

Zusammenfassung

Titel: Die natürliche Variation der Gewebeanteile sowie der Länge von Gefäßzellen und Fasern im Holz älterer Bäume der nördlichen Roteiche (*Quercus rubra* L.).

Gefäßzellen, Fasern, axiales Parenchym und Markstrahlen wurden untersucht in 10 markfernen Jahrringen (38. bis 47. Jahrring) an 50- bis 100jährigen Bäumen von unterschiedlichen Standorten. Bei mittleren Werten für die auf Holzquerschnitten ermittelten Anteile von 20% Gefäßzellen, 41% Fasern, 23% Parenchym und 16% Markstrahlen betrug die Variabilität in gleicher Reihenfolge 30%, 20%, 22% und 22%. Die Länge der Gefäßzellen betrug im Mittel 0,45 mm bei einer Variabilität von 29% und die der Fasern 1,35 mm und 27%.

Von der Variabilität in den einzelnen Merkmalen konnte nur ein relativ geringer Anteil auf die unterschiedlichen Wuchsbedingungen verschiedenartiger Standorte zurückgeführt werden.

Zur Klärung von Möglichkeiten einer Verbesserung der Holzqualität durch Züchtung auf einen höheren Faseranteil und auf längere Fasern werden Provenienzversuche zur Einschätzung von Heritabilitäten und genetischem Gewinn empfohlen.

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

I. A. Field Study

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Introduction

Eucalypt plantations constitute a considerable proportion of the world's exotic hardwood forests. Adaptability, phenomenal growth rate under suitable conditions, and an expanding world market for hardwood fibres are the major reasons for the exceptional interest that many *Eucalyptus* species enjoy outside their native range.

Proper management and silvicultural techniques, combined with applied breeding programmes are resulting in greatly increased output from forest lands. However, reports on genetic work on eucalypts are scarce, and it is only in recent years that they received substantial attention in this field.

Considerable variation between and within species has been reported (GREEN, 1971; DADSWELL, 1972; BROWN *et al.*, 1972; DAVIDSON, 1973); and low heritability estimates were obtained for tree height, diameter, straightness, and branching habit of open-pollinated *E. regnans* families (ELDRIDGE,

1971). Controlled pollination experiments by HODGSON (1975) and ELDRIDGE (1970) on *E. grandis* and *E. regnans* respectively demonstrated the incidence of selfing and subsequent inbreeding depression in these species.

More than 350 000 hectares have been planted to *Eucalyptus grandis* in the Republic of South Africa, and this species is generally the most important in a number of subtropical countries.

In the present work control-pollinated seed from a diallel crossing scheme was used to raise full-sib families in a greenhouse in North Carolina and in a field test in south-central Florida, U.S.A. The major objectives of the study were:

1. To gain information on the mode of inheritance of quantitative traits in *E. grandis* by investigating:
 - a. the magnitude of additive and non-additive variances.
 - b. maternal and reciprocal effects,

- c. genetic and phenotypic correlations among selected characteristics.
 - d. the relationship between cross-, open-, and self-pollinated seedlings of several clones.
2. To determine the extent to which greenhouse performance is predictive of the performance of relatively young field material.

Materials and Methods for the Field Test

Parent trees were selected in even-aged stands in the Republic of South Africa with the emphasis on desirable characteristics for the production of sawtimber. Trees selected had a straight trunk, light branches, high volume production, little spiral grain, and minimum splitting upon felling. Eleven of the parents were located in the same geographical area (Letaba district, Northern Transvaal), three parents (44, 47 and 50) came from Eastern Transvaal and one (01) was selected in a stand in the South Cape. Grafts from the parent trees were established in a clone bank where pollination work was done for this study. A complete diallel mating design was adopted and emasculation and bagging of flowers were done on each of 15 clones just prior to fall of the inner opercula. Pollinations were made five to seven days after emasculation, at which stage stigmas are most receptive. Most of the pollinations were done in March through June 1972 and seed was harvested six months after pollination. The success of crossing parent trees was quite remarkable and made available a 13×13 full diallel with 20,1% missing cells for the greenhouse experiment, and a 15×15 half-diallel, excluding selfs, with only 5,7% missing cells for the field test. In most tree breeding experiments maternal and reciprocal effects are considered negligible. Since results in the greenhouse partially support this, some reciprocal crosses were used to "fill" the half-diallel cells to obtain an almost complete half-diallel, excluding selfs.

