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Genetic Variation in Growth of Outcrossed, Selfed and Open-Pollinated Progenies of *Eucalyptus regnans* and some Implications for Breeding Strategy

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Summary

Open-pollinated, selfed and outcrossed progenies were derived from thirteen parent trees in natural stands of *Eucalyptus regnans*, and evaluated in a field trial. Forty-five months after planting, volume of outcross progenies averaged 37% more than the selfs. From the growth of open-pollinated progenies relative to selfs and outcrosses, the average outcrossing rates for the parent trees was estimated to be 0.69. The mixed mating system of this species complicates genetic interpretation of open-pollinated progeny test results. Heritability (h^2) for volume growth at 45 months was estimated as 0.16 from the selfs and 0.18 from the outcrossed progeny, compared with an apparent value of 0.45 from the open-pollinated progeny. The variance between open-pollinated progeny appeared to be inflated by heterogeneity in both outcrossing rates and inbreeding depression.

The ranking of parents on outcross progeny performance was more highly correlated with self rankings than with open-pollinated rankings. It was concluded that vigorous open-pollinated progeny were indicative of high breeding value, but that the converse could not necessarily be claimed. Important implications for breeding strategy are that the role of family selection during the initial phase of domestication of *E. regnans* requires re-examination. Also that selfed progeny (which are more easily produced than outcrosses) may prove useful for estimation of genetic parameters and future breeding.

Key words: *Eucalyptus*, progeny testing, breeding, inbreeding.

Zusammenfassung

Nachkommenschaften, entstanden aus freier Abblüte, Selbstbefruchtung und Kreuzungen, von 13 Elternbäumen aus natürlichen Beständen von *Eucalyptus regnans* wurden im Feldversuch untersucht. Fünfundvierzig Monate nach dem Auspflanzen lag das Volumen der Kreuzungsnachkommenschaft durchschnittlich 37% höher als das der Selbststun-

gen. Die durchschnittlichen Fremdungsraten der Elternbäume wurden auf 0,69 geschätzt basierend auf der Wachstumsrelation von Selbst- und Fremdbefruchtungsnachkommenschaften. Das Paarungssystem dieser Art komplizierte die genetische Interpretation der Ergebnisse frei abgeblühter Nachkommenschaften. Die Heritabilität (h^2) für das Volumenwachstum im Alter von 45 Monaten betrug 0,16 für die Selbststungen, 0,18 für die Fremdungen und bei den frei abgeblühten Nachkommenschaften 0,45. Die Varianz zwischen frei abgeblühten Nachkommenschaften schien durch die Heterogenität der Fremdbefruchtungsraten und durch die Inzuchtdepression erhöht worden zu sein. Eine Rangordnung der Eltern aufgrund des Erscheinungsbildes der Fremdungen war mit der Rangordnung der Selbststungen enger korreliert als mit der der Nachkommenschaften aus freier Abblüte. Es wird geschlossen, daß lebensfähige (kräftige) frei abgeblühte Nachkommenschaften ein Anzeichen für einen hohen Zuchtwert sind, aber daß der gegenteilige Schluß nicht notwendigerweise gezogen werden muß. Wichtige Folgerungen für die Züchtungsstrategie sind, daß die Rolle der Familienselektion für die Anfangsphase der Kultivierung von *E. regnans* eine erneute Untersuchung erfordert. Die Selbststungen, die leichter erzeugt werden können als Fremdungen, können sich für die Schätzung genetischer Parameter und die zukünftige Züchtung als nützlich erweisen.

Introduction

Eucalyptus regnans F. MUELL. is a major commercial timber species in south-eastern Australia (BOLAND *et al.*, 1984) and the subject of several genetic improvement programs (ELDRIDGE, 1971; PEDERICK, 1976; GRIFFIN *et al.*, 1982a). It is pollinated by a variety of insects and in common with other eucalypts has a mixed mating system (MORAN and BELL, 1983; GRIFFIN *et al.*, 1987). Open-pollinated seed from natural stands of *E. regnans* thus consists of a mixture of outcrossed and inbred seed resulting from selfing and from mating of related individuals. The actual outcrossing rate for any particular seed crop of an individual tree will be determined by a variety of genetic and environmental factors including self-fertility (ELDRIDGE and GRIFFIN, 1983),

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flowering phenology relative to neighbouring trees in the stand (GRIFFIN, 1980) and weather conditions during the flowering period which influence pollinator activity (GRIFFIN and C. P. OHMART, unpubl.).

Clearly it is not valid to regard such open-pollinated progenies as half-sibs for the purpose of estimating individual heritability (WILCOX, 1980). The actual coefficient of relationship (r) among progeny will be higher than the $r = 1/4$ for true half-sibs, and individual heritabilities based on the assumption of $r = 1/4$ will therefore be biased upwards (NAMKOONG, 1966; SQUILLACE, 1974). Earlier studies of open-pollinated eucalypt progenies (e.g. ELDRIDGE, 1972; KEDHARNATH and VAKSHASYA, 1977; KAGEYAMA and VENCOSKY, 1983; KEDHARNATH, 1982) have not taken sufficient account of this complication, although ELDRIDGE (1976) drew attention to the need to consider the consequences of a mixed breeding system for development of breeding strategy for eucalypts. No assumptions regarding coefficients of relationship of open-pollinated progeny are required for estimating genetic parameters such as family heritability or genetic correlations.

The experiment described in this paper compared sets of controlled outcrossed (O), selfed (S) and open-pollinated (OP) progeny in order to assess inbreeding effects, calculate genetic variances and covariances, and explore bias in individual heritability estimates based on evaluation of OP progeny.

