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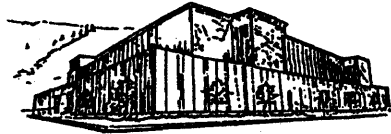
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**White Pine Blister Rust, Whitebark Pine, and *Ribes* species
in the Greater Yellowstone Area**

by

maria newcomb

presented in partial fulfillment of the requirements

for the degree of

Master of Science

School of Forestry

The University of Montana

May 2003

Approved by:



Chairperson



Dean, Graduate School

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White Pine Blister Rust, Whitebark Pine, and *Ribes* species in the Greater Yellowstone AreaDirector: Dr. Diana L. Six *DL S*

White pine blister rust is a tree disease caused by an introduced fungal pathogen (*Cronartium ribicola*) that has resulted in devastating impacts in many coniferous forests of North America. The pathogen alternates between white pine hosts and currant and gooseberry hosts (members of the genus *Ribes*). In western North America, regional differences in disease intensities within and among species of white pine are recognized. Whitebark pine is an ecologically valuable, high-elevation pine host that commonly occurs in relatively pristine habitats including portions of the Greater Yellowstone Area. Chapter 1 presents a study that was aimed at detecting and describing spatial patterns, or associations, between white pine blister rust disease severity in whitebark pine hosts and landscape features related to the *Ribes* host species distributions. No previous studies have related the spatial, landscape distribution of *Ribes* species to the variation in rust severity in whitebark pine stands. In order to relate variation in rust severity to such landscape features, it was necessary to address the fact that whitebark pine trees vary considerably in growth form and size both among and within stands. Host trees from site to site present very different targets to the pathogen. Consequently, a comparison of rust severity among stands with different size distributions requires adjustment for canker capacity (maximum number of cankers expected for trees of a particular size) with a relative severity index. Significant relationships between disease severity and distances to landscape features that relate to *Ribes* species distributions and susceptibilities were found in this study, showing that a spatial pattern of disease severity exists. Moreover, it is possible that the pattern of blister rust disease severities among whitebark pine stands relates to proximities between pine and *Ribes* hosts.

Given the possible role of *Ribes* species proximities in explaining current blister rust disease severities in whitebark pine of the GYA, Chapter 2 addresses the information gap resulting from the fact that recent research programs have generally neglected the role of the *Ribes* hosts. The ecology of *Ribes* hosts in the Greater Yellowstone Area is characterized, initiating the development of a more comprehensive approach to the white pine blister rust pathosystem that considers both host groups. Each *Ribes* species is a unique host that exhibits a distinct spatial association with the pine hosts and a distinct genotypic and phenotypic susceptibility to infection by *Cronartium ribicola*. An overview of nine *Ribes* taxa known to occur in the GYA is presented, with discussion of the ecology and pathology of each.

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“...our ideas grow from our work within a community. To fail to acknowledge the context of our ideas is in part to weaken that community.”

-anonymous

This project received invaluable support in the form of funding and other resources, shared knowledge and insights, and gifts of time and effort. At the most fundamental level all contributions had in common the truest gift of freedom to detour, with accompanying limits on how far the detours could extend. It follows that I refer to the evolution of this project rather than its directional progression. The influences these contributions had on how the project evolved are intertwined, to a degree that I am unable to disentangle, with influences on my education and development. My words of thanks, therefore, carry a depth of meaning that is beyond what words can fully express.

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reviews by Brian Geils, particularly in the development of a disease severity index. Additionally, shared ideas and insights from Jim Hoffman, Holly Kearns, Bill Jacobi, John Guyon, GERAL McDonald, Kim Hummer, and Robert Keane are greatly appreciated. I also learned a lot from the perspective that Detlev Vogler provided as a plant pathology research geneticist.

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CHAPTER ONE:

Patterns of White Pine Blister Rust Severity Among Whitebark Pine Stands of the Greater Yellowstone Area: Relationships with Landscape Features and Site Factors

ABSTRACT

White pine blister rust is a tree disease caused by an introduced fungal pathogen (*Cronartium ribicola*) that has resulted in devastating impacts in many coniferous forests of North America. The pathogen alternates between white pine hosts and currant and gooseberry hosts (members of the genus *Ribes*). Regional differences in disease intensities within and among species of white pine are recognized. Whitebark pine is an ecologically valuable, high-elevation pine host that commonly occurs in relatively pristine habitats including portions of the Greater Yellowstone Area (GYA). Surveys of whitebark pine have found that disease intensities vary greatly across its range. It is known that the pathogen has been present in white pines of the GYA since at least 1945. At present it remains unknown whether ecological conditions in some portions of the GYA are such that whitebark pine populations will remain sustainable even in the continued presence of the pathogen. This study was aimed at detecting and describing spatial patterns, or associations, of white pine blister rust disease severity in whitebark pine hosts and landscape features related to the ecology of the *Ribes* host species. Meeting this objective requires both the determination of a means of quantitatively assessing blister rust disease severity in whitebark pine that enables examination of the variation in disease severity among sites, and the determination of an appropriate spatial scale for investigation.

Field data on tree characteristics and disease severity were collected at 45 sites in whitebark pine stands throughout portions of the GYA over the summers of 2001 and 2002. Additional variables were measured for all these sites using topographic maps of the GYA. A relative index of disease severity was derived to account for problematic differences in tree sizes among sites. This GYA Relative Severity Index was used as the dependent variable in correlation and linear regression analyses of disease severity on independent variables of site factors and distances to landscape features. The landscape features that were considered were selected based on information on the alternate *Ribes* hosts, at the species-level, gained from observations during both field seasons. Significant relationships were found between the GYA Relative Severity Index and two variables that show autocorrelation: distances to 5th order streams and distances to nearest streams at or below 2621 m, a common upper-elevational limit for *Ribes hudsonianum* and *R. lacustre*. Additionally, a possible threshold extended forest cover metric value was detected such that sites with extended forest cover metrics greater than 0.65 all were associated with low estimated disease severities, consistent with findings of other studies. When the GYA Relative Severity Index was only used for sites with extended forest cover metrics less than 0.65, linear regression analysis of disease severity on the mean total and forested distances to streams at or below 2621 m showed that 61 percent of the variability in disease severity was explained by the mean total and forested distances to streams at or below 2621 m. The significant relationships between disease severity and distances to landscape features found in this study show that a spatial pattern of disease severity exists, implying that predictive abilities related to disease progression in this system may be possible.

INTRODUCTION

Research motivation: Rapid global transport of organisms across natural geographic barriers has resulted in considerable ecological, evolutionary, and economic consequences. Many of the exotic species that are introduced are plant pathogens, some of which have resulted in severe ecological and evolutionary impacts (Haack and Byler 1993, Liebhold et al. 1995, Chapin et al. 2000, Palumbi 2001). Several case studies have demonstrated that introduced pathogens can cause catastrophic impacts on forest ecosystem diversity and function (Haack and Byler 1993) and may result in dramatic alterations of evolutionary patterns (Palumbi 2001). For example, the introduced causal agent of Chestnut blight, *Cryphonectria parasitica* (Murrill) Barr, has led to the near elimination of American chestnuts from eastern North American forests. The causal agent of Dutch elm disease, *Ophiostoma ulmi* (Buisman) Nannf., has had devastating impacts on American elms, with only a small proportion of the original population that exhibit genetic resistance or tolerance to the disease still remaining (Kendrick 1992, Schlarbaum et al. 1997, Allen and Humble 2002).

White pine blister rust is a tree disease caused by an introduced fungal pathogen (*Cronartium ribicola*) that has resulted in severe economic and ecological damage in many coniferous forests of North America (Haack and Byler 1993). All North American white pine species (members of the subgenus *Strobos*) are highly susceptible to the pathogen. Because of catastrophic losses in three commercially valuable white pine species [eastern white pine (*Pinus strobus* L.), western white pine (*P. monticola* Dougl.), and sugar pine (*P. lambertiana* Dougl.)], white pine blister rust is recognized as the most damaging conifer disease in North American forests (Maloy 1997, Neuenschwander et al. 1999, Geils 2001). The significance of damage to ecologically valuable tree species in western North America such as whitebark pine (*Pinus albicaulis* Engelm.) (Zeglen 2002), limber pine (*Pinus flexilis* James), foxtail pine (*P. balfouriana* Grev. and Balf.), and southwestern white pine (*P. strobiformis*) has also recently been recognized (Tomback 2003). As the research emphasis on white pine blister rust expands to include not only the economically important species but the ecologically valuable white pines as well, there has also been a corresponding shift in perspective from one focused strictly on protection of economic interests to one that considers ecological impacts of biological invasions. The fact that white pine blister rust is not

restricted to managed forests but also impacts relatively pristine and otherwise intact ecosystems demonstrates that the detrimental impacts from this pathogen in these environments fits within the broader category of global change concerns. This study was broadly aimed at increasing our understanding of impacts from introduced pathogens to relatively unmanaged ecosystems, and more specifically impacts to whitebark pine within the Greater Yellowstone Area (GYA).

The GYA is one of the few largely intact ecosystems remaining in temperate regions (Patten 1991, Noss et al. 2002). It is comprised of about 23,000 square kilometers spanning seven national forests, two national parks, three federal refuges, and Bureau of Land Management and state lands in Wyoming, Montana, and Idaho (Craighead 1994, Reinhart et al. 2001). Relatively few direct anthropogenic-driven changes are evident in whitebark pine forests of the GYA, with the presence of exotic species being a notable exception (Reinhart et al. 2001). Because these whitebark pine forests remain relatively pristine and un-managed, they present researchers with an exceptional model to assess how natural ecosystems might be altered by biological invasions and other global-scale anthropogenic stresses (Keiter 1991).

Disease Cycle: Characteristics of the fungal pathogen, in part, explain the pathogen's ability to invade remote forests such as those of the GYA. The white pine blister rust disease system is an interaction among three groups of organisms. The pathogen, *C. ribicola*, alternates between white pine hosts (subgenus *Strobilus*) and gooseberry and currant hosts (*Ribes* spp.). *Cronartium ribicola* is a Basidiomycete in the order Uredinales (rust fungi). Rust fungi are obligate biotrophs, meaning they can only grow within living hosts (Kendrick 1992). They are associated with major leaf and stem diseases in agricultural and forest systems (Manion 1981). *Cronartium ribicola* is a macrocyclic heteroecious rust (Kendrick 1992) and must successfully infect and alternate between both host plants to complete its life cycle. Thus, pine hosts can only be infected by spores from *Ribes* hosts (Mielke 1943, Kendrick 1992).

Cronartium ribicola has a three- to six-year life cycle, with two spore stages developing on white pines and three on *Ribes* plants. Aeciospores are thick walled (2.0-5.5 μm) and durable (Peterson 1967). These relatively large spores (19 x 25 μm) (Peterson 1967) travel from pine to *Ribes* hosts via air currents, remaining viable for distances up to 500 km or more (Mielke 1943). This step in the life cycle allows for long-distance disease transmission. Aeciospores are predominantly released in early to mid-summer, but can be released even

in late summer and fall (Smith et al. 2000, m. newcomb, personal observation). For successful infection of a *Ribes* leaf, specific moisture and temperature conditions are required (Van Arsdel et al. 1956, McDonald et al. 1981) coupled with compatible genetic interactions of the host plants (Van Arsdel 1972, McDonald and Andrews 1981). Fungal penetration of the *Ribes* leaves occurs through stomata that are located on lower leaf surfaces (Woo and Martin 1981).

Once a *Ribes* plant is infected, uredia develop on the under-side of infected leaves after an incubation period of 13 to 30 days (Mielke 1943), depending, in part, upon temperature (Mielke 1943, Van Arsdel et al. 1956). Throughout summer, urediniospores are produced clonally on the undersides of *Ribes* leaves and can spread infection from *Ribes* plant to *Ribes* plant several times within a season (McDonald et al. 1981, Agrios 1997). The number of uredial generations that develop during a summer depends on the occurrence and timing of favorable meteorological conditions. In different locales and years in western North America, generations of uredia have been observed to range in number from 1 to more than 7 (Mielke 1943).

In late summer or early fall, with the onset of shorter day lengths and cooler temperatures, urediniospore production is replaced by teleiospore production on the infected *Ribes* leaves. Teliospores germinate in place on the leaves during periods of saturated air and low temperatures (Bega 1959, McDonald and Andrews 1980) to produce haploid basidiospores, the products of meiosis (Gitzendanner et al. 1996). Basidiospores are wind dispersed from *Ribes* leaves to needles of white pines from July to October (Agrios 1997). Basidiospores are small (5 to 10 μm in diameter), thin-walled, and ephemeral (they are readily destroyed by ultraviolet light and desiccation). It is believed that production and survival of these spores is restricted to a limited range of environmental conditions and that dispersal distances are generally short (Kinloch et al. 1998, McDonald and Hoff 2001). Processes of basidiospore germination on the needles and subsequent infection of pines are affected by the temperature and moisture conditions on the needle (Hanson and Patton 1977). Germination and infection occurs in the presence of free water or very high (above 97%) relative humidities (Van Arsdel et al. 1956). Infection by basidiospores occurs when germ tubes grow into stomatal pits of the needle and penetrate between guard cells (Patton and Johnson 1970). The resulting mycelium then grows through the conducting tissue of the needle to the living bark tissue of the stem where it persists as a perennial infection, eventually producing a canker (Mielke 1943, Agrios 1997).

For pine infection to occur, it is believed that wet conditions with saturated air are required for cumulative time periods that allow for the production, release, and transport of basidiospores, germination of the spores on needles, and penetration of the needle by germ tubes. The time required for these processes is estimated to be 48 hours (Van Arsdel et al. 1956). Prolonged rain events have been considered to be most important for providing conditions favorable for pine infection (Hirt 1942). Fog has also been considered as a source of moisture that allows for successful pine infection (Hirt 1942). Yet the spatial and time scales involved throughout the entire spore processes that lead to and include needle infection make it difficult to pinpoint the specific atmospheric conditions that are involved.

The pycniospore (spermatia) stage occurs within cankers two to four years following needle infection (Agrios 1997). These spores are produced in a nectar-like secretion (Buller 1950). The mating system of *C. ribicola* is highly outcrossing, with haploid pycniospores presumably involved in cross-fertilization (Gitzendanner et al. 1996). It is believed that insects are attracted to the nectar-like medium in which pycniospores are released, and may facilitate transport of the spores to other pycnia (Hunt 1985, Kinloch et al. 1998). If the pycnia are compatible, fusion and fertilization may occur (Gitzendanner et al. 1996). Generally, aeciospores are first produced within the cankers during the spring or summer months three to six years after the initial needle infection. Haploid fungal mycelium is maintained on the periphery of the cankers and continues to produce pycnia and haploid pycniospores every summer (Agrios 1997, Hunt 1997). Aecia form under living tree bark surrounding the canker. When these aecia push through the bark and aeciospores are dispersed, the bark in that region is ruptured and dies. Fungal mycelium then moves to the surrounding healthy bark. This results in annual canker expansion and the eventual girdling of the tree or branch as the fungus continues to spread. In general, the location of a canker within the tree dictates the degree and type of damage that occurs to the tree (Mielke 1943). Bole cankers, and branch cankers that originate near and subsequently move into the bole, are eventually lethal if the foliage between the girdled portion of the stem and the roots cannot sustain the tree (Moss 1953). In small-diameter trees, death can occur relatively rapidly and often results from girdling. Larger trees may persist with infections for 40 years or more, depending in part on the number and location of cankers (Mielke 1943, McDonald et al. 1981).

The complicated life cycle of *C. ribicola* spans vastly different spatial scales, from microscopic (spore development and interactions with host plants), to macroscopic (long dispersal distances). Thus, studies of the fungus and its life history under natural conditions are inherently difficult. To date, knowledge of the etiology of this fungal pathogen has largely been based on circumstantial evidence, and much remains unknown about the environmental limits and requirements of the different spore types (Hamelin et al. 1998). Studies on the life cycle and conditions affecting production of the different spore stages have been conducted primarily in controlled settings with a limited number of host groups. Information from these studies has then been generalized to field conditions and other hosts (Van Arsdell et al. 1956, Bega 1959, Hanson and Patton 1977, McDonald and Andrews 1980, Hunt 1985).

Disease distribution: White pine blister rust is present throughout the entire geographic range of some host pines, particularly western white pine and sugar pine (Neuenschwander et al. 1999, Tomback 2003). However, regional differences in disease intensities (defined here as the amount of disease present in a host population, (Nutter et al. 1991)) within and among species of white pine are recognized (Smith and Hoffman 2000, Kendall and Keane 2001). Some host species (bristlecone pines: *Pinus aristata* Engelm. and *P. longaeva* D.K. Bailey and Mexican white pine: *P. ayacahuite* Ehrenberg ex. Schlechtendahl.) that exhibited susceptibility when artificially inoculated with *C. ribicola* have not been observed to be infected in their native ranges (Schoettle 2003, Geils 2003). For some other host species, including whitebark and limber pines, disease intensities vary across their ranges.

Surveys of whitebark pine have documented that disease intensities vary across its range (Zeglen 2002, Tomback 2003). Average incidence of infection in living trees is as high as 83% in the Bob Marshall Wilderness Complex in Montana (Keane et al. 1994), with more recent studies of that region reporting close to 100% infection and mortality in some stands (Tomback 2003). Yet recent surveys in some other areas show lower incidences of infection and demonstrate high variability in disease intensities across geographic areas. For example, surveys have found an average of 71% of host trees infected at four sites in the Selkirk Mountains (Kegley et al. 2001), 46% in southwestern Oregon (Goheen et al. 2002), and 31% (Zeglen 2002), 30% (Stuart-Smith 1998), and 27% (Campbell and Antos 2000) across the Canadian Rockies and British Columbia, respectively. Across eastern Idaho and western Wyoming, 31% of trees

were found to be infected (Smith and Hoffman 2000), 20% in Crater Lake National Park (Murray and Rasmussen 2000), and 7.6% in central Idaho (Smith and Hoffman 1998).

Pine host – pathogen interaction: Disease results from complex interactions between host, pathogen, and environment that relate, in part, to the following factors: phenotypic and genotypic characteristics of both host and pathogen (Et-touil et al. 1999, Roy and Kirchner 2000, Hovmoller 2001, Thrall and Burdon 2003) edaphic and site factors that determine host condition (Zufa, floor discussion in Var Arsdel 1972, Maxwell et al. 1997, Wennstrom and Hagner 1999, Stanosz et al. 2001), macro- and micro-climatic factors (Van Arsdel 1965, Chellemi and Britton 1992), and host densities and arrangements relative to topography (Jacobi et al. 1993, Geils et al. 1999). Across the western United States the ecological setting is highly heterogeneous. The interaction between whitebark pine hosts and *C. ribicola* may exhibit conditionality relative to this heterogeneity. As defined by Bronstein (1994), interactions are conditional when the outcomes, or net costs and benefits, vary in space and time as they are affected in predictable ways by current ecological conditions. Recent surveys across western North America suggest that *C. ribicola* infection in whitebark pine may exhibit conditionality, allowing for the possibility that an ecological context exists in which whitebark pine and *C. ribicola* can coexist in a dynamic equilibrium.

