Summary

Title of the paper: Thornlike formations on a hybrid from section Tacamahaca.

The occurrence of thorn-like growth on the cork ridges of a hybrid between P. *candicans* and P. trichocarpa is reported.

Résumé

Titre de l'article: *Présence* de *formations* epineuses sur un *peuplier* hybride de la section Tacamahaca. —

On a observé la présence de pousses a aspect epineux sur les côtes liégeuses d'un peuplier hybride entre P. *candicans* et P. trichocarpa.

Vigor, Disease Resistance, and Field Performance in Juvenile Progenies of the Hybrid Pinus monticola Dougl. × Pinus strobus L.

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Introduction

In North America and Europe today there are at least a dozen different agencies working toward the improvement of resistance to blister rust (caused by Cronartium ribicola FISCHER) in various white pines. Two principal lines attack are employed: (1) intraspecies breeding wherein the breeder attempts to select and cross resistant phenotypes from within a species inherently low in rust resistance but preferred for inherently rapid growth and good timber quality, and (2) interspecies breeding wherein the hybridizer attempts to combine resistance inherent within one entire species with rapid growth and good quality inherent within a second species. In intraspecies breeding there is perhaps a better possibility of maintaining the superior growth and qualitiy characteristics of a good species, and probably less danger of encountering serious problems in acclimatization. In interspecies breeding there is the advantage of working with known resistant genotypes, plus the possibility of obtaining the bonus of hybrid vigor. At present there is little actual basis for choosing one method in preference to the other since concrete evidence of the desirability of one method over the other is lacking. Probably the safest approach is to recognize the advantages of both intra- and interspecies breeding, and above all to make long range plans providing for the inclusion of proved materials developed by either method.

In this respect, results of early growth and rust resistance in interspecies hybrid progenies from controlled pollinations among pairs of rust resistant *Pinus* monticola DOUGL. and P. strobus L. selections are of specific interest to those engaged in breeding for C. ribicola resistance. Since the results are analysod with an eye to exploring the efficacy of selection, as reflected in the inheritance of desirable growth and resistance characteristics, they are of general interest to most workers engaged in forest tree improvement.

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The history of the hybrid P. monticola X P. strobus in the United States began with its production at the Institute of Forest Genetics, Placerville, California, about 15 years ago by RIGHTER (1945). Work in C. ribicola resistance of P. strobus began over 20 years ago with the pioneering experiments by RIKER et al. (1943) at the University of Wisconsin. In 1950 several North American workers joined forces in an attack on certain of the problems of securing increased resistance in native white pines (ANONYMOUS, 1951). The cooperative approach accelerated exchange of resistant white pine materials including scionwood, grafts, pollens, and seed from controlled pollinations. Exchanges between BINGHAM and SQUILLACE,

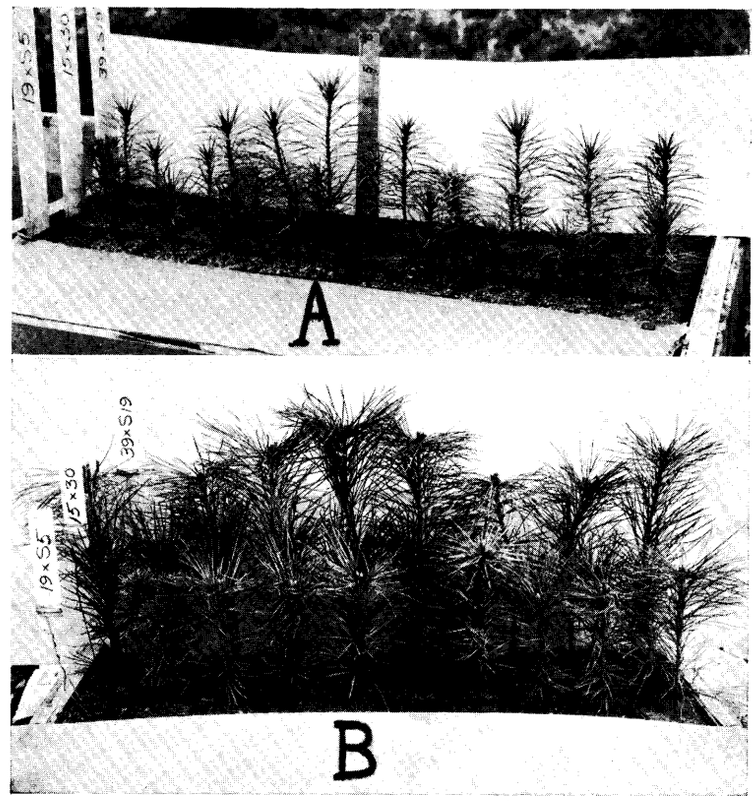

Figure 1. — First-year (A) and second-year (B) hybrid and Pinus monticola seedlings as grown in the Spokane, Washington nursery. Two hybrid progenies (P. mt. 19 × P. st. 5 and P. mt. 39 × P. st. 19), in the front and rear 10-seedling rows running across the photograph, bracket a P. monticola intraspecies progeny (P. mt. 15 × P. mt. 30). Hybrids in the front row appeared no more vigorous than the P. monticola seedlings of the middle row, but those of the rear row express definite hybrid vigor.

stationed at Spokane, Washington, and RIKER and PATTON, at Madison, Wisconsin, were numerous. This led to an interagency project in appraising the performance of hybrids which had been cooperatively produced by controlled pollinations between rust-resistant *P. monticola* and *P. strobus* selections.

Prior to undertaking the project in appraising hybrid performance, many intraspecies progenies of both species had been produced by BINGHAM et al. (1953) and RIKER and PATTON (1954). It had already been shown by SQUILLACE and BINGHAM (1954) that significant, if not strong correlations existed between height growth in *P. monticola* intraspecies progenies and height growth in the corresponding *P. monticola* parental selections. It seemed probable, therefore, that similar relationships might exist between vigor of interspecies hybrid progenies and that of corresponding parent trees, grafts of parent trees, and intraspecies progenies from parent trees. Preliminary observations indicated that certain hybrid progenies displayed outstanding hybrid vigor, while others were little better, if as good as the best intraspecies progenies (Figure 1). Early observations also indicated that wide differences existed in the apparent rust resistance of hybrid and intraspecies progenies. Accordingly, these and other aspects of hybrid performance were investigated.

