White pines, *Ribes*, and blister rust: integration and action

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Summary

The preceding articles in this series review the history, biology and management of white pine blister rust in North America, Europe and eastern Asia. In this integration, we connect and discuss seven recurring themes important for understanding and managing epidemics of *Cronartium ribicola* in the white pines (five-needle pines in subgenus *Strobus*). Information and action priorities for research and management of the pathogen, telial and aecial hosts, and their interactions are listed in a detailed Appendix. Syntheses focused on genetics, plant disease, invasive species or forest management have provided alternative but knowledgeable lessons on the white pine blister rust pathosystem. Two critical issues for the conservation of white pines are to sustain ecosystems affected by blister rust and to maintain genetic diversity for adaptive traits such as disease resistance. Forest genetics includes tree improvement and molecular techniques for research; their application can increase rust resistance by artificial and natural selection. Silviculture augments genetics with methods to deploy and enhance resistance as well as to regenerate and tend white pine stands. Although cultivated or wild *Ribes* might serve as inoculum sources, silviculture and horticulture can reduce the risk of serious impacts from blister rust using genetics for breeding and epidemiology for hazard assessment and disease control. Climate change threatens to cause major alterations in temperature and precipitation regimes, resulting in maladapted conifers succumbing to various diseases and insect outbreaks. In contrast, many white pine species have broad ecological ranges and are tolerant of harsh environments—traits that permit successful establishment and growth over wide geographic and altitudinal zones. Given appropriate management, white pines could thrive as valuable commercial and ecologically important keystone species. In an uncertain environment, adaptive management provides a learning and participatory approach for sustaining resilient ecosystems.

1 Introduction

The preceding articles on white pines (five-needle pines in subgenus *Strobus*), currants and gooseberries (*Ribes*), and *Cronartium ribicola* J.C. Fisch. in Rabh. present a comprehensive review of the history, biology and management of the white pine blister rust pathosystem. These articles synthesize the literature on economically and ecologically important white pines, wild and cultivated *Ribes*, and blister rust fungi of North America, Europe and eastern Asia. With a knowledgeable interpretation, this information provides a scientific basis for managing white pines and *Ribes* and for mitigating blister rust impacts by genetics, silviculture and horticulture. In this synopsis, we discuss seven integrating themes from the preceding review articles.

2 Historical lessons

Several well-studied authors, each with a distinctive perspective, have attempted to derive critical historical lessons on the genetics and ecology of invasive species, including *C. ribicola*. Besides revealing diversity and complexity in the white pine blister rust
pathosystem, their conclusions have provided a caution on the limits of our understanding and ability to control natural ecosystems (Geils et al. 2010; Kim et al. 2010; Zhang et al. 2010).

Using white pine blister rust as a model genetic system, Ekramoddoullah and Hunt (2002) described multiple mechanisms of host defence and pathogen evasion, including R-gene inheritance, protein synthesis and gene regulation. New techniques may soon provide additional observations on the molecular bases of disease, resistance and virulence (Richardson et al. 2010). But, understanding and applying these processes would require further development of concepts and procedures, such as how to recognize genetically controlled seedling responses (King et al. 2010). Knowledge of rust diseases has rapidly advanced in recent studies of annual or fast-growing agronomic crops (Pei and McCracken 2005). Kinloch (2004), however, warned that these models translate poorly to the long-lived, genetically-complex forest trees that are aecial rather than uredinial hosts. For such trees, understanding resistance and virulence is difficult and may require new approaches using controlled genetic material (Nelson et al. 2009). McDonald et al. (2004) identified gaps in our comprehension of gene-by-environment interactions, phenotypic plasticity, ecophysiological maladaptation, induced defence and attenuated disease. The meaning and implication of these concepts, however, challenge both forest pathologists and managers (Kim et al. 2010; Zambino 2010).

Callaway and Maron (2006) related how decades of study on exotic plant species have altered fundamental concepts in ecology and evolutionary biology. For example, biologists, who accept that macroevolution requires millennia to produce new species, now suggest that population-level microevolution over a few generations can effect significant genetic change with important ecological consequences. Several processes that might instigate rapid evolution are introduction of an invasive species and emergence of a ‘new’ pathogen by host-shifting, hybridization or host–pathogen coevolution.

An invasive or emergent pathogen may have been involved in the several infestations in eastern Asia on Pinus koraiensis Siebold & Zucc or P. strobus L. (eastern white pine, native to North America) (Kim et al. 2010). Likewise, the realized and potential capability of North American C. ribicola to utilize telial host species other than Ribes or hybridize with other Cronartium species are difficult to interpret (Joly et al. 2006; Geils et al. 2010; Richardson et al. 2010). These phenomena may demonstrate the rapid, localized coevolutionary dynamics described by Thompson (2005) or the phenotypic plasticity and importance of gene regulation suggested by McDonald et al. (2004). Such rapid and major changes have important implications for quarantines, white pine–bark beetle–blister rust interactions and forest management strategies (Schwandt et al. 2010; Tomback and Achuff 2010; Zhang et al. 2010).

