Modeling Blister Rust Incidence in Whitebark Pine at Northern Rocky Mountain Alpine Treelines: A Geospatial Approach

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ABSTRACT

The status of whitebark pine (*Pinus albicaulis*), a foundation and keystone species and a pioneer establisher at alpine treeline, is threatened by the invasive and exotic fungal pathogen (*Cronartium ribicola*) that causes white pine blister rust in five-needled pines. Originally thought to be limited to moderate environments, the disease is now found extensively throughout colder and dryer regions east of the Continental Divide, including alpine treeline. My research objective was to determine how blister rust infection of treeline whitebark pine varies across Glacier National Park. I present findings from field sampling conducted in July 2008 in Glacier National Park, Montana. Thirty plots were randomly placed at 6 different treeline study sites on the eastern slopes of the Continental Divide. Vegetative and geomorphic characteristics, along with presence/absence and level of blister rust intensity, were detailed within each plot. Vegetation measurements included conifer composition, tree island dimensions and windward growth patterns, evidence and intensity of blister rust, as well as shelter type. Field-measured topographic characteristics included elevation, aspect, and slope. In addition, high resolution GPS-derived DEMs were created at each plot in order to model the land surface and calculate detailed environmental variables in a GIS. Environmental and blister rust intensity variables were used to determine spatial correlates of blister rust infection at treeline. The resulting blister rust prediction model ($P < 0.001$, $F(4,25) = 6.79$, $R^2 = 0.52$, Adjusted $R^2 = 0.44$) suggests that areas exhibiting increased wind speed, northwest facing slopes, high flow accumulation rates, and close proximity to perennial streams have a higher likelihood of blister rust intensity, specifically total canker density. Results of this research may contribute to the understanding of the dynamics of this disease, and prove useful in whitebark ecosystem management and conservation.

Dedication

For my mom – the first to believe in me.

For John – whose humor kept me sane.

For my cats – who kept my lap warm on many a late working night.

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My decision to go back to school after a long hiatus proved to be one of the best decisions I have made in my life. The transition from a professional work life to academia was a daunting task, and unfamiliar territory. I was lucky to have the encouragement and support from so many. It is amazing what you can do when colleagues, friends, and family believe in you.

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Fieldwork was a big component of this research study. Conducting the vegetation sampling and GPS collection was a huge task in a short amount of time. Thank you to Lynn Resler, Amos Desjardins, Allisyn Hudson-Dunn, and Cyndi Smith for hiking all those miles with me through grizzly territory in Glacier N.P., and to Matt Foley for his help in my GPS pilot Study in Blacksburg. Fieldwork was funded through a College of Natural Resources Virginia Tech Seed Grant awarded to Dr. Lynn Resler and Dr. Bill Carstensen, and a research award I received from the Graduate Research and Development Program.

It seems that no GIS study is without technical difficulty, software bugs, and setbacks, and my study was certainly no exception. I spent countless hours researching ESRI forum threads and thanks to the GIS community, I found many resolutions. Pat Donovan, a great friend and GIS expert, was an excellent resource in spatial interpolation and geostatistical analysis-related trouble shooting. We bounced many a GIS idea off each other during this study. Katherine Smith provided the LiDAR data for my pilot study. I also appreciate the help I received with various GIS/LiDAR related technical questions from Peter Sforza, Steve Prisley, Valerie Thomas, Thomas Dickerson, and Andrew Foy.

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Chapter 1. Introduction

Evidence indicates that climate change is influencing tree growth patterns at alpine treelines worldwide (Lloyd and Graumlich, 1997; Dullinger et al., 2004). Given results of paleoreconstructions of treelines (e.g. Lloyd and Graumlich, 1997), one predicted response of trees to climate warming is advancement of subalpine vegetation to higher elevations (Dullinger et al., 2004; Körner and Paulsen, 2004; Bekker, 2005; Baker and Moseley, 2007). Thus, tree elevation serves as an indicator of climate conditions and other environmental and biological conditions. Whitebark pine (*Pinus albicaulis*) is a pioneer establisher at alpine treeline and may facilitate the growth of successive alpine tree species. Tolerant of the harsh, cold environment found at high elevations, whitebark pine serves an important role as a tree island initiator (Ogilvie, 1990; Resler and Tomback, 2008; Resler and Fonstad, 2009), provides food for wildlife (Kendall and Arno, 1990) and stabilizes soil, rock and snowpack (Arno and Hoff, 1989). However, since the early 1900s, the introduced disease, white pine blister rust, caused by the fungal pathogen *Cronartium ribicola*, has devastated populations of whitebark pine. Given its critical role as a keystone and foundation species (Kendall and Arno, 1990), the decline of whitebark pine populations has serious implications for treeline establishment in the alpine treeline ecotone (Tomback and Resler 2007).

White pine blister rust incidence in whitebark pine populations was thought to be more prevalent in the milder, moist climates (Van Arsdel et al., 1956) west of the Continental Divide and typically found within subalpine ecosystems (Hoff and Hagle, 1990; Campbell and Antos, 2000). Within the last decade, however, research has indicated that this disease is found in the dryer, colder regions, east of the Continental Divide in the Rocky Mountains (Resler and

Tomback, 2008). Evidence of blister rust incidence in the highest extents of the alpine treeline ecotone is limited within the literature.

The goal of this research was to determine environmental correlates of blister rust infection incidence and intensity in whitebark pine located within the alpine treeline ecotone on the eastern slopes of Glacier National Park, Montana (GNP). The specific objectives of this research were to:

1) Characterize geographic variation in the disease incidence at sampling locations across a North-South transect of the Park, east of the Continental Divide.

And

2) Determine how blister rust infection rates in treeline whitebark pine is influenced by key environmental variables (i.e., topographic characteristics, proximity to alternate host species, proximity to water) at 6 alpine treeline locations in GNP through field data collection and spatial analysis.

This research has both basic and applied significance. From a basic research standpoint, the focus of this research will be to examine the extent of blister rust in cold arid alpine ecotones, and to determine what environmental variables (if any) may influence this disease. From an applied research standpoint, understanding the patterns and processes of white pine blister rust may help predict where the disease may spread and improve preventive management strategies applied by government and conservation organizations. My primary research question is: What are the spatial correlates of blister rust intensity and proportion in whitebark pine at alpine treeline? Three key geographic components I will examine in this research are spatial pattern, physical geography, and GIS technologies.

Chapter 2. Literature Review

Whitebark pine populations are being threatened by the exotic, invasive fungal pathogen white pine blister rust, which was introduced to North America in the early 1900s (Keane and Arno, 1993; Kendall, 1994; Tomback et al., 1995; Campbell and Antos, 2000; McDonald et al., 2006). Whitebark pine is an important foundation and keystone species not only in subalpine forest ecosystems, but also in alpine treeline ecosystems in the Northern Rocky Mountains (Tomback et al., 1995; Murray et al., 2000; Ellison et al., 2005). Whitebark pine is an important biogeographic component of treeline, therefore the presence of blister rust in whitebark pine at alpine treeline has implications for treeline dynamics in the context of climate change (Tomback and Resler, 2007; Resler and Tomback, 2008).

WHITEBARK PINE ECOSYSTEMS

Whitebark pine is a foundation and keystone species in subalpine and alpine ecosystems in the western United States and southwestern Canada (Kendall and Arno, 1990). As such, the species provides numerous ecosystem services such as providing a food source for wildlife (Kendall and Arno, 1990); tree island establishment and facilitating the establishment of other tree species (Arno and Weaver, 1990); and stabilizing soil, rock, and snowpack in even the harshest alpine environments (Arno and Hoff, 1989).

Whitebark pine trees provide seed cones as a high energy food source for many wildlife species (including red squirrels, Clark's nutcrackers, and grizzly bears), as well as canopy shelter for animals inhabiting cold, high elevation regions of the Rocky Mountains (Kendall and Arno, 1990). Seed dispersal of whitebark pine is primarily dependent on Clark's nutcrackers (*Nucifraga columbiana*), which co-evolved with whitebark pine. Clark's nutcrackers have the capability of carrying up to 150 seeds in its throat pouch at one time, and can transport seeds as far as 12.5 km from harvested tree to cache site (Tomback, 1982; Tomback et al., 1995). The collected whitebark pine seeds are buried in the ground as food storage sites (caches), with as many as 1-15 seeds found per cache (Tomback, 1982, Tomback et al., 1995). The Clark's nutcracker caches seeds in subalpine and alpine 'safe-sites' at the base of trees, logs, or rocks; open areas such as meadows and burned sites; and in the loose substrate of exposed slopes above treeline (Tomback, 1982; Tomback et al., 1990; Hutchins, 1990). These cache sites can be retrieved by the nutcrackers during times when food supplies are scarce. Unharvested seed cache sites typically result in the propagation of this tree species across expansive areas high in elevation (Tomback, 1982; Tomback et al., 1995).

DISTRIBUTION OF WHITEBARK PINE

Severely cold environments with heavy snowfall, short growing seasons, and strong winds are prime habitat for whitebark pine (McCaughey and Schmidt, 1990; Weaver, 1990). Much of the distribution of whitebark pine can be found in high-elevation subalpine forests and in the alpine treeline ecotone of western North American mountain ranges: the Rocky Mountains, the Columbia Mountains, the Interior Plateau, the Cascade Mountains, and the Coast Mountains (McCaughey and Schmidt, 1990; Ogilvie, 1990). The distribution extends from northern British Columbia (~55ºN latitude) to south-central California (~36ºN latitude), and from the westward reaches of the Pacific coastal range extending eastward to Wyoming's Wind River range (~107ºW longitude) (Arno and Hoff, 1989; McCaughey and Schmidt, 1990). Major occurrences of whitebark pine can be found in the Rocky Mountains east and west of the

Continental Divide. Within western Canada whitebark pine is found in British Columbia and Alberta, restricted to high elevation mountain environments (Ogilvie, 1990).

The topography in high elevation mountain ecosystems also creates ecological niches important for species richness, and areas with complex topography tend to provide more habitat potential than flat terrain (MacDonald, 2003). The spatial distribution of whitebark pine is strongly influenced by geology and geomorphology. Glacially scoured sites, moraine and landslide deposits, and thin-soiled steep slopes in the high elevation mountain environment are conducive to the growth of whitebark pine (Hansen-Bristow et al., 1990). Whitebark pine has a competitive advantage over other species such as fir and spruce due to its tolerance of cold sites on rugged topography, allowing it to dominate while competitor species are hampered by the harsh conditions (Arno and Weaver, 1990).

Whitebark pine is a pioneer establisher at alpine treeline. The species is also thought to facilitate the growth of other alpine conifers (Resler et al., 2005; Resler, 2006; Resler and Tomback, 2008; Resler and Fonstad, 2009). Whitebark pine trees may grow up to 700 m below and 300 m above the treeline. In more exposed areas at higher elevations in the treeline ecotone, whitebark pine grows in a dwarfed, krummholz form (shrub-like, wind and weather battered trees), typically initiating colonies of tree islands (Ogilvie, 1990). Tree islands are typically formed by dense clumping of krummholz trees, gathered together for protection from wind and cold climates, and increased moisture availability, for the mutual reward of survival (Arno and Hammerly, 1984). The growth and shape of krummholz vegetative forms is strongly influenced by wind exposure and snow cover (Daly, 1984). Cushion krummholz is an example of extremely wind-deformed trees growing together under protection from the harsh conditions into a hedge-like form; another tree island form, these colonies spread in the leeward direction, retreating from the wind (Arno and Hammerly, 1984).

