

Epidemiology for Hazard Rating of White Pine Blister Rust

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Abstract—The ability to assess the potential for a severe infestation of white pine blister rust is an important management tool. Successful hazard rating requires a proper understanding of blister rust epidemiology, including environmental and genetic factors. For the blister rust caused by *Cronartium ribicola*, climate and meteorology, and the ecology, distribution, and pathology of ribes and other telial hosts affect spread and intensification of rust on white pine hosts (several sections in subgenus *Strobos* of genus *Pinus*). The importance of ribes (genus *Ribes*) for supporting effective inoculum production varies according to differences in susceptibility, diversity, distribution, and abundance by taxon and population. Temperature and humidity regimes and air circulation patterns at micro to synoptic scales influence the development and dispersal of the rust. Spatial and temporal variations in the dispersal processes are expressed as differences in rust severity distributions. These differences can be mapped as hazard zones and used to choose among alternative management prescriptions. When *C. ribicola* was first introduced to North America, its epidemiological behavior displayed a limited range of hosts and environments. The diversity of related rusts, however, suggests that *C. ribicola* may have the capacity to adapt to previously unrecognized hosts and environments. Pine populations have also shown some ability to respond with lower susceptibility to this introduced pathogen, indicating that the North American pathosystems are dynamic and evolving. Efforts to manage such high-elevation species as whitebark pine would be aided by continued research in the epidemiology of this pathosystem in diverse hosts and environments.

Ribes and Meteorology Affect Spread

Success in protecting, sustaining, and restoring white pine ecosystems (Samman et al. 2003) requires the understanding that epidemics of *Cronartium ribicola* (white pine blister rust) differ by region, landscape, and site. These differences result, in part, from variation in the

biology and pathology of ribes¹, limitations imposed by weather and climate, and genetic interactions of the hosts and pathogen. Both ecological and evolutionary processes determine where, how often, and how much the rust spreads and multiplies.

Mielke (1943) illustrated that an epidemiological approach could explain the early spread of the rust in western North America. In the coastal pine region of British Columbia, rust spread was more rapid to the north than to the south because of more favorable winds, hosts, and climate. Winds also had carried aeciospores to the interior white pine belt; but limited distributions of highly susceptible ribes retarded buildup of the rust, even where moisture was adequate. Spread in the western white pine stands of the Inland Empire (northern Idaho, eastern Washington, and far western Montana) was early and rapid—white pine and very susceptible ribes were abundant neighbors in a favorable climate. In spite of adequate winds, however, spread into higher mountains farther east or south was delayed and slow (because the temperatures were usually too low for ribes infection). At cool elevations, even on highly susceptible whitebark pine, canker growth was slow; there were few generations of rust; and growing seasons were short. In the southern Cascades, precipitation diminished, but adequate moisture still permitted infection; susceptible white and sugar pines and very susceptible ribes were present. Winds to transport spores from north to south were more frequent in the Coast Range (early spread) than in the Cascade Range (later spread). Winds capable of transporting spores were even less frequent near the California state line where a sharp, wind deflection to the east limited spread to northern California, a region with susceptible hosts and an otherwise favorable climate.

In this paper, we review selected historical literature and identify developing concepts and technologies for applying epidemiological information to mapping potential losses from white pine blister rust. Observations on the present distribution and damage from blister rust provide baseline data for monitoring and initial modeling of hazard. A defensible projection of future trends and

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¹ Species of currants and gooseberries are in the genus *Ribes*. These plants are also identified with the common noun, 'ribes' and in some, older literature, the proper noun, 'Ribes'. In this paper, we refer to these plants by their common, general name unless a technical, taxonomic name is required.

expected impacts, however, requires a greater understanding of the ecological and genetic interactions of hosts and pathogen and the environmental effects of temperature, moisture, and air circulation. This understanding begins with knowledge about the principal telial hosts in the genus *Ribes*.

Ribes Diversity, Susceptibility, and Importance

There are numerous species, subspecies, varieties, ecotypes, and cultivars of ribes that differ in their response to blister rust infection, to their proximity to white pine, and to their epidemiological importance. Susceptibility is the capacity of a ribes to become infected and support inoculum production. Susceptibility is a genetic trait that varies by plant and environment (reviewed in Zambino and McDonald 2004). It can differ with the growth and habitat of the ribes and with exposure to different strains or pathogenic races of the rust. Susceptibility may be quantified or ranked from field observations, or from inoculations in the field, greenhouse, or petri-dishes. Because of genetic interactions and host physiology, assessment of susceptibility can be affected by technique.

Clinton and McCormick (1924) reported limited success with inoculations of detached leaves. More recently, Zambino (2000) examined R-gene resistance in horticultural ribes using single-leaf cuttings. McDonald and Andrews (1981) described leaf-disk inoculations; and McDonald (2000) demonstrated geographic variation in susceptibility and interactions between rust and ribes. Other recent assessments used relative infection in common gardens, under natural, or artificial inoculation conditions (Hummer and Finn 1999; Hummer and Picton 2002).

Environment and developmental stage of the ribes greatly affect infection rate efficiency. Young, succulent, greenhouse-grown plants or leaf cuttings inoculated in moist chambers can show very high levels of infection that are well above levels seen in hardened, open-grown, field plants. Leaves are more readily infected after full expansion, and then decrease in receptivity with age (Harvey 1972; Lachmund 1934; Pierson and Buchanan 1938; Spaulding 1922a; Zambino 2000). The period when aging leaves can be infected is extended if shoots become dormant (Harvey 1972). Previous work also suggests that infection is significantly greater in the less hardened plants that grow in full or partial shade than in open-grown plants in full sun (Hahn 1928; Kimmey 1938; Mielke et al. 1937). Van Arsdel attributes much of the difference in natural infection of open-grown versus shaded plants to duration of conditions adequate for infection (temperature and dew period) rather than other

leaf attributes (Van Arsdel et al. 1956; Van Arsdel 1965b). The type of infecting spores can also have an effect. Urediniospores¹ can cause significant infection in ribes leaves that would be 1 to 2 weeks too mature for aeciospore-initiated infection (Pierson and Buchanan 1938).

