# Juvenile Blister Rust Resistance and Height Growth of Pinus strobus × P. peuce F<sub>1</sub> Hybrids

By I. BLADA

Statiunea Experimentală Forestieră, Pădurea Verde, Timișoara, Romania

(Received 29th October 1987)

#### Summary

Twenty one P. strobus imes P. peuce full-sib and two halfsib families were artificially inoculated with C. ribicola. The families were arranged in a randomized completeblock design. Each family was represented by a 10-seedling plot in each of 3 blocks. The results after 5 years of testing are, as follows: (1) differences both among parents and hybrids were significant for resistance and growth; (2) the hybrids' performances in resistance and growth were intermediate between the 2 parents' performances; (3) GCA variance for resistance is 7 times larger than the SCA one, suggesting that the additive variance is most important in the parent populations; (4) concerning growth, the GCA: SCA variance ratio was 1:1; (5) resistance and growth narrow-sense heritabilities were 0.521 and 0.408 respectively; (6) expected genetic gain for resistance and growth would be  $26^{\circ}/_{0}$ ,  $20^{\circ}/_{0}$ ,  $11^{\circ}/_{0}$  and  $4^{\circ}/_{0}$  and  $7^{\circ}/_{0}$ ,  $5^{\circ}/_{0}$ ,  $3^{\circ}/_{0}$  and  $1^{\circ}/_{0}$  respectively if the best 3, 6, 12 and 18 families were selected; (7) there were good general combiners among the parents.

Key words: Pinus strobus, P. peuce, hybrid, resistance, additive variance, heritability, genetic gain, combining ability, Cronartium ribicola.

#### Introduction

*P. strobus* L. has wide genetic variability and high productivity in plantations in North America, Europe and the Far East (Kriebel, 1983). In Romania, it is a fast growing species as it is able to produce 20.2 m³/year/ha (Radu, 1974).

Cronartium ribicola Fisch. ex Rabenh. migrated from its Siberian gene centre 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 genetic improvement of resistance. P. strobus improvement has been based both on intraspecific crosses (Riker et al., 1943; Heimburger, 1972a; ZSUFFA, 1981) and interspecific ones (PATTON, 1966; HEIMBUR-GER, 1972b; ZSUFFA, 1979). To date, there has been no significant increase in the resisitance of selected P. strobus  $F_1$  progenies to blister rust (Kriebel, 1983). Therefore, the introduction of resistance genes in P. strobus may be the only way to form a realistic program with P. strobus (Heim-BURGER, 1972a). P. strobus X P. peuce GRISEB. F, hybrids have demonstrated good resistance (PATTON, 1966; HEIM-BURGER, 1972a; SOEGARD, 1972; BLADA, 1986) and growth Leandru, 1982; Blada, 1986). However, the P. peuce  $\times$  P. strobus hybrids is of doubtful value to forestry in North America because it is slower-growing than P. strobus Fowler and Heimburger, 1958; Wright, 1962). Recently, an eastern white pine tree used as a female in reciprocal crosses to Balkan pine, exhibited a favourable significant cytoplasmatic effect in resistance but not in growth (Blada,

The most remarkable scientific and practical results have been obtained in Moscow, Idaho, where develop-

ment of blister rust resistant *P. monticola* by genetic recombination, has been underway since 1950 (BINGHAM *et al.*, 1953; Hoff and McDonald, 1980). These results were published in many papers and will not be detailed here. The first 25 years work resulted in the establishment of three seed orchards as a result of 2 cycles of selection (phase I) and a more complex program (phase II) is underway now Hoff and McDonald, 1980).

In Romania, the blister rust appeared in 1934 on *Ribes nigrum* L. and in 1936 on *P. strobus* (Georgescu *et al.*, 1957) but heavy attacks have been noticed on *P. strobus* since 1973 (Blada, 1978, 1980; Petrescu, 1980). Because of the importance of *P. strobus* and the potential danger that the rust represents a genetic resistance improvement program started in 1977 (Blada, 1980).

The purpose of this paper is to present data on blister rust resistance and height growth in five years old  $P.\ strobus \times P.\ peuce$  hybrids.

