DIALLEL CROSS IN *Pinus cembra:* II THE NURSERY TEST AT AGE 6

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Abstract. A 10 x 10 full diallel cross was made in a native population of *Pinus cembra* L. from high elevation, to provide information about genetic variation and inheritance of important breeding traits, for the species. In October 1991, seeds were sown in individual polyethylene pots, in spruce humus. The families, including selfed and open pollinated parents, were arranged in a randomized complete block design with 4 replication and 12 seedlings per plot. Six traits were measured, prior to field planting, when the progenies were 6 years old: total height (H.6), height increment in the 6th year (h.6), diameter at root collar (DRC), number of buds around the leader bud (NBAL), total number of branches (TNB) and lamma shoots formation (LS). In addition, the weights of 100 seeds (100 SW) of each family were measured prior to sowing and cotyledon number (CN) was counted after seed germination. Computer analysis of balanced modified full diallel using Schaffer and Usanis' DIALL program produced the results presented below. The most important result was that significant ($p < 0.05$) and highly significant ($p < 0.01$; $p < 0.001$) differences occurred in the all 8 traits for g.c.a., s.c.a., maternal and reciprocal effects. This suggest that the traits were controlled by nuclear (additive and non-additive) and extra nuclear genes, and by nuclear x extra nuclear gene interactions. Additive and non-additive genetic variances accounted for 25% and 27% for H.6 and 25% and 17% for h.6 of the phenotypic variance, respectively, indicating that both variances were important for height growth in this population. There were found parents with significant g.c.a. effects for growth and other traits. Narrow - sense heritability estimates varied between 0.081 to 0.477 for CN and LS, respectively, while the H.6 accounted for 0.292. By selecting the best 10 to 40 families, a genetic gain in H.6, between 6.0% and 3.1% could be achieved. In conclusion, the improvement of the growth by using both additive and non - additive gene effects should be possible.

Key words: *Pinus cembra,* diallel cross, additive variance, combining ability, genetic correlation, heritability.

I NTRODUCTION

The natural distribution area of the stone pine *(Pinus cembra* L.) is restricted to the high elevations of the Alps and Carpathians (Holzer, 1963; Critchfield and Little, 1963). In the Alps, the species ranges between 1200 and 2500 m elevation (Contini and Lavarelo, 1982) but the main zone is between 1500 and 2000 m (Holzer, 1975). In Romania, stone pine ranges between 1350 and 1880 m elevation in the northern Carpathians (Gubesh, 1971) and between 1350 and 1986 m in the southern Carpathians (Beldie, 1941; Tataranu and Costea, 1952; Oarcea, 1966).

The stone pine is important for : (1) reforestation of the subalpine zone to raise the timber line, to its initial limit, where it plays a leading part in watersheds, for stabilizing avalanche areas

and for reducing the effects of the flash floods (Holzer, 1972a, 1975); (2) spruce-larch-cembra mixed stands creation at high elevation in order to increase their windbreak resistance (Blada, 1996); (3) its dense - brown - reddish wood useful for handicrafts (Contini and Lavarelo, 1982); (4) its high resistance to blister-rust caused by *Cronartium ribicola* Fisch. ex Rabenh. (Bingham,1972; Holzer,1975; Hoff et al., 1980; Blada, 1982; 1987; 1990a; 1994); (5) landscaping purposes due to its conic - oval shape when grown as single tree (Blada, 1996);

Insofar, as can be determined, not too many breeding work with stone pine have been reported. Until now, the main experiments have concentrated on cone and seed studies (Rohmeder and Rohmeder,1955, Nather 1958, Holzer 1972b; Blada and Popescu, 1992), provenances testing (Blada,1997), half-sib families testing (Holzer, 1975; Blada, 1996), full-sib families testing (Blada, 1995) and interspecific hybridization (Blada, 1987; 1994).

A genetic improvement program with stone pine have been started in Romania (Blada, 1990 b, 1995) that has the following objectives : (1) phenotypic selection of parents in natural populations; (2) testing provenance and half-sib families; (3) intra and interspecific crosses; (4) full-sib families testing, estimates of genetic parameters and selection of the best combiners and families; (5) seed orchard establishment with the best combiners for both mass seed production and base population for advanced - generation breeding. Four papers, as part of this program, have been published until now (Blada and Popescu, 1992; Blada, 1994, 1995, 1997), and one is presented now. The objective of this paper was to provide information about genetic variation and inheritance of important breeding traits useful in the breeding of the stone pine.

MATERIALS AND METHODS

Initial material and mating design

The 10 parents trees used in the crossing scheme were randomly chosen from Gemenele old natural population located in the Retezat Mountains from Southern Carpathians, at about 1800 m elevation. Actually, reproductive fertility was taken into consideration in parent selection in order to obtain the necessary number of flowers for pollination. The flowers were isolated in paper bags prior to local pollen dissemination. Fresh pollen was used for all crossings. A full - diallel mating design according to Griffing's (1956) Method 1 was used, during July 1989.

Progeny test and experimental design

One hundred seedlots from controlled crossing were collected in October 1990. Before sowing, the filled seeds were separated from empty seeds by immersing each seedlot in 90° alcohol. This procedure was good because only the full seeds were sown; but, from statistical standpoint, it may not be correct because it produced a decrease of environmental error variance and an increase of other components of phenotypic variance, such as SCA and reciprocal variances.

