Ann. For. Res. 51: 53-66, 2008

ANNALS OF FOREST RESEARCH
www.e-afr.org

White pine blister rust resistance in North American, Asian and European species - results from artificial inoculation trials in Oregon

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Sniezko R.A., Kegley A.J., Danchok R., 2008. White pine blister rust resistance in North American, Asian and european species - results from artificial inoculartion trials in Oregon. Ann. For. Res. 51: 53-66.

Abstract. Dorena Genetic Resource Center (DGRC) has used artificial inoculation trials to evaluate progenies of thousands of *Pinus monticola* and *P. lambertiana* selections from Oregon and Washington for resistance to white pine blister rust caused by *Cronartium ribicola*. In addition, early results are now available for *P. albicaulis* and *P. strobiformis*. DGRC has also recently evaluated seed orchard progenies of *P. strobus*, as well as bulked seedlots from *P. armandii* and *P. peuce*. The majority of *P. monticola, P. lambertiana, P. albicaulis*, and *P. strobus* progenies are very susceptible to blister rust. However, resistance exists in all these species. *P. strobiformis* showed relatively high levels of resistance for the eight progenies tested. Resistance in *P. armandii* was mainly reflected in the very low percentage of cankered seedlings; for *P. peuce*, the high percentage of cankered seedlings alive three years after inoculation was notable. *R*-genes are present in some of the North American five-needle pine species, but partial resistance traits (e.g. bark reaction) will play a major role in breeding activities for *P. monticola* and *P. lambertiana* and will likely be the key to developing durable resistance.
Keywords: white pines, progenies, inoculation, blister rust resistance, canker, *R*-genes

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Introduction

All North American species of five-needle pines (*Pinus* subsection *Strobus*) are susceptible to white pine blister rust (WPBR), caused by the non-native, invasive pathogen *Cronartium ribicola* J.C. Fisch. (Hoff et al. 1980). WPBR is now present in ecosystems of eight of the nine species of five-needle pines in the United States and Canada, and its range continues to expand (Blodgett & Sullivan 2004, Johnson & Jacobi 2000, Conklin 2004). Infection levels and mortality from WPBR can exceed 95% (Kegley & Sniezko 2004a, 2004b, Tomback et al. 2001), and the future viability of these species in some of the areas of highest rust hazard is bleak. Fortunately, all species examined to date show one or more types of resistance (Hoff et al. 1980, Kinloch & Dupper 2002, Sniezko et al. 2004, Kegley & Sniezko 2004, Bingham 1983, Sniezko et al. in press, Jurgens et al. 2006).

Operational programs to develop WPBR resistant populations of *Pinus monticola* Dougl. ex D. Donn. (western white pine), *P. lambertiana* Dougl. (sugar pine), and *P.*

strobus L. (eastern white pine) have long been established (Bingham 1983, Daoust & Beaulieu 2004, King & Hunt 2004, McDonald et al. 2004, Kriebel 2004, Sniezko 1996, Samman & Kitzmiller 1996). The objective of these programs is to produce resistant material for reforestation and restoration. Due to the availability of a reliable artificial inoculation methodology, seedling progeny of thousands of field selections of *P. monticola* and *P. lambertiana* have been evaluated for resistance. The resistance work in *P. monticola* is among the most successful to any non-native pathogen in North America (Sniezko 2006), but further breeding is still needed. Although most of the efforts to-date have involved the three species of the highest commercial value, recent concerns about the high mortality of several high elevation species of white pines have raised awareness of the need to evaluate the level of resistance in those species (Samman et al. 2003, Schoettle 2004, Schwandt 2006, Conklin 2004).

This paper will provide an overview on resistance testing results for five North American white pine species inoculated with sources of *C. ribicola* from Oregon and Washington. Results from resistance screening of *P. armandii* and *P. peuce* will also be presented. In addition to the standard resistance traits, results from testing for major gene resistance, which is expressed as a hypersensitive reaction (HR) in the needles, will also be presented. Field results and research needs will also be briefly discussed.

Operational screening

The Pacific Northwest Region of the Forest Service (Region 6), US Department of Agriculture, which encompasses both Oregon and Washington, has been actively engaged in blister rust resistance evaluations since 1956. Most of this work occurs at Dorena Genetic Resource Center (DGRC) in Cottage Grove, Oregon. At DGRC seedling progeny (usually two-year-old seedlings) of *P. monticola* and *P. lambertiana* are artificially inoculated and assessed for the development of disease symptoms and mortality for five years in operational screening trials (Kegley & Sniezko 2004, Sniezko & Kwgley 2003a, 2003b). The majority of the seedlots tested ('screened') are open-pollinated seed collections from individual parent trees. These initial forest selections are either free of rust or show little impact of rust relative to other trees in the stands; however, the level of rust infection in forest stands can vary widely from very low to nearly 100 percent. Full-sib families of *P. monticola* and *P. lambertiana* have also been tested for resistance.

Operational screening of seedling families of *P. albicaulis* Engelm. (whitebark pine) began in 2002. In addition, a small number of seedling families of *P. strobus* and *P. strobiformis* Engelm. (southwestern white pine), as well as one bulked seedlot of *P. peuce* Gris. (Balkan pine) and two bulked seedlots of *P. armandii* Franch. have been inoculated at DGRC.

