Developing Proactive Management Options to Sustain Bristlecone and Limber Pine Ecosystems in the Presence of a Non-Native Pathogen

A. W. Schoettle[1]

***Abstract**—Limber pine and Rocky Mountain bristlecone pine are currently threatened by the non-native pathogen white pine blister rust (WPBR). Limber pine is experiencing mortality in the Northern Rocky Mountains and the infection front continues to move southward. The first report of WPBR on Rocky Mountain bristlecone pine was made in 2003 (Blodgett and Sullivan 2004), at a site that is more than 220 miles away from the former infection front. No mortality has been observed in this recently infected area but the species is highly susceptible. There are no ecological reasons to suspect that WPBR on bristlecone and the southern distribution of limber pine will not expand over time. Learning from experiences in impacted ecosystems will facilitate the development of proactive measures to mitigate impacts in these southern populations in the future. If no action is taken, and the pathogen takes its course, we risk losses of aesthetic landscapes; impacts to ecosystem boundaries, successional pathways, and watershed processes; and shifts from forested to treeless sites at some landscape positions. This paper introduces an interdisciplinary approach to developing proactive management options for limber and bristlecone pines in the southern Rocky Mountains. Managers, researchers, operational professionals and interested public groups will have to work together and share their knowledge and perspectives to sustain these ecosystems for future generations.*

Introduction

Limber pine (*Pinus flexilis* James) and Rocky Mountain bristlecone (*Pinus aristata* Engelm.) are white pines (subgenus *Strobus*) yet limber pine is in section *Strobus*, subsection *Strobi* and Rocky Mountain bristlecone pine is in subgenus *Parrya*, subsection *Balfournianae* (Lanner 1990). They both have 5-needles per fascicle. Limber pine and bristlecone pines can grow as erect trees, clusters of erect trees and as wind-sculpted wedge-shaped shrubs (krummholz). Limber pine has a very broad elevational distribution ranging from the grassland treeline to the alpine treeline as well as a broad latitudinal distribution from Canada southward into New Mexico (Schoettle and Rochelle 2000). Bristlecone has a narrower distribution, primarily occupying higher elevation sites in central and southern Colorado with a small distribution into North New Mexico and a peripheral population in the San Francisco Peaks of Arizona. Their often bushy growth form and slow growth rate combined with the inaccessibility of the rocky sites that they dominate make them poor timber species and ones that have long been overlooked by the forestry community. The most basic ecological information has not been quantified for these species (Schoettle 2004).

Limber pine and bristlecone pine are currently threatened by the non-native pathogen white pine blister rust (*Cronartium ribicola* J. C. Fisch.). The impact of white pine blister rust on commercial North American white

[1] USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

pines has been a focus of attention since its introduction from Europe in the early 1900s. In the mid-1980s, the focus expanded to impacts of the disease to the non-commercial whitebark pine (*Pinus albicaulis* Engelm.) as forest practices shifted toward management of ecosystems. White pine blister rust's threat to whitebark pine and the resultant impacts to the habitat of the endangered grizzly bear (*Ursus arctos horribilis*) have brought whitebark pine ecosystems into view by the management and research community (e.g., Schmidt and McDonald 1990, Tomback and others 2001). Limber pine has been infected in the Northern Rocky Mountains for decades and the infection front continues to move southward; infections in Colorado were found in 1998 (Johnson and Jacobi 2000). White pine blister rust was first reported on Rocky Mountain bristlecone pine in 2003 (Blodgett and Sullivan 2004). This new infection site supports infected limber pine and bristlecone pine and appears disjunct from the more continuous infection front more than 200 miles to the north. The disease appears to have jumped over a near continuous corridor of limber pine from the infection front to the bristlecone/limber pine forests (figure 1). Introduction of the rust into the southern ecosystems may have occurred from infected nursery stock planted in the growing communities of the urban-wildland interface or long-distance transport of rust spores from California or other infected areas.

