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REVIEW

White pine blister rust in Korea, Japan and other Asian regions: comparisons and implications for North America

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Summary

This article briefly reviews the history of white pine blister rust, attributed to *Cronartium ribicola*, and addresses current research and management issues in South Korea, Japan and other regions of eastern Asia (China, Russia and Himalaya). For each region, the distribution, damage, aecial hosts, telial hosts and management of *C. ribicola* and other blister rust fungi on native and introduced white pines are summarized. In addition, blister rust behaviours in eastern Asia and North America are compared; and the potential evolutionary and management implications are discussed.

1 Introduction

In an era of expanded world trade, introduction of exotic pathogens critically threaten the stable functioning of natural ecosystems (Liebhold et al. 1995). *Cronartium ribicola* J.C. Fisch. in Rabh., a blister rust pathogen, was introduced into North America a century ago and has since caused significant mortality and serious impacts in white pine ecosystems (Samman et al. 2003). The life cycle of *C. ribicola* requires aecial and telial hosts (see Geils et al. 2010;. Aecial hosts of *C. ribicola* are species in the genus *Pinus*, subgenus *Strobus*, subsections *Balfourianae*, *Strobi*, and *Cembrae*, the white pines (Price et al. 1998). Telial hosts are known from the genus *Ribes* (Grossulariaceae, currant family) and from the genera *Castilleja* and *Pedicularis* (Orobanchaceae, broom-rape family).

Asia is identified as a centre of diversity for blister rust fungi and the putative source of the *C. ribicola* introduced first to Europe and then to North America (Leppik 1970; Hunt 2003a). Although the systematics of the blister rust fungi infecting white pines is unresolved, numerous *Cronartium* taxa are endemic to Asia that were not known to occur in Europe or North America.

This article briefly reviews the history, distribution, status, research and management of *C. ribicola* and related blister rust fungi in eastern Asia, including Korea, Japan, China, Russia and Himalaya (Fig. 1). Aecial and telial hosts of *C. ribicola* are identified and discussed for each region (Tables 1 and 2). We compare blister rust behaviors in eastern Asia and North America and discuss the potential evolutionary and management implications gained from that comparison. A companion article by Zhang et al. (2010) focuses on blister rusts in China.

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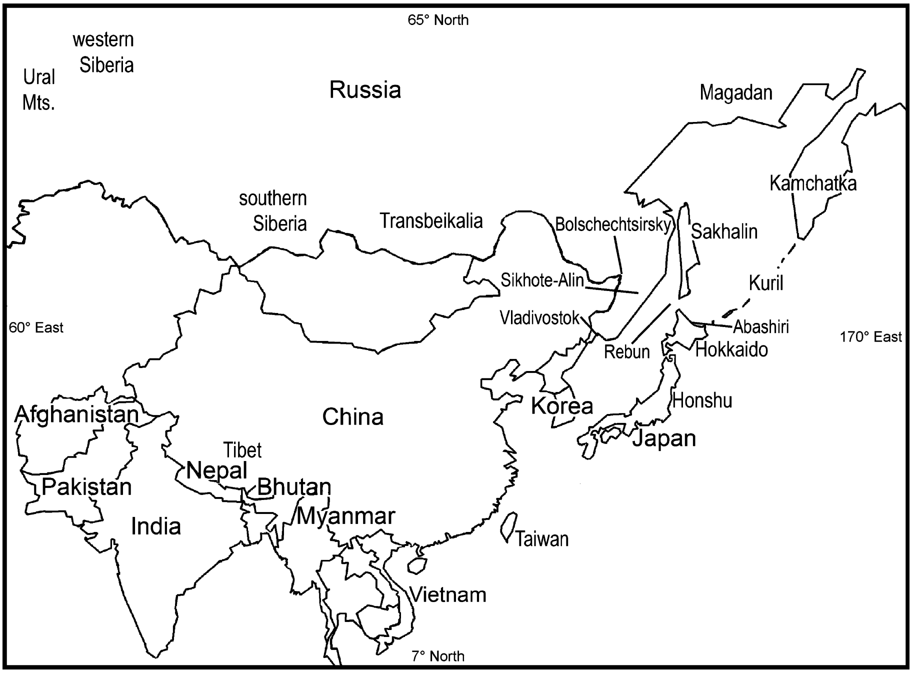

Fig. 1. Regions and sites within Asia noted for presence of white pines (*Pinus*, subgenus *Strobus*) and associated blister rusts (*Cronartium*).

2 South Korea

2.1 History

In 1937, Takagi (cited from Hyun 1972) reported the first known observation of *C. ribicola* in South Korea when an infestation of white pine blister rust was discovered in the central region of the Korean peninsula (Fig. 1) in an 8-year-old plantation of *Pinus koraiensis* Siebold and Zucc. Prior to 1963, there was little concern over blister rust because the Korean infestation was limited to 20 ha and affected only 650 trees (Hyun and Koo 1981).

After 1963, however, a serious blister rust infestation developed in young plantations of *P. koraiensis* and continued until 1978 (Hyun and Koo 1981). Between 1972 and 1978, more than one million trees were killed and the continuation of white pine plantation forestry was seriously threatened (La and Yi 1995). The most severely infested plantations were <20 years old and located at elevations between 600 and 1000 m (La and Yi 1976). Major efforts to control *C. ribicola* were undertaken. The principal methods used were sanitation of infected trees and removal of the common telial host, *Pedicularis resupinata* L. Since 1990, blister rust incidence has remained low; and *C. ribicola* has been found only occasionally in white pine plantations (Fig. 2). The causes of this brief but severe infestation are unknown; however, planting many susceptible *P. koraiensis* on high hazard sites (with abundant telial hosts and a favourable climate) may have contributed. Although *Pedicularis* is still controlled to protect forest plantations, white pine blister rust is no longer considered a major forest disease in Korea.

