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REVIEW

Biology and pathology of *Ribes* and their implications for management of white pine blister rust

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Summary

Ribes (currants and gooseberries) are telial hosts for the introduced and invasive white pine blister rust fungus, *Cronartium ribicola*. Knowledge of wild and introduced *Ribes* helps us understand the epidemiology of blister rust on its aecial hosts, white pines, and develop disease control and management strategies. *Ribes* differ by species in their contribution to initial establishment and subsequent intensification of blister rust. Their significance to pine infection depends on their inherent capacities to become infected and support spore production, their abundance and environmental interactions. *Ribes* and white pines are adapted to disturbance and frequently co-occur in forest and woodland ecosystems. Differences in light and moisture requirements affect how long various species of *Ribes* occupy a site. Natural or artificial selection increases rust resistance in white pines, *Ribes*, and other host genera; but selection also affects virulence and aggressiveness of *C. ribicola*. Blister rust pathosystems evolve. Local pathosystems wherein the rust and its hosts coexist with reduced damage could arise by several processes.

1 Introduction

The white pine blister rust fungus, *Cronartium ribicola* J.C. Fisch. in Rabh., is a macrocyclic pathogen that must alternate between hosts during its life cycle. The aecial stage of *C. ribicola* occurs on white pines (*Pinus*: *Balfouriana*, *Cembrae* and *Strobi*) and the telial stage primarily on currants and gooseberries (*Ribes*) (Geils et al. 2010). Inherent and ecological factors account for differences among *Ribes* species in their production of the inoculum (basidiospores) that infects white pines and for some species playing greater roles in white pine blister rust in North America. Such species differences have influenced white pine management since *C. ribicola* introduction into North America. Since 1909, several species of *Ribes* were targeted for eradication in order to halt blister rust spread and eliminate the disease (Spaulding 1914; Maloy 1997). *Ribes* eradication has since been largely abandoned in North America (but see Ostrofsky et al. 1988; Kim et al. 2010; Zhang et al. 2010). However, knowledge of the occurrence and prevalence of individual *Ribes* species remains useful for disease prediction and stand management, as illustrated by recent hazard models (Kearns 2005).

This paper reviews information on *Ribes* important to white pine blister rust management in North America (Canada and United States). *Ribes* biology, susceptibility, species co-occurrence, ecology and interactions with forest management are discussed. Hummer and Dale (2010) present additional information on the systematics, biology and horticulture of cultivated *Ribes*.

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Conditions necessary for *Ribes* to contribute to pine infection are numerous: (1) ecological niches or habitats must overlap or be in sufficient proximity for aeciospores or urediniospores to infect the *Ribes*; (2) a population must be susceptible to a local pathogen race; (3) leaves must be susceptible when infective spores are present; (4) infected leaves must not be shed before subsequent spore stages are produced and (5) spores must remain viable until conditions allow for dispersal, germination and infection. Because infections on pines can sporulate for many years, these conditions need to be fulfilled only occasionally for a *Ribes* species to effect blister rust spread and intensification. This paper addresses these factors for the regionally important *Ribes* species of North America. Silvicultural practices are discussed in terms of their effects on *Ribes* and not as management recommendations. Integrated approaches to white pine management are described by Zeglen et al. (2010) and Ostry et al. (2010). Several factors important to the white pine blister rust disease, namely, resistance of host populations, virulence and aggressiveness in *C. ribicola*, and physical distribution of hosts are discussed for their potential effects on pathosystem evolution (also see Kim et al. 2010). The significance of *Pedicularis* and *Castilleja* (Orobanchaceae) as non-*Ribes* telial hosts of *C. ribicola* (McDonald et al. 2006; Zambino et al. 2006, 2007) is also reviewed.

2 *Ribes* biology

2.1 *Ribes* diversity

To assess the interactions of different *Ribes* with *C. ribicola*, taxa and populations must be recognized and differences in their biology and susceptibility identified. The species number reported for North America varies among taxonomists (Berger 1924; Sinnott 1985; Holmgren 1997) and may be as high as 100 taxa (Coville and Britton 1908). The Pacific Northwest (Washington and Oregon) is a centre of diversity for *Ribes* (Messinger et al. 1994), particularly gooseberries (section *Grossularia*). *Ribes* taxonomy at specific and infraspecific levels may be further revised as new phylogenetic analyses (Lanham and Brennan 1999; Messinger et al. 1999; Senters and Soltis 2003; Schultheis and Donoghue 2004) reveal relationships and detect differences not indicated by morphology (see Hummer and Dale 2010). Natural hybridization occurs among gooseberry species (Mesler et al. 1991); but fertile, natural crosses between species of other and more distantly related sections are lacking (Keep 1962).

2.2 Cycles of abundance in relation to forest stand history

Successional stage of a forest stand affects presence of *Ribes* and white pines and potential for infection by *C. ribicola*. Both hosts establish early in succession and readily exploit large- to small-scale openings with mineral soil exposed by fire, blow-down and the action of root disease or insect outbreak (Fivaz 1931; Moss and Wellner 1953; Quick 1954; Arno 2000; Hunt 2000). *Ribes* persist in many stands for a shorter period than white pines, as light becomes limiting for early seral shrubs as overstory canopy cover closes.

Most *Ribes* grow best on well-drained soils with surface moisture in the growing season. They primarily regenerate after prolonged survival in the seed bank or by resprouting from the crown (Moss and Wellner 1953). *Ribes* species adapted to very-moist, mixed-light conditions of riparian areas or swamps also reproduce by layering (Davis and Moss 1940; Van Arsdel et al. 1961). Because such clonal patches can maintain themselves over prolonged periods of competition (Moss and Wellner 1953), they depend less on a seed bank than upland species. *Ribes* respond to pruning or low-intensity fire with vigourous re-sprouting (Littlefield 1930); some *Ribes* sprout if broken or cut roots are exposed to light (Cheyney 1920).

2.3 *Ribes* seed biology

2.3.1 *Production, dispersal, deposition and seed-bank formation*

Insects pollinate most *Ribes* species (McGregor 1976); hummingbirds pollinate species (*R. sanguineum* Pursh, *R. malvaceum* Sm., and *R. speciosum* Pursh) with bright red, tubular flowers (Grant and Grant 1966; Stiles 1982; Temeles et al. 2002). Wind and water contribute little to pollination (Offord et al. 1944). Most *Ribes* produce fruit within several years of establishment. Five years after logging, 2230 *R. roezlii* Regel plants produced 61,500 fruits and 2.3 million seeds per ha (Quick 1954); within 5 years of a fire, other *R. roezlii* were in fruit (Quick 1962b). *Ribes* generally become non-reproductive as low light reduces vigour and pollination declines (Moss and Wellner 1953).

Birds and mammals both disperse and consume seed (Lyon and Stickney 1976; Piper 1986; Usui et al. 1994). Birds of open habitats are important consumers of fruits and agents of seed dispersal, whereas forest birds play little role in dissemination (Cooper 1922). Seeds of *R. cereum* Dougl. and *R. nevadense* Kellogg with high germination rates were recovered from the droppings of chickadees, robins and other thrushes (Offord et al. 1944; Quick 1954). Perch sites have a high probability of receiving viable seeds. Seed are also dispersed by grazing animals such as elk (Edge et al. 1988), deer (Quick 1954; Habeck 1960), and cattle. Grizzly bear consume *Ribes* fruits, particularly those of *R. lacustre* (Pers.) Poir. (Mealey 1975; Zager 1980; Hamer et al. 1991; Hunt 2000); seeds in scat retain high germination rates (Quick 1954). Gravity and water also disseminate seed (Moss and Wellner 1953; Quick 1954).

Ribes seed banks accumulate at the mineral–humus interface and in the lower humus (Davis and Moss 1940; Stewart 1957) as a result of the rapid regeneration of *Ribes* after disturbance, seed deposition from fallen, unconsumed fruit and decomposition of organic materials in older duff (Moss and Wellner 1953; Stewart 1957; Stickney 1991). In the Inland Northwest (northern Idaho and adjacent areas), the *Ribes* species most important for the spread of *C. ribicola* rely primarily on banked seed for regeneration (Moss and Wellner 1953).