We use the term 'importance' of different ribes to describe their relative roles in blister rust spread and intensification. Epidemiological importance combines susceptibility (pathology and genetics) with abundance and distribution of ribes and pines (ecology). A very susceptible ribes can be rated low in importance if it were rarely associated with the pine hosts. Conversely, the importance of a ribes would be elevated if its proximity to other ribes and pines resulted in a synergistic increase of infection. For example, *Ribes cynosbati* is very susceptible to infection, whereas *R. americanum* has low susceptibility. Where only *R. cynosbati* is abundant, infection of the pine is uncommon because infected leaves of this species are usually shed before telia mature. Where only *R. americanum* is abundant, infection of the pine is nearly absent because infection on the ribes is infrequent and late so very few telia develop despite a large, host-leaf surface area. Where both ribes occur, pine infection may occur because abundant uredinia on the *R. cynosbati* cause some infection of the *R. americanum* which then produce a few telia. Other susceptible and early-defoliating species are *R. pinetorum* in the Southwest and *R. roezlii* in California. *Ribes montigenum* is an alpine species that often grows next to or under whitebark pine or limber pine but is seldom observed to be heavily rusted. *Ribes hudsonianum* var. *petiolare* is a western, riparian plant that grows below the alpine zone; it is very susceptible and capable of supporting a large inoculum potential. This ribes may occasionally act synergistically with *R. montigenum*. Occasionally, urediniospores from distant *R. hudsonianum* var. *petiolare* cause heavy infections of *R. montigenum* in close proximity to pine and may lead to heavy pine infection (see Newcomb 2003). Importance is thus a function of the susceptibility of individual ribes plants and inoculum potential of the alternate host community.

The susceptibility and infection potential of western ribes had been reported by numerous authors. Spaulding and Gravatt (1917) conducted an early susceptibility test but did not rank species. Taylor (1922) quantified basidiospore production per unit area for several species. Hahn (1928) found that most ribes of the Northwest were susceptible to both *Cronartium ribicola* and *C. occidentale*. Mielke (1937) and Mielke et al. (1937) noted differences in susceptibility for the ribes associated with

¹ Uredospores or urediospores of older literature, terminology here follows that of the current American Phytopathological Society glossary of terms at <http://www.apsnet.org/education/IllustratedGlossary/>.

western white pine. Kimmey (1935, 1938, 1944), Buchanan and Kimmey (1938), Kimmey and Mielke (1944), and Kimmey and Wagener (1961) made field observations and inoculations in other western regions. As mentioned, the expression of susceptibility may be influenced by leaf age, shading, or leaf temperature and wetness. More recently, Hummer and Finn (1999) reported on three years of uredinia production on 55 accessions of ribes exposed to natural infection in an open-grown garden. They noted variation within taxonomic sections of the genus (see table 1), between species, and within species. Van Arsdel and Geils (2004) interpreted and summarized results of these studies for the ribes of the interior, western states (table 2).

Table 1—Sections of genus *Ribes* (by subgenera) with representative species

Subgenus <i>Ribes</i>		currant
<i>Calobotrya</i>	<i>R. cereum</i>	stinky
<i>Coreosma</i>	<i>R. hudsonianum</i>	black
<i>Heritiera</i>	<i>R. laxiflorum</i>	dwarf
<i>Ribes</i>	<i>R. rubrum</i>	red
<i>Symphocalyx</i>	<i>R. aureum</i>	golden
Subgenus <i>Grossularioides</i>		gooseberry
		currant
<i>Grossularioides</i>	<i>R. lacustre</i>	spiny currant
Subgenus <i>Grossularia</i>		gooseberry
<i>Grossularia</i>	<i>R. oxyacanthoides</i>	

Identification of Ribes

Ribes are shrubs, to 3 m tall or with prostrate or sprawling growth, and distinguished from similar shrubs by several characteristics (see Van Arsdel and Geils 2004). Leaves are alternate, simple, palmately veined, palmately lobed, with doubly serrate edges. Flowers have five petals, five sepals, five stamens, and a one-chambered ovary with a double style. The withered flowers remain attached to the berry as it ripens. The alternate leaves differ from the opposite leaves of maple and viburnum. Leaves lack a bitter taste, in contrast to the bitter leaves of ninebark. Ribes have no stipules at the base of the petiole, unlike ninebark and thimbleberry. Leaves of *Ribes americanum* have trichomes; the otherwise similar leaves of New Mexico raspberry lack these glandular hairs.

The genus *Ribes* includes three subgenera found in the interior western states. The currants (subgenus *Ribes*) have no spines or bristles and a mature berry which detaches cleanly from its jointed petiole (bearing several fruits); the gooseberries (subgenus *Grossularia*) are usually armed with nodal spines and the petiole remains attached to the berry; spiny currants or gooseberry currants (subgenus *Grossularioides*) are armed with spines and internodal bristles and have jointed floral petioles. The several sections of the genus represented in the interior West provide a natural classification below the subgenus level (table 1).

It is necessary to identify ribes by species because they vary greatly in epidemiological importance. We recognize 19 species in the interior western states (table 2, expanded from list in Van Arsdel and Geils 2004); several of these species are further classified into subspecies or varieties (not presented here). Usually only a few species occur in a given forest, although many more may occur in the region. Identification begins with a review of the ranges and ecological distributions of the local ribes flora (e.g., Holmgren 1997). Floral and fruit characteristics are diagnostic. Ribes flower early in the growing season; fruit develop and persist to mid-season. Familiarity with the local ribes in flower and fruit allows confident identification of specimens later in the season when leaves are infected.