Raising and Establishment

Approximately 40 seedlings per family were raised in $2,5 \times 10$ cm styrene tubes in the greenhouse for 6 weeks, and in a nursery in Florida for a further 10 weeks. The tubes were placed on a screen wire with mesh small enough to support the rooting medium. This technique provides for air pruning of the roots and is believed to make the plant more resistant to planting shock. The seedlings suffered somewhat upon exposure to nursery conditions after removal from the greenhouse environment, but weekly application of fertilizer resulted in very healthy and uniform planting stock at four months.

Ninety-nine cross-pollinated families, comprising the half-diallel, and 11 open-pollinated families were tested. In June 1973, the seedlings were field planted in single-tree plots in an "unbalanced" randomized block design. In this design each of 63 blocks contained approximately 70 of the 110 families. Since single-tree plots were used, each family occurred in approximately 40 of 63 blocks.

The planting site is on a palmetto prairie with Leon fine sand. These prairies are natural treeless expanses of saw-palmetto, wire-grass, runner-oak, etc. (MESKIMEN, 1972). Intensive site preparation included double chopping and cross disking to kill palmettos and other vegetation, broadcast of rock phosphate at a rate of one ton per acre, and bedding to suppress herbaceous vegetation and to elevate seedlings out of standing water during the rainy season. Immediately after planting, the stock survived a short dry

spell that was followed by heavy rains which caused standing water between the beds for several weeks.

Measurements

Height growth was recorded at six (Ht-6) and 15 months (Ht-15) after planting. Stem diameter was measured approximately five centimeter above the root collar at 6 months (referred to as root collar diameter, DRC-6), while the 15 month measurement was done at breast height (DBH-15). An index of volume production was obtained by applying the volume formula for a cone at 6 months (VOL-6), and the formula for a cone plus a cylinder at 15 months (VOL-15).

The width of the crown was taken on both occasions (CRDM-6 and CRDM-15) and four ratios were computed expressing crown diameter as a ratio of height and diameter at the respective ages (CRDM-6/Ht-6; CRDM-6/DRC-6; CRDM-15/Ht-15; CRDM-15/DBH-15). A subjective straightness score was done at 15 months, grading the trees into four classes, good, medium, bad and a class that contained trees that did not recover normally after frost damage.

In December 1973, trees were damaged by low temperatures twice, and frost damage (Frost) was subjectively assessed according to a 5-point scale. Frost damage obviously occurred in the form of thermal layers. Therefore, family means for frost score were adjusted (ADJSCOR) using height growth as covariable. After obtaining the regression coefficient for the regression of frost score on height at six months the value was used to obtain an adjusted frost score value for each tree.

A general least squares analysis on an individual tree basis was performed employing the computer programme prepared by SCHAFER and USANIS (1969). The linear model included replications, general combining ability (GCA), specific combining ability (SCA) and residual as sources of variation. The analysis was based on the random model assuming that the experimental material is a random sample from a parent population of selected trees. Genetic correlations were provided for in the programme and phenotypic product-moment correlations were obtained with the aid of a programme from the Statistical Analysis System (SERVICE, 1972). The expected mean squares are listed in Table 1.

Results and Discussion

Genetic variation

Enough genetic variation was demonstrated to encourage selective breeding for most characteristics that were studied. At six months the best family was 2,13 m tall, while the worst family measured 1,47 m. At 15 months the best family, measuring 4,74 m, was 1,95 m taller than the poorest and produced 4,86 cubic decimeters more in volume. Subjective straightness values for family means ranged from 2,7 to 1,5 on a 4-point scale. Also, the percentage of trees that were deformed after frost damage varied from one full-sib family to the other, even among overall means of offspring, from parent to parent, *e. g.* family percentages for deformities ranged from 2,6 to 34,3%, and for parental groups from 9,8 to 18,0%. In all cases the total number of trees tested per family did not vary enough to have a significant influence on the range in means. Crown width expressed as a ratio of height or diameter of the tree at the various ages also showed substantial family variation.

