3. Bei der Rückkreuzung, wabei als väterlicher Elter der Hybrid P. nigra X P. densiflora und als Mutter P. nigra gewählt wurde, kommen bei dem anatomischen Bau der Nadeln mehr die Merkmale der Mutter (P. nigra) zum Ausdruck, als in dem Fall, bei dem als väterlicher Elter der Hybrid P. densiflora X P. nigra ausgewählt worden ist und die Mutter dieselbe blieb.
4. Die zweijährigen Hybridpflanzen von P. nigra X P. *densiflora* zeigen nicht immer ein größeres Höhenwachstum als die reine Art P. nigra. Die Wuchsleistung der jungen Hybridpflanzen hängt von den einzelnen Individuen des weiblichen Elters ab.
5. Bei der Rückkreuzung des Hybrids mit der Schwarzkiefer weisen dreijährige Pflanzen größere Höhen als die Kontrollpflanzen auf, d. h. als die reine Art P. nigra. In diesem Falle wurden aber als weibliche Eltern andere Schwarzkiefernstämme als die unter Punkt 1 angeführten ausgewählt.
6. Die Verhältnisse zwischen den Durchmessern der Hybridpflanzen und denen der Kontrollpflanzen der Schwarzkiefer stimmen mit den Ergebnissen überein, welche für die Höhen der Pflanzen erhalten worden waren.

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Breeding Blister Rust Resistant Western White Pine

III. Comparative Performance of Clonal and Seedling Lines from Rust-Free Selections

By R. T. BINGHAM[1])

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In 1950, the Forest Service began its program in breeding western white pine (Pinus monticola DOUGL.) resistant to blister rust caused by *Cronartium* ribicola J. C. FISCH. ex. RABENH. Progress has been reported in this journal and elsewhere (BINGHAM et al. 1953, 1960; and BINGHAM 1963).

During the 15 years through 1964 more than 400 phenotypically resistant selections have been located in rust-decimated, natural western white pine stands of northern Idaho and adjacent States. These remarkable trees, completely rust-free or with few infections, their branches often interlaced with those of neighboring trees bearing thousands of rust cankers, comprise the basic plant material for a practical breeding program aimed toward mass production of resistant planting stock.

Presently, the only economical means for mass producing resistant western white pine stock is by seed. Consequently, each of the field selections is under test to determine its ability to transmit resistance via seed. Some selections exhibit general combining ability for resistance (i. e., they transmit an above-average level of resistance to several test progenies). These are considered to have the greatest breeding value and are entered in the long-range breeding and seed orchard programs (BINGHAM et al. 1960).

Other experimentation is also underway. To gain insight into the efficacy of phenotypic selection for resistance and into the mode of inheritance of resistance, a representative group of field selections has been under study as grafted clonal lines exposed to heavy, natural blister rust infection. Comparative performance of these clonal lines and of related seedling progenies is the subject of this paper.

Materials and Methods

Clonal lines. — In early December of 1950 and 1951, scionwood from 36 rust-free selections was collected, often in remote localities in the mountains, packed with snow in polyethylene bags, and stored in an accessible snowbank. Greenhouse grafting began about 2 months later (**Fig.** 1) on well-established, actively growing, 4- to 5-year-old western white pine seedlings of a single Coeur d'Alene National Forest nursery seed lot. In early May of 1951 and 1952, suseeptible rootstock foliage was removed by pruning all branches below successful graft unions. Grafted plants were then transferred to an outdoor coldframe for hardening-off. In early June of the same year grafts were planted in three 5-acre field plots, located in areas of heavy, natural blister rust infection. Plots were at Elk River, Idaho; at Tepee Creek near Coeur d'Alene, Idaho; and at Randolph Creek near Saltese, Montana.