Ribes Distribution and Abundance

Although ribes occurs across North America, there are notable differences in the mixture of species in the local flora and in their distribution and abundance by region, landscape, and site. Ribes eradication, successional stage, natural disturbance, duration of exposure to rust, and chance events can each potentially affect ribes populations, their genetics, and their epidemiological importance. In the eastern states and provinces, the single most epidemiologically-important ribes had been the cultivated *Ribes nigrum*; wild ribes there are much less susceptible and less important. Ribes eradication in northeastern states had been aggressive and effective. In these areas, continued low levels of ribes, along with other characteristics (such as the preponderance of pine in abandoned fields that previously lacked ribes) have resulted in a low level of lethal infection of young pine. Present levels of disease in these pines cannot be taken as an indication that future rust damage would not occur if *R. nigrum* were again widely cultivated in proximity to pine. In the southern Appalachians, the important host is *R. cynosbati*. This ribes grows at higher elevations than eastern white pine, co-occurs at mid-elevation, and is absent at lower elevations of the white pine distribution (fig. 1). In the interior West, ribes are rare in certain portions of the range of white pines, such as the Davis Mountains, TX, Santa Rita, AZ, and Snake Range, NV. There are, however, diverse susceptible rust-infested communities of ribes in the Sacramento Mountains, NM and Jarbidge Mountains, NV (Vogler and Charlet 2003). Even small, isolated populations of ribes can support a rust outbreak. Examples include the Black Hills, SD; Gallinas Peak and San Francisco Mountains, NM; and the Sangre de Cristo, CO (Blodgett and Sullivan 2004). Reconnaissance of areas such as these provides an initial assessment of rust hazard and the potential role of disease escape in the developing epidemic. A genetic inventory of *Cronartium ribicola* populations across its entire range would greatly improve our understanding of evolutionary

Table 2—Importance of *Ribes* species of the interior West^a to the spread and intensification of white pine blister rust.

Species	Section	Class ^b	Comments
<i>R. nigrum</i>	black	A	cultivated
<i>R. hudsonianum</i>	black	A	= <i>R. petiolare</i> ; northern (to n. NV and UT, w WY); wet
<i>R. americanum</i>	black	C	western
<i>R. wolfii</i>	black	C	
<i>R. laxiflorum</i>	dwarf	B	= <i>R. coloradense</i> ; northwestern to UT (one locality) and CO
<i>R. rubrum</i>	red	D	cultivated
<i>R. viscosissimum</i>	stinky	B	western; disturbed
<i>R. cereum</i>	stinky	D	includes several ssp.; western
<i>R. mescalerium</i>	stinky	D	NM endemic
<i>R. aureum</i>	golden	C	native, cultivated; western; important host for <i>C. occidentale</i>
<i>R. lacustre</i>	spiny	B	western; forest
<i>R. montigenum</i>	spiny	B	western; alpine
<i>R. pinetorum</i>	gooseberry	A	NM and AZ
<i>R. inerme</i>	gooseberry	B	western; may hybridize with <i>R. o. setosum</i>
<i>R. hirtellum</i>	gooseberry	B	eastern but listed for SD
<i>R. niveum</i>	gooseberry	B–C	northwestern and CO (one locality)
<i>R. oxyacanthoides</i>	gooseberry	D	with var. <i>hendersonii</i> (NV) and <i>setosum</i> ; UT, ID, WY, SD
<i>R. leptanthum</i>	gooseberry	D	AZ, NM, UT
<i>R. velutinum</i>	gooseberry	B	AZ, NM, UT, NV; important host for <i>C. occidentale</i>

^a southern ID, WY, CO, UT, NM, and adjacent portions of MT, SD, AZ, and NV.

^b *Ribes* are classified on the basis of their susceptibility to infection and capacity to produce telia under field conditions. “Class A” species have the highest potential for contributing to spread; “Class B” species have moderate or variable potential; “Class C” species have low potential; and “Class D” species are usually insignificant.

potential in the pathosystem (McDonald et al. 2004, 2005, and in press; see also Zambino et al. submitted).

Disturbance and succession change the distributions and age structures of pine and ribes, alter ribes-to-pine proximity, affect ribes population structure, and influence local microclimate. Therefore, disturbance regime and successional patterns influence blister rust epidemiology, and consequently, hazard. For example, wild or prescribed fire creates regeneration opportunities for the white pine; but also benefits ribes regeneration. Ribes regenerate primarily from the soil seed-bank or from bases of surviving plants. As the overstory develops, the abundance of each ribes species declines according to its shade tolerance. With succession, species are lost from the ribes community and others assume dominance. In the moister forest habitats, canopy closure can virtually eliminate the shrubby component of the understory. Within the range of western white pine in the Inland Northwest, four well-represented species of ribes ranked by epidemiological importance are *Ribes hudsonianum* var. *petiolare*, *R. inerme*, *R. viscosissimum*, and *R. lacustre* (Mielke et al. 1937). Shade tolerance is lowest for *R. viscosissimum*, intermediate for *R. inerme* and *R. hudsonianum*, and greatest for *R. lacustre*. Although neither *R. viscosissimum* nor *R. lacustre* rank high for importance, where they co-occur on some sites, *R. viscosissimum* produce abundant urediniospores which infect *R. lacustre* which then produces teliospores (Zambino, pers. observation). Loss of *R. viscosissimum* after canopy closure ends this synergism.

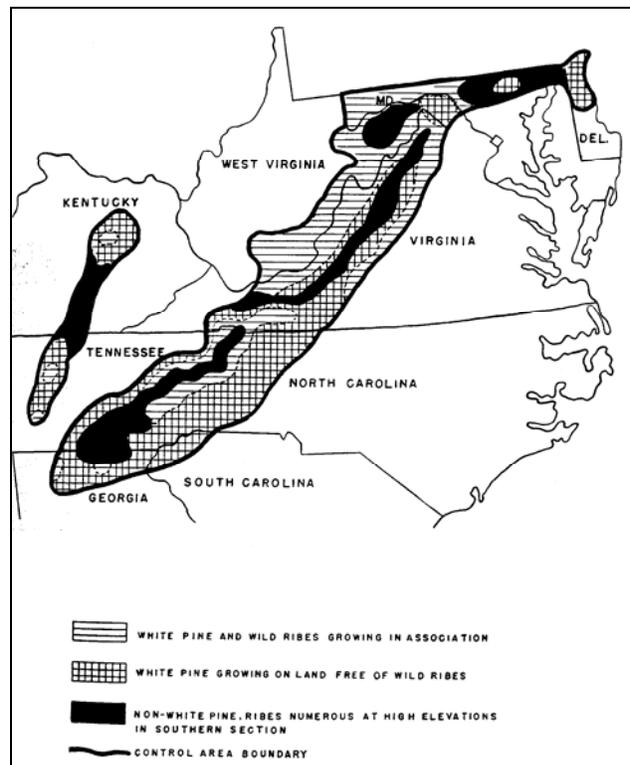


Figure 1—Association of white pine and wild ribes in the southern Appalachians (adapted from Ball 1949).