Seeds was sown in November 1989 in individual polyethylene pots (22cm x 18cm) in a potting spruce humus. Based on results of previous local experiments (Blada, 1996), by sowing the stone pine seed during the autumn, the seed develop its embryo and germinate in the next spring eliminating a complicated, costly and risky 180 days stratification period as Kriebel (1973) recommended. But, if sowing was done during autumn, control measures for seed predation by mice

in the nursery beds was compulsory.

After sowing, the seeded pots were placed in nursery beds and arranged in a randomized complete block design. Each of 100 families was represented by a 12 seedling plot in each of 4 blocks. The seedlings were kept in pots throughout the 6 years testing period.

Measurements

Six traits were measured, prior to field planting, when the progenies were 6 years old. In addition, the weights of 100 seeds of each family were measured prior to sowing and cotyledon lumber was counted after seed germination (Table 1). Lamma shoots was measured using 5 indices: H no lamina shoots; 2 = only a small number of new needles present; 3 = slight flushing on leader and secondary branches; 4 = leader and / or branches with 1 - 2 cm growth; 5 = leader and / or Branches with more than 2 cm of growth. The other traits listed in table 1, do not require additional ;explanation. The plot means comprised the basic data for statistical analysis.

Statistical analysis

Although initially a full diallel mating design was used, the analysis was performed Lccording to the modified full diallel mating design known as Griffing's (1956) Method 3, where he parents (selfed) were excluded; such analysis leads to unbiased estimates. However, the parents vere included in the material grown in the experiment so that comparisons of hybrids with their parents could be made in other type of analyses.

The mathematical model for analysis was a combination of Hayman (1954a) and Griffing's 1956) models, such as:

$$x_{kij} = u + b_k + g_i + g_j + s_{ij} + m_i - m_j + r_{ij} + e_{kij} \qquad (1)$$

where: x_{kij} = the mean performance in k-th block of the i-th parent mated to the j-th parent; u = the general mean; b_k = the effect of the k-th block; g_i and g_j=the general combining ability effects for the i-th and j-th parents, respectively; s_{ij} = the specific combining ability effect for the cross between the i-th and j-th parents so that $s_{ij} = s_{ji}$; m_i and m_j = the maternal effects of the i-th and j-th parents; r_{ij} = the difference caused by the direction of the cross between i-th and j-th parents, such that $r_{ij} = -r_{ji}$; e_{kij} = the random error.

Plot means of the eight measured traits were analysed using the least - squares method by means of the computer DIALL program prepared by Schaffer and Usanis (1969). The analysis of balanced modified full diallel according to Griffing's (1956) Method 3, was based upon the random model assuming that the parents were random samples from a random mating population. This assumption make possible estimates of the additive and non-additive genetic variance of the parent population.

The model of analysis of variance, expected mean squares and formulas for estimating the variance components were listed in table 2.

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

$$SE(\sigma^2_j) = \sqrt{\sum_i \frac{2a_i^2 (MS_i)^2}{df_i + 2}} \qquad (2)$$

where: a_i are the coefficients of the inverse of the matrix of expected mean squares used to estimate the j-th variance component.

The component of variance σ^2_{GCA} was used to estimate the variance in general combining ability among all of the parents in this experiment and is used as an estimator of $1 / 4\ \sigma^2_A$. It is assumed that all epistatic components of genetic variance were insignificantly small. The component σ^2_{SCA} , the estimated variance in specific combining ability, is an estimator of $1/4\ \sigma^2_D$.(with the same assumptions). Therefore, an estimator of the additive genetic variance is $4\sigma^2_{GCA}$ and an estimate of the dominance genetic variance is $4\sigma^2_{SCA}$.

The narrow-sense heritability estimates at half-sib family level (h^2) was calculated using the formulas given by Kriebel, et al. (1972), adapted to this case, as follows:

$$h^2 = \frac{\sigma^2_{GCA}}{\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{Mat} + \sigma^2_{Rec} + \sigma^2_p/k + \sigma^2_w/kn} \qquad (3)$$

where: σ^2_p = plot error = $\sigma^2_e - \sigma^2_w/n$; σ^2_w = within plot error variance ; n = number of seedlings per plot; k = number of replications; the other symbols are as defined in table 2.

The general combining ability (g_i) effects were calculated by the computer according to the DIALL program (Schaffer and Usanis, 1969).

Genetic correlations (r_g) were directly calculated by the computer, according to the following formula (Falconer,1960):

$$r_g = \frac{cov_{GCA(xy)}}{\sqrt{\sigma^2_{GCA(x)} \sigma^2_{GCA(y)}}} \qquad (4)$$

where: $cov_{GCA(xy)}$ = additive covariance component between the traits x and y; $\sigma^2_{GCA(X)}$ and $\sigma^2_{GCA(Y)}$ = the variances due to GCA for traits x and y, respectively.

The genetic gain (ΔG) was calculated by Falconer's (1960) formula :

$$\Delta G = i\, h^2\, \sigma_P \qquad (5)$$

where i = intensity of selection taken from Becker (1984) and σ_P = phenotypic standard deviation.