## **Materials and Methods**

Materials, mating and experimental design

The breeding design and genetic model followed that of Сомsтоск and Robinson's (1952) experiment II, which was conceived for intraspecific crosses. There is not such a design for interspecific crosses, that is why it was adapted in the respective case. Both populations and parent trees were selected according to their great number of flowers but without regard to blisher-rust resistance and to height growth. Other informations in this context are given in Table 1-A. The 7 P. strobus female and 3 P. peuce male parents chosen from the non-inbred populations were mated in 1979 according to a factorial design. Before factorial crosses, the parental trees were tested neither for growth nor for resistance to blister-rust. The seeds were stratified according to KRIEBEL'S (1973) methodology and then they were sown, in spring 1981, in individual polyethylene bags (22 cm imes 18 cm imes 18 cm) filled up with a mixture consisted of 70% spruce humus and 30% sand. Over the testing period, the seedlings grew in these bags and for this reason it is presumed that potential growth could be higher than the realized one because of the bags stress on seedling roots. During inoculation, the 21 hybrid families were placed in a randomized complete-block design; each family was represented by a 10-seedling plot in each of the 3 blocks. Two half-sib progenies, representing the mean of the open-pollinated parent trees, were included in the test.

## Inoculation

Test seedlings were artificially inoculated three times, between August 20 and 25 in 1982, 1983 and 1984, when they were two, three and four years old. The inoculum was obtained from heavily infected leaves of *R. nigrum* 

Table 1-A. — General information about parent populations and parent trees.

Parent	Р			
specles	Number	Location	Origin	Parent trees
P. strobus	1	Dofte ana 1)	Unknown	7
P. peuce	1	Dofteana 1)	Unknown	3

1) Dofteana Arboretum, Romania

harvested from a single plantation. Other inoculation details were similar to those described by BINGHAM (1972).

Rust and growth assessment

The growth was measured at age 5 whereas the blister-rust resistance was assessed both at age 5 and 6. Rust-susceptibility was measured according to Blair's (1970) "c-score" (adapted), that is a 1 to 10 scale, where 1 = nolesions (total resistance) and 10 = seedling dead (total susceptibility). The c-score, as used in case of fusiform rust (Cronartium fusiforme Hedge. and Hunt ex Cumm.) takes into consideration both the number and severity of the stem and branch lesions and presumably all resistance mechanisms were assessed.

The family means were the basic data for statistical analysis.

#### Statistical analysis

The statistical model assumes that the replicates were fix and male and female random samples from non-inbred populations. The formula for this model is as follows:

$$X_{ijkh} = m + M_i + F_j + (MF)_{ij} + B_k + (MFB)_{ijk}$$
 (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, ... I);  $F_j=$  the effect of the j-th female (j = 1, 2, ... J);  $B_k=$  the effect of the k-th block (k = 1, 2, ... K); (MF)<sub>ij</sub> = the effect of the interactions of the i-th male and j-th female; (MFB)<sub>ijk</sub> = the effect of the interactions of the interactions of the i-th male, j-th female and the k-th block.

The analysis of variance with the expectations of mean squares and formulas for estimating the variance components are given in *Table 1*.

Table 1. — Model for analysis of variance.

Source of variation	d.f.	м. s.	E (MS)
Blocks (B)	K-l	MS <sub>B</sub>	
Males (M)	I-l	MS <sub>M</sub>	$\sigma_{e}^{2} + \kappa \sigma_{MF}^{2} + \kappa J \sigma_{M}^{2}$
Females (F)	J-1	$^{ m MS}_{ m F}$	$\sigma_{e}^{2}$ + k $\sigma_{MF}^{2}$ + ki $\sigma_{F}^{2}$
Males x Females	( I-l)(J-l)	MS <sub>MF</sub>	$\sigma_e^2 + \kappa \sigma_{MF}^2$
Pooled error	( LJ-l)(K-l)	MS <sub>e</sub>	$\sigma_{e}^{2}$
$\sigma_{\mathbf{M}}^2 = (\sigma_{\mathbf{M}}^2 - \sigma_{\mathbf{M}}^2)/$	$\kappa J;  \sigma_{\mathbf{F}}^2 = (\sigma)$	<sup>2</sup> <sub>F</sub> -σ <sub>MF)</sub>	$\sigma_{MF}^{2} = (\sigma_{MI}^{2}, -\sigma_{e}^{2})/K$