Table 1. **Synopsis of aecial host status for *Cronartium ribicola* (*sensu lato*) in Asia.**

Region	Subregion	*Pinus*	Disease status
Korea		*P. koraiensis*	Was severely infested in plantations
		P. parviflora	Putatively immune
		P. pumila	Putatively escapes
		P. strobus[1]	Susceptible to Korean *C. ribicola*
Japan		*P. koraiensis*	A plantation infested in 1970s
		P. parviflora	Common but not infested
		P. pumila	Natural host; also host to several related endocyclic blister rusts
		P. strobus[1]	Many plantations infested in 1970s
China	Northern	*P. sibirica*	Natural host
	Northeastern	*P. pumila*	Natural host
		P. koraiensis	Severely infested in plantations; alternates with *Ribes* or *Pedicularis*; ITS similar to rust from Korea and to *P. lambertiana* in North America
	Central and southern	*P. armandii*	Infestation widespread and serious; pathogen ITS differs from *P. koraiensis* pathogen in northeast China
	Southern	*P. wallichiana*	Natural host
Russia	Far East: Sikhote-Alin, Vladivostok, Bolschechtsirsky	*P. koraiensis*	Rarely infected; natural host alternating with *Ribes* and *Pedicularis*
	Far East, Magadan area	*P. pumila*	Severe infestation; natural host alternating with *Ribes*
	Far East, Kamchatka	*P. pumila*	Severe infestation; natural host alternating with endemic *Castilleja* and *Pedicularis*
	Far East, North Kuril, Sakhalin	*P. pumila*	Severe infestation; natural host; identified as *Endocronartium sahoanum* var. *hokkaidoense*
	Western to southern Siberia	*P. sibirica*	Natural host; severe infestations in southern Siberia; other portions not well studied
Himalaya	India, Pakistan and Bhutan	*P. wallichiana*	Natural host; infestations ranging from light to severe associated with genetics and environment

[1]Non-native.

2.2 White pines and telial hosts

Korea has relatively small populations of native *Pinus koraiensis*, *P. parviflora* Siebold and Zucc., and *P. pumila* Regal; *P. strobus* L. is introduced from North America (Table 1). *Pinus koraiensis* is the only native species known to be naturally infected by *C. ribicola*; natural infection has not been reported for *P. parviflora* or *P. pumila*. Plantations of *Pinus strobus* have apparently escaped infestation (La and Yi 1976), but caution would be warranted before large-scale planting of *P. strobus* is undertaken. In three Korean trials, >40% of *P. strobus* seedlings exposed to natural infection by *C. ribicola* were infected (Yi and Kim 1983; La and Yi 1995). In these same trials, about 20% of *P. koraiensis* seedlings

Table 2. **Synopsis of telial host status for *Cronartium ribicola* (*sensu lato*) in Asia.**

Region	Subregion	*Ribes*, *Pedicularis*, *Castilleja*	Disease status
Korea		*Pe. resupinata*	Natural host
		R. fasciculatum *R. hudsonianum*[1] *R. nigrum*[1]	Hosts by artificial inoculation with Korean isolates
Japan		*Pe. chamissonis* *Pe. yezoensis*	Natural hosts associated with *P. pumila* at high elevation
		R. latifolium *R. sachalinense*	Natural hosts at low elevation; not associated with *P. pumila*
		R. rubrum	Once found infected
China	Northeastern	*R. manshuricum*	Natural host
		Pe. resupinata *Pe. spicata*	Natural host; close to *P. koraiensis* plantation results in severe infestation
	Central	*R. glacial* var. *laciniatum*	Rust alternates with *P. armandii*
	Southern	*Ribes?*	Endemic species: *R. himalense*, *R. orientale*, *R. takare* but host status of individual species unknown
Russia	Far East, Sikhote-Alin area	*R. mandshurica* *R. latifolium* *Pe. resupinata* *Pe. mandshurica*	Natural hosts, but uncertain if *Pedicularis* is a host for *C. ribicola*, *C. flaccidum* or both
	Far East, Vladivostok area	*R. latifolium* *Pe. resupinata*	Natural hosts, but uncertain if *Pedicularis* is a host for *C. ribicola*, *C. flaccidum* or both
	Far East, Bolschechtsirsky area	*R. mandshurica* *Pe. resupinata*	Natural hosts, but uncertain if *Pedicularis* is a host for *C. ribicola*, *C. flaccidum* or both
	Far East, Magadan area	*R. dikuscha* *R. fragrans* *R. triste*	Natural hosts, alternating with *P. pumila*, only pine of area; *Pedicularis* present, not infected
	Far East, Kamchatka	*R. latifolium* *R. triste* *C. pallida* *Pe. chamissonis* *Pe. resupinata*	Natural hosts alternating with *P. pumila*; *Pe. resupinata* is common host
Himalaya	India Pakistan	*R. rubrum* *R. orientale*	Natural hosts

[1]Non-native.

but no *P. parviflora* seedlings were infected. As *P. pumila* in Korea is restricted to remote locations, blister rust symptoms, phenology and occurrence are not well known (La and Yi 1995). In 2006, we (M.-S. Kim pers. obs.) examined *P. pumila* stands north of Sorak Mountain (Yangyang, Korea) for the occurrence of blister rust on *Pedicularis resupinata.* Although this telial host was abundant, we did not find *C. ribicola*. Blister rust had been a problem in Korea on *P. koraiensis*; it is now uncommon in plantations and rare in native stands. The causes of these differences are unknown but likely result from a combination of genetic and environmental factors.

By inoculation, Korean isolates of *C. ribicola* can infect species of either *Ribes* or *Pedicularis*; but the rust has been found in nature only on *Pedicularis* (Table 2; Yi and La 1974). Although 12 *Ribes* species occur in Korea (Lee 1966), they are seldom found within white pine stands. La and Yi (1995) reported that *Ribes fasciculatum* Siebold and Zucc. var.