Literature Reviewed

The interspecies hybrid *P. monticola* × *P. strobus,* or reciprocal, has been produced and reported by several workers including (in chronological order of reporting) RIGHTER (1945), RIGHTER and DUFFIELD (1951), BINGHAM, SQUILLACE and DUFFIELD (1953), HEIMBURGER (1953), and RIKER and PATTON (1954). Furthermore, in the juvenile stages the hybrid is reported to display hybrid vigor or at least to be vigorous by all of the same workers except BINGHAM et al. (1953), as well as by BUCHHOLZ (1945), STOCKWELL and RIGHTER (1949), and DUFFIELD and RIGHTER (1953).

BUCHHOLZ (1945) discussed the embryological aspects of hybrid vigor in pines and, since neither the embryo nor meristematic growing points were larger than in ordinary seed, concluded that the real explanation of hybrid vigor should be sought in biochemical or other physiological investigations. PAULEY and PERRY (1954) working with *Populus* clones found that certain clones apparently had gene combinations enabling more complete exploitation of the growing season at a given locality. Possibly hybrid vigor in pines might be due to some such gene combination. JOHNSON (1955) seems to follow this line of reasoning when he states "One acceptable definition of hybrid vigor can be simply stated to be better adaptability to given environmental conditions than that shown by parent lines." BUCHHOLZ (1945) showed that pine hybrid embryos mature at a more rapid rate and perhaps this tendency to differentiate cells at a more rapid rate persists in the hybrid plants. No attempt was made to review the extensive literature on hybrid vigor and heterosis in plants other than white pines, and in other pines and angiospermous trees other than as related to the problem at hand. For a thorough discussion of heterosis and hybrid vigor, the reader is referred to the article by WHALEY (1944) or the book edited by GOWEN (1952).

CHILDS and BEDWELL (1948) and HIRT (1940) have reported on the relative susceptibility of various white pines to attack by *C. ribicola,* concluding that *P. strobus* was relatively resistant when compared with *P. monticola* but that neither species could be considered resistant in comparison to the Eurasian white pines (*P. griffithi* MCCLELL., *P. cembra* L., *P. peuce* GRISEB., *P. armandi* FRANCH. and *P. koraiensis* SIEB. and ZUCC.).

Materials and Methods

Interspecies hybrid progenies with corresponding parent trees, clonal lines (grafts), and intraspecies progenies utilized in this study are outlined below. Throughout this study hybrid progenies are compared only with their *P. monticola* or *P. strobus* parents, with grafts from these parent trees, or with intraspecies progenies involving either the *P. monticola* or *P. strobus* parents. In all cases hybrid progenies were those produced on a single mother tree by controlled pollination with a single pollen parent.

Type of material	Measured at or near Spokane, Washington	Measured at or near Wisconsin Rapids, Wisc.
	Number	*Number*
Hybrid progenies:		
(1) *P. mt.* × *P. st.* (av. 42 plants per progeny)	14	3
(2) *P. st.* × *P. mt.* (av. 65 plants per progeny)	—	2
Parent trees:		
(1) *P. mt.* selections	7	—
(2) *P. st.* selections	—	8
Clonal lines:		
(1) *P. mt.* clones (av. 7 grafts per line)	6	—
(2) *P. st.* clones (av. 3 grafts per line)	—	7
Intraspecies progenies:		
(1) *P. mt.* × *P. mt.* (av. 57 plants per progeny)	76	1
(2) *P. st.* × *P. st.* (av. 70 plants per progeny)	7	55

Measurements of hybrid progenies, parent trees, clone members, and corresponding intraspecies progenies were recorded in feet, later transposed into metric equivalents. Progenies and clones were measured after the cessation of terminal growth in the late summer or fall, or before the start of terminal growth in the spring. Parent trees were measured during a single year with current growth excluded, after the method of SQUILLACE and BINGHAM (1954). BINGHAM and SQUILLACE contributed measurements on the Spokane materials, taken during the years 1952 through 1955. PATTON contributed measurements on the Wisconsin Rapids materials, taken during 1954. In the tables and discussion which follow, heights of hybrid or corresponding intraspecies progenies are averages of all progeny seedlings. *P. monticola* clone heights are averages of the third- through fifth-year annual height growth of grafts growing on several outplantings in northern Idaho and northwestern Montana. First- and second-year growth of grafts was excluded from averages because of inequalities introduced by early differences in rate of graft healing, size of scion, vigor of stock plants, and other factors. Clone heights in *P. strobus* are averages during the last 10 years of annual height growth in grafts growing at an outplanting near Wisconsin Rapids.

The variety of materials and their treatment permitted a more critical examination of the hybrid than has heretofore been possible. Hybrid growth performance can be appraised at 2 localities representative of the geo-

graphic range of the parental lines. Simultaneously, investigations of the relative performance of corresponding phenotypes, clonal lines, and intraspecies progenies are possible. Materials had been inoculated with *C. ribicola* and evidence on inheritance of rust resistance could also be gathered.

At the outset of the project it was found that in *P. monticola*, significant variation in height growth was introduced by measurable factors other than heritable height growth capacity. Growth rate of the parent trees was found directly correlated with site quality, inversely correlated with tree age. Graft height growth was directly correlated with relative vigor of the stock plant, but only for the first 3 of 5 years of growth; also with outplanting site quality. Progeny heights were found directly correlated with average progeny seed weight and with relative excellence of the growing season, but only for the first 3 of 4 years of growth. Accordingly, calculated averages of all materials measured at Spokane were adjusted for seed weight, growing season, stock vigor, tree age, and site quality wherever applicable. Adjustment techniques, and the relationships upon which they were based, will be the subject of a later paper by SQUILLACE and BINGHAM.

