

# Age Trends in Genetic Parameters of Blister Rust Resistance and Height Growth in a *Pinus strobus* x *P. peuce* F<sub>1</sub> hybrid population

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**Abstract**—This paper reports information about genetic variation in blister rust resistance (BRR), survival (TS) and total height growth (H) over 20 years in a *Pinus strobus* x *P. peuce* hybrid population. Highly significant ( $p < 0.001$ ) differences among hybrid families were found for the three traits. With minor exceptions, female and male x female effects were significant ( $p < 0.05$ ) or highly significant ( $p < 0.01$ ;  $p < 0.001$ ) over the whole testing period for BRR, TS and H. However, male effects were significant ( $p < 0.05$ ) only for H. This suggested that the traits were controlled by additive and non-additive genes. Over 20 years, the additive variances ranged between 26 and 39 percent for BRR, between 17 and 62 percent for TS and between 31 and 44 percent for H. Non-additive variances ranged between 37 and 60 percent for BRR, between 34 and 78 percent for TS and between 31 and 54 percent for H. Therefore, both variances were important for the traits involved. Narrow-sense heritability estimates at the family level ranged between 0.290 and 0.430 for BRR, between 0.177 and 0.633 for TS and between 0.382 and 0.531 for H. Heritabilities at the individual level ranged between 0.024 and 0.067 for BRR and between 0.064 and 0.167 for H. Parents of good general combining ability were found for both BRR and H. Strong age-age genetic correlations were found between BRR and TS while correlations between BRR and TS on one hand and H on the other were low. The high-parent heterosis was negative while the mid-parent one was positive, accounting for 21.3 percent for BRR, 35.4 percent for TS and 10.4 percent for H. A variable genetic gain for the three traits could be expected, suggesting that hybrid planting could be profitable.

**Key words:** *Pinus strobus*, *P. peuce*, factorial cross, hybrid, additive variance, heritability, combining ability, genetic correlation

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## Introduction

It is well known that eastern white pine (*Pinus strobus* L.) has wide genetic variability and high productivity in plantations in North America, Europe and the Far East (Kriebel 1983).

The blister rust (*Cronartium ribicola* J.C. Fisch. in Rabenh.) migrated from its Siberian gene center to Europe (Leppik 1967) and by 1900 to North America where it caused losses in *P. strobus*, *P. monticola* Dougl. and *P. lambertiana* Dougl. (Bingham and Gremmen 1971). The inefficiency of conventional control methods of the pathogen has stimulated interest in genetic improvement of resistance. The eastern white pine improvement program was based on both intraspecific crosses (Riker and others 1943; Heimburger 1972a; Zsuffa 1981) and interspecific ones (Patton 1966; Heimburger 1972; Zsuffa 1979).

Interspecies breeding with white pines was tried in attempts to introduce resistance factors into eastern white pine from related more resistant species, like Balkan pine (*Pinus peuce* Griseb.) and Himalayan pine (*Pinus wallichiana* Jacks.). According to Heimburger (1972a), introduction of resistance genes in eastern white pine may be the only way to form a realistic program with this species. In a previous investigation, an F<sub>1</sub> hybrid population from reciprocal crosses between eastern white pine and Balkan pine supported evidence that extranuclear genes controlling blister-rust resistance and growth traits could be found in eastern white pine (Blada 1992). In addition, more recent investigations (Blada 2000a) suggested that parents with a good general combining ability were found in eastern white pine, not only for growth traits but also for blister-rust resistance.

The *P. strobus* x *P. peuce* F<sub>1</sub> hybrids have demonstrated good blister rust resistance (Patton 1966; Heimburger 1972a; Blada 1989; 2000a) and growth traits (Leandru 1982; Blada 2000a; 2000b).

Introduction to Romania of eastern white pine took place at the end of the 19<sup>th</sup> century, but it was intensified after 1960 when about 300,000 ha were planted with this species; with its 20.2 m<sup>3</sup>/year/ha it proved to be a fast growing species (Radu 1974). At the same time, blackcurrant (*Ribes nigrum* L.), one of the alternate hosts of the blister rust pathogen, was planted on large scale to produce fruits. Very soon, coincident with blackcurrant spreading, heavy attacks of blister rust occurred all over the country (Blada 1987; 1990).

Because the blister rust cannot be controlled by conventional methods (Bingham and others 1953), a genetic improvement

program was launched in Romania in 1977 (Blada 1990). The program included both intra- and inter-specific crossing. The practical objective of the program was to establish hybrid seed orchards consisting of parents with high general combining ability for blister rust resistance (Blada 1982). Because of financial reasons, this objective has been only partially fulfilled. Several progress reports on this subject were previously published or presented in symposia (Blada 1987; 1989; 1990; 1992; 1994; 2000a; 2000b).

The objective of this paper is to present the age trends in genetic parameters for blister rust resistance, tree survival and total height growth over 20 years of testing in a *P. strobus* x *P. peuce* F<sub>1</sub> hybrid population.

## Materials and Methods

### Parents, Mating Design, and Progenies

The initial material consisted of five eastern white pine female and five Balkan pine male parents selected in non-improved planted populations free of blister rust and of unknown origin. The selections could be considered random samples with respect to any trait, except reproductive fertility. In 1979, a 5 x 5 factorial mating design (Comstock and Robinson, 1952) was completed. The seed samples were stratified according to Kriebel's (1973) recommendations and then sown (spring 1981) in individual polyethylene pots (22x18 cm) in a potting mixture consisting of 70 percent spruce humus and 30 percent sand. The progenies grew in pots throughout the first six years and they were the subjects of the nursery test reported earlier (Blada 1987).

### Inoculation and Experimental Design

The 25 full-sib hybrid families and two open pollinated progenies were artificially inoculated three times with blister rust, in late August 1982, 1983 and 1984, when they were two, three and four years old, respectively. During each inoculation period, the potted trees were introduced into a polyethylene tent and arranged in randomized complete block design with 14-seedling row-plots in each of the three blocks. The two open pollinated progenies, representing the means of the two parent species, were included as controls. Inoculum consisted of heavily infected leaves of *Ribes nigrum* L. collected from a single plantation. Other details concerning inoculation and inoculation tents were similar to those described by Bingham (1972).

At age six, the hybrids and controls were planted out at 3x3 m spacing, in the Caransebes-Valisor Forest District, at about 45°27' N latitude and 22°07' E longitude and 310 m

altitude. As expected, owing to the heavy controlled artificial inoculation, a variable number of seedlings per family were killed during the nursery stage, so that only about 10 seedlings per plot could be used for planting in the field test. Hence, a randomized complete block design with 10-seedling row-plots in each of the three blocks was used. No thinning was carried out by age 20.

### Measurements

Several traits were assessed when the hybrids were 5-, 9-, 11-, 13-, 17- and 20-years-old. However, only three traits for each age were presented in this report. (table 1). The blister rust resistance was scored using an index that took into account both the number and severity of the lesions. Its numerical values assigned were: 1 = dead tree or total susceptibility (all trees killed by rust in previous years were included in this cumulative category); 2 = four or more serious stem lesions; 3 = three severe stem lesions; 4 = three more or less severe stem lesions; 5 = two severe stem lesions; 6 = two more or less severe stem lesions; 7 = one severe stem lesion; 8 = one more or less severe stem lesion; 9 = branch or very light stem lesions; 10 = free of lesions or total resistance. Percentages of the trees surviving were calculated based on blister rust resistance index data, i.e. all trees with a score 2 to 10 were considered tree survivors. All percentages were transformed to the arc sin square root for analysis.

