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Genetic Variation in Growth and Blister-Rust Resistance in a *Pinus strobus* x *P. wallichiana* Hybrid Population

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Summary

This experiment consists in a controlled crossing according to a factorial design performed between 7 female trees of *P. strobus* and 4 male trees of *P. wallichiana* to combine the rapid growth of former species with high resistance to *Cronartium ribicola* of the latter one. The hybrid families were artificially inoculated at age 2, and field planted at age 6. Blister rust resistance (BRR), tree survival (TS), total height growth, (H) annual height growth (h), diameter (D), basal area (BA), stem volume (V), stems straightness (SS) and branch thickness (BT) were the traits measured at age 17. Statistical analysis produced the results presented below.

Significant ($p < 0.05$) and highly significant ($p < 0.01$; $p < 0.001$) differences were found among hybrid families. Differences among female effects were highly significant ($p < 0.001$) for all tested traits including BRR, suggesting that nuclear additive genes controlled these traits. Significant differences were found among male parents for H but no significant differences for BRR; therefore, all four male parents transmitted a

similar level of resistance. The ratio $\sigma^2_{GCA}/\sigma^2_{SCA}$ variance accounted for 8.1 for BRR, 8.5 for H, 3.5 for V, 9.3 for SS and 1.9 for BT. Similarly, the ratios of $\sigma^2_{GCA-F}/\sigma^2_{GCA-M}$ variance due to female parents were 70.5 for BRR, 23.6 for H, 1.0 for V, 0.4 for SS and 1.0 for BT, were found. Narrow-sense heritabilities, at individual level, were low to moderately high, ranging between 0.085 for BT and 0.421 for BRR. By comparison with the mean of *P. strobus* parent species, the BRR heterosis was highly positive, but negative for all growth traits. If the hybrids will be used in operational planting programs, a significant genetic gain for BRR and growth traits could be achieved.

Key words: *Pinus strobus*, *P. wallichiana*, *Cronartium ribicola*, hybrid, heterosis, additive variance, heritability, genetic correlation, genetic gain.

Introduction

Blister rust (*Cronartium ribicola* FISCH. ex RABENH.) caused severe damages throughout the commercial range of eastern white pine (*Pinus. monticola* DOUGL.) and over extensive high-

rust-hazard areas within the ranges of eastern white pine (*Pinus strobus* L.), and *Pinus lambertiana* DOUGL. (BINGHAM et al., 1969). Because the conventional methods of blister rust control (through *Ribes* eradication and antibiotic treatments) proved to be inefficient (DIMOND, 1966; KETCHMAN et al., 1968), several programs aiming at developing rust-resistant pines were initiated (RIKER et al. 1943; HIRT, 1948; BINGHAM et al., 1953; HEIMBURGER 1956, 1962; PATTON and RIKER, 1958; MEAGHER and HUNT, 1985. The objective of breeding was to exploit both within and between species variation and the eastern white pine and western white pine and some Euro-Asian species were the main species taken into account.

Eastern white pine is well adapted to a diversity of plantation environments and it has wide genetic variability and high productivity in plantations in North America, Europe and the Far East (KRIEBEL, 1983). Unfortunately, it has been ranked as a susceptible species to the blister rust disease (BINGHAM, 1972a; HOFF et al., 1980).

Blue pine (*P. wallichiana* JACK. syn. *P. griffithii* McCLELL.) is an important species in breeding for resistance to blister rust. For this reason, the IUFRO Committee on (resistance to) White Pine Blister Rust selected this species as its first choice because of the following: its good performance and relatively high level of resistance exhibited in central and southern Europe and United States; its extensive range, and thus, probable great genetic variability for resistance, growth and hardiness (BINGHAM, 1972a). The potential of hybridization was early recognized by STOCKWELL and RICHTER (1947), RICHTER (1955), and DUFIELD and SNYDER, A. (1958), but the key to success in the future use of most hybrids will be the degree to which vegetative propagation can be used operationally because obtaining seeds of hybrids is usually difficult and expensive (ZOBEL and TALBERT, 1984). However, this is not the case in species with abundant female strobili/seed production like most of the five needle pines (BLADA, unpublished data).

In the United States and Canada, interspecies breeding with white pines was tried in attempts to introduce resistance genes into eastern white pine from related more resistant species, such as *Pinus peuce* GRISEB and *P. wallichiana*. Based on artificial inoculations, PATTON (1966) found evident differences among both eastern white pine and blue pine selections in ability to transmit resistance to progenies. Also, hybrid progenies of *Pinus strobus* x *P. griffithii* contained the highest percentages of resistant seedlings among all other interspecific hybrids tested. In addition, first-year progenies of the crosses between *P. strobus* x *P. griffithii* showed considerable variability in height, crown size, and needle length. With regard to within species crossing, HEIMBURGER (1972) found no differences among *P. strobus* individual progenies; therefore, he hypothesized a lack of certain resistance genes in this species; if this is the case, the introduction of such genes from other species may be the only way to form a reasonably realistic breeding program with *P. strobus*. However with evidence at hand, RIKER et al. (1943), PATTON (1966) and BLADA (1992a), based on their experiments, demonstrated that resistant individuals within eastern white pine species exist. Unfortunately, the existing results with regard to the North American experiments with *P. strobus* x *P. wallichiana* hybrids refer, with minor exceptions, to juvenile stage of the trees, only.

Owing to its remarkable growth performances, the eastern white pine was introduced in Romania since 1861 where it showed good qualities and adaptation to the excessive continental climate (RADU, 1974). Intensive introductions have rapidly increased after 1960. Because of high occurrence of black currant (*Ribes nigrum* L.) across the country, since 1970

a heavy blister rust attack took place (BLADA, 1982). Encouraged by the previous successfully trials with white pines interspecific hybrids (LEANDRU, 1982) and because of potential importance of *P. strobus* species for Romanian silviculture and because of the danger the blister rust represents, a genetic improvement program was launched in 1977. Initially, the program included both intra- and interspecific hybridizations, but later on, because of financial constraints, the research project has been continuing on a small scale, i. e. at present only interspecific hybrid trials, initially established, are taken into account.