Fig. 2. Asian white pines. (a) plantation of *Pinus koraiensis*, South Korea; (b) native stand of *P. pumila*, South Korea; (c) native stand of *P. pumila*, Japan; (d) foliage and cone of *P. pumila*, Japan.

chinese (native to Korea), *Ribes hudsonianum* var. *petiolare* (Dougl.) Jancz. (native to North America), and *R. nigrum* L. (native to Europe) were successfully inoculated with Korean isolates of *C. ribicola*.

2.3 Current research and disease management

Currently, *C. ribicola* is not considered a major problem for white pine forestry in Korea. Some disease management approaches begun in 1973, however, are still used. The primary methods of disease control are removal of infected trees and eradication of telial hosts; silvicultural practices include pruning and chemical control (La and Yi 1976, 1995; Yi et al. 1981; Kim and Yi 1988). In 1975, a blister rust resistance breeding program was initiated in Korea. After selecting >1500 candidate trees and a decline in blister rust incidence, the program was discontinued.

3 Japan

3.1 History

In Japan (Fig. 1), *C. ribicola* was first reported on *Ribes rubrum* L. in Hokkaido (Takahashi 1905). In the 1930s, *P. pumila* was discovered to be infected by a blister rust pathogen then described as *Cronartium kamtschaticum* Jørst. (Hiratsuka 1935; Ito 1938).

This blister rust fungus has since been referred to as *C. ribicola* (Yokota and Uozumi 1976; Hama 1987). After World War II, *P. strobus* was introduced into Japan for commercial reforestation (Uozumi 1972; Yokota et al. 1975; Yokota and Uozumi 1976). In 1972, *C. ribicola* was found in a plantation of *P. strobus* in eastern Hokkaido (Uozumi 1972; Yokota et al. 1975). By the late 1970s, blister rust had spread over 334 ha and infested 95 plantations of *P. strobus* and a plantation of *P. koraiensis* (Uozumi 1978; Imazu and Kakishima 1995). Since that time, however, there have no additional reports of blister rust damage to white pine plantations; but other blister rust pathogens have been discovered in native stands of *P. pumila*.

3.2 White pines and telial hosts

In addition to the introduced *Pinus strobus*, Japan has five native white pine taxa—*P. pumila*, *P. koraiensis*, *P. parviflora*, *P. hakkodensis* Makino, and *P. armandii* Franch. var. *amamiana* (koidz.) Hatus (Table 1). The last *armandii* var. is endemic on two small islands in southern Japan, and populations were substantially reduced by previous harvesting (Kanetani et al. 2004). The serious threats to *P. amamiana* are inbreeding depression and pine wilt disease not blister rust. *Pinus parviflora* refers to a complex of white pine taxa, including a natural hybrid with *P. pumila* called *P. hakkodensis* (Saho 1972). No native stands of *P. parviflora* are known to be infested by blister rust fungi (Imazu and Kakishima 1995); but Bingham (1972) reported two provenances displayed moderate resistance when inoculated with North American *C. ribicola*. Natural infection of *P. koraiensis* in Japan is limited to the infested plantation discovered during the 1970s infestation on *P. strobus* (Imazu and Kakishima 1995). Yokota et al. (1975) described a study wherein potted seedlings of *P. strobus* and of *P. koraiensis* were exposed to infected *Ribes* on Rebun Island, Japan; blister rust only developed on the seedlings of *P. strobus*. *Pinus pumila* is native to high elevations of central Honshu (Fig. 2) and infected by multiple blister rust fungi, including *C. ribicola* (Imazu and Kakishima 1995).

Species of *Ribes* and *Pedicularis* serve as telial hosts of *C. ribicola* in different regions of Japan (Table 2). In addition to the *Ribes rubrum* reported in Hokkaido, *R. sachalinense* Nakai and *R. latifolium* Jancz. are infected by *C. ribicola* on Rebun Island and in Abashiri (Takahashi 1905; Saho 1972). No *Ribes* occur within the range of *P. pumila*; where *Ribes* have been located in native stands of other Japanese white pines, none have been found infected by *C. ribicola* (Imazu and Kakishima 1995). The telial hosts of *C. ribicola* associated with *P. pumila* are *Pedicularis chamissonis* Steven var. *japonica* and *Pe. yezoensis* Maxim. (Hiratsuka 1935; Ito 1938).

In central Honshu, the distribution of *C. ribicola* is limited to sites where *P. pumila* occurs with *Pedicularis chamissonis* or *Pe. yezoensis*. Because blister rust infection of *P. pumila* does not produce the resinosis and branch swelling typical of the disease on other pines and in other regions, *C. ribicola* is nearly impossible to detect unless it is sporulating on a pine or present on a telial host (S. Kaneko, pers. obs.). In 2006, we visited two *P. pumila* stands in central Honshu when *C. ribicola* was not sporulating on *P. pumila*. Uredinia and telia of *C. ribicola*, however, were commonly found on *Pedicularis* plants growing abundantly at each sites (Fig. 2).

3.3 Other white pine blister rust fungi

An unexpected discovery was the existence of a blister rust fungus in Hokkaido and northern Japan—*Peridermium yamabense* Saho and I. Takah.—that spread directly from one *P. pumila* tree to another (Saho and Takahashi 1976; Saho 1981, 1987). Evidence for an autoecious (pine-to-pine) life cycle was first provided by an injection inoculation method used on several white pine species, including *P. strobus* (Saho 1984). The ability of spores from one pine to directly infect another was later demonstrated by a spray inoculation method which was successful but produced only a low infection rate (Kaneko and Harada 1995).

