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Blister Rust Incidence in Treeline Whitebark Pine, Glacier National Park, U.S.A.: Environmental and Topographic Influences

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Abstract

Whitebark pine (*Pinus albicaulis*) is a foundation and keystone species of upper subalpine and treeline ecosystems throughout the western United States and Canada. During the past several decades, *Cronartium ribicola*, an introduced fungal pathogen that causes white pine blister rust in five-needled pines, has caused significant declines in whitebark pine throughout its range. Our research objectives were to examine geographic variation in blister rust infection (total canker density) in whitebark pine found at six alpine treelines east of the Continental Divide in Glacier National Park, Montana, and to determine which environmental factors have the greatest influence on blister rust infection at treeline. Within a total of 30 sampling quadrats (five at each treeline study site), we measured the number of cankers on each whitebark pine in order to assess how blister rust infection varied throughout our study area. We created high-resolution digital elevation models to characterize surface microtopography, and used a geographic information system (GIS) to derive environmental variables of interest. A mixed effects, Poisson regression model determined environmental correlates of blister rust from the resulting set of field and GIS-derived variables. We found that rates of infection varied considerably among treelines, and that treeline sites exhibiting high flow accumulation rates, greater distances to wetlands, slopes facing southwest, higher curvature, greater wind speeds, and close proximity to *Ribes* and perennial streams had the highest rates of blister rust infection.

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Introduction

Landscape pathology is an interdisciplinary field that integrates theory and methods from landscape ecology and forest pathology in order to understand the spread, dynamics, and influence of pathogens on landscape spatial pattern, as well as the influence of landscape on disease (Holdenrieder et al., 2004; Lundquist, 2005). One understudied, yet increasingly important application of landscape pathology is examining how pathogens may affect ecosystem dynamics through mortality of keystone and/or foundation species. Both keystone and foundation species play essential roles in the stability of forested ecosystems; keystone species sustain ecosystem functioning and biodiversity to a greater proportion than their biomass would suggest (Paine, 1995), and foundation species, because of their abundance, define structure and ecosystem dynamics. The loss of keystone and foundation species could result in ecosystem instability through loss of biodiversity and changing species interactions (Ellison et al., 2005). Such changes could have profound effects on vegetation pattern and landscape functioning; however, the specific impacts of resulting changes in many forested ecosystems remains to be seen.

Whitebark pine (*Pinus albicaulis*) is a keystone and foundation species of high-elevation subalpine and treeline ecosystems of western United States and southwestern Canada (Kendall and Arno, 1990; McCaughey and Schmidt, 1990; Tomback et al., 1995; Murray et al., 2000; Ellison et al., 2005). White pine blister rust, caused by the fungal pathogen *Cronartium ribicola,* is an introduced disease that infects five-needled white pines (Family Pinaceae) and has devastated populations of whitebark pine, the pine most susceptible to the disease (Hoff and Hagle, 1990; Tomback et al., 1995). The decline of whitebark pine populations due to blister rust is likely to have serious landscape consequences, given its many ecosystem services, which include stabilizing soil, rock, and snowpack (Arno and Hoff, 1989); providing a food source for several wildlife species (Kendall and Arno, 1990); and facilitating the establishment of other tree species (Arno and Weaver, 1990). In exposed areas within the alpine treeline ecotone (ATE), whitebark pine grows in a dwarfed, krummholz form (shrub-like, wind- and weather-battered trees) (Ogilvie, 1990; Holtmeier, 2009), and in some locations, initiates tree island establishment (Resler and Tomback, 2008). Seed dispersal of whitebark pine is dependent on the Clark's nutcracker (*Nucifraga columbiana*), which co-evolved with whitebark pine and typically results in the propagation of whitebark pine across expansive areas high in elevation (Hutchins and Lanner, 1982; Tomback, 1982; Tomback and Linhart, 1990; Tomback et al., 1995). Though fire suppression and mountain pine beetle infestations have also contributed to declines in whitebark pine populations throughout its range, (Kendall and Arno, 1990; Keane and Arno, 1993), more than 90% of whitebark pine mortality in the northwestern portion of its range is due primarily to blister rust (Kendall and Arno, 1990), with mortality especially prevalent in the northern Rocky Mountains (Kendall and Arno, 1990; Keane et al., 1994).

The complex blister rust life cycle involves a white pine host, an alternate host species, and the development of five kinds of spores (Hoff and Hagle, 1990; McDonald and Hoff, 2001). Currants and gooseberries (members of the genus *Ribes*) have long

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been recognized as the most common alternate host species for blister rust since the introduction of the disease to North America in the early 1900s, though McDonald et al. (2006) suggested that the sickletop lousewort (*Pedicularis racemosa*), and scarlet Indian paintbrush (*Castilleja miniata*) also may serve as alternate hosts. The potential for blister rust infection of white pine tree species exists in areas where white pines and *Ribes* coexist (which is across the entire range of some white pine species) (Kinloch, 2003), though regional variation in disease intensities have been documented both within and among different species of white pine (Smith and Hoffman, 2000; Kendall and Keane, 2001).

In many mild, moist environments (Van Arsdel et al., 1956) white pine blister rust is prevalent in subalpine whitebark pine populations (Hoff and Hagle, 1990; Campbell and Antos, 2000). Though studies of blister rust incidence in the highest extents of the alpine treeline ecotone are limited, Resler and Tomback (2008) revealed that blister rust infection in whitebark pine is also found in the continental environments of alpine treelines on the eastern slopes of the northern Rocky Mountains (Resler and Tomback, 2008), which is also the focus area of this study.

