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Nuclear and Extranuclear Genetic Effects in F_1 Reciprocal Hybrids between Pinus strobus and P. peuce

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(Received 7th March 1991)

Summary

Three *P. peuce* and one *P. strobus* parents were reciprocally crossed. The 6 families were artificially inoculated with *C. ribicola* then transplanted in the field. The results after 9 years of testing are, as follows: (1) Nuclear gene effects in hybrids were significant in height growth and highly significant in blister rust resistance; (2) Extranuclear gene effects were highly significant in blister rust resistance, diameter, basal area and volume growth rate; (3) There is evidence that the parent 62 of *P. strobus* is a carrier and transmitter of extranuclear genes involved in blister rust resistance and in some growth traits such as, diameter, height growth, basal area and volume growth rate; (4) The superiority in blister rust resistance, diameter, basal area and volume growth, due to extranuclear genes effects was about 218%, 34%, 80% and 88%, respectively.

Key words: Pinus strobus, P. peuce, Cronartium ribicola, reciprocal hybrids, nuclear genes, extranuclear genes, genetic correlations, phenotypic correlations.

Introduction

For many decades, the chromosolal theory of heredity has been the cornerstone of genetics. Consequently, concentration on the study of chromosome heredity led to the exclusion of investigations of the extranuclear complement of the cell. But, as far back as 1909, CORRENS and BAUER (cited from JINKS, 1964) found instances of non-Mendelian inheritance of some flowering plants. Although correctly interpreted as examples of extranuclear heredity, this and other exceptions aroused little interest. However, for some decades the cell was recognized as an integrated unit whose properties were more than a mere composite of its nuclear and extranuclear contents (JINKS, 1964).

Extranuclear or maternal effects were found both in plants and animals. The most common maternal effect in plants is caused by a variation in seed size. It is well known that seeds of different sizes may vary in speed of germination and in subsequent growth rate. Some authors (HOUGH, 1952; SCHELL, 1960; GREEN, 1971; BRAMLETT et al., 1983) have shown that fast germinating seeds yield seedlings that initially grow more vigorously than those from smaller seeds, but this initial difference may decrease or disappear after several months or after a few years.

Maternal effects were most often considered of little importance in tree improvement programmes, and BARNES and SCHWEPPENHAUSER (1978) had shown that these effects are indeed ngligible in most traits studied in *Pinus patula* SCHIEDE and DEPPE.

But, in some other cases, significant maternal or extranuclear effects were found in several traits and species, such as:

— volume production and diameter, branch length, number of branches, dry-weight and stem-index in *Eucalyptus grandis* (HILL) MAIDEN (WYK, 1976);

— diameter growth in hybrids resulting from crossing *Eucalyptus camaldulensis* DEHNH. as female with *E. tereticornis* SM. as male (VENKATESH and SHARMA, 1977);

— germination percentage and cotyledon number in black spruce (MORGENSTERN, 1974);

— cone length, number of seeds per cone and 100-seed weight in *Pinus cembra* L. (BLADA, in preparation);

— blister-rust resistance in F_1 hybrids resulting from cressing *Pinus strobus* L. as female with *P. peuce* GRISEB. as male (BLADA, 1986 and 1987);

— one thousand-seed weight in radiata pine, where the author (WILCOX, 1976) mentioned that the maternal effects of each parental line was the most important effect in that experiment.

Results concerning nuclear and extranuclear gene effects on resistance to *Cronartium ribicola* FISCH. ex RABENH. and some growth traits in reciprocal hybrids between *P. strobus* and *P. peuce* are reported in this paper.

Materials and Methods

Initial material and mating design

Three parental trees of *P. peuce* and one of *P. strobus* selected according to their flowering coincidence only, within mature plantations, of unknown origin, were used in a simple reciprocal mating design, as follows:

Group 1		Group 2	
♀	♂	♀	♂
62 x	13	13 x	62
62 x	15	15 x	62
62 x	18	18 x	62

where: 62 = *P. strobus* and 13,15,18 = *P. peuce*.

Prior to crossing, the parents were tested neither for blister-rust resistance nor for growth traits.