Peridermium yamabense and several additional autoecious taxa found to infect Japanese white pines are placed in the endocyclic genus *Endocronartium* (Imazu et al. 1989, 1991; Imazu and Kakishima 1992; Imazu 1994). The described white pine blister rust fungi in Japan are: (1) *Cronartium ribicola*; (2) *Endocronartium yamabense* (Saho and I. Takah.) Paclt; (3) *E. sahoanum* Imazu and Kakish. var. *sahoanum*; and (4) *E. sahoanum* var. *hokkaidoense* Imazu and Kakish. (Imazu and Kakishima 1995). Although macroscopic symptoms of all the blister rust fungi on Japanese white pines are similar, the morphological and genetic features of these endocyclic rusts are distinct from each other and from *Cronartium ribicola* (Imazu and Kakishima 1995; Imazu et al. 2000). The Japanese *Endocronartium* are only known to occur in the mountainous areas of Tohoku and eastern/central Hokkaido where the only blister rusts on *Pinus pumila* are *Endocronartium* and where *Cronartium ribicola* appears to occur only on *Pedicularis*.

3.4 Current research and disease management

The diversity of epidemic behaviors and life cycles of the Japanese blister rust fungi open numerous questions regarding *C. ribicola* and related rust fungi. Early reports of blister rust fungi on *Ribes* and *P. pumila* suggest that *C. ribicola* is native to Japan, but the origin of the invasive blister rust in plantations of *P. strobus* is unknown. Native white pines either escape infection or, as with *P. pumila*, display tolerance by their cryptic symptoms. The phylogeny of blister rust fungi—which apparently only occur on either *Ribes* or *Pedicularis*, alternate to *Pedicularis* but not *Ribes*, or bypass both *Ribes* and *Pedicularis*—is unknown (but see Richardson et al. 2010; : Fig. 1). The white pine blister rust pathosystems of Japan provide a valuable and unique laboratory for biogeographic studies in evolutionary and invasive biology.

Cronartium ribicola was a serious concern to forest managers in the 1970s. *Pedicularis* could be controlled in plantations, but they are naturally shaded out without eradication. In Honshu, blister rust damage to *P. pumila* is not severe; although *Pedicularis* are infected, they are judged more an ecological asset than a rust hazard. Blister rust is no longer deemed a major disease in Japan.

4 Other Asian regions

4.1 China

Zhang et al. (2010) review the history, biology and management of blister rust fungi and associated hosts in China. We provide here a brief synopsis on the white pine blister rust pathosystems in China for a synthesis across eastern Asia and comparison to North America. In particular, we summarize information on history, biogeography, pathology and phylogeny to illustrate the paucity of data for blister rust in China and possible confusion in the literature over several pathogens referred to as *C. ribicola*.

4.1.1 History

Although Asia is the putative evolutionary origin of *C. ribicola* (Leppik 1970), Xu et al. (2006) identified *C. ribicola* as an alien, invasive pathogen in China (also see Zhang et al. 2010). Early reports of a white pine blister rust in China include those of Clinton (1919), Spaulding (1922b), and Cummins and Ling (1950). Cheng et al. (1995) conducted isozyme analysis of aeciospores from *P. koraiensis* in three locations of Liaoning province (see Zhang et al. 2010 for map of Chinese provinces). They identified the fungus as *C. ribicola* because it possessed a similar isozyme pattern to that obtained by Powers et al. (1989) for *C. ribicola* on *P. strobus* in eastern North America.

In 1933, Hashioka found uredinia typical of *Cronartium* on *Ribes formosanum* Hayata in Taiwan; so, the rust was referred to as *C. ribicola* for 'dwelling on *Ribes*' (Chen 1967). Decades later, aecia were found on *Pinus taiwanensis* Hayata, subgenus *Pinus* (Chen 1967). *Cronartium flaccidum* (Alb. and Schwein.) G. Winter has a broad aecial host range, including many species of the subgenus *Pinus* but none of subgenus *Strobus* (Peterson 1967). Although no *Ribes* species are known as telial hosts of *C. flaccidum*, the telial hosts of this rust are distributed among many diverse families with Taiwanese species (Jørstad 1934; Jing et al. 1995). Therefore, these rusts on *R. formosanum* and *P. taiwanensis* might be more closely related to *C. flaccidum* than to *C. ribicola.* DNA-based diagnostics would be useful to resolve the status of *C. ribicola* in Taiwan.

4.1.2 White pines and susceptibility to blister rust

China has the greatest diversity of white pine species in Asia (Wang and Hong 2004). Zhang et al. (2010) lists the 12 taxa occurring in China and provide a map for their distributions in China. The major white pines are *Pinus sibirica* Du Tour in northwestern China, *P. pumila* and *P. koraiensis* in northeastern China, *P. armandii* in central and southern China, and *P. wallichiana* A.B. Jacks. (syn. *P. griffithii* McClellan, *P. excelsa* Wall. ex D. Don) in southern China (Table 1).

All these white pines are infected in China by native blister rust pathogens (Zhang et al. 2010). North American isolates of *C. ribicola* are able to infect these species and to elicit diverse resistance responses in *P. armandii* and *P. wallichiana* (Bingham et al. 1971; Bingham 1972). Given the large number of white pine species, their wide distributions and variations in pathosystem interactions, China is an important centre of genetic diversity for potential resistance to white pine blister rust.

4.1.3 White pine blister rust pathosystems

Across China, species of *Ribes* or *Pedicularis* vary by region, association with the endemic white pine, and function as telial hosts for a *Cronartium* rust (Tables 1 and 2). These differences can be used to identify distinct pathosystems comprised of a white pine, telial host(s) and blister rust pathogen. The pathosystems in northwestern, northeastern and southern China resemble the respective pathosystems in neighbouring countries where the pathogen is referred to as *C. ribicola*. Although the issue is not resolved, it appears the *Cronartium* rust on *P. armandii* in central China is distinct from *C. ribicola*.