The concept of *C. ribicola* and whitebark pine conditionality can be framed by what is known about the role of plant pathogens in wild systems. Pathogens influence plant populations (Thrall and Burdon 2003). Yet evaluating the role of pathogens in wild systems is difficult because of the multiplicity of interactions (Lenne et al. 1994) and the often long period of time required for examining their full effects (Kranz 1990). Accounts of the functions of pathogens in such complex ecosystems are largely based on observed host-pathogen interactions, and causal pathogen influences on host population dynamics are inferred (Burdon and Shattock 1980, Dinoor and Eshed 1984, Augspurger 1988, Lenne et al. 1994). Observations of pathogens on an ecosystem scale rarely find extensive damage, and discernable impacts on host population structure and function are generally limited (Dinoor and Eshed 1984, Augspurger 1988, Kranz 1990, Garcia-Guzman and Dirzo 2001). Yet it is also commonly observed that frequencies of resistant hosts across geographical space varies (Wahl 1970, Hunt and Van Sickle 1984, Ericson et al.

2002), implying that pathogens may be influential in defining host population composition and/or distribution, even if such influences have rarely been detected.

Increasing evidence supports the hypothesis that pathogens can influence plant distributions, both locally and geographically. Local patterns in host distributions may result from influences of pathogens through the following processes: prohibition of host-plant regeneration near parental hosts (Augspurger 1984, Gilbert et al. 1994); restriction of host plants to patches of limited sizes such that host densities are maximized while pathogen densities are limited (Burdon and Shattock 1980, Jennersten et al. 1983); restriction of hosts to microsite refuges (Rochow 1970, Jarosz and Burdon 1988), and spatially patterned limitations on host phenologies (Dinoor 1970). It has also been hypothesized that pathogens may limit the broader geographic distributions of hosts (Wilde and White 1939, Weltzien 1972). Factors that may interact with pathogens to influence geographic ranges of hosts include climate (Weltzien 1972), soil conditions (Wilde and White 1939), and for some host-pathogen interactions the distribution of alternate hosts is an additional ecological factor (Weltzien 1972).

While it is inherently difficult to determine causal effects of pathogens on hosts in wild systems, which exhibit numerous intricate species-environment interactions, natural experiments exist in the form of deliberately-introduced bio-control, and accidentally-introduced, exotic pathogens. These examples demonstrate the ability of pathogens, in particular contexts, to dramatically impact host populations (Burdon et al. 1981, Hiers and Evans 1997). White pine blister rust disease development in western North America is a similar natural experiment. The outcome of the introduction of *C. ribicola* could ultimately result in either of the following situations: complete devastation throughout the range of white pines such that only genetically resistant pines persist, or a conditional host-pathogen interaction such that only resistant pine hosts persist in regions with ecological conditions favorable to pathogen infection, while pine hosts in regions with less favorable ecological contexts may include both resistant individuals and susceptible ones that persist through escape or avoidance mechanisms (Lenne et al. 1994).

Evidence supporting a possible conditional host-pathogen outcome for North American white pines may be found in the form of detectable patterns in disease intensities relative to some ecological factor or factors. Detection of patterns in disease intensities requires the use of both a meaningful and

effective metric for quantifying disease intensity and an appropriate spatial scale for examination (Levin 1992). For blister rust in whitebark pine, both of these requirements are challenging and have not yet been adequately defined. Standard measures used in disease assessments (incidence of infection, or the proportion of surveyed trees infected; and severity ratings, or assigned numerical or descriptive values representative of the proportion of area or volume affected by disease) (Nutter et al. 1991) that are appropriate for purposes of monitoring may not be equally appropriate for comparisons among sites and detection of patterns across complex landscapes. Despite a recent increase in disease surveys within whitebark pine (Zeglen 2002, Tomback 2003), no methods or metrics have been developed that facilitate among-stand examinations of disease intensity relative to specific ecological factors. This may, in part, explain why few clear or consistent patterns have emerged relating standard measures of white pine blister rust infection to predictive factors (Campbell and Antos 2000, Schwandt 2001, Smith and Hoffman 2001, Zeglen 2002).

Defining an index of disease severity: In many systems, appropriately describing disease intensities in a manner that allows for analysis and prediction of disease progression is a challenging task (Seem 1984, Waggoner and Aylor 2000). This is especially so for complex pathosystems such as blister rust in whitebark pine. In such natural systems, interactions which occur between hosts and pathogens are influenced by the diverse climatic and edaphic conditions which hosts encounter, as well as the diverse host ages and conditions which the pathogens encounter. Standard methods for studying the effect of plant diseases were developed within agricultural systems which exhibit more uniformity among hosts and their environments. Effective methodologies and measures for use in complex forest systems are generally lacking (Lenne et al. 1994). Most estimates of white pine blister rust in field sites are reported as incidence of infection measured as the proportion of trees infected (Keane et al. 1994, Harris 1999, Campbell and Antos 2000, Smith and Hoffman 2001, Murray and Rasumussen 2000, Zeglen 2002), or disease severity measured as a percentage or category of damage (Keane et al. 1994, Goheen et al. 2002), or as the average number of cankers per tree (Keane et al. 1994, Stuart-Smith 1998). These measures have been useful for providing valuable information about the status of whitebark pine hosts, but may not adequately allow for studies of factors related to predictions of disease progression.

For all of the above measures, the unit of investigation is a single tree. Whitebark pine trees differ substantially in growth form and size potential. They can exhibit remarkably variable crown shapes and sizes, and can occur as single trees or multi-stemmed clusters with straight and tall or short and contorted stems (Weaver 2001). From the perspective of pathogen infection, this variability in tree size and shape and in the related factors of tree age and condition, results in highly diverse host targets. Tree form can differ within a site, but the most striking differences occur among sites. Therefore, detection of patterns in disease intensities necessitates development of a measure that removes tree-level differences in host target characteristics to allow for comparisons of disease levels among pine stands.

Probability of infection of any single tree most likely relates to several interacting factors, including canopy or foliage target size (Buchanan 1936), tree height within the canopy (McDonald et al. 1981, Stuart-Smith 1998), position within the stand, and relative susceptibility that may be related to tree age (Stuart-Smith 1998) and vigor, which is affected by site quality and competing vegetation (Posey and Ford 1924, Snell 1928, Mielke 1943). Tree diameter is correlated, to varying degrees, with all of these factors. Studies on whitebark pine have reported that tree diameters were associated with differences in infection incidences or severities (Stuart-Smith 1998, Campbell and Antos 2000, Murray and Rasmussen 2000, Smith and Hoffman 2001, Zeglen 2002, and Goheen et al. 2002). A similar correlation has been reported for western white pine (Hunt 1983). Diameter is a factor that is easy to measure. Therefore, a useful metric of disease severity may be one that accounts for tree diameter. For the purposes of this study, an index of disease severity was devised that relates the measured disease severity of each surveyed tree to a calculated expected capacity disease severity for a tree of that size. This index of disease severity allows stand-to-stand comparisons of disease severity to the factors of interest.

Disease patterns and spatial scale: Pattern and scale are tightly linked (Levin 1992). Therefore, in addition to determining an effective metric for disease intensity, detection of pattern in the whitebark pine blister rust pathosystem is challenged by the need to recognize the appropriate spatial scale for examination. Primarily because research on the epidemiology of blister rust in whitebark pine is in a relative stage of infancy, consideration of potential pattern in disease levels in recent studies has been a secondary priority to surveys of pathogen distribution and intensity across geographical regions. When

relationships between blister rust levels and other variables have been examined, the following factors were considered: elevation, slope, aspect, latitude, longitude, west-east distribution across mountain ranges, topographic position, mean summer precipitation, mean temperature of warmest month, mean number and average duration of frost-free days, tree canopy cover, density and basal area, whitebark pine density and basal area, average whitebark pine diameter, canopy structure, stand age, plant community and habitat types, and presence/absence of on-site *Ribes* plants (see Stuart-Smith 1998, Campbell and Antos 2000, Smith and Hoffman 2001, Zeglen 2002). Few strong associations were discovered. Campbell and Antos (2000) reported significant, but weak, associations with tree canopy cover and presence/absence of *Ribes* species. Smith and Hoffman (2001) found elevation, mean summer precipitation, and average diameter to be important explanatory factors. Finally, Zeglen (2002) found an association with transect location within the west to east mountain range locations. In summary, results that suggest patterns of infection levels remain inconclusive.

Review of the available information on whitebark pine forests and blister rust dynamics illustrate that there has been a nearly complete lack of attention given to the alternate hosts in surveys of white pine blister rust (Schwandt 2001). No studies have been conducted to look at the relationships between *Ribes* species distributions and abundances and whitebark pine infection level. Considering that for nearly a century there has been an interest and investment in protecting commercially valuable white pines from white pine blister rust in North America, and furthermore, that it has been recognized throughout that time that *Ribes* species play at least some role in the disease system as the obligate intermediate host for the pathogen, it is somewhat surprising that there is at present a general lack of consensus regarding how and if *Ribes* patterns influence pine infection patterns. The relative neglect of this essential component of the disease cycle may be at least partly based in history. Present white pine blister rust studies remain influenced by a forestry perspective with emphasis on the pine hosts (Vogler 1999). Moreover, any examination of patterns between pine and *Ribes* hosts is a study of an indirect interaction (mediated by another species group – the pathogen). These higher order interactions present problems during investigation and statistical analysis since common research and statistical methods typically strive to reduce interdependence (Laska and Wootton 1998, Wootton 1994a and 1994b). With few recent

exceptions, indirect interactions in complex terrestrial systems have not been effectively investigated (Wootton 1994a).

An investigation of patterns of blister rust disease levels relative to *Ribes* host factors requires recognition that distinct *Ribes* species cannot effectively be amalgamated into a single category of “*Ribes* sp.” and that the spatial scale of analysis must be expanded beyond that of the associated whitebark pine stand (Newcomb and Six, in press). With few exceptions, there has been little recognition that each *Ribes* species is a distinct host with its own relationship with the pathogen, and thereby, its own distinct role in the disease system. The important correlative to this fact is that one model or explanation for the pathogen’s distribution cannot be generalized across regions with different *Ribes* species compositions. Recognizing that the composition of *Ribes* species is important, and that the relationship between pine and *Ribes* species is an indirect interaction, provides a starting point for selecting an appropriate spatial scale for detecting patterns. The concept of pattern in natural systems is inseparable from that of scale (Levin 1992). If patterns are undetectable at one scale, it may be that there is another scale (either spatial or temporal) that is more appropriate for examination. For white pine blister rust, the area examined should be inclusive enough to allow for processes of basidiospore dispersal from *Ribes* to pine (a phenomenon that is still poorly understood in natural conditions), but not so inclusive to extend into an area with different *Ribes* species compositions.

White pine blister rust in the Greater Yellowstone Area: White pine species that inhabit the GYA include whitebark and limber pines. Both are hardy trees that can sometimes grow in harsh areas where other tree species cannot. Whitebark pine is a slow-growing, long-lived tree that grows in high elevation forests up to timberline. The species is a critical component of high mountain ecosystems, providing watershed protection and wildlife habitat (Kendall and Arno 1989). The large seeds have a high lipid and protein content (Lanner 1996) and are a nutritious, year-round food source for animals. In particular, federally protected grizzly bears (*Ursus arctos*) make use of the seed cones for food, as well as red squirrels (*Tamiasciurus hudsonicus*), Clark’s nutcrackers (*Nucifraga columbiana*), and black bears (*Ursus americanus*) (Kendall and Arno 1989, Mattson and Reinhart 1997). Limber pine covers less area

within the Greater Yellowstone Area than whitebark pine and often occurs in small stands or groups of scattered individuals. Both white pine species are considered critical components of the ecosystem.

At least nine *Ribes* species occur in the GYA, and seven species are listed in the Flora of Yellowstone National Park (Despain 1975). Observations (m. newcomb) revealed the following species to be common in the GYA. As hosts to *C. ribicola*, they may have minor to important roles in the blister rust pathosystem:

- ◆ *Ribes cereum* – grows on dry montane slopes, forest edges, and rocky areas; generally observed growing as single plants;
- ◆ *R. hudsonianum* – a riparian species, limited to moist soil, often observed in patches;
- ◆ *R. inerme* – present on stream banks, swamps and floodplains, often associated with willows;
- ◆ *R. lacustre* – consistently (although sometimes sparsely) found in moist woods and slopes, most abundantly along stream banks;
- ◆ *R. montigenum* – primarily limited to subalpine and alpine areas, observed growing in patches or as single plants;
- ◆ *R. oxycanthoides* ssp. *setosum* – (synonymous with *R. setosum*) present on open slopes and valley bottoms;
- ◆ *R. viscosissimum* – present in moist or mesic open forests, observed growing as single plants, often in recently disturbed areas.

(Dorn 1984, Sinnott 1985, Lackschewitz 1991)

While the ecological role of native *Ribes* has received less research attention than that of the white pine hosts, the genus is a common component of coniferous forests. In the presence of *C. ribicola*, the ecological role of *Ribes* species is critical because of the indirect detrimental impacts (via the pathogen) on white pines.

Consideration of patterns in blister rust disease intensities, and the implications for pine host-pathogen conditionality, is especially pertinent in the GYA. The data that are available on blister rust levels show wide variation in infection incidences among sites (Kendall et al. 1996, Harris 1999, Smith and Hoffman 2000). While some areas contain sites with as high as 88% infection level (Smith and Hoffman 2000), other sites exhibit very low incidences of infection (Kendall et al. 1996, Harris 1999, Smith and Hoffman 2000). It is known that the disease has been established in pine hosts within the GYA since the 1940s (Krebill 1969). The fact that the pathogen has had a long-term presence in the area but still occurs in variable intensities could be explained by conditionality of the host-pathogen interaction across the diverse topography of the GYA.

Moreover, understanding the potential for conditionality may help increase predictive abilities related to the extent of future damage to pine stands by the pathogen. The GYA is often described as one of the largest remaining temperate, reasonably intact, ecosystems (Patten 1991), and there is great interest in conserving this status and maintaining native species populations (Noss et al. 2002). Unfortunately, little is known about white pine blister rust disease dynamics in the GYA. When there is a strong interest in obtaining information for use in management and conservation efforts, vacuums in available data tend to be filled with unsubstantiated generalizations. While a careful analysis of the present status of blister rust throughout the GYA seems to illustrate that the extent of future damage to white pines is as yet unknown, statements regarding the future of GYA whitebark pine stands have claimed there is “little room for optimism” (Koteen 2002), and predicted an “inevitable spread of the disease and, along with it, eventual loss of most whitebark pine” (Reinhart et al. 2001). However, such statements are mostly unsubstantiated with data. Thus there is a critical need to increase both our knowledge of disease dynamics and our ability to predict future damage within this ecologically valuable area.

Project objectives: This work is broadly aimed at increasing our understanding of impacts from exotic pathogens to natural ecosystems. Prediction of impacts to ecosystems, such as the extent of blister rust damage in whitebark pine forests, requires determining a measure of impact (disease), detecting and describing patterns of impact (disease), and finally discovering the drivers of pattern (Levin 1992). While it is beyond the scope of this work to determine causal factors of patterns within this system, the theoretical framework for the study is based on reducing knowledge gaps that must be filled prior to prediction of future impacts. The immediate goal of the project was therefore to better understand spatial patterns (and thus conditionality) of white pine blister rust disease intensity in whitebark hosts within the GYA.

Specific objectives of the project were the following:

- To determine a means of quantitatively assessing blister rust disease severity in whitebark pine that enables examination of the variation in disease severity among sites relative to ecological factors that may be suggestive of conditionality between the pathogen and pine hosts.

- To use this metric of disease severity to determine associations, or patterns, between disease intensity and landscape features related to the ecology of the *Ribes* host species.

By examining which landscape features may be useful in explaining variation in disease severity, this study is unique among white pine blister rust research projects in its consideration of a spatial scale and landscape context that is large enough to incorporate processes of pathogen dispersion and proximities of whitebark pine and *Ribes* populations (but see Jacobi et al. 1993 in comandra blister rust system).

MATERIALS AND METHODS

Field Methods 2001: Disease measures and host plant factors were investigated in 17 whitebark pine stands throughout portions of the Gallatin, Bridger Teton, and Targhee National Forests, as well as Yellowstone and Grand Teton National Parks. Study site locations and characteristics are summarized in Table 1. Stands were selected, as much as possible, such that whitebark pine was the major tree species. Site selection attempted to include a wide range of blister rust disease intensities among stands. In each stand, 28 live trees or trees obviously killed by blister rust (which were rarely encountered in the sites surveyed) were inspected for disease symptoms. Disease intensity was assessed using two methods. The first method involved counting, with aid of binoculars, all discernable active and old cankers (on branches and the main stem) in the upper, middle and lower thirds of the tree canopy. For the few trees (10 total from both years) for which blister rust was recognized as the cause of mortality, detection of cankers was too difficult to accomplish reliably and therefore only live trees were considered. Yet because these rarely occurring trees (present in only a few sites) are important as evidence for the site disease intensity, their presence was recorded. The second method of disease assessment provided a numerical disease severity rating, based on the percentage of visible disease-related damage on the main stem (bole) and in the canopy of examined trees (Six, in prep.). This method requires visually dividing the foliage and the bole into thirds and designating a rating of zero to three (zero representing no infection and three representing more than 50 percent impacted by infection) for each third (see Figure 1). Since trees that die due to blister rust are important in describing disease intensity, these trees were included in this second method of assessment and were assigned a maximum severity rating of 18 (maximum possible percentage of disease-related damage).

The stem diameter at a height of 1.4 m (DBH, diameter at breast height) and canopy position relative to neighboring trees (open, overstory, subdominant, or overtopped) were recorded for each sample tree assessed for infection. The area immediately surrounding sample trees was used to measure whitebark pine density, spatial association between whitebark trees and on-site *Ribes*, and percent tree canopy cover. Whitebark pine density was estimated using a wandering-quarter transect method (Catana 1963) oriented to remain within a fairly homogeneous forest stand. At each whitebark pine tree encountered along the wandering quarter transect, distance was also measured from the tree to the nearest *Ribes* shrub (if *Ribes* were present within 25 m in any direction). A line transect was then established along the general midline of the wandering transect. At stratified random points along the line percent tree canopy cover was measured (using a convex densiometer) and the distance from the point of measurement to the nearest *Ribes* shrub was recorded (if *Ribes* were present within 25 m in any direction). *Ribes* species were present at fewer than half of the sites that were characterized. When *Ribes* plants were present, a variable-area transect (Parker 1979) was established perpendicular to the line transect at every fourth stratified random point to estimate *Ribes* densities by species. The direction of the variable-area transect alternated between upslope and downslope directions. Additional variables recorded at each site included elevation, slope, and aspect.

