

estimating likely survival of grafts of different clones retained after stage-2.

Conclusions

Pooled (or standard) estimates of genetic parameters from open-pollinated progeny trials in central Portugal suggest that early selection of *E. globulus* based on height, and to a lesser extent on sectional area, can be very effective in indirectly improving growth at the end of the plantation rotation. Absolute gains from early selection can be maximised by using indices combining phenotypic and family mean values of juvenile traits and taking account of juvenile-mature genetic correlations.

Efficiencies of early selection were higher when the plantation rotation was longer. However, the optimum stage of growth for early selection to improve mature sectional area of *E. globulus* in central Portugal appears to be when trees reach around 8 m tall, regardless of rotation, or whether selection is based on phenotype or combined indices.

It is possible to complete early selection in two stages with the initial stage-1 selection at say two years and the final stage-2 at four years but maintaining a generation interval equivalent to selection at two years. Stage-1 selection may be on HT2 with at least twice as many trees grafted into breeding arboreta as are ultimately required for future breeding. Stage-2 selection is carried out two years later when the breeding arboreta have reached sexual maturity and controlled-pollinations can proceed. There are strong theoretical and practical advantages in favour of two-stage selection at different times in the one generation.

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Genetic Parameters and Selection Strategies for *Eucalyptus nitens* (Dean and Maiden) in Victoria

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Summary

Genetic parameters were estimated for growth and form traits in a nine year old progeny trial containing 32 open-pollinated families of *Eucalyptus nitens* collected from native stands in the central highlands of Victoria. Estimates of individual heritabilities were moderate for stem

diameter ($h^2 = 0.18$), height ($h^2 = 0.23$), stem straightness ($h^2 = 0.20$), and branch retention ($h^2 = 0.21$), low for branch angle ($h^2 = 0.11$) and very low for branch thickness ($h^2 = 0.04$). Stem diameter, height and stem straightness were all strongly positively correlated with each other. Both growth traits had strong adverse correlations with branch thickness ($r_A = -0.50$ to -0.51) and branch retention ($r_A = -0.34$ to -0.53) but more favourable correlations with branch angle ($r_A = -0.09$ to 0.20).

Index selection strategies were formulated to examine the implications of these genetic parameters when the breeding objective is either to improve growth for pulp

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production or to improve branching characters for sawn structural and appearance products. Indices combined stem diameter, stem straightness and branch retention using both individual and family information with increasing emphasis placed on traits deemed economically important for the particular end uses. Results show that the presence of the adverse genetic correlation between both growth and stem straightness with branch retention make it impossible to satisfy both breeding objectives with the same selection criteria.

Key words: *Eucalyptus nitens* heritability, genetic and phenotypic correlations, combined index selection, selection strategy, breeding objective.

Introduction

There is increasing interest in *Eucalyptus nitens* as a fast growing plantation species in cooler temperate regions where frosts are moderate to severe (PURNELL and LINDQUIST, in press). Variation across the natural range of the species has been extensively described by FEDERICK (1979). Very little information is available, however, about genetic parameters for growth and form traits in this species in Australia and these parameters are required if effective breeding strategies are to be formulated. The only documented estimates of genetic parameters for *E. nitens* appear to be those for growth and straightness in provenance trials in South Africa (PURNELL, 1986; PURNELL and LINDQUIST, in press) and information based on family means within provenances from New Zealand (KING and WILCOX, 1988).

The aim of this paper is to present estimates of genetic parameters for growth and form traits from a nine year old progeny trial of central highland families of *E. nitens* on one site in Victoria. The likely response to various selection options in this population is considered by constructing selection indices using different combinations of pedigree, economic and genetic information.

Materials and Methods

Trial Site and Design

The progeny trial was established on a site which previously carried *E. regnans* regrowth. The site is located in Gippsland in Eastern Victoria (latitude 38° 28'S, longitude 146° 30'E, altitude 600 m). This region experiences a cool temperate climate, having an annual average rainfall of 1200 mm.

Open-pollinated offspring were raised from seed collected from 32 dominant trees occurring naturally in the central highlands of Victoria. Trees were planted at a spacing of 3 m x 2 m in complete randomised blocks with five replications of 8-tree row plots.

