



## REVIEW

# A review of genetic approaches to the management of blister rust in white pines

By J. N. KING<sup>1,5</sup>, A. DAVID<sup>2</sup>, D. NOSHAD<sup>3</sup> and J. SMITH<sup>4</sup>

<sup>1</sup>British Columbia Ministry of Forests and Range, Victoria, BC V8W 9C2, Canada; <sup>2</sup>North Central Research and Outreach Center, University of Minnesota, Grand Rapids, MN 55744, USA; <sup>3</sup>Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria BC V9L 5W1, Canada;

<sup>4</sup>School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611 USA;

<sup>5</sup>E-mail: John.King@gov.bc.ca (for correspondence)

## Summary

Since introduced a century ago, *Cronartium ribicola* has devastated many populations of North American white pines. However, significant genetic resistance to white pine blister rust occurs naturally and can be exploited. In this review, we discuss the progress and different approaches to breeding for resistance in North American white pines. Three broad categories of resistance are: (1) ontogenetic resistance, (2) R-gene resistance and (3) partial resistance. Ontogenetic resistance is associated with increased host age and indicated by higher susceptibility to infection in primary needles and young seedlings than in grafts and older trees. R-gene resistance (major gene resistance) is an example of the classic gene-for-gene system common in many rust diseases. R-gene resistance provides immunity but may not be durable. Host resistance and the corresponding rust virulence which defeats it are well described for sugar pine and western white pine. Host plants with partial resistance are able to retard or tolerate disease development without eliminating the pathogen. Partial resistance is also called slow-rusting resistance or low-level resistance and is revealed in seedlings by several responses, including slow-canker-growth, difficult-to-infect, needle-shed and bark-reaction. Most of these seedling responses are presumed to be multigenic; but needle-shed may be controlled by recessive genes. Long-term, field trials for verification of screening and selection results are sparse. Although 100% higher survival of selected material over unselected occurs in some trials, mortality is high under conditions of high hazard and heavy inoculum load. In several, long-term trials, some full-sib crosses expressed a strong phenotypic resistance that indicates specific combining ability between complimentary parents. These and other observations suggest that we might yet find strong and durable resistance. Study of Eurasian white pines infected by blister rust fungi could help us better understand endemic pathosystems. Different strategies are identified for deploying material selected for either R-gene or partial resistance. Current research suggests that resistance is more complex than previously modelled, but new molecular techniques offer useful methods for investigating the white pine blister rust pathosystem.

## 1 Introduction

### 1.1 White pine blister rust

*Cronartium ribicola* J.C. Fisch. in Rabh., the cause of white pine blister rust, has been in North America for over 100 years. It has a complex life cycle involving five different spore stages, alternating hosts, and exacting environmental conditions. Even though the pathogen appears quite fragile, it has proved remarkably successful in colonizing most of the native ranges of the white pines (KINLOCH 2003; GEILS et al., this issue). Several other exotic pathogens were also introduced in the early 20th century, in particular, chestnut blight caused by *Cryphonectria parasitica* (Murrill) Barr. on American chestnut (*Castanea dentata* Marsh. Borkh.) and Dutch elm disease caused by *Ophiostoma ulmi* (Buism.)

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Nannf. and *O. novo-ulmi* Brasier on elm species (*Ulmus*). Unlike these other pathosystems, however, North American white pines have demonstrated considerable resistance to blister rust. This resistance has enabled genetics and breeding to be a feasible method of managing the disease (BORLAUG 1972; KINLOCH 2003; SНИЕZKO 2006).

Genetic management of white pine blister rust is actively conducted in breeding programs for eastern white pine (*Pinus strobus* L.), western white pine (*P. monticola* Dougl. ex D. Don) and sugar pine (*P. lambertiana* Dougl.). Investigations and preliminary screenings are started for whitebark pine (*P. albicaulis* Engelm.), southwestern white pine (*Pinus flexilis* James var. *reflexa* Engelm. syn. *P. strobiformis* Engelm.), Rocky Mountain bristlecone pine (*P. aristata* Engelm.) and limber pine (*P. flexilis*, James) (MAHALOVICH and DICKERSON 2004; SCHOETTLE and SНИЕZKO 2007; CONKLIN et al. 2009). In this review, we discuss the general advances in breeding programs for genetic resistance against blister rust and examine potential, future strategies. More detailed reviews of specific programs are provided by SAMMAN and KITZMILLER (1996), DAOUST and BEAULIEU (2004), KING and HUNT (2004), KRIEBEL (2004), McDONALD et al. (2004) and LU and DERBOWKA 2009;. We use AGRIOS (2005) for specific phytopathology terms, WHITE et al. (2007) for genetics terms and generally follow PRICE et al. (1998) for pine systematics.

## 1.2 Background to the eastern white pine programs

Eastern white pine has been difficult to manage because fire suppression removes its best regeneration environment, ungulates browse young regeneration and white pine weevil (*Pissodes strobi* Peck) damage shoots. Upon arrival of *C. ribicola* to eastern North America, blister rust was viewed as the most harmful agent. Because white pine had significant economic and ecological values, researchers began surveys in the 1920s to find trees with disease-resistant phenotypes (RIKER et al. 1943, 1949; PATTON and RIKER 1966).

A prominent plantation in the search for resistant white pine was established at Pointe Platon, Quebec, in 1908 with seedlings imported from Germany (HADDOW 1969; HEIMBURGER 1972a). Although some seedlings appeared resistant, in only 40 years, *C. ribicola* reduced the plantation from 400 individuals to 36. In 1948, grafts and seedlings of the 36 survivors were relocated to Connaught Range, Ontario and Maple, Ontario and augmented with other collections. These plantations were established with *Ribes* bushes interspersed to provide the rust inoculum for identifying resistant phenotypes adapted to local conditions. Carl Heimburger worked in the Ontario program from 1948 to 1968 and was followed by Louis Zsuffa at the Maple station from 1968 to 1984. They acquired 17 different species of Eurasian white pines, hybridized with North American white pines and tested in nursery beds (HEIMBURGER 1972b; ZSUFFA 1981). Although temporarily abandoned, this work has been revived with new and interesting results (LU et al. 2005; LU 2009; LU and DERBOWKA 2009; see Section 4).