Field methods 2002: A total of 32 whitebark pine stands were sampled across much of the GYA between June and September, 2002 (site location and characteristics summarized in Table 1). Plots were located throughout portions of the GYA to fill in areas that had not been sampled previously. Many of the sample locations were fairly remote, and therefore, data were not biased towards easily-accessible sites. Again, plots were generally located so that whitebark pine was the dominant tree species. Transect positions within stands were arbitrarily selected to best represent the stand, and transect direction was determined to follow the countour. The first 50 trees (live or dead) encountered within variable-length belt transects, 4.57 m in width, were assessed. Disease level was assessed in the same manner as in 2001 with one exception. In 2001 the number of cankers, number of stems, and diameter of each stem were reported for each tree cluster, while in 2002 numbers of cankers and diameter were reported per stem and tree clusters were not noted. This difference in methodology does not interfere with calculation of total cankers

per stem or total cankers per diameter of sampled trees. Another difference in methods between years was the use of different types of transects (wandering quarter in 2001 and variable-length belt in 2002). Other variables recorded at each site included elevation, slope, aspect, slope position (valley bottom, toeslope, footslope, backslope, shoulder, or ridge) (USDA Soil Conservation Service 1993), slope configuration (undulating, linear, convex, concave, or broken), stand structure (closed canopy single-storied, closed canopy multi-storied, open canopy scattered individuals, or open canopy scattered clumps). Variables recorded for each sampled tree (stem) included diameter, tree status (healthy, declining, dying, recent dead, or old dead), crown class (open-grown, dominant, codominant, intermediate, suppressed, or remnant), a crown ratio estimate (to the nearest five percent), and other damage. (Definitions of all codes except slope position were taken from current Forest Service Natural Resources Information System Field Sampled Vegetation Module (NRIS FSVeg) codes).

Landscape feature analysis: Field observations from 2001 and 2002 showed that *Ribes* species compositions and abundances tended to change with increasing stream orders. Also, it was observed that disease levels in pines varied with large-scale topographic position (edge versus interior of a mountain range). Relationships of disease intensity to spatial factors such as stream order, position within mountain ranges, and distances that potentially are involved in spore dispersion can be assessed using topographical maps. Therefore, in the fall of 2002 the following variables were measured for all sites visited in 2001 and 2002 using maps of the GYA: distances from sampled plots to the nearest 3rd, 4th, and 5th order streams (with stream orders being assessed at the map scale of 1:327,360 using National Geographic Topo! Interactive Map software); distances to the nearest perennial stream; distances to the nearest perennial stream at or below 2621 m (an elevation commonly observed as the upper elevation of many *Ribes* species, including the most susceptible *Ribes hudsonianum*); and the forested distances (distance through forested cover) to the nearest perennial stream and the nearest perennial stream at or below 2621 m (the zone containing the riparian *Ribes* species recognized as being highly susceptible). Distance to 3rd order streams was considered as a variable since *Ribes* species abundances and compositions were observed to change between 2nd and 3rd order streams. Distances to 4th and 5th order streams, which occur in larger river valleys, were considered to represent relative topographic position within mountain ranges. Additionally,

because both the total distance and the distance through forest cover may be important for processes of spore dispersal, the mean of the total and forested distances to streams and streams at or below 2621 m were recorded. Taking the mean of the total and forested distances essentially weights the forested distance, since the total distance is comprised of both forested and non-forested components. The mean of the total and forested distances, therefore, doubles the importance of the forested components which may be reasonable for spore dispersal processes. The final map-level variable assessed was the percentage of adjacent forest cover on the map using a rectangular 32-grid overlay, covering 0.18 square kilometers extending downslope from the survey site. The number of grids overlaying forested cover was counted and recorded as a proportion of the total number of grids (32). A metric of extended forest cover for each site was then defined as the product of the adjacent (downslope) forest cover and the on-site canopy cover estimated in the field. Selection of all of the above factors incorporated information on species-level *Ribes* ecology gained from observations during both field seasons, as well as understandings of spore dispersal processes.

Data analyses: All statistical analyses were performed using STATISTICA (StatSoft, 1998). Data from 45 sites surveyed were included in most analyses. Wilcoxon matched pairs tests were used to examine relationships between tree-diameter sizes and standard measures of disease intensities (estimated infection incidences, numbers of cankers per stem, and the disease severity rating (Figure 1)) for trees surveyed in 2002. Assumptions of the Wilcoxon matched-pairs test, that the variables were measured on a scale that allows rank ordering of observations and that differences between variables also allow for rank ordering (StatSoft 1998), were met by these data.

In order to devise an index of disease severity (B.W. Geils, US Forest Service Rocky Mountain Research Station plant pathologist, personal communication), numbers of cankers on stems with infection (single-stemmed trees examined in 2001 and all stems examined in 2002) were plotted against stem diameter. Bins (or intervals) of data points were established for variable-width classes of diameter sizes, such that the count for each bin was 40 points, or 45 in the case of the bin for the upper diameter sizes. The relationship between the mean stem diameter for each bin, and the values of the 90th percentiles for numbers of cankers were used to derive a formula for the expected capacity number of cankers for any tree

of a particular size. A linear trend was detected for the lower nine of ten bins when the 90th percentile numbers of cankers were plotted against the mean stem diameter for each bin. The tenth bin showed a decrease in the 90th percentile value. Different equations were derived for trees with diameter less than 45 cm and those with diameter greater than or equal to 45 cm. For tree diameters less than 45 cm, simple linear regression was used to evaluate the relationship between numbers of cankers and stem diameter. For tree diameters greater than or equal to 45 cm a linear relationship was calculated from the inflection point (diameter=45 cm) to the 90th percentile value for that bin, which was established as the minimum value for the expected infection capacity of trees with diameters above 45 cm. Several different alternative functions were tested for large-diameter trees, which demonstrated that the results that make use of these calculations are not sensitive to the particular function(s) used for large diameter trees. The three designated linear functions were used to calculate a representative value for expected infection capacities for trees of a particular stem diameter at surveyed sites.

An index of severity (the GYA Relative Severity Index) was defined as the ratio of the number of observed cankers at a site to the sum of the reference infection capacity numbers of cankers for trees by diameter size. The GYA Relative Severity Index for each of the 45 surveyed sites was calculated. Relationships between the GYA Relative Severity Index as the dependent variable and site factors and distances to landscape features as independent variables were first assessed using Spearman's rank order correlations and scatter plots. Spearman's rank order is a non-parametric method of correlation. The assumptions of this method are that the individual observations of the measured variables can be ranked into two ordered series, which are met for all variables used in the analysis. Variables were determined to be unrelated using three criteria: the Spearman-R level of significance ($p > 0.1$), visual assessments of possible non-linear trends, and the biological importance of the variable. Regression analysis was used to investigate relationships between the GYA Relative Severity Index and independent variables of distances to landscape features, subsequent to log-log transformation of the data to increase linearity and meet assumptions of linear regression. The assumptions include that the error terms are independent, have constant variances, and are normally distributed (StatSoft 1998). Assumptions were determined to be met

through examinations of plots of the residuals against the independent variables. Significantly related ($p < 0.05$) independent variables were tested for autocorrelation using Pearson product-moment correlations.

A possible threshold value was detected for the extended forest cover metric from descriptive assessments, again taking into account the biological importance and meaning of the variable from accounts in the literature. Thus regression analysis was used to relate the GYA Relative Severity Index and distances to landscape features for only those stands with extended forest cover metrics less than or equal to 0.65 (subsequent to the removal of five sites with extended forest cover metrics greater than 0.65).

Relationships among proportions of cankers in different thirds (by height) of the canopy of individual trees were investigated using Pearson product-moment correlations. Pearson correlation analysis assumes that the data pairs are randomly selected and that the variables are measured on at least interval scales, which holds true for these data sets.

RESULTS

Locations, characteristics, and the GYA Relative Severity Index for 45 sites in 10 mountain ranges sampled over the summers of 2001 and 2002 are shown in Table 1. Sites typically had a southerly aspect, with an average aspect of 200° . Site elevations ranged between 2746 and 3261 m, and averaged 2919 m. A summary of the GYA Relative Severity Index values by mountain range, a natural geographic range for this high elevation pine (Zeglen 2002), is presented in Table 2.

Data collected in 2002 were used in Wilcoxon matched pairs tests to compare means of three measures of infection; percent of infected trees, number of cankers per stem, and the disease severity rating (Figure 1), for small and large trees. 2001 data considered tree clusters to be tree units for canker counts and severity ratings and thus could not be pooled with 2002 data. Small and large trees were categorized as having stem diameters less than or equal to 15.24 cm and greater than 15.24 cm, respectively.

Comparisons of the small and large tree classes illustrate significant differences in means for small and large trees for all three measures (percent of trees infected, $p=0.00018$; numbers of cankers per stem, $p=0.000072$, and disease severity rating, $p=0.0058$) (Figure 2).

Numbers of cankers by stem diameter for stems with detected infection (single-stem trees from 2001 and all stems from 2002) are plotted in Figure 3. Two outliers [(101.6, 3) and (139.7, 0)] with very

large diameters were removed. Both these data points met the following condition to be characterized as extreme values: the data point values are greater than the 75th percentile value plus 3*(the 75th percentile value minus the 25th percentile value). As extreme values, they are considered members of a different population of rare and very large-diameter trees. Ten bins of equal counts of points (nearly equal for the upper bin) were created and 90th percentile values determined for each bin (Figure 4) to represent an expected upper-value infection “capacity” number of cankers for trees of a particular stem diameter, in current GYA conditions. Values for the first 9 of 10 bins, plotted against mean stem-diameter for the bin, show strong linear relationship (Figure 4). The regression equation and the linear equation connecting the 90th percentile of the 10th bin (the largest trees) as a minimum value for large-diameter trees are presented in Figure 4 as a formula for calculation of the expected capacity number of cankers for a given size of tree (infection capacity). A relative disease severity index for whitebark pine trees in present conditions in the GYA is then defined as the ratio of the number of observed cankers at a site to the sum of the “capacity” values of live trees assessed at the site. Comparisons of values of the GYA Relative Severity Index and other disease metrics are shown in Figure 5 with the GYA Relative Severity Index values plotted by ascending rank order with standard metrics of disease (proportion of trees infected, mean number of cankers per stem, and the value assigned by the disease severity rating (Figure 1)) for 28 sites surveyed in 2002.

Potential predictors of disease severity were initially investigated, using the GYA Relative Severity Index by site as the dependent variable, with Spearman’s rank order correlations and scatter plots. Figure 6 presents results for two site factors (extended forest cover metric and elevation) as independent variables. Figures 7 and 8 present results for independent variables of distances to landscape features. Elevation (Figure 6), and distances to 3rd and 4th order streams (Figure 7) did not exhibit a detectable relationship with the dependant variable ($p=0.13$, $p=0.49$, $p=0.54$ respectively), while all others were further assessed for relationships with disease severity.

Univariate linear regression analysis of log-log transformed data was used to investigate straight-line relationships between the remaining distance-to-landscape-feature variables and the GYA Relative Severity Index. Data was log-log transformed to meet assumptions of linear regressions (as tested by

examinations of the residuals). Regression equations, correlation coefficients, and levels of significance for these analyses are presented in Figures 9-11. Distances to the nearest 5th order stream, as well as the total, forested, and the mean of total and forested, distances to the nearest stream at or below 2621 m are all significantly related to the GYA Relative Severity Index ($p < 0.0003$). Pearson product-moment correlation coefficients indicate that distances to the nearest 5th order stream are significantly related to all versions of distances (total, forested, and the mean of the total and forested) to the nearest stream at or below 2621 meters (Table 3). This degree of autocorrelation among these factors prohibits their use in a multiple regression analysis.

Log-transformed GYA Relative Severity Index values plotted against transformed distances to nearest streams at or below 2621 m are shown in Figure 11. It is possible that some other factor accounts for low disease severities at sites with severities notably less than predicted by the regression equation. In fact, some of the sites with low disease severities that fall distinctly below the regression line are associated with high extended forest cover metric values. The extended forest cover metric may be associated with low disease severities above a certain threshold value (Figure 3). All sites with extended forest cover metrics above 65 percent are associated with consistently low disease levels. This fact, in addition to accounts in the literature relating high vegetative densities with reduced potential for white pine blister rust impacts (in conditions of relatively low spore loads as exhibited throughout much of the GYA) support the use of the GYA Relative Severity Index limited to stands with moderate and low extended forest cover metrics. Stands with high extended forest cover metrics may have predictably low severities that preclude the use of the severity index.

Figure 12 depicts linear regression equations (of log-log transformed data) for GYA Relative Severity Index values on distances (total, forested, and mean of forested and total) to the landscape feature of a stream at or below 2621 meter, for sites with extended forest cover metrics less than or equal to 0.65 (excluding five sites with metrics greater than 0.65). The R-squared values obtained by these regressions (0.57, 0.52, and 0.61) indicate that within the GYA a large amount of the variation in blister rust disease severities in whitebark stands with extended forest cover metrics less than or equal to 0.65 can be accounted for by these distances to the nearest stream at 2621 m.

In addition to comparisons of the GYA Relative Severity Index values, indicative of quantities of cankers, comparisons of the relative distributions of cankers within tree canopies among sites may also be informative. Table 4 presents results of Pearson product-moment correlations between the distances to the nearest stream at or below 2621 m and relative proportions of cankers in the lower, middle, and upper thirds of tree canopies. A significant ($p < 0.005$) inverse relationship was found between versions of distances (total, forested, and mean of total and forested) to streams at 2621 m and the proportion of cankers in the lower third of the canopy.

DISCUSSION

Metric of disease severity: For the purposes of this study, a relative disease severity index was derived for comparisons of whitebark pine stands under the present conditions occurring in the GYA. The value of this severity index is that, by definition, it is directly applicable to a specific place and time. The specific formula presented here is not expected to be applied in other forests, although the concept could be widely applicable. It is also expected that the derived index will need adjustment as disease conditions change over time in the GYA. There is a remarkably rich and extensive, century-long history of white pine blister rust research on the commercially important white pine hosts (Maloy 1997) which can be drawn upon to understand blister rust in whitebark pine stands. However, the use of information from other systems presents simultaneously both a benefit and a risk. It remains a challenge to make use of pertinent knowledge about disease dynamics without making inappropriate generalizations. The relative severity index used here borrowed from concepts relating probabilities of infection with tree size that were first developed back in the early 1900s in eastern and western white pine, but translated them to present GYA whitebark pine stands.

The few data that exist for whitebark pine relating percent infection with tree size classes (based on diameter) show a general, rough agreement with trends found in this study (Campbell and Antos 2000, Murray and Rasmussen 2000, Smith and Hoffman 2001, Zeglen 2002, Goheen et al. 2002). Assessment of the upper values, or capacities, for recorded numbers of cankers by diameter size clearly shows an increase in infection capacity up to a diameter size (DBH) of roughly 40 to 50 cm. The trend for trees with larger diameters is not as consistent. The 90th percentile for the upper diameter-size bin (Figure 4) is less than for

the adjacent 2 bins (with smaller diameters). It is possible that the infection capacity does not simply level off but actually decreases for these larger-diameter trees.

Potential causes for a decreasing capacity for infection can only be speculated. It is possible that trends observed in this study are simply artifacts of a sampler's ability to detect cankers in small trees (where infections quickly kill branches or stems and then appear similar to other types of tree stress or damage) or in large trees (where cankers are difficult to see). It is also likely that target size and target location are important causal factors related to infection capacities (Buchanan 1936, Mielke 1943, McDonald et al. 1981, Stuart-Smith 1998). Induced defenses, known in other pines (Paine and Stephen 1987, Davis et al. 2002), may be more important for larger, older trees. Finally, it is recognized that host-age affects susceptibility to infection by other pine-stem rust pathogens, such as pine twisting rust in Scots pine (Mattila et al. 2001). Age-related (and associated vigor-related) effects on susceptibility to white pine blister rust in pine hosts have also been conjectured for a long time (Posey and Ford 1924, Snell 1928, Mielke 1943).

Patterns of disease severity: For seven of the 45 sites surveyed in this study, no infection was observed on the sample-trees. Yet at all seven of these sites, signs of infection were observed on host trees in the vicinity. Moreover, observations in stands that were not quantitatively surveyed demonstrate that the pathogen is widely present, at least at low levels, throughout much of the GYA. The pathogen is well established in the area, and the potential for future disease intensification and associated negative impacts to whitebark pine exists. However, whether the disease will increase to high levels in all locations is questionable. The disease has been present in many areas of the GYA for at least half a century (Brown and Graham 1969), yet considerable differences still exist in disease intensities among sites (Harris 1999, Smith and Hoffman 2000, Tables 1 and 2). Furthermore, results of this study suggest a pattern of disease severity relative to landscape features that is unlikely to be due to chance alone. The pattern detected in this study indicates an association with two factors, distance to a landscape feature (the nearest stream at or below 2621 m) related to expected habitat for the susceptible riparian *Ribes hudsonianum* and the common *R. lacustre*, and distance to a feature (the nearest 5th order stream) that serves as a descriptor for large-scale topographic position.

The possible trend detected in this study for stands associated with high extended forest cover metrics to exhibit low disease severities is consistent with numerous accounts in the literature (Spaulding 1929, Kimmey and Wagener 1961, Hunt 1998, Campbell and Antos 2000). The trend is often explained as the result of vegetative barriers trapping or impeding spore dispersal (Spaulding 1929, Kimmey and Wagener 1961, Hunt 1998, Campbell and Antos 2000). Vegetative density is a difficult factor to characterize accurately. The description of extended forest cover used in this study could likely be improved upon in future work, perhaps through use of aerial photography or remote sensing assessments. This study made use of a calculated metric that includes an on-site estimation of forest canopy cover and a map-level estimation of the percent forest cover in a 0.18 square km rectangle extending out in the down-slope direction from the survey site. The concept behind the calculation is that vegetative density at both the spore source and the host target, as well as at the ground between the two, all potentially affects the probability of infection (as a trap or hindrance for dispersing spores). If canopy cover is dense immediately above *Ribes* hosts, principles of spore dispersion imply that a high percentage of dispersing spores would be trapped and removed from air currents at that site (Aylor 1999). Canopy cover above potentially important spore sources (*Ribes* hosts) was not assessed. However, all sites with high forest cover in the near-proximity of the pine host targets showed consistently low disease levels. Consideration of vegetative density, or forest cover, in the near-proximity of spore-source *Ribes* plants may be worthy of future investigation.

Two factors show significant associations with the relative disease severity in whitebark pine stands. Both distances to 5th order streams and distances to the nearest stream at 2621 m are correlated with disease severity, but are also correlated with each other. A biologically meaningful interpretation of the autocorrelation between the two variables is that sites that are distant from 5th order streams (major river valleys of the Yellowstone and Snake rivers) tend to be more within the interior of mountain ranges and also tend to be distant from streams at elevations below 2621 m. These tend to be sites on high-elevation plateaus, or where the base-level relief (upper stream valleys) is at high elevations.

For investigating relationships between landscape features within the near vicinity and disease levels, distances to streams at 2621 m are more meaningful and descriptive. Yet the variable of distance to

5th order streams may include more features associated with disease level distributions. Distances to 5th order streams could include components of large-scale meteorological processes that are important for explanations of disease severity, perhaps including influences of long-distance spore dispersal. It is also possible that the relationship detected with 5th order streams is more appropriately described as being strong above a particular threshold distance, and weak for lesser distances. Additional surveys to increase the sample of whitebark stands would clarify the trend with distances to 5th order streams.

