

History of western white pine and blister rust in British Columbia¹

by Richard S. Hunt²

ABSTRACT

Blister rust (*Cronartium ribicola*) entered Europe about 300 years after eastern white pine (*Pinus strobus*) was first planted in Europe. North America imported millions of infected seedlings after blister rust was firmly established throughout Europe. Blister rust probably entered into western North America on multiple occasions and spread throughout British Columbia (BC) by about 1930. Two large saw mills solely cutting western white pine (*P. monticola*) started in the 1920s with the main production for matches. Blister rust surveys in the 1940s painted a poor picture for the future of western white pine in BC, so it was discriminated against in forest management plans. Harvest volumes declined and the 2 mills ceased production about 1960. Selection of resistant clones from mature parents occurred between 1948 and 1960, but when it was evident that mature tree resistance was not likely to be in their seedlings the program was terminated. A program based on screening seedlings was started in 1983. The selected seedlings are hypothesized to possess age-related resistance that is being expressed at an early age. These and the better parents are incorporated into orchards.

Key words: *Cronartium*, white pine, surveys, match blocks, rust resistance, PR proteins

RÉSUMÉ

La rouille vésiculeuse (*Cronartium ribicola*) a envahi l'Europe il y a près de 300 ans au tout début de l'utilisation du pin blanc de l'Est (*Pinus strobus*) en plantation en Europe. L'Amérique du Nord a importé des millions de semis infectés une fois que la rouille se fut propagée définitivement dans toute l'Europe. La rouille vésiculeuse a été probablement introduite dans l'ouest de l'Amérique du Nord à plusieurs reprises et s'est répandue dans l'ensemble de la Colombie-Britannique (C.-B.) au cours des années 1930. Deux importantes scieries utilisant seulement du pin blanc de l'Ouest (*P. monticola*) ont débuté la production principalement d'allumettes dans les années 1920. Les relevés de propagation de la rouille vésiculeuse effectués dans les années 1940 laissant entrevoir un avenir sombre du pin blanc de l'Ouest en C.-B., il fut mis de côté dans les plans d'aménagement forestier. Les volumes récoltés diminuèrent et les deux scieries mirent un terme à leur production vers 1960. La sélection de clones résistants à partir d'arbres à maturité a été effectuée entre 1948 et 1960, mais lorsqu'il devint évident que la résistance des arbres à maturité ne se retrouvait pas parmi leurs descendants, le programme fut annulé. Un programme reposant sur la sélection de semis a été amorcé en 1983. Les semis sont retenus selon l'hypothèse qu'ils détiennent une résistance qui s'exprime avec le temps mais qui est déjà présente à un jeune âge. Ces derniers ainsi que des parents mieux choisis sont introduits dans des vergers.

Mots clés : *Cronartium*, pin blanc, relevés, allumettes, résistance à la rouille, protéines PR



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Introduction

White pine logging started on the east coast, moved to the Great Lakes Region, then to Idaho and British Columbia (BC). By the time logging started in BC, a disease caused by an Asian fungus, *Cronartium ribicola* J.C. Fisch. in Rab., already had been introduced to North America. This rust pathogen produced cankers that were readily invaded by a host of secondary insects (Furniss *et al.* 1972) and other fungi (Williams 1972) that caused die-back and extensive mortality (Byler *et al.* 1972). It had been previously determined that *C. ribicola* was

obligated to alternate between currants or gooseberries (*Ribes* spp.) and white pines, such as *Pinus strobus* L. in eastern North America and *P. monticola* D. Don in western North America. Also the infection in the currants was limited to the leaves, so infection ceased in the fall, while in pines it was perennial in cankers. *C. ribicola* could spread from *Ribes* spp. to *Ribes* spp. or white pines, but it could not spread from pine to pine.

A Brief History of *Cronartium ribicola* and Eastern White Pine in Europe

Although eastern white pine first arrived in France (Moir 1924) and Britain (Carroll 1973), in 1553 and 1605, respectively, it was not until about 1705 that Britain established the first plantations. These produced copious seed by 1726, which was used to start additional British plantations (MacDonald *et al.* 1957). Because seed was readily available plantations

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were established throughout northern Europe from about 1750 to 1810 (Spaulding 1929). At the same time black currants (*R. nigrum* L.) were commonly grown (Hedrick 1919) and *C. ribicola* was first recorded on them in 1830 from Austria (Unger 1836, Poelt and Zwetko 1997) and again in 1846 from the Crimea (Peterson 1973). Normally, we would attribute these collections to *C. ribicola* that originated in Asia on the assumption that *C. ribicola* was not endemic to Europe (Spaulding 1922, Leppick 1970, Hunt 2003). However, because eastern white pine plantations had already been established for 50 to 100 years without any reports of cankering, it can be argued that these collections on *Ribes* spp. are of a rare, and relatively benign, European strain of *C. ribicola* (Gäumann 1945, 1959).