The standard errors (SE) of the variance components were obtained from the following formula (Anderson and Bancroft, 1952):

SE = 
$$\sqrt{\frac{2}{K^2} \sum_{f_5} \frac{MS}{f_{g}^{+}} \frac{g}{2}}$$
 (2)

where: K = coefficient of the variance component;  $MS^2_g = \text{the g-th mean square}$  used to estimate the variance component; f = the degrees of freedom of the g-th mean square.

The narrow-sense (h<sup>2</sup>) and broad-sense (H<sup>2</sup>) heritabilities formulas, at family level (Grafius and Wiebe, 1959), were:

$$h^{2} = \frac{C_{M}^{2} + \sigma_{F}^{2}}{\sigma_{M}^{2} + \sigma_{F}^{2} + \sigma_{e}^{2}/K}$$
(3)

$$H^{2} = \frac{\sigma_{M}^{2} + \sigma_{F}^{2} + \sigma_{MF}^{2}}{\sigma_{M}^{2} + \sigma_{F}^{2} + \sigma_{MF}^{2} + \sigma_{e}^{2}/K}$$
(4)

Two kind of genetic gain was calculated, such as: (1) as compared to parents mean and (2) as compared to hybrid population mean. In the first case the formula was  $\triangle G = \mathrm{Sh^2}$  and in the second one was  $\triangle G = \mathrm{ih^2}\sigma_\mathrm{p}$  where:  $S = \mathrm{selection}$  differential expressed as the mean of the hybrid families selected for the next generation minus the general mean;  $i = \mathrm{intensity}$  of selection;  $\sigma_\mathrm{p} = \mathrm{phenotypic}$  standard deviation.

Estimation of combining abilities followed Griffing's (1956) method 4 and formulas adapted to a factorial design.

The calculation formula for synthetic indices of selection ( $I_{\rm s})$  was (Cabulea, unpublished data):  $I_{\rm s}=A.B/100$  where: A and B = the progress in height and in blister rust resistance respectively, of a family, calculated (in  $^{9}\!/_{\! 0}$ ) as compared to the parents mean.

## **Results and Discussions**

Genetic variability (Table 2)

There were significant (p < 0.05) differences among hybrid families in resistance and highly significant (p < 0.001) differences in growth rate.

Response of parental trees varied with sex and the character tested. Thus, there were highly significant (p <0.01; p <0.001) differences among females in both resistance and growth, whereas among males there were highly significantly (p <0.001) differences in growth but no differences in resistance. Therefore, growth in males and females and resistance in females were controlled by genes with additive effects.

The male  $\times$  female interactions were highly significant (p < 0.001) in growth but negligible in resistance, suggesting a non-additive genetic effect for the former character.

Table 2. — Analysis of variance of resistance to C. ribicola and height growth of P.  $strobus \times P$ . peuce hybrids.

Source of		Resi	stance	Height 1	growth
variation	df	MS	è	MS	F
Total	62				
Replications	2	o. 56	1. o	96.15	14.4
Hybrid families	20	1, 26	2,2+	41.46	6. 2
-Females (F)	(6)	2.60	4.5++	66.12	9.9++
-Males (M)	(2)	o. 96	1.6	59.2o	8.9++
-Males x Females	(12)	o. 64	1.1	26,17	3.9++-
Pooled error	40	o. 58		6.66	

Table 3. — Blister rust resistance, height growth and synthetic index of selection rankings for P.  $strobus \times P$ . peuce hybrids (DUNCAN test).

