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Genetic Control of Growth of *Eucalyptus globulus* in Portugal

II. Efficiencies of Early Selection

By N. M. G. BORRALHO¹⁾, P. P. COTTERILL¹⁾ and
P. J. KANOWSKI²⁾

(Received 19th March 1991)

Summary

Weighted average genetic parameters from three open-pollinated trials of *Eucalyptus globulus* in central Portugal were used to estimate efficiencies of early phenotypic and combined index selection in improving mature sectional area of stem at end of 8, 13, and 18 year rotations. It was apparent that the relative benefits of early selection increased as plantation rotation increased. However, even under short eight-year rotations, early phenotypic selection on height at four years (when trees were ca. 8 m tall) almost doubled the gains expected in sectional area at eight years, compared with later direct selection. The optimum stage of growth for early selection remained constant at around the time trees reach 8 m tall, regardless of rotation age, or whether selection is based on phenotype or combined indices. The efficiency of early selection is based on phenotype or combined indices. The efficiency of early selection can be increased by strategies which employ preliminary stage-1 selection where grafts of candidate trees are established in breeding arboreta. A final stage-2 selection is carried out when arboreta reach sexual maturity. In this way the testing and breeding phases can be overlapped to some extent and the final phase (stage-2) selection delayed without extending generation interval. Efficiencies of early selection increased substantially with rotation lengths.

Two-stage selection, with an initial index selection at two years and a second at four years, considerably improved the efficiencies of early selection. Efficacy of this procedure, compared with simple one-stage selection, depends largely on the phenotypic correlation between traits at the two stages.

Key words: Early selection, index selection, *Eucalyptus globulus*.

Introduction

Shortening the generation intervals in forest tree breeding is essential to maximizing genetic gains per unit time (COTTERILL, 1985). Generation intervals are dependent on the durations of both a test phase and a breeding phase. The testing phase is the time between establishing trees in the field (or some other testing environment) and being able to assess which selections should be used as parents for the next generation. The breeding phase is the time required to cross the newly selected parents and produce in the nursery the new generation of progeny.

The testing phase may be reduced by selecting trees as early as possible. The optimum time of selection depends on changes in heritabilities and additive genetic correlations over time for the species and region (*e. g.* NAMKOONG *et al.*, 1972; LAMBETH, 1980; LAMBETH *et al.*, 1983; KANG, 1985; FOSTER, 1986; McKEAND, 1988; COTTERILL and DEAN, 1988; DEAN and COTTERILL, 1991). In the case of *Eucalyptus* spp. there appear to be no previous reports on changes in genetic parameters over the plantation rotation, despite breeding programs being established in many parts of the world.

Further reductions in the generation interval may be achieved by two-stage selection with the testing and breeding phases overlapping to some extent (DEAN and COTTERILL, 1991). The breeding phase may also be minimized by accelerating flowering of the selected parents.

This paper examines efficiencies of early selection in improving sectional area of stem at the end of plantation rotation for *Eucalyptus globulus* LABILL. in central Portugal. These estimates of efficiencies are based on pooled estimates of genetic parameters for height and sectional area taken from Part I of this study (BORRALHO *et al.*, 1992). The implications of early selection combining phenotypic and family information, and two-stage selection, are also investigated.

¹⁾ CELBI, Forest Research Centre, Quinta do Furadouro, Amoreira 2510 Obidos, Portugal.

²⁾ Oxford Forestry Institute, South Parks Road, Oxford OX1 3RB, United Kingdom.

Results are presented for mature sectional area after three plantation rotations of 8, 13, and 18 years. Presently, rotations of *E. globulus* in Portugal range from 10 years to 15 years. However, there is a clear trend in recent years, particularly in small scale forestry, toward shorter rotations (PEREIRA and PEREIRA, 1988). A general reduction in rotation length is also expected in the future as a consequence of better soil preparation, more intensive fertilization (with some irrigation), and the use of genetically improved trees.

Materials and Methods

Genetic and Phenotypic Parameters

Pooled estimates of individual heritabilities and additive genetic correlations were determined as weighted averages of the parameters presented in Part I of this study for three open-pollinated progeny trials of *E. globulus* established by Celulose Beira Industrial (CELBI) S.A. in central Portugal (BORRALHO *et al.*, 1992). The weightings used in obtaining pooled estimates were based on the inverse of each parameter's variance for each progeny trial (following CUNNINGHAM *et al.*, 1977; WOOLASTON *et al.*, 1990). For example, the pooled estimates of individual heritability (h^2) of a particular trait were calculated as the weighted average of heritabilities (h_i^2) estimated for n progeny trials - (1)

$$h^2 = \sum_{i=1}^n z_i \times h_i^2 \quad (1)$$

where the weighting factor (z_i) represents the inverse of the variance σ_i^2 of the heritability for the i th trial - (2)

$$z_i = \frac{1/\sigma_i^2}{\sum_{i=1}^n 1/\sigma_i^2} \quad (2)$$

with σ_j^2 representing the variance of heritability summed across all trials. The standard errors of pooled estimates of h^2 were calculated as - (3)

$$s.e.(h^2) = \sum_{j=1}^n z_j^2 \times \sigma_j^2 \quad (3)$$

Pooled estimates of additive genetic correlations and their standard errors were calculated in the same way.