Plot-mean data were subject to randomized block and factorial analysis of variance (Hallauer and Miranda 1981) and within-plot variance was calculated by a separate analysis (Becker 1984) where only six (out of 10) planted trees per plot were taken into account. It should be stressed that a few families had only six surviving trees / block; this is the reason why only six trees per block, taken at random, were included in the analysis.

### Statistical Analyses

In order to estimate the genetic components of variance the following statistical model, applied to plot means, was assumed:

$$x_{ijkh} = m + M_i + F_j + (MF)_{ij} + B_k + e_{ijkh} \quad (1)$$

where:  $x_{ijkh}$  = the observation of the  $h$ -th full-sib family from the cross of the  $i$ -th male and  $j$ -th female in the  $k$ -th block;  $m$  = general mean;  $M_i$  = the effect of the  $i$ -th male ( $i = 1, 2, \dots, I$ );  $F_j$  = the effect of the  $j$ -th female ( $j = 1, 2, \dots, J$ );  $(MF)_{ij}$  = the effect of the interaction of the  $i$ -th male and  $j$ -th female;  $B_k$  = the effect of the  $k$ -th block ( $k = 1, 2, \dots, K$ ) and  $e_{ijkh}$  = the random error.

**Table 1**—Traits measured for 25 full-sib hybrid families and two open pollinated families.

Traits	Measured at ages....	Units	Symbols
Blister-rust resistance	5, 9, 11, 13, 17, 20	Scale 1...10	BRR. 5 ... BRR. 20
Survival	5, 9, 11, 13, 17, 20	%	S. 5 ... S. 20
Total height growth	5, 9, 11, 13, 17, 20	dm	H. 5 ... H. 20

Since the parents were assumed to be random samples from a random mating population, and the hybrid families were planted in a complete randomized block design, a random model for statistical analysis (table 2) was used (Comstock and Robinson 1952).

Standard errors (SE) of variance components were computed by the formula given by Anderson and Bancroft (1952).

To estimate effectiveness of selection for early traits, three types of heritabilities were calculated.

The first heritability is the one commonly used for estimating the ratio of genetic (additive and non-additive) to total phenotypic variance which is appropriate for estimating gain from selection among hybrid families when they are vegetatively propagated. This is broad-sense heritability ( $h^2_1$ ) and was estimated by Grafius and Wiebe's (1959) formula:

$$h^2_1 = \sigma^2_G / \sigma^2_{Ph.1} = (\sigma^2_M + \sigma^2_F + \sigma^2_{MF}) / (\sigma^2_M + \sigma^2_F + \sigma^2_{MF} + \sigma^2_e / k) \quad (2)$$

where  $k$  = number of blocks.

Mass selection genetic gain (Falconer 1981) was estimated by:

$$\Delta G_1 = i_1 h^2_1 \sigma_{Ph.1} \quad (3)$$

where:  $i_1$  = the selection intensity taken from Becker (1984);  $\sigma_{Ph.1}$  is the phenotypic standard deviation of the family mean.

The second heritability is appropriate for estimating gain from selection among half-sib hybrid families when they are sexually propagated. This is narrow-sense heritability ( $h^2_2$ ) at the family level and was estimated by Grafius and Wiebe's (1959) formula:

$$h^2_2 = \sigma^2_A / \sigma^2_{Ph.1} = (\sigma^2_M + \sigma^2_F) / (\sigma^2_M + \sigma^2_F + \sigma^2_{MF} + \sigma^2_e / k) \quad (4)$$

and gain from half-sib family selection was estimated by:

$$\Delta G_2 = i_1 h^2_2 \sigma_{Ph.1} \quad (5)$$

The third heritability is the one commonly used for estimating genetic gain from mass selection among randomly placed seedlings. This is individual tree narrow-sense heritability ( $h^2_3$ ) and was estimated by:

$$h^2_3 = \sigma^2_A / \sigma^2_{Ph.2} = (\sigma^2_M + \sigma^2_F) / (\sigma^2_M + \sigma^2_F + \sigma^2_{MF} + \sigma^2_p + \sigma^2_w) \quad (6)$$

where:  $\sigma^2_w$  = within plot variance;  $\sigma^2_p$  = plot error =  $\sigma^2_e - \sigma^2_w/n$ ;  $n$  = seedlings per plot.

The mass selection gain was estimated by:

$$\Delta G_3 = i_1 h^2_3 \sigma_{Ph.2} \quad (7)$$

where  $\sigma^2_{Ph.2}$  is the phenotypic standard deviation and it refers to individual tree values.

If the best general combining ability parents ( $gca$ ) are to be selected and intermated, then the genetic gain was calculated as twice the average of  $gca$ 's or the average of the breeding values of the three selected parents for the next breeding works (table 10).

The heterosis was calculated according to Hallauer and Miranda's (1981) formula:

$$He_1 = [(H_y - HP) / HP] \cdot 100 \quad (8)$$

$$He_2 = [(H_y - MP) / MP] \cdot 100 \quad (9)$$

where:  $H_y$ ,  $HP$  and  $MP$  are the hybrid mean, the high-parent mean and the mid-parent mean, respectively. As shown above, two estimates of heterosis were computed: one that compared to the best parent ( $He_1$ ) and the other that compared to the mean of the parents from open pollinated controls ( $He_2$ ). According to the broad, modern concept, there exists positive or negative heterosis, luxuriant, adaptive, selective or reproductive heterosis and labile or fixed heterosis (Mac Key 1976). Only positive and negative heterosis was estimated in this experiment.

Genetic coefficient of variation ( $GCV$ ) was calculated by formula:

$$CGV = (\sqrt{\sigma^2_G} / X) 100 \quad (10)$$

where:  $\sigma^2_G$  and  $X$  are the genetic variance and trait mean, respectively.

General combining ability ( $gca$ ) effects of each parental tree were calculated, using Griffing's (1956) method 4, adapted to a factorial mating design. The statistical model was:

$$X_{ij} = X... + g_i + g_j + s_{ij} + e_{ijk} \quad (11)$$

where:  $X_{ij}$  is the mean of the  $i$ -th female tree crossed to the  $j$ -th male tree over  $k$  replications;  $X...$  is the general mean;  $g_i$  is the  $gca$  effect associated with the  $i$ -th female tree;  $g_j$  is the  $gca$  effect associated with  $j$ -th male tree;  $s_{ij}$  is the  $sca$  effect associated with the cross between the  $i$ -th female tree and  $j$ -th male tree;  $e_{ijk}$  is the residual effect.

The computational formulae were as follows:

$$gca_i = x_i - X... \quad (12)$$

$$gca_j = x_j - X... \quad (13)$$

**Table 2**—Analysis of variance of factorial mating design random effects model, in a random complete block in one environment.