Measurements

All surviving trees were measured for growth and form traits in April 1987 (at approximately nine years). Growth measurements included stem diameter (over bark at 1.3 m) and total height. Components of tree form were assessed following COTTERILL and DEAN (1990) either visually on a six point scale: stem straightness (6 = straightest), branch angle (6 = most perpendicular to main stem), and branch thickness (6 = thinnest); or as a count: branch retention (the actual number of branches retained by the tree to a height of 1.5 m).

Data Analyses

Individual tree data were analysed using a least squares analysis of variance and covariance program written by

HARVEY (1977). The model used for the analysis is described as follows — (1)

$$Y_{ijk} = \mu + f_i + b_j + fb_{ij} + e_{ijk} \quad (1)$$

where Y_{ijk} represents an individual tree observation, μ the overall mean, f_i the effect of the i th open-pollinated family, b_j the effect of the j th randomised block, fb_{ij} the effect of the family x block interaction and e_{ijk} the within plot error. Components of variance due to blocks (σ_b^2), families (σ_f^2), family x block interaction (σ_{fb}^2) and within-plot error (σ_w^2) were calculated from the analysis.

MORAN and BELL (1983) and GRIFFIN and COTTERILL (1988) report a range of outcrossing rates in open-pollinated seed collected from natural stands of *Eucalyptus* species with the average outcrossing rate of 70%. For the purposes of estimating heritability this outcrossing rate corresponds to an average coefficient of relationship of $r = 1/2.5$. Individual heritabilities (denoted h^2) were thus estimated as — (2)

$$h^2 = \text{additive variance} / \text{variance of individual phenotype} \\ = 2.5 \sigma_f^2 / (\sigma_f^2 + \sigma_b^2 + \sigma_{fb}^2 + \sigma_w^2). \quad (2)$$

Standard errors of individual heritabilities were estimated according to SWIGER et al. (1964). Genetic correlations (denoted r_A) were calculated from estimates of additive genetic variances following HAZEL et al. (1943) and the standard errors of these correlations according to TALLIS (1959). No assumption regarding the coefficient of relationship is required for estimating genetic correlations. Phenotypic correlations (r_p) were estimated as simple correlation coefficients.

Selection Indices

Selection options for *E. nitens* were considered that would lead either to increased volume production for pulp wood, or to improvement in branching and knot characters for sawn structural and appearance products. Seven different selection indices were constructed using the computer program RESI4 (described by COTTERILL and DEAN, 1990). All indices integrated stem diameter, stem straightness and branch retention and varied in the type of information used (individual or family information or both), the emphasis placed on either growth or branch retention, and whether or not various traits were allowed to change.

Genetic gains that might be expected in each trait (denoted ΔG_{DBH} for stem diameter, ΔG_{STEM} for stem straightness and ΔG_{BRN} for branch retention respectively) as a consequence of selection on each of the indices are calculated routinely by the RESI 4 program (COTTERILL and

Table 1. — Estimates of overall means ($\mu \pm$ standard deviations) and individual heritabilities ($h^2 \pm$ standard errors) for growth and form traits in *E. nitens* in Victoria.

Trait	$\mu \pm$ s.d.	$h^2 \pm$ s.e.
Stem diameter (cm)	18.22 \pm 5.32	0.18 \pm 0.06
Height (m)	18.47 \pm 4.09	0.23 \pm 0.07
Stem straightness (point)	3.74 \pm 0.71	0.20 \pm 0.06
Branch angle (point)	3.40 \pm 0.79	0.11 \pm 0.05
Branch thickness (point)	4.33 \pm 0.68	0.04 \pm 0.03
Branch retention (count)	9.08 \pm 3.79	0.21 \pm 0.07

Table 2. — Estimates of genetic ($r_A \pm s.e.$; above diagonal) and phenotypic (r_p ; below the diagonal) correlations for growth and form traits in *E. nitens* in Victoria.