Pooled estimates of phenotypic parameters (*e. g.*, phenotypic correlations, overall means of traits and their standard deviations) were calculated by simple averaging across sites. Intermediate values between pooled estimates of parameters measured at different ages were estimated by linear interpolation.

Single-Stage Early Selection

The early selection strategies considered in this paper involve selection on juvenile traits at either one time (single-stage) or two different times (two-stage) in the same generation. In all cases the objective of early selection is to maximize indirect genetic gains in "mature" sectional area of stem measured either 8, 13, or 18 years after planting (*i. e.*, three different plantation rotations). The single-stage selection strategies are based on selection for phenotypic values or indices -

(1) Phenotypic Selection

Involves single-stage early selection on phenotypic

(measured) values of individual trees for height or sectional area measured at two, four, six, or eight years after planting.

(2) Combined Index Selection

Early selection is on indices (I_j) combining phenotypic (P_j) and weighted family mean (F_j) information for the j th juvenile trait - (4)

$$I_j = P_j + b.F_j \quad (4)$$

The weighting factor (or index coefficient) b in equation 4 is calculated to maximize indirect gain in mature sectional area (at either eight, 13 or 18 years). This is achieved by setting the breeding objective or genetic worth (usually denoted H) equal to breeding value for the mature trait - (5)

$$H = A_{SAT} \quad (5)$$

where A_{SAT} represents the true breeding value of an individual tree for sectional area at t years (with t being the rotation age). The economic weightings of juvenile traits included in the combined index are set to zero (following procedures given in COTTERILL and DEAN, 1990, chapter 9). The indices defined by equations 4 and 5 take account of juvenile-mature correlations and follow similar indices used previously in tree breeding (COTTERILL and JACKSON, 1981; FOSTER, 1986; COTTERILL and DEAN, 1988 and 1990; DEAN and COTTERILL, 1991).

The indices considered in this study were constructed using the RESI program outlined by COTTERILL and DEAN (1990, Chapter 11). In constructing indices it was assumed that the family mean F_j is based on 30 open-pollinated progeny with coefficients of relationship $r = 1/3$ (as discussed in BORRALHO *et al.*, 1992).

Results presented include the regression (β_{HI}) of genetic worth H on the index value I . This coefficient gives a guide to the reliability of the index in reflecting a tree's genetic potential for mature performance.

The indices defined in equation 4 combine information on only one juvenile trait. Indices combining multiple juvenile height or sectional area traits were also calculated but, as juvenile height and sectional area are generally highly correlated (BORRALHO *et al.*, 1992), the multiple trait indices produced only marginally greater gains than comparable single-trait indices.

Two-Stage Early Selection

Two-stage early selection involves a preliminary stage-1 selection on a particular juvenile trait (say height at two years, HT2) followed by a final stage-2 selection on another juvenile trait (say height at four years, HT4) measured at a different time in the same generation. The objective is, of course, to improve mature performance for sectional area at either 8, 13, or 18 years. For the sake of simplicity, the two-stage selection strategies are compared in terms of selection on phenotypic values of juvenile traits at both stages. However, the general conclusions apply equally to selection on combined indices at each stage.

Two-stage selection was evaluated in terms of expected gains in mature traits and the final number of stage-2 selections correctly identified at stage - 1 -

(1) Gains in Mature Traits

Suppose stage-1 selection is on phenotypic performance for trait X and stage-2 selection is on phenotypic per-

formance for another trait Y. The indirect gain (denoted ΔA_Z) in the breeding objective trait Z (i. e., breeding value for sectional area at say eight years) can be calculated from theory given in COTTERILL and JAMES (1981, equation 6) - (6)

$$\Delta A_Z = i_X r_{XZ} + i_Y \frac{(r_{YZ} - r_{XY} r_{XZ} S)}{(1 - r_{XY}^2 S)^{1/2}} \quad (6)$$

expressed in units of additive genetic standard deviation ($\sigma_{A(Z)}$). The r_{XY} , r_{XZ} , and r_{YZ} represent phenotypic correlations between traits X, Y, and breeding objective Z, i_X and i_Y standardized selection differentials for stage-1 and 2 selection; and $S = i_X(i_X - x)$ with x being the standardized culling level for stage-1 selection on X. The correlations involving the breeding objective Z can be expressed in terms of genetic parameters (following COTTERILL and JAMES, 1981, equation 8) - (7) and (8)

$$r_{XZ} = r_{A(XZ)} h_X \quad (7)$$

$$r_{YZ} = r_{A(YZ)} h_Y \quad (8)$$

In this case h_X and h_Y are square roots of individual heritabilities of X and Y, and the r_A are the additive genetic correlations between each trait and Z.

Equation 6 has been solved for varying intensities of selection at stage-1, denoted P_1 , including $i_1 = 2.665$ (i. e. retaining 1% of population at stage-1), 2.421 (2%), 2.225 (3%) and 2.154 (4%). The final selection intensity after both stage-1 and 2 is fixed at $i = 2.665$ (1% of original population finally selected), so that i_Y will vary according to i_X . Genetic and phenotypic parameters (r_{XY} , r_{XZ} , r_{YZ} , h_X^2 and h_Y^2) are assigned the pooled values calculated previously.

