



REVIEW

White pines, *Ribes*, and blister rust: a review and synthesis

By BRIAN W. GEILS^{1,4}, KIM E. HUMMER² and RICHARD S. HUNT³

¹USDA Forest Service, Rocky Mountain Research Station, Flagstaff, AZ 86001, USA; ²USDA Agriculture Research Service, National Clonal Germplasm Repository, Corvallis, OR 97333, USA; ³Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC V8Z 1M5, Canada (retired); ⁴E-mail: bgeils@fs.fed.us (for correspondence)

Summary

For over a century, white pine blister rust (*Cronartium ribicola*) has linked white pines (*Strobus*) with currants and gooseberries (*Ribes*) in a complex and serious disease epidemic in Asia, Europe, and North America. Because of ongoing changes in climate, societal demands for forests and their amenities, and scientific advances in genetics and proteomics, our current understanding and management of the white pine blister rust pathosystem has become outdated. Here, we present a review and synthesis of international scope on the biology and management of blister rust, white pines, *Ribes*, and other hosts. In this article, we provide a geographical and historical background, describe the taxonomy and life cycle of the rust, discuss pathology and ecology, and introduce a series of invited papers. These review articles summarize the literature on white pines, *Ribes*, and blister rust with respect to their status, threats, and management through genetics and silviculture. Although the principal focus is on North America, the different epidemics in Europe and Asia are also described. In the final article, we discuss several of the key observations and conclusions from the preceding review articles and identify prudent actions for research and management of white pine blister rust.

1 Introduction

1.1 Historical and geographical background

For over a century, white pine blister rust, caused by the fungus *Cronartium ribicola* J.C. Fischer in RABENHORST (1872), has linked white pines and *Ribes* into a disease pathosystem of serious economic and ecological consequences (Fig. 1). The current epidemics in Asia, Europe, and North America (CABI 2000) occur in a dynamic, interconnected world (see FOLKE et al. 2004). White pine blister rust is not a single pandemic of ubiquitous severity; rather, there are different epidemics in several regions, each with a unique history and environment that locally determines impacts and evolutionary trends (see THOMPSON 2005). Sustaining resilient ecosystems is one approach to managing these epidemics, but the task is made difficult by climate change, other invasive species, and disturbances, as well as conflicts over resources and their management (MILLAR et al. 2007).

The review and synthesis in this article and the following series of papers were developed from a 1999 workshop (HUMMER and SNIETKO 2000) to promote an international dialog on white pines, *Ribes*, and blister rust. The workshop participants discussed whether the cultivation of currants and gooseberries (*Ribes*) could be pursued without impairing white pine forestry. They identified the need for a contemporary summary on white pines, *Ribes*, and blister rust that included information on biology, management, and research needs. A second inspiration for this compilation developed from a serious concern for the sustainability of white pine populations threatened by complex ecological changes. SCHWANDT (2006) described the nearly distribution-wide decline of whitebark pine (*Pinus*

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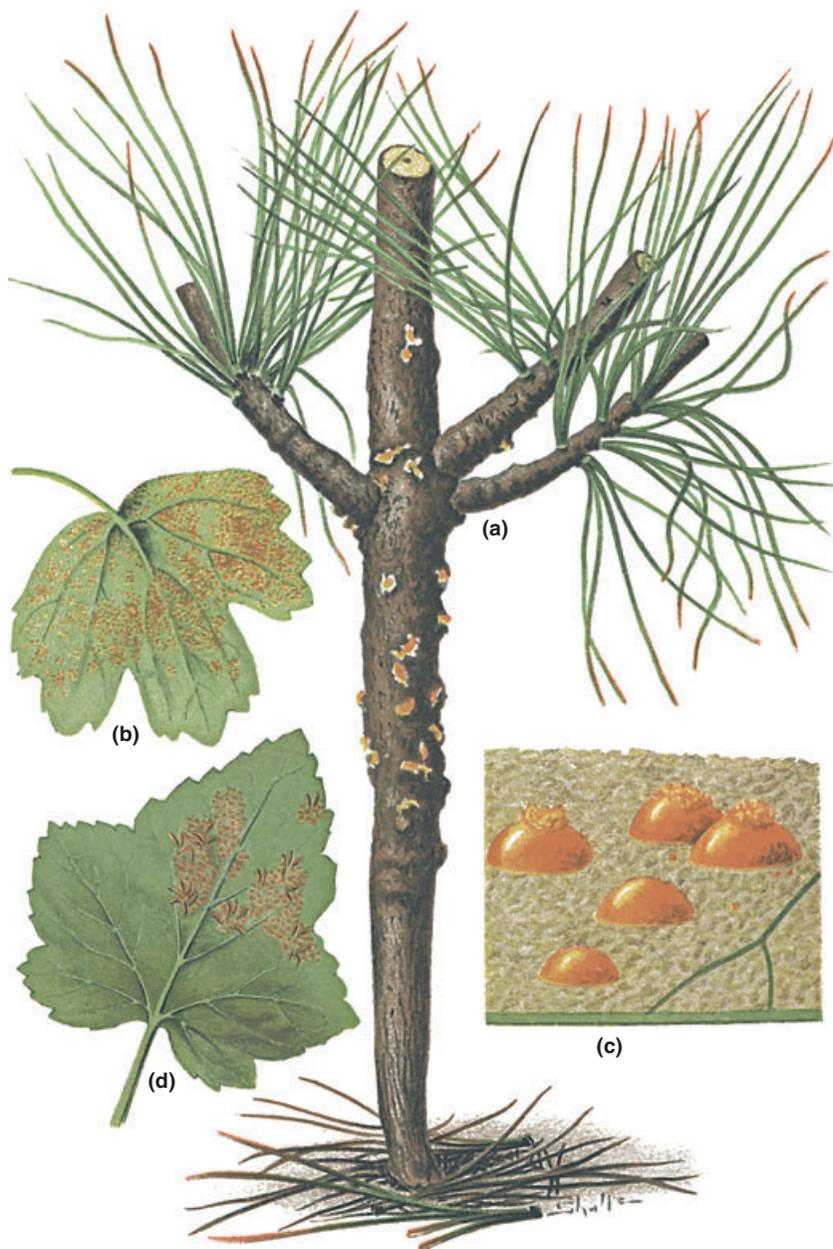


Fig. 1. *Cronartium ribicola* on *Pinus strobus* and *Ribes*. Reprinted Plate I (Frontispiece.) from Bulletin No. 206, *The Blister Rust Of White Pine* by SPAULDING (1911). From original description: (a) A 4-year-old white-pine tree diseased with blister rust. Note the slight swelling of the stem in the area bearing the yellow spore pustules. (b) Leaf of *Ribes aureum* bearing many pustules of uredospores (urediniospores). (c) Enlarged detail of uredo (uredinial) pustules. (d) Leaf of *Ribes americanum* with a number of the hair-like growths of the teleutospore (teliospore) stage. These spores are capable of infecting pine, while the first two forms cannot, but can infect the leaves of *Ribes*.

albicaulis Engelm.) and attributed losses to several biological factors including blister rust. Although climate change alone could render many presently occupied habitats unsuitable for whitebark pine (WARWELL et al. 2007), blister rust and other disturbances can contribute to population decline and ecosystem disruption (KLIEJUNAS et al. 2009). SCHOETTLE and SNIEZKO (2007) identified limber pine (*P. flexilis* James), a species with broad geographic distribution and ecological range, as another pine threatened by blister rust. Our intent for this series is to assist managers, researchers, and stakeholders, who often have conflicting interests, in making better-informed decisions for managing ecosystems with white pines, *Ribes*, and blister rust.

The review in this introductory article is based on our examination of over 1200 reports and publications on white pines, more than 400 on *Ribes*, and 2400 on white pine blister rust. Of these, nearly 1300 are available as a compiled bibliography published as supporting information (References S1). Other bibliographies selected from a digital literature database are available on request from the corresponding author. In this section, we focus on identifying the primary and most influential papers for a general, historical overview, and geographical synthesis of the readily available literature on white pine blister rust. We briefly review the biology and history of the rust and its status in Europe. For more detailed information on white pines, *Ribes*, other hosts, genetics, silviculture, and blister rusts of Asia, we refer readers to the other articles in the series.

1.2 White pines

Taxonomically, the genus *Pinus* is divided into two major groups consisting of the subgenus *Pinus* for the diploxylon, hard, or yellow pines and the subgenus *Strobus* for the haploxylon, soft, or pinyon and white pines (GERNANDT et al. 2005). All pines of subgenus *Strobus* are clearly distinguished by a single vascular bundle per leaf (i.e., haploxylon), but further segregation into sections, subsections, and species is disputed. Difficulty with the systematics of *Strobus* is attributed to a lack of distinct traits unique to a single group (i.e., feature coalescence, SYRING et al. 2007) and to insufficient reproductive isolation (as in *Abies*, see HUNT 1993). In this review, we generally follow the systematics of PRICE et al. (1998) and include as *white pine* all the species in subsection *Strobi* (white pines, narrow sense) along with those in subsections *Balfourianae* (foxtail pines) and *Cembrae* (stone pines). All these pines are typically five-needled (section *Quinquefoliae* of GERNANDT et al. 2005) and susceptible to infection by *C. ribicola*. The pinyon pines (subsection *Cembroides*) are also in subgenus *Strobus* but typically have 1–4 needles per fascicles. Numerous taxa in subgenus *Pinus* have five needles per fascicle and occur in the American Southwest, Mexico, and Central America (most in ‘Pseudostrobus group’). Neither the pinyons nor the ‘Pseudostrobus’ pines are natural hosts of *C. ribicola*.

