Selection age and risk: finding the compromise. Silvae Genet. **42**: 25–40 (1993). — NAMKOONG, G. and CONKLE, M. T.: Time trends in genetic control of height growth in ponderosa pine. Forest Science **22**: 2–12 (1976). — NAMKOONG, G., USANIS, R. A. and SILEN, A. R.: Age-related variation in genetic control of height growth in Douglas-fir. Theor. Appl. Genet. **42**: 151–159 (1972). — PHARIS, R. P., WEBBER, J. E. and ROSS, S. D.: The promotion of flowering in forest trees by gibberellin $A_{4/7}$ and cultural treatments: a review of the possible mechanisms. For. Ecol. Manage. **19**: 65–84 (1987). — REHFELDT, G. E.: Genetic variance and covariances in *Pinus contorta*: estimates of genetic gains from index selection. Silvae Genet. **34**:26–33 (1985). — SAKAI, K., MUKAIDE, H. and TOMITA, P. H.: Intraspecific competition in forest trees. Silvae Genet. **17**: 1–5 (1968). — SAS Institute: SAS Procedures Guide. Release 6.03 Ed. Cary. NC (1988). — SATTERTHWAITE, F. E.: An approximate distribution of estimates of variance components. Biom. Bull. **2**: 110–114 (1946). — SMITHERS, L. A.: Lodgepole Pine in Alberta. Bulletin 127. Department of Forestry, Ottawa, Canada (1961). — WU, X.: Theoretical and experimental evaluation of early selection in lodgepole pine (*Pinus contorta* ssp. *latifolia* ENGLM.). Ph. D. thesis, the University of Alberta, Edmonton (1993). — WU, H. X. and YING, C. C.: Genetic parameters and selection efficiencies in resistance to western gall rust, stalactiform blister rust, needle cast and sequoia pitch moth in lodgepole pine. (Submitted) (1995). — XIE, C.-Y., JOHNSTONE, W. D. and YING, C. C.: Spacing and provenance effects on the performance of shore pine (*Pinus contorta* var *contorta*) – twenty-year test results. Can. J. For. Res. **25**: 567–576 (1995). — XIE, C.-Y. and YING, C. C.: Genetic architecture and adaptive landscape of interior lodgepole pine (*Pinus contorta* ssp. *latifolia*) in Canada. Can. J. For. Res. **25**: 2010–2021 (1995). — YANCHUK, A. D., YEH, F. C. and DANCIK, B. P.: Variation of stem rust resistance in a lodgepole pine provenance-family plantation. For Sci. **34**: 1067–1075 (1988). — YING, C. C., ILLINGWORTH, K. and CARLSON, M.: Geographic variation in lodgepole pine and its implications for tree improvement in British Columbia. *In*: Lodgepole pine the species and its management. D. M. BAUMGARTNER *et al.* (eds.). Coop. Ext. Serv., Wash. State Univ., Pullman (1985). — ZOBEL, B. and TALBERT, J.: Applied Forest Tree Improvement. John Wiley & Sons, New York (1984).

Genetic Analysis of Survival in *Eucalyptus globulus* ssp. *globulus*

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Summary

Genetic parameters for survival and diameter were estimated from measurements from 4 to 5 year old progeny trials of *Eucalyptus globulus* ssp. *globulus* in Australia and Portugal. The trials comprised over 660 open-pollinated families, covering the natural range of species. Individual narrow sense heritabilities for survival were moderate to high (average h^2_{op} = 0.31). Correlations between survival at different sites were also moderate to high ranging from 0.16 to 0.92 (average of 0.48), suggesting that in some instances survival ability can be determined by different genes. Diameter and survival were also positively correlated within sites (average r_g = 0.54).

Key words: REML, heritabilities, genetic correlations, binomial scale.

FDC: 165.3; 232.11; 176.1 *Eucalyptus globulus*; (94); (469).

Introduction

In *Eucalyptus globulus* ssp. *globulus*, as in most tree species, plantation programs usually aim to improve the productivity on an area basis, thus combining growth rate per tree with survival per unit area. However, while there are several reported studies on the genetic control of growth in *E. globulus* ssp. *globulus* (VOLKER *et al.*, 1990; BORRALHO *et al.*, 1992), the genetic control of survival in a plantation forestry context has not received much attention. As a consequence, survival, and particularly early survival, has not been included as a trait in eucalypt selection programs (e. g. BORRALHO *et al.*, 1993; JARVIS *et al.*, 1995), although its impact on plantation productivity can be large. Furthermore, failure to account for survival in the evaluation of other traits is known to bias the prediction of breeding values if traits are significantly correlated with survival. For example, differential or size dependent mortality (MAGNUSSEN, 1993), or culling of smaller trees prior to assessment age (MATHESON and RAYMOND, 1984), have been shown to result in inflated breeding value predictions.