The aim of this hybridization was to establish whether or not:

- the eastern white pine fast growth can successfully and positively be combined, via pollen, with the blue pine blister rust resistance in the *P. strobus* x *P. wallichiana* hybrid genotype;
- the newly acquired characteristics of the hybrid are long lasting;
- the blister rust can be controlled through this hybridization.

The aim of this paper is to provide new information about genetic variation within a 17 year old *P. strobus* x *P. wallichiana* F1 hybrid population. The previous paper concerning the same trial was published when the hybrids were nine years old (BLADA, 1992b) and its outcome will be discuss in parallel with the present results.

Materials and Methods

Initial material and mating design

The eastern white pine was selected as the best species for growth traits, whereas the blue pine was the best parent species for traits related to blister-rust resistance. In order to obtain the hybrid families, in 1979 seven eastern white pine as females, and four blue pine as males were factorially crossed according to COMSTOCK and ROBINSON's (1952). Experiment II. Both populations and parents were taken at random without regard to any trait except female strobili production. All parents were untested and of unknown origin. The seeds were stratified according to KRIEBEL's (1973) methodology and then sown (spring 1981) in individual polyethylene pots (22 x 18 x 18 cm) in a potting mixture consisting of 70% spruce humus and 30% sand.

Inoculation, experimental design and testing

Hybrid and control material was placed in a big tent and artificially inoculated with *C. ribicola* in 1982, 1983 and 1984, at the end of August, when it was two, three and four years old. During each inoculation, the pots with seedlings were placed in a polyethylene tent and arranged in a randomized complete block design. Each family was represented by a 14-seedling plot in each of the three blocks. Two half-sib progenies, representing the mean of the open-pollinated parents, were included as control.

Inoculum material consisted of heavily infected leaves of *Ribes nigrum* collected from a single population. Other details concerning inoculation and inoculation tent were more or less similar to those described by BINGHAM (1972b).

At age 6, the seedlings were transplanted to the field (Valiug Forest District) in row plots using the same experimental design as in the inoculation tent. The planting distance was 3 m within and between rows. But, it should be stressed that only 6 - 12-seedling per plot were planted in the field; the rest of the seedlings died during the nursery test because of blister

Table 1. – Traits measured at age 17.

Trait	Unit	Symbol
Blister-rust resistance	Scale 1...10	BR
Tree survival	%	TS
Total height	dm	H
Annual height growth	dm	h
Diameter at 1.30m	cm	D
Basal area	dm ²	BA
Stem volume	dm ³	V
Stem straightness	Scale 1...5	SS
Branch thickness	mm	BT

rust, but they were taken into account at age 9 (BLADA, 1992b) and age 17 (this paper) when the trial was assessed.

Measurements

Nine traits at six trees per plot were measured in the autumn of 1997, when the trees were 17 years old (Table 1). The blister-rust resistance was measured by two indices. The first index (BRR) was measured by a 1 to 10 scale (1=dead tree because of blister rust and 10=totally resistant tree) and it reflects the economical and biological impact as well as the incidence of disease. The second index (TS), was calculated in percent based on the BRR index data, i.e. all trees with a score higher than 1 were considered survivors. To normalise the variance, before statistical analysis, the percents were transformed to the arc sin of their square roots. A subjective 1 to 5 index was used for the assessment of the stem straightness, where 1 = sinuous and 5 = very straight. The other traits from table 1 do not require additional explanation.

Statistical analysis and genetic gain

Statistical analysis was performed at both the family and individual level. The statistical model assumes that the replicates were fixed and the males and females were random samples from base population. The formula for this model was:

$$X_{ijkh} = m + M_j + F_i + (MF)_{ji} + B_k + e_{ijkh} \quad (1)$$

where: X_{ijkh} = the observation of h -th full-sib family from the cross of the j -th male and i -th female in the k -th block; m = the general mean; M_j = the effect of the j -th male ($j = 1, 2, \dots, J$); F_i = the effect of the i -th female ($i = 1, 2, \dots, I$); $(MF)_{ji}$ = the effect of the interaction of the j -th male and i -th female; B_k = the effect of the k -th block ($k = 1, 2, \dots, K$); e_{ijkh} = the random error. It should be noted that M x B, F x B and M x F x B interactions were pooled for the error term.

As parents were random samples from random mating populations and because the families were planted in a complete randomized block design, a random model for statistical analysis was used. The analysis of variance with the expectations of mean squares and formulas for estimating the variance components are presented in table 2 (HALAUER and MIRANDA, 1981).

Table 2. – Analysis of variance of the design II mating design in one environment (HALAUER and MIRANDA, 1981).

Source of variation	DF	MS	E(MS)
Blocks (k)	$k - 1$		
Males (m)	$m - 1$	M_3	$\sigma^2 + k \sigma_{mf}^2 + k f \sigma_m^2$
Females (f)	$f - 1$	M_4	$\sigma^2 + k \sigma_{mf}^2 + k m \sigma_f^2$
Males x Females (m x f)	$(m - 1)(f - 1)$	M_3	$\sigma^2 + k \sigma_{mf}^2$
Pooled errors	$(k - 1)(mf - 1)$	M_2	σ^2
Total	$k m f - 1$		
Within plot	$k m f(n - 1)$	M_1	

M_1 = the within plot mean square and includes the within plot genetic variance and environmental variance; n = the number of hybrid trees measured in each plot.

Since data on individual trees was available, a separate analysis was performed in order to estimate the within plot variance. Because of unequal survival within plots, at age 17, only six hybrid trees per plot were taken at random into account for within plot variance calculation.

Standard error (SE) of variances was computed with the formula given by ANDERSON and BANCROFT (1952).

The average dominance of genes (d) was calculated according to COMSTOCK and ROBINSON (1952).

