A Natural History of *Cronartium ribicola*

Brian W. Geils, Research Plant Pathologist, USDA, Forest Service, Rocky Mountain Research Station, Flagstaff, AZ; **Detlev R. Vogler,** Research Geneticist, USDA Forest Service, Pacific Southwest Research Station, Institute of Forest Genetics, Placerville, CA

Abstract–*Cronartium ribicola* is a fungal pathogen that causes a blister rust disease of white pines, *Ribes,* and other hosts in the genera *Castilleja* and *Pedicularis.* Although blister rust can damage white pine trees and stands, the severity and significance of these impacts vary with time, place, and management. We use a natural history approach to describe the history, biology, and management of *C. ribicola.* We review its status as a non-native pathogen, likely ecological and evolutionary behavior, and implications for management.

Introduction

The history of white pine blister rust is little more than 100 years old. European interest first began in response to an epidemic that devastated plantations of introduced North American white pines. Then shortly after 1900, concern developed in the United States and Canada due to multiple rust introductions and severe commercial losses. Although *Cronartium ribicola* is native to Asia, brief local epidemics have occurred there. In North America, the pathogen has recently spread into the Southwest and intensified in high-elevation stands of the Pacific and Rocky Mountain regions. A typical pattern for blister rust epidemics has three phases—latent establishment, exponential growth, and endemic persistence. Demographic, ecological, and genetic factors determine the duration and severity of these phases. In the past, managers have used quarantine, eradication, sanitation, and genetics with variable success in controlling the rust. The present management strategy is to protect and sustain white pines through silviculture and genetics.

Similar to most pine stem rusts, *C. ribicola* is an obligate parasite of living hosts and has a complex life cycle comprising multiple spore stages for reproduction, dispersal, and perennial survival. *Cronartium ribicola* and related taxa are distributed across temperate Asia, Europe, and North America almost everywhere susceptible hosts occur. Most species of North American white pines have naturally infested populations, but disease severity ranges widely by location because of differences in site hazard and stand history. Most white pines and *Ribes* escape infection by geographic isolation or other environmental factors. Disease in susceptible white pines can result in death of individual branches, the upper crown, or an entire tree. Resistant white pines recognize pathogen presence and respond with physiological defenses that confer immunity if the pathogen is eliminated or tolerance if both survive. Subject to multiple, complex, ecological interactions, the long-term course of an epidemic and its effects on pathogen and host populations depend on their fitness in passing genes to the next generation.

Managers have historically considered *C. ribicola* as an introduced invasive pathogen causing unacceptable losses that can be reduced by silvicultural and genetic intervention. Economic rust control in commercial timber stands has often been difficult to achieve. Rust control to protect ecological values in natural high-elevation forests presents even greater difficulties. Important questions include the dispersive capability of the pathogen, distribution of hazardous sites, vulnerability of susceptible populations, rate of co-evolutionary adaption, resilience of affected ecosystems, and criteria for assessing values and risk. We agree with those who believe that management should be based on real understanding, support healthy ecosystems, and value life.

A Natural History Perspective

> *It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living.*
>
> *—Sir David Attenborough, 2006*

Many people might profess that an alpine meadow of white pines makes life worth living (Figure 1). Few, however, would see *Cronartium ribicola,* the disease agent causing white pine blister rust, as interesting and anything but a pest. We view the *Cronartia* (pine stem rust fungi) as organisms with value in themselves. They exercise a creative role in the evolution and dynamics of biotic communities. They form enduring, intimate associations with their hosts and co-evolve with these and other dependent species. In contrast to native stem rusts, however, *C. ribicola* is often perceived only as an introduced, invasive pathogen that can and should be controlled to reduce loss of ecological values. Although there are scientific and philosophical bases for this perception, our consideration of an alternative perspective leads to several questions with different implications for management. Is *C. ribicola* naturalizing? Can affected ecosystems remain diverse, productive, and attractive? Are the dynamics of the white pine blister rust pathosystem significantly different

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

Figure 1. A high-elevation meadow of whitebark (*Pinus albicaulis*) and limber pine (*P. flexilis*), upper Lamoille Canyon, Ruby Mountains, NV. Photo by B. Geils.

from those of native blister rust pathosystems? What are the ethical responsibilities for preserving existing biotic entities such as populations, species, and communities? In wildlands, should maintaining natural ecological and evolutionary processes have precedence over management intervention? How do we ensure that management in the long-run does not cause more harm than good?

Our objective in raising these questions is not to dispute *what* to think about these issues but to encourage deeper reflection on *how* to think about them. Conservation biologists are motivated to act, but selection among strategies from a single-species focus to ecosystem management is problematic and fraught with ambiguity and contradiction (Simberloff 1998). Reiners and Lockwood (2010) provided a philosophical framework for examining how ecologists select and interpret facts according to their perceptions of what is relevant, attractive, and ethical. A thorough presentation of the history, biology, and management of blister rust and application of the Reiners and Lockwood model would require an entire monograph. For a comprehensive review of white pine blister rust, we refer the reader to the synthesis by Geils and others (2010) and to additional reviews in the same issue of Forest Pathology (Shaw and Geils 2010). Here, we only briefly describe several observations from the natural history of *C. ribicola,* offer our interpretations, and urge serious scientific investigation and philosophical discussion of the goals and means for stewardship of the natural world.