RESULTS AND DISCUSSIONS

Genetic variation

The most prominent feature of this experiment was that significant ($p < 0.05$) and highly significant ($p < 0.01$; $p < 0.001$) differences occurred in all traits for g.c.a. , s.c.a. and reciprocal effects. Maternal effects were statistically significant ($p < 0.05$) for H.6, DRC and TNB and highly significant ($p < 0.01$; $p < 0.001$) for 100 SW and CN (Table 3). This suggest that all traits, including growth ones, were controlled by nuclear (additive and non-additive) genes and by nuclear x extra nuclear gene interactions, whilst the extra nuclear genes were involved only in five traits.

Table 4 presents the best and the poorest six full-sib families indicating large genetic variation among family means for several traits. Thus, the H.6 mean of the poorest 6 families averaged 19.7 cm whilst the best 6 families averaged 28.2 cm, i.e. 43% taller. The differences between the two groups were even larger for some other traits, such as : 96% for DRC, 46% for TNB and 94% for LS (see D_1 in table 4) In the same context, the mean top 6 families surpassed the test mean in 100 SW, CN, H.6, h.6, DRC, NBAL, TNB and LS by 22%, 5%, 18%,18%, 77%, 17%, 19% and 37%, respectively (see D_2 in table 4).

Low to high genetic variation coefficients were found among full-sib families (Table 7). The value of this coefficients varied between 3% for CN and 19% for LS, while the H.6 one accounted for 12%.

Large genetic variation was found not only among cross-pollinated families but among self-pollinated ones, as well. Two-way variance analysis of the 10 selfed parent families showed that significant ($p < 0.05$) and highly significant ($p < 0.01$; $p < 0.001$) differences were found among them for all tested traits (Table 5). This result demonstrated that the variation within S_1 population in still very high.

Surprisingly, higher genetic coefficients of variation (GCV) were calculated within self- than within cross-pollinated population, i.e., the GCV values of the self- and cross-pollinated families ranged between 10% and 37% (Table 5) and between 3% and 19% (Table 7) respectively. Self-pollinated families (SP) have strongly contrasted with those from cross-pollinated (CP) ones, in 7 out 8 traits (Table 6). A comparison of overall means indicated that, CP trees performed 52% and 39% better in H.6 and DRC, respectively, than SP trees. However, CP mean was almost equal in CN and lower in LS than SP mean.

In conclusion, progeny testing has demonstrated a high within population genetic variation that could be exploit in a breeding program.

Variance components

Variance component estimates, standard errors and dominance ratios were listed in table 7. The diallel analysis indicated that GCA and SCA variance components were important sources of variation for all eight tested traits. Additive and non-additive genetic variances accounted for 25% and 27% for H.6, 25% and 17% for h.6 and 14% and 22% for DRC, respectively, of the phenotypic variance. Therefore, the magnitude of GCA variance relative to SCA variance for these traits suggested that additive gene effects may be almost as important as non-additive ones, in this young population indicating that progress under selection is possible to a considerable degree.

Dominance variances exceeded additive ones in five out of eight traits, i.e. in 100 SW, CN, H.6, DRC and TNB. For example, the ratios of non-additive to additive variances were 2.1 : 1.0 for 100 SW, 1.1 : 1.0 for H.6 and 1.6 : 1.0 for DRC , indicating a clear over dominance in these traits, while a partial dominance was noticed in h.6, NBAL and LS with the following ratios: 0.7 : 1.0 and 0.9 : 1.0, and 0.4 1.0, respectively.

The maternal component of variances significantly contributed to the phenotypic variances. The largest maternal component of this study was 10% of the phenotypic variance and it was associated with 100 SW, while the smallest one of 1% was associated with both NBAL and LS. The maternal variance of the H.6 and DRC accounted for 4% and 5%, respectively, of phenotypic variance. Thus, with one exception, the experimental material of six years old, supported evidence that maternal effects were moderately large.

The reciprocal variance components accounted for between 6% for LS and 31% for 100 SW of the phenotypic variance. High proportion of reciprocal variance was calculated in H.6 and DRC, i.e. 25% and 21%, respectively. Consequently, the contribution of reciprocal variance was large in growth traits, accounting for about the same percentage of the phenotypic variance as did GCA and SCA variances. Therefore, reciprocal, as well as maternal variances could be important in a breeding program for stone pine.

It must be stressed that GCA, SCA, maternal and reciprocal variance component estimates were associated with small standard errors at all but one cases, indicating their reliability.

The above mentioned results offered support for adopting full diallel mating design (though it is very costly) for estimation not only GCA and SCA but maternal and reciprocal variance components, as well.

It was evident that all variances were well represented in almost all traits, suggesting that a selective breeding program utilizing not only nuclear but maternal gene effects, as well, could be adopted.

General combining ability

General combining ability effects calculated for each parent tree were listed in table 8. Both positive and negative g.c.a. effects which significantly differed from the test mean were found for 7 out of 8 traits. Parent X had the largest positive g.c.a. effects for 100 SW, H.6, h.6 and DRC, whereas parent Z was the second highest for both H.6 and h.6. On the other hand, parents 3 and 45 had the largest negative values for H.6 and h.6. Consequently, parents X and Z should be selected for their high positive g.c.a. effects and breeding value for growth traits whereas parents 3 and 45 and some others have to be rejected because of their high negative g.c.a. effects for the same growth traits.