In the West Big Hole Range of Idaho and Montana, whitebark pine has historically dominated forest stands mixed with subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) (Murray and Bunting, 2000). However, since the decline of whitebark pine largely attributed to blister rust infection, the percentage of subalpine fir and Engelmann spruce is increasing (Murray and Bunting, 2000).

WHITE PINE BLISTER RUST

White pine blister rust is an invasive disease caused by the fungal pathogen *Cronartium ribicola* that infects five-needled white pines (Family Pinaceae). Within this family, whitebark pine is the most susceptible to blister rust disease, resulting in devastating decline of whitebark pine populations (Hoff and Hagle, 1990; Tomback et al., 1995). More than 90 percent of whitebark pine mortality in the northwestern portion of its range can be blamed on blister rust disease (Kendall and Arno, 1990). While fire suppression and mountain pine beetle infestations have contributed to declines in whitebark pine populations, trees stressed from blister rust infection increase their susceptibility and further the decline (Hoff and Hagle, 1990; Kendall and Arno, 1990; Keane and Arno, 1993). The blister rust fungus, which is native to Asia, was accidentally introduced to western and eastern coasts of North America by way of transported blister rust-infected white pine nursery stock grown in Europe around the turn of the 20th century (Samman et al., 2003). Boats carrying white pine nursery stock transported the fungus to western North America in 1910 to the ports of Vancouver, British Columbia. By 1922 blister rust cankers were observed 100 miles north of Vancouver, throughout eastern British Columbia and in Washington state. Five years later, cankers were found in Idaho, the southern extent of western white pine (Hoff and Hagle, 1990).

The blister rust life cycle requires both a host species and an alternate host, (Samman et al., 2003). The rust must spread between the white pine host and the alternate host species, returning to the white pine host in order to complete the life cycle (Hoff and Hagle, 1990). *Ribes* spp. (currants or gooseberries) have long been known as the common alternate host species for blister rust since the introduction of the disease in the early 1900s. Recently however, research conducted in 2004 revealed that the list of alternate plant species capable of hosting blister rust may be expanded (McDonald et al., 2006). Additional alternate host species may include the plants: sickletop lousewort (*Pedicularis racemosa*), and scarlet Indian paintbrush (*Castilleja miniata*) (McDonald et al., 2006). Campbell and Antos (2000) reported a significant relationship between stands of infected whitebark pine and the presence of *Ribes* spp. Areas where white pine and *Ribes* spp. coexist have the potential for blister rust infection of white pine tree species (Kinloch, 2003). Historically, foresters attempted to remove infected trees as well as *Ribes* spp. bushes. By 1965 these eradication attempts proved futile (Hoff and Hagle, 1990).

Originally thought to be restricted to mild temperatures and moist climates (Van Arsdel et al., 1956), a lower incidence of blister rust infection was anticipated in dryer and cooler environments (Hoff and Hagle, 1990; Campbell and Antos, 2000). The presence of blister rust in the cold and dry environments, such as the alpine treeline ecotone of the eastern slopes of the Northern Rocky Mountains proves that this is not the case (Resler and Tomback, 2008). Kinloch (2003) discussed the perplexity of the spread of blister rust to drier areas thought to have climates inhospitable to this disease. Based on the aggressive track record of blister rust spread, there is no assurance that any North American climate is exempt from blister rust wherever alternate host plants can grow (Kinloch, 2003).

PATTERN AND PROCESS OF BLISTER RUST INCIDENCE

Simply stated, landscape pathology is the study of diseases across a landscape. This interdisciplinary field integrates landscape ecology and forest pathology in examining the spread, dynamics, and influence of a pathogen on landscape spatial patterns, as well as the influence of landscape on disease (Holdenrieder et al., 2004; Lundquist, 2005). Holdenrieder et al. (2004) examined the spatial patterns of forest pathology at the landscape scale and acknowledged that further research in landscape pathology may fill the gaps in our understanding of landscape disease, the extent of exotic infestations in our forests, and of how climate change might affect the susceptibility of landscape vegetation and the spread of plant diseases.

The potential effects of climate on the spread of rusts has received some attention from researchers. For example, Frank (2006) and Frank et al. (2008) explored the meteorological conditions conducive to the spread of white pine blister rust in the Sacramento Mountains of New Mexico. In one study on the incidence of the comandra blister rust (*Cronartium comandrae*), Jacobi et al. (1993) used simulations of wind speed and direction to determine fungal spore dispersion and compare rust incidence with lodgepole pine infection. These studies show that examining the role of wind in dispersing blister rust fungal spores may reveal important information regarding the spatial pattern of the spread of this disease. However, gaps still exist in our understanding of the role of topoclimatic variables, and their effect on landscape structure and disease incidence (Holdenrieder et al., 2004).

Spatial modeling coupled with detailed landscape analyses is a useful method for understanding relationships between pathogen dynamics and the intensity of the disease across the landscape (Holdenrieder et al., 2004). In several studies examining the spread of Sudden Oak Death, understanding disease dynamics by studying the spatial behavior of the disease is crucial (Kelly and Meentemeyer, 2002; Kelly et al., 2007; Liu et. al., 2007; Anacker et al., 2008). Sudden Oak Death (SOD) is caused by a pathogen (*Phytophthora ramorum*) requiring a foliar host (much in the way that *Ribes* spp. hosts blister rust) and is devastating coastal oak forests in California and southern Oregon (Kelly and Meentemeyer, 2002; Meentemeyer et al., 2004; Kelly et al., 2007; Liu et. al., 2007). Foliar host plants play a key role in the spread of *P. ramorum*, by providing a source of inoculum easily dispersed, potentially infecting oak species (Garbelotto et al., 2003). Kelly and Meentemeyer (2002) examined several landscape variables to correlate with spatial patterns of oak mortality incidence. It was found that a shorter distance to forest edge, lower topographic moisture indices (dryer slopes), higher density of nearby host plants, such as California Bay (*Umbellularia californica*), closer proximity to trails, and low summer solar insolation levels resulted in an increased risk of SOD (Kelly and Meentemeyer, 2002). If the spatial pattern of sudden oak death disease is an important component in SOD research, it may likely play an important role in blister rust incidence. Closer examination of similar variables may prove beneficial in understanding the spatial patterns of blister rust.

ALPINE TREELINE

The effect of climatic change on vegetation distribution at the treeline ecotone has received much attention among researchers. Evidence suggests climate change may influence the elevational position of treeline on a mountain slope (e.g. Lloyd and Graumlich, 1997). There has been much debate among researchers over the possible causes of the forest to shrub and herbaceous transitional patterns found at treeline; typically the causes fall within the categories of anthropogenic influences (logging practices, livestock grazing, prescribed burning) and harsh geomorphic terrain creating unfavorable conditions for tree growth (avalanches, steep slopes) (Körner and Paulsen, 2004). In natural climatic treeline environments high in elevation and latitude, anthropogenic influences are scarce. Körner and Paulsen (2004) examined several natural climatic treelines at a global scale where temperature appears to play a key climatic factor in determining treeline. However, Holtmeier (2003) emphasized that climate is not the only controlling factor in changing treeline pattern. Many physiognomic and ecological factors influence treeline, requiring a complex landscape-ecological approach when examining treeline dynamics (Stevens and Fox, 1991; Holtmeier, 2003; Malanson et al., 2007)

Positive feedback mechanisms have strong influences on ecological patterns at alpine treeline (e.g. Alftine and Malanson, 2004; Bekker, 2005). Positive feedback systems create a cycle of change that intensifies the original condition (Starr, 1994). Positive plant interactions are positive feedbacks within an ecological context. For example, an existing tree may modify and improve its surrounding environment by providing protection from wind or increasing soil moisture, thereby enabling subsequent seedling establishment, growth and survival (e.g. Resler, 2006). In the forest-tundra ecotone in Glacier National Park (GNP), Alftine and Malanson (2004) found wind to play an important role in influencing the spatial pattern of alpine treeline and examined the responses of treeline due to climate change. In a separate study, Alftine et al. (2003) examined the role of snow as a positive feedback mechanism in the establishment of treeline pattern. Bekker (2005) examined the relationships between pattern and process in the establishment of tree seedlings and the role of existing trees in the advancement of subalpine forest in GNP. Pattern and process may change over time due to changes in climatic conditions (Bekker, 2005). According to Holtmeier and Broll (2005), climate change alone does not control the sensitivity of treelines; many other environmental variables are influential. A good indicator of treeline sensitivity to environmental change is the advancement of forest into areas beyond the tree limit (Holtmeier and Broll, 2005). Baker and Weisberg (1997) discussed the altering role of climate change on vegetation composition in the alpine forest-tundra ecotone in Rocky Mountain National Park. In their study, they employed GRASS GIS technology in mapping tree population parameters as a tool for monitoring vegetation change in response to climatic variation (Baker and Weisberg, 1997).

UTILIZING GIS TO CHARACTERIZE BLISTER RUST INCIDENCE IN WHITEBARK PINE

Mapping forest diseases has become a priority in forest management (Van Arsdel, 1964; Geils et al., 1999; White et al., 2002; Sturdevant and Kegley, 2006). However, there has been relatively little work conducted in mapping landscape disease at the alpine treeline ecotone, much less blister rust infection among treeline whitebark pine. The emphasis of most mapping studies related to whitebark pine has focused on subalpine ecosystems. For example, in the mountains of Helena National Forest Montana, the U.S. Forest Service conducted field and mapping surveys of whitebark pine stands with incidences of mountain pine beetle damage and blister rust infection (Sturdevant and Kegley, 2006). White et al. (2002) discussed the importance of delineating white pine blister rust hazard areas on maps in the Lake States region of Minnesota, using Geographic Information System techniques and spatial databases. Spatial analyses of these hazard areas show that “climate, topographic characteristics, and distance from water bodies and wetlands have a strong influence on white pine blister rust infection hazard" (White et al., 2002:1639).

Remote sensing applications have also proved useful in tracking the incidence of blister rust in five-needled pines. In the Bob Marshall Wilderness Complex Montana, within the Northern Rocky Mountain range, satellite imagery (LANDSAT TM) data in conjuction with field data proved useful in analyzing subalpine forest and determining the extent of whitebark pine stand deaths due to the spread of blister rust (Keane et al., 1994).

Global Positioning Systems (GPS) and Geographic Information Systems (GIS) are important tools in estimating disease risk in natural landscape systems (Nutter, 2006). Nutter (2006) emphasized the crucial role of GPS and GIS in an epidemiological study analyzing the spread of Moko disease of bananas in subsistence farmland in the Amazon region of Brazil. Utilizing GIS in the study of whitebark pine at treeline enables a broader scope of landscape dynamics, allows the input of many environmental factors into a model, and can incorporate a larger study area too extensive to reach by foot.

Many modeling approaches coupled with GIS have been used in the assessment and prediction of pathogenic impacts and spread. For example, Desprez-Loustau et al (2007) used the CLIMEX model to examine the geographic extent and impact of forest pathogenic fungi. This model is a dynamic simulation system that is capable of predicting the distribution/location of a given species based on the species climatic requirements (Desprez-Loustau et al., 2007).