Traits	Correlations					
	Stem diameter	Height	Stem straightness	Branch angle	Branch thickness	Branch retention
Stem diameter		0.92±.04	0.55±.18	0.20±.26	-0.51±.41	-0.53±.18
Height	0.83		0.41±.20	-0.10±.26	-0.50±.37	-0.34±.21
Stem straightness	0.38	0.38		-0.29±.25	-0.17±.35	-0.73±.15
Branch angle	0.12	0.08	-0.03		-0.20±.38	-0.23±.25
Branch thickness	-0.61	-0.47	-0.17	0.06		-0.11±.35
Branch retention	-0.26	-0.22	-0.13	0.0	0.16	

Table 3. — Genetic gains in stem diameter, stem straightness and branch retention following index selection to (a) improve growth and (b) reduce branch retention in *E. nitens* in Victoria. These calculations are for selection of superior individuals (on the basis of their index values) at an intensity of one tree in every 100.

Index Selection Options	Genetic Gain ^A		
	ΔG_{DBH}	ΔG_{STEM}	ΔG_{BRN}
(a) Establish Response Baseline :			
$I_1 = .03 P_{DBH} + .15 P_{STEM} - .03 P_{BRN}$	18	12	-27
(b) Increase Growth :			
$I_2 = .06 P_{DBH} + .09 F_{DBH} + .20 P_{STEM} + .12 F_{STEM} - .07 P_{BRN} - .02 F_{BRN}$	20	12	-28
$I_3 = .06 P_{DBH} + .09 F_{DBH} + .32 F_{STEM} - .09 F_{BRN}$	17	9	-20
$I_4 = .03 P_{DBH} + .07 F_{DBH} - .04 P_{STEM} - .05 F_{STEM} [+ .01 P_{BRN} + .06 F_{BRN}]^B$	10	1	-
(b) Reduce Branch Retention :			
$I_5 = [.001 P_{DBH} + .005 F_{DBH} + .03 P_{STEM} + .11 F_{STEM}]^B + .01 P_{BRN} + .03 F_{BRN}$	-	-	9
$I_6 = .01 P_{DBH} - .04 P_{STEM} + .04 P_{BRN}$	-3	-6	18
$I_7 = .01 P_{DBH} + .03 F_{DBH} - .04 P_{STEM} + .03 F_{STEM} + .03 P_{BRN} + .06 F_{BRN}$	-1	-6	18

A) Genetic gain is expressed as percentage change in the mean for each trait.
 B) Traits within parentheses are restricted to no change by index.

DEAN, 1990; Chapter 8). The intensity of selection is assumed to be one tree in every 100 ($i = 2.67$; BECKER, 1985).

Results and Discussion

Overall means and their standard deviations and individual heritabilities and their standard errors are given in table 1. Genetic and phenotypic correlations are presented in table 2. Genetic gains following selection on multi-trait selection indices integrating both individual

and family information for stem diameter, stem straightness and branch retention are compared in table 3 with the overall aim of improving either growth or branch retention.

Heritabilities

Estimates of individual heritabilities of growth traits were moderate with low standard errors and ranged from $h^2 = 0.18 \pm 0.06$ for stem diameter to $h^2 = 0.23 \pm 0.07$ for height (Table 1). These heritabilities are similar to those

estimated by PURNELL (1986) who also reported a lower heritability for stem diameter ($h^2 = 0.11$) than for height ($h^2 = 0.27$) in two *E. nitens* provenance progeny trials up to age three years in South Africa. KING and WILCOX (1988) reported a family heritability of $h^2_f = 0.8$ for stem diameter which, converted using the equations of FALCONER (1986), gives an estimate of individual heritability of $h^2 \approx 0.24$. These indications of moderate heritabilities for growth traits in *E. nitens* suggest that substantial genetic gains should follow individual selection for growth in this species.

In the trial reported here stem straightness also had a moderate heritability with a low standard error ($h^2 = 0.20 \pm 0.06$; Table 1). This estimate of heritability for stem straightness is much lower than the high estimate of $h^2 = 0.65$ for stem form reported by PURNELL (1986) but very similar to the estimate $h^2 \approx 0.23$ derived (as above) from the study of KING and WILCOX (1988). In the South African study an eight point subjective score was used to assess form (with 8 being best) and appears to have discriminated well between trees. The South African trials were assessed at very young ages (17 months and 39 months) and it is possible that the stem form assessed in these trials was quite a different trait from the stem straightness assessed at nine years in the study reported here. In the New Zealand trial stem form was assessed on eight year old trees as a nine point score of sawlog quality and is closer to the scoring system used here.