Methods

Thirteen trees growing in two natural stands of *E. regnans* F. MUELL. were chosen for study. No selection criteria were applied other than that each tree had to have accessible flowering branches. Six of the parents (N1–6) were growing at Narracan, Victoria (lat. 38°20'S, long. 146°14'E; see GRIFFIN (1980) for stand description), and the remainder (T7–14) in a similar stand nearby at Thorpdale.

The mean distance between designated male and female parents was 250 m at Narracan with a minimum of 50 m, and for Thorpdale 106 m with a minimum of 20 m. For purposes of this study trees were assumed to be unrelated, although in such natural populations the possibility of some degree of relatedness between individuals cannot be discounted.

Mating designs

The O progeny were produced by mating the six Narracan parent trees in a 3 female \times 3 male design II (factorial) and those from Thorpdale in a 3 \times 4 design II. All parent trees were also self pollinated and OP seed was harvested from each. The controlled pollinations were carried out over two successive flowering seasons. Procedures are described in GRIFFIN *et al.* (1982b) and ELDRIDGE and GRIFFIN (1983).

Trial Establishment and Measurement

Ripe capsules were harvested, seed extracted, moist-stratified for four weeks at 5°C and germinated in punnets. Germinants were pricked out into peat pots and raised in an open nursery for seven months prior to outplanting. In the nursery all 47 families of the three population types were established in randomised blocks with 12 replicates of 5-seedling row plots.

The field planting site was a fertile ex-pasture which, judging from adjacent vegetation, had originally carried *E. regnans*. Weeds were controlled by strip-spraying prior to ploughing, and trees were planted at 2 \times 3 m spacing in August 1979. The field design was 12 replicates of 3-tree non-contiguous family plots. This design was intended to

Table 1. — Expectations of mean squares relevant to estimating genetic parameters from analyses of S and OP progeny.

Source of variation	d.f.	Expectations of mean squares ^A
Female	f-1	$\sigma_w^2 + k_1 \sigma_f^2$
Female \times block	(f-1)(b-1)	$\sigma_w^2 + k_2 \sigma_{fb}^2$
Within-plots	N-bf	σ_w^2

^A) There are f female parents, b randomised complete blocks, and a total of N open-pollinated or selfed progeny in the trial. The variance component σ_f^2 is due to female parents, σ_{fb}^2 female \times block interactions, and σ_w^2 within-plot error. Coefficients of variance components, for the open-pollinated and selfed progeny were $k_1 = 18.71$ and 12.77 , respectively, and $k_2 = 1.77$ and 1.66 .

simulate the intimate mixture of progeny of the different mating types which would occur under natural regeneration, while still retaining a degree of blocking necessary for reliable comparison of families and estimating variance components. A single row of buffer trees was planted around the whole trial but there were no internal buffers.

Height (Ht) of all trees was measured at 3, 11, 21, 30 and 45 months after planting; diameter (Dia) at breast height (over-bark) was also measured on the latter two occasions, permitting computation of conic volume (Vol) per tree. Only trees which survived to 45 months with little distortion from wind damage were included in analyses. Average family sizes analysed were $n_{op} = 19$, $n_s = 14$, $n_o = 20$ progenies.

Analyses of Data

1) Open-pollinated and Selfed Progeny

Individual tree data for OP and S progeny were analysed separately using a least-squares program written by HARVEY (1977). The analysis of each set of data was based on the mixed model —

$$Y_{ikl} = u + f_i + b_k + fb_{ik} + e_{ikl} \quad (1)$$

where Y_{ikl} represents the individual tree observations, u the overall mean, f_i the effect of the i th female parent of either the OP or S progeny, b_k the effect of the k th randomised complete block, fb_{ik} the female \times block interaction, and e_{ikl} the within-plot error. The effect of blocks was assumed fixed in the Model 1 above, and in subsequent models used to analyse design II data. The effect of female parents was considered random. Variance due to female parents (σ_f^2), female \times block interactions (σ_{fb}^2), and within-plot error (σ_w^2) were obtained by equating the expectations of mean squares given in Table 1.

MORAN and BELL (1983) estimated that the outcrossing rate in natural stands of *E. regnans* is, in common with other eucalypt species, around 0.70. Extending the calculations of SQUILLACE (1974, Table 7) it can be shown that 30% selfing gives an average coefficient of relationship among OP progeny of $r = 1/2.5$. This calculation is based on the assumption of five 'equally effective local males' (using SQUILLACE's terminology) and no non-local pollen. In the case of S progeny the coefficient of relationship is $r = 1/1.5$ (BARKER and LIBBY, 1974; SQUILLACE, 1974).

The component σ_f^2/r was used to provide separate estimators of additive genetic variance (σ_a^2) for OP (i.e. $\sigma_a^2 = 2.5 \sigma_f^2$) and S progeny ($\sigma_a^2 = 1.5 \sigma_f^2$). Likewise individual heritabilities (h_i^2) were calculated separately for OP and S progeny as —

$$h_i^2 = \sigma_a^2 / (\sigma_f^2 + \sigma_{fb}^2 + \sigma_w^2) \quad (2)$$

Table 2. — Expectations of mean squares relevant to estimating genetic parameters from analyses of O progeny.