Other major programs emphasized the search for resistant phenotypes in native stands. AHLGREN (1961) made selections in Minnesota and planted progeny and parental grafts at several sites in the Boundary Waters and at Tofte, Minnesota. The most promising of the Tofte progeny along with other selections are grafted into the breeding arboretum at the University of Minnesota Cloquet Forestry Experiment Station.

RIKER et al. (1953) selected trees from west-central Wisconsin growing close to *Ribes* and, by inference, long exposed to *C. ribicola*. Grafts from these trees were used in several breeding programs (RIKER et al. 1943; HEIMBURGER 1962; PATTON 1972; SINCLAIR 2003). PATTON (1972) made additional selections in the 1950s and 1960s from native stands in Michigan, Minnesota, and Wisconsin and propagated many by grafting. These selections are still used in breeding programs and maintained at several locations, including the USDA Forest Service, Oconto River Seed Orchard, Wisconsin. Eastern white pine clone P327 has consistently yielded progeny with increased resistance and was included in several

studies of the mechanisms of resistance (PATTON 1967, 1972; ZAMBINO and MICHLER 1999; JURGENS et al. 2003). Seedlings from open-pollinated and controlled-crosses from these plantings were artificially inoculated with *C. ribicola* to study resistance (ZAMBINO and MICHLER 1999; JURGENS et al. 2003; JACOBS et al. 2009). In addition to these programs, small-scale breeding and rust resistance research has been conducted in Ohio, Tennessee, New England and Quebec (DAOUST and BEAULIEU 2004; KRIEBEL 2004).

### 1.3 Background to white pine programs in western regions

In western North America, *C. ribicola* was not as widely and frequently introduced as in the East (GELLS et al., this issue). Infected white pine seedlings were imported into Vancouver, British Columbia prior to 1914 (HUNT 2009). Blister rust rapidly spread through the distributions first of western white pine (MIELKE 1943) and later of sugar pine (SMITH 1996). It has now affected all the indigenous white pine species of Canada and the United States except *P. longaeva* D.K. Bailey. The white pines of Mexico and Utah appear to have escaped infestation (Schwandt et al., this issue). The Inland Northwest (northern Idaho and adjacent areas) where western white pine formerly grew in almost single-species stands has been severely infested and seriously impacted (NEUENSCHWANDER et al. 1999; FINS et al. 2002).

#### 1.3.1 Western white pine

BINGHAM (1983) initiated the first resistance breeding program for western white pine in 1946. McDONALD et al. (2004) reviewed this program of the USDA Forest Service Region 1 (Idaho and Montana) and the program of Region 6 (Oregon and Washington). The Region 1 program has been conducted at Moscow and Coure d'Alene, Idaho. The Region 6 program at Cottage Grove, Oregon began a decade later and is continued by the Dorena Genetic Resources Center. Initially, both programs rigorously selected healthy survivors and produced crosses in standing trees (BINGHAM 1983). The later, Phase II of these programs relaxed selection criteria and screened open-pollinated progeny. Since rust severity in Idaho often averaged more than 150 cankers per tree and few trees were apparently canker-free, Phase II candidates were selected from trees with fewer than three cankers (McDONALD et al. 2004). Region 1 introduced their Phase II program in 1965 and has screened over 3000 trees (McDONALD et al. 2004). Region 6 began an open-pollinated phase in 1971; the Dorena Center has screened over 4900 western white pine and 4500 sugar pine candidates (SNIETKO 1996; SNIETKO and KEGLEY 2003b).

The early program in British Columbia screened ramets (grafted cuttings) from canker-free field selections following the protocols developed for white pine in Wisconsin and Minnesota (KING and HUNT 2004). This initial effort was soon abandoned when progeny from these resistant, older individuals proved quite susceptible. In 1983, a program based on the USDA Phase II program was established. Since rust severity was generally lower in British Columbia than in Idaho, candidate trees were selected from canker-free individuals with intact lower branches. Open-pollinated seedlots (progeny) were screened from parent trees widely distributed from the coastal (291 trees) and the interior (216) regions (HUNT 2004a).

#### 1.3.2 Other white pines

There has been a recent effort to find resistance in the other North American species of white pine. This interest includes limber pine, southwestern white pine and bristlecone pine (SCHOETTLE and SNIETKO 2007; SNIETKO et al. 2008; CONKLIN et al. 2009). The major effort has been for whitebark pine, a keystone species in subalpine and alpine environments. Many populations of whitebark pine are seriously impacted or at risk from mountain pine beetle, succession, climate change, and blister rust (Schwandt et al., this

issue; Tomback and Achuff, this issue). Both Region 1 and Region 6 have screening programs for whitebark pine (MAHALOVICH and DICKERSON 2004; SNIETKO et al. 2007). Early but marked differences in resistance at population and family levels (MAHALOVICH et al. 2006; SNIETKO et al. 2007) have provided an impetus for developing screening and breeding programs for this species (VOGLER 2007; AUBRY et al. 2008).

#### 1.4 Discovery of major gene resistance in white pines

##### 1.4.1 Summary of sugar pine breeding programs

The USDA Forest Service Region 5 program to select and screen sugar pine in the Pacific Southwest began in the 1950s. The program is located at the Placerville Nursery and supported by the Institute of Forest Genetics, Placerville, California (KITZMILLER 1976; KINLOCH 1982; SAMMAN and KITZMILLER 1996; McDONALD et al. 2004). The program conducts large-scale inoculation and screening using open-pollinated progeny of canker-free trees selected across California (KITZMILLER 1976). A key difference from the other programs developed from the discovery of a simply-inherited, dominant gene that confers immunity to sugar pine trees carrying the *Cr1* gene (KINLOCH et al. 1970).