The seeds were stratified according to KRIEBEL's (1973) methodology and then, in the spring of 1981, they were sown in individual polyethylene pots (22 cm x 18 cm x 18 cm) in a mixture consisted of 70% spruce humus and 30% sand. The seedlings were grown in pots throughout the first seven years; because of the "pot stress" the realized height growth of the hybrids was about half the size of the control hybrids that were transplanted in the field at age 4.

Inoculation, experimental design and testing

The seedlings were artificially inoculated three times, between August 20 and 25 when they were two, three, and four years old. During each inoculation, the pots with the seedlings were placed in a polyethylene inoculation chamber using a randomized complete block design; each family was represented by a 10-seedling plot in each of the 4 blocks. Inoculum material consisted of heavily infected leaves of *Ribes nigrum* L. collected from a single plantation. Other details concerning inoculation and space of inoculation were similar to those described by BINGHAM (1972).

The seedlings were transplanted to the field when they were 7 years old, by using the same experimental design as in the inoculation chamber. So, the nursery test took place between 1981 and 1987 and the field test between 1988 and 1989.

Measurements

Blister-rust resistance was assessed during the autumn at age 5, 6, 7, 8, 9 (BR.5, BR.6, BR.7, BR.8, BR.9) by using a 1 to 10 scale, where: 1 = seedling dead or total susceptibility and 10 = no lesions or total resistance. This scale reflects the economical and biological impact as well as the incidence of the disease within the hybrid population because it takes into consideration both the number and severity of the stem and branch lesions or cankers. The other measured traits were height growth (Ht.9) and diameter at 1/2 t (D.9) at age 9; by using Ht. 9 and D.9, basal area (BA.9) and stem volume (V.9) were calculated, such as:

$$(BA.9) = (3.14)\, D^2/4 \qquad (1)$$

$$(V.9) = (BA.9)\,(Ht.9) \qquad (2)$$

Family means were the basic data for statistical analysis.

Statistical analysis

A fixed model was used; the formula for this model was:

$$x_{ce_xk} = m + g_c + g_{e_x} + s_{ce_x} + b_k + e_{ce_xk} \qquad (3)$$

where: m = the general mean; g_c = the general effect of the c-th nuclear action (c = 1 . . . C); g_{e_x} = the general

Table 1. — Model for analysis of variance.

Source of variation	DF	MS	E(MS)
Blocks	K-1	MS_K	
Hybrids	H-1	MS_H	
-Nuclear effects (C)	C-1	MS_C	$\sigma_e^2 + KEx\sigma_C^2$
-Extranuclear effects (Ex)	Ex-1	MS_{Ex}	$\sigma_e^2 + KC\sigma_{Ex}^2$
-Interactions (C x Ex)	(C-1)(Ex-1)	MS_{CEx}	$\sigma_e^2 + K\sigma_{CEx}^2$
Error	(H-1)(K-1)	MS_E	σ_e^2

Table 2. — Variance analysis of several traits of reciprocal hybrids between *P. strobus* and *P. peuce.*

Source of variation	DF	BR.5	BR.6	BR.7	BR.8	BR.9	Ht.9	D.9	BA.9	V.9
					Mean squares for...					
Total	23									
Blocks	3	7.1	3.2	3.0	0.6	0.8	0.3	0.004	0.017	0.0004
Hybrids	5	10.5^{+}	22.1^{+++}	22.9^{+++}	31.4^{+++}	31.8^{+++}	1.6^{+}	0.159^{++}	0.704^{+++}	0.0059^{++}
-Nuclear effects (C)	(2)	9.1	6.5^{+}	6.0	3.3^{+}	3.3^{+++}	2.3^{+}	0.010	0.055	0.0016
-Extranuclear effects (Ex)	(1)	33.8^{+++}	94.4^{+++}	99.6^{+++}	150.0^{+++}	151.5^{+++}	1.1	0.735^{+++}	3.080^{+++}	0.0236^{+++}
-Interactions (C x Ex)	(2)	0.3	1.5	1.4	0.2	0.8	1.2	0.020	0.165	0.0014
Error	15	2.8	1.6	1.9	0.5	0.3	0.5	0.023	0.047	0.0008

Table 3. — Adjusted means for several traits to illustrate family differences between reciprocal hybrids in terms of extranuclear effects.

