Juvenile-Mature Correlations and Trends in Genetic Variances in Sitka spruce in Britain

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Abstract

The value of early testing to breeding programmes is described. Pre-rotation age selection is essential if cost-effective breeding is to be achieved and rate of genetic gain maximised. Judging the effectiveness of early family selection requires a knowledge of genetic correlations between juvenile and adult traits, while gain prediction further requires that the additive variance of the mature population is known. The effectiveness of early testing is reviewed and the concept of the coefficient of family variation (the quotient of the square root of the family component of variance and the trait mean) is introduced. Declining coefficients of additive variance as evidenced in several studies in the literature diminish the magnitude of genetic gains by the time rotation age is reached.

Two investigations into juvenile-mature correlations and trends in additive variance in Sitka spruce in Britain are described. The first concerns a small 27 year-old progeny test and the second a larger set of 15 year-old tests replicated on several sites. Both studies show high correlations between height as early as 3 years and later measures of vigour, and it is concluded that retention of progeny tests to 15 years gives little further advantage in terms of selection for vigour, over selection at 6, or even 3 years. The second study shows a decline in additive variance with age, although significant additive variance remains at 15 years. There is no evidence of the decline occurring earlier at faster growing sites as might be expected if the decline were associated with the onset of inter- and intra-family competition. Frequency of assessments and differences in test design may have had an obscuring effect.

Key words: Juvenile-mature correlations, genetic variances, Sitka spruce, *Picea sitchensis.*

Zusammenfassung

Der Wert von Frühtests in Züchtungsprogrammen wird untersucht. Eine Selektion bereits vor dem Umtriebsalter ist notwendig, wenn eine kosteneffektive Züchtung angestrebt und der genetische Gewinn maximiert werden soll. Die Beurteilung der Effektivität einer Frühselektion von Familien erfordert Kenntnisse der genetischen Korrelation zwischen Merkmalen in der Jugend und im Alter, während für die Vorhersage des genetischen Gewinnes darüber hinaus die additive Varianz der hiebsreifen Population bekannt sein muß. Die Effektivität von Frühtests wird besprochen und das Konzept des Koeffizienten der Familienvariation (Quotient aus der Quadratwurzel der Familienvarianzkomponente und dem Mittelwert des Merkmals) wird eingeführt. Abnehmende additive Varianzkomponenten, wie in verschiedenen Studien gezeigt wird, verringern die Größe der genetischen Gewinne bis das Rotationsalter erreicht wird.

Zwei Untersuchungen über Jugend-Alter-Korrelationen und Trends bei additiver Varianz bei Sitka in Großbritannien werden dargestellt. Die erste bezieht sich auf einen kleinen 27 Jahre alten Provenienzversuch, die zweite auf mehrere 15 Jahre alte Versuche, die auf verschiedenen Standorten wiederholt sind. Beide Studien zeigen enge Korrelationen zwischen der Höhe im Alter 3 und späteren Messungen der Wuchsleistung, und es kann gefolgert werden, daß die Erhaltung von Nachkommenschaftsprüfungen bis zum Alter 15 geringe Vorteile hinsichtlich der Selektion auf Lebensfähigkeit gegenüber einer Selektion im Alter von 6 Jahren oder sogar 3 Jahren bietet. Die zweite Studie zeigt eine Abnahme der additiven Varianz mit dem Alter, obwohl eine signifikante additive Varianz auch noch im Alter 15 besteht. Es gibt keinen Nachweis, daß diese Abnahme auf besseren Standorten eher auftritt, was erwartet werden könnte, wenn die Abnahme mit dem Einsetzen von inter- und intrafamiliärer Konkurrenz in Verbindung stehen würde. Jedoch könnten die Häufigkeiten der Schätzungen sowie Unterschiede in der Versuchsanordnung einen abschwächenden Einfluß gehabt haben.