Most eucalypt species are sensitive to frost damage. In this population of *E. grandis* subjective unadjusted frost

Table 1. — Variance analysis format used to estimate variance components from 99 control-pollinated families grown in the field (analysis is on an individual tree basis).

Source of Variation ¹⁾	DF	Expected Mean Squares ²⁾
Replications	62	$\sigma_e^2 + 0,41^3) \sigma_{sca}^2 + 0,62\sigma_{gca}^2 + 63,96\sigma_r^2$
GCA	14	$\sigma_e^2 + 40,79 \sigma_{sca}^2 + 495,98\sigma_{gca}^2$
SCA	84	$\sigma_e^2 + 40,39 \sigma_{sca}^2$
Residual	3870	σ_e^2

¹⁾ GCA = General Combining Ability.

SCA = Specific Combining Ability.

²⁾ σ_r^2 = Variance due to replications.

σ_{gca}^2 = Variance due to GCA.

σ_{sca}^2 = Variance due to SCA.

σ_e^2 = Residual Variance.

³⁾ Coefficients are given to two decimals only. It should be noted that the coefficient for GCA is close to that of a complete 14×14 half-diallel without selfs and 41 replications.

score values ranged from 2,85 to 4,27 and values adjusted for height growth ranged from 3,42 to 4,40. All family means were adjusted for block differences.

In an analysis of variance highly significant F-values for general combining ability (GCA) were obtained for most traits (Table 2). For specific combining ability (SCA) F-values were significant for all characteristics except adjusted frost score and ratios involving crown width, height and diameter of the tree. A study of the GCA values of the parent trees indicated a large range for all growth characteristics, i.e. height, diameter, and volume produced. General combining ability for volume production for instance ranged from -0,56 to 0,91 with a mean of 2,85 cubic decimeter at 15 months. Generally the best parents at 6 months ranked highest at 15 months for height, diameter, and volume, production, but it was found that the change in ranking for GCA caused non-significant rank correlation coefficients and that parents cannot be ranked reliably for 15-month performance of progeny from 6-month results.

Variance components

In a selection programme that utilizes additive genetic variance, the variance component attributable to general combining ability (σ_{gca}^2) is of major interest. From Table 2 it is clear that the specific combining ability variance component (σ_{sca}^2) is larger than σ_{gca}^2 for most of the traits, suggesting that non-additive genetic variance is most important in this population of *E. grandis* and a breeding programme other than one utilizing only additive variance could be adopted with advantage.

All variance component estimates are associated with relatively small standard errors indicating their reliability. Non-additive variance of this relative magnitude has been rarely reported for random mating populations in forestry, or in agriculture.

Various factors may influence variance component estimates, e.g. (1) clerical or key punching errors causing a substantial deviation of some family means from the population mean, (2) existing maternal or reciprocal effects will be included in the estimate for σ_{sca}^2 in the DIALL (SCHAFER and USANIS, 1969) programme if they are not separated in the model, (3) differences in gene and genotypic frequencies of different populations that are inter-mated, (4) the degree of dominance, (5) linkage disequilibrium and epistasis, and (6) inbreeding. Since experimental data was checked with care, and since greenhouse data partially supported the disappearance of maternal effects and showed non-signifi-

Table 2. — Components of variance (upper line) and standard errors (lower line) estimated from 99 control-pollinated families grown in the field. Significance levels, obtained from F-tests, are indicated for general and specific combining ability.