Little is known about *C. ribicola* on *P. sibirica* in Xinjiang province of northwestern China other than it alternates to species of *Ribes* (Jing et al. 1995). This region is adjacent to southern Siberia, Russia, where blister rust is also not well known (Spaulding 1922b; Iroshnikov and Politov 2004).

Pinus pumila occurs in northeastern China in Heilongjiang and Jilin provinces and Inner Mongolia. Its distribution overlaps with that of *P. sibirica* and is adjacent to portions of southeastern Russia (see below). Jing et al. (1995) did not mention any rust on *P. pumila* in their review of pine rusts in northwest China.

Cronartium ribicola is common throughout the native distribution of *P. koraiensis* in Heilongjiang, Jilin and Liaoning provinces (Shao 1980). The telial hosts in northeastern China include *Pedicularis resupinata*, *Pe. spicata* and *Ribes manshuricum* Kom. (Chen 2003). In Liaoning province, *C. ribicola* alternates to *Pedicularis* and causes severe impacts to *P. koraiensis* plantations (Jia et al. 2000).

Pinus armandii is the most widely distributed white pine in China; it occurs across central China from Hebei to Yunnan provinces and Tibet. A blister rust of *P. armandii* is widespread in the Beilongjiang Forest of Gansou and the Qinling Mountains of Shaanxi province (JING et al. 1995). JING et al. (1995) were unable to inoculate either *Ribes* or *Pedicularis* from the Qinling Mountains with aeciospores from *P. armandii* and speculated the blister rust might be autoecious. Using aeciospores collected on *P. armandii* in the Chi Mountains bordering Shaanxi and Sichuan provinces, YANG (2003) demonstrated *Ribes glacial* var. *laciniatum* (Hook f. et Thoms) Clarke serves as telial host for a *Cronartium* rust.

HEI et al. (2003) used sequences of internal transcribed spacers (ITS) to compare a diverse group of *Cronartium* rust fungi. They sequenced rusts on *P. koraiensis* from Dandong and Liaoning provinces and on *P. armandii* from Guangyuan and Sichuan provinces; for reference, they included GenBank sequences for *C. ribicola* on *P. koraiensis* from Korea and *P. lambertiana* Dougl. from California. They concluded the rust on *P. koraiensis* was similar to other sequences for *C. ribicola* but the rust on *P. armandii* was sufficiently different that it might be recognized as a distinct species.

CHEN (1979) reported *P. wallichiana* and *P. armandii* in Tibet were infected with *C. ribicola*; other surveys only confirmed its presence on *Ribes* (ZHUANG 2003). The common species of the Sino-Himalayan plateau that often occurs with *P. wallichiana* are *Ribes himalense* Royle, *R. orientale* Desf., and *R. takare* D. Don (CHEN 2003; WANG and HONG 2004). Taxonomic confusion over the *Cronartium* rust on *P. wallichiana* is discussed below for Himalaya.

RICHARDSON et al. (2010): Fig. 1 illustrates tentative phylogenic relationships among *C. ribicola* populations from northeastern Asia, Europe and North America, not including isolates from *P. armandii*. Thus, it remains likely that a different species of blister rust pathogen can infect *P. armandii* in China; but its affinity to the *C. ribicola* on other Chinese hosts and from other regions is unresolved.

4.2 Asiatic Russia

4.2.1 Far East

In the Russian Far East (Fig. 1), *P. pumila* and *P. koraiensis* are widely distributed (KAKISHIMA et al. 1995). Although reports for this region list both *C. ribicola* and *C. kamtschaticum*, studies have concluded that *C. kamtschaticum* should be considered synonymous with *C. ribicola* (HIRATSUKA et al. 1992; AZBUKINA et al. 1999). *Cronartium ribicola* is common on the aecial hosts *P. koraiensis* and *P. pumila* (Table 1). It occurs on several telial hosts (Table 2) including *Ribes dikuscha* Fisch. ex Turcz., *R. fragrans* Pall., *R. latifolium*, *R. manshuricum*, *R. nigrum*, *R. palczewskii* Pojark., *R. pallidiflorum* Pojark., *R. pauciflorum* Turcz. ex Ledeb. (= *R. nigrum*), *R. procumbens* Pall., *R. rubrum*, and *R. triste* Pall. (KAKISHIMA et al. 1995), *Castilleja pallida* Spreng., *Pedicularis chamissonis* Steven, *Pe. resupinata*, *Pe. sudetica* Willd., and *Pe. lanata* Willd. ex Steven (AZBUKINA 1995; KAKISHIMA et al. 1995).

Unlike Korea and Japan, severe infestations of *P. pumila* caused by *C. ribicola* (formerly *C. kamtschaticum*) were observed in the Kamchatka Peninsula and Magadan region. In some areas, nearly 100% of trees were infected and considerable mortality had occurred (AZBUKINA 1995). Numerous blister rust infections on *P. pumila* were reported in Kamchatka during the 1960s along with simultaneous infections by *Coleosporium pini-pumilae* Azbukina (AZBUKINA 1995). In 1964, extensive mortality of *P. pumila* attributed to blister rust was observed in the Magadan region (AZBUKINA 1995). Another severe blister rust infestation on *P. pumila* was known on Schmidt Peninsula, Sakhalin Island in 1971 (AZBUKINA 1995). In the Kamchatka Mountains, *C. ribicola* was collected on *Castilleja pallida* (Azbukina 1995) and was confirmed on *Pedicularis resupinata* and *Ribes triste* in Kamchatka (Imazu et al. 2000). *Pinus pumila* is the only pine in the Magadan region; and it was heavily infected with *C. ribicola* in several locations (Kakishima et al. 1995). Uredinial and telial stages of *C. ribicola* were found on *Ribes fragrans*, *R. triste*, and *R. dikuscha*, but not on *Pedicularis*. (Kakishima et al. 1995).