Geils (2001) interpreted the management history of white pine blister rust in United States using an adaptive cycle metaphor of crisis and re-organization ( Gunderson and Holling 2002). Applying this model, blister rust management proceeded through three principal phases as a result of changing environments and management objectives (crises) that led to strategic changes in management programs (re-organization). The first phase began soon after C. ribicola was established (Geils et al. 2010). The strategy then was to reduce pine infection by eradicating Ribes; control relied on public support and financing for a major government program (Zeglen et al. 2010). The second phase began with the loss of inexpensive labour and adoption of a strategy characterized as cost-effective disease control. The new tactics emphasized biocides, biological agents, pruning, and use of silviculture to reduce Ribes regeneration. The program was re-organized as a Forest Service responsibility, and most control operations were incorporated into silvicultural activities conducted at a District level. Investment in regional genetics programs, the third and present phase, promised improvement in white pine survival by increasing host resistance or tolerance (King et al. 2010; but see Zeglen et al. 2010). In the western states, genetics
programs began work on the economically important western white pine (\textit{P. monticola} \textit{Dougl. ex D. Don}) and sugar pine (\textit{P. lambertiana} \textit{Dougl.}); however, in response to new crises, these programs now include species of principally ecological value (\textit{Tomback} and \textit{Achuff} 2010).

Although the history of epidemics and control in other locations such as Europe and Korea have differed in details, they have also followed the pattern of crisis and re-organization (\textit{Geils} et al. 2010; \textit{Kim} et al. 2010). The lessons from these historical reviews are that invasive or emergent pathogens appear, strategic goals change, control tactics fail, and new techniques are developed (see Appendix). The challenge is to apply these lessons to new circumstances.

### 3 Conservation of white pines

Two concerns for the conservation of white pines have recently emerged that are directly related to impacts from infestation by \textit{C. ribicola}. The first is blister rust damage to white pines grown for commercial, fibre production. Eastern white pine and western white pine have desirable qualities for wood production, including broad genetic transferability and rapid growth. In a warmer world of increased resource demand, these white pines—under genetic and silvicultural management—could outperform many other conifer species afflicted with their own diseases and climatic stresses (\textit{Ostry} et al. 2010; \textit{Schwandt} et al. 2010). The second concern is over the impacts of blister rust to white pines within wilderness and biodiversity reserves. Whitebark pine (\textit{P. albicaulis} \textit{Engelm.}), limber pine (\textit{P. flexilis} \textit{James}), and foxtail pine (\textit{P. balfouriana} Grev. & Balf.), are recognized for their ecological and aesthetic roles, but they are threatened by the multiple factors of climate change, bark beetles and blister rust (\textit{Schwandt} et al. 2010; \textit{Tomback} and \textit{Achuff} 2010). Conservation of these and other high-elevation white pines is especially difficult owing to biological and management constraints (\textit{Zeglen} et al. 2010). These constraints might be overcome with informed management and sustained public support (see Appendix).

White pines contributing to fibre production in North America, Europe and eastern Asia have experienced severe blister rust infestations (\textit{Geils} et al. 2010; \textit{Kim} et al. 2010; \textit{Zhang} et al. 2010). Many infestations initially caused serious losses of white pines, and blister rust remains a serious threat if an invasive or emergent rust pathogen were to establish. Nonetheless, white pines can be grown with commercial success if planting stock is adapted to the site and appropriate silviculture is used (\textit{Radu} 2008; \textit{Ostry} et al. 2010; \textit{Zeglen} et al. 2010).

\textit{Tomback} and \textit{Achuff} (2010) present the argument for conservation of whitebark pine as a keystone species in high-elevation ecosystems. Whitebark pine seeds are a critical resource for the threatened grizzly bear (\textit{Ursus arctos}) and Clark’s nutcracker (\textit{Nucifraga columbiana}). Trees often occur in small groups scattered over the landscape; genetic diversity is low; and dispersal is dependent on seed caching by nutcrackers (\textit{Syring} et al. 2007; \textit{Richardson} et al. 2010). Severe outbreaks of mountain pine beetle (\textit{Dendroctonus ponderosae} Hopkins) can kill most of the seed-producing trees in a population, and infestations of \textit{C. ribicola} can lead to regeneration failure of susceptible trees (\textit{Schwandt} et al. 2010). Because of various disturbances, many whitebark pine populations are in a decline spiral (\textit{Tomback} and \textit{Achuff} 2010).

Silvicultural and genetic approaches are identified by \textit{Schwandt} et al. (2010) and \textit{Tomback} and \textit{Achuff} (2010) to increase the regeneration and survival of whitebark pine and other high-elevation white pines. Specific techniques, however, would require additional evaluation and refinement (see Appendix). For example, fire can create seed-caching sites used by nutcrackers; but fire also increases blister rust hazard by stimulating \textit{Ribes} (\textit{Zambino} 2010). Although only limited screening for rust resistance has been conducted on the high-elevation white pines, early results are encouraging (\textit{Sniezko} et al. 2010).
King et al. (2010) reports that hybridization and backcrossing was successful with *P. strobus* and several related Eurasian pines. This work could be repeated with whitebark pine and the related Eurasian stone pines. Crossbreeding might be especially successful because whitebark pine is closely related to the Eurasian stone pines (Krutovskii et al. 1995 even questions whitebark pine as separate species) and some Eurasian pines appear resistant to *C. ribicola* (Kim et al. 2010).