	HT-6		HT-15		DRC-6		DBH-15		VOL-6		VOL-15		Frost		Adjscore		CRDM-6		CRDM-15		CRDM-6		CRDM-15		CRDM-15		DBH-15				
σ_r^2	0,0644	0,3102	0,0592	0,4583	0,2603	0,4583	0,0897	0,4583	35258,7	6613,8	1,2382	0,2227	0,4205	0,0013	0,0013	2,2831	0,0021	0,0013	0,0003	263,77	56,01	0,0013	0,0003	2,2831	0,0021	0,0013	0,0003	2,2831	0,0021	3,3944	1,9522
σ_{gca}^2	0,0032***	0,0312***	0,0160	0,0520***	0,0058*	0,0520***	0,0037	0,0520***	958,1**	609,0	0,1481***	0,0187***	0,0247***	0,0018***	0,0018***	22,213***	22,213***	0,0018***	0,0018***	76,43***	35,18	0,0018***	0,0006	2,4316***	0,0008***	0,0008***	0,0003	2,4043***	1,1429	2,4043***	1,1429
σ_{sca}^2	0,0090***	0,1285***	0,0253	0,2200***	0,0359***	0,2200***	0,0450	0,2200***	5828,1***	1368,5	0,4750***	0,0197*	0,0031NS	0,0009NS	0,0009NS	31,113*	31,113*	0,0009NS	0,0007	194,85***	42,08	0,0009NS	0,0007	0,6297NS	0,002NS	0,002NS	0,0001	-2,0760NS	1,5425	-2,0760NS	1,5425
σ_e^2	0,1570	1,5142	0,0344	3,0163	0,7606	3,0163	0,0686	3,0163	134879,8	3065,4	7,1062	0,7443	0,4925	0,0149	0,0149	1004,6	1004,6	0,0149	0,0003	3265,4	74,2	0,0149	0,0003	38,753	0,0163	38,753	0,0163	486,01	11,05	486,01	11,05

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

cant reciprocal effects, the model used is regarded as not unduly influenced by the first two factors. Additive genetic variance σ^2_A and σ^2_D is larger than dominance genetic variance σ^2_D when the gene frequencies of the undesirable allele is relatively low in the case of complete dominance, or in the case of "pure" over-dominance, at intermediate frequencies (FALCONER, 1960). Since the *E. grandis* population showed fairly large amounts of additive variance, and is regarded as non inbred, the degree of dominance in this study may be "pseudo-overdominance" caused by allelic or linkage disequilibrium, or both.

The average level of dominance in the F_2 generation of corn, thought to be a possible case of true overdominance was shown to be not significantly different from the value of complete dominance after 12 generations of breeding (MOLL *et al.*, 1963), and they concluded that the degree of dominance in the F_2 generation was biased upwards due to linkage effects. The effects of linkage and epistasis on the estimates of σ^2_A and σ^2_D were discussed by COCKERHAM (1956, 1963) and SCHNELL (1963). Since crosses from divergent populations typically cause linkage effects, the present *E. grandis* population might have been influenced by these factors because "wide crosses" were included in the design.

In view of the results the parental population of this study was examined more intensively. As mentioned earlier, 4 of the 15 parents came from a different geographical area in South Africa than did the others. Eleven parents were selected from plantations owned by a private company, Merensky Trust. The policy of this company has been to collect seed from better than average trees, resulting in the circulation of better than average genetic stock for several generations. Thus, this population (hereafter referred to as "close" population) could have approached equilibrium due to random mating in successive generations. Three of the other four trees were selected in different government plantations ca 240 kilometers away, while one tree came from a plantation several hundred kilometers away. Crossing of these four parents with the others resulted in 48 families, referred to as "wide crosses."

A least squares analysis was conducted upon the 51 crosses obtained from the matings in the close population, employing the DIALL programme of SCHAFER and USANIS (1969). The estimates of variance components and their standard errors for eight traits are presented in Table 3 in

comparison with estimates from the original population. The relative contribution of σ^2_{sca} to the total among family genetic variance is shown as $\sigma^2_{sca}/(2\sigma^2_{gca} + \sigma^2_{sca})$. The remarkable change of the ratio from one population to the other suggests that estimates for σ^2_{sca} in the original population are inflated by one or more of the factors discussed above. It is concluded that biased estimates of dominance will be obtained if σ^2_{gca} , as estimated from the original population, is used as the estimator, i.e. $\sigma^2_{sca} = 1/4\sigma^2_D$. Epistatic effects, linkage and allelic disequilibrium may be important in this population, and heritability estimates using σ^2_{gca} as estimator of $1/4\sigma^2_A$ may be biased upwards.