A blister rust of *P. pumila* in the North Kuril Islands (southeast of Kamchatka) was suspected to be endocyclic because uredinia and telial were not found on nearby plants of either *Castilleja* or *Pedicularis* (Imazu et al. 2000). Earlier, this blister rust fungus was considered to be distinct from *Cronartium ribicola* and was described as *Peridermium kurilense* Diet. (Dietel 1905). Later, it was placed in synonymy with *C. kamtschaticum* (Jørstad 1934; Hiratsuka 1944; Hiratsuka et al. 1992); then most recently, it has been referred to as *Endocronartium sahoanum* var. *hokkaidoense* based on morphology and DNA analysis (Imazu et al. 2000).

In southeastern Russia, Kakishima et al. (1995) reported blister rust was rare on *P. koraiensis* in the Sikhote-Alin Reserve. No blister rust was found on *P. pumila* which occurs only in high-elevation locations; however, uredinia and telia were commonly found on *Ribes* and *Pedicularis* where they occurred. In areas where *P. koraiensis* was common, *C. ribicola* occurred on *Ribes latifolium* (Ussuri Reserve–Vladivostok region) and *R. manshuricum* (Bolschechtsirsky Reserve). Kakishima et al. (1995) found uredinia and telia on *Pedicularis resupinata* (a telial host of *C. ribicola* in Korea and Japan) and *Pe. mandshurica* Maxim.; but could not confirm whether the fungus was *C. ribicola* or *C. flaccidum*, common in the region on *P. sylvestris* L.

4.2.2 Siberia

Pinus sibirica occurs across northeastern European Russia, the Ural Mountains, western Siberia, and the mountains of southern Siberia and Transbeikalia (Spaulding 1922b; Iroshnikov and Politov 2004; Fig. 1). *Cronartium ribicola* occurs throughout the western (Iroshnikov and Politov 2004) and middle distributions of *P. sibirica* (Spaulding 1922b). Some sources of *P. sibirica* appear to inherit resistance to *C. ribicola* (Bakshi 1972; Bingham 1972; Stephan 2004).

4.3 Himalaya

4.3.1 Blue pine and red currant

Pinus wallichiana displays considerable intraspecific variation which permits a large distribution from Afghanistan to Pakistan, India (Jammu, Kashmir, Himachal Pradesh, Uttar Pradesh), Nepal, China, Bhutan, and Myanmar (Fig. 1) and a broad elevational range from 1500 to 3800 m (Critchfield and Little 1966; Ahsan and Khan 1972; Dogra 1972; Shams-Ur-Rehman 2000). The phylogenetic relationships of *P. wallichiana* with other species of the subgenus *Strobus* are poorly understood (Gernandt et al. 2005; Syring et al. 2007); but it is interfertile with *P. peuce* Griseb., *P. parviflora*, *P. ayacahuite* Ehrenb. ex Schltdl., *P. monticola* Dougl. ex D. Don, *P. strobus*, and *P. flexilis* James (Critchfield 1986).

In the Himalayan region, several *Ribes* species are reported as telial hosts of *C. ribicola*. In 1923, Mr Greswell (Deputy Conservator of Forests) collected *C. ribicola* on *R. rubrum* at 2286 m elevation in the Kamalban Range, Upper Kagan, Hazara (Khan 1928). R. R. Stewart collected *C. ribicola* on *R. orientale* near Gulmarg, Kashmir in 1929 (Arthur and Cummins 1933).

4.3.2 Taxonomy and history

The taxonomic relationships among blister rust pathogens (*Cronartium* and *Peridermium*) of *Pinus wallichiana* are not yet well understood and are quite confusing in early reports. Peterson (1967) listed *Peridermium indicum* Colley and Taylor (Colley and Taylor 1927) as a rust on *Pinus wallichiana* (as *P. griffithii*) and *Ribes* species of Himalaya. Khan (1960) considered *Cronartium ribicola* and *Peridermium indicum* as synonymous species. Peterson (1967), however, considered *Peridermium indicum* morphologically distinct from *Peridermium strobi* and *Peridermium kurilense*; but Bagchee (1950) attributed the differences to climatic factors. Further uncertainty developed because *Peridermium indicum* was commonly regarded as synonymous with *Peridermium strobi* (Peterson 1967) which was often considered to be synonymous with *Cronartium ribicola* (Colley and Taylor 1927). According to Hiratsuka (1995a), *Peridermium indicum* should be considered as aecial state of *Cronartium ribicola sensu lato* (i.e., 'in a wide sense'), and *Peridermium strobi* should be considered as an aecial state of *Cronartium ribicola sensu stricto* ('in a narrow sense').

According to Khan (1928), the search for *Peridermium* and *Cronartium* species on *Pinus wallichiana* began when Stuart Moir became aware of an herbarium specimen with uredinia and telia of *Cronartium ribicola* on a *Ribes* leaf collected by Jacquemont from northwestern Himalaya. This specimen at the Botanical Museum of Paris was identified by Léveillé (1846) and linked with a European specimen from Crimea into a single taxon, *Cronartium asclepiadeum* var. *ribis* (*nomen nudum*) (Peterson 1973). Although the taxonomic identity of this historical rust sample from India cannot be determined at present, its existence prompted a 1923 survey.

Historical reports of blister rust fungi on *Pinus wallichiana* identified the rust as either *Cronartium ribicola* or *Peridermium indicum*. An early specimen on *Pinus wallichiana* of what is now tentatively recognized as *Cronartium ribicola sensu lato* was collected in May, 1894 by J. Nisbet at 3050 m elevation from Lambathatch, Chakrata division (Khan 1928). R.S. Troup collected a blister rust on *Pinus wallichiana* from Pluga, Kulu in 1914; the fungus was later referred to as *Peridermium indicum* (Colley and Taylor 1927). Bagchee (1950) collected additional specimens from the same area during 1933–1935. Other blister rust collections were made from the North West Frontier province of Pakistan and several regions of northern India where *Pinus wallichiana* and *Ribes* co-occurred (Bagchee 1950). From 1932 to 1935, Bagchee (1950) searched extensively but without success for the blister rust on *Pinus wallichiana* south of the Tons Valley, India. However, *Cronartium ribicola* was collected in 1934 from Brauchthatch at 3164 m elevation—only 19 km from the 1894 collection site of Nisbet (Bagchee 1950).