Each field plot contained six grafts (ramets from each of the 36 canker-free parent trees [ortets]), the total number of 216 ramets being subdivided into six randomized, complete blocks, each block containing one ramet of each ortet. Grafts were row-planted at 30 X 30 feet, but with planting spots of adjacent rows shifted 15 feet to increase spacing

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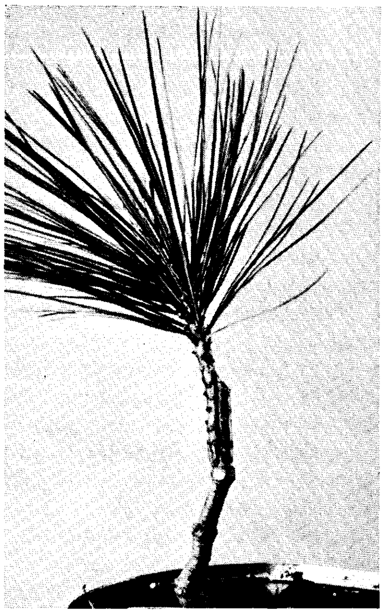

Figure 1. — The standard type of greenhouse, side-graft of western white pine used in the study. All blister rust susceptible foliage of the stock plant was removed prior to outplanting on field plots.

between plants. At each planting spot the graft was set 1 foot from a numbered planting stake. A 5- to 6-year-old control seedling was set 5 feet away from the graft on the row line. These controls were from one of three ordinary nursery lots assigned at random to two of the six blocks in the plot. Centered between the graft and control but 5 feet to one side of the row line was set a *Ribes lacustre* (Pers.) Poir. A *Ribes viscosissimum* Pursh. plant was set 5 feet to the other side *(Figs. 2 and 3)*.

Grafts and control seedlings were inspected for survival in August of 1952 and 1953, then for survival and blister rust infection in August or September of 1954 through 1956, 1959, and 1964.

Corresponding seedling lines. — Thirty-five of the selections tested by performance of clonal lines were also tested for seed-transmission of resistance. Test materials were artificially inoculated seedling progenies from (a) a series of four "test-crosses" made by outcrossing each selection with the same four "testers", and (b) where possible, self-pollinations.

Pollinations, attempted in the years 1950 to 1960, were not always successful, so the progeny tests which followed in 1952 to 1962 were sometimes incomplete with only one to three of the four "test-crosses" and no self represented.

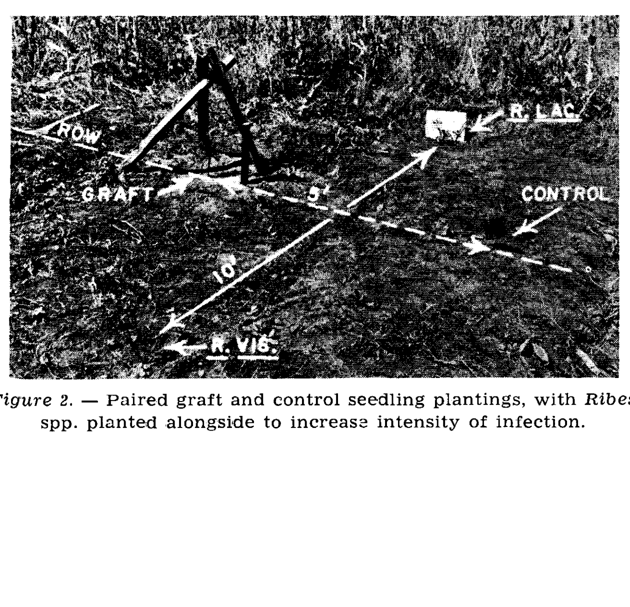

Figure 2. — Paired graft and control seedling plantings, with *Ribes* spp. planted alongside to increase intensity of infection.

Figure 3. — A similar unit planting 14 years later. The control seedling, on the left in front of the camera box, has been killed by blister rust.

In other cases the entire set of four outcrosses might be repeated, or the self repeated, in successive years. As a result the various selections were represented by from one to nine outcross progenies, and by zero to three selfed progenies.