Results and Discussion

Vigor of the hybrid investigated at both parental localities

The average progeny height for 16 juvenile hybrids, arrayed for comparison with corresponding intraspecies progenies of both parents, is shown in Table 1. In the sandy loam, mildly acid (pH 5.0 to 6.5) soil at Spokane and vicinity, the juvenile hybrids as a group displayed definite hybrid vigor, exceeding the height of either parent. Mean differences in average height between the groups of hybrid progenies and corresponding groups of intraspecies progenies were significantly different for the first 2 years of growth — in favor of the hybrids. Third-year height differences between the hybrids and corresponding *P. strobus* progenies were not significant, but the lack of significance is meaningless since only 3 comparisons were possible. Also, in 2 of the 3 three-year-old hybrids compared (*P. mt.* 19 × *P. st.* 5 and *P. mt.* 19 × *P. st.* 19) the hybrids appeared inherently inferior through 3 seasons' growth. In the sandy, mildly acid (pH 5.0 to 6.5) soil at the Wisconsin Rapids nursery data were limited, and differences in hybrid and intraspecies progeny height were based at the most on 4 comparisons. In the 4 comparisons of second-year height of hybrids and intraspe-

Table 1. — Hybrid progeny height versus corresponding *P. monticola (P. mt.)* and *P. strobus (P. st.)* intraspecies progeny heights, at Spokane and Wisconsin Rapids

Hybrid designation		First-year height			Second-year height			Third-year height		
P, mt. seed parent	*P. st.* pollen parent	Hybrid progeny	Corresponding intraspecies progenies		Hybrid progeny	Corresponding intraspecies progenies		Hybrid progeny	Corresponding intraspecies progenies	
			P. mt.	*P. st.*		*P. mt.*	*P. st.*		*P. mt.*	*P. st.*
Selection number	Selection number	*Millimeters*								
					At Spokane, Washington					
19	5	40	40	38	90	71	98	139	117	163
	7	46	40	34	90	71	75			
	19	47	40	34	100	71	86	136	117	164
	174	50	40	52	108	71	139			
21	107	67	46	52	182	87	139			
39	18	55	43		141	77		212	128	
	19	65	43	34	151	77	86	230	128	164
54	107	65	43	52	171	82	139			
	129	70	43		183	82				
	174	67	43	52	167	82	139			
63	18	47	38							
	30	46	38							
69	30	56	43							
70	19	55	46	34						
Number of pairs		14			10			4		
Means		55.4		41.8	138.3		77.1	179.2		122.5
Mean differences		13.6[1]			61.2[1]			56.7[1]		
Number of pairs		9			8			3		
Means		55.8		42.4	132.4		112.6	168.3		163.7
Mean differences		13.4[1]			19.8[1]			4.6[2]		
					At Wisconsin Rapids, Wisconsin					
39	19				86		62			
54	174	48		42	66	58	68			
70	19	40		44						
P. st.	*P. mt.*									
6	30				66		62			
7	30				56		62			
Number of pairs					1					
Means					66.0		58.0			
Mean differences					8.0[2]					
Number of pairs		2			4					
Means		44.2		43.3	68.6		63.3			
Mean differences		0.9[2]			5.3[2]					

[1]) Mean difference indicated between paired means is significant at the 1 percent level of probability, determined by paired „*t*"-test.
[2]) Insufficient data for reliable paired "*t*"-test.

cies progenies of *P. strobus*, the *P. strobus* progenies outgrew the hybrids in 2 cases. In 2 comparisons of first-year height the *P. strobus* progenies outgrew the hybrids in 1 case. Even the hybrid *P. mt.* 54 × *P. st.* 174, which definitely displayed hybrid vigor during its first 2 years at Spokane, was outgrown by intraspecies progenies of *P. st.* 174 in its second year at Wisconsin Rapids. It would seem that at Wisconsin Rapids the hybrid was perhaps outside its optimal range. In fact, hybrids grown there had an abnormal yellowish, off-color appearance to the foliage. Reactions of this type are not uncommon in hybrids and have been explained by JOHNSON (1955) on the basis that hybrids may be able to exploit a wider range of optimal growth conditions while being confined within a narrower range of survival conditions than the parental types.

Results at Spokane, Washington shown in Table 1 were strikingly similar to those of the earlier but less extensive study of RIGHTER (1945) at Placerville, California, as shown below. Thus despite possible racial differences, to say nothing of widely different environmental influences, hybrid and corresponding intraspecies progenies performed similarly at locations over 600 miles apart in the western United States. Even the third-year *P. strobus* performance, partly overtaking the hybrid progeny height, was duplicated.

Species or hybrid	First-year height		Second-year height		Third-year height	
	Placerville, Calif.	Spokane, Wash.	Placerville, Calif.	Spokane, Wash.	Placerville, Calif.	Spokane, Wash.
	Millimeters					
Average *P. mt.* progeny	43	42	61	77	94	122
Average hybrid progeny	59	55	117	138	200	179
Average *P. st.* progeny	43	42	70	113	152	164

The juvenile hybrid *P. monticola* × *P. strobus* progenies have already been reported by RIGHTER (1945), BUCHHOLZ (1945), and DUFFIELD and RIGHTER (1953) as displaying hybrid vigor in comparison with progenies of either parent, when growing within the range of *P. monticola*. Also the reciprocal hybrid has been reported as "very vigorous" by HEIMBURGER (1953), or as displaying "marked and encouraging hybrid vigor" by RIKER and PATTON (1954) in eastern North America. Much of this evidence is confirmed by the present study. In summing up the evidence, it can be said that the hybrid progenies as a group displayed hybrid vigor for the first 2 years' growth at Spokane and vicinity, but probably did not display hybrid vigor at Wisconsin Rapids.

Hybrid seed germination in relation to hybrid vigor

The fact that hybrid vigor may be in part merely the better adaptability of the hybrid organism to the growing season at a given locality was demonstrated for first-season hybrids by results of seed germination. Germination checks on stratified seed made at intervals during the 1953 through 19955 growing seasons showed that seed of hybrid progenies always germinated more rapidly and more completely than did seed of corresponding *P. monticola* progenies. During a 128-day period (May 1 — September 5, only slightly shorter than the complete Spokane growing season) 85 percent of the hybrid versus 50 percent of the *P. monticola* seed emerged in the seedbeds.

Table 2. — First-season growth advantage of hybrid over *P. monticola* progenies as determined by seedbed emergence at various check dates, 1953 through 1955 seasons, Spokane, Washington[1])

Check dates	Remainder of growing season	Hybrid seed (14 progenies)		*P. monticola* seed (36 progenies)	
		Newly emerged seed	Emergence % × days remaining	Newly emerged seed	Emergence % × days remaining
Days from sowing	*Days*	*Percent*	*Seedling-days*	*Percent*	*Seedling-days*
22	106	10	1060	6	636
33	95	78	7410	58	5510
48	80	8	640	12	960
89	39	2	78	14	546
128	0	2	0	10	0
Totals		100	9188	100	7652
Difference			← 1536 →		

[1]) Seedbed emergence during a 128-day period considered as 100 percent emergence.