Details of the inoculation process and assessments have been discussed elsewhere (Kegley & Sniezko 2004, Sniezko & Kegley 2003a); this paper will focus on types of resistance responses observed in operational testing and provide summary information from several resistance screening trials. The operational screening results for *P. monticola* and *P. lambertiana* will be briefly discussed; the results for *P. strobus, P. albicaulis, P. strobiformis, P. peuce*, and *P. armandii* will be discussed in greater depth.

Resistance traits

Since the underlying mechanism and the inheritance of many of the resistance responses is still unknown, and because there may be geographic differences in types of resistance, the DGRC WPBR resistance screening program currently focuses on broad resistance categories. These categories include complete resistance (which prevents stem infection) and partial resistance (which reduces the number of infections, increases latency, or minimizes the impact to the tree).

Complete resistance ('immunity') is very rare and is often controlled by single genes. Several mechanisms or types of resistance that result in a canker-free phenotype have been described; they include *R*-gene, or major gene, resistance (Kinloch et al. 1999, 2003) as well as several other needle-based resistances (Bingham 1983, Hoff & McDonald 1971, McDonald & Hoff 1970, 1971). Unfortunately, at least some forms of complete resistance can be overcome by evolution of the pathogen (e.g. Kinloch et al. 2004). In addition, some of these resistances may be less effective in some environments (Hunt 2004a, 2004b).

Most of the partial resistance (or 'slow rusting') traits are hypothesized to be controlled by several to many genes. These resistances are thought to be less influenced by the strain of rust and to be more durable. Partial resistances reduce the number of infections, increase the length of time it takes for an infection to reach the stem, or enable the tree to survive with infection. Some types of partial resistance may have immediate utility; however, further breeding may be necessary to increase the usability of other types. Because trees are long-lived organisms, Region 6 program goals include the incorporation of as many types of resistance as is operationally practical. Several types of partial resistance are described below.

Reduced Number of Infections: A significant reduction in the number of stem infections on a tree could increase the tree's chances of survival. Under artificial inoculation, some families have fewer needle lesions than others ('reduced needle lesion frequency'); this was hypothesized to yield a reduction in the number of stem infections (Hoff & McDonald 1980). Reduced needle lesion frequency is variable, and its utility in the field needs further examination (Hunt 2002, Kegley & Sniezko 2004). The frequency of stem symptoms on inoculated seedlings have been assessed at DGRC since 2000; this is likely the first assessment of this trait in operational screening trials of *P. monticola, P. lambertiana, P. albicaulis, P. strobus*, and *P. strobiformis.* These counts may provide a more direct measure to relate to field performance.

Latency: After artificial inoculation, some seedling families tend to develop stem symptoms one or two years later than the most susceptible families. This latency may be due to slow fungus growth in the needles (Hoff 1988) and may provide more time for other resistances or other factors to slow down or inactivate the fungus. These families or individual seedlings may also exhibit mortality at a later time relative to most susceptible genotypes (Hoff 1988).

Increased Survival: Some seedlings with stem symptoms survive. A small percentage of seedlings in some families exhibit tolerance; active stem symptoms may be present, but there is little or no observed reduction in tree vigor (Hoff 1988). Others may exhibit incompatible (bark reaction), inactive, or slow-growing (slow canker growth) stem infections. Bark reaction is an incompatible interaction with the fungus (Theisen 1988, Hoff 1986). Bark reaction manifests as a sunken necrotic lesion, often at the base of a needle fascicle, on stem tissue. When no fungal activity is observed, the bark reaction is considered 'complete.' An 'incomplete' or 'partial' bark reaction does not completely halt fungal growth (Kinloch & Davis 1996, Franc 1988). Slow canker growth resistance has been described as latent development of cankers in which necrosis is present; fungal mycelium is still present, but the extent is minimal (Hunt 1997, 2004a, 2004b, Hoff & McDonald 1980).

Seedling families can also exhibit a combination of the types of resistance discussed above (Kegley & Sniezko 2004, Sniezko & Kegley 2003b). Five years after artificial inoculation, all resistances are in low frequency in open-pollinated progenies of *P. monticola, P. lambertiana*, and *P. albicaulis* of the first generation selections (generally <10% of trees), but a few families show much higher levels (Kegley & Sniezko 2004, Sniezko & Kegley 2003a, 2003b, Sniezko et al. in press).

Species variation-operational screening results

In September 2002, six species were inoculated with blister rust. Four species were from North America; one species was from Europe, and one species was from Asia. Five of the species were inoculated at the same time, while the *P. monticola* were inoculated a week earlier. *P. albicaulis, P. peuce* and *P. armandii* seedlings were planted together in a randomized complete block (RCB) design with three blocks of up to 10 trees per seedlot per block; the *P. strobus* and *P. lambertiana* were in adjacent RCB trials with six blocks of up to 10 trees per seedlot per block. The *P. monticola* also included 6 blocks with up to 10 trees per family per block. For *P. monticola*, *P. lambertiana*, and *P. albicaulis*, only the results from the open-pollinated progeny of phenotypic selections are reported; for *P. strobus* all families were open-pollinated seed orchard lots, and the parents had previously been selected for some degree of resistance. The *P. peuce* and *P. armandii* were bulked collections of unknown resistance.