Design and treatment of the nine-replicate, 90-seed progeny tests established prior to 1960 have been described earlier (Bingham *et al.* 1960). The 1960 and 1962 tests included 10 randomized blocks, each block including one 16-seed replicate of each progeny. Naturally some seed — especially in selfed progenies — failed to germinate, and some seedlings were killed by damping-off fungi or died from other causes besides blister rust. Expecting these extraneous losses, when extra seed was available up to three seeds were sown in each planting spot. Later, extra seedlings were removed at random, leaving one per planting spot. Even so, in the 1952 test the average replicate was reduced from full stocking of ten to nine seedlings, the 1962 test from 16 to 10 seedlings. Several progenies were reduced to only a few seedlings per replicate, and those represented by a total of fewer than 15 full-sib or selfed seedlings were dropped from the analysis.

Adequacy of the artificial inoculations was determined from sporecast slides placed on test bed surfaces at the time of inoculation and from mapping the position of infected seedlings in the test beds. Over 7 years, basidiospore casts averaged about eight spores per square millimeter of vaseline-coated glass-slide surface, with about 2½ spores per sq. mm. seen germinating in place on the slides. Thus an average 2-year-old seedling with, say, 25 sq. mm. of upper needle surface on each of 50 needles intercepted perhaps 10,000 spores, of which more than 3,000 were germinable. Even so, seedlings in some parts of the beds escaped inoculation. Maps of seedbed rust distribution showed that little or no infection occurred in some small "escape" areas, and seedlings in these areas were eliminated from analyses.

Susceptibility (conversely, resistance) in individual test progenies was expressed as the percentage of seedlings in the progeny which became infected under the intense rust exposure, increased by percentage of seedlings which escaped infection in the average control lot of the same progeny test. Susceptibility in seedling lines was expressed as the percentage of infected seedlings in the average test progeny of the line.

Results and Discussion

Comparative resistance of clonal lines from rust-free selections. — In the three graft plots, mortality from causes other than blister rust infection (i. e., from graft-union failure, drought, snow breakage, rodent damage) averaged 80 percent for grafts, 30 percent for control seedlings. Thus, mortality of grafts was high enough to preclude sensitive analysis of variations in resistance between clonal lines. However, the number of grafts that survived, 133, was adequate for gross comparisons of resistance in clones vs. control seedlings.

Relative performance of grafts and control seedlings at the three locations is shown in *Table 1*. It is noteworthy that only 5 of 133 grafts — about 4 percent — became infected over a 13-year period of exposure to the rust. Meanwhile, 89 percent of the 452 control seedlings became infected; this indicated that rust spreading from planted and naturally occurring *Ribes* spp. had been both intense and adequate. Statistically, the 85-percent difference in infection between grafts and controls is highly significant.

In eastern white pine *(P. strobus* L.), it appears that grafting *per se* lowers susceptibility for a time, and that in grafts susceptibility is inversely proportional to age of ortet (Patton 1961). The author has observed identical reactions in western white pine grafts; so it is likely that much of the observed difference between infection of grafts (from ortets 22 to 67 years old at grafting) and of control seedlings (at ages 5 to 19 years) is due to these extraneous effects of grafting and tree age. But the grafts in this experiment have long since recovered from grafting or pruning shock *(Figs. 1 and 2);* in fact, they now present a "rust target" which is on the average larger than that of the surviving control seedlings. Hence, in respect to susceptibilty, one would expect the grafts to behave like the normal, older trees occurring in natural stands bordering the field plots. The 25- to 50-year-old trees in the adjacent natural stands, however, have become heavily infected in the experimental period. Thus the difference between infection of grafts and control seedlings in this experiment is considered to represent a genetic difference in susceptibility.

Infection of control seedlings was significantly different between plantations *(Table 1,* 5- to 18-percent differences), but not between seedling provenances *(Table 2,* 0- to 1-percent differences). The significant plantation effect probably reflected conditions at the different sites, because differences in degree of natural infection in adjacent natural white pine stands followed the same pattern. The slight differences in infection of grafts on the three plantations were not significant.