Source of variation	Df	MS	E (MS)
Total	KIJ-1		
Blocks (B)	K-1	MS <sub>B</sub>	
Hybrids (Hy)	IJ-1	MS <sub>Hy</sub>	
-Females (F)	J-1	MS <sub>F</sub>	$\sigma^2_w + \sigma^2_p + K\sigma^2_{MF} + K\sigma^2_F$
-Males (M)	I-1	MS <sub>M</sub>	$\sigma^2_w + \sigma^2_p + K\sigma^2_{MF} + K\sigma^2_M$
-M x F	(J-1)(I-1)	MS <sub>MF</sub>	$\sigma^2_w + \sigma^2_p + K\sigma^2_{MF}$
Pooled error	(IJ-1)(K-1)	MS <sub>E</sub>	$\sigma^2_w + \sigma^2_p$
Within plot	KIJ(n-1)	MS <sub>w</sub>	$\sigma^2_w$

where:  $x_i$  = the mean of the F<sub>1</sub> resulting from crossing the *i*-th female tree with each of the male parent;  $x_j$  = the mean of the F<sub>1</sub> resulting from crossing the *j*-th male parent with each of the female tree;

To examine relationships among traits, genetic correlations coefficients were estimated using Falconer's (1981) formula.

## Results and Discussions

### Blister Rust Attack Evolution

Table 3 summarizes survival at ages 6 and 20. At the end of the nursery test, survival in the F<sub>1</sub> hybrid population was 74.3 percent, while in open pollinated control populations of *P. strobus* and *P. peuce*, the survival was 22.7 percent and 98.2 percent, respectively (table 3, column 3). The field test showed that, at age 20, survival in hybrids, *P. strobus* and *P. peuce* was 70.7 percent, 15.5 percent and 88.9 percent, respectively (table 3, column 5). Blister rust susceptibility was high in eastern white pine, very low in Balkan pine and low in hybrids. The mortality was due mostly to blister rust and only a few to other causes (see table 3, columns 7 and 8). It should be emphasized that the field test had been laid out in a site free of any *Ribes* species and blister rust, as well. Consequently, no new infections took place, so that the trees were killed only due to the infections that resulted from the control inoculation. Also, it was noticed that during the nursery test, both stem and branch cankers were evident, but later only stem basal cankers occurred. This suggests the absence of the local secondary infections.

Concerning the tree growth, the following phenomenon was observed:

- when the canker was marginal to the stem, the infected tree grew normally up to about 12-15 years of age;
- when the canker spread and reached the half stem diameter, the growth was slow and the tree was dead after a few years;
- when the canker had spread over half the stem diameter, the tree was dead in the same or in the next season of vegetation.

### Genetic Variation

The analysis of variance indicated highly significant ( $p < 0.001$ ) differences among hybrid family means for blister

rust resistance, survival and total height growth at all ages (table 4, row 2). At age 20, blister rust resistance varied from 6.3 to 9.1, survival between 49.9 percent and 91.3 percent and total height from 88.3 dm to 110.0 dm. Hence, selection at the family level within the hybrid population could be carried out for the three economically important traits.

There was a large genetic variation among parents within each sex (species) for the three traits examined over years. An important finding of this experiment was that the effects of eastern white pine female parents were significant ( $p < 0.05$ ) for blister rust resistance and highly significant ( $p < 0.01$ ;  $p < 0.001$ ) for survival at most ages. Significant differences among eastern white pine female parents for total height growth were found by the end of the testing period, i. e. at ages 17 and 20 (table 4, row 3).

Balkan pine as male parents had significant ( $p < 0.05$ ) effects on height growth through age 17 but had no significant effects on blister rust resistance and survival at any age (table 4, row 4). The results suggested that: (i) an additive genetic control in these three traits occurred; (ii) high *gca* parents could be selected within the eastern white pine parental population. Similar results were found in other experiments with *P. strobus* x *P. peuce* hybrids (Blada 1989).

Male x female interaction effects were highly significant ( $p < 0.01$ ;  $p < 0.001$ ) for the three traits at all ages (table 4, row 5), suggesting non-additive gene action.

The genetic coefficient of variation at the family level (table 5) was, in general, moderate ranging between 8.0 and 12.3 percent for blister rust resistance, between 7.6 and 18.3 percent for survival and between 5.0 and 10.8 percent for total height growth.

### Variance Components

Variance component estimates, standard errors and dominance ratios were listed in table 5.

The contribution of the *GCA* variance to the total phenotypic variance ranged over years from 26 to 39 percent for blister rust resistance, 17 to 62 percent for survival and 31 to 44 percent for total height growth. The contribution of *SCA* variance for the same traits ranged from 37 to 60 percent, 34 to 78 percent and 31 to 54 percent, respectively.

The ratio of dominance to additive variance for blister rust resistance was greater than 1 at all ages indicating that dominance variance was of higher importance. However, the additive variance was only slightly lesser than dominance variance, suggesting that both variances could be used in a

**Table 3**—Tree survival and evolution of blister rust attack.

Genotype	Nursery test at age 6		Field test at age 20				
	Inoculated trees at age 2 No.	Survival No. (%)	Planted trees No. (%)	Survival No. (%)**	Total killed trees No. (%)**	Killed trees by rust No. (%)***	Killed by other causes No. (%)***
1	2	3	4	5	6	7	8
<i>P. strobus</i>	150	34 (22.7)	34	23 (15.5)	127 (84.5)	124 (97.6)	3 (2.4)
Hybrids	1050	780 (74.3)	780*	742 (70.7)	308 (29.3)	299 (97.1)	9 (2.9)
<i>P. peuce</i>	109	107 (98.2)	107	97 (88.9)	12 (11.1)	4 (33.3)	8 (66.7)

\* Some families had more and some other less than 10 trees / block; \*\* calculated as against inoculated trees (column 2).

\*\*\* Calculated as against total killed trees (column 6).

**Table 4**—Mean squares and F-tests for the *P. strobus* x *P. peuce* F<sub>1</sub> hybrid factorial analyses.

Source of variation	DF	Traits <sup>a</sup>								
		BRR.5	BRR. 9	BRR. 11	BRR. 13	BRR. 17	BRR. 20	S. 5	S. 9	S. 11
Replications	2	0.054	0.035	0.036	0.054	0.171	0.146	2.675	1.418	2.13
Hybrids	24	2.520***	1.503***	2.775***	2.520***	2.537***	2.590***	112.328***	295.800***	332.71***
-Females (F)	(4)	5.527*	2.692	6.702*	5.527*	7.261*	7.512*	184.804	904.224**	1259.58***
-Males (M)	(4)	2.398	2.248	1.121	2.398	1.526	1.671	108.036	229.358	191.20
-M x F	(16)	1.799***	1.020**	2.207***	1.799***	1.609***	1.589***	95.282***	160.304***	136.37***
Error	48	0.142	0.246	0.154	0.142	0.130	0.120	1.953	2.241	5.80
Within plot <sup>b</sup>	540	3.480	6.407	8.348	8.684	14.980	14.950	-	-	-
Source of variation	DF	Traits								
		S. 13	S. 17	S. 20	H. 5	H. 9	H. 11	H. 13	H. 17	H. 20
Replications	2	7.842	3.03	3.26	0.075	0.242	0.314	0.792	5.796	3.647
Hybrids	24	287.044***	312.92***	262.08***	0.491***	2.243***	7.730***	14.793***	50.217***	113.538***
-Females (F)	(4)	832.042**	1145.85**	901.62**	0.123	3.408	6.967	19.628	105.040*	243.275*
-Males (M)	(4)	249.610	95.72	101.45	1.765**	4.410*	19.029*	35.662*	87.649*	149.623
-M x F	(16)	160.153***	158.99***	142.35***	0.265**	1.410***	5.096***	8.366***	27.153***	72.082***
Error	48	4.240	5.27	2.88	0.056	0.263	1.013	0.862	5.215	2.765
Within plot <sup>b</sup>	540	-	-	-	2.484	3.006	10.568	14.124	38.801	75.871

<sup>a</sup> See Table 1 for list of traits.

