

traits, along with a highly significant variation ensures the success of blue pine improvement.

(5) A lack of significant correlation between blister rust resistance and growth traits suggests that indirect selection is not applicable. A tandem selection, starting with blister rust resistance as the most important trait, appears to be a suitable improvement method.

(6) Both blister rust resistance and growth traits seem to be polygenically controlled. Such control confers a "horizontal" resistance which is equally effective against all races of *C. ribicola*.

(7) A significant genetic gain could be achieved by planting the best families on suitable sites.

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## Inheritance of Initial Survival and Rooting Ability in *Eucalyptus Globulus* Labill. Stem Cuttings

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#### Summary

Additive genetic variances and covariances and their corresponding heritabilities and genetic correlations were estimated for the initial survival of *Eucalyptus globulus* LABILL. stem cuttings (in the propagation environment) and the rooting ability of the survivors. Cuttings were harvested on four occasions from 494 clones of 10 full-sib

families. Percentage survival of cuttings was moderately heritable, with an estimated overall heritability of  $\hat{h}^2=0.20$ , whereas the percentage of survivors which rooted had a higher estimated heritability ( $\hat{h}^2=0.41$ ). There were no genetic or phenotypic correlations between these traits ( $\hat{r}_g=-0.12$  and  $\hat{r}_p=-0.02$ , respectively). The magnitude of the genotype-occasion interaction was marked for survival ( $P<2\%$ ) but small and not significant for rooting ( $P>50\%$ ). These results indicate that genetic improvements of propagation characteristics in *E. globulus* could be made, and that survival and rooting ability of the survivors should be assessed separately. Selection accuracy appeared to increase with higher overall levels of survival and rooting.

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FDC: 165.3; 165.441; 181.51; 176.1 *Eucalyptus globulus*.

### Introduction

Propagation by stem cuttings can be an effective way of transferring genetic gain to plantations. However, when rooting ability varies markedly between individuals selected as potential progenitors of clones, a proportion have to be discarded from subsequent clonal production because of propagation difficulties, resulting in the loss of genetic gain. Knowledge of the inheritance of propagation traits and their genetic relationship with economically important traits is needed either to select directly for better propagation characteristics or to develop optimal breeding and clonal propagation strategies. Moderate to high genetic control of rooting ability has been reported for some conifers (FOSTER et al., 1984; SKRØPPA and DIETRICHSON, 1986; FOSTER, 1990), but there have been no such studies on eucalypts.

When cuttings invariably survive the propagation period, the number of cuttings rooted as a proportion of the original number is a meaningful measure of rooting ability. However, if some cuttings die before rooting is assessed, this measure becomes a composite of the proportion of cuttings that initially survived and the proportion of surviving cuttings which rooted (WILSON, 1993). In *E. globulus* there was no strong or consistent relationship between survival and the rooting ability of the survivors (WILSON and PEREIRA, 1992; WILSON and REIS, 1992). Thus, when necessary, the ability of the cutting to survive initially in the propagation environment and the ability of surviving cuttings to root should be considered as 2 independent variables. In this study the nature of the variation associated with initial survival and rooting in *E. globulus* stem cuttings is investigated and the heritabilities and genetic correlations of these traits are estimated.

### Material and Methods

#### Clones

The clones were developed from seed of 10 crosses between 10 unrelated parents, as detailed in table 1. The parent trees were originally selected in genetically unimproved stands of *E. globulus* in several locations in central Portugal. From young seedlings of these crosses, 494 clones were successfully propagated (with an average number of 49 clones per cross).

#### Propagation Techniques

Stem cuttings were harvested from seedling-origin or clonal-origin mother plants growing in 10 litre pots in a double-skin plastic greenhouse. There were no effects on propagation characteristics due to the position of the mother plants in the greenhouse (WILSON and REIS, 1993).

Table 1. — List of the crosses represented in the four propagation trials.

