Provenance Variation in Western White Pine (*Pinus monticola*): The Impact of White Pine Blister Rust

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Abstract—The five-needle pines have been an important part of the landscape of North America, but they have been severely affected by the introduction of white pine blister rust (causal agent: *Cronartium ribicola*). However, most of these species have one or more types of some inherent resistance to this exotic disease, such as major gene resistance (complete resistance), and some forms of partial resistance. Long-established provenance trials in western white pine (WWP, *Pinus monticola*), established with unselected populations, allow us to investigate and compare genetic variation in our native populations for this resistance. These trials in British Columbia (Canada) and Washington and Idaho (USA) include seed sources that cover all the native range of WWP; the Canadian trials also include some of the selected populations from the ongoing genetic improvement effort. Trends shown here for growth (and survival) are similar to other reports on WWP—a large rather genetically undifferentiated northern population above latitude 45° N and a highly diverse but much less vigorous southern population. But also reported here, after 20 years of cumulative rust infection in the trials, is a trend in this northern population, sometimes significant, showing much higher levels of resistance in the Northern Cascades and lower elevation North Coastal sources compared to interior sources from Idaho and elsewhere. We describe several factors that could have caused these differences, such as natural selection after the early introduction; selection for traits involved in general constitutive defenses, which also gives resistance to this nonnative disease; or refugium differences in the primarily undifferentiated northern population. We also note the high effectiveness of the selection programs and discuss the inherent resistance defenses to this exotic pathogen that exist in native American species of white pine.

INTRODUCTION

Provenance testing is an important feature in understanding the background genetic variability of forest tree species (Morgenstern 1996). In the five-needle pines (also known as “white pines” and “soft pines”) of North America, this has been especially important since the accidental introduction of the exotic white pine blister rust (WPBR). The fungal pathogen *Cronartium ribicola*, the causal agent of WPBR, has been in North America for about 100 years. Although it appears very fragile, with a complex life cycle involving five different spore stages, alternating hosts, and exacting environmental conditions, it has proved remarkably successful in its colonization throughout most of the native ranges of the very susceptible North American white pines (Geils et al. 2010; Kinloch 2003). However, unlike other exotic pathogens that were also introduced in the early 20th century, in

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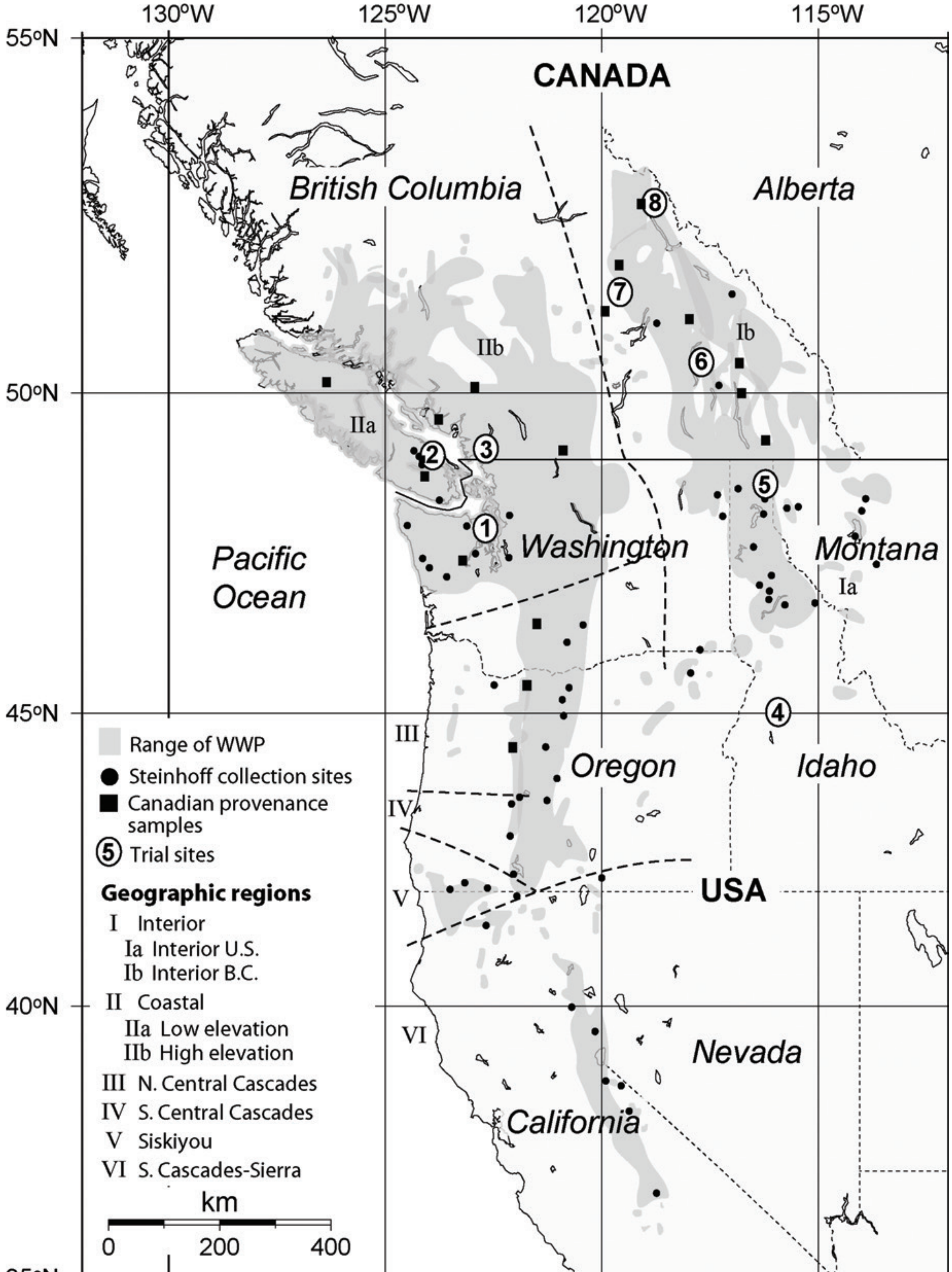

Figure 1—Western white pine distribution, sample locations, and trial sites.

particular chestnut blight caused by *Cryphonectria parasitica* on American chestnut (*Castanea dentata*), and Dutch elm disease caused by *Ophiostoma ulmi* and *O. novo-ulmi* on elm species (*Ulmus* spp.), there appears to be considerable native resistance in North American white pines to this exotic disease, albeit at low frequencies in natural populations (Kegley and Sniezko 2004; Kinloch et al. 2003; Sniezko et al. 2014).

Western white pine (WWP, *Pinus monticola*), has both a wide geographic distribution and one of the most comprehensive series of long-term provenance tests for the native North American five-needle pines. This paper summarizes results from these provenance trials, distributed both in the United States and Canada now that WPBR has had sufficient time to affect them. It draws some conclusions about geographic variability in genetic resistance in native WWP to the nonnative WPBR, and also about how this important tree species is perhaps evolving with this exotic pathogen.

Background to Provenance Research in Western White Pine

Two features were earlier noted in studies on the geographic variation and genecology of WWP:

1. There is a marked difference between the widely distributed northern populations (Regions I–III) and more narrowly distributed southern populations (fig. 1).