	Resistance			Н	eight growth	Syntha	tic
Family	Mean	DUNCAN	Family	Mean	index of		
	(c-score)	test		(c-score)	test	selection	
		(p<0. 05)			( p<0. o5)	Family	Value
491	1. 07		567	43.3		594	26. 6
589	1. 23		594	4o. 8		491	23. 7
486	1. 33		483	38.4		567	19.8
490	1. 33		481	38.3		488	18. 6
594	l. 37		564	38. o		587	15, 2
570	l. 5o		593	36. 5		589	13.8
587	1. 57		587	36.3		593	12.6
488	1. 67		563	35. 9		564	12.3
59o	1. 73		592	35. 5		5 <b>7</b> 0	12. o
483	l. <b>7</b> 3		589	34.7		592	lo. 6
593	2. 00	111	570	34. 5		59o	lo. o
592	2. 07		59o	34. l		561	8. o
561	2. 07		561	33.9		483	7. 9
485	2.2o		569	33.6		569	4.8
567	2.3o		598	33. <b>3</b>		598	4.2
564	2.33		483	33. о		490	4.1
600	2.37		485	31.4	1	485	3.8
569	2. 70		Sol	31. 1		486	1. 8
598	2.77		490	30. 6		553	1. 7
601	3. o7		485	29.6		6ol	1.5
563	3.53	1	600	28. o		600	- 1.1

According to the Duncan test (*Table 3*), the families were distributed into 5 and 9 undifferentiated groups for resistance and growth, respectively. According to c-score, the resistance of the families ranged between 1.07 to 3.53. Height growth appeared as a more heterogenous character. The first 7 families were the best in growth.

The ranking of the hybrid families according to the synthetic index of selection (that into consideration both resistance and growth values) is shown in the last part of the *Table 3*.

The performances of hybrids are shown in Figure 1. Compared to each parental species, the hybrids were 68% more resistant than P. strobus and 43% more susceptible than P. peuce. The hybrids grew 10% slower than P. strobus and 86% faster than P. peuce. The frequency of non-infected seedlings within parent and hybrid populations was 16% in P. strobus, 71% in P. peuce and 70% in hybrids. The results demonstrate the ability of Balkan pine and eastern white pine to transmit to hybrids their resistance and active growth respectively.

## Variance components

The analysis of variance revealed a highly significant general combining ability (GCA) variance both in resistance and growth, whereas specific combining ability (SCA) variance was highly significant only in growth (*Table 2*).

The structure of the phenotypic variance for resistance demonstrated that the GCA variance was 7 times larger than SCA variance, and GCA variance due to females effects was 14 times larger than GCA variance due to males effects. These data suggest that the additive genetic variance for resistance is most important in parent (mostly in *P. strobus*) populations, and a breeding strategy for resistance based on additive variance could be advantageously adopted (*Table 4*).

The amount of GCA variance for growth was about equal to that of SCA variance and GCA variance due to females effects was 3 times larger than GCA variance due to males effects. It appears that a program for height growth improvement could be based on both additive (that is most important in *P. strobus*) and non-additive variance (*Table 4*).

## Combining ability (Table 5)

Parents 2 and 63 from *P. strobus* and parent 14 from *P. peuce* had positively significant GCA effects for growth and could be saved as good combiners. Parents 65 and 6-1 from *P. strobus* and parent 18 from *P. peuce* had negatively significant GCA effects for growth and must be rejected.

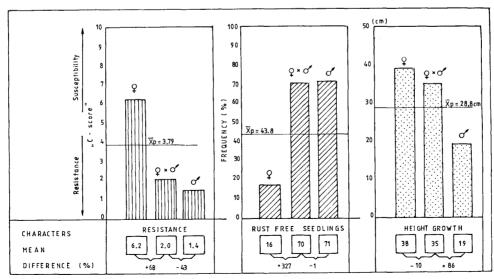


Figure 1. — Performance of P. strobus  $\times$  P. peuce hybrids in blister rust resistance and height growth as compared to P. strobus  $(\mathfrak{P})$  and P. peuce  $(\mathfrak{F})$   $(\overline{\mathbf{x}})$  = the parents mean).

Table 4. — Variance component estimates, standard error and heritabilities, at family level, estimated from P. strobus  $\times$  P. peuce families.