Female parent	Male Parent						
	A	B	C	D	F	G	I
B			X				
E	X	X		X	X	X	X
H				X			
I			X				
J			X				

Each mother plant, and the cuttings harvested from it, represented one clone. The mother plants were harvested for cuttings every 2 to 4 weeks to maintain a globular crown on a low (up to 50 cm) woody framework. Harvested shoots were 15 cm to 30 cm long, each yielding one decapitated two-node cutting from the distal part of the shoot. Leaves were trimmed to give little or no overlap at an initial stocking in the propagation environment of 400 cuttings/m<sup>2</sup>. Cuttings were immersed for 30 seconds in Benomyl fungicide solution (2g/l) then set in 1:1 (v:v) peat and perlite medium, mixed with 3 kg/m<sup>3</sup> Osmocote slow-release fertilizer (N:P:K=15:12:10). The cuttings were set in a glasshouse (Trials 1 to 3) or an outdoor shadehouse (Trial 4) and were kept well wetted with intermittent mist. They were shaded with 85 % shade (glasshouse) or 25 % shade (shadehouse); day temperatures ranged between 20 °C and 30 °C, and relative humidity was 70 % to 95 % (glasshouse) or unknown (shadehouse).

#### Testing for Propagation Characteristics

Four propagation trials were conducted with shoots harvested on 21/3/91, 28/4/91, 5/6/91 and 18/7/91. On each occasion, a single plot of 5 cuttings per clone was randomly assigned in the glasshouse. Initial survival per plot was enumerated 35 days to 40 days later and the number of cuttings rooted per plot was enumerated after hardening and several weeks of growth, when rooted and unrooted cuttings could be distinguished. Survival (denoted S) was calculated as the number of cuttings surviving as a percentage of the original number and rooting (denoted R) was calculated as the number of cuttings rooted as a percentage of the number surviving at the end of the propagation period.

#### Statistical Analyses

Analyses of the data followed the provisional genetic model, denoted Model 1:

$$y = Xb + Za + e \quad (1)$$

where  $y$  is the vector of observations for S and R on a plot basis,  $a$  is a vector of additive genetic effects (i.e. the breeding values) of the clones,  $b$  is a vector of propagation trials assumed fixed,  $X$  and  $Z$  are design matrices and  $e$  is a vector of the residual errors. Observations of the same clone across propagation trials were treated as environmentally uncorrelated repeated measurements. In the single propagation trial analyses, Model 1 reduces to:

$$y = 1' \mu + Za + e \quad (2)$$

where  $1$  is a vector of ones and  $\mu$  is the overall mean.

The models assume all random terms are multivariate normally distributed with null means and (co)variances as follows:

$$\text{var} \begin{bmatrix} y \\ a \\ e \end{bmatrix} = \begin{bmatrix} ZGZ' + R & ZG' & R \\ GZ' & G & 0 \\ R & 0 & R \end{bmatrix} \quad (3)$$

where  $G = A \oplus T$ , is the direct product operation (SEARLE, 1982) between  $A$  (the numerator relationship matrix between trees), and  $T$  (the matrix of additive genetic covariances of traits). If  $G$  and  $R$  are known (and non-singular) then the best linear unbiased predictor (BLUP) of  $a$  (the random effects) is  $\hat{a}$ , which can be obtained from the equations (HENDERSON, 1975):

(4)

$$\begin{bmatrix} X' R^{-1} X & X' R^{-1} Z \\ Z' R^{-1} X & Z' R^{-1} Z + G^{-1} \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \end{bmatrix} = \begin{bmatrix} X' R^{-1} y \\ Z' R^{-1} y \end{bmatrix}$$