Regions for the southern populations, particularly in the Sierra Nevada and Warner Mountains (fig. 1: Region VI), are reported as quite distinct both with isozyme data (Steinhoff et al. 1983) and with growth and frost hardiness data (where it is noted these populations show lower growth potential but higher hardiness) compared to the northern populations (Rehfeldt et al. 1984). In both these studies the populations from Region V (Siskiyou) and Region IV, the southern Oregon (USA) Cascades, appear transitional between the northern population and the Sierra Nevada population.

The observations made from Steinhoff and colleagues' wide-ranging collections are also noted in other collections and studies and many observers have commented on the distinct difference in growth and needle characteristics of the Sierra Nevada white pine. In Canadian studies, Hunt (1994) and Meagher and Hunt (1998, 1999) noted southern sources of white pine (Southern Cascades, Siskiyou, and Sierra Nevada) are distinct from northern sources and are far more susceptible to WPBR. An evaluation of early growth and survival in a large progeny test of WWP in southwestern Oregon by Bower and Sniezko (2004) showed higher growth potential from northern sources of WWP. Bower and Sniezko (2004) also reported a distinct Californian population and a transition zone in the southern Oregon Cascades and confirmed Steinhoff's designation of a broad northern population from northern Oregon and eastward into Montana (USA).

2. There is exceptionally wide phenotypic plasticity for the northern populations (fig. 1: Regions I–III).

A commonly observed phenomenon is the wide transferability between the interior (Montana, Idaho, interior British Columbia [BC]) and coast for growth potential (Bower 1987; Steinhoff 1981), but a slightly less although still very wide amplitude for cold hardiness (Rehfeldt et al. 1984; Thomas and Lester 1992). This is highly unusual as strong genetic differences are typically noted between coastal and interior populations of most conifers; and strong latitudinal, elevational, and other environmental clines are the observed norm (Rehfeldt et al. 1984). Steinhoff et al. (1983) noted in an isozyme analysis that among-source population variability within this northern group was very low and even within-source variability was generally lower than in other regions. Even though populations from the Inland Empire (Idaho, eastern Washington, and Montana) and interior BC are now separated from the Northern Cascades and Coastal populations (fig. 1), the isozyme and the growth and adaptive trait data show a lack of strong differentiation within this large region, indicating they probably disseminated from a common gene pool after the last ice age (Critchfield 1984; Steinhoff et al. 1983).

Less has been noted on infection and survival differences among WWP provenances to exposure to WPBR, but it is interesting to note that the major R-gene (major gene resistance; MGR) that confers a hypersensitive response resistance (Kinloch et al. 1970) identified as Cr2 (Kinloch et al. 1999) appears absent throughout this northern population and shows higher frequencies in the Sierra Nevada (0.005–0.008) compared to only 0.001 in the southern Oregon Cascades (Kinloch et al. 2003). This observation fits well with Critchfield's hypothesis of a common gene pool and bottleneck that did not allow Cr2 to become established in the northern population. Another observation on resistance is based on assessment of various plantations and trials in BC (Hunt 1994, 2004). Hunt (2004) suggests that some of the resistance responses selected for in Idaho (e.g., needle shed) can do well in the shorter growing season of interior BC, but may not perform as well in the longer growing season found in coastal environments.

In a study of the genetic architecture of the Steinhoff WWP rangewide seed collections using amplified fragmented length polymorphism markers, Kim and others (2010) showed with nonmetric multidimensional scaling of genetic distance (Kim et al. 2010: fig. 4) a potential for a more diverse population structure than that described by Steinhoff and others (1983). They confirmed the divergence between a northern population of relatively low genetic diversity and the more diverse southern population at about 45° N latitude. Kim et al. (2010) also found that the transition areas between these populations (which they identified as clades) east and west of the ridge of the Southern Cascades could be quite marked (also Richardson et al. 2009).

METHODS

Provenance Samples and Field Trial Descriptions

Figure 1 shows the distribution of WWP, the provenance source population, and trial locations. Details of the U.S. provenance collection information are provided by Steinhoff et al. (1983), and the Canadian populations and trial sites are described in detail in Meagher and Hunt (1998). The Steinhoff collection (U.S. trials) had 60 populations in total with 3 to 25 trees per population. These were considered random samples, which means they did not come under the intense selection identified for the WPBR screening (King et al. 2010; McDonald et al. 2004). The Canadian collection of more than 100 samples (trees or mixed seedlots) included random samples encompassing more of the Canadian range of WWP (both Coastal and Canadian Rockies). The Canadian collection also used the Steinhoff collections for the U.S. Northern Rockies Region (Region I-a; fig. 1), and also some selected populations. This selected material came from various screening programs and included: (1) *The Porter families*—early intensive selections with some screening (as described by King and Hunt [2004]); (2) *The Westar families*—selections made in southern interior BC using the Idaho protocols (McDonald et al. 2004) without screening; (3) *Dorena Genetic Resource Center MGR seedlot*s from Oregon; and (4) some exotics, of which *P. koraiensis* is reported here.

Table 1 details the trials we report here with ages, final height measurements, and the overall percentage of trees with cankers from blister rust as well as blister rust frequency (incidence) for the Idaho collection (U.S. Northern Rockies Region I-a) subset of seedlots (as this was common to both the U.S. and Canadian trials). Rust incidence (presence or absence) was recorded as canker frequency in the *Results and Discussion* section (tables 2–7), and canker severity (counted number of cankers, up to 30) was also recorded in the U.S. trials. The U.S. trial sites have not previously been described, but are randomized complete block (RCB) designs of three 10-tree row blocks per seedlot (collection sample) and were established in 1983. The Whidbey Island site (Lone Lake) established by Washington State Department of Natural Resources (WA DNR) in cooperation with the U.S. Department of Agriculture, Forest Service (USDA FS) Moscow Forestry Sciences Laboratory (1 in fig. 1) and the Lost Valley site (located near McCall, Idaho outside the range of WPP on USDA FS land; 4 in fig. 1) both provided high survival. Another Idaho site located at Priest River Experimental Forest (USDA FS) lost two full blocks due to early plantation failure (5 in fig. 1). One block provided nearly full survival and was assessed. The Canadian sites described by Meagher and Hunt (1998) are also RCB with 25 replicated blocks of 4-tree row plots and were planted in 1988; they are described in greater detail later.

DATA ANALYSIS

Analysis of the trial information, which included both height and blister rust canker incidence (Canker) and severity (Canker Severity), was conducted by using a linear mixed-effects model that included the effects of

Table 1—Site descriptions of provenance trials reported.

	Site	Agency	Location	Latitude °N	Longitude °W	Elevation m	Mean height and (age)	% Blister rust incidence for overall plantation and (Idaho collection)	References to sites or materials
1	Whidbey Is.	WA DNR	Washington, Coastal	48° 03'	122°46'	50	123 –(20)	50% - (54%)	a,b
2	Ladysmith	Canadian For. Serv.	BC Coastal	49° 00'	123° 52'	75	62 – (12)	68% - (79%)	c,d,e,f
3	Sechelt	Canadian For. Serv.	BC Coastal	49° 30'	123° 44'	250	45 – (12)	91% - (96%)	c,d,e,f
4	Lost Valley	USDA For. Serv. Region 1	Idaho South	44° 59'	116° 30'	1800	35 – (21)	85% - (91%)	a,b
5	Priest River	USDA For. Serv. Region 1	Idaho North	48° 20'	116° 42'	730	95 – (20)	22% - (24%)	a,b
6	Nakusp	Canadian For. Serv.	BC Interior (South)	50° 15'	117° 46'	680	46 – (12)	35% - (45%)	c,d,e
7	Barrière	Canadian For. Serv.	BC Interior (Central)	51° 19'	119° 54'	725	52 – (12)	16% - (19%)	c,d,e
8	Valemount	Canadian For. Serv.	BC Interior (North)	52° 41'	119° 03'	760	49 – (12)	76% - (81%)	c,d,e

[a] Steinhoff et al. (1983).
[b] Rehfeldt et al. (1984).
[c] Hunt (1994).
[d] Meagher and Hunt (1998).
[e] Meagher and Hunt (1999).
[f] King and Hunt (2004).