The term *history* in natural history derives from the Greek for *inquiry* or *knowing*. A natural history is a description of one kind of organism in its natural environment. It is a narrative on the development, behavior, relationships, evolution, and significance of a subject organism. We are inspired by Charles Darwin and E. O. Wilson. Their work demonstrates that natural history is not just for charismatic species, but also for ‘lowly’ barnacles and ants. Natural history unites biology and philosophy. What we perceive depends on how we observe and integrate that observation into an operational model of reality (see Hawking and Mlodinow 2010). What we perceive determines what we accept as true, beautiful, and right—therefore, what motivates our action.

Our own perceptions emerge from the sciences of biogeography and genetics. We have studied rust distribution and epidemiology to investigate how the pathogen finds its host or, conversely, how the host escapes infection. We have studied the pathology and genetics of rust–pine interactions to learn how the rust evades host defenses and how the host resists or tolerates the pathogen[1]. The scientific and historical literature provides a wealth of observation and interpretation on the white pine blister rust pathosystem. The articles in Shaw and Geils (2010) serve as a synthesis and guide to original references and additional scholarly reviews.

Diverse scientists, managers, and other concerned individuals hold various perspectives on blister rust. A widely held perspective in the mode of *command-and-control* (Holling and Meffe 1996) considers blister rust as a forest health problem that can and should be solved through management intervention. This perspective emphasizes blister rust as: 1) a recently introduced disease; 2) caused by an aggressively invasive non-native pathogen; 3) infecting highly susceptible host species; and 4) causing dire economic and ecological impacts. Along with fire, succession, bark beetles, and climate change, blister rust contributes to the decline

---

[1] Use of active verbs such as *find* do not imply purposeful intent by the pathogen or host. The statement *the pathogen finds* is a contraction for “the fungus produces and releases myriad spores, diffusion and mass transport widely disperse these spores, and some spores randomly impact and adhere to the leaf surfaces of potential hosts.”

of white pine populations and loss of biodiversity (Tomback and others, The Magnificent High-Elevation Five-Needle White Pines: Ecological Roles and Future Outlook these proceedings). Therefore, damaged ecosystems ought to be restored and maintained to historical conditions by management intervention using silviculture and genetics to control pests and to mitigate losses (Schwandt and others 2010).

Our alternative perspective highlights other aspects of the blister rust pathosystem. Fungi are living organisms that participate in ecological and evolutionary processes. Fungi have intrinsic biotic value regardless of their nutritional strategy as saprophytes or parasites and distribution as endemic or cosmopolitan. Our natural history perspective views the organism called *Cronartium ribicola* as comprising diverse genetic lineages and interbreeding populations. Their interactions with hosts and other organisms develop from the processes of speciation, migration, extirpation, reproduction, dispersal, parasitism, co-evolution, and ecosystem dynamics. *Cronartium ribicola* itself is a keystone species for communities of fungi, insects, and other animals which depend on blister rust cankers for food and habitat (Furniss and others 1972; Stillinger 1944).

Because *C. ribicola* is an introduced invasive exotic, blister rust could be seen as a novel challenge requiring intervention to protect threatened white pine species. But, the biological behavior of the organism is wholly analogous with that of blister rust fungi native to North America. The presence of both genetic resistance and ecological tolerance in its hosts indicates that they are not defenseless to the pathogen. Our perspective is not meant to justify selection of the "do nothing" management option. It is intended to provide a useful and realistic contrast for assessing the costs and long-term results of intervention to manage complex natural systems.

We value natural ecosystems as vital to human welfare, but so complex as to require an adaptive approach such as that first described by Holling (1978). We recognize biotic systems as *complex*—exhibiting non-linear behavior, embedded in hierarchical structures, and affected by various, often obscure contingencies. We consider *change* as the most common attribute of biotic systems. Resilient systems persist; adaptable systems evolve. Prudent stewardship requires adaptive learning that strives for desired results within a context of social and economic constraints, an appreciation of beauty, and regard, if not fondness, for all living organisms.

The reason for our caution with management intervention is that forest ecosystems are sufficiently complex that either treatment or neglect can produce unexpected or unwanted results. Therefore, a pragmatic strategy should be based on an understanding of ecosystem dynamics and biotic evolution and should recognize the limits of our knowledge and ability. We do not judge the sincerity of others. Rather, we urge use of observations from history and long-term monitoring for adapting management practice to changing environments and goals. For example, the history of blister rust includes many cases where control failed, was inappropriate, or ill-applied (Van Arsdel 2011). Early in the epidemic of eastern North America, losses were so severe that warnings of the blister rust threat and declarations of need for control were strongly voiced (e.g., Detwiler 1918). When managers realized that they could not readily eliminate blister rust, they abandoned white pine silviculture (Van Arsdel 2011). This fear of blister rust, however, was unjustified—eventually, white pines displayed their great reproductive potential and the epidemic progressed into an endemic phase. Even within a region of high rust hazard, a dedicated and knowledgeable land manager can produce white pine timber along with wildlife dependent on white pine snags and *Ribes* (Van Arsdel 2011).

