of climate variables recorded from weather stations

Site	**Divide NE**	**Divide SW***	**Wyoming C. NE**	**Wyoming C. SW**
Temperature (°C)				
Max	22.3	22.6	22.1	21.0
Min	-1.4	-1.7	-8.6	-7.9
Range	23.6	24.3	30.7	29.0
Mean	9.7	9.6	9.0	9.0
S.D.	5.2	5.5	5.4	5.2
Humidity (%)				
Max	94.9	96.1	95.0	99.0
Min	18.7	14.6	17.0	13.6
Range	76.2	81.5	78.0	85.4
Mean	64.4	63.0	55.6	54.7
S.D.	18.2	20.7	19.8	20.8
Wind Speed (km/h)				
Range	0 - 35.4	0 - 59.4	0 - 38.1	0 - 45.4
Mean	7.9	9.3	9.8	8.9
S.D.	4.7	9.2	6.0	8.0
Gust Speed (km/h)				
Range	0 - 88.8	0 - 84.8	0 - 70.8	0 - 76.1
Mean	18.0	14.8	18.0	17.9
S.D.	11.1	13.5	10.3	12.6

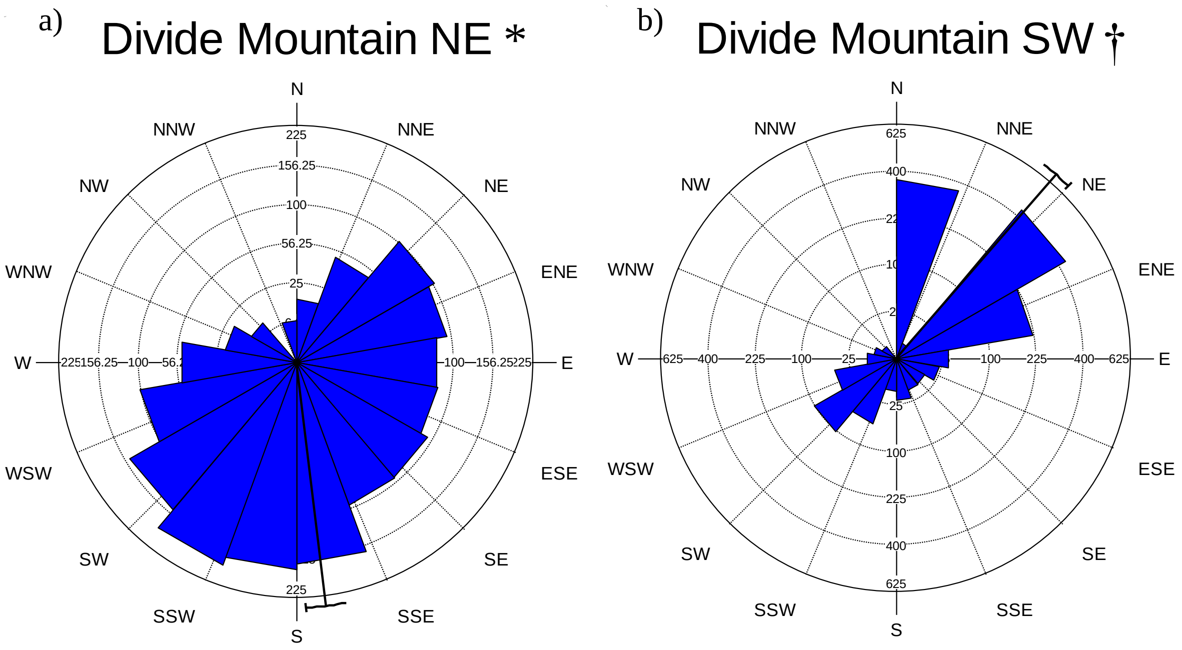
**Wind sensor broke during high winds on the morning of August 27, 2010*