4 Genetics of white pines and their rust pathogens

King et al. (2010) reviews the North American genetics programs investigating resistance of white pines to infection by *C. ribicola*. They describe four types of host reaction: (1) partial resistance (or tolerance) such as slow-rusting resistance where infection or mortality rates are reduced; (2) ontogenic resistance where susceptibility decreases with host age; (3) R-gene resistance where specific *Cr* genes provide immunity to avirulent pathogen races; and (4) resistance attributed to recessive genes such as inferred for a needle-shed response. Gene-by-environment interactions can affect expression of partial resistance or ontogenic resistance. Although R-gene resistance actively arrests pathogen development, it can be defeated by a virulent race. Planting white pines with increased resistance to blister rust is an important component to the strategy for conservation of white pines in western North America (Schwandt et al. 2010). Unfortunately, performance of some improved planting stock has been disappointing (Zeglen et al. 2010).

Genetic improvement programs for white pines have relied on traditional breeding techniques—selecting for phenotypic traits of seedlings inoculated with *C. ribicola* and verifying field resistance in long-term out-planting trials (King et al. 2010; Zeglen et al. 2010). Richardson et al. (2010) identifies new molecular techniques for investigating population genetics, phylogenies, and host–pathogen interactions. These techniques could provide molecular makers to identify specific genes, determine their regulation and function, and track gene flows among demes and hybrids. A greater understanding of genetics using either traditional or molecular approaches could provide management with better operational methods for screening, breeding, and deploying genetically improved seedlings (see Appendix).

A goal of genetic improvement is to provide managers with white pine seedlings that have ‘strong durable resistance’ (King et al. 2010). These seedlings would have low rates of infection and mortality not compromised by emergence of a virulent race of *C. ribicola*. One genetic strategy for achieving this goal is to combine strong R-gene resistance with durable slow-rusting or ontogenic resistance. R-gene resistance has already been combined with slow-rusting resistance for sugar pine in California and for western white pine in British Columbia (Zeglen et al. 2010). Ontogenic resistance appears to be a general disease response controlled by multiple developmental genes found in many pine families; it is not defeated by virulent pathogens (see Ziller 1974; Liu et al. 2005b).

R-gene resistance is present in at least three taxa of white pines capable of crossing with other white pine species (King et al. 2010); these taxa are sugar pine, western white pine and southwestern white pine (*Pinus flexilis* var. *reflexa* Engelm). Eastern white pine has ontogenic resistance; western white pine carries the *Cr2* gene and is highly resistant to the white pine weevil (*Pissodes strobus* Peck) (Wilkinson 1981). If these resistance traits were combined, improved seedlings could be planted no matter what the hazard zone, no matter how high the *Ribes* population, and whether or not there were commercial currants nearby. Accomplishing this would be challenging, but very rewarding.

Additional objectives of genetic resource management are to conserve genetic diversity and protect potential sources of resistance and other adaptive traits (Schwandt et al. 2010). In Canada and United States, selection and screening for blister rust resistance has been conducted longer and more extensively for the commercial species (eastern white pine,
western white pine and sugar pine) than for the high-elevation species (King et al. 2010). As these high-elevation white pines occur in limited, fragmented populations and are threatened by numerous disturbances, there is a special urgency to bank resistant candidates of these species (Tomback and Achuff 2010). Schwandt et al. (2010) discuss protecting resistance candidates: (1) in situ, location documented, marked, and monitored; (2) grafted and banked in seed orchards or clone banks; and (3) stored as candidate seed. Molecular technologies are developing that could evaluate candidates without the expensive and time-consuming methods of traditional screening (Richardson et al. 2010).

5 White pine silviculture

Although there are common principles and practices in the silviculture of white pines, differences in ecology and management objectives dictate that methods fit the region, species, and site. Ostry et al. (2010) describes site selection, regeneration, and stand tending of eastern white pine in North America. Zeglen et al. (2010) reviews blister rust hazard and risk, planting genetically improved seedlings, and blister rust control for western white pine, sugar pine, and the high-elevation white pines of western North America. Zambino (2010) adds information on the ecology of North American Ribes useful for reducing rust hazard. Kim et al. (2010) and Zhang et al. (2010) discuss control practices for white pine plantations in eastern Asia. Silvicultural intervention is an important tool for conserving white pines in western North America and for restoring whitebark pine populations (Schwandt et al. 2010; Tomback and Achuff 2010); but techniques could still be improved (see Appendix).

Historically, eastern white pine and western white pine were major timber species seriously impacted by blister rust (Geils et al. 2010). Western white pine remains an important timber species, especially in British Columbia; it is productive, commands premium value, and has the silvicultural advantages of large seed-transfer zones and resistance to root disease (Schwandt et al. 2010; Tomback and Achuff 2010; Zeglen et al. 2010). Although eastern white pine is still grown commercially and also has resistance to root disease (Gerlach et al. 1997), its principal values now resemble those of whitebark pine—biodiversity, aesthetics and wildlife (Wilkins 1994; Ostry et al. 2010: Fig. 2).