At alpine treelines, the distinct characteristics of tree structure (e.g. patchy, heterogeneous, and environmentally stunted growth forms), environment (e.g. high microclimatic variability, exposure to wind), and susceptibility of treeline to impacts from climate change may create potential for blister rust infection that is distinct from that found in the subalpine. Furthermore, given the importance of whitebark pine as a biogeographic component of treeline, and its role as a keystone and foundation species (Kendall and Arno, 1990), the decline of whitebark pine populations has potentially serious implications for treeline ecosystems (Tomback and Resler, 2007). In order to understand more about the current and potential future impacts of blister rust–induced whitebark pine mortality on treeline dynamics, the goal of this study was to determine which environmental factors influence blister rust infection incidence and intensity specifically at alpine treeline. Through field sampling, analysis of environmental variables derived from geospatial technologies, and subsequent statistical modeling, our specific objectives were (1) to characterize geographic variation in the disease incidence at sampling locations situated east of the Continental Divide in Glacier National Park (GNP), and (2) to determine key environmental variables (i.e., topographic characteristics, proximity to alternate host species, proximity to water) influencing blister rust infection rates in whitebark pine at six alpine treeline locations in GNP.

This study makes use of both global positioning systems (GPS) and geographic information systems (GIS), which are important tools in estimating disease risk in natural landscape systems (Nutter et al., 2002). Relatively little work has been conducted in mapping landscape disease at the alpine treeline ecotone, with most whitebark pine–related mapping studies focusing on subalpine ecosystems. Several studies (Van Arsdel, 1964; Geils et al., 1999; White et al., 2002; Sturdevant and Kegley, 2006) cite the need to consider topographic and environmental variables when analyzing the spatial patterns of blister rust disease across the landscape. Utilizing GIS to study blister rust incidence among treeline whitebark pine enables a broad scale approach to the study of treeline landscape dynamics, and allows the simultaneous input of many environmental factors into a model.

Study Area

Study sites were located on the eastern slopes of the Lewis Range in Glacier National Park, Montana, U.S.A., which is part of the Waterton-Glacier International Peace Park that extends from Montana into Alberta, Canada. GNP is situated in northwest Montana and straddles the Rocky Mountain Continental Divide, which creates two characteristic 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 (Finklin, 1986). Due to a rain shadow effect, decreasing rainfall and winter snow accumulation results with an eastward progression from the Divide (Harris et al., 1997).

The rugged terrain in GNP was sculpted by ice during the Pleistocene Epoch, with some additional modifications associated with Holocene neoglacial and periglacial activity (Butler and Malanson, 1989, 1999; Carrara, 1990; Harris et al., 1997). The mountains and valleys of GNP exhibit geology distinct from the granite and metamorphic bedrock of its southern Rocky Mountain counterparts (Whipple, 1992). 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 biodiverse 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 (Carrara, 1990; NPS, 2008).

Methods

The purpose of field sampling was to determine where and to what degree blister rust has infected treeline whitebark pine, to locate and document alternate host species, and to measure site conditions and characterize the microtopography of the sampling sites. Our fieldwork was conducted in July 2008 at six alpine treeline study sites east of the Continental Divide, situated roughly along a north-south latitudinal transect: Gable Pass, Ptarmigan Lake, Otokomi Lake, White Calf Mountain, Triple Divide Pass, and Firebrand Pass (Fig. 1). These locations were chosen based on presence of whitebark pine as determined through the authors' knowledge of the area and through investigation of a vegetation base map that delineated whitebark pine woodlands and krummholz ecosystems developed under the U.S. Geological Survey–National Park Service Vegetation Mapping Program (USGS, 2007). At the treeline study sites, whitebark pine grew as part of tree islands, or as solitary individuals independent of tree islands (typically stunted or in krummholz growth form). Tree islands were defined as spatial clusters of at least two trees with overlapping foliage. Many solitary whitebark pines were found in the protection of rocks or other microshelters. Table 1 lists the range of site characteristics at each of the treeline study sites.

The methodology involved three primary tasks: (task 1) conduct a field study to quantify blister rust intensity (total canker density) among alpine treeline whitebark pine populations, measure the proximity of these populations to potential host species, and record site conditions (wind speed, general slope, and aspect readings) at each sampling quadrat; (task 2) create a fine-scale Digital Elevation Model (DEM) that represented the surface microtopography of each quadrat, derive topographic variables from these DEMs, and measure the proximity of each quadrat to water bodies using GIS; and (task 3) determine how the selected environmental and topographic variables (independent variables) influence blister rust infection rates (dependent variable) observed in GNP, using statistical modeling.