Resistance is defined by AGRIOS (2005) as the ability of an organism to overcome the effect of a pathogen either completely, ['total resistance' see KINLOCH (2003)] or in some degree ['partial resistance']. *Cr1* was the first dominant R gene ('resistance gene') reported in a forest tree species (KINLOCH et al. 1970). Upon recognition of the pathogen, this gene promotes a hypersensitive response (HR) in needle tissue. This HR reaction produces a necrotic lesion on the needle around the entry point of *C. ribicola* that prevents further progress of the rust (KINLOCH and LITTLEFIELD 1977). The terms major gene resistance (MGR) or R-gene resistance are used synonymously and characterized as 'vertical resistance' (VANDERPLANK 1968). Typical for rust diseases, a gene-for-gene interaction (FLOR 1971) between the *Cr* gene in the pine and a corresponding virulence *vc* gene in the rust demonstrates classic co-evolution in the white pine blister rust pathosystem. *Cr1* is distributed along a north-south cline ranging in frequency from <0.01 in the northern distribution of sugar pine to 0.06–0.08 in the southern Sierra Nevada (KINLOCH 1992). Unlike multigenic or partial resistance, R genes do not act additively but are expressed as a dominant phenotype (one copy of the gene provides immunity), so *Cr1* masks expression of partial-resistance genes. R-gene resistance can be identified in very young tissue, primary needles and is even expressed under high inoculum loads.

##### 1.4.2 Gene-for-gene co-evolution

The Happy Camp race of *C. ribicola* was first recognized at the Region 5 outplanting site on the Klamath National Forest, California. The virulence conferred by *vc*r1 (KINLOCH and COMSTOCK 1981) defeats the HR reaction of the host *Cr1* gene. Virulence to *Cr1* has been recorded at only one other location, 700 km to the south (KINLOCH et al. 2004). Region 5 has used this virulent race of *C. ribicola* to find additional, resistance traits. After identifying the *Cr1* status of seedlings in inoculation chambers, selected seedlings are outplanted at Happy Camp where virulent *C. ribicola* is abundant. By interplanting test trees among *Ribes* bushes, these individuals are screened for partial resistance traits such as slow-rusting resistance, SRR (KINLOCH 2003). Seed from individuals with the best combination of R-gene and SRR resistance are then planted in production orchards which supply the seedlings used in forest regeneration (KINLOCH 1982; SAMMAN and KITZMILLER 1996).

A similar R gene, *Cr2*, has been identified from a small valley near the Champion Mine in the Oregon Cascades (KINLOCH et al. 1999). It produces an HR reaction similar to *Cr1*

but in western white pine rather than sugar pine. It is distinct from *Cr1* because the *vcr1* and *vcr2* virulence genes in different races of *C. ribicola* are not effective on the other host's R gene (KINLOCH and DUPPER 2002). A third R gene, *Cr3*, has been identified in southwestern white pine; an HR reaction has been observed in limber pine (KINLOCH and DUPPER 2002; VOGLER et al. 2006).

No R genes have been observed in eastern white pine. But artificially inoculated, open-pollinated (ZAMBINO and MICHLER 1999; JURGENS et al. 2003) and full-sib seedlings of P327 (JACOBS et al. 2009) exhibit a reaction similar to a hypersensitive response. Four weeks after infection, responsive primary needles include spots of collapsed, dead, mesophyll cells with compact, restricted, fungal mycelia and surrounding host tissues with no intercellular hyphae. No R gene is known to be involved in this reaction, but SMITH et al. (2006b) found functional protein homologues in eastern white pine that are related to proteins with known roles in disease resistance.

The frequency of *Cr2* in western white pine is generally lower than *Cr1* in sugar pine (1:1000 vs. 1:100); but both *Cr1* and *Cr2* are more frequent in the Sierra Nevada (KINLOCH et al. 2003). *Cr2* appears to be absent north of the Columbia River Gorge through the Cascades. The Champion Mine race of *C. ribicola* carrying the *vcr2* gene is widely distributed throughout the Oregon Central Cascades (KINLOCH et al. 2004), unlike the narrow distribution of the Happy Camp race (*vcr1*) in California. This difference is unexplained but could be a result of mutation rates, genetic fitness costs or stochastic rather than genetic factors (B. Kinloch and R. Sniezko, pers. comm.). Before the *Cr2* gene was recognized, numerous selections of western white pine from the Champion Mine area were planted in the Dorena seed orchards; these could have spread the *Cr2* gene to progeny through pollen or seed. Because *Ribes* leaves used for screening were collected in the Champion Mine area, *vcr2* could have been spread to field trials and other plantations.

Although naturally occurring *Cr2* has not been found in British Columbia, many trials and plantations have been established with Champion Mine and other Dorena seedlots carrying this R gene. After 20-years of exposure in severely infested areas, the presence of *vcr2* is unlikely to have gone undetected because the *Cr2* seedlots are often the only survivors and these show typical, dominant-gene segregation (HUNT et al. 2004).

## 2 Screening for resistance: characterization of white pine blister rust resistance mechanisms

Early screening of eastern white pine relied upon grafts of selected trees planted within *Ribes* gardens for inoculum. Early observations showed that older individuals and grafted ramets tolerated or overcame infections, whereas seedlings and young trees usually died (PATTON 1961; Kinloch and Byler 1981; KINLOCH and DAVIS 1996). Resistance that increases with age or developmental tolerance is called 'mature-tree', 'ontogenetic' or 'age-related' resistance (WHALEN 2005). To avoid selecting for resistance of little value in young plantations, most screening is now done on seedlings (the most vulnerable stage).

Screening is usually conducted with artificial inoculation in chambers laden with heavily-infected *Ribes* leaves. These controlled environments can process seedlings faster, insure more even inoculation, and facilitate monitoring. Tens of thousands of western white and sugar pine open-pollinated families have been inoculated and screened for their response (KITZMILLER 1976; HOFF and McDONALD 1980; THEISEN 1985; HUNT 2004b; McDONALD et al. 2004). This protocol has also been adapted for eastern white pine (ZAMBINO and MICHLER 1999; JURGENS et al. 2003).