Source of variation	d.f.	Expectations of mean squares ^A
Analysis of individual tree data —		
Within-plots	N-bfm	σ_w^2
Analysis of plot mean data —		
Female	f-1	$\sigma_p^2 + (1/k_a)\sigma_w^2 + k_8\sigma_{fm}^2 + k_{11}\sigma_f^2$
Male	m-1	$\sigma_p^2 + (1/k_s)\sigma_w^2 + k_9\sigma_{fm}^2 + k_{12}\sigma_f^2$
Female × male	(f-1)(m-1)	$\sigma_p^2 + (1/k_e)\sigma_w^2 + k_{10}\sigma_{fm}^2$
Female-male × block	(fm-1)(b-1)	$\sigma_p^2 + (1/k_r)\sigma_w^2$

A) There are f female parents, m male parents, b randomised complete blocks, and N trees in each design II mating. The variance component σ_f^2 is due to females, σ_m^2 males, σ_{fm}^2 female × male interactions, σ_p^2 between-plot error and σ_w^2 within-plot error. Coefficients of variance components relevant to genetic parameter estimation were estimated for the pooled design II analysis as: $k_7 = 1.90$, $k_{10} = 9.70$, $k_{11} = 34.46$ and $k_{12} = 29.79$.

Standard errors of the individual heritabilities were estimated according to SWIGER *et al.* (1964). Additive genetic correlations (denoted r_a) were estimated using the additive genetic variances and covariances from analyses of individual tree data of OP and S progeny. Standard errors of r_a were estimated according to TALLIS (1959).

2) Outcrossed Progeny

In order to simplify the analysis, data for each separate design II mating were analysed using two analyses of variance (following the method outlined in KEMPTHORNE, 1969; COTTERILL *et al.*, 1987; and others): (a) an analysis of individual tree data to determine mean squares within-plots, and (b) an analyses of plot means to determine mean squares (and mean cross-products) due to female parents, male parents, and female × male parent interactions. The purpose of the analysis of individual tree data is only to provide estimates of σ_w^2 which are necessary for determining heritability on an individual tree basis.

The analysis of plot means was according to the model —

$$\bar{Y}_{ijkl} = u + f_i + m_j + b_k + fm_{ij} + \epsilon_{ijkl} \quad (3)$$

where \bar{Y}_{ijkl} are the plot mean observations, u the overall mean, f_i the effect of the i th female parent, m_j the effect of the j th male parent, fm_{ij} the female × male parent interaction, b_k the effect of the k th block, and ϵ_{ijkl} the experimental error. The effects of blocks are assumed fixed while the effects of female and male parents are assumed to be random.

Sums of squares (and cross products) and degrees of freedom for the analyses of each of the two separate design II matings were summed and used to calculate pooled estimates of mean squares. Equating these pooled mean squares with the expectations presented in Table 2 provides estimates of variance due to female parents (σ_f^2), male parents (σ_m^2), female × male parent interactions (σ_{fm}^2), and between-plot error (σ_p^2). The estimation of σ_p^2 actually requires subtraction of σ_w^2 from the individual tree analysis.

It can be shown that twice the sum of the maternal and paternal components of variance (or $2(\sigma_f^2 + \sigma_m^2)$) provides an estimate of additive genetic variance for the O progeny, while the component $4\sigma_{fm}^2$ estimates dominance variance (see COTTERILL *et al.*, 1987). Individual heritabilities for O progeny were calculated as —

$$h_i^2 = 2(\sigma_f^2 + \sigma_m^2)/(\sigma_f^2 + \sigma_m^2 + \sigma_{fm}^2 + \sigma_p^2 + \sigma_w^2) \quad (4)$$

The additive genetic correlations (r_a) presented for the O progeny were calculated from averages of the maternal and paternal components of covariance and variance.

3) Constant Estimates

Least-squares means were estimated for each of the S and OP families using either: (a) all progeny measured, or (b) the largest 50% only of the S or OP progeny of each family. (The least-squares means in this case are adjusted for bias due to inequalities in the numbers of individuals of each family; COTTERILL *et al.*, 1983). The 50% truncation has been used to study the consequences (if any) of estimating breeding potential of parents from the performance of only their better progeny. BARKER and LIBBY (1974) suggest that the truncation of S family data may reduce the expression of major deleterious gene effects and hence make the performance of inbred progeny of parents a more reliable guide to the performance of the same parents under outcrossing.

Least-squares means were also estimated for each of the half-sib O families generated under design II matings. Corrections were made to the least-squares means of the O families to take account of minor differences in the overall means of all progeny in each of the two separate design II matings. Least-squares means of half-sib progeny are equivalent to the least-squares estimates of breeding value described in COTTERILL *et al.* (1983) and elsewhere.

4) Apparent Outcrossing Rate of OP Progeny

Under the assumption that inbreeding depression (ID) changes linearly with increasing levels of inbreeding, the apparent rate of outcrossing (t) under open-pollination may be estimated as —

$$t = (u_2 - u_1)/(u_3 - u_1) \quad (5)$$

where u_1 , u_2 and u_3 represent the overall least squares means for S, OP and O progeny respectively. Estimates of t were also derived using the least-squares family means of each of the individual parent trees under test.

5) Inbreeding Depression

The average depression of growth rate of selfs relative to outcrossed progeny was estimated as —

$$ID = [(u_3 - u_1)/u_3] \times 100\% \quad (6)$$

Table 3. — Mean squares for analysis of variance for traits assessed at 45 months for S, OP and O progeny.