Introduction

One of the principal aims of the breeding programme for Sitka spruce (*Pitcea sitchensis* (BONG.) CARR) in Britain is to improve the productivity of the species in terms of volume per hectare. Sitka spruce is the main species used in commercial forestry, accounting for 32% of existing conifer plantations and 54% of current planting (CAS, 1980, p 145). The economic advantages of improved yield are easily quantified and are substantial (GILL, 1982). Justification of investment in tree improvement requires that the cost of an improvement programme is more than met by the expected returns. The most expensive element of most tree breeding programmes, and Sitka spruce is no exception, is the essential process of progeny testing. Any reduction in progeny test costs can greatly increase the financial viability of the breeding programme.

Sitka spruce in Britain reaches its maximum mean annual increment at age 45—65 years depending on site quality (Forestry Commission, 1981). Commercial rotations are of similar length except where foreshortened by risk of premature wind-blow. Progeny tests designed to allow family comparisons of rotation-age volume production would be prohibitively expensive in terms of the plot size required, the delay in realising gain and the length of the generation cycle. To maximise the rate of genetic gain, the breeder must utilize progeny test results as soon as family performance can be reasonably predicted. The optimum time of assessment occurs when the additional gain, achieved by more accurate later selection, equals the additional costs of retaining the progeny tests.

Selection at an age earlier than rotation age, with the aim of improving rotation age yields, is effectively indirect selection on a juvenile trait with reliance on a correlated response in a mature trait (NANSON, 1969). When heritability is defined (h^2) as the ratio of utilisable genetic variation to phentotypic variation, correlated gain in the mature trait after selection on the juvenile trait is given by:

$$CG_M = i_J \ h_J \ h_M \ r_G \ \sigma_{PM}$$

where:

CG = correlated gain
i = selection intensity
h = square root of heritability
r_G = genetic correlation between juvenile and mature traits calculated as the family component of covariance of the 2 traits divided by the square root of the product of the respective family components of variance.
σ_P = square root of the phenotypic variance

and where subscripts J and M refer to parameters measured on the juvenile and mature traits respectively.

In the case of half-sib progeny tests, family heritability (h^2) is given by $\frac{1}{4}\ \sigma^2_A/\sigma^2_P$ (WRIGHT, 1976, NAMKOONG, 1979) where σ^2_A = additive genetic variance. Thus the formula for correlated gain may be expressed as:

$$CG_M = i_J\ h_J\ \sqrt{\frac{\frac{1}{2}\sigma_{AM}^2}{\sigma^2_{PM}}}\ r_G\ \sigma_{PM}$$

$$= i_J\ h_J\ \frac{1}{2}\sigma_{AM}\ r_G$$

Allowing for the different definition of heritability, these formulae are equivalent to those of FALCONER (1960). Thus there are two parameters which cannot be measured on the juvenile trait but require to be known before correlated gain at maturity can be calculated:

a. the additive variance of the mature population and
b. the genetic correlation between the juvenile and mature traits.

Tree breeders generally are not well placed to obtain estimates of these parameters. Most progeny tests are relatively young and usually have plot sizes too small to permit measurement of volume yield when rotation age is reached. CANNELL (1982) points out that plot sizes must be sufficient to avoid inter-genotypic competition, otherwise high juvenile-mature correlations may indicate only a correlation between 'isolation' and 'competition' ideotypes and not necessarily a correlation between juvenile traits and the desired 'crop' ideotypes. Provenance trials are often older with larger plot sizes but there is no reason to expect that high juvenile-mature correlations for provenances will also apply to families. NAMKOONG et al. (1972) with Douglas fir (*Pseudotsuga menziesii* (MIRB) FRANCO) and NAMKOONG and CONKLE (1976) with Ponderosa pine (*Pinus ponderosa* LAWS) found that although population differences were established at an early age and maintained, family differences were not predictable.