There are several complications when dealing with survival. The first is that survival of seedlings at different sites can be determined by various causes: temporary or prolonged frost or drought, wind, competition or diseases. To measure the importance of different causes of mortality, and thus allow accurate genetic prediction across trials, the pattern and scale of genotype-environment interactions for survival must be known. Such interactions can be examined by genetic correlations (BURDON, 1977; BULMER, 1980), with survival at different trials treated as distinct traits. Since in most cases, the same genotypes are not represented in different trials, genetic covariances must be obtained from related individuals. ANOVA-based methods have been commonly used in forestry (BURDON, 1977; WOOLASTON *et al.,* 1991). A more flexible procedure is to use Restricted Maximum Likelihood to calculate these genetic covariances as initially suggested by SCHAEFFER *et al.* (1978) and later extended to individual models by JUGA and THOMPSON (1990) and MEYER (1991).

A difficulty in the analysis of open-pollinated eucalypt progeny, such as in this study, is that differences in the rate of inbreeding amongst open-pollinated families may occur (POTTS *et al.,* 1995). Several authors (GRIFFIN and COTTERILL, 1988; BORRALHO, 1994; HODGE *et al.,* 1995) have drawn attention to the fact that this variation in selfing may affect variance estimates, and this is likely to be even more important in traits such as early survival (HARDNER and POTTS, 1995). A further complication is the binomial nature of survival, which has only 2 distinct non-continous phenotypes: dead or alive. Groups of individuals, for example families, can have any value for survival, expressed as a percentage of those individuals that have survived, also denoted incidence (MCGUIRK, 1989). However, the phenotypic scale in which the incidence is expressed

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is inappropriate for comparing survival across trials of different incidence, since on this scale variances differ according to the mean (GIANOLA, 1982; FALCONER; 1989; MCGUIRK, 1989). An alternative is to analyse survival as a continuous trait by postulating an underlying continuous distribution of phenotypes, termed the liability scale in this paper, which maps into the observed distribution via a fixed threshold (GIANOLA, 1982). The phenotype and genotype of a dead tree is considered to lie below the threshold, whereas that of an alive tree, would lie above the threshold. Hence by assuming that survival is distributed on an underlying (liability) scale, variances can be compared across trials (MCGUIRK, 1989). The objective of this paper is to analyse the genetic control of survival in a base population of *Eucalyptus globulus* ssp. *globulus* grown on a diverse range of sites in Portugal, Western Australia and Tasmania, and to determine its genetic relationship with growth. This is believed to be the first published report on the genetic control of survival and its relationship with juvenile growth for *Eucalyptus*.

Materials and Methods

Genetic Material

The progeny in this study were obtained from a range wide collection undertaken by the CSIRO Australian Tree Seed Centre in collaboration with several international forestry companies, in 1987 and 1988, as detailed in JORDAN *et al.* (1995). It consisted of over 660 open-pollinated families covering the entire natural range of *Eucalyptus globulus* ssp. *globulus* (hereafter abbreviated spp. *globulus*) (*Figure 1*).

Trial Site and Design

The trials included in this study are located in Tasmania (5 sites established by North Forest Products and 1 site established by Forestry Tasmania), Western Australia (3 sites established by Bunnings Tree Farms) and Portugal (2 sites established by Soporcel). Climatic conditions range from dry Mediterranean in Portugal and Western Australia, with 500 mm to 840 mm annual rainfall; to wetter more temperate sites in Tasmania with 950 mm to 1600 mm annual rainfall (*Table 1*).

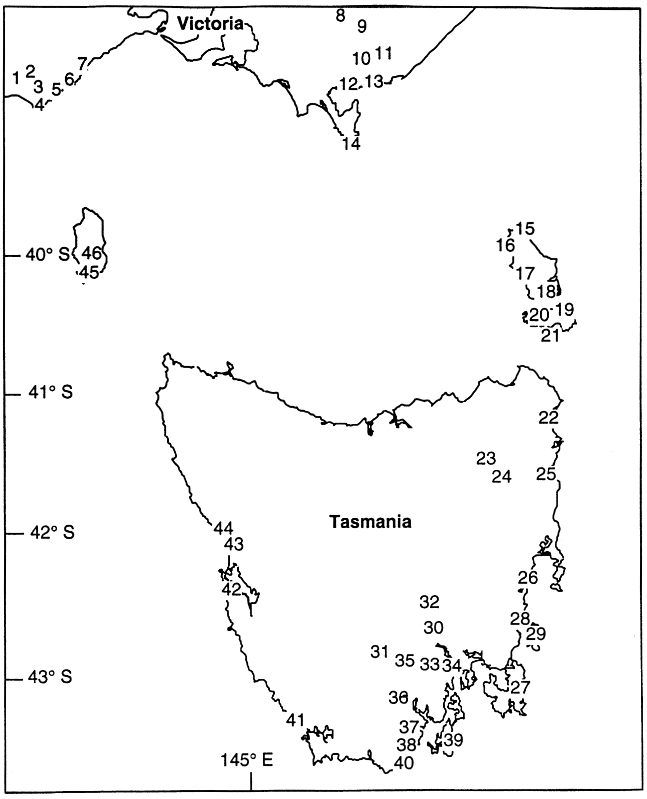

Figure 1. – Location of sampling plots throughout the natural distribution of *E. globulus* ssp. *globulus*, the numbers corresponding to separate localities as defined by JORDAN *et al.* (1994).