In another study, Kluza et al (2007) used an ecological niche modeling approach in a research study investigating the potential risk and spread of Sudden Oak Death (SOD) in California. In this study Genetic Algorithm for Rule-Set Prediction (GARP) was the model employed to predict the geographic range of species distribution (Stockwell and Peters, 1999).

Environmental inputs for this model study are in GIS raster format and include variables such as: topography (including elevation, aspect, flow direction and accumulation), monthly normalized difference vegetation index used to infer climate conditions, and climate (yearly mean diurnal temperature values, ground frost, min/max/mean temperatures, precipitation, solar radiation) (Kluza et. al., 2007). Examining similar variables (as examined in these studies) in blister rust incidence at alpine treeline deserves consideration.

APPLICATIONS OF A BLISTER RUST INCIDENCE MODEL

One of the 'big questions' in geography most applicable to this thesis is, "How has the earth been transformed by human action?" (Cutter et al., 2002). The spread of blister rust disease to North America is a classic example of human-impact on the environment. The transport of blister rust-infected white pine nursery stock to North America from Europe and Asia and the subsequent introduction of this exotic, invasive fungal pathogen, has certainly made an impact. Human-induced global warming is the main cause of the spread of blister rust to dry, continental alpine treeline locations. In terms of global biodiversity, blister rust may potentially extirpate whitebark pine as a viable species, thus decreasing biodiversity in the subalpine forest and alpine tundra ecosystems. On the other hand, as some tree species develop natural resistance to this disease either by hybridization or genetic resistance, a new species will perhaps evolve, thus increasing biodiversity. In fact, from a management standpoint, the introduction of white pines genetically resistant to blister rust in problematic areas with a high prevalence of blister rust may be a key strategy in forest management.

From the literature it is clear that topographic and environmental variables must be considered when analyzing the spatial patterns of blister rust disease across the alpine treeline landscape. Operationalizing the presence and absence of blister rust within a given study area into quantitative variables for determining correlations with these environmental variables will be a challenge in this thesis study. Many different modeling tools and methods may be used to evaluate the scale, direction and distance of the spread of a pathogen to determine a spatial pattern. With the advancement of geospatial tools, remote sensing applications coupled with GIS and GPS prove to be highly useful tools in determining spatial pattern and process, furthering the progress in the field of biogeography.

Chapter 3. Methods

The goal for this research project was to quantify blister rust incidence and intensity using field techniques, and to determine, through spatial analysis, what environmental variables correlate strongly to the intensity of blister rust incident areas. The first objective was to determine to what extent blister rust is infecting treeline whitebark pine, and to characterize the geographic variation of blister rust incidence across a north-south transect, east of the continental divide in Glacier National Park, Montana (GNP). The second objective was to determine how these blister rust infection rates may be influenced by key environmental variables (i.e., topographic characteristics, proximity to alternate host species, proximity to water). By combining both the Spatial and Earth Science traditions of Geography (Robinson, 1976), these influential environmental variables were stratified and analyzed spatially using GIS, comparing blister rust incidences found in different study sites of the northern Rocky Mountains.

The methodology I employed involved four primary tasks, as stated below:

Task 1: Conduct a field study to measure blister rust incidence/ intensity among alpine treeline whitebark pine populations, the proximity of these populations to potential host species, and site conditions (wind speed, general slope and aspect readings) at each study site.

Task 2: Test and develop a fine-scaled Digital Elevation Model (DEM) that best represents the surface of each study site.

Task 3: Derive topographic variables from these DEMs (elevation, slope, aspect, flow accumulation, curvature, potential solar radiation), and measure the proximity of each study site to water bodies (perennial streams, lakes, wetlands) using GIS.

Task 4: Use multivariate statistical analysis to determine how the selected environmental and topographic variables (independent variables) influence blister rust infection intensity (dependent variables) observed in GNP.

STUDY AREAS

Study sites were located in the northern Rocky Mountains of Glacier National Park, Montana U.S.A. The Park is part of the Waterton-Glacier International Peace Park, which extends from Montana into Alberta, Canada. Situated in northwest Montana, GNP straddles the Rocky Mountain Continental Divide, forcing drainage from the western slopes to the Pacific Ocean and drainage from eastern slopes to the Gulf of Mexico. One unique exception however, is Triple Divide Peak, where water drains into three basins. From the peak, water drains west to the Pacific, northeast to the Hudson Bay, and southeast to the Gulf of Mexico. The Continental Divide also creates two very different climates in GNP east and west of the Divide. West of the Divide, the Park receives moist maritime weather from the Pacific which cools as it rises over the mountains releasing rain and snow on the western slopes (Harris et al., 1997). The eastern side of the Park is exposed to dryer, windier, continental climate conditions, funneled from the north through Canada (NPS, 2008). Due to a rain shadow effect, progressing eastward from the Divide there is much less rainfall and winter snow accumulation then in the western portion of the Park (Harris et al., 1997).

The extreme mountainous terrain in GNP is a result of landforms sculpted by ice during the Pleistocene Epoch, with present day glaciers and associated periglacial features having developed just a few thousand years ago during the “Little Ice Age” (Harris et al., 1997). Glacially carved and modified, the mountains and valleys of GNP exhibit unique geology quite different from the granite and metamorphic bedrock of its southern Rocky Mountain counterparts (NPS, 2008). Precambrian metasedimentary rocks thrusted over younger bedrock dominate the underlying terrain structure of the Park (Harris et al., 1997). Although the resulting bedrock soils are thin, and much of the terrain is steeply sloping, the plant cover of GNP is dominated by coniferous forests (almost 50%) and is home to 30 endemic species, most of which are limited to the northern Rocky Mountains, and thrive in these cold, harsh, post-glacial environments (NPS, 2008).

The purpose of field sampling was to document where and to what degree white pine blister rust is infecting whitebark pine trees within the alpine treeline ecotone (ATE), locate alternate host species, measure site conditions, and characterize the topography.

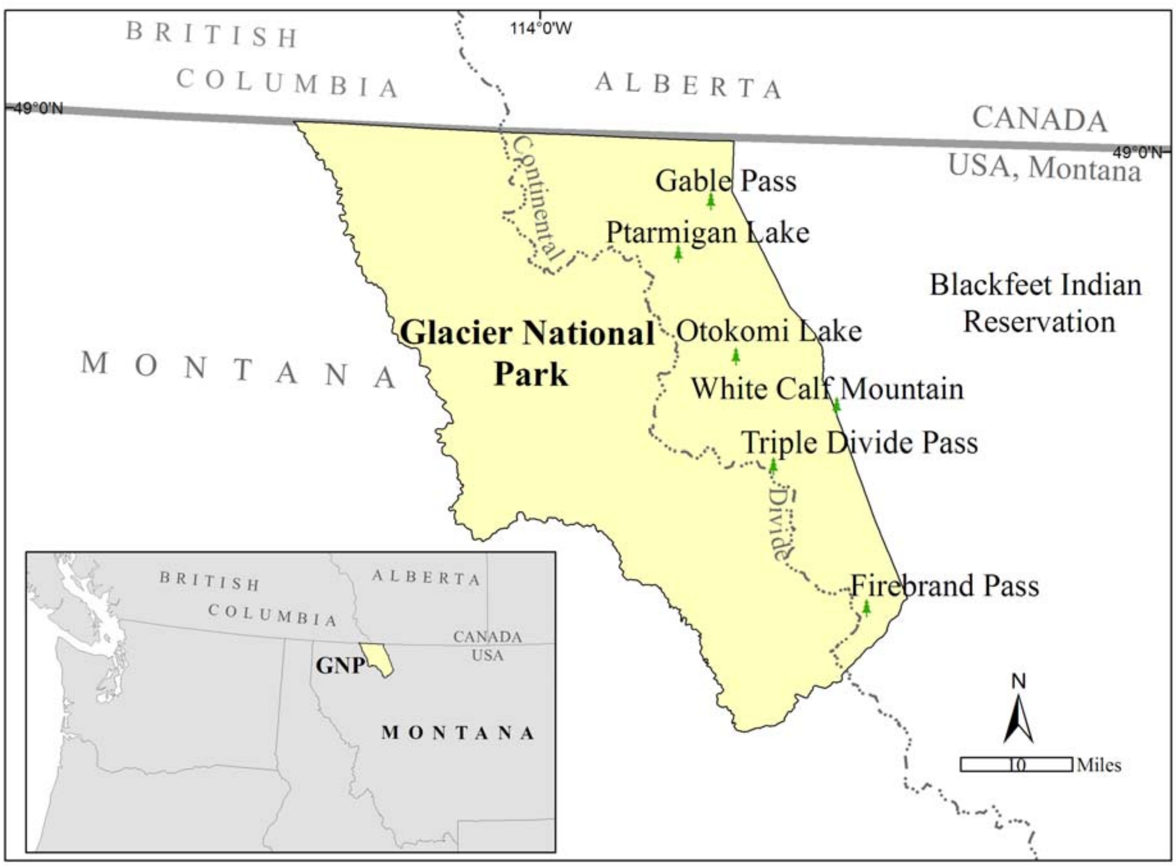

Figure 3.1 Treeline study sites within Glacier National Park, east of the Continental Divide.

The fieldwork conducted in July of 2008 comprised of six representative, alpine treeline study sites east of the Continental Divide. Study sites chosen for sampling are located along a north-south latitudinal transect. Locations of the treeline study sites included: Gable Pass (48.92° N, 113.65° W), Ptarmigan Lake (48.85° N, 113.71° W), Otokomi Lake (48.72° N, 113.59° W), White Calf Mountain (48.66° N, 113.39° W), Triple Divide Pass (48.58° N, 113.51° W), and Firebrand Pass (48.4° N, 113.32° W) (Figure 3.1). These treeline study sites had whitebark pine present, and were selected based on consultation with Park Scientists and through GIS analysis of a vegetation base map developed under the USGS-NPS Vegetation Mapping Program (2007). Areas on the map that delineated whitebark pine woodlands and krummholz ecosystems were particularly helpful in identifying potential locations of treeline whitebark pine. In some cases, the treeline whitebark pine sampled was in solitary growth form, and in other cases it was part of tree islands. Table 3.1 lists the range of site characteristics at each of the treeline study sites.

Table 3.1 Site Characteristics: Range of values observed at each treeline site.

Treeline Site	Elevation (m)	Slope (°)	Aspect
Gable Pass	2,213 - 2,240	16 - 23	N, W, SW
Ptarmigan Lake	2,086 - 2,129	19 - 31	E, SE, SW
Otokomi Lake	1,962 - 2,090	27 - 38	S, SE
White Calf Mountain	2,170 - 2,220	21 - 24	N, E, SE
Triple Divide Pass	2,177 - 2,259	13 - 31	S, W
Firebrand Pass	1,951 - 2,171	18 - 31	NE, NW, E

TASK 1: FIELD DATA COLLECTION: WHITEBARK PINE, BLISTER RUST INCIDENCE, ALTERNATE HOSTS, AND SITE CONDITIONS

Equal-area quadrats delineated boundaries for sampling whitebark pine and blister rust incidence. Area sampling methods are suitable for providing statistically representative samples (Lounsbury and Aldrich, 1986: 110-112). In reviewing other landscape studies involving quadrat sampling methods, Kelly and Meentemeyer's (2002) landscape scale study on sudden oak death (SOD) indicated that plots smaller than 1 hectare may not represent the overall spatial pattern occurring at a broader scale. Because readily available remote sensing resources can detect the incidence of SOD, larger sample sizes were appropriate. However, in this blister rust study where traditional fieldwork methods are used to gather detailed information, quadrat plots of such a large size would not be feasible. Though large quadrat plots sparsely distributed across a study area could have yielded a large amount of detailed observations within each quadrat, smaller quadrat plots spaced more regularly across the study area enabled broader coverage and yielded more representative data of the landscape.