Various species of white pine occur nearly wherever pines are able to grow (for natural distributions see CRITCHFIELD and LITTLE 1966). The compilation by RICHARDSON (1998) is a milestone in the ecology and biogeography of all pines and provides a comparison of previous systematics of the genus. TOMBACK and ACHUFF (2010) review the taxonomy, ecology, and biogeography of the white pines of western Canada and United States (western North America). SCHWANDT et al. (2010) describe the present status and management of these western pines. OSTRY et al. (2010) discuss the modern silviculture of eastern white pine (*Pinus strobus* L.); ZEGLEN et al. (2010) do likewise for western white pine (*P. monticola* Dougl. ex D. Don) and sugar pine (*P. lambertiana* Dougl.). This review presents additional information on the history of *P. strobus* in North America (as eastern white pine) and Europe (as Weymouth pine). ZHANG et al. (2010) and KIM et al. (2010) describe the history, status, and taxonomy of white pines, respectively, in China and eastern Asia.

1.2.1 History

White pines have long been valued. Their-easily worked wood and large seeds were important to many early peoples (ABRAMS 2001). The white pine, *P. strobus*, became a key naval resource for great masts in the 1600s and spurred British colonization of New England and Canada (ALBION 1926). Conflicts in white pine forest policy contributed to the American sentiment for independence from Britain (CARROLL 1973) and to the development of a distinctly British Canadian forestry (LOWER 1973). In North America, the primary white pine lumber region shifted during the period 1850–1875 from the eastern and maritime regions to the upper Great Lakes region (RANEY 1935; LARSON 2007). During the same time, a California gold rush spurred growth of a timber industry based on sugar pine. With the white pine supply in the Great Lakes region nearly gone, and with the arrival in the 1900s of mining and railroads to eastern Washington, northern Idaho, and western Montana, timber companies set up logging camps and mills in the Inland Northwest and British Columbia (ROCKWELL 1911; HUNT 2009).

Although *P. strobus* was first planted in Europe two centuries earlier, its silviculture greatly expanded, especially in Germany, in the late 1800s and early 1900s (RADU 2008). With the availability of inexpensive seedlings from Europe, interest grew for restoration of eastern white pine as a North American timber crop. Soon, however, enthusiasm turned to anxiety when epidemics of an invasive blister rust spread across Europe (GÄUMANN 1950) and North America (SPAULDING 1922b). Foresters had already seen an invasive blight eliminate chestnut forestry (LIEBHOLD et al. 1995). Would the new disease likewise devastate the prized white pines?

1.2.2 Reviews and conferences

Numerous review publications provide information on the biology and conservation of white pines with an emphasis on local forest concerns and management. The history, silvics, and importance of eastern white pine were reviewed by FROTHINGHAM (1914), MARQUIS (1959), and HORTON and BEDELL (1960). WILSON and HOUGH (1966) provided an extensive bibliography. STIELL (1994) recounted the history from 1918 to 1994 of Ontario's Petawawa National Forestry Institute, where many studies on eastern white pine were conducted. HOLZER (1972) described three European species of white pine; KRIEBEL (1972) provided information on the adaptability, growth, and resistance of the American white pines. One of the most important commercial white pines is western white pine for which HOFF (1987) supplied a comprehensive bibliography. Whitebark pine is now a species of special concern; TOMBACK et al. (2001c) described its ecology and restoration (also TOMBACK and ACHUFF 2010). For Europe, RADU (2008) provided a current review of white pine forest history, breeding, and its return to silviculture.

The proceedings of conferences that focused on white pines, their management, conservation, or genetics are also sources of information. CAMERON (1978) compiled a silvicultural symposium at Chalk River for eastern white pine; similar issues with additional concerns over economics surfaced at a Durham conference (FUNK 1986). At a Duluth conference (STINE and BAUGHMAN 1992), ecosystem and non-commodity values of eastern white pine emerged as critical interests. Although focused on whitebark pine conservation, a Bozeman conference (SCHMIDT and McDONALD 1990) was the first to consider the special status of alpine white pines. The theme was repeated for stone pines at a St. Moritz conference (SCHMIDT and HOLTMEIR 1994). BAUMGARTNER et al. (1994) compiled a Spokane proceedings on forest management and ecology in the western white pine type. Sugar pine conservation and management were topics of a Davis symposium (KINLOCH et al. 1996). Serious concern over various white pines was reflected in several, recent conferences—Calgary (PARKS CANADA, 2003), Ottawa (WILSON and BARKELY 2003),

Ashland (GOHEEN and SNIETKO 2007), and Whistler (CENTRE FOR FOREST CONSERVATION GENETICS 2007). Several recent international conferences have focused on the genetics of white pines. SNIETKO et al. (2004b) compiled proceedings for a Medford conference, BLADA et al. (2008) for a 2006 meeting in Valiug, Romania, and NOSHAD et al. (2009a,b) for a 2008 meeting in Yangyang, Korea.

1.3 *Ribes*: Currants and gooseberries

Currants and gooseberries are fruit-bearing shrubs of the genus *Ribes*, family Grossulariaceae (Fig. 2). They thrive in sunny, cool gardens, or forests and produce flavourful, vitamin C-rich berries. White pine blister rust causes both 'felt-blight' and early defoliation of *Ribes* in areas of severe infestation. Where the pathogen does not reproduce well, fruit crops and long-term health of *Ribes* bushes are little affected. In central Europe during the 1900s, foresters valued Weymouth pine as a fast-growing, timber species; but given the choice of food or fibre, most Europeans preferred their cultivated black currant (*Ribes nigrum* L.; SPAULDING 1929). In the eastern United States, however, a vigorous, government campaign convinced Americans to favour white pine forestry and support a programme of aggressive, *Ribes* eradication (DETWILER 1923). Cultivated currants and gooseberries, however, retained many proponents. Because *Ribes* species and varieties differed greatly in susceptibility to rust infection, efforts were made early to select and breed cultivars resistant to *C. ribicola* (DARROW and DETWILER 1929; SNELL 1941).

Presently in the United States, the *Ribes*-agribusiness is small but has potential for expansion (BARNEY 2000; BARNEY and HUMMER 2005). Canadian production of currants and gooseberries exceeds that of the United States. Although resistant varieties are available, concern remains that with expanded cultivation an aggressive (fast increasing) and/or virulent (resistance-defeating) race of *C. ribicola* might develop and impact the economic and ecological values of white pines (MUIR and HUNT 2000). HUMMER and DALE (2010) describe *Ribes* horticulture and success in breeding for resistance (also see BRENNAN et al. 2002a). ZAMBINO (2010) reviews wild *Ribes*, their ecology, and their role in blister rust epidemiology and coevolution.

1.4 White pine blister rust

The fungus *C. ribicola* is a rust of pine which, like stem rust of wheat, is in the order Pucciniales (AIME et al. 2006). Typical of many rusts, this obligate, biotrophic (requiring a living host) pathogen alternates with very different appearances between a telial host (a leaf rust of *Ribes* as *Cronartium*) and an aecial host (a stem rust of *Pinus* as form-genus *Peridermium*). The early history of white pine blister rust was marked by taxonomic confusion arising from insufficient information on host range and rust phylogeny (lineage relationships). This confusion was thought to have been resolved by the time of SPAULDING's (1922b) major review for North America and Europe. Spaulding and most others of the time considered *C. ribicola* as a single, sexually reproducing, rust species that alternated between white pines and *Ribes*. Although the frequently observed white pine blister rust pathogen of Europe and North America might share a closest common ancestor, there appear to be additional lineages of ambiguous relationship such as a native European rust (GÄUMANN 1945, 1950) and several Asian rusts (KIM et al. 2010; ZHANG et al. 2010). Revision of the systematics for the *Cronartium* rusts on white pines would require appropriate use of molecular diagnostic techniques (RICHARDSON et al. 2010). The existence of different blister rust pathogens has important implications on quarantines (HUNT et al. 2010).

GÄUMANN (1945, 1950), BINGHAM and GREMMEN (1971), and recently HUNT (2003a) described the international history of *C. ribicola* as an invasive forest pathogen of Europe and North America. PETERSON and JEWELL (1968) summarized the epidemiology, damage,