Several concepts are especially useful for developing that understanding which can serve as a basis for management. Gunderson and Holling (2002) described a conceptual model of the creative renewal of ecosystems that incorporates resilience as a fundamental dimension of change. Their approach of adaptive management is derived from studies of complex natural and human systems and serves as an alternative to the command-and-control approach appropriate to definable engineering projects. Thompson (2005) offered hypotheses on the geographic mosaic of co-evolution between parasites and hosts that integrate both spatial and temporial aspects of genetic interactions. The specifics of co-evolutionary patterns vary with the life histories of parasite–host systems, but one generality is that significant genetic changes occur at a local scale from one generation to the next. To move from hypothesis to theory, however, studies have to be installed and monitored. Keane and Arno (2001) identified seven steps for developing and executing whitebark pine restoration projects that could be extended to other white pine species. These steps are: 1) multiscale inventory of existing conditions; 2) identification of key natural processes; 3) ranking landscapes and stands for treatment priority; 4) selection of sites potentially benefiting from treatment; 5) design of treatments specific to individual sites; 6) efficient implementation; and 7) response monitoring.

The importance Keane and Arno (2001) placed on monitoring is consistent with the Gunderson and Holling (2002) approach of adaptive management. Monitoring is an opportunity for learning how stands and landscapes change over time and for testing hypotheses of co-evolution. For example, rust incidence and host mortality can be high early in a regional epidemic or in a young stand (Zambino 2010; Tomback and others 1995). These early trends, however, may not extend into later epidemic stages or to older stands. Ostrofsky and others (1988) re-assessed the regional incidence of blister rust after 70 years of *Ribes* eradication in Maine. They learned that incidence was only 3.8% in treated areas and less than 10% in areas not treated.

Paleobiology

The evolution and biogeographical history of stem rust fungi can be inferred from life-cycles, morphologies, host ranges, extant distributions, disease symptoms, and phylogenetic relationships. Although fungi are mostly absent from the geological record, the pines are well represented as fossils and pollen. Millar and Kinloch (1991) used a phylogenetic tree indicating evolutionary relationships among the pine hosts to hypothesize about former hosts and the distributions of stem rusts. A similar study with the non-pine hosts would likely also be instructive. Richardson and others (2010) reviewed molecular approaches for producing gene-based phylogenetic trees of stem rusts and *Cronartium ribicola*.

Evidence from diverse sources (above, and review by Van Arsdel 2011) suggests that the association of an ancestral *C. ribicola* with *Strobus* pines dates to the Cretaceous Period before Laurasia broke into Eurasia and North America (about 65 million years ago). In the warm Tertiary epochs, pines in North America retreated to refugia too cold for blister rust while hosts and pathogens in Eurasia survived in more diverse refugia. During the Pleistocene, distributions of stem rusts, white pines, and other hosts shuffled across the northern continents repeatedly for several million years in response to the advances and retreats of glaciers. By the Holocene, only a few species of white pines remained in isolated alpine locations in Europe; but a diversity of white pines persisted in Asia along with their stem rusts (Kim and others 2010). The white pines in North America consisted of one species widely distributed in the East and representatives of the stone pines, foxtail pines, other five-needle pines, and pinyon pines in the West. The only stem rust on any of these species was *C. occidentale* on pinyon pines (Kinloch and others 2003).

Several ideas emerge from considering paleobiology in light of recent history. White pines and stem rusts have long shared a co-evolutionary history characterized by co-incidence, migration over continental distances, separation, and reunion. *Cronartium ribicola* and *C. occidentale* share common hosts in the genus *Ribes* and, though long separated, are closely related genetically (Vogler and Bruns 1998). Kinloch and others (2003) observed that the distribution of resistance in sugar pine (*P. lambertiana*) to *C. ribicola* correlates with the distribution of pinyon pines and surmised that, before the recent introduction of *C. ribicola* to North America, natural selection for blister rust resistance in sugar pine may have been induced by prior challenge from *C. occidentale*. For *C. ribicola*, the distinction between native and non-native may be less relevant than for other introduced plant pathogens.