Juvenile-Mature Correlations

Several published studies estimate juvenile-mature correlations, some as phenotypic correlations of family means and rather fewer as genetic correlations. SQUILLACE and GANSEL (1974), with Slash pine (*Pinus elliottii* ENGELM.) families in single-plant plots, found family-mean correlations between height at age 25 and height at age 3, 8, 14 and 18 of 0, 0.80, 0.96 and 0.98 respectively for open-pollinated families and generally lower for full-sib families. They concluded that maximum gain per year could be achieved by selecting at about age 10 for a rotation age of 25 years. WAKELEY (1971), with Slash, Loblolly (*Pinus taeda* L.), Longleaf (*P. palustris* MILL.) and Shortleaf (*P. echinata* MILL.) pines found good correlations for height and diameter between ages 20 and 30 but poor correlations with ages earlier than 15 years. His correlations were based on individual phenotypes thus including all non-additive and environmental variances.

GIERTYCH (1974) found poor correlations of family means for height at age 16 and diameter at age 59 with Scots pine (*Pinus sylvestris* L.) YING and MORGENSTERN (1979) found genetic correlations of 0.60—0.92 between height at ages 8 and 11 and height at age 22, for open-pollinated White spruce (*Picea glauca* (MOENCH) VOSS) families with plot sizes of 49—50 plants. VAN HAVERHEKE (1983) found very high and consistent genetic correlations (0.94) between height as early as 3 years and height at 17 years for a mixture of origins and families of *Pinus flexilis* JAMES and *P. strobiformis* ENGELM. The correlations are however exaggerated by the effect of species and origin and correlations between families within origins are likely to be lower. NAMKOONG and CONKLE (1976) obtained genetic correlations between height at 29 years and height at 3, 5, 7, 8, 12, 20 and 25 years of 0.05, 0.19, —0.4, 0.47, —0.60, 0.64 and 0.85 respectively for open-pollinated Ponderosa pine families with 1 or 2 measureable trees per plot. Open-pollinated families of Douglas fir (NAMKOONG et al. 1972) yielded genetic correlations between height at 33 years of age and height at 5, 10, 12, 15, 18, 23 and 28 of —0.57, —0.74, —1.00, 0.24, 0.93, 0.97 and 0.96 respectively. Intergenotypic competition may have exaggerated the correlations as families were planted in row plots.

In a review of juvenile-mature correlation studies, LAMBETH (1980) concludes that 5—6 years is the optimum test-period in terms of maximum gain per year for 20-year rotations and 7—8 years for 50-year rotations. This is rather earlier than the 10 years suggested as optimum for 25-year rotations of slash pine (SQUILLACE and GANSEL, 1974) and FRANKLIN (1979) suggests that selection be delayed until the middle of the mature genotypic phase which is typically about half the economic rotation age.

Time trends in additive variance

Fewer studies have examined time trends in additive variance. Relative additive variance in half-sib progeny tests can be expressed as the coefficient of family variation, calculated as the square-root of the family component of variance divided by the mean. FRANKLIN (1979) shows trends in additive variance for a number of studies but the data presented are in absolute rather than relative terms. NAMKOONG et al. (1972) showed that small height differences between half-sib families of Douglas fir disappeared after 40 years indicating declining relative additive variance. NAMKOONG and CONKLE (1976) (*Table 1*) found a marked decrease in additive variance between ages 5 and 7 for height of half-sib families of Ponderosa pine. Additive variance increased slightly in relative magnitude after age 20, but at 29 years had not regained earlier levels.

Half-sib families of White spruce (*Table 2*) generally show a decline in relative additive variance between height at 8 or 11 years and height at 22 years. Diameter variance is usually smaller than height variance at 22 years.

Further evidence of declining additive variance with increasing inter-tree competition is given by CANNELL (1982) where open-pollinated families of Sitka spruce at wide spacing continued to show significant family differences at age 4, whereas the same families at very close spacing, and therefore under intense inter-tree competition, failed to show significant variation.