Resistance screening has spurred interest in characterizing both the infection process and the mechanisms of resistance. Hindrances to hyphal colonization of needles at any age include phenolic compounds, stomatal openings and wax deposits (WOO et al. 2001; JURGENS et al. 2003; SMITH et al. 2006a). A major effort has been to evaluate and

characterize seedling responses to blister rust infections after artificial inoculation. These seedling responses are thoroughly described by THEISEN (1985), HUNT (2004b), KEGLEY and SNIETKO (2004) and McDONALD et al. (2004). Seedling responses include: (1) zero or few infection spots (low spots); (2) needles drop soon after spotting (needle shed); (3) needle spotting with no subsequent development of cankers (spots only); (4) fewer and slower-growing cankers (slow canker growth) and (5) various, necrotic responses in the stem (bark reaction). Slow canker growth and bark reactions express tolerance rather than resistance because seedlings display symptoms but are able to survive with severe damage. Numerous other responses on long surviving seedlings have been reported recently, such as Mechanism X (SNIETKO and KEGLEY 2003b). Responses that appear as a continuous phenotype are interpreted as controlled by multiple genes (HOFF and McDONALD 1980). Responses that appear as qualitative phenotypes, particularly needle-shed and spots-only responses, have been interpreted as being regulated by recessive genes (HOFF and McDONALD 1971; McDONALD and HOFF 1971).

Challenges in evaluating seedling responses include variation in symptoms among seedlings, inconsistent and uneven inoculation rates, spore loading far above natural levels, and variation in susceptibility by needle age or type as primary or secondary needles (PATTON 1961; PATTON and RIKER 1966; HUNT and JENSEN 2001; HUNT 2004b). There is, thus, a need to link young seedling responses observed after artificial inoculation with the mechanisms of response and phenotypes of forest or plantation trees. The validity and interpretation of many seedling responses are questionable (HUNT 1997, 2002b, 2004a, 2005; WOO et al. 2001; JURGENS et al. 2003; SNIETKO and KEGLEY 2003b; ZAMBINO and McDONALD 2004; KINLOCH et al. 2008), especially as they relate to field resistance. Characterizing the genes responsible for observed seedling responses and demonstrating a link to the phenotypes of forest or plantation trees would put screening by artificial inoculation on a sound biological basis.

A more practical, alternative approach to measuring individual seedling responses is to simply monitor mortality over time. Mortality can be quantified either by counting dead seedlings or, where inoculation systems ensure near 100% early stem infection in susceptible seedlings, by plotting mortality curves (ZAMBINO and MICHLER 1999). This is an expedient approach in a mass-screening program; but a mortality response has limited value since it does not differentiate between resistance, tolerance, and escape.

### **3 Field verification of genetic resistance**

Although seedling inoculation and evaluation is now standard practice among screening programs, selection is based on different seedling traits and these traits are variously defined. For example, seedlings with the needle-shed trait are selected in the Region 1 and 6 programs but not in the Region 5 and British Columbia programs; the term 'bark reaction' refers to different traits in the different programs. Field trials verify whether the seedling traits used to select for resistance are correlated to long-term performance of plantation or forest trees. A commonly understood terminology is necessary to communicate information on which seedling traits and adult phenotypes are actually associated.

Field verification of genetic resistance in eastern white pine has begun. An un-replicated, progeny trial of 874 open-pollinated families and over 40,000 seedlings was established in the early 1970s near Tofte, Minnesota; and progeny were examined for blister rust infection at 10, 20, and 30 years. Some trees survived infection through apparent responses like SRR and bark reaction (A. David, unpublished data), but no evidence of R-gene resistance has been seen (MERRILL et al. 1986).

An unpublished trial at the Oconto River Seed Orchard investigated the heritability of rust resistance in open-pollinated seedlings from putative rust-resistant individuals. Seedlings were planted in 1983 and 1984 on eight sites in combinations with open or

understorey conditions on high or low hazard sites. These seedlings were re-measured for vigour and rust incidence. Early results indicate significant differences in blister rust resistance among families and support a gene-by-environment ( $G \times E$ ) interaction for rust incidence (PIKE et al. 2003).

Early results of seedling inoculations in Idaho forecast that plantations of improved  $F_2$  progeny would display 71% freedom from rust (HOFF et al. 1980). SCHWANDT and FERGUSON (2003) summarized monitoring of 60  $F_2$  field-trial plantations; 0–96% of trees became infected. Although these results were too variable to validate the initial forecast, they were encouraging.  $F_2$  plantation trees generally performed better than trees of the surrounding natural forest as  $F_2$  trees had fewer infections and greater longevity. For some plantations, the  $F_2$  trees had twice the survival rate of natural, unimproved trees; survival of  $F_2$  seedlots was better even at the heavily infested Merry Creek site (FINS et al. 2002; McDONALD et al. 2004). Although the large variation in incidence among trials was not explained by environmental predictors of site hazard (e.g., within-stand *Ribes* abundance), some weak trends related to topography and geography indicated a possible  $G \times E$  interaction (MULLER 2002; ZEGLEN et al., this issue).

The present approach for evaluating field resistance is the realized-gain trial consisting of long-term, replicated, block plots (M.F. Mahalovich, pers. comm.; McDONALD et al. 2004). On Vancouver Island, British Columbia, three sites of replicated  $8 \times 8$  tree block-plot trials were established in 1999 with 1-year-old stock. The blocks represented seedlots from full-sib crosses of parents in the British Columbia program that had been screened for specific seedling responses (HUNT 2004b). Block differences were marked between any of the selected and screened seedlots and the unselected, wild seedlot by 100% or better increase in survival. Over three sites with different rust intensities and between replicates within sites, this difference was maintained. Similar realized-gain plots in interior British Columbia demonstrated a marked superiority of selected, Idaho seedlots over unselected wild controls (HUNT 2004a: 82 vs. 38% canker-free; M. Carlson, unpublished data).