Past Management

Literature on blister rust reveals that divergent epidemiological and management histories have unfolded in geographic regions with different environments and different host–pathogen combinations (Geils and others 2010). In the 1800s, foresters planted *Pinus strobus*, a valuable North American timber species, across northern and central Europe to western Russia (Gäumann 1950). Once introduced into Russia, *P. strobus* was exposed to *Cronartium ribicola* alternating between *Ribes* and the native Siberian white pine (*P. sibirica*). The combination of a favorable climate and close proximity of susceptible white pines and European black currants (*R. nigrum*) permitted rapid development of a severe epidemic in Europe. Although the silviculture of *P. strobus* was mostly abandoned in Europe by the early 1900s, European nurseries continued to ship inexpensive white pine seedlings to North America. Since blister rust infection can be latent in young seedlings, the rust was carried in cryptically-infected white pines that were planted at many locations across eastern North America. The pathogen was soon introduced as well to western North America. Inspection, quarantine, seedling destruction, and other early control responses failed to prevent widespread establishment of *C. ribicola*.

Foresters had been unable to stop the rapid and nearly complete destruction of American chestnut (*Castanea dentata*) from an introduced blight (Anagnostakis 1987), raising concern that the white pine blister rust might be similarly intractable and potentially disastrous. But, *C. ribicola* was more vulnerable to control because its life cycle required alternation between pines and *Ribes* (see historical reviews in Geils and others 2010 and Zambino 2010). Government-managed and publicly-supported blister rust control programs focused on eradicating cultivated European black currant first and then wild native *Ribes*. Eradication was easier and relatively more effective in eastern North America than in western regions because of differences in labor costs and *Ribes* biology. The impact of eradication on the blister rust epidemics varied greatly, and its long-term consequences are still unresolved. Perhaps eradication’s most important contributions were employment and fire protection. The experience of working in the woods exposed many young men (and some women) to the beauty, challenge, and reality of forestry in North America (Shaw 2010).

Besides eradication, silvicultural methods have been used to regenerate and tend white pine stands and have reduced blister rust damage (Ostry and others 2010; Zeglen and others 2010). Direct control of the disease on pine was attempted for a brief time; but antibiotics, biocontrol, and pine-removal ultimately proved impractical in North America. Sites differ in the expected severity of rust damage because of variations in climate and spatial distributions of hosts. Rating and mapping site hazard have been used to select favorable sites for regenerating white pines and determining appropriate treatments for site preparation, thinning, and sanitation. Stand treatments include pruning branches to remove infections or reduce the risk of future infections that would be lethal to the host. Although these methods impose additional costs with uncertain benefits, they remain important management tools in North America (Schwandt and others 2010).

In North America, genetic resistance programs have provided planting stock selected for improved performance in response to *C. ribicola* (King and others 2010). Improved stock is available for western white pine (*P. monticola*) and sugar pine, and it is being developed for high-elevation white pines (Sniezko and others, Past and Current Investigations of the Genetic Resistance to *Cronartium ribicola* in High-elevation Five-needle Pines these proceedings). Although increasing genetic resistance through artificial or natural regeneration is an important component along with silviculture in sustaining white pine populations, this approach faces several challenges. Schwandt and others (2010) cited a lack of planting opportunities as fewer sites are managed intensively and poor long-term field performance resulting from interactions of complex environmental and genetic factors. Restoration programs involving thinning and controlled burning can increase planting opportunities. Sniezko and others (Past and Current Investigations of the Genetic Resistance to *Cronartium ribicola* in High-elevation Five-needle Pines these proceedings) provide a realistic appraisal of the potential for developing durable resistance in high-elevation white pines and identify additional needs in methods and monitoring for successful deployment.

Life History and Parasitism

Cronartium ribicola is a fungus comprised of a thallus (or body) of filamentous and often multinucleate hyphae and reproducing sexually by spores borne on a basidium (a club-like structure). Common to the Pucciniales or rust fungi, *C. ribicola* is an obligate parasite of vascular plants. That is, the fungus requires a live host to grow and regenerate—when the host tissue dies, the fungus dies. Typical of parasites, its life cycle has multiple spore stages (it is macrocyclic) and alternates between phylogenetically unrelated hosts (it is heteroecious).

The distinguishing visible signs of *C. ribicola* become apparent on infected white pine and *Ribes* (see Geils and others 2010). The first signs on a pine are the darkening spermogonia, which produce sweetish exudates, microscopic non-infective spores (spermatia), and receptive hyphae. Next produced are the blister-like aecia with powdery, bright orange aeciospores erupting through a white peridium. Since infection is perennial on pine, spermogonia and aecia from present and past years may be found on an infected pine stem. Uredinia form as pustules on the undersides of leaves of the annual host, usually a *Ribes*. Several cycles of urediniospores from the uredinia may be produced in a season. The fungus produces brown, hair-like masses of telia visible in late summer or early fall on leaves of the non-pine host.

Colley (1918) described the cytology and parasitism of *C. ribicola*. Spermatia and receptive hyphae provide for genetic outcrossing. Aeciospores effect long-distance dispersal from pine and infection of a telial host. Urediniospores spread and intensify the fungus on the telial host within a season. Teliospores aggregated into telia germinate *in situ* and produce basidia, from which basidiospores are discharged to infect nearby pines.

Cummings and Hiratsuka (2003) conceptualized the nuclear cycle of a heteroecious *Cronartium* rust. The strategy of the rust is a combination of: 1) sexual reproduction and outcrossing for genetic diversity; 2) short- and long-distance dispersal for spatial diversity; 3) persistence on a perennial host for longevity; and 4) intensification on an annual host for amplification.