Declining additive variance must be a source of major concern to tree breeders. If stands at rotation age show no additive variance then there is no prospect of obtaining

Table 1. — Coefficient of family variation (%) for height of ha'f-sib families of Ponderosa pine. Data from NAMKOONG and CONKLE (1976).

Age (years)	3	5	7	8	12	20	25	29
Coeff family variation	9.4	8.6	4.8	3.6	2.7	3.4	3.6	4.4

Table 2. — Coefficient of family variation (%) for height and diameter of half-sib families of White spruce. Data from YING and MORGENSTERN (1979).

Study	8/11 height	22 height	22 diameter
		Age (years)	
91A	4.9	6.0	3.5
91B	9.0	1.4	0
92A	7.6	5.6	4.6
92B	10.6	6.4	6.6

genetic gain by traditional methods of breeding. Significant additive variance in juvenile stages means that selection of families for rapid establishment and early growth on specific microsites is likely to be successful (NAMKOONG and CONKLE, 1976) but unless there is genetic variance present at rotation age, the aim of improved volume production cannot be achieved.

The following reports on two investigations into juvenile-mature correlations and trends in additive variance in Sitka spruce, first in a small 27-year-old progeny test and secondly in a larger set of 15-year-old tests replicated on several sites.

Study 1
Materials and Methods

In 1953, a progeny test of 11 half-sib families derived from open-pollinated Sitka spruce plus trees was planted at Kilmichael Forest, Strathclyde Region, Scotland.

The plus trees, although of unknown origin, can be considered as representative of the population of plus trees growing and selected in British forests. The original experiment design had 5 complete randomised blocks and 10 × 10 = 100 plant plots. Plant spacing was 1.7 m × 1.7 m, and an unplanted row was left between all plots. At 26 years, parts of the experiment had grown very poorly, exhibiting slow and stunted growth caused primarily by poor soil drainage. One block showed satisfactory and regular growth and some plots in a further two blocks also showed satifactory, regular growth. As these blocks were adjacent and on a similar site type they were combined to form a second replication of 9 of the 11 families.

Height had been assessed at 1, 3 and 6 years, and breast height diameter was assessed at 26 years. An analysis of residual diameters (actual diameter less mean plot effect) of trees at different positions in the plot indicated that the outer row of the plot contributed significantly to within-plot variance, and further analysis of this and subsequent assessments was, therefore, confined to the inner 8 × 8 plants.

At age 27, random samples of 25 trees per plot (excluding the outer rows) were measured for breast height diameter, felled, and measured for total height. Measurements were also taken to allow stem volumes to be calculated according to Procedure 1 in Forestry Commission (1975) Booklet No 39. Analysis of variance and expected mean squares are given in Table 3.

Table 3. — Analysis of variance model used. where n is the harmonic mean number of plants per plot.

Source of variance	df	Expected mean square
Blocks	1	$\sigma^2_W + n\,\sigma^2_{fb} + 9n\sigma^2_b$
Families	8	$\sigma^2_W + n\,\sigma^2_{fb} + 2n\sigma^2_f$
Blocks x families	8	$\sigma^2_W + n\,\sigma^2_{fb}$
Within plots		σ^2_W

Results

Survival of most families was similar, being above 97% at the 6th year, and 86—94% at the 26th year. The family of plus tree 210 was exceptional with survival falling to 59% by the 26th year. The fact that this family's low survival was similar in both blocks discounts the possibility of catastrophic death due to plot position. The same family has occurred in only one other progeny test, in north Wales, where survival after 20 years was 50% compared to 69—75% for other families in that test. The low survival had a marked effect on mean tree volumes, but volume per plot was similar to that for other families.

With the reduced experimental design, few traits show significant differences between families (Table 4), and for several traits family components of variance were zero or negative, so that no coefficient of family variation could be calculated. Due to the inability of the design to detect family differences, few genetic correlations can be calculated. Phenotypic correlations of family means are, however, shown in Table 5. The correlation coefficients show very poor correlations between 1 year height and any 27 year trait.