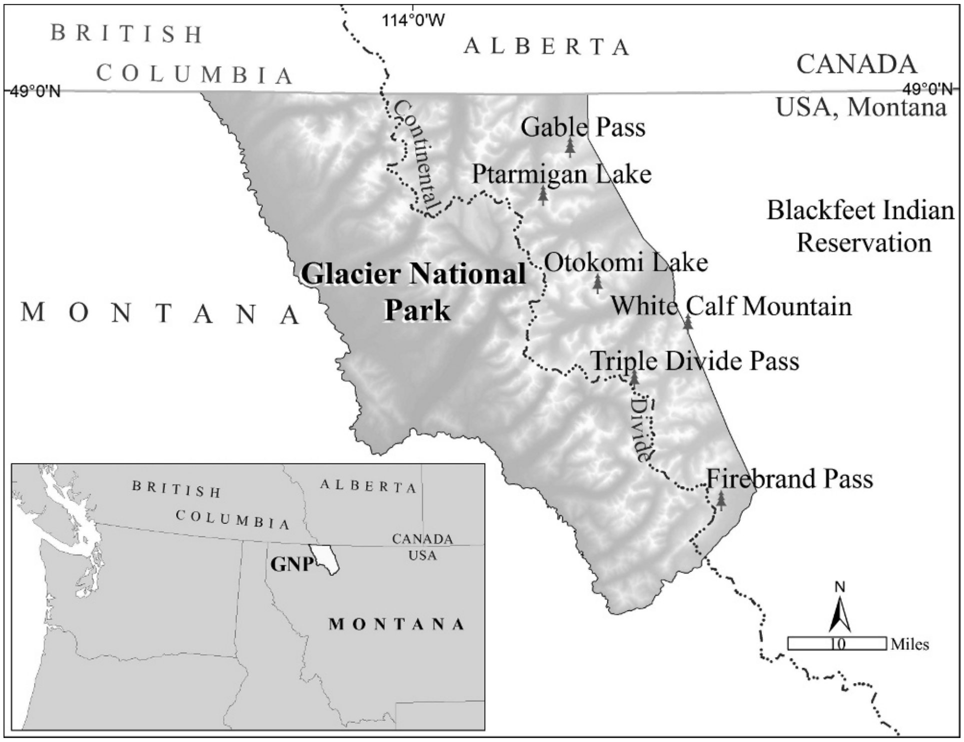

FIGURE 1. Treeline study sites within Glacier National Park, Montana, east of the Continental Divide.

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

A total of 30 quadrats (five at each treeline site), each with a 15 m fixed-dimension, delineated boundaries for sampling whitebark pine and blister rust incidence (Smith, 2009). The purpose of selecting fixed-area quadrats was to establish a standard area for examining whitebark pine trees that were distributed spatially over the landscape, and also to enable density measurements (Kent and Coker, 1994). Quadrats were placed using a random pin toss, and represented varying slopes, aspects, and elevations observed at our treeline sites. Within a treeline site, the distance between adjacent sampling quadrats ranged from 50 to 545 m apart. We conducted vegetation inventories within the sampling quadrats following similar field methods outlined in Resler and Tomback (2008). Species composition, length, width, and height dimensions were recorded for each individual tree and tree island. Each whitebark pine tree was examined for the presence or absence of blister rust. If blister rust was present, we enumerated and characterized the number of cankers per tree. Following Hoff (1992), canker classes denoted 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) (Fig. 2). In a few instances, lengths of the tree islands were in excess of 35 m; in these cases, only whitebark pine trees that fell within the sampling quadrat were examined for blister rust. In addition, if blister rust was present, percent canopy kill (to roughly quantify needle die-off) was visually estimated and 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.

TABLE 1

Site Characteristics: range of values observed at each treeline site.

Treeline site (latitude/longitude)	Elevation (m)	Slope (°)
Gable Pass (48.92°N, 113.65°W)	2213–2240	16–23
Ptarmigan Lake (48.85°N, 113.71°W)	2086–2129	19–31
Otokomi Lake (48.72°N, 113.59°W)	1962–2090	27–38
White Calf Mountain (48.66°N, 113.39°W)	2170–2220	21–24
Triple Divide Pass (48.58°N, 113.51°W)	2177–2259	13–31
Firebrand Pass (48.4°N, 113.32°W)	1951–2171	18–31

Generally, finding the presence of a host species and alternate host species within close proximity across a landscape may increase the likelihood for finding disease-infected trees (Holdenrieder et al., 2004). Since several species of *Ribes* can serve as hosts for white pine blister rust (Newcomb, 2003), the location of these hosts in relation to infected whitebark pine is potentially important information for determining the spatial distribution of blister rust. While hiking to each sampling quadrat, we scouted out locations of *Ribes* plants and recorded their locations with a GPS. In circumstances where we found several different *Ribes* plants within close proximity, we designated the entire area as a *Ribes* location due to time constraints associated with geolocating every plant. Upon returning from the field, we calculated the distances from the sampling quadrats to these potential host plant areas in a GIS using a spatial analysis proximity tool.

Wind speed and direction, which are highly influenced by topography, 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 due to the spatio-temporal variability of the topographically channeled winds, measuring the general wind

FIGURE 2. **Active blister rust canker found on whitebark pine, exhibiting aecial sacs.**

speed for a fixed time period was possible. Using a Kestrel® handheld anemometer, we recorded wind speed for two minutes, at two different locations within each quadrat. These measurements were then averaged in order to estimate wind speed for each sampling quadrat. Though these measurements represent a snapshot in time, they served to characterize the nature of topographically influenced wind at each study site and sampling plot.

Topographic orientation and gradient control the exposure of a given surface to oncoming weather systems, sunlight, wind, and overall drainage. Sufficient moisture, cooler temperatures, and steeper slopes have been associated with higher incidences of blister rust (Van Arsdel et al., 1956; White et al., 2002). For this reason, we recorded aspect and slope measurements at each quadrat during field data collection, using a compass and clinometer. These field measurements are based on visual estimates and a general one-dimensional plane of the surface for each study site, and were used to validate the DEM-derived topographic variables (Task 2).

TASK 2: CHARACTERIZING TERRAIN: DEVELOPING A GPS-DERIVED DEM AND DERIVING MODEL VARIABLES IN GIS

The second task of the methodology involved the creation of high-resolution GPS-derived DEMs to characterize the terrain for each ATE site and sufficiently represent curves, depressions, and slopes; and derive topographic variables to correlate with blister rust incidence. Publicly available DEM data in 10 m (1/3 Arc Second) resolution data sets are available for GNP from the USGS (http://seamless.usgs.gov). However, because we were interested in characterizing the topography for 15 m × 15 m sampling quadrats, a 10 m resolution USGS DEM was insufficient for representing terrain variability for such a small area. Since all of the sampling sites for this study were in open areas at the ATE with virtually no tree cover, it was anticipated that GPS-derived DEMs created in this environment would yield representative terrain surfaces.

