Early Growth Results in a Diallel Progeny Test of Eucalyptus grandis (Hill) Maiden

II. A Greenhouse Study

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Introduction

Raising, planting, and evaluating thousands of offspring from selected parent trees result in large expenses in time, effort and money. Therefore, reliable predictions from early testing procedures, such as greenhouse studies, would mean a greatly increased return on capital invested in a tree improvement Programme.

The present investigation is part of the same study reported as Part I.* Hence the objectives are the same as stated before, especially with reference to genetic variances, maternal and reciprocal effects, and the relationship between greenhouse and field planted material.

Materials and Methods

Fifteen selected parents from even-aged *Eucalyptus* grandis stands in the Republic of South Africa were used in a complete diallel mating design, but due to failure of some crosses and limited space in the greenhouse, a 13 X 13 diallel was used there (Fig. 1). Selfing was not very successful and failure of certain crosses resulted in 20,1% missing cells.

♂ ♀	04	10	36	37	44	45	60	47	50	38	39	15	22
04	X	X	X	X	X		X	X	X	X	X	X	X
10	X		X	X	X	X	X	X	X	X	X		X
36	X	X		X	X	X	X	X	X	X	X	X	
37	X	X				X	X		X		X	X	
44	X	X		X	X	X	X		X		X	X	X
45	X	X	X	X	X			X	X	X		X	X
60	X	X	X	X	X	X	X	X	X	X	X	X	X
47	X	X		X		X	X	X	X	X	X		X
50		X	X			X	X	X		X	X	X	X
38		X		X	X	X		X	X		X	X	X
39	X		X	X			X	X	X	X		X	
15	X	X	X	X	X	X	X	X	X	X		X	
22	X	X	X	X	X	X	X	X		X	X	X	

Fig. 1. — Mating design of the breeding experiment in the greenhouse.

Seed size effect was found to last up to 2 months in E. *obliqua* (Green, 1971) but its influence is not known for E. grandis. Therefore, seed were screened and only seed from a 0,589 mm screen were used.

Seed were gerrninated on moist filter paper and transferred to 114 mm pots, filled with a 3:1 sandy loam-peat moss mixture. The pots were placed on greenhouse benches of which 8 were temporarily constructed in addition to 10 permanent ones to accommodate the entire experiment. The temporary benches had a base of wood boards while the others had a base of river pebbles. This difference in the two groups of benches caused a large and unexpected differential response in the two groups of material planted in the respective pots. Seedlings developed normally over the first two months after planting. Then the roots protruded through holes in the bottom of each pot and further root development occurred on either the boards of the temporary benches, or in the river pebbles of the permanent benches. Apparently the combination of moisture and aeration was more favourable on the temporary than on the permanent benches with the result that plants on the former were twice as large as plants on the latter at age 5 months.

Although it was not expected that different benches would influence plant development, differential influences due to moisture and temperature gradients were expected in the greenhouse. Therefore, it was decided to adopt a special statistical design using incomplete blocking to reduce experimental error caused by environmental influences. Five selfed, nine open pollinated and 130 control-pollinated families were used in a 12 X 12 quadruple lattice design. Four five-tree family plots were arranged over the 4 replications and 5 surplus trees were planted per family to provide for replacement of early failures.

Measurements

Height measurements were taken at 2, 3, 4 and 5 months after planting (Ht-2, Ht-3, Ht-4, Ht-5), while diameter was measured just above the root collar at 4 months (Dm-4). The 4 height measurements were used to determine growth rate per month (Rate) using the following linear equation;

$$L = (3X_5 + X_4 - X_3 - 3X_2)/10$$

where L = a least squares estimate of linear height growth per month, and

X_5, X_4, X_3, and X_2 = height measurements at 5, 4, 3 and 2 months respectively.

Dry weight (Dry-wt) was determined at 5 months and an index of stem volume (Stem-Ind) was computed using the volume formula for a cone. Branch measurements included the length (Br-len) and diameter (Br-dm) of the two largest branches, and the number of branches (No. Br) at 4 months. The size of the branches were indicated by a volume index (Br. Ind), again using the volume formula for a cone. Four ratios were computed: Number of branches / Height at 4 months (No. Br/Ht-4), branch diameter/branch length (Br-dm/Br-len), branch diameter/root collar diameter at 4 months (Br-dm/Dm 4), and branch length/height at 4 months (Br-len/Ht-4).

Data were analysed with the aid of the Statistical Analysis System (Service, 1972) and DIALL (Schaffer and Usanis, 1969). With the former, adjusted family means were computed based on the analysis of variance for lattice de-

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* Silvae Genetica 25: 126—132 (1976).