The relative rapidity of the hybrid seed emergence was shown by the fact that hybrid emergence as early as 33 days after sowing (88 percent) was almost equal to *P. monticola* emergence 89 days after sowing (90 percent).

Data from periodic checks of seed emergence permitted rough calculations of the relative advantage in period of growth accruing to first-season hybrids, through their ability to germinate more rapidly and more fully exploit the growing season. Calculations of this sort are shown in Table 2. Many hundreds of seed were involved in the calculated percentages of seed emerging on the various check dates (Table 2, columns 3 and 5), but for a better understanding of the calculations visualize the hybrid and *P. monticola* progenies shown in Table 2 as each containing a total of only 100 germinable seed (i. e. 1 percent emergence equals 1 seed emerged). The 10 percent or 10 hybrid seed which had emerged by the 22-day check date thus could grow for at least 106 days before the termination of the 128-day growing season, contributed 10 × 106, or 1060 seedling-days of growth to the hybrid total. The 6 corresponding *P. monticola* seedlings emerging by the same check date contributed 6 × 106, or 636 seedling-days growth to the *P. monticola* total. Repeating the above process for newly emerged seedlings at each successive check date and totaling the numbers of seedling-days, the 100-seedling hybrid progeny accumulated a total of 9188 seedling-days, the 100-seedling *P. monticola* progeny a total of 7652 seedling-days. This was a growth-time advantage for the hybrids of 1536 seedling-days, or roughly 20 percent growth advantage for the hybrids. It was interesting to note that in respect to height growth (Table 1) the hybrids in their first season averaged 33 percent taller than corresponding *P. monticola* progenies. The greater rate of growth of the hybrids, even during their first year, is not completely explained by germination behavior.

Degree of hybrid vigor displayed by different hybrids

Table 1 and Figure 1 demonstrate yet another feature of hybrid vigor not heretofore reported in the American literature on white pine hybrids — namely that wide differences in height growth existed between different hybrids. For instance, a "*t*"-test for significance of the observed differences (25, 61, and 91 mm.) between hybrids *P. mt.* 19 × *P. st.* 5 and *P. mt.* 39 × *P. st.* 19 during their first 3 years' growth at Spokane showed the differences to be significant at the 1 percent level of probability. Also,

the average height of all hybrid progenies which had *P. mt.* 19 as a seed parent was significantly less than that of hybrids having either *P. mt.* 39 or *P. mt.* 54 as seed parents. Similarly, at Wisconsin Rapids hybrid *P. mt.* 54 × *P. st.* 174 was significantly superior to hybrid *P. mt.* 70 × *P. st.* 19 the first year (difference 8 mm), and hybrid *P. mt.* 39 × *P. st.* 19 was significantly superior to hybrid *P. mt.* 54 × *P. st.* 174 (difference 20 mm.) the second year.

Degree of hybrid vigor as related to vigor of corresponding parents, clones, and intraspecies progenies

The success or failure of many projects in forest tree improvement will be measured in the efficacy of selection, as reflected in the degree of inheritance of desirable characters like growth rate. If through selection the differences in growth of hybrid progenies shown above could have been predicted, then perhaps the work of securing hybrids of greater vigor would have been expedited. Preliminary analyses and observations led to the belief that selection of hybrid parents for growth rate might be productive. First, the foreknowledge that in accordance with theoretical expectations, average height in *P. monticola* intraspecies progenies was correlated with height growth in the 2 parent trees. Second, that fast-growing *P. monticola* progenies (i. e. like those of trees 21, 39, and 54, Table 1) were associated with vigorous hybrids, while slow-growing *P. monticola* progenies (i. e. like those of 19 and 63) were associated with slow-growing hybrids. Third, an analysis of variance showed hybrids having different *P. monticola* parents had significantly different heights.

With these facts in mind a series of multiple correlation analyses was run, aimed at determining whether significant relationships existed between hybrid height growth and height growth in corresponding parental materials. Included were first- and second-year height growth of hybrid progenies (1) versus average annual height growth of corresponding *P. monticola* and *P. strobus* parents at their respective localities, (2) versus average annual height growth of grafts of both parents at their respective localities, and (3) versus average first- and second-year height growth of corresponding *P. monticola* and *P. strobus* intraspecies progenies at their respective localities. Results of the analyses are shown in Table 3.

Hybrid progeny height for the first 2 years was highly and significantly correlated with that of corresponding intraspecies progenies (*R* equals .90 and .99 significant at the 1 percent level). Hybrid height the first year was significantly correlated with graft height growth (*R* equals .78, significant at the 5 percent level). The other 3 analyses of hybrid first- and second-year height versus parent-tree height growth, and hybrid second-year height versus graft height growth gave multiple correlation coefficients ranging from .35 to .65, moderately high but not significant. The relative strength or weakness of the basic data was obvious, in that where adequate numbers of parental progenies or clone members were available high and significant indices were found; where numbers of clone members or of parent trees were low and where the experimental materials were growing under less controlled conditions, lower and nonsignificant indices resulted. It seemed from these data that the vigor of hybrids and that of their parents, as reflected in grafts and progenies, was quite closely related; but that the relationship of hybrid vigor with that of the parent trees was obscured, probably because of insufficient data.

Nevertheless, results of the correlation analyses suggested that selection of parental types for proposed hybrids would be profitable. From a practical standpoint segregation of wild parents into at least 2 classes — those above and below average in height growth rate — with breeding restricted to the better class apparently would be good practice. Where grafts of parent trees or parental intraspecies progenies were available, it appeared that any selection for parental vigor based upon them would be even more productive in securing faster growing hybrids. In breeding poplars VLOTEN (1954) has recognized the individuality of different inter-racial and interspecies hybrids and has pointed out that individual parent tree selection is not only possible but necessary for obtaining the greatest degree of hybrid improvement. Pine hybridizers like RIGHTER (1955) have for some time employed selection in hybrid seedbeds, and both RIGHTER (1954) and DUFFIELD (1954) have suggested that selection, either among genotypes or races, is the next step in developing improved hybrids. It would seem from results reported here that there is ample possibility for improving hybrid vigor by selection of parent trees.