The different threats to eastern white pine and western white pine call for different silvicultural treatments (Ostry et al. 2010; Zeglen et al. 2010). The main threats to eastern white pine are herbivory, white pine weevil, competing vegetation, and blister rust. Eastern white pine may be severely browsed by white-tailed deer (Odocoileus virginianus) or snowshoe hare (Lepus americanus); but the dominant browsing animal in the western white pine region, mule deer (Odocoileus hemionus), does not eat western white pine. The white pine weevil is the most damaging agent to eastern white pine on many sites; western white pine is resistant (Soles et al. 1970; Wilkinson 1981). Especially on productive sites for eastern white pine, brushing to remove competing vegetation is usually more important than controlling C. ribicola. Blister rust hazard is low on many eastern white pine sites, especially in southern reaches of its distribution. In the West, blister rust hazard varies by region and site; but C. ribicola is a serious threat throughout the distribution of western white pine (Schwandt et al. 2010). Minimizing losses in eastern white pine relies on site selection, site preparation, and early cultural treatment (vegetation control; pruning to correct weevil damage and to prevent lethal cankers). Eastern white pine seedlings resistant to blister rust are not available. For western white pine (and sugar pine) resistant planting stock is recommended for all sites and available for many sites; if resistant stock is not available, early pruning (delayed for sugar pine) can be used (Zeglen et al. 2010).

Across the distribution of white pines in North America (Ostry et al. 2010: Fig. 1; Schwandt et al. 2010: Fig. 1) blister rust hazard varies regionally with climate and the occurrence of different Ribes species (Zambino 2010). Hazard also varies from site-to-site
sufficiently to be important in decisions of site selection and treatment (Ostry et al. 2010). Although herbicides have been used to control Ribes (Zambino 2010; : Fig. 1), chemical and mechanical eradication methods are now rarely used (Zeglen et al. 2010; but see Zhang et al. 2010). Ribes regeneration and persistence are affected by site preparation and canopy management (Zambino 2010).

Although silvicultural management can increase white pine regeneration, growth, and survival on sites over a wide range of environments, intervention is expensive owing to costs for planning, implementing and monitoring treatments. Foresters already preoccupied with the duties of management might benefit from more specific information and local demonstrations of the effectiveness of various stand treatments. For example, specific data on canker heights within a jurisdiction could help determine the return from a treatment such as pruning branches near the ground. A trial plantation within the local forest that shows good growth and survival of rust-resistant trees might overcome reluctance to risk planting white pines.

6 Ribes cultivation and management

Hummer and Dale (2010) and Zambino (2010) summarize information on the biology, horticulture and ecology of cultivated and wild Ribes. They also discuss managing Ribes with genetic and cultural approaches to minimize the threat of Ribes contributing to spread of C. ribicola. Rust hazard and Ribes control in North America are also discussed by Ostry et al. (2010) and Zeglen et al. (2010). Kim et al. (2010) and Zhang et al. (2010) identify the Ribes and other telial hosts present in eastern Asia and describe control methods used.

Worldwide currant production, which predominantly occurs in northern Europe, exceeds 600,000 metric tons per year; production is negligible in North America (Hummer and Dale 2010). A thriving currant industry that existed in Canada and United States prior to blister rust introduction was eliminated by laws favouring white pines over currants. Recently, many of these laws have been repealed, thus opening the door to resume large-scale Ribes production.

Although the risk to white pine increases as currant production expands close to pine plantations, genetic and horticultural mitigations could be developed (Hummer and Dale 2010). High-yielding cultivars bred in Europe are selected for resistance to their important insects and pathogens, but not to C. ribicola. To be acceptable in North America, cultivars would require resistance to powdery mildew (Sphaerotheca) and C. ribicola. Although an R gene for blister rust has been available since 1935, the Cr gene has little commercial acceptance because the first varieties released have inferior fruit quality and low yield under mechanical harvesting. Because the genus Ribes includes five subgenera, genetic diversity is high and could provide numerous useful traits including multiple mechanisms for rust resistance. Unfortunately, crossing between subgenera is difficult. Genetic maps are being developed which could determine linkages between resistance and other traits and expedite breeding (Richardson et al. 2010). Numerous horticultural practices could control development of blister rust in commercial Ribes operations and reduce the likelihood of inoculum escaping to infect white pines. Both breeding and horticulture would benefit from additional research (see Appendix).

Because of the great diversity among species, populations and individuals, Ribes can affect the epidemiology of C. ribicola in many different ways. Zambino (2010) discusses Ribes susceptibility, inoculum production, habitat occurrence, and synergism. Forest management activities can affect the abundance of Ribes as well as the conditions permitting rust spread from Ribes to white pines (e.g., spore production, dispersal, longevity, germination and infection). A knowledge of the role of Ribes in blister rust epidemiology is helpful for reducing blister rust hazard by silviculture (Ostry et al. 2010;
Our understanding of Ribes biology and its management has gaps that further research could investigate (see Appendix).

7 Climate change

The preceding chapters only touched upon climate change, but rapid global warming could have serious consequences for white pine conservation (Schwandt et al. 2010; Tomback and Achuff 2010). During the past four million years, global surface temperatures cooled at such a gradual rate that Pliocene conifers were able to respond to alternating ice-ages and interstitials (Jacobson and Dieffenbacher-Krall 1995; Ravelo et al. 2004). However, global warming is now considerably accelerated (Tomback and Achuff 2010). Because the seeds of long-lived pines might be maladapted for their parental sites and as animal-dispersed and wind-borne seeds might not reach suitable distant habitats (Richardson et al. 2002a), white pines may only accommodate climate change with management intervention (Weaver 2004). The British Columbia and Alberta Forest Services already add seed from southern zones into mixtures for northern zones (Alberta Forest Genetic Resource Council 2005).