These results indicate significant progress with material produced from seedlings subjected to inoculation screening and selection. Selected material might show 100% or better improvement in survival; but on very high hazard sites or challenged by a reproductively aggressive rust, nearly all the seedlings could still be infected and killed. This has led to some disappointment with traditional selection and tree breeding (ZEGLEN et al., this issue).

Some of the most interesting field-trial results have come from sites with older, pedigreed, full-sib material. One such trial is at Grass Creek and Blodgett Creek, within 20 km of the Champion Mine. Using block plots established between 1968 and 1974 and subjected to persistent, heavy, rust infection, Sniezko et al. (2004) reported family-level survival rates that demonstrate presence of resistance not related to known R genes but stronger than typically produced by screening for partial resistance. Although *Cr2*-resistance may have been initially present, an abundance of the virulent Champion Mine race there now precludes *Cr2* as the resistance factor operating at present. Although blister rust has completely eliminated most families and the adjacent natural white pine, over 66% of the trees in some families have survived. Evidence for resistance in these families includes: (1) up to 30% of individuals remain canker-free; (2) low infection frequency and few cankers; (3) tolerant individuals, surviving with large, bole cankers and (4) a bark reaction showing healed or inactive cankers (Sniezko et al. 2004a).

At Happy Camp, the rust load is usually high, controls experience 100% mortality, and the *vr2*-race is present. Nonetheless, KINLOCH et al. (2008) observed that some western white pine crosses showed strong, durable resistance not attributable to *Cr2*. A few, specific crosses from Bingham's Idaho selections stabilized at 50% canker-free survival. Evaluations at Happy Camp plus monitoring at other sites over many years demonstrating

repeatable performance from some seedling response traits indicate there may be a basis for both a durable and strongly expressed resistance (SNEZKO and KEGLEY 2003b).

#### 4 Research on Eurasian white pines and hybridization

Most early programs recognized that Eurasian white pines which co-evolved with *C. ribicola* might cross with North American white pines to provide improved, genetic resistance (HEIMBURGER 1962; PATTON 1966; BINGHAM 1972; KRIEBEL 1972; CRITCHFIELD and KINLOCH 1986). Eurasian white pines in the native range of *C. ribicola* are typical of endemic pathosystems in that, although blister rust occasionally damages some seedlings and saplings (AHSAN and KHAN 1972), it was not considered a major forestry problem (WANG and HONG 2004). However, with the increase of plantation forestry in eastern Asia, blister rust became a greater concern (Kim et al., this issue; Zhang et al., this issue). Species comparisons, in their native environment (IROSHNIKOV and POLITOV 2004), western Europe (S øegaard 1972) and North America (PATTON 1966; BINGHAM 1972; HEIMBURGER 1972a), indicate that North American white pines are generally more susceptible than Eurasian species.

Of all the Eurasian white pines with greater resistance than North American species, *Pinus wallichiana* A.B. Jacks. (syn. *P. griffithii* McClelland) is a special favourite. This Himalayan white pine displays a growth potential equal to that of eastern white pine (BINGHAM 1972). A thorough assessment of *P. wallichiana* has not been done because of its large distribution, broad environmental range and high variability from population to population (KHAN 2004). Many populations show poor survival and variable growth (HEIMBURGER 1972a); but some crosses of *P. strobus* × *P. wallichiana* grow so exceedingly well they out-perform pure *P. strobus*. Other species of interest include in the *Strobi* pines—*Pinus peuce* Griseb., *P. parviflora* Siebold & Zucc., and *P. armandii* Franch. (HEIMBURGER 1972b) and the *Cembrae* pines—*P. koraiensis* Siebold & Zucc. and *P. sibirica* Du Tour (BINGHAM 1972; CRITCHFIELD and KINLOCH 1986; IROSHNIKOV and POLITOV 2004). These species generally lack the growth rate and form of *P. strobus*.

North American and Eurasian species within the section *Strobus* (consisting of *Strobi* and *Cembrae*) are generally crossable with each other; the exception is sugar pine (CRITCHFIELD and KINLOCH 1986). The most comprehensive program of species testing and hybridization was conducted at Ontario, Canada, between 1956 and 1965. Although many of the early F<sub>1</sub> crosses among numerous species combinations were lost to frost and maladaptation (HEIMBURGER 1972b), the survivors were naturally pollinated by surrounding eastern white pine. LU et al. (2005) and LU (2009) inoculated this surviving material, including F<sub>3</sub> crosses and backcrosses, with a heavy rust load. Although all the *P. strobus* died, there were mortality differences between families suggesting partial resistance (JURGENS et al. 2003; ZAMBINO and McDONALD 2004). *Pinus wallichiana* was the most promising species for hybridizing and backcrossing with *P. strobus* (BINGHAM 1972; LU et al. 2005). Family variability ranged from 0% survival for *P. strobus* to 40–70% for hybrid families. This ratio near 50% suggests genetic segregation in the hybrid-mother trees for a single or very few genes controlling resistance (LU et al. 2005). Although no hypersensitive response is known for *P. wallichiana* crosses, a hypersensitive response is reported for *P. armandii* (HOFF and McDONALD 1972; LU et al. 2005).

### 5 Deployment

#### 5.1 Deployment of genetic resistance

Seed orchards are now able to capture and transmit genetic resistance for eastern white pine, western white pine and sugar pine. Guidelines for deploying resistant material

describe use of scarce, high-quality, rust-resistant material where it can be most effective. Efficient use is especially relevant for eastern white pine for which resistant material is limited and decision models for blister rust hazard are available (cf. HAGLE et al. 1989).