Components	Resistance	Height growth
$\sigma_{\rm p}^2$ (GCA - females)	o. 217 ± o. o34	4. 439 ± 3. 834
$\sigma_{ m M}^2$ GCA - males)	a. ol5 + o. o21	1. 573 <sup>+</sup> 2. 048
Total GCA-variance	o. 232	6. ol2
σ <sub>MF</sub> (SCA -variance)	o. o2o = o. o9!	6, 502 + 3, 332
Total genetic variance	o. 252	12.514
σ <sup>2</sup> <sub>MFR</sub> (environment)	o. 193	2. 221
Phenotypic variance	o. 444	14, 735
h <sup>2</sup> (narrow-sense)	o. 521	0.403
H <sup>2</sup> (broad-sense)	o. 566	o. 819
$\sigma^2_{ ext{GCA}( extbf{f})}$ : $\sigma^2_{ ext{GCA}( ext{M})}$	14:1	3:1
$\sigma_{\text{GCA}}^2$ : $\sigma_{\text{SCA}}^2$	7:1	1:1

GCA and SCA = general and specific combaining ability

Of all parents, only one (65) had positively (i.e. susceptibility) significant effects for resistance, and no one had negatively (i.e. resistance) significant GCA effects. For this reason, the progeny test should be carried out to identify good combiners for resistance.

Table 5 shows the SCA effects for each parental couple. Genetic control

Histograms illustrated in Figures 2 (A) and (B) represent the hybrid distribution according to their blister-rust resistance at age 5 and 6 respectively. The frequency (A) departs from the normal but the frequency (B) accords with normal distribution. Therefore, the resistance in hybrids at age 5 seems to be inherited in a pattern that can be attributed to the effects of major genes while at age 6, the resistance seems to be under polygenic control. However, the question as to whether or not the resistance is under major genes or polygenic control remains to be answered.

Height growth of individual trees within the hybrid population resulted in a frequency distribution very close to the normal curve (Fig. 2-C). This pattern of distribution

Table 5. — Estimates of GCA and SCA effects for resistance to C. ribicola (R) and height growth (H) of P. strobus ( $\circlearrowleft$ ) and P. peuce ( $\circlearrowleft$ ) parents.

\ ₫	14	1	18		20		G€	A (Q)
\$	Н	R	н	R	H	R	n	R
1	-3, 5	-o. 58	1. 8	o. 68	1. 7	-o, lo	1.1	0, 63
2	4, 7	o. o9	-1. 7	o. 35	-3. o <sup>+</sup>	-0.41	2.3	o. 17
62	- o. 2	0.06	1. 5	-o. <b>4</b> 9	- 1, 3	o. 43	o. 3	o. 5o
63	- 3.5	o, 23	o. 7	- o. o2	2.8	- o. 21	2.8	-o. 17
65	1.1	- o. ol	l. o	-o. 55	- o. l	o. 56	- 4. o <sup>+</sup>	o. 77 <sup>+</sup>
6-l	o. 3	-o. o8	1. 9	o. 28	-2.1+	- o. 2o	- 3.5 <sup>+</sup>	- o. 27
6-2	1, 2	o. 29	- 3.3+	- o. 25	2.1+	- o. o4	1.0	-0, 63
GCA (O)	1.4+	0, 04	- 1, 8+	o. 19	o. 4	- o. 23	0, 0	0, 0

Legend: + = p < 0.05; GCA and SCA = general and special combining ability; positive values in case of resistance means susceptibility, and negative ones means resistance.

is specific to continuously-variable characters (Mather and Jinks, 1977), and it is therefore assumed that the height growth of the hybrids is controlled by polygenes.

### Heritability

Blister-rust resistance and height growth estimates of narrow-sense heritabilities on plot mean were 0.521 and 0.408 respectively (*Table 4*). Broad-sense heritabilities, as expected, had higher values due in part to a high level of non-additive variance. The results indicate that selection on the basis of family comparisons could be effective.

#### Genetic gain

If the hybrids are planted on suitable sites a substantial genetic gain will be achieved by family selection. Thus, if selected the best 3, 6, 12 and 18 of 21 hybrid families, a genetic gain of  $26^{0}/_{0}$ ,  $20^{0}/_{0}$ ,  $11^{0}/_{0}$  and  $4^{0}/_{0}$  respectively, for resistance and  $7^{0}/_{0}$ ,  $5^{0}/_{0}$ ,  $3^{0}/_{0}$  and  $1^{0}/_{0}$  respectively, for growth would be expected. The size of genetic gain is different if calculated against the parental mean ( $Table\ 6$ ).