Early results from these trials are presented in table 1. All six species had a very high incidence of needle lesions ('spots'); species' means ranged from 95.5 to 100% (table 1); however, the two sources of *P. armandii* had fewer seedlings with spots 17 months after inoculation (4.5%, and 16.7%, for *P. armandii*-China and Taiwan, respectively) relative to the North American species (48.9 to 96.3%) or *P. peuce* (70%) (figure 1). The *P. armandii* shed more infected needles relative to the other species. The percentage of *P. armandii* and *P. peuce* seedlings with needle spots was much higher in this trial than that reported by Hoff et al. (1980).

The *P. peuce* and the two geographic sources of *P. armandii* had fewer spots than the North American species. Eight months after inoculation, *P. peuce* averaged 13 spots/tree, while the China and Taiwan sources of *P. armandii* aver aged 5.3 and 3.1 spots/tree, respectively. In contrast, *P. strobus* averaged 36.3 spots/tree, and the two sources of *P. albicaulis* averaged 34.1 and 25.6 spots. Hoff et al. (1980) also reported more spots present in North American species. Spot counts were not recorded for the *P. lambertiana* and *P. monticola*. The number of spots for these species was assessed using classes (e.g. Kegley & Sniezko 2004), and both *P. lambertiana* and *P. monticola* averaged many more spots than the *P. armandii* (unpublished data).

The exotic species, especially the two geographic sources of P. armandii, had fewer seedlings with stem symptoms (% SS, table 1) and fewer SS per tree relative to the North American species (table 1). Many of the *P. peuce* seedlings had stem infections (76.7% SS) but averaged only 2.4 SS/tree. In contrast the Wyoming source of *P. albicaulis* as well as *P. strobus, P. lambertiana*, and *P. monticola* had many more SS/tree. The Oregon sources of *P. albicaulis* averaged only 3.5 SS/tree;

Table 1 Rust infection traits of six species of five-needle pines inoculated at Dorena Genetic Resource Center in 2002

Species[a]	# families	height (cm)	% spotted[b]	# spots[c]	% SS[d]	# SS[e]	% RSURV3[f]
P. peuce	1	9.2	96.7	13.0	76.7	2.4	69.0
P. armandii, China	1	21.0	95.5	5.3	9.1	1.5	100.0
P. armandii, Taiwan	1	17.4	96.7	3.1	3.3	1.0	100.0
P. albicaulis, Wyoming, US	1	12.9	100.0	34.1	96.2	10.5	7.4
P. albicaulis, Oregon, US	4	4.3	100.0	25.6	96.6	3.5	1.9
P. strobus	10	19.1	99.8	36.3	99.3	8.1	3.7
P. lambertiana	23	34.8	99.7	--	99.5	14.0	1.3
P. monticola	33	23.9	99.8	--	97.7	11.0	18.2

[a] The *P. lambertiana* and *P. monticola* are open-pollinated progeny of phenotypic selections from Oregon and Washington; the Oregon sources of *P. albicaulis* are open-pollinated progeny of phenotypic selections while the Wyoming source of *P. albicaulis* is a bulked collection; the *P. peuce* and *P. armandii* are from bulked collections; the *P. strobus* are wind-pollinated seedlots from a seed orchard in Wisconsin.

[b] The percentage seedlings that developed needle lesions ('spots').

[c] The mean number of spots per seedling approximately 8 months after inoculation; spots were not counted on *P. lambertiana* or *P. monticola*.

[d] The percentage seedlings that developed stem symptoms (SS).

[e] Mean number of stem symptoms approximately 17 months after inoculation; average includes only seedlings with stem symptoms.

[f] Percentage infected seedlings surviving approximately 3 years after inoculation.

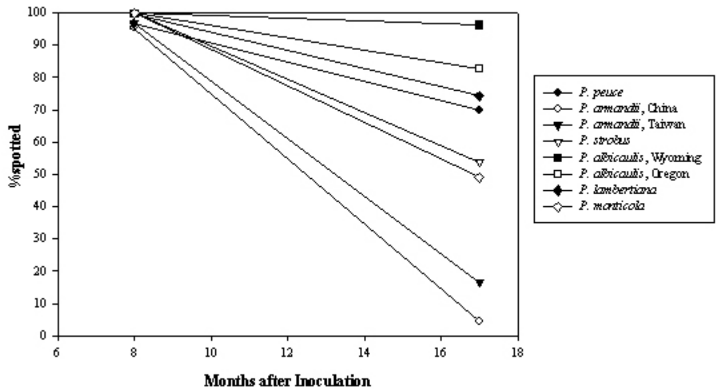

Figure 1 Percentage seedlings with spots at approximately 8 and 17 months after inoculation for 6 species of five-needle pines inoculated with *Cronartium ribicola* in 2002

however, these seedlings were very small (table 1).

Throughout the first three years following inoculation, survival of the infected trees was very high for *P. peuce* and *P. armandii* (69% and 100% RSURV3, respectively), while the survival of the North American species was much lower: less than 7.5% RSURV3 for *P. albicaulis, P. strobus,* and *P. lambertiana* and 18.2% for *P. monticola* (table 1). Both *P. peuce* and *P. armandii* had been previously shown to have higher levels of resistance than *P. strobus* and *P. lambertiana* when inoculated with a source of rust from Idaho (Hoff et al. 1980, Bingham 1972). *P. armandii* seedlings also had high survival when inoculated with sources of rust from eastern North America (Lu et al. 2005). Results here reflect the status three years after inoculation (Hoff et al. 1980 reported four-year data), but two additional years of assessments are scheduled.