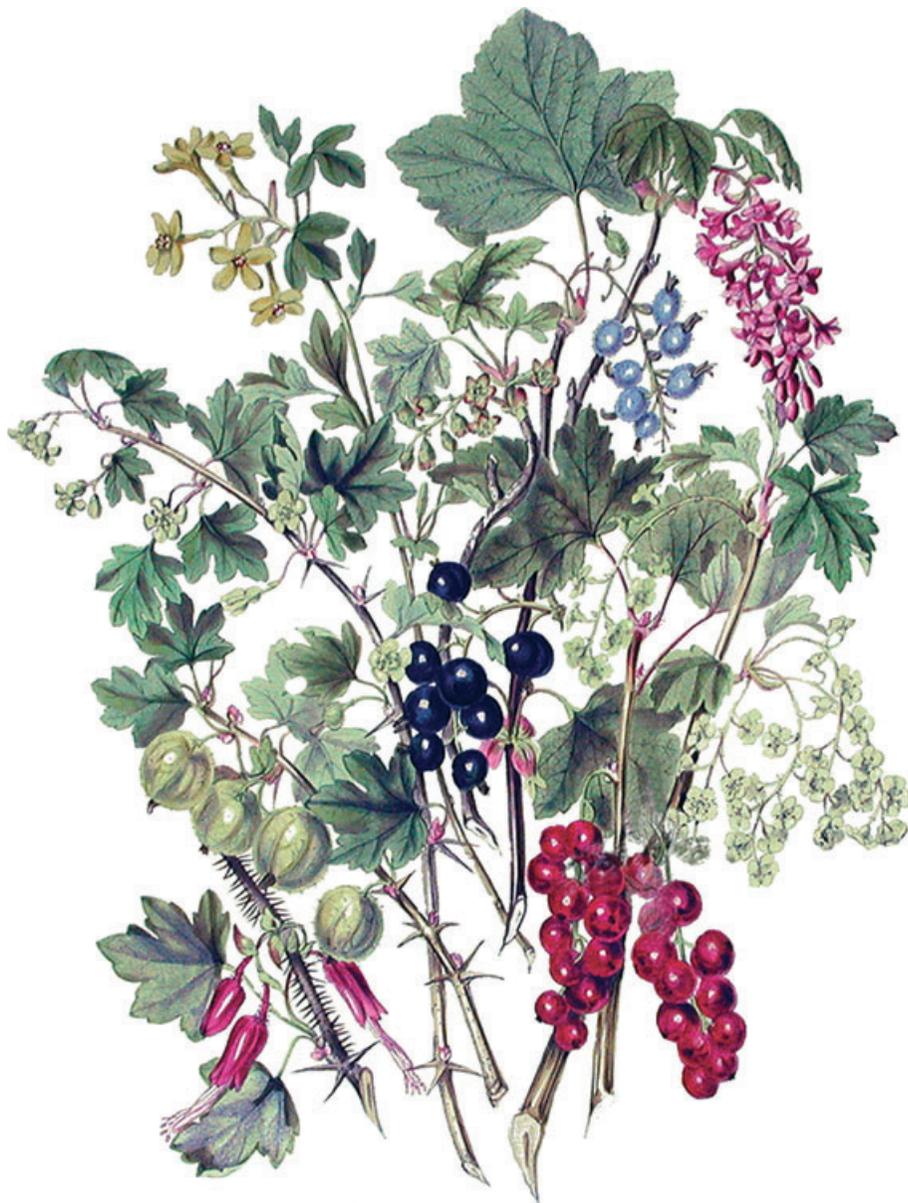


Fig. 2. Grossulariaceae: the currants and gooseberry tribe. Adapted from *Illustrations of the natural order of plants* by TWINING (1949). Species represented are *Ribes grossularia*, *R. rubrum*, and *R. nigrum* from Europe and *R. aureum*, *R. sanguineum*, and *R. speciosum* from North America.

and control of pine stem rusts. KINLOCH (2003) and McDONALD et al. (2005b) summarized the North American epidemics in terms of genetic changes and speculated on the potential for surprise in future blister rust epidemics (also see ZAMBINO 2010). Because white pine

blister rust is a disease of special concern, it is modelled as a cause of mortality in the (United States) National Insect and Disease Risk Map (KRIST et al. 2006).

Although not restricted to *C. ribicola*, proceedings have been published for recent conferences on the biology of rusts of forest trees. The international symposium edited by BINGHAM et al. (1972) focused on disease resistance with emphasis on the stem rusts of pines. Five conferences on conifer rusts have been held since 1989 by groups associated with the International Union of Forest Research Organizations. The Canada meeting (HIRATSUKA et al. 1991) included papers on phylogeny, history, taxonomy, epidemiology, genetics, distribution, and management. For the Japan conference, KANEKO et al. (1995) compiled information from Asia, especially on taxonomy and distribution. For Finland, JALKANEN et al. (1998) assembled papers on white pine blister rust taxonomy, epidemiology, genetics, and control. For China, XU et al. (2003) published papers on life history, epidemiology, resistance, and taxonomy. The most recent meeting was held in 2006 at King's Beach, California (chaired by J. Walla, North Dakota State University).

Management and research on blister rust in North America has consistently benefited from collaboration and information exchange between Canadian and American forest pathologists. Since 1954, the Western International Forest Disease Work Conference (WIFDWC) has provided a forum for cooperation of forest pathologists from North America, Europe, Asia, and other regions. Through its annual meetings and working group on rusts, WIFDWC is an effective group for promoting international dialogue on the pathology of forest trees.

2 Taxonomy and life cycle

2.1 Stem rusts of pine, *Cronartium*

CUMMINS and HIRATSUKA (2003) provided a recent synopsis of the rust genera with illustrations and comparisons of spore stages and life cycles. *C. ribicola* is one of 12 species of stem rusts of pine examined by PETERSON (1967, 1973); he suggested more study is needed to resolve the taxonomy of the several rusts infecting white pines. For rusts, parasites with simple and similar morphologies, data on life cycle, host range, and molecular genetics are especially useful for inferring their evolutionary history and providing a basis for systematics.

VAN ARSDEL (1969) speculated on the evolution of a pine stem rust that originated during the Pliocene in Asia and rapidly coevolved along with the white pines during the Pleistocene. MILLAR and KINLOCH (1991) also speculated on the evolutionary history of pines and stem rusts in their review of taxonomy, genetics, and biogeography. They agreed with Van Arsdel that alternating glacial and interglacial periods were important in formation of the present taxa and distributions. They inferred that several pine-to-pine rusts might have evolved during the Quaternary. VOGLER and BRUNS (1998) used DNA sequences to construct phylogenies of the *Cronartium/Peridermium* complex. They also recommended a systematic re-evaluation of the group to better account for host affinities and life cycles. RICHARDSON et al. (2009) presented preliminary results of a currently active but incomplete survey of the blister rusts of white pines (see RICHARDSON et al. 2010; : Fig. 1).

2.2 Races and relatives

Although the blister rust pathogen of white pines in North America and Europe is now known as '*C. ribicola* J.C. Fisch. in Rabh.', numerous synonyms and other authorities have been used in the literature (HIRATSUKA 1995b). Some of this confusion developed because a collector recognized that a rust on a white pine was a *Peridermium* (i.e., with aecia) but lacked the telial host (an angiosperm) to make the connection to a *Cronartium* species. For

example, COLLEY and TAYLOR (1927) described *P. kurilense* and *P. indicum* from white pine collections now referred to as *C. ribicola*. However, IMAZU and KAKISHIMA (1995) described several Japanese stem rusts on white pines with microcyclic life cycles, whereby spores produced on pine directly infect other white pines (see KIM et al. 2010). Even for macrocyclic pine rusts (alternating between aecial and telial hosts), there are differences in host susceptibility at the genus, species or variety level that some (e.g., YOKOTA 1983) infer as requiring taxonomic or racial recognition. Although the *Cronartium* rusts typically exhibit host specialization that would promote reproductive isolation, they might be capable of genetic exchange across well-accepted species lines. For example, JOLY et al. (2006) described a hybrid between *C. ribicola* and *C. comandrae* Peck from the aecial stage; it is unknown if the hybrid is infective or fertile and how frequent introgression occurs.

2.3 Survival, reproduction, and dispersal

2.3.1 Life history

Although European mycologists (KLEBAHN 1889) first described the life cycle of the white pine blister rust fungus, SPAULDING (1911, 1916) was the first American to present a simplified illustration of *C. ribicola* in several of its life stages (Fig. 1). Orange spores produced on a pine in spring (aeciospores) are blown to and infect an alternate host, *Ribes*; several weeks later, spores of a second stage are produced on a *Ribes* and infect other *Ribes* over the summer (urediniospores). After repeating this stage for several generations (several weeks each), the rust produces brown, hair-like telia from which another set of spores are produced which infect the white pine (basidiospores). A rust on a newly infected pine produces aeciospores several years later. A more complete, technical description of parasitism and morphology was given by COLLEY (1918) and the sexual process by BULLER (1950). VAN ARSDEL et al. (2006) summarized the literature and their observations on the environmental conditions for growth, sporulation, germination, and infection. ONO (2002) reviewed the nuclear behaviour of rusts with an endocyclic life cycle, a form of the microcyclic life history proposed for some rusts of Asian white pines (see KIM et al. 2010; ZHANG et al. 2010).

2.3.2 On pine, aecial host

COLLEY (1918) described the initial spore stage on pine—the spermogonium (formerly pycnium) as having dispersive spermatia and receptive hyphae. The life cycle process at this stage is analogous to pollination in flowering plants, including attractive nectar, and genetic transfer vectored by insects (PIERSON 1933). The function of the spermogonium in fertilization, however, had long remained in doubt. Using molecular markers, HAMELIN et al. (1998) demonstrated genetic uniformity within single, haploid (with one set of chromosomes) infections, long-distance dispersal, and extensive sexual recombination. COLLEY (1918) described development of the aecial stage that arises from dikaryotic hyphae (two nuclei per fungus cell) and releases aeciospores upon rupture of a blister-like peridium. RHOADS (1920) described development of aecia and expansion of the aecia-producing region over a single season and multiple years. Aeciospores are thick-walled and pigmented (KASANEN 1997); they are aerially dispersed and infect leaves of *Ribes* and other susceptible hosts at distances to 1200 km (FRANK et al. 2008).

2.3.3 On *Ribes* and other telial hosts

COLLEY (1918) described the repeating uredinial (formerly uredial) stage that produces dikaryotic urediniospores which asexually intensify and spread the fungus among telial

hosts during a growing season. SPAULDING (1922a) reported some early observations of the development of the telium which bears teliospores (formerly telutospores). These spores germinate in place to produce a basidium in which sexual fusion and reduction leads to formation of haploid basidiospores (formerly sporidia). HANSEN and PATTON (1975, 1977) described basidiospore germination and the growth leading to and including pine infection. Basidiospores are relatively thin-walled, delicate spores which are dispersed to infect nearby white pine (meters to a few kilometres) (ZAMBINO 2010). As infection of *Ribes* is generally limited to the leaves and leaves are typically shed in autumn (except some coastal California sites), the rust only rarely overwinters on *Ribes* (STEWART and RANKIN 1914; HAHN 1939). Year-to-year survival occurs almost exclusively on the pine host. Other telial hosts of *Cronartium* pathogenic on white pines are species of *Pedicularis* and *Castilleja* in the Orobanchaceae (HIRATSUKA and MARUYAMA 1976; PATTON and SPEAR 1989; McDONALD et al. 2006). As these telial hosts are also infected by several *Cronartium* taxa (PETERSON 1973), they might provide a common, susceptible host on which a hybridized rust could develop (see BRASIER 2001; JOLY et al. 2006).