Knowledge of the hazard posed by *C. ribicola* is important for supporting deployment decisions (OSTRY et al., this issue; Zeglen et al., this issue). In the past, only broadly-based ratings such as the Lake States hazard map (VAN ARSDEL 1964) were available to identify landscapes and sites at risk of infestation and serious impact. Advances in GIS technology make it possible to generate high-resolution, digital maps that rate site hazard arising from aspect, topography, proximity to water and infestation history (WHITE et al. 2002). Because many sites cannot be easily described and model projections require informed interpretation, knowledge of a practising professional forester is essential to successfully apply a hazard model.

The various hazard rating systems used in western North America are reviewed by VAN ARSDEL et al. (2006). But, given the variable results of Idaho  $F_2$  field trials (SCHWANDT and FERGUSON 2003; ZEGLEN et al., this issue), predicting stand hazard is akin to picking 'winning and losing stocks in the market'. Mapping hazard zones has been used more in the East than in the West; but mapping could be useful wherever there are discernable environmental differences influencing blister rust spread and intensification (VAN ARSDEL et al. 2006).

Another decision factor is whether resistance is deployed as R-gene resistance, partial resistance, or both. Breeding programs can combine R-gene resistance and partial resistance to produce seedlings that have both vertical and horizontal resistance and thereby provide the best features of each (KINLOCH 2003). In the Region 5 sugar pine program where *Cr1* is endemic, this is routinely done. In British Columbia, where the *Cr* gene is not endemic, the *Cr* gene is incorporated into seed from production orchards by pollen dispersal (KING and HUNT 2004).

For British Columbia, deployment of the combination of R-gene and partial resistance is used only on sites of the greatest hazard, such as low elevation, coastal regions. The inclusion of R-gene resistance provides reliable protection for the first 12–14 years after planting. Results from the sugar pine program in California (KINLOCH 1997) and the western white pine program in coastal British Columbia (HUNT et al. 2004) suggest that R-gene protection for 12–14 years provides sufficient time for seedlings to mature enough that ontogenetic resistance becomes effective. Where R-gene resistance has been defeated by a virulent rust, partial-resistance genes limit the size and spread of infections to branch cankers. To limit the likelihood of *vr* evolution and prolong the effectiveness of R-gene resistance, use of the combination approach is restricted within any landscape block to a single, 20-year window (S. Zeglen, pers. comm.).

For coastal British Columbia, the combination approach for deploying both R-gene and partial resistance is considered feasible and effective. In the British Columbia interior, early observations from realized-gain trials suggest that partial resistance alone would be adequate (M.R. Carlson, unpublished data). Site hazard might be so high in the western white pine forests of northern Idaho, that R-gene resistance would soon be defeated by an emergent, virulent race. In the Oregon Cascades, virulence to *Cr2* is already widely distributed. In eastern white pine, with no known *Cr* gene, back-crossing with western white pine could prove a feasible approach for deploying effective resistance for seedling and mature white pine.

In unmanaged stands that rely primarily on natural regeneration with minimal site maintenance, alternative resistance strategies are difficult to assess. Would the natural evolution of SRR be slowed by planting R-gene seedlings that would eventually cross with native trees? Perhaps or not. DOWKIW and BASTIEN (2007) provided some evidence that defeated R genes could in fact add to partial resistance. ZAMBINO and McDONALD (2004) suggested disease attenuation in a natural system is one possible outcome, but if a more

aggressive rust was to arrive or emerge, then other courses could develop. Although white pines may not be totally eliminated in unmanaged systems, they may not persist in some natural ecosystems as a key species without some intervention.

Decisions on deployment strategy also consider other silvicultural practices. If R genes are active, then no cankers are produced and sanitation pruning would be unnecessary. Branch pruning and other silvicultural interventions can act in a complementary, additive fashion with SRR, other forms of partial resistance, or ontogenetic resistance. Ontogenetic effects are used to advantage in other systems such as reducing mechanical, bole instability in seedlings of *P. radiata* D. Don (AIMERS-HALLIDAY et al. 1999). Using cuttings from 3- to 4-year-old seedlings can add significant resistance that acts additively with SRR. Full-sib crosses grown in cutting beds allow strong phenotypic specific-cross effects to combine additively with ontogenetic resistance. Although the outplanting of cuttings is usually associated with an intensively managed, economically productive forestry, production costs for cuttings are becoming competitive with those of seedlings (MENZIES and AIMERS-HALLIDAY 2004). Cuttings could provide a worthwhile augmentation in stands primarily regenerated by natural seeding. Another type of resistance that could be used in an additive manner with SRR and ontogenetic resistance is that induced by endophytes; inoculating seedlings with certain fungal endophytes might increase seedling survival (GANLEY et al. 2008).

## 5.2 Deployment for adaptability

Deployment decisions are guided not only by consideration of resistance to *C. ribicola* but also by other, adaptive traits such as coldhardiness. Although some early provenance trials of eastern white pine were established (WRIGHT 1970; Wright et al. 1979), relatively little research has proceeded to develop seed-source recommendations or seed-transfer guidelines and to consider the potential impacts of climatic changes. Northern regions of the white pine distribution especially lack important information. Provenance tests with 7-year-old, Ontario seedlings identified opposing clinal gradients; seed can be moved northward 2.0–2.5° latitude without sacrificing growth potential or cold hardiness (LU et al. 2003a; b). However, to avoid significant reduction in growth potential, southward seed transfer is limited to 1.5–2.0° latitude (JOYCE et al. 2002). In Quebec, a provenance progeny test measured 4-year heights and 3-year bud burst and bud set; the test revealed a southwest–northeast clinal gradient for growth potential. Based on this test, the province has been divided into two, large, breeding zones (LU et al. 1997). Seed-transfer guidelines for some portions of the Upper Great Lakes region are expected to be similar to those in Ontario and Quebec (MOHN et al. 1976; MERRILL et al. 1986).