In conclusion, if two out of ten randomly selected parents exhibited significant positive g.c.a. effects for growth, then one may assume that 20% of trees within natural population, (where the parents have been growing), could be selected as good combiners.

Correlations

Both phenotypic and genetic correlations between traits were calculated (Table 9). There were found significant ($p < 0.05$) and highly significant ($p < 0.01$; $p < 0.001$) positive phenotypic correlations between: 100 SW and H.6, 100 SW and h.6; 100 SW and DRC; CN and DRC; H.6 and h.6, H.6 and DRC, H.6 and NBAL, H.6 and TNB; h.6 and DRC, h.6 and NBAL, h.6 and TNB; DRC and NBAL, DRC and TNB.

Substantial positive genetic correlations were found between: 100 SW and DRC; CN and DRC; H.6 and h.6; H.6 and DRC; h.6 and DRC.

According to indirect selection principle, the strong positive genetic correlations between H.6, h.6 and DRC imply genetic gain in any of these traits even if selection was practiced on only one. On the other hand, due to some positive correlations one could expect some negative economical results. For example, total number of branches, will increase with H.6, h.6, DRC and NBAL, and for this reason a conscious effort should be made to find fast growing trees with a small number of branches.

The previous results needed to be confirmed from long-term juvenile-adult correlations and correlations with additional characters of economic and ecologic value.

Heritability and genetic gain

Estimates narrow-sense heritability on a plot mean basis were fairly consistent for five traits, such as: 0.292 for H.6, 0.354 for h.6, 0.293 for NBAL, 0.267 for TNB and 0.477 for LS. However, the heritabilities were low for the other three traits (Table 7).

Table 10 showed that the highest genetic gain could be achieved in LS. But this genetic gain is doubtful because lamma shoots formation in species growing in temperate or at higher latitudes could frequently be positive correlated with frost susceptibility. By selecting the best 10, 20, 30 or 40 out of 90 full-sib tested families, a genetic gain in H.6 and DRC of 6%. 4.7%, 3.9%, 3.1% and 2.7%, 2.1%, 1.7%, 1.4%, respectively, could be expected. Such a gain could be economically important if the improved planting material will be used on a large area. These gains at age 6 may be good predictors of later results. However, later age correlations, wich are not available, will be more reliable for final gain estimation.

It should be noted that the parental selections were random with regard to vigor and all were selected in a single native population. In this situation, some parents were probably related and there was, therefore, a closer than half-sib average relationship among the progenies. For this reason, heritabilities and genetic gains probably were underestimated.

The results indicated that selection on the basis of family comparisons could be effective and might be economically acceptable if the loss in selection differential and testing time could be made small.

CONCLUSIONS

The results illustrated the existence of sufficient additive as well as non-additive genetic variance within the breeding population for growth traits to utilize in an improvement program.

Maternal and reciprocal variance could also be taken into consideration for stone pine improvement.

Parents with a good general and specific combining ability for growth traits to be used in a breeding program could be found within *P. cembra* natural population where the parents have been growing. Narrow - sense heritabilities of the traits were low to fairly large.

The existence of substantial positive genetic correlations between several traits, including growth ones, suggested that indirect selection could be applied.

A genetic gain in growth, and other traits, could be achieved by selecting and planting the best families and individuals from tested population.

This test supports the adoption of a full diallel mating design in *P. cembra* even if it requires more effort than a half diallel one; by this way is possible to detect the maternal and reciprocal effects.

An effort to improve the growth traits by exploiting g.c.a., s.c.a. and perhaps maternal effects seems to be rewarding.

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Figure 1 . Full diallel mating design according to GRIFFING's (1956) Method 1

Parents	2	**3**	**45**	**50**	**205**	**206**	**209**	**X**	Y	Z
2	X	x	x	x	x	x	x	x	x	x
3	x	X	x	x	x	x	x	x	x	x
45	x	x	X	x	x	x	x	x	x	x
50	x	x	x	X	x	x	x	x	x	x
205	x	x	x	x	X	x	x	x	x	x
206	x	x	x	x	x	X	x	x	x	x
209	x	x	x	x	x	x	X	x	x	x
X	x	x	x	x	x	x	x	X	x	x
Y	x	x	x	x	x	x	x	x	X	x
Z	x	x	x	x	x	x	x	x	x	X

Table 1. Measured traits

Traits	**Units**	**Symbol**
100 seed weight	g	100 SW
Cotyledon number	No	CN
Total height at age 6	cm	H.6
Height increment in the 6-th year	cm	h.6
Diameter at root collar	mm	DRC
Number of buds around the leader bud	No	NBAL
Total number of branches	No	TNB
Lamma shoots	Index 1-5	LS

Table 2. Analysis of variance of modified full diallel, random effects model, in a randomized block layout in one environment.