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

The first heritability is the one commonly used for estimating the ratio of genetic (additive + non additive) to total variance which is appropriate for estimating gain from selection among families when they are vegetatively propagated. This is a broad sense heritability (H^2) and it is estimated by the following formula (GRAFIUS and WIEBE, 1959):

$$H^2 = \sigma_G^2 / \sigma_{Ph,1}^2 = (\sigma_M^2 + \sigma_F^2 + \sigma_{MF}^2) / (\sigma_M^2 + \sigma_F^2 + \sigma_{MF}^2 + \sigma_e^2 / k) \quad (2)$$

where σ_G^2 = the total genetic variance; $\sigma_{Ph,1}^2$ = the phenotypic variance which refers to family means; σ_M^2 , σ_F^2 , σ_{MF}^2 , σ_e^2 = males, females, M x F interactions and error, variances, respectively.

Mass selection genetic gain (ΔG_1) was estimated (FALCONER, 1981) by:

$$\Delta G_1 = i_1 H^2 \sigma_{Ph,1} \quad (3)$$

where i_1 = the selection intensity for family selection, taken from BECKER (1984); $\sigma_{Ph,1}$ = the phenotypic standard deviation which refers to family means.

The second heritability is appropriate for estimating gain from selection among families when they are sexually propagated. This is a narrow-sense heritability (h_A^2) at family level, and it is estimated by:

$$h_A^2 = \sigma_A^2 / \sigma_{Ph,1}^2 = (\sigma_M^2 + \sigma_F^2) / (\sigma_M^2 + \sigma_F^2 + \sigma_{MF}^2 + \sigma_e^2 / k) \quad (4)$$

where: σ_A^2 = the additive genetic variance;

Genetic gain (ΔG_2) from family selection was estimated by:

$$\Delta G_2 = i_1 h_A^2 \sigma_{Ph,1} \quad (5)$$

The third heritability is the one commonly used for estimating genetic gain from mass selection among randomly placed trees within plot (h_w^2); this heritability was estimated by:

$$h_w^2 = \sigma_A^2 / \sigma_{Ph,2}^2 = (\sigma_M^2 + \sigma_F^2) / (\sigma_M^2 + \sigma_F^2 + \sigma_{MF}^2 + \sigma_p^2 + \sigma_w^2) \quad (6)$$

where: $\sigma_{Ph,2}^2$ = the phenotypic variance and it refers to individual tree values; h_w^2 = within plot variance; σ_p^2 = plot error = $\sigma_e^2 - \sigma_w^2 / n$; n = 6 trees per plot.

The mass selection gain (ΔG_3) was estimated by:

$$\Delta G_3 = i_2 h_w^2 \sigma_{Ph,2} \quad (7)$$

where: $\sigma_{Ph,2}$ = phenotypic standard deviation and it refers to individual tree values and i_2 = the selection differential for individual tree selection.

If the best parents are to be selected and intermated, i_1 should be doubled to give the expected genetic gain (ΔG_4) such as:

$$\Delta G_4 = 2i_1 h_A^2 \sigma_{Ph,1} \quad (8)$$

The general combining ability (gca) effects of each parent and the specific combining ability (sca) effects of each male-female cross were estimated according to GRIFFING (1956), adapted to a factorial mating design. The statistical model was:

$$x_{ij} = X... + g_i + g_j + s_{ij} + e_{ijk} \quad (9)$$

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 the j -th male tree; s_{ij} is the sca effect

Table 3. – Analysis of variance of the tested traits in a *P.strobus* x *P.wallichiana* hybrid population.

Source	Df	Mean squares								
		BRR	TS	H	h	D	BA	V	SS	BT
Blocks	2	0.097	6.05	1.58	0.667	0.0595	0.0009	3.8	0.1515	0.1737
Hybrids	27	4.068***	154.70***	30.77***	0.886***	1.7138*	0.1209**	841.8***	0.3406***	5.8975
- Females	(6)	15.518***	472.27***	120.3***	2.977***	4.9818***	0.3941***	3117.6***	0.4725***	15.2655**
- Males	(3)	0.711	233.17	12.56**	0.383	0.4394	0.1248	88.6	1.6403***	2.9658
- M x F	(18)	0.802	35.73	3.95***	0.273***	0.8369***	0.0292*	208.8***	0.0800	3.2635***
Error	54	0.326	40.86	0.37	0.063	0.0398	0.0143	0.5	0.0487	0.0897
Within plot	420	1.542	-	19.65	1.4286	2.2266	0.1236	610.4	0.5381	9.6983

*p < 0.05; **p < 0.01; ***p < 0.001.

associated with the cross between the *i*-th female tree crossed to the *j*-th male tree; e_{ijk} is the residual effect.

The computational formulae for gca effects were as follows:

$$gca_i = x_i - X... \quad (10)$$

$$gca_j = x_j - X... \quad (11)$$

where: gca_i and gca_j are the effects attributable to female and male parents, respectively.

Heterosis

MACKEY (1976) recognizes both *positive* and *negative heterosis*. The high parent heterosis has the same meaning as *hybrid vigor* which refers to size superiority over both parents, but it is essentially to understand that the term may be properly used for traits other than size (ZOBEL and TALBERT, 1984). *High parent (HPH)* and *mid-parent (MPH)* heterosis was calculated according to the HALAUER and MIRANDA (1981) formula:

$$HPH = [(Hy - HP) / HP] 100 \quad (12)$$

$$MPH = [(Hy - MP) / MP] 100 \quad (13)$$

where: *Hy*, *HP* and *MP* = hybrid, high parent and mid-parent means, respectively.

Results and Discussions

Genetic variation

The analysis of variance indicated significant ($p < 0.05$) and highly significant ($p < 0.01$; $p < 0.001$) differences among hybrid families for all traits except branch thickness (Table 3, row 2). Hence, effective selection at the family level within hybrid population could be carried out for the most economically important traits, including blister-rust resistance.

There was large genetic variation among parents within each sex for all traits examined. Effects of eastern white pine female parents were highly significant ($p < 0.01$; $p < 0.001$) not only for all growth traits but for the two traits related to blister-rust resistance, too (Table 3, row 3). Similar results were detected at age nine of the same hybrid trial (BLADA, 1992b). This suggest: (a) that, even if the eastern white pine is very susceptible to blister rust, resistance genes can be found in the species individual genotypes; (b) an additive genetic control of all growth traits and blister rust resistance, and (b) parents with high GCA could be selected for breeding.