Northern populations of western white pine are not strongly differentiated. Perhaps these north populations originated from a common gene pool after the last ice age (STEINHOFF et al. 1983; CRITCHFIELD 1984) and a bottleneck eliminated any *Cr2* genes. Western white pine appears to have a broad, phenotypic plasticity for several adaptive traits. There is wide seed-transferability for growth potential between interior (Montana, Idaho, British Columbia) and coastal populations (STEINHOFF 1981; MEAGHER and HUNT 1998; D. De Bell, pers. comm.; J. King, unpubl. data). The amplitude for cold hardiness is more narrow (REHFELDT et al. 1984; THOMAS and LESTER 1992). Some types of resistance have limited transferability. Oregon Cascade seedlots with *Cr2* have a high susceptibility to *Dothistroma* needle blight on some sites in coastal British Columbia (R. Hunt, unpublished data). Blister rust resistance that appears effective in Idaho is not effective in coastal British Columbia sites (HUNT 2004a). Populations of western white pine from the Klamath Mountains and Sierra Nevada are quite distinct from northern populations; seed transfer between northern and southern regions are not advised (HUNT 1994; MEAGHER and HUNT 1998, 1999).

Sugar pine has been comprehensively tested for various adaptive traits (KITZMILLER 2004); and there has been a concerted study of general adaptability in whitebark pine and other western species of white pines (MAHALOVICH et al. 2006; BOWER and AITKEN 2008). These species do not show the great plasticity of northern populations of western white pine, but they do show a general capacity for south to north transfer of blister rust resistance. The geographic variation in resistance observed in some western species needs more investigation. Partial resistance is less common in southern sources of western white pine, sugar pine and whitebark pine than northern sources (KITZMILLER 2004; MAHALOVICH et al. 2006; SНИЕZKO et al. 2007). The opposite trend occurs for R-gene resistance in sugar pine (KINLOCH 1992).

## 6 Genetic models of resistance

A genetic model of blister rust resistance is a descriptive hypothesis of the inheritance and mechanisms by which a host white pine responds to infection by *C. ribicola*. The genetic model for most selection and breeding is slow-rusting resistance (SRR) or partial resistance, referred to by Bingham as 'low-level resistance'. SRR will not stop blister rust development in an infected host, but it reduces the rate of infection or delays mortality. SRR is probably under the control of several genetic factors (HOFF and McDONALD 1980; LIU et al. 2004) and expresses horizontal resistance (*sensu* Vanderplank). The Idaho needle-shed traits, however, might be controlled by individual, recessive genes. Although attempts have been made to estimate heritabilities for SRR and the component seedling response characteristics (BINGHAM et al. 1960; YANCHUK et al. 1994), the environmental sensitivities make such universal estimates of heritability difficult (as demonstrated in the F<sub>2</sub> field trial, SCHWANDT and FERGUSON 2003). Genes expressed as continuous phenotypes are called quantitative trait loci (QTL), or for partial resistance traits quantitative resistance loci (QRL). These genes are distinct from the qualitative, R genes that express vertical resistance (*sensu* Vanderplank). The distinction between horizontal and vertical resistance, however, is not always meaningful. Evidence from rice (*Oryza sativa* L.) to the bacterial pathogen, *Xanthomonas oryzae* pv. *oryzae* indicates that there is significant, genetic overlap between QRL and R genes (LI et al. 2006b). DOWKIW and BASTIEN (2007) showed that defeated R genes can affect the partial resistance observed in the *Populus-Melampsora* pathosystem by adding positively or negatively to the phenotypic expression of partial resistance.

An increasingly complex view of host-pathogen interactions is emerging for the indigenous, fusiform rust pathosystem of *C. quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme* on various oaks and southern pines such as loblolly pine (*P. taeda* L.). A new model of resistance proposes the action of several host R genes and a series of matching rust avirulence genes to replace the previous model of partial resistance (WILCOX et al. 1996; KUBISIAK et al. 2005). SCHMIDT et al. (2000) suggested that components of partial resistance may be present as well. CARSON and CARSON (1989) and KINLOCH and WALKINSHAW (1991) have cautioned that distinguishing among outcomes by just examining phenotypes is difficult. Variability in environments, host susceptibility, races for virulence or aggressiveness, and G × E interactions can all produce a continuous distribution of resistance whereby either a multiple R-gene model or a partial resistance model could account for the observed outcome.

Partial resistance may be the principal resistance in endemic systems (downstream resistance), and R-gene resistance may be an early, ephemeral resistance (up-front resistance; BURDON 2001; SCHMIDT et al. 2000). But, this is not always the case. Some endemic pines (e.g., *P. armandii*, but see Zhang et al., this issue) in the presumed native environment of *C. ribicola* display HR reactions typical of R genes; while others do not show a typical HR reaction but express segregation ratios expected for dominant genes (LU et al. 2005). Strong phenotypic traits not linked to observable HR reactions are also noted

in several North American white pines that express ratios expected for dominant genes (e.g., Mechanism X: SNIEMKO and KEGLEY 2003b or P327: JACOBS et al. 2009).

LU et al. (2005) in eastern white pine with Eurasian crosses and KINLOCH et al. (2008) in western white pine with native resistance examined segregation ratios in long-term, pedigreed material. They reported large phenotypic effects that could result from just a few segregating genes and some specific combining effects resulting from crossing complimentary individuals. Similarly, LI et al. (2006a) noted strong, specific-combining-ability (SCA) effects in particular crosses of loblolly pine in the fusiform rust pathosystem. One cross would regularly allow only 75% gall infections, whereas other crosses would express nearly 100% infection. They considered models of multiple recessive genes matched to rust races and of epistatic interactions among R genes to explain this anomaly (LI et al. 2006a). In specific crosses, modifier genes in a host that suppress resistance or in a pathogen that suppress virulence can alter alternative dominant or recessive expression. But, strong partial resistance (e.g., strong SCA effects in the Grass Creek plantation or as reported by KINLOCH et al. 2008) could also be explained by genes controlling QRL.