The long-term survival of *Ribes* in a seed bank is shown by: (1) rapid regeneration in freshly exposed soils after fire, tip-ups from windstorms or management in successionally advanced stands; and (2) seed counts and viability from soil samples obtained from intact, mature forests (Strickler and Edgerton 1976; Kramer and Johnson 1987).

In New York, Fivaz (1931) observed the emergence of *R. rotundifolium* Michx. and *R. glandulosum* Grauer from the seed bank; more than 152,000 *Ribes* plants per ha regenerated where *Ribes* had been actively growing but removed several years prior. *Ribes rotundifolium* equivalent to 9,316–24,263 seedlings per ha appeared after road-building in an apparently *Ribes*-free forest; and *R. glandulosum* and *R. rotundifolium* germinated from tip-up-exposed soil predating the establishment of a 70-year-old stand. In California (Quick 1956), soil from sugar pine (*P. lambertiana* Dougl.) stands of different ages yielded viable seed of *R. roezlii* at roughly equivalent rates of about 395,000 seeds per ha. Davis and Moss (1940) claimed that a conifer rotation of 120–130 years was not sufficiently long to eliminate the *Ribes* seed bank. After 17 years in a laboratory, dried seed stored at room temperature and without special maintenance still germinated (Pfister and Slone 2005). However, germination decreases with age; so, even where *Ribes* is long persistent (e.g., open forest pastures), the most recently deposited seed would have the highest germination rate and contribute the most to the next generation.

2.3.2 Seed dormancy and germination

Dormancy of *Ribes* seed is constitutive and varies by species (Mielke 1943; Moss and Wellner 1953). Dormancy is broken by scarification, exposure to light, fire or vernalization (Janczewski 1907; Fivaz 1931; Smith and Fischer 1997; Miller 2000; Baskin and Baskin 2001). Physical dormancy is imposed by an impermeable seed coat in a few species (e.g., *R. lacustre*) (Fivaz 1931; Moss and Wellner 1953). The ability of acid scarification (Fivaz 1931) to break dormancy suggests there is a germination advantage for fresh seed consumed, digested and deposited by mammals or birds. Physiological mechanisms of dormancy common in *Ribes* are reversed by environmental factors that promote seed germination near the soil surface after disturbance (Baskin and Baskin 2001).

Ribes seed can be artificially germinated after treatments either at a constant, low temperature or at alternating temperatures over an extended period. Exposure to a higher temperature allows for a check of germination status; if dormancy has not broken, then vernalization can be resumed (Barton 1939; Offord et al. 1944; Quick 1956; Pfister 1974; Shaw 1974). Depending on the species, vernalization treatments can be as short as 60 days (*R. aureum* Pursh: Shaw 1974) or as long as 300 days (*R. montigenum* McClatchie: Pfister 1974).

2.3.3 Seed bank depletion and Ribes *regeneration after fire and other disturbances*

Soil disturbance by fire, other natural processes or management stimulates germination of stored seed but also alters the soil condition which had enabled long-term, viable storage (Moss and Wellner 1953; Reynolds et al. 2000). Seeds are re-deposited by disturbance and erosion to different soils depths (Quick 1954).

Fires that remove organic soil layers destroy banked seed. However, patches of low to moderate intensity in a mixed-severity fire allow *Ribes* to regenerate from seed lower in the soil or from the base of surviving plants (Littlefield 1930; Moss and Wellner 1953; Arno 2000; Miller 2000). Fire stimulates surviving seed to germinate (Lyon and Stickney 1976) by a variety of mechanisms including: (1) fissuring of seed coats (Miller 2000); (2) volatilization of soil allelopathic factors (Miller 2000); (3) increased light and diurnal temperature fluctuations (Miller 2000); (4) increased soil pH (Fivaz 1931; Haddow 1969; Miller 2000; Baskin and Baskin 2001; Dahir and Cummings 2001); (5) generation of stimulatory compounds in smoke (Brown and van Staden 1997; Flematti et al. 2004) and (6) increased soil oxygen (Moss and Wellner 1953). Seedling establishment is greatest in the first year after fire (Quick 1954) and is particularly high where slash piles have burned (Moss and Wellner 1953). Low competition and increased light favour seedlings established after moderately hot fires (Quick 1954); therefore, after fire, *Ribes* often become a significant component of the shrub layer. Re-burns can destroy sensitive *Ribes* regeneration before the seed bank is replenished (Moss and Wellner 1953; Haddow 1969).

For stands that are not burned, banked *Ribes* seed germinate or are devitalized more quickly if a stand is clearcut than if it is harvested with a light, selection cut (Moss and Wellner 1953). Three years after harvest, *Ribes* survival and growth is poor under the canopy conditions of partial shade suitable for western white pine seedlings (*Pinus monticola* Dougl. ex D. Don). Half of *Ribes* seedlings may die in the first year (Davis and Moss 1940).

3 *Ribes* traits affecting epidemiology of white pine blister rust

Even where abundant near white pines, *Ribes* species differ in their contributions to the spread and intensification of *C. ribicola.* Important differences related to pathology and phenology include: (1) the capability of a plant to become infected; (2) inherent ability to produce inoculum; (3) tendency for inoculum to be inactivated or cast; (4) occurrence and abundance in different habitats and (5) synergistic interactions.

3.1 *Ribes* susceptibility

3.1.1 Assessing susceptibility

In the blister rust literature, susceptibility refers to the capacity of a plant to become infected by *C. ribicola* or its ability to support rust development. Expression of susceptibility depends on both genetics and physiology interacting with the environment (reviewed in Zambino and McDonald 2004). *Ribes* susceptibility has variously been quantified as the percent of leaves that become infected (infection rate or receptivity) or a measure of leaf surface-area that supports production of uredinia or telia (infection level). Susceptibility differs with the developmental age of a leaf or stem; growth conditions of light, moisture and fertility; and exposure to different strains or virulent races of the rust. Species ranking or ratings are obtained from: (1) field observations (Quick 1954); (2) whole plants naturally or artificially inoculated *in situ* or in gardens representing particular growth conditions (Spaulding 1922b; Mielke and Hansbrough 1933; Kimmey 1935, 1938; Mielke 1937; Hummer and Finn 1999; Hummer and Picton 2002); (3) plants in greenhouses (Spaulding and Gravatt 1917; Spaulding 1922b; Hahn 1928; Pierson and Buchanan 1938; Zambino 2000); (4) cuttings in growth chambers (Zambino 2000); and (5) leaves (Clinton and McCormick 1924) as well as leaf-discs in Petri dishes (McDonald and Andrews 1981).

Developmental stage of the leaf affects susceptibility. Leaves are immune when immature, are most readily infected after full expansion, and decrease in receptivity with age (Spaulding 1922a; Lachmund 1934a; Pierson and Buchanan 1938; Harvey 1972; Zambino 2000). Presence or absence of infected leaves early in the season might not reflect plant infection status late in the season. Receptivity in leaves decreases with age at a species-dependant rate (Pierson and Buchanan 1938). Exposure to sunlight hastens the decrease in receptivity (Hahn 1928; Mielke et al. 1937; Kimmey 1938), but openings on south-facing aspects also shorten the duration of dew and temperature conditions required for infection (Van Arsdel et al. 1956; Van Arsdel 1965b).

Elevated nitrogen level increases susceptibility in pines and *Ribes* (Van Arsdel 1972; McDonald and Dekker-Robertson 1998; author, pers. obs.). Association with forest-inhabiting nitrogen-fixing plants or artificial fertilization may increase *Ribes* susceptibility; for example, *R. roezlii,* a nitrophilous species often associated with nitrogen-fixing species, is very susceptible (Moss and Wellner 1953). Young, well-fertilized, succulent, greenhouse-grown plants can develop high infection levels, well above those usually displayed by hardened, open-grown, field plants.

Inoculum spore stage also affects age-related receptivity and the rate of rust development. Urediniospores can cause significant rates of infection on *Ribes* leaves that would be 1–2 weeks too mature for aeciospore-initiated infection (Pierson and Buchanan 1938). In addition, for susceptible leaves of *R. nigrum* L. (European black currant) under the most favourable conditions for infection, uredinia appear 2–3 days earlier if inoculated with urediniospores than with aeciospores (author, personal observation). Disks from 14- to 21-day-old leaves of *R. hudsonianum* var. *petiolare* (Dougl.) Jancz. develop fewer infections after inoculation with aeciospores than with urediniospores (McDonald and Andrews 1981).