Relative rust resistance of hybrid progenies

The hybrids between blister rust resistant selections of *P. monticola* and *P. strobus* made in this project were the first such hybrids produced in the United States. Since both species are classed as susceptible to blister

Table 3. — Relationships between heights of hybrid progenies at Spokane and height of corresponding *P. monticola (P. mt.)* and *P. strobus (P. st.)* parent trees, clones, and intraspecies progenies at their respective localities

Item	First-year height				Second-year height			
	Basis			Multiple correlation indices (*R*)	Basis			Multiple correlation indices (*R*)
	Hybrid progenies	Corresponding parental materials			Hybrid progenies	Corresponding parental materials		
		P. mt.	*P. st.*			*P. mt.*	*P. st.*	
Height growth of parent trees (average annual growth for last 10 years)	14	7	6	.35	8	4	5	.52
Height growth of clones (average annual growth of grafts, 3 years in *P. mt.*, 10 years in *P. st.*)	10	5	7	.78[1])	8	4	6	.65
Height growth of intraspecies progenies (average height first or second year as applicable)	12	73	5	.90[2])	10	40	5	.99[2])

[1]) Significant at the 5 percent level of probability.

[2]) Significant at the 1 percent level of probability.

Table 4. — Incidence and intensity of *Cronartium ribicola* infection on juvenile hybrid and corresponding intraspecies progenies, Spokane, 1954 and 1955

Measure of resistance	Hybrids	Basis	*P. monticola*	Basis	*P. strobus*	Basis
		Number of progenies		*Number of progenies*		*Number of progenies*
Average percent of seedling with typical foliage infections 1 year after artificial inoculation	89.6	8[1])	84.7	37	88.4	4
Average number of typical foliage infections per 450-needle foliage sample	254	8[1])	162	33	169	4
Average percent of seedlings with typical bark infections 2 years after artificial inoculation	88.5	4[2])	67.9	21	84.0	3
Average height of seedlings when inoculated, millimeters	148	8[1])	78	37	102	4

[1]) Included were hybrid progenies *P. mt.* 19 × *P. st.* 5, 19 × 19, 21 × 107, 39 × 18, 39 × 19, 54 × 107, 54 × 129, and 54 × 174.

[2]) Included were hybrid progenies *P. mt.* 19 × *P. st.* 5, 19 × 19, 39 × 18, 39 × 19.

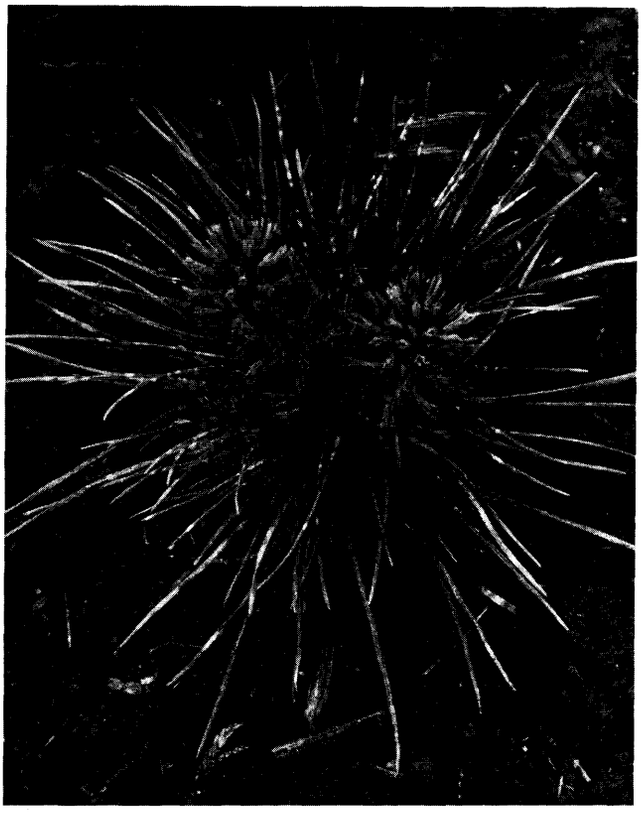

Figure 2. — Needle spot infections caused by *Cronartium ribicola*, on a *Pinus monticola* seedling, 10 months after artificial inoculation. Large, susceptible plants may support upwards of 1,000 such light yellow colored infections.

rust in comparison with Eurasian species a limited hybridization program employing resistant phenotypes seemed a logical approach for investigating the possibility of securing both resistance and hybrid vigor. In this respect early performance of hybrids in rust resistance tests is of interest. Relative resistance (or susceptibility) of 8 juvenile hybrids and corresponding *P. monticola* and *P. strobus* intraspecies progenies, all growing at Spokane, is shown in Table 4. Results may change as the progenies mature.

Three different measures of susceptibility to *C. ribicola* were employed including (1) the percentage of the seedlings having 1 or more typical needle-spot infections (Figure 2), (2) the total number of such foliage infections in a foliage sample of 450 needles, and (3) the percentage of the seedlings having 1 or more typical bark infections. The percentages of seedlings which displayed typical needle symptoms were quite similar in the hybrid and both corresponding intraspecies progenies, varying less than 5 percent. The relative intensity of needle infections on hybrid progenies was much greater than in corresponding intraspecies progenies, averaging over 1½ times as many infection foci per unit foliage sample. Similarly. hybrid progenies supported roughly 1⅓ as many bark cankers as did corresponding *P. monticola* progenies; but 3 corresponding *P. strobus* progenies supported almost as many cankers as did the hybrids.

It was interesting to note that in relation to vigor (as expressed by average progeny height) the *P. strobus* progenies were more similar to the hybrids than were the *P. monticola* progenies. The old axiom that obligate parasites like *C. ribicola* develop more luxuriantly in a vigorous host plant was borne out. Correlation analyses showed that second-year seedling height was directly and significantly associated with the number of needle spots occurring in a foliage sample of a given size. Thus in the larger plants it appeared that it was the vigor of the plant, rather than the greater number of needles or more favorable exposure under artificial inoculation, which made the needles more susceptible to spotting. Since the vigor of the hybrid and *P. strobus* progenies could not be classified as due to environmental conditions (seed weight and growing season effects having already been neutralized by progeny height adjustments) it appeared that no valid adjustment for the effect of inherent seedling height superiority on needle spotting could be made. It remains to be seen whether the effect persists with age.