Volume per plot is, however, very highly correlated with height at both 3 and 6 years. When the family of plus tree 210 (having low survival and large mean-tree size) is ex-

Table 4. — Analysis of variance.

Trait	Mean	Range	Significance of family variance	Coefficient of family variance %
1 year height	20.4 cm	15.8-24.7	*	12.6
3 year height	50.9 cm	43.5-59.3	NS	-
6 year height	1.70 m	1.44-2.01	NS	-
26 year diameter	15.9 cm	14.5-19.4	**	9.2
27 year diameter	15.9 cm	14.4-19.6	*	8.8
27 year basal area/tree	212 cm^2	170-328	*	20.7
27 year basal area/plot	1.15 m^2	0.95-1.36	NS	-
27 year height	15.9 m	14.2-17.0	NS	-
27 year volume/tree	0.169 m^3	0.137-0.269	NS	19.8
27 year volume/plot	8.94 m^3	6.86-10.14	NS	-

Table 5. — Phenotypic correlations of family means (bracketed figures exclude the family of plus tree 210).

	27 year height	27 year diameter	27 year volume/tree	27 year volume/plot
1 year height	-0.15 (0.08)	-0.34 (0.18)	-0.44 (0.17)	0.32 (0.39)
3 year height	0.39 (0.65)	0.15 (0.95)	-0.08 (0.92)	0.84 (0.93)
6 year height	0.28 (0.42)	0.30 (0.93)	0.06 (0.86)	0.86 (0.89)

Table 6. —

where n is the harmonic mean number of plants per plot
b is the harmonic mean number of block per site
s is the number of sites
f is the number of families

Source	df	Expected mean square
Families	45	$\sigma^2_W + n\sigma^2_{fb} + nb\sigma^2_{fs} + nbs\sigma^2_f$
Sites	6	$\sigma^2_W + n\sigma^2_{fb} + nb\sigma^2_{fs} + nbf\sigma^2_s$
Families x sites	270	$\sigma^2_W + n\sigma^2_{fb} + nb\sigma^2_{fs}$
Blocks within sites	27	$\sigma^2_W + n\sigma^2_{fb} + nf\sigma^2_b$
Families x blocks within site	1215	$\sigma^2_W + n\sigma^2_{fb}$

cluded, 27 year volume per tree and 27 year mean diameter both become highly correlated with 3 and 6 year height. Height at 27 years is not well correlated with 3 or 6 year height irrespective of whether the family of plus tree 210 is excluded. In the absence of significant family variation, these correlations must be considered largely environmental but they do show that plots tallest at 3 or 6 years will give he greatest volume production at 27 years, and, if survival is similar, the largest-diameter trees.

Study 2

Materials and Methods

In 1970, progeny tests of half-sib families derived from open-pollinated Sitka spruce plus trees were established on 8 sites throughout Britain. These sites and experimental designs are described by JOHNSTONE and SAMUEL (1978). One site (Brendon) failed to make regular growth, and this investigation is confined to the 46 families which are fully replicated on the 7 remaining sites. As in the first study, the families are representative of the population of plus tree families in Britain. All experiments were planted as complete randomised blocks based on line-plots of 4 or 8 plants or square plots of 16 plants, thus some inter-genotypic competition is likely to have occurred by the 10th year, at least on the more vigorous sites, and intensified by the 15th year.

At all sites, height was assessed after planting (HT00) except at Aultmore, except at 3 years (HT03) Farigaig, except at 6 years (HT06) and at 10 years (HT10). Diameter at breast height was assessed at 10 (DM10) and 15 (DM15) years. Analysis of variance and expected mean squares are

Table 8. — Genetic Correlations.
(Correlations with HT00 and HT03 are based on 6 sites, correlation between HT00 and HT03 is based on 5 sites).