Tab. 1. — Variance analysis format for estimating variance components from 130 control-pollinated families grown in the greenhouse.

Source of Variation1)	D.F.	Expected mean squares3)
Replications	3	$\sigma^2_w + 5\,\sigma^2_p + 54{,}6\,\sigma^2_{b(r)} + 650\,\sigma^2_r$
Blocks/Replications	44	$\sigma^2_w + 5\,\sigma^2_p + 4{,}9\,\sigma^2_{rec} + 10{,}5\,\sigma^2_{mat} + 5{,}1\,\sigma^2_{sca} + 9{,}4\,\sigma^2_{gca} + 54{,}1\,\sigma^2_{b(r)}$
GCA	12	$\sigma^2_w + 5\,\sigma^2_p + 3{,}7\,\sigma^2_{rec} + 7{,}4\,\sigma^2_{mat} + 33{,}2\,\sigma^2_{sca} + 331{,}8\,\sigma^2_{gca}$
SCA	63	$\sigma^2_w + 5\,\sigma^2_p + 6{,}0\,\sigma^2_{rec} + 11{,}8\,\sigma^2_{mat} + 30{,}8\,\sigma^2_{sca}$
Maternal	12	$\sigma^2_w + 5\,\sigma^2_p + 36{,}2\,\sigma^2_{rec} + 325{,}0\,\sigma^2_{mat}$
Reciprocal	42	$\sigma^2_w + 5\,\sigma^2_p + 36{,}3\,\sigma^2_{rec}$
Plot error	343	$\sigma^2_w + 5\,\sigma^2_p$
Within plot2)	2080	σ^2_w

1) GCA: General combining ability
SCA: Specific combining abliity

2) The analysis was done on a plot mean basis and within plot variance was obtained in a separate analysis

3) σ^2_{gca} : variance due to general combining ability
σ^2_{sca} : variance due to specific combining ability
σ^2_{mat}: variance due to maternal effects
σ^2_{rec} : variance due to reciprocal effects
σ^2_r : replication variance
$\sigma^2_{b(r)}$: variance due to blocks within replications
σ^2_p : plot variance; σ^2_w: within plot variance

signs, and the latter was used for computation of genetic parameters. The use of adjusted family means in the DIALL programme leads to biased estimates of variance, especially for specific combining ability, because no within family variance is entered into the analysis. Therefore, the least squares analysis (Schaffer and Usanis, 1969) to estimate variance components were based upon plot means with replications, blocks within replications, general combining ability (GCA), specific combining ability (SCA), maternal effects, reciprocal effects, plot error and within plot error as sources of variation *(Tab. 1).* Adjusted family means were only used to determine general combining abilities for different clones, and in correlation studies.

Results and Discussion

Genetic Variation

Large variation among family means clearly illustrated the existence of genetic variation for most traits. Mean height growth of the poorest family in the greenhouse, for instance, was only 38, 61, and 68 percent of that of the best family at 2, 3, and 4 months respectively. Since a full table of family means cannot be presented, *Tab. 2* shows the adjusted family means of the 5 best and the 5 poorest families (excluding selfs) for each trait, indicating the magnitude of family variation.

General combining ability (GCA), *i.e.* the average performance of the progeny of an individual tree mated to a number of other trees, calculated as a deviation from the population mean, was determined for each clone. When clones were ranked according to GCA a large change in ranking was found for height growth at 2 months and the same at 5 months. Correlation studies of GCA values at different ages indicated that results at 2 months cannot be used reliably to accept or reject parent trees. Seed sizes do influence initial growth, and since some clones produce only small seed, a potentially good clone will be rejected if selection is based upon early height growth performance.

Variance Components

From *Tab. 1* it is clear that approximate F-tests can be computed for general combining ability, and for maternal and reciprocal effects. Variance components are presented in *Tab. 3.* For specific combining ability (SCA) an F-test should be constructed using Satterthwaite's (1946) approximation. However, since estimates of variance components and their standard errors were obtained, F-tests are redundant, and may even be misleading. For instance, direct F-tests for GCA indicates significance for all but three traits; for reciprocal effects no significance is obtained. Maternal effects for height growth seem to disappear in older material, but may exist in branch characteristics and volume production. The estimates of some variance components, however, are associated with large standard errors so are not realiable.