Since the data in Table 4 represent all that the authors know at present about the rust resistance of hybrids from rust-resistant phenotypes, and since relatively few young hybrids and few parent trees are involved, it would not be wise to discard the growth advantage of the hybrids in favor of apparently greater rust resistance of the intraspecies progenies. In fact, in the one hybrid where a parent apparently having at least partially dominant resistance factors is involved in hybrid parentage, the resistant parent was known to have transmitted a measurable degree of resistance to the hybrid. Among the hybrids of Table 4, resistance tests as outlined in the text and table showed that all of the *P. monticola* or *P. strobus* selections involved in hybrid parentage failed in transmitting appreciable resistance to their first generation intraspecies progenies, with the exception of *P. mt.* 21. For example, 2 selections (*P. mt.* 21 and *P. mt.* 54) involved in the parentage of the hybrids in Table 4 were each crossed with the other, with *P. mt.* selections number 59, 62, and 63, and by wind. It was noteworthy that the 5 progenies of selection 21 contained on the average over 3 times as many spot-free seedlings, and supported only

about 40 percent as many needle spots, as did the 5 progenies of selection 54. The extent of resistance transmission by selection *P. mt.* 21 as compared with *P. mt.* 54 was also demonstrated by the hybrid progenies involving these *P. monticola* seed parents when both were crossed with selection *P. st.* 107, as shown below:

Hybrid progeny		Spot-free seedlings	Needle spots per 450-needle foliage sample
P. mt. × *P. st.*		*Percent*	*Number*
21	107	5.1	147
54	107	1.6	248

The hybrid progeny *P. mt.* 21× *P. st.* 107 contained approximately 3 times as many spot-free seedlings and supported only about 60 percent as many needle spots as did hybrid *P. mt.* 54 × *P. st.* 107. It was apparent that both intraspecies and hybrid progenies of *P. mt.* 21 were relatively resistant, while those of *P. mt.* 54 were relatively susceptible. Thus through continued breeding with better parents an even higher degree of resistance could have been found in first generation hybrids. Backcrossing to the more resistant parent might also be productive, both in increasing resistance of the hybrids and in securing plants with better climatic adaptability.

Observations on acclimatization of hybrid progenies

Early observations on the acclimatization of the juvenile hybrid progenies are probably not diagnostic of later performance, but it appeared that the relatively spindly stems of the hybrids often resulted an their being broken or permanently crooked under conditions of heavy snow-press holding in north Idaho and northwestern Montana. Four-year-old hybrids were about 3 dm. tall but had ground-line diameters no larger than the 2 dm. *P. monticola* seedlings of the same age. Hybrids were pressed horizontal by the time of snow melt and returned to an upright position slowly, if at all, often with kinked or cracked stems. The *P. strobus* progenies being tested in the same areas were even more spindly than the hybrids and were more seriously damaged by heavy snow. Backcrossing to the stockier *P. monticola* parent is indicated. In the Wisconsin Rapids area needles and branch tips of *P. monticola* suffered severely from winter killing, the dead needles becoming red by early spring. The 3 *P. monticola* × *P. strobus* hybrids were intermediate between the severely injured *P. monticola* and the healthy *P. strobus,* the needles becoming quite yellow, sometimes with reddened tips, but with needles or branch tips only rarely killed; but 2 reciprocal hybrids were indistinguishable from the *P. strobus* intraspecies hybrids in this respect.

Conclusions and Summary

Juvenile performance of 16 different hybrid progenies from controlled pollinations beween *Cronartium ribicola* resistant selections of *P. monticola* and *P. strobus* is reported and discussed in detail.

Comparisons of hybrid progeny height growth for the first 3 growing seasons are made with corresponding heights of more than 100 intraspecies progenies involving either the *P. monticola* or *P. strobus* parent of the hybrids. For their first 2 years the hybrids express definite hybrid vigor at Spokane, Washington, exceeding progenies of both parents in height. Some question exists as to the expression of hybrid vigor under conditions at Wisconsin Rapids, Wisconsin. A good part of the superiority of hybrids during their first year can be explained on the basis of their early germination and more effective use of the growing season. Hybrid seed germinated both more completely and more rapidly than did seed from *P. monticola* intraspecies crosses. From records on germination it was estimated that hybrids averaged about 20 percent better utilization of the growing time of the first season.

Juvenile hybrid progenies had significantly different average height growth rates, both at Spokane, Washington and Wisconsin Rapids, Wisconsin. The fastest growing hybrids averaged from 1.6 to 2 times as tall as the slowest growing hybrids. Average height growth in hybrid progenies was significantly correlated with that of intraspecies progenies representative of the hybrid parents, or with that of grafts of the corresponding parents; probably correlated with height growth of the parent trees themselves. Selection for rapid growth rate among proposed hybrid parents probably will be productive in developing more vigorous hybrids. Selection of parents on the basis of superior growth rate of intraspecies progenies or grafts would definitely be reflected in improved juvenile hybrid height growth.

Preliminary evaluations of rust resistance among 8 juvenile hybrid progenies tested to date indicate that in hybrids resistance may be lower than in corresponding intraspecies progenies. Hybrids supported over 55 percent as many needle infections per unit foliage sample, and over 30 percent more bark cankers than did corresponding *P. monticola* progenies. Indicated differences in infection may change as the trees mature. From resistance displayed by one hybrid progeny it appears that more highly resistant first generation hybrids can be produced. Among 4 *P. monticola* parents included in the hybrids tested, the one with a proved ability to transmit resistance to its inraspecies progenies also transmitted resistance to a hybrid.

Acclimatization of the hybrids under conditions of the northern Rocky Mountains or of central Wisconsin remains conjectural. Preliminary observations indicate that the hybrids are intermediate between the 2 parents in respect to their ability to remain erect and withstand mechanical injuries under heavy snow-press conditions in the northern Rocky Mountains, or in their susceptibility to winter injury of foliage and young shoots in central Wisconsin.

Zusammenfassung

Titel der Arbeit: *Wüchsigkeit, Krankheitsresistenz und Verhalten im Freiland bei dreijährigen Nachkommenschaften des Bastards Pinus monticola Dougl.* × *Pinus strobus L.* —

Das Verhalten 16 verschiedener Bastardnachkommenschaften aus künstlichen Kreuzungen zwischen strobenrostresistenten *P. monticola* und *P. strobus* wird behandelt und im einzelnen beschrieben.