The five infected ramets all originated from different ortets. Two of them, from ortets 22 and 59, supported lethal stem infections that caused their death. Two others, an 8-foot-tall graft of ortet 28 and a 15-foot-tall graft of ortet 33, were living and each supported two living, normal branch cankers. The remaining infected ramet, a 4-foot-tall graft from ortet 9, was also living and supported a normal and potentially lethal stem canker in 1956. But by 1959 the margins of the canker were producing wound phellogens; by 1964 the canker was completely "corked-out". This corking-out phenomenon was reported by Struckmeyer and Riker (1951) as a resistance mechanism in eastern white pine and by Bingham *et al.* (1960) in western white pine.

Among the 400 infected control seedlings, 251 had already been killed by one or more lethal stem cankers. The remaining 149, while alive, supported from one to more than 20 stem and branch cankers. Almost one-third of the healthy control plants — 17 of 52 — were extremely low-vigor, frost-damaged runts, averaging about 1½ feet tall. Compared to the 128 rust-free ramets (average height 7 feet), these runts were poor rust suscepts both in respect to plant vigor and "target" size.

Intensity of infection was much greater on control seedlings than on grafts *(Table 3).* There were almost 30 times as many cankers on controls — an average of 1.47 cankers per control tree, only 0.05 canker per graft.

Comparative resistance of clonal vs. seedling lines. — Relative performance of grafts and control-pollinated seedlings from the 36 selections is shown in *Table 4*. Infection of ortets and of their related clonal and seedling lines followed no discernible pattern. Nine of the 36 ortets were known to have supported from one to three blister rust cankers, but none of the 33 ramets in the nine corresponding clonal lines became infected. Instead, the five infected ramets all came from uninfected ortets. Related cross- and self-pollinated seedling lines in four of the five infected clonal lines were correspondingly low in resistance (90 to 100 percent infected). But in the remaining infected clonal line (No. 22) the related seedling lines were among the most resistant observed. Related seedling progenies of 30 uninfected clonal lines also showed wide variation in resistance.

Selfed progenies gave a moderately good indication of the performance of crossed progenies. Using angles equal to arc sin of the square root of the percent infected for the progenies of single trees as items, the product-moment correlation was $r = .428$, almost significant at the 5 percent level with 17 d. f. However, the rank-correlation coefficient was $r_s = .486$, significant at the 5 percent level.

Table 1. — Blister rust infection in grafts vs. control seedlings.

Location of plantation	Average height	Trees exposed to blister rust		Trees infected by rust[1])	
		Grafts	Seedlings	Grafts	Seedlings
	(Feet)	(Number)		(Percent)	
Elk Creek	12	28	144	4	99
Tepee Creek	9	42	129	5	81
Randolph Creek	4[2])	63	179	3	86
Average or total	7	133	452	4	89

[1]) Between-plantation differences in seedling infection were significant at 5 percent level. At all plantations, graft-seedling differences in infection were significant at 1 percent level.
[2]) Randolph Creek plantation is at a high elevation and has a brief growing season.

Table 2. — Blister rust infection in three control seedling lots.

Control lot	Surviving or rust-killed seedlings	Blister rust infected seedlings	
(No. and origin)	(Total no.)	(No.)	(%)[1])
226 (Coeur d'Alene N. F.)	160	140	88
227 (St. Joe N. F.)	153	136	89
229 (Kaniksu N. F.)	139	124	89
Totals and Averages	452	400	89

[1]) Small differences between lot percentages nonsignificant.

Table 3. — Intensity of infection in grafts vs. control seedlings.

Plant class	Grafts			Control seedlings		
	No. plants	No. cankers	Av. no. cankers per plant	No. plants	No. cankers	Av. no. cankers per tree
Rust-infected, living	3	5	1.7	149	361	2.4
Rust-infected, killed	2	2	1.0	251	304	1.2
Subtotal infected	5	7	1.4	400	665	1.7
Healthy (uninfected)	128	—	—	52	—	—
Totals	133	7	0.05	452	665	1.47

Table 4. — Comparative performance of clonal lines and corresponding seedling progenies from phenotypically resistant selections.