There are several oddities in the life history of *C. ribicola*. A form of rust on Asian white pines appears to have a simplified, autoecious or pine-to-pine life cycle that bypasses an alternate host (Kaneko and Harada 1995; Zhang and others 2010). Rust collections by Joly and others (2006) at a few sites in southern Alberta indicate that spermatia of *C. comandrae* from lodgepole pine (*P. contorta*) can fertilize the receptive hyphae of *C. ribicola* on limber pine (*P. flexilis*). The hybrid aeciospores produced are not known to be infective.

Combes (1995) reviewed the very successful strategy of parasitism in diverse groups of organisms, including intricate modes of dispersal and reproduction as well as multiple evolutionary pathways. Parasites are wholly dependent upon their hosts except during periods of spore dispersal. Although a parasite can damage a host and reduce its fitness, natural selection upon a biotrophic parasite favors host fitness, not lethality. Rapid, local, cell death in the host (hypersensitivity) is a common defense. Typical of parasites, *C. ribicola* obtains from its host protection from the external environment, an elevated position from which to launch its propagules, and the nutrition necessary for growth and reproduction. *Cronartium ribicola* infects its host by means of hyphae entering host stomates, ramifying between host cells, and extracting nutrition from host cells with a specialized structure called an haustorium (Colley 1918).

Hosts and Distribution

The most common telial hosts of *Cronartium ribicola* in North America are plants in the genus *Ribes* (Grossulariaceae), but several species of *Pedicularis* and *Castilleja* (Orobanchaceae) are also infected and can support telial production and subsequent infection of pine (Zambino 2010). In eastern Asia, hosts occur in all three genera, but the genus-host range is reported to vary by location (Kim and others 2010).

In North America, most species of *Ribes* appear to be compatible hosts; but species, populations, and individual plants vary in susceptibility and tolerance because of genetic and ecological factors (Zambino 2010). Although resistance is found among the cultivated black currants, they are often the most contagious hosts. The spiny alpine gooseberry, *R. montigenum,* often occurs under whitebark pine (*P. albicaulis*) in high-elevation meadows, but becomes infected in summer from urediniospores produced on western black currants (*R. hudsonianum*) that are restricted to riparian zones in lower-elevation forests. The widely distributed wax currant (*R. cereum*) is susceptible to *C. ribicola* and contagious in some regions. But in the American Southwest, the currant referred to as *R. cereum* is commonly infected by a leaf rust of pinyon (*Coleosporium ribicola*), but not by *Cronartium ribicola* even where other *Ribes* species are severely infested.

Judging from natural and artificial inoculations, all species of five-needle white pines (subgenus *Strobus,* section Quinquefoliae) can serve as aecial hosts (Tomback and Achuff 2010). Extraordinarily, other pines such as *P. radiata* in subgenus *Pinus* may be infected, and the infections endure without producing spores (D. Vogler, personal observation). Typically infected pines are the white pines related to *P. strobus*, the stone pines (e.g., *P. albicaulis*) and the foxtail-bristlecone pines (e.g., *P. aristata*). *Pinus pumila* is a high-latitude pine of eastern Asia related to whitebark pine and with a similar low, bushy form. This native pine is susceptible to white pine blister rust but co-exists well with the parasite.

Some susceptible species of white pines in North America are not known to be naturally infected. The white pines such as *P. ayacahuite* of Mexico and central America occur with *Ribes* in habitats that appear to be environmentally suitable for rust infection. But their geographic isolation from rust-infested regions in the United States may have allowed them to escape infection (so far). In contrast, *P. longaeva* (Great Basin bristlecone pine) and associated *Ribes* appear to be within the dispersal range of *C. ribicola* aeciospores (Frank and others 2008). The environment of the Great Basin may be so unfavorable for rust infection that these susceptible hosts have also escaped infection.

Biotic Interactions

Each white pine blister rust pathosystem is nested within a larger ecosystem and network of biotic interactions including competition, herbivory, predation, and various forms of symbiosis. The best recognized of these interactions is between host and pathogen—expressed at the organism level as a physiological disease and at the population level as an epidemic with ecological and genetic dimensions.

The symptoms of blister rust result from the altered physiological responses of a host to the presence and action of a pathogen and secondary agents (Geils and others 2010). Pathogenesis in an aecial host proceeds from needle spots to shoot, branch, and stem reactions including localized necrosis, resinosis, and altered cell growth and division. As a consequence of rust sporulation, desiccation, and attack by insects and other fungi, the inner bark within a branch or bole canker is killed. After a stem is girdled, distal portions die, producing either a branch flag or top-kill; mortality results from crown decline and/or insect attack. Growth of an infection may be slowed or halted before or after the rust sporulates as result of a hypersensitive host reaction in the needle or bark or from external processes such as rodent feeding. The likelihood and impact of infection varies with host age. Disease is more damaging on seedlings, but more infections are likely found on large trees because of their size, exposure, and retention of infected branches. Infection in a telial host is usually limited to deciduous leaves. Symptoms of infection are necrotic spots; signs of the fungus are uredinia and telia. Damage results from early defoliation. For each aecial or telial host, environmental and genetic factors affect the severity and outcome of pathogenic interactions.