Cross				Traits					
♀ x ♂	BR.5	BR.6	BR.7	BR.8	BR.9	Ht.9	D.9	BA.9	V.9
Group 1									
62 x 13	8.9	7.3	7.1	7.2	6.8	7.6	1.4	1.6	0.12
62 x 15	7.1	5.8	5.2	6.7	6.8	8.6	1.6	2.0	0.17
62 x 18	9.4	8.4	7.6	8.3	8.4	8.2	1.5	1.8	0.15
Mean 1	8.5	7.2	6.6	7.4	7.3	8.1	1.5	1.8	0.15
Group 2									
13 x 62	6.3	3.0	2.6	2.3	2.2	7.7	1.2	1.1	0.09
15 x 62	5.1	2.9	2.1	2.0	2.0	8.5	1.1	1.0	0.09
18 x 62	6.9	3.9	3.0	2.9	2.6	6.9	1.1	1.0	0.07
Mean 2	6.1	3.3	2.5	2.4	2.3	7.7	1.1	1.0	0.08
Group 1- Group 2	2.4	3.9	4.1	5.0	5.0	0.4	0.4	0.8	0.07

effect of the e_x-th extranuclear action ($e_x = 1 \ldots Ex$); s_{ce_x} = the specific effect of the interaction of the c-th nuclear action and e_x-th extranuclear action; b_k = the effect of the k-th block; e_{ce_xk} = the error; The analysis of variance with the expectation of mean squares are given in *table 1.*

Genetic and phenotypic correlations among traits were calculated by the formula:

$$r_{AB} = \frac{Cov_{AB}}{\sqrt{\sigma^2_A \cdot \sigma^2_B}} \quad (4); \text{ and } Cov_{AB} = 1/2\,(\sigma^2_{AB} - \sigma^2_A - \sigma^2_B) \quad (5)$$

where: Cov_{AB} = covariance of the traits A and B; σ^2_{AB} = variance of the cross-product of the trait A and B; σ^2_A and σ^2_B = variance of the traits A and B (Wilcox, 1975).

Results

There were statistical differences ($p < 0.05$; $p < 0.01$; $p < 0.001$) among hybrids in all tested traits (*Table 2*, row 3). Such genetic differences indicate the possibility for selection within hybrid population.

The nuclear gene effects in hybrids at age 9 were significant ($p < 0.05$) in height growth and highly significant ($p < 0.001$) in blister-rust resistance (*Table 2*, row 4).

The extranuclear effects were highly significant ($p < 0.001$) in blister-rust resistance throughout the testing period, that is from age 5 to 9. Also, highly significant differences were present in diameter, basal area and volume growth rate, but not in height growth (*Table 2*, row 5). A comparative analysis of the two groups of reciprocal hybrids listed in *table 3*, revealed that each hybrid family from Group 1 exhibited higher performances in all traits, except height growth, as compared to the homologous hybrid family from Group 2. This result provided evidence of extranuclear inheritance. Therefore, the female tree 62 of *P. strobus* seems to be an outstanding tree within the basal population; perhaps, it is a carrier