Table 4.6: Summary of periods when relative humidity (RH) was above 90%

Date/Time	Mean RH (%)	Duration (Hrs)	Date/Time	Mean RH (%)	Duration (Hrs)
Divide NE			**Divide SW**		
7/27/2010 0:40	92.79	8	7/27/2010 0:34	93.59	7
8/3/2010 2:40	93.05	35	8/3/2010 2:34	93.55	34
8/12/2010 18:40	93.41	44	8/12/2010 18:34	94.92	45
8/29/2010 2:40	91.07	9	8/29/2010 2:34	91.81	20
			9/1/2010 4:34	91.15	7
			9/5/2010 17:34	92.25	7
9/8/2010 6:40	92.15	7	9/8/2010 5:34	92.76	8
9/8/2010 17:40	93.50	34	9/8/2010 18:34	94.93	34
Wyoming C. NE			**Wyoming C. SW**		
8/3/2010 21:56	92.28	7	8/3/2010 20:24	94.32	8
8/4/2010 18:56	93.55	8	8/4/2010 17:24	95.59	10
8/14/2010 16:56	93.18	16	8/14/2010 15:24	96.18	15
8/29/2010 23:56	92.54	12	8/29/2010 23:24	95.52	12

Analysis of predominant wind direction at the Divide Mountain northeast station reveals that there is more variation in wind directions at that site compared to the Wyoming Creek stations (Figure 4.1a-d). There is a significant difference in the predominant wind direction at the Divide Mountain southwest station compared to the pattern recorded at the northeast station, and compared to the similarities between aspects at the stations at the Wyoming Creek site. This could be due to an incomplete data set recorded when the wind sensor broke before sampling had concluded.

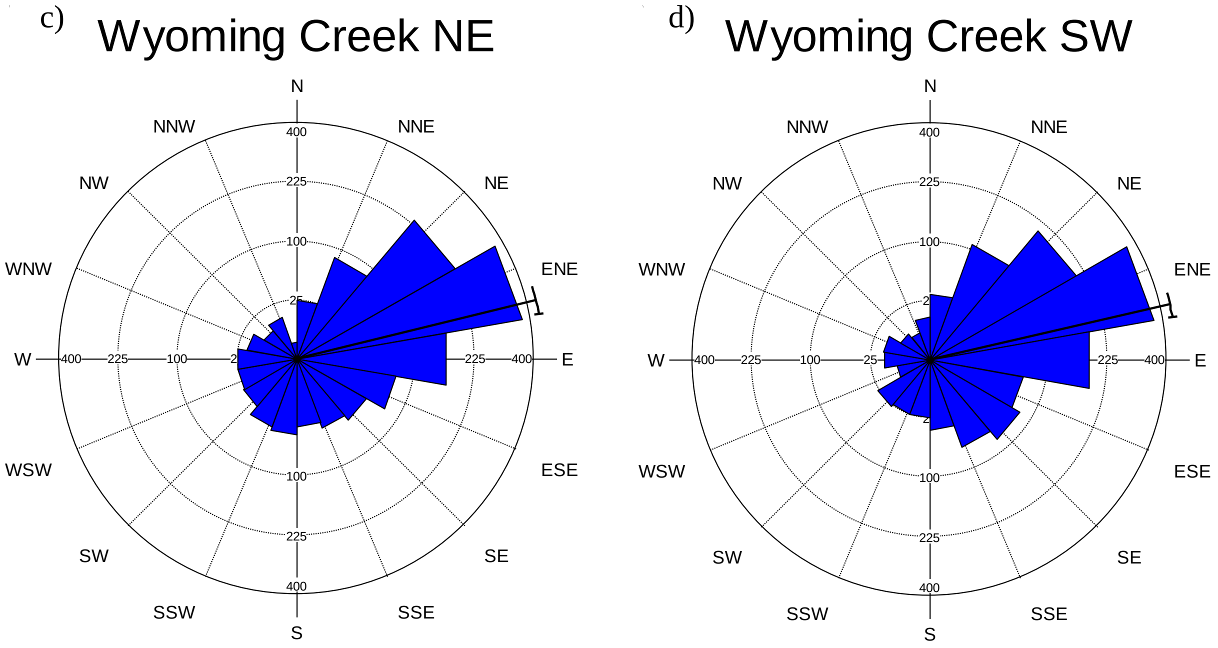
Figure 4.1: Rose diagrams of predominant wind directions by aspect at Divide Mountain (a and b) and Wyoming Creek (c and d). Numbers on axes indicate number of records (Wind roses created using Oriana 3.21, 2010)


a) Divide Mountain NE *

b) Divide Mountain SW †

*See Appendix B for modified diagram representing the end of data recording on August 27