Differences in disease severities in whitebark pine across the GYA were found to be linked with distances to streams at or below 2621 m. This variable was considered in the analysis because it is a riparian feature at the general upper-elevational limit of riparian *Ribes* species (m. newcomb, personal observations, Rocky Mountain Herbarium collection reports, 2001), recognized as being highly susceptible. The elevation 2621 m was selected primarily because of observed (m. newcomb) distributions and infection tendencies of *Ribes hudsonianum* and *R. lacustre*. This landmark is particularly pertinent for *R. hudsonianum*, which requires perennially wet soils such as those associated with streams and seeps (Lackschewitz 1991). While this species may sometimes occur above this elevation it was observed below this elevation much more commonly. This species is widely recognized as the most susceptible of those found in the GYA (KimmeY 1938, Maloy 1997). The range of *R. hudsonianum* covers the entire GYA (Hitchcock and Cronquist 1973) although its occurrence is locally patchy and its abundance can vary greatly from place to place. It was not observed in the lower drainages of many sites visited during this study.

In contrast, *R. lacustre* has a relatively consistent occurrence across the GYA. It is a common, although sometimes sparse, member of the shrub component of forests up to roughly 2621 m. Again, while this species occurs sporadically in transition zone forests above 2621 m, it occurs much more commonly at elevations below 2621 m. When *R. lacustre* does occur at higher elevations it is restricted to rock outcrops or talus slopes. In these rocky exposed microsites it typically exhibits a distinctive growth form that is stunted and highly branched, with small leathery, dark green leaves. This growth form appears to be rather resistant (m. newcomb, personal observations) and is unlikely to play much of a role in disease progression. With the exception of this growth form, *R. lacustre* is recognized as being moderately susceptible (KimmeY

1938, Maloy 1997). This species occurs throughout mesic and moist forested slopes but tends to be more common in drainages and stream bottoms and in some areas may be restricted to those sites (m. newcomb, personal observations, Lackschewitz 1991).

Factors not related to disease severities: Site elevation, distances to 3rd and 4th order streams, and straight distance and forested distance to the nearest perennial streams were all factors with very little or no detectable association with differences in disease severities. Results from this study demonstrate that high elevation conditions are not limiting for pine infection, and in fact one of the two highest-elevation sites (at 3139 m) was found to have a relative index of disease severity among the top five severities recorded (Table 1). Moreover, all five spore stages were observed at these high elevations (m. newcomb, personal observations).

There are several possible reasons why no relationships were detected between 3rd and 4th order streams and the GYA Relative Severity Index values. Third-order streams are numerous across the landscape. Any relationship with a distance to a particular 3rd order stream is likely to be confounded by another nearby 3rd order stream. Fourth-order streams are less frequent and include streams such as the Lamar, the Buffalo Fork, the Gros Ventre, and the Snake (above the confluence with the Gros Ventre) Rivers. These are all waterways associated with fairly broad and non-forested valleys and often bordered by patches of *Ribes inerme* (m. newcomb, personal observations). The 4th order segments of these rivers vary in length, so that distances from pine stands to these segments may have little descriptive meaning. If there is a correlation with disease level it is hidden by other complicating factors and is difficult to detect. This holds true for the factors of total and forested distances to the nearest perennial stream as well.

It is informative that distances to nearest streams are not correlated with disease while distances to streams at or below 2621 m are. The fact that distances to the two landmarks differ significantly in explanatory importance implies that the important correlative factor of 2621 m – elevation streams is absent in the nearest streams. Thus it does not appear that the isolated features of perennial water, or topographical draws, are the correlative features since these are also characteristics of the nearest streams, which are not related to disease severities. Furthermore, it does show support for the explanation that spore source *Ribes* may be limited to the streams and associated forests at or below 2621 m.

The potential role of *Ribes* species: Additional inferences can be made in support of *Ribes* species being an important component of the landscape feature of streams at or below 2621 m. The relative height-position of cankers within pine canopies provides some information about distances from spore source *Ribes* to the infected pine hosts. Knowledge of spore dispersal processes indicates that spores that travel longer distances can be in higher air currents than those that travel shorter distances (Aylor 1999). Cankers that are located in the upper portions of pine canopies may result from spores that originate from sources more distant than those associated with cankers in the lower portions of the canopies. Moreover, spores that travel longer distances are likely to be trapped by various obstacles in lower air currents such that cankers in the lower portions of pine canopies may result primarily from short-distance dispersal. It might be expected therefore that percentages of cankers in the lower third of canopies would be negatively correlated with distances to susceptible *Ribes* species. Thus the significant negative correlation found in the assessment of the proportions of cankers in the lower canopy third relative to the distances to streams at 2621 m (Table 4) indicates that it is possible that when the distance to streams at 2621 m is greater, the spores involved in pine infection are also coming from a greater distance, resulting in fewer cankers in the lower canopy third. This suggests that *Ribes* species present at or near the streams at or below 2621 may be involved in the infection process of the assessed pines.

The site factors that were selected for this analysis relate to observed trends in distributions of the *Ribes* species believed to be more highly susceptible in the GYA. However, the *Ribes* species that most commonly occurs in close proximity to whitebark pine stands is *Ribes montigenum*, a high-elevation species. While it does not appear that *R. montigenum* is strongly associated with present blister rust disease level patterns in the GYA, its role in the disease system should not be discounted. Two distinct steps leading to present disease levels are those of pathogen establishment and pathogen intensification. It may be that *R. montigenum* is only involved in the intensification stage. If so, then pines near an abundance of *R. montigenum* but distant from the more susceptible *Ribes* may remain at low levels of infection, while pines in areas with synergistic proximities of *R. montigenum* and more susceptible *Ribes* may show higher disease levels than pines that are near only the more susceptible *Ribes*. *Ribes montigenum* was present at

only 11 of 45 sites surveyed in this study, and a larger sample size is necessary for meaningful comparisons of trends between sites with and without *R. montigenum*. The topic is worthy of further study.

A descriptive assessment of the untransformed data for the GYA Relative Severity Index values plotted against the distance to streams at or below 2621 m (Figure 8) fits the shape of an inverse power law function. This function is also a commonly accepted basis for diffusion models (Okubo and Levin 1989, 2001). The physical phenomenon of diffusion has been used as the framework for modeling spatial movement of biological organisms and populations (Andow et al. 1990, Okubo 2001). Atmospheric diffusion theory has been the basis for investigations of spore, pollen, and diaspore (seed and fruit) dispersion (Okubo and Levin 1989, Okubo et al. 2001). Use of diffusion models has allowed for calculations of the expected extent of spore dispersal for various values of diffusivity, settling velocity (related to particle size), and wind velocity. These mathematical interpretations have been useful in rough analyses of real-world processes (Okubo et al. 2001).

Various diffusion models have been empirically tested and generally support the idea that some quantities of spores (and other small particles) can be expected to disperse relatively long distances. For example, in a study of ragweed (*Ambrosia* spp.) pollen dispersal, it was estimated that approximately 1% of dispersed pollen grains would remain airborne at a distance of 1 km from the pollen source. Considering the enormous quantities of both pollen and spores that are typically released, even 1% can be a significant quantity (Okubo et al. 2001). Moreover, in a study specific to spore dispersal, it was found through spore-trapping methods that basidiospores of a white-rotting fungus (*Phlebia centrifuga* P. Karst) in natural old-growth forest conditions continued to settle at distances of 1 km from the source at an estimated rate of 28.5 spores per square meter (Norden and Larsson 2000). These authors reviewed their results and those from other studies of wood-decaying fungi as evidence that spore dispersal over distances of 1 km and greater may be a frequent event. Results of this study indicate that it may be valuable in the future to consider white pine blister rust in the context of diffusion models. Consideration of processes that may drive the statistically significant pattern between disease level and distance to particular landmarks will be useful for developing further investigations within this system.

Concluding remarks: This study is only an initial step toward detecting and describing patterns within this complex pathosystem. Results presented here suggest a simplified spatial pattern that supports a link between relative blister rust disease severities in whitebark pine and distances to expected habitat for susceptible *Ribes* species. The significant relationships between disease severity and distances to landscape features (the nearest stream at 2621 m and the nearest 5th order stream) found in this study imply that predictive abilities related to disease progression in this system are possible. Further research may increase our understanding of disease dynamics in whitebark pine forests and thereby support management and conservation efforts within the GYA. Ultimately such research, as initiated in this project, will also increase our understanding of impacts of introduced pathogens in natural systems.

TABLES AND FIGURES

Table 1. Locations, characteristics, and the Greater Yellowstone Area (GYA) Relative Severity Index values (see Results section) of sites in the GYA where whitebark pine trees were assessed for white pine blister rust.

Site Name	Severity	Elevation (m)	Aspect	UTM coordinates	Ribes species present (4.57 m)
Ski Lake	0.88	2947	220	12T 0505986 4819682	<i>R. montigenum</i>
Teewinot	0.71	2880	100	12T 0519399 4844512	None
Ramshorn Peak 2001	0.71	2810	160	12T 0492327 4998691	None
Upper Hoback	0.48	3139	275	12T 0537126 4767449	<i>R. montigenum</i>
Elephanthead Mtn.	0.47	2804	270	12T 0545020 5043607	None
25-Short	0.36	2982	70	12T 0517239 4838083	None
Swift Creek	0.25	3005	205	12T 0548960 4803717	None
South Fork Deep Creek	0.25	2944	195	12T 0543238 5039781	None
Ramshorn Peak 2002	0.24	2947	165	12T 0492588 4999699	None
Rock Creek	0.22	2829	110	12T 0491445 5003238	None
Surprise/Ampitheater Lakes	0.16	2932	190	12T 0518099 4841836	None
Flat Creek	0.16	2984	290	12T 0533073 4808440	None
North Fork Bear Creek	0.16	2707	150	12T 0528063 4996969	<i>R. lacustre</i>
Horse Creek Divide	0.13	2941	230	12T 0535094 4997979	None
Jackson Peak	0.12	2890	290	12T 0530602 4813500	<i>R. montigenum</i>
Sheep Mtn (Sleeping)	0.094	2900	160	12T 0535996 4822526	<i>R. montigenum</i> and <i>R. cereum</i>
Elbow Lake	0.076	2746	225	12T 0540669 5024803	<i>R. lacustre</i>
Fish Lake	0.066	2752	130	12T 0529390 4999893	None
Sheep Mountain-Lulu Pass	0.060	2941	220	12T 0584448 4990595	<i>R. montigenum</i>
Palmer Mountain	0.055	2835	270	12T 0532674 4989140	<i>R. lacustre</i> and <i>R. viscosissimum</i>
Lady of the Lake	0.055	2800	150	12T 0587911 4990692	None
Pine/Crevice Creeks	0.053	2807	290	12T 0533888 4991797	None
Shedhorn Ridge	0.052	2853	75	12T 0466690 4992812	None
Lambert/Colley Divide	0.045	2800	210	12T 0544836 5008875	None
Blue Miner Lake	0.042	3050	110	12T 0539555 4823662	<i>R. montigenum</i>
Wolverine Pass	0.035	2880	225	12T 0577234 4990654	None
Mt. Leidy	0.032	2950	145	12T 0548037 4841129	<i>R. montigenum</i>
Upper Thorofare Creek	0.028	2883	270	12T 0594825 4875555	<i>R. montigenum</i>
Lower Open Creek	0.023	3043	170	12T 0581748 4889624	None
Sentinel Creek	0.015	2903	170	12T 0464886 4979387	None
Bald Knoll	0.012	2954	290	12T 0541516 4693797	<i>R. montigenum</i>
Red Mountain	0.012	2804	155	12T 0489602 4975895	None
Upper Open Creek	0.012	2926	195	12T 0591042 4900111	<i>R. montigenum</i>
Lookout Mountain	0.0096	2934	195	12T 0561881 4993737	None
Hayden Creek	0.0093	2917	190	12T 0586761 4982841	None
Edmond Lake	0.0056	3078	335	12T 0618616 4752943	<i>R. lacustre</i>
Rainbow Lake	0.0046	3261	180	12T 0593938 4775089	None
Island Lake	0.0027	2978	185	12T 0615999 4978710	None
Camp Creek	0	2984	260	12T 0586817 4878873	<i>R. montigenum</i>
Surprise Lake Beartooths	0	2975	220	12T 0608088 4983320	None
Deer Creek Pass	0	3139	195	12T 0598698 4888230	None
Mt. Washburn	0	2813	265	12T 0544081 4960450	<i>R. montigenum</i>
Fawn Lake	0	2730	230	12T 0536195 4991446	<i>R. lacustre</i>
Beauty and Night Lakes	0	3050	140	12T 0613093 4979793	None
Avalanche Peak	0	2920	225	12T 0568814 4925354	None
Mean (SE)		2919 (17.0)	200 (9.2)		

Table 2. Summary of white pine blister rust severity (see Results section) by mountain range for 45 whitebark pine stands of the Greater Yellowstone Area (GYA) surveyed during 2001 and 2002. (North and South Absaroka Mountains divided at headwaters of the Lamar River.)

Mountain Range	Number of transects	Mean GYA Relative Severity Index	Standard Error of Severity Index
Teton	4	0.53	0.16
South Gallatin	3	0.39	0.16
Wyoming	2	0.25	0.23
Gros Ventre	5	0.13	0.036
North Absaroka	13	0.10	0.036
Mt. Leidy Highlands	1	0.032	-
Madison	3	0.026	0.013
Beartooth	5	0.024	0.014
South Absaroka	6	0.011	0.0054
Wind River	2	0.0051	0.00052
Washburn	1	0	-
Totals	45		

Table 3. Pearson product-moment correlation coefficients between independent variables (distance to nearest 5th order stream and total, forested, and mean of total and forested, distances to nearest stream at or below 2621 m). N=45 sites within whitebark pine sites.

Distance to nearest 5 th order stream related to the following variables:	Coefficient of Correlation (r)	Level of significance (p)
Distance to nearest stream at 2621 m	0.73	<0.000001
Forested distance to stream at 2621 m	0.70	<0.000001
Mean total & forested distance to stream at 2621 m	0.73	<0.000001

Table 4. Results of Pearson product-moment correlation analysis between distance variables to the nearest stream at or below 2621 m and relative canopy positions (by tree crown height thirds) of white pine blister rust cankers in whitebark pine trees. N= 37 sites with observed cankers.

Distance variable (to nearest stream at or below 2621 m) (km)	Relative tree crown height (by thirds)	Proportion of cankers within height class	Coefficient of correlation (r)	Level of significance (p)
Total	Lower	0.22	-0.45	0.0047
Forested			-0.48	0.0028
Mean total & forested			-0.47	0.0033
Total	Middle	0.32	0.017	0.44
Forested			0.0080	0.96
Mean total & forested			0.081	0.63
Total	Upper	0.46	0.20	0.24
Forested			0.30	0.067
Mean total & forested			0.25	0.14

Step 1: Divide tree into foliage and bole categories. Rate each category separately.

Step 2: Divide foliage / bole into thirds.

Step 3: Rate each third separately. The rating should be 0, 1, 2 or 3 (see below).

- 0 = no visible infection
- 1 = < 25% infected
- 2 = 25-50% infected
- 3 = > 50% infected

Step 4: Add ratings of thirds to obtain total foliage and total bole ratings.

Step 5: Add total foliage and bole ratings together for a total tree rating.

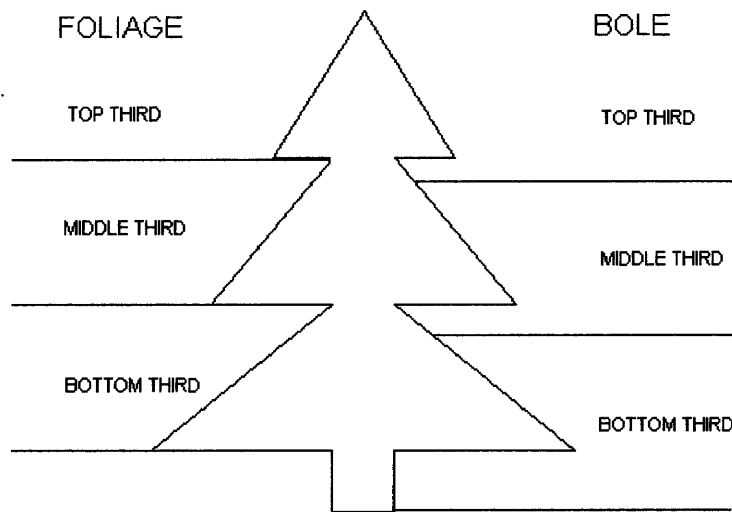


Figure 1. Numerical disease severity rating, from Six in prep., for use in assessing white pine blister rust in whitebark pine trees. Each of six visually-determined divisions of the tree (three within the foliage and three within the bole) is rated separately with a rating of zero, one, two, or three such that a minimum tree severity rating is represented by zero (no visible infection), and a maximum rating is represented by 18 (more than 50 percent of each of the six divisions is impacted by infection).

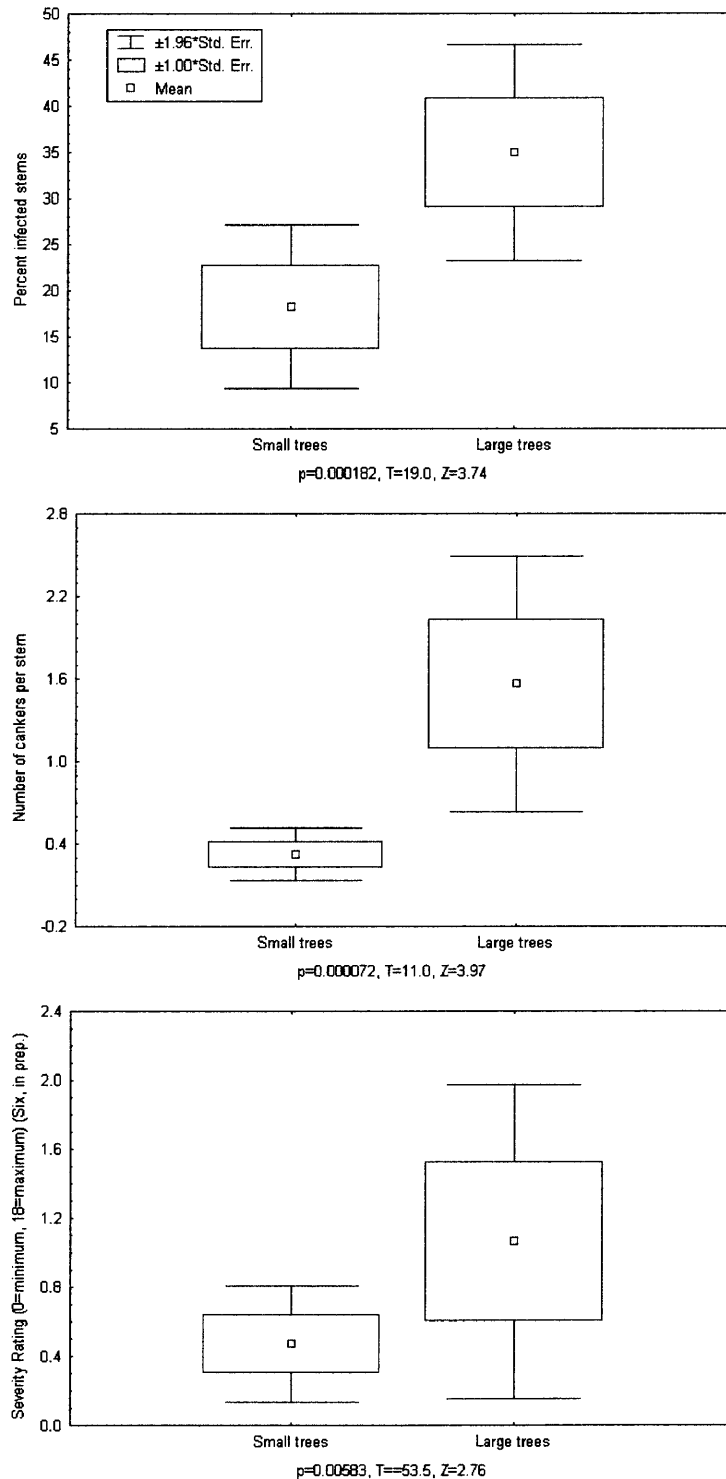


Figure 2. Comparisons of means of small and large trees, for standard measures of disease intensity (a. percent trees infected, b. number of cankers per stem, c. disease severity rating (see Figure 1)). Small and large trees are defined as those with diameter (dbh) less than or equal to 15.24 cm and greater than 15.24 cm respectively. N=24 sites with infection visited in 2002. Test statistics (T and Z) and levels of significance (p) from Wilcoxon matched pairs test (paired by means of small and large stems by site) are shown.