Dietrich's 1854 collection in Estonia (Spaulding 1922, Lepik 1970) is the first European report on white pine. Subsequently, reports of cankers on eastern white pine show the rust spreading westward from country to country across Europe (Spaulding 1922; Gäumann 1959). The spread rate calculates to 36 km/year against the prevailing winds. Spread was aided by infection on nearby black currants and by pine seedling sales throughout Europe from infested nurseries in Germany and Belgium (Spaulding 1922, Moir 1924). Some believe this epidemic was caused by a *C. ribicola* strain newly introduced from Asia, which was more severe on eastern white pines and black currants than the European strain (Gäumann 1959).

An endemic European strain of *C. ribicola* would certainly explain why native European pines are regarded as blister rust-resistant (Søegaard 1972, Blada and Popescu 2004). The rust arrived in Britain in 1892 (Hunt 2003). Consequently, we can be reasonably certain that by 1895 white pine seedlings over 1 year in age growing anywhere in continental Europe likely would be exposed to *C. ribicola*. The most commonly imported stock was 2-year-old seedlings. Surveys of these imports into the eastern USA in the early 1900s revealed that some lots were so infested that they were destroyed. In contrast, retained lots only averaged about 1% infection (Spaulding 1914).

History of *Cronartium ribicola* in Western North America

Because Mielke (1943) produced a thorough history of blister rust in western North America, general texts and forestry schools have perpetuated his view of *C. ribicola* arriving in western North America. He attributes all the *C. ribicola* in the West to a single importation of 1000 eastern white pine seedlings from France into Vancouver in 1910. Additionally, he shows the rust spreading both 200 km north and south (southern Washington State) by 1913, and 500 km south into Oregon by 1917 or 1918 on pine. This calculates to a spread rate of 66 to 71 km/year against the prevailing winds with little or no aid from black currants and without any known pine infection between Vancouver and these southern points. This shot-gun spread seems strange compared to the slower and more contiguous spread in Europe. To account for this long distance spread the inoculum density must have been massive at this point source in 1913. But, subsequently to Mielke's (1943) publication we know from resistance screening programs that if the inoculum density was high, the survival of the young imported stock would be near zero within 6 years (Patton and Riker 1965, Gremmen 1972, Heimbürger 1972). However, when found after 12 years, 18% of the stock was still

alive even with black currants on-site (Davidson 1922)! To account for such high survival the inoculum density must have been very low. Thus, it would appear that the Vancouver importation was not responsible for infection in southern Washington and Oregon. Evidently the imports were 1-year-old seedlings (Davidson 1922), so it is possible that they were lifted prior to basidiospore release and were shipped free of infection. Possibly they were infected in Vancouver later than 1910 from some other importation, thus accounting for the high survival observed in 1922.

Shortly after the initial discovery of blister rust in BC in 1921 (Eastham 1922, Güssow 1923), Pennington (1925) reported a *P. strobus* importation into Victoria prior to 1910. Metcalf (1929) was convinced that many other importations provided inoculum sources. Certainly, Güssow (1923) could not rule out this possibility. In BC, importation records were not kept prior to 1910 and the quarantine of 1914 (Güssow 1916, Eastham 1923) stopped importations (Güssow 1923). During that 4-year window, 27 importations were recorded, but by the time of the first surveys in the 1920s most of the stock had already been sold off and distributed throughout the province, or possibly destroyed (Davidson 1922). These other importations totalled at least 350 seedlings (Güssow 1923). If we conservatively estimated that there were equal importations prior and post 1910 then there would be an additional 53 potential foci in BC contributing to the epidemic in the west. At the same time similar imports were possibly sent to Seattle, Fort Vancouver, Portland, Coos Bay, Corvallis, San Francisco and perhaps other points in the western USA, but apparently no records were kept. However, unknown to Mielke, Joy (1939) recorded, but did not publish, that a nursery in Washington State had ignored the 1914 quarantine (Spaulding 1922). It imported eastern white pine from known infested sources in eastern North America (E.P. Van Ardel, retired professor, Texas A&M University, College Station Texas, unpublished)—a few in 1913 from Ohio and 50 from Illinois in 1915 (Joy 1939). It is much easier to explain the early disjunct distribution and apparent rapid spread of *C. ribicola* in western North America by acknowledging that there were multiple introductions at several different points, rather than a single point source for all western North American infections.