Source	Df	MS	E (MS)	F-test
Replications (R)	k-1	MS_R	$\sigma^2_e + p\,(p-1)\,\sigma^2_{Rep}$	
GCA	p-1	MS_{GCA}	$\sigma^2_e + 2k\,\sigma^2_{SCA} + 2k\,(p-2)\,\sigma^2_{GCA}$	
SCA	p(p-3)/2	MS_{SCA}	$\sigma^2_e + 2k\,\sigma^2_{SCA}$	
Maternal (Mat)	p-1	MS_{Mat}	$\sigma^2_e = 2k\,\sigma^2_{Rec} + 2kp\sigma^2_{Mat}$	
Reciprocal (Rec)	(p-1)(p-2)	MS_{Rec}	$\sigma^2_e + 2k\,\sigma^2_{Rec}$	
Error	$(k-1)(p^2-p-1)$	MS_E	σ^2_e	
Total	kp(p-1)			

$\sigma^2_e = MS_E$; $\sigma^2_{Rec} = (MS_{Rec} - MS_E)/2k$; $\sigma^2_{Mat} = (MS_{Mat} - MS_{Rec})/2kp$; $\sigma^2_{SCA} = (MS_{SCA} - MS_E)/2k$;
$\sigma^2_{GCA} = (MS_{GCA} - MS_{SCA})/2k(p-2)$; $MS_{Rep} = (MS_{Rep} - MS_E)/p(p-1)$

Table 3. Analysis of variance of modified full diallel of *P. cembra* tested traits

Source of variation	Df	Mean squares for the traits...							
		100 SW	CN	H.6	h.6	DRC	NBAL	TNB	LS
Repl.	3	2.963	0.241	5.407	2.880	1.865	0.459	3.542	0.434
GCA	9	133.113●●●	1.391●	182.958●●●	43.882●●●	12.155●●●	4.75●●●	8.761●●●	8.886●●●
SCA	35	27.715●●●	0.479●	23.779●●●	4.407●●●	2.425●●●	0.609●●●	1.321●●●	0.641●●●
Mat	9	93.261●●●	2.250●●	49.702●	8.487	6.572●	0.723	3.018●	0.911
Rec	36	23.026●●●	0.661●●●	21.540●●●	4.187●●●	2.298●●●	0.627●●●	1.039●●●	0.446●●●
Plot error	266	0.410	0.267	1.885	0.996	0.421	0.140	0.349	0.247

Table 4. Means of the 6 best (upper part) and the 6 poorest (lower part) full-sib families

Rank	Traits							
	100 SW	CN	H.6	h.6	DRC	NBAL	TNB	LS
1	24.7	10.8	29.7	12.9	12.6	4.4	5.4	3.5
2	24.3	10.6	28.6	12.8	11.8	4.4	5.2	3.4
3	23.3	10.4	28.2	12.3	11.8	4.3	5.1	3.4
4	21.7	10.4	27.6	12.2	11.6	4.2	5.0	3.4
5	21.5	10.3	27.5	12.2	11.5	4.1	5.0	3.1
6	20.9	10.3	27.4	12.0	11.5	4.1	5.0	3.0
Sub-mean	22.7	10.5	28.2	12.4	18.8	4.2	5.1	3.3
40	15.7	9.7	21.1	9.1	9.8	3.1	3.8	1.8
41	15.5	9.6	20.5	9.0	9.7	3.1	3.7	1.8
42	15.4	9.6	19.9	9.7	9.7	3.1	3.6	1.7
43	15.3	9.5	19.6	8.3	9.6	2.9	3.5	1.7
44	13.7	9.5	18.8	8.0	9.6	2.8	3.3	1.5
45	13.3	9.3	18.6	7.7	9.3	2.8	3.0	1.4
Sub-mean	14.8	9.5	19.7	8.5	9.6	3.0	3.5	1.7
Test mean	18.6	10.0	23.9	10.5	10.6	3.6	4.3	2.4
D1(%)	53	11	43	46	96	40	46	94
D2(%)	22	5	18	18	77	17	19	37

D_1 and D_2 = differences (%) between the poorest 6 and the best 6 families and between test mean and the best 6 families, respectively

Table 5. Two-way ANOVA of self-pollinated families, variance components (σ^2), standard errors (SE) and genetic coefficients of variation (GCV)

Source of variation	DF	Mean squares for the traits...							
		100 SW	CN	H.6	h.6	DRC	NBAL	TNB	LS
Replications(R)	3	1.29	0.38	4.17	0.34	1.17	0.11	1.02	0.29
Selfed-families	9	25.09●●●	2.08●	20.26●●	6.84●●●	3.18●	0.66●●●	4.18●●●	3.64●●●
Error	27	0.62	0.75	5.62	1.22	1.02	0.13	0.13	0.32
Components									
$\sigma^2_F \pm$ **SE**		6.12 ± 2.68	0.33 ± 0.23	3.66 ± 2.19	1.40 ± 0.73	0.54 ± 0.35	0.13 ± 0.07	0.99 ± 0.45	0.83 ± 0.39
$\sigma^2_e \pm$ **SE**		0.62 ± 0.16	0.75 ±0.20	5.62 ± 1.48	1.22 ± 0.32	1.02 ± 0.27	0.13 ± 0.03	0.23 ± 0.06	0.32 ± 0.08
σ^2_p		6.74	1.08	9.28	2.62	0.26	0.26	1.22	1.15
GCV (%)		14	10	19	24	16	27	37	33