Source	d.f.	Height (m)	Diameter (cm)	Volume (dm ³)
Selfed progeny (S):				
Block	11	3.60**	9.42*	442**
Family	12	2.88*	11.89**	413**
Family × Block	79	1.20 ^{ns}	3.94*	167 ^{ns}
Within-plot	74	1.30	2.58	143
Open-pollinated progeny (OP):				
Block	11	2.58**	7.12 ^{ns}	347 ^{ns}
Family	12	5.94**	26.94**	1491**
Family × Block	113	1.27 ^{ns}	5.66**	313 ^{ns}
Within-plot	112	1.11	4.04	240
Design II progeny (O):				
Female	4	0.34 ^{ns}	11.73*	663*
Male	5	3.86**	7.32 ^{ns}	619*
Female × Male	10	0.51 ^{ns}	2.75 ^{ns}	139 ^{ns}
Experimental error	172	0.70	2.23	192
Within-plot	202	0.98	3.52	276

** P < 0.01; * P < 0.05; ns not significant.

with u_1 and u_3 defined above. Estimates were also derived for progeny of each of the individual parents under test.

Results

The results presented and subsequent discussion concentrate on the most advanced available index of tree growth, i.e. relative volume at 45 months (denoted Vol-45), but the extent to which earlier measurements are correlated with Vol-45 is also explored. Mean squares and genetic parameter estimates for all traits derived from each of the mating designs are given in Tables 3 and 4, together with additive genetic and phenotypic correlations between Vol-45 and the other traits.

Genetic Parameters

There was fairly close agreement for all traits studied between estimates of individual heritability based on the control-pollinated S and O progeny. For instance, respective heritabilities for Vol-45 were $h_1^2 = 0.16$ for S and 0.18 for O (Table 4). In contrast, heritabilities based on OP progeny (even assuming $r = 1/2.5$) were often over twice as large (e.g. $h_1^2 = 0.45$ for Vol-45). The standard errors of heritabilities for all offspring were reasonably high relative to the absolute magnitudes of individual estimates. These higher standard errors reflect the limited number of parents and progeny analysed for each mating design.

Levels of additive genetic variance (σ_a^2) for height of S, OP and O progeny increased steadily from three to 45 months after planting (Table 4). The within-family variance (σ_e^2) for height also increased as trees grew larger. There was a particularly dramatic increase in σ_e^2 for height between three and 11 months (after the first growing

Table 4. — Individual heritabilities (h_1^2), additive genetic variance (σ_a^2) and within-family variance (σ_e^2) for each trait, and genetic (r_a) and phenotypic (r_p) correlations with volume at 45 months estimated for S, OP and O progeny. Dominance genetic (σ_d^2) is estimated for O progeny only.

Trait	$h_1^2 \pm \text{s.e.}$	σ_a^2	σ_d^2	σ_e^2	$r_a \pm \text{s.e.}$	r_p
Selfed progeny (S):						
Ht-3	.25 ± .18	.0041		.0136 ^A	.10 ± .44	.20
Ht-11	.04 ± .09	.0072		.1660	.84 ± .48	.50
Ht-21	.16 ± .14	.1185		.6734	.81 ± .48	.50
Ht-30	.13 ± .13	.1152		.8212	.63 ± .28	.81
Dia-30	.27 ± .18	.6048		1.820	.95 ± .06	.88
Vol-30	.19 ± .16	3.669		16.85	.96 ± .05	.91
Ht-45	.13 ± .13	.1862		1.297	.56 ± .33	.78
Dia-45	.23 ± .17	.9155		3.399	.97 ± .03	.97
Vol-45	.16 ± .14	28.53		157.6		
Open-pollinated progeny (OP):						
Ht-3	.26 ± .20	.0045		.0159 ^A	.65 ± .25	.36
Ht-11	.37 ± .25	.0828		.1897	.93 ± .09	.55
Ht-21	.38 ± .25	.3238		.7262	.88 ± .09	.74
Ht-30	.41 ± .26	.3795		.7742	.91 ± .07	.79
Dia-30	.55 ± .31	1.535		2.190	.96 ± .03	.85
Vol-30	.53 ± .30	15.81		23.53	.98 ± .02	.92
Ht-45	.43 ± .27	.6210		1.201	.83 ± .12	.78
Dia-45	.46 ± .28	2.815		4.956	.98 ± .01	.97
Vol-45	.45 ± .28	156.1		281.4		
Design II progeny (O):						
Ht-3	.27 ± .19	.0042	neg	.0137 ^A	.31 ± .48	.10
Ht-11	.07 ± .07	.0160	neg	.2457	.74 ± .16	.48
Ht-21	.11 ± .10	.0868	.0480	.7067	.64 ± .11	.69
Ht-30	.19 ± .16	.1822	neg	.8663	.76 ± .16	.66
Dia-30	.20 ± .16	.4556	neg	2.066	.92 ± .09	.83
Vol-30	.22 ± .17	7.658	neg	31.07	.95 ± .06	.85
Ht-45	.18 ± .16	.2246	neg	1.162	.76 ± .14	.70
Dia-45	.19 ± .17	.8284	.2156	3.946	.98 ± .02	.93
Vol-45	.18 ± .17	62.73	neg	322.7		

^A) Within-family variance estimated as $\sigma_{fb}^2 + \sigma_w^2$ for S and OP progeny and $\sigma_{fm}^2 + \sigma_p^2 + \sigma_w^2$ for O progeny.

Table 5. — Overall means for S, OP and outcrossed O progeny. Figures in brackets are percentage reductions in the means for S or OP progeny compared with the outcrossed progeny. Also given is the estimated outcrossing rate (t) of OP progeny.