Prior to fieldwork in Glacier National Park, we tested and validated a method for creating GPS-derived DEMs by comparing our handheld, submeter differential GPS-derived elevations with LiDAR data. Smith (2009) provides a description of the validation technique and the methods that we used to generate DEMs in the ATE study sites of Glacier National Park. In GNP, we collected GPS points while traversing each vegetation sampling quadrat and represented the land surface by considering changes in slope gradients (breaklines), recording high and low points, and molding depressions and ridges present across each quadrat. After field collection, differentially corrected GPS points were spatially interpolated through a series of GIS analyses using spatial analysis and geostatistical tools outlined in Smith (2009). A representative terrain (in the form of a DEM) of submeter resolution was achieved for each quadrat. Subsequently, ArcGIS Spatial Analyst and ModelBuilder (ESRI, 2006) were used to calculate topographic surface raster layers from each DEM for inclusion as variables in a regression model to predict blister rust occurrence. These DEM-derived layers were slope, aspect, curvature, flow accumulation, and potential solar radiation. Examples of a final DEM raster surface and some of the derived topographic variables included in the initial model run are shown in Figure 3.

We considered shape and orientation of the landscape as factors that could potentially influence blister rust incidence given their effects on surface water collection and distribution, and the established relationship between moisture and spore production in the blister rust life cycle (Van Arsdel et al., 1956). From a hydrological perspective, topography influences flow rate, direction, and retention of water, and is widely used in land surface analyses (Zevenbergen and Thorne, 1987). Curvature surfaces derived from each of the DEM quadrat study sites represent the concavity and convexity of a surface and were included in the analysis because we suspected that increased concavity may help retain snowpack, or capture snowmelt or runoff from rain events. ‘Flow accumulation,’ which indicates how much drainage flows through the DEM surface, was an additional moisture indicator used in this study. High amounts of flow accumulation indicate topographically low areas of a surface where drainage accumulates (ESRI, 2006).

Orientation of the land surface affects the amount of exposure of a tree to wind (and fungal spore transport), sun, and weather; therefore, we considered the influence of slope and aspect on rates of blister rust in our analysis. Slope and aspect raster layers 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 and were comparable to the field measured aspect values. This comparison helped support the DEM creation process, and helped validate surface representation.

Warm surfaces exposed to sunlight (especially those within a rain shadow) 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. We derived potential solar radiation from each of the DEM quadrat surfaces using GIS, calculating the amount of incoming solar radiation received by each cell of a surface throughout the year (in this case the year 2008 was used). It was anticipated that

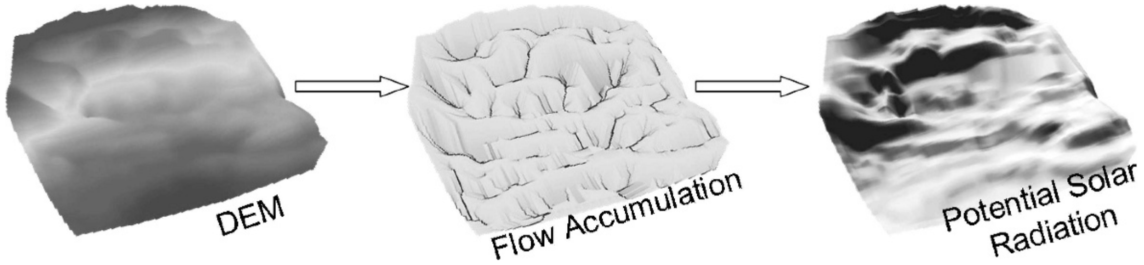

FIGURE 3. Schematic example of derived topographic variables from a submeter DEM quadrat surface (site WC-Quad2), 3D terrain surfaces displayed in ArcScene.

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).

Finally, we considered 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). For this study, GIS hydrography layers were obtained from the National Park Service (NPS) GIS Data Store (http://science.nature.nps.gov/nrdata/). We considered areas of year-round water availability to be potentially important factors contributing to blister rust infection; therefore, we incorporated perennial streams, lakes, and wetlands in this analysis. We calculated distances from quadrats to each of the streams, lakes, and wetlands GIS layers using a spatial analyst proximity tool and a USGS 10 m DEM. Due to the mountainous terrain of our study area, which may serve as obstacles or barriers to wind-spread fungal spores, we calculated the surface path distance, which takes into account terrain characteristics, rather than the Euclidean distance. The resulting mean distances to water bodies from each quadrat (averaging all cell distances within the quadrat) were incorporated in the regression analysis.

The final independent variables examined in this study are either field-derived, GIS-derived, or a combination thereof (Table 2). The dependent variable used to quantify blister rust incidence, total canker density, was compared with these independent environmental variables in the Poisson regression analysis (task 3). Total canker density is defined as the number of blister rust cankers found within the sampled whitebark pine population, controlling for the number of whitebark pines.

TASK 3: STATISTICAL ANALYSIS

Since spatial dependence among our quadrats within each treeline site was suspected, we used a mixed-effects rate model to address potential problems associated with pseudoreplication (Hurlbert, 1984). The purpose of the statistical model was to uncover important environmental and topographic correlates of blister rust infection in treeline whitebark pine. Ideally, we would have conducted a cell-by-cell comparison of DEM-derived topographic variables and blister rust intensity through spatial analysis in GIS. However, given time, personnel, and cost limitations, rates of blister rust were quantified at the quadrat level; therefore, we aggregated detailed topographic and field-derived variable statistics for each quadrat. DEM-derived, raster values were summarized for each quadrat in a GIS using zonal statistics. We feel confident that the detail of these surface variables was not lost; far more information went into characterizing the terrain than could be achieved from a readily available USGS 10 m DEM. Furthermore, the submeter DEM allowed us to calculate the proportions of each quadrat surface within four aspect categories which could not have been done at this level of scale with a USGS 10 m DEM.