<sup>b</sup> The within plot variance was calculated by a separate analysis; \*p = 5 percent; \*\*p = 1 percent; \*\*\*p = 0.1 percent.

breeding program. The ratio of dominance to additive variance for both survival and total height growth did not show a clear trend over the testing period. But each of these variances was sufficient for their practical use for the improvement of blister rust resistance, survival and total height growth. The trend in the contribution of the error variance to the phenotypic variance for blister rust resistance and height growth declined significantly with age, that is, from 35 percent at age nine to 12 percent at age 20 and from 29 percent at age 11 to 7 percent at age 20, respectively. In contrast, for survival, the error variance displayed a slight continuous decline, ranging from 5 percent at age five to 3 percent at age 20. This decline supports the expectation that genetic estimates of the three traits become more accurate with age.

The additive variance component associated with female parent (*P. strobus*) effects ranged from 16 to 39 percent for blister rust resistance, from 15 to 59 percent for survival and from 0 to 27 percent for total height growth of the phenotypic variance. The contribution of male parent effects to the same traits ranged from 0 to 12 percent, 0 to 6 percent and 12 to 44 percent, respectively. Thus, it is evident that the magnitude of the variance component associated with female parent effects was far greater than that associated with male parent effects over the whole testing period. These results were consistent with those reported elsewhere (Blada 1989) for another experiment with *P. strobus* x *P. peuce* hybrids.

The female additive variance components were associated with standard errors smaller than the estimates themselves in all but four cases thus making heritability estimates fairly reliable. However, the standard errors of the male variances for blister rust and survival were higher in six cases than the estimates themselves, at most ages, and suggesting non-accurate estimates.

## Heritability

The broad-sense ( $h^2_1$ ) and narrow-sense ( $h^2_2$ ) heritabilities at the family level, as well as individual-tree narrow-sense ( $h^2_3$ ) heritabilities calculated over testing period are represented in table 6.

The magnitude of heritability estimates for blister rust resistance, survival and total height growth indicated that these traits may be under moderate to high genetic control, but there is an apparent age dependency. For blister rust resistance, the estimated narrow-sense heritability at the family level was 0.325 at age 5 and increased to 0.430 at age 20. Similarly, for survival the heritability was lowest at age five ( $h^2_2 = 0.177$ ), but increased to 0.516 at age 20. The family narrow-sense heritability for total height growth ranged between 0.382 and 0.531. According to table 6, the trend in the three types of heritability for blister rust resistance and height growth was in general consistent over the 20 years testing period. The change in heritability in long rotation crops such as trees is not surprising since genes involved in height growth control may change with age (Namkoong and others 1988) and these changes may be related to different growth phases (Franklin 1979). Perhaps the accumulative nature of blister-rust resistance and tree survival was responsible for increasing heritability with age and the age-age genetic correlations.

Individual narrow-sense heritabilities differed over years. Their estimates were low ranging from 0.024 to 0.067 for blister rust resistance and low to moderate ranging between 0.064 and 0.167 for height growth.

As expected, the broad-sense heritability estimates were much greater than the narrow-sense estimates. The narrow-sense heritabilities are used in conventional breeding while broad-sense ones are also important as vegetative propagation methods and economical methods of producing specific

**Table 5**—Variance components (percents in brackets), standard errors (SE), dominance ratios, genetic coefficient of variation (GCV) and trait means (X).

Parameters	Traits <sup>a</sup>								
	BRR. 5	BRR. 9	BRR. 11	BRR. 13	BRR. 17	BRR. 20	S. 5	S. 9	S. 11
$\sigma^2_{GCA-F} \pm SE$	0.248 (25) ±0.216	0.111 (16) ±0.106	0.300 (26) ±0.263	0.249 (25) ±0.216	0.377 (38) ±0.282	0.395 (39) ±0.291	5.968 (15) ±7.421	49.594 (46) ±34.985	74.881 (59) ±48.576
$\sigma^2_{GCA-M} \pm SE$	0.040 (4) ±0.100	0.082 (12) ±0.089	-0.072 (0) ±0.065	0.040 (4) ±0.101	-0.006 (0) ±0.069	0.005 (0) ±0.073	0.850 (2) ±4.666	4.604 (4) ±9.520	3.655 (3) ±7.959
Total $\sigma^2_{GCA}$	0.288	0.193	0.300	0.289	0.377	0.400	6.818	54.198	78.536
$\sigma^2_{SCA} \pm SE$	0.592 (56) ±0.200	0.258 (37) ±0.114	0.648 (60) ±0.245	0.552 (56) ±0.200	0.493 (49) ±0.179	0.490 (49) ±0.177	31.110 (78) ±10.588	52.688 (48) ±17.812	43.523 (34) ±15.157
Total $\sigma^2_G$	0.840	0.451	0.984	0.841	0.870	0.890	37.928	106.886	122.059
$\sigma^2_e \pm SE$	0.142 (15) ±0.028	0.246 (35) ±0.049	0.154 (14) ±0.031	0.142 (15) ±0.028	0.130 (13) ±0.026	0.120 (12) ±0.024	1.953 (5) ±0.390	2.241 (2) ±0.448	5.803 (4) ±1.160
$\sigma^2_{Ph}$	0.982	0.697	1.138	0.983	1.000	1.010	39.881	109.127	127.861
$\sigma^2_W$	3.480	6.407	8.348	8.684	14.980	14.950	—	—	—
$\sigma^2_p$	-0.438	-0.822	-1.237	-1.305	-2.367	-2.372	—	—	—
$\sigma^2_{SCA} : \sigma^2_{GCA}$	1.9 : 1.0	1.3 : 1.0	2.3 : 1.0	1.9 : 1.0	1.3 : 1.0	1.2 : 1.0	4.6 : 1.0	1.0 : 1.0	0.6 : 1.0
$\sigma^2_{GCA-F} : \sigma^2_{GCA-M}$	6.2 : 1.0	1.3 : 1.0	1.0 : 0.0	6.2 : 1.0	1.0 : 0.0	1.0 : 0.0	7.0 : 1.0	10.8 : 1.0	20.5 : 1.0
GCV (%)	11.5	8.0	12.1	11.5	12.1	12.3	7.6	14.9	16.7
Mean	8.0	8.4	8.2	7.9	7.7	7.7	81.4 Arc 97.8 %	69.3 Arc 87.4 %	66.0 Arc 83.5 %