These are called the Mixed Model Equations. When variance and covariances in  $G$  are not known, the preferred method to estimate them is by restricted maximum likelihood (or REML) procedures (PATTERSON and THOMPSON, 1971), since they use all the information available and optimize only the part of the likelihood that does not depend on the fixed effects. REML is an iterative procedure where each iteration comprises an evaluation of the likelihood for a given set of variance components. The process is repeated until the likelihood is maximized. Assuming normality, an expression for this likelihood, or equivalently,  $-2$  its logarithm, is (HARVILLE, 1977):

$$-2 \log L = \text{const} + \log |R| + \log |G| + \log |C| + y' P y \quad (5)$$

where  $R$  and  $G$  are as defined before, and  $C$  is the coefficient matrix in equation 4. The matrix  $P$  is called the projection matrix and is given by:

$$P = V^{-1} - V^{-1} X (X' V^{-1} X)^{-1} X' V^{-1}. \quad (6)$$

with  $V = ZGZ' + R$ . To locate the maximum of  $L$  (or the minimum of  $-2\log L$ ) most REML algorithms utilize information from its derivatives. It is apparent from equation 6 that this requires the inversion of a matrix of size equal to the number of random effects ( $V$ ) in each round of iteration, limiting the method to small problems. A derivative-free approach (DFREML) has been developed by GRASER et al. (1987). The advantage of DFREML over other REML procedures is that it finds solutions for  $\log |C|$  and  $y' P y$  simultaneously and without needing to invert  $V$ , by a series of Gaussian elimination steps. The remaining terms required to evaluate  $\log L$ ,  $|R|$  and  $|G|$ , can also under certain conditions be evaluated indirectly, as discussed by MEYER (1989). For univariate analysis, a direct solution for the residual variance is given by:

$$\hat{\sigma}_e^2 = \frac{y' P y}{N - r(X)} \quad (7)$$

where  $N$  is the number of observations and  $r(X)$  the rank of matrix  $X$ . The process is subsequently repeated for a range of additive genetic variances, and  $\log L$  is evaluated for each one. To improve the rates of convergence, GRASER et al (1987) suggested maximising the likelihood with respect to one parameter ( $\lambda = \hat{\sigma}_a^2 / \hat{\sigma}_e^2$ ), since  $\hat{\sigma}_e^2$  can be estimated from (7). An estimate of the additive genetic variance ( $\hat{\sigma}_a^2$ ) can be obtained from  $\lambda$  and (7). Heritability ( $\hat{h}^2$ ) is estimated as:

$$\hat{h}^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_a^2 + \hat{\sigma}_e^2} \quad (8)$$

A similar approach can be used in multivariate analyses, by maximizing the likelihood with respect to the matrix of residual covariances, and its ratio with the additive genetic covariances (JUGA and THOMPSON, 1990; MEYER, 1991).

Sampling errors of estimated parameters and their ratios can be approximated by the inverse of the matrix of second derivatives (also called the Hessian matrix) of the log likelihood function with respect to the parameters

Table 2. — Generalised least square means and approximate standard errors, in parenthesis, of survival (S) and rooting (R) in propagation trials 1, 2, 3 and 4 and overall trials mean  $\pm$  standard deviation.

Trial	S (s.e.)	R (s.e.)
1	50.0 (5.42)	32.7 (8.18)
2	63.1 (5.42)	37.0 (8.17)
3	52.2 (5.42)	24.5 (8.18)
4	80.5 (5.42)	35.8 (8.17)
Across	61.5 $\pm$ 34.5	32.6 $\pm$ 37.5

being estimated. The Hessian matrix is not obtained with derivative-free REML algorithms but approximations by numerical differentiation have been described (NELDER and MEAD, 1965) and seem to work well for models with up to two random effects (MEYER, 1989).

To investigate the importance of genotype-occasion interaction, a second model was used (denoted Model 2), which included an additional random term for the interaction:

$$y = Xb + Za + Wd + e \quad (9)$$

where  $d$  is a vector of interaction effects and  $W$  is the incidence matrix for the interaction term. Significance of differences between Model 1 and Model 2 were tested using the chi-square ratio test (e.g. McCULLAGH and NELDER, 1989).

Estimates of variance and covariances for Models 1 and 2 were carried out using a DFREML program written by MEYER (1991b).