The North Forest Products' trials contained 5 replicates, each with between 21 to 28 incomplete blocks of 20 to 25 families in 2-tree continuous plots (JORDAN *et al.*, 1995). The Western Australian trials had between 5 to 9 replicates of between 10 to 13 incomplete blocks with families planted in 5 (Bridgetown and Busselton) or 10 tree line plots. The Portuguese trials comprised 5 to 7 randomised complete blocks of 20

Table 1. – Location, soil, climate, experimental design, and data structure for each trial.

Trial	*Established*	*Latitude*	*Longitude*	*Altitude (m)*	*Annual Rainfall (mm)*	*Soil Type*	*No. Trees*	*No. Families*	*Mean Survival (%) (± s.d.)‡*	*Mean Diam. (cm) (± s.d.) ‡*
Portugal										
Ameixoeira	Nov-88	39°05'N	08°55'W	100	700-800	Gradational	4626	177	0.63±0.43	5.79±2.21
Nave Redonda	Nov-89	38°35'N	07°30'W	100	500-600	Lithosol	4428	123	0.81±0.38	4.70±1.05†
Western Australia										
Mumballup	Jul-88	33°33'S	116°04'E	240	633	Sandy duplex	5322	120	0.86±0.37	13.81±4.02
Bridgetown	Jul-90	33°57'S	116°17'E	260	592	Lateritic	5153	104	0.91±0.33	10.02±1.84
Busselton	Jul-90	33°45'S	115°24'E	100	838	Sandy duplex	4966	104	0.47±0.41	6.40±2.01
Tasmania										
Woolnorth	Jul-89	40°49'S	144°53'E	60	1163	Yellow podzolic	5469	494	0.91±0.25	7.48±2.74
West Ridgley	Jul-89	41°08'S	145°48'E	180	1273	Kraznozem	4983	450	0.88±0.27	10.71±3.28
Massy Greene	Jul-89	41°05'S	145°54'E	120	1130	Kraznozem	6150	596	0.95±0.18	12.69±3.95
Latrobe	Jul-89	41°17'S	146°27'E	100	953	Yellow podzolic	5930	569	0.91±0.24	8.56±2.02
Exeter	Jul-89	41°17'S	146°51'E	120	974	Sandy duplex	5723	551	0.96±0.17	8.57±2.19
Meunna	Aug-88	41°05'S	145°30'E	250	1614	Kraznozem	1240	84	0.46±0.40	9.95±4.19

†) Estimate based on height (m), not diameter (cm).

‡) Standard deviations are obtained from the variation of individual trees as opposed to family means.

tree line plots. The data analysed consisted of 4 year diameter or height growth measurements, except at Mumballup (Western Australia) and Meunna (Tasmania) where 5 year data was used. Site, climatic and design characteristics for all trials are detailed in *table 1*.

Statistical Analysis

Estimates of variance and covariance components and associated heritabilities of survival, and correlations between survival and growth were obtained by Restricted Maximum Likelihood methods (REML), using a derivative free algorithm (DFREML; MEYER, 1991), with the following model:

$$y = Xb + Zu + Wp + e \qquad (1)$$

where y is the vector of N observations for survival and growth; b is the vector for the fixed effects, namely race as defined by JORDAN *et al.* (1995) and blocks; p is the vector for the additional random effect (plot), and u is the vector for the additive genetic effects. X, W and Z are incidence matrices for the fixed and random effects respectively.

To correct for the uncertainty in the rate of relatedness amongst the open-pollinated progeny collected from natural stands, a stand-type classification was added to the genetic model (BORRALHO and POTTS, 1995). This classification of stand-types ranged from 1 to 4, according to the number of potential pollinators surrounding the parent tree. The assumption that survival had an underlying continuous normal distribution, was shown to be appropriate (CHAMBERS, 1994). The expected mean and variances of the parameters y, b, u, p and e are as follows:

$$E\begin{bmatrix} y \\ e \\ p \\ u \end{bmatrix} = \begin{bmatrix} Xb \\ 0 \\ 0 \\ 0 \end{bmatrix}, \qquad Var\begin{bmatrix} y \\ e \\ p \\ u \end{bmatrix} = \begin{bmatrix} V & R & WG_p & ZG_u \\ R & R & 0 & 0 \\ G_pW' & 0 & G_p & 0 \\ G_uZ & 0 & 0 & G_u \end{bmatrix} \qquad (2)$$

where:

$$V = R + ZG_uZ' + WG_pW' \qquad (3)$$

$R = \bigoplus_{j=1}^{m} \boldsymbol{R}_{oj}$, with m = number of records,

$G_p = \boldsymbol{I}_p \otimes