Family means of the "wide crosses" were generally better than the test average, while families from the "close population" had a lower mean than the test mean. In Table 4 this is illustrated for one trait, namely height growth at 15 months.

Height, Diameter and Volume Production

From Table 2 it is clear that height and diameter are inherited in a non-additive as well as in an additive fashion. The results suggest that breeding strategies that utilize non-additive gene action should be adopted for *E. grandis*. This may be a practical approach for seed production in immediate generations, but in the light of the above discussion on the fluctuating results of different populations, it may not be the most effective breeding method over successive generations. As the genetic population stabilizes, dominance variance may turn out to be much less important than additive variance, upon which the latter will be used to maximize gain.

Frost Resistance

Additive gene action appears to be the controlling factor for frost resistance. Since the evaluation of frost damage was strongly related to the size of the tree, frost score was adjusted minimizing the effect of height differences. The adjusted frost score, therefore, is regarded as the better indicator of frost resistance, and it has negligible dominance gene action.

In practice, however, selection should not be based on frost score values only, because slow growing families might have received a better frost evaluation than fast growing ones due to the adjustment based upon height growth. Selection should, primarily, be based on height

Table 3. — Comparisons of estimates of variance components (upper line) and standard errors (lower line) between two populations.¹⁾

Population A	Ht-6	Ht-15	DRC-6	DBH-15	VOL-6	VOL-15	CRDM-6	CRDM-15
σ^2_{gca}	0,0032	0,0312	0,0058	0,0520	958,1	0,1481	22,213	76,43
±	0,0015	0,0160	0,0037	0,0272	609,0	0,0718	9,500	35,18
σ^2_{sca}	0,0090	0,1285	0,0359	0,2200	5628,1	0,4750	31,113	194,85
±	0,0020	0,0253	0,0084	0,0450	1369,5	0,0993	8,556	42,08
Ratio ²⁾	0,58	0,67	0,76	0,68	0,75	0,62	0,41	0,56
Population B	Ht-6	Ht-15	DRC-6	DBH-15	VOL-6	VOL-15	CRDM-6	CRDM-15
σ^2_{gca}	0,0042	0,0476	0,0095	0,0591	1806,4	0,1749	31,166	116,773
±	0,0021	0,0243	0,0058	0,0319	981,3	0,0867	14,346	55,854
σ^2_{sca}	0,0035	0,0574	0,0183	0,0788	1944,6	0,1463	8,823	77,780
±	0,0016	0,0210	0,0082	0,0333	1050,6	0,0664	7,149	35,682
Ratio	0,29	0,38	0,49	0,40	0,35	0,29	0,12	0,25

¹⁾ Population A includes crosses among all 15 parents.

Population B includes crosses among only 11 parents belonging to a "close" population.

²⁾ Ratio = $\frac{\sigma^2_{sca}}{2\sigma^2_{gca} + \sigma^2_{sca}}$

but it is well known that vigorous plants are more susceptible to frost damage than dormant ones. The change to negative values at 15 months indicates a differential response of trees after frost damage, namely the faster growing trees recovered better after damage than the slower growing ones. This is in agreement with the phenotypic correlations which shows an increase in correlation between frost score and height, diameter, or volume with age. In other words, phenotypically the bigger tree is damaged less by frost than the smaller one; genetically it is not, but since it is inherently a fast growing tree, and frost damage occurred mostly in the lower region of the tree, the phenotypic damage will be less at a later age because it can recover quickly after frost damage.

The size of the crown is moderately correlated with height or diameter at the respective ages. A very high genetic correlation between CRDM-6 and CRDM-15 was obtained. If these traits are standardized by expressing them as a ratio of height or diameter at the different ages, trees of different sizes are on a comparable basis. High correlations between such ratios indicate that efficient selection for branch features (or crown width) can be done at an early age, especially if crown width is expressed as a ratio of root collar diameter.