Selection	Age in 1951	Ramets tested	Outcrosses			Selfs		
			Progenies tested	Seedlings		Progenies tested	Seedlings	
				Tested	Infected		Tested	Infected
(No.)	(Yrs.)	(No.)	(No.)	(No.)	(%)	(No.)	(No.)	(%)
1	59	3	7	627	76	1	20	68
5	37	4	—	—	—	—	—	—
9	30	4[2])	9	875	98	—	—	—
10	27	7	1	83	92	—	—	—
12[1])	67	2	3	74	96	—	—	—
15[1])	25	4	5	515	88	—	—	—
16	31	2	3	199	92	1	18	100
17	25	3	5	324	69	2	75	74
18[1])	32	6	4	425	91	1	32	86
19	34	5	4	341	72	1	83	73
20	35	8	8	701	84	1	140	99
21[1])	35	7	4	249	76	1	41	90
22	30	8[2])	4	276	70	1	18	62
23	55	1	4	145	89	1	30	87
24	24	—	6	580	78	—	—	—
25	32	2	5	296	80	1	38	94
27	30	4	2	34	91	—	—	—
28	56	4[2])	2	80	90	—	—	—
29[1])	59	3	4	264	97	—	—	—
30[1])	46	4	6	389	85	2	40	100
33	56	2[2])	1	18	100	—	—	—
34	56	4	1	22	89	—	—	—
35	36	3	1	15	96	—	—	—
37	40	4	3	181	77	1	15	87
38	35	3	1	73	85	—	—	—
39	45	1	3	197	91	1	47	86
45[1])	38	4	6	494	73	1	31	73
54[1])	46	2	9	835	96	3	99	76
57[1])	38	1	1	24	90	—	—	—
58	34	6	7	1142	70	2	561	65
59	31	3[2])	4	363	96	1	40	100
61	22	3	6	580	71	—	—	—
62	26	2	2	84	89	—	—	—
63	52	2	9	842	95	1	17	61
64	26	5	3	229	84	—	—	—
65	25	6	9	748	97	2	88	94

[1]) Selection supported one to three blister rust cankers.
[2]) One ramet of the clone infected, with one or two cankers.

None of the selfed progenies was completely or even highly resistant. This indicates that resistance was not controlled by one or a few recessive genes. The correlation between selfed and crossed progenies and the high general combining ability of some parents indicates that genes with additive effects may be more important.

Conclusions and Summary

Efficiency of phenotypic selection. — In view of the very minor and irregular infection of grafts from rust-free or very lightly infected selections, relative to the massive infection or ordinary control seedlings on the same plots, it appeared that most of the selections were genotypically as well as phenotypically resistant. Thus, phenotypic selection for relative freedom from rust in heavily infected natural stands was highly efficient. It follows that phenotypic selection in seedbeds of sexual propagules should be similarly efficient. This does not mean that all canker-free trees in natural stands have high breeding value. In fact, as already shown (Bingham *et al.* 1960) and as shown here again, only about one in four of the canker-free selections has a high breeding value — i. e., exhibits general combining ability for seed-transmission of resistance.

Mode of inheritance of resistance. — The occasional but irregular infection in clonal lines also suggests that resistance is a threshold character sometimes overcome under field conditions particularly favorable for infection. The same threshold-type resistance seems to hold in seedling progenies. We are convinced that with repeated artificial inoculations under ideal conditions for infection we can induce infection on the most "resistant" seedlings available. Resistance is thus relative. Probably we shall never produce completely immune western white pine.

Blister rust resistance is known to exist in both eastern and western white pine (PATTON and RIKER 1958; BINGHAM *et al.* 1960), but so far there has been little concrete evidence concerning the numbers or kinds of genes involved in the resistance system. Both HEIMBURGER (1962) and BINGHAM (1963) have suggested that resistance is controlled by polygenes. The fact that resistance is seated in both foliage and bark tissues, and has quantitative-like inheritance (see *Table 1*, BINGHAM *et al.* 1960), indicates that more than one partially dominant gene is involved. The performance of selfed lines further strengthens this hypothesis by showing that control is not by single or multiple recessive genes.