3.1.2 Species of greatest susceptibility

Most North American species of *Ribes* are susceptible to infection by *C. ribicola*. Kimmey (1938) summarized over 20,000 tests with both artificial and natural inoculations of western species grown in open, partial-shade and shade. Rankings among species and populations are made by multiple comparison tests and field observations. In general, but not without exception, species with higher receptivity also produce more telia (Kimmey 1938). *Ribes nigrum* is often included in a test as a susceptible control. It consistently develops a high percentage of leaf surface area infected. Especially when grown in the open, it supports production of abundant urediniospores and teliospores (Kimmey 1938; Snell 1942; Mielke 1943).

Of all the *Ribes* native to western North America, *R. hudsonianum* var. *petiolare* is the most susceptible (Hahn 1928; Mielke et al. 1937) under either open-canopy or partial-shade conditions (Kimmey 1938). *Ribes bracteosum* Dougl. ex Hook., *R. roezlii* under open-canopy or partial-shade conditions (Kimmey 1938), and *R. inerme* Rydb. (Lachmund 1934a) are also highly susceptible. However, *R. hudsonianum* var. *petiolare* produces many more telia than *R. roezlii* or open-grown *R. inerme* (Mielke and Hansbrough 1933; Mielke et al. 1937; Kimmey 1938). Mielke (1937) suggested that low production of telia in open-grown *R. inerme* results from the combined stress of severe infection and drought. However, in some natural settings, abundant urediniospore production has been observed on *R. inerme* next to *R. hudsonianum* var. *petiolare* that were only producing telia (author, pers. obs.). *Ribes lacustre*, *R. viscosissimum* Pursh and *R. sanguineum* produce relatively few telia, in amounts typical of less susceptible species (Lachmund 1934a; Kimmey 1938). *Ribes tularense* (Coville) Fedde and *R. montigenum* are both rated as medium in susceptibility (Kimmey and Mielke 1944). Almost all the common species of southern Oregon are highly susceptible (Kimmey 1935).

For some species, regional populations vary in both aspects of susceptibility—receptivity and capacity to produce telia. Xeromorphic forms of *R. cereum* with smaller, waxy leaves appear to be less receptive to infection than other forms of this generally resistant, telia-poor species. But some populations of *R. cereum* under certain conditions are readily infected and support abundant telia production (Kimmey 1938; Kimmey and Mielke 1944). *Ribes roezlii* populations from southern California have the highest susceptibility expressed by the species; those from British Columbia have intermediate susceptibility (Kimmey and Mielke 1944; Kimmey and Wagener 1961). *Ribes roezlii* from northern California are the most variable in susceptibility; compared with populations from British Columbia, these have lower average infection rates but produce more telia.

3.2 Inoculum loss, vigour and species interactions affecting pine infection

Even among *Ribes* with similar rates of *C. ribicola* infection, their contribution to the effective inoculum pool varies. Differences occur for casting infected leaves and preference for habitats with different environment potentials for infection (riparian or upland). Spore vigour and duration of viability may be related to host species. In addition, for *Ribes* that differ in phenology of susceptibility, production of spore types, or casting of infected leaves, co-occurrence can synergistically increase pine infection over the contributions of the individual species.

3.2.1 Leaf casting

Abscission of infected leaves occurs in many susceptible *Ribes*, is extreme in some species, and is affected by environment and disease severity. *Ribes* planted at an open-canopy site more readily shed infected leaves than at a partial-shade site (Kimmey and Wagener 1961). In nearly any species, defoliation can occur in severely infested bushes. At one planting in Oregon, nearly 90% of the leaves of the susceptible *Ribes* were prematurely cast (Kimmey 1935). Species in the West particularly prone to leaf casting are *R. divaricatum* Dougl., *R. inerme*, *R. roezlii* and *R. pinetorum* Greene (Mielke 1943; Van Arsdel et al. 2006). In the East, *R. cynosbati* L. and *R. rotundifolium* are similarly prone to leaf casting (Spaulding 1922a; Van Arsdel et al. 2006).

Patterns and effects of leaf casting are well illustrated by *R. roezlii*. In its native California habitat, this species readily defoliates in response to infection, frost, exposure to sun or low-soil moisture (Mielke and Hansbrough 1933; Mielke et al. 1937; Kimmey 1944). This species casts even lightly infected leaves when planted outside of its native range (Kimmey and Wagener 1961). Unlike most other *Ribes*, *R. roezlii* retains some leaves for more than one year; infected leaves of the previous year are more likely to be cast than current-season leaves (Kimmey 1944). As occurs in other susceptible and easily defoliated species, leaf drop by *R. roezlii* early in the season may be followed by a flush of new, very receptive leaves.

3.2.2 Teliospore timing and inactivation

Leaves of *R. lacustre* shift to teliospore production earlier than those of other, more susceptible *Ribes*. This early formation supports Waters (1928) hypothesis that the onset of maturity-related resistance, stress or depletion of photosynthate reserves in the host shifts many rusts from production of urediniospores to teliospores. Early telia production may advance the timing of pine infection from fall to spring. In the cool climate of coastal British Columbia, *R. bracteosum*, *R. lacustre* and *R. lobbii* A. Gray support telia beginning early in the growing season and could produce inoculum as early as spring (Buchanan and Kimmey 1938; Hunt and Jensen 2000).

Telia on leaves of *R. cynosbati* cast early in autumn-lacked germination, whereas those telia on similar leaves of *R. nigrum* retained a high germination rate (Spaulding 1922a). Viability was retained longer for harvested leaves of *R. nigrum* and *R. americanum* Mill. than from *R. cynosbati* and *R. rotundifolium*. Teliospores survived 87 days on *R. nigrum* leaves, over 4-times longer than those on *R. rotundifolium* (Spaulding and Rathbun-Gravatt 1925). Comparisons are lacking for the common susceptible species in the West.

3.2.3 Basidiospore vigour

Basidiospores from *R. nigrum* have a higher survival rate after drying and brief exposure to sunlight than those from seven native species under identical experimental conditions (Spaulding and Rathbun-Gravatt 1926b).

3.2.4 Habitat preferences

Habitat preferences and topographic position affect *Ribes*' capacity to support production of viable basidiospores that are effective inoculum to infect white pine. Teliospores on *R. hudsonianum* var. *petiolare* (and presumably other *Ribes*) in moist valleys can become ineffective shortly after production by early germination (Mielke 1943). Telia on heavily infected *R. viscosissimum* and *R. lacustre* in low, riparian areas may be less effective than lightly infected upland bushes because dew formation promotes early germination that precedes the time when pine infection can occur (Mielke 1937). In the East, frequent, short periods of rain or dew in July and August can initiate teliospore production and germination but not allow sufficient time for pine infection. These special meteorological conditions can identify areas of low hazard (Charlton 1963).

3.2.5 Synergism

For telial host species to have a synergistic interaction, they must be close enough for urediniospore dispersal between them. Typical of rusts, dispersal curves (viable spores deposited over distance from source) display a steeply declining slope and very long, right tail; the rate of decline depends on several characteristics of the environment and of the spore (McCubbin 1918; Van Arsdel 1960; Frank et al. 2008). Snell (1920) recovered viable urediniospores only within 15 m of their source. Spaulding (1922b) found infected *R. glandulosum* and *R. cynosbati* within 91 m of a source *R. nigrum* and recovered viable urediniospores 274 m downwind. Although high atmospheric moisture favours bush-to-bush infection, it also causes urediniospores to adhere in clumps that limit long-distance dispersal (author, personal observation).

In eastern North America, *Ribes cynosbati* is very susceptible but usually sheds infected leaves prior to telia production; *R. americanum* has low susceptibility and late rust development but produces telia. Synergism occurs where urediniospores from *R. cynosbati* increase the numbers of *R. americanum* infections, consequently increasing local telia and pine infection. In the Sierra Nevada, *Ribes roezlii* often defoliates early but produces a flush of susceptible leaves that are infected from the co-occurring, non-defoliating, *R. nevadense* (Mielke and Hansbrough 1933; Kimmey 1944).