Genetic gain and heritability from the "Close" Population

Additive genetic variance is usually larger than dominance variance in most agricultural and forestry experiments. In this study the relative ratio of these components of variance follows a similar pattern when estimated from progeny data obtained from matings among parents that had been selected in the same geographical area. Therefore, it is assumed that this "close" population complies more closely with the normal genetic assumptions and that the covariance of relatives can be translated to genetic variances.

Low heritability (h^2) estimates were obtained for growth characteristics as well as for crown width expressed as a ratio of height or diameter growth. The ratios CRDM-6/DRC-6 and CRDM-15/Ht-15 have higher h^2 estimates than the other two ratios (Table 6), indicating the change in these ratios over time. Because of this and the correlation values, one would select for the best CRDM/DRC ratio at six months and for the best CRDM/Ht ratio at 15 months. The predicted gain for these variables is also higher than for the other two ratios. These values are based upon a mass selection scheme and may be expected to be higher when a selection index is used.

Fifteen percent gain in volume at 15 months is a considerable increase in timber production. Even smaller increases than this 15% would result in appreciable improvement in yield, especially when considered in relation to large scale afforestation programmes.

While it would be theoretically feasible to do selections at 6 months of age, results indicate that selection would be better at age 2 to 3 years. At this stage also, generation turnover will not be delayed since trees do not flower until the second or third year after planting. Selection at 15–24 months will be valuable, especially if strong correlations exist between two-year-old and older trees (*i.e.* of pulpwood rotation age), and the risk of rejecting potential "winners" at an early age is reduced.

Open-pollinated versus Control-pollinated offspring

A comparison of open-pollinated and control-pollinated family means indicated that the latter performs better than the former. The difference in height growth between the

Table 6. — Heritabilities¹⁾ and gain predictions²⁾ for several characteristics from progeny of the "close" population³⁾

Trait	Heritability	Gain ⁴⁾	Test mean	Gain as % of the mean
Ht-6	,10	,082 m	1,74 m	4,7
Ht-15	,11	,292 m	3,51 m	8,3
DRC-6	,05	,084 cm	3,55 cm	2,4
DBH-15	,08	,268 cm	3,31 cm	8,1
VOL-6	,06	42,0 cc	664,7 cc	6,3
VOL-15	,10	,452 cub.dm.	2,85 cub.dm.	15,9
CRDM-6				
Ht-6	,08	,030	,771	3,9
CRDM-15				
Ht-15	,22	,048	,149	32,0
CRDM-6				
DRC-6	,26	3,36	37,28	9,0
CRDM-15				
DBH-15	,01	,614	136,9	0,4

$$1) \text{ Heritability} = \frac{4\sigma_{gca}^2}{2\sigma_{gca}^2 + \sigma_{sca}^2 + \sigma_e^2}$$

$$2) \text{ Gain} = i \cdot \frac{4\sigma_{gca}^2}{(2\sigma_{gca}^2 + \sigma_{sca}^2 + \sigma_e^2)^{1/2}}$$

where σ_{gca}^2 = variance due to general combining ability,
 σ_{sca}^2 = variance due to specific combining ability,
 σ_e^2 = residual variance, and
i = selection intensity.

3) "close" population refers to a group of parents selected in the same geographical area.

4) Selecting 120 individuals from 2040 (51 families) gives a selection intensity of 2 which is the multiplier in the gain calculation. (NAMKOONG and SNYDER, 1969).

two types of offspring was 0,27 m at 15 months. The variation in an open-pollinated family is much larger than within a cross-pollinated family, and one would suspect the occurrence of selfed trees in the former. At later ages selfed trees tend to lag behind out-crossed trees although they might have performed equally well over the first few months. None of the 11 open-pollinated families in this study were included among the best 20 families when ranked for height growth at 15 months, and only one was among the best 20 for volume production at the same age.

The sample of open-pollinated families was not adequate in this study, but in an intensive study HODGSON (1975) confirmed the general trend observed in this research. He found that the cross-pollinated families generally outperform open-pollinated families, and that the height depressions in opens compared with crosses varied from 2% in one clone to 26% in another at age 11 to 18 months.