	HT00	HT03	HT06	HT10	DM10
HT00					
HT03	0.363				
HT06	0.407	0.948			
HT10	0.339	0.870	0.926		
DM10	0.492	0.810	0.903	0.828	
DM15	0.294	0.722	0.778	0.790	0.917

given in *Table 6*. Analyses of covariance have the same coefficients and degrees of freedom as analysis of variance.

Results

Family differences were highly significant (P = 0.001) for all traits. Variance components were calculated from expected mean-squares and are shown in *Table 7*. Variance components were used to calculate the appropriate phenotypic variances for a half-sib progeny test:

$$\sigma^2_P = (\tfrac{1}{n}\sigma^2_W + \sigma^2_{fb})\,(bs)^{-1} + \sigma^2_{fs}\,(s)^{-1} + \sigma^2_f$$

Family heritabilities were then calculated. These, along with trait means ($\bar{x}$) are also shown in *Table 7*. Genetic correlations were calculated and are shown in *Table 8*.

Figure 1 shows the trend in the coefficient of family variation. Similar declining trends in family variation occurred at each individual site as shown in *Table 9*.

Correlated gains in all traits resultant on selection on any particular trait were calculated using the formula:

$$\%CG_M = i_J\,h_J\,\tfrac{1}{2}\,\sigma_{AM}\,r_G \cdot \frac{100}{\bar{x}_M} \cdot 2$$

where a selection intensity of 1:10 (equivalent to $i_J = 1.755$, BECKER, 1984) is assumed for the purpose of this illustration. Heritability, additive variance and trait mean are taken from *Table 7* and genetic correlations from *Table 8*. The factor of 2 is introduced on the assumption that genetic gain will be achieved by means of a random-mating multi-clone orchard where both female and male parents have been selected on the basis of progeny test results. Correlated gains are shown in *Table 10*.

Thus the maximum gain achievable in 6th year height is 20.6%, 8.9% of this being achievable by selection on height-

Table 7. — Variance components and half-sib family heritabilities.

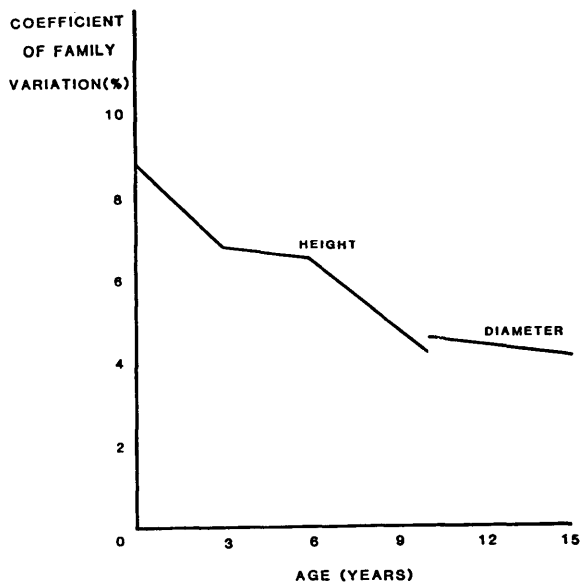| Trait	Unit	Variance component					Mean
		$(\tfrac{1}{n}\sigma^2_W + \sigma^2_{fb})$	σ^2_{fs}	$\sigma^2_f = \tfrac{1}{4}\sigma^2_A$	σ^2_P	h^2	$\bar{x}$
HT00	cm	8.30	1.99	6.50	7.18	0.91	28.9
HT03	cm	100.9	22.0	37.9	45.7	0.83	90.8
HT06	cm	534.3	125.4	166.5	202.6	0.82	199.1
HT10	m	0.246	0.029	0.039	0.051	0.75	4.63
DM10	cm	0.918	0.071	0.102	0.144	0.71	6.99
DM15	cm	1.650	0.125	0.219	0.293	0.75	11.44

Figure 1. — Trend in coefficient of family variation.

at-planting and 19.6% selecting an 3rd year height. Due to declining additive variance, the maximum achievable gain in 10th year height has fallen to 12.9%, but 11.8% or 12.5% of this can be achieved by selecting on 3rd or 6th year height respectively. The table shows the high predictive value of assessments at 3 and particularly 6 years.