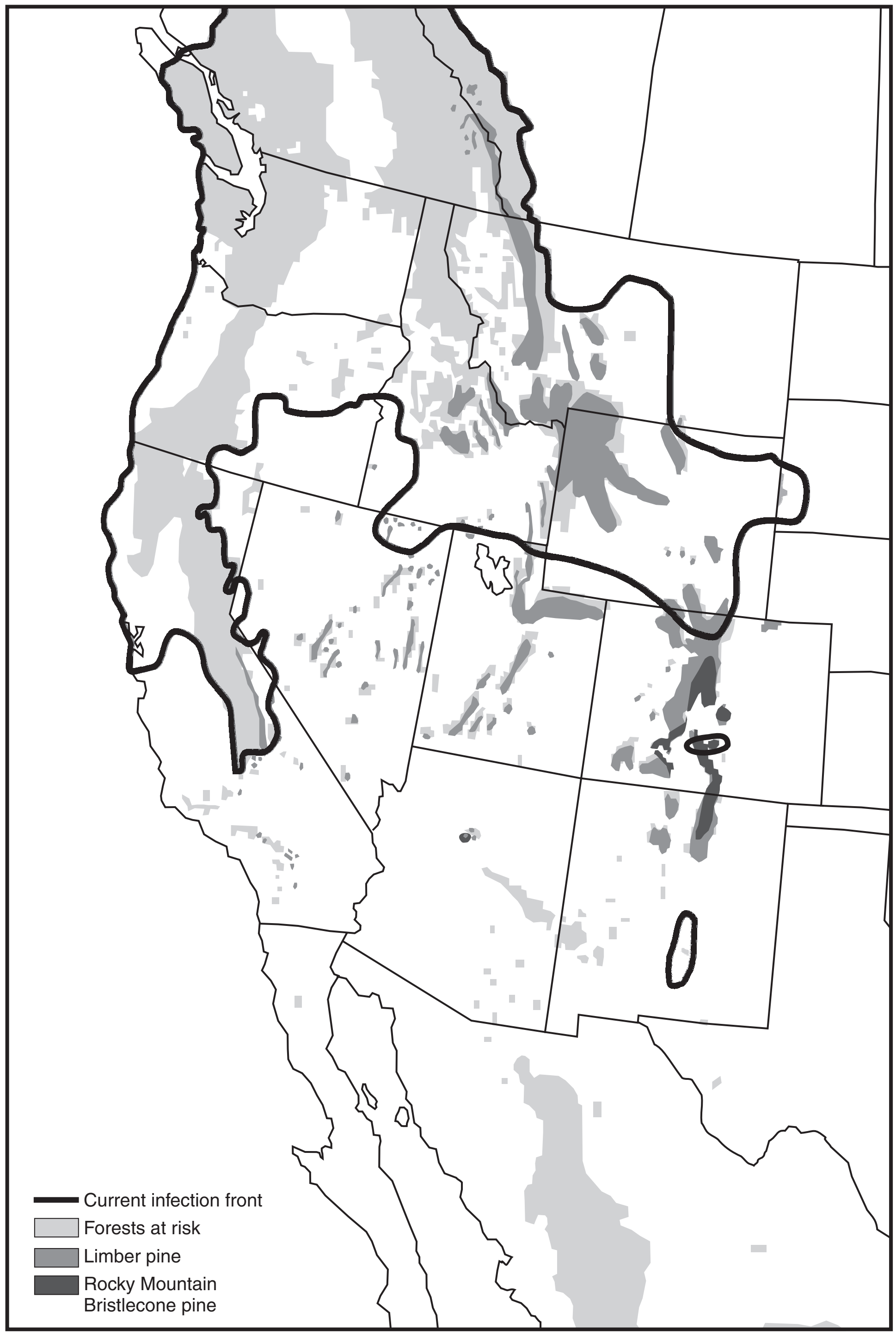

Figure 1—A map of the distribution of forest at risk in western North America for white pine blister rust impacts (light shading) and the distribution of limber pine (medium shading) and Rocky Mountain bristlecone pine (dark shading). Forests at risk are all those containing the 5-needle pine species that are susceptible to the rust. The dark line denotes the current white pine blister rust infection front; not all stands are infected within the lined areas but the rust has been documented on the pines in those areas.

Screening studies reveal that all of the North American 5-needle white pines are highly susceptible to the rust. It is estimated that less than 5 percent of the population of each species has any genetic resistance to the rust. Heavily infected areas have experienced almost complete mortality of the white pine component of the forest and the replacement forest communities are more prone to epidemics of native pests and pathogens. Despite significant efforts to contain the pathogen after its introduction in the early 1900s, this fungus continues to spread. Blister rust is now a permanent resident of North America affecting even the high elevation and drier forest ecosystems once thought to escape infection.