Table 2—Results for canker frequencies (incidence and severity) at the Whidbey Island, Washington DNR Trial Site.

Trait	Canker 13 yrs		Canker 21 yrs		Canker_Severity 21	
Random effect	**variance**	**S.E.**	**variance**	**S.E.**	**variance**	**S.E.**
Block	0	n/a	0.0933	0.1039	0.6646 ns	0.6816
Population (Region)	0.1081	0.1908	0.2358.	0.0866	0.521 ***	0.1251
Fixed effect	**DF**	***P*** [a]	**DF**	***P*** [a]	**DF**	***P*** [a]
Region	5,66	<0.0001	5,57	<0.0001	5,57	0.0002
Region level	**Estimated canker incidence**	**Confidence limits**	**Estimated canker incidence**	**Confidence limits**	**Estimated canker severity**	**Confidence limits**
I N - Interior	0.028	0.017, 0.046	0.537	0.384, 0.682	**1.513**	-0.268, 3.294
II N - Coastal	0.050	0.028, 0.087	**0.302**	0.190, 0.444	**0.675**	-0.955, 2.305
III N - N. Cascades	0.019	0.006, 0.060	**0.200**	0.111, 0.334	0.574	-0.979, 2.126
IV T - S. Cascades	0.025	0.009, 0.067	0.488	0.327, 0.652	1.884	0.334, 3.433
V T - Siskiyou	0.046	0.011, 0.182	0.680	0.430, 0.857	3.097	1.362, 4.833
VI S – Sierra	**0.204**	0.136, 0.293	**0.712**	0.564, 0.826	2.328	0.757, 3.899
Comparison of regions	**Difference in canker incidence**	***P*** [b]	**Difference in canker incidence**	***P*** [b]	**Difference in severity score**	***P*** [b]
Interior vs. Coastal	-0.05	0.1445	**0.235**	**0.0001**	0.838	0.0141
Interior vs. N. Cascades	0.009	0.1450	**0.337**	**<0.0001**	0.940	0.0242
Coastal vs. S. Cascades	0.025	0.2374	-0.186	0.0187	-1.208	0.0107
Coastal vs. Siskiyou	0.004	0.9359	**-0.388**	**0.0115**	-2.422	0.0013
Coastal vs. Sierra	**-0.154**	**0.0408**	**-0.441**	**0.0007**	-1.653	0.0002

**** significant <0.0001,*** significant <0.001, ** significant <0.01, n.s. non significant >0.05, n.a. not available
[a] *P*-value for testing whether all Fixed Region effects are zero is derived from an *F* distribution.
[b] *P*-value for testing whether each difference is zero is derived from a *t* distribution.

interest: *Region (R)*, provenance *Population (P)*, *Trial* site *(T)*, and *Block (B)*. Region was based on the original seven regions as designated in Steinhoff et al.'s (1983) survey (shown in figure 1), but we also discuss the division in terms of northern populations (fig. 1: N, Regions I–III), southern Sierra populations (S, Region VI), and transitional populations (T, Regions IV and V). In the Canadian trials, which had larger sampling within the defined northern regions, we also looked at regions defined as: Coastal Low elevation (Region II-a), Coastal High elevation (or Northern Cascades, Region II-b), Idaho (Region I-a), and Interior BC (Region I-b) (fig. 1).

In the mixed model the random *Population* (trees sampled) is nested in *Region*, which is the principal fixed effect. The MIXED procedure of SAS® (SAS Institute Inc., Cary, North Carolina, USA) was used for the normally distributed height data and for canker severity; and the GLIMMIX procedure was used for rust frequency (incidence), a 1,0 binomial dataset (Littell et al. 1996; SAS Institute Inc. 2004). Contrast statements allowed testing hypotheses about the fixed regional effects or groupings of these fixed effects using t-tests. In the analysis of estimates of variance of the components associated with random effects of *Trial*, *Block*, and *Population*, the significance of each of these effects was tested by individually removing it from the model and assessing the change in the model fit via the observed log likelihood. The reduced model lies on the boundary of the parameters' space for the variance component; therefore, the *P*-value associated with these likelihood ratio tests was determined by using the technique described in Verbeke and Molenberghs (2000: section 6.3.4). All tests have a level of significance $\alpha = 0.05$. In the analysis of the Canadian sites, two models were run: one excluded the selected populations, and another included these populations.

Table 3—Results for heights in decimeters at the Whidbey Island Trial (Washington DNR).

Trait	Height 4 yrs		Height 13 yrs		Height 21 yrs	
Random effect	**variance**	***P*** [a]	**variance**	***P*** [a]	**variance**	***P*** [a]
Block	0.1600	0.2132	11.81	0.1986	22.12	0.2118
Population (Region)	0.4801	**0.0018**	24.06	**< 0.0004**	69.69	**< 0.0001**
Tree (Population Region)	0.4159	0.0014	146.74	< 0.0001	429.24	< 0.0001
Fixed effect	**F value**	***P*** [b]	**F value**	***P*** [b]	**F value**	***P*** [b]
Region	39.40	<0.0001	37.81	<0.0001	58.41	**< 0.0001**
Region level	**Least squares mean**	**Confidence limits**	**Least squares mean**	**Confidence limits**	**Least squares mean**	**Confidence limits**
I N - Interior	11.036	10.2, 11.9	70.17	63.2, 77.2	**123.64**	113.7, 133.6
II N - Coastal	10.545	9.67, 11.4	64.37	57.3, 71.5	114.19	103.9, 124.5
III N - N. Cascades	10.312	9.35, 11.3	64.56	57.1, 72.0	114.36	103.2, 125.5
IV T - S. Cascades	9.388	8.41, 10.4	54.94	47.4, 62.5	100.12	88.78, 111.5
V T - Siskiyou	7.775	6.34, 9.17	43.30	33.3, 53.3	70.38	54.39, 86.37
VI S – Sierra	5.493	4.60, 6,39	29.95	22.8, 37.1	41.96	31.25, 52.66
Comparison of regions	**Difference in least squares**	***P*** [c]	**Difference in least squares**	***P*** [c]	**Difference in least squares**	***P*** [c]
Interior vs. Coastal	0.492	0.2468	5.804	0.0823	9.45	0.0801
Coastal vs. S. Cascades	1.156	0.0321	9.430	0.0183	14.07	0.0282
Coastal vs. Siskiyou	2.790	0.0004	21.07	0.0002	43.81	<0.0001
Siskiyou vs. Sierra	2.262	0.0038	13.34	0.0131	28.42	0.0017

[a] *P*-value for testing whether each variance component is zero is derived from a mixture of χ^2 distributions.
[b] *P*-value for testing whether fixed Regional effects are zero is derived from an *F* distribution.
[c] *P*-value for testing whether each difference is zero is derived from a *t* distribution.