Trait	Selfed (S)	Open-pollinated (OP)	Design II (O)	t_{op}
Ht-3(m)	0.45 (10)	0.50 (0)	0.50	1.0
Ht-11(m)	1.45 (22)	1.77 (5)	1.87	0.76
Ht-21(m)	4.41 (17)	4.98 (6)	5.29	0.65
Ht-30(m)	6.63 (12)	7.17 (5)	7.51	0.61
Dia-30(cm)	6.46 (17)	7.37 (6)	7.83	0.66
Vol-30(dm ³)	8.07 (37)	11.18 (13)	12.83	0.65
Ht-45(m)	9.77 (11)	10.43 (4)	10.92	0.57
Dia-45(cm)	10.35 (18)	11.88 (6)	12.64	0.67
Vol-45(dm ³)	29.40 (37)	41.45 (12)	46.98	0.69

season) which was not accompanied by similarly large increases in σ_a^2 in the case of S and O progeny. Consequently individual heritabilities decreased from $h_1^2 = 0.25$ and 0.27 for Ht-3 of the S and O offspring, respectively, to low values of $h_1^2 = 0.04$ and 0.07 for Ht-11. The same trend was not evident for OP progeny because the σ_a^2 estimated for this population increased more than σ_e^2 to 11 months.

Between 11 and 30 months (when the mean height of the outcrossed O progeny had reached 7.5 m; Table 5) the individual heritabilities for height of the S and O progeny followed the same trend as σ_a^2 and increased steadily to moderate values of $h_1^2 = 0.13$ and 0.19 (Table 4). In the case of OP progeny the apparent heritabilities for height remained fairly stable over time, increasing slightly from $h_1^2 = 0.37$ at 11 months to 0.43 at 45 months.

Individual heritabilities for diameter decreased marginally between 30 and 45 months in all three populations because the levels of σ_e^2 increased slightly more than σ_a^2 . Individual heritabilities for diameter were higher than those for height at 30 and 45 months for the S and OP progeny, but about the same for O progeny. The trends in heritability of volume reflected those for diameter.

It is worth noting that both σ_a^2 and σ_e^2 were generally lower for S progeny, particularly for diameter and volume traits (Table 4). However, when the lower overall means of S progeny (Table 5) are taken into account the coefficients of variation can be shown to be about the same. For instance, in the case of Vol-45 the coefficients of within-family variance (u/σ_e) were 0.37 for S, and 0.29 for OP and O progeny.

Negative components of dominance variance were estimated for all traits except Ht-21 and Dia-45. It may be that these negative components reflect very low levels of true dominance variance in *E. regnans* or, alternatively, they may be due to sampling effects associated with the relatively few parents studied. The levels of dominance variance were certainly low in the instances where an estimate was actually obtained. For example, Ht-21 exhibited almost twice as much additive as dominance variance ($\sigma_a^2/\sigma_d^2 = 1.79$; Table 4), while for Dia-45 $\sigma_a^2/\sigma_d^2 = 3.84$. However, these low estimates of dominance variance in the O progeny are somewhat at odds with the inbreeding depression evident in the S progeny (discussed later). A change in the population mean following inbreeding (i.e. inbreeding depression) should depend, to a fairly large extent, on the level of dominance variance (see MARYO, 1980; and others).

Additive genetic correlations between the very early Ht-3 and subsequent Vol-45 tended to be low (r_a between 0.10

and 0.65; Table 4) with high standard errors. There was a marked increase in correlation after the first growing season with Ht-11 fairly strongly genetically correlated with Vol-45 (r_a between 0.74 and 0.93). In the case of O progeny the genetic correlations between height and Vol-45 remained fairly stable between 11 and 45 months. However, in the case of S and OP progeny the genetic correlations actually diminished as pairs of measurements became closer in time. For instance, genetic correlations for S progeny were estimated at $r_a = 0.84$ between Ht-11 and Vol-45 and only $r_a = 0.56$ between Ht-45 and Vol-45. Phenotypic correlations between heights traits and Vol-45 generally remained stable or increased as measurements became increasingly closer in time.

The genetic correlations between diameter and Vol-45 were substantially higher than those involving height with low standard errors. This reflects the greater contribution of diameter to the estimated conical volume of trees. The genetic correlations between Dia-30 and Vol-45 ranged between $r_a = 0.92$ and 0.96 for all offspring, while the corresponding correlations between Dia-45 and Vol-45 ranged between $r_a = 0.97$ and 0.98.

In general, genetic correlations for OP progeny were reasonably similar to those estimated for the S and O progeny. This may be due to the fact that determination of genetic correlations requires no assumption regarding the coefficient of relationship among OP progeny.

Estimated Inbreeding Depression and Outcrossing Rates

Mean values over all progeny of each mating type are given in Table 5 together with the percentage reduction of growth of OP and S progeny relative to O families, and the estimated rate of outcrossing (t) for the OP progeny.

ID for height growth of S progeny was greatest at 11 months with the mean height of selfs some 22% less than the mean of O progeny (1.45 m c.f. 1.87 m; Table 5). ID for subsequent height measurements of S progeny decreased to 17% for Ht-21, 12% for Ht-30 and 11% for Ht-45. ID was more severe for diameter, and particularly volume, with Dia-45 and Vol-45 of S progeny averaging 18 and 37% reductions, respectively. Results given in Table 6 show that

Table 6. — Least-squares means of parents for volume (dm^3) at 45 months as estimated using S and OP progeny, before and after culling, and OP progeny. Also given are estimates of inbreeding depression (ID) for the S progeny and apparent outcrossing rate (t) for the OP progeny. The top four ranked parents according to the means of each group of progeny are indicated by rankings in square brackets.