Conclusions

The progeny test data from this research illustrated the existence of sufficient additive as well as non-additive genetic variance to utilize in a selective breeding programme for most characteristics. The magnitude of non-additive variance indicated the possible influence of allelic or linkage disequilibrium in this population of *E. grandis*; a situation which might easily arise in exotic plantations where divergent genotypes will be allowed to intermate.

Phenotypic and genetic correlations indicate that correlated responses for several traits will be obtained if selection is done on only one. However, a study of correlations and ranking of general combining abilities at different ages indicate that, for this population, many erroneous decisions will be made if selections are done too early.

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Summary

A half-diallel progeny test of *Eucalyptus grandis* was raised, planted and assessed in the field at ages 6 and 15 months after planting. The 15 parent trees involved were selected in evenaged stands in the Republic of South Africa. The objectives were to investigate the relative magnitude of genetic variances, and phenotypic and genetic correlations of several traits. Results indicated the importance of additive as well as non-additive variances. The magnitude of the latter raised the question of possible allelic or linkage disequilibrium that could have arisen due to intermating of divergent genotypes in the exotic plantations. High correlations illustrated the possibility of simultaneous improvement of several characteristics in a selective breeding programme.

Key words: *Eucalyptus grandis*, half-diallel, progeny test, variance components, correlations.

Zusammenfassung

Bei der Prüfung der Nachkommenschaften aus einem Kreuzungsdiallel mit 15 ausgewählten Einzelbäumen von *Eucalyptus grandis* (HILL) MAIDEN war im Alter von 6 bzw. 15 Monaten der Sämlinge deutlich additive und nicht additive Varianz festzustellen. Die Untersuchungsergebnisse zeigen, daß in einem solchen Auslesezüchtungsprogramm Möglichkeiten zur Verbesserung verschiedener Eigenschaften gegeben sind.

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Microsporogenesis, pollination and potential yield of seed of *Larix* in NE Scotland

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Introduction

It is widely known that the yield of seed from Larch seed orchards is poor. KIELLANDER (1966) suggested that thirty percent germination could be considered normal in European Larch, *Larix decidua* (MILL.) and Japanese Larch, *L. kaempferi* (SARG.) and MESSER (1956) found that the percentage of empty seeds in *L. decidua* ranged from 59.8% to 80.1%. Similar yields of seed from controlled hybrid crosses by the authors have resulted in 20 or fewer full seed per cone which is one third or less of the potential yield.

Seed production in seed orchards is affected by a variety of factors and failure at, or prior to, fertilization, due to either maternal, paternal or environmental effects, with subsequent disturbances in embryogeny is known to have an important effect on yield of seed (SARVAS 1962, MATTHEWS 1963, ANDERSON 1965 and ERIKSSON *et al.* 1972). Failure at this stage may be due to variation in quality and/or quantity of pollen leading to non-fertilization or be due to genetic and/or environmental factors which cause early failure of the zygote. Swedish workers have shown that low seed

yield may be due to unfavourable climatic conditions during microsporogenesis (ERIKSSON 1968, ERIKSSON *et al.* 1972). In Larch, microsporogenesis takes place between October and March (EKBERG *et al.* 1968). Low temperatures during the active stages of meiosis appear to result in chromosomal irregularities, disturbances of cell division and non-functioning pollen. Disturbance of meiosis due to low temperatures has been reported to occur in many conifers for example in *Abies sachalinensis* (MAST.) MERTEN and LESTER 1961, *Picea abies* L. (KARST), ANDERSON 1965, *Pinus edulis* (ENGEL.) VOSS, CHIRA 1967 and *Larix laricina* (K. KOCH), CHANDLER and MAVRODINEAU 1965. In some species abnormally high temperatures are also known to disturb meiosis as reported for *Picea abies*, CHIRA 1965 and *Taxus baccata* L., CHIRA 1964. Because of the reported detrimental effects of local climate on microsporogenesis in Sweden it is felt that the location of seed orchards for the production of forest tree seed is an important consideration (ERIKSSON *et al.* 1972).

Winter temperatures in North-east Scotland are not as low as in Sweden but temperatures below the critical level