† Wind sensor broke August 27, 2010


c) Wyoming Creek NE

d) Wyoming Creek SW

Chapter 5. Discussion

The goal of this research was to obtain a better understanding of the relationship between landscape pattern and white pine blister rust infection at alpine treeline and if geographical differences in study site location influenced landscape pattern and infection. Furthermore, a secondary goal was to understand the climate conditions at alpine treeline during the three month germination period of the blister rust life cycle. I found that although whitebark pine is an important treeline component at both Divide Mountain and the Beartooth Plateau, there were several geographic differences and similarities between the two sites with respect to landscape pattern, blister rust infection, and climate.

SUMMARIZING WHITEBARK PINE INCIDENCE AND LANDSCAPE PATTERN AT ALPINE TREELINES AT DIVIDE MOUNTAIN AND THE BEARTOOTH PLATEAU

Field sampling revealed that the total number of whitebark pine and whitebark pine density, as measured in the sampling quadrats, is higher at Divide Mountain than Wyoming Creek, indicating that whitebark pine is a more important treeline component at Divide Mountain. Whitebark pine at Divide Mountain was found to be part of a tree island 54.91% of the time, which indicates that the role of whitebark pine at Divide Mountain is important in tree island composition. At Wyoming Creek, whitebark pine was found as an individual tree the majority of the time (58.23%), possibly indicating that tree island formation is not as frequent at this site with whitebark pine as the colonizing species. The higher rates of individual whitebark pines at Wyoming Creek may also be influenced by the fewer number of trees sampled at that site compared to Divide Mountain.

Landscape metric analysis revealed that the landscape pattern at both alpine study sites was similar, even though the two sites are separated by considerable latitude. Specifically, tree island size, connectivity, Euclidean nearest neighbor and contagion at the two sites were comparable. This finding possibly indicates that the difference in latitude between the two sites does not have a significant effect on the growth patterns of alpine treeline and therefore pattern and process is likely not influenced by latitude, but more sites would need to be sampled to determine this relationship.

Tree island size is important at treelines because patch size can affect positive feedback mechanisms, whereby trees can alter the microclimate of their environment, and thus perpetuate establishment (and pattern) at treelines (Alftine and Malanson 2004). Average patch area was similar at both study sites. This finding reveals that treeline vegetation pattern and growth habits are similar at both treeline sites in the northern Rocky Mountains. Similarities between average patch perimeter and percent of landscape also confirm this finding that vegetation pattern, specifically patch area and functions of area, has similar characteristics at both treeline sites.

Connectivity is another important measurement in landscape ecology and landscape pathology studies (Turner et al., 2001; Ellis et al., 2010). Average patch contiguity at both Divide Mountain and Wyoming Creek was fairly low (0.27 and 0.29 respectively) on a scale of 0-1 in connectedness. Low contiguity indicates that spatial connectedness of patches is not very high, which could be a result of competition and limited resources in the alpine environment. The patchy nature of treeline is a result of many processes, such as dispersal, establishment, and growth conditions, that interact in the treeline ecotone (Malanson et al., 2007). Low connectivity and patchiness could facilitate disease spread because the patchy nature creates conditions for transmission of blister rust since it is a wind borne pathogen.