Ribes genetics

One might expect that a ribes species or community with similar densities and other characteristics would

contribute to hazard in a simple, predictable manner at every site. Ribes at different sites, however, belong to different populations with different histories and different genetics and frequencies of resistance mechanisms. Site-to-site differences of ribes for resistance to blister rust have been largely unexplored. Variability in resistance among individuals within a species is well documented by early and repeated studies (Hahn 1928; Kimmey 1938; Mielke et al. 1937). Resistance in wild ribes may be due to both R-gene and multigenic inheritance, as demonstrated for cultivated, European species (reviewed in Zambino and McDonald 2004). A complex distribution of R-gene resistance within the genus *Ribes* is also further indicated by recently identified clones of North American species that are completely immune to *C. ribicola* but susceptible to *C. occidentale*, and clones of the European species *R. nigrum* that are highly susceptible to *C. ribicola* but immune to *C. occidentale* (Zambino pers. observation). The highest proportion of apparently immune clones of North American ribes reported by Mielke and others (1937) was about 15 percent in *Ribes hudsonianum* var. *petiolare*—a taxon usually considered highly favorable for rust development.

Ribes populations exposed to severe and prolonged rust may have changed significantly in resistance from those with only recent or moderately low rust presence. Rust has been shown to cause premature defoliation in both European and North American species of ribes and to lower survival in winter dormancy. The genetic cost of supporting rust infections could also cause more susceptible ribes to be prematurely stressed and to drop out of the population more readily, even before low light levels usually limiting to survival have been reached. As mentioned, ribes can regenerate from banked seeds even several hundreds of years after canopy closure. There is the potential that ribes established after a severe disturbance may “reset the clock” that is, re-gain a high susceptibility similar to pre-rust levels, even at sites where resistance had increased over the century. These topics require further investigation.

Meteorology Influences Development and Dispersal _____

Environmental factors besides moisture, especially temperature regime and air circulation, control the timing and pattern of rust spread (Van Arsdel 1965b). Temperature affects rate of pine-host tissue colonization, development of spore-bearing structures, spore release, spore germination, and infection. Temperature responses differ at the various stages of the life cycle. Wind is important for carrying spores for local spread and long distance dispersal. Desiccation and solar radiation each affect spore viability, with differences among spore stages. Because reproduction and dispersal of blister rust

is strongly affected by meteorological phenomena, climatic information, including daily and seasonal patterns and storm frequencies, are useful for predicting hazard. The following, selective review summarizes the micrometeorological requirements for blister rust as described by Spaulding (1922b), Spaulding and Rathbun-Gravatt (1925, 1926a, 1926b), Hirt (1935, 1937, 1942), Mielke (1943), Riker et al. (1947), Van Arsdel (1952, 1954), Van Arsdel et al. (1956), Bega (1959, 1960), McDonald and Andrews (1980), and Zambino et al. (1997). These investigations of rust spores and infected plants represent a limited number of populations; various authors use different rust and host populations and methods; they report different responses. Further refinements can be expected as behaviors of newly established populations in different regions are studied over time.

Aecial Stage

Aeciospores produced from perennial cankers on white pines can disperse few to hundreds of kilometers, land, and infect telial hosts (mostly ribes). Aeciospores are usually produced in the spring, over a wide range of moderately warm temperatures from 16 to 28° C. They are discharged in day or night when the air is saturated and within a few hours of blister opening. Fresh aecia are uncommonly found at some high-elevation sites as late as the end of August. McDonald et al. (in press) report that such late-season spores from whitebark pine at one site in northern Idaho were still infective on locally-collected specimens of *Pedicularis racemosa* under artificial inoculation conditions. Although it is unknown whether local conditions would allow natural infection this late in the growing season, leaves and flowers were still being produced on the *Pedicularis*, and all the local hosts (*Ribes hudsonianum* var. *petiolare*, *R. lacustre*, *R. inerme*, *P. racemosa*, and *Castilleja miniata*) bore young telia. If recent infections from aeciospores had occurred there, the environment appeared to favor the teliospore stage on the alternate hosts required to infect pine, as predicted by local temperature regimes (see below). So, aeciospores produced even late in the season could still have epidemiological importance.

Aeciospores are stimulated to germinate by freezing or exposure to 32 to 36° C for 8 hrs, but germination is restricted if they are exposed for 36 hrs to 36° C (fig. 2). Free water or saturated air is required, but the necessary duration of exposure depends on temperature, varying from 5 to 25 hrs over a temperature range from 8 to 24° C. The minimum duration is 5 hrs at an optimum temperature of 12 to 16° C; minimum temperature for germination is from 5 to 8° C; maximum is from 19 to 24° C. Under normal conditions, spores can remain viable for several weeks to an extreme of 6 months (longer under

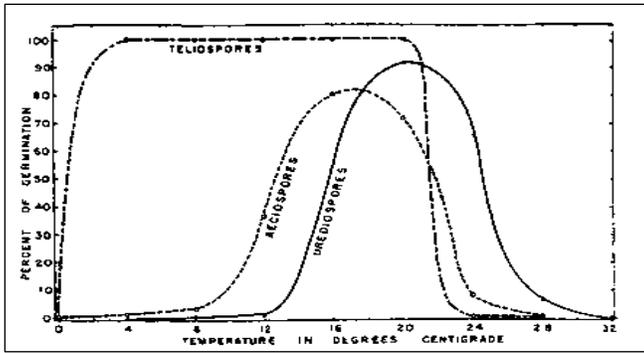


Figure 2—Germination of spores of the white pine blister rust as affected by temperature (from Van Arsdel et al. 1956).

low-temperature storage; Zambino 1997). Strong light rapidly reduces viability of most spores. The minimum time for ribes infection by aeciospores is 7 to 8 days of moderately warm weather for production of aeciospores, followed by 12 hrs of saturated air for spore release, and another 5 hrs at 16 to 20° C at >97% RH and wet ribes leaves for germination and infection.