The estimates for general combining ability for most traits have a standard error about 1/2 the size of the estimates themselves, indicating that GCA is real, and that a selective breeding program, utilizing additive variation, will be effective in improving the population mean. The standard error for height growth increased with increasing age suggesting that environmental variation is affecting estimates of genetic variance components. This phenomenon is more pronounced for estimates of SCA, since specific combinations are inflated by increasing environmental variation in older material. Therefore, estimates for σ^2_{sca} for height growth at 2 and 3 months have relatively small standard errors, indicating the existence of real SCA variation, but in the older material these estimates are less reliable. Consequently, SCA variance components for most traits, measured at 4 or 5 months, are associated with fairly large standard errors, with the exception of branch length and number of branches. These two traits, even expressed as a ratio per unit length, indicate a possible presence of strong nonadditive genetic effects.

The magnitude of σ^2_{gca} relative to σ^2_{sca} for most traits suggests that non-additive gene effects may be almost as important as additive gene action in very young *E. grandis.* The magnitude of these components, however, is influenced by various factors such as gene frequencies, or linkage, or both, as discussed in Part I.

The existence of additive variation is clearly shown in the greenhouse material suggesting that early screening of greenhouse or nursery trees may be beneficial in a breeding program. However, since some families may be „slow starters", an early screening should be done with caution and usually only the extremes rejected or selected. At three months 70 percent of the families that ranked among the 30 best full-sib families at 2 months, were still included with these 30 families, but this figure dropped to 60 percent and 50 percent at four and five months respec-

Tab. 2. — Adjusted means for several characteristics of the 5 best and the 5 poorest families (excluding selfs) grown in the greenhouse to illustrate family differences.

Rank	Ht-2[1] cm	Ht-3 cm	Ht-4 cm	Ht-5 cm	Dm-4 mm	Drywt gm	Rate cm	Stem. Ind. cc
1	13,7	27,6	50,3	74,0	3,8	5,0	28,8	2,6
2	12,48	27,2	49,2	73,8	3,7	4,9	22,2	2,6
3	12,46	26,5	49,1	73,8	3,7	4,8	21,5	2,6
4	12,45	26,1	49,0	72,6	3,7	4,7	21,1	2,4
5	12,3	25,6	49,0	72,6	3,7	4,7	21,0	2,4
Sub-mean	12,6	26,6	49,3	73,4	3,7	4,8	22,9	2,5
135	7,0	17,2	36,2	52,3	2,8	2,0	14,7	0,9
136	6,9	17,2	36,0	52,1	2,8	1,9	14,7	0,9
137	6,7	16,8	36,0	52,1	2,8	1,8	14,6	0,9
138	6,1	16,6	35,0	51,9	2,8	1,7	14,4	0,9
139	5,1	16,1	33,1	51,0	2,7	1,3	14,3	0,6
Sub-mean	6,4	16,8	35,3	51,9	2,8	1,7	14,5	0,8
Test mean	9,6	21,1	42,0	61,5	3,2	3,0	17,7	1,5
Std. Dev.[2]	3,3	6,5	20,9	35,9	1,0	2,2	12,4	1,8
LSD[3]	2,6	4,8	8,6	12,3	0,5	1,7	4,0	0,9

Rank	Br-dm mm	Br-len cm	No. Br.	Br-Ind. cc	$\frac{\text{Br-len}}{\text{Ht-4}}$	$\frac{\text{Br-dm}}{\text{Dm-4}}$	$\frac{\text{Br-dm}}{\text{Br-len}}$	$\frac{\text{No. Br.}}{\text{Ht-4}}$
1	0,32	4,0	1,6	0,012	0,06	0,07	0,0025	0,043
2	0,36	4,8	2,2	0,015	0,09	0,11	0,0032	0,058
3	0,43	5,6	2,3	0,026	0,11	0,11	0,0037	0,061
4	0,45	5,7	2,3	0,028	0,11	0,12	0,0039	0,063
5	0,45	6,1	2,4	0,030	0,12	0,13	0,0041	0,064
Sub-mean	0,40	5,2	2,2	0,022	0,10	0,11	0,0035	0,058
135	0,95	14,1	8,5	0,118	0,32	0,29	0,0097	0,190
136	0,95	14,2	8,8	0,121	0,33	0,30	0,0098	0,199
137	0,98	14,6	8,8	0,121	0,33	0,30	0,0108	0,215
138	1,01	14,9	9,7	0,136	0,34	0,31	0,0110	0,217
139	1,04	15,8	10,6	0,138	0,38	0,51	0,0123	0,243
Sub-mean	0,99	14,7	9,3	0,127	0,34	0,34	0,0107	0,215
Test mean	0,73	10,2	5,0	0,069	0,23	0,21	0,0065	—
Std. Dev.	0,49	8,2	5,2	0,094	0,16	0,15	0,0048	—
LSD	0,28	4,3	3,0	0,051	0,10	0,11	0,0032	—

[1] The numbers accopanying the abbreviations for height and diameter growth indicate the age of the seedling in months.