(2) Number of Stage-2 Selections Correctly Identified at Stage-1

Simulations were carried out using data from progeny trials 2 and 4 described in BORRALHO *et al.* (1992). The stage-1 of selection in trial 2 was on phenotypic value for height at two years (denoted HT2) with the best 25, 50, 75, or 100 trees chosen from the total 2500 trees in the trial (i. e., selecting 1%, 2%, 3%, or 4% of the population). Stage-2 selection involved choosing the best 1% of the original population on height at four years (HT4). In trial 4, the stage-1 selection was sectional area at four years (SA4) with the best 10, 20, 30, and 40 trees chosen from the total 1000 trees. Stage-2 selection involved choosing the best 1% of the original population on sectional area at six years (SA6). The number of common (correctly identified) trees in the groups selected at stages-1 and 2 was recorded.

Efficiencies of Early Selection

(1) Phenotypic Selection

Efficiencies of early selection have been calculated as the genetic gain per year in mature sectional area (at rotation age) produced by indirect selection on juvenile traits, compared with the gain per year from later direct selection on the mature trait itself. Efficiency (denoted Q_{year}) of early selection on phenotypic value of juvenile trait (denoted X) to improve a mature trait (Z) would be calculated as - (9)

$$Q_{year} = \frac{\text{Gain per year in Z from early selection on X}}{\text{Gain per year in Z from phenotypic selection on Z}} \quad (9)$$

which can be converted to the well known equation given in LAMBETH (1980), and elsewhere - (10)

$$Q_{year} = \frac{h_X r_{A(XZ)} T_Z}{(h_Z T_X)} \quad (10)$$

Efficiency is expressed as a percentage and $Q_{year} > 100\%$ indicates that early selection is expected to produce more gain per year in the mature trait than later direct selection on the mature trait itself. The T_X and T_Z represent generation intervals under early selection on X and later direct selection on Z, respectively. These generation intervals were calculated as the age (t) of trees at time of selection plus a constant four-year breeding phase (i. e., $T = t + 4$, in years). Therefore, $T_{HT2} = 6$ years for early selection on HT2, $T_{SA8} = 12$ years, and so on. The four-year breeding phase would usually be required for *E. globulus* in Portugal under well managed breeding programs. Equation 10 has been solved using pooled estimates of heritabilities and correlations.

(2) Index Selection

Efficiency per year (Q_{year}) under early indirect index selection to improve mature traits was calculated as - (11)

$$Q_{year} = \frac{\text{Gain per year in Z from early index selection on X}}{\text{Gain per year in Z from direct index selection on Z}} \quad (11)$$

which reduces to an identity equivalent to equation 10 with heritabilities and correlations of indices replacing those for phenotypic measurements. The generation intervals are calculated as $T = t + 4$.

(3) Two-Stage Selection

In this case the numerator used to calculate Q_{year} in equation 9 can be derived from equation 6 and the denominator from equation 10 to give - (12)

$$Q_{year} = \frac{i_X r_{XZ} + i_Z [(r_{YZ} - r_{XY} r_{XZ} S) / (1 - r_{XY}^2 S)^{1/2}] T_Z}{i_Z h_Z T_X} \times 100\% \quad (12)$$

Note that in this case the generation interval for early selection, T_X , is calculated for stage-1 selection on X (i. e., $T_X = t_X + 4$).

Results and Discussion

Pooled Parameter Estimates

Pooled estimates of genetic and phenotypic parameters are given in table 1. It should be noted that the parameters given for most height traits are based on only one progeny trial (i. e., either trials 2 or 4, BORRALHO *et al.*, 1992). The parameters given in table 1 for HT1 and HT2 do not correspond exactly to values in BORRALHO *et al.* (1992) because these traits were not measured at exactly one and two years, respectively. Hence, heritability of HT1 in table 1 represents the linear interpolation of values for HT1 (actually measured at 6 months) and HT2 (actually measured at 17 months) in Part I of this study. Likewise, HT2 in table 1 represents the linear interpolation of values for HT2 and HT4 in Part I. In the case of HT8 in table 1, the parameter values represent the

Table 1. — Pooled estimates of means and standard deviations ($\bar{x} \pm \sigma_p$), individual heritabilities and standard errors ($h^2 \pm s. e.$), additive genetic correlations ($r_A \pm s. e.$) and phenotypic correlations (r_p) between juvenile height or sectional area traits and mature sectional area at 8, 13, and 18 years.

| Trait | $\bar{x} \pm \sigma_p$ | $h^2 \pm s. e.$ | SA8 | | SA13 | | SA18 | |
|-------|-------------------------|-----------------|-----------------|-------|-----------------|-------|-----------------|-------|
| | | | $r_A \pm s. e.$ | r_p | $r_A \pm s. e.$ | r_p | $r_A \pm s. e.$ | r_p |
| HT1 | 1± 0.4 m | 0.21±.08 | 0.40±.24 | 0.45 | 0.40±.24 | 0.40 | 0.40±.23 | 0.35 |
| HT2 | 3± 0.8 m | 0.20±.07 | 0.77±.14 | 0.61 | 0.75±.15 | 0.54 | 0.70±.16 | 0.47 |
| HT4 | 8± 1.2 m | 0.29±.09 | 0.93±.05 | 0.80 | 0.90±.06 | 0.73 | 0.85±.07 | 0.66 |
| HT6 | 14± 2.0 m | 0.34±.02 | 0.98±.03 | 0.82 | 0.95±.05 | 0.80 | 0.90±.05 | 0.70 |
| HT8 | 18± 2.5 m | 0.35±.02 | 0.98±.03 | 0.86 | 0.97±.04 | 0.83 | 0.95±.05 | 0.80 |
| SA4 | 70± 30 cm ² | 0.16±.02 | 0.98±.03 | 0.88 | 0.98±.04 | 0.80 | 0.95±.05 | 0.71 |
| SA6 | 140± 55 cm ² | 0.15±.02 | 0.98±.03 | 0.96 | 0.98±.03 | 0.89 | 0.95±.04 | 0.82 |
| SA8 | 185± 80 cm ² | 0.14±.03 | 1.00 | 1.00 | 0.98±.03 | 0.97 | 0.95±.04 | 0.83 |
| SA13 | 270±145 cm ² | 0.14±.03 | | | | | | |
| SA18 | 350±200 cm ² | 0.13±.03 | | | | | | |