The early studies of rust susceptibility for RM bristlecone pine are confounded by taxonomic confusion associated with the species. The bristlecone pines throughout the western United States were thought to be one species (*P. aristata*) until 1970 when Bailey (1970) distinguished the populations into two species. The populations in Colorado, northern New Mexico and the isolated population in Arizona were designated Rocky Mountain bristlecone pine and retained the name of *P. aristata* and the populations in Utah, Nevada and California were called Great Basin bristlecone pine and newly named *P. longaeva*. The results from the rust-screening studies of Hoff and others (1980) and Bingham (1972) are confounded by the combining of seed collections from the two bristlecone pine species. Only the Childs and Bedwell (1948) study explicitly sampled a Colorado population (RM bristlecone pine) and shows that while this species is susceptible to the rust, it appears to have slighter greater resistance than western white pine or sugar pine. Although these early studies were conducted with bulk seed lots, they suggest that sustaining bristlecone pine forests through management may be more successful than other species.

Taking advantage of learning from experiences in impacted ecosystems and using the time to develop and instigate proactive measures to help prepare the bristlecone pine and southern limber pine ecosystems for the pathogen provide the opportunity to attempt to mitigate impacts in the future. This paper will discuss the reasons for developing information and management options now, even in these early stages of pathogen infection, and introduce an interdisciplinary approach to developing a proactive management strategy for limber pine and Rocky Mountain bristlecone pine in the central Rocky Mountains.

The White Pine Blister Rust Threat: The Situation

White pine blister rust has a complex life cycle that requires two obligate hosts: the 5-needle white pine and the currant or gooseberry species (*Ribes* ssp.) (figure 2). Infection of the *Ribes* occurs in the spring through wind transport of aeciospores released from cankers on the pines. Several spore stages are completed on the *Ribes* leaves until finally the basidiospores are released in late summer or early fall. The fungus is confined to the leaves of the *Ribes* plants where it completes it life stages. *Ribes* are deciduous and shed their leaves and the fungal infection each year. As a result the fungus does not cause mortality of the *Ribes* plant. In contrast, once infected the fungus is persistent, perennial, and invasive within the pine. The white pine blister rust basidiospores enter pine needles through stomatal openings and the fungus grows into the twig (McDonald and Hoff 2001). Aecia (which

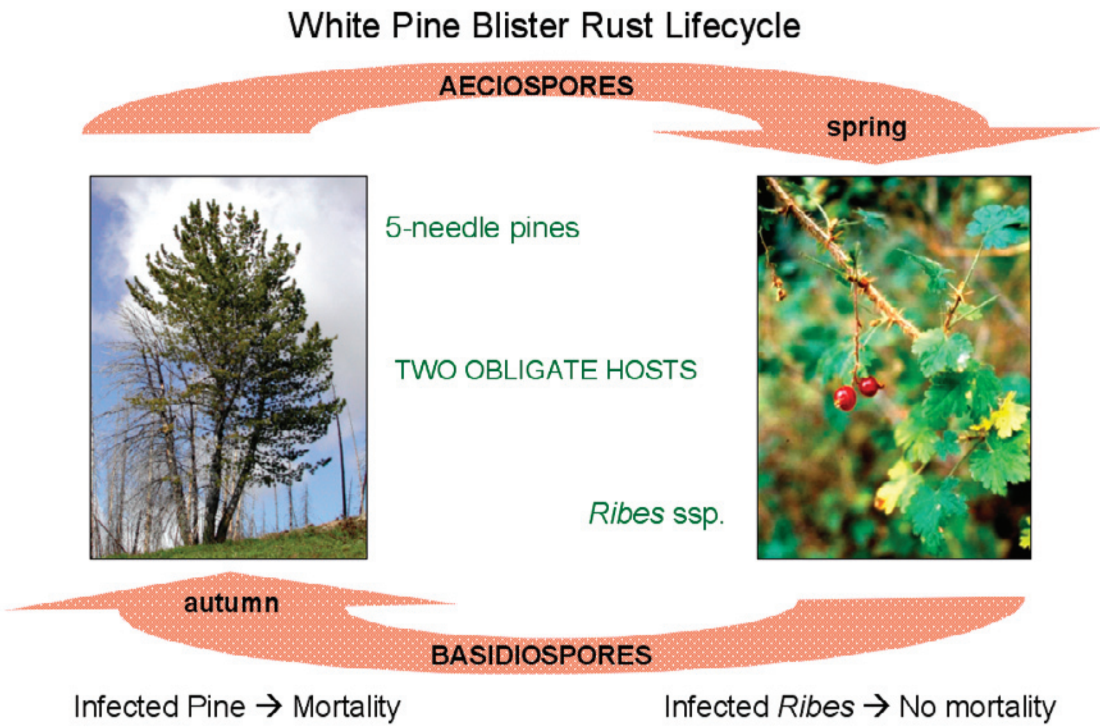

Figure 2—Simplified schematic of the life cycle of white pine blister rust.