Table 6. Performance comparisons between control-cross-pollinated (CP) and control-self-pollinated (SP) progenies from the same parents

Parents	100 SW g		CN No.		H.6 cm		h.6 cm		DRC mm		NRAL No.		TNB No.		LS Index	
	CP	SP	CP	SP	CP	SP	CP	SP	CP	SP	CP	SP	CP	SP	CP	SP
2	19	17.0	9.8	9.7	23.7	15.1	10.5	6.4	10.5	7.1	3.8	2.3	4.4	2.6	2.4	3.5
3	18	16.4	9.9	9.8	22.0	13.6	9.8	5.7	10.6	6.6	3.5	1.4	3.9	1.5	2.2	2.7
45	19	17.8	10.1	9.9	21.3	12.8	9.1	4.7	10.3	7.6	3.4	2.0	4.3	2.9	2.4	3.4
50	20	22.2	9.8	8.2	23.9	15.6	10.7	6.2	10.5	7.0	3.1	1.3	4.2	3.0	2.8	3.9
205	19	20.3	10.2	11.1	24.2	14.4	10.2	5.0	11.1	8.3	3.8	2.2	4.4	3.6	2.8	4.4
206	18	14.8	10.0	9.9	24.9	15.5	11.2	6.8	10.5	7.2	3.6	1.6	4.0	2.5	2.2	2.7
209	17	16.9	9.9	9.8	23.4	18.0	10.1	7.1	10.4	8.6	3.7	2.6	4.9	5.2	2.7	3.7
x	21	17.3	10.1	10.1	26.2	20.3	11.7	9.2	11.5	9.4	3.5	2.2	4.8	3.9	2.2	2.0
y	20	21.4	9.9	10.1	23.8	17.2	10.5	7.6	10.4	7.7	3.6	1.9	4.0	2.3	1.8	1.5
z	18	15.7	9.9	10.4	25.7	14.6	11.0	6.9	10.5	6.8	3.9	1.9	4.1	2.8	2.7	4.2
Mean	19	18.0	10.0	9.9	23.9	15.7	10.5	6.6	10.6	7.6	3.6	1.9	4.3	3.0	2.4	3.2
SUP (%)	5		1		52		59		39		89		43		-25	

SUP = superiority above the self-pollinated progenies

Table 7. Variance components (precents in brackets), standard errors, dominance ratios, genetic variation coefficients, narrow-sense heritabilities on both family and individual seedling basis

Components	100 SW	CN	H.6	h.6	DRC	NBAL	TNB	LS
σ^2_{GCA}±SE	1.6514(18) ±0.8951	0.0143(4) ±0.0095	2.4941(25) ±1.2255	0.6185(25) ±0.2936	0.1525(14) ±0.0817	0.0649(20) ±0.0318	0.1166(17) ±0.0587	0.1292(28) ±0.0594
σ^2_{SCA}±SE	3.4211(37) ±0.80789	0.0265(7) ±0.0143	2.7433(27) ±0.6934	0.4274(17) ±0.1289	0.2511(22) 0.0708	0.0588(18) ±0.0178	0.1218(17) ±0.0387	0.0497(11) ±0.0189
σ^2_{Mat}±SE	0.8806(10) ±0.50316	0.0199(5) ±0.0122	0.3530(4) ±0.2729	0.0539(2) ±0.0470	0.0536(5) ±0.0358	0.0012(1) ±0.0043	0.0248(4) ±0.0164	0.0058(1) ±0.0050
σ^2_{Rec}±SE	2.8364(31) ±0.6625	0.0494(13) ±0.0192	2.4650(25) ±0.6201	0.4002(16) ±0.1209	0.2354(21) ±0.0663	0.0610(18) ±0.0181	0.0866(12) ±0.0301	0.0249(6) ±0.0131
$\Sigma\sigma^2_G$	8.7895	0.1102	8.0554	1.5000	0.6924	0.1859	0.3498	0.2093
σ^2_e ± SE	0.4098(4) ±0.0354	0.2669(71) ±0.0231	1.8849(19) ±0.1628	0.9960(40) ±0.0860	0.4213(38) ±0.0364	0.1404(43) ±0.0121	0.3486(50) ±0.0301	0.2472(54) ±0.0214
σ^2_p	8.8919	0.1769	8.5266	1.7490	0.7978	0.22109	0.4369	0.2711
σ_p	2.9819	0.4206	2.9200	1.3225	0.8932	0.4701	0.6610	0.5206
$\sigma^2_{SCA}/\sigma^2_{GCA}$	2.0717	1.8565	1.0999	0.6910	1.6468	0..9059	1.0448	0.3818
GCV (%)	16	3	12	12	7	12	14	19
h^2_A	0.186	0.081	0.292	0.354	0.191	0.293	0.267	0.477

Table 7. Variance components (precents in brackets), standard errors, dominance ratios, genetic variation coefficients, narrow-sense heritabilities on both family and individual seedling basis