Unlike many other conifers, eastern white pine and western white pine have wide ecological amplitudes and are transferable over large geographic regions (King et al. 2010; Ostry et al. 2010; Zeglen et al. 2010). For example, western white pine growth and resistance to some pathogens can be improved by shifting populations northward or up-slope (Hunt and Ying 2005). These major white pine species are good choices for ameliorating the effects of climate change on commercial production of softwoods. Western white pine would be particularly desirable because its rapid growth permits a short rotation (Muir and Hunt 2000). Productive sites for commercial white pine forestry, however, are also likely to have a climate favourable for C. ribicola; so, maintaining rust resistance could be important (Schwandt et al. 2010).

The high-elevation white pines in western North America occur as isolated, small populations; but some have large geographic distributions and tolerate environmentally harsh sites (Tomback and Achuff 2010). These white pines mature slowly, and their seedlings and saplings are especially vulnerable to lethal cankering by blister rust because their branches are close to the ground and they lack ontogenic resistance (King et al. 2010; Zeglen et al. 2010). Consequently, few new recruits would survive into old-growth. The current old-growth had already passed through that vulnerable early stage before the introduction of C. ribicola. However, abiotic stresses, fire and mountain pine beetle outbreaks—which may be more severe as result of global warming—could drastically reduce the longevity and fecundity of this old-growth.

With the world’s glaciers receding and continental plates rebounding, global warming could lead to serious coastal flooding, volcanic eruptions and earthquakes. During these unsettled times, government priorities may not include planting non-commercial white pines in remote locations. Sustaining and restoring high-elevation white pines could require partnerships of foresters and other technical professionals with environmental activists to collect seeds, rear and plant white pine seedlings (Schwandt et al. 2010).

The species of Ribes are numerous, occupy diverse habitats, and easily dispersed (Hummer and Dale 2010; Zambino 2010). In spite of climate change, they are not likely to require assistance in finding suitable habitats. Likewise, by natural dispersal or with human assistance, C. ribicola seems able to reach and establish in any site where hosts are present in a suitable environment (Geils et al. 2010; Zambino 2010). The history of blister rust and diversity of Cronartium rusts in Eurasia suggest that introduction of an invasive pathogen could pose a considerable threat to North American white pines (Kim et al. 2010; Zhang et al. 2010). An introduced or emergent pathogen could alter host-range relationships, shift hazard-zone boundaries, and nullify gains in breeding for resistance.
In North America, we rely on natural regeneration for sustaining most white pine populations, especially the western high-elevation species (Schwandt et al. 2010). Soon—if not already—conserving white pines and preserving familiar ecosystems may require extensive planting of adapted species. Different responses among species (including mountain pine beetle) and new niche openings created by global warming means that novel assemblages and disturbance regimes could develop; climatic warming may not merely ‘push’ whole plant communities to cooler sites, higher in elevation or latitude (see Plessa et al. 2005; Frey 2005). The supply in storage of white pine seeds with putative resistance currently exceeds reforestation demand (Schwandt et al. 2010). Some of this surplus could be used for assisted migration (McLachlan et al. 2007). But, where to plant? Many white pines tolerate dry, exposed sites better than their competitors; so, climate change could allow white pines to succeed on warmer sites formerly held by competitors (Tomback and Achuff 2010). Past and recent droughts have been associated with pole blight of western white pine and a decline of eastern white pine (Tainter and Baker 1996; Livingston et al. 2005). Neither natural nor artificial regeneration may be sufficient to prevent loss of some white pine populations (Tomback and Achuff 2010).

In some regions, blister rust is not a major cause of white pine mortality and regeneration failure; in other regions, it is an important contributor to losses in white pine populations (Geils et al. 2010; Kim et al. 2010; Schwandt et al. 2010). Until now, land managers have had practical tools for assessing blister rust hazard and risk (Ostry et al. 2010; Zambino 2010; Zeiglen et al. 2010). But with a rapidly changing and uncertain environment, could hazard and epidemiology models be sufficiently reliable to justify long-term silvicultural investments (Kliejunas et al. 2009)? New approaches may be required (see Appendix).

8 Adaptive management

To be effective for conserving white pine populations, management interventions would not only have a scientific basis but also be adaptable to unpredictable environmental and societal changes. Managers are confronted with dynamic ecosystems, changing goals and policies, and unforeseen responses to treatment. The processes of forest dynamics include biotic succession and disturbance, climate change, and introduction of invasive species (Schwandt et al. 2010). Policy evolves with changing emphases in priorities and investments (Geils et al. 2010). For example, the government hires crews to eradicate Ribes for saving white pines until they can be harvested for timber; then later, the policy shifts to rely on partners for protecting white pines as wildlife habitat (Ostry et al. 2010; : Fig. 2). Intervention treatments can have unintended consequences—such as aggressive fire suppression that leads to loss of early-successional species (Tomback and Achuff 2010). Ecosystem dynamics, policy changes and treatment responses can be expected to occur but not predicted in their details. To deal with these contingencies, an adaptive approach would promote research, management and stakeholders working in concert to develop, implement, monitor, assess and revise effective treatments for sustaining desirable resilient ecosystems.