The blue pine as male parents had highly significant ($p < 0.01$; $p < 0.001$) effects on total height and stem straightness but no significance on blister rust resistance and diameter and volume (Table 3, row 4). The lack of significant differences in blister rust resistance could be attributable to the small sample (only four males), and, consequently, further confirmation is needed. As the blue pine male parents exhibited the same level of blister-rust resistance, all of them could either be removed or selected for further breeding works. Taking into

account that the present hybrid population inherited most of resistance from these parent trees, the latter option would be applied. A similar lack of significance on blister rust resistance in blue pine selections was found in the same trial assessed at age nine (BLADA, 1992b). Opposite, PATTON (1966) and BLADA (1987) based on much younger tests found differences among blue pine selections in their ability to transmit resistance to progenies, and consequently, for best results, selection of individuals within a resistant species is perhaps as important as the selection and progeny testing of individuals within the susceptible species.

Male x female interaction effects were significant ($p < 0.05$) and highly significant ($p < 0.001$) for all traits except for blister rust, tree survival and stem straightness (Table 3, row 5), suggesting a non-additive gene action on growth traits, only.

Large variation among means of the hybrid families was found (Table 4). The group poorest in blister-rust resistance (X_2) scored an average of 6.3 points and 63.2% survival, while those for the best group (X_1) scored an average of 8.5 points and 91.2%, i. e. 35% and 44% more, respectively. At the same time, the difference (D1) between the two groups of families accounted for 13% in total height and 34% in stem volume growth rate. These data demonstrate both the magnitude of family variation and the possibilities of selection at family level.

The genetic coefficient of variation at family level (Table 5) was high enough (15.8%) for blister-rust resistance, moderate (11.7%) for volume growth rate and low (4.0%) for diameter.

Table 4. – Means of the best and poorest five hybrid families.

Rank	Traits								
	BRR	TS	H	h	D	BA	V	SS	BT
1	8.8	94.2	81.7	8.9	16.7	2.23	174.4	3.7	33.5
2	8.5	91.4	81.4	8.8	16.5	2.17	173.9	3.6	33.2
3	8.5	90.5	80.3	8.8	16.4	2.13	171.3	3.6	32.6
4	8.4	90.1	79.6	8.7	16.4	2.13	170.3	3.6	32.2
5	8.2	89.7	79.4	8.7	16.3	2.10	168.6	3.5	31.8
X ₁	8.5	91.2	80.5	8.8	16.5	2.15	171.7	3.6	32.7
24	7.5	75.4	73.0	7.7	14.7	1.63	134.2	2.8	29.1
25	7.2	63.3	72.9	7.2	14.6	1.60	128.9	2.7	28.8
26	6.6	62.6	72.5	7.2	14.4	1.57	128.3	2.7	28.7
27	5.1	57.5	69.4	7.0	14.3	1.57	124.0	2.7	28.5
28	5.1	57.0	69.1	7.0	14.1	1.50	123.5	2.5	28.3
X ₂	6.3	63.2	71.4	7.2	14.4	1.6	127.8	2.7	28.7
X	7.6	81.9	75.8	8.2	15.4	1.9	150.8	3.1	30.6
D ₁ (%)	35	44	13	22	15	34	34	33	14
D ₂ (%)	12	11	6	7	7	13	14	16	7

D₁ = differences (%) between mean of the best (X_1) and the poorest group (X_2) of five families; D₂ = differences (%) between mean of the best group of five families (X_1) and the test mean (X).

Table 5. – Variance components (σ^2) (percents in brackets), standard errors (SE), variance ratios (σ^2_{GCA} , σ^2_{SCA} , σ^2_{GCA-F} , σ^2_{SCA-M}) and genetic coefficients of variation (GCV).

Parameters	BRR	TS	H	h	D	BA	V	SS	BT
$\sigma^2_{GCA-F} \pm SE$	1.269 (72) ± 0.648	35.950 (42) ± 19.688	9.698 (83) ± 5.015	0.225 (62) ± 0.124	0.345 (53) ± 0.209	0.030 (56) ± 0.016	242.40 (77) ± 130.01	0.033 (20) ± 0.020	1.001 (47) ± 0.642
$\sigma^2_{GCA-M} \pm SE$	0.018 (1) ± 0.022	9.157 (11) ± 7.032	0.410 (4) ± 0.383	0.005 (1) ± 0.012	-0.019 (0) ± 0.018	0.005 (9) ± 0.004	-5.72 (0) ± 4.13	0.074 (45) ± 0.049	-0.014 (0) ± 0.102
Total σ^2_{GCA}	1.287	45.107	10.108	0.230	0.345	0.035	242.40	0.107	1.001
$\sigma^2_{SCA} \pm SE$	0.159 (9) ± 0.087	-1.710 (0) ± 4.562	1.195 (10) ± 0.417	0.070 (19) ± 0.029	0.266 (41) ± 0.089	0.005 (9) ± 0.003	69.41 (22) ± 22.01	0.010 (6) ± 0.009	1.057 (49) ± 0.344
Total σ^2_G	1.446	45.107	11.303	0.300	0.611	0.040	311.81	0.117	2.058
$\sigma^2_e \pm SE$	0.327 (18) ± 0.062	40.863 (47) ± 7.722	0.369 (3) ± 0.070	0.063 (18) ± 0.012	0.040 (6) ± 0.008	0.014 (26) ± 0.003	0.53 (1) ± 0.09	0.049 (29) ± 0.009	0.090 (4) ± 0.017
σ^2_{Ph}	1.773	85.970	11.672	0.363	0.651	0.054	312.34	0.166	2.148
σ^2_W	1.542	-	19.648	1.429	2.227	0.124	610.4	0.538	9.698
$\sigma^2_{GCA} : \sigma^2_{SCA}$	8.1:1.0	1.0:0.0	8.5:1.0	18.6:1.0	1.3:1.0	7.0:1.0	3.5:1.0	9.3:1.0	1.9:1.0
$\sigma^2_{GCA-F} : \sigma^2_{GCA-M}$	70.5:1.0	3.9:1.0	23.6:1.0	42.3:1.0	1.0:0.0	6.7:1.0	1.0:0.0	0.4:1.0	1.0:0.0
GCV(%)	15.8	8.4	4.4	6.7	4.0	10.5	11.7	11.0	4.7
Average dominance	$0 < d < 1$	$d = 0$	$0 < d < 1$	$0 < d < 1$	$0 < d < 1$	$0 < d < 1$	$0 < d < 1$	$d = 0$	$d = 1$

Legend: $d = 0$ denote no dominance; $0 < d < 1$ denote partial dominance; $d = 1$ denote complete dominance.