weighted averages of HT8 in trial 3 and HT9 in trial 4 of BORRALHO *et al.* (1992).

The pooled parameter estimates for sectional area traits (with the exception of SA13 and SA18) are based on at least two of the three progeny trials in BORRALHO *et al.* (1992). However, the parameter estimates for SA13 are calculated by linear interpolation (as mentioned in Materials and Methods).

COTTERILL and DEAN (1990, chapter 4) refer to these type of pooled values of genetic parameters as "standard parameter estimates". These authors argue that standard parameters should be more generally applicable and useful for constructing selection indices and estimating average gains from selection for particular species and regions.

Table 2. — Efficiencies (Q_{year}) and genetic gains from selection on either phenotype or indices combining phenotypic values and family means of height or sectional area traits. Calculations are based on improving mature sectional area at eight, 13 or 18 years and use pooled estimates of genetic and phenotypic parameters. The absolute genetic gains are calculated for selection intensity $i=2.665$.

| Trait | Q_{year} | | | Genetic Gains (cm ²) | | |
|-----------------------------|------------|------|------|----------------------------------|------|------|
| | SA8 | SA13 | SA18 | SA8 | SA13 | SA18 |
| Phenotypic Selection | | | | | | |
| HT1 | 108 | 168 | 218 | 15 | 27 | 34 |
| HT2 | 173 | 259 | 319 | 29 | 49 | 60 |
| HT4 | 191 | 287 | 355 | 43 | 73 | 90 |
| HT6 | 169 | 256 | 315 | 48 | 82 | 99 |
| HT8 | 141 | 203 | 286 | 48 | 83 | 105 |
| SA4 | 142 | 215 | 290 | 33 | 59 | 73 |
| SA6 | 118 | 167 | 225 | 33 | 59 | 73 |
| SA8 | 100 | 139 | 187 | 34 | 59 | 73 |
| SA13 | | 100 | | | 54 | |
| SA18 | | | 100 | | | 69 |
| Index Selection | | | | | | |
| I_{HT1} | 120 | 141 | 173 | 22 | 34 | 40 |
| I_{HT2} | 171 | 217 | 288 | 39 | 63 | 79 |
| I_{HT4} | 174 | 219 | 293 | 52 | 85 | 108 |
| I_{HT6} | 151 | 194 | 257 | 54 | 94 | 118 |
| I_{HT8} | 125 | 163 | 223 | 56 | 95 | 123 |
| I_{SA4} | 146 | 199 | 272 | 44 | 77 | 100 |
| I_{SA6} | 118 | 160 | 218 | 44 | 78 | 100 |
| I_{SA8} | 100 | 134 | 181 | 53 | 78 | 100 |
| I_{SA13} | | 100 | | | 82 | |
| I_{SA18} | | | 100 | | | 101 |

Efficiencies of Early Selection

Efficiencies of early selection based on phenotypic values for height or sectional area, or indices combining phenotypic values and family means, are presented in table 2.

(1) Plantation Parameters

Efficiencies per year (Q_{year}) increased considerably as the rotation increased from eight to 13 and, finally, to 18 years. For example, the Q_{year} values associated with indirectly improving SA18 were approximately double those associated with improving SA8 (Table 2).

It is also apparent that, as well as being lower in magnitude, the Q_{year} values were less variable under shorter rotations. Early selection on height to indirectly improve SA8 gave efficiencies ranging from $Q_{year}=108\%$ (for selecting HT1) to 191% (for HT4, Table 2). In other words, the early phenotypic selection is expected to produce 8% to 91% more gain per year in SA8 than later selection on phenotypic value for SA8 itself. However, the corresponding range in efficiencies for indirect selection to improve SA13 was $Q_{year}=168\%$ (HT1) to 287% (HT4), and in the case of SA18 the range was $Q_{year} = 218\%$ to 355% .

In conclusion, it is clear that there is relatively less benefit from early selection under short rotation forestry, and the precise timing of the early selection is a little less critical. These findings may be intuitively obvious but do not appear to have received much attention in the literature. However, even under very short eight-year rotations for *E. globulus*, early selection can still be very important. For example, selection at two years on HT4 is expected to produce almost twice as much gain per year in SA8 ($Q_{year}=191\%$) compared to later direct selection on SA8 itself.