Parameters	Traits								
	S. 13	S. 17	S. 20	H. 5	H. 9	H. 11	H. 13	H. 17	H. 20
$\sigma^2_{GCA-F} \pm SE$	44.793 (42) ±32.222	65.791 (54) ±44.245	50.618 (51) ±34.847	-0.009 (0) ±0.008	0.133 (14) ±0.135	0.125 (4) ±0.291	0.751 (13) ±0.778	5.192 (24) ±4.088	11.413 (27) ±9.500
$\sigma^2_{GCA-M} \pm SE$	5.964 (6) ±10.245	-4.218 (0) ±5.105	-2.727 (0) ±5.025	0.100 (44) ±0.068	0.200 (20) ±0.173	0.929 (27) ±0.741	1.820 (31) ±1.385	4.023 (18) ±3.427	5.169 (12) ±5.978
Total $\sigma^2_{GCA}$	50.757	65.791	50.618	0.100	0.333	1.054	2.571	9.225	16.582
$\sigma^2_{SCA} \pm SE$	51.971 (48) ±17.797	51.237 (42) ±17.669	46.492 (46) ±15.818	0.070 (31) ±0.030	0.382 (39) ±0.158	1.361 (40) ±0.325	2.502 (42) ±0.931	7.313 (34) ±3.037	23.106 (54) ±8.011
Total $\sigma^2_G$	102.728	117.028	97.110	0.170	0.715	2.415	5.073	16.538	39.688
$\sigma^2_e \pm SE$	4.240 (4) ±0.848	5.276 (4) ±1.055	2.877 (3) ±0.575	0.056 (25) ±0.111	0.263 (27) ±0.053	1.013 (29) ±0.203	0.862 (14) ±0.172	5.215 (24) ±1.043	2.765 (7) ±0.553
$\sigma^2_{Ph}$	106.978	122.304	99.987	0.225	0.978	3.428	5.935	21.753	42.453
$\sigma^2_W$	—	—	—	2.484	3.006	10.568	14.124	38.801	75.871
$\sigma^2_p$	—	—	—	-0.192	-0.238	-0.748	-1.492	-1.252	-9.880
$\sigma^2_{SCA} : \sigma^2_{GCA}$	1.0 : 1.0	0.8 : 1.0	0.9 : 1.0	0.7 : 1.0	1.1 : 1.0	1.3 : 1.0	1.0 : 1.0	0.8 : 1.0	1.4 : 1.0
$\sigma^2_{GCA-F} : \sigma^2_{GCA-M}$	7.5 : 1.0	1.0 : 0.0	1.0 : 0.0	0.0 : 1.0	0.7 : 1.0	0.1 : 1.0	0.4 : 1.0	1.3 : 1.0	2.2 : 1.0
GCV (%)	15.8	18.3	17.2	10.8	5.9	5.6	5.0	5.5	6.6
Mean	64.1 Arc 80.8 %	59.0 Arc 73.5 %	57.2 Arc 70.7 %	3.8	14.2	27.8	44.7	73.6	96.1

<sup>a</sup> See Table 1 for list of traits. $\sigma^2_{GCA-F}$  and  $\sigma^2_{GCA-M}$  = additive variance due female and male parent trees, respectively.

**Table 6**—Estimates of phenotypic variance ( $\sigma^2_{Ph,1}$ ,  $\sigma^2_{Ph,2}$ ), phenotypic standard deviations ( $\sigma_{Ph,1}$ ,  $\sigma_{Ph,2}$ ), family broad sense and narrow sense heritabilities ( $H^2_1$ ,  $h^2_2$ ) and individual narrow sense heritabilities ( $h^2_3$ ).

Parameters	Traits <sup>a</sup>								
	BRR. 5	BRR. 9	BRR. 11	BRR. 13	BRR. 17	BRR. 20	S. 5	S. 9	S. 11
$\sigma^2_{Ph,1}$	0.888	0.533	1.035	0.888	0.913	0.930	38.579	107.633	123.993
$\sigma^2_{Ph,2}$	4.320	6.858	9.332	9.525	15.850	15.840	—	—	—
$\sigma_{Ph,1}$	0.942	0.730	1.017	0.942	0.955	0.964	6.211	10.375	11.135
$\sigma_{Ph,2}$	2.078	2.619	3.055	3.086	3.981	3.980	—	—	—
$H^2_1=h^2_{bs}$	0.947	0.847	0.951	0.947	0.953	0.957	0.983	0.993	0.984
$h^2_2=h^2_{ns}$	0.325	0.363	0.290	0.325	0.413	0.430	0.177	0.503	0.633
$h^2_3=h^2_W$	0.067	0.028	0.032	0.030	0.024	0.025	—	—	—

Parameters	Traits								
	S. 13	S. 17	S. 20	H. 5	H. 9	H. 11	H. 13	H. 17	H. 20
$\sigma^2_{Ph,1}$	104.141	118.786	98.089	0.188	0.803	2.753	5.359	18.276	40.610
$\sigma^2_{Ph,2}$	—	—	—	2.654	3.721	12.983	19.197	55.339	115.559
$\sigma_{Ph,1}$	10.205	10.899	9.904	0.434	0.896	1.659	2.315	4.275	6.373
$\sigma_{Ph,2}$	—	—	—	1.629	1.929	3.603	4.381	7.439	10.750
$H^2_1=h^2_{bs}$	0.966	0.985	0.990	0.901	0.891	0.877	0.946	0.905	0.977
$h^2_2=h^2_{ns}$	0.487	0.554	0.516	0.531	0.415	0.382	0.480	0.505	0.408
$h^2_3=h^2_W$	—	—	—	0.064	0.089	0.081	0.134	0.167	0.143

<sup>a</sup> See Table 1 for list of traits.

$H^2_1=h^2_{bs} = \sigma^2_G / \sigma^2_{Ph,1}$ ;  $h^2_2=h^2_{ns} = \sigma^2_{GCA} / \sigma^2_{Ph,1}$ ;  $h^2_3=h^2_W = \sigma^2_{GCA} / \sigma^2_{Ph,2}$ ;  $\sigma^2_G = \sigma^2_M + \sigma^2_F + \sigma^2_{MF}$ ;  $\sigma^2_{GCA} = \sigma^2_M + \sigma^2_F$ ;  $\sigma^2_{Ph,1} = \sigma^2_M + \sigma^2_F + \sigma^2_{MF} + \sigma^2_e/R$ ;  $\sigma^2_{Ph,2} = \sigma^2_M + \sigma^2_F + \sigma^2_{MF} + \sigma^2_p + \sigma^2_W$ ;  $\sigma^2_p = \text{plot error} = \sigma^2_e - \sigma^2_W/n$ ;  $n = 6$ ;  $\sigma^2_e = \text{variance error}$ .

crosses, such as supplemental mass pollination, become available (Zobel and Talbert 1984). However, heritability estimates were high enough to ensure genetic progress in improving blister rust resistance, survival and height growth using *P. strobus* x *P. peuce* F<sub>1</sub> hybrids.

## Combining Abilities

The general combining ability (*gca*) effects estimated for 10 parents and 18 traits over years were presented in table 7.

Both positive and negative *gca* effects which differed from the test mean were found for both male and female parents for most traits. The range of estimated *gca* effects among parents suggested that it may be possible to select parents with superior breeding values for blister rust resistance, tree survival and height growth.