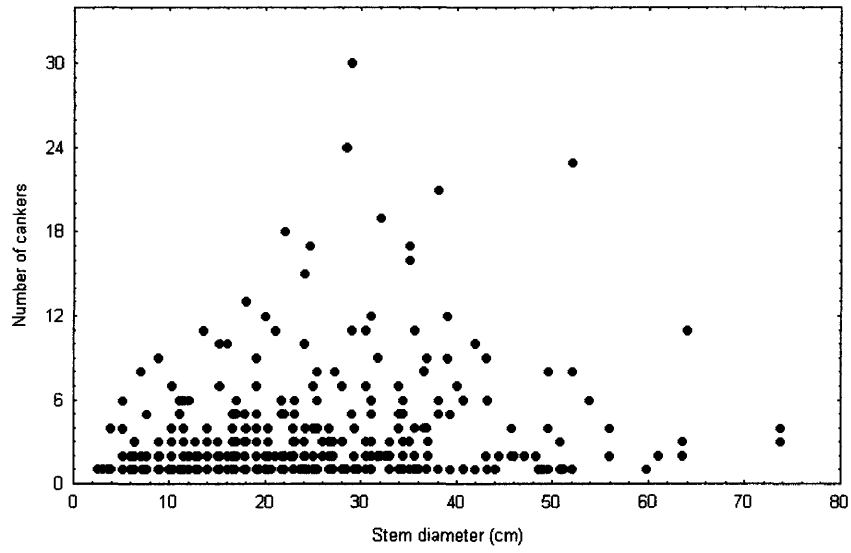


Figure 3. Number of white pine blister rust cankers by tree diameter (cm). N=405 stems with infection (includes all stems with infection surveyed in 2002, and single-stem trees with infection surveyed in 2001).

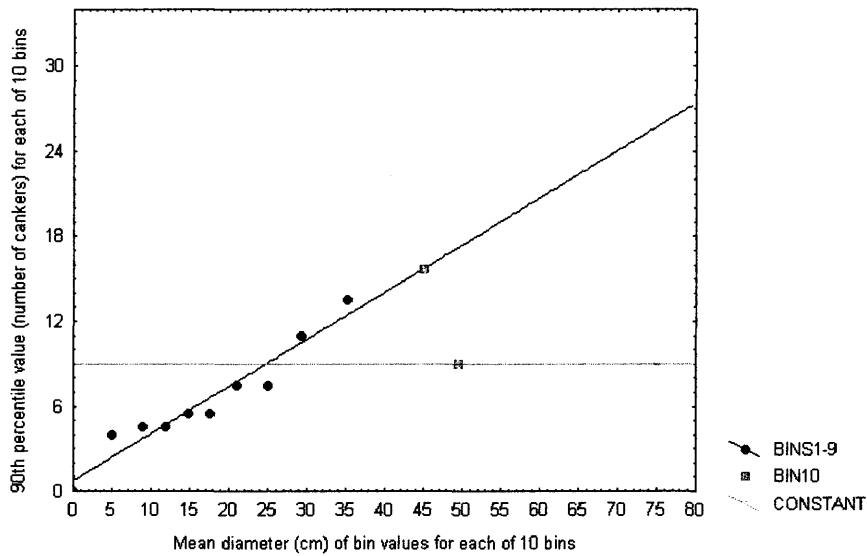


Figure 4. Expected infection capacity number of white pine blister rust cankers for whitebark pine trees in the Greater Yellowstone Area based on data collected during 2001-2002 grouped in 10 bins with counts of 40 or 45 per bin. Capacity numbers derived by the regression equation ($p=0.000006$, $R^2=0.93$) for 90th percentile values (number of cankers) against mean diameter (cm) for the lower 9 bins. The 90th percentile value for the 10th bin is shown in a straight-line relation with the inflection point at (45.0, 15.72). A straight-line relationship is shown with no slope for diameter values above the 90th percentile break-point diameter (49.45, 9.0).

Expected capacity – an upper value for the number of cankers per stem by tree diameter.

Expected capacity = $0.723 + 0.333(x)$ if diameter < 45 cm

Expected capacity = $83.615 - 1.509(x)$ if $45 \leq$ diameter < 49.45 cm

Expected capacity = $9 + 0(x)$ if diameter \geq 49.45 cm

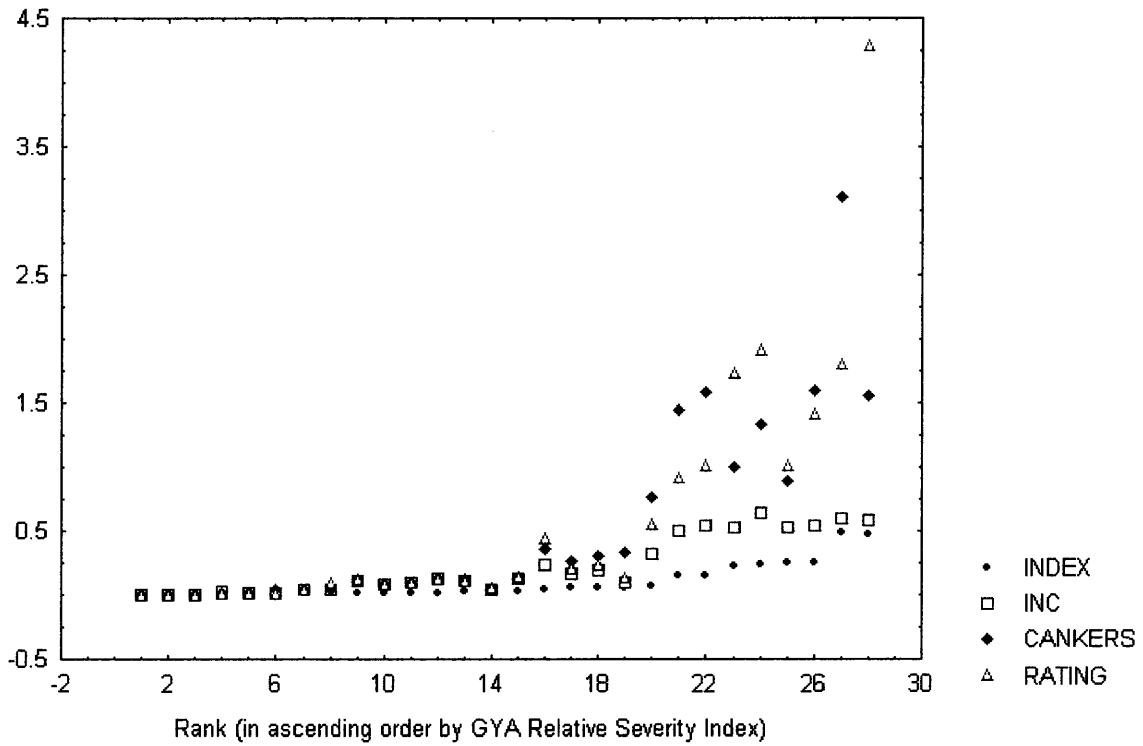


Figure 5. Four measures of disease intensity plotted against the derived GYA Relative Severity Index (N=28 sites surveyed in 2002). INDEX=GYA Relative Severity Index, INC = proportion of trees infected, CANKERS=mean number of cankers per stem, RATING=disease severity rating (see Figure 1).

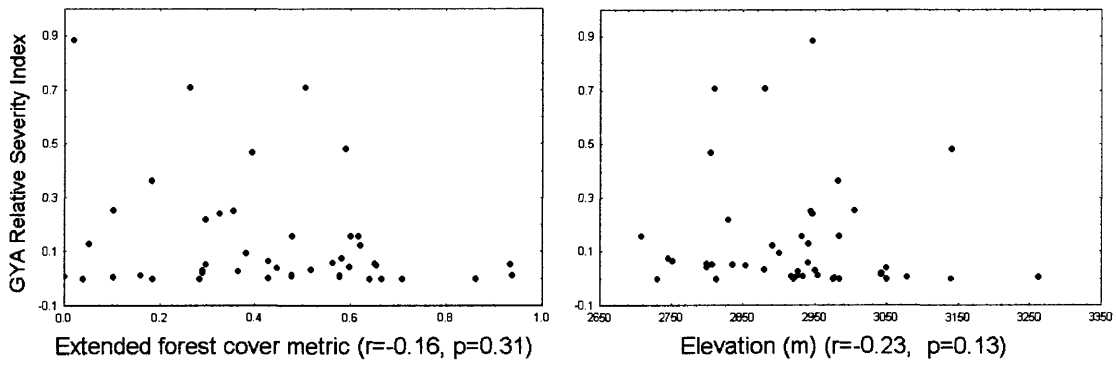


Figure 6. Spearman's rank order correlation coefficient (r) and level of significance (p) from correlation analysis comparing the index of white pine blister rust disease severity ($N=45$ whitebark pine sites) and the site factors of a metric of extended forest cover (calculated as the on-site canopy cover multiplied by the percent forest cover in the downslope, 0.18 square km) and elevation.

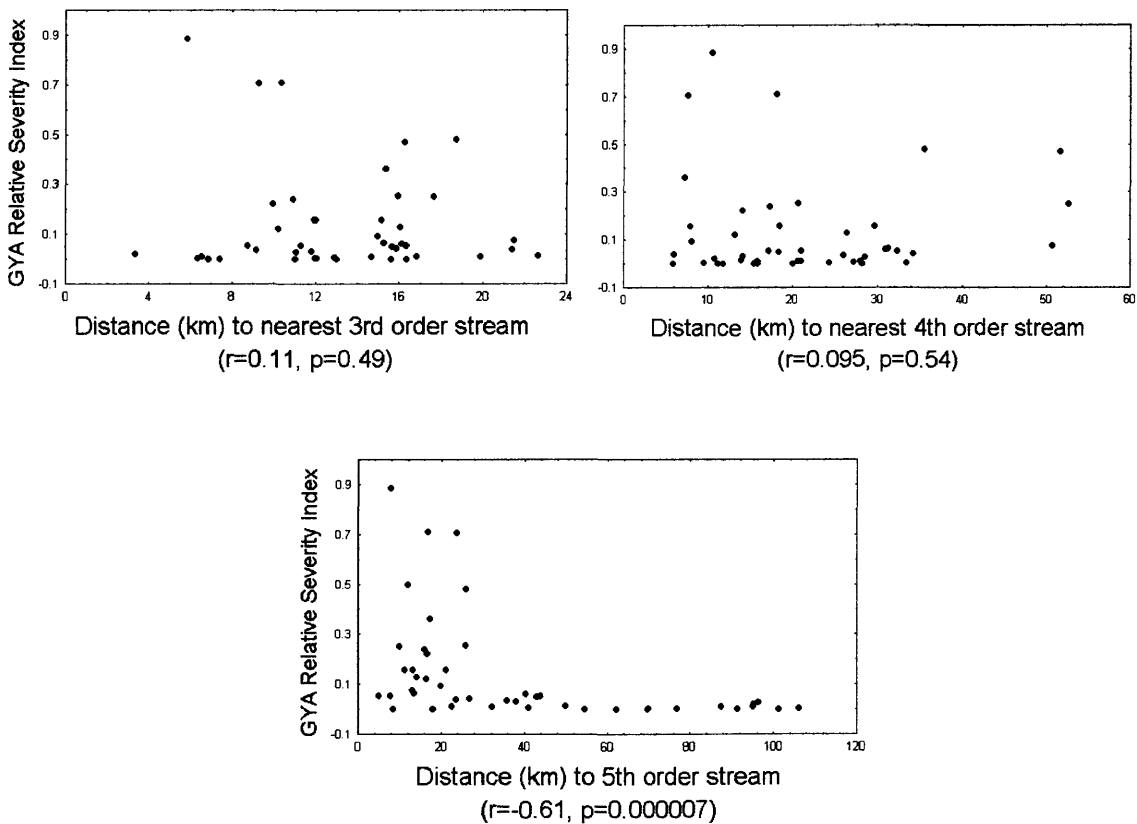


Figure 7. Spearman's rank order correlation coefficient (r) and level of significance (p) from correlation analysis comparing the white pine blister rust GYA Relative Severity Index ($N=45$ whitebark pine sites) and distances to the landscape features of the nearest 3rd, 4th, and 5th order streams.

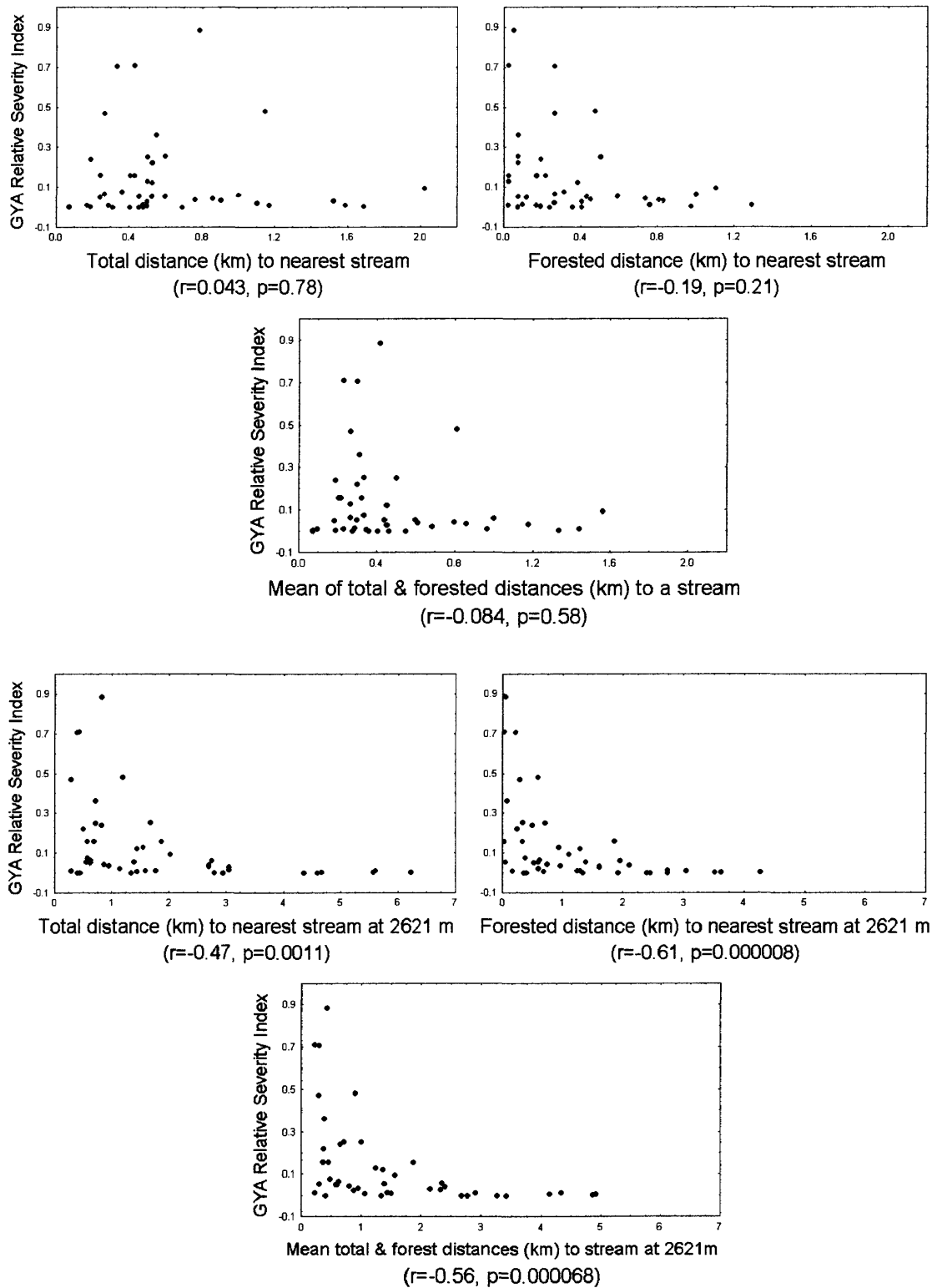


Figure 8. Spearman's rank order correlation coefficients (r) and levels of significance (p) from correlation analysis comparing the white pine blister rust GYA Relative Severity Index ($N=45$ whitebark pine sites) and distances to the landscape features of total, forested, and mean of the total and forested, distances to the nearest stream and the nearest stream at or below 2621 m.