Components	100 SW	CN	H.6	h.6	DRC	NBAL	TNB	LS
σ^2_{GCA}±SE	1.6514(18) ±0.8951	0.0143(4) ±0.0095	2.4941(25) ±1.2255	0.6185(25) ±0.2936	0.1525(14) ±0.0817	0.0649(20) ±0.0318	0.1166(17) ±0.0587	0.1292(28) ±0.0594
σ^2_{SCA}±SE	3.4211(37) ±0.80789	0.0265(7) ±0.0143	2.7433(27) ±0.6934	0.4274(17) ±0.1289	0.2511(22) 0.0708	0.0588(18) ±0.0178	0.1218(17) ±0.0387	0.0497(11) ±0.0189
σ^2_{Mat}±SE	0.8806(10) ±0.50316	0.0199(5) ±0.0122	0.3530(4) ±0.2729	0.0539(2) ±0.0470	0.0536(5) ±0.0358	0.0012(1) ±0.0043	0.0248(4) ±0.0164	0.0058(1) ±0.0050
σ^2_{Rec}±SE	2.8364(31) ±0.6625	0.0494(13) ±0.0192	2.4650(25) ±0.6201	0.4002(16) ±0.1209	0.2354(21) ±0.0663	0.0610(18) ±0.0181	0.0866(12) ±0.0301	0.0249(6) ±0.0131
$\Sigma\sigma^2_G$	8.7895	0.1102	8.0554	1.5000	0.6924	0.1859	0.3498	0.2093
σ^2_e ± SE	0.4098(4) ±0.0354	0.2669(71) ±0.0231	1.8849(19) ±0.1628	0.9960(40) ±0.0860	0.4213(38) ±0.0364	0.1404(43) ±0.0121	0.3486(50) ±0.0301	0.2472(54) ±0.0214
σ^2_p	8.8919	0.1769	8.5266	1.7490	0.7978	0.22109	0.4369	0.2711
σ_p	2.9819	0.4206	2.9200	1.3225	0.8932	0.4701	0.6610	0.5206
$\sigma^2_{SCA}/\sigma^2_{GCA}$	2.0717	1.8565	1.0999	0.6910	1.6468	0..9059	1.0448	0.3818
GCV (%)	16	3	12	12	7	12	14	19
h^2_A	0.186	0.081	0.292	0.354	0.191	0.293	0.267	0.477

Table 8. Adjusted general combining ability effects

Parents	Traits							
	100.SW	CN	H.6	h.6	DRC	NBAL	TNB	LS
2	-0.217	-0.154	-0.236	0.004	-0.122	0.210	0.147	-0.047
3	-0.673*	-0.026	-1.869***	-0.697	-0.076	-0.106	-0.355	-0.205
45	0.127	0.107	-2.627***	-1.358***	-0.330	-0.215	-0.006	-0.041
50	1.449***	-0.185	-0.027	0.240	-0.161	-0.498**	-0.131	0.409*
205	0.552*	0.253	0.317	-0.260	0.503	0.209	0.108	0.398
206	-0.559*	0.045	0.985	0.760	-0.127	0.050	-0.292	-0.194
209	-2.266***	-0.020	-0.496	-0.393	-0.260	0.091	0.574*	0.311
x	2.002***	0.101	2.328***	1.192**	0.894***	-0.077	0.490*	-0.280
y	0.853**	-0.079	-0.143	-0.017	-0.220	-0.005	-0.342	-0.590**
z	-1.308***	-0.042	1.774**	0.535	-0.106	0.344*	-0.188	0.242
$SE(g_i - g_j)$	0.068	0.055	0.146	0.106	0.069	0.040	0.063	0.053

Table 9. Genetic correlations at GCA level (upper line) and phenotypic correlations (lower line with 43 degree of freedom)

	CN	H.6	h.6	DRC	NBAL	TNB	LS
100.SW	0.02	0.14	0.26	0.53	-0.72	-0.13	-0.24
	0.20	0.39*	0.41*	0.60***	-0.13	0.15	-0.33*
CN		0.03	-0.18	0.71	0.31	0.34	0.09
		0.13	-0.01	0.35*	0.16	0.13	0.04
H.6			0.95	0.56	0.32	0.13	0.10
			0.94***	0.67***	0.49***	0.42**	-0.13
h.6				0.50	0.11	0.03	-0.09
				0.58***	0.34*	0.32*	-0.20
DRC					0.03	0.38	0.04
					0.30*	0.56***	-0.19
NBAL						0.05	0.08
						0.31*	-0.07
TNB							0.40
							0.10

Table 10. Expected genetic gain (AG) for the main traits

Traits	AG (%) if the best 10, 20, 30, 40 of the 90 families were selected			
	10	20	30	40
H.6	6.0	4.7	3.9	3.1
h.6	8.9	7.1	5.8	4.7
DRC	2.7	2.1	1.7	1.4
LS	17.4	13.7	11.2	9.1