Uredinial Stage

Urediniospores are produced on ribes leaves and dispersed within the same bush, to nearby bushes or, less frequently, to distant bushes. The period of urediniospore production starts 7 to 24 days after initial infection, up until mid-August when conditions are usually unfavorable for urediniospore production. The optimum temperature range for urediniospore production is from 14 to 20° C, with a nocturnal lower limit of 2° C. Formation of urediniospores can be inhibited by several days exposure to temperatures above 35° C before resuming optimum conditions, and prevented by 10 days exposure to this temperature. Under most natural conditions, viability of mature urediniospores declines rapidly and is less than 2 weeks; germination is best from fresh spores but can be poor in cool weather. Germination begins 4 to 6 hrs after spores are released and exposed to warm, saturated air and free water on the ribes leaves. A minimum temperature for germination ranges from 8 to 16° C, the maximum is from 25 to 28° C; and the optimum is 14 to 20° C (fig. 2). Provided that plants have not been exposed to very warm temperatures, the scenario for ribes to be infected by urediniospores is a daytime temperature of 16 to 28° C for 7 to 24 days to produce the spores, followed by 4 to 12 hrs at 20 to 24° C, saturated air, and wet target leaves for urediniospore release, germination, and fresh infection.

Telial Stage

Teliospores are produced on alternate hosts and germinate in place to produce probasidia and basidiospores. The season of teliospore production on ribes begins a minimum of 2 weeks after aecial or uredinial infection. Production is stimulated by cool temperatures but inhibited by 3 consecutive days above 28° C, nocturnal lows above 20° C, or daily highs above 35° C. The favorable range for teliospore formation is 1 to 20° C, with optimum at 16° C. Warm (>20° C) or cold (0° for 12 hrs) temperatures at formation affect germination, but spores can recover from freezing. Teliospores remain viable for several weeks and germinate best at an age of 4 to 9 days, after exposure for about 12 hours to free moisture (rain, fog, or dew), and at temperatures (fig. 2) from 10 to 18 (optimum 16)° C (range 0–1 to 21–22° C).

Basidial Stage

Basidiospores¹ are delicate, short-lived spores produced from telia on the non-pine host, and are dispersed up to several kilometers to infect white pine. The season for basidiospore production begins when viable teliospores are present and moisture is present as free water or relative humidity exceeds 97% (germination is best at 100% RH when teliospores are in contact with water). The temperature range for basidiospore germination is from 0–1 to 20–21° C, but is best at 10 to 18° C. Basidiospore viability and germination are inhibited by a number of factors: extremes of drying and wetting (but cycles of moderate drying and re-wetting at 4° C can enhance germination rate, Zambino, pers. observation), temperature exceeding 21° C (>35° C lethal), exposure to direct light, sustained low humidity at moderate temperatures (26 hrs at 58% RH). The minimum time required at favorable temperature and humidity for the rust to proceed from teliospores to infections is variously reported as about 11 to 19 hrs; the process is usually complete by 36 hrs. Basidiospores may either germinate to form a germination tube for pine infection, or may produce secondary spores for re-dispersal. The minimum time course for pine infection given that ribes have been infected is 2 weeks of cool temperatures to produce telia, then 4 to 9 days for teliospore maturation, then (provided there had been no exposure to a 5-day period of temperature >35° C that would reduce pine infection or prolonged temperature >21° C to reduce infection), a minimum period of 48 hrs with saturated air, free moisture on leaves, and a cool temperature (<20° C); the latter provides for teliospore germination, basidial development, basidiospore germination, and germination tube penetration.

¹ Sporidia in older literature—terminology here follows Ziller (1974).

Temperature Effect

Although moisture has long been recognized as a potential constraint on rust spread, temperature can also be the critical factor in some locations. Portions of the north-central states and southern California are too warm for pine infection. In other parts of southern California, pine infections may only have resulted from infection in spring (McDonald 1996). The high western mountains—above 2700 m (9000 ft) in northern Rockies and Yellowstone plateau (Hendrickson 1970) or 3000 m (10,000 ft) in the Southwest—can be too cold for development and intensification on the ribes. Although each spore and rust infection is actually responding to its own microclimatic environment, meteorological summaries and models can be statistically useful for conditions at larger scales. Canopy and site topography may affect the temperature and control the outcome for individual rust spores or infections, but the sheer numbers in rust populations and large sizes of air masses allow properly adjusted climatic averages to be meaningful for predicting epidemics. For modeling at the landscape scale, Kearns (2005 and these proceedings) demonstrates that monthly, climatic statistics adjusted to specific sites correlate well with corresponding rust incidence. For modeling at the synoptic scale¹, Frank et al. (in preparation) illustrates that upper-level weather data with a 6-hr resolution could identify periods when surface temperature and humidity might be sufficiently favorable to allow viable long-distance dispersal and successful establishment of a new rust outbreak area.

Graphs of the percent germination of basidiospores by time and temperature (fig. 3; unpublished data from R. Krebill) illustrate that rust populations might be adapted to different temperature regimes. Graphs for rusts originating from both limber pine in a warmer environment and whitebark pine in a cooler environment demonstrate that regardless of source, teliospores produce fewer basidiospores and production is delayed at sub-optimal temperatures. However, when teliospores of rust from whitebark pine were exposed to cool temperatures at which rust from the limber pine rust produced no basidiospores, some teliospores did germinate and produce basidiospores. Also, the upper elevation rust had a longer delay prior to teliospore germination at all temperatures, suggesting an adaptation that reserves teliospores for germination during periods that will be sufficiently long to allow the complete pine infection process. This implies that at the cooler elevations where whitebark pines are found, there is a selected portion of

the rust population adapted to completing its life cycle under locally prevalent conditions.