(2) Optimum Time or Stage of Growth for Selection

The optimum time for early selection of *E. globulus* in Portugal is best judged in terms of height traits which were evaluated earlier in the progeny trials studied. Efficiencies of early selection to improve SA8 increased from $Q_{year}=108\%$ for indirect selection on HT1 to $Q_{year} = 173\%$ for HT2 and reached a maximum $Q_{year} = 191\%$ for HT4 (Table 2). Thereafter, efficiencies decreased to 169% for HT6 and 141% for HT8. The substantial improvement in efficiency of early selection on height at two years versus one year is due to the much stronger juvenile-

mature genetic correlations between HT2-SA8 versus HT1-SA8 (Table 1). The pooled heritabilities of height traits and juvenile-mature correlations continue to increase between four and six years but, in the case of indirect gains in SA8, these improvements in genetic parameters were not sufficient to compensate for the time lost by further delaying selection.

The situation was similar under longer rotations. In the case of indirect selection to improve SA18, efficiencies were again higher at four years ($Q_{\text{year}} = 355\%$ for HT4 cf. 319% for HT2, Table 2). It is apparent that, as mentioned previously, the peak efficiency at four years becomes increasingly more pronounced as the plantation rotation increases.

In conclusion, it appears that around four years is the optimum time for early selection on height to improve mature growth of *E. globulus* under 8-, 13-, or 18-year plantation rotations in central Portugal. COTTERILL and DEAN (1988) suggest that optimums for early selection may be better expressed in terms of stage of growth (tree size) rather than age. Stage of growth avoids the problem that mean size of constant-age-stands can vary considerably from one site to another, although efficiencies on a yearly basis will obviously be affected. In the progeny trials studied by BORRALHO *et al.* (1992) age 4-years corresponds, on average, to a plantation height of ca. 8 m (Table 1). Selection may be made before four years if plantation height reaches 8 m sooner. It is interesting to note that for *Pinus radiata* in Australia, COTTERILL and DEAN (1988) report an optimum stage of growth of ca. 7 m for indirect selection to improve growth at 16 years.

Recent advances in site preparation and genetic improvements of *E. globulus* in Portugal have led to stands commonly reaching 7 m to 8 m after two years on good sites. It is now considered a poor stand which reaches only 3 m at two years (which was the case in trials reported in this study, planted as long ago as 1966).

(3) Early Selection on Height versus Sectional Area

Early selection on height was always more efficient than early selection on corresponding sectional area measured at the same age (Table 2). This is because the juvenile height traits were more highly heritable and exhibited approximately equivalent juvenile-mature correlations to corresponding sectional area traits (Table 1).

The efficiencies Q_{year} for early selection on sectional area were greatest at four years (Table 2) because SA4 was equally heritable as other sectional area traits and had strong juvenile-mature correlations (Table 1). It is interesting to compare efficiencies of selection on HT8 and SA8. In the case of improving SA8 the selection on SA8 is, of course, direct selection and $Q_{\text{year}} = 100\%$ (Table 2). Indirect selection on HT8 to improve SA8 offers no advantage in time saved but $Q_{\text{year}} = 141\%$ due to the much higher heritability of HT8 ($h^2 = 0.35$ Table 1) compared with SA8 ($h^2 = 0.14$), and the strong genetic correlation between the two traits.

(4) Combined Index versus Phenotypic Selection

Early selection on indices combining phenotypic and family information generally resulted in lower Q_{year} efficiencies than phenotypic selection (Table 2). This is because the Q_{year} for early index selection is determined relative to gains from mature index selection (Equation 11), while Q_{year} for early phenotypic selection, is determined relative to gains from mature phenotypic selection

(Equation 9). It is apparent from table 2 that while Q_{year} is often lower for index selection the absolute genetic gains in mature traits are considerably higher. These absolute gains given in table 2 assume a selection intensity of one tree in every 100 ($i = 2.665$). Hence, selection on say I_{HT4} can be expected to produce ca. 52 cm² gain per generation in SA8. This gain represents a 29% improvement in the mean SA8 given in table 1. The corresponding gain expected in SA8 from early phenotypic selection on HT4 is less than 43 cm² per generation (or 23%). The higher absolute gain from combined index selection is due to the fact the index provides a more reliable guide to the true breeding values of individual trees for mature traits. BURDON (1990), COTTERILL and DEAN (1990) and DEAN and COTTERILL (1991) also comment on the potential of combined indices with restrictions in maximizing gains from early selection.

The main finding in table 2 regarding early index selection is that optimum time for selection remains at around four years (as for phenotypic selection). However, under index selection the optimum is far less clearly defined and differences in Q_{year} between early selection at two (I_{HT2}) or four years (I_{HT4}) are very small, regardless of plantation rotation.

Table 3 presents estimates of β_{HI} , which reflect the reliability of indices in indirectly improving mature performance. The efficacy of prediction of breeding values for mature sectional area increased substantially with the time of early selection, but not much with rotation length. For example in the case of SA13, regression values increased from $\beta_{\text{HI}} = 0.20$ at two years (I_{HT2}) to $\beta_{\text{HI}} = 0.43$ at eight years (I_{HT8} , Table 3). Accuracy of the indices based on sectional area were intermediate between these values, between $\beta_{\text{HI}} = 0.26$ and 0.29, and were little affected by timing of early selection. In the case of indices integrating height traits it is apparent that the increased reliability (β_{HI}) of indices after two to four years was not sufficient to make up for additional time lost by delaying selection (as mentioned previously).