At each of the 6 treeline sites, 5 quadrats randomly placed represented varying slopes, aspects, and elevations across the ATE landscape for a total of 30 quadrats. Each had a fixed dimension of 15 m x 15 m (with the exception of site WC-Quad1 where a 20m sampling scheme was tested and determined too time intensive at this level of detailed data collection).

I conducted vegetation inventories within the sampling quadrats following field methods outlined in Resler and Tomback (2008). Species composition was recorded for each individual tree and tree island. Some of the treeline whitebark pine trees assumed solitary growth forms, attributing self-establishment to the protection of rocks or other microshelters from the harsh climates found in the ATE. In other cases, whitebark pine grew near other tree species in krummholz tree islands, defined as clusters of dwarfed tree species dependent on one another in this cold and windy environment. Each whitebark pine tree was examined for the presence or absence of blister rust. If blister rust was present, I enumerated and characterized the number of cankers per tree. Following Hoff (1992), canker classes were described and used to denote levels of blister rust infection: potential (showing signs of canker development, swelling of stem, but no sporulation present), inactive (evidence of past canker development, with cracked old bark leftover from past sporulation), and active (signs of aecial sacs either in the developed stage or previously burst, showing recent active sporulation) (Figure 3.2). In addition, if blister rust was present the percent canopy kill was noted using seven categories: 1 (0%), 2 (0-5%), 3 (5-25%), 4 (25-50%), 5 (50-75%), 6 (75-95%), and 7 (95-100%). Sampling results convey the density of whitebark pine trees and the intensity of blister rust infection.

Figure 3.2 Active blister rust canker found on whitebark pine, exhibiting aecial sacs.

Finding the presence of both the alternate host species as well as the pathogen within the landscape may increase the likelihood for finding disease-infected trees (Holdenreider et al., 2004), and may serve as a key component in determining the severity of blister rust hazard in a given area. Since plants of the *Ribes* spp. can serve as hosts for white pine blister rust, the location of these potential hosts in relation to infected whitebark pine is important spatial information. While hiking to the ATE sampling quadrats, it was possible to scout out locations of *Ribes* spp. and record GPS locations of individual plants. In cases where there were multiple *Ribes* plants within a quadrat, I designated the entire quadrat area as a *Ribes* location due to the time constraints of recording each GPS position. In similar circumstances where several locations of this alternate host plant were within a concentrated area, a radial area was designated as a *Ribes* location. Upon returning from fieldwork, I calculated the distances from the study sites in the ATE to these potential host plant areas in a GIS using a spatial analysis proximity tool.

Highly influenced by topography, wind speed and direction are environmental factors that can potentially influence the spatial pattern of fungal spore transport (e.g. Jacobi et al., 1993; Frank et al., 2008). Though wind direction was difficult to quantify at each quadrat location, measuring the general wind speed was possible. Using a hand-held anemometer, wind measurements recorded for a duration of 2 minutes, at two different locations within each quadrat, were averaged in order to estimate wind gusts. These measurements are but a snapshot in time, but they may help characterize the nature of topographically influenced wind at each study site.

Topographic orientation and gradient control the exposure of a given surface to oncoming weather systems, sunlight and wind, as well as the overall drainage. Sufficient moisture, cooler temperatures, and steeper slopes have been associated with higher incidences of blister rust (Van Arsdel, 1956; White et al., 2002). For this reason, I recorded aspect and slope measurements at each quadrat during field data collection, using a compass and clinometer. These general measurements are based on sight and a general one-dimensional plane of the surface for each study site, and served as validation for the DEM-derived topographic variables.

TASK 2: CHARACTERIZING TERRAIN: DEVELOPING A GPS-DERIVED DEM

The second task was to create a representative surface model of each study site in order to derive topographic variables to correlate with blister rust incidence. Topographic variables are important factors to consider when examining landscape dynamics of a disease. The geomorphology of the landscape influences wind speed/direction and vegetation distribution in the ATE (Geddes et al., 2005; Butler et al., 2007). Incorporating topographic variability into a GIS model allows for a digital description of the land surface (Bishop and McBratney, 2002). In order to characterize the terrain, detailed information was required to sufficiently represent curves, depressions, and slopes of the land in the form of a DEM. These characteristics are essential when comparing topographic variables (such as moisture and sun exposure) with blister rust incidence. The accuracy and resolution of DEM data are important factors to consider in environmental modeling applications (Thompson et al., 2001). For these reasons, in an attempt to improve upon currently existing DEMs, testing and developing high resolution DEMs was a priority in this study.

Publicly available DEM data in 10 m (1/3 Arc Second) resolution datasets are available for GNP, and may be downloaded from the United States Geological Survey (USGS) website (http://seamless.usgs.gov) (USGS, 2008). However, as the sampling quadrats are only

15 m x 15 m, a 10 m USGS DEM does not provide a good representation of terrain variability for such a small area. Additionally, errors found in USGS DEM digital datasets can have a large impact on the quality of DEM-derived terrain attributes such as slope, aspect, or flow accumulation (Holmes et al., 2000). One study compared USGS DEM-derived terrain attributes from 10 m and 30 m DEMs to those derived from Real-Time Kinematic (RTK) GPS estimates (Pike et al., 2006). The USGS DEMs, generated by stereo photogrammetric techniques, were more prone to error, and the RTK GPS-derived elevations proved more accurate. Finer-scaled DEMs are necessary to represent the landform variability of the study sites in GNP.

Several researchers have analyzed DEMs derived from Light Detection and Ranging (LiDAR) data, GPS, and photogrammetrical techniques for their accuracy in representing landform surface variability (Baily et al., 2003; Mills et al., 2003; Geddes et al., 2005; Heritage and Hetherington, 2005; Webster and Dias, 2006). Webster and Dias (2006) compared ground elevations between high-precision GPS and LiDAR surveys within a GIS workstation. Using the collected ground points, they interpolated from Triangular Irregular Networks (TIN) in order to create DEMs with a resolution of 2 meters. Surveys conducted in open field areas showed comparable vertical specifications between GPS and LiDAR points when overlaid in a GIS. Results of survey tests covering areas of dense shrubland and tree canopy showed interference with LiDAR, with instances of height errors occurring due to tops of vegetation cover interpreted as ground.

Strong results were anticipated with a GPS-derived DEM created in the alpine treeline ecotone.

Geddes et al. (2005) generated a 5 m resolution DEM using a differential GPS and aerial photographs (scale=1:15,000) in a mountain environment in northwestern Montana and compared the results to a 30 m resolution USGS DEM. Results showed that the GPS-derived

DEM had errors in valleys, possibly due to tree cover, but overall the surface of the ridge was represented better with the GPS 5 m DEM than with the 30 m USGS DEM. Since all of the study areas for this thesis project are in open areas at ATE with virtually no tree cover, this study suggests similar success with a GPS-derived DEM.

For the purpose of characterizing terrain at the ATE study sites it was necessary to create a high resolution, submeter GPS-derived DEM for each whitebark pine and blister rust sampling quadrat. These digital elevation models served as a higher resolution model of the study site terrain than any DEM currently available (a USGS 10 m DEM) and as a base layer for GIS analyses.

Prior to fieldwork and GPS collection in Glacier National Park, I conducted a pilot study in Blacksburg, VA in order to test the DEM creation process. Using a Trimble GeoXT differential GPS unit with submeter accuracy, I compared differentially corrected GPS elevation positions on varying terrain to high accuracy elevation measurements from LiDAR data obtained from the Town of Blacksburg, VA. Some of the "testing" ground for creating DEMs included flat areas of an athletic field, uneven surfaces of a boulder drainage ditch, and a steeply sloping hill face. All terrain types were void of tree canopy or building obstruction (to simulate an alpine environment, and reduce interference from multipath environments). After successful completion of the DEM test sites, I found the elevations to be comparable between GPS and LiDAR surfaces (on average within 1 meter) (Figure 3.3).

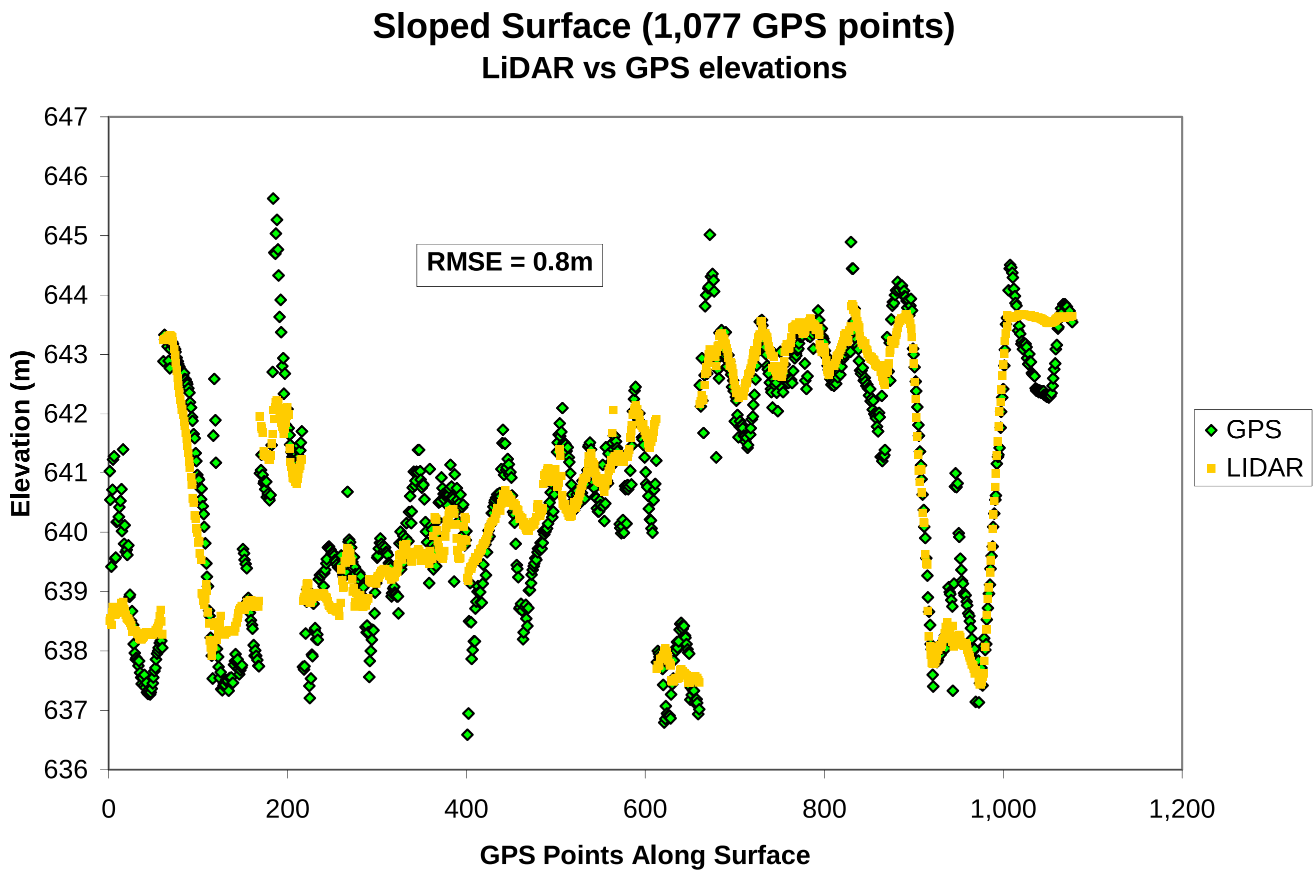

Figure 3.3 Example of GPS/LiDAR elevation comparison on a sloping surface.