Although hosts are often ranked on a scale from susceptible to resistant, the pathogen–host interaction may be better characterized by the four modes of escape, susceptibility, resistance, and tolerance (Vogler and Delfino Mix 2010). A plant *escapes* if geographic isolation or other external, environmental factors prevent challenge by the rust. Most host plants remain uninfected because of escape. A plant is *susceptible* to infection if the pathogen can establish an intimate and enduring presence in the host to meet its nutritional and reproductive requirements. A plant demonstrates host *resistance* when it recognizes an invading pathogen and responds with active defensive mechanisms. *Virulent* genotypes of the pathogen can evade detection in an infected host and thus are capable of causing disease in a plant that would otherwise be characterized as resistant. A *tolerant* host can survive and reproduce in spite of established infection. Because susceptible and tolerant plants allow the pathogen to reproduce, they are contagious.

Years of research have unraveled some of the biochemical mechanisms behind pathogenesis and the modes of pathogen–host interactions (see reviews in Shaw and Geils 2010). Observations in genetics have increased our knowledge of the inheritance of specific traits associated with resistance. However, we are only beginning to understand the population genetic consequences of artificial selection in natural white pine ecosystems. New introductions and gene movement at larger scales of landscapes to regions are infrequent and subject to random effects. Because of heterogeneity in effective population size, outcrossing, dispersal, extirpation, and other metapopulation dynamics, co-evolution of rust and host may occur rapidly at the fine scale of individual stands. Many epidemics have demonstrated a common temporal pattern in the frequency of infected trees (discussed in Zambino 2010). In the latent period, infections are too uncommon to be detected; then the number of infections seems to explode among highly vulnerable young trees. Later in an epidemic and in older stands, the infection rate and percentage of diseased trees appears to decline or fluctuate at a low level. This pattern could result from demographic and ecological processes such as host maturation and aging, succession and reduction in *Ribes* density, or population genetic processes (naturalization).

Management using silvicultural and genetic approaches has focused on young stands and plantation forestry. If we are to sustain natural stands of white pine in high-elevation forests, we need to better understand disease processes at the pathogen-host level and epidemiological processes over generations of trees. Both ecological and evolutionary processes are critical.

Human Relations

In this review of the natural history of *Cronartium ribicola*, we have identified several instructive features of its biology and management. We have also described our perspective on the blister rust pathosystem and implications for white pine management. Science provides a method for assessing the likelihood an intervention would be cost-effective and reliable for achieving a specified objective. Ethics provides a frame for discussing whether a manager ought to act, given the costs, risks, tradeoffs, and consequences of intervention. Ethics also describes the utilitarian or intrinsic values implicit in human relations to other humans and other beings that determine what are right and good objectives.

In *A Sand County Almanac*, Aldo Leopold (1949), father of wildlife conservation, introduced the concept of a *land ethic*. Leopold recounted Odysseus's return to Ithaca and discovery that his palace was occupied by suitors seeking to take his wife and kingdom. Odysseus slew not only the suitors but also his unfaithful servants. He was considered justified by the ethics of the age in disposing of the servants because they were his property. Today's ethics require that servants be treated as persons with human rights not as property. Leopold thought of the 'land' as more than property, but as the soil, water, and whole biotic community upon which life depends. By a land ethic, we do not have a right to abuse the land; rather we have a responsibility to care for it.

Human self-interest leads to valuing plants, animals, and nature for their utility in providing food, shelter, comfort, and pleasure. Formerly, predators such as wolves were hunted for bounty because they destroyed game and livestock. Although some Americans still view wolves as varmints, others esteem wolves as aesthetic symbols of wild nature and agents for maintaining healthy wildlife herds. Charismatic predators such as wolves have worthy qualities of personality and behavior that humans view as intelligent and beautiful. White pines are still harvested for timber and other products, but their stature and grace have earned them aesthetic value and protection (Tomback and Achuff 2010). Mistletoes are parasites of forest trees that foresters have long considered a scourge because they reduce timber yield. But, the Druids considered them a symbol of the divine. Artists are inspired by them, and biologists protect them for wildlife habitat. A forest wildfire can be threatening and destructive. Many older foresters thought fire had no place in managed stands. But, fire displays an awesome beauty if viewed from a safe vantage. At the urging of a new generation of fire ecologists, land managers now use fire to renew forest stands.