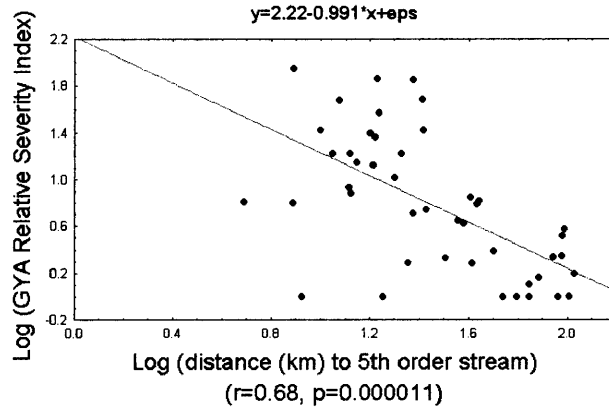


Figure 9. Correlation coefficient (r), level of significance (p), and regression equation from univariate regression of log-log transformed data relating the white pine blister rust GYA Relative Severity Index against distance to nearest 5th order stream. (N=45 sites surveyed in whitebark pine stands)

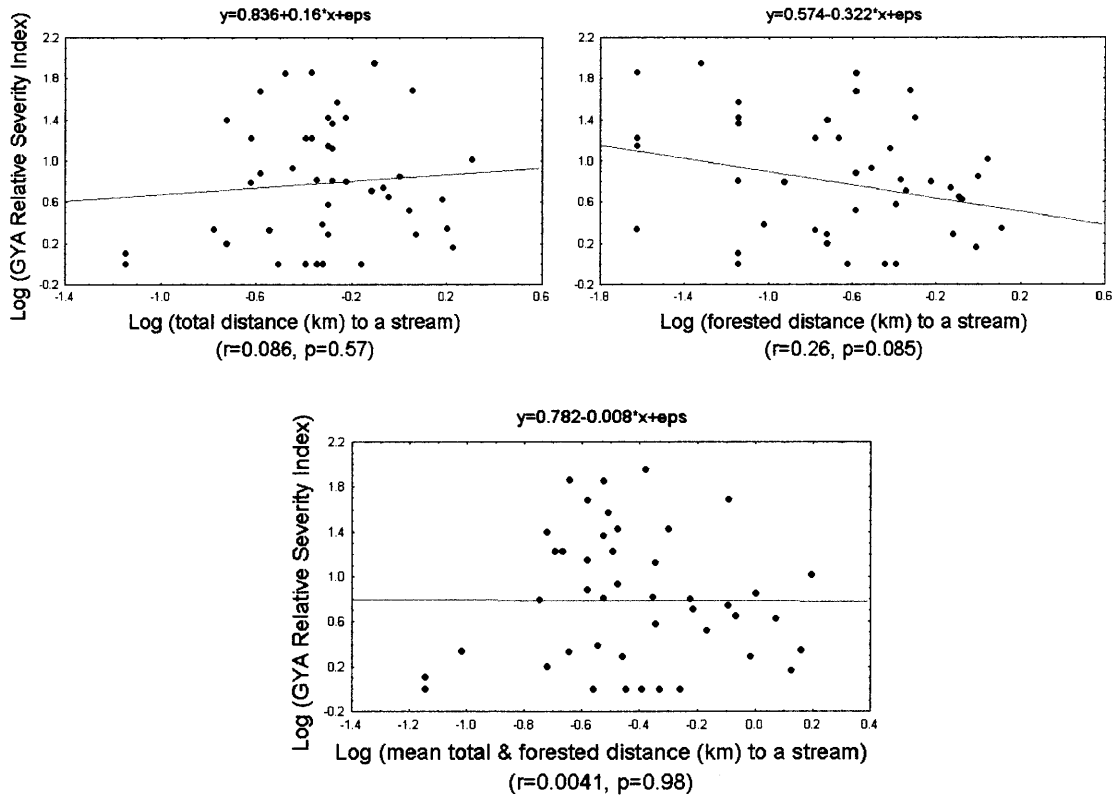


Figure 10. Correlation coefficients (r), levels of significance (p), and regression equation from univariate regression of log-log transformed data relating the white pine blister rust GYA Relative Severity Index (N=45 sites surveyed in whitebark pine stands) against total, forested, and mean total and forested, distances to nearest perennial stream.

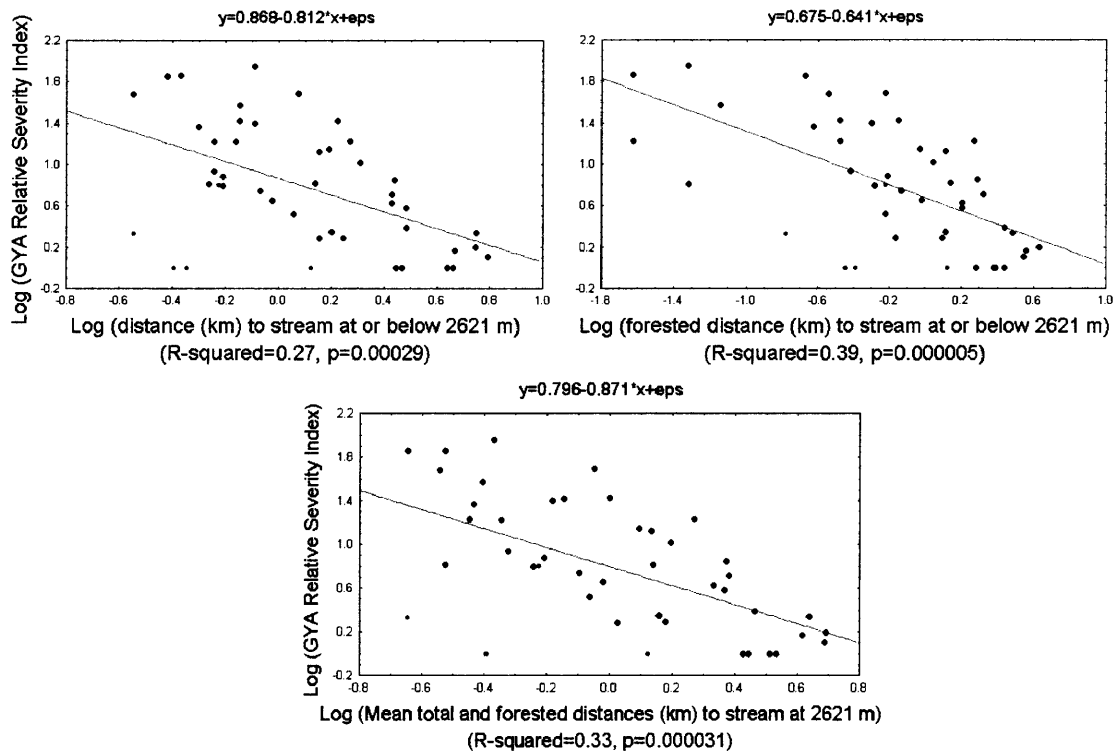


Figure 11. Correlation coefficients (r), levels of significance (p), and regression equation from univariate regression of log-log transformed data relating the white pine blister rust disease GYA Relative Severity Index (N=45 sites surveyed in whitebark pine stands) against total, forested, and mean total and forested, distances to nearest perennial stream at or below 2621 m.

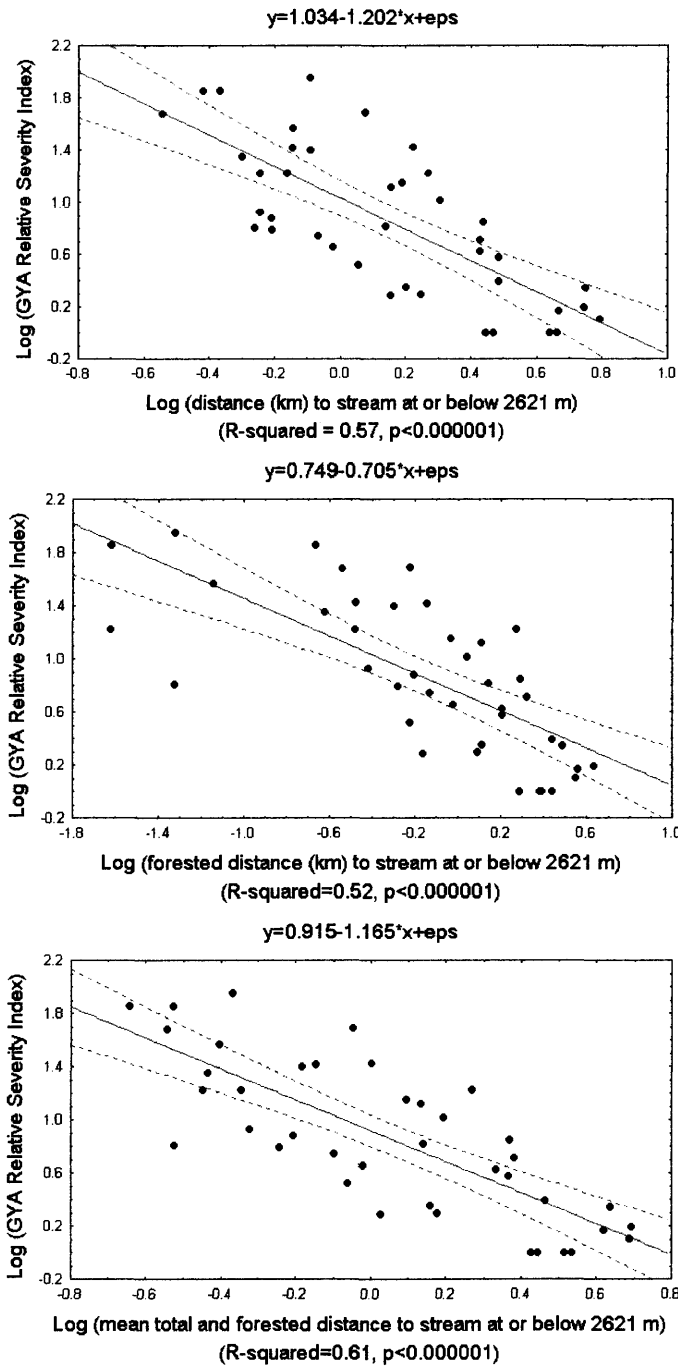


Figure 12. Coefficients of determination (R-squared), levels of significance (p), and regression equations from simple linear regressions of log-log transformed data relating the white pine blister rust GYA Relative Severity Index against total, forested, and mean total and forested, distances to nearest perennial stream at or below 2621 m. for sites with extended forest cover metrics less than or equal to 0.65.

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CHAPTER TWO:

The Ecology of the *Ribes* species of the Greater Yellowstone Area in Relation to White Pine Blister Rust in Whitebark Pine

ABSTRACT

Cronartium ribicola, the causal fungus of white pine blister rust, is an introduced pathogen that alternates between white pine hosts and currant and gooseberry hosts (members of the genus *Ribes*). The pathogen has had devastating impacts on white pine hosts in some areas. Recent research programs related to white pine blister rust have emphasized molecular and controlled-environment studies of the pine hosts while neglecting the role of the *Ribes* hosts and ecological aspects of the disease in general. Whitebark pine, one of two pine host species within the Greater Yellowstone Area (GYA), is an ecologically important high-elevation tree species. The role of the GYA *Ribes* species and *Ribes* – pine hosts proximities in disease dynamics within whitebark pine stands remains poorly understood. This paper characterizes the ecology of *Ribes* hosts in the GYA and initiates the development of a more comprehensive approach to the white pine blister rust pathosystem. Each *Ribes* species is a unique host group that exhibits a distinct spatial association with the pine hosts and a distinct genotypic and phenotypic susceptibility to infection by *Cronartium ribicola*. An overview of nine *Ribes* taxa known to occur in the GYA is presented, with discussion of the ecology and pathology of each.

INTRODUCTION

White pine blister rust is a disease caused by an introduced fungal pathogen (*Cronartium ribicola*). The disease system is a complex cross-Kingdom interaction between three groups of organisms (white pines, *Ribes*, and a fungus). The pathogen alternates between white pine hosts (members of the *Pinus* subgenus *Strobus*) where it persists as a perennial and often lethal infection, and currant and gooseberry hosts (members of the genus *Ribes*) where it infects only the deciduous leaves and results in relatively minor impacts. In many areas of North America, white pines are severely threatened by the disease, which is often recognized as the most devastating disease of conifers (Klinkowski 1970). Since the early 1900s when the pathogen first arrived in North America, forest managers have been challenged by the difficulties of blister rust control and prediction of damage and spread.

Two white pine species occur within the Greater Yellowstone Area (GYA): whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*). Whitebark pine inhabits more acreage in the GYA than limber pine. It is a slow-growing, high-elevation species that provides valuable watershed protection near headwaters, wildlife cover, and an important food source for birds, small mammals, and bears, including the federally protected grizzly bear (Tomback 2003). At least eight *Ribes* species are found in the GYA (Dorn 2001, m. newcomb, personal observation). These host plants and their interactions with the fungal pathogen are influenced by the climatic conditions and meteorological events of the GYA. Claims have been made that ecological conditions in the GYA generally limit the spread and intensification of the blister rust pathogen (Carlson 1978). White pine blister rust has been present in white pines of the GYA since the 1940s (Krebill 1969), and at present, disease intensities among whitebark pine stands are known to be highly variable, ranging from barely detectable incidences of infection to relatively high percentages of infected trees within a stand (Harris 1999, Smith and Hoffman 2000, m. newcomb, unpublished data). The fact that the disease still occurs in variable intensities after such a long presence leaves unanswered the question of whether the pathogen will threaten the existence of whitebark pine hosts within the GYA, or whether the ecological context in at least some portions of the GYA are such that whitebark pine hosts may be sustainable even in the presence of this exotic pathogen.

The objective of this paper is to address gaps in current knowledge of dynamics of white pine blister rust in the GYA. Information on the ecology of local *Ribes* species presented herein addresses an aspect of the disease that is vitally important, but which has generally been neglected in recent research programs. An extensive history of white pine blister rust research exists, dating back to the early 1900s when the introduction of the pathogen to North America led to the first active program to control an exotic disease outbreak within the developing forestry programs (Geils 2001). White pine blister rust research efforts have persisted to present times in various forms (Maloy 1997), resulting in a large library of literature on the topic. However, our present understanding of white pine blister rust disease dynamics could benefit greatly from a more comprehensive perspective that includes the *Ribes* hosts. Recent research has often disregarded the role of the *Ribes* hosts, and ecological aspects of the disease in general. An ecological perspective considers relationships between organisms and their environment, and all the associated inherent complexities of the affected ecosystem (Kendrick 1992).

The general lack of attention to the *Ribes* alternate hosts is evident when searching existing literature on this pathosystem. For the purposes of this paper, a search was conducted using the Cambridge Scientific Abstracts Plant Science and Biological Sciences databases (inclusive of 250 primary research journals and approximately 5700 serials). Categorical results (by host group and study setting) of a keyword search using “white pine blister rust” or “*Cronartium ribicola*” from 1995 to present are shown in Table 1. Only 4 of 44 published works have considered *Ribes* species relative to white pine blister rust disease. These studies (Zurawicz et al. 1996, Hummer 1997, Pedersen 1997; 1998) were all based on improving, in part through disease resistance, *Ribes* cultivars, as horticultural crops. Only one of the four studies (Hummer 1997) included *Ribes* species native to North America. Furthermore, only 5 of 44 papers (reporting results from 4 studies) considered pine hosts in forested habitats while 32 considered pine hosts and/or the pathogen only under artificial conditions (either laboratory or controlled greenhouse or nursery environments). Thus, recent (published in 1995-2003) white pine blister rust studies conducted under natural conditions (forest and plantation) comprised only 27% of all studies. Moreover, studies of native *Ribes* species that occur in North American forests comprise only 2% of all recently published works, and no studies have been published during that time period on *Ribes* species occurring in natural conditions.

Results from the above studies show a consistent trend toward use of molecular approaches in research both within forest pathology (Lundquist and Klopfenstein 2001) and general plant population studies (Jelinski 1997). There has also been a considerable number of mechanistic experiments carried out under controlled conditions designed to reduce the tremendous complexity that exists in forest systems. Molecular and mechanistic studies are incontrovertibly important for understanding many aspects of the disease. However, without corresponding studies that further test these results under natural conditions, and characterize the natural field conditions in which the small-scale processes occur, some level of doubt will accompany their conclusions (Innes 1993, Brown et al. 2001, Harvey 2001). Comprehensive knowledge of this and other pathosystems requires that ecological and ecosystem studies keep pace with controlled-environment and molecular studies (Zadoks 1999, Hatcher and Paul 2000, Bergelson et al. 2001, Harvey 2001).

Manipulations of plant communities (Miller 1994, Callaway et al. 2002), natural enemy-host systems (Bjornstad et al. 2001), intertidal food-web systems (Berlow 1999), and desert shrubland and pinyon-juniper woodland ecosystems (Brown et al. 2001) have all documented the importance of intricate interactions between community members and that indirect effects can sometimes be stronger than direct effects on population and community functions. Weak interactions can ultimately act as strong community stabilizers, and disparate taxa from diverse trophic levels can be tightly linked through cascading interactions. Most, if not all of these effects and interactions would be eliminated in simplified experimental systems. Additionally, long-term ecological studies have shown that episodic abiotic events can cause significant shifts in species interactions (Brown et al. 2001). The important community-level impacts that result from such episodic events are not only undetectable in controlled-environment studies, but also in short-term field studies. Finally, the importance of considering ecological contexts is well illustrated by the fact that even host plants of the same species occurring in variable environments can relate to pathogens as dissimilarly as separate species (Loomis and Adams 1983). Thus, biological insights into complex systems generally arise through a process that combines analyses of simplified, isolated factors, with analyses of real-world contexts and consideration and knowledge of the ecological context.

This characterization of the ecology of *Ribes* hosts in the GYA can, therefore, serve as a beginning step in developing a more comprehensive approach to the white pine blister rust pathosystem.

THE GREATER YELLOWSTONE AREA

Among all the North American white pines, whitebark pine forests are unique in that they typically occupy vast, contiguous expanses of lands that have experienced little direct human-impact. The GYA has been referred to as the largest expanse of connected wild areas in the lower forty-eight states and is viewed as a national, even global, treasure (Keiter 1991, Patten 1991, Noss et al. 2002). It is comprised of about 23,000 square kilometers, encompassing significant natural resources and the headwaters of three major watersheds (the Snake-Columbia, the Green-Colorado, and the Yellowstone-Missouri Rivers) (Keiter 1991). By jurisdiction, the area spans seven national forests, two national parks, three federal refuges, and Bureau of Land Management and state lands in Wyoming, Montana, and Idaho (Craighead 1994, Reinhart et al. 2001). This relatively pristine and un-manipulated character of GYA whitebark pine forests defines the nature and importance of potential impacts from white pine blister rust to these pine hosts as an environmental problem in the category of global-change issues.

HISTORICAL PERSPECTIVE

In contrast to the recent lack of focus on the role of the *Ribes* hosts in white pine blister rust management and research efforts, *Ribes* species were the center of focus during a massive historical blister rust control program conducted from 1909 to 1967 (Maloy 1997). Management for control of the disease began shortly after discovery of the disease in North America in the early 1900s. Under the blister rust control program, the restriction of cultivated, and the destruction of wild, *Ribes*, was seen as the best means of disease control. As part of this program, an extensive *Ribes* eradication program was conducted in the United States. Eradication efforts focused on manually, mechanically, and chemically destroying wild *Ribes* shrubs. The program cost millions of dollars, caused undetermined ecological consequences, and employed as many as 11,000 workers at one time during its peak (Maloy 1997).