Euclidean nearest neighbor has been used in previous studies to summarize landscape pattern and understand disease spread and transport vectors on the landscape (Ellis et al., 2010). Euclidean nearest neighbor analysis found that patches at Divide Mountain and Wyoming Creek were on average fairly close to each other (1.28m and 1.91m respectively). Euclidean nearest neighbor, as used in this study, may have been influenced by its calculation being based on the sampled quadrats only, and not the entire landscape. The importance of the Euclidean nearest neighbor metric could change if proximity distance increases as sample area increases, since disease vectors may be modified if the average distance between patches increased. However, the short average distances found in this study may result in reduced distance a spore would have to travel with wind before infecting a tree. Average contagion at Divide Mountain and Wyoming Creek was fairly high (85.68 and 87.81 out of 100, respectively) indicating that the vegetation is well aggregated, or clustered.

RELATIONSHIP BETWEEN LANDSCAPE PATTERN AND BLISTER RUST INFECTION AT TREELINE

Field sampling found a slightly greater percentage of infected trees (23.59%) at Divide Mountain compared to Wyoming Creek (19.21%). Though there were more total cankers at Divide Mountain, whitebark pine trees at Wyoming Creek have a higher canker density (average number of cankers per tree; WC=1.33; DM=0.86). Higher canker density at Wyoming Creek could be a result of larger tree islands on average at that site compared to Divide Mountain. Since blister rust is a wind borne pathogen, a larger surface area of a patch collects more spores leading to higher canker densities per tree. Higher canker densities could result in more rapid mortality rates, as more cankers per tree mean that the infection could soon spread to the main stem if it has not already, and kill the tree.

Results of Spearman's Rank Correlation analysis found that only patch area ($P<0.001$), patch perimeter ($P<0.001$), percent of landscape ($P<0.01$), and patch contiguity ($P<0.01$) were metrics that had a significant relationship to canker density and blister rust infection at Divide Mountain. At Wyoming Creek, only patch area ($P<0.05$), patch perimeter ($P<0.05$), percent of landscape ($P<0.05$), and number of patches ($P<0.05$) were metrics with a significant relationship to canker density and blister rust infection. Identification of patch area as significant at both study sites confirms previous findings that patch area is significant for higher blister rust infection rates (Resler and Tomback 2008). Both patch perimeter and percent of landscape, which were found to be correlates of infection at Divide Mountain and Wyoming Creek, are functions of patch area. The higher canker density at Wyoming Creek is likely due to the comparably few number of sampled whitebark pine. The lack of statistical correlations between blister rust incidence and the other metrics used in this, and previous landscape pathology studies, indicates that some aspects of landscape pattern may not be related to blister rust infection rates (Ellis et al., 2010, Grilli, 2010).

Results from the Kruskal-Wallis one way ANOVA found no significance between slope aspect and landscape metrics (patch area, patch perimeter, number of patches, percent of landscape, contiguity, Euclidean nearest neighbor, and contagion). These findings reveal that vegetation pattern is not necessarily influenced by aspect. Results of the Puri and Sen two-way ANOVA found a slight significance ($P<0.1$) between study site, and the interaction between study site and aspect, and canker density. This finding does not support previous research that aspect is a significant factor in canker density at alpine treeline (Smith et al., 2011). This could also indicate that a latitudinal gradient between study sites is not a significant factor in blister rust infection rates, as there was no difference between sites, but more data would need to be collected to determine this relationship and if latitude is a factor.

Predicting blister rust infection in whitebark pine is a complex task. This research analyzed the relationship between infection and landscape pattern at treeline, as opposed to the relationship between disease and host distribution. As seen in many plant diseases, a complex interaction must occur between three components that favor disease, pathogen, host, and environment as visualized by the “disease triangle” in pathology studies (Agrios, 2005; p. 79). These complex interactions of blister rust infection require the appropriate factors before infection will occur: the host—whitebark pine, the pathogen—blister rust spores from alternate hosts in surrounding areas, and environment—the conditions required for viability and transmission. Not only do certain aspects of landscape pattern influence infection rates among whitebark pine at treeline, but the pattern of alternate host locations is also important. Simple visual observations of areas in and around our quadrats found the presence of *Ribes* as well as other less common alternate hosts such as sickletop lousewort and Indian paintbrush, indicating that the source of spores is within range and could infect any viable whitebark recipient in the area. Genetic resistance to blister rust is rare in whitebark pine and it has been suggested that because of interactions between spore dispersal and microclimate conditions, non-infected trees are “escapes” of infection genetically resistant (Hoff et al., 2001).