In order to create DEM surfaces, GPS observations were recorded every second at a slow walking pace (attempting to model every depression and varying topographic feature) with a hand-held submeter GPS. Occupation period, the amount of time spent in one position collecting GPS readings, is more important in poor collection conditions (canopy cover, high multipath environment) than in good collection conditions and environments (open spaces, clear skies) (Trimble GPS Pathfinder® Office, 2003). Averaging GPS observations at one position can help improve precision (not accuracy), but averaging one position over a 20-60 second interval would likely not be different then recording individual points per position since factors contributing to error change very little in this short time interval (such as satellite arrangement, ionospheric density) (Oderwald and Boucher, 2003). All of the ATE study sites in which I sampled had good collection conditions, and recording GPS positions every second proved to be a viable technique for producing DEMs of the study sites.

In order to generate points for the DEM, I collected GPS points while traversing each vegetation sampling quadrat. In order to represent the land surface accurately, I took special consideration to changes in slope gradients (breaklines), recording high and low points, molding depressions and ridges present across the quadrat. Along with other environmental variables such as blister rust intensity, and wind speed, this DEM served as a key modeling component for deriving topographic variables used in the regression analysis (Task 3).

TASK 3: DERIVATION OF MODEL VARIABLES IN GIS: TOPOGRAPHIC CHARACTERISTICS AND PROXIMITY TO WATER

As previously noted, topographic variables may play a key role in modeling environmental processes such as disease spread and incidence across a landscape (Holmes et al., 2000; Thompson et al., 2001; Bishop and McBratney, 2002; Pike et al., 2006). After field collection, I code-processed differentially corrected GPS data using a base station provider located at an average distance ~31 km from the study sites (well within the GPS requirements for submeter accuracy) using Trimble® GPS Pathfinder Office (2003). The steps taken to create 3D surfaces were as follows: created mass points from filtered/corrected GPS features for each quadrat, applied a transformation to convert the GPS unit default of WGS84 to NAD 83, and generated triangulated irregular networks (TINs) using ArcGIS (ESRI, 2006). When trying to mold topographic features to a model, a TIN represents the dynamics of land very well, capturing drainages, depressions, ridges, and other geomorphic surface features (Zeiler, 1999), and was the last step before creating a preliminary DEM raster surface. First-hand knowledge of the terrain through field reconnaissance, photo documentation, and numerous GPS locations recorded, proved to be the best tools in characterizing the terrain at all study sites.

A series of GIS analyses of TINs and surface points using ArcScene and Geostatistical Analyst's semivariogram/covariance clouds (ESRI, 2006), helped me to determine that the most representative surface could be achieved through a few steps of removing outliers and applying smoothing algorithms to the GPS-derived DEM. The Spatial Analyst (ESRI, 2006) "fill" tool provided the means of comparing neighboring points for examining outliers, and removing the resulting pits and peaks within the surface. Using the neighborhood spatial analyst function 'focal statistics' to smooth surfaces, a representative terrain of submeter resolution was achieved for each quadrat.

Finally, I used ArcGIS ModelBuilder (ESRI, 2006) to generate topographic raster data layers from each DEM, for inclusion as variables in a regression model. These layers were: slope, aspect, curvature, flow accumulation, and potential solar radiation (Figure 3.4). All variables were analyzed in spatial reference UTM NAD 1983 zone 12 meters projection (Figure 3.5).

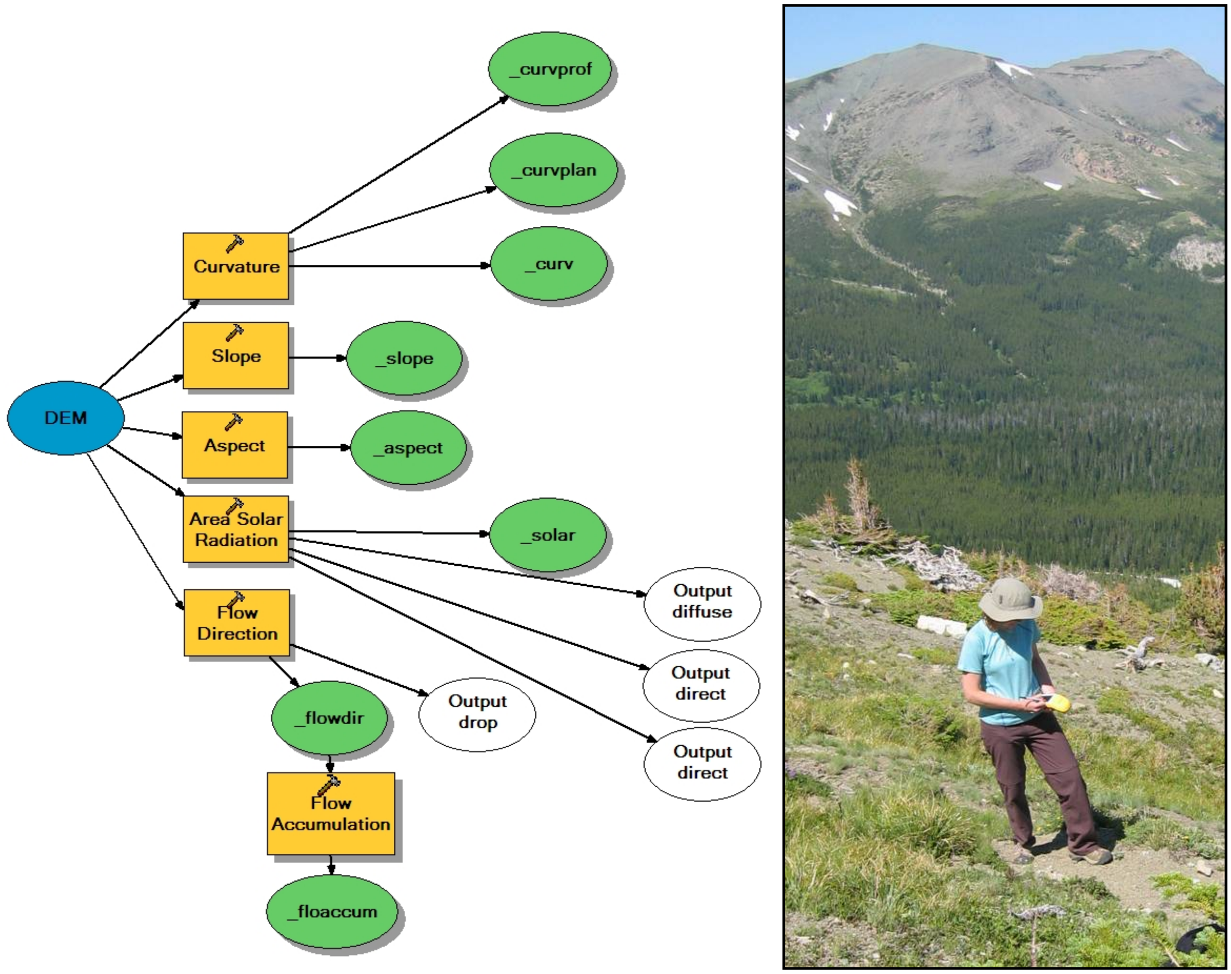

Figure 3.4 DEM-derived topographic variables using Model Builder, and GPS data collection.

The shape and orientation of the land are important characteristics to consider in this blister rust study. Hydrologically speaking, topography influences flow rate, direction, and retention of water (potential factors when considering blister rust prevalence), and are widely used in land surface analyses (Zevenbergen and Thorne, 1987). Moisture is an important resource for blister rust development and growth of alternate host plants. Orographically speaking, orientation of the land surface affects the amount of wind, sun, and weather exposure. As previously mentioned, mountain winds may play a role in fungal spore transport. Warm surfaces (especially those within a rain shadow) exposed to sunlight are prone to dry soils, which may inhibit the blister rust life cycle, but at the same time favor whitebark pine habitat (Arno, 2001) and may encourage growth of alternate host plants. The topographic variables considered in the blister rust incidence model deserve further discussion.

Slope and aspect variables (topographic gradient and orientation factors affecting hydrologic and orographic processes) derived from each DEM were compared to field measurements of slope and aspect for validation purposes. Though the field measured slope and aspect readings were based on a one-dimensional plane, the DEM-derived slope and aspect took into account all cells within the DEM raster surface. Aspect, being circular data, cannot simply be averaged within each quadrat. Therefore, the mode of DEM-derived aspect values of each quadrat was compared to each field measurement. The DEM-derived aspect values were comparable, with nearly half of the study sites having azimuth values within 6 degrees of the field measured aspect value. This comparison helped support the DEM creation process, and helped validate surface representation.

Curvature surfaces derived from each of the DEM quadrat study sites represent the concavity and convexity of a surface. Rationale for including this variable in the regression analysis was as follows: as the slope of a surface becomes more concave and less steep, soil water retention tends to increase (Pachepsky et al., 2001; Thompson et al., 2006). Increased concavity in the terrain surface may help retain snowpack, as well as capture snowmelt or runoff from rain events--a potential moisture source that may prove hospitable to blister rust. Two types of curvature considered in this study were profile curvature and planimetric curvature. Profile curvature accounts for the curvature of the surface in the direction of maximum slope, and influences flow acceleration and deceleration (affecting erosional and depositional processes) (Zevenbergen and Thorne, 1987; Moore et al., 1991). Planimetric curvature, measured perpendicular to the direction of maximum slope, serves as an indicator of how much the flow converges and diverges across a surface (Zevenbergen and Thorne, 1987).

An additional moisture indicator used in this study was 'flow accumulation', which indicates how much drainage flows through the DEM surface. High amounts of flow accumulation on a surface may indicate the presence of a stream channel or topographic lows; conversely, low amounts of flow may indicate topographic highs or ridges (ESRI, 2006). Quantifying how much surface drainage an upslope area may contribute and accumulate for each quadrat may prove an important relationship when correlating blister rust incidence.

The amount of sunlight received on a surface can influence soil moisture, species composition of plants, and plant growth conditions (e.g. Kelly and Meentemeyer, 2002). I derived potential solar radiation from each of the DEM quadrat surfaces using GIS, calculating the amount of incoming solar radiation each cell of a surface receives throughout the year (in this case the year 2008 was used). It was anticipated that areas with high potential solar radiation may indicate drier soils, and warmer conditions for plant growth (conditions that may inhibit blister rust, but favor growth of alternate host plants).