[2] Standard Deviation.

[3] Least significant difference at the 5% level obtained from the Lattice analysis of variance in the Statistical Analysis System (SERVICE, 1972).

tively. Unless the number of families is very high, making early screening of paramount importance, and the risk of rejecting too many potential „winners" is therefore not large, nursery selection or rejection of families is not recommended. Runt seedlings in the nursery will be culled but families should not be evaluated only upon nursery performance.

Maternal Effects

An additional influence of the female parent to the variation among offspring, known as maternal effects, is found in animals more often than in plants. 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. Various studies (GREEN, 1971; HOUGH, 1952; SCHELL, 1960) have shown that fast germinating seeds yield seedlings that initially grow more vigorously than those from smaller seeds but this initial difference may decrease and even disappear after several months, or after a few years. A strong correlation between seed size, speed of germination, and initial seedling size has been found in these studies. In unpublished studies HODGSON [1] and the author have found similar trends in *E. grandis.*

Maternal effects are most often considered of little importance in tree improvement programmes, and BARNES (1973) has shown that these effects are indeed negligible in most traits studied in *P. patula.* An exception to this statement is in short term studies where seed size effects are critical and must be accounted for.

Since different eucalypt clones produce capsules of varying size and, hence, seeds of different size, the study of maternal effects in juvenile material was one objective of this research. Although seed was screened to obtain a uniform size, it is interesting to note that clones 36, 38, 47 and 50 which were observed to have large seed, ranked among the first 5 (of 13) clones for height growth at 2 and 3 months, while clone 37 with small seed held the 12th po-

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[1] L. M. HODGSON, J. D. M. Keet Research Station, Politsi, Republic of South Africa.

Tab. 3. — Components of variance (upper line) and standard errors (lower line) estimated from 130 control-pollinated families grown in the greenhouse. Significance levels[1]), obtained from F-tests, are indicated for general combining ability, maternal and reciprocal effects.

Component	Ht-2	Ht-3	Ht-4	Ht-5	Dm-4	Rate	Dry-wt	Stem. Ind.
σ^2_r	1,4968 ±1,0066	0,6656 1,0912	—23,517 6,0486	—76,15 18,67	—0,0227 0,0070	—8,22 2,559	—0,2824 0,0601	—0,0896 0,0276
$\sigma^2_{b(r)}$	0,7974 ±0,2616	11,1142 2,5934	317,99 67,103	1007,4 211,7	0,3244 0,0708	122,6 25,7	3,2890 0,7150	1,3020 0,2799
σ^2_{gca}	0,3511*** ±0,1643	0,8646*** 0,4208	1,0094** 0,6353	1,0303^{NS} 1,0079	0,0039* 0,0025	0,0568^{NS} 0,0838	0,0171^{NS} 0,0154	0,0079* 0,0059
σ^2_{sca}	0,2438[3]) ±0,1627	0,6226 0,4697	0,5576 1,2890	3,2949 3,0131	0,0044 0,0054	0,2861 0,2982	—0,0001 0,0457	0,0110 0,0144
σ^2_{mat}	0,1317** ±0,0741	0,0376^{NS} 0,0893	0,1690^{NS} 0,3231	0,0756^{NS} 0,6505	0,0031* 0,0021	0,0054^{NS} 0,0576	0,0256* 0,0183	0,0071* 0,0047
σ^2_{rec}	0,0569^{NS} ±0,1227	—0,0636^{NS} 0,3599	0,1980^{NS} 1,2384	2,2180^{NS} 2,8716	0,0021^{NS} 0,0049	0,0301^{NS} 0,2600	—0,0075^{NS} 0,0043	—0,0105^{NS} 0,0106
σ^2_e	3,5640 ±0,2714	11,9411 0,9092	38,405 2,924	77,6030 5,9086	0,1422 0,0108	8,1371 0,6195	1,4341 0,1092	0,4068 0,0310
σ^2_p	2,470	7,977	14,304	8,643	0,0392	0,1171	1,4341	0,1208
σ^2_w	5,472	19,82	120,5	344,8	0,515	40,1	0,0000	1,73