Pearson correlations and scatterplot matrices for all variables generated in JMP® v. 7 (SAS, 2007) helped to determine which variables were contributing redundant information. The plots indicated that two curvature variables (flow acceleration and deceleration, flow convergence and divergence) supplied redundant information and, therefore, we chose only to include the curvature profile variable in the analysis. Using GIS we partitioned and reclassified our aspect raster layers, and calculated the numeric proportion of each quadrat falling within four aspect categories: NE, SE, SW, and NW. These four categories represent mesic, xeric, and intermediate conditions and are commonly used

TABLE 2

Field and GIS-derived independent and dependent variables.

Field/GIS measurements	Variable	Unit of measure	Independent/dependent variable
Field	Wind speed —	miles per hour	Independent
Field and GIS	Elevation —	meters	Independent
GIS	Slope —	degrees (0–90°)	Independent
GIS	Aspect —	azimuthal direction (0–360°)	Independent
GIS	Curvature —	1/100 m	Independent
GIS	Potential solar radiation —	watt hours/m^2	Independent
GIS	Flow accumulation —	#cells contributing to flow	Independent
Field and GIS	Distance to *Ribes* spp. —	meters	Independent
GIS	Distance to perennial streams —	meters	Independent
GIS	Distance to lakes —	meters	Independent
GIS	Distance to wetlands —	meters	Independent
Field	Total canker density (total cankers per whitebark pine) —	cankers/tree	Dependent

in forest ecology studies (Beers et al., 1966; Jain et al., 2004; Letts et al., 2009). We calculated numeric proportions to provide a range of aspect values within the quadrat rather than assign one predominant aspect. For example, the terrain surface for WC-Quad4 is predominantly facing SE; however, the proportion within each of the four aspect categories is: NE (26%), SE (37%), SW (19%), and NW (18%).

Fourteen independent environmental variables (including field and GIS-derived variables) were included in the initial Poisson regression models. These were: mean elevation, proportion of aspect (four categories), mean slope, mean wind speed, mean curvature profile, maximum flow accumulation, maximum potential solar radiation, mean distance to *Ribes*, mean distance to perennial streams, mean distance to lakes, and mean distance to wetlands. The statistical method of aggregation (minimum, mean, maximum, etc.) for these quadrat variables was chosen based on which method was the most logical and easiest to interpret. Using R v. 2.11.0 (R Development Core Team, 2010) we determined the environmental correlates of blister rust infection by fitting a rate model (Faraway, 2006) to our dependent variable, total canker density. The Poisson regression used the independent environmental variables to explain the infection of blister rust by controlling for the total number of whitebark pines within each quadrat by adding it as an offset term. We used forward and backward stepwise regression to choose our final model based on which in the series of candidate models had the lowest Bayesian Information Criterion (BIC). BIC evaluates how well the independent variables explain the dependent variable, but subtracts a penalty for the total number of variables in the model.

Results

A total of 390 individual trees and tree islands were sampled at the six treeline study sites. Of the combined sample, 279 (71.5%) were solitary trees, and 111 (28.5%) were tree islands. Density of trees and tree islands was highest at White Calf Mountain (98.4 trees 1000 m^{-2}) and lowest at Otokomi Lake (19.5 trees 1000 m^{-2}). Species richness among the tree islands ranged from 1 to 7, with *Pinus albicaulis, Pinus flexilis*, *Abies lasiocarpa*, *Picea engelmannii*, *Pinus contorta*, *Pseudotsuga menziesii*, and *Larix lyallii* present among the study sites. Tree islands ranged in length from 0.23 m to 35 m ($\bar{x}$ = 10.5 m ± 9.6), with a maximum threshold value set to 35 m due to their extensive growth habit in our study area. The longest dimensions of individual trees ranged from 0.04 m to 3.74 m ($\bar{x}$ = 0.65 m ± 0.69). A significant but weak correlation existed between the length of the tree island and canker incidence ($r_s = 0.32$, $P < 0.001$).

WHITEBARK PINE AND VARIATION OF BLISTER RUST INCIDENCE AMONG TREELINE STUDY SITES

Among the sampled trees and tree islands, 333 living five-needled white pines were present. Additionally, 97 dead, five-needled pine trees found within the sampling quadrats exhibited evidence of blister rust–induced mortality. Of the total living white pines, 311 were whitebark pine (*Pinus albicaulis*), and 22 were possibly limber pine (*Pinus flexilis*). Limber pine, which has strikingly similar characteristics to whitebark pine especially at alpine treelines where cone presence is diminished (Kendall and Arno, 1990; Kendall, 1994; Kendall and Schirokauer, 1997), is a five-needled white pine [*Pinus* subgenus (*Strobus*)] that also is susceptible to blister rust infection and occasionally found in overlapping habitats. Limber pine was present in small numbers at three of our study sites (White Calf Mountain, Gable Pass, and Firebrand Pass) and, therefore, our analyses and results include the combined occurrence of blister rust in both species and are reported collectively as "whitebark pine."

Of the 333 living whitebark pine sampled at the six treeline study sites, 47% were infected with blister rust. In total, 678 cankers were present on all infected whitebark pine. Of the 219 whitebark pines found in tree islands, 56% were infected with blister rust (581 cankers total were found on tree island whitebark pines, with a range of 1–39 cankers found per tree). However, only 29% of solitary whitebark pines (n = 114) were infected with blister rust (97 cankers in total were found on individual trees, with a range of 1–14 cankers found per tree.). Whitebark pine in tree islands (n = 219) had more cankers per tree ($\bar{x}$ = 2.65 ± 4.66) than solitary whitebark pine (n = 114, $\bar{x}$ = 0.85 ± 1.91); total cankers, $Z = -4.83$, $P < 0.0001$, Mann Whitney U test).