release the aeciospores) erupt through the bark of the twig and form the telltail canker. The fungus continues to grow into the branch and ultimately the main stem of the tree. Cankers girdle the infected branch or stem killing the distal tissue. Branch cankers often will not kill the tree until the reduction in leaf area is so great that the tree cannot survive or the canker grows to affect the main stem. The contribution of rust-caused branch mortality to reduced cone production and an increase in sensitivity of the tree to other stresses such as drought, competition, and bark beetle attacks deserves research attention to fully assess the impacts of the disease. Cankers on the main stem of a tree cause top-kill and will usually kill the individual. White pine blister rust exerts strong selective pressure at the seedling-sapling stage and can cause high rates of seedling mortality within several years of infection. Very old trees that have significant partial cambial dieback, such that all of the tree's surviving foliage is supported on a few branches, may be rapidly killed by white pine blister rust once infected (Schoettle 2004).

White pine blister rust has its own set of environmental constraints as influenced by the tolerances of its biology as well as the distribution of its two hosts, the five-needle white pines and *Ribes* ssp. The degree of overlap between the rust's potential habitat with that of limber pine and bristlecone pine's distributions has not been fully defined. While the selective pressure exerted by the rust on these five-needle pines will not be uniform across their distribution, existing information on *Ribes* distributions suggests that it may be extensive; three-fourths of the limber pine sites sampled along the elevation gradient of Colorado's Front Range contained *Ribes* ssp. (8 of 12 stands; Schoettle and Rochelle 2000) and more than half of the bristlecone pine sites evaluated by Ranne and others (1997) contained *Ribes* ssp. (27 of 50 stands). Long-range transport of rust spores may be possible (Mielke 1943) but may not be necessary for the rust to spread through these ecosystems. The suitability of different *Ribes* species to host the rust varies (Van Arsdel and others 1998) but unfortunately, those species that support good rust spore production are present throughout the range of both bristlecone and limber pine (Kearns and others, in press).

Consequences of Non-intervention

Bristlecone and limber pine ecosystems are unique and valued. The effects of blister rust-caused mortality in these systems will be greater than the loss of the individual trees. In addition to their ecological roles, which will be discussed below, these species are appreciated by people for their artistic forms and extreme longevity (e.g., Cohen 1998). Bristlecone pine and limber pine are often used as symbols of perseverance and tolerance. In central Colorado, over 100,000 people a year pay an entrance fee to visit an ancient bristlecone pine forest in a Research National Area. Also, because these species occupy ridge tops they are often the species that surround forest visitors as they enjoy the mountain vistas at their hike's destination. The loss of these species to a non-native pathogen would be a national loss.

Ecologically, bristlecone and limber pines species play critical roles in maintaining the resilience and integrity of many Rocky Mountain ecosystems. Wildlife relies on these species for food. Limber pine has large wingless (or near wingless) seeds and has a mutualistic relationship with corvid species (e.g., Clark's nutcracker, *Nucifraga columbiana* Wilson) such that the corvids feed on the seed and serve to disperse the seeds (Lanner and Vander Wall 1980, Tomback and Kramer 1980). As for whitebark pine, seeds of limber pine are also an important food source for black and grizzly bears (*Ursus* ssp.; Kendell 1983, McCutchen 1996), red squirrels (*Tamaisciurus hudsonicus*; Hutchins and Lanner 1982) and other small rodents. For the grizzly bear it is known that during years of low whitebark pine seed production the fecundity of bears is reduced and they depend more heavily on limber pine seed to fulfill their nutritional needs. Low limber pine seed production likely affects squirrel populations and the carnivore species that depend on them, including possibly the Canada lynx (*Lynx canadensis*).