History of Rust Distribution Surveys and White Pine Utilization

The early surveys in the 1920s were carried out by the BC Forest Service, Ministry of Agriculture, the federal Division of Botany and the US Forest Service. The US Forest Service established white pine species trials (Childs and Bedwell 1948) and disease intensification plots (Lachmund 1934) near Whistler. The rust had spread throughout BC by the 1930s so surveys stopped, and the Americans went home as there was plenty of it within the western USA.

Most early inventories show western white pine at about 1% of the total timber volume (BCDL 1941). Most of the concentrations were on Vancouver Island, the Fraser Valley and the West Kootenays. Western white pine grew mainly with Douglas-fir at the coast and was harvested in clear cuts. The usual practice throughout the interior was to selectively cut western white pine from mixed stands of Douglas-fir, western hemlock, and western redcedar, as pure western white pine stands did not exist as they did in Idaho.

White pine has always commanded premium prices (e.g., BCLD 1921, 1941; BCDLF 1961; BCMF 1981)³, and because the logs were valuable, loggers in the west Kootenays went out long distances for individual trees. They were cut in special runs, or mills, for paneling, furniture, pattern stock and match blocks. In the interior, the WW Powell Co. Ltd. opened in Nelson in 1921 cutting only white pine with their major volume being in match blocks sent to Quebec. Similarly, The Canadian White Pine Company was established in Vancouver in 1923 and they bought logs from various coastal operators. In Mission, the Eddy Match Co. opened in 1947 and the Dominion Match Co. operated in Victoria. Shortly thereafter the need for matches started declining as wood stoves were replaced by electric ranges. There was a major mountain pine beetle outbreak in 1957/1961 (Collis and Alexander 1966), and at the same time white pine inventories were declining throughout the province from aggressive salvage harvesting. There was no re-planting of white pine. In the 1960s the match factories and the Nelson sawmill closed, while the Vancouver sawmill converted to cut western redcedar (Heal 2002). However, export to the east of rough 1-inch boards continued at past volumes until 1990; since then, even bolstering the depleting volumes with white bark pine, the volume of white pine cut has continued to decline (e.g., BCMF 1992, 1997, 2001, 2006).

History of Damage Surveys

In 1946, Buckland, and in 1947, Thomas and Roff, surveyed white pine stands for blister rust incidence. As a result, salvage logging was recommended for severely damaged stands, while for less severely damaged stands maintaining crown closure by replacing selective cutting with clearcutting at normal rotation was recommended. Crown closure was thought to discourage *Ribes* growth and lessen the impact of blister rust. However, in general, *Ribes* were abundant, the terrain rough, and most white pines scattered, making *Ribes* eradication too expensive (Porter 1948). Even in the less severely attacked stands “the situation appears to be beyond hope of survival”, for the next crop (Thomas and Roff 1947). Thus, western white pine was cut without re-planting white pine, and because natural young growth was not counted towards a successfully regenerated stand, it was frequently spaced out during precommercial thinning operations. Consequently, volumes declined, and at the coast some white pine stands no longer exist (Hunt *et al.* 1985). Policies that eliminated white pine remained in effect until the early 1980s when it was demonstrated that most cankers are close to the ground so pruning would permit trees to grow to a harvestable size (Hunt 1982). However, the former volumes of white pine will not be restored until resistant stock is routinely planted in high numbers.

History of Resistance Programs to 2004

The first screening of BC western white pines occurred in Ontario in 1946 to 1948 (Heimbürger 1972) from seed collected in the BC interior and sent by Dr. C.D. Orchard, the chief forester for BC (Heimbürger 1948, Heimbürger, personal communication). Six selected clones were eventually

established at the UBC forest at Haney, BC but these were subsequently culled. In Wisconsin, Riker *et al.* (1943) discovered resistance in a few clones of mature eastern white pine inoculated with *C. ribicola*. Following Riker's methods, Porter (1948) initiated a resistance program in BC. He rated clones for blister rust resistance after inoculation for several years in a *Ribes* garden. Shortly after the program started, Riker *et al.* (1949) reported that seedlings were more susceptible than their parents. Later, by using a range of clone ages, Patton (1961) clearly demonstrated that resistance increased with age. He explained his results by observing *C. ribicola* basidiospores failing to develop in needles of mature pines, but readily developing in seedlings (Patton 1967). Thus, inoculated mature trees will have fewer needle infection spots and subsequently fewer cankers than inoculated seedlings. Porter's (1960) program was terminated in 1960 because it seemed that his resistant clones would produce susceptible offspring (King and Hunt 2004).