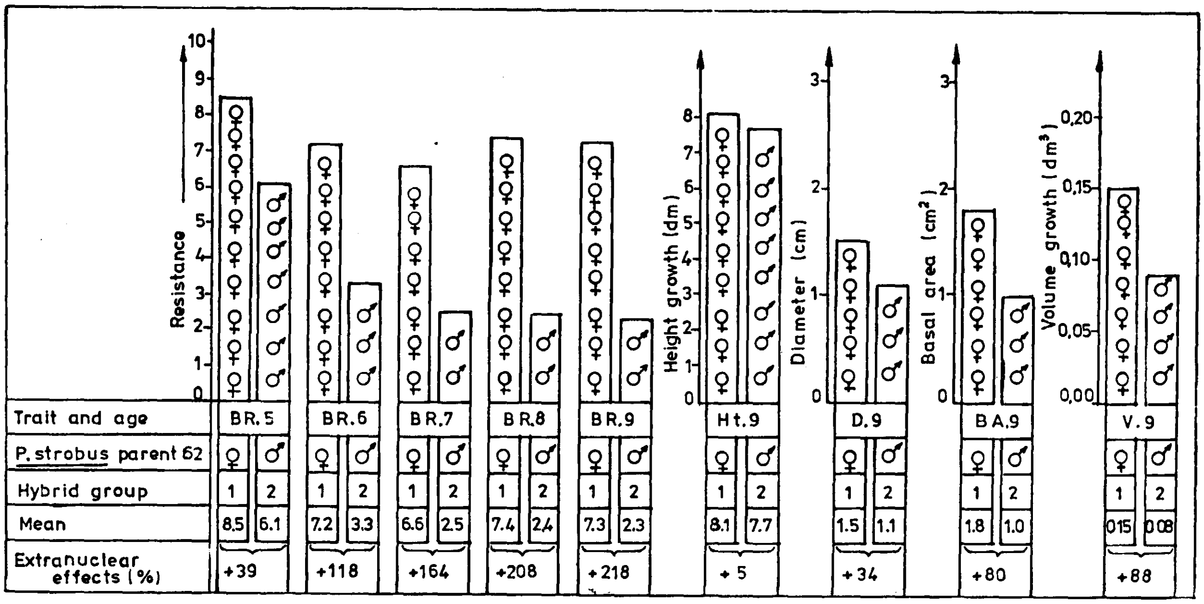

Figure 1. — Phenotypic expression of extranuclear genes on C. *ribicola* resistance and on some growth traits in reciprocal hybrids between *P. strobus* and *P. peuce*.

of extranuclear resistance genes responsible for the high resistance of the hybrids from group 1. This result suggests that within *P. strobus* species some valuable female parents could be selected; if hybridization to *P. peuce* follows, it may lead to an additional genetic gain due to extranuclear genes.

Quantitatively, the phenotypic effects of the extranuclear genes in some traits were remarkable. Thus, because of these effects, the hybrids from Group 1 (*Table* 3) exceeded those of Group 2 by about 34%, 80% and 88% in diameter, basal area and volume growth, respectively; their superiority in blister rust resistance, at age 5, 6, 7, 8 and 9 was 39%, 118%, 164%, 208%, and 218%, respectively (*Fig. 1*). These data showed that the phenotypic expression of the extranuclear resistance genes grew stronger and stronger with age.

The interaction, nuclear x extranuclear genetic effects, in the hybrid population was statistically insignificant for all traits (*Table* 2, row 6).

Correlations (Table 4).

Highly significant ($p < 0.001$) age-to-age genetic correlation in blister rust resistance was found throughout the testing period; this strong correlation suggests that the resistance could be persistent in advanced ages.

Also were found genetically significant correlations between:

— blister rust resistance and some growth traits, such as diameter, basal area and volume;

— diameter and other growth traits, such as basal area and volume.

— basal area and volume;

Other details concerning genetic and phenotypic correlations are given in *table 4*.

Discussion

The detection of plasmagene effects can be made by means of reciprocal crosses. So, where strains differ only by nuclear genes, the progeny of reciprocal crosses be-

Table 4. — Genetic correlations (above diagonal line) and phenotypic correlations (below diagonal line) for several traits of the hybrids (DF = 4).