Bristlecone and limber pines have a suite of structural and physiological traits that enable them to be very stress tolerant and occupy sites that other species cannot (Schoettle 2004). Mortality caused by the rust in these harsh sites will transition these forested sites to treeless areas affecting slope stability, snow retention and watershed hydrology. While these rocky ridges are the most obvious habitat occupied by bristlecone and limber pine, scattered occurrence of these species throughout the high-elevation forested region of the Colorado is typical (Schoettle 2004). On these more mesic sites, limber pine's early post-disturbance dominance succeeds over time to other conifer species (Rebertus and others 1991). Limber pine acts as a nurse tree, mitigating the harsh open environment after disturbances and facilitating the establishment of Engelmann spruce and subalpine fir in the subalpine (Rebertus and others 1991, Donnegan and Rebertus 1999) and of Douglas-fir at the lower treeline (Baumeister 2002). Engelmann spruce and subalpine fir are able to become established in the lee of bristlecone pine at the alpine treeline at elevations where they cannot become established alone (personal observations). The loss of limber and bristlecone pines in these more mesic areas would alter successional trajectories and future forest composition.

The ecological trade-off of the traits that confer stress tolerance is slow growth and poor competitive ability. These species have long tree and leaf lifespans (see Schoettle 1994). Both limber and bristlecone pine have delayed reproduction such that it takes more than 50 years for a seedling to mature to become cone-bearing. As a result, after a disturbance, there is a long lag before the reforested site is ecologically functional with respect to seed production and the species and processes that depend on them. This posed a compelling reason for attempting to establish rust-resistant seedlings of these species as soon as possible to minimize this lag period and accelerate the natural production and dispersal of rust-resistant seeds.

The effects of white pine blister rust on five-needle pines will interact with the changing fire regimes in the Rocky Mountains. As fire regimes get more frequent and unpredictable due to past fire suppression and forest practices, large wildfires may jeopardize the usually less-flammable five-needle pine ecosystems on dry sites. In addition, branch and tree mortality caused by white pine blister rust may contribute to fuel loading in white pine stands, increasing the susceptibility of these stands to sustain and be consumed by fire. In the event of larger fires, especially those covering a larger area than cannot be seeded effectively by wind dispersal mechanisms, the loss of bird-dispersed pines as colonizers may be especially pronounced.

In summary, these species and their ecosystems provide aesthetic and spiritual experiences for forest visitors and diet and habitat for wildlife. In addition, they have unique structural and physiological traits that lead to unique ecological functions on the landscape including post-fire recovery and facilitating succession. These species are, however, very slow growing and the ecosystems are slow to recover after disturbance. The mortality and reduced cone production caused by the non-native pathogen white pine blister rust will further slow the post-disturbance recovery of these ecosystems. Observations of effects caused by this pathogen in the northern Rockies shows that the impacts can be devastating and far reaching (Tomback and others 2001). Learning from experiences in other ecosystems and initiating proactive measures provides the opportunity to help sustain these ecosystems during their pending persistent assault by white pine blister rust. There is no ecological reason to suspect that WPBR won't continue to spread through bristlecone and limber pine ecosystems in the southern Rocky Mountains. If no action is taken, and the pathogen takes its course, we risk losses of aesthetic landscapes, impacts to ecosystem boundaries and successional pathways, and shifts from forested to treeless sites at some landscape positions causing changes in slope stability and watershed hydrology.

Developing Management Options

The Need for an Interdisciplinary Approach

Development of strategies for sustaining limber pine and bristlecone pine ecosystems in the presence of the non-native pathogen requires an interdisciplinary approach (figure 3). Information is very limited for these non-timber species and ecosystems. Information and integration is needed in the areas of (1) pathology, including etiology and epidemiology, (2) genetics of both hosts and the genetics of resistance mechanisms, and (3) ecology of both hosts and the fungus as well as the interactive effects of the disease on ecosystem function. The integration of existing information and the gathering of new information in each of these areas will help the development of management options to sustain white pine ecosystem function and maintain the species' existing distribution. The goal of this effort is to provide

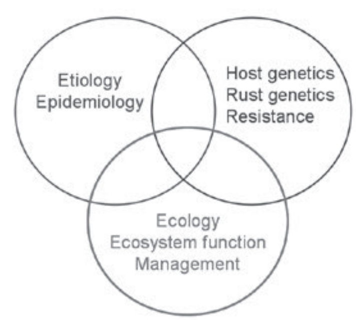

Figure 3—The need for an interdisciplinary approach in developing management options to sustain white pine ecosystem function in the presence of the non-native pathogen white pine blister rust.