Zwischen den Bastarden und mehr als 100 intraspezifischen Kreuzungsnachkommen beider Arten stellte man nach den ersten drei Vegetationsperioden einen Vergleich des Höhenwachstums an. In den ersten beiden Jahren übertreffen die Bastarde in Spokane/Washington die reinen Nachkommen beider Eltern sehr deutlich. In Wis-

consin Rapids/Wisconsin scheint dagegen Bastard-Heterosis fraglich zu sein. Die Überlegenheit der Bastarde im ersten Jahr kann man zum großen Teil mit deren besonders früher Keimung und damit besseren Ausnutzung der Vegetationsperiode erklären. Bastardsaatgut keimte vollständiger und schneller als das der intraspez. *P. monticola*-Kreuzungen. Im Durchschnitt nutzten die Bastarde die erste Vegetationszeit um etwa 20% besser aus.

Sowohl in Spokane als auch in Wisconsin Rapids wurden zwischen den Bastardnachkommenschaften signifikante Unterschiede im Höhenwachstum festgestellt. Die wüchsigsten Hybriden waren 1,6 bis 2mal höher als die niedrigsten. Das Durchschnittshöhenwachstum der Bastardnachkommenschaften korreliert mit dem der intraspez. Nachkommenschaften beider Eltern. Es stimmt außerdem mit dem Wachstum der Eltern-Pfropflinge und wahrscheinlich mit dem Höhenwachstum der Eltern selbst überein. Um noch wüchsigere Bastarde zu erzielen wird es für erfolgversprechend gehalten, unter den Bastardeltern eine Selektion auf Wüchsigkeit durchzuführen.

Eine vorläufige Bonitierung auf Rostresistenz bei acht jungen Bastardnachkommenschaften ergab, daß unter den Bastarden die Resistenz geringer sein dürfte als vergleichsweise bei den Nachkommen intraspez. Kreuzungen. Bastarde wiesen 55% mehr Nadelinfektionen pro Einheit Blattmasse und über 30% mehr Rindenherde auf als reine *P. monticola*-Nachkommenschaften. Es ist möglich, daß sich die genannten Infektionsunterschiede im Alter ändern.

An der Resistenz einer bestimmten Bastardnachkommenschaft läßt sich erkennen, daß wahrscheinlich noch widerstandsfähigere F_1-Hybriden erzielt werden könnten. Von vier in die Bastardprüfung einbezogenen *P. monticola* gibt es einen Mutterbaum, der seine Rostresistenz nicht nur auf die Nachkommen gleicher Art, sondern auch auf die Bastarde überträgt.

Die erfolgreiche Anpassungsfähigkeit der Bastarde an die Klimabedingungen in den nördlichen Rocky Mountains und dem mittleren Wisconsin wird vermutet. Nach vorläufigen Beobachtungen nimmt man an, daß sich die Bastarde bezüglich ihrer Widerstandsfähigkeit gegen Schneedruck (in den Rocky Mountains) und der Empfindlichkeit ihrer Nadeln und jungen Triebe gegen Winterfröste (in Wisconsin) zu den Elternarten intermediär verhalten.

Résumé

Titre de l'article: *Vigueur, résistance aux maladies et comportement de descendants âgés de trois ans de l'hybride Pinus monticola Dougl. × P. strobus L.*

Les auteurs étudient et discutent les caractères de 16 descendances différentes d'hybrides provenant de croisements contrôlés entre des *Pinus monticola* et *P. strobus* sélectionnés pour leur résistance à *Cronartium ribicola*. On compare l'accroissement en hauteur des hybrides pour les 3 premières années avec celui de plus de 100 descendances issues de croisements intraspécifiques comprenant soit le parent *P. monticola*, soit le parent *P. strobus*. Dans les deux premières années les hybrides cultivés à Spokane, Washington, surpassent nettement les deux parents, manifestant un hétérosis marqué. A Wisconsin Rapids, Wisconsin, cependant cet hétérosis semble plus douteux. La supériorité des hybrides pendant la première année peut être expliquée partiellement par leur germination précoce et une meilleure utilisation de la période de végétation. Les graines hybrides avaient une meilleure faculté germinative et une germination plus rapide que celles issues des croisements intraspécifiques de *P. monticola*. D'après les données de la germination, on a pu estimer que les hybrides pouvaient utiliser en moyenne 20% de plus de la saison de végétation.

On constata des différences significatives de l'accroissement en hauteur entre les descendances hybrides, à Spokane aussi bien qu'à Wisconsin Rapids. Les hybrides ayant la croissance la plus rapide étaient 1,6 à 2 fois plus hauts que ceux ayant la croissance la plus lente. La hauteur moyenne des descendances hybrides est en corrélation avec celle des descendances intraspécifiques correspondant aux mêmes parents, et avec la croissance des greffes de ces parents; et probablement aussi avec la croissance en hauteur des parents eux-mêmes. La sélection des parents en ce qui concerne la vitesse de croissance permettra donc d'obtenir des hybrides plus vigoureux. La sélection des parents d'après la croissance des descendances intraspécifiques ou des greffes aboutirait à une amélioration de la croissance juvénile des hybrides.

Une évaluation préliminaire de la résistance à la rouille vésiculeuse parmi 8 descendances hybrides montra que la résistance des hybrides pourrait être moindre que celle des descendances des croisements intraspécifiques correspondants. Les hybrides avaient 55% de plus d'infections des aiguilles et 30% de plus de chancres de l'écorce que les descendances correspondantes de *P. monticola*. Il est possible que ces différences dans les infections changent avec l'âge.

D'après l'étude de la résistance chez une descendance hybride, il semble qu'on pourrait produire une génération F_1 d'hybrides plus résistants. De quatre *P. monticola* compris dans l'étude des hybrides, le seul qui transmette nettement sa résistance aux descendances intraspécifiques la transmet également à une descendance hybride.

L'acclimatation des hybrides dans les conditions des Montagnes Rocheuses septentrionales et en Wisconsin central reste incertaine. On conclut, des observations préliminaires, que les hybrides sont intermédiaires entre les deux parents en ce qui concerne la résistance à la neige dans les Montagnes Rocheuses, et la sensibilité des aiguilles et jeunes pousses aux froids hivernaux en Wisconsin.