It was not until 1983 that a resistance program based on screening seedlings was jointly established in BC by the Canadian and BC Forest Services. The results of this program were summarized by Hunt (2004). The program started out trying to select for the 5 main traits reported in seedlings from Idaho, i.e., “reduced spotting,” “early shedding of spotted needles,” “fungicidal short shoot,” “bark reactions” and “no spots.” Reduced spotting was found in a few families, but this did not correlate to less cankering in field plots (Hunt 2002). Making this correlation was further confounded by having the current needles frequently more resistant than older needles, but only on older trees (Hunt and Jensen 2000). At an informal meeting “rust busters” in 1990, Bro Kinloch, (emeritus research geneticist, US Forest Service) challenged the western white pine resistance programs to demonstrate that the “early needle shed” and “fungicidal short shoot” resistance traits were reproducible when re-inoculated. When confirmed, the selected materials should be made available for other programs to evaluate. Since then, the BC program spent many years trying to find “early needle shed” and “fungicidal short shoot” resistance in BC test materials and in materials already selected in Oregon and Idaho without any success. In fact, research found that the timing of the reported “early needle shed” was actually happening after the stems were already infected (Hunt *et al.* 2007).

Most early “bark reactions” observed on BC test seedlings were not reproducible on re-inoculation, and were attributed to attack by secondary fungi, or other primary fungi (Hunt 1997). Slightly later “bark reactions” were called “slow-canker-growth” (SCG) resistance and it usually was reproducible on re-inoculation. This was further sub-divided into 4 sub-types based on morphology (Hunt 1997, 2004). Re-inoculating “no spot” seedlings in a disease garden usually resulted in spotting and copious cankering, while a few had considerably reduced cankering. These few were marked as resistant and called “difficult to infect” or “DI” for short. It was hypothesized that this is the trait described by Patton; i.e., having reduced spotting and cankering because of mature tree resistance, but in these particular cases it was occurring at an early age. There is a tendency for both SCG resistance and DI resistance to be found in the same families. It is hypothesized that all these seedlings are displaying the phenomenon known as age-related resistance (ARR), but at an early age. Age-related resistance is also called ontogenetic

³Annual reports of the BC Ministry of Forests and its antecedent organizations are available at <http://www.for.gov.bc.ca/hfd/pubs/docs/mr/annual/annualrpt.htm>

resistance because it is a developmentally regulated defence response as clearly demonstrated in *Arabidopsis* (Kus *et al.* 2002). The defence proteins involved contribute to both developmental functions and to non-specific resistance.

Although the inheritance and age of onset are little known in conifers, it is believed that AAR in western white pine is genotype specific. It is hypothesized that some pathogenesis-related proteins (PR proteins) are regulated as a tree ages. It is further hypothesized that PR proteins such as PmPR10 (Liu *et al.* 2003) and anti-microbial peptide (PmAMP1) (Ekramoddoullah *et al.* 2006) are responsible for this effect in western white pine (Liu *et al.* 2004). For instance, older needles and twigs contain more PmAMP1 than younger tissues during the late summer. PmPR10 has ribonuclease activity and this inhibits fungal growth. There are at least 19 isoforms of this protein in western white pine (Liu *et al.* 2003) so the effectiveness against *C. ribicola* may vary by isoform and the relative amount of the better isoform types, plus the quantity of the protein produced. It has been demonstrated that the quantity of PmPR10 may increase by pathogen attack and by dormancy (Liu *et al.* 2003, 2004). Selections of BC trees are more resistant at high-elevations test sites where the dormancy is longer than that at low-elevation sites (Hunt 2005). Also, Idaho orchard stock is highly resistant in the BC interior and less so in southern Idaho, and very susceptible at the BC coast where the dormancy is shorter. A long dormancy would favour the production and retention of PmPR10 compared to locations where the growing season is long.

In BC we have established orchards with seedlings selected for DI and SCG resistance and from parents that produced seedlings with these traits. Current and future research includes crossing among orchard selections and screening offspring for resistance. Parallel field trials will also be established, to see if there is congruency with screening trials. These studies will identify the poorest parents so they can be culled from the orchards.

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