CLIMATE CONDITIONS AT ALPINE TREELINE AND THE LIFECYCLE OF BLISTER RUST

Descriptive analyses of the weather station data revealed that climate conditions varied by aspect and by study site. Slight differences in temperature and relative humidity patterns between study sites could be a factor of differences in synoptic weather patterns between the two sites, as they are separated by considerable distance. These synoptic weather patterns could explain the similarities in maximum temperature among the stations, even though the Wyoming Creek stations were at a higher elevation, and the lesser amounts of moisture and high relative humidity conditions at that site, since the Beartooth area is drier than the Glacier area. Synoptic frontal boundaries dividing the two sites are evident when looking at the data on a daily basis where recorded wind directions were easterly for the northern Divide Mountain site and southerly for the southern Wyoming Creek site, indicating differences in weather patterns between study sites.

Other similar patterns in climate conditions occur with relative humidity between aspects, where the northeast stations at both sites have higher average percent relative humidity, but the southwest stations have more variability in percent relative humidity. Wind speed and gust speed also exemplifies similar patterns between the northeast and southwest aspects at both sites where higher speeds were recorded on the southwest aspects, with the exception of Divide Mountain southwest where the sensor broke two weeks before the end of the sampling period. High winds and relative humidity at these sites are crucial for dispersal of basidiospores during the late summer months when constant high humidity was recorded, keeping the basidiospores viable and carrying them up to 300 meters to the needles of whitebark pine trees (McDonald and Hoff, 2001).

According to McDonald and Hoff (2001), near 100% relative humidity (RH) is required for a 6-8 hour period in late summer-early fall to trigger teliospore germination which then generates basidiospores that also require constant high humidity to stay viable as they are carried by the wind to whitebark pines. Analysis of relative humidity at all four stations resulted in six periods of time where the conditions were above 90% RH for at least six hours at the Divide northeast station and eight periods of time at the Divide southwest station. At Wyoming Creek, there were four periods of time at both stations where the same conditions were recorded for relative humidity and duration of time. The differences in RH between study sites may also be attributed to a geographic difference between the sites, but more data is needed to determine that relationship. This finding indicates that the higher infection rates at Divide Mountain may be influenced by more frequent periods of high RH observed at that site, which is required by blister rust for germination and survival. Kendall and Keane (2001) found higher mortality rates of whitebark pine due to blister rust in the Glacier area compared to the Beartooth area. These higher mortality rates could be a result of the differing relative humidity conditions between the sites, as indicated in this study.

Another significant finding that there were two periods when the southwest aspect reached this threshold and the northeast aspect did not may indicate a pattern of higher average relative humidity on southwest aspects compared to northeast aspects. This may indicate that southwest aspects have higher average relative humidity during the three month period than northeast aspects, since both sites exhibited higher average relative humidity on southwest aspects.

Observations of prolonged periods of high relative humidity are significant to the life cycle of blister rust at alpine treeline. Previous research (Campbell and Antos, 2001) has suggested that the conditions at alpine treeline are too harsh and cold for blister rust to remain viable. However, the findings of this study, as obtained through field observations of infection and weather conditions, reveal that blister is active at alpine treeline and the conditions are present for the disease to reproduce and spread throughout the alpine treeline ecotone.

LIMITATIONS

Since the data were non-normal, I was unable to use a linear regression model to analyze the data, so simple correlation analyses were used to determine which landscape metrics were significantly correlated with blister rust infection. The most significant limitation to this study was the issues with classification methods and accuracy from satellite imagery analysis. Neither a 0.5 meter panchromatic image nor a 2.4 meter multispectral image could be classified accurately above 50%. This is unacceptable for a study of this kind, as the target of analysis is at the individual tree level. However, the alternative method did provide meaningful results and was a viable method for analysis.