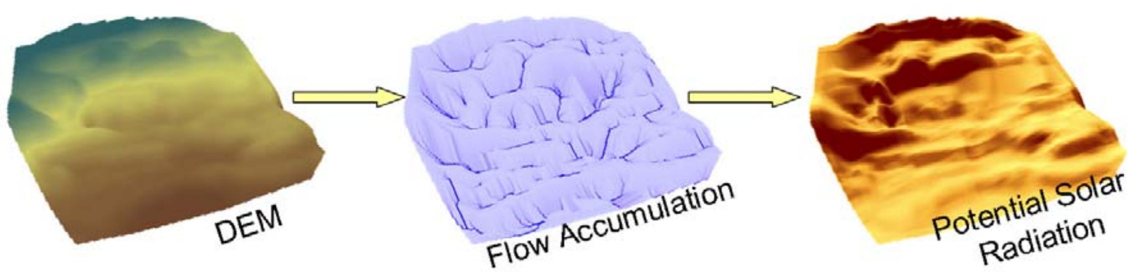

Figure 3.5 Examples of derived topographic variables from a DEM quadrat surface

The last set of variables considered for the blister rust model was the distance from each quadrat to water bodies such as perennial streams, lakes, and wetlands. Previous research findings have indicated that a relationship exists between blister rust incidence and distance to water bodies (Van Arsdel, 1965; White et al., 2002). In Van Arsdel's (1965) study, blister rust infected areas were associated with topographically high areas near lakes.

For this study, GIS layers of streams, lakes, and wetlands were obtained from the National Park Service (NPS) GIS Data Store (http://science.nature.nps.gov/nrdata/). Similar to the National Hydrography Dataset high resolution GIS layers with the scale based on 1:24,000 USGS 7.5' Quads, the NPS data parses out non-natural features, and separates out glacier and ice mass features in separate files (features not considered in blister rust correlation). I considered areas of year-round water availability important factors in examining blister rust correlation; therefore, I incorporated perennial streams, lakes and wetlands in this analysis. I calculated distances from quadrats to each of the streams, lakes, and wetlands GIS layers using a spatial analyst proximity tool. Rather than calculate the Euclidean distance (as a crow flies) to these features, I calculated the surface path distance, which takes into account the surface terrain (using a USGS 10 m DEM as the surface raster) when calculating distances. The resulting mean distances to these water bodies from each quadrat (averaging all cell distances within the quadrat) were incorporated in the regression analysis.

The eleven independent variables examined in the multiple regression analysis, presented in Table 3.2, are either field-derived, DEM-derived, or a combination thereof. The dependent blister rust variables measured in the field resulted in two categories compared with environmental variables: proportion of whitebark pine infected with blister rust, and total canker density.

Table 3.2 Field and DEM-derived independent and dependent variables.

Field / Derived Measurements	Variable	Unit of Measure	Independent/ Dependent Variable
Field	Wind Speed	--- miles per hour	Independent
Field-DEM creation	Elevation	--- meters	Independent
Derived from DEM	Slope	--- degrees (0-90°)	Independent
Derived from DEM	Aspect	--- azimuthal direction (0-360°)	Independent
Derived from DEM	Curvature	--- 1/100 m	Independent
Derived from DEM	Potential Solar Radiation	--- watt hours/m^2	Independent
Derived from DEM	Flow Accumulation	--- #cells contributing to flow	Independent
Field and Derived	Distance to *Ribes* spp.	--- meters	Independent
Derived	Distance to Perennial Streams	--- meters	Independent
Derived	Distance to Lakes	--- meters	Independent
Derived	Distance to Wetlands	--- meters	Independent
Field	Proportion of trees infected with Blister Rust	--- percentage	Dependent
Field	Total Canker Density (total cankers/per whitebark pine)	--- cankers/tree	Dependent

TASK 4: STATISTICAL ANALYSIS

A multiple regression analysis determined the combined influence of important environmental and topographic correlates of blister rust infection in treeline whitebark pine. Because dependent variables related to blister rust intensity were quantified at the quadrat level, it was necessary to aggregate detailed topographic and field derived variables for each quadrat. A cell-by-cell comparison of dependent and independent variables through spatial analysis in GIS was not possible, because assigning a spatial location to each tree analyzed for blister rust would have been too costly and time-intensive for this study. The detail of these surface variables was not lost, however; far more information went into characterizing the terrain than could be achieved from a readily available USGS 10 m DEM.

All data were tested for normality following standard procedures, and transformations were applied when appropriate (Sokal and Rohlf, 1981). Data were described and analyzed using JMP v.7 (JMP, 2007). Prior to analyses, I applied a log transformation to the dependent variable, total canker density. Examination of Pearson correlations and scatterplot matrices for all variables helped to determine which variables had high multicollinearity and should therefore be excluded from regression analyses. The plots indicated that two curvature variables (flow acceleration and deceleration, flow convergence and divergence) supplied redundant information and therefore, I chose only the curvature profile variable for this analysis. Distance to perennial streams and lakes were somewhat correlated, although not so much that they were excluded from regression analysis.

For consistency, all variables analyzed in the regression model were kept in numeric format. I partitioned and reclassified the aspect variable into 8 azimuthal categories using GIS: NW (292.5-337.5°), N (337.5-360° and 0-22.5°), NE (22.5-67.5°), E (67.5-112.5°), SE (112.5-157.5°), S (157.5-202.5°), SW (202.5-247.5°), and W (247.5-292.5°). I included the proportion of each quadrat falling within these 8 aspect categories in the statistical analysis, thereby eliminating the inconsistency of incorporating nominal aspect data and numeric data of other variables in the model, and keeping all variables in numeric format. For example, the terrain surface for FP-Quad1 is predominately facing NE, however the proportion within each aspect group is: N (29%), NE (34%), E (10%), SE (4%), S (8%), SW (5%), W (3%), and NW (7%). Assigning a numeric proportion for each of the 8 categories also provides more information on the range of aspect values within the quadrat, and whether it strongly suggests one or more directional categories.

A total of eleven independent environmental variables (including field and GIS-derived variables) met the assumptions for multiple linear regression analysis and were included in the initial multiple regression models. These were: mean elevation, aspect (8 categories), mean slope, mean wind speed, mean curvature profile, maximum flow accumulation, maximum potential solar radiation, mean distance to *Ribes* spp., mean distance to perennial streams, mean distance to lakes, and mean distance to wetlands. The statistical method of aggregation (min, mean, maximum, etc.) for these quadrat variables was chosen based on which one had highest significance in statistical analyses, as well as which method was the most logical. I analyzed these variables through a series of stepwise regressions using JMP v.7 (JMP, 2007), in order to predict overall blister rust intensity. Independent variables and interactions among variables (for example, variables that share similar characteristics may be grouped together into one interaction) were eliminated and added, one at a time, through forward, backward and mixed stepwise regressions in order to test and build candidate regression models. From these candidate models, I ultimately selected the strongest model for blister rust prediction. The final model was chosen based on statistical significance, statistically significant predictor variables, high R^2 and adjusted R^2 values, low Mean Square Error, and met the assumptions of multiple linear regression.

Chapter 4. Results

SAMPLING RESULTS OF WHITEBARK PINE AND BLISTER RUST INCIDENCE

Field sampling within the 30 treeline quadrats resulted in measurements of 333 living five-needled white pines. Of this total, 311 were whitebark pine (*Pinus albicaulis)*, and 22 were limber pine (*Pinus flexilis)*. In addition to these living trees, 97 dead whitebark pines found within the quadrats exhibited evidence of blister rust-induced mortality. Like whitebark pine, limber pine is a five-needled white pine and is susceptible to blister rust infection. Due to the small number of limber pine trees found among whitebark pine populations, and difficulty in distinguishing needle morphology between the two species, herein results of blister rust occurrence between both tree species will be combined and termed "whitebark pine".

Conifer species composition (aside from whitebark and limber pine) found within the quadrats included: subalpine fir *(Abies lasiocarpa)*, Engelmann spruce *(Picea engelmannii)*, common juniper *(Juniperus communis)*, creeping juniper *(Juniperus horizontalis)*, lodgepole pine *(Pinus contorta)*, douglas fir *(Pseudotsuga menziesii)*, and subalpine larch *(Larix lyallii)*. Of the 333 total whitebark pine sampled, 47% were infected with blister rust. A total of 678 cankers were counted on all blister rust infected whitebark pine. Of the 219 whitebark pine found in multi-tree or tree island communities, 56% had blister rust infection, totaling 581 cankers found on tree island whitebark pine. Compared to the 114 whitebark pine trees growing solitarily, only 29% were infected with blister rust with 97 cankers found on individual whitebark pine.

Geographic variability existed in blister rust infection incidence along the latitudinal sampling transect (Table 4.1). Though the highest density of whitebark pine was found in the White Calf Mountain quadrat sites (WC) where nearly 60 whitebark pine were found in one study quadrat, the highest blister rust infection rates were found at the southernmost treeline quadrats near Firebrand Pass (115 cankers were enumerated within just one quadrat). Quadrats located at the Otokomi Lake treeline site had the second highest infection rate and blister rust canker density. Almost all the quadrats sampled at Firebrand Pass and Otokomi Lake sites had 100% blister rust infection among the whitebark pine populations.

Table 4.1 Total canker density and percent whitebark pine infection within quadrats.

	Site	N (# of PIAL*)	Total Canker Density per PIAL	% PIAL Infected
	GP-Quad1	18	1.94	44
North	GP-Quad2	15	2.87	73
	GP-Quad3	5	1.00	20
	GP-Quad4	9	0.67	22
	GP-Quad5	9	1.33	33
	PL-Quad1	3	0.00	0
	PL-Quad2	4	0.50	50
	PL-Quad3	3	2.00	33
	PL-Quad4	3	0.67	33
	PL-Quad5	2	0.50	50
	OL-Quad1	4	4.75	75
	OL-Quad2	5	5.60	100
	OL-Quad3	2	16.50	100
	OL-Quad4	6	4.00	100
	OL-Quad5	4	0.50	50
	WC-Quad1	42	1.21	45
	WC-Quad2	23	0.13	13
	WC-Quad3	27	0.59	22
	WC-Quad4	57	1.33	47
	WC-Quad5	49	1.14	33
	TD-Quad1	6	3.50	83
	TD-Quad2	4	1.00	50
	TD-Quad3	1	0.00	0
	TD-Quad4	3	3.33	100
	TD-Quad5	5	2.00	60
	FP-Quad1	3	2.00	100
	FP-Quad2	2	2.50	100
	FP-Quad3	10	11.50	100
South	FP-Quad4	3	20.33	100
	FP-Quad5	6	4.33	83

*PIAL = *Pinus albicaulis* (whitebark pine)

By reexamining the spatial scale and comparing each of the 6 treeline sites, it is apparent which treelines have the highest incidence of blister rust. Treelines ranked in order of highest to lowest blister rust incidence are: Firebrand Pass, Otokomi Lake, Triple Divide Pass, Gable Pass, White Calf Mountain, and Ptarmigan Lake treeline sites (Table 4.2).

Table 4.2 Total canker density and percent whitebark pine infection per treeline.