Component	Br-dm	Br-len	No. Br.	Br. Ind.	Br-len / Ht-4	Br-dm / Dm-4	Br-dm[2]) / Br-len	No. Br. / Ht-4
σ^2_r	—0,0039 ±0,0022	—1,8202 0,5394	0,2943 0,6314	—0,000238 0,000051	0,000916 0,000719	0,000306 0,000392	0,036D-5 0,031D-5	0,000824 0,000580
$\sigma^2_{b(r)}$	0,0736 ±0,0163	25,726 5,599	7,6389 1,7074	0,002779 0,000611	0,002114 0,000572	0,003097 0,000772	0,112D-5 0,035D-5	0,000907 0,000249
σ^2_{gca}	0,0026*** ±0,0013	0,5592*** 0,2959	0,3250*** 0,1744	0,000099*** 0,000047	0,000229** 0,000147	0,000231*** 0,000125	0,021D-5*** 0,011D-5	0,000125* 0,000090
σ^2_{sca}	0,0021 ±0,0017	0,5929 0,4228	0,6121 0,2457	0,000049 0,000051	0,000698 0,000288	0,000080 0,000199	—0,003D-5 0,017D-5	0,000781 0,000195
σ^2_{mat}	0,0007* ±0,0005	0,2482** 0,1481	0,0821** 0,0488	0,000016* 0,000012	0,000093* 0,000066	—0,000039^{NS} 0,000042	0,0^{NS} 0,005D-5	0,000031* 0,000020
σ^2_{rec}	—0,0005^{NS} ±0,0012	—0,1849^{NS} 0,2807	—0,2593^{NS} 0,0985	—0,000065^{NS} 0,000032	—0,000072^{NS} 0,000155	0,000328^{NS} 0,000246	0,028D-5^{NS} 0,023D-5	—0,000097^{NS} 0,000045
σ^2_e	0,0427 ±0,0033	10,1752 0,7747	4,7678 0,3630	0,001426 0,000109	0,005431 0,000413	0,005742 0,000437	0,544D-5 0,041D-5	0,002045 0,000156
σ^2_p	0,0112	2,0152	1,4478	0,000204	0,001327	0,002748	0,152D-5	0,000458
σ^2_w	0,1573	40,8	16,6	0,00611	0,020518	0,014972	1,96D-5	0,007933

[1]) Significance levels: ***, 0,5%; **, 1%; *, 5%; NS, Not significant.

[2]) D-5 denotes multiplication by 10^{-5}.

[3]) F-tests were not constructed for specific combining ability. See text.

sition. This ranking changed with older material. When used as males, ranking of clones did not follow a similar pattern. These results suggest that clones that normally produce big seed tend to have a more viable endosperm and embryo than those producing smaller seed, and initially produce the largest seedlings.

Maternal effects were statistically highly significant for height growth at two months but became non-significant at 3 months and the F-value even decreased in the older material. This may indicate that seed size effect, or differential viability in the endosperm, if it were present, diminished rapidly and „washed" out in older trees. The variance components in *Tab. 3*, however, show real maternal effects in 2 month old seedlings, but in the older trees these estimates have large standard errors.

Significant maternal effects were found for volume production and diameter, which were measured at 5 and 4 months respectively. It might be that maternal effects are slower to disappear in these traits, because they are more sensitive to environmental effects. A strong maternal influence seems to exist for branch features, especially branch length even when expressed as a ratio of height growth at 4 months. This is also strongly reflected in the estimates of variance components which show that maternal effects are real for Dm-4, Dry-wt, Stem-Ind, Br-len, and number of branches.

The maternal components of variance contribute little to the total among plot genetic variation, especially for height growth. Its contribution for diameter and volume is larger and may be meaningful, while it is small for the other characteristics. The experimental material supported evidence that maternal effects for growth characteristics, *i.e.* height and possibly diameter growth, disappear in older trees. It also indicated that branch features may be under stronger maternal influence than height and diameter growth, but the trees were not old enough to come to conclusive inferences on the possible decrease of maternal effects in these traits.

Reciprocal Effects

Reciprocal effects, defined as the contrast in specific combining ability between two 2-parent crosses, were computed for all traits. No significant results were found *(Tab. 3)* and it is clear that the contribution of the variance components for reciprocal effects to the total among plot genetic variation is small. Most of the estimates of variance components for reciprocal effects were associated with large standard errors.

These results indicate that reciprocal, as well as maternal effects, are of minor importance in a breeding program for young *E. grandis* but material should be grown for a longer period to be positive. The results offer some support for adopting mating designs for the estimation of GCA and SCA only, especially for height and diameter growth. In other words, a complete diallel pollination programme would not be necessary because reciprocal and maternal effects will not be estimated. Simplified mating designs like the tester series or a partial diallel would result in considerable saving in effort and money.