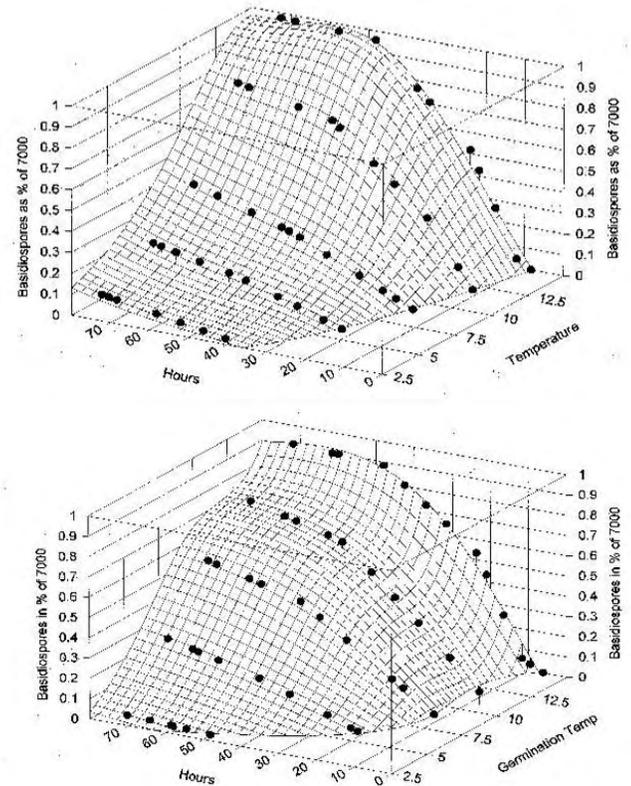


Figure 3—Germination of basidiospores from telia on *Ribes lacustre* artificially inoculated with aeciospores collected from whitebark pine (upper graph) or limber pine (lower graph). Aeciospores had been collected from Yellowstone National Park from whitebark pine at Tom Miner Basin (2900 m) and limber pine at Golden Gate Pass (2130 m). Telia of the two sources were produced in a common environment on plants inoculated on the same date. Data from unpublished work by R. Krebill; graphs adapted from G. McDonald and presented by Zambino et al. (2002). Erratum: multiple scale by 100 for percent.

Dispersal

There are two forms of dispersal—diffusion and transport. Diffusion occurs on a local scale as the density of spores for deposition and infection from a single source declines in magnitude with distance according to a power function (e.g., the square root function). Although diffusion-like models were developed in early rust studies, Van Arsdel (1967) demonstrated that spores are also commonly dispersed by transport within an air mass (fig. 4). Transport occurs at multiple scales as a result of laminar flow of distinct air masses differing in density, which are eventually disrupted by turbulent mixing. Such transport provides a “pipeline” which directs spores from an

¹ Pertaining to meteorological phenomena occurring at the scale of migratory high and low pressure systems of the lower troposphere, with length scale of 1000–2500 km and time scales exceeding 24 hrs (Whiteman, Mountain Meteorology).

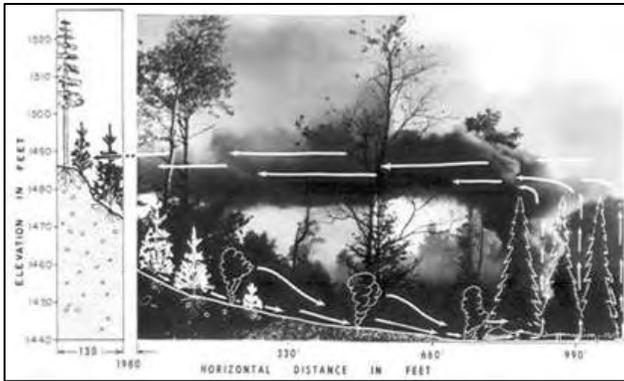


Figure 4—Smoke movements show air currents that match the spread of white pine blister rust from swamp ribes to upland white pines in northeastern Wisconsin.

inoculum source to a corresponding deposition sink; the resulting infection pattern at the sink can appear in spatially diffuse as well as in defined patches. If source–sink transport were infrequent or shifting, the resulting infection pattern would appear random or as indistinct patches. Transport may disperse rust spores locally, as with valley air circulation (this occurs frequently over a length scale of kilometers); across landscapes, as where land–water temperature differences drive air circulation (occasionally and over tens of kilometers); and even regionally, as with flow of large air masses and long distance dispersal (this occurs rarely and over many hundreds of kilometers). As an example of transport at the local scale, Quick (1962) relates canyon physiography to pine infection and basidiospore dispersal from individual ribes bushes in California. Van Arsdel (1965a, 1967) describes intermediate, landscape scale dispersal in Wisconsin from areas of high density ribes by laminar transport with an air circulation pattern driven by land–water temperature differences. Frank et al. (in preparation) discuss the relative likelihood of transport with large air masses moving from the Sierra Nevada eastward to the Rocky Mountains and Southwest.

Distribution

The observed patterns of blister rust canker distribution are the result of dispersal, infection, establishment, and recognition. Not only must spores be transported to a site, they must germinate and infect a host, intensify to a detectable level, and persist over years until chance recognition. Patterns of infection vary the most where distributions of hosts are discrete and climates favoring infection are irregularly distributed or are only marginally favorable. At a regional scale, new outbreaks or satellite infestations are seen as young cankers (3 to 25 years old) that are quite remote from previously reported infestations. Frank et al. (in preparation) suggest that long distance dispersal can transport spores, at least

occasionally, to nearly all sites downwind of a large infestation, but that further spread from and intensification at these remote sites may be limited by conditions at the deposition site. Important site factors are the distribution and size of the local telial host population, its proximity to pine, and the extent or frequency of a suitable environment (temperature and humidity regime). On a local scale, we recognize four distinctive patterns of canker distribution. Where a discrete inoculum source is nearby and climate is favorable, the number of cankers decreases with distance from source. Where there are many recognized or unrecognized sources of rust at various distances from the observed pines, canker distribution appears to be random—*incorrectly interpreted as a lack of relationship between ribes and canker abundance*. Where climate, topography, and pine–ribes distributions develop strong source–sink relationship, the rust occurs in discrete patches. Where the source–sink relationship is less strong, patches are less distinct. Where a cold climate usually prevents infection of the ribes in very close proximity to the pine (e.g., *Ribes montigenum* and whitebark pine), rust abundance on the pine is usually low and random; at these sites infection may result from infrequent transport from ribes at lower, warmer sites. The newly identified, non-ribes alternate hosts (*Pedicularis* and *Castilleja* species; McDonald et al. in press; Zambino et al.) are abundant in some upper montane sites, but their epidemiology importance and interactions require more investigation.