Synergistic interactions can occur between species of different but connected habitats. The alpine *R. montigenum* often grows with whitebark pine (*Pinus albicaulis* Engelm.) or limber pine (*P. flexilis* James) but is heavily infected only rarely. *Ribes hudsonianum* var. *petiolare* is a riparian species that grows below the alpine zone; it often supports abundant production of urediniospores. If urediniospore transport on updrafts from a lower riparian area to the alpine zone were occasionally to increase *R. montigenum* infection, basidiospore production and infection of the nearby pine could also increase (Newcomb 2003).

Early phenological development in a susceptible species can foster synergism. *Ribes lacustre* produces leaves susceptible to infection by aeciospores very early in the season; urediniospores from *R. lacustre* infecting nearby bushes of slower-developing *Ribes* species could then initiate longer and more productive cycles of *C. ribicola* intensification leading to more pine infection.

3.3 *Ribes* of greatest importance to blister rust

A final factor in the contribution of *Ribes* to infection of white pine is the stage of the *C. ribicola* epidemic in the region. Initial establishment of an epidemic has been attributed to several highly susceptible *Ribes* species—*R. nigrum*, *R. hudsonianum* var. *petiolare*, *R. inerme*, *R. bracteosum*, *R. sanguineum*, *R. divaricatum*, *R. nevadense* and *R. roezlii* (Pennington 1925; Detwiler 1928; Lachmund 1934a; Mielke et al. 1937; Mielke 1938, 1943; Kimmey and Wagener 1961). These susceptible hosts can be infected at distances to hundreds of kilometres from aecial and uredinial sources. Inoculum produced on these *Ribes* and on white pines then infects less susceptible but locally abundant or synergistic *Ribes* species which then intensify an infestation.

3.3.1 Eastern states and provinces

Ribes nigrum was the most significant source of inoculum for early spread in the northeastern states because this highly susceptible species occurred on abandoned farms in close proximity to eastern white pine, *Pinus strobus* L. (Spaulding 1914; Reynolds 1918; Posey and Ford 1924). Itself an introduced species, *R. nigrum* rapidly decreased in importance as eradication programs quickly eliminated it (Spaulding 1914; Maloy 1997). The important native *Ribes* were *R. cynosbati*, *R. rotundifolium*, *R. glandulosum* and *R. americanum* (Reynolds 1918; Littlefield 1930; Fivaz 1931). *Ribes lacustre* was a minor species in the region and rarely infected (Detwiler 1920; Cooper 1922; Fivaz 1931). Robust *R. cynosbati* was abundant in pastures and open areas and was frequently infected (Cooper 1922). In Vermont, this species was a major target of early eradication, even though there were only 12–15 bushes per ha (Spaulding 1922b). The few *Ribes* that now persist in New England occur primarily in the midst of stone walls or in lowlands, and only infrequently in forests. However, Bergdahl and Teillon (2000) found nearly all the *Ribes* present were infected.

In southern Appalachia, the principal *Ribes* are *R. cynosbati* and *R. rotundifolium*. Blister rust only occurs on eastern white pine and *Ribes* at sites with frequent fogs and dews in a narrow elevational zone above 917 m (Yost and Hepting 1947; Ball 1949; Powers and Stegall 1971). Although the range of eastern white pine includes lower elevations, *Ribes* are restricted to higher elevations and blister rust is limited to favourable infection sites supporting both hosts.

There are several important *Ribes* species in Ontario—*R. glandulosum*, *R. triste* Pall., *R. hudsonianum* var. *hudsonianum*, *R. americanum*, *R. hirtellum* Michx and *R. inerme* (Haddow 1969). Other species present are *R. lacustre*, *R. cynosbati*, *R. oxyacanthoides* L. and *R. rotundifolium* (Zavitz and Duff 1922). The formerly cultivated lands in eastern Ontario are virtually *Ribes*-free but roadsides, fence rows and pastures within the agricultural zone support *Ribes* (Haddow 1969). In Quebec, the principal species is *R. hirtellum* (Lavallée 1992).

The blister rust epidemic in the Lakes States started at the border between Minnesota and Wisconsin and was initially carried only by *R. cynosbati* (Washburn 1917). In southern Wisconsin, the important *Ribes* are *R. cynosbati*, *R. missouriense* Nutt. and *R. americanum.* In northern Wisconsin, *R. glandulosum* and *R. triste* (Van Arsdel et al. 1961) are the important species; *Ribes lacustre* is a minor host (Habeck 1960). *Ribes glandulosum*, *R. hirtellum* and *R. triste* are important in northeastern Minnesota (Stewart 1957).

3.3.2 Northwestern states and provinces, including the inland white pine region

In the West, *C. ribicola* was first detected in southern, coastal British Columbia on *Ribes nigrum* (Hunt 2009). In settled areas, this cultivated species contributed significantly to early spread, but the infestation soon spread across British Columbia, including the dry, pine-free, interior areas. Even in far southeastern Washington, *R. nigrum* was infected at an early date, even though there were no white pines nearby and the nearest infestation was 300 km away.

Intensification and spread of blister rust occurred on additional species as *C. ribicola* established in less populated areas. In British Columbia, the most important and abundant native *Ribes* were *R. lacustre*, *R. bracteosum*, *R. divaricatum*, *R. sanguineum* and *R. viscosissimum*. The first four were also important in western Oregon and Washington (Mielke 1943). West of the Cascade crest in these states, *R. bracteosum* was important for early establishment of blister rust and continues to be a major host (Bedwell and Childs 1943; Mielke 1943). East of the crest, the important species was *R. inerme* (Bedwell and Childs 1943).

For interior populations of western white pine, the important *Ribes* in British Columbia were *R. viscosissimum* and *R. lacustre* (Buchanan and Kimmey 1938; Hunt 1983). In northern Idaho, these species were important along with *R. hudsonianum* var. *petiolare* and *R. inerme*. Mielke (1943) attributed the initial establishment of blister rust in northern Idaho to the later two species. *Ribes hudsonianum* var. *petiolare* was the most important species for epidemic spread across the region; within a few years, *C. ribicola* was common across the Inland Northwest on western white pine. After an infestation was established, the less-susceptible, upland species, *R. viscosissimum* and *R. lacustre* were infected and contributed to further intensification.

Within Yellowstone National Park (northwest Wyoming and adjacent states), eradication was meant to protect whitebark pine and limber pine from blister rust produced on

R. lacustre, *R. viscosissimum*, *R. inerme*, *R. hudsonianum* var. *petiolare* and *R. oxyacanthoides* ssp. *setosum* (Lindl.) Q. P. Sinnott (Gynn and Chapman 1949; McDonald and Hoff 2001). More recently and more widely across the area, *R. oxyacanthoides* ssp. *setosum* on open slopes and *R. montigenum* sheltered under whitebark pine were only found to be infected infrequently (Newcomb 2003).

3.3.3 Other pine regions of western coastal states

For the sugar pine region of Oregon and California, Mielke (1938) implicated the highly susceptible *Ribes roezlii* var. *cruentum* (Greene) Rehder in the original, upper-slope establishment of the rust. *Ribes sanguineum* var. *glutinosum* (Benth.) Loudon and *R. bracteosum* were important for infestations on lower slopes. The highly susceptible *R. nevadense* was infected up to 200 km from known infestations on white pine (Mielke 1938).

Several susceptible *Ribes* species occur in southern Oregon (Kimmey 1935). *Ribes roezlii* var. *cruentum* occurs above the Rogue River, *R. klamathense* (Coville) Fedde in riparian and lakeshore areas, *R. marshallii* Greene at sites that are wet in spring but dry in the late season, *R. sanguineum* on open sites, *R. binominatum* A. Heller on steep slopes with shifting soil, *R. erythrocarpum* Coville & Leiberg at upper elevations under whitebark pine and mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière), and *R. velutinum* Greene on rocky, dry slopes.