2.3.4 Infection of pine

Because conditions are often limiting for infection of the economically important pine host, much study has been directed at this stage of the life cycle. SPAULDING and RATHBUN-GRAVATT (1926a) recognized that season, weather, and especially moisture were necessary requirements. LACHMUND (1933) described infection through a pine needle, latency, and development in the pine bark. HIRT (1939, 1942) observed that a single exposure of 12–24 h of suitable weather resulted in a few trees being infected and that an entire season of such exposure episodes resulted in a majority of trees becoming infected. VAN ARSDEL et al. (1956) reported similar findings from their extensive and detailed studies in Wisconsin. VAN ARSDEL (1967) described the importance of night-time release of spores and landscape effects on dispersal. Much of current management and research is directed toward producing pines with inherited resistance to blister rust (see KING et al. 2010). But, the principal limit on spread of the rust is host escape owing to various environmental factors and morphological barriers (e.g., HUNT 2005). Site hazard is typically an assessment of the potential for the presence and increase of the rust as limited by environmental rather than genetic factors (see OSTRY et al. 2010; ZEGLEN et al. 2010).

2.4 Heterothallism and outcrossing

Transfer of spermatia from a spermogonium of one thallus (fungal body) to the receptive hyphae of a different thallus provides a means for genetic outcrossing. Although HIRT (1964) interpreted his observations as not supporting obligate heterothallism, HUNT (1985) concluded that *C. ribicola* is heterothallic (supported by GITZENDANNER et al. 1996; HAMELIN 1996). HAMELIN et al. (2005) quantified sexual recombination in two populations and concluded that genetic exchange over distances of hundreds of kilometres might be important for a pathogen subject to population bottlenecks (KINLOCH et al. 1998). Along with variation and selection, outcrossing and genetic exchange are therefore important processes affecting the potential for and rate of evolution by *C. ribicola*.

3 Pathology and ecology

Other than its brief periods of dispersal, *C. ribicola* exists as a parasite in a durable, intimate association within a host (COMBES 1995). Because the parasite pathologically alters host plant physiology and anatomy (pathogenesis) as well as host population demography and genetics, the host–parasite combination constitutes the core of an interactive, coevolving

pathosystem. Additional components are other biotic associates and the physical environment.

3.1 Parasitism and histology

3.1.1 On aecial host

Cronartium ribicola sustains its growth and reproduction by parasitism of pine needles, shoots, inner bark, and outer xylem to a limited extent (HUDGINS et al. 2005). SPAULDING (1925) stated that infection begins with penetration of a stoma (leaf opening for gas exchange) and suggested some differences in susceptibility are related to variation in needle characteristics. Histological and cellular changes to infected needles were described by BOYER and ISAAC (1964). HUNT and JENSEN (2000) concluded, for some populations at least, all needle ages are susceptible. WOO et al. (2001) attributed some mechanisms of disease escape to needle morphology. STRUCKMEYER and RIKER (1951) reported formation of a necrotic bark periderm could limit pathogen development. As infection proceeds, the rust grows through intercellular spaces of the bark (WELCH and MARTIN 1974). Histological reactions by the host include increased cell division, swelling, and development of traumatic resin ducts (HUDGINS et al. 2005).

Cankers (woody stems with localized swellings, resinosis, and dead tissues; see Fig. 3) range from those with aggressive sporulation and little defensive response by the host to those rare cases where the rust is apparently inactive (HUNGERFORD 1977; ECKERT 2007). The rate of canker expansion is quantified by numerous authors and recently by KEARNS et al. (2009). Aecial sporulation exposes the phloem (inner bark) and cambium to desiccation and attracts secondary attack by insects and other fungi (WILLIAMS 1972; KEARNS et al. 2008). Symptoms of girdling cankers include branch flagging and topkill wherein the foliage distal to the canker is dead and the stem has been attacked by bark and twig beetles. Death occurs rapidly in young trees after a lethal canker encircles the main stem. Older, larger trees can survive from years to decades depending on the amount of crown killed by flagging or topkill; cankers in the lower bole are often lethal (SLIPP 1953). A rust infection (living host and the parasitic rust) may itself encounter several different fates. Besides the active resistance of the host that slows or limits fungal growth, the pathogen may fail to reach the main stem before the host branch dies or the fungus is removed by rodents, thereby killing the obligate biotrophic fungus (MIELKE 1935).

3.1.2 On telial host and in culture

Rust spores enter *Ribes* leaves through stomates. Hyphae develop in the intercellular spaces; and rust haustoria penetrate host cells (WOO and MARTIN 1981). PATTON and SPEAR (1989) described similar hyphal growth in *Ribes*, *Castilleja*, and *Pedicularis* up to development of haustorial mother cells; however, they found haustoria only in the *Ribes*. Axenic culture of an obligate rust is difficult to obtain, but it provides a useful tool for examining the genetic structure and sexual behaviour of the rust (KINLOCH and DUPPER 1996).

3.2 Genetics

Because planting white pines was a profitable cultural practice and host response to blister rust appeared to be inherited, several resistance screening, and tree breeding programmes have been established. These programmes and associated research have contributed to the understanding of the genetics of the host, the pathogen, and their coevolution. Use of molecular techniques has also accelerated our knowledge of the pathosystem. Here, we



Fig. 3. Interactions of *Cronartium ribicola* with *Pinus lambertiana* trees about 10-years old. (a) Discoloration of the bark, early symptom of infection. (b) Typical, blister rust canker of susceptible host with a rough-barked, fusiform branch through which the infection originated and a diamond pattern of aecia (blisters). (c) Canker on a resistant host displaying a bark-reaction trait and healing at the margins. (Photo by D. Burton at Happy Camp, CA, USA).

provide a general introduction to the genetic biology of *C. ribicola* and its hosts. KING et al. (2010) review these topics in greater detail and relate their implications for breeding white pines better able to escape, tolerate, or resist rust infection. RICHARDSON et al. (2010) elaborate upon molecular genetic techniques and describe their use for investigating evolutionary trends in the pathosystem.

3.2.1 Pathogen virulence and host resistance

Although the existence of genetic variation in resistance was initially doubted (e.g., HAHN 1949), BINGHAM et al. (1971) proposed that resistance genes were widely dispersed within host populations and operated by various mechanisms. Putative genetic resistance (survival mechanisms of unknown inheritance) is described in seedlings (HOFF et al. 1980) and ontogenic resistance (age-related) in mature pines (PATTON 1961; KINLOCH and BYLER 1981). From resistance studies, WOO et al. (2004) demonstrated that gene-by-environment interactions are important to infection success. General host responses that appear to be controlled by multiple genes are described variously as non-race specific, horizontal, quantitative, partial resistance, or slow rusting, referring to modes of inheritance or

expression. KINLOCH et al. (1970) reported a simply-inherited resistance of major effect (no rust development beyond a short, initial stage in needles only) that confers immunity except to specific virulent races [‘race-specific, vertical, qualitative, total resistance, or major gene resistance (MGR)’]. KINLOCH et al. (1999) characterized the Champion Mine strain of *C. ribicola* as specifically virulent to western white pines that are typically resistant to other races of the rust. KINLOCH and DUPPER (1999) identified a resistance gene which permits the host to react to needle infection with hypersensitive necrosis (sacrificing some tissue, killing the parasite). A specific resistance gene is referred to as an R gene; for host resistance to *Cronartium*, an R gene is referred to as a *Cr* gene. Virulent pathogens have a complementary gene to the R gene that defeats the mechanism of host resistance (FLOR 1971; section ‘Gene mapping and proteomics’). A host with an active-resistance genotype carries resistance genes and expresses an interaction phenotype (resistance trait) in response to an encounter with a pathogen—inoculation, infection, detection, and reaction—(COMBES 1995).

Numerous trials in North America, Europe, and Asia reveal that white pines vary by species, age, and population in their response to artificial inoculation. Common measures of host response are disease incidence (percent of plants that develop disease symptoms), disease severity (amount of disease on a plant), and rate of disease development (often measured as host longevity after inoculation). Studies by DELATOUR and BIROT (1982) and STEPHAN (1986) support hypotheses of geographic variation in virulence and resistance. The ability of a rust to infect, cause disease, and reproduce on a potential host (parasitism) varies genetically and geographically.

3.2.2 Population genetics

Cronartium ribicola was subjected to genetic restrictions by population bottlenecks in its introductions from Asia to Europe and then to North America (KINLOCH 1998). In addition, outcrossing appears to be extensive, and rust populations display genetic differences at various spatial scales. Among the hosts, at least western white pine and sugar pine display geographic variation in resistance (KINLOCH 1992; KINLOCH et al. 2003; and see THOMPSON 2005 on ‘Red Queen dynamics’). A study by KINLOCH et al. (1998) on the population structure of the rust found genetic diversity was not related to geographic distance but might have resulted from genetic drift that typically occurs in small, isolated populations (i.e., with limited outcrossing). Additional observations (KINLOCH et al. 1999, 2004) suggested that selection for virulence could be locally intense but spread of virulence be very limited. ET-TOUIL et al. (1999) concluded that long-distance spore dispersal, new colonization, and genetic drift are important evolutionary processes within the eastern Canadian epidemic. HAMELIN et al. (2000) reported that rust populations from eastern and western North America formed two distinct clusters. RICHARDSON et al. (2007), however, found rust isolates from either the eastern or western populations shared a capability to infect a western endemic species of *Pedicularis*. RICHARDSON et al. (2008) also showed the western rust population is not genetically uniform and selection for R-gene resistance could affect genetic diversity. Geographic variations of *C. ribicola* in virulence and aggressiveness have important implications for disease control.