In Canada and United States, the management of white pines, Ribes, and C. ribicola is conducted by setting and implementing public policy in the form of regulations and practices. We have attempted in these review articles to provide a summary on the blister rust pathosystem to serve as a scientific basis for that management. In setting rules for managers to follow, policy-makers need not only incorporate the best-available science from researchers but also balance conflicting objectives among diverse stakeholders. Because nature, society and science are complex and dynamic, regulations and practices eventually require modification; and their outcomes are never certain. Gunderson and Holling (2002) described a theory of adaptive change and its application to management of natural ecosystems. Their approach of participation and learning provides a general,
conceptual framework for setting, implementing and revising policy and for resolving issues of conflict, change and uncertainty. The white pine blister rust pathosystem has proved to be complex and dynamic; its management issues have included conflicts over objectives, changes of tactics, and uncertainties in outcomes. Therefore, an approach like that of Gunderson and Holling (2002) would appear to be helpful for managing white pine ecosystems threatened by blister rust.

Within the North American public arena, management of white pine blister rust involves several groups with different roles. Administrators supervise programs and set policy; regulators enforce rules; foresters implement practices, scientists and other technical specialists develop and transfer new information and tools; various stakeholders (Ribes growers, woodlot operators, industrial forest stewards and environmental activists) help determine strategic goals and acceptable tactics. Most of the administrators, regulators and foresters responsible for managing white pine resources are associated with federal, state or provincial governments; but there are some private or corporate managers. Likewise, researchers and other technical specialists are usually government or university employees engaged in research, development and technology transfer and assistance (e.g., http://www.fs.fed.us/rm/highhelevationwhitepines/). Stakeholders are citizens representing their economic or environmental interests.

Plant pathologists and geneticists have organized several working groups to exchange information and develop cooperative projects. The International Union of Forest Research Organizations (http://www.iufro.org/) houses numerous working parties that organize international conferences held about every 4 years. The working parties dealing with white pine blister rust are Rusts of Forest Trees in the Forest Health Division and Breeding and Genetic Resources of Five-needle Pines in the Physiology and Genetics Division. Many research and forest protection pathologists in western North America are members of the Western Forest Disease Work Conference (http://www.fs.fed.us/foresthealth/technology/wif/index.htm). This group provides a discussion forum and field trips covering the range of western forest pathology topics; the Conference encourages participation of pathologists from Mexico and other countries in their annual meetings. Several other groups with western North American interest in white pine blister rust and genetics are Rust Busters (http://www.fs.fed.us/r6/dorena/rustbusters/), the Western Forest Genetics Association (http://www.fsl.orst.edu/wfga/), and the Ecological Genomics and Forest Health Network (http://www.pinegenome.org/egfhn/). The Central Rockies White Pine Group is an informal discussion group including pathologists, geneticists, physiologists, foresters and ecologists working mostly in Wyoming, Colorado, New Mexico and adjacent states.

Although numerous ecological and environmental groups are advocates for the conservation and restoration of white pines in western North America, several foundations are especially active with regards to white pine blister rust. The Whitebark Pine Ecosystem Foundation (http://www.whitebarkfound.org/) is a member-sponsored organization which publishes a newsletter, organizes conferences, and forms partnerships to accomplish research and restoration goals. The Sugar Pine Foundation (http://www.sugarpinefoundation.org/) is concerned with sustaining and restoring sugar pines, especially in the California–Nevada, Lake Tahoe region.

This synopsis has identified seven major challenges for those concerned over white pines, Ribes, and blister rust: (1) applying the lessons of history; (2) conserving white pines; (3) developing strong durable resistance; (4) integrating silviculture and genetics into operational practices; (5) reconciling Ribes cultivation and white pine forestry; (6) accommodating the environmental and social consequences of climate change; and (7) developing and supporting programs to mitigate the impacts of blister rust. The various participants have different roles in management, research and partnership and bring alternative perspectives and priorities. Rather than being a cause of conflict, this diversity can be a source for creative approaches to meeting these challenges. The following
Appendix is our attempt to identify from the entire review how these challenges might be met with specific actions for understanding and managing the white pine blister rust pathosystem.

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Appendix: Information and action priorities
*Cronartium ribicola* is the pathogen that connects aecial-host white pines (subgenus *Strobus*) and telial hosts (*Ribes, Pedicularis* and *Castilleja*) into a white pine blister rust pathosystem. At times and places, the risks posed by blister rust to economic resources and biodiversity values are sufficient to engage managers and stakeholders in actions to prevent and mitigate avoidable impacts. Geils et al. (2010) pose four questions that are addressed in the subsequent articles of 2010. Briefly, these questions relate to: (1) the role of the pathogen in causing impact; (2) the potential for management by genetic and silvicultural techniques; (3) the knowledge base for developing and deploying these techniques; and (4) support for implementing management and monitoring results. In their reviews, the authors have identified numerous information and action priorities consistent with present challenges and opportunities. The items listed in this appendix are compiled from these identified priorities, organized by topic question, and presented as general and specific actions for understanding and managing white pine blister rust pathosystems.