At age 20, (fig. 1), the eastern white pine female Parent 7 had the largest positive *gca* effects for both blister rust resistance (*gca* = 0.827 points) and survival (*gca* = 8.070 arc sin) whereas the Parent 1 was the second highest for blister rust resistance but the fourth for survival. At the same age, among Balkan pine parents, the male Parent 20 had the largest positive *gca* effects for both blister rust resistance (*gca* = 0.420 points) and total height growth (*gca* = 5.185 dm). On the other hand, the female Parent 2 and Parent 8 were the worst because of their negative effects for all traits at age 20. With one exception, the Balkan male parents had low effects on both blister rust resistance and height growth. A

primary objective of tree breeding involves choosing the best parents for mating, especially when the trait to be improved is quantitatively inherited. Hence the parents 7 and 1 should be selected as good *gca* parents for blister rust resistance and, on the other hand, parents 3 and 20 should be selected as good parents for height growth. Taking into account that blister rust resistance trait has the first priority in improvement, the parents 7, 1, and 20 should be used for blister-rust resistance breeding, as they have the ability of transmitting to their offspring a good level of resistance.

## Genetic Correlations

Genetic correlations for traits involved in 5-, 9-, 11-, 13-, 17- and 20-year-old hybrids are presented in table 8.

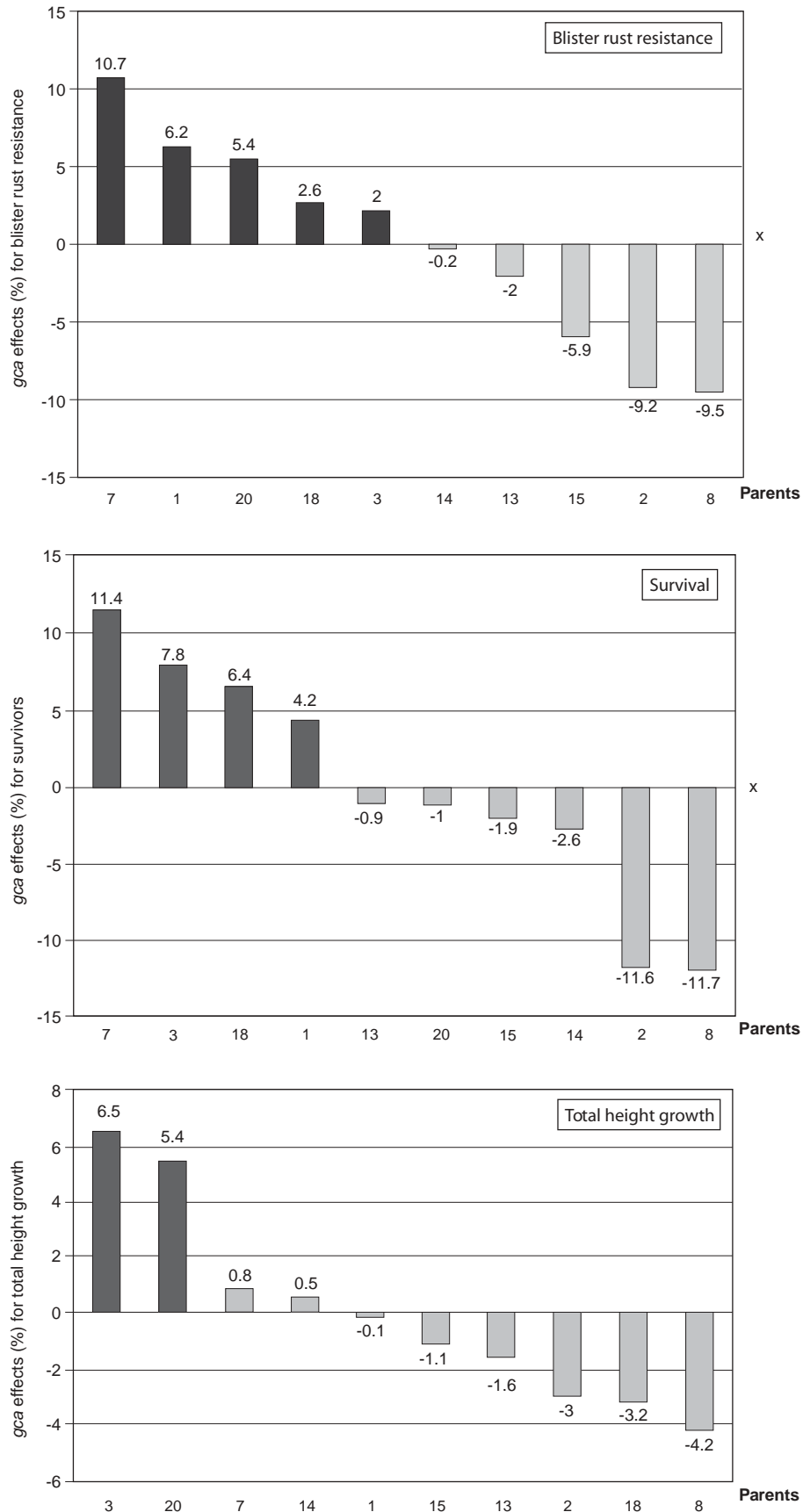
Within trait age-age genetic correlations ranged from 0.406 to 1.00 for blister rust resistance, 0.106 to 0.963 for survival and 0.010 to 0.926 for total height growth. Correlations between blister rust resistance and survival at the same age, except age five, were moderate to high ranging between 0.425 and 0.897. They appear to have a significant predictive value for early selection purposes. Based on these data, one may expect that selection for high blister rust resistance at age five or survival at age nine should result in high blister rust resistance and a high survival at age 20.

Trait-trait genetic correlations between blister rust resistance or survival, on one hand, and height growth on the other, were low and very low. These results suggested that

Table 7—General combining ability (*gca*) effects of 10 parents for tested traits.

Parents	Traits <sup>a</sup>																			
	BRR. 5	BRR. 9	BRR. 11	BRR. 13	BRR. 17	BRR. 20	S. 5	S. 9	S. 11	S. 13	S. 17	S. 20	H. 5	H. 9	H. 11	H. 13	H. 17	H. 20		
	<b><i>gca</i> - females</b>																			
1	0.338	-0.014	0.660	0.338	0.490	0.480	-3.875	0.678	3.358	0.917	6.148	2.964	-0.017	-0.277	-0.388	-1.392	-1.731	-0.068		
2	-0.876	-0.508	-0.860	-0.876	-0.730	-0.726	-1.695	-7.335	-9.228	-6.443	-9.112	-8.216	0.094	0.463	0.112	-0.192	-1.511	-2.928		
3	0.138	0.092	0.600	0.138	0.156	0.154	4.072	3.025	3.872	0.370	2.435	5.484	-0.146	-0.444	0.992	2.288	4.529	6.252		
7	0.698	0.639	0.093	0.698	0.796	0.827	3.365	11.065	11.545	11.690	9.715	8.070	0.036	-0.310	-0.834	-0.645	0.189	0.812		
8	-0.296	-0.208	-0.493	-0.296	-0.710	-0.733	-1.869	-7.435	-9.548	-6.536	-9.188	-8.303	0.032	0.570	0.119	-0.059	-1.477	-4.068		
	<b><i>gca</i> - males</b>																			
13	-0.289	-0.561	-0.340	-0.289	-0.137	-0.153	1.178	-2.215	-1.135	-1.656	1.008	-0.636	0.464	-0.250	0.232	0.015	-1.697	-1.528		
14	0.031	-0.054	0.060	0.031	0.010	-0.013	1.152	-3.455	-2.082	-3.090	-3.138	-1.870	0.168	-0.290	-1.281	-1.539	-0.131	0.478		
15	-0.509	0.019	-0.207	-0.509	-0.450	-0.453	2.125	-1.642	-2.568	-3.996	-1.405	-1.350	0.022	-0.564	-0.728	0.832	-0.411	-1.095		
18	0.371	0.072	0.340	0.371	0.196	0.200	-4.642	0.925	-0.428	4.144	3.562	4.564	-0.402	0.330	-0.092	-0.279	-1.864	-3.042		
20	0.398	0.526	0.147	0.398	0.383	0.420	0.185	6.385	6.212	4.597	-0.028	-0.710	-0.254	0.776	1.686	2.635	4.103	5.185		

<sup>a</sup> See Table 1 for list of traits.