4.3.3 Importance and resistance

Bagchee (1952) reported the blister rust caused by *C. ribicola* was an economically important disease of *P. wallichiana* in Indian Himalaya (Table 1). Blister rust, however, was reported only sporadically in western Himalaya (Bakshi 1972). Although *C. ribicola* causes a damaging blister rust on 3- to 10-year-old seedlings or saplings of *P. wallichiana*, infestations are rare (Ahsan and Khan 1972). In 1956, Ahmad collected *C. ribicola* on *Ribes rubrum* from the Pakistani village of Shogran (Zakaullaii 1994); and Sultan et al. (2009) collected *C. ribicola* on *R. orientale* from northern Pakistan. Damage from *C. ribicola* was reported in *P. wallichiana* plantations in Pakistan (Zakaullaii 1994). A blister rust was found recently on *P. wallichiana* at several locations in Bhutan, but the rust had caused little impact (Kirisits et al. 2007).

Based on inoculation studies with North American isolates, *P. wallichiana* possesses moderate to high levels of resistance to *C. ribicola* (Heimburger 1962; Bingham 1972;

Hoff et al. 1980; Stephan 1986). In Romania, tests of open-pollinated *P. wallichiana* families suggested that polygenic resistance to blister rust was negatively correlated to rainfall (Blada 1994; Shams-Ur-Rehman 2000). Heimburger (1972b) reported that breeding programs successfully crossed *P. wallichiana* with *P. monticola*, *P. strobus*, *P. parviflora*, and *P. peuce*. but further research on hybrid crossing to increase resistance was discontinued (see King et al. 2010).

Although blister rust fungi that infect white pines and *Ribes* have long been known to occur in Himalaya (Table 2), many questions remain for all the organisms involved in this pathosystem. Additional work on *Cronartium* using molecular techniques could aid an understanding of the taxonomy of Himalayan blister rusts and their evolutionary relationship to blister rusts of other regions. Population genetic studies of *Pinus wallichiana* could help to differentiate populations in relation to distribution and blister rust susceptibility and resistance. Botanical surveys of the *Ribes* and other potential telial hosts could provide useful information on their distribution, ecology and susceptibility.

5 Blister rust in Asia and North America: Comparisons and implications

5.1 Evolutionary relations

The ultimate biogeographic origin of *C. ribicola* in North America is unknown. The source of the invasive blister rust introduced to Europe and then to North America might be from either northern Asia or Himalaya since those regions appear to have the genetic diversity and resistance which suggests a long history of coevolution (Leppik 1970; Hunt 2003a). The white pine blister rusts of Asia include taxa with different macrocyclic or microcyclic life cycles (Imazu and Kakishima 1995) and different telial hosts among the *Ribes*, *Pedicularis* and *Castilleja* (Wicker and Yokota 1976; Yokota and Uozumi 1976; Shao et al. 1980; Yi and Kim 1983; Kakishima et al. 1995; McDonald et al. 2006). Although native white pine (especially *P. wallichiana*, *P. pumila*, *P. sibirica* and *P. koraiensis*) are susceptible at the species level, many trees display a high degree of genetic resistance or tolerance to blister rust infection (Søegaard 1972; Hoff et al. 1980; McDonald et al. 2005b). Likewise, *Ribes* also show considerable variation in response to infection (Yi and Kim 1983; Brennan 1996). Although the phylogeny of the *Cronartium* rust on *P. armandii* in central and southern China remains unresolved, it appears to be more remotely related to the North American *C. ribicola* than fungi of northeastern China (Hei et al. 2003).

Molecular genetic studies have characterized North America populations of *C. ribicola* (Kinloch et al. 1998; Hamelin et al. 2000; Richardson et al. 2008); the molecular genetic characterization of Asian and European populations has begun (Richardson et al. 2009). Initial data from DNA sequencing of selected Eurasian and North American populations of *C. ribicola* indicate that *C. ribicola* comprises at least three distinct genetic groups (Richardson et al. 2010; : Fig. 1). Isolates from Korea and northeastern China form one clade; Japanese isolates form a second clade that is intermediate to a clade of isolates from USA and Germany. Based on limited data, these Asian *C. ribicola* isolates are closely related but represent separate lineages; Japanese isolates are phylogenetically closer to North American isolates than are Korean and northeastern Chinese isolates. However, additional isolates from Japan and northwestern China would be needed to confirm these results. Collaborative efforts to collect and genetically analyse *C. ribicola* isolates from Siberia, Himalaya, and other Eurasia sources could help resolve the ultimate origin of European and North American rusts.

5.2 Ecology and pathology

Regardless where the North American *C. ribicola* ultimately originated, comparing the ecology and pathology of the blister rusts in eastern Asia and North America could provide insight useful for regulation and silviculture. The history and behavior of *C. ribicola* in North America is briefly reviewed in Geils et al. (2010) and expanded upon in other articles of 2010.