Family variation

Pinus monticola. The majority of open-pollinated *P. monticola* progeny of field selections in Oregon and Washington are highly suscptible; five years after inoculation, usually less than 10% of the open-pollinated seedlings survive (figure 2) (Kegley & Sniezko 2004). However, some families exhibit moderate to high survival; these families usually show greater levels of stem-symptom-free and bark reaction (Sniezko & Kegley 2003a, 2003b, Kegley & Sniezko 2004). This performance is repeatable (for example, figure 3) and will provide a source of material for advanced generation breeding. A subset of the top families is now in field tests to gauge field performance and durability of resistance.

Table 2 shows the performance of four families from the 1998 inoculation; these families include three full-sib resistant families as well as a half-sib (open-pollinated) susceptible family. Five years after inoculation all of the seedlings in the susceptible family (03024-532 x w) were dead (0% RSURV5, table 2). In contrast, the three full-sib families had 47.3% to 88.1% RSURV5. One of the families, had only 5.7% stem symptoms (% SS); this family is known to have major gene resistance. The other two full-sib families had only 42.3 and 47.7% stem symptoms, of which 79.2 and 55.5% had bark reaction (complete or partial) (table 2). There was also higher latency (delayed development of stem symptoms) in the full-sib families relative to the susceptible half-sib control family; the percentage of seedlings exhibiting stem symptoms within one year of inoculation (% ESS) ranged from 14.2 to 33.3% in the full-sib families and 69.5% ESS for the susceptible family (table 2). The full-sib families had higher levels of resistance for all traits relative to the susceptible family.

Pinus lambertiana. As with *P. monticola*, the majority of open-pollinated progeny of *P. lambertiana* field selections is highly susceptible; on average less than 10% of the seedlings survive five years after infculation (figure 4)(Kegley & Sniezko 2004, Sniezko 1996). However, both complete resistance and partial resistances appear to be present in *P. lambertiana* (Kinloch et al. 1970, Kinloch & Davis 1996, Kegley & Sniezko 2004). Information on the hypersensitive response (HR) in needles is well documented for sugar pine (Kinloch & Littlefield 1977), but less is known about the frequency of partial resistance (Kegley & Sniezko 2004). For the Oregon populations of sugar pine, some families show a low frequency of partial resistances, but no non-HR resistance canker-free phenotypes as in *P. monticola* have been described for *P. lambertiana* (Kinloch & Davis 1996, Kegley & Sniezko 2004). However, since most of the range of sugar pine occurs in California, it is possible that parents with higher levels of resistance may be present there.

Pinus albicaulis. The first large inoculation of individual families *of P. albicaulis* at DGRC was in 2004. Forty-three families

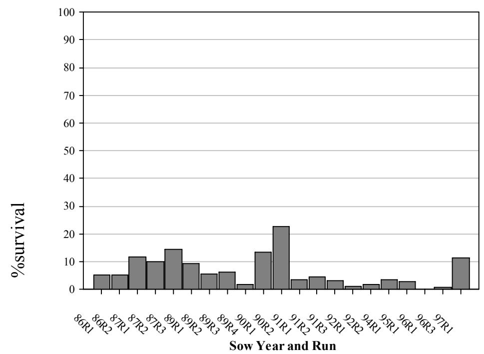

Figure 2 Mean survival five years after inoculation of half-sib seedling progeny of *Pinus monticola* field selections in operational blister rust screening trials at Dorena Genetic Resource Center (5 to 116 families per trial)

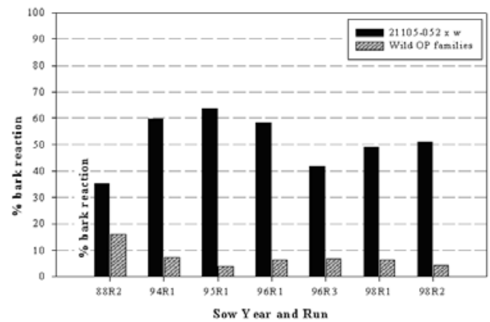

Figure 3 High level of bark reaction of one half-sib *Pinus monticola* family (21105-052 x w) compared with mean of other half-sib progeny of phenotypic selections (Wild OP) included in seven operational blister rust screening trials at Dorena Genetic Resource Center

Table 2 Means for rust resistance traits for four *P. monticola* families included in the 1998 inoculation

Seed parent	Pollen Parent	% infected[a]	% BR[b]	% SS[c]	% SSAL[d]		% ESS[e]	% RSURV5[f]
					3 yr	5 yr		
06024-506	06024-504 x 511	96.7	79.2	42.3	82.5	50.8	14.2	69.4
06024-506	06024-506	94.8	55.5	47.7	55.0	19.5	26.0	47.3
15045-844 x 862	15045-814 x 837	100.0	0.0	5.7	66.7	33.3	33.3	88.1
03024-532	w	100.0	0.0	100.0	8.5	0.0	69.5	0.0

[a] Percentage seedlings with needle lesions ('spots') or stem symptoms.
[b] Percentage seedlings with bark reaction.
[c] Percentage seedlings with stem symptoms (normal cankers, partial bark reactions, complete bark reactions.
[d] Percentage seedlings with stem symptoms surviving 3 and 5 years after inoculation.
[e] Percentage seedlings with early stem symptoms, those that show up within one year of inoculation; high % ESS indicates lower levels of latency.
[f] Percentage survival of infected seedlings five years after inoculation.