3.2.3 Gene mapping and proteomics

An R gene codes for synthesis of a protein that recognizes the presence of a pathogen and leads to a cascade of resistance responses (EKRAMODDOULLAH and HUNT 1993). In sugar pine, the R gene associated with a hypersensitive reaction (HR) response has been mapped by proximity to six markers (DEVEY et al. 1995; also see JERMSTAD et al. 2006), thereby providing a beginning point for gene cloning. Early synthesis of a protein normally

associated with cold-hardiness is known to be induced (up-regulated) by western white pine infected with *C. ribicola* (EKRAMODDOULLAH et al. 1998). Although most of the progress in plant disease resistance at the molecular level has been made in other pathosystems, LIU et al. (2004) used white pine blister rust to describe a molecular model of resistance. They modelled resistance as a process of recognition by the plant of a signal from the pathogen, followed by a cascading transcription of factor genes inducing production of pathogenesis-related, anti-pathogen proteins. Virulent pathogens do not produce the avirulence factor (*avr*) that triggers the resistance response. If the *avr* factor were critical for pathogen metabolism, then virulence could reduce the pathogen's genetic fitness (competitive ability to reproduce) or aggressiveness (capability in producing spores). Host proteins involved in pathogen recognition and response resemble those used protection from cold injury; specific disease resistance could be an appropriation of a general defence mechanism (and see GOULD 2002 : 662 for discussion of exaptation).

3.3 Biotic associates

Although the white pine blister rust pathosystem principally comprises a pathogen, an aecial host, and a telial host, many other organisms are directly involved in spermatial transfer, spore dispersal, predation upon the rust or rust-infected tissue, activating host defences, or performing other symbiotic functions. The purple mould, *Tuberculina maxima* Rostr., is an antagonistic fungus occasionally found on blister rust cankers. Although *T. maxima* was studied in depth by Carl von Tubeuf (MALOY and LANG 2003) as a potential biological control agent, WICKER (1981) eventually determined that it is a competitor of *C. ribicola* for host nutrients, not a rust pathogen. Recently, GANLEY et al. (2008) suggested that fungal endophytes (external symbionts) on white pine needles could mediate or activate host resistance.

3.4 Plant disease epidemiology

The proportion of diseased plants (incidence) or plant parts (severity) can be described and related to time (disease progression) or to biotic and abiotic environmental factors (hazard). For early blister rust epidemics in North America, MERRILL (1991) determined that incidence increased logistically at different rates in different environments. He characterized the areas with the least incidence as low hazard and those with an average three-fold greater rate of increase in incidence as high hazard. VAN ARSDEL et al. (1961) related patterns of disease distribution within trees and stands to landscape features associated with climate (e.g., a lake-effect) and to host population characteristics (e.g., paucity of *Ribes* on some soils). Using these relations, they mapped hazard across the Great Lakes area at a regional scale. Later, CHARLTON (1963), GROSS (1985), LAVALLÉE (1986a,b), and KEARNS (2005) developed climate-based hazard maps for the northeastern states, Ontario, Quebec, and Colorado, respectively.

MCDONALD et al. (1981) constructed a computer program to model blister rust epidemics in stands of western white pine. Their model simulated canker numbers and disease effects on pine growth and survival from various life history studies and a site-level index of disease (based on cankers developed per unit of host exposed). At an interregional scale, FRANK et al. (2008) modelled the likelihood of *C. ribicola* spread from the California Sierra Nevada to the Great Basin, southern Rocky Mountains, and Southwest. Their analysis of synoptic-level patterns of air flow and simple assumptions of environmental conditions for infection accounted for the recent epidemics in these western regions. Epidemiological models (see MADDEN 2006; SCHERM et al. 2006), along with local knowledge, are important tools for assessing silvicultural options at specific locations, including deploying or promoting inherited resistance. The dynamics of evolutionary and

ecological changes in a plant disease epidemic is complex; but it can be described in terms of incidence, severity, damage (mortality and reduced fitness), and impact (resource and biotic community consequences).

4 Historical biogeography

The histories of white pine blister rust migrations, impacts, and controls differ among the different major epidemics of Asia, Europe, eastern North America, and western North America. ZHANG et al. (2010) review blister rust and white pines in China. KIM et al. (2010) synthesize blister rust history and status in eastern Asia and discuss the international implications of genetically diverse and mobile pathogens. Here, we review the history of blister rust in Europe from early discoveries to the present. OSTRY et al. (2010) provide, along with information on the silviculture of eastern white pine, their perspective on the current threat of *C. ribicola* in eastern North America. We add historical information for New England and mid-Atlantic States, Lake States, southern Appalachia, and eastern Canada. Values, threats, and management of the white pine species of western North America are discussed by TOMBACK and ACHUFF (2010), SCHWANDT et al. (2010), and ZEGLEN et al. (2010). We supplement these with a brief history of the introduction, establishment, and initial spread in the western states and provinces as a context for our following introductory reviews on control and management.

4.1 Europe

Although there are three native white pines in Europe, the recorded history of white pine blister in Europe begins a few hundred years after the initial introduction of *P. strobus* from North America (RADU 2008; HUNT 2009). Two species are the slow-growing, high-elevation stone pines *Pinus sibirica* Du Tour of the Urals on the eastern border of Europe (the western Russia Empire of the 19th century is included here as part of Europe) and *P. cembra* L. of the Alps (see KLUMPP 2008). The third species is *P. peuce* Griseb., found in the Balkans and southeastern Europe and closely related to *P. strobus*. Eastern white pine was first recognized as valuable for the large masts essential to naval power as a result of George Weymouth's 1605 voyage along the northeastern American coast (see ALBION 1926; WINSHIP 1905). The colonies of New England and Canada supplied England with valuable timber and naval stores for many years, but not without political friction (CARROLL 1973; LOWER 1973). In the early 1700s, eastern white pine was successfully established in Britain on the Weymouth estate (SPALDING 1899). Soon, the pine was planted widely across central Europe as Weymouth or Strobe pine. Now, it is found occasionally in gardens and as a naturalized escape (ESSL 2007).

GÄUMANN (1945, 1950) described *C. ribicola* as having two populations in Europe—a rare native and an invasive exotic. The earliest report (seen by the authors) of a *Cronartium* rust in Europe is by UNGER (1836) who listed an 1830 collection from the Austrian Alps on *Ribes alpinum* L. (now at the Herbarium of the Karl-Franzens Universität, Graz, Austria). LEPPIK (1970) suggested the genetic origin of rust would be found where host populations have developed a high degree of resistance after long association with the pathogen. *Pinus cembra* populations are ranked as very resistant by HOFF et al. (1980); and in the Alps, it is rarely found to be infected and then displaying a tolerant interaction (both host and pathogen reproducing) (T. Kirisits and O. Holdenrieder, personal communication). According to GÄUMANN (1945, 1950), the extensive planting of susceptible Weymouth pines in climates favourable for rust infection provided the pathway for introduction of an Asian blister rust fungus on *P. sibirica* into northern and central Europe. Other early discoveries include a collection on *Ribes* from Crimea that may be a native European rust (LÉVEILLÉ 1846) and an 1854 observation by DIETRICH (1856) of a rust in Estonia that may

have migrated from western Siberia (see LEPIK 1934). By 1904, *C. ribicola* was well established in central Europe.

DUFRENOY (1922) attributed a 1904 Swiss infestation of blister rust to introduction of an invasive rust from the north; his description of older Swiss infestations as ‘different’ suggested these had been caused by a native rust (see FISCHER 1915). Because there is a geographic and altitudinal separation of the pine host populations and lack of bridging *Ribes* populations, it would be possible for two, different biotypes of *C. ribicola* to coexist in the Alps. *P. cembra* occurs in natural, high-elevation stands; *P. strobus* is not found in the Alps except at low-elevation sites where it is only rarely grown (such as the healthy, garden trees of Ticino, southern Alps; T. Kirisits and O. Holdenrieder, personal communication). Although European forest pathologists may have accepted GÄUMANN (1945, 1950) conjecture for the existence of a native *C. ribicola*, this idea has been considered unsubstantiated by many North American forest pathologists. Whether there are alpine and lowland biotypes or native and invasive rusts would require additional study. RICHARDSON et al. (2010); and see their Fig. 1) identify molecular diagnostic techniques now being used to better understand blister rust phylogeny and biogeography. KIM et al. (2010) discuss the relevance to North America of Eurasian blister rust fungi.

Because of the severity of blister rust in several plantations of Weymouth pine and western white pine, SOMERVILLE (1909) warned of the threat to North America and described white pine culture in England as a failure. Raphael Zon, who was educated in Europe and became the first Chief of Silvics for the U.S. Forest Service, described (in PETTIS 1909) blister rust as being widespread in northern Europe (especially Germany) which was then shipping seedlings to America. In Europe, continued silviculture of white pines was debated for decades (see MÜLDER 1960; PAWSEY 1963; SPAULDING 1926, 1929), but numerous international efforts have been made in resistance genetics and tree breeding (e.g., BINGHAM and GREMMEN 1971; BLADA and POPESCU 2004).

Plantings of Weymouth pine in northern and central Europe are now uncommon outside of gardens and resistance trials (SCHMITT 1972; KIRISITS 2007). Endemic white pines persist in the Alps, Balkans, and Carpathians of southern Europe (BLADA 1990; RADU 2008). Although *C. ribicola* still threatens white pines in regions favourable for infestation, RADU (2008) argued that disease control can be successful with silvicultural management and genetic improvement.

4.2 Eastern North America

4.2.1 United States, New England, and mid-Atlantic States

The importation of *C. ribicola* was first widely recognized as a result of STEWART's (1906) discovery of infection on currant at Geneva, New York. STEWART and RANKIN (1914) recounted the history of this infestation. POSEY and FORD (1924) reported an earlier epidemic they dated to 1897 and attributed to black currant imported from England. In the early 1900s, numerous shipments of white pine seedlings were imported into the United States from Germany, France, and Holland; many of these seedlings, although infected, were planted across the region (PETTIS 1909; HIRT 1956). Although there was some initial concern over importation of infected currants and gooseberries, cryptically infected eastern white pines—not leafless *Ribes* cuttings were the principal pathway of disease introduction into North America.