RESULTS AND DISCUSSION

The results are discussed in four sections: (1) the Washington State DNR trial at Lone Lake on Whidbey Island, which was one of the most informative trials for survival and completeness of seed sources; (2) the coastal sites including analysis of Canadian sites, plus in combination with the Whidbey Island (Lone Lake) site;(3) the Canadian interior sites analyzed separately; and (4) Idaho sites analyzed separately and combined.

Blister Rust and Height, Lone Lake on Whidbey Island, Washington

The Lone Lake trial site on Whidbey Island was the most comprehensive of the provenance trials analyzed, having the complete Steinhoff collection. White pine on this site had good vigorous growth and high overall survival but moderate (50 percent) rust incidence measured over several years.

The frequency (incidence) of cankers from blister rust was low at age 13, with no region having more than 21 percent, and most having less than 5 percent (Cankers 13 years, table 2). This allowed the trees to display vigorous growth on this productive site and get ahead of later rust development. A significant incidence of both branch and stem cankers was recorded only for Region VI (the Sierras), where a 20 percent incidence of blister rust cankers was significantly different from 0 percent. The 21-year assessment was quite different and by this time the overall incidence (proportions of stems infected) of cankering in the trial was 50 percent (table 2). Although the Sierra population samples again showed the highest frequencies (>70 percent), other populations were also higher than 50 percent. But the two local populations—the Coastal (Region II) and North Cascades (Region III)—had significantly lower rust incidence (20–30 percent) than most other regions (table 2). Noticeable within the broad region

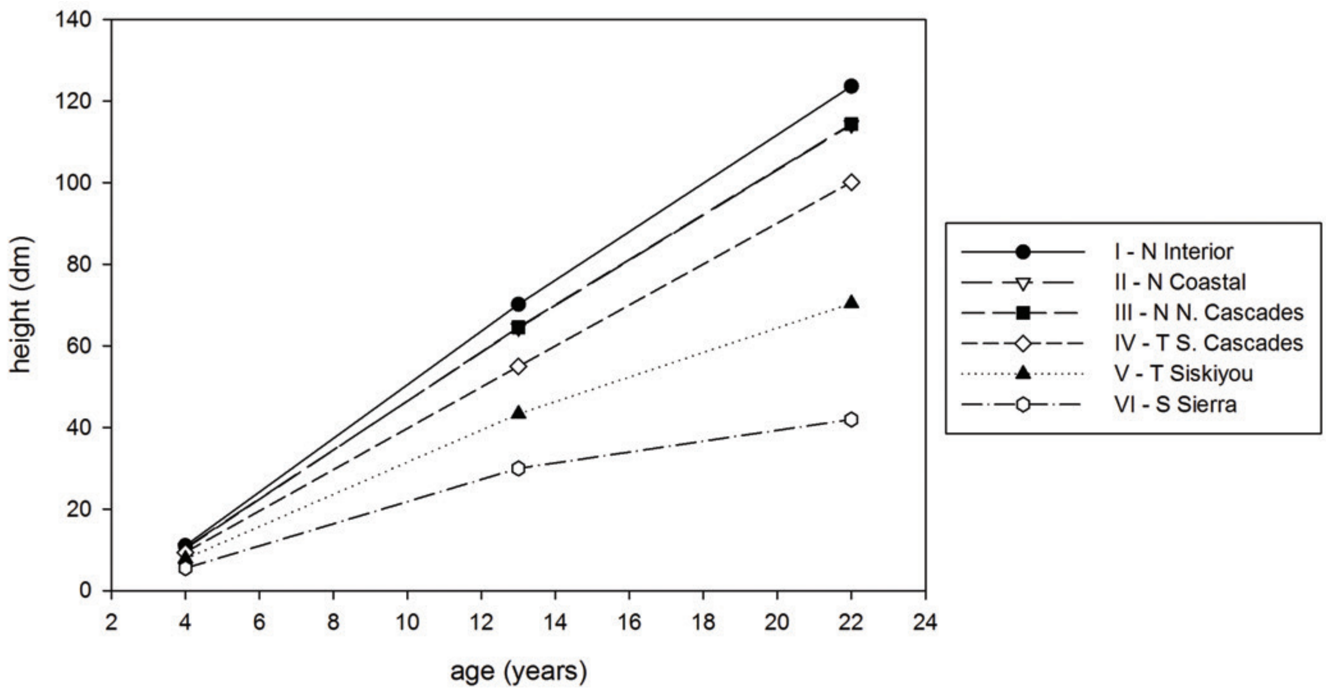

Figure 2—Height measurements (decimeters) over time at the Whidbey Island site.

for the northern populations is that interior populations have significantly higher rust incidence than the local Coastal populations (Pr > |t| 0.0001) and the North Cascades populations (Pr > |t| <0.0001, table 2). Canker incidence and canker severity (number of cankers) tracked each other closely on the U.S. sites where this was measured. The Idaho Region populations had twice the severity of the local Coastal or Northern Cascades populations (table 2).

Table 3 shows the three height measurements at the Whidbey Island site (diameter at age 21 was also recorded; it is not reported, but tracked height closely). The vigor especially of the Interior populations (>12 m on average at age 21) was very marked; they were on average 1 m taller than the local populations. The southern regions all showed poorer growth compared to local sources. The Sierra sources at one-third the height of the northern regions suffered poor survival caused not only by higher rust incidence but also by overgrowth of bigger trees. Very few of the Region VI trees were still alive at the 21-year assessment. Figure 2 shows the increasing height trends of the different regions over time.

Blister Rust and Height on Canadian and All Coastal Sites

The Ladysmith site, about 200 km north of Whidbey Island, is a similar low-elevation productive site with average height of more than 6 m at 12 years. Mean canker incidence was 68 percent, and showed significant discrimination between the regional groups, as did the Whidbey Island site (table 4). Five of the eight groups showed greater than 75-percent rust incidence; only the North Cascades among the unselected populations had a lower incidence (67 percent). This difference was significant compared to Northern Interior BC (Region I-b; Pr > |t| 0.0339). All the selected populations had a significantly lower incidence than the unselected, most notably the *Dorena MGR population* with only 27 percent versus nearly 70 percent overall. Also of interest were the *Porter families*, which were selected quite early in the outbreak and screened on rather simple resistance attributes; they showed statistically significant higher levels of resistance than the local unselected populations (83 percent vs. 46 percent, Pr > |t| 0.0006, table 4; King and Hunt 2004).

Table 4—Results for canker frequencies (incidence) at the Canadian sites in Coastal BC.