(wind-pollinated progeny of field selections) from six different collection areas in Oregon and Washington as well as one bulked seedlot from the Shoshone National Forest, Wyoming, were exposed to two inoculum sources (Trial 1 and Trial 2). The parent trees selected for seed collection were in areas of low to moderate blister rust infection. In addition, 80 families of *P. monticola* were also included in the two trials; the *P. monticola* families included a susceptible full-sib control that provides a comparison with the *P. albicaulis*. Each trial was composed of three complete blocks with up to 10 seedlings per family per block.

Trial Comparison. All of the seedlings in both trials developed spot (Sniezko et al. in press). Both trials had similar levels of seedlings with stem symptoms (87.7 and 89.8% SS for Trials 1 and 2, respectively), and survival two years after inoculation was also comparable for the two trials (25.6 and 24.4% RSURV2, table 3). An earlier prototype inoculation of a bulked seedlot showed similar trends; the % SS and % survival were roughly the same for the two inoculum sources (Kegley et al. 2004). The implication of these early results is that the geographic source of inoculum used in testing (at least from areas in Oregon and Washington) may make little difference for the presence of infections and overall survival.

Family Variation: Family means varied from 39.9 to 100% SS in Trial 1 and from 23.3 to 100% SS in Triaf 2 (figure 5). Families tended to perform similarly with both inoculum sources (r = 0.75, p<0.0001), but a few families showed differences of 30% or more (figure 5). The more northern sources (Mt. Hood and Colville) had fewer seedlings with stem symptoms and had higher survival (table 3, figure 5). This early data suggests that in Oregon and Washington, resistance, as indicated by % SS and % RSURV2, may be in higher frequency in the northern part of the geographic range. In a study of Interior Northwest seed sources, principally from Idaho and Montana, an increase in some types of resistance was noted from southeast to northwest (Mahalovich et al. 2006). This trend in resistance is also evident in preliminary data from a larger sample of families from Oregon and Washington (Sniezko, unpublished data).

The moderate to high frequency of families with relatively low % SS in the 43 field selections tested is higher than that found in tests of field selections in the Pacific Northwest of *P. monticola* or *P. lambertiana* (e.g. Kegley & Sniezko 2004). However, the *P. albicaulis* averaged more SS per tree and had more rapid mortality relative to the susceptible *P. monticola* control (Sniezko et al. in press). This trial is still in progress, and additional mortality is expected.

Pinus strobiformis. Eight families of *P. strobiformis* were tested for WPBR resistance at DGRC. These families were open-pollinated

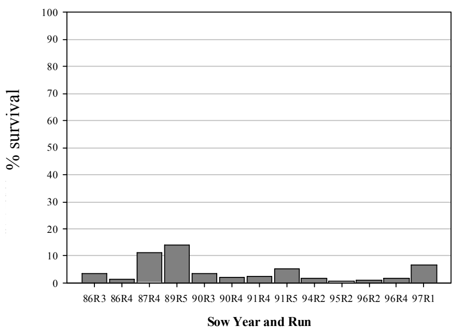

Figure 4 Mean survival five years after inocula tion of half-sib seedling progeny of *Pinus lambertiana* field selections in operational blister rust screening trials at Dorena Genetic Resource Center (50 to 117 families per trial).

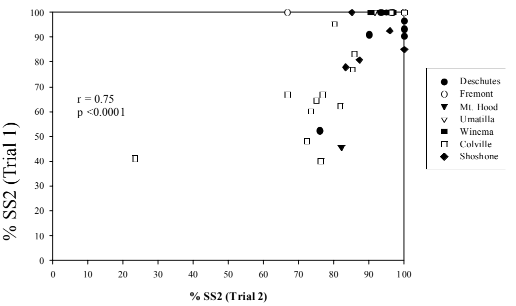

Figure 5 Percentage seedlings with stem symp toms two years after inoculation (% SS2) in Trial 1 vs. Trial 2 for 44 *Pinus albicaulis* seedlots from seven National Forests

Table 3 Population and trial means for *P. albicaulis* and a susceptible *P. monticola* inoculated in 2004 with two sources of white pine blister rust.