Characterizing the climate of treeline is a challenge due to the harsh conditions. As this data only represents a three month period, it only gives us a glimpse into the conditions during a single season, and therefore does not consider periodic climate cycles that have been shown to affect treeline dynamics, such as the Pacific Decadal Oscillation (PDO) which has been tied to increased snowfall and seedling establishment pulses during the negative phase (Alftine and Malanson, 2004). Seasonal data is still very useful and a good beginning into describing the climate conditions, but further research and extended time that the weather stations are assembled in the field would provide a more complete understanding of the relationship between blister rust infection and climate at alpine treeline.

Chapter 6. Conclusion

Blister rust is a very active disturbance agent at the alpine treeline ecotone in the northern Rocky Mountains. Analysis of landscape metrics found that landscape pattern at alpine treeline is similar at both treeline sites, indicating that latitude is not a factor in landscape pattern. Using landscape metrics to determine which aspects of landscape pattern were significant in higher infection rates found that there is variability between sites as to which metrics are important in blister rust infection at treeline. Analysis of weather data found that there was a difference in weather conditions between sites. This study also revealed that relative humidity during the recording period was higher overall at Divide Mountain where there was more infection of whitebark pine. As the stations are assembled in future field seasons, the data will provide an opportunity to compare conditions during this three month germination period and hopefully find similar patterns that will help to better understand how the life cycle continues in alpine treeline conditions.

Landscape analysis helps better understand how landscape pattern is influenced by processes at treeline, such as limited resources, difficult growing conditions, and topographic influences (e.g. Resler, 2006; Malanson et al., 2007; Elliott and Kipfmueller, 2010). Several studies in landscape ecology and landscape pathology have shown clear relationships between landscape pattern and the process of disease spread (e.g. Turner et al., 2001; Holdenreider, et al., 2004; Condenso and Meentemeyer, 2007; Ellis et al., 2010). However, as this study shows, the landscape pattern, as measured here may not influence blister rust-infection of whitebark pine to the degree originally thought. It is important to continue researching the relationships between landscape and disease in whitebark pine and other keystone species in future studies (Tomback et al., 2001; Ellison et al., 2005).