Hazard Management Zones

An understanding of blister rust epidemiology allows one to better map hazard and therefore manage white pine ecosystems. Hazard zones are two or more levels of potential for rust damage as mapped at a regional scale. Assumptions are that the combined presence of rust and its hosts and climate are predictable and that pines are susceptible to disease. Site hazard rating makes similar assumptions but is scaled to a defined stand or locality rather than across a landscape. Zone boundaries are delimited by pine and ribes distribution with primary consideration of regional climate and their modification by elevation, soil type, landform, and landscape structure (land–water interactions). Zones are intended to reflect the potential abundance, distribution, and infection frequency of the rust on pine. Zones should identify where different sets of management options are most appropriate and effective.

The first mapping of rust hazard zones is described by Van Arsdel (1961) for the Lake States and is updated here using a recent review of the historic, early pattern of rust spread in southern Michigan (fig. 5). Van Arsdel (1961) describes five infection-level zones and their corresponding control needs.

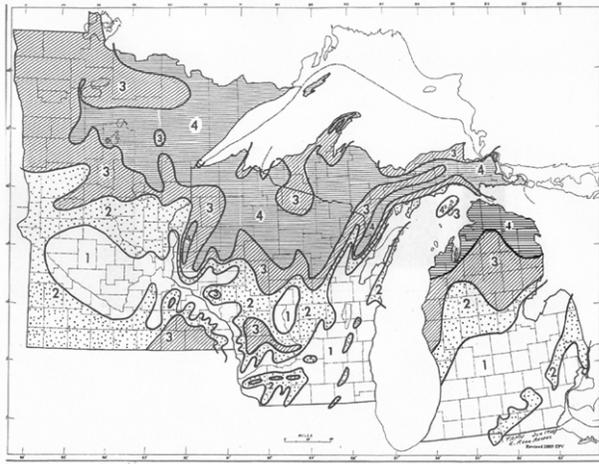


Figure 5—Hazard zones from white pine blister rust in the Lake States, updated 2005.

Zone 0 includes all areas with a mean July temperature above 23° C, which are too warm for rust development. No infestation or damage is expected.

Zone 1 includes areas where the regional climate is too warm and dry for the blister rust infection in all but those few sites where several microclimatic factors combine to moderate temperature and humidity. These sites are small canopy openings (gap diameter less than tree height) at the base of a slope where nocturnal, cold air collects. Rust infection is infrequent, and even without disease control, pine losses are expected at less than 5 percent. White pine could be cultivated without disease control.

Zone 2 is that area where the regional climate is too warm and dry for blister rust infection in most locations but a single, microclimatic factor (fig. 6) is sufficient to moderate temperature and humidity, allowing rust infection. Infections may occur on such sites as the open or brushy ground northwest of the edge of a woodlot or row of trees, which would shade morning sun and prolong the dew period. Disease control is usually not required for cultivation of white pine.

Zone 3 is that area where the regional climate is cool and moist enough for pines to become infected every few years, even on sites without any features that modify microclimate. In open fields and brush, scattered trees may be infected in the lower 2 m of crown. Damage can become severe, and disease control is recommended for commercial white pine plantations.

Zone 4 is that area where the regional climate is so cool and wet that all sites are suitable for infestation, and infection may occur throughout the crown. The extent of infestation and distribution of infections indicate that rust dispersal can occur over distances of several kilometers, resulting in severe damage. Special disease control or

avoidance measures are necessary to minimize disease impacts.

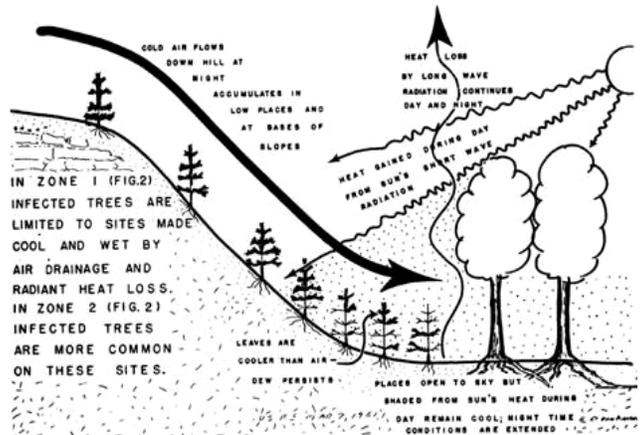


Figure 6—Drainage of cold air at night and radiant heat loss make locally cool wet spots.

Numerous hazard maps and general observations for blister rust have been published; some are reviewed here. Although control maps were routinely prepared (e.g., Ball 1949), Van Arsdel (1961, 1964 and fig. 5) expanded the mapping concept to include a more explicit consideration of climatic influences and generate a regional map of potential damage for the Lake States. Other relevant factors to be considered are the lack of ribes locally due to eradication or site characteristics (e.g., sandy soil) and lack of inoculum due to early defoliation of the locally prevalent ribes species. McDonald et al. (2004, 2005) suggest that over time, natural selection would alter the population structures of hosts and pathogens in regards to resistance and aggressiveness. Less lethal rust infections on pine, whether due to host or pathogen, would tend to survive and propagate after epidemics had removed susceptible trees, moving the pathosystem to behaviour more similar to those of endemic rusts. The regional and local effects of global climate change could also alter environmental factors with sufficient rapidity and magnitude to affect host and pathogen abilities to reproduce. Considering these historic, ecological, genetic, and climatic factors along with changing management objectives, a hazard map should be recognized as a spatial model with numerous, explicit and implicit assumptions, data dependencies, and resolution. A hazard map should be judged not for accuracy in predicting current levels of disease incidence or loss but for leading to appropriate management within a given policy framework (such as “sustaining healthy ecosystems”).

Several regions have been mapped for potential rust damage. Brown et al. (1999) adapted available map data to produce a GIS hazard map for Minnesota. Ostrofsky et al. (1988) recognized that prevailing incidence in Maine was less than predicted by Charlton (1963), and suggested

Table 3—Comparison of signs and symptoms of *Cronartium ribicola* and *C. occidentale* on ribes ^a.