Discussion

The first study shows high phenotypic correlations between heights at 3 or 6 years, and volume at 27 years in a case where inter-family competition is absent. The second study shows high genetic correlations between height as early as 3 years and later heights and diameter; the correlations possibly being exaggerated to an unknown extent by inter-family competition. Correlations are sufficiently strong to suggest that retention of progeny tests to 15 years gives very little further advantage over selection at 6, or even 3 years. Progeny tests for vigour can therefore be designed for short duration. Savings in test costs may well outweight the slight additional gains achievable by retention to 15 years. Additional unpublished work indicates that morphological traits at 15 years, particularly stem straightness, can also be predicted from 6th year assessments, although assessment at 3 years is unlikely to be effective. Work is currently underway to investigate the age at which wood quality characteristics can be efficiently predicted, and present progeny test designs must continue to allow for the possibility of a longer testing-phase being required. Potential gains in wood quality will have to be sufficient to offset any additional testing costs and this aspect is also being investigated.

Table 10. — Correlated Genetic Gains (%).

Selection Trait	Correlated gain in					
	HT00	HT03	HT06	HT10	DM10	DM15
HT00	29.6	8.2	8.9	4.8	7.5	4.0
HT03		21.7	19.6	11.8	11.9	9.5
HT06			20.6	12.5	13.2	10.1
HT10				12.9	11.6	9.9
DM10					13.6	11.1
DM15						12.4

While selection for vigour appears to be effective at early ages, declining additive variance must be taken into account in making gain predictions. Selections estimated to give a 20% gain in terms of 6th year height will yield only a 12% gain in terms of 10th year height and 15th year diameter. Hence the importance of quoting genetic gains not only by reference to a base population but also in terms of a trait at a specified age. Although additive variance has declined by 15 years, a 12% gain in height and diameter is equivalent to a volume gain of 40% at this age, so gains can still be substantial.

What happens beyond 15 years is not known. Long-term experiments are required to investigate whether strong genetic correlations continue, and whether additive variance continues to decline. Such experiments require to be carefully designed with large plots to avoid the effects of inter-family competition throughout the rotation. An adequate range of families must be included to ensure that significant additive variance is present and which is capable of being detected by a suitable experiment design.

Reasons for the decline in additive variation to 15 years can only be speculative. High initial additive variance may be due to maternal effects, such as seed weight, which diminish with time after planting. Further decline in additive variation occurs between 6 and 10 years and may be associated with the onset of inter- and intra-family competition. *Table 9,* however, provides no evidence of the decline occurring earlier on the faster growing sites. It may be that assessments were insufficiently frequent to display site-dependent trend differences. Differences in test design between sites could also have a confounding effect. A later series of tests (described by SAMUEL and JOHNSTONE, 1979) may be better able to provide an explanation.

Conclusions

Both studies show high correlations between height as early as 3 years and later measures of vigour, such that progeny testing for vigour to 3 or 6 years may well be more cost-effective than progeny testing to 15 years. Additive variance declines with age, but significant additive variance remains at 15 years. Further experimentation is required to investigate correlations and trends in variance beyond the age of 15 years.

Table 9. — Coefficient of family variation (%) and significance of family variance.