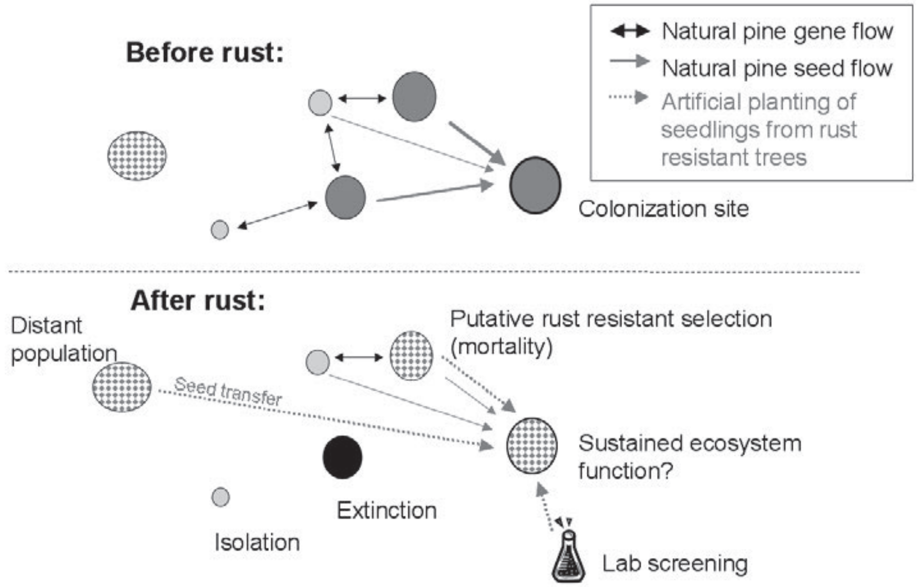

Figure 4—Schematic of potential effects of white pine blister rust on limber pine and bristlecone pine populations. The rust may cause extinction of some stands and isolation of others. After the rust has impacted an area, creating a colonization site may promote establishment of rust-resistant individuals if seeds are available. Artificial seed transfer, via outplanting of rust resistant seedlings, may accelerate the establishment of rust-resistant seedlings in the colonization site. Creating small regeneration sites before the rust arrives will result in young stands on the landscape for efficient rust-resistance selection upon invasion.

managers with the ability to (1) create regeneration opportunities for limber and bristlecone pines, (2) accelerate the establishment of rust resistant individuals, (3) prioritize stands for management intervention and assess some management options for those stands, and (4) sustain the functioning and resilience of these forest ecosystems for the future.

The goal is to accelerate the establishment of white pine blister rust resistant genotypes of limber pine and bristlecone pine across the landscape. Exploring the use of natural processes in addition to tree-planting approaches deserves attention with these species (figure 4). Protecting seed source stands and creating nearby regeneration opportunities to provide for rapid selection of rust-resistant genotypes in the presence of the rust may be an option. The susceptibility of trees to rust infection is not constant with age; young susceptible trees are killed rapidly by the rust while some older trees appear to develop resistance over time (ontogenetic resistance). Ontogenetic resistance can be significant in sugar pine yet the degree this occurs in bristlecone and limber pine is not known. If present, the older stand may be less impacted by the rust yet the progeny of those ontogenetically resistant trees are susceptible to infection by the rust. Therefore in the event of a disturbance such as a fire these older stands may not ensure the recovery of the area in the presence of the pathogen. Because ontogenetic resistance does not contribute to true genetic rust resistance it may serve to retain trees on the landscape for a generation but does not ensure future landscape sustainability over longer time scales. As a result, to accelerate the establishment of rust-resistant seedlings, it will be important to provide an opportunity in portions of the landscape for rust-resistant selection of reproductive seed trees and regeneration of their progeny. Creating a mosaic of mixed age classes and regeneration opportunities across the landscape before the pathogen is present may retain bristlecone and limber pine attributes in the area while rust-resistant selection occurs rapidly in the young stands and slowly in the older stands. This approach may sustain the present and future resiliency of the ecosystem in the presence of the pathogen.

Alternatively, selecting rust resistant genotypes through research studies and outplanting is another approach. Identifying resistant individuals can be done, as has been done for other white pines, by field assessment in areas already challenged by white pine blister rust or by screening seedlings in nursery trials with artificial inoculations. This more active management approach also requires sufficient knowledge to generate seed transfer guidelines to avoid outplanting resistant individuals that are maladapted to the site. This process will take time. A combination of approaches may be useful: prepare the landscape before infection by creating a diverse age class structure; promote natural regeneration from resistant trees after infection; and augment, if needed, with artificial regeneration of selected genotypes.