**Figure 1**—General combining ability (*gca*) effects for blister-rust resistance, survival and total height growth at age 20.

**Table 8**—Genetic correlations among traits.

Traits <sup>a</sup>	BRR. 9	BRR. 11	BRR. 13	BRR. 17	BRR. 20	S. 5	S. 9	S. 11	S. 13	S. 17	S. 20	H. 5	H. 9	H. 11	H. 13	H. 17	H. 20
BRR. 5	0.809	0.676	1.000	0.926	0.918	0.281	0.816	0.803	0.874	0.751	0.754	-0.405	-0.178	0.019	0.078	0.227	0.232
BRR. 9	—	0.406	0.809	0.759	0.759	0.312	0.868	0.774	0.783	0.568	0.661	-0.561	-0.187	-0.108	0.031	0.236	0.148
BRR. 11	—	—	0.676	0.644	0.626	0.106	0.474	0.506	0.425	0.559	0.487	-0.397	-0.285	0.037	0.135	0.328	0.352
BRR. 13	—	—	—	0.926	0.918	0.281	0.816	0.803	0.874	0.751	0.754	-0.405	-0.178	0.019	0.078	0.227	0.232
BRR. 17	—	—	—	—	0.998	0.342	0.869	0.871	0.891	0.790	0.778	-0.306	-0.265	0.053	0.098	0.303	0.344
BRR. 20	—	—	—	—	—	0.348	0.877	0.880	0.897	0.792	0.775	-0.316	-0.253	0.070	0.114	0.325	0.361
S. 5	—	—	—	—	—	—	0.398	0.414	0.379	0.324	0.390	0.229	-0.383	0.110	0.232	0.395	0.363
S. 9	—	—	—	—	—	—	—	0.963	0.906	0.762	0.817	-0.378	-0.278	0.061	0.174	0.351	0.309
S. 11	—	—	—	—	—	—	—	—	0.917	0.841	0.851	-0.247	-0.290	0.087	0.175	0.365	0.408
S. 13	—	—	—	—	—	—	—	—	—	0.845	0.839	-0.323	-0.208	0.054	0.086	0.210	0.237
S. 17	—	—	—	—	—	—	—	—	—	—	0.921	-0.232	-0.452	-0.038	-0.032	0.148	0.304
S. 20	—	—	—	—	—	—	—	—	—	—	—	-0.287	-0.430	-0.045	-0.001	0.143	0.231
H. 5	—	—	—	—	—	—	—	—	—	—	—	—	0.043	0.073	0.010	0.093	0.093
H. 9	—	—	—	—	—	—	—	—	—	—	—	—	—	0.567	0.454	0.065	0.016
H. 11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.926	0.660	0.564
H. 13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.829	0.702
H. 17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.876

<sup>a</sup> See Table 1 for list of traits.

the two categories of traits were inherited independently, and hence, tandem selection cannot be applied.

Contradictory age-age within trait correlation estimates was found in total height growth. Thus, correlations involving height growth at ages five and nine were very low with two exceptions. In contrast, correlations involving ages between 11 and 20 were high and very high, ranging between 0.564 and 0.926. Consequently, early selection at age 11 could result in height growth improvement at age 20, and presumably at rotation age, too.

## Heterosis

Parent and hybrid performances and the two types of heterosis exhibited at age 20 are illustrated in figure 2.

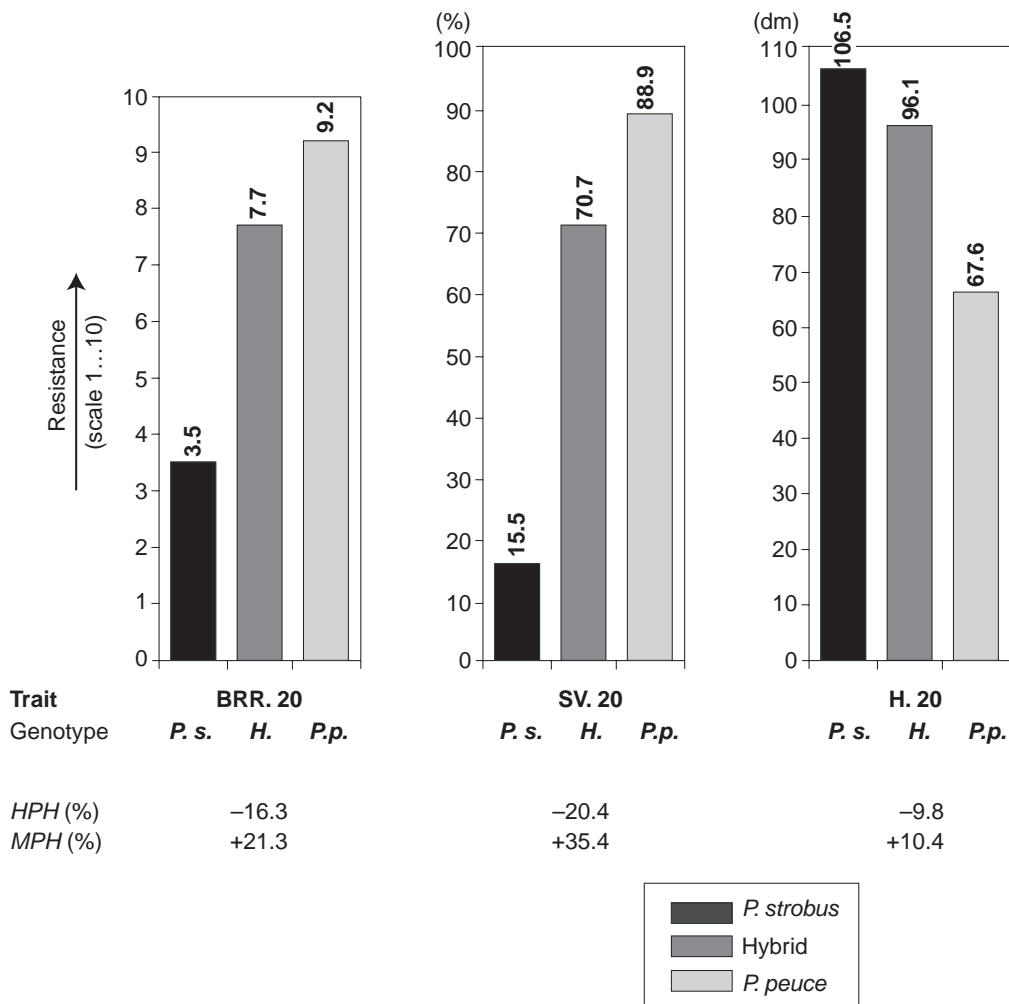
It should be pointed out that the eastern white pine is the best parent species for growth whereas the Balkan pine is the best parent species for blister rust resistance.