Trait	Sechelt 1995		Sechelt 2001		Ladysmith	
Random effect	**variance**	**S.E.**	**variance**	**S.E.**	**variance**	**S.E.**
Block	0.4848	0.1825	1.158	0.4874	0.7671	0.2766
Population (Region)	0.1084	0.7112	0.2173	0.2231	0.4005	0.1771
Fixed effect	**DF**	***P*** [a]	**DF**	***P*** [a]	**DF**	***P*** [a]
Region (only unselected)	4, 26	0.4343	4, 23	**0.3759**	4,24	0.0405
Region (with selected)	7, 66	0.0184	7, 52	0.2582	9,88	<.0001
Region level	**Estimated canker incidence**	**Confidence limits**	**Estimated canker incidence**	**Confidence limits**	**Estimated canker incidence**	**Confidence limits**
I-a Inland Empire	0.54	0.42, 0.67	0.96	0.91, 0.98	0.80	0.65, 0.89
I-b BC Interior unselected	0.49	0.39, 0.60	0.93	0.95, 0.97	0.86	0.78, 0.92
Westar families	0.39	0.30, 0.50	0.94	0.89, 0.97	0.76	0.68, 0.83
II-a - Coastal (unselected)	0.48	0.36, 0.60	0.95	0.89, 0.98	**0.83**	0.71, 0.90
Porter families	0.24	0.12, 0.41	0.91	0.74, 0.97	**0.46**	0.30, 0.62
II-b… high elevation	**0.58**	0.45, 0.70	0.97	0.91, 0.99	0.92	0.83, 0.96
III N - N. Cascades	0.44	0.30, 0.58	0.92	0.82, 0.97	**0.67**	0.45, 0.83
IV *T - S. Cascades (Dorena)*	**0.20**	**0.07, 0.45**	**0.72**	**0.33, 0.93**	**0.27**	0.08, 0.62
Comparison of regions	**Difference in canker incidence**	***P*** [b]	**Difference in canker incidence**	***P*** [b]	**Difference in canker incidence**	***P*** [b]
Coastal (II-a) vs Interior BC	0.01	0.7318	0.02	0.4187	0.03	0.4579
Coastal (II-a) unselect vs *Porter*	**0.24**	**0.0328**	0.03	0.6647	**0.37**	**0.0006**
Interior (BC) vs. *Westar families*	0.10	0.1379	0.01	0.6911	**0.10**	**0.0160**
N. Cascades (III) vs. Interior BC	0.05	0.2286	0.01	0.8123	**0.20**	**0.0339**
N. Cascades (III) vs. Idaho (I-a)	0.10	0.1951	0.01	0.1575	0.13	0.2019
Idaho – I-a vs. *Dorena*	**0.34**	**0.0200**	**0.24**	**0.0144**	**0.53**	**0.0052**

[a] *P*-value for testing whether all fixed Regional effects are significantly different is derived from an *F* distribution.
[b] *P*-value for testing whether each difference is zero is derived from a *t* distribution.

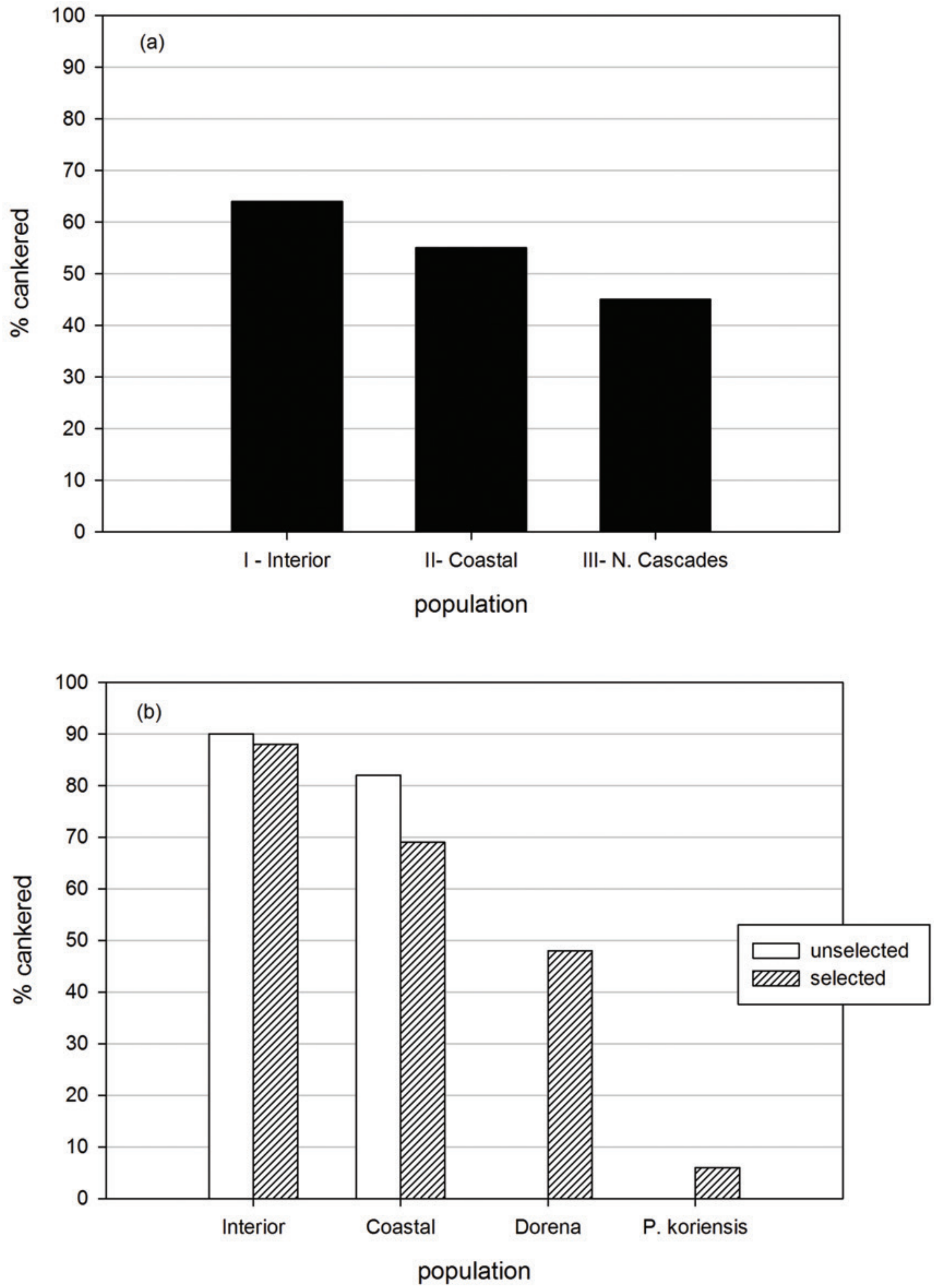

Figure 3—Canker frequencies in the coastal trials.

The Sechelt site is another low-elevation coastal site on the mainland side of the Salish Sea. This site had the highest incidence of rust of all the trials surveyed with greater than 90-percent infection at 12 years old, a dramatic increase from the 1995 assessment, when no group showed more than 58 percent infection. The regional differences are nonsignificant (Pr > F 0.3795) unlike at Ladysmith or Whidbey Island. Only the *Dorena MGR* seedlot at 72-percent infection (increasing from 20 percent at the 1995 assessment) had a significantly lower incidence than the others. Although a frequency of 72 percent is higher than what might be expected from the segregating Cr2 expression, this figure is not in fact significantly different from the expected 50 percent (confidence intervals of 33–93 percent, table 4). Thus, it does not conclusively indicate a breakdown of resistance due to vcr2; further monitoring would be needed to verify if in fact vcr2 was present. This site has not had any other detailed assessment, but a walk-through in 2008 indicated a still marked proportion of white pines in the stand structure (30 percent or greater), many living with pronounced cankers.