The coefficients (b) for family means in the indices based on height decreased substantially with increasing age of early selection. Coefficients ranged from $b = 4.1$ for the index I_{HT2} to $b = 2.3$ for the index I_{XT6} (Table 3). For sectional area, the index coefficients remain constant and relatively high ($b = 5.2$) over the range of ages. The

Table 3. — Regression coefficients (β_{HI}) of genetic worth (H) on index value (I). The genetic worth (H) is based on breeding values for sectional area at 8, 13, or 18 years. Also given are coefficients (b) for the indices combining phenotypic values and family means for traits measured between two and eight years after planting.

| Index | β_{HI} | | | b |
|------------------|---------------------|------|------|-----|
| | SA8 | SA13 | SA18 | |
| I_{HT2} | 0.22 | 0.20 | 0.18 | 4.1 |
| I_{HT4} | 0.36 | 0.36 | 0.31 | 2.7 |
| I_{HT6} | 0.42 | 0.42 | 0.37 | 2.3 |
| I_{HT8} | 0.44 | 0.43 | 0.42 | 2.4 |
| I_{SA4} | 0.29 | 0.28 | 0.26 | 5.2 |
| I_{SA6} | 0.29 | 0.29 | 0.27 | 5.2 |
| I_{SA8} | — | 0.29 | 0.26 | 5.2 |

weighting coefficient is dependent on the heritability of the trait, assuming the number of progeny per family and the coefficient of relationship remain consistent. The lower the heritability the more important family information becomes as a guide to a tree's true breeding value (COTTERILL and DEAN, 1990). The decrease in index coefficients with time is therefore a consequence of increasing heritability of height.

Putting strong emphasis on family information, by assigning higher values for b , can lead to a reduction in effective population size in the longer term. COTTERILL and DEAN (1990) suggest overcoming this problem by either setting an arbitrary limit on the number of individuals chosen per family, or deliberately reducing the emphasis on family information. However, either approach will reduce genetic gains in the short-term. Therefore, for two indices giving comparable gains in the mature trait, the one which accords less emphasis to family information is likely to be preferred for practical purposes. In this case the index I_{HT4} would usually be preferred to I_{HT2} .

Two-Stage Selection

(1) Reliability of Stage-1 Selection

The success of two-stage selection at different times in one generation depends largely on identifying at stage-1 the trees which are ultimately retained for crossing at stage-2. In practice this will usually involve selecting more trees at stage-1 than are finally required after stage-2. Results of simulation studies carried out on progeny trial data from BORRALHO *et al.* (1992) are given in figure 1. In these studies, stage-1 selection was on HT2 and stage-2 selection on HT4 for progeny trial 2, and stage-1 selection on SA4 and stage-2 selection on SA6 for trial 4. The 4%, 3%, 2% or 1% of trees selected at stage-1 included 25, 25, 24 or 15, respectively, of the 25 trees ultimately chosen at stage-2 in trial 2, and 10, 9, 7, or 6, respectively, of the 10 trees ultimately chosen at stage-2 in trial 4. In Figure 1 these results are presented in terms of probability of the ultimate stage-2 selections being correctly identified at stage-1.

The simulations suggest that selecting around twice as many trees at stage-1 as are ultimately required at

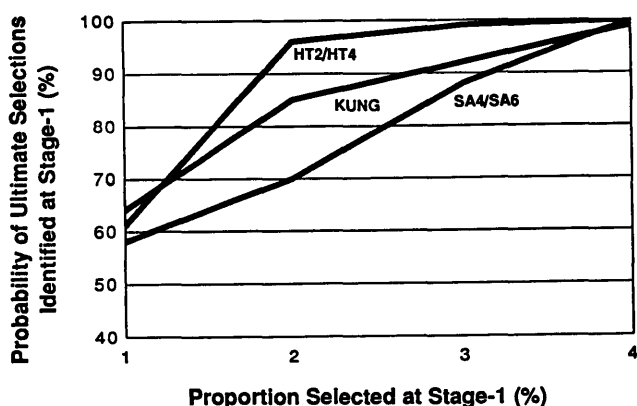


Figure 1. — Probability of trees selected at stage-2 being included in the group of trees selected previously at stage-1. Values are based on HT2/HT4 phenotypic selection from trial 2, SA4/SA6 phenotypic selection from trial 4, or results from KUNG (1974). A constant 1% of the total population are finally retained after both stages and, in the case of KUNG (1974), phenotypic correlation $r_p = 0.9$.

stage-2 may be appropriate for early selection of *E. globulus* in central Portugal, when both measurements are strongly correlated (*i.e.*, r_p greater than say 0.8). It is interesting that DEAN and COTTERILL (1991) reached the same conclusion for two-stage early selection of *Pinus radiata* in Australia. It also agrees well with simulated results presented by KUNG (1974, Figure 1). An appealing strategy under these conditions is to graft the group of candidate trees selected on HT2 (*i.e.*, stage-1 selection) into breeding arboreta. Accelerated flowering techniques can be applied to ramets in the arboreta but, in the case of *E. globulus*, it will take one or two years to induce flowering. The stage-2 selection to confirm which trees will finally be crossed for future breeding purposes is delayed until the arboretum reaches sexual maturity (*i.e.*, stage-2 selection on HT4). The selection and breeding phases are therefore overlapped to some extent, and stage-2 selection can be delayed without adversely affecting the generation interval.