Site	TG	KE	GA	TY	GD	AU	FG	Mean
HT00	9.2***	8.7***	10.0***	8.9***	10.6***	N/A	8.5***	8.8***
HT03	8.7***	8.8***	6.8***	6.8***	8.1***	7.5***	N/A	6.8***
HT06	7.8***	8.7**	7.0***	6.2***	8.5***	6.9***	9.5***	6.5***
HT10	4.2^{NS}	6.8***	4.5***	5.6***	4.8*	5.5***	4.0**	4.2***
DM10	– ^{NS}	5.7*	4.7***	6.8***	5.8*	6.8***	4.8*	4.6***
DM15	2.8^{NS}	4.0*	4.9***	4.4***	3.8^{NS}	6.0***	5.4*	4.1***

(N/A – not assessed; – = negative family component of variance; *** significant at
p = 0.001, ** p = 0.01, * p = 0.05, NS = not significant)

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Inbreeding and Interspecific Hybridization in Eucalyptus gunnii

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Summary

The success and vigour of plants arising from self and close matings of *Eucalyptus gunnii* are compared with wide intraspecific crosses and a range of interspecific crosses. The barriers to inbreeding in *E. gunnii* are strong, in many cases stronger than the barriers to interspecific hybridization. The success (number of plants obtained/flower pollinated) of self-pollination and close intraspecific crosses was less than wide intraspecific crosses and most interspecific crosses investigated, as was the height and survival after 1 year's plantation growth. *E. gunnii* females demonstrate wide crossability, with the success of most interspecific hybrid combinations tried with species from the section *Maidenaria*, not significantly different from that of wide intraspecific crosses. The only major barrier to interspecific hybridization found was with *E. globulus*. There was not a strong association between crossability and the taxonomic/genetic distance between parents, although after 1 year's plantation growth, F_1 hybrids from the only interseries cross examined (*E. gunnii* × *ovata*) showed reduced vigour. The implications of these results for the development of breeding strategies as well as for gene flow and hybridization in natural populations are discussed. Strong barriers to inbreeding in *Eucalyptus* may result in a disparity between pollen dispersal and gene flow in natural stands, with more distant matings favoured.

Key words: Eucalyptus, breeding system, inbreeding depression, self-incompatability, hybridization, crossability, gene flow.

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Zusammenfassung

Erfolg und Wüchsigkeit von Pflanzen aus Selbstbestäubung und Kreuzung naher Verwandten von *Eucalyptus gunnii* werden mit intraspezifischen Kreuzungen weiter entfernter Verwandter und mit Artkreuzungen verglichen. Die Kreuzungsbarrieren gegen Inzucht sind bei *Eucalyptus gunnii* groß, in vielen Fällen größer als bei Artbastardierung. Der Erfolg (Anzahl entstandener Pflanzen pro bestäubter Blüte) war bei Selbstungen und bei Kreuzungen naher Verwandter innerhalb der Art geringer als bei Kreuzung weiter entfernter Verwandter und als bei den meisten Artkreuzungen. Dies gilt auch für Höhe und Überlebensrate nach einjährigem Wachstum in einer Plantage. *E. gunnii*-Mütter weisen eine große Kreuzbarkeit auf. Der Erfolg der meisten Bastarde aus versuchten Artkreuzungskombinationen mit Arten der Sektion *Maidenaria* war nicht signifikant anders als der bei Kreuzungen weiter entfernter Verwandter innerhalb der Art. Die einzige Hauptbarriere gegen Artbastardierung wurde bei *E. globulus* gefunden. Dort bestand keine enge Beziehung zwischen Kreuzbarkeit und dem taxonomisch-genetischen Abstand zwischen den Eltern, obwohl die F_1-Bastarde der einzigen untersuchten Interserienkreuzung (*E. gunnii* × *ovata*) nach einjährigem Wachstum auf der Plantage eine reduzierte Wüchsigkeit zeigten. Die Folgerungen dieser Ergebnisse für die Entwicklung von Züchtungsstrategien wie auch für die Genverteilung und Hybridisierung natürlicher Populationen werden diskutiert. Große Inzuchtbarrieren bei *Eucalyptus* können eine Ungleichheit zwischen Pollen- und Genverteilung in einheimischen Beständen zur Folge haben, mit einer Bevorzugung der Paarung entfernter Verwandter.

Résumé

La réussite et la vigueur des plants issus d'autoféconda-tion et de croisements de parents génétiquement proches