Proposed Strategy

Achieving the integrated interdisciplinary approach to sustain white pine ecosystems requires the cooperation of diverse partners and expertise. Developing the necessary knowledge to create regeneration opportunities to accelerate the selection for and establishment of a rust-resistant population will require information on the colonization dynamics of both the pines and *Ribes*, the geographic pattern of local adaptation of both hosts and the pathogen, and the identification of rust-resistance mechanisms and their distributions in the pine populations (figure 5).

Programs within Region 2 Forest Health Management, Colorado State University, and Rocky Mountain Research Station have begun to tackle this problem. Ongoing studies in the area of geographic patterns of local adaptation suggest that local differentiation among bristlecone pine populations is sufficient to warrant the definition of seed transfer zones. Studies have also begun to screen bristlecone for rust-resistance to identify possible resistant individuals and assess the possibility of differential distribution of resistance among populations. Extensive monitoring of rust infection, meteorological conditions, and host distributions are being used to generate rust hazard models for southern Wyoming and Colorado. Studies of the regeneration dynamics of bristlecone and limber pine show that they establish well after

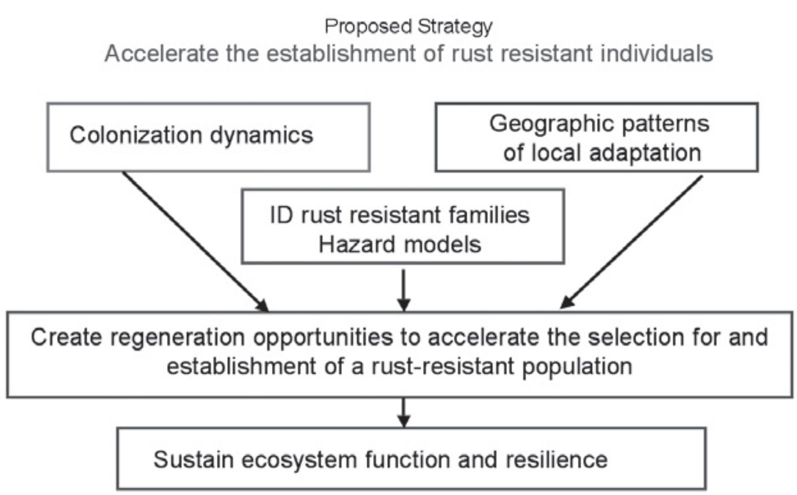

Figure 5—Schematic of a strategy to develop management options to sustain white pine ecosystem function in the presence of the non-native pathogen white pine blister rust.

fire and are able to colonize the interior of large burned areas. However, *Ribes* densities are greatly increased after fire (Schoettle 2003), elevating the risk of rust in the area. Therefore fire can be used to generate colonization sites for bristlecone and limber pines but prior to its use in an area one should consider whether *Ribes* is also likely to proliferate.

Ongoing Needs

The program to develop restoration options for high-elevation white pines will take time and time is running short. Gathering, integrating, and synthesizing information is critical for the development of management options in a timely manner to help sustain bristlecone and limber pine ecosystem function and resilience. Increasing awareness of the threat to these valued ecosystems will stimulate work to fill the information gaps. In addition, education to encourage recognition of the hosts and the symptoms of the disease will facilitate efforts to learn the extent of the disease and to restrict the transplanting of infected horticultural stock. Other ecosystems that have been affected by the non-native rust for longer periods offer learning opportunities. While information may not be directly transferable among ecosystems, insights from past experiences in other systems regarding what restoration treatments might work in bristlecone and limber pine ecosystems may be valuable. Information from the uninfected ecosystems can provide baselines to help managers in infected areas better assess the effectiveness of restoration treatments in their areas. Finally, managers, researchers, operational professionals and interested public groups must work together and share their knowledge and perspectives to develop and implement effective management options to sustain and restore these ecosystems for future generations.

References

Bailey, D. K. 1970. Phytogeography and taxonomy of Pinus subsection Balfourianae. Annals of the Missouri Botanical Garden. 57: 210-249.

Baumeister, D. A. 2002. Effects of *Pinus flexilis* on the dynamics and structure of plant communities on the northern Rocky Mountain Front. Missoula, MT: Division of Biological Sciences, University of Montana, PhD Dissertation.

Bingham, R. T. 1972. Taxonomy, crossability, and relative blister rust resistance of 5-needled pines. Biology of rust resistance in forest trees. Proceedings: NATO-IUFRO Advanced Study Institute. Misc. Publ. # 1221. Moscow, ID: U.S. Department of Agriculture, Forest Service. 271-280.