Traits	BR.5	BR.6	BR.7	BR.8	BR.9	Ht.9	D.9	BA.9	V.9
BR.5		0.997^{+++}	0.995^{+++}	0.998^{+++}	0.994^{+++}	-0.083	0.775	0.753	0.631
BR.6	0.950^{++}		0.996^{+++}	0.990^{+++}	0.996^{+++}	0.265	0.905^{+}	0.878^{+}	0.800
BR.7	0.955^{++}	0.993^{+++}		0.990^{+++}	0.989^{+++}	0.249	0.927^{++}	0.898^{+}	0.814^{+}
BR.8	0.897^{+}	0.981^{+++}	0.978^{+++}		0.998^{+++}	0.322	0.985^{+++}	0.959^{++}	0.886^{+}
BR.9	0.875^{+}	0.973^{++}	0.964^{++}	0.996^{+++}		0.400	0.996^{+++}	0.984^{+++}	0.922^{++}
Ht.9	-0.120	0.163	0.142	0.259	0.320		0.496	0.494	0.611
D.9	0.665	0.823^{+}	0.820^{+}	0.916^{+}	0.929^{++}	0.485		0.994^{+++}	0.966^{++}
BA.9	0.647	0.802	0.797	0.900^{+}	0.916^{+}	0.488	0.998^{+++}		0.975^{+++}
V.9	0.523	0.713	0.704	0.823^{+}	0.853^{+}	0.632	0.969^{+++}	0.971^{++}	

tween them are generally identical in phenotype. Consequently, when some differences occur, these differences could be attributed to plasmagenes though some irregular exceptions usually result from preferential segregation and sex linkage (MATHER, 1958). The question mark is: how can one recognise the true extranuclear heredity? According to JINKS (1964), persistent differences between reciprocal crosses are diagnostic of exranuclear heredity.

In this experiment, reciprocal hybrids between *P. strobus* and *P. Peuce* demonstrated a highly significant extranuclear effect in blister rust resistance and some growth traits. But the question is how long will this effect persist? The F_1 hybrids showed that extranuclear effects were very strong throughout the testing period. However, the question as to whether or not this extranuclear effect will persist in the F_2 generation remains to be answered.

Cell investigations revealed that the main carriers of extranuclear genes are: mitochondria, plastids, kinetosomes and centrioles (JINKS, 1964). Research in F_1 and the following generations of maize, mitochondria and plastids (chloroplasts) and some nucleo-citoplasmatic interactions proved to be both heritable and involved in the heterosis process (HOOKER, 1972; CARLSON, 1982; BERVILLE and CHARBONIER, 1982).

Recent investigations using molecular markers have demonstrated that in conifers, mitochondria are largely transmitted maternally (NEALE and SEDEROFF, 1987; OWENS and MORRIS, 1990), while chloroplasts are transmitted paternally (NEALE et al., 1986; SZMIDT et al., 1987; NEALE and SEDEROFF, 1987; STINE and KEATHLEY, 1987; WAGNER et al., 1987; WAGNER et al., 1989). Therefore, in our case there are two possible hypotheses: (a) either the mitochondria of the parent 62 contains one or more genes for blister rust resistance or (b) the cholorplasts of the same parent contain one or more genes for blister rust susceptibility. The F_1 reciprocal hybrids between *P. strobus* and *P. peuce* are already producing flowers, so that backcrosses in the near future will or will not confirm the two hypotheses.

Concluding Remarks

Experimental material supported evidence that extranuclear genes controlling blister rust resistance, diameter, basal area and volume growth rate could be found within the *P. strobus* species.

Testing F_1 reciprocal hybrids as well as the hybrids from forthcoming backcrosses have to be continued; if the extranuclear actions of the genes persist, a breeding strategy for blister rust resistance and volume growth rate improvement could be advantageously adopted.

In order to achieve an extra-genetic gain, according to the present results, the following approaches would have to be followed:

(a) To establish grafted clonal seed orchards by using the clone 62 of *P. strobus* as female parent and about 100 clones of *P. peuce* as male parents; the seed, with a broad genetic diversity, will be used in operational planting programmes;

(b) To perform specific crosses between the female tree 62 of *P. strobus* and many *P. peuce* male trees by using a mix-pollen.

In some cases, as this one, the phenotypic nuclear genes effects are less important than extranuclear ones.

Acknowledgements

My thanks are due to Dr. I. CABULEA from the Agricultural Research Station (Turda-Romania) for the guidance in statistical analysis. Also, I gratefully acknowledge the most useful comments of Prof. Dr. J. P. VAN BUIJTENEN from Texas University in reviewing the article and making useful suggestions.

Literature

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