Branch angle and branch retention had moderate heritabilities of $h^2 = 0.11 \pm 0.05$ and $h^2 = 0.21 \pm 0.07$ respectively, indicating that these traits should also show reasonable improvement following individual selection. Branch thickness, on the other hand, was very poorly inherited with $h^2 = 0.04 \pm 0.03$ indicating that it would not be easily improved by individual selection.

With the exception of branch thickness, the heritabilities presented here for form traits suggest that reasonable gains may be expected from individual tree selection on either stem straightness, branch angle or branch retention for *E. nitens* in Victoria. However, little or no response to individual selection for branch thickness is likely. If improvement in this trait is desired, other methods such as family selection, should be considered.

Genetic and Phenotypic Correlations

Strong positive genetic ($r_A = 0.92 \pm 0.04$) and phenotypic ($r_p = 0.83$) correlations were exhibited between stem diameter and height suggesting that selection for one trait would lead to a strong indirect response in the other. The standard errors of these correlations amongst growth traits are low.

Stem straightness was favourably correlated with both growth traits and had relatively low standard errors. The genetic correlation with stem diameter ($r_A = 0.55 \pm 0.18$) was higher than with height ($r_A = 0.41 \pm 0.20$). The phenotypic correlation ($r_p = 0.38$) was the same for both growth traits. Branch angle was positively genetically correlated with stem diameter ($r_A = 0.20 \pm 0.26$) and adversely correlated with height ($r_A = -0.10 \pm 0.26$). The standard errors of these correlations among growth traits and branch angle are higher than the estimates themselves, indicating that these correlations must be interpreted with caution. In addition, the phenotypic correlations are low ($r_p = 0.12$ and 0.08 with stem diameter and height respectively). Further work is required to confirm these findings.

Branch thickness was strongly adversely correlated with stem diameter ($r_A = -0.51 \pm 0.41$) and height ($r_A = -0.50 \pm 0.37$). Standard errors of these genetic correlations are also quite high in this instance but are less than the correlations themselves and the phenotypic correlations between growth traits and branch thickness are also strong and negative ($r_p = -0.61$ and -0.47 with stem diameter and height respectively). These results suggest that selection for fast growth (in particular fast stem diameter growth) in *E. nitens* would lead to improvement in straightness and branch angle but a deterioration in branch thickness. However, the much lower heritability of this latter trait reduces the significance of this adverse correlation. This finding is similar to the negative association between growth and branch size reported for *E. globulus* grown in Australia (VOLKER et al., 1990).

Both genetic ($r_A = -0.53 \pm 0.18$ and -0.34 ± 0.21) and phenotypic correlations ($r_p = -0.26$ and 0.22) between the branch retention count and both stem diameter and height respectively are strongly adverse. (Note that the sign of the correlations involving branch retention have been reversed to indicate that an increase in the number of branches below 1.5 m is not desirable). The genetic correlation between branch retention and stem straightness ($r_A = -0.73 \pm 0.15$) is also very strongly adverse while the phenotypic correlation is also adverse but smaller in magnitude ($r_p = -0.13$).

Of the other associations between traits, stem straightness showed adverse correlations with branch angle ($r_A = -0.29 \pm 0.25$) and branch thickness ($r_A = -0.17 \pm 0.35$) but with large standard errors. Phenotypic correlations were also adverse but smaller in magnitude ($r_p = -0.03$ and -0.17 for branch angle and branch thickness respectively). Branch angle had moderate to low correlations with branch thickness and branch retention. The standard errors of these genetic correlations are large and phenotypic correlations between these traits are near zero. The correlations between branch retention and branch thickness are low and inconsistent.

Selection Strategies and Breeding Objectives

Plantation grown *E. nitens* can be used for either: (i) pulp production, in which case increased volume production is perceived to be the economically most important breeding objective (CAMERON, J. N., pers. comm); or for (ii) sawn structural and appearance products, in which case incidence of knots in the butt log is the critical factor (McKIMM et al., 1988). Index selection strategies necessary to achieve these simple breeding objectives for these very different production systems are examined here.

Particular advantages of index selection are described in detail by COTTERILL and DEAN (1990) and include: selection applied simultaneously to more than one trait; use of additional sources of information (ie family means as well as phenotypic values); differential economic weightings; and the ability to impose restrictions to prevent changes in chosen traits. Table 3 lists seven different indices combining various of these index selection options to investigate methods of breeding *E. nitens* to increase volume production for pulp (as assessed by stem diameter) or to improve branching characters for sawn structural and appearance products (as assessed by the number of branches retained below 1.5 m).