Numerous records were made of the extensive blister rust control activities in Yellowstone National Park which occurred over more than 20 years (Galusha, no date). Throughout the Yellowstone program, *Ribes* removals occurred only within designated control areas, totaling 115,470 acres

(Hendrickson 1967). Concern for Yellowstone's white pine hosts increased in 1937, when *C. ribicola* was found on *Ribes hudsonianum*, in an area 19 miles northwest of the park boundary (Galusha, no date). The first significant scouting effort for signs of the pathogen within and adjacent to the park occurred in 1940 when several thousand *Ribes* and approximately 1,000 white pines were surveyed, all with negative results (Joy 1940). By 1944, momentum for the *Ribes* eradication program was building. A ten-day disease survey in early September of that year revealed 20 infected leaves on two *R. hudsonianum* plants within the park. The first efforts to remove *Ribes* in the park occurred in 1945 (Riley and Chapman 1945, Galusha, no date). By 1947, blister rust control work crews were an organized and hard-working battalion. The 1947 section of H.D. Galusha's undated summary of blister rust control work in Yellowstone National Park includes words of respect for the war veterans who dominated the work crews of the time, and who "established a degree of excellence that is unparalleled in easier times – undoubtedly at the expense of much blood, sweat, and tears, the phenomenal figures of ribes eradication pay silent tribute to what was probably a very colorful era marked by very dedicated leaders and hard-working men."

An infected pine was found within Yellowstone National Park for the first time in 1950 (Gynn and Chapman 1950), and by 1956 infected limber pine and *Ribes viscosissimum* were discovered in nearby Grand Teton National Park. *Ribes* removal work continued, and between 1945 and 1952, a total of 1,785,000 shrubs had been destroyed (Galusha no date). *Cronartium ribicola* was continuing to spread and was found in southeastern parts of Wyoming in 1952 and 1956 (White Pine Blister Rust Control Annual Report 1956).

In 1966, Region 1 (Idaho, Montana, and Wyoming) of the Forest Service began a study to evaluate the results of the *Ribes* eradication program that had been in place for over 30 years. Results showed a similar average infection rate in pines whether *Ribes* had been removed or not (Toko et al. 1967). Therefore, the Region 1 *Ribes* eradication program was halted. In Yellowstone National Park, a similar study in 1975 also found that the removal of *Ribes* did not appear to affect the level of pine infection and it was recommended that the eradication program in force in the park also cease (Berg et al. 1975). Surveys completed from 1968-1971 throughout portions of the park reported 959 (0.3%) infected trees out of

325,641 examined. Because of the generally low infection levels observed, the authors concluded that “blister rust will never eradicate the white pine type in Yellowstone” (Berg et al. 1975).

Yet, more than 25 years after that proclamation, it is now known that disease intensification has occurred in some areas within and adjacent to the park (Smith and Hoffman 2000, Chapter 1 of this thesis) indicating that over time white pine blister rust may result in impacts to whitebark pine in at least some localized areas of the GYA. The same questions that were of concern in 1975 (Berg et al. 1975) remain unanswered: (1) Do the conditions within Yellowstone National Park limit rust spread, and (2) what roles do *Ribes* species play in rust spread and intensification? Results reported in Chapter 1 of this thesis show a pattern of pine infection related to the distance to the nearest stream at or below 2621 m, a landmark selected for consideration because of its association with the upper-elevational limit of most *Ribes* species occurring in the GYA. Thus, while reduction of *Ribes* abundance in localized areas during eradication efforts did not appear to lead to a reduction in overall infection level, it is possible that *Ribes* distributions may still be an important factor in the observed pattern of white pine blister rust infection. The characterization of the *Ribes* species of the GYA can provide an additional layer of information to facilitate better understanding of the dynamics of this disease.

OVERVIEW OF RIBES

The genus *Ribes* L. (Grossulariaceae) is a large taxon that includes 120 to 150 species of wild and cultivated currants and gooseberries. *Ribes* species are found across much of the temperate regions of the Northern Hemisphere, as well as in western North Africa, in the Andes of South America, and at high elevations in Central America creating a nearly continuous distribution from Alaska to Tierra del Fuego (Messinger et al. 1999, Sinnott 1985). Members of the genus are shrubs with alternate or clustered, simple leaves, and that produce fruits that are succulent berries.

Ribes plants are obligate alternate hosts for two species of rust fungi (*Cronartium ribicola* and *C. occidentale*) that can cause considerable damage to pines while causing relatively little damage to *Ribes*. In North America, *C. occidentale* is a native rust and is less damaging ecologically than the introduced *C. ribicola* (Hahn 1930). The life cycles of the two species of *Cronartium* are similar except that *C. occidentale* infects pinyon pines while *C. ribicola* infects white (five-needle) pine hosts (Van Arsdell and

Krebill 1995). The spore stages that occur on *Ribes* leaves are similar in appearance for these two species, and are difficult to distinguish visually (Hahn 1930). Both have been reported to occur in the GYA (White Pine Blister Rust Annual Report 1964, Graham 1966), although *C. ribicola* is much more commonly found.

There are historical references to human use of gooseberries and currants that extend at least back to an herbal printed in 1578 (Sinnott 1985). More recently, a large commercial market for products from cultivated *Ribes* has developed, including ornamentals, medicinal extracts, and edibles such as juices, jams, jellies and dessert berries. Most commercial *Ribes* production is in northern Europe (Brennan 1996). In North America, the popularity of *Ribes* species as commercial and ornamental plants has been impacted by their role as alternate hosts in forest diseases (Newman 2002). However, there has been a recent increase in the appeal of *Ribes* as commercial plants in North America (Brennan 1996, Newman 2002).

Blackcurrant reversion disease continues to impact *Ribes* production outside the Americas. Blackcurrant reversion disease is caused by a virus (genus *Nepovirus*), and results in severe crop losses (Jones 2000). American production of currants and gooseberries may, therefore, fill an increasing demand as European crops decline. However, increased plantings of *Ribes* in North America may negatively impact native white pine populations if these *Ribes* are susceptible to white pine blister rust and can act to intensify the disease. For these reasons, the emphasis of recent research has been rust disease resistance in commercial *Ribes* cultivars (Hummer 1997) and has generally excluded wild, native *Ribes* species. Thus, little is known of the ecology or pathology of *C. ribicola* in wild *Ribes*.

RIBES SPECIES OF THE GYA

The following nine *Ribes* taxa are known to occur in the GYA (Despain 1975, Dorn 2001, Craighead 1994, m. newcomb, personal observation):

- * *Ribes aureum* Pursh
- * *Ribes cereum* Dougl.
- * *Ribes hudsonianum* Richards. (previously reported as *R. petiolare*)
- * *Ribes inerme* Rydb.
- * *Ribes lacustre* (Pers.) Poir.
- * *Ribes montigenum* McClatchie
- * *Ribes oxyacanthoides* ssp. *hendersonii* (C.L. Hitchc.) Sinnott (previously reported as *R. hendersonii*)
- * *Ribes oxyacanthoides* ssp. *setosum* (Lindl.) Sinnott (previously reported as *R. setosum*)
- * *Ribes viscosissimum* Pursh

Each of the above taxa occur in distinct habitats, resulting in a unique relationship with the abiotic environment (relative humidity; exposure to wind, sun, and frost; topography- and canopy-determined temperature influences; etc.) and a distinctive spatial association with pine hosts. Moreover, it is recognized that taxon-specific variation exists in genetically-based biochemical and morphological plant defenses, with wide variation in disease resistance exhibited among species, and among individuals within a species (Mielke 1937). Each taxon is a unique host whose relationship with the pathogen can vary within and among habitats. Therefore, it is critical to consider the role of *Ribes* in disease intensification at a species-level taxonomic resolution (or even at the subspecies-level in the case of *R. oxyacanthoides*). A general overview of the biology of each species, its occurrence in the GYA, and what is known of its relative susceptibility to infection by *C. ribicola* follows.

***Ribes lacustre*:** *Ribes lacustre* is widely distributed and occurs in both eastern Asia and North America (Messinger et al. 1999). This species is the only Yellowstone area *Ribes* whose geographic range extends beyond North America (Messinger et al. 1999). In North America it ranges from Alaska south to California and east to Newfoundland, with occurrences in the Dakotas, Michigan, Pennsylvania, Colorado and Utah (Hitchcock and Cronquist 1973, Lackschewitz 1991). The broad distribution of this species, along with its production of edible fruits that are utilized by chipmunks, other small mammals, birds and bears, suggest that *R. lacustre* has great ecological value in the forested areas where it is found (Martin et al. 1951, Hamer et al. 1991).

Ribes lacustre can be found throughout the GYA in most woods, on forested slopes, and along stream banks at elevations up to approximately 2650 m, and in some rocky sites above that elevation (Hitchcock and Cronquist 1973, Lackschewitz 1991, m. newcomb, personal observation). Rocky Mountain Herbarium records of *R. lacustre* collection locations within Wyoming (data request April 2001) support this distributional range with 93 of 98 collections reported either from below 2650 m in elevation, or from rock outcrops at elevations above 2650 m. While herbarium records are not necessarily a representative sample of a population, they can contribute to collective information on a species distribution. Although the distribution of *R. lacustre* is characterized by high constancy (presence in a high proportion of stands) (Steele et al. 1983), it often only exhibits low cover values in the stands where it occurs (Oosting and Reed

1952, Coates et al. 1990). *Ribes lacustre* is commonly associated with wet or moist areas (Despain 1973, McLean 1970, Applegate 1939, St. John and Warren 1937). In the Alberta Rockies, *R. lacustre* has been classified as hygro-mesic, with a rating of four in a five-point scale (one being associated with xeric sites and five with moist sites) (La Roi and Hnatiuk 1980). However, it appears to be a fairly tolerant species that is not restricted only to wet areas but is also observed in open forests and openings (Mielke 1937). It has a low- to moderate-shade tolerance and is the most shade tolerant of the *Ribes* species that occur in western intermountain forests (Oosting and Reed 1952, Coates et al. 1990, Moss 1953).

The ability to do well in disturbed areas and when subjected to stress is typical of *Ribes* species in general. *Ribes lacustre* appears to fit these characteristics well. In northwestern Oregon, *R. lacustre* was present at a frequency of 4% in a burned area while not observed in adjacent undisturbed forest (Neiland 1958). A post-logging recolonization study in central Canada led to classification of *R. lacustre* as a facultative stress tolerator, implying an ability to grow rapidly following a disturbance that increases available light and nutrients, as well as an ability to persist under low light and nutrient conditions (Brumelis and Carleton 1989).

Many shrubs, including *R. lacustre*, produce adventitious roots in response to damage and stress. A study of plants buried by volcanic tephra after the Mount Saint Helens eruption showed that *R. lacustre* produced 2 to 5 adventitious roots per centimeter of stem (Antos and Zobel 1985). This is an effective adaptive response to many disturbances, although apparently not to highly intense burns that may destroy roots. *Ribes lacustre* was found to decrease significantly in frequency following slash burns that created high soil temperatures in the Mission Mountains of Montana (Vogl and Ryder 1969). Thus *R. lacustre*'s ability to respond to an increase in resources following a disturbance is variable, depending upon the type and intensity of damage.

Moreover, evidence suggests that this species is also adapted to stress that does not directly increase available resources. A comparison of vegetation in and out of deer yards showed a tendency for *R. lacustre* to be a "moderate increaser", meaning it can tolerate, and even benefit from, deer browsing (and/or associated presence) (Habeck 1960). Additionally, Mielke (1937) reported that *R. lacustre* tolerates some level of chemical herbicide stress and responds to mechanical damage by vegetative layering. It is likely

that *R. lacustre* has evolved under browsing pressure. It is known to be a food source for browsers such as deer (Wallmo et al. 1972, Singer 1979), elk (Edge et al. 1988), and mountain goats (Saunders 1955). It is plausible that *R. lacustre* exemplifies most species in the genus in its ability to respond positively to disturbance and tolerate different forms of stress.

Studies conducted in the 1930s found that *R. lacustre* generally exhibits low susceptibility to white pine blister rust (measured as percent of leaves infected and percent of leaf-area supporting infection) (Kimmey 1938). However, additional studies suggested that the species was none-the-less important as a source of spores for pine infection (Mielke 1937, Buchanan and Kimmey 1938). Thus, the amount of infection supported per leaf or per shrub may not translate directly to the amount of pine infection that occurs. This may indicate that some component of the ecological context, such as the consistent distribution of *R. lacustre*, its proximity to white pines, features of the microsites it tends to inhabit, or some other related factor, may ultimately play a critical role in disease dynamics.

***Ribes viscosissimum*:** *Ribes viscosissimum* ranges from British Columbia, south along the east side of the Cascade Range to the Sierra Nevada Mountains in California. The species is found in northern Arizona, and its range extends east to include Montana, western Wyoming, and northwestern Colorado (Hitchcock and Cronquist 1973, Lackschewitz 1991). In the Yellowstone area, the distribution of *R. viscosissimum* overlaps somewhat with that of *R. lacustre*. Like *R. lacustre*, *R. viscosissimum* is more commonly found at elevations below 2600 m, and generally occurs above that elevation only in specific microsites (m. newcomb, personal observation). Both species are commonly found where soils are generally moist (Applegate 1939, Daubenmire and Slipp 1943). However, *R. viscosissimum* has a deeper taproot than *R. lacustre*, and can grow in drier areas. *Ribes viscosissimum* has a low tolerance for shade and cannot persist under closed canopies (Moss 1953). A study in a red fir forest of the Sierra Nevada found that *R. viscosissimum* shrubs were short and spindly when occurring in closed canopy conditions, while in more open conditions they were robust and flourishing (Oosting and Billings 1943). *Ribes viscosissimum* has often been observed thriving after canopy removal events (fire, logging, blow-downs) in association with reproducing pines (Pack 1934). In areas where light is not limiting, the distribution of *R. viscosissimum* has been measured as intermediate between a random and a contagious distribution pattern.

This could be explained by initial seed dispersal (most likely by birds) being fairly random, and then over time the plants that establish become centers of localized reproduction (Fracker and Brischle 1944).

Even though *R. viscosissimum* does not tolerate low-light conditions as a shrub, it can persist under these conditions in the seed bank. Fruits of *R. viscosissimum* have plentiful seeds. A small sample of berries from southeast Washington showed an average of 71 seeds per *R. viscosissimum* fruit (Piper 1986). In central Idaho, samples from soil layers of three forest types were analyzed for seed content. A total of 91 viable seeds from *R. lacustre* and/or *R. viscosissimum* were found, for a maximum density of 567 viable seeds per square meter (Kramer and Johnson 1987). Some data suggest that the seeds may not only be abundant in forest soils, but also remain viable in these soils for a long period of time. The seeds are generally not windborn, but may be dispersed by birds and mammals. A study of seedling emergence from soil samples collected from mixed conifer forests showed that samples of soils from areas where *R. viscosissimum* and *R. cereum* plants were absent produced seedlings of both species, implying a seed-bank or animal-dispersed source (Strickler and Edgerton 1976). This indicates adaptive means by this plant of persisting through unfavorable conditions, and thriving from disturbance.

The susceptibility of *R. viscosissimum* to *C. ribicola* is generally believed to be similar to that of *R. lacustre* (Kimmey 1938). Moreover, results of an experiment conducted in forested conditions showed both *R. viscosissimum* and *R. lacustre* to be similarly capable of facilitating disease progression in nearby pines (Buchanan and Kimmey 1938). Thus, even with a relatively low susceptibility rating, the role of *R. viscosissimum* in disease dynamics cannot be discounted. An additional factor to consider is the proclivity of this species for establishment and increasing productivity following disturbances. Disturbance is a fundamental process for both host groups (*Ribes* and whitebark pine), and thereby, for the pathogen as well. It appears that disturbance may be particularly significant for *R. viscosissimum* since it thrives as an early-successional shrub in reproducing stands (Pack 1934, Lackschewitz 1991, m. newcomb, personal observation).

Ribes hudsonianum: This riparian species ranges from Alaska to northern California, east to Hudson's Bay and is found in Minnesota, Wyoming, and Utah (Hitchcock and Cronquist 1973, Lackschewitz 1991). While *R. lacustre* and *R. viscosissimum* are sometimes found growing in moderately

mesic conditions, *R. hudsonianum* requires a wet rooting medium to persist (Davis 1952, Lackschewitz 1991) and is often seen growing in running water (m. newcomb, personal observation). This species has a national wetland indicator status of facultative obligate-wetland (USDA, NRCS 2001) meaning that it is at least as likely to occur within a designated wetland as not, and in some areas it occurs almost exclusively in wetlands. While *R. hudsonianum* shrubs generally occur in narrow belts along streams or seeps, they can also occur in dense thickets as a dominant component of the riparian vegetation. There is some historic evidence suggesting that *R. hudsonianum* is of intermediate importance as a summer browse plant for Yellowstone deer (Russell 1932) and browsed stems are common (m. newcomb, personal observation).

The distribution of *R. hudsonianum* within the GYA is more variable than that of *R. lacustre* and *R. viscosissimum*. Drainages within some regions support very dense patches, while other drainages have either no apparent occurrences, or support only a few small or scattered patches (m. newcomb, personal observation). While there are regional trends in distribution, even adjacent drainages can differ in relative abundance of *R. hudsonianum*. This distributional variability is notable enough that *R. hudsonianum* was not selected as a habitat type indicator species for use in a system of forest-type classifications developed from vegetation composition patterns (Pfister et al. 1977, Steele et al. 1983). Like *R. lacustre*, this species was rarely observed above an elevation of 2650 m (m. newcomb, personal observation). Rocky Mountain Herbarium collection locations are again consistent with my observations, with only 2 of 40 collections were reported from elevations above 2650 m (data request April 2001).

Ribes hudsonianum is widely recognized as the most susceptible of the *Ribes* that inhabit the GYA (Lachmund 1934, Kimmey 1938, Pierson and Buchanan 1938, Moss 1953). Yet the role this species plays in disease progression in whitebark pine is still largely unknown since the high susceptibility of this species may be ameliorated some by the fact that the shrub is limited to wet habitats, often at elevations lower than where whitebark pine stands occur, and therefore, frequently occurs at some distance from whitebark pine stands.

***Ribes inerme*:** The range of *R. inerme* extends from British Columbia south along the eastern side of the Cascade Range to the Sierra-Nevada Mountains in California and Nevada east to Montana, Wyoming, Colorado and New Mexico from 1200 to 3000 m (Hitchcock and Cronquist 1973, Sinnott 1985,

Lackschewitz 1991). In the GYA, the species is most commonly found below about 2550 m, along streams and in wet bottomlands, and is frequently associated with willows (Rocky Mountain Herbarium collections, m. newcomb, personal observation). In many sites in the GYA, *R. inerme* growth is essentially restricted to willow patches, but can still be quite abundant in large willow bottoms.

Ribes inerme and *R. oxyacanthoides* ssp. *setosum* co-occur in geographic range and habitat (Dorn 2001) and when not in flower are challenging to distinguish (J. Whipple, Yellowstone National Park botanist and B.W. Geils, US Forest Service Rocky Mountain Research Station plant pathologist, personal communications; m. newcomb, personal observation). In fact, where both taxa are known to overlap, population studies have revealed apparent hybrids with intergraded morphological features (Sinnott 1985). In many contexts they are distinguishable; however, *R. inerme* is more restricted to wet sites, it tends to grow in a more sprawling form, and is often less defended with spines than *R. oxyacanthoides* ssp. *setosum* (m. newcomb, personal observation).

Ribes inerme is thought to be a relatively highly susceptible species, although somewhat less than *R. hudsonianum* (Kimmey 1938). It also is generally more distant in its proximity to whitebark pines since it inhabits wetter areas, often at lower elevations than whitebark pine stands.