	Treeline Site	N (# of PIAL)	Total Canker Density per PIAL	% PIAL Infected	BR* Intensity Rank (1=highest)
North	Gable Pass	56	1.80	45	4
	Ptarmigan Lake	15	0.73	33	6
	Otokomi Lake	21	5.05	86	2
	White Calf Mtn	198	1.02	36	5
	Triple Divide Pass	19	2.37	68	3
South	Firebrand Pass	24	8.88	96	1

* BR = Blister Rust

ENVIRONMENTAL CORRELATES: MODEL RESULTS

Of the eleven independent variables analyzed in stepwise regression, four variables: northwest aspect, mean wind speed, maximum flow accumulation, and mean distance to perennial streams, proved to be statistically significant ($P < 0.05$) predictors of total canker density (Table 4.3). Reported in Table 4.4 are the ranges of values observed at each treeline site for these four predictor variables.

Table 4.3 Results of least square regression analysis for independent variables.

Independent Variable	Probability (*P*)	Coefficient (β)
Mean Wind Speed	0.0163*	*0.107396*
Mean Elevation	0.4221	-
Mean Slope	0.5878	-
NW Aspect (292.5-337.5°)	0.0287*	*3.250409*
N Aspect (337.5-360° and 0-22.5°)	0.7347	-
NE Aspect (22.5-67.5°)	0.6603	-
E Aspect (67.5-112.5°)	0.7637	-
SE Aspect (112.5-157.5°)	0.6925	-
S Aspect (157.5-202.5°)	0.2754	-
SW Aspect (202.5-247.5°)	0.3242	-
W Aspect (247.5-292.5°)	0.2041	-
Mean Curvature Profile	0.1921	-
Max. Potential Solar Radiation	0.9386	-
Max. Flow Accumulation	0.0202*	*0.00126*
Mean Distance to *Ribes* spp.	0.7072	-
Mean Distance to Perennial Streams	0.0208*	*-0.000321*
Mean Distance to Lakes	0.4368	-
Mean Distance to Wetlands	0.2664	-

* Statistically significant at $P < 0.05$

Table 4.4 Ranges of observed values for predictor variables at each treeline study site.

Treeline Site	Aspect	Mean Wind Speed (mph)	Maximum Flow Accumulation (# cells)	Mean Distance to Perennial Streams (m)
Gable Pass	N, W, SW	2.4 - 5.7	1,948 - 4,094	519 - 1,111
Ptarmigan Lake	E, SE, SW	1 - 4.2	3,170 - 10,885	227 - 690
Otokomi Lake	S, SE	3 - 6.7	2,312 - 8,573	116 - 267
White Calf Mountain	N, E, SE	2.9 - 13.1	1,355 - 7,063	2,780 - 2,949
Triple Divide Pass	S, W	1.6 - 7.1	3,319 - 6,023	602 - 1,095
Firebrand Pass	NE, NW, E	2.5 - 12	4,180 - 9,478	114 - 897

The resulting multiple regression model for the prediction of total canker density:

log(y+1)=0.058316 + 3.250409 * Aspect (NW)+ 0.107396 * Wind +

0.000126 * Flow Accumulation + -0.000321 * Distance to Perennial Stream

Overall, the results show a highly significant model (P < 0.001, F(4,25)=6.79). The R^2 value (0.52; Adjusted R^2 = 0.44) indicates that over half of the variance in blister rust incidence can be explained by the combined influence of these four variables. This predictive model suggests that areas exhibiting increased wind speed, northwest facing slopes, high flow accumulation rates, and close proximity to perennial streams have a higher likelihood of blister rust intensity, specifically total canker density.

Chapter 5. Discussion

The objectives of this study were 1) to characterize geographic variation in blister rust incidence at 6 alpine treeline sampling locations in Glacier National Park across a North-South transect of the Park, east of the Continental Divide and 2) to determine environmental correlates of blister rust through field data collection and spatial analysis. Overall, the results of the field study indicate that blister rust incidence varied across the study sites, with the highest infection rates found in the most southerly site. The results of the blister rust model indicated that 4 environmental variables (northwest aspect, wind speed, flow accumulation, and distance to perennial streams) significantly correlated with blister rust total canker density. From the field and model results it is clear that a combination of factors must be considered when determining patterns of this complicated disease.

GEOGRAPHIC VARIABILITY OF BLISTER RUST INTENSITY

The intensity of blister rust infection was variable within the treeline ecotone. Field results show that nearly half of all treeline whitebark pines exhibit evidence of blister rust infection, with a total density of approximately 2.04 cankers per tree. Whitebark pine exhibited anywhere from 1 - 115 cankers per tree (potential, inactive, or active cankers). The majority of whitebark pine trees infected with blister rust were part of tree island communities, yielding a density of 2.65 cankers per tree. To a lesser extent, solitary growing whitebark pines infected with blister rust had a lower density of 0.85 cankers per isolated tree. This higher density of blister rust cankers per tree found among whitebark pine in tree island communities is similar to findings of Resler and Tomback's (2008) study. Perhaps a higher infection rate of tree island whitebark pine rather than solitary whitebark pine could be attributed to the shear size, or footprint, of a tree island, which may increase the likelihood of trapping fungal spores in transport. One other possibility is that the dense grouping of trees in a tree island provides shelter and creates more humidity than a solitary whitebark pine, and thus may serve as a potential moisture source for blister rust development as well as shelter and survival of the alternate host, *Ribes* spp.

Study findings show that blister rust intensity is geographically variable across the latitudinal transect. The highest number of cankers (115) and canker density (8.88/tree) were found in the southernmost treeline site near Firebrand Pass, yet another similar finding to that of Resler and Tomback's (2008) study where they found a higher total canker incidence in their southernmost site at Divide Peak. This finding seems to contradict the conception that blister rust incidence increases with colder more northerly latitudes, and suggests it favors more southerly latitudes. However based on blister rust intensity found at the site with the second highest blister rust intensity (Otokomi Lake, midway up the sampling transect) (Figure 5.1), there does not appear to be a clear relationship between blister rust intensity and latitude. In this study, only two of the quadrat sampling sites showed no signs of blister rust - these sites were Ptarmigan Lake (PL-Quad1) and Triple Divide Pass (TD-Quad3). Again, these results do not indicate a relationship between blister rust incidence and latitude, at least within the range of latitudes represented in this study. Expanding the latitudinal range of the study sites may yield different results. However, in this fine scale study, findings suggest other factors play a role in blister rust incidence and intensity.

Blister rust incidence and intensity have topographic variation. The topographic characteristics of the sites with the highest blister rust infection show an apparent pattern between total canker density and the shape and orientation of the land. Quadrat sampling sites near Firebrand Pass had the highest proportion of northwest facing slopes, very close proximity to perennial streams, the highest average flow accumulation, and among the gustiest wind speeds. All of the sampling sites at Otokomi Lake, the site that exhibited the second highest blister rust density, had the closest proximity to perennial streams, and had high wind speeds. It is evident that these topographic variables and total blister rust canker density have a high degree of correlation.

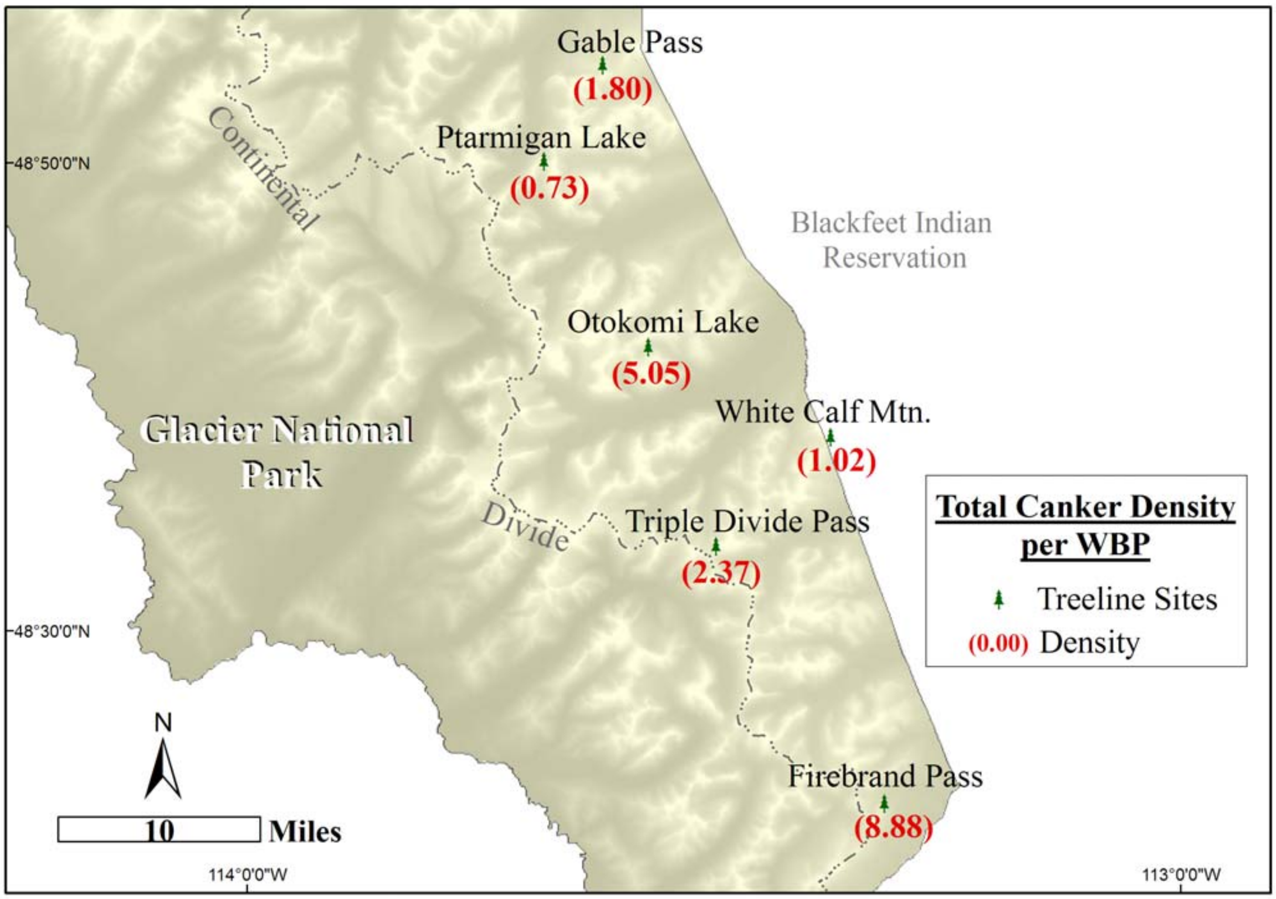

Figure 5.1 Total canker density per whitebark pine at each of the treeline sites.

THE ENVIRONMENTAL CORRELATES OF BLISTER RUST INTENSITY: WIND, ASPECT, FLOW ACCUMULATION, AND PROXIMITY TO PERENNIAL STREAMS

The model results show that a combination of the right factors of wind, northwest facing aspect, flow accumulation and distance to perennial stream may lead to potential areas of blister rust hazard. An important question to ask after model regression analyses is, do the results make sense? I believe these variables do make sense.