Establishing a Response Baseline

Index 1 (abbreviated I_1) in table 3 integrates phenotypic values for stem diameter, stem straightness and branch retention (denoted P_{DBH} , P_{STEM} , and P_{BRN}). In I_1 equal economic weighting was placed on one standard deviation change in each trait to establish a baseline of response to index selection for each trait. The gains expected from selection on I_1 ($\Delta G_{DBH} = 18\%$, $\Delta G_{STEM} = 12\%$ and $\Delta G_{BRN} = -27\%$) confirm the indications from moderate estimates of heritability, strong positive genetic correlations between stem diameter and stem straightness and the strong adverse correlations between both of these traits and branch retention. Indeed it was not possible to improve all of these traits using any of the index combinations examined. If these three traits are to be used as selection criteria it will therefore be necessary to employ quite different selection strategies to achieve the two breeding objectives outlined above.

Improving Growth

Index 2 combines individual and family mean values for all three traits (family mean for stem diameter abbreviated as F_{DBH} and so on) as well as double the economic weighting being placed on growth. Selection on I_2 gave the highest response in growth ($\Delta G_{DBH} = 20\%$) from any index combination studied, however, as expected from the genetic parameters it also led to the greatest increase in the number of branches retained below 1.5 m ($\Delta G_{BRN} = -28\%$). When a restriction was imposed so there is no increase in branches retained (I_4) the response in growth is only half the maximum achievable from combined selection on all traits in I_2 ($\Delta G_{DBH} = 10\%$ for I_4 cf. $\Delta G_{DBH} = 20\%$ for I_2 ; Table 3).

When considering alternative selection strategies and breeding objectives it is also important to consider cost factors. A differential of almost 3:1 between cost of assessing form scores such as stem straightness and branch characters compared to stem diameter is reported for large (10 m tall) plantation grown radiata pine trees by DEAN (1990). It is quite likely that these relative costs will be similar for such measurements made on other forest tree species which are grown in plantations. A major advantage of combined index selection may well be that these traits which are expensive to measure can be included in the index (and hence selected on) as family means only. Index 3 combines the phenotypic value and family mean of stem diameter (to maximise the response in growth) with the less expensive to measure family means for stem straightness and branch retention. It is interesting that the response to selection on I_3 is only 3% less than the best growth response achieved here ($\Delta G_{DBH} = 17\%$ for I_3 cf. $\Delta G_{DBH} = 20\%$ for I_2) and in addition there will be less branches retained below 1.5 m ($\Delta G_{BRN} = -20\%$ for I_3 cf. $\Delta G_{BRN} = -27\%$ for I_2). Clearly the next step is to be able to properly compare the relative cost advantages of these likely gains and to express them as a function of the overall processing system.

Reducing branch retention

The best response in branch retention is found when the economic weighting placed on this trait is increased ten fold (I_6 and I_7). It is interesting to note that including

family information did not increase the response expected for branch retention ($\Delta G_{DBH} = 18\%$ for I_6 and I_7) but did reduce deterioration in growth from $\Delta G_{DBH} = -3\%$ when only phenotypic values are integrated in I_6 to $\Delta G_{BRN} = -1\%$ when family values are included in I_7 . The response in branch retention when a restriction (that there be no deterioration in stem diameter or straightness) is imposed is again only half the maximum expected for this trait in this system ($\Delta G_{BRN} = 9\%$ for I_5 cf. $\Delta G_{BRN} = 18\%$ for I_6 and I_7).

It is obvious from these rather simplistic deliberations that further studies are needed to define more clearly the economic aspects of improving growth versus improving branch retention in *E. nitens* and indeed to verify whether these traits, measured on nine year old trees should be included in the breeding objective at all. In reality the breeding objective should consist of a group of traits with the importance of each component trait not depending on how easy it is to change genetically but rather depending on the rate at which the value of a particular end product increases per unit change in that trait. The breeder can then make objective decisions about which traits to use as selection criteria based on the genetic associations between traits which are readily measured on individuals in the population under scrutiny and traits which are included in the breeding objective.

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