## Results and Discussion

### Means

Table 2 shows S and R for each trial and across trials. Overall mean survival was 62 %, but varied across trials. Survivals in the first 3 trials, set in the glasshouse, ranged between 50 % and 63 %, while S in the fourth trial, set in the shadehouse, was 81 %. Of the survivors, an average of 33 % rooted, ranging across trials from 25 % to 37 %, giving an overall propagation success of 20 % (i.e. 62 %  $\times$  33 % = 20 %). Similar values were reported by DE LITTLE and RAVENWOOD (1991) for the same species.

### Variance Components and Heritability

Estimates of additive genetic and environmental variances and corresponding heritabilities for S and R are presented in table 3. Overall trial heritabilities were moderate for S ( $\hat{h}^2 = 0.20 \pm 0.04$ ) and high for R ( $\hat{h}^2 = 0.41 \pm 0.03$ ), and associated with small standard errors. However, for S, estimates were similar across the four trials, with values ranging between  $\hat{h}^2 = 0.22$  and  $\hat{h}^2 = 0.30$ , whereas they were less consistent for R, ranging between  $\hat{h}^2 = 0.44$  and  $\hat{h}^2 = 0.83$ . In Trial 4, the analysis converged to the boundary of the parameter space, i.e. to a value of  $\hat{\sigma}_a^2$  equivalent to a heritability of one.

Differences in heritabilities across trials were associated with changes in magnitude of the variance components. Additive variances ( $\hat{\sigma}_a^2$ ) of S were similar in the first three trials (with  $\hat{\sigma}_a^2$  from 251.6 to 217.3; Table 3), whereas in Trial 4, where mean survival was significantly higher,  $\hat{\sigma}_a^2 = 319.5$ . Since no trend was apparent for environmental variance, higher heritabilities were also associated with

Table 3. — Estimates of additive genetic ( $\hat{\sigma}_a^2$ ) and residual ( $\hat{\sigma}_e^2$ ) variance components, heritabilities ( $\hat{h}_a^2$ ) and approximate standard errors (in parenthesis), of survival (S) and rooting (R) in propagation trials 1, 2, 3 and 4 and across trials.

Trial	$\hat{\sigma}_a^2$	$\hat{\sigma}_e^2$	$\hat{\sigma}_p^2$	$\hat{h}^2$ (s.e.)
<i>Survival</i>				
1	265.4	777.7	1043.2	0.25 (0.14)
2	271.3	810.3	1081.5	0.25 (0.14)
3	251.6	895.3	1146.9	0.22 (0.13)
4	319.5	751.3	1070.8	0.30 (0.14)
Across	223.1	887.8	1110.9	0.20 (0.04)
<i>Rooting</i>				
1	1052.0	712.4	1764.3	0.60 (0.23)
2	1438.3	293.1	1731.3	0.83 (0.26)
3	547.2	696.2	1243.5	0.44 (0.20)
4	†	†	†	†
Across	529.8	773.5	1303.2	0.41 (0.03)

† Search terminated at the boundary of the parameter space.

Table 4. — Estimates of additive ( $\hat{\sigma}_a^2$ ), genotype x interaction ( $\hat{\sigma}_{a \times o}^2$ ) and residual ( $\hat{\sigma}_e^2$ ) variances for initial survival (S) and rooting (R) under Model 2, and the likelihood ratio test for the null hypothesis  $\hat{\sigma}_{a \times o}^2 = 0$ .

Trait	$\hat{\sigma}_a^2$	$\hat{\sigma}_{a \times o}^2$	$\hat{\sigma}_e^2$	$\chi^2$ Ratio Test
S	222.8	669.6	218.3	5.74 (2%)
R	530.0	75.1	701.4	0.42(n.s.)

higher mean survival. Differences in magnitude of  $\hat{\sigma}_a^2$  and  $\hat{\sigma}_e^2$  for R were more marked (with  $\hat{\sigma}_a^2$  between 547.2 and 1438.3), but higher heritabilities were still associated with more successful (higher percentage rooted) propagation trials.