## **Conclusions**

Fast growth of *P. strobus* can be combined with rust-resistance of *P. peuce* in a valuable intermediate hybrid.

There is sufficient additive genetic variance in parent

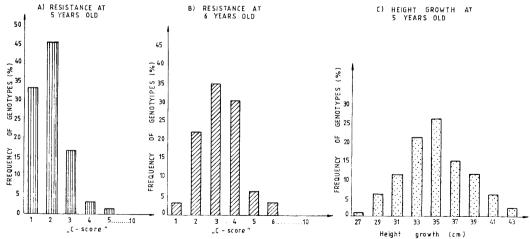


Fig. 2. — Frequency distribution in the P. strobus × P. peuce hybrid population evaluated for blister rust resistance and height growth.

Table 6. — Expected genetic gain (%) at family level for P. strobus  $\times$  P. peuce hybrids as compared to their mean and parents mean (in brackets).

Characters	Genetic gain if selected the best families				
	3	С	12	18	
Resistance	23	20	11	4	
	(+1	(fe)	(6,	(2)	
Height growth	7	5	3	ı	
	(8)	(6)	(4)	(1)	

populations to utilize in a selective breeding program for resistance and growth.

Some parents had positively and some negatively significant GCA effects for growth. No one parent combines significantly favourably the resistance to *C. ribicola*.

Growth seems to be under polygenic control, but the question of whether or not resistance is under single gene or polygenic control remains to be answered.

Narrow-sense heritabilities had moderate values both for resistance and growth, but if the hybrids are planted on a large scale a substantial genetic gain should be achieved, particularly in resistance.

#### Acknowledgements

Grateful acknowledgment is made to Dr. Val. Enescu for reviewing the Romanian version of the paper and to Dr. I. Cabulea for his assistance in the statistical analysis. Dr. H. Kriebel made English corrections, suggested some improvements and presented the paper in the 18th IUFRO World Congress, Ljubljana, 1986; for all these I would like to express my gratitude.

## Literature

Anderson, R. L. and Bancroft, T. A.: Statistical theory in research. McGraw-Hill Book Co., New York, 399 pp. (1952). — Bingham, R. T.: Artificial inoculation of large numbers of P. monticola seedlings with C. ribicola. In: Bingham et al. (eds). Biology of rust resistance in forest trees. USDA For. Serv., Misc. Publ. 1221, p. 357—372 (1972). — Bingham, R. T., Squilace, E. A. and Duffield, J. E.: Breeding blister rust resistant western white pine. J. For. 51: 161—163 (1953). — Bingham, R. T. and Gremmen, J.: A proposed international program for testing white pine blister rust resistance. Eur. J. For. Path. 1: 93—100 (1971). — Blada, I.: Ameliorarea pe cale genetică a rezistentei la boli si insecte a speciilor