In California, *R. roezlii* is the most abundant, widespread, and important *Ribes*; *R. nevadense* also occurs (Kimmey and Wagener 1961). *R. roezlii* is the only *Ribes* in portions of the Siskiyou Range and comprises 90% of the population in the Sierra Nevada (Kimmey and Wagener 1961). The susceptibility of this species allows it to become infected from sources several kilometres distant, but most telia-bearing leaves are shed by late October (Kimmey and Wagener 1961). This *Ribes* can be a significant inoculum source in the occasional years when August weather is favourable for rust development and pine infection (Kimmey and Wagener 1961). Although the riparian *R. nevadense* is less prevalent, it can become heavily infected if there is a local inoculum source; and because it retains infected leaves, it contributes to infection of *R. roezlii* and white pines. *Ribes cereum* is common in some locations (Mielke 1943).

3.3.4 Regions of recent spread

Cronartium ribicola has recently spread eastward and southward across the Rocky Mountains (southern Idaho, Wyoming and adjacent areas) and the Southwest (Arizona and New Mexico). Isolated populations of limber pine, whitebark pine, southwestern white pine (*Pinus flexilis* James var. *reflexa* Engelm. syn. *P. strobiformis* Engelm.), and Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.) have been infested (Geils et al. 2010; Schwandt et al. 2010). Van Arsdel and Geils (2004) and Kearns et al. (2008) identified the *Ribes* species, their distribution, habitats and apparent importance in these regions.

Krebill (1964) found infected limber pine in southeastern Idaho near infected *R. viscosissimum*. Later observations in the general area found infected *R. hudsonianum* var. *petiolare* (B. Geils, pers. comm.).

Both *R. cereum* and *R. montigenum* occur in the whitebark pine stands of the Jarbidge Mountains (northeast Nevada). Vogler and Charlet (2004) found only *R. cereum* to be infected which suggested it may be the important telial host of the area, but *R. hudsonianum* var. *petiolare* also occurs (B. Geils, pers. comm.) and may have played a role in establishing an epidemic. Because the incidence and severity of *Ribes* infection varies so much from year-to-year in warm, dry regions, a few, incidental observations may not be sufficient to determine the relative importance of *Ribes* species. When Smith et al. (2000)

first discovered a white pine infestation in western Nevada, neither *R. cereum*, *R. montigenum* nor *R. nevadense* appeared to be infected.

Custer State Park, South Dakota is presumably the eastern-most extent of the western population of *C. ribicola* (DNA marker evidence in Zambino et al. 2003). Lundquist et al. (1992) found blister rust on *R. cereum* with the first discovery of infected limber pine. Blodgett (2005) reported *R. oxyacanthoides* ssp. *setosum* and ssp. *oxyacanthoides* are also common in the area.

Kearns et al. (2008) identified *R. cereum*, *R. inerme*, *R. lacustre* and *R. montigenum* as the most common *Ribes* in Wyoming and Colorado associated with limber pine. Although several species can be found together in any of the isolated ranges of central and southern Wyoming, each *Ribes* displayed its own, typical habitat preferences—*R. cereum* for dry, open sites; *R. inerme* for wet, rocky sites; *R. lacustre* for mesic forest sites; and *R. montigenum* for alpine and subalpine sites.

Blister rust infection of southwestern white pine generally occurs where *R. pinetorum* is abundant (Van Arsdel et al. 1998, 2006; Geils et al. 1999). But, the *Ribes* flora of the Southwest varies by mountain range and habitat; so, in certain localities, other *Ribes* species such as *R. inerme, R. montigenum*, *R. lacustre* or even *R. velutinum* may be more important inoculum sources (Van Arsdel and Geils 2004; Van Arsdel et al. 2006). *Ribes pinetorum* generally occurs at elevations above 2740 m or in canyon bottoms on north aspects. *Ribes cereum* is often locally abundant with white pines but is commonly infected with *Coleosporium ribicola* Arthur rather than *Cronartium ribicola*. Van Arsdel and Geils (2004) reported that *R. mescalerium* Coville, *R. wolfii* Rothr. and *R. aureum* were infrequent species with little to no importance for blister rust.

3.4 Pine infection relationships to distance from telial host species

Sources, modes of transport and sinks for viable basidiospores of *C. ribicola* are critical factors for white pine infection. Basidiospores form on hair-like columns of teliospores on the leaves of telial hosts. Forcible ejection of basidiospores effects dissemination from the leaf surface. Airborne transport is affected by numerous processes—gravimetric flow of cooling air, prevailing winds, weather patterns, localized funnelling of air flow by physiographic features and temperature inversions, convective air circulation over lakes and diffusion and dissipation within turbulent air. Regional geography and local physiographic features dictate whether pine infections originate predominately from sources within the pine stand (local spread) or from distant sources (long-distance dispersal). Distance estimates of basidiospore transport range from 15–18 m (Buchanan and Kimmey 1938), 0.8 km (York 1926), 1.6 km or greater (Mielke 1943; Martin 1944), to 16–27 km (Van Arsdel 1965b). The relationship between *Ribes* source and pine infection is obscured with increasing distance and the multiplicity of weather events and air-flow patterns favouring dispersal and infection (Buchanan and Kimmey 1938). Patterns of pine infection and distances of effective dissemination also differ from year-to-year with annual variation in the weather (Pennington 1925).

3.4.1 Local spread from Ribes *bushes*

The incidence of pine infection declines sharply with distance from a source (Van Arsdel 1960). Most pine infection is limited to several hundred meters (Posey and Ford 1924; Buchanan and Kimmey 1938; Kimmey and Wagener 1961). The decrease of effective infection with distance results from dilution, settling of condensation droplets carrying basidiospores (Gregory 1945; Kimmey and Wagener 1961; Pruppacher and Klett 1997), screening by vegetation (Spaulding 1929), and loss of basidiospore viability (Spaulding and Rathbun-Gravatt 1926b; Mielke 1943).

The directional distribution of pine infection results from repeated patterns of air flow such as the wind vectors of late summer and autumn storms (POSEY and FORD 1924). In the sugar pine region, warm fronts and down-slope air flow on open slopes and in ravines control the process (BUCHANAN and KIMMEY 1938; KIMMEY and WAGENER 1961). Rains from cyclonic warm fronts increase soil moisture and relative humidity near the ground; subsequent calm and clear nighttime conditions permit radiant heat loss and the down-slope flow of cool, moist air that initiates germination, carries basidiospores, and allows infection (KIMMEY and WAGENER 1961).

3.4.2 Long-distance dispersal

Long-distance transport of basidiospores is demonstrated in the landscape patterns of pine infection and the distributions of tracer compounds or rust cankers. The adiabatic cooling of moist air masses accounts for the high occurrence of blister rust on slopes facing prevailing or storm winds. Rising air generates fog; with condensation, the air mass releases sufficient heat to cool it to a temperature conducive for inoculum formation and pine infection (VAN ARSDEL 1965b). Valley temperature inversions limit down-slope transport and protect germinating spores from the cooling effect of radiant heat loss (VAN ARSDEL 1967; VAN ARSDEL and KREBILL 1995).

In California, fall storms initiate mass-air flow by adiabatic cooling that leads to a high rust incidence of sugar pine in stream basins and at the head of canyons (QUICK 1962a). Infection of western white pine and whitebark pine in moist, maritime or upland areas of the Northwest may have similar origins. In stands where there are few to no upland *Ribes*, white pines may be infected by mass-air flow over distances of 0.4–1.6 km from large populations of riparian *Ribes* (BEDWELL and CHILDS 1943; MIELKE 1943). MARTIN (1944) attributed infection of whitebark pine at creek heads to basidiospores from heavily infected *Ribes* growing along the lower creeks.

Ribes growing in the open and above a pine stand present a particularly severe hazard by long-distance dispersal (MARTIN 1944; MOSS and WELLNER 1953; HUNT 1983). Based on release and recovery of silver iodide particles in Idaho, LLOYD et al. (1959) attributed rust incidence in a *Ribes*-free pine stand to a distant patch of upland *Ribes.* Basidiospores originated on the upper north slope of Diamond Peak under clear fall conditions with a prevailing north wind; the spores were transported down-slope and southward by cold air drainage, then lofted upward in warm air rising over Petit Lake, and carried over the pass to the white pines 1.6 km south of the lake.

The position of rust cankers within an infested crown also implicate the occurrence of long-distance dispersal. Within western white stands in British Columbia, cankers near the ground result from *Ribes* inoculum produced in the stand; cankers high in the crown result when inoculum from a distant source is carried into the stand by down-slope air flow (HUNT 1983).