Even if the correlation between measurements at the two stages is high, selecting twice as many trees at stage-1 cannot guarantee that every tree finally chosen at stage-2 will be represented in breeding arboreta. However, the few trees which are overlooked at stage-1 can be either excluded from breeding without greatly influencing genetic gain (results presented later), or used in the controlled-crossing as pollen parents only (with pollen collected from ortets in the field trials if they happen to be flowering).

The results discussed above attempt to define optimum proportions selected at stage-1 in terms of numbers of stage-2 selections correctly identified. Another approach is to determine genetic gains expected from various proportions selected at the first stage. BROWN (1967) made these calculations for stage-1 and 2 selection on the same trait and not taking account of juvenile and mature heritabilities. Figure 2 presents genetic gains expected in SA8, SA13 or SA18 following stage-1 selection on HT2 and stage-2 on HT4 (*i.e.* taking account of the additive genetic and phenotypic correlations and heritabilities required to solve Equation 6). It is apparent that gain (ΔA_z) per generation expected in mature sectional area increased markedly as the proportion (p_1) retained at stage-1 is increased from 1% to 2% (Figure 1). Further increase in ΔA_z occurs as p_1 is increased from 2% to 4% but the curve is clearly beginning to plateau, particularly for SA8.

In practice it may be difficult for breeding operations to justify the additional costs of establishing any more than twice the number of selections finally required in breeding arboreta. The plateauing gain-curves in figure 2 indicate that it is realistic to simply abandon the few selections which may be missed in the 2% stage-1 selection. In other words, never consider selecting at stage-1 more than twice the number finally required. However, as already mentioned, some selections overlooked at stage-1 may be introduced to subsequent matings as pollen parents.

(2) Efficiency

Efficiencies of early selection in two stages, rather than only in one stage, are presented in table 4. In the case of early selection on height traits the efficiencies of two-stage options exceed those of corresponding single-stage options. This is because the two-stage selection can take advantage of increasing heritabilities and juvenile-

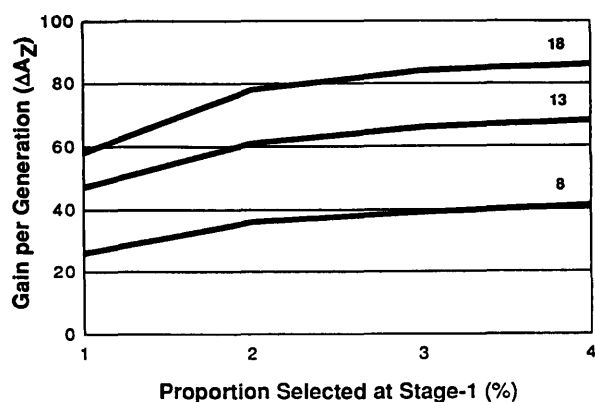


Figure 2. — Genetic gain (ΔA_z) per generation expected in sectional area at 8, 13, or 18 years following stage-1 selection on HT2 and stage-2 selection at HT4. Gains are given for a range of proportions of the overall population selected at stage-1. The final proportion retained after both stages of selection is set at 1% ($i=2.665$), and genetic and phenotypic parameters required to solve equation 6 are taken from pooled estimates. The gains are expressed in cm^2 per generation.

mature correlations of height traits over time (*i. e.*, increasing reliability of selection) without extending the generation interval. The most efficient option in table 4 is stage-1 selection on HT2 and stage-2 on HT4 which is expected to produce $Q_{\text{year}}=222\%$ gain in SA8 compared with later direct selection on SA8 itself (when 2% of the trees are selected at stage-1). The corresponding efficiency of single-stage selection on HT2 alone is $Q_{\text{year}}=173\%$, and on HT4 alone is 191% (Table 2).

Two-stage selection on juvenile sectional area traits (*e. g.*, SA4/SA6) produced only a marginal increase in efficiency compared with single-stage selection (on SA4, Tables 2 and 4). This is because the sectional area traits

Table 4. — Efficiencies (Q_{year}) and absolute genetic gains from two-stage selection on phenotypic values with either 1%, 2%, 3%, or 4% of the population selected at stage-1, and a final proportion of 1% retained after both stages. Calculations are based on improving mature sectional area at 8, 13, or 18 years and use pooled estimates of genetic and phenotypic parameters. The absolute genetic gains are for selection intensity $i=2.665$.