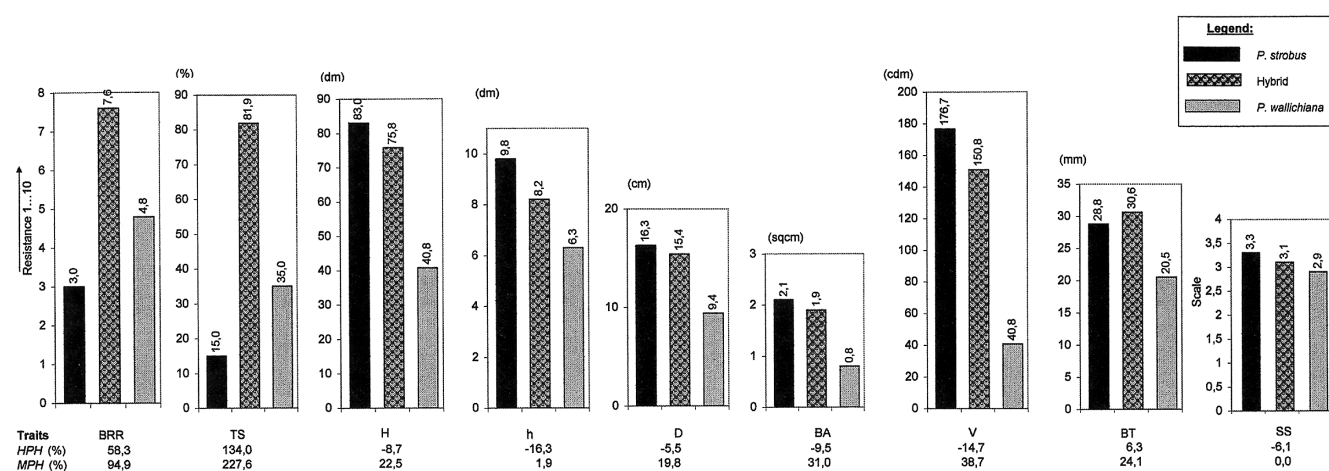


Figure 1. – *Pinus strobus* x *P. wallichiana* hybrid performance, high-parent heterosis (HPH) and mid-parent heterosis (MPH).

Performances and Heterosis

Parent and hybrid performances and the two estimates of heterosis are illustrated in figure 1.

Estimates of high-parent heterosis were positive only for three traits and negative for the rest. Average estimates of high parent heterosis were positive and very high for blister-rust resistance and tree survival, i.e. 58.3% and 134.0%, respectively. Thus, the hybrids displayed hybrid vigor. At the same time, estimates of high parent heterosis were negative for all growth traits, as follows: -8.7% for total height, -5.5% for diameter and -14.7% for volume growth rate. However, KRIEBEL (1982); pointed out that in Ontario, the best hybrid families were from 22% to 44% superior in volume to the best eastern white pine families in three 17 to 22 years old progeny test.

Estimates of mid-parent heterosis were positive for all tested traits. For example, hybrids exceeded mid parent values by 94.9% for blister-rust resistance, 22.5% for total height, 19.8% for diameter and 38.7% for volume growth rate. The respective results suggest that hybrids brought together their parental genes for both rapid growth and blister-rust resistance. These results may justify the use of F_1 *P. strobus* x *P. wallichiana* hybrid production.

There are both similarities and differences between high parent heterosis assessed at age nine (BLADA, 1992b) and that assessed at age 17, as follows:

- at both testing ages, the high parent heterosis was positive for blister rust resistance and tree survival, as well; therefore, the hybrid population mean outgrew the blue pine parent mean at both ages;
- at age nine, the high parent heterosis was positive for all growth traits but negative at age 17; it means that at this age, the mean of the eastern white pine parents outgrew the hybrid population mean
- in the Romanian excessive continental climate, the hybrids exhibited hardiness across the 17 years testing period (BLADA, unpublished data).

Variance components

Variance component estimates, standard errors and additive to dominance ratios, genetic coefficients of variance and average dominance are listed in table 5. The contribution of σ^2_{GCA} to the total phenotypic variance was 87% for total height, 53% for diameter and 77% for volume growth, whereas the contribution of σ^2_{SCA} to the same traits was much lower, i.e. 10%,

41% and 22%, respectively. However, both additive and dominance variances could be used for improvement in wood production.

The contribution of σ^2_{GCA} to the phenotypic variance was predominant i. e. 73% for blister-rust resistance and 53% for tree survival, while the contribution of σ^2_{SCA} to the same traits was only 9% for the former and zero for the latter trait.

The estimated variance components were associated with standard errors smaller than the estimates themselves in all but five cases thus making the heritability estimates fairly reliable.

The $\sigma^2_{GCA}/\sigma^2_{SCA}$ ratios for all traits were by far in favour of additive variance. However, according to KRIEBEL (1983) the non-additive variance was most important in interspecific hybridization of white pines.

The $\sigma^2_{GCA-F}/\sigma^2_{SCA-M}$ ratios showed that estimates of GCA variance among females were much greater than estimates among males for all traits, except stem straightness.