Inoculum sources vary greatly, even in the relatively low-relief Lake States (VAN ARSDEL and KREBILL 1995). In lake-free areas, the *Ribes* mostly responsible for pine infection occur in the immediate vicinity. But near a lake, diurnal breezes can interact with the surrounding land to effect long distance dispersal, as demonstrated by smoke patterns (VAN ARSDEL 1965a, 1967). For the northern, coolest regions, along the Great Lakes, *Ribes* plants near the shore are generally rust-free because cool spring temperatures delay or prevent infection; but *Ribes* 8 km inland may be heavily infected. Basidiospores from these inland *Ribes* can be carried down-slope toward a large lake, lofted in a convective updraft over the water, deposited 16–27 km from their source, and cause infection even where *Ribes* are locally rare or absent (VAN ARSDEL 1965a; DAHIR and CUMMINGS 2001). Numerous infections often develop high in the canopy where a lateral convective flow approaches a lake shore slope. Smaller-scale convective patterns occur over smaller lakes and marshes of the southern, warmer regions of the Lakes States; here the most important inoculum sources are *Ribes* inhabiting marshes or near shorelines (Van Arsdel 1972).

4 Implications for management of white pine blister rust

4.1 Management to alter *Ribes* presence and retention

Management of *Ribes* includes the practices of eradication, forest harvesting and burning to deplete seed bank reserves and manipulating canopy density to reduced *Ribes* persistence. Controlling *Ribes* within a stand could have a benefit for local spread, but reducing *Ribes* at a larger scale could lower the landscape hazard. This review focuses on practices directly affecting *Ribes*. Integrated forest management benefits from a strategic approach (Schwandt et al. 2010) and includes use of genetics (King et al. 2010) and silviculture (Ostry et al. 2010; Zeglen et al. 2010).

4.1.1 Ribes *in assessment of hazard*

Hazard assessments rate the environmental potential for infection of susceptible pines. Factors used to estimate hazard include: (1) incidence (percent infected) and rust index (infections per unit of needle area) (Hunt 1983; Goddard et al. 1985; Hagle et al. 1989); (2) weather and climate (Charlton 1963; Van Arsdel 1965b; Van Arsdel and Krebill 1995); (3) topographic and site characteristics of slope, aspect, elevation, latitude and proximity to lakes or streams (Van Arsdel and Krebill 1995; Geils et al. 1999; White et al. 2002) and (4) forest density, age and canopy closure (Van Arsdel 1967; Van Arsdel and Krebill 1995). Epidemiological models use these factors to simulate their effects on components of rust development, such as aeciospore production, repeating infection cycles, teliospore production and inactivation, basidiospore production and dispersal and pine infection (McDonald et al. 1981, 1991).

Many hazard assessments directly account for the effects of *Ribes* abundance and distribution (Stillinger 1944; Moss and Wellner 1953; McDonald et al. 1981, 1991; Lavallée 1986a; Hagle et al. 1989). Other assessments indirectly consider *Ribes* by a proxy factor of distance to potential *Ribes* habitat (Van Arsdel et al. 1961; Charlton 1963). Because *Ribes* may be absent from suitable habitats (Haddow 1969) and their density is variable, even in similar habitats (Newcomb 2003; Kearns et al. 2008), hazard estimates are improved with data for *Ribes* abundance and distribution. In many cases, recognizing the different roles of *Ribes* species and combinations that contribute to infection further improves the assessment (cf. Muller 2002; Kearns 2005).

Sampling for *Ribes* density presents several challenges, because populations change over time and present different statistical distributions (Fracker and Brischle 1944). Populations with a random distribution are easier to describe (e.g., *R. rotundifolium* in New York; Fracker 1936) than populations with a clustered distribution (e.g., *R. rotundifolium* in Pennsylvania or riparian species). Where a significant portion of the pine infection results from long-distance dispersal, *Ribes* abundance within a stand may be uncorrelated to hazard (Van Arsdel et al. 1961).

4.1.2 Ribes *eradication*

Historically, the principal approach for control of blister rust was *Ribes* eradication (Maloy 1997; Geils et al. 2010). Differences in the relative contribution of various *Ribes* species to pine infection were recognized early in the eradication program; *R. nigrum* and *R. glandulosum* were initially targeted as the most important species (Reynolds 1918). Eradication guidelines recommended removal of all *Ribes* plants, of all species, within

180–275 m of the pines to be protected (ANONYMOUS 1920); but complete protection was not expected (DETWILER 1920).

Intensive hand labour to eradicate *Ribes* was expensive (OFFORD et al. 1940, 1958; Fig. 1). The entire eradication program for the United States was about one-billion current US dollars (MCDONALD et al. 2006; : calculating from figures in MALOY 1997). These costs were no longer justifiable as reserves of white pine timber dwindled, incidence fell and correlations between *Ribes* abundance and infection declined. For example, TOKO et al. (1967) and CARLSON and TOKO (1968) determined that annual infection rates after eradication in 53 young, white pine stands averaged only 3% per year and were not correlated to the number of remaining *Ribes* bushes. They concluded that further eradication in northern Idaho would provide little additional benefit.

The long-term effects of *Ribes* eradication are difficult to ascertain. After 70-years of eradication in Maine, rust incidence in eastern white pine was lower for treated stands than for untreated stands (3.8 *vs.* 9.1%, respectively; OSTROFSKY et al. 1988). In the Lake States, less-than-complete eradication (<62 bushes per ha) proved effective for minimizing infection in eastern white pine (MARTIN 1944). Even in northern Idaho, rates of infection and mortality were markedly lower after eradication than generally occurred during the initial incursion of blister rust prior to establishment of the eradication program (TOKO et al. 1967). Besides eradication, other factors may effect changes in rust incidence and the correspondence between rust incidence and *Ribes* abundance. Factors proposed by MCDONALD et al. (2004) as deserving additional study include: (1) infection from telial hosts in genera other than *Ribes*; (2) telial hosts that have little urediniospore cycling and (3) infections from long-distance dispersal.

4.1.3 Telial hosts in other genera

In eastern Asia, several genera in addition to *Ribes* serve as telial hosts of blister rust fungi infecting white pines (KIM et al. 2010; ZHANG et al. 2010). Telial hosts of *C. ribicola* in genera other than *Ribes* occur in North America (ZAMBINO et al. 2005, 2006, 2007; MCDONALD et al. 2006). These telial hosts are *Pedicularis racemosa* Dougl. ex Benth. (sickle top lousewort), *P. bracteosum* Benth. (bracted lousewort), and *Castilleja miniata* Dougl. ex Hook. (scarlet paintbrush) in the Orobanchaceae (formerly Scrophulariacaeae). A fourth species, *C. rhexifolia* Rydb. (alpine paintbrush), produced urediniospores and teliospores after artificial inoculation (ZAMBINO et al. 2005, 2006). The two genera are similar to *Ribes* in their adaptation to disturbance, but are hemiparasitic on roots of various host species and have wind-blown seed dispersal (ALLARD 2001). Thus far, blister rust has been confirmed on non-*Ribes* telial hosts at two upper montane sites in Idaho (ZAMBINO et al. 2005, 2006; MCDONALD et al. 2006) and one site in California (D. Vogler, pers. comm.). Since only telia have been found so far on natural infections, these might only infrequently effect uredinial intensification of inoculum common on *Ribes* hosts.

4.1.4 Stand management effects on Ribes

Because management alters stand composition and environment, practices such as thinning, harvesting and even grazing can affect the prevalence of telia hosts and the microclimate of rust development (DAVIS and MOSS 1940; MOSS and WELLNER 1953). Management objectives include depleting the *Ribes* seed bank, minimizing growth and persistence of *Ribes* bushes, promoting establishment of white pine and avoiding climatic conditions that favour pine infection.