Population[a]	# lots	% SS2[b]		% RSURV2[c]		% SSAL2[d]	
		Trial 1	Trial 2	Trial 1	Trial 2	Trial 1	Trial 2
All families	**48**	**87.7**	**89.8**	**25.6**	**24.4**	**18.3**	**18.1**
Deschutes	10	92.4	95.2	19.7	12.1	17.5	8.1
Fremont	14	100.0	97.3	8.8	5.1	8.8	2.7
Mt Hood	1	45.6	82.0	82.6	81.5	61.9	77.5
Umatilla	1	100.0	91.7	4.2	0.0	4.2	0.0
Winema	4	100.0	94.1	6.8	15.8	6.8	11.4
Colville	13	69.6	76.3	55.3	58.5	35.8	46.0
DGRC-grown Shoshone	1	85.0	100.0	20.6	10.0	5.6	10.0
CDA-grown Shoshone	4	87.8	87.8	14.2	15.4	4.5	4.2
Susceptible *P. monticola*	1	100.0	93.3	100.0	100.0	100.0	100.0

[a] Source of material; there were two groups of material from the Shoshone National Forest —those grown at Dorena Genetic Resource Center (DGRC) and those grown at the Forest Service nursery in Coeur d'Alene, Idaho (CDA).
[b] The percentage seedlings with stem symptoms 2 years after inoculation.
[c] Percentage infected seedlings surviving 2 years after inoculation.
[d] Percentage seedlings surviving with stem symptoms 2 years after inoculation.

progeny of canker-free parents in a heavily infected stand in Bradford Canyon, New Mexico (D. Conklin, pers. comm.). Seed from a susceptible *P. strobiformis* tree was not available for this test, so performance of the eight half-sib *P. strobiformis* families was compared to that of *P. monticola* and *P. lambertiana*. Study design was randomized complete block, with four blocks of up to 10 seedlings of *P. strobiformis* per family per block. The controls were 23 *P. lambertiana* and 54 *P. monticola* seedlings comprising a variety of both resistant and susceptible genotypes. Results are available through 39 months after inoculation.

Species Variation. *P. strobiformis* averaged fewer seedlings with needle lesions (spots) than *P. monticola* or *P. lambertiana* (83.9% vs. 100 and 98.1%, tespectively) (table 4) and had fewer needle spots per tree at all assessments (unpublished data); at 10 months after inoculation, *P. strobiformis* averaged 10.5 spots/tree compared with 24.2 and 32.8 spots for *P. lambertiana* and *P. monticola*, respectivety (table 4). *P. strobiformis* not only had fewer trees with stem symptoms relative to *P. monticola* and *P. lambertiana* (42.5% vs. 91.3 and 70.4%, respectively) but also had fewer stem symptoms 17 months after inoculation (3.2 vs. 7.7 and 6.1) and higher survival (75.5% vs. 41.5 and 43.5% RSURV3, respectively)(table 4). More *P. strobiformis* seedlings with stem symptoms survived three years after inoculation (50.8% SSAL3) relative to *P. lambertiana* (38.1%) and *P. monticola* (21.1%) (table 4). In an earlier test of *P. strobiformis* from uninfected stands, Hoff et al. (1980) reported a high incidence of spots and cankers, but also reported a high incidence of cankered trees alive three years after inoculation.

Family Variation. For the eight *P. strobiformis* families, the percentage of trees with spots (SPOT%) varied from 66.7 to 100%, and the number of spots per tree varied from 5.0 to 18.2 (table 4). The percentage of trees with stem symptoms varied from 12.5 to 67.7% SS. Many of the seedlings with stem symptoms were surviving; family means ranged from 36.4 to 78.6 % SSAL at 39 months after inoculation (table 4), excluding Family SWWP-563 x w, which had only one seedling with stem symptoms. The high survival observed in *P. strobiformis* is encouraging, and the results suggest that several types of resistance are present (see section on Major Gene Resistance).

Pinus strobus. Ten wind-pollinated seedlots of *P. strobus* from a Forest Service orchard in Wisconsin were inoculated in 2002. There are differences in population structure of eastern and western populations of *C. ribicola*

(Hamelin et. al. 2000), so a main objective of the trial was to evaluate the relative level of resistance in seedling families of *P. strobus* exposed to a source of rust in the western United States.

Nearly 100% of the seedlings were infected; more than 99% of the seedlings developed spots and stem symptoms (table 5). Family means varied from 95 to 100% stem symptoms, and families averaged 5.3 to 11.5 stem symptoms per tree (table 5). Survival of infected trees three years after inoculation was very low for the *P. strobus*; on average 3.7% RSURV3, with family means ranging from 0 to 15.5% (table 5). Although overall survival of the *P. strobus* was low, an average of 37.7% of the seedlings exhibited some degree of bark reaction (table 5). However, since bark reactions can vary in effectiveness, this did not lead to increased survival of the young seedlings in this test. Similar results were found in a 1996 inoculation, which included four *P. strobus* families; the *P. strobus* averaged 38.2% bark reaction and 3.6% survival (Sniezko & Kegley 2003a). *P. strobus* seedlings have also shown generally low survival in inoculation tests in eastern North America using rust from those geographic areas (Lu et al. 2005, Berrang pers. comm.).

Major gene resistance screening

Although the number of resistance mechanisms and their inheritance is for the most part unknown, one form of complete resistance is known. This resistance is expressed as a hypersensitive reaction (HR) in the needles; HR generally stops the progression of the fungus in the needles and thus prevents stem infection (e.g. Kinloch et al. 1999, 2003, 2004). This resistance is under the control of a single, do-minant gene (*R*-gene); 50 to 100% of offspring of parents with HR would also have HR and would show high survival in the absence of blister rust with specific virulence to that gene.