In general, *C. ribicola* has not caused major problems in native stands of white pines in Korea and Japan, perhaps because the disease is endemic and naturalized. In Korea, native *P. pumila* stands are apparently free from blister rust. In Japan, *C. ribicola* occurs in *P. pumila* stands; but infection is rare and symptoms cryptic. In both countries, *P. pumila* shows apparent immunity or at least tolerance to blister rust. The few reports of serious blister rust impacts in Japan and Korea pertain to plantations of *P. strobus* and *P. koraiensis* occurred during several years of severe infestations which have since ended (Yokota et al. 1975; La and Yi 1995). Although the causes for different blister rust behaviours in native stands and plantations are unknown, several possible factors can be identified. In contrast to native stands, plantations could present a different environment (hazard) owing to site selection and preparation, species composition, stocking and silviculture. Comparing stands and plantations, genetic differences in either host resistance or pathogen virulence and aggressiveness could be significant. The source of these differences could have been an introduction of a non-native *C. ribicola* or unintended artificial selection that increased susceptibility in plantation trees. Gene-by-environment interactions (G $\times$ E) could have further magnified differences between native stands and plantations.

Compared with native stands of *P. pumila* in Korea, Japan and the Sikhote-Alin Reserve, the white pine blister rust(s) of Kamchatka, Magadan and North Kuril Islands have caused severe damage and mortality to *P. pumila* (Azbukina 1995; Kakishima et al. 1995). The causes of this striking, epidemiological contrast are unknown but could be the results of environmental or genetic factors and their interactions. Differences in life cycles and telial hosts could provide clues to the importance of blister rust genetics (at specific or intraspecific levels) for infestation severity.

An examination of the telial host ranges of *Cronartium ribicola* comparing and contrasting northeastern Asia and North America could also be informative. Blister rust fungi in northeastern Asia infect different combinations of the *Pedicularis*, *Castilleja* and *Ribes* species present in different locations (McDonald et al. 2005b). In spite of apparently similar environments for infection, populations of putatively related taxa are infested in some regions but not others. Genetic differences in either pathogenicity or susceptibility could be responsible.

As a further complication, telial host range can perhaps change as a result of genetic adaptation, developmental plasticity and/or trait reversion in a population (McDonald et al. 2006). Until 2004, only species of *Ribes* were known to be the natural, telial hosts of *Cronartium ribicola* in North America (see Zambino 2010). Hiratsuka and Maruyama (1976) had inoculated *Castilleja miniata* Dougl. ex Hook. plants which produced telia in a greenhouse. Later inoculations of *Castilleja miniata* and *Pedicularis racemosa* Dougl. using different inoculum sources either had been unsuccessful or produced a non-host response (Hunt 1984; Patton and Spear 1989). Since 2004, *Castilleja miniata*, *Pedicularis racemosa* and *Pe. bracteosa* were found bearing telia of *Cronartium ribicola* in natural stands of white pines in Idaho and California (McDonald et al. 2006; D. Vogler pers. comm.). Although additional cases of species other than *Ribes* serving as natural telial hosts in North America are unknown, Richardson et al. (2007) showed that *Cronartium ribicola* isolates from either eastern or western North America were capable of infecting *Pedicularis racemosa* under greenhouse conditions.

Observations in eastern Asia and North America of apparent differences and changes in telial host range have several possible explanations and implications. First, telial hosts might be present but are overlooked owing to insufficient search and recognition (inspection, survey, monitoring and identification of host and pathogen). Underestimation of potential inoculum sources could affect hazard assessment; but DNA-based diagnostics could improve detection and identification. Second, the realized host range of a blister rust population might reflect genetic differences in pathogen virulence and fitness and in plant susceptibility (including non-host incompatibility, specific resistance and tolerance). Introduction of a novel pathogen or host (i.e., with a different genetic potential) could initiate a new epidemic. Evidence is lacking that *Pedicularis* changed from a non-host to a telial host; however, such changes could result from a cryptic introduction. Such new introductions could pose a serious threat to the achievements of the North American genetic improvement programs (Kinloch 2003). Likewise, we do not know whether *C. ribicola* was introduced into Asia on *P. strobus*; but it was introduced into North America on multiple occasions. Knowledge of the host range and susceptibility of native plant populations could help in risk assessment, inspection and regulation of invasive pathogens. Third, with a general capacity to infect multiple plant genera, *C. ribicola* could possess an innate capacity for switching to new telial host species. Such switches could result from phenotypic plasticity or gene regulation, which could cause major and abrupt change.

6 Conclusions

Eastern Asia represents a vast geographic area comprising diverse biotic communities and considerable variation in the behaviours of white pine blister rust fungi. Continued study of the genetic and environmental influences on host–pathogen interactions in this region would enhance our general understanding of the blister rust pathosystem worldwide. The two subject areas where progress could made are the history and evolution of blister rusts in eastern Asia.

The history of white pine blister rust in Asia includes information on the discovery, identity and behavior of various blister rust fungi with regard to their life cycles, host ranges and severities of infestation. The utility of historical reports has been limited by a lack of voucher specimens, variability in taxonomy and identification methods, and indefinite geographic references. DNA-based diagnostics now provide more reliable and informative data for comparing blister rust fungi. Geographic positioning systems (GPS) allow for precise determination of locations, including elevation. Use of these tools for identifying recent collections and herbarium specimens and for mapping their distributions could aid in interpreting the records of the past century.

Cronartium ribicola in eastern Asia is reputed to be a native pathogen and a potential progenitor of the invasive blister rust of Europe and North America. Phylogenic and population genetics studies could help resolve the biogeography and evolution of *C. ribicola*. Understanding blister rust where it has long been resident could provide insights into ecological stabilization for promoting naturalization and interactions with biotic associates for developing biological control. Understanding coevolution in white pines and blister rust fungi could help identify potential sources and alternative modes of resistance and tolerance in association with pathogen response. The future is uncertain; managers should expect that major, abrupt ecological and genetic changes are likely to occur even if they can not forecast what will incite those changes and exactly how a ecosystem will respond. Understanding the behaviours of white pine blister rust pathosystems could assist in developing genetic and silvicultural strategies and tactics for sustaining resilient populations of white pines and maintaining ecosystem services.

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