Parent	Selfed (S)	Culled selfed (S ^c)	Open-pollinated (OP)	Culled open-pollinated (OP ^c)	Design II (O)	ID%	t_{op}
N1	32.64 [4]	39.12 ^A	49.29 [2]	63.2 [2] ^A	51.43 [3]	36.6	0.89
N2	17.88	19.48	25.57	34.13	43.15	58.6	0.30
N3	34.56 [2]	45.22 [2]	45.81	61.5 [3]	46.17	25.1	0.97
N4	28.11	42.19	35.13	45.74	46.34	39.3	0.39
N5	24.37	32.53	37.68	49.53	45.75	46.7	0.63
N6	31.08	41.11	35.03	49.54	49.0 [4]	36.6	0.22
T7	22.90	27.50	25.06	31.71	43.52	47.4	0.06
T8	22.77	33.14	48.14 [3]	63.96 [1]	48.55	53.1	0.98
T9	33.02 [3]	45.03 [3]	53.88 [1]	61.20 [4]	48.88	32.4	1.31
T10	31.50	42.20	45.82 [4]	59.63	53.40 [1]	41.0	0.65
T11	15.22	16.24	36.51	48.20	40.95	62.8	0.83
T12	28.32	43.87 [4]	43.46	57.87	41.82	32.2	1.12
T14	37.17 [1]	46.55 [1]	45.68	53.86	51.76 [2]	28.2	0.58
Overall mean	29.40	38.77	41.45	53.48	46.98		

A) Computed following truncation of slowest growing 50% of trees in each family.

B) Least-squares estimates of breeding value of parents (COTTERILL *et al.*, 1983) may be calculated from the above as — breeding value = 2 (least-squares parent mean — overall mean).

Table 7. — Correlations among means of parents for volume at 45 months as estimated for S and OP progeny, both before and after 50% culling, and O progeny.

	Culled selfed (S ^c)	Open-pollinated (OP)	Culled open-pollinated (OP ^c)	Design II (O)
Selfed (S)	.94***	.62*	.57*	.72**
Culled selfed (S ^c)		.64*	.62*	.61*
Open-pollinated (OP)			.96***	.58*
Culled open-pollinated (OP ^c)				.54

the ID calculated for each of the 13 parents is very variable, with values for Vol-45 ranging from 25.1% for parent 3 to 62.8% for parent 11.

The growth of OP progeny relative to their respective S and O siblings provides an estimator (t) of the degree of natural outcrossing. As for ID, calculations of t have been made on a population basis (Table 5) and for each separate parent (Table 6). The population estimates of t proved quite stable from the second year (Ht-21) onwards for all traits measured, with a value of $t = 0.69$ for Vol-45 (Table 5). However, there was substantial variation in t calculated for each parent (Table 6), ranging from apparent complete outcrossing ($t \geq 1.0$) for parents 9 and 12 to strong inbreeding for parents 2, 6 and 7 (t values of 0.30, 0.22 and 0.06, respectively; Table 6).

Relative Breeding Values of Parents

Of the three mating designs, controlled outcrossing (design II) was considered to provide the most reliable estimates of the breeding potential of parents. The least-squares means (or breeding values) estimated from half-sib O progeny were therefore used as a basis for evaluating the reliability of the least-squares means estimated from the S and OP progeny.

For Vol-45 the correlation between S and O progeny from the same parents was higher than the corresponding correlation between parental means for OP and O progeny ($r = 0.72$ c.f. 0.58; Table 7). The 50% truncation of the S and OP data sets failed to improve these associations, in fact the reverse occurred and the correlation coefficients actually declined. For example, the correlation of O least-square means with S and culled-self (denoted S^c) means for Vol-45 were $r = 0.72$ and 0.61, respectively.

The above correlations are reflected in the accuracy of the ranking of parents. For instance, the best four parents for Vol-45 on the basis of least-squares means of O progeny were the parents 1, 6, 10 and 14 (Table 6). Selection of parents on the performance of uncultured S progeny would have correctly identified two of these top four parents, with the others ranked fifth and sixth. Selection on performance of S^c progeny would have correctly identified only one of the top four parents according to O performance. Selection on OP performance would also have correctly identified two of the top four parents, but with the others ranked sixth and eleventh.

Discussion

Genetic Parameters

The moderate individual heritabilities of between 0.13 and 0.18 estimated for all growth traits of S and O progeny from 30 months after planting onward (Table 4), suggest that substantial gains can be expected from selection at this age. The heritabilities for earlier height measurements were generally lower and selection at less than two years

(or when trees are less than about 5 m tall) may not be as efficient. In the only other report of a controlled-pollinated progeny test of a eucalypt species VAN WYK (1976) estimated an individual heritability of 0.10 for height of *E. grandis* at six years in South Africa.

An important finding of this study is that individual heritability estimates for eucalypt species may be seriously biased upwards when they are based on OP progeny grown from seed collected in natural stands. The coefficient of relationship of $r = 1/2.5$ used to estimate heritability in this study seems reasonable in the light of the apparent rates of outcrossing of between $t = 0.57$ and 0.76 listed in Table 5. Therefore the inflation of heritability estimates cannot be attributed merely to incorrect assumptions regarding the true r value of OP progeny of *E. regnans*.

Another major factor contributing to bias in genetic parameters (including heritabilities and genetic correlations) derived from OP seed from natural stands, is the substantial variation in ID across families (Table 6). This variation in inbreeding is completely confounded with the effects of families *per se* and would substantially inflate the estimates of additive genetic variance (and perhaps covariance). Eucalypt breeders clearly need to be cautious in using genetic parameters estimated from such OP progeny as a basis for construction of selection indices or for gain estimation.

The genetic correlations estimated using OP progeny in the present study were, surprisingly, reasonably similar in magnitude and direction to correlations estimated using S and O progeny. Perhaps any upwards bias in additive genetic covariance (the numerator) was cancelled to some extent by similar upward bias in additive variance components (the denominator).