1 Role of the pathogen

- Complete a global review of *Cronartium* phylogeny and systematics, especially those infecting white pines using molecular markers and reconciling morphology, host, and life history characteristics, including:
  - complete distribution-wide spore collections;
  - conduct DNA sequencing, develop an EST library, and survey with microsatellite and AFLP markers using an assignment test; and
  - determine a taxonomic identity for the blister rust on *P. armandii*.
- Conduct biogeographical and epidemiological studies on the white pines blister rust fungi to better understand their origins, migrations and other dynamics of their distribution patterns, including:
  - estimate divergence times for extant *Cronartium* species;
  - evaluate the evolution of the different rust populations by DNA analyses and cross-inoculation using geographically different inocula and hosts;
  - test hypotheses using biological and historical data for the possible introduction of non-native biotypes of white pine blister rust fungi into Japan or China; and

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develop methods to identify biotypes of white pine blister rust fungi and to predict pathways by which various biotypes might move into new regions (previously infested or not).

- Investigate lesser-known aspects of rust life history and reproductive biology important for assessing its potential for spread and intensification, including:
  - demonstrate the viability of hybrid aeciospores (C. ribicola × comandrae) by inoculation of alternate hosts;
  - assess the role of common telial hosts in allowing hybrid rusts to complete their life cycle;
  - conduct new research on the telial stage of the rust, especially season of production under various environments, potential for overwintering, and the longevity of teliospores (especially on cast leaves of western Ribes and cultivars);
  - determine the factors that induce basidiospores to form, develop, dispersal, and survive within cultivated Ribes plantings to reduce the inoculum potential from commercial operations; and
  - study rust spread (dispersal and establishment processes) from telial hosts in genera other than Ribes, telial hosts that have little urediniospore cycling, and infections resulting after long-range transport.

2 Potential for management by genetic and silvicultural techniques

- Obtain and apply information for genetic resource management based on the organization of genetic diversity in a spatial hierarchy from demes to species, including:
  - complete a phylogenetic and systematics review applying molecular techniques to the white pines, especially the P. flexilis complex and P. wallichiana, and sampling multiple individuals within each taxon to account for non-monophyly;
  - conduct rust susceptibility studies for various taxa and populations of white pines;
  - map resistance and other adaptive traits, beginning with whitebark pine and P. wallichiana, across their distributions and relate these to environmental features (ecological genomics);
  - produce artificial embryos of clonal lines of pedigreed material for breeding programs;
  - develop pine hybrids for native species with minimal or lacking resistance;
  - use genetic transformation to introduce useful but difficult to incorporate genes and combine with mass in vitro propagation to accelerate tree improvement;
  - select, bank and incorporate rust-resistant trees into breeding programs that concentrate on naturally occurring resistance to blister rust;
  - develop seed source recommendations and transfer guidelines where not available; and
  - develop genetic approaches for stands relying on natural regeneration.

- Determine and implement silvicultural treatments for successful regeneration and survival of white pine, including:
  - improve nursery and artificial regeneration techniques such as sowing or planting;
  - monitor regeneration for long-term genetic gains and to trigger silvicultural treatments such as pruning;
  - apply prescribed fires and other silvicultural techniques to prepare seedbeds and monitor Ribes;
  - encourage natural regeneration where required;
  - adapt methods for protecting high-value trees such as seed trees, super-canopy trees, and whitebark pines from diseases, insects, and abiotic stresses with various methods such as irrigation, hand removal of competing vegetation, insecticides, baits and repellents, pruning, and scribing; and
increase species and age diversity by planting and managing white pine within various forest types and maintain a sufficient numbers of healthy old-growth white pines for wildlife and aesthetic purposes.

- Develop, test and improve silvicultural techniques for reducing damage to white pine seedlings and poles, including:
  - survey and monitor pine mortality and causes, regeneration failure, blister rust incidence, severity and damage to identify priority areas for intervention;
  - identify, monitor and protect trees with genetic resistance to blister rust from injury and death;
  - initiate trials with deer protectors as a solid barrier to basidiospores;
  - develop environmentally safe triadimefon-like fungicides that can be used in nurseries and for protection of out-planting until they can be pruned or develop ontogenic resistance;
  - explore and operationally evaluate chemical control in the field and biocontrol agents such as parasitizing fungi and endophytic microorganisms; and
  - develop methods to reduce damage from bears and other mammals.

- Develop epidemiological models for assessing site hazard and treatment efficacy, especially to explain high levels of damage in some stands, behaviour in endemic pathosystems, and for projecting risks in China, Mexico, and future climates, including:
  - discern the height cankers may be found in different geographic locations on different white pine species as an aid for assessing the value of pruning to control blister rust;
  - investigate the mechanisms by which fungal endophytes affect infection and host resistance;
  - continue or establish large-scale and long-term field with putatively resistant stock types, replicated over different sites to study gene-by-environmental interactions and to discern and demonstrate various types of resistance or tolerance.