Character	<i>Cronartium ribicola</i>	<i>Cronartium occidentale</i>
Onset of telial formation	later	earlier
Form of teliospore columns and telial mats	straight, sparse, never “fur-like” in mass	bent, very dense, “fur-like”,
Color of mature, un-germinated telia	straw brown, orange-tinge	dark brown
Color of older, germinated telia	retains orange color longer but may have lavender-purple tinge	soon develops a lavender-purple tinge
Extent of telial production on infected portions of the leaf	much of the infected portion of the leaf without telia	most of the infected portion of the leaf with telia
Pattern of infection on leaf	small, scattered spots	large, continuous areas
Hardman symptom characteristics ^b , in order of increasing severity	slight necrosis by spotting (from rust or secondary fungi); general necrosis of infected area; “blister necrosis” as large raised or sunken dead areas of leaf; angular necrosis delimited by veins; necrotic areas bear uredinia but no telia.	telia present with no visible host reaction; chlorosis around telia visible on dorsal side of leaf; “green island effect” ^c ; purpling ^d on dorsal leaf side

^a Table based on descriptions by Kimmey (1946), Miller (1967), and our observations.

^b Symptoms by D. Hardman, unpublished work described by Miller (1967).

^c A condition commonly caused by leaf spot fungi where green, infected patches are surrounded by yellow or light green areas.

^d Marked by a purple-black or -brown discoloration different from the usual reddening of diseased or aging leaves.

that the significant reduction in rust was due to effective ribes eradication. Later, Lombard and Bofinger (1999) concluded that rust distribution in New Hampshire was consistent with Charlton (1963). Regional hazard maps were prepared for Ontario (Gross 1985) and Quebec (Lavallée 1986). For the Sacramento Mountains of New Mexico, Geils et al. (1999) mapped expected rust potential early in the outbreak history. Smith and Hoffman (2001) modeled rust distribution for southern Idaho and western Wyoming using site and stand descriptors. Kearns (2005 and these proceedings) developed alternative models and maps for southeastern Wyoming and Colorado using site, vegetation and climatic data. In regions such as British Columbia at which zonal hazard is uniformly high and management is intensive, site and stand hazard rating have been more commonly used than hazard zone mapping (e.g., Hunt 1983 or McDonald 2000).

Rates and incidence of infection in current, naturally regenerating stands in many of the areas in North America first affected by rust are much lower than during the early outbreak, and cankers on many trees in these areas are slow-growing, with little or no sporulation. Such changes in blister rust pathosystems do not invalidate the concept of rust hazard, but reaffirm the idea that hazard is relative to cultural treatments employed, including resistance and ribes density, and that ecosystem recovery might also be modeled. In the interior West, populations of white pines, ribes, and rust are more insular than the

expansive forests of the Pacific and northern regions. Hazard zones may be especially useful where there are large, distinct differences in rust potential from forest to forest. Finally, reassessment of management tools associated with hazard zones may be needed, as changes to pine and ribes populations in response to decades of exposure to blister rust become recognized.

Diversity of Rust Species and its Relevance to White Pine Blister Rust Pathosystems

Several taxa of rusts occur on either white pines or ribes (Gooding and Bethel 1926). These rusts include *Coleosporium ribicola* (pinyon leaf rust); *Puccinia* spp. (on ribes and sedges); *Cronartium ribicola* (white pine blister rust); *Cronartium occidentale* (pinyon blister rust, on ribes and pinyon), and *Melampsora ribesii-purpureae* (on ribes and willows). Identification of these rusts can be made from the appearance of macroscopic characteristics of the rust on ribes (see Van Arsdel and Geils 2004 for a key and illustrations). *Melampsora ribesii-purpureae* is a typical rust of the *Melampsora epitea*-complex, but appears to be quite rare (see Ziller 1974). The *Puccinia* rusts are uncommon, usually seen as a single or few cup-like pustules, visually quite distinct from *Cronartium* and *Coleosporium* rusts. *Coleosporium ribicola* is common in the Southwest, especially on *Ribes cereum* and *R. leptanthum*; it may be found in other regions, on other

ribes (*R. inerme*), and many kilometers from the nearest pinyon (Hedgcock et al. 1918). The telia of *Coleosporium ribicola* appear as a waxy cushion and should not be mistaken for uredinia of a *Cronartium*. On ribes, the two blister rust fungi *Cronartium ribicola* and *C. occidentale* are indistinguishable by their uredinia (Kimmey 1946, Miller 1967). Differences between the telia of the two species are recognizable if many leaves are carefully examined, but they can still be easily mistaken (table 3, previous page). Ribes host and time of onset for telia formation are more useful characteristics than differences in form, color, extent, pattern and development of infections, which are not consistently reliable for most observers. Vogler (these proceedings) resolves this difficulty with a molecular determination technique.

Among species of *Cronartium* (*C. ribicola*, related Asian rusts, *C. occidentale*, and others) there is notable variation in host range, pathogenicity, environmental requirements, life history, population genetics, evolutionary history and tendencies (Vogler and Bruns 1998; McDonald et al. 2005; Zambino et al., submitted). McDonald et al. (2005) suggest given this diversity, the pine stem rusts have a potential for genetic or epigenetic adaptation (or exapatation, see Gould 2002 page 43), allowing a rust to exploit new hosts and new environments. This could include the aforementioned changes in aggressiveness, exploitation of non-ribes alternate hosts as utilized at blister rust's center of diversity in Asia, but only recently discovered in North America, and adaptations for sporulation and spore germination at different ranges of temperatures than have been observed (e.g., McDonald et al. 2005, McDonald et al. submitted, Zambino et al. submitted). Future models of rust hazard as estimated potential for causing unacceptable management impacts may need to broaden from a primarily ecological perspective (host community and climate) to include a population genetic perspective with gene flow (long distance dispersal) and isolation (local adaptation).

Conclusions

A great deal has been learned about how blister rust spreads from ribes to pine and the environmental factors that constrain it. This knowledge was gained from observing the results of early Blister Rust Control programs, from research, and from various management projects. To effectively address new management objectives, spread to new regions and hosts, and other new developments, much more can be learned about rust epidemiology. Especially useful would be investigations into the development and dispersal of the rust in alpine microclimates, and changes in pine, ribes, and rust populations and responses that have occurred over time in North American pine ecosystems with long exposure to rust. This information would provide a basis to predict

hazard and long-term outcomes for whitebark pine and other species and locations having only recent infection histories.

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