Thinning depletes *Ribes* seed banks through germination. As little as 20–30% open canopy in western white pine habitats stimulate germination of *Ribes* while minimizing their long-term survival (DAVIS and MOSS 1940; MOSS and WELLNER 1953). However, a

Fig. 1. Use of herbicides in 1927 to eradicate *Ribes* in northern Idaho. (a) Crew mixing herbicide and filling backpack sprayers. (b) Several decades after major fires in the region, *Ribes* had grown to form large, upland bushes and riparian thickets that were a challenge to handheld sprayers. These images were taken soon after blister rust was discovered in northern Idaho and illustrate how, at the time, protecting white pine by controlling blister rust was considered of paramount importance; intangible costs to health and environment were underrated by today's standards; and accomplishing control in northern Idaho was difficult compared to reforested farmlands of New England.

tradeoff is that low-intensity thinning provides insufficient light to regenerate western white pine (Jain et al. 2004). The potential effectiveness of thinning depends on which *Ribes* species are present. For *Ribes* common in the Inland Northwest, the order of shade tolerance is *R. viscosissimum* (eliminated at 60% open canopy) < *R. hudsonianum* var. *petiolare* < *R. lacustre*. The latter species establishes at 40% open canopy, fruits at 30% and layers at 10% (Davis and Moss 1940; Mielke 1943; Moss and Wellner 1953). Fins et al. (2001) suggested caution in thinning and advised use of low-to-moderate intensity thinning only after *Ribes* have been shaded out.

Clearcutting without subsequent *Ribes* control allows *Ribes* resurgence (Quick 1954); however, dense establishment of early seral conifers speeds *Ribes* suppression. Broadcast burns 3–5 years after clearcutting kill young *Ribes* before they seed; if burn intensity is low, then a second burn can eliminate survivors (Davis and Moss 1940; Moss and Wellner 1953). Small openings are more attractive than large openings to the rodents that consume *Ribes* seed and damage stems (Quick 1954).

Management also changes the microenvironment that affects teliospore germination, basidiospore dispersal and infection of *Ribes* and of pine. In different white pine ecosystems, pine infection may be favoured if *Ribes* are shaded (Kimmey and Wagener 1961), in small openings (Van Arsdel et al. 1961), or within or at the edge of openings of different sizes and aspects (Van Arsdel and Krebill 1995). By decreasing the density of undergrowth screening basidiospore dispersal, grazing favours pine infection (Habeck 1960).

4.2 Pathosystem change

There are numerous examples of precipitous decline in blister rust incidence where native white pines have long been in contact with the introduced *C. ribicola* (Haddow 1969; McDonald et al. 2005b). Such examples seem encouraging, but require explanation. A variety of factors are suggested—natural selection for constitutive or induced resistance, increase in natural biological control and diversification of pathogen populations to include variants that are less aggressive (Zambino and McDonald 2004; McDonald et al. 2005b). A change in a host population (either *Ribes* or pine) by natural selection for resistance represents progress in disease reduction unless overcome by new virulence or aggressiveness in the pathogen population. Stands have also been altered for decreased host density, less inoculum, increased *Ribes*-to-pine distance and screening conditions that promote disease escape. The major concern is whether reduced pine infection will prove to represent progress toward a persistent population of white pines or whether *C. ribicola* would rebound if management increased the populations of white pines and *Ribes*.

4.2.1 Costs of rust susceptibility: driving force for natural selection of resistance in Ribes

Natural selection for disease resistance occurs whenever a pathogen poses a significant selective disadvantage to susceptible plants and resistant plants are present. Blister rust affects the survival and fecundity of *Ribes*. Pennington et al. (1921) reported a case of the complete loss of *R. cynosbati*, *R. rotundifolium* and *R. glandulosum* after two consecutive years of rust-induced defoliation. Pluta and Broniarck-Niemiec (2000) noted that a heavy, natural infection of *R. nigrum* resulted in defoliation, decreased winter survival and subsequently poor fruit production. Competition among *Ribes* seedlings can be intense; in one case, fewer than 2% of seedlings regenerating after eradication survived for more than 2 years (Pennington et al. 1921). Rust susceptibility had to affect seedling survival; but little is known whether natural selection for resistance is more effective in leaf-shedding or non-leaf-shedding species, in seedlings or established bushes, and with or without additional physiological stress, such as shade.

4.2.2 Variability within species and rust strain-specific interactions

Two types of resistance—R-gene and multigenic resistance—are known in European currants and appear to be present in North American species (Zambino and McDonald 2004). R-gene resistance (or major gene resistance, see King et al. 2010) results from specific recognition by a plant of a factor (product of an *avr* gene) produced by a pathogen. R-gene resistance is the most prevalent form of plant resistance to rusts and other biotrophic fungi. R-gene resistance is expressed in tissues of all ages, is effective across diverse environments and levels of inoculum, and can only be overcome by strains that do not express the *avr* allele. R-gene resistance is positively identified by: (1) segregation analysis (inheritance as a single, usually dominant trait; Ekramoddoullah and Hunt 2002; Zambino and McDonald 2004); (2) DNA sequence motifs and (3) reversals in susceptibility of different hosts to different strains of rust (see Richardson et al. 2010). R-gene resistance is treated as a qualitative trait that is simply inherited.

Multigenic resistance is treated as a quantitative trait with complex inheritance (Zambino and McDonald 2004; King et al. 2010). Its effectiveness varies with host physiology, pathogen aggressiveness and environment. Multigenic resistance is least effective in young plants and non-hardened tissues; infection occurs where partial-resistant hosts have increased exposure to inoculum or remain in juvenile, succulent states. Multigenic resistance is indicated if individuals rank in the same order for disease susceptibility with exposure to different conditions and strains.

The best documented R-gene resistance of *Ribes* to infection by *C. ribicola* is the *Cr* gene. It has single-gene, dominant inheritance and confers immunity (Brennan 1996; Luffman 2000). The *Cr* gene of *Ribes* is effective even under experimental conditions that favour rust development (Zambino 2000). The *Cr* gene has been transferred to commercial European black currant cultivars by crossing *R. nigrum* with *R. ussuriense* Jancz. (see Hummer and Dale 2010).

Evidence for R-gene resistance in North American *Ribes* is found in patterns of immunity and reversals in susceptibility. Immunity has been reported by Hahn (1928), Mielke (1937) and Kimmey (1938). In the highly susceptible *R. hudsonianum* var. *petiolare* (a close relative of *R. nigrum* and *R. ussuriense*; Senters and Soltis 2003), 10–15% of clones were immune to blister rust under even the most favourable conditions for infection (Mielke 1937). Other clones of this and additional species (*R. viscosissimum* and *R. inerme*) display strong resistance but lack immunity; for these, the least infection occurs among open-grown plants (Mielke 1937). Several possible mechanisms could explain this response, such as (1) multigenic resistance whereby either sunlight enhances maturation and resistance, or (2) R genes which confer less-than-complete immunity (a common situation in other rust pathosystems; Zambino and McDonald 2004), or (3) a combination of responses to a mixed-rust inoculum.

Ribes lacustre displays the most difference in infection between open-grown and partial-shade plants (Mielke 1937). This difference and the typical, early development of telia in the species suggest these responses are related to tissue maturity and multigenic control. However, Anderson and French (1955) found significant reversals in relative resistance of genets of both *R. cynosbati* and *R. lacustre* exposed to rust sources from different hosts and geographical regions, which implies R-gene resistance.

Inoculations of leaf disks from 50 genets of four *Ribes* species with four rust sources (McDonald and Andrews 1980, 1981, 1982) showed evidence of both R-gene and multigenic resistance (McDonald 2000; Zambino and McDonald 2004). Infection rate was highest with pairings of genet and inoculum from the same location, a result that would be expected if rust populations were genetically better fit to their local hosts than to other populations. One genet of *R. hudsonianum* var. *petiolare* remained uninfected after inoculation with a rust source from western white pine growing near Champion Mine, Oregon. A strain of *C. ribicola* at this location is virulent on western white pine carrying the *Cr2* gene (see McDonald et al. 1984; Kinloch et al. 1999); but this strain also appears to be less aggressive on both *Ribes* (McDonald 2000) and white pines without the *Cr2* gene (McDonald et al. 1984). Adaptation enabling the rust to overcome R-gene resistance in the pine may impose a 'cost of virulence' in terms of its genetic fitness on both pines and *Ribes*. McDonald (2000) concluded that the lack of infection in the one *R. hudsonianum* genet could be due to either R-gene or multigenic resistance.