The problem of upward bias in genetic parameter estimates may not be as serious for open-pollinated seedlots collected from trees growing in seedling seed orchards or plantations of bulk origin. Two published studies using OP progeny from plantations, both assuming a half-sib relationship within families, reported heritabilities for growth rate of *E. grandis* which were more comparable with those derived from our O and S data than from our OP data. KAGEYAMA and VENCOVSKY (1983) estimated individual heritabilities of between 0.11 and 0.39 for height at two years over five sites in Brazil, while MUBITA (1986) reported a value of 0.11 for height at 10 years in one trial in Zambia. In eucalypt plantations there should be far less relatedness between neighbouring trees than is found in natural stands. Tree-to-tree variation in flower production should also be reduced because crown sizes are more uniform. The overall level of outcrossing could therefore be enhanced and, more importantly, be more uniform across families. Recent results from mating system studies in *E. regnans* seed orchards (G. F. MORAN and W. T. ADAMS, unpubl.) support this contention with values of t estimated at around 0.9.

The low genetic and phenotypic correlations between very early measurements of growth (e.g. Ht-3, Table 4), and subsequent growth, is important for practical breeding and has been observed in a number of other trials involving a range of eucalypt species (e.g. ELDRIDGE, 1972; KARSCHON, 1974; KEDHARNATH and VAKSHAYA, 1977). Even for such fast-growing plants it clearly takes at least one growing season to overcome maternal and nursery effects. Height measured in the first year after planting, or when trees are below

about 2 m tall, appears not to be a reliable guide to subsequent growth.

Inbreeding Depression and Apparent Outcrossing Rates of OP Progeny

The conclusion that S progeny are generally less vigorous than O, but that degree of inbreeding depression varies substantially among parents, supports earlier indications for *E. regnans* (ELDRIDGE, 1970; ELDRIDGE and GRIFFIN, 1983) and the results of similar experiments with *E. grandis* HILL ex MAID. (HODGSON, 1976). VAN WYK (1981) has also shown that progeny from mating of full-sibs of *E. grandis* grow more slowly than outcrosses. If the relationship between coefficient of inbreeding (F) of a progeny and degree of ID is linear for *E. regnans*, as has been demonstrated for early height growth of the coniferous species *Pinus radiata* D. DON (GRIFFIN *et al.*, 1986), then comparison of the relative growth of the selfs ($F = 0.5$) and outcrosses ($F = 0$) in the current experiment (Table 5) indicates an average decline of 2.1% in height at 45 months per 0.1 increase in F , and 7.5% for volume at 45 months. These results show that it is clearly in the interests of forest growers to maximise the degree of outcrossing in seed crops used in establishing their plantations.

It is interesting that the population mean estimate of $t = 0.69$ (Table 6) determined by simply comparing growth of the respective O, S, and OP progeny is comparable to outcrossing rates estimated by more sophisticated isozyme techniques for the same *E. regnans* stands (GRIFFIN *et al.*, 1987) and more generally for natural populations of eucalypts (MORAN and BELL, 1983). The t estimate from this study is quite robust over time, with little variation in values derived from population means of all traits from Ht-21 onwards (Table 5).

An important finding, particularly for interpretation of progeny test data and genetic parameter estimation, is the demonstration that t varies substantially between individual parents (Table 6). OP progeny from four parents (3, 8, 9 and 12) were apparently completely outcrossed while those from three other parents (2, 6, 7) were estimated to contain less than 30% outcrosses. As noted, both genetic and environmental effects contribute to this variation. Parents differ in self fertility (ELDRIDGE and GRIFFIN, 1983; GRIFFIN *et al.*, 1987), while opportunities for outcross pollination are not constant for a variety of environmental reasons (FRIPP *et al.*, 1987). It was certainly predictable that a large tree such as parent 6, which was isolated from its nearest neighbour by 400 m (GRIFFIN, 1980), would produce a high proportion of inbred seed ($t = 0.22$ Table 6), while the fact that trees 2 and 7 were large open grown trees on the margins of the stands probably contributed to their low outcrossing rate.

In general the prediction of high outcrossers from such simple observations as size and location would not be possible. However, in order to maximise the proportion of outcrossed seed it would seem good policy to restrict seed collection to reasonably dense, even-aged, stands after a good flowering year. Direct experimental support for this assertion is not available, but it accords with the finding of ZANI and KAGEYAMA (1984) that, for *E. grandis*, a management regime encouraging heavy general flowering gave a high yield of viable seed per kg. For this species outcrossing is known to increase seed yield relative to that following inbreeding (HODGSON, 1976).

Truncation of the data, using the most vigorous 50% of progeny in each OP family, may have been expected to reduce the effects of the inbred component and thereby enhance the reliability of the OP^c mean as a guide to the outcrossed O family mean. Similarly culling the S families might be expected to minimise the effects of segregants expressing major deleterious genes (BARKER and LIBBY, 1974). Neither expectation eventuated, and in each case correlations of the means of S^c or OP^c progeny with their respective O values were less than those for S or OP (Table 8). The lower correlations after truncation may have been due to the reduced family size and the approach might have worked better if families size had been larger at the beginning (COTTERILL and JAMES, 1984). However, no practical degree of truncation could have been helpful in substantially reducing the level of coancestry within the OP families which were highly inbred. In the case of agricultural crops it seems that any major deleterious recessive genes uncovered by increased homozygosity following selfing have generally led to such rapid and severe inbreeding depression that the entire line (family) is often abandoned within a couple of generations (MAYO, 1980). In this case truncation of data would do little to influence the interpretation of results.