Blodgett, J. T.; Sullivan, K. F. 2004. First report of white pine blister rust on Rocky Mountain Bristlecone pine. Plant Disease. 88: 311.

Childs, T. W.; Bedwell, J. L. 1948. Susceptibility of some white pine species to *Cronartium ribicola* in the Pacific Northwest. Journal of Forestry. 46: 595-599.

Cohen, M. P. 1998. A garden of bristlecones – tales of change in the Great Basin. Reno, NV: University of Nevada Press. 308 p.

Donnegen, J. A.; Rebertus, A. J. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. Ecology. 80: 1370-1384.

Hoff, R. J.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology. 10: 307-316.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Johnson, D. W.; Jacobi, W. R . 2000. First report of white pine blister rust in Colorado. Plant Disease. 84: 595.

Kearns, H. S. J.; Jacobi, W. R.; Sullivan, K. F.; Geils, B. W. In press. Is the alternate host for white pine blister rust in Colorado? In: B. W. Geils, comp. 2004. Proceedings of the 51st Western International Forest Disease Work Conference; 2003 August 18–22; Grants Pass, OR. Flagstaff, AZ: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Kendell, K. C. 1983. Use of pine nuts by black and grizzly bears in the Yellowstone area. International Conference on Bear Research and Management. 5: 166-173.

Lanner, R. M. 1990. Biology, taxonomy, evolution, and geography of stone pines of the world. Proceedings: Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 14-24.

Lanner, R. M.; Vander Wall, S. B. 1980. Dispersal of limber pine seed by Clark's nutcracker. Journal of Forestry. 78: 637-639.

McCutchen, H. E. 1996. Limber pine and bears. Great Basin Naturalist. 56(1): 90-92.

McDonald, G. I.; Hoff, R. J. 2001. Blister rust: an introduced plaque. In: Whitebark Pine Communities, edited by D. F. Tomback, S. F. Arno, and R. E. Keane. Washington, D.C.: Island Press. 193-220.

Mielke, J. L. 1943. White pine blister rust in Western North America. New Haven, CT: Yale University School of Forestry Bulletin. 52.

Ranne, B. M.; Baker, W. L.; Andrews, T.; Ryan, M. G. 1997. Natural variability of vegetation, soils and physiography in the bristlecone pine forests of the Rocky Mountains. Great Basin Naturalist. 57: 21-37.

Rebertus, A. J.; Burns, B. R.; and Veblen, T. T. 1991. Stand dynamics of *Pinus flexilis*-dominated subalpine forests in the Colorado Front Range. Journal of Vegetation Science. 2: 445-458.

Schmidt, W. C.; McDonald, K. J., comps. 1990. Proceedings: Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Schoettle, A. W. 1994. Influence of tree size on shoot structure and physiology of *Pinus contorta* and *Pinus aristata*. Tree Physiology 14: 1055-1068.

Schoettle, A. W. 2004. Ecological roles of five-needle pine in Colorado: potential consequences of their loss, p. 124-135. In: Sniezko, Richard A.; Samman, Safiya; Schlarbaum, Scott E.; Kriebel, Howard B., eds. 2004. Breeding and genetic resources of five-needle pines: growth, adaptability, and pest resistance; 2001 July 23-27; Medford, OR, USA. IUFRO Working Party 2.02.15. Proceedings RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 259 p.

Schoettle, A. W.; Berger, C. A.; Bonnet, V. H. 2003. Proactive conservation options for bristlecone pine forests in the presence of an exotic pathogen – use of fire? In: Abstracts – The Ecological Society of America 88th Annual Meeting, August 3-8 2003, Savannah, GA. Washington, D.C.: The Ecological Society of America. 301.

Schoettle, A. W.; Rochelle, S. G. 2000. Morphological variation of *Pinus flexilis* (Pinaceae), a bird-dispersed pine, across a range of elevation. American Journal of Botany. 87: 1797-1806.

Tomback, D. F.; Kramer, K. A. 1980. Limber pine seed harvest by Clark's nutcracker in the Sierra Nevada: timing and foraging behavior. Condor. 82: 467-468.

Tomback, D. F.; Arno, S. F.; Keane, R. E., eds. 2001. Whitebark pine communities. Washington, D.C.: Island Press. 440 p.

Van Arsdel, E. P.; Conklin, D. A.; Popp, J. B.; Geils, B. W. 1998. The distribution of white pine blister rust in the Sacramento Mountains of New Mexico. Finnish Forest Research Institute Research Papers. 712: 275-283.