Measurements of whitebark pine and blister rust incidence (specifically, total canker density and percent infection) for each of the 30 sampling quadrats are shown in Table 3. Total canker density and percent infection (our measures of blister rust incidence) varied both within and among treeline study sites. All treelines exhibited infection of whitebark pine by blister rust; however, only two quadrats had 0% blister rust infection: Ptarmigan Lake (PL-Quad1) and Triple Divide Pass (TD-Quad3). Firebrand Pass and Otokomi Lake treeline sites had the highest blister rust incidence. At Firebrand Pass, four out of five quadrats exhibited 100% infection rates, and at Otokomi Lake three out of five quadrats had 100% blister rust infection, with ranges from 2 to 20.33 cankers per tree (Table 3). The treeline sites with total cankers (potential, inactive, and active) ranked from highest to lowest were Firebrand Pass (213), White Calf Mountain (202), Otokomi Lake (106), Gable Pass (101), Triple Divide Pass (45), and Ptarmigan Lake (11). However, when considering the number of cankers per whitebark pine tree, total canker densities ranked from highest to lowest were found at treeline sites: Firebrand Pass (8.87 cankers per tree), Otokomi Lake (5.05 cankers per tree), Triple Divide Pass (2.37 cankers per tree), Gable Pass (1.8 cankers per tree), White Calf Mountain (1.02 cankers per tree), and Ptarmigan Lake (0.73 cankers per tree). We sampled the highest number of whitebark pine trees at White Calf Mountain (nearly 60 trees in one quadrat), and though this treeline site had the second highest number of cankers, this site exhibits comparatively low blister rust incidence since our measure of blister rust incidence and intensity reflects the whitebark pine population.

ENVIRONMENTAL CORRELATES OF BLISTER RUST INFECTION: MODEL RESULTS

We used a Poisson regression mixed-effects rate model to determine the environmental correlates of blister rust incidence. The model relates the total number of blister rust cankers to the environmental variables, while controlling for the number of whitebark pines trees within each quadrat. We added a random effect for 'treeline site' to the rate model, since canker rates among our five quadrats within the same treeline site were correlated (Fig. 4). Using stepwise regression we determined that of the 14 independent variables considered for our model, 8 variables (flow accumulation, distance to wetlands, northeast aspect, curvature, distance to *Ribes*, distance to perennial streams, wind speed, and southwest aspect) were statistically significant ($P < 0.05$) predictors of total canker density (Table 4). The resulting Poisson regression mixed-effects model for the prediction of canker density

TABLE 3

Total canker density, percent whitebark pine infection, canker and canopy kill classes within quadrats.

	Site[‡]	N (# WBP[*])	Total canker density per WBP[*]	% WBP infected[**] per quadrat	# potential cankers	# inactive cankers	# active cankers	Canopy kill class (mode)	% WBP infected[**] per treeline	BR intensity rank per treeline[‡‡] (1 = highest)
	GP-Quad1	18	1.94	44	0	8	27	1	45	4
North	GP-Quad2	15	2.87	73	1	26	16	1		
	GP-Quad3	5	1.00	20	0	3	2	1		
	GP-Quad4	9	0.67	22	0	4	2	1		
	GP-Quad5	9	1.33	33	0	6	6	1		
	PL-Quad1	3	0.00	0	0	0	0	1	33	6
	PL-Quad2	4	0.50	50	0	2	0	1		
	PL-Quad3	3	2.00	33	0	6	0	1		
	PL-Quad4	3	0.67	33	1	1	0	1		
	PL-Quad5	2	0.50	50	0	1	0	1,6 [†]		
	OL-Quad1	4	4.75	75	1	15	3	6	86	2
	OL-Quad2	5	5.60	100	2	23	3	5		
	OL-Quad3	2	16.50	100	1	20	12	1		
	OL-Quad4	6	4.00	100	3	18	3	6		
	OL-Quad5	4	0.50	50	1	1	0	2		
	WC-Quad1	42	1.21	45	10	36	5	2	36	5
	WC-Quad2	23	0.13	13	0	1	2	1		
	WC-Quad3	27	0.59	22	2	11	3	1		
	WC-Quad4	57	1.33	47	5	53	18	1		
	WC-Quad5	49	1.14	33	7	23	26	1		
	TD-Quad1	6	3.50	83	0	11	10	1	68	3
	TD-Quad2	4	1.00	50	4	0	0	1		
	TD-Quad3	1	0.00	0	0	0	0	1 [†]		
	TD-Quad4	3	3.33	100	2	5	3	1,2,7 [†]		
	TD-Quad5	5	2.00	60	1	4	5	2		
	FP-Quad1	3	2.00	100	4	2	0	3	96	1
	FP-Quad2	2	2.50	100	3	1	1	1		
	FP-Quad3	10	11.50	100	3	110	2	3		
South	FP-Quad4	3	20.33	100	0	40	21	3,4,6 [†]		
	FP-Quad5	6	4.33	83	0	17	9	3		

[‡] Site = GP (Gable Pass), PL (Ptarmigan Lake), OL (Otokomi Lake), WC (White Calf Mountain), TD (Triple Divide Pass), FP (Firebrand Pass).

[*] WBP includes whitebark pine at all sites and limber pine at White Calf Mountain, Gable Pass, and Firebrand Pass.

[†] No mode exists, therefore all canopy kill classes are shown.

[**] %WBP infected = (number of WBP with blister rust infection)/(number of total WBP) × 100.

[‡‡] BR (blister rust) intensity rank based on percent whitebark pine infection.