Correlations

Phenotypic correlation is the association between two characteristics that can be observed directly, which can be partitioned into the correlation of breeding values, or genetic correlation, and the environmental correlation (Falconer, 1960). The genetic cause of correlation is mainly pleiotropy, though linkage may also be involved.

A strong phenotypic correlation is obtained among all characteristics *(Tab. 4)*. Height growth at increasing age shows increasingly stronger correlations with other growth traits, which may be expected from young material in an active growing condition.

Strong genetic correlations are obtained among all characteristics except between growth rate and number of branches indicating that the formation of branches is relatively independent of rate of growth. Correlations greater than one are obtained on two occasions, which could be caused by an inaccurate estimate of the genetic variance and covariance components for height growth at 4 and 5 months, as indicated by the size of the standard errors in *Tab. 3*.

High and positive genetic correlations for branch diameter and branch length with height and diameter growth respectively suggest a strong relationship between the latter and the size of the crown. The importance of this was pointed out in Part I where it was indicated that selection for crown width at 6 months should be based on the ratio of crown width to stem diameter.

Correlated response between different characters is dependent upon heritability of the traits under question, genetic correlation, phenotypic variation, and upon selection intensity. Strong positive correlations between height, diameter growth, and volume production imply genetic gain in any of these traits even if selection is practised on only one. Branch diameter and length, however, will increase with diameter and height growth, and a conscious effort should be made to find fast growing trees with thin branches of moderate length.

Self-, cross-, and open-pollinated offspring

The greenhouse included 5 self-pollinated families as well as 8 open-pollinated families. Unfortunately not enough families from the same parents occur in each pollination group for statistical comparison, but they can be compared with cross-pollinated families *(Table 5)* to indicate the general trend that may exist in growth performance. The cross-pollinated data are the mean female values over all males used in the mating design.

The lack of sufficient data is recognized, but if each group of material is considered as a small sample from a larger population, a comparison of overall means indicates that self-pollinated (SP) trees perform 10—20% worse than open-pollinated (OP) or cross-pollinated (XP) trees. On the other hand, OP seedlings do not differ significantly from XP ones. Overall means of the samples may be ignored and individual comparisons made between 5 SP and 5 XP families, and between 5 OP and 5 XP families. A variation in performance is illustrated that indicates that some SP families may initially perform as well as XP families, but there is a tendency for the former to drop behind the latter as trees become older. Other SP families are obviously inferior to either OP or XP families.

The initial equality of the OP seedlings and XP seedlings suggests that the amount of selfing in the former may be negligible, or if selfing did occur, that the selfed trees performed as well as the XP. Again, the same variation is demonstrated among clones within each group, but the differences are not as pronounced as they are in the self/cross comparisons. Hodgson (1974) found that XP trees performed significantly better than OP trees at 3 years.

The data presented are, admittedly, inadequate to make conclusive remarks about inbreeding depression, but the trend toward inferiority of selfs is evident. Even if some selfs exist among OP trees, the probability exists that the selfed trees will be eliminated either in the nursery, or in the first thinning of a commercial stand, or even in a progeny test/seedling seed orchard. The comparisons among

Tab. 4. — Genetic correlations (above diagonal line) based upon plot mean analysis of variance with adjustment for block effects, and phenotypic correlations* (below diagonal line) based upon individual observations for several traits in the greenhouse.

Trait	Ht-2	Ht-3	Ht-4	Ht-5	Dm-4	Dry-wt	Rate	Br-dm.	Br-len	No. Br.
Ht-2		0,85	0,82	0,76	0,65	0,88	0,24	0,80	0,69	0,82
Ht-3	0,56		0,87	0,79	0,74	0,65	0,35	0,44	0,40	0,57
Ht-4	0,13	0,68		0,95	0,74	1,04	0,68	0,56	0,63	0,63
Ht-5	0,07	0,60	0,97		0,76	1,06	0,80	0,80	1,00	0,40
Dm-4	0,28	0,66	0,78	0,76		0,65	0,51	0,64	0,62	0,28
Drywt	0,14	0,52	0,78	0,79	0,65		0,89	0,84	0,88	0,66
Rate	—0,03NS	0,54	0,97	0,99	0,73	0,78		0,48	0,87	0,08
Br-dm	0,34	0,52	0,59	0,59	0,72	0,56	0,54		0,94	0,44
Br-len	0,30	0,58	0,72	0,73	0,80	0,70	0,68	0,92		0,31
No. Br.	0,28	0,53	0,65	0,64	0,74	0,62	0,60	0,77	0,82	

* Significant at the 0,1% level unless indicated otherwise.

Tab. 5. — Height-growth comparisons between open-pollinated, self-pollinated, and control-pollinated progenies from the same parents.