The S progeny test proved reasonably useful in screening families for outcross performance, with the top four parents identified in the O test ranked in the top six in the S test. The OP progeny performance also proved fairly reliable for ranking parents with three of the top four parents in O tests also in the top six on OP results. The OP test would, however, have failed to identify the potential of the spatially isolated tree 6 which ranked 11th from OP data and 4th from O performance. It seems that good growth in an OP test is likely to indicate high breeding value, but poor OP performance does not necessarily indicate a genetically undesirable parent. Given these difficulties in interpreting OP family data, breeding strategies which place reduced emphasis on family selection during the initial stage of domestication, would seem desirable for *E. regnans*.

It is important to emphasise that, in spite of the problems identified in this study, open-pollinated seed is clearly of value in applied eucalypt breeding programs. In most cases it is the only practical means of taking the all-important first step of obtaining a comprehensive sample of the gene resource. As has been demonstrated in Florida for *E. robusta* (FRANKLIN and MESKIMEN, 1973) and *E. grandis* (MESKIMEN, 1983), large genetic gains can be obtained by individual tree selection among open-pollinated seed source introductions. In these programs additional gain was obtained by a combination of individual and family selection in advanced generation progeny tests.

The present study has also demonstrated that selfed progeny are useful in estimating both genetic parameters and parental breeding values. Since the flowering biology of eucalypts is such that controlled self pollination is much simpler and less expensive than outcrossing (ELDRIDGE and GRIFFIN, 1983), the role of this mating design in genetic studies and applied breeding warrants serious consideration. Indeed it may be that some form of inbred line development (LINDGREN, 1975; HALLAUER and MIRANDA, 1981; LINDGREN, 1986) could have a place in advanced generation breeding strategy for eucalypts.

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Ecological Genetics of *Pinus contorta* from the Rocky Mountains (USA): a Synthesis

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Abstract

Studies of population differentiation in *Pinus contorta*, which were conducted in common gardens, are summarized according to the growth, freezing tolerance, and the periodicity of shoot elongation of seedlings from 173 Rocky Mountain (USA) populations. Regression models accounted for 45 to 77% of the variance among populations, coordinated the results of previous studies and described clinal patterns of variation that generally reflect elevational and geographic gradients in the frost-free period.

Key words: Population differentiation, genecology, adaptive variation.

Zusammenfassung

Studien über Differenzierungen bei *Pinus contorta*-Populationen, die in öffentlichen Parks durchgeführt wurden, werden zusammenfassend dargestellt. Es wurde das Wachstum, die Frosttoleranz und die Periodizität der Sproßstreckung an Sämlingen von 173 Rocky Mountain (USA) Populationen untersucht. Regressionsmodelle erklärten 45 bis 77% der Variation zwischen Populationen, koordinierten die Resultate vorausgegangener Studien und beschrieben klinale Variationsmuster, die allgemein geographische und Höhengradienten der frostfreien Periode reflektierten.

Introduction

Population differentiation in *Pinus contorta* var. *latifolia* from the Rocky Mountains (USA) occurs along clines that parallel gradients in the frost-free period (REHFELDT, 1983; 1985a, b, c; 1987). As a result, clines are elevationally steep and geographically gentle. The clines also involve a coadaptive complex of traits, many of which are components of an annual sequence of developmental events that begins with shoot elongation in the spring and culminates with cold acclimation in the fall. Adaptation to spatially heterogeneous environments thus reflects a balance between selection for a suite of traits that provide a high growth potential in mild environments and selection for a suite that

provide high tolerance to early autumn frosts in severe environments.

Both the development and perpetuation of the clines are strongly influenced by the ecology and demography of the species. In the Rockies, *P. contorta* is a seral species that occupies almost any forest habitat (PFISTER and DAUBENMIRE, 1973). The species is distributed across more than 2,000 m of elevation and thus occupies extremely heterogeneous environments that differ, for example, by 100 frost-free days (Fig. 1). Even-aged natural populations commonly develop under repetitive cycles (LOTAN *et al.*, 1984) that include: (1) wildfire, (2) profuse reproduction of as many as a half million seedlings/ha from either serotious or open cones, (3) intense natural thinning to less than 1,000 trees/ha, (4) epidemics of the mountain pine beetle, which supplement competitive mortality to provide the fuel for (5) wildfire. As a result, conditions are provided that are ideally

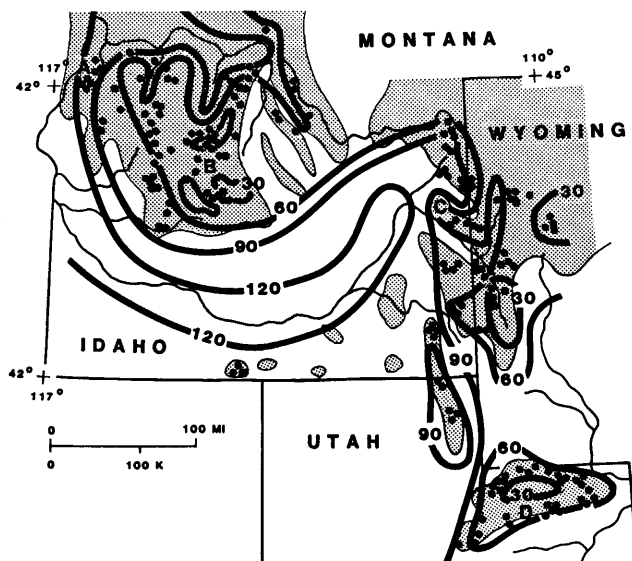


Figure 1. — Region of study showing the distribution (shading) of *P. contorta* (from LITTLE, 1971), location of populations (dots), and average frost-free period (from U. S. Department of Commerce, 1968). Localities A to D position the elevational clines of Figure 2.

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