At age 20, the estimates of the high-parent heterosis were negative for the three traits, that is, the hybrid performances

were lower than those of the best parent for each trait. For example, for height growth, the hybrid mean was 9.8 percent lower than the mean of the white pine but greater than Balkan pine. Similarly, the mean blister rust resistance and tree survival were 16.3 and 20.4 percent, respectively, lower than the mean of Balkan pine bulk lot.

Mid-parent heterosis was positive for the three involved traits. The heterosis estimates accounted for 21.3 percent for blister rust resistance, 35.4 percent for survival and 10.4 percent for height growth.

The hybrids inherited a high blister rust resistance and were fast growing. Thus, the eastern white pine measured an average of 3.5 points in blister rust resistance and 15.5 percent in tree survival while the hybrid measured 7.7 points and 70.7 percent, respectively; that is, 120 percent and 356 percent more. Also, the hybrid mean exceeded the mean of the Balkan pine in height growth. The Balkan pine measured 67.6 dm in height while the hybrid measured 96.1 dm, or 42 percent more. Therefore, the hybrids inherited high blister rust resistance and faster growth from their parents.



**Figure 2**—*Pinus strobus*, *P. peuce* and *P. strobus* x *P. peuce* F<sub>1</sub> hybrid performance at age 20, high-parent heterosis (HPH) and mid-parent heterosis (MPH).

## Selection and Genetic Gain

Based on these results, selection could be made at both the family and individual level. The genetic gain that could be achieved in all traits and all ages are presented in table 9.

If the best 5, 8, 11, or 14 out of 25 hybrid families were selected at age 20, a genetic gain of 7.2, 5.8, 4.7, and 3.7 percent in blister rust resistance, 12, 9.7, 7.7 and 6.1 percent in survival and 3.6, 2.9, 2.3, and 1.8 percent in height growth could be expected.

Selection at individual level could make an additional gain. So, if at age 20 the best 5, 10, 15, and 20 percent individuals within the best hybrid families were selected, a genetic gain of 2.7, 2.3, 2.0, and 1.8 percent in blister rust resistance and 3.3, 2.8, 2.5, and 2.2 percent in total height growth could be achieved.

Genetic gain was calculated as twice the average of the *gca*s, at age 20. The average breeding value of the best parents was presented in table 9.

The best three parents for blister rust resistance were female trees 7 and 1 and male tree 20. Their average breeding value was 1.151 points, which represent a genetic gain of 15 percent in the overall mean (7.7 points), for blister rust resistance (table 10, column 4). Similarly, for total height growth, the best three parents were 3, 7, and 20, and their average breeding value was 8.165 dm, which represent a genetic gain of 8.5 percent in the overall mean (96.1 dm) for height growth

The estimated genetic gains indicated that a program aimed at improving blister rust resistance and height growth through interspecific hybridisation could be successfully achieved.

**Table 9**—Expected genetic gain ( $\Delta G$ ) according to the intensity of selection and hybrid age.

Traits <sup>a</sup>	$\Delta G$ (%) selecting the best 5, 8, 11 or 14 hybrid families of 25 tested				$\Delta G$ (%) selecting the best 5, 10, 15 or 20% individuals within the best hybrid families			
	5	8	11	14	5	10	15	20
	BRR. 5	5.1	4.1	3.3	2.6	3.6	3.0	2.7
BRR. 9	4.2	3.4	2.7	2.2	1.8	1.5	1.4	1.2
BRR. 11	4.8	3.9	3.1	2.5	2.5	2.1	1.8	1.7
BRR. 13	5.2	4.2	3.4	2.6	2.4	2.1	1.8	1.6
BRR. 17	6.9	5.5	4.4	3.5	2.6	2.2	1.9	1.7
BRR. 20	7.2	5.8	4.7	3.7	2.7	2.3	2.0	1.8
S. 5	1.8	1.5	1.2	0.9	—	—	—	—
S. 9	10.1	8.1	6.5	5.1	—	—	—	—
S. 11	14.4	11.5	9.3	7.3	—	—	—	—
S. 13	10.4	8.4	6.7	5.3	—	—	—	—
S. 17	13.8	11.1	8.9	7.0	—	—	—	—
S. 20	12.0	9.7	7.7	6.1	—	—	—	—
H. 5	8.2	6.6	5.3	4.1	5.7	4.8	4.3	3.8
H. 9	3.5	2.8	2.3	1.8	2.5	2.1	1.8	1.7
H. 11	3.1	2.5	2.0	1.6	2.2	1.8	1.6	1.5
H. 13	3.3	2.7	2.2	1.7	2.7	2.3	2.0	1.8
H. 17	3.9	3.2	2.5	2.0	3.5	3.0	2.6	2.4
H. 20	3.6	2.9	2.3	1.8	3.3	2.8	2.5	2.2

<sup>a</sup> See Table 1 for list of traits.

**Table 10**—General combining ability (*gca*) estimates, breeding values (BV) and genetic gains ( $\Delta G$ ) if selected the best three parents for blister-rust resistance, tree survivors and total height growth.

Select parents	Blister-rust resistance			Select parents	Survival			Select parents	Total height growth		
	<i>gca</i>	BV	$\Delta G^a$		<i>gca</i>	BV	$\Delta G^a$		<i>gca</i>	BV	$\Delta G^a$
	--- Points ---		%		-----%-----			----- dm -----		%	
7	0.827	1.654	21.5	7	11.4	22.4	31.7	3	6.252	12.50	13.0
1	0.480	0.960	12.5	3	7.8	15.6	22.1	20	5.185	10.37	10.8
20	0.420	0.840	10.9	18	6.4	12.8	18.1	7	0.812	1.624	1.7
Mean	0.577	1.151	15.0		8.5	17.1	24.0		4.083	8.165	8.5

<sup>a</sup> Calculated against test mean, that is, 7.7 for blister-rust resistance, 70.7 percent for survival and 96.1 dm for total height growth.

## Conclusions

At age 20, the *P. strobus* x *P. peuce* F<sub>1</sub> hybrids exhibited a mid-parent heterosis in blister rust resistance, survival and total height growth.

Highly significant genetic variation over 20 years was detected in the hybrid population to warrant improvement for the three traits involved, using additive as well as non-additive genetic variances.

Additive variance for height growth was found within both *P. strobus* and *P. peuce* parent populations, whereas the additive variance associated with blister rust resistance and survival was found within female parent (*P. strobus*) population, only. Non-additive variance was also consistently involved in the three tested traits.

The magnitude of variation in *gca* effects suggested that in both initial populations it is possible to detect parents with high breeding values for the traits under study. An important finding was that good *gca* parents were found within eastern white pine, not only for growth but for blister rust resistance, as well.

Narrow sense heritability estimates at the hybrid family level suggested that the tested traits were under moderate to high genetic control over all ages.

The within trait age-age genetic correlations suggested that selection for blister rust resistance and height growth at an early age should result in high improvement of the respective traits, at age 20.

Because of the weak trait-trait correlations, at all ages, between growth and blister rust resistance, no tandem selection can be applied.

The estimated genetic gains indicated that planting *P. strobus* x *P. peuce* F<sub>1</sub> hybrids in operational planting programs seems to be promising

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