We suggest that *Cronartium ribicola* is worthy of thoughtful and creative consideration. Darwin found grandeur in that "endless forms most beautiful" could evolve from fixed laws. So simple a thing as the blister rust fungus has survived with its hosts for millions of years; it can find its hosts a thousand kilometers from its origin, and adapt to and create new environments in which to thrive. *Cronartium ribicola* is now a permanent resident of the white pine ecosystems of North America. In response, we suggest that pragmatic, science-based management of these ecosystems consider three principles:

- Management based on an informed and deep understanding will be met with positive reinforcement from nature;
- The health of an ecosystem is best judged by its beauty of form and function;
- Good management respects both the utility and intrinsic value of all living organisms.

Acknowledgements

We thank the many colleagues who have helped us develop the ideas in this paper through discussion, collaboration, and inspiration. Our critics have pointed to the need for objective evidence and sound reason. Skeptics have identified the difficulty of the work and the importance of practical approaches. Supporters have encouraged us to acquire knowledge of an extensive literature and better understanding of a complex pathosystem. We credit Frank Hawksworth, Roger Peterson, Fields Cobb, and Bohun Kinloch for instilling in us the values of nature and science. We appreciate the thoughtful reviews of this paper by Diana Tomback, Mary Lou Fairweather, and Annette Delfino Mix.

References

Anagnostakis, S. L. 1987. Chestnut blight: the classical problem of an introduced pathogen. Mycologia. 79(1): 23-37.

Colley, R. H. 1918. Parasitism, morphology, and cytology of *Cronartium ribicola*. Journal of Agricultural Research. 15: 619-659.

Combes, C. 1995. Parasitism, the Ecology and Evolution of Intimate Interactions. Chicago, IL: University of Chicago Press. 728 p.

Cummins, G. B.; Hiratsuka, Y. 2003. Illustrated Genera of Rust Fungi. St. Paul, MN: American Phytopathological Society Press. 225 p.

Detwiler, S. B. 1918. Battling the pine blister rust. American Forestry. 24 (296): 451-457.

Frank, K. L.; Geils, B. W.; Kalkstein, L. S.; Thistle, H. W., Jr. 2008. Synoptic climatology of the long distance dispersal of white pine blister rust. II. Combination of surface and upper-level conditions. International Journal of Biometeorology. 52: 653-666. [Online]. doi: 10.1007/s00484-008-0158-3

Furniss, M. M.; Hungerford, R. D.; Wicker, E. F. 1972. Insects and mites associated with western white pine blister rust cankers in Idaho. Canadian Entomologist. 104: 1713-1715.

Gäumann, E. 1950. Principles of plant infection, a text-book of general plant pathology for biologists, agriculturists, foresters, and plant breeders. In: Brierley, W.B. [English ed.] New York: Hafner Publishing. 543 p.

Geils, B. W.; Hummer, K. E.; Hunt, R. S. 2010. White pines, *Ribes*, and blister rust: a review and synthesis. Forest Pathology. 40: 147-185. [Online]. doi: 10.1111/j.1439-0329.2010.00654.x Available: http://www.treesearch.fs.fed.us/pubs/36222

Gunderson, L. H.; Holling, C. S., eds. 2002. Panarchy, Understanding Transformations in Human and Natural Systems. Washington, DC: Island Press. 507 p.

Hawking, S.; Mlodinow, L. 2010. The Grand Design. New York: Bantam Books. 198 p.

Holling, C. S., ed. 1978. Adaptive Environmental Assessment and Management. Caldwell, NJ: Blackburn Press. 377 p.

Holling, C. S.; Meffe, G. K. 1996. Command and control and the pathology of natural resource management. Conservation Biology. 10: 328-337. [Online]. doi: 10.1046/j.1523-1739.1996.10020328.x

Joly, D. L.; Langor, D. W.; Hamelin, R. C. 2006. Molecular and morphological evidence for interspecific hybridization between *Cronartium ribicola* and *C. comandrae* on *Pinus flexilis* in southwestern Alberta. Plant Disease. 90: 1552. [Online]. doi: 10.1094/PD-90-1552A

Kaneko, S.; Harada, Y. 1995. Life cycle of *Endocronartium sahoanum* and its nuclear condition in axenic culture. In: Kaneko, S.; Katsuya, K.; Kakishima, M.; Ono, Y.; 4th IUFRO Rusts of Pines Working Party Conference; 1994 October 2-7; Tsukuba, Japan. Kukizaki, Japan: Forestry and Forest Products Research Institute, Forest Microbiology Section: 95-100.

Keane, R. E.; Arno, S. F. 2001. Restoration concepts and techniques. In: Tomback, D. F.; Arno, S. F.; Keane, R. E. Whitebark pine communities: Ecology and restoration. Washington, DC: Island Press: 367-400.