HR has been identified in four North American five-needle pine species-*P. lambertiana, P. monticola, P. strobiformis* and *P. flexilis* (Kinloch & Dupper 2002). There are separate genes controlling HR in *P. lambertiana, P. monticola*, and *P. strobiformis*. Only a bulked seedlot of limber pine has been confirmed to have HR (Kinloch & Dupper 2002), but additional trials are now underway.

Table 4 Family and species means for *P. strobiformis* (SWWP), *P. monticola* (WWP), and *P. lambertiana* (SP)

Family	# sdl	ht2 (cm)	% infected[a]	% spotted[b]	# spots[c]	% SS	# SS[d]	% SSAL3[e]	% RSURV3[f]
SWWP-73 x w	39	20.2	71.8	66.7	5.8	33.3	4.0	46.2	75.0
SWWP-77 x w	6	12.7	100.0	100.0	10.2	50.0	1.7	66.7	66.7
SWWP-563 x w	8	8.9	100.0	87.5	18.2	12.5	--	0.0	75.0
SWWP-876 x w	40	25.6	82.5	77.5	5.0	52.5	4.0	61.9	75.8
SWWP-877 x w	29	8.9	82.8	82.8	10.3	34.5	4.3	50.0	75.0
SWWP-988 x w	49	27.1	85.7	77.6	8.2	57.1	1.0	78.6	85.7
SWWP-989 x w	31	11.9	100.0	93.5	16.7	67.7	4.0	66.7	74.2
SWWP-997 x w	34	18.9	88.2	85.3	9.6	32.4	3.8	36.4	76.7
SWWP avg		16.8	88.9	83.9	10.5	42.5	3.2	50.8	75.5
SP avg	23	25.7	100.0	100.0	24.2	91.3	6.1	38.1	43.5
WWP avg	54	12.7	98.1	98.1	32.8	70.4	7.7	21.1	41.5

[a] The seedling developed needle lesions ('spots') or stem symptoms (SS).

[b] The seedling had spots at either the 8, 10, or 17 month assessment.

[c] Mean number of spots present at the 10 month assessment; means include only those seedlings that had spots.

[d] Mean number of stem symptoms present at the 10 month assessment; means include only those seedlings that developed SS.

[e] The % seedlings surviving with SS 39 months after inoculation. The denominator includes only those seedlings that developed SS.

[f] The percentage infected seedlings surviving 39 months after inoculation.

Table 5 Means for seedling height and blister rust infection traits from 2002 inoculation of 10 families of *P. strobus* at Dorena Genetic Resource Center

Family	n	height	%	#	% SS	#	%	%
ON-519	49	22.8	98.0	48.2	100.0	9.6	41.7	0.0
ON-516	31	15.3	100.0	23.6	100.0	6.1	17.2	0.0
ON-469	32	21.5	100.0	27.9	100.0	9.0	56.3	9.4
ON-491	21	18.3	100.0	37.4	95.0	5.3	47.4	4.8
ON-466	27	17.7	100.0	32.9	100.0	9.2	50.0	0.0
Q-327	58	17.9	100.0	34.7	98.3	7.2	50.9	15.5
ON-477	49	20.4	100.0	35.0	100.0	8.6	45.8	4.1
ON-459	25	16.8	100.0	40.7	100.0	6.6	21.7	0.0
ON-539	20	20.7	100.0	42.1	100.0	11.5	20.0	0.0
ON-638	27	20.0	100.0	40.1	100.0	8.1	25.9	3.7
Average		**19.1**	**99.8**	**36.3**	**99.3**	**8.1**	**37.7**	**3.7**

[a] Mean total seedling height after two growing seasons.
[b] Percentage seedlings that developed needle lesions ('spots').
[c] Mean number of spots/tree approximately 8 months after inoculation.
[d] Mean number of stem symptoms per **infected** tree approximately 17 months after inoculation.
[e] Percentage seedlings with any type of bark reaction - complete or partial.
[f] Percent survival of infected seedlings approximately 3 years after inoculation.

DGRC has been screening seedlings for the presence of HR since the late 1990s; seedlings are inoculated at the cotyledon or primary needle stage. To-date, 7 species of pine-5 North American species (*P. lambertiana, P. monticola, P. strobiformis, P. strobus* and *P. albicaulis*)-and 2 Asian species (*P. armandii* and *P. morrisonicola*) have been screened at DGRC. The *P. lambertiana* and *P. monticola* families selected for HR testing have been identified based on operational screening results. These families have been tested because they have a high proportion of seedlings that did not develop stem symptoms in previous operational tests at DGRC and are the most likely candidates to have the *R*-gene. The incidence of HR in these species generally is low and is very low or not present in the northern populations of each species (Kinloch et al. 2003).

Table 6 presents some results from DGRC's major gene resistance screening trials for five of the seven species. Both of the Asian species (*P. armandii* and *P. morrisonicola*) exhibited HR. Hoff & McDonald (1975) reported HR in a bulked collection of *P. armandii* from the Shansi province of China.

All five *P. strobiformis* families exhibited HR. Three of the five *P. strobiformis* had low percentages of HR and appear to be pollen receptors (table 6). Similar results for these families have been found using a California source of *C. ribicola* (Vogler pers. comm.). Further work is also needed to clarify whether the HR resistance in *P. strobiformis* can be evaluated using the same criteria as for *P. lambertiana* and *P. monticola*, or whether some of the canker-free seedlings may not develop the diagnostic necrotic bands around the needle spots characteristic of HR in *P. lambertiana* and *P. monticola*. The high incidence of seedlings without stem symptoms for the eight *P. strobiformis* families in the operational test suggests that there may be other resistances in addition to HR in this species.