Ribes oxyacanthoides* ssp. *setosum* and ssp. *hendersonii: Currently there are five accepted subspecies of *R. oxyacanthoides* (Sinnott 1985). Two subspecies occur in the GYA. These are *R. oxyacanthoides* ssp. *setosum* and ssp. *hendersonii*. Many floras distinguish these taxa at the species-level as *R. setosum* and *R. hendersonii* (Lackschewitz 1991). The two subspecies are allopatric and occupy distinct localized areas, as do all five subspecies of *R. oxyacanthoides* across North America (Sinnott 1985). They also differ significantly in morphology. Ecologically, they also merit consideration as distinct taxa. *Ribes oxyacanthoides* ssp. *setosum* is found at elevations between 1500 and 2700 m in the Rocky Mountains of central and southern Montana, eastern Idaho, northern Utah and Wyoming (Sinnott 1985). The more northerly *R. oxyacanthoides* ssp. *oxyacanthoides* is not a montane species, and while it is unlikely that it occurs in the GYA, it may occur in some valley bottoms within the area (Sinnott 1985). In the GYA, *R. oxyacanthoides* ssp. *setosum* is found along stream bottoms and open wooded slopes (m. newcomb, personal observation). It thrives in disturbed sites, and a White Pine Blister Rust Control

Annual Report for Yellowstone National Park (1967) stated that *R. setosum* seedlings flourished in disturbed and wet areas.

Ribes oxyacanthoides ssp. *hendersonii* is primarily a subalpine and alpine shrub that occurs in rocky areas up to and beyond treeline in mountain ranges of eastern Idaho, Montana, and places in Nevada and Wyoming (Sinnott 1985, Lackschewitz 1991, m. newcomb, personal observation). In the GYA, *R. oxyacanthoides* ssp. *hendersonii* appears to be relatively uncommon, although it can be locally abundant on some slopes (m. newcomb, personal observation).

Kimme (1938) reported *R. oxyacanthoides* ssp. *setosum* as exhibiting relatively low-susceptibility to *C. ribicola*. However, shrubs supporting moderate levels of infection in sites in the GYA have been observed, along with many shrubs with no infection (m. newcomb, personal observation). While there is not enough available information to dismiss *R. oxyacanthoides* ssp. *setosum* as unimportant in disease intensification, it is likely that it plays a lesser role than some other GYA *Ribes* species. There are no reports on the relative susceptibility of *R. oxyacanthoides* ssp. *hendersonii* to *C. ribicola*. Infection has not been observed on this species in the GYA (m. newcomb, personal observation). The tendency of this species to grow in open, dry, exposed sites makes it less likely that this species will commonly be infected as it is generally recognized that *Ribes* plants in open, high-light conditions show decreased tendencies for infection (Kimme 1938, m. newcomb, personal observation).

Ribes aureum: The only species in the GYA with yellow flowers, *R. aureum*, is restricted to the lower elevations of the GYA. Its range extends along the east slopes of the Rocky Mountains from Alberta to New Mexico and eastward, and it is found in the eastern slopes of the Cascade Range and from north-central Washington south to California (Hitchcock and Cronquist 1973, Lackschewitz 1991). Common habitats for *R. aureum* include valley floodplains and stream banks of valleys and foothills (Lackschewitz 1991). The relative susceptibility of *R. aureum* has been reported as moderate to high (Maloy 1997). However, the fact that the species is typically limited to lower elevations in the GYA makes it an unlikely factor in whitebark pine infection processes.

Ribes cereum: The geographic and elevational range of *R. cereum* is remarkably broad. This species ranges from dry foothills to rocky and exposed alpine sites (1500 to 4000 m in elevation) from

British Columbia, on the east side of the Cascade Range to the Sierra Nevadas and east and south to Nebraska, Colorado, and New Mexico (Hitchcock and Cronquist 1973, Lackschewitz 1991, Hickman 1993). *Ribes cereum* is widespread throughout the GYA, although it is rarely observed in high densities. It exhibits a great deal of morphological variability across different environments. A study in the northern Sierra Nevadas showed *R. cereum* to be resistant to a post-fire herbicide treatment applied to limit shrub growth and allow pine establishment. Instead, *R. cereum* was significantly more abundant in the herbicide treatment than in the control (Bock et al. 1978). These findings are congruent with the general adaptive trend of high stress tolerance exhibited by a number of *Ribes* species.

In general, *R. cereum* is considered to have very low susceptibility to *C. ribicola* (Kimmey 1938). However, this highly variable and wide-ranging species has also demonstrated population-level variability in susceptibility. Kimmey and Mielke (1944) found that *R. cereum* originating from the southern Sierra Nevadas, or from Lassen Park to the north, differed in relative amounts of infection when inoculated under identical conditions. The high variability in this species, and its wide distribution over much of the GYA, indicates a need for further research to understand its role in disease intensification.

Ribes montigenum: This high-elevation (*montigenum* is derived from “mountain-born”) species ranges geographically from southern British Columbia south along the eastern slopes of the Cascade Range to the Sierra Nevadas and mountains of southern California, and east to the Rocky Mountains in Montana and New Mexico (Hitchcock and Cronquist 1973). Across this broad latitudinal gradient range, *R. montigenum* grows within different elevational ranges (Allen et al. 1991). Within the GYA, *R. montigenum* tends to thrive at higher elevations, generally above 2600 m. Of all the GYA *Ribes*, it has the closest spatial and ecological association with whitebark pine. It often grows predominantly beneath patches of trees that include whitebark pines. These tree “islands” can establish unique microenvironments (Marr 1977), and in some conditions *R. montigenum* is limited to these sites (Marr 1977, Cox 1933). Particularly near the upper treeline where conditions are harsh, *R. montigenum* often exists only beneath or at the edge of these tree islands (Holtmeier and Broll 1992). Moreover, a study of subalpine vegetation in Utah showed that *R. montigenum* may in turn create a special microenvironment that favors the establishment of a number of herbaceous species. *Ribes montigenum* can exhibit vegetative layering when winter pocket

gopher soil mounds cover the drooping outer shrub branches which then form adventitious roots (Ellison 1954). In this process, the species can expand its shrub “island” and associated microenvironment.

Research conducted in the GYA over 2001 and 2002 also found evidence for tree-shrub island patterns under some contexts. Data collection efforts in 2001 were, in part, directed at testing the hypothesis that *R. montigenum* shrubs and whitebark pine occur in a positive, non-random spatial association. Six sites surveyed in whitebark pine stands supported notable amounts of *R. montigenum*. In three of these sites *R. montigenum* was located significantly ($p < 0.05$) closer to a whitebark pine tree than to a random point (Figure 1). The two sites that clearly showed a non-significant association between whitebark pines and *R. montigenum* had high tree canopy cover estimations, exhibiting a relatively closed, and thus sheltering, canopy that may have altered environmental conditions affecting *Ribes* distributions. The fact that there is a positive relationship between whitebark pine and *R. montigenum* when sites consist of exposed open stands suggests that there could be a facilitative association between the two host groups at these sites. It is intriguing to contemplate the long-term consequences of such an association, conceptualized in the context of co-evolutionary theory (Burdon and Thrall 1999). The historic positive association between these species prior to the interaction with the introduced blister rust pathogen, may now drive an indirect negative interaction between the pine and shrub. This close spatial association increases the need for consideration of the relationship between *R. montigenum* and the pathogen and how this interaction fits into larger disease dynamics.

Ribes montigenum has been classified as moderately susceptible (Kimmey and Mielke 1944). This general category fits with observations from the GYA (m. newcomb, personal observation). This species was frequently observed with infection by *C. ribicola* in 2001 and 2002 when near infected pines (inoculum sources). Yet it was rarely observed with infection when no infected pines were within sight of the shrubs. It may be that *R. montigenum* plays a significant role in local intensification but not initial establishment (see Chapter 1). This species merits additional research consideration because of its close proximity to whitebark pine hosts throughout much of the GYA.

FUTURE DIRECTIONS

There has been a century-long interest in improving our understanding of white pine blister rust in North American white pines. While much has been learned, there remains much that is unknown about the dynamic effects of *C. ribicola* in white pine forests. In recent times, considerable work has focused on the molecular aspects of the white pine hosts (Kinloch and Dupper 2002), the pathogen (Et-touil et al. 1999, Hamelin et al. 2000), and pine host-pathogen interactions (Yu et al. 2002). However, research that addresses the ecological contexts of the hosts and their environment in relation to the distribution and intensification of the pathogen is needed.

Using the GYA as a model system, this paper characterizes the local *Ribes* species in relation to their role in white pine blister rust in whitebark pine stands of the area. The GYA provides a useful setting for investigations of the dynamics of interactions between the pathogen and its hosts because of the variability in disease intensities that exists among different host pine stands, allowing for natural experiments across the variable conditions. Additionally, the GYA is an important setting for studies of white pine blister rust host dynamics because of its ecological importance and the associated impelling need to understand threats to the whitebark pine forests of the area. These forests are critical components of this valuable ecological treasure.

Thus the GYA can provide a model study system for addressing future research needs. Data describing the distributions and abundances of the *Ribes* species and their proximities to white pine hosts are needed. Investigations of the relative susceptibilities of the *Ribes* hosts to *C. ribicola* are needed through intra-specific, spatial and temporal comparisons. Moreover, very little is known about *Ribes* species' phenologies and the timing of rust development on the *Ribes* hosts. Information on these topics would be a valuable contribution to current knowledge of the white pine blister rust pathosystem. Additionally, such studies would provide essential data from an ecological context to accompany the important accomplishments on the molecular front of host-pathogen research.

TABLES AND FIGURES

Table 1. Results of a March, 2003 keyword search for “white pine blister rust” or “*Cronartium ribicola*” using the Cambridge Scientific Abstracts Plant Science and Biological Sciences databases. Conference proceedings, review articles, and articles that only incidentally mention the disease were not included.

Host group(s) considered	Artificial conditions (Lab, greenhouse, or nursery)	Plantation or Crop	Forest	TOTAL
Major focus on white pine alone	9	3	5	17
Major focus on white pine and <i>Cronartium ribicola</i>	9	0	0	9
Major focus on <i>Cronartium ribicola</i> alone	14	0	0	14
Major focus on <i>Ribes</i> spp. alone	0	4	0	4
TOTAL	32	7	5	44

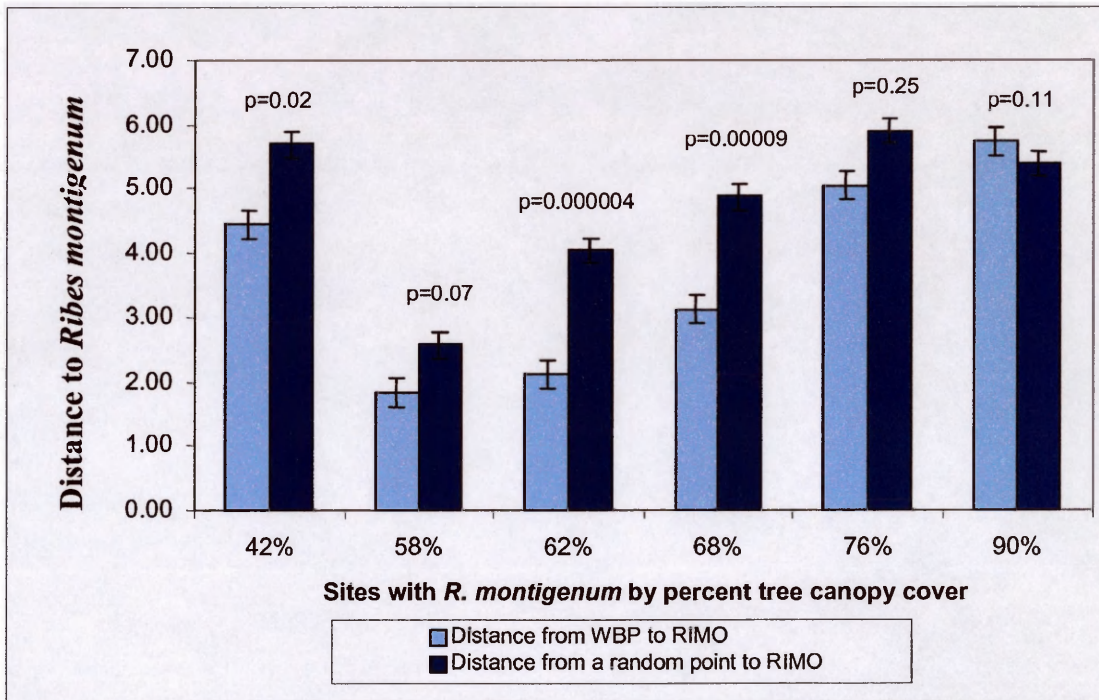


Figure 1. Spatial associations between whitebark pine (WBP) and *Ribes montigenum* (RIMO) shrubs at six sites with differing estimated percent tree canopy cover. Error bars equal one standard error. P-values represent levels of significance from student’s t-tests comparing mean distances at a site from a whitebark pine tree to the nearest *Ribes montigenum* shrub, and from a random point to the nearest *Ribes montigenum* shrub.

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APPENDIX: TREE-LEVEL DATA

Table A-1. White pine blister rust disease metrics and crown ratios for whitebark pine trees assessed at 25 sites, by crown class. Metrics include the GYA Relative Severity Index (see Results section for description); numbers of cankers in lower, middle, and upper canopy thirds; and severity rating (see Figure 1) by relative stem and canopy thirds. SE = one standard error.

	Suppressed	Intermediate	Codominant	Dominant	Open	Remnant
Mean GYA Relative Severity Index (SE)	0.044 (0.018)	0.11 (0.014)	.11 (0.011)	0.13 (0.048)	0.25 (0.096)	0.28 (0.056)
Mean Cankers in Lower Third (SE)	0.029 (0.018)	0.16 (0.023)	0.21 (0.034)	0.18 (0.10)	0.46 (0.22)	0.5 (0.5)
Mean Cankers in Middle Third (SE)	0.022 (0.013)	0.17 (0.025)	0.27 (0.031)	0.45 (0.19)	0.41 (0.16)	1.5 (0.5)
Mean Cankers in Upper Third (SE)	0.044 (0.018)	0.15 (0.025)	0.34 (0.042)	0.33 (0.11)	0.16 (0.073)	0.5 (0.5)
Mean Total Cankers (SE)	0.066 (0.024)	0.38 (0.047)	0.64 (0.065)	0.91 (0.30)	0.92 (0.36)	2.5 (0.5)
Mean Severity Rating in Lower Canopy Third (SE)	0.029 (0.015)	0.12 (0.017)	0.12 (0.016)	0.12 (0.058)	0.27 (0.11)	0.5 (0.5)
Mean Severity Rating in Middle Canopy Third (SE)	0.022 (0.016)	0.15 (0.021)	0.18 (0.019)	0.21 (0.084)	0.22 (0.079)	1.0 (0)
Mean Severity Rating in Upper Canopy Third (SE)	0.051 (0.022)	0.14 (0.023)	0.21 (0.023)	0.24 (0.076)	0.22 (0.10)	0.5 (0.5)
Mean Severity Rating in Lower Stem Third (SE)	0.0074 (0.0074)	0.0091 (0.0045)	0.0078 (0.0039)	0 (0)	0.081 (0.081)	0 (0)
Mean Severity Rating in Middle Stem Third (SE)	0.022 (0.016)	0.034 (0.012)	0.039 (0.011)	0.061 (0.042)	0.27 (0.27)	0 (0)
Mean Severity Rating in Upper Stem Third (SE)	0.015 (0.015)	0.088 (0.021)	0.055 (0.015)	0.061 (0.042)	0.22 (0.12)	0 (0)
Mean Severity Rating (SE)	0.14 (0.064)	0.54 (0.071)	0.57 (0.058)	0.70 (0.20)	0.92 (0.32)	2.0 (1.0)
Mean Crown Ratio (SE)	31.9 (1.4)	49.5 (0.72)	53.6 (0.66)	67.0 (2.1)	67.2 (2.9)	27.5 (2.5)
Count (N)	136	441	510	33	37	2

Table A-2. White pine blister rust disease metrics for whitebark pine trees assessed at 25 sites, by crown ratio classes. Metrics include the GYA Relative Severity Index (see Results section for description); numbers of cankers in lower, middle, and upper canopy thirds; and severity rating (see Figure 1) by relative stem and canopy thirds. SE = one standard error.

	Crown Ratio 5 – 30%	Crown Ratio 35 & 40%	Crown Ratio 45 & 50%	Crown Ratio 55 & 60%	Crown Ratio 65 & 70%	Crown Ratio 75 – 95%
Mean GYA Relative Severity Index (SE)	0.059 (0.012)	0.11 (0.020)	0.080 (0.016)	0.12 (0.017)	0.13 (0.024)	0.18 (0.039)
Mean Cankers in Lower Third (SE)	0.053 (0.018)	0.12 (0.028)	0.088 (0.022)	0.24 (0.043)	0.28 (0.079)	0.35 (0.097)
Mean Cankers in Middle Third (SE)	0.10 (0.026)	0.18 (0.040)	0.14 (0.023)	0.27 (0.044)	0.32 (0.063)	0.38 (0.088)
Mean Cankers in Upper Third (SE)	0.12 (0.027)	0.26 (0.055)	0.18 (0.032)	0.28 (0.055)	0.33 (0.087)	0.17 (0.042)
Mean Total Cankers per Stem (SE)	0.24 (0.045)	0.47 (0.084)	0.35 (0.051)	0.57 (0.088)	0.68 (0.14)	0.80 (0.17)
Mean Severity Rating in Lower Canopy Third (SE)	0.080 (0.024)	0.10 (0.025)	0.064 (0.016)	0.14 (0.023)	0.14 (0.029)	0.21 (0.050)
Mean Severity Rating in Middle Canopy Third (SE)	0.14 (0.039)	0.13 (0.027)	0.12 (0.021)	0.16 (0.025)	0.20 (0.033)	0.22 (0.047)
Mean Severity Rating in Upper Canopy Third (SE)	0.20 (0.046)	0.19 (0.037)	0.15 (0.028)	0.17 (0.032)	0.14 (0.029)	0.14 (0.35)
Mean Severity Rating in Lower Stem Third (SE)	0 (0)	0.01 (0.0071)	0.012 (0.0069)	0.0044 (0.0044)	0.0056 (0.0056)	0.045 (0.030)
Mean Severity Rating in Middle Stem Third (SE)	0.085 (0.031)	0.01 (0.01)	0.020 (0.010)	0.044 (0.015)	0.011 (0.0079)	0.054 (0.022)
Mean Severity Rating in Upper Stem Third (SE)	0.15 (0.044)	0.075 (0.026)	0.044 (0.020)	0.049 (0.024)	0.050 (0.024)	0.036 (0.022)
Mean Severity Rating (SE)	0.63 (0.16)	0.47 (0.086)	0.40 (0.068)	0.54 (0.069)	0.52 (0.080)	0.69 (0.12)
Count (N)	188	200	251	225	179	111