Epistatic interactions between QRL in different parts of the genome can be a significant feature of resistance. These epistatic interactions reflect either the addition of enhancing genes, removal of susceptible genes (e.g., MA et al. 2006; : wheat *Fusarium* head blight; LI et al. 2006b; : rice), or the combination of favourable alleles affecting a single but highly effective metabolic pathway conferring resistance. The mechanisms and genetic control of these observed, strong phenotypic effects in specific cross combinations outside of R-gene resistance have yet to be validated. KINLOCH et al. (2008) suggested a 50% resistance level or 1:1 ratio could fit a recessive gene model (as postulated by HOFF and McDONALD 1971; McDONALD and HOFF 1971), but they warned there are too many inconsistencies to make an unambiguous interpretation of inheritance.

Gene-by-environment interactions may be key features of partial resistance, but they are difficult to interpret (ZSUFFA 1981). Observed interactions may be explained by variability in expression of different genotypes in different environments; environmental sensitivity in the blister rust pathosystem is well documented (VAN ARSDEL et al. 2006). HUNT (2004a) reported rank change in expressed resistance as resulting from G × E interaction. The Idaho F<sub>2</sub> material that is resistant in at interior British Columbia sites shows no resistance in the coastal region at low-elevation sites but does at high-elevation sites (HUNT 1994, 2004a). One hypothesis to explain these and other observations of the Idaho material posits an interaction of host-growing season and pathogen-lifecycle phenology. Although inoculum-source effects were controlled in Hunt's study, the gene-for-gene model could still account for strong G × E interactions by the presence of multiple R genes (KINLOCH and DUPPER 2002).

Ontogenetic resistance is usually associated with strong and replicated resistance shown in grafted ramets of highly resistant individuals that is not transferred to their open-pollinated progeny. There is ample evidence of an ontogenetic effect both in maturity of needle tissue within a growing season and by tree age (WOO et al. 2001; HUNT 2005). Ontogenetic resistance, however, is not always effective strong resistance, as demonstrated by the loss of old western white pine trees during the initial wave of *C. ribicola* in northern Idaho (McDONALD et al. 2004). The loss of resistance in open-pollinated progeny of strongly resistant grafts could be a result of the disruption of recessive or epistatic genes by sexual recombination. Ontogenetic resistance can still be an effective, additive component of resistance (see Section 5.1).

## **7 Considerations and future approaches and in the genetic management of white pine blister rust**

Appreciable gains have been made from all the programs engaged in phenotypic selection and screening. The western North American programs are producing seedlings with

increased survivability of 100% and higher. Native populations of white pines have considerable, inherited resistance to *C. ribicola*; selection and screening has been effective. However, there is a strong environmental component; on high-hazard sites, we can still expect heavy mortality.

We have generally interpreted resistance in two different, heritable forms as R-gene resistance and partial resistance. R-gene resistance is implemented in the sugar pine program. Although R-gene resistance has the advantage of dominant resistance, there are serious concerns of its durability to an evolving rust. Much of the breeding effort has relied on partial resistance that is durable, but will not contain an aggressive pathogen. Partial resistance holds up in some environments such as interior British Columbia; but safe deployment remains uncertain because the environment is complex and changing. The two models of R-gene and partial resistance are overly simplistic; many features of the host-pathogen genetic system are yet to be discovered. Strongly expressed, full-sib effects of specific combining ability are especially interesting because they provide both strong and durable resistance. The recessive gene hypothesis has long provided a conceptual basis for the Idaho approach and may account for the good performance of Idaho material in interior British Columbia. Strong phenotypic resistance has also been observed in several, unique genotypes expressing certain seedling response characteristics.

Our understanding of the dynamics of resistance and virulence is incomplete and due in part to differences in characterizing seedling responses. Because we now have breeding populations of known pedigree, we can re-evaluate our models of the underlying mechanisms of resistance and their inheritance. Two approaches are proposed. First, we need to return to basics by carefully defining the seedling response characteristics and then relating these to the mechanisms of resistance. For example, the difficult-to-infect characteristic (HUNT 2004b) might be related to stomatal wax deposits (NOSHAD et al. 2009a). Although this type of avoidance mechanism has been postulated before (WOO et al. 2001; JURGENS et al. 2003; SMITH et al. 2006a), relating specific response characteristics with selected genotypes is the important, next step. Emerging molecular and genomics techniques for phenotyping selected lines could facilitate this work.

Rapid advancements in molecular techniques provide many new approaches to investigate the pathosystem. Richardson et al. (this issue) identify methods to examine the phylogenetics of aecial hosts (pine) and telial hosts (*Ribes*, *Pedicularis* and *Castilleja*) and to detect the protein precursors of HR and SRR. Two specialized fields of genomics could advance genetic approaches for the management of blister rust. Functional genomics investigates dynamic aspects such as gene transcription, translation and protein-protein interactions that can lead to phenotyping and describing the whole biological system underlying resistance. Molecular breeding uses molecular markers to identify linkages among QTL. Although not yet applied to blister rust, the technique has proved useful in other breeding programs (SCHENKEL et al. 2006). An ecological genomics approach is currently being developed in a widely-cooperative, management and research venture (ECOSYSTEM GENOMICS and FOREST HEALTH NETWORK 2008).

Other approaches in molecular biology are *in vitro* screening, microscopic techniques, tissue culture, and micropropagation. *In vitro* fertilization assists in development of hybrid crosses. Embryogenesis produces clonal lines for a pedigreed breeding program. Genetic transformation introduces genes otherwise difficult to incorporate. Along with *in vitro* propagation, regeneration of transgenic conifers could accelerate tree improvement (TRONTIN et al. 2007; NOSHAD et al. 2009b). Genomics and molecular biology forces more rigorous models of resistance to clarify understanding of this complex pathosystem. Intensive genomics studies in systems such as rice indicate there is a complex relationship between QRL and R genes that may someday also be described for white pine blister rust. Combining traditional selection and breeding with the insights of molecular biology could provide desired high-level, durable resistance (LI et al. 2006a).

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