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Veränderungen der Pollengröße bei Lärche nach Blütenbehandlung mit Colchicin

Von Z. M. ILLIES

(Eingegangen am 24. 4. 1956)

Im Gegensatz zu der Polyploidiezüchtung mit Colchicin bei krautigen Pflanzen hatte man bisher bei holzigen Gewächsen nach Colchicineinwirkung auf die diploiden, im Wachsen begriffenen Körperzellen mehrere Jahre lang abzuwarten, bis die so entstandenen mixoploiden Pflanzen (C_0-Generation) blühreif geworden waren und diploide Geschlechtszellen entwickelten. So konnten erst nach mehreren Jahren die erforderlichen Kreuzungen zur Erzeugung einheitlicher polyploider Pflanzen durchgeführt werden (ILLIES 1951/52, dort ausführliches Literaturverzeichnis). Nachfolgend wird bei *Larix leptolepis* der Versuch unternommen, die bisherige C_0-Generation dadurch entscheidend abzukürzen, daß männliche Blüten während der Meiose colchiciniert wurden, um auf diese Weise unreduzierten Pollen zu erhalten. Die C_0-Generation würde dann nur auf die colchicinierten unreduzierten Geschlechtszellen beschränkt bleiben, und die aus Kreuzungen mit diesen C_0-Pollen hervorgegangenen Nachkommen wären bereits die C_1-Generation.

Die Versuche wurden an Blütenknospen von fünf Pfropflingen von *Larix leptolepis* mit einer 0,2%igen warmen Colchicinlösung vorgenommen. Das Colchicin wurde auf 40°—60° C erwärmt, um das Diffundieren in die verharzte Knospe zu erleichtern. Als Zeitpunkt der Colchicineinwirkung auf die bis zu Beginn des Versuches normal im Freien überwinterten Pfropflinge wurde der 15. 3. gewählt, an dem durch Stichproben an Kontrollblüten festgestellt worden war, daß sich die Meiose in der Diakinese bis Interphase befand. Um das Colchicin direkt an die Blüten heranzubringen, wurde die von OLDÉN (1954) bei Kirsche und Apfel beschriebene Methode etwas abgewandelt angewendet[1]). Wie Abb. 1 zeigt, wurde dazu ein mit Blüten besetzter Zweig durch den durchbohrten Gummistopfen des Deckels eines WITTschen Topfes gesteckt und der Zwischenraum zwischen Zweig und Gummistopfen gut mit Watte und Hahnfett abgedichtet. An diesem Zweig wurde ein Reagenzglas mit warmer Colchicinlösung befestigt und in einem Becher in den Topf gestellt, dessen angeschliffener Deckel danach ebenfalls gut abgedichtet wurde. Das Absaugen der Luft geschah durch eine dem Topf angeschlossene Wasserstrahlpumpe. Da der Wasserdruck sehr wechselnd war, mußte von einer Überprüfung des Unterdrucks mittels Manometer abgesehen werden. Als Kriterium, daß das Colchicin in die Knospen eingedrungen war, wurde das erste Auftreten von Luftblasen genommen, was je nach der Stärke des Wasserdrucks nach 10 bis 30 Minuten eintrat. Von da an wurde noch 20 Minuten lang weiter abgesaugt. Nachdem der Unterdrucktopf abgebaut war, wurden die

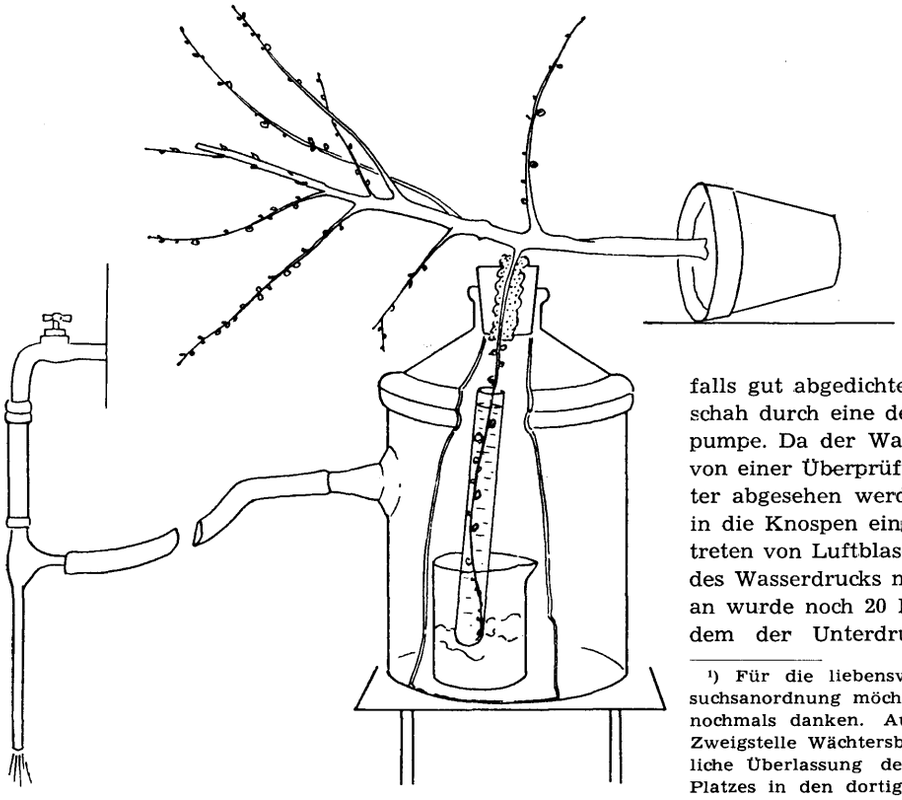

Abb. 1. — Versuchsanordnung.

[1]) Für die liebenswürdige ausführliche Mitteilung der Versuchsanordnung möchte ich Herrn Dr. OLDÉN auf diesem Wege nochmals danken. Außerdem danke ich dem Leiter unserer Zweigstelle Wächtersbach, Herrn Dr. HEITMÜLLER, für die freundliche Überlassung des für die Versuchsanordnung benötigten Platzes in den dortigen Gewächshäusern, und Fräulein L. MAY für ihre unermüdliche Hilfe bei der Colchicinbehandlung.