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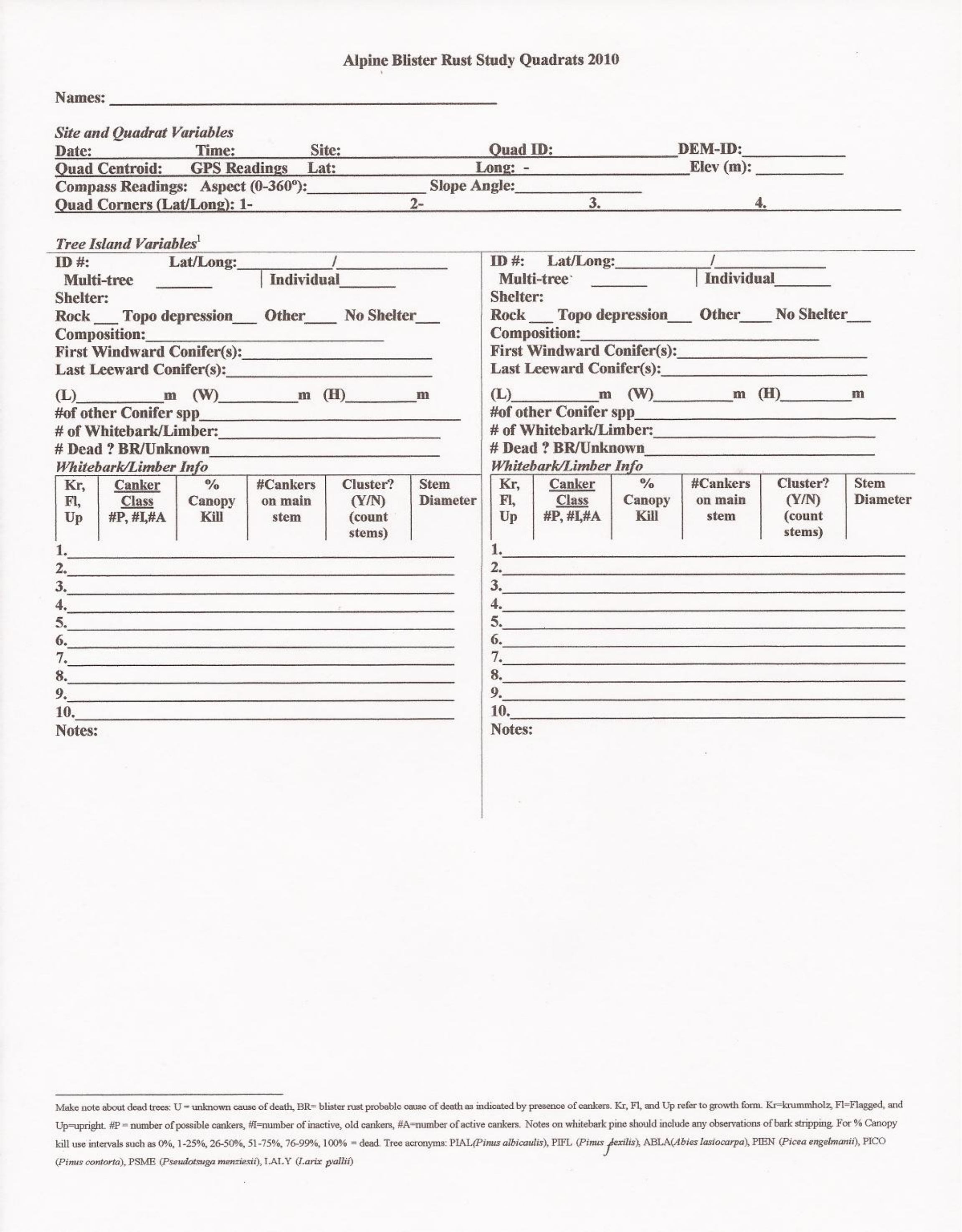
Appendix A. Example of field data sheet



Alpine Blister Rust Study Quadrats 2010

Names: ______________________________

Site and Quadrat Variables

Date: Time: Site: Quad ID: __________ **DEM-ID:** __________

Quad Centroid: GPS Readings Lat: Long: - __________ **Elev (m):** __________

Compass Readings: Aspect (0-360°): __________ **Slope Angle:** __________

Quad Corners (Lat/Long): 1- 2- 3. 4.

Tree Island Variables[1]

ID #: Lat/Long: ________/________

Multi-tree ______ | **Individual** ______

Shelter:

Rock ___ Topo depression___ Other___ No Shelter___

Composition: ______________________

First Windward Conifer(s): ______________________

Last Leeward Conifer(s): ______________________

(L)________**m (W)**________**m (H)**________**m**

#of other Conifer spp ______________________

# of Whitebark/Limber: ______________________

 # Dead ? BR/Unknown ______________________

Whitebark/Limber Info

Kr, Fl, Up	Canker Class #P, #I,#A	% Canopy Kill	#Cankers on main stem	Cluster? (Y/N) (count stems)	Stem Diameter

1.

2.

3.

4.

5.

6.

7.

8.

9.

10.

Notes:

ID #: Lat/Long: ________/________

Multi-tree ______ | **Individual** ______

Shelter:

Rock ___ Topo depression___ Other___ No Shelter___

Composition: ______________________

First Windward Conifer(s): ______________________

Last Leeward Conifer(s): ______________________

(L)________**m (W)**________**m (H)**________**m**

#of other Conifer spp ______________________

# of Whitebark/Limber: ______________________

 # Dead ? BR/Unknown ______________________

Whitebark/Limber Info

Kr, Fl, Up	Canker Class #P, #I,#A	% Canopy Kill	#Cankers on main stem	Cluster? (Y/N) (count stems)	Stem Diameter

1.