Results from a combined mixed model run of all the coastal sites—Whidbey, Ladysmith, and Sechelt—based on the last assessment for rust incidence demonstrate the difference between the unselected North Cascades (Region III—45 percent cankered) and the Interior (Region —64 percent cankered) (fig. 3a; Pr > |t| 0.0443). The local Coastal Region II was 54 percent cankered and was not significantly different from either of these. Figure 3b shows the combined summary of coastal Canadian sites and includes selected populations. Differences are noted between the Interior (Idaho and North BC at 90 percent) and the North Cascades at 82 percent. Selected populations also showed up well. The *Dorena MGR* at 48 percent had a significantly lower incidence of cankers than all other populations except the *Porter families* at 69 percent. The exotic *P. koriensis* had only a 6-percent infection rate. The *Westar families*, representing the selected interior families, were not much better than the Interior unselected and certainly not as good as the North Cascades (Region III). The *Westar families* representing selections from wild stands in the southern interior of BC were not screened.

Heights in the coastal Canadian trials showed the same trends as at Whidbey Island with the Idaho Region having some of the greatest growth, but unlike Whidbey these regional differences were not significant (table 5). However, if the variation in provenance samples within regions is investigated more closely, some significant trends did emerge. If we split off the Northern Rocky Mountain BC samples from the Southern Interior (I-b), it shows significantly poorer growth than Idaho, Southern Interior BC, and the local Coastal population (II-a). These are 18 parent trees sampled from areas such as Mount Revelstoke and Valemount at the very northern edge of WWP's inland distribution (e.g., trial site 8, fig. 1). It would indicate that although this broadly defined northern population (Regions I–III) is relatively homogeneous, some differentiation is occurring at the species' edge. Another feature on the more detailed redefinition of regions is the significant and superior growth of the selected *Porter families*. If this group is taken out of the Coastal high elevation group (II-b) and treated separately, it shows a marked effect. Individuals in the *Dorena MGR* seedlot (Region IV) as at Whidbey Island were significantly smaller at the Ladysmith site; but on the heavily rusted Sechelt site they performed well, as one of the few healthy populations on this site.

Blister Rust and Height on the Canadian Interior Sites

Among the three Canadian trial sites in Interior BC, Nakusp, a moderate productivity site in the Southern Interior, had just 35-percent overall infection. Barrière in the Thompson River Valley was a more northern and severe site but with only 16-percent overall infection. The Valemount site was more than 75 percent overall infected and located at the northern edge of WWP distribution. The regions (without any of the selected populations) were nonsignificant at all sites, but most discriminating at the Valemount site. The same trend as the coast was shown: interior populations (Region I) had a higher incidence of cankers than the low elevation Coastal (Region II-a) or North Cascades (Region III) populations (table 6).

This trend of regional differences is shown graphically for the Valemount site in figure 4, with the lower canker incidence of North Cascades and low elevation Coastal

Table 5—Results of the mixed-effects model for heights in decimeters for the Coastal Canadian sites.

Trait	Ladysmith		Sechelt	
Random effect	**variance**	***P*** [b]	**variance**	***P*** [b]
Block	7607	0.0005	1760	0.0128
Population(Region)	NE[a]		NE	
Tree (Seedlot Region)	36299	<.0001	32446	<.0001
Fixed effect	**DF**	***P*** [c]	**DF**	***P*** [c]
Region	5, 2900	0.2084	5, 1048	0.1583
Region (with selected)	7, 2900	<.0001	6, 1048	0.0077
Region level	**Least squares mean**	**Confidence limits**	**Least squares mean**	**Confidence limits**
I-a Inland Empire	63.09	58.82, 67.35	45.42	42.25, 48.60
I-b BC Interior - Westar	62.84	59.05, 66.63	45.74	43.29, 48.18
I-b BC Interior - Northern	58.22	53.54, 62.90	38.03	34.11, 41.95
II-a - Coastal	62.71	NE, NE	44.65	40.54, 48.75
II-b - Coastal high elevation	58.51	NE, NE	45.64	41.29, 49.84
II-a&b Coastal Porter	67.14	64.25, 70.03	47.93	42.28, 53.58
III N - N. Cascades	59.58	55.00, 64.15	41.51	37.52, 45.51
IV Dorena MGR	56.80	51.04, 62.55	44.67	36.28, 53.06
Comparison of regions	**Difference in least squares**	***P*** [d]	**Difference in least squares**	***P*** [d]
Local (II-a) vs Idaho	0	0.8341	0.7	0.7323
Local (II-a) vs N Interior	**4.5**	**0.0287**	**6.6**	**0.0097**
Local vs coastal high (II-b)	2.4	0.0776	0	0.7340
Local vs N. Cascades (III).	2.5	0.1160	3.1	0.2255
Local vs S. Cascades (IV).	**3.6**	**0.0276**	0	0.9957

[a] NE – Not estimable
[b] *P*-value for testing whether each variance component is zero is derived from a mixture of χ^2 distributions.
[c] *P*-value for testing whether all Fixed Region effects are zero is derived from an *F* distribution.
[d] *P*-value for testing whether each difference is zero is derived from a *t* distribution.

Table 6—Results of the analysis for canker frequencies (incidence) at the Canadian sites in Interior BC.

Trait	Nakusp		Barrière		Valemount	
Random effect	**variance**	**S.E.**	**variance**	**S.E.**	**variance**	**S.E.**
Block	0.0349	0.0366	0.0793	0.05692	0.2553	0.0916
Population (Region)	0.1190	0.07049	0.1600	0.0646	0.6147	0.1511
Fixed effect	**DF**	***P*** [a]	**DF**	***P*** [a]	**DF**	***P*** [a]
Region (only unselected)	5,25	0.0866	4,31	0.4395	4, 38	0.0852
Region (with selected)	9,92	<.0001	7,63	0.0738	8, 56	**0.0007**
Region level	**Estimated canker incidence**	**Confidence limits**	**Estimated canker incidence**	**Confidence limits**	**Estimated canker incidence**	**Confidence limits**
I-a Inland Empire	0.456	0.355, 0.561	0.186	0.134, 0.253	0.809	0.661, 0.902
I-b BC Interior	0.444	0.372, 0.520	0.198	0.152, 0.255	0.858	0.782, 0.911
Westar families	0.39	0.30, 0.50	0.127	0.094, 0.170	**0.713**	0.593, 0.809
II-a - Coastal	0.425	0.333, 0.522	0.203	0.147, 0.274	**0.662**	0.549, 0.759
Porter families	**0.181**	0.123, 0.258	**0.076**	0.033, 0.165	**0.451**	0.252, 0.667
II-b… high elevation	0.333	0.240, 0.440	0.151	0.099, 0.224	0.827	0.715, 0.902
III N. Cascades	0.338	0.229, 0.467	0.137	0.087, 0.210	**0.736**	0.510, 0.882
IV S. Cascades (Dorena)	0.190	0.080, 0.386	0.049	0.015, 0.152	**0.297**	0.074, 0.692
Comparison of Regions	**Difference in canker incidence**	***P*** [b]	**Difference in canker incidence**	***P*** [b]	**Difference in canker Incidence**	***P*** [b]
Interior vs. *Westar. Families*	0.06	0.0015	0.06	0.0309	0.145	**0.0121**
Interior vs. Coastal unselect	0.12	0.1271	0.04	0.2215	0.196	**0.0043**
Interior vs. Porter families	0.27	**<0.0001**	0.10	0.0891	0.407	**0.0001**
Interior vs. Dorena	0.25	**0.0275**	0.12	0.0115	0.561	**0.0019**

[a] *P*-value for testing whether all Provenance effects are zero is derived from an *F* distribution.
[b] *P*-value for testing whether each difference is zero is derived from a *t* distribution.

populations (70 percent) and the marked and significant effect in the selected populations—particularly the greater survival shown by the Region IV *Dorena MGR* population (30 percent), the *Porter families* selections (II-Coast select; 45 percent), and even the Westar compared to unselected Interior populations (70 vs. 85 percent).