| Traits | Q_{year} | | | | Genetic Gain (cm^2) | | | |
|-----------------------|-------------------|-----|-----|-----|--------------------------------|-----|-----|-----|
| | 1% | 2% | 3% | 4% | 1% | 2% | 3% | 4% |
| Improving SA8 | | | | | | | | |
| HT1/HT2 | 120 | 170 | 186 | 194 | 17 | 23 | 26 | 27 |
| HT2/HT4 | 170 | 222 | 237 | 244 | 28 | 37 | 39 | 40 |
| HT4/HT6 | 191 | 208 | 211 | 211 | 42 | 46 | 46 | 46 |
| HT6/HT8 | 171 | 177 | 175 | 173 | 47 | 49 | 48 | 48 |
| SA4/SA6 | 141 | 145 | 144 | 142 | 31 | 32 | 32 | 31 |
| SA6/SA8 | 114 | 118 | 118 | 117 | 31 | 33 | 32 | 32 |
| Improving SA13 | | | | | | | | |
| HT1/HT2 | 182 | 252 | 275 | 285 | 29 | 40 | 44 | 45 |
| HT2/HT4 | 250 | 324 | 346 | 356 | 48 | 62 | 66 | 68 |
| HT4/HT6 | 278 | 307 | 312 | 313 | 74 | 78 | 79 | 77 |
| HT6/HT8 | 254 | 263 | 261 | 258 | 81 | 84 | 83 | 82 |
| SA4/SA6 | 214 | 220 | 218 | 215 | 54 | 56 | 55 | 55 |
| SA6/SA8 | 173 | 179 | 178 | 176 | 55 | 57 | 57 | 56 |
| Improving SA18 | | | | | | | | |
| HT1/HT2 | 244 | 325 | 350 | 362 | 38 | 51 | 55 | 57 |
| HT2/HT4 | 315 | 414 | 444 | 457 | 60 | 78 | 84 | 86 |
| HT4/HT6 | 358 | 392 | 397 | 398 | 90 | 99 | 100 | 100 |
| HT6/HT8 | 323 | 341 | 341 | 339 | 102 | 107 | 107 | 107 |
| SA4/SA6 | 278 | 286 | 283 | 280 | 70 | 72 | 71 | 71 |
| SA6/SA8 | 225 | 230 | 228 | 225 | 71 | 73 | 72 | 71 |

SA4 and SA6 have equal heritability and similar juvenile-mature correlations with SA8 (Table 2). Consequently the extended testing phase under two-stage selection leads to little increase in reliability of selection.

Note that the selection options given in table 4 are for early traits spaced two years apart in time. It is assumed that grafts established in breeding arboreta after stage-1 can be induced to flower within two years. Hence any delay of stage-2 selection more than two years after stage-1 would extend the breeding phase and therefore the generation interval.

(3) Practical Considerations

There are a number of important practical considerations which represent both advantages and disadvantages of two-stage selection at different times in one generation. The main disadvantage is the additional costs of grafting and establishing more clones in breeding arboreta than are ultimately needed for future breeding. However, after stage-2 selection the unwanted clones can be removed from arboreta. In the CELBI *E. globulus* breeding program in Portugal it is normal practice to establish grafted ramets in large (60 liter volume) pots after stage-1 selection. These arboreta of potted grafts are easily culled and rearranged into a smaller area after stage-2 selection.

The main practical (and theoretical) advantage of two-stage selection is, of course, that the selection and breeding phases may be overlapped to some extent. Another advantage is that the stage-1 selection allows candidate clones to be concentrated into breeding arboreta. These arboreta greatly simplify the subsequent task of control-pollinations. In companies, such as CELBI, where plantations and progeny trials are spread widely apart it would be impossible to do control-pollinations on the ortets themselves after stage-2 selection. Establishing arboreta also simplifies the practicality of applying treatments (*e. g.*, fertilizer, irrigation, hormone, ring-barking) to accelerate the flowering of grafts. For *E. globulus* it is evident that grafts can be induced to flower after one to two years while ortets in plantations may not flower before six to 10 years (Mrs. A. LEAL, CELBI, personal communication).

The two-stage selection may be especially convenient where traits are expressed at different ages or have different costs of measurement. In the case of *E. globulus* the stage-1 selection may be on HT2 and stage-2 on an index combining height and wood traits at four years. Wood traits are usually expensive to measure and the advantage of delaying selection until stage-2 is that the actual measurements of wood characteristics should be more reliable (higher juvenile-mature correlations), and may only need to be carried out on those trees, or families, selected at stage-1 (rather than measuring all trees and families in the progeny trials).

Another practical advantage of two-stage selection is that the breeding arboreta established after stage-1 can provide a large and convenient source of scion material for future grafting of superior trees finally retained after stage-2. In many programs the stage-2 selections are not only control-crossed for future breeding, but also established in clonal orchards to provide commercial quantities of seed for plantations. The rapid establishment of orchards after stage-2 selection depends on having plenty of scions available for grafting. The experience gained in grafting after stage-1 can also be particularly useful in

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.

Acknowledgements

The genetic and phenotypic parameters reported here are based on progeny trials established and maintained in Portugal by Celulose Beira Industrial (CELBI), S. A.. This series of papers are part of both CELBI's Project D95 and the senior author's post-graduate studies at Oxford Forestry Institute. It is a pleasure to acknowledge CELBI for financial and other support of the pro-

ject. We are very grateful to Dr. THOMAS LEDIG for his useful review of this paper.

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

By P. H. WHITEMAN¹⁾, C. A. DEAN²⁾, J. C. DORAN³⁾ and J. N. CAMERON¹⁾

(Received 19th April 1991)

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

¹⁾ APM Forests Pty Ltd., PO Box 37, Morwell, Vic. 3840, Australia.
²⁾ Division of Forestry, CSIRO, PO Box 946, Mount Gambier, SA 5290, Australia.
³⁾ Division of Forestry, CSIRO, PO Box 4008, Queen Victoria Terrace, ACT 2600, Australia.