The results concerning variance component estimates showed that:

- high amount additive variance for blister-rust resistance and growth traits was found within parent populations to be used in a breeding program.
- the greatest amount of additive variance associated with both blister-rust resistance and growth traits was found within the eastern white pine parent population; this suggests that selection should be done within eastern white pine species; the blue pine male parent contributions to additive variance was insignificant for blister-rust resistance but significant for total height growth;

There is a living parallel between the amount of genetic variances recorded at age nine (BLADA, 1992b) and those from age 17, such as:

- at both ages of testing, the $\sigma^2_{GCA}/\sigma^2_{SCA}$ ratios for all traits were in favor of additive variance;
- at both ages of testing, the $\sigma^2_{GCA-F}/\sigma^2_{SCA-M}$ ratios for all but one trait (stem straightness) were in favor of the variance attributable to female parents; this suggest a much higher variation within eastern white pine base population and a lower genetic variation within blue pine base population.

The measure of the average dominance of genes in the expression of the traits analyzed was calculated and the major results presented in table 5, are, as follows:

- no dominance ($d = 0$) was found in tree survival and stem straightness;
- partial dominance ($0 < d < 1.0$) was found in blister rust resistance and growth traits;
- complete dominance ($d = 1$) was found in branch thickness, only.

Heritability

The broad-sense (H^2) and narrow-sense (h^2_A) heritabilities at the family level, as well as individual-tree narrow-sense heritabilities (h^2_w) are presented in table 6.

At age 17, narrow-sense heritability estimates at family level were high or very high for all traits. For example, estimates of 0.828 and 0.885 and 0.777 for blister-rust resistance, total height and volume growth, respectively, were obtained. Roughly, estimates of the same magnitude were obtained when this trial was nine year old (BLADA, 1992b). These high heritability estimates were due to the high level of additive variance attributable to the female parents.

The individual-tree narrow-sense heritabilities appeared to be high for blister-rust resistance ($h^2_w = 0.421$), moderately high for total height ($h^2_w = 0.327$), low for diameter ($h^2_w = 0.122$) and very low for branch thickness ($h^2_w = 0.085$).

As expected, the broad-sense heritability estimates were much greater than the narrow-sense ones. The narrow-sense heritabilities are used in conventional breeding, but broad-sense estimates will become important as vegetative propagation methods and economical methods of producing specific crosses, such as supplemental mass pollination, become available.

Both individual and family heritability estimates were high enough to ensure a significant genetic progress in improving blister-rust resistance and growth traits by using *P. strobus* x *P. wallichiana* F1 hybrids.

Combining abilities

The general combining ability (*gca*) effects estimated for 11 parents and 9 traits were presented in table 7. Both positive and negative *gca* effects were found for female parents for all traits. The eastern white pine female parents 2, 3 and 5 exhibited highest blister-rust resistance effects (*gca* = 0.854; 0.537 and 0.654 points, respectively) and volume growth rate (*gca* = 11.9; 19.4 and 13.4 dm³, respectively). In percents (Fig. 2) the same parents exceeded the trial mean in blister rust resistance and volume growth rate with 11.2%, 7.0%, and 8.5%, respectively and by 7.9%, 12.9% and 8.7%, respectively. For the same traits, the Parent 9 was -31.9% and -13%, respectively, under trial mean. It is evident that in eastern white pine, an increase in blister-rust resistance was associated with an increase in volume growth rate. Opposite, for blue pine male parents, highly significant ($p < 0.01$; $p < 0.001$) *gca* effects were found only for total height growth and stem straightness. These parents did not exhibit significant *gca* effects in blister-rust resistance and consequently, they have had about the same level of resistance; thus, all of them could be selected for further breeding work as sources for resistance genes.

Table 6. – Estimates of phenotypic variances (σ^2_{Ph}), phenotypic standard deviations (σ_{Ph}), broad-sense (H^2) and narrow-sense heritabilities at family level (h^2_A) and individual level (h^2_w).

Parameter	Traits								
	BRR	TS	H	h	D	BA	V	SS	BT
$\sigma^2_{Ph.1}$	1.555	58.73	11.426	0.321	0.624	0.045	311.387	0.134	2.088
$\sigma^2_{Ph.2}$	3.057	-	30.951	1.729	2.838	0.164	922.210	0.656	11.756
$\sigma_{Ph.1}$	1.247	7.664	3.380	0.567	0.790	0.212	17.663	0.366	1.445
$\sigma_{Ph.2}$	1.748	-	5.563	1.315	1.685	0.404	30.368	0.810	3.429
H^2	0.930	0.768	0.989	0.935	0.979	0.894	0.999	0.879	0.986
h^2_A	0.828	0.768	0.885	0.717	0.553	0.781	0.777	0.800	0.479
h^2_w	0.421	-	0.327	0.133	0.122	0.214	0.263	0.163	0.085

Table 7. – Estimates of general combining ability (*gca*) effects for 11 parents.

Parent	Trait								
	BRR	TS	H	h	D	BA	V	SS	BT *
Females									
2	0.854***	3.357	2.554***	0.250*	0.448***	0.188***	11.90***	-0.019	0.127
3	0.537*	1.690	4.971***	0.109	0.481***	0.146**	19.40***	-0.102	-2.015***
5	0.654**	3.357	0.979***	0.475***	0.773***	0.188***	13.14***	0.214*	0.056
9	-2.463***	-13.976***	-1.779***	0.225*	-1.069***	-0.170**	-19.56***	-0.261**	-0.198
10	0.387	3.690	-0.704**	0.009	-0.190*	-0.013	3.17***	0.314***	0.494***
11	0.254	1.024	-1.246***	0.000	-0.352***	-0.112*	-7.59***	-0.102	-0.156
12	-0.221	0.857	-4.771***	-1.066***	-0.469***	-0.245***	-20.44***	0.044	1.802***
Males									
21	0.177	3.047	-0.465*	0.122	0.140	0.071	-1.37	-0.167*	-0.107
26	-0.175	3.047	0.797***	0.112	0.130	0.062	2.10	0.295***	0.446
27	0.139	2.714	-0.832***	-0.107	-0.132	-0.062	-2.10	-0.300***	-0.449
28	-0.142	-2.714	0.502*	-0.126	-0.137	-0.072	1.37	0.171*	0.108

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$;

Note: For simplification, the labels of the parents 2, 62, 65, 68, 215, 315, 326, 21, 26, 21-B, 26-B from previous paper (BLADA, 1992 b) became 2, 3, 5, 9, 10, 11, 12, 21, 26, 27, and 28, respectively, in this paper.