Species of *Ribes* also serve as telial hosts for *Cronartium occidentale* Hedgc., Bethel, & N. Hunt (Hedgcock et al. 1918). Hahn (1928) inoculated various species of *Ribes* with *C. ribicola* and *C. occidentale*; some individual plants were susceptible to just one or the other pathogen. Similar results were obtained with genets of *R. hudsonianum* var. *petiolare* from an Idaho location exposed for 80 years to *C. ribicola* but 500 km from known populations of *C. occidentale* (author, unpubl. data). The observation that genets were immune to only *C. occidentale*, to only *C. ribicola*, to both rust species, or highly susceptible to both suggests resistance that depends on recognition of a specific rust (as in R-gene resistance) may be common among the *Ribes*.

4.2.3 Selection, adaptation and change in Ribes *rust, and environment*

Resistance in *Ribes* appears to be sufficiently prevalent for natural selection to occur, but *C. ribicola* also evolves. The occurrence of natural selection for resistance can be investigated by comparing the relative proportions of resistant *Ribes* in populations challenged by the pathogen. Contrasts could be made between areas with older epidemics to areas with younger epidemics or by comparing bushes that have survived long exposure to the rust to plants from seed banks that predate arrival of the rust. Resistance that persists after a cycle of forest regeneration indicates development of *Ribes* populations that produce less inoculum. Additional studies might identify rust strains that overcome resistance and assess the resulting costs of virulence.

Other factors that can alter relationships between *C. ribicola* and its hosts include rust expansions into new geographic areas and climatic changes that shift the distributions of hosts and pathogen. Rust spread to new areas, particularly to high-elevation sites, provides an opportunity for adaptation to climatic factors through altered temperature-germination profiles and for acquiring or fine-tuning adaptation to other telial hosts (i.e., *Pedicularis* and *Castilleja*).

Knowledge of the biogeographical history of *C. ribicola* is incomplete, but the pathogen in North America has experienced at least two genetic bottlenecks as result of its leaps first to northern Europe and then to North America (Kinloch et al. 1998; Hamelin et al. 2000; McDonald et al. 2004; Richardson et al. 2008; Geils et al. 2010). The North American rust has an eastern and a western population, and both populations primarily utilize *Ribes* as the telial host. In Asia, blister rusts infect either *Ribes*, *Pedicularis* or both (Kim et al. 2010; Zhang et al. 2010). Although non-*Ribes* telial hosts, *Pedicularis* and *Castilleja*, were only recently found in nature in North America, inoculations (Hiratsuka and Maruyama 1976; but see Hunt 1984) and histology (Patton and Spear 1989) demonstrate a fundamental compatibility of the rust with these genera. Vogler (2000) and Vogler and Bruns (1998) suggested that specialization on telial hosts drives evolution in the *Cronartium* rusts. *Castilleja* is a common host for species of *Cronartium* that infect yellow pines (subgenus *Pinus*) and have broad telial host ranges (Hunt 1992; Vogler and Bruns 1998). Strains of *C. ribicola* from diverse hosts and locations across the United States have a shared ability to infect *Pedicularis* (Richardson et al. 2007). Further study of rust strains and plant populations from diverse regions would significantly contribute to an understanding of the role of non-*Ribes* telial hosts, including their distribution, epidemiology and threat.

4.3 Potential effects of increased *R. nigrum* cultivation

Several states have removed restrictions on cultivation of *R. nigrum* (McKay 2000); and some growers are interested in adding this black currant to their operations (Mashburn 2000). Although this *Ribes* was considered the agent most responsible for spread of *C. ribicola* in early epidemics, the situation now is quite different and deserves re-appraisal. Would cultivation of *R. nigrum* pose a significant threat to white pine stands and ecosystems (Bergdahl and Teillon 2000; Muir and Hunt 2000; and see Hummer and Dale 2010)? Considerations include whether: (1) cultivation is restricted to resistant cultivars (Barney 2000); (2) resistant cultivars remain resistant to all strains (Bergdahl and Teillon 2000; Zambino 2000); (3) basidiospores from susceptible cultivars affect local pines (Barney 2000; Muir and Hunt 2000); (4) routine disease control by fungicides or dormant oils minimizes risk; (5) susceptible *R. nigrum* or hybrids establish beyond production areas by seed or pollen; (6) pollen dispersed from susceptible, heterozygous resistant cultivars pollinate native species (Bergdahl and Teillon 2000); and (7) these hosts affect the genetic diversity of the rust population (Barney 2000; Bergdahl and Teillon 2000).

Other threats are a lesser concern. Cultivated *Ribes* establishment in forest plantations and wildlands is unlikely because local species should be better adapted to their native habitats than domesticated cultivars. The opportunity for hybridization is low if plants are not sufficiently close to allow cross-pollination. As with other plants, hybrids of *Ribes* may also be less fit, more susceptible to parasites, and more readily eliminated by natural selection than native species (see Combes 1996).

4.4 Species of special concern

Although some *Ribes* species are abundant or even considered noxious weeds, a few taxa are rare endemics in at least a part of their distribution (USDA NRCS 2009). *Ribes echinellum* (Coville) Rehder is threatened (Department of Interior, Fish and Wildlife Service 1985, 2007), but it is endemic to Florida and South Carolina, well outside the distribution of white pines. Twelve additional taxa are endangered, threatened, of special concern, or sensitive. *Ribes cereum* var. *colubrinum* Hitchc. is endangered in Washington state (Washington Natural Heritage Program, 1990) and a sensitive species in Montana (Lesica and Shelly 1991). *Ribes oxyacanthoides* ssp. *irriguum* (Dougl.) Sinnott is threatened in Washington (Washington Natural Heritage Program, 1990). *Ribes oxyacanthoides* ssp. *cognatum* (Greene) Sinnott is a sensitive species in Montana (Lesica and Shelly 1991) and a candidate of federal concern (Sinnott 1985). Chumley and Hartman (2000) discovered a small population of *R. niveum* Lindl. in Colorado, far removed from the Pacific Northwest where it is endemic. Even telial hosts significant in the spread of blister rust (*R. hudsonianum* and *R. glandulosum*) are threatened in some states (USDA NRCS 2009).

Several *Ribes* are critical resources for wildlife. *Ribes malvaceum* and *R. speciosum* provide Anna's hummingbird (*Culype anna*) with an important source of nectar in its breeding territory (Stiles 1982). Grizzly bear (*Ursus arctos*), a threatened species (Department of Interior, Fish and Wildlife Service 2007) feed on the fruits of *Ribes*, particularly *R. lacustre* (Mealey 1975; Zager 1980; Hamer et al. 1991; Hunt 2000).

The occurrence of rare *Ribes* and animals dependent on *Ribes* can complicate efforts to manage white pine ecosystems (Schwandt et al. 2010). A practical response for their conservation is to manage for a state of ecosystem function in which both *Ribes* and pines retain or regain their significance as early seral species within a dynamic ecological community. The disturbances necessary to sustain rare *Ribes* and dependent species can also maintain the white pines that are the keystone species of such communities. The requirements of rare species and functional white pine ecosystems dictate careful selection and application of management practices, and a sound conceptual understanding of the interplay among white pines, *Ribes*, and associated species.

5 Implications

Ribes differ by species and population in their importance to the spread and epidemiology of *C. ribicola*. Their effects on pine infection derive from their distributions and abundance, ecological persistence, ability to support rust infection, and occurrence in habitats and environments that favour or disfavour spore production and dispersal. Knowledge of these differences and their effects on pine infection contribute to an improved understanding of blister rust hazard and to better approaches for white pine management. The analysis and modelling of the population dynamics of telial hosts at species and species-interaction levels and across landscapes can assist management planning. Appropriate information includes the aspects of landscape pattern and disturbance history that affect *Ribes* presence, differences in persistence of inoculum from different telial hosts, patterns of spore dispersal from various hosts (including commercial *Ribes* where this is a concern), and differences in resistance among *Ribes* populations.

The unfolding evidence is that over time, all the major organisms in the pathosystem – *Ribes*, white pines and blister rust—are adapting and evolving. Understanding the interactions between natural selection for resistance in aecial and telial hosts and the evolution of *C. ribicola* to its hosts and adaptation to its environments is therefore critical for managing natural and cultivated ecosystems of white pines and *Ribes* at risk from white pine blister rust.

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