Clone	Self-pollinated			Open-pollinated			Cross-pollinated		
	Ht-2 cm	Ht-3 cm	Ht-4 cm	Ht-2 cm	Ht-3 cm	Ht-4 cm	Ht-2 cm	Ht-3 cm	Ht-4 cm
04	4,32	9,39	15,98	—	—	—	9,18	20,36	40,48
44	10,09	22,52	39,51	—	—	—	10,42	22,33	42,67
60	8,27	18,95	36,39	—	—	—	9,37	21,18	43,77
15	5,88	18,58	34,28	10,62	20,32	40,50	8,71	20,60	41,59
47	9,47	20,08	38,84	9,58	20,81	42,02	10,57	22,22	44,79
10	—	—	—	10,19	21,46	37,91	9,87	20,49	42,20
37	—	—	—	9,14	19,49	41,01	8,47	19,67	40,20
50	—	—	—	10,81	22,47	46,74	10,85	21,57	42,99
35	—	—	—	9,63	21,46	45,68	—	—	—
06	—	—	—	10,18	22,06	40,35	—	—	—
17	—	—	—	10,11	21,74	42,45	—	—	—
Mean	7,61	17,90	33,00	10,03	21,23	42,08	9,68	21,05	42,34

open-pollinated and cross-pollinated families of older trees in Part I support this.

Extrapolation of Greenhouse Results to Field Results. Vigour and Branch Characteristics.

Generally no significant correlations were obtained between growth traits, *i.e.* height and diameter, in the greenhouse and the same traits in the field. When general combining ability of clones were compared between the greenhouse and the field data, very small, and nonsignificant, correlations were obtained.

Ratios involving branch length and diameter, and height of the seedling at 4 months in the greenhouse were correlated with different combinations of ratios involving crown-, root collar-, breast height diameter, and height of the trees at 6 and 15 months after planting in the field (CRDM, DRC, DBH, Ht). Greenhouse branch length/height at 4 months is significantly (P = 95%) correlated with CRDM-6/Ht-6 indicating that this ratio determined on very young seedlings may be predictive of the same ratio in young field plantings. When general combining ability for the ratios in the two experiments were compared, the correlation was not significant at the 5% level but significance was obtained at the 13% level which indicates some relationship between general combining ability for the ratios.

Significant (P = 95%) negative correlations were obtained for branch diameter and Br-dm/Dm-4 with the ratio CRDM-15/DBH-15 which show that the rate of change in the field for CRDM-15/DBH-15 is not proportionate to the change of the same ratio in the greenhouse. One would expect that the greenhouse traits would rather be correlated with the 6-month field ratio (CRDM-6/DRC-6). A weak relationship between these traits and the non-significance may be ascribed to the relative position of the branch measurements in the greenhouse. In the field the longest branches are produced close to the root collar at 6 months, but in the greenhouse the longest branches occurred about half-way up the shoot, especially on the fast growing trees.

From the data in the two experiments it is concluded that early greenhouse measurements on height, diameter, and volume are not predictive of field performance of older trees from the same families. Research workers in Europe (Herbert, 1971) also feel that the inherent capacity for rapid growth is unlikely to be detected in artificial greenhouse environments, but that some promise lies in early evaluation of stem and branch characters. The author's data support this even though the same members of a family were not carried from the greenhouse stage through the field planting. Simple random segregation within a family will further weaken comparisons of field and greenhouse studies, unless the same individuals are studied in each stage.

Variance Components

Meaningful additive as well as dominance variances were detected in both experiments indicating that selective breeding in *E. grandis* will be effective. In both groups of data specific combining ability variance was greater than general combining ability variance for most traits, and for height growth an increase in the former was obtained. It is not expected that dominance variance will keep increasing after crown competition in the field sets in, but its magnitude indicates that breeding methods should be adopted that utilize dominance effects, *e.g.* two-clone seed orchards or clonal propagation. Although some factors such as inbreeding, linkage and allelic disequilibrium, maternal and reciprocal effects, etc. probably influenced the estimates, it is important that competition effects may change the pattern in the field. In the greenhouse, competition did exist, and since trees were growing so rapidly, slower growing families were suppressed soon and specific combining ability variance was increased. In the field, when competition sets in it will reduce height growth variation and may very well reduce SCA variance.

The comparison of the greenhouse and the field tests showed that growth characteristics of seedlings in a greenhouse are not related to the same traits in the field. Greenhouse studies are useful for genetic studies on juvenile material, but in general it is concluded that greenhouse results cannot be extrapolated to field tests for traits related to volume production. For branch and crown characteristics meaningful trends were sometimes obtained, and more intensified research should be undertaken to determine the relative merit of early appraisal of such traits.