Kim, M.-S.; Klopfenstein, N. B.; Ota, Y.; Lee, S. K.; Woo, K. S.; Kaneko, S. 2010. White pine blister rust in Korea, Japan and other Asian regions: Comparisons and implications for North America. Forest Pathology. 40: 382-401. [Online]. doi: 10.1111/j.1439-0329.2010.00664.x

King, J. N.; David, A.; Noshad, D.; Smith, J. 2010. A review of genetic approaches to the management of blister rust in white pines. Forest Pathology. 40: 292-313. [Online]. doi: 10.1111/j.1439-0329.2010.00659.x

Kinloch, B. B., Jr.; Sniezko, R. A.; Dupper, G. E. 2003. Origin and distribution of *Cr*2, a gene for resistance to white pine blister rust in natural populations of western white pine. Phytopathology. 93: 691-694. [Online]. doi: 10.1094/PHYTO.2003.93.6.691

Leopold, A. 1949. A Sand County Almanac and Sketches Here and There. New York: Oxford University Press. 228 p.

Millar, C. I.; Kinloch, B. B. 1991. Taxonomy, phylogeny, and coevolution of pines and their stem rusts. In: 3rd IUFRO Rusts of Pine Working Party Conference, Banff, AB, 1989 September 18-22. Ed. By Hiratsuka, Y.; Samoil, J. K.; Blenis, P. V.; Crane, P. E.; Laishley, B. L. Info. Rep. NOR-X-317. Edmonton, AB: Forestry Canada, Northern Forestry Centre. pp. 1-38.

Ostrofsky, W. D.; Rumpf, T.; Struble, D.; Bradbury, R. 1988. Incidence of white pine blister rust in Maine after 70 years of a *Ribes* eradication program. Plant Disease. 72(11): 967-970. [Online]. doi: 10.1094/PD-72-0967

Ostry, M. E.; Laflamme, G.; Katovich, S.A. 2010. Silvicultural approaches for management of eastern white pine to minimize impacts of damaging agents. Forest Pathology. 40: 332–346. [Online]. doi: 10.1111/j.1439-0329.2010.00661.x

Reiners, W.A.; Lockwood, J. A. 2010. Philosophical Foundations for the Practice of Ecology. New York: Cambridge University Press. 212 p.

Richardson, B. A.; Ekramoddoullah, A. K. M.; Liu, J.-J.; Kim, M.-S.; Klopfenstein, N. B. 2010. Current and future molecular approaches to investigate the white pine blister rust pathosystem. Forest Pathology. 40: 314-331. [Online]. doi: 10.1111/j.1439-0329.2010.00660.x

Schwandt, J. W.; Lockman, I. B.; Kliejunas, J. T.; Muir, J. A. 2010. Current health issues and management strategies for white pines in the western United States and Canada. Forest Pathology. 40: 226-250. [Online]. doi: 10.1111/j.1439-0329.2010.00656.x

Shaw, C. G. 2010: Foreword [to Special Issue. White Pines, *Ribes*, and Blister Rust]. Forest Pathology. 40: 145-146. [Online]. doi: 10.1111/j.1439-0329.2010.00653.x

Shaw, C. G.; Geils, B. W., guest eds. 2010. Special Issue: White Pines, *Ribes* and Blister Rust. Forest Pathology. 40: 145-417. Woodward, S., editor-in-Chief. Berlin, Germany: Blackwell Verlag GmbH.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? Biological Conservation. 83: 247-257.

Stillinger, C. R. 1944. Damage to conifers in northern Idaho by the Richardson red squirrel. Journal of Forestry. 42(2): 143-144.

Thompson, J. N. 2005. The Geographic Mosaic of Coevolution. Chicago, IL: University of Chicago Press. 443 p.

Tomback, D. F.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology. 40(3/4): 186-225. [Online]. doi: 10.1111/j.1439-0329.2010.00655.x

Van Arsdel, E. P. 2011. Blister Rust in North America: What We Have Not Learned in the Past 100 Years. In: Fairweather, M. Comp. 2011. Proceedings of the 58th Annual Western International Forest Disease Work Conference; 2010 October 4-8; Valemount, BC. U.S. Forest Service, AZ Zone Forest Health, Flagstaff, AZ: in press.

Vogler, D. R.; Bruns, T. D. 1998. Phylogenetic relationships among the pine stem rust fungi (*Cronartium* and *Peridermium* spp.). Mycologia. 90: 244-257. [Online]. Available: http://www.jstor.org/stable/3761300

Vogler, D. R.; Delfino Mix, A. 2010. Resistance: What is it? In: Cleary, M.; 3rd Western White Pine Management Conference; 2008 June 17-18; Vernon, BC. Kamloops, BC: BC Ministry of Forests and Range: 24-30.

Zambino, P. J. 2010. Biology and pathology of *Ribes* and their implications for management of white pine blister rust. Forest Pathology. 40: 264-291. [Online]. doi: 10.1111/j.1439-0329.2010.00658.x

Zeglen, S.; Pronos, J.; Merler, H. 2010. Silvicultural management of white pines in western North America. Forest Pathology. 40: 347-368. [Online]. doi: 10.1111/j.1439-0329.2010.00662.x

Zhang, X. Y.; Lu, Q.; Sniezko, R. A.; Song, R. Q.; Man, G. 2010. Blister rusts in China: hosts, pathogens, and management. Forest Pathology. 40: 369-381. [Online]. doi: 10.1111/j.1439-0329.2010.00663.x