(λ) is (Equations 1–3; for site $i = 1, \ldots, 6$ and quadrat $j = 1, \ldots, 5$):

$$Total\ number\ of\ blister\ rust\ cankers_{ij} \sim Poisson(\lambda_{ij}). \qquad (1)$$

$$\log(\lambda_{ij}) = -1.71 + \log(total\ number\ of\ whitebark\ pines_{ij}) + \sum_{k=1}^{8} X_{kij}\beta_{kij} + \theta_i. \qquad (2)$$

$$\theta_i \sim Normal(mean = 0,\ sd = 1.681). \qquad (3)$$

Overall, the results show a highly significant model ($P < 0.001$, $\chi^2 = 175.78$, df = 8). The deviance for the null model (including only an intercept and a random effect for site) was 268.4. Adding the above eight environmental variables to the model resulted in a deviance of 92.62. A significant amount of the deviance in our rate model for blister rust incidence could be explained by the combined influence of these eight variables. In fact, the deviance $R^2 = 0.655$ can be interpreted as the fraction of uncertainty explained by the fitted model (Cameron and Windmeijer, 1997). This predictive model suggests that, accounting for the number of whitebark pine trees present, areas exhibiting high flow accumulation rates, farther distances from wetlands, less northeast-facing slopes, higher curvature, close proximity to *Ribes* and perennial streams, increased wind speed, and southwest-facing slopes have a higher rate of blister rust infection.

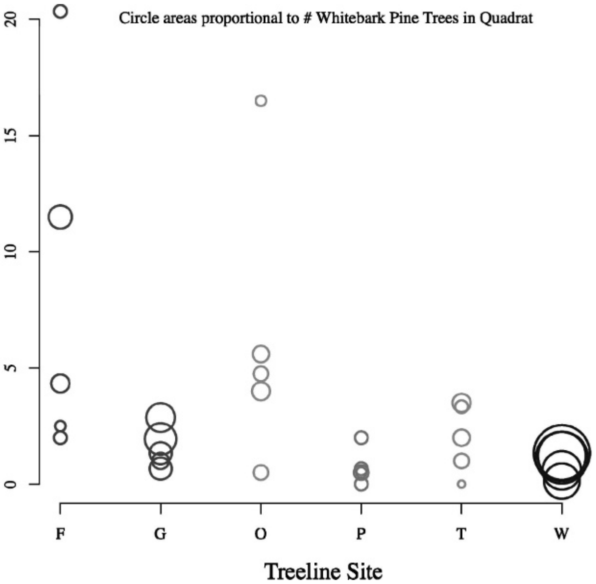

FIGURE 4. Bubble chart showing rate of blister rust cankers per tree, by treeline site. Circle size is proportional to number of whitebark pine trees in each of the sampling quadrats. Five quadrats were sampled at each treeline site. Treeline sites: (F) Firebrand Pass, (G) Gable Pass, (O) Otokomi Lake, (P) Ptarmigan Lake, (T) Triple Divide Pass, (W) White Calf Mountain.

TABLE 4

Results of Poisson regression rate model for predictor variables.

	Independent variable $(X_{1,\ldots,8})$	Estimate $(\beta_{1,\ldots,8})$	Probability (P)	Significance level	BIC* criteria order of importance
(X_1)	Flow accumulation	0.0003445	2.00E-16	$p < 0.001$	Most important (lowest BIC)
(X_2)	Distance to wetlands	0.001934	3.52E-13	$p < 0.001$	↓
(X_3)	NE aspect category (0–90°)	–5.027	1.22E-09	$p < 0.001$	
(X_4)	Curvature	0.1199	1.88E-07	$p < 0.001$	
(X_5)	Distance to *Ribes* spp.	–0.002969	1.14E-06	$p < 0.001$	
(X_6)	Distance to perennial streams	–0.001076	0.000548	$p < 0.001$	
(X_7)	Wind speed	0.05089	0.019589	$p < 0.05$	
(X_8)	SW aspect category (180–270°)	2.027	0.02707	$p < 0.05$	Least important (highest BIC)

* Bayesian Information Criterion (BIC) evaluates how well the independent variables explain the dependent variable.

Discussion

GEOGRAPHIC VARIABILITY OF BLISTER RUST INTENSITY

Our findings indicate that blister rust and its impacts on whitebark pine are well established in treeline ecosystems of the eastern slopes of Glacier National Park. Nearly half of all treeline whitebark pine trees in our study areas exhibited evidence of blister rust infection, with total numbers of cankers ranging from 0 to 115 per sampling quadrat. Similarly to the findings of Resler and Tomback's (2008) study, we found a significant correlation between total cankers and longest dimension of whitebark pine trees and tree islands, and higher canker densities among tree island whitebark pine (total density of 2.65 cankers per tree) compared to those growing solitarily (0.85 cankers per tree). These findings suggest that a relationship exists between landscape pattern at treeline (specifically, the size of tree islands and possibly their connectivity) and blister rust infection, possibly as a result of increased capacity of larger surface areas to trap spores. Foliage area and position within a stand may relate to the probability of infection (McDonald and Andrews, 1981), possibly by creating areas of shelter and moist environments. However, more research needs to be conducted to understand the relationship between patch size and infection, and also to investigate whether tree and tree island microclimates generate humid environments conducive to spore development and germination and survival of alternate hosts.

Blister rust incidence among the six treeline sites selected in this study ranged from 0.73 to 8.87 cankers per tree. However, a high infection rate at a site may not result in high mortality rates if whitebark pine density at a site is low. For example, in our study, the site with the highest canker density (Firebrand Pass, 8.87 cankers per tree, our southernmost site) was characterized by a relatively small number of whitebark pine (24 total whitebark pine). White Calf Mountain, in comparison, had the highest number of whitebark pine among our treeline sites (198 total whitebark pine), though it had one of the lowest canker densities (1.02 cankers per tree). Given the biogeographic importance of whitebark pine at treeline in the White Calf area (Resler and Tomback, 2008), the high density of whitebark pine at this site may suggest a greater long-term impact on treeline ecosystems and dynamics than would be found in sites with a lower pine density.