The rank of the estimated *gca* effects suggested that it may be possible to select parents with superior breeding values for blister-rust resistance and growth traits. Hence, the parents 2, 3 and 5 should be selected as good *gca* combiners for both blister-rust resistance and volume growth. Also, taking into consideration that blister-rust resistance has first priority in

improvement the male parents 21, 26, 27 and 28 may all be used for resistance breeding, as they have a similar level of resistance. All the other parent trees should be removed.

There were striking differences between the magnitude of the *gca* effects at age nine (BLADA, 1992b) and the magnitude of the same-effects at age 17, as follows:

- at age nine, the ranking of the 11 parents according to magnitude of their *gca*-effects differing from the ranking established at age 17;
- at age nine, for blister rust resistance, the parents 3, and 12, and 27 ranked first, second and third, respectively while at age 17, for the same trait, the parents 2 and 3 and 5 occupied the first three positions in the rank; therefore, only Parent 3 kept its position in the rank whereas, the other two were replaced by parents 2 and 5;
- similar differences were noticed in other traits; thus, the parent rank changes according to the hybrid age.

Estimated specific combining ability (*sca*) effects for blister-rust resistance and volume growth are presented in table 8. Of the 28 crosses among the 11 parents used in the factorial mating design, ten for volume growth had highly significant positive *sca* effects, but no significant effects were found for blister rust resistance. The positive highly significant crosses involved the three best *gca* combiners in volume growth rate.

Once desirable crosses are identified, several techniques exist to exploit them for increased genetic gain. For example, large quantities of seed from full-sib families could be produced by supplemental mass pollination. Then vegetative propagation, including somatic embryogenesis, provides the potential of (i) expanding the number of seedlings produced from a small number of full-sib seed and (ii) selecting superior individuals within full-sib families for propagation. In an improvement program, the most desirable parents would be the ones that had high *gca* effects. They could be combined with other parents to consistently produce families with high *sca*. The high *gca* would insure a high expected full-sib family mean when the parents were crossed, and the high *sca* potential would provide the possibility of producing better than expected specific crosses.

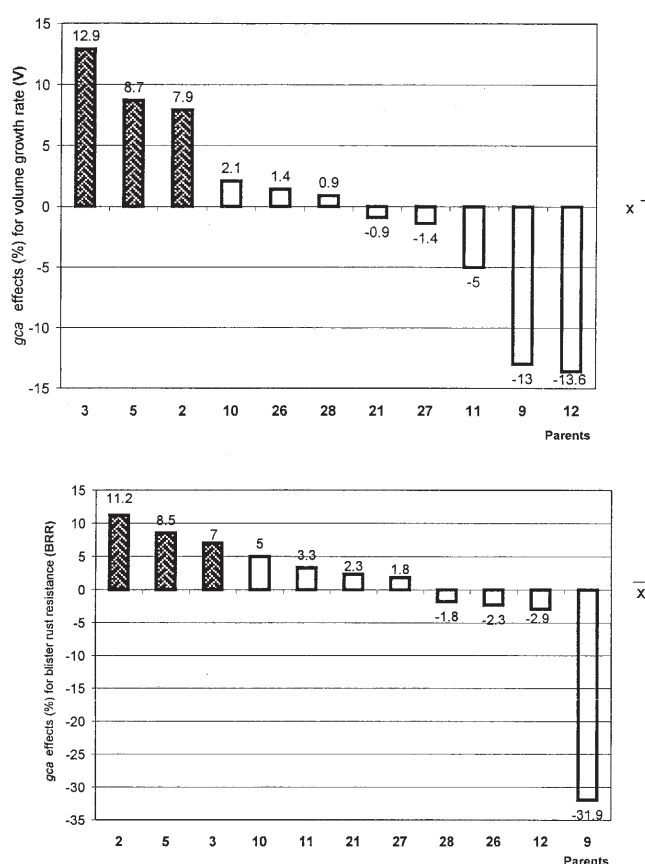
Figure 2. – General combining ability (*gca*) effects (in percents over general mean) for volume growth (V) and blister-rust resistance (BRR).

Table 8. – Specific combining ability effects (*sca*) for volume (upper line) and blister-rust resistance of the parents (lower line).

Parents	21	26	27	28
2	10.00** 0.23	-9.77*** -0.21	9.71*** 0.24	-10.04*** -0.21
3	5.60** -0.22	-5.77*** 0.24	5.81*** -0.22	-5.54*** 0.23
5	2.46** 0.10	-2.41*** -0.14	2.27*** 0.11	-2.38*** -0.14
9	-0.94 -0.16	0.89 0.17	-0.83 -0.15	0.82 0.16
10	-12.47** 0.26	12.56*** -0.25	-12.26*** 0.27	12.29*** -0.25
11	0.29 -0.81	-0.28 0.83	0.00 -0.80	-0.05 0.81
12	-4.96** 0.60	4.77*** -0.57	-4.75*** 0.58	4.90*** -0.61

*** p < 0.001

Correlations

Genetic and phenotypic correlations among traits were presented in table 9. In general, high and positive genetic and phenotypic correlations were found among growth traits, such as: total height, diameter, basal area and volume growth. Such positive correlations imply positive genetic gain in these traits even if selection was practiced on only one trait.

Genetic and phenotypic correlations between stem straightness and growth traits were relatively low, ranging between 0.143 and 0.288. Both types of correlations between branch thickness and growth traits were negative or close to zero. This indicates that the large trees produced thinner branches and this means timber of high quality.