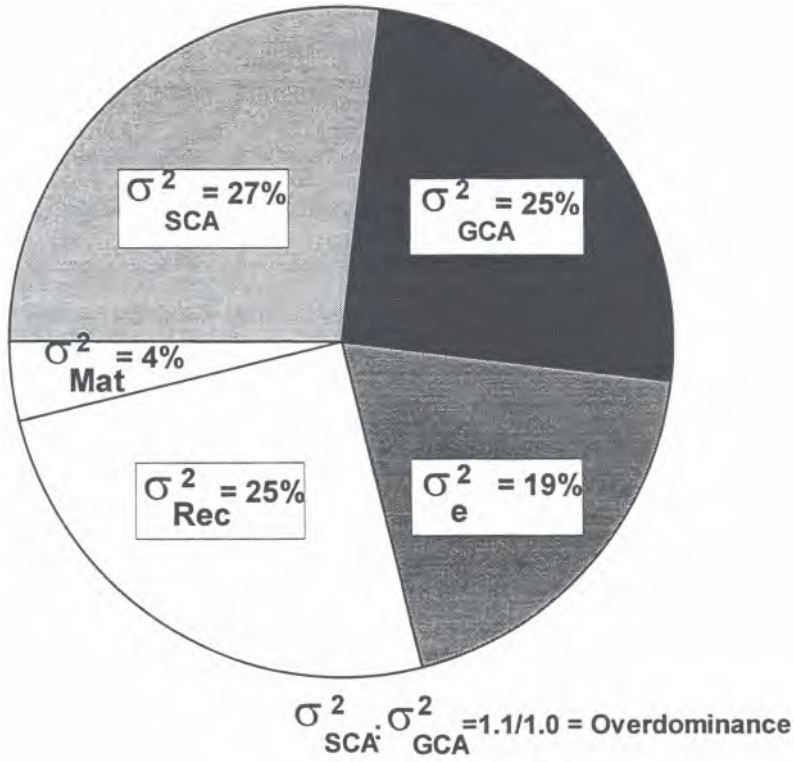

Fig. 2 - The structure of the phenotypic variance for total height

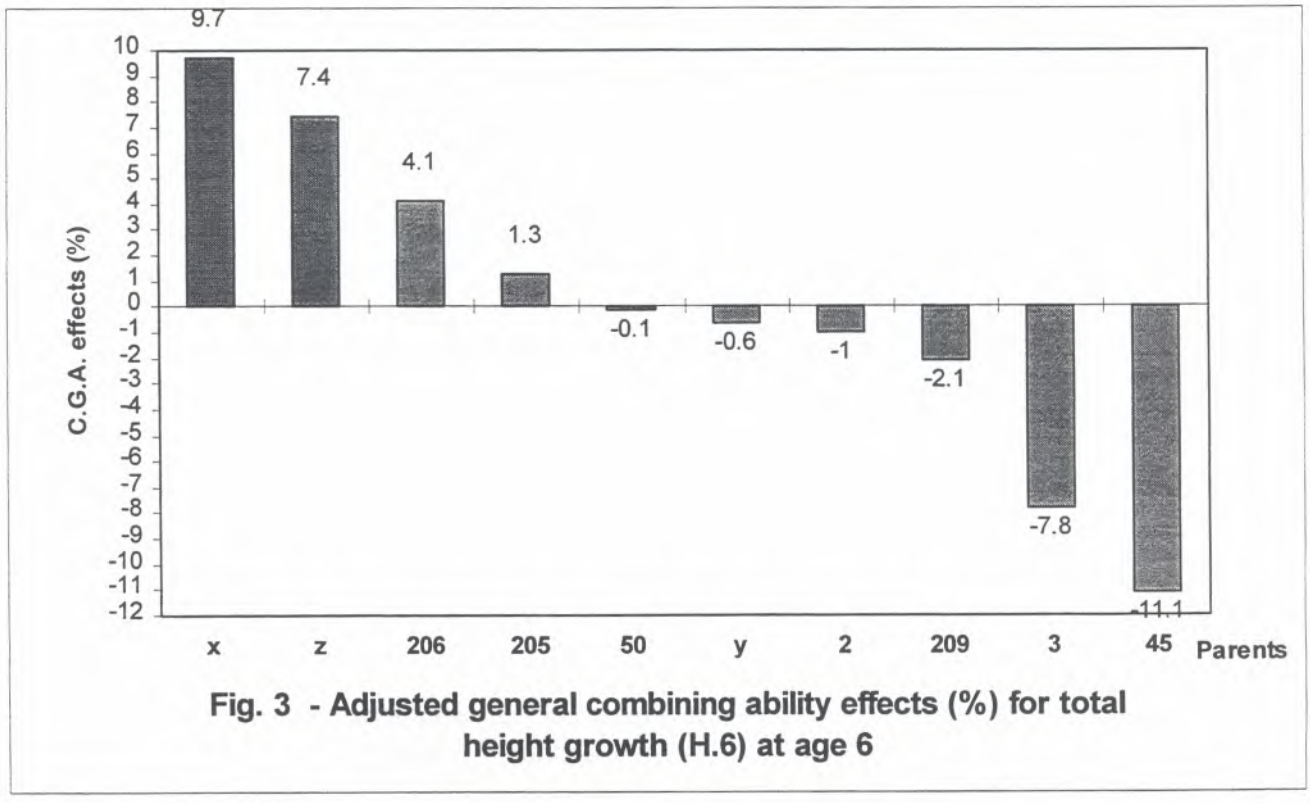

Fig. 3 - Adjusted general combining ability effects (%) for total height growth (H.6) at age 6