Cronartium ribicola severely affected white pine stands for the first half century after introduction and remains a damaging pathogen within some portions of the eastern white pine distribution. At Kelm Mountain, New York, SNELL (1931) reported 96% mortality. At Waterford, Vermont, RUSDEN (1952) quantified harvest losses at about three-fourths of

potential crop trees and volume. By 1986, blister rust interacting with economic and social interests had reduced eastern white pine to commercial insignificance (MARTY 1986). But, effective programmes for *Ribes* eradication had reduced blister rust incidence (OSTROFSKY et al. 1988). Although blister rust may preclude growing susceptible white pine on certain high-hazard sites, blister rust is no longer a constraint on white pine forestry using good silviculture (LOMBARD and BOFINGER 1999; BERGDAHL and TEILLON 2000; OSTRY et al. 2010).

4.2.2 United States, Lake States

Cronartium ribicola was introduced to Wisconsin and Minnesota from infected European stock in 1916 (SAMPSON 1918). Several years later, Michigan was infested. The several infestations in the Great Lakes region expanded to include most of the white pine distribution—but with notable variations in severity. VAN ARSDEL et al. (1961) observed a near absence of disease in southern Wisconsin, even where *Ribes* and pines were abundant as close neighbours. They related disease distribution to the environment at several climatic scales, including a site or micro-scale and a landscape or meso-scale. Areas of greatest severity were characterized as high-hazard zones.

As in the northeastern states, white pine populations were reduced by disease, harvest, and site conversion; likewise, *Ribes* populations were reduced by eradication. Recent surveys by DAHIR and CUMMINGS (2001) and ROBBINS et al. (1988) in the climatically high-hazard zone of northern Wisconsin and Michigan's Upper Peninsula found blister rust to be uncommon at the time of their surveys. Besides climate, factors such as host distribution, abundance, and genetics are also important in determining rust incidence and severity. As elsewhere in eastern North America, blister rust remains a potential contributor to pine mortality; but it is no longer the dominant disturbance agent controlling forest composition and growth in the Great Lakes region.

4.2.3 United States, southern Appalachia

Eastern white pine and *Ribes* occur as scattered populations along the length of the Appalachian chain. By 1941, blister rust had made a series of southward jumps to North Carolina (PIERCE 1942). In this region, the coincidence of pine, *Ribes*, and favourable weather for infection are less common than farther north. CORDELL (1968) reported the absence of *Ribes* and low incidence of blister rust on a series of plots in Virginia. Over time, the effects of blister rust can eliminate white pine saplings and decimate larger trees at some sites (POWERS and STEGALL 1971); but the distribution of blister rust in southern Appalachia is limited and predictable (ANDERSON et al. 1980).

4.2.4 Eastern Canada

GÜSSOW (1916) gave an early warning of the threat posed by the imported *C. ribicola* to eastern white pine. MCCALLUM (1923) reported that the Canadian epidemic extended from the Maritimes, through Quebec, to Ontario; ZALASKY (1959) added Manitoba. By 1938, DICKSON (1943) described blister rust as distributed across Ontario with a modest incidence of 10–20% near settlements and low incidence of 1–2% on Crown Lands. He attributed the greater rust incidence to the proximity of cultivated black currant and more favourable climate infection. Even without a serious effort to eradicate *Ribes*, Ontario had a lower abundance of *Ribes*; and thus, it experienced less severe infestation and lower mortality rate than regions to the south and east (HADDOW 1956, 1969). POMERLEAU and BARD (1969) acknowledged that losses were greater in Quebec, but they also noted that impact was minimal where *Ribes* had been controlled. PLOURDE et al. (1991) suggested

that, with good management (including hazard assessment and tree breeding), blister rust need not be an impediment to white pine reforestation.

4.3 Western North America

The blister rust epidemic in western North America contrasted strongly with that in eastern North America owing to several fundamental differences. In the East, there were many introductions over many years and locations; whereas in the West, there were few introductions of limited duration and area (Metcalf 1923; HUNT 2009). Furthermore, in the West, a greater diversity of white pine and *Ribes* species were widely distributed across environments ranging from temperate rainforests to arid woodlands. Another complication in the West was the occurrence of the native pinyon blister rust (HEDGCOCK et al. 1918), *Cronartium occidentale* Hedgcock, Bethel & Hunt. Because *C. occidentale* alternated to *Ribes* and was nearly indistinguishable from *C. ribicola*, the two rusts were easily misidentified (VAN ARSDEL and GEILS 2004) and incorrectly assumed to be very closely related (see VOGLER and BRUNS 1998).

The biogeography of the western North American epidemic was characterized by introduction and rapid spread through very favourable maritime and montane environments (MIELKE 1943 but see HUNT 2009). Over many decades, blister rust continued spreading to and within continental and alpine environments to the east and south (BROWN 1970; GEILS et al. 2003). SCHWANDT et al. (2010); their Fig. 1) describe the current distribution of white pine blister rust in this region.

4.3.1 Western Canada

The initial discoveries of *C. ribicola* in western North America clearly date to 1921 with several collections from British Columbia—Vancouver Island, North Vancouver, and the Fraser Valley (GÜSSOW 1922). The date of the first introduction and whether there was only a single western introduction, however, are unknown. MIELKE (1943) presented the simple and often repeated story of a sole importation in 1910 from France that spread throughout the entire West. HUNT (2009) argued for a more complex history, one with multiple, cryptic introductions in the decades around 1910 to several locations in British Columbia and the Pacific Northwest (see section ‘Pacific Northwest’). MCCALLUM (1923) described a sudden appearance of blister rust throughout the coastal regions. The rapidly developing severity of the infestation was illustrated by LACHMUND (1934b) who attributed mortality rates of 66–90% at Garibaldi, British Columbia to the innumerable dead branches caused by *C. ribicola* and other damaging agents. Although the primary hosts were western white pines on coastal sites, only several decades later, nearly all the whitebark pine and limber pine trees on some subalpine sites in Alberta (~1000 km east of Vancouver) were infected (THOMAS et al. 1960). SMITH (1971) summarized blister rust distribution in the Canadian Rocky Mountains; ZEGLEN (2002) reported a survey for whitebark pine in British Columbia. Blister rust is widespread, common, and a serious management concern in British Columbia and Alberta.

4.3.2 Pacific Northwest

Although scouting for *C. ribicola* in the Puget Sound region began in 1917, the first Washington discoveries on black currant and western white pine date to 1921 (DETWILER 1922). In the following two years, scouts collected infected *Ribes* from 11 counties in northwestern Washington (herbarium records for Bureau of Plant Industry). By 1942, blister rust had been detected throughout Washington and Oregon—including white pines estimated to have been infected in 1913 and 1917 (Northwest Region 1948: map).

PENNINGTON (1925) attributed this sudden appearance to aerial dispersal of aeciospores over hundreds of kilometres during several years especially favourable for blister rust spread (wave years). MIELKE (1943) extended and elaborated upon Pennington's description under the assumption there had been only a single introduction in 1910 near Vancouver, British Columbia. Metcalf (1923) acknowledged, however, that both *Ribes* and white pines had been repeatedly imported to the region before quarantines were enacted and speculated that some had been diseased. HUNT (2009) computed that if there were a single introduction, the western North American epidemic would have spread (sometimes against prevailing winds) at a rate 1.4 times faster than spread of the European epidemic. He concluded that Mielke's assumption of one introduction at Point Grey, British Columbia in 1910 is not supportable.

CHILDS et al. (1938) documented the early appearance of blister rust on whitebark pine. By 1926, populations of whitebark pine in the Pacific coastal mountains were infested; in 1936, blister rust was discovered on Mt. Hood, in the inland Oregon Cascades. WARD et al. (2006) reviewed the history of whitebark pine and blister rust in the Pacific Northwest. SHOAL and AUBRY (2006) assessed the current epidemic status and described incidence as less in the rain-shadow forests of east-side Cascades, southern Oregon than wet, rainforests in northwestern Washington.

4.3.3 Northern Rockies and Yellowstone

Cronartium ribicola was present at numerous sites in northern Idaho by 1923 and in Montana by 1928 (PUTNAM 1931). The few cankers initially observed at these sites increased to tens of thousands within several years. After a few decades, blister rust had spread across Montana to the greater Yellowstone area, including the Teton and other ranges of western Wyoming and southeast Idaho (BROWN 1970). Because northwestern portions of this region receive maritime weather favourable for reproduction of the rust, wave years were frequent; but, because eastern and southern locations are more continental, wave years there were less common. The principal aecial hosts were whitebark pine and limber pine. These species occur in a variety of habitats and locations, including the cold and dry Yellowstone plateau which HENDRICKSON (1970) described as low hazard. NEWCOMB (2003) reported that the blister rust severity for whitebark pine in the greater Yellowstone area ranged from very high to very low and was related to tree size and proximity of potential inoculum sources.

TOMBACK et al. (1995) reported severe mortality and reproductive failure of whitebark pine in northwestern Montana resulted from a combination of fire, competition, bark beetles, and blister rust. JACKSON and LOCKMAN (2003) updated and confirmed a previous study for limber pine in central Montana. In that study area, a foliar pathogen [*Dothistroma septospora* (Doroguine) Morelet] was the principal mortality agent; blister rust was a minor contributor. Although nearly half the limber pines were infested with blister rust, the multi-stem form of limber pine provided a form of tolerance whereby damage was limited to branch flagging and non-lethal topkill. Across the whole region, the blister rust epidemic has displayed a notable geographic trend from northern Idaho to central Wyoming whereby arrival occurred later, wave years were less frequent, and infected trees survived longer (BROWN 1978a,b; SMITH and HOFFMAN 2000).