de rășinoase. Manuscris ICAS, 30 p. (Unpublished) (1978). BLADA, I.: Relative blister rust resistance of native and introduced white pines in Romania. In: HEYBROEK, H. et al. (eds). Resistance to diseases and pests in forest trees. PUDOC, Wageningen, 415-416 (1980). — Blada, I.: Rezistența genetică la Cronartium ribicola și creșterea hibrizilor F<sub>1</sub> reciproci între *P. strobus* și *P. peuce.* Revista Pădurilor 3: 132—135 (1986). —— Blair, R. T.: Quantitative inheritance of resistance to fusiform rust in loblolly pine. Ph. D. Thesis, N. C. State Univ. Releigh, 87 pp. (1970). — Comstock, R. E. and Robinson, H. F.: Estimation of average dominance of genes. In: Gowen, J. W. (ed). Heterosis, Iowa State Coll. Press, Amnes, (1952). — Fowler, D. P. and Heimburger, C.: The hybrid P. peuce × P.strobus, Silvae Genetica 7, 81—86 (1958). — - Georgescu, C. C. Petrescu, M., Stefanescu, M. and Miron, V.: Bolile și dăunătorii pădurilor. EAS, București. 638 pp. (1957). — Grafius, J. E. and Wiebe, G. A.: Expected genetic gain in yield in small grain. A geometrical interpretation. Agron. Jour. 51: 560-562 (1959). - GRIF-FING, B.: Concept of general and specific combining ability in relation to diallel crossing systems. Austral. J. Biol. Sci. 9: 465-493 Heimburger, C.: Relative blister rust resistance of native and introduced white pines in eastern North America. In: BINGHAM, R. T. et al. (eds). Biology of rust resistance in forest trees. USDA For. Serv. Misc. Publ. 1221 (1972a). - Heimburger, C.: Breeding of white pine for resistance to blister rust at the interspecific level. In: BINGHAM, R. T. et al. (eds). Biology of rust resistance in forest trees. USDA For. Serv. Misc. Publ. 1221 (1972b). Hoff, R. J. and McDonald, G. I.: Improving rust resistant strains of inland western white pine. USDA For. Serv. Res. Pap. - Kriebel, H. B.: Methods for germinating Int. 245, 13 p. (1980). seed of five needle pines. IUFRO Instructions, 2 p. (1973). Kriebel, H. B.: Breeding eastern white pine: a world wide perspective. For. Ec. and Mariag. 6: 263-279 (1983). - LEANDRU, L.: Hibrizi interspecifici la pin. S. II ICAS București, 78 p. (1982). LEPPIK, E. E.: Some viewpoints on the phylogeny of rust fungi. VI. Biogenic radiation. Mycologia 59: 568-579 (1967). and JINKS, J. L.: Introduction to biometrical genetics. Chapman and Hall, London. 223 pp. (1977). - PATTON, R. F.: Interspecific hybridization in breeding for white pine blister rust resistance. In: Gerhold, H. et al. (eds). Breeding pest-resistant trees. Perg. Press, Oxford (1966). — Petrescu, M.: Cercetări privind biologia, prevenirea și combaterea lui Cronartium ribicola la pin. Manuscris ICAS. (Unpublished). 1980. — RADU, S.: Cultura și valorificarea pinului strob. Ed. CERES, București. 304 p. (1974). -- RIKER, A. J., KOUBA, T. F., BRENER, W. H. and BYAM, L. E.: White pine selections tested for resistance to blister rust. J. For. 41: 753-760 (1943). -SOEGAARD, B.: Relative blister rust resistance of native and introduced white pine species in Europe. In: BINGHAM. R. T. et al. (eds). Biology of rust resistance in forest trees. USDA For. Serv. Misc. Publ. 1221, 681 pp. (1972). — WRIGHT, J. W.: Genetics of forest tree improvement. FAO, Rome. 399 pp. (1962). — ZSUFFA, L.: The genetic improvement of eastern white pine in Ontario. In: Scar-RATT, J. B. (ed). Proc. tree improv. symp. COJFRC Publ. 0-P-7, 153-160 (1979). -- ZSUFFA, L.: Experience in breeding P. strobus for resistance to blister rust. In: Proc. 17-th IUFRO World Congress, Kyoto, 181-183 (1981).

## Age-to-Age Correlations in Growth Processes with fixed and random Effects

By S. Magnussen<sup>1</sup>)

(Received 29th November 1987)

## Summary

A model to predict phenotypic single tree age-to-age correlations is developed. Correlations are predicted from variance ratios and a factor d which depicts the relative proportion of size dependent growth in a quantitative juvenile trait. Observed age 10 to age 35 correlations of stem volume in a *Pinus resinosa* (Atr.) spacing trial indi-

cated that the model is a good first approximation at a spacing of 2 m  $\times$  2 m. Correlations were underestimated at closer spacings and overestimated at wider spacings. Prediction bias could be explained by spacing dependent changes in d. With time, d approached an upper limit asymptotically. Accurate predictions were possible once d was close to its limit. Examples from the literature illustrated the potential for predicting age-to-age correlations of tree height. An application of the model as a tool for tree breeders to settle questions about selection age is demonstrated.

Research Scientist, Canadian Forestry Service, Petawawa National Forestry Institute, Chalk River, Ontario K0J 1J0, Canada