ENVIRONMENTAL AND TOPOGRAPHIC CORRELATES OF BLISTER RUST INTENSITY IN TREELINE WHITEBARK PINE

The results of the blister rust model indicated that eight of the field and GIS-derived environmental variables (flow accumulation, distance to wetlands, northeast and southwest aspects, curvature, distance to *Ribes*, distance to streams, and wind speed) were significantly correlated with total canker density. The model reveals that whitebark pine trees located in close proximity to areas with more moisture potential and *Ribes* species, and in areas prone to gusty winds, have a higher potential to be infected by blister rust.

Our model results suggest that treeline locations fostering relatively moist conditions may encourage blister rust infection—a result that has been substantiated by many other studies of blister rust infection in white pine communities (Van Arsdel et al., 1956; McDonald and Hoff, 2001; White et al., 2002). Areas with high moisture potential, as characterized by our model, have high flow accumulation rates, increased curvature or concavity of the surface terrain, and are relatively close to perennial streams. The relationship between high blister rust infection and topographically low areas can be explained by the tendency for topographic depressions to encourage the settling of cool air masses, to accumulate snowmelt and rain runoff, and to foster soil water retention. Topographic depressions and nearby perennial streams appear to provide optimal wet conditions for pine infection (Newcomb, 2003) by creating favorably moist environments for both blister rust spore development (Van Arsdel et al., 1956), and growth of *Ribes* species which tend to be abundant in moist locations such as near streams or within valley bottoms (Kendall and Keane, 2001; Kearns et al., 2008).

Treeline areas associated with high blister rust incidence were also found to be prone to high wind speeds, and tended to be within close proximity to *Ribes*. Areas prone to gusty wind episodes (such as mountain environments, e.g. Barry, 2008) may indeed create 'hot spots' for blister rust fungal spore transport, primarily because wind is an important vector of spore dispersal that causes blister rust in whitebark pine. Specifically, basidiospores, the spores that are wind-dispersed from *Ribes* to whitebark pine from late July to October (Agrios, 2005), form only in environmentally limited conditions and dispersal distances tend to be short (McDonald and Hoff, 2001). The relationship between the distance to *Ribes* and blister rust incidence may be explained by the relatively short distance required for successful spore transmittal between the whitebark pine host and alternate host. In our study areas, we frequently observed *Ribes* growing within the protection of tree islands; it was also observed as individual plants in exposed, unsheltered locations. In many instances *Ribes* was located close to our sampling quadrat boundaries, if not within the sampling quadrat. From what we observed and modeled at our treeline sites, the abundance of *Ribes*, and prevalent orographic winds, provide the fungal spore transport resources needed for blister rust development and proliferation in the alpine treeline ecotone.

One unanticipated finding from the model was the positive relationship between blister rust infection rates and distance to wetlands. Though our model indicates that farther distances from wetlands is related to increased blister rust infection, this finding seems to contradict the result that nearby moisture sources and close proximity to *Ribes* plants are important factors in finding blister rust infection. Our results do, however, seem to agree with White et al.'s (2002) study, which found a positive relationship between blister rust incidence and distances 200–1000 m from wetlands. In our study, the distances between sampling quadrats and wetlands exceeded 300 m, and networks of perennial streams near our treeline sampling sites were more prevalent than lakes and wetlands.

Our model results also revealed that blister rust incidence shared a positive relationship with southwest-facing slopes, yet a negative relationship with northeast-facing slopes (Table 4). We found these associations perplexing because, as discussed above, many of our moisture-related topographic variables were positively associated with blister rust infection, and historically, blister rust has had more of an impact throughout mesic portions of the whitebark pine range (Kendall and Keane, 2001). Yet, typically, in the northern hemisphere, southwest-facing slopes are considered to be xeric environments due to the long duration and high intensity of sunlight these slopes receive throughout the growing season (Beers et al., 1966; Jain et al., 2004; Letts et al., 2009). White et al.'s (2002) study found similar relationships between southwest aspect, northeast aspect, and blister rust incidence, and suggested a temperature-related explanation for the negative association between northeasterly aspects and blister rust infection in *Pinus strobus*; they suggested that a shorter growing season may inhibit infection rates on northerly aspects in their northern Minnesota study region. Another possible explanation for our finding is that the large-scale, westerly synoptic weather systems characteristic of our study area create a stronger influence on environment (and thus spore development and pine infection) than does the local, small-scale influence of aspect. West-trending slopes in Glacier National Park typically receive a considerable share of moisture from weather systems that move southeastward from Canada and cross over the Continental Divide; passing of these weather systems typically results in relatively cool and moist conditions due to orographic uplift of airflow from the prevailing westerly winds (Finklin, 1986).

Conclusion

The focus of the model we presented here was to understand environmental factors that relate to blister rust intensity at alpine treelines. However, it is important to note that blister rust infection results from a number of complex interactions among host, pathogen, and environment that ultimately relate to a number of biotic components that were not explicitly evaluated in this study. For example, our study doesn't consider geographic variation of resistant hosts or a full assessment of the density and distribution of all species of alternate hosts.

'Treeline site' was an important random effect in this model, which highlights the importance of geography. Also, the ability to extrapolate our results to treeline locations beyond the sampling quadrats selected for this research is limited. However, we would expect that similar environmental dynamics, if not the specific variables revealed as important in this study, will have a similar influence on blister rust infection throughout its range. The widespread distribution of the pathogen throughout our study sites suggests it is possible that the disease will intensify at these treelines in the future, as will the associated negative impacts on whitebark pine and treeline dynamics. Implications of the spread of blister rust into the alpine treeline ecotone include hastening the decline of whitebark pine, and the associated decline of high-elevation tree islands (Tomback and Resler, 2007). 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, in light of the loss of a keystone and foundation species.

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