HR has not yet been detected in *P. albicaulis* (whitebark pine), but relatively few seedlots have been examined thus far (table 6), and more work is planned. The high levels of canker-free seedlings found in the first operational test of whitebark pine suggest that HR or another type of resistance controlled by a major gene may be present.

Field testing

Field resistance is the ultimate test of the level and durability of the blister rust resistance.

Table 6 Number of families tested for and exhibiting a hypersensitive reaction (HR) in the needles for five of the species examined in major gene resistance screening trials at Dorena Genetic Resource Center

Species	# families tested	# families with HR
P. albicaulis	8	0
P. armandii	2	2
P. morrisonicola	2	2
P. strobus	4	0
P. strobiformis	5	5[a]

[a] Three of the five families appear to be pollen receptors (the maternal parent does not have the R-gene but received pollen from a tree that does have the gene).

Until recently, there have been relatively few well-documented field tests for blister rust resistance. Most of the older tests of *P. monticola* and *P. lambertiana* have high levels of infection but also show some families with good survival 20 to 30 years later (Sniezko et al. 2004a, Kinloch et al. 2007).

Working with an array of cooperators, DGRC has now established a relatively large set of tests to examine field resistance and durability of resistance in *P. monticola* and *P. lambertiana*. These trials will examine which types of resistance are effective under different conditions (e.g. climate, races of rust, rust hazard, etc.), as well as which types of resistance or combinations of resistance are durable. At this time there is good correspondence between early field results and operational screening results for *P. monticola* (Sniezko et al. 2004b). However, mortality is just starting in some of these tests. Survival is the variable of most importance when evaluating the utility of partial resistance. More information about field infection and survival of *P. monticola* and *P. lambertiana* should be available in the next five years.

Research needs

Several avenues of research would help increase the efficiency of these operational programs. There are still important questions relating to how many resistance mechanisms are present and how they are inherited. Research using single spore isolates of blister rust on a subset of families will probably be essential to help further elucidate some of these questions. Knowledge about the worldwide genetic diversity in blister rust, especially relating to virulence and aggressiveness would be invaluable in helping to evaluate the potential evolution of this non-native pathogen and the durability of resistance in our native tree species. It would also be of interest to know how many and which types of resistance are present in Asian and European species of white pine which seem to survive well in their native range even when rust is present.

Summary

Blister rust is now a permanent resident of North American ecosystems. Artificial inoculation provides a method of evaluating hundreds or thousands of progenies over relatively short-time periods. The methodology is well established in *P. monticola* and *P. lambertiana* and seems to transfer readily to allow operational screening in other species.

Development of blister rust resistant populations of *P. monticola* and *P. lambertiana* give hope that the same can be done for some of the other North American species of white pines, such as *P. albicaulis*. Early screening results for these other species indicate the presence of some resistance. However, more work is still needed to raise the level of resistance coming from *P. monticola* and *P. lambertiana* seed orchards and to examine which types of resistance are durable.

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Centrul de Resurse Genetice Dorena (DGRC) a efectuat teste de inoculare artificială pentru a evalua rezistenta la rugina veziculoasă cauzată de *Cronartium ribicola* a descendențelor aparținând la mii de arbori selecționați de *Pinus monticola* şi *P. lambertiana* din Oregon şi Washington pentru. In prezent există rezultate obținute la vârste timpurii pentru *P. albicaulis* şi *P. strobiformis*. De asemenea, DGRC a evaluat recent descendențele livezilor semincere (plantaje) de *P. strobus*, precum şi unele loturi de semințe amestecate (în cadrul speciei) aparținând speciilor *P. armandii* şi *P. peuce.* Majoritatea descendențelor de *P. monticola, P. lambertiana, P. albicaulis* şi *P. strobus* sunt foarte susceptibile la rugina veziculoasă. Oricum, în toate aceste specii există rezistență la rugină. *P. strobiformis* a etalat un nivel relativ ridicat de rezistență în cazul celor opt descendențe testate. Loturile de puieți rezultate din semințe amestecate (în cadrul fiecărei specii) de *P. armandii* şi *P. peuce* au manifestat o rezistență mult mai mare decât majoritatea descendențelor aparținând speciilor de pini albi nord americani. Rezistenta speciei *P. armandii* a fost in principal reflectată de procentul foarte scăzut al puieților canceroşi; la *P. peuce*, procentul mare al puieților supraviețuitori infectați cu cancer a fost remarcabil la trei ani de la inoculare. Genele-*R* sunt prezente la unele specii de pini cu cinci ace din America de Nord dar caracterul rezistenta parțială (ex. reacția scoarței) va juca un rol important in activitățile de ameliorare pentru *P. monticola* şi *P. lambertiana* şi probabil va fi cheia obținerii rezistenței durabile.
Cuvinte cheie: pini albi, descendențe, inoculare, rezistența la rugina veziculoasă, cancer, gene-*R*.
(Tradus de I. Blada)