4.3.4 Pacific Southwest

By 1929, *C. ribicola* was established in sugar pine in northwestern California (WAGENER and MIELKE 1936). MIELKE (1938) reported a blister rust infestation on *Ribes* in 1937 that extended more than 160 km south of the Oregon border in both the Coastal Range and Sierra Nevada. In the favourable environment of northern California, blister rust severity

was sufficient to cause sugar pine mortality from the damage of numerous branch cankers rather than a single lethal stem canker. MILLER (1968) discovered the rust had also advanced into the high-elevation, northern population of foxtail pine (*Pinus balfouriana* Grev. & Balf.). By 1960, blister rust had spread to the central Sierra Nevada; but its distribution there was restricted to favourable canyon sites (QUICK 1962a,b).

BYLER and PARMETER (1979) made several observations and conclusions on blister rust incidence and damage in California. Although more than 50% of the white pines on some examined sites were infected and most of these were expected to die, the mean incidence for all the examined sites was only 20% and most trees on the least affected sites were expected to survive. SMITH (1996) summarized blister rust epidemiology in California. *C. ribicola* spread by a series of long-distance dispersal events during infrequent wave years. Although the climate limited the number of sites infested and the subsequent rate of intensification, it did not preclude blister rust spread throughout the Sierra Nevada. DURISCOE and DURISCOE (2002) and KLIEJUNAS (2002) reported the current status of blister rust in the southern Sierra Nevada; KLIEJUNAS and DUNLAP (2007) described the present distribution of blister rust in high-elevation populations of California white pines. Although blister rust is distributed throughout the region, it is still not known to occur south of the southern Sierra Nevada. Within an infested landscape, incidence varies from site to site and ranges from moderate to absent.

4.3.5 Southern Rocky Mountains, Southwest, and Great Basin

The history of *C. ribicola* over most of the interior western states is a story of the discovery of new infestations in disjunct populations of various taxa of white pines and subsequent local spread and intensification. As with the other American regions, much of the history was first recorded in the annual reports of the Office of Blister Rust Control (BRC) and later by the Northern and Rocky Mountain Regions of the Forest Service. BROWN (1978b) summarized the distribution of limber pine blister rust in Wyoming (exclusive of Yellowstone); he reported that northern forests had been generally infested since or before 1935 but that the Laramie Peak area in east central Wyoming was not infested until 1950. LUNDQUIST et al. (1992) discovered blister rust in the small and isolated population of limber pine in the Black Hills, South Dakota.

A renewed search for blister rust in the interior West was inspired by HAWKSWORTH's 1990 discovery of a well-established epidemic in southwestern white pine (*Pinus flexilis* James var. *reflexa* Engelm. syn. *P. strobiformis* Engelm.) in the Sacramento Mountains of south central New Mexico (HAWKSWORTH 1990; VAN ARSDEL et al. 1998). FRANK et al. (2008) demonstrated how this and other infestations in the Southwest and adjacent regions could have resulted from long-distance (>100 s of km), aerial dispersal of aeciospores from the Pacific Southwest. CONKLIN (2004) described blister rust intensification in the Sacramento Mountains epidemic.

Although blister rust had been known for several decades across the Wyoming border, it was not found in northern Colorado until 1998 (JOHNSON and JACOBI 2000). BLODGETT and SULLIVAN (2004) reported an infestation in southern Colorado (Sangre de Cristo Range and Wet Mountains) on limber pine and Rocky Mountain bristlecone pine (*P. aristata* Engelm.). SMITH and HOFFMAN (2000) and KEARNS and JACOBI (2007) recently summarized the blister rust distribution in portions of the interior western states. VOGLER and CHARLET (2004) described a local infestation in northern Nevada on the edge of the Great Basin. Within this whole region, infestations varied from widespread in the Sacramento Mountains to highly localized as in the Sangre de Cristo Range. By late 2009, the only white pine species not known by us to be naturally infected was *Pinus longaeva* D.K. Bailey; and the only western state not known to be infested was Utah.

4.4 Mexico

White pines, *Ribes* and several *Cronartium* rusts are broadly distributed across the diverse forests of Mexico (PERRY 1991; CIBRIAN TOVAR et al. 2007). Specimens of over 30 taxa of *Ribes* are deposited at the Missouri Botanical Garden; distribution maps indicate *Ribes* occur in almost all of the forested Mexican states (<http://www.tropicos.org>, examined September 2009). PERRY (1991) lists five species of white pine in Mexico—*P. ayacahuite* Ehrenb. ex Schldl. (Mexican white pine, with several varieties), *P. chiapensis* (Martínez) Andresen (rare species, southern Mexico and Guatemala), *P. lambertiana* (restricted to small area in Baja), *P. flexilis* (limber pine, in Mexico rare or misidentified), and *P. strobiformis* (southwestern white pine, widespread in Sierra Madre). Although recent works by GERNANDT et al. (2005) and by SYRING et al. (2007) have advanced our phylogenetic understanding of the white pines, the systematics and consequently specific distributions of white pines in Mexico remain unclear. Especially important is the relationship among the very similar and blister-rust-susceptible taxa of the *P. flexilis*-complex (limber pine, southwestern white pine, and Mexican white pine). Additional unknowns are the likelihood of *C. ribicola* establishing in Mexico and the rust hazard in 'cloud forests' of high-montane regions. White pines in the Mexican Sierra Madre are separated from the epidemic in southern New Mexico by only 400 km (SCHWANDT et al. 2010; : Fig. 1). Some Mexican populations are as close to the southern Sierra Nevada epidemic (an inferred inoculum source) as are the infested sites recently discovered in Arizona. We know of no confirmed reports for *C. ribicola* in Mexico.

5 From disease control to silviculture and genetics

Because several species of North American white pines had great economic value, foresters quickly mobilized to control *C. ribicola* by quarantine, eradication, silviculture, and genetic resistance (BENEDICT 1981; MALOY 1997; HUNT 2009). Silviculture and genetics remain important tools in managing white pines (KING et al. 2010; OSTRY et al. 2010; ZEGLEN et al. 2010). Molecular tools help characterize hosts and pathogens for their phylogeny, systematics, and biochemistry (RICHARDSON et al. 2010). The articles by TOMBACK and ACHUFF (2010) and by SCHWANDT et al. (2010) present the status, current management, and future prospects for white pines in western North America; their reviews include discussions of protection, conservation, and restoration. Here, we briefly review the history of blister rust management and research to identify significant changes in perspective and practice over the past 100 years.

5.1 Prevention and quarantine

In the early 1900s, enthusiasm for reforestation of white pine in eastern North America created an unwary demand for inexpensive seedlings grown in Europe. Although some pathologists and foresters such as Raphael Zon may have known *C. ribicola* was devastating Weymouth pine across Europe, there initially was little effort to prevent introduction and establishment of white pine blister rust (SPAULDING 1909). This rapidly changed after STEWART's 1906 discovery with nursery inspections, destruction of infected plants, formation of action committees, public education, and the first American plant disease quarantines (SPAULDING and PIERCE 1917). These quarantines were meant to prevent further importation of infected stock from Europe into eastern North America and to prevent either European or eastern North American importations into western North America. Unknown at the time, however, the quarantine was already breached by infected pine seedlings. Although early detection surveys and pre-infestation measures such as *Ribes* eradication were undertaken, establishment of new epidemics was not prevented

(BENEDICT and HARRIS 1931). Some states retain restrictions on the cultivation of *Ribes* (McKAY 2000). Regulatory and research functions remain to be important national responsibilities in protecting forests from invasive species (ALLEN and HUMBLE 2002; HAIN 2006).

5.2 Disease control

After early detection and elimination of infected plants had failed to prevent establishment of *C. ribicola* (SPAULDING 1922b), disease control was directed at eradication of *Ribes* by mechanical and chemical means. The objective was to protect commercial white pines from infection by inoculum produced within or near to a plantation or stand. Therapeutic and preventative sanitation included canker treatments with biocides, biological control agents, branch pruning, and bole scribing to reduce blister rust severity and infection rate.

5.2.1 *Ribes* eradication

In 1917, the U.S. Department of Agriculture (USDA) began a general programme of blister rust control in the northeastern states to eradicate cultivated black currants and wild *Ribes* (FILLER 1924). This programme included state and community partnership, communication and education, and detailed reporting of accomplishment in terms of plants removed, acres treated, and costs. Much of the field work was accomplished with labour from the Civilian Conservation Corps under direction of the Office BRC. This programme was extended to other regions, re-organized, and eventually transferred to the USDA Forest Service. Today, Forest Health Protection supports managers with technical expertise; Forest Research and Development is responsible for providing basic and applied science. Much of the BRC information was presented in annual meetings and reported in unpublished government documents. *Ribes* eradication (or simply eradication) was intended to protect designated white pines from infection by removing *Ribes* bushes to specific standards of distance and efficiency with one or more entries ('local control'). Occasionally, eradication was begun even before an area became infested in order to estimate future operational costs and to reduce disease potential (BENEDICT and HARRIS 1931).

Many of the early control programmes were organized at a state or province level and included operations research and economic assessment. MANDENBERG (1937) reported on the history of control in Michigan. DICKSON (1943) contrasted control efforts in Canada as poorly coordinated among licensees and governmental authorities. He recommended a plan that was typical of approaches used by various agencies—survey a region, map control zones, eliminate cultivated black currants, organize and train crews, and track the progress of eradication. Initial research was mostly directed by managers for the primary purpose of developing practical tools for improving eradication efficiency and secondarily for understanding fundamental ecological and genetic processes (see MOORE 1916). MARTIN (1944) judged the American programme for protecting white pines by eradication as successful. VAUX (1948) reviewed the California programme in detail, including its economics and higher post-war labour costs. Eradication for BRC was deemed cost-effective by MATTHEWS and HUTCHISON (1948) and by GUTHRIE et al. (1949). ZAMBINO (2010) examines the biological rationale behind *Ribes* eradication; HUMMER and DALE (2010) review development of *Ribes* cultivars resistant to blister rust.