Regional differences in height were nonsignificant at the moderate Nakusp site as they were on the coastal sites (table 7). But in the more northern sites the *Dorena MGR* seedlot begins to suffer in performance and at the Valemount site even the coastal low elevation sources (IIa) begin to suffer (5.1 m vs. 4.3 m (Pr > |t| <0.0001). A later walk-through of the Valemount site at 20 years showed the *Dorena MGR* seedlots still alive, but starting to be overgrown by the remaining white pine survivors.

Blister Rust and Height on the Lost Valley and Priest River, Idaho Sites

The Lost Valley site near McCall, Idaho was similar in scope to the Lone Lake site on Whidbey Island; it had the complete Steinhoff collection, good growth, and high overall survival but a high (85 percent) rust incidence measured at 21 years. Although outside the normal range of WWP, this area had one of the highest incidences of rust among the sites we investigated. The Priest River Experimental Forest trial site lost two full blocks due to early plantation failure; thus, only the one surviving block was assessed. The Priest River site was a low rust environment with just over 20 percent rust incidence overall.

Overall regional differences in canker frequency were nonsignificant in the highly rust-infected Lost Valley site (table 8). But contrasts in the Priest River site, and the overall analysis, picked up the same results as in the Whidbey Island and the Canadian trials. Unselected white pines in Idaho (Region I) had overall higher susceptibility than the unselected Northern Cascades (Region III) (79 percent vs. 49 percent cankered) (Pr > |t| 0.0092 in the combined analysis, table 8).

The Lost Valley and Priest River Planting 21-year data were also included in a separate analysis (McDonald, unpublished data, on file at USDA FS, Moscow

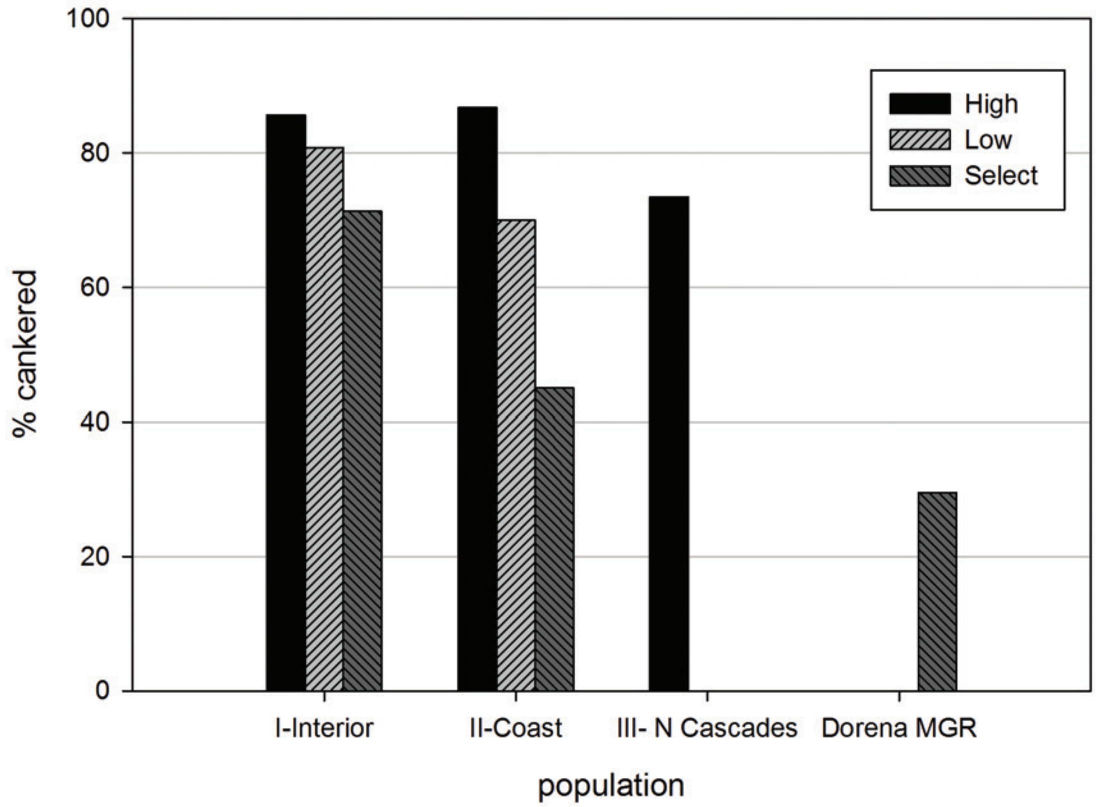

Figure 4—Canker frequencies at the Valemount site.

Forestry Sciences Laboratory, Moscow, Idaho). Seedlots in this analysis were portioned in a slightly different manner based on the separations shown in Kim et al. (2010: fig. 4) and data from an unpublished nursery and greenhouse experiment conducted at the Moscow Forestry Sciences Laboratory. Results suggest some small adjustments to the boundaries shown in figure 1 of this paper. These data suggest that the Region II and Region III boundary could be shifted to the Columbia River along the Oregon-Washington boundary. Other subdivisions concurrent with the present-day distribution of WWP are also noted: a North/South subdivision that follows the Bitteroot Divide in the United States and the Columbia River (Arrow Lakes) in Canada. Although this still may be considered a rather homogenous population, differences between the northern populations of Regions I–III are starting to emerge as was shown in the Canadian Northern Interior sites (Valemount). Molecular marker data suggest that a single refugia event may be an oversimplification for the northern Rocky Mountains.

DISCUSSION OF RESULTS

A result that is consistent but varying in magnitude indicates that in the random population selections, as in the Steinhoff collection, Region II (North Central Cascades) and III (low elevation Coastal) can have as much as one-half the level of infections compared to the Interior Region I samples or the higher elevation Region II (II-b in figure 1). Possible explanations include:

1. The effects of natural selection since the WPBR introduction to the Port of Vancouver in the early 20th century. The spread has been primarily south and west, so it is not surprising to see the Northern Cascades and low elevation North Coastal areas displaying higher native levels of resistance.

2. Details of mortality from WPBR are not shown here, but as noted in the Introduction, Hunt (2004) has suggested that some of the resistance responses valuable in the Interior (e.g., needle

Table 7—Results for height measurements for the Interior Canadian Sites.