The additive genetic and phenotypic correlations between S and R were moderately negative ( $\hat{r}_g = -0.12$  and  $\hat{r}_p = -0.02$ , respectively) and not significantly different from zero (Chi-square ratio test,  $P > 15\%$ ). Moreover, no relationship was evident between trial mean S and trial mean R. In particular, Trial 4, which had a good survival (S=81%) did not show exceptional rooting (R=36%), compared with the other trials.

Thus, the results suggest that rooting, as the percentage of initially surviving cuttings which rooted, is under stronger additive genetic control than survival, and these traits are genetically independent. Since the initial survival of cuttings, particularly the relatively fragile apical cuttings of *E. globulus*, is expected to be strongly dependent on the propagation environment, selection for better rooting ability should be made independently of survival. With such a poor genetic relationship between the 2 traits, the heritability estimate of R is reduced (data not shown) if percentages are based on the total number of cuttings set, instead of only on those which initially survived. For example, the overall heritabilities would have dropped from  $\hat{h}^2 = 0.41$  (as in Table 3) to 0.36. Similar reductions in heritability estimates occur in each separate trial.

#### Genotype-Occasion Interactions

Comparisons between Model 1 (without genotype-occasion interaction) and Model 2 (with interaction) showed a significant interaction effect for S at the 2% level, with interaction variance,  $\hat{\sigma}_{a \times o}^2 = 670$ , accounting for 55% of the total variance (Table 4). On the other hand, interaction did not seem to be significant for R, with  $\hat{\sigma}_{a \times o}^2 = 75.1$ , which accounted for less than 5% of total variance. This suggests that, for the range of propagation conditions tested, a few propagation trials would be sufficient for a reliable selection for R in *E. globulus*, but not for S.

An alternative way of looking at the impact of interactions between trials is to use the correlations between estimated breeding values (BLUP of a) among different pairs of trials. These are presented in table 5, using the BLUP's of breeding values of the 10 parents, for S and R. For S, correlations were generally low but positive across pairs of trials, with values ranging between 0.01 to 0.63. Correlations between survival in Trial 4, which had a high

Table 5. — Correlations of expected breeding values (BLUP) of parents, between trial i and j for initial survival (below diagonal) and rooting (above diagonal).

Trial	1	2	3	4
1				
2	0.36			
3	0.63	0.59		
4	0.01	0.10	0.43	

mean survival of 81%, and earlier trials, were particularly poor. This marked interaction indicated by the unpredictability of breeding values for S across propagation trials, may reflect clone-propagation system interactions due to season (since the trials were made from mid-winter to late spring), as well as to the difference in the propagation environments (Trials 1 to 3 in the glasshouse, Trial 4 in the shadehouse). In contrast, correlations between predicted breeding values of R across the four trials were consistently high, values ranging between 0.66 and 0.94.

### Conclusions

Estimates of genetic parameters for propagation traits and the relative importance of genotype-propagation system interactions, such as those presented in this study, are needed if breeding programs are to rely on vegetative propagation to transfer gains into plantations. The way in which propagation traits should be incorporated into selection and breeding strategies aimed at improving growth or wood quality traits is still uncertain (HAINES, 1992), but there is no doubt that success of large-scale vegetative propagation depends on high survival and rooting ability of the propagules (HAINES and WOOLASTON, 1991). Results from this study show that this should be achievable, under appropriate propagation systems, through breeding. Initial survival and rooting are both heritable, but survival was under only poor additive genetic control, whereas rooting was strongly inherited. The two traits were not genetically correlated indicating the involvement of different genes. Although genetic improvement of propagation characteristics can combine selection for both survival and rooting, for example using multitrait indices, it was apparent that substantial improvements in mean survival could be achieved simply by refining the propagation system. The poor relationship between survival and rooting, the lower heritability of the former and the substantial genotype-trial interactions found for survival makes it a less attractive trait to use than rooting. The results also suggest that improving overall survival, by changing the propagation environment, should not affect the accuracy of selection for rooting. Further studies are needed, however, to incorporate this information into tree selection and breeding schemes.

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