After the eradication programme came under Forest Service direction in 1959, management interests shifted and eradication programmes were terminated. Fire suppression had been an important secondary activity for BRC crews; but dedicated fire crews assumed this duty under Forest Service control. Outside of the Inland Northwest where

western white pine was 'king' (TOMBACK and ACHUFF 2010) and *Ribes* were very abundant (ZAMBINO 2010), populations of white pines and *Ribes* were relatively small and dispersed; so, by comparison, eradication was less cost-effective. Other tree species and their associated insects and diseases had taken on increased importance (HEPTING and JEMISON 1958). KETCHAM et al. (1968) discontinued eradication in Idaho and Montana in favour of managing for other tree species. HENDRICKSON (1970) cited a low incidence of rust in Yellowstone as a rationale for dropping the eradication programme there (see KENDALL and ASEBROOK 1998). MACGREGOR (1969) announced the cessation of eradication in California. A state-supported programme, however, remained in Maine where BRADBURY (1989) concluded that targeted eradication to protect young eastern white pine plantations still returned positive economic value.

5.2.2 Chemical biocides

Moss et al. (1960) announced that a cycloheximide formulation (Actidione BR) and similar biocides (then called 'antibiotics') killed the blister rust pathogen without seriously damaging the white pine host. Applications were tested as a therapeutic by direct basal spray or aerial canopy spray and as a protective seedling dip. Although results of numerous trials and toxicity studies were well publicized (as were many bulletins on application methods) statistics on the area and costs of treatment were mostly limited to unpublished reports. VICHE et al. (1962), however, did publish on an operational spray project in northern Idaho, wherein 6500 ha were treated with biocide at a cost of \$4.00/ha. Although such treatment costs were considered acceptable, results in eliminating infections without tree damage were unreliable from such trials and operational projects (BENEDICT 1966). When numerous research studies with rigorous methods and long-term observations determined that initial conclusions were probably confounded by several natural processes and that biocides were actually ineffective, their use and further development was suspended (DIMOND 1966; LEAPHART and WICKER 1968).

5.2.3 Biological control

The concept of plant disease control with an antagonistic, biological agent was developed a century ago by Carl von Tubeuf in the *C. ribicola*-*T. maxima* system (VON TUBEUF 1930). Although much research was conducted on *T. maxima*, WICKER (1981) concluded its mode of action was to destroy the rust's food base. *T. maxima* might prolong host survival, but it did not eliminate the pathogen. BYLER et al. (1972) demonstrated that several opportunistic, secondary organisms can invade cankers and cause a die-back reducing inoculum production. BÉRUBÉ et al. (1998) and GANLEY et al. (2008) suggested using fungal endophytes to inhibit blister rust infection. Like biocides, biological agents (including fungi, arthropods, slugs, and rodents) have not yet provided an operational tool for blister rust control in North America.

5.2.4 Pruning

Pruning white pine to increase the volume of clear wood was already an established management practice when STILLINGER (1947) reported on pruning for sanitation. As most lethal cankers occur low in the crown, pruning had the additional benefit of prolonging tree survival. The relevant economic, silvicultural, and disease control questions have been addressed in long-term studies of various species and regions (HUNT 1998; LAFLAMME et al. 1998; SCHWANDT and MARSDEN 2002). Where justified by economic or ecological objectives and often combined with other silvicultural treatments, pruning remains a useful disease control technique (ZEGLEN et al. 2010).

5.3 Forest and stand management

HUBERT (1928) recognized the critical management and disease control issues in the diverse and recently infested forests of northern Idaho were: (1) choice of tree species to retain in thinning and regeneration; (2) natural succession of species; and (3) amount of *Ribes* regeneration. DETWILER (1933) used economic and ecological arguments to justify the value of continued investment in white pine forestry and BRC. DAVIS and MOSS (1940) advocated thinning and harvest practices on Idaho white pine sites that minimized *Ribes* regeneration by shading; they admonished foresters to assess disease control in terms of timber production rather than *Ribes* abundance. Several years later, WELLNER (1946) described how Idaho management practices encouraged retention of shade-tolerant tree species which gave rise to new silvicultural problems such as root disease (HAGLE et al. 2000). In Nova Scotia, MCGINN and DAVIDSON (1953) reported that *Ribes* establishment bore little relation to the amount of timber harvest and that blister rust was a minor factor in white pine regeneration. They suggested a modest effort in site selection and cost-effective eradication was sufficient to maintain white pine forestry in the region.

Not only did silviculture vary by region, but it also continued to evolve (see OSTRY et al. 2010; ZEGLEN et al. 2010). WOODS (1953) was especially critical of single-species preference for white pine and advocated alternative approaches based on genetically selected and modified trees and highly regulated stands that would 'bear little resemblance to those through which our forefathers walked'. BYLER and PARMETER (1979) recognized that, although some stands were seriously infested, there were also many sites where sugar pine could significantly contribute to stand composition—if it were judiciously planted and favoured during thinnings. HAGLE et al. (1989) elaborated on integrated management and use of hazard assessment for western white pine. DENITTO (1996) emphasized long-term tree survival as a key management objective and forest health monitoring as a necessary part of management.

For many white pine forests of North America, blister rust has been one of the most important factors in selection of management objectives and choice of silvicultural treatments. The significant trend for these forests in the past century has been a shift from efficient disease control to commercial timber production and then to ecosystem management (for last see SCHOETTLE 2004a; AUBRY et al. 2008; BURNS et al. 2008; CONKLIN et al. 2009). Effective ecosystem management requires adaptive learning (management as experiment) and involving participation of diverse groups (managers, researchers, and various stakeholders) (see HUNT et al. 2010).

5.4 Selection for resistance and tree improvement

Differences in the susceptibility of various white pine species and trees led early investigators to deduce there might be a heritable basis for resistance which could be exploited with selective tree breeding (SPAULDING 1925). Several factors contributed to building support for genetics research and resistance screening. These included pre-existing programmes for white pine reforestation, progress in understanding resistance and virulence in non-forest crops (FLOR 1971), and realization of the limitations of quarantine, eradication, and silviculture (see HUNT 2004b).

Historically, genetics programmes began with screening for the rare individuals which were phenotypically resistant (apparently not escaped and not diseased). Several programmes tried creating hybrids by crossing trees of desirable, but susceptible species with trees of less susceptible species. Little of that work is still continued. Most applied genetics programmes have advanced to the stage of selecting parents whose families had higher-than-average survival in screening trials. Outplanting seedlings from selected

families is used in reforestation; long-term performance is monitored in realized-gain trials. Progress has also been made with investigations on the modes and inheritance of resistance. Research programmes are studying the genetics of white pines and *Cronartium* rusts and investigating the molecular basis of host–pathogen interactions (see RICHARDSON et al. 2010).

The institutional nature of genetics programmes provided numerous histories describing their approaches and accomplishments (see KING et al. 2010). For eastern white pine, PATTON and RIKER (1966) reviewed a 20-year effort in the Great Lakes region. KRIEBEL (1983, 2004) prepared a worldwide summary and an update for the eastern states. DAoust and BEAULIEU (2004) wrote a 50-year summary for Canada. GREMMEN (1972) reported on 40 years of genetic study for several white pine species in Europe; BLADA and POPESCU (2004) provided a recent update. For western white pine, BINGHAM (1983) described his 25 years of study in Idaho; and KING and HUNT (2004) related progress in Canada. SAMMAN and KITZMILLER (1996) described the sugar pine programme. Sniezko (2006) reviewed resistance efforts in North America, particularly including examples from the Dorena, Oregon screening centre. HUNT et al. (2010) lists many of the specific opportunities for genetics research to contribute to management of white pine ecosystems.

6 Synopsis

As evident in the following articles, the threats described by SAMMAN et al. (2003) in managing white pine ecosystems are geographically diverse. In regions such as British Columbia with long and severe epidemics of *C. ribicola*, sustaining a white pine forest industry remains an important objective; and planting resistant western white pine is the practice of choice (HUNT 2009). In other regions such as the southern Rocky Mountains where blister rust is a more recent arrival and hazard varies by forest and site, protecting biodiversity values is the chief objective. For high-elevation species such as limber pine, SCHOETLE and Sniezko (2007) advocated immediate, proactive intervention to facilitate white pine reproduction and natural selection for resistance and other adaptive traits. In the Pacific Northwest, Canadian and northern Rocky Mountains, whitebark pine populations have been so damaged by numerous factors that ecological rehabilitation by planting improved stock are recommended (SCHWANDT 2006; AUBRY et al. 2008; TOMBACK and ACHUFF 2010). Europe and eastern Asia provide additional stories of not only sudden and severe infestations but also of endemic native pathosystems with diverse hosts and blister rust fungi (see KIM et al. 2010; ZHANG et al. 2010).

VOGLER (2007) posed a set of questions that he suggested should precede embarking on a selection and breeding programme for disease resistance in whitebark pine. To expand and generalize from his four questions, we ask: (1) Is blister rust the driving cause of decline in a white pine population of concern? (2) Can this decline be reversed by deploying seedlings from resistance-screened families or by encouraging natural regeneration and natural selection? (3) Do we have operationally feasible methods of deploying or encouraging resistance and a sufficient understanding of the modes and inheritance of host–pathogen interactions and the distribution of adaptive genetic traits to act effectively? And, (4) how do we acquire and maintain the institutional and public support necessary for resolving complex, evolving problems? Although these basic questions have been alternatively addressed for several earlier blister rust epidemics, we now face different circumstances, expectations, and opportunities in a great variety of situations. In response to these challenges, we offer this series of reviews on the current status and various threats to white pines, horticulture and biology of *Ribes*, and the genetics and silviculture of white pines.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

References S1. White Pines, *Ribes*, and Blister Rust: REFERENCES.

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