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Germination of Blue Spruce and Ponderosa Pine Pollen After Eleven Years of Storage at 0° to 4° C[1])

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Pollen of blue spruce *(Picea pungens* ENGELMANN), ponderosa pine *(Pinus ponderosa* LAWSON), lodgepole pine *(Pinus contorta* DOUGLAS), and limber pine *(Pinus flexilis* JAMES) was stored in 1954 at each of two temperatures (0 to 4 degrees C. and 25 to 27 degrees C.) and under each of three relative humidities (0, 25, and 50 percent). Periodic estimates have been made of the germination of this pollen after 24 hours of culture *in vitro* at room temperature on two culture media: agar (1.2 percent plus 2.0 percent sucrose), and a 10 percent aqueous sucrose solution shown by preliminary tests in 1954 to give the highest germination and/or longest pollen-tube growth of fresh pollen.[3]) The procedures used for culturing the pollen and estimating germination have been described (FECHNER, 1958). After six years of storage at 25 to 27 degrees C., the pollen of none of the species studied germinated, regardless of the relative humidity of storage (FECHNER, *et al.*, 1960). This paper presents the results of cultures made during June, 1965 of the pollen which had been stored for approximately eleven years at 0 to 4 degrees C. and under the three relative humidities mentioned.

Samples of blue spruce and ponderosa pine pollen which had been stored for eleven years at 0 to 4 degrees C. and 50 percent relative humidity were also cultured on six aqueous sucrose solutions (0, 5, 10, 15, 20, and 25 percent concentration) in each of two Petri dish culture chambers to determine whether any change in the sucrose requirement for germination had occurred during storage.

Results

Pollen of lodgepole pine and limber pine which had been stored for eleven years at 0 to 4 degrees C. did not germinate on either culture medium used, regardless of the relative humidity at which it had been stored. Blue spruce and ponderosa pine pollen stored for eleven years at 0 to 4 degrees C. germinated as much as 30 and 70 percent, respectively. Highest germination of blue spruce pollen was obtained when the pollen was stored at 50 percent relative humidity; germination of ponderosa pine pollen was highest when the pollen was stored at 25 percent relative humidity but not significantly higher (as determined by the F-test) than that stored at 50 percent relative humidity. The germination of blue spruce pollen was not significantly affected by the medium on which the pollen was cultured, but germination of ponderosa pine pollen was approximately two to three times greater on the 10 percent sucrose medium than on the agar medium at each storage relative humidity *(Table 1)*.

Table 1. — Germination of blue spruce and ponderosa pine pollen after 24 hours of culture at room temperature, following eleven years of storage at 0 to 4 degrees C.

Species	Storage Relative Humidity, Percent		
	0	25	50
	Germination, Percent		
Blue spruce	0.5	19.0	29.5
Ponderosa pine			
10 percent sucrose	19.0	71.0	63 0
1.2% agar + 2.0% sucrose	6.0	33.0	30.0

Pollen of blue spruce which had been stored for eleven years at 0 to 4 degrees C. and 50 percent relative humidity showed the highest germination on a 15 percent sucrose solution, when different aqueous concentrations were compared *(Figure 1)*. There was no significant difference in germination percent between Petri dish culture chambers in any of the concentrations tested. Following eleven years of storage at the same temperature and relative humidity conditions, however, germination of ponderosa pine pollen was significantly affected (5 percent level of probability) by the concentration of sucrose in aqueous solution, greatest germination occurring on a 5 percent solution *(Figure 1)*.

[1]) Published with approval of the Director of the Colorado Agricultural Experiment Station as Scientific Series Paper No. 1064.

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[3]) The aqueous medium used for limber pine was distilled water.