Areas prone to gusty wind episodes (such as mountain environments) (e.g. Barry, 2008) may indeed facilitate 'hot spots' for blister rust fungal spore transport. The blister rust life cycle involves a complex process of spore development, and frequent transfer between white pine host and alternate host (Hoff and Hagle, 1990). Wind is a logical transport mechanism for the dispersal of blister rust spores, and faster wind speeds enable fungal spores to travel longer distances.

The relationship of northwest facing slopes with higher likelihood of blister rust intensity supports previous research (White et al., 2002). At a larger scale, slopes with northwest aspects in Glacier National Park and other parts of the Northern Rocky Mountains experience cooler, moister conditions due to orographic uplift of airflow from the prevailing westerly winds (Finklin, 1986) that may prove conducive to fungal spore development. Northwestern-facing slopes receive a share of moisture from weather systems that move southeastward from Canada and cross over the Continental Divide; a condition that ecosystems on the western slopes of the Divide frequently endure. At a finer scale, the study site quadrats exhibiting northwest facing terrain had a higher density of blister rust cankers per whitebark pine tree. These findings seem to support the assumption that cool, moist conditions encourage blister rust development, and that southeast facing slopes (having more sun exposure than northwest facing slopes) may be too warm and dry for spore development.

Areas with high flow accumulation are characterized by downslope flows of runoff that tend to concentrate in low topographic areas. This flow accumulation concept may also apply to cool air masses that settle down in low drainage depressions. Low areas with poor drainage are environments that foster soil water retention, and may provide hospitably cool and moist conditions for blister rust development.

Lastly, the regression model shows an inverse relationship between the distance to perennial streams and blister rust density. Based on GIS analysis, I observed networks of perennial streams to be more extensive in the higher reaches of the mountains, and found more prevalent near the ATE sampling sites, compared to lakes. Perennial streams provide moist environments, and may provide favorable conditions for fungal spore development in the blister rust life cycle. The prediction model suggests the closer a whitebark pine is to a perennial stream, the higher likelihood of infection by blister rust.

THE INSIGNIFICANT VARIABLES IN BLISTER RUST PREDICTION: PROXIMITY TO RIBES, AND OTHER TOPOGRAPHIC VARIABLES

Contrary to my initial prediction that strong correlations may exist between blister rust intensity and the proximity of *Ribes* spp., multiple regression analyses did not find the distance to *Ribes* to be a significant predictor of blister rust infection ($P > 0.10$). One possible reason for this finding is that *Ribes* plants were found extensively throughout the alpine treeline ecotone, and there seemed to be no limitation as to where it could grow. Often found growing within the protection of tree islands, it was also observed as individual plants in exposed, unsheltered locations. In many instances, *Ribes* spp. was located close to the sampling quadrat boundaries, if it was not within the sampling quadrat, (Figure 5.2). Due to the frequency of *Ribes* plant locations within the proximity of quadrats, any correlation pattern between its presence and blister rust incidence may be indiscernible.

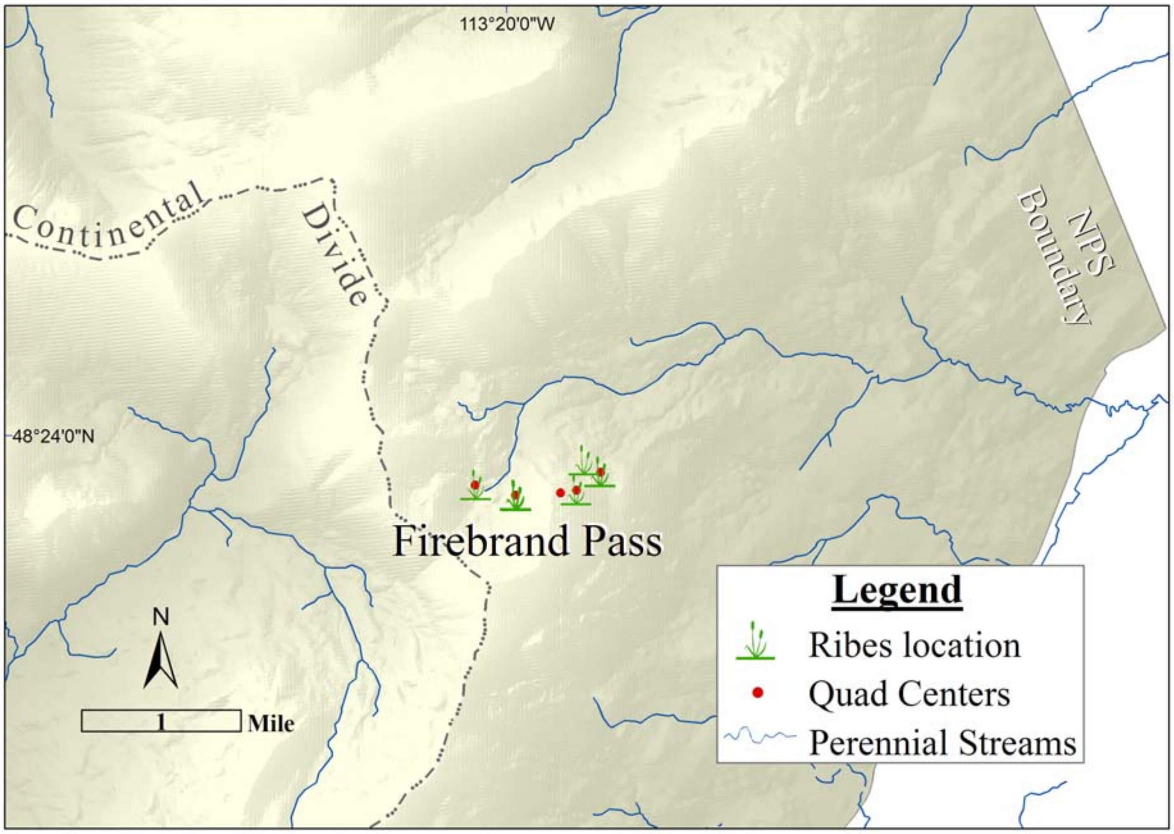

Figure 5.2 Example of *Ribes* spp. locations at a treeline site, and proximity to quadrats.

Curvature was a variable I felt could be a potentially important factor in explaining variability of blister rust incidence. Undulating terrain surfaces have a higher potential for increased soil water retention, preservation of snowpack, and higher retention of snowmelt and runoff. Increased curvature in the terrain seemed to be a viable source for moisture and could potentially facilitate blister rust incidence. Many of my study sites were characterized by alternating hummock and hollow topography intermixed with miniature patterned ground (e.g. Butler and Malanson 1989; 1999). However, curvature was not a significant predictor of blister rust incidence in this model. Alternatively, the variable flow accumulation, another indicator of moisture, was a significant predictor of blister rust incidence ($P < 0.05$).

Slope, elevation, and close proximity to open water bodies were expected to be additional important predictor variables of blister rust incidence. In previous studies, (Van Arsdel, 1965; Geils et al., 1999; White et al., 2002) topographically high areas characterized by steep slopes, and a close proximity to lakes and wetlands, have been associated with a higher hazard for blister rust incidence. These research studies showed that areas located on ridges with high slope gradients, are the initial receivers of wind-dispersed fungal spores. Lakes generate breezes that pick up speed and moisture as they travel across the waterbody, potentially carrying spores and transporting blister rust several miles away.

Although the Otokomi Lake sampling sites (second highest total canker density) had the steepest slopes, and were close to waterbodies and streams, these variables were determined insignificant in predicting blister rust incidence ($P > 0.1$). Despite the insignificance of these particular variables in this blister rust model, moisture (in the form of flow accumulation and proximity to perennial streams) and wind were highly correlated with blister rust incidence. Small lakes (such as cirques) and larger waterbodies (the largest being St. Mary’s Lake, Sherburne Lake, and Two Medicine Lake) were within proximity of most of the study sites. However, perennial streams in the highest extents of our treeline study sites were more prevalent. Topographic depressions, nearby perennial streams, and orographic winds appear to provide the moisture and transport resources needed for blister rust development and proliferation in the alpine treeline ecotone.

I anticipated that the amount of sun exposure on a surface (potential solar radiation) could influence blister rust incidence in two possible ways, and therefore it was included in the regression analyses. First, increased sunlight on a terrain surface could result in dry soil conditions, which could inhibit blister rust incidence. On the other hand, warmer conditions associated with an increase in solar radiation could favor the growth of *Ribes* spp., enabling this alternate host plant to grow extensively throughout the alpine treeline ecotone, and potentially increase the risk of blister rust incidence. Nevertheless, potential solar radiation was not a significant predictor in blister rust incidence ($P > 0.1$).

POTENTIAL USES FOR THE BLISTER RUST MODEL

Previous studies conducted in the Midwestern region of the United States have mapped white pine blister rust hazard based on environmental variables similar to those used in this study (Van Arsdel, 1961; Van Arsdel, 1964; White et al., 2002). As technology develops and detailed data becomes more readily available, maps predicting potential blister rust hazard areas can be improved and extended to mountainous regions. Such predictive maps may prove useful for implementation of conservation management practices, such as those that investigate genetic resistance of white pines to blister rust disease (e.g. McDonald and Hoff, 2001). Knowing where potential hazard areas are may help target strategic planting of genetically resistant trees. Also, identifying areas with high potential for infection may save time and money in planning reconnaissance trips for future studies of blister rust. This study provides important baseline data for such future initiatives.

FURTHER RESEARCH FOR THE BLISTER RUST MODEL

The integration of additional variables into the regression model would have been desirable if time had permitted. Climate in particular, is an important variable that I would like to consider in the blister rust prediction model. Specifically, the variability in temperature, precipitation and relative humidity are seemingly important variables to consider when examining the dynamics of fungal diseases. Climatic data, which integrates the effects of elevation, is an especially important consideration within mountainous terrain.

CONCLUSIONS AND CONSEQUENCES FOR TREELINE

The fieldwork conducted for this study in Glacier National Park provided a first hand look at the alarming extent of blister rust in the alpine treeline ecotone, and the serious consequences this disease has for whitebark pine and treeline. Some of the oldest krummholz whitebark pine, surviving for many years at higher and steeper slopes than any other tree species in the harsh climate of the ATE, were found covered in blister rust cankers. This disease appears to have no bounds.

Blister rust intensity exhibited geographic variation within the ATE study sites. While a latitudinal trend of blister rust intensity was not apparent in this particular 40-mile swath of sampling sites, two distinct relationships were found. These relationships are 1) an increase in blister rust canker density among whitebark pine tree islands, and 2) a high degree of correlation between blister rust canker density and the combination of 4 topographic factors, northwest aspect, wind speed, flow accumulation, and distance to perennial streams.

This study provides additional evidence that the spatial distribution of blister rust continues to expand; the cold, dry regions that were thought to be inhospitable regions for the pathogen are clearly no longer a barrier to its proliferation. Implications of the spread of blister rust into alpine treeline include hastening the decline of whitebark pine, and the associated decline of high elevation tree islands. Furthermore, the devastating toll of blister rust infection on whitebark pine has numerous ramifications for treeline dynamics, including changes in our understanding of treeline response to climate change and the potential loss of high mountain ecosystem processes that rely on this important foundation and keystone species. Expanding our knowledge of the patterns and processes of blister rust, and furthering this research in the realm of landscape ecology and forest pathology is essential for conservation management in whitebark pine ecosystems.

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