Summary

Control-pollinated seed from 13 selected *Eucalyptus grandis* trees were used to raise a full-diallel progeny test in the greenhouse. Several characteristics were assessed at monthly intervals on four occasions, starting at the second month after sowing. The objectives were to estimate the relative magnitude of genetic variances, maternal and reciprocal effects, phenotypic and genetic correlations, and to investigate the relationship between greenhouse and field planted trees belonging to the same full-sib family. Like the field material, the data illustrated considerable additive as well as non-additive genetic variances. Maternal effects were significant at two months but seemed to disappear in older trees, indicating a possible effect of seed size and endosperm viability. Reciprocal effects were generally negligible, and high correlations were obtained between most traits.

General combining ability of the parents showed much fluctuation from two to five months, and extrapolation of greenhouse results to field data generally showed poor correlations for growth characteristics. An exception was for branch features where a meaningful trend was found between the two groups of material. It was concluded that, for traits related to volume production, early appraisal of offspring is not recommended, but for branch and crown features such early assessments might have merit.

Key words: *Eucalyptus grandis*, greenhouse, full-diallel, progeny test, variance components, maternal effects, reciprocal effects, correlations.

Zusammenfassung

Zur Prüfung der Nachkommenschaften aus einem vollen Kreuzungsdiallel unter kontrollierter Bestäubung wurden zugleich im Freiland und im Gewächshaus 13 Einzelbaumabsaaten von *Eucalyptus grandis* vorgenommen. Danach erfolgte an 4 Stichtagen im Monat die Untersuchung, die auf vier Ziele gerichtet war: 1. Abschätzung relativer Größen genetischer Varianzen, 2. mütterliche und wechselseitige Wirkungen, 3. phaenotypische und genetische Verhältnisse und 4. das Verhältnis zwischen im Treibhaus und frei ausgepflanzten Bäumen der gleichen Familie.

Sowohl an den Nachkommenschaften im Freiland als auch an denen im Gewächshaus war beträchtliche additive und nicht additive genetische Varianz zu erkennen. Mütterliche Einflüsse waren bis zum Alter von etwa 2 Monaten zu bemerken. An Hand der meisten Eigenschaften wurde ein hoher Grad an Wechselbeziehungen ermittelt. Die allgemeine Kombinationseignung der Elternbäume schwankte innerhalb von 5 Monaten beträchtlich. Die Wachstumsunterschiede waren insgesamt gesehen unerheblich im Gegensatz zur Ästigkeit, bei der sowohl bei den Nachkommenschaften im Freiland als auch im Gewächshaus gemeinsame Trends zu beobachten waren.

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Estimation of Number of Embryonic Lethal Alleles in Conifers: I. Self-Pollinated Seed

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Introduction

Controlling seed losses is a major concern in forestry, especially in tree breeding programs. One cause for seed losses is embryo abortion resulting from the matching of recessive embryonic lethal alleles after inbreeding.

Reduced seed yield following inbreeding has been reported for *Pseudotsuga menziesii* (Mirb.) Franco by Orr-Ewing (1957), *Pseudotsuga menziesii* var. *menziesii* by Sorensen (1967, 1969, 1971), *Picea abies* L. and *Pinus sylvestris* L. by Sarvas (1962, 1968), *Pinus peuce* Griseb. by Hagman and Mikkola (1963), *Picea glauca* (Moench) Voss. by Mergen *et al.* (1965), *Pinus banksiana* Lamb and *Pinus resinosa* Ait. by Fowler (1965), *Picea abies* L. and *Pinus sylvestris* L. by Koski (1971), *Pinus taeda* L. by Franklin (1972), and *Pinus virginiana* Mill. by Bramlett and Pepper (1974).

Assuming that losses due to injury of ovules and fertilization failure are negligible and accounting for the polyembryonic reproduction system in conifers, Bramlett and Popham (1971) and Koski (1971) postulated a model for probability of unsound seed. With self fertilization in a tree having n loci heterozygous for embryonic recessive lethal alleles, they found the probability of unsound seed to be

$$p = \mathrm{P}\,(\text{Unsound seed}) = \sum_{r=0}^{n} \frac{1}{2^r}\binom{n}{r}\left(1 - 2^{-r}\right)^f. \qquad (1)$$

In this formula, the quantity $\frac{1}{2^r}\binom{n}{r}$ represents the binomial probability that in a particular female gamete there are r loci containing recessive lethal alleles. The quantity f is the number of fertilizations in an ovule, assumed to be the same for all ovules.

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