3 Knowledge base for developing and deploying these techniques

- Conduct research on the ecology, genetics and evolutionary biology of white pine blister rust fungi and develop tools for applying results to management, including:
  - characterize metapopulation structure and gene flow for various regions and scales, and in particular examine the potential of gene flow from other *Cronartium* taxa to *C. ribicola*;
  - describe the interactions of adaptive traits (e.g., Cold hardiness), aggressiveness, virulence and fitness in terms of physiological, evolutionary and ecological processes;
  - compare the ecological and genetic behaviours of host specialization, epidemiology, genetic adaptation, developmental plasticity, virulence and/or trait reversion in populations from eastern Asia with those in North America and contrasting populations from eastern and western North America;
  - develop axenic systems and controlled genetic material for examining rust genetic structure and sexual behaviour;

- Conduct research on *Ribes* biology useful for reducing potential blister rust hazard to white pine, including:
  - explore the genetic diversity and susceptibility of American *Ribes* for horticultural potential and presence of resistance mechanisms other than the *Cr* gene;
  - conduct species-level analysis of *Ribes* population dynamics across landscapes as they relate to blister rust incidence and fire regime;
determine the relative genetic fitness of *R. nigrum* to native species and consequent affects to community susceptibility; and

determine whether natural selection for resistance is more effective in leaf-shedding or non-shedding species, in seedlings or established bushes, with or without additional physiological limitations, such as low-light conditions, in areas with long or short exposure to rust, and in bushes surviving rust or plants regenerated from seed banks.

Assess and mitigate the risk from expanded *Ribes* cultivation for a virulent race of rust to develop and impact economic resources and ecosystem services of white pine in North America, including:

- develop suitable country markets and a system for reporting and monitoring where currant production is increasing;
- review by government agency their policies and encourage agreement on uniform regulations to address the potential biological threat from commercial and hobby plantings of *Ribes* to the current and future white pine resource;
- determine the impact of blister rust and its control on commercial yield in North America *Ribes* plantations;
- develop a system of monitoring and reporting the potential defeat of the R-gene *Cr* in *Ribes* cultivars and a test to assure the phytosanitary health in the movement of *Ribes* propagules;
- develop currant cultivars with resistance to rust and powdery mildew and that produce acceptable fruit quality (and high vitamin C content) and yield and that can be readily picked by mechanical harvesters;
- assess the potential for threat reduction to white pine production if *Ribes* cultivations were restricted to durable, immune or highly resistant cultivars or routinely employed disease control by fungicides or dormant oils; and
- re-examine the processes of long-distance spore dispersal to better model the risk of infection to susceptible *Ribes* by aeciospores and pine by basidiospores and the potential for movement of susceptible genes from cultivated *Ribes* into native species through pollen from either production areas or escaped populations.

Conduct further testing of strains and plant populations from diverse regions to determine where non-*Ribes* telial hosts may be contributing to pine infection (in both North American and Eurasia) and their contribution to blister rust hazard and the genetic diversity of the rust.

Investigate the genetic and proteomic factors that control pathogenesis, resistance and virulence, including:

- improve methods to account for variation in symptoms among seedlings, inconsistent and uneven infection rates and variation in susceptibility by needle age with more precise descriptions of seedling responses (interaction phenotypes);
- determine the occurrence, susceptibility, distribution of resistance, and potential impacts of blister rust in unstudied or understudied white pine species;
- continue work on molecular characterization of the genes and proteins involved in resistance and virulence to improve the understanding of function, evolution and stability in the white pine blister rust pathosystem;
- test and improve alternative models of R-gene resistance and partial resistance;
- compare the variability in the R-protein structures that determine pathogen specificity to obtain useful information about ontogenetic resistance of long-lived individuals;
- conduct hybridization experiments to look for the up- or down-regulated genes using a cDNA library and sequenced ESTs;
○ use advanced sequencing technology to sequence the whole cDNA library simultaneously and provide an understanding of DNA changes and ultimately amino acid and protein structural changes unavailable with microarrays;
○ identify and clone avirulence genes of *C. ribicola* to identify R genes among white pine RGAs;
○ resolve protein functionality using yeast two-hybrid analysis;
○ utilize previously developed molecular markers and new high-throughput sequencing technologies to map resistance and other adaptive traits in white pines and virulence in *C. ribicola*;
○ utilize association genetics techniques for gene discovery;
○ conduct genome scans to detect putative loci under positive selection;
○ use genecolgical approaches to identify putative selective signatures and draw comparisons between adaptive traits and molecular markers;
○ purify the Cro rI protein from *C. ribicola* to determine if it is active as an elicitor or virulence factor;
○ continue to research the regulation of PmAMP1 and class IV chitinases to improve operational screening for slow-canker growth defence; and
○ determine gene associations for various, partial resistance seedling responses (such as the slow-rusting trait).

4 Support for implementing management and monitoring results

○ Acquire and maintain long-term public support for the coordinated efforts of various management and research agencies, their partners and stakeholders for sustaining or rehabilitating white pine ecosystems.
○ Develop and implement plans at regional and local levels to assess the condition and trend of white pine ecosystems, identify threats to ecosystem health and productivity, set treatment and site priorities, apply mitigation treatments, establish monitoring and adaptive management systems, and communicate with partners and stakeholders.
○ Continue to provide expertise in forest pathology and other specialized fields for technical advice and research to aid development, monitoring, and assessment of program strategies, tactics, and applications.

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