Very high and positive genetic and phenotypic correlations were obtained between the two traits connected with blister-rust resistance ($r_G = 0.928$ and $r_p = 0.916$). Also, high and positive genetic correlations were obtained between blister-rust resistance, and diameter, basal area and volume growth ($r_G = 0.680$; $r_G = 0.655$; $r_G = 0.608$). This suggests that trees with higher resistance possess a higher volume and that tandem selection should be effective.

Comparing correlation estimates obtained at age nine with those from age 17, the following remarks can be done: at age nine no significant phenotypic correlations were found between blister rust resistance and any growth trait (BLADA, 1992), while at age 17, both genetic and phenotypic correlations were significant ($p < 0.05$) and highly significant ($p < 0.01$; $p < 0.001$).

Selection and genetic gain

Selection could be made at both the family and the individual level and the genetic gains that could be achieved are presented in table 10. If the best 5, 10 or 15 out of 28 full-sib families were selected and vegetatively propagated, a genetic gain of 21.5%, 15.5% and 11.0% in blister-rust resistance and 16.5%, 11.9% and 8.4% in volume-growth, respectively, could be expected. Similarly, at the same intensity of selection but using sexual propagation, the achieved genetic gain could be 19.1%, 13.8% and 9.8% in blister-rust resistance and 12.8%, 9.2% and 6.6% in volume growth.

Assuming that the three best *gca* parents of the 11 were selected and crossed, a genetic gain of 30.6% in blister-rust resistance and 20.5% in volume growth could be made.

In summary, such genetic gains represent a considerable increase in both blister-rust resistance and timber production. Even smaller increases in resistance and volume growth would give appreciable improvement in yield, especially when considered in relation to large-scale plantation programs. Such gains plead for developing *P. strobus* x *P. wallichiana* hybrids to be used in operational forest regeneration.

Conclusions

Improving blister-rust resistance and growth traits, through hybridization, using preponderantly additive genetic variance, is possible.

Compared to additive variance, the amount of non-additive one was low in both blister-rust resistance and growth traits

The significant magnitude of variation in *gca* effects suggested that it would be possible to detect parents with high breeding value for both blister-rust resistance and growth traits. Good *gca* parents were found within eastern white pine, not only for growth traits, but for blister-rust resistance, as well, whereas all the blue pine parents exhibited a similar level of blister-rust resistance.

Table 9. – Genetic (upper line) and phenotypic (lower line) correlations among traits of the hybrid families (Df = 26).

Traits	TS	H	h	D	BA	V	BT	SS
BRR	0.928 0.916***	0.321 0.314	0.140 0.126	0.680 0.652***	0.665 0.595**	0.608 0.586**	-0.107 -0.097	0.182 0.159
TS		0.084 0.072	0.056 0.057	0.506 0.451*	0.537 0.395*	0.384 0.338	-0.117 -0.117	0.025 -0.013
H			0.537 0.515**	0.591 0.585**	0.720 0.688***	0.859 0.855***	-0.543 -0.533**	0.218 0.202
h				0.213 0.219	0.572 0.547**	0.414 0.400*	-0.440 -0.426*	0.192 0.143
D					0.821 0.786***	0.912 0.901***	0.031 0.030	0.279 0.261
BA						0.864 0.826***	-0.275 -0.252	0.239 0.211
V							-0.270 0.268	0.288 0.268
BT								0.312 0.302

*p < 0.05; **p < 0.01; ***p < 0.001.

Table 10. – Expected genetic gain (ΔG) in percent if selecting the best families (ΔG_1 , ΔG_2), the best individuals within family (ΔG_3) and the best *gca* parents (ΔG_4).

Traits	$\Delta G_1 = i_1 H^2 \sigma_{Ph.1}$			$\Delta G_2 = i_1 h^2_A \sigma_{Ph.1}$			$\Delta G_3 = i_2 h^2_W \sigma_{Ph.2}$			$\Delta G_4 = 2i_1 h^2_A \sigma_{Ph.1}$
	Selected 5, 10 or 15 families of 28						Selected individuals (%)			Selected parents
	5	10	15	5	10	15	10%	15%	20%	3 of 11
BRR	21.5	15.5	11.0	19.1	13.8	9.8	17.0	15.1	13.6	30.6
TS	12.8	9.2	6.5	12.8	9.2	6.5	-	-	-	20.4
H	6.2	4.5	3.2	5.6	4.0	2.9	4.2	3.7	3.4	8.9
h	9.1	6.6	4.7	7.0	5.0	3.6	3.7	3.3	3.0	11.2
D	7.1	5.1	3.6	4.0	2.9	2.1	2.3	2.1	1.9	6.4
BA	14.1	10.1	7.2	12.3	8.9	6.3	8.0	7.1	6.4	19.6
V	16.5	11.9	8.4	12.8	9.2	6.6	9.3	8.2	7.4	20.5
SS	14.6	10.5	7.5	13.3	9.6	6.8	7.5	6.6	6.0	21.3
BT	6.6	4.7	3.4	3.2	2.3	1.6	1.7	1.4	1.2	5.1

ΔG_1 and ΔG_2 = genetic gain if the best 5, 10, 15 families are selected out of 28; ΔG_3 = gain from mass selection if the best 10%, 15%, 20% of individuals are selected within a family; ΔG_4 = gain if the best 3 out of 11 parents are selected.

As narrow-sense heritability estimates were high, a breeding program could be successful.

High and positive genetic correlations between blister-rust resistance and volume growth indicated that indirect selection could be effective in improving these traits.

Estimates of positive high parent heterosis for blister-rust resistance showed that the hybrids outgrew the two parents in resistance and this may justify *P. strobus* x *P. wallichiana* hybrids as a breeding objective.

Selection can be done at both hybrid family and individual within hybrid family level, as well as at individual parent level within eastern white pine base population.

A substantial genetic gain in both blister-rust resistance and volume growth rate could be achieved. Planting these F_1 hybrids in operational programs seems to be promising.

The aim of this experiment was reached, i. e. there were brought together the two desirable characteristics from the two parental species, so that the hybrids display nearly as fast growth as eastern white pine and nearly the same resistance to blister rust as blue pine

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