Trait	Nakusp		Barrière		Valemount	
Random effect	**variance**	***P*** [a]	**variance**	***P*** [a]	**variance**	***P*** [a]
Block	21.0	0.0006	57.1	0.0005	30.8	0.0008
Seedlot(Region)	20.3	< 0.0001	0	n/a	9.09	0.0033
Tree * Seedlot (Region)	91.05	< 0.0001	156.68	< 0.0001	208.86	< 0.0001
Fixed effect	**DF**	***P*** [b]	**DF**	***P*** [b]	**DF**	***P*** [b]
Region	7,91	<0.0001	6,160	<0.0001	6, 47	<0.0001
Region level	**Least squares mean**	**Confidence limits**	**Least squares mean**	**Confidence limits**	**Least squares mean**	**Confidence limits**
I-a Inland Empire	45.7	41.1, 50.3	52.4	48.9, 55.8	48.6	44.7, 52.5
I-b BC Interior - Westar	**48.0**	45.5, 50.5	52.9	49.6, 56.2	51.5	48.5, 54.6
I-b BC Interior - Northern	44.9	41.7, 48.0	**49.5**	45.9, 53.0	**50.5**	47.2, 53.8
II-a - Coastal	47.5	44.5, 50.4	49.4	46.0, 52.8	**42.9**	39.8, 46.1
II-b… high elevation	45.6	42.0, 49.3	48.2	44.4, 52.0	47.1	43.1, 51.0
III N - N. Cascades	45.5	39.8, 51.3	49.4	45.7, 53.0	46.6	41.8, 51.3
IV S. Cascades (Dorena)	44.4	34.7, 54.0	46.1	41.7, 50.6	**35.9**	28.4, 43.5
Comparison of regions	**Difference in least squares**	**P** [c]	**Difference in least squares**	**P** [c]	**Difference in least squares**	**P** [c]
local vs. other interior	3.1	0.0475	3.4	0.0018	1.9	0.1316
local vs. coastal (II-a)	0.5	0.7095	0.1	0.9563	**7.5**	<0.0001
local vs. coastal high (II-b)	2.4	0.1904	1.3	0.3780	3.4	0.0998
local vs. N. Cascades (III).	2.5	0.3949	0.1	0.9454	3.9	0.1104
local vs. S. Cascades (IV).	3.6	0.4548	3.3	0.0777	14.6	0.0005

[a] *P*-value for testing whether each variance component is zero is derived from a mixture of χ^2 distributions
[b] *P*-value for testing whether all Fixed Region effects are zero is derived from an *F* distribution.
[c] *P*-value for testing whether each difference is zero is derived from a *t* distribution.

shed) that do well in the shorter growing season of the Interior may do less well in the longer growing season of the coast. We found the greatest discrepancy in mortality in the coastal sites.

3. Various constitutive defenses valuable against WPBR, but evolved against other unknown pathogens or pests, might have arisen faster in these more resistant populations after the postglacial northward migration.

4. The evolutionary history of the northern populations appears to be more complex than a single introduction, and a great deal more variability might exist (see following).

Besides the regional difference within the northern population for rust resistance, we also note that the northern population did not perform uniformly well for growth and survival across all sites. Samples from Southern Interior BC and Northern U.S. Rockies (Idaho I-a in tables) performed particularly well for growth across all sites—at the very favorable sites of Whidbey Island and Ladysmith (VI)—nearly 10 percent higher than the local populations. However, the Northern Canadian Rockies samples (I-b) (from the far north of its range) do poorly for growth on coastal sites, and Coastal populations have poor growth in the Northern Canadian Rockies. Kim et al. (2010) suggest that the glacial refugia in the Rockies and subsequent recolonizations might be more complex than a simple founder effect and that genotypic diversity is more likely to arise at the fringes of the range for a species (Kim et al. 2010; Petit et al. 2003) and McDonald (unpublished data, on file at USDA FS, Moscow Forestry Sciences Laboratory, Moscow, Idaho).

Table 8—Results of the GLIMMIX analyses for canker frequencies (incidence) at the Idaho sites.

Trait	Lost Valley		Priest River		Combined Idaho	
Random effect	**variance**	**S.E.**	**variance**	**S.E.**	**variance**	**S.E.**
Population (Region)	1.3839	0.4914	0.4442	0.3457	0.7646	0.2715
Block * Region					0	.
Fixed effect	**DF**	***P*** [a]	**DF**	***P*** [a]	**DF**	***P*** [a]
Region	5,52	0.6577	5,56	0.3457	5,53	0.1226
Region level	**Estimated canker incidence**	**Confidence limits**	**Estimated canker incidence**	**Confidence limits**	**Estimated canker incidence**	**Confidence limits**
I N - Interior	0.91	0.78, 0.97	0.24	0.16, 0.35	**0.79**	0.21, 0.98
II N - Coastal	0.90	0.73, 0.97	0.21	0.085, 0.43	0.78	0.21, 0.98
III N - N. Cascades	0.76	0.44, 0.93	0.03	0.004, 0.21	**0.49**	0.069, 0.92
IV T - S. Cascades	0.84	0.56, 0.96	0.22	0.094, 0.43	0.71	0.16, 0.97
V T - Siskiyou	0.92	0.39, 0.99	0.31	0.053, 0.79	0.83	0.24, 0.99
VI S – Sierra	0.89	0.69, 0.97	0.40	0.18, 0.68	0.83	0.28, 0.98
Comparison of regions	**Difference in canker incidence**	***P*** [b]	**Difference in canker incidence**	***P*** [b]	**Difference in canker incidence**	***P*** [b]
Interior vs. Coastal	0.01	0.8902	0.03	0.7795	0.10	0.8247
Interior vs. N. Cascades	0.14	0.1079	0.20	**0.0378**	0.30	**0.0092**

[a] *P*-value for testing whether all Provenance effects are zero is derived from an *F* distribution.
[b] *P*-value for testing whether each difference is zero is derived from a *t* distribution.

The results also show that early first generation phenotypic selection programs have been very effective against WPBR. The *Porter families* selected and screened in the 1950s (King and Hunt 2004) proved particularly effective as a group. This adds to the evidence from the unselected populations that low frequency, probably constitutive defenses, exist for resistance to this disease beyond just the MGR expression of Cr2. The value of ongoing selective breeding to take advantage of the inherent resistance found in the North American white pine and accelerate the natural selection process is well documented (King et al. 2010; Sniezko et al. 2014). In the most heavily infected sites (Sechelt at 90 percent and Valemount at 80 percent) the MGR seedlot from the Dorena program appeared the only effective resistant lots although many non-MGR trees still survived in later surveys of these severe sites with both active and non-active cankers. More recent trials that include seedlots with known partial resistance have shown good field resistance in very severely infected sites and in artificial inoculation trials (Sniezko et al. 2014; Ukrainetz and King, poster presented at IUFRO meeting, March 2016, Rotorua, New Zealand). In the long term this approach is likely to be more successful for stable resistance.

The existence of this genetic variation to WPBR is the foundation for the breeding work with western white pine. This paper shows that at least low-to-moderate differences exist in the level of resistance between geographic populations of WWP, with perhaps the highest incidence of resistance (but still relatively low) in the North Cascades populations. Previous work has shown geographic variation in one type of resistance, MGR (Kinloch et al. 2003). It also suggests that the efficacy of resistance might vary by site conditions (coastal or interior, high or low elevation) (Hunt 2004), and effectiveness under a changing climate will need to be monitored. Resistance programs seek to capture this resistance, and they are well underway in much of the range of WWP (King and Hunt 2004; McDonald et al. 2004; Sniezko et al. 2014). A new series of trials involving many of the best resistant seedlots known (from BC, Idaho, Oregon, and Washington) is being established in Oregon, Washington, and BC in 2014 and 2015 to further examine the efficacy of resistance from different geographic sources.

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