2.

3.

4.

5.

6.

7.

8.

9.

10.

Notes:

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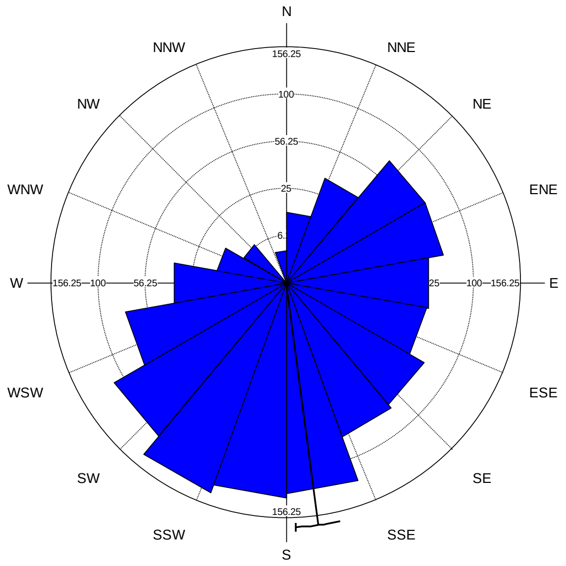
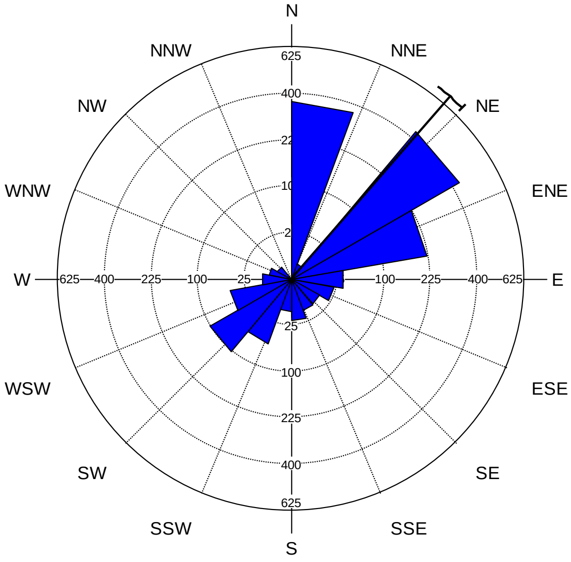
[1] Make note about dead trees: U = unknown cause of death, BR= blister rust probable cause of death as indicated by presence of cankers. Kr, Fl, and Up refer to growth form. Kr=krummholz, Fl=Flagged, and Up=upright. #P = number of possible cankers, #I=number of inactive, old cankers, #A=number of active cankers. Notes on whitebark pine should include any observations of bark stripping. For % Canopy kill use intervals such as 0%, 1-25%, 26-50%, 51-75%, 76-99%, 100% = dead. Tree acronyms: PIAL(*Pinus albicaulis*), PIFL (*Pinus flexilis*), ABLA(*Abies lasiocarpa*), PIEN (*Picea engelmanii*), PICO (*Pinus contorta*), PSME (*Pseudotsuga menziesii*), LALY (*Larix lyallii*)

Appendix B. Modified wind direction data


Divide Mountain NE - Modified


Divide Mountain SW

The predominant wind direction patterns at Divide Mountain were not similar when comparing the northeast and southwest aspects. Since the wind sensor on the southwest aspect broke on August 27th, 2010 before sampling was complete, I created another wind rose diagram to represent the same time period for the northeast station to compare and determine if the same, random wind pattern was evident on the northeast station. When comparing the modified northeast wind rose to the southwest wind rose, the wind pattern is still very different and did not change much at all when compared to the non-modified wind rose. By comparing the wind roses representing the same dates, it can be inferred that the anomalies and sporadic wind direction changes on the southwest aspect are not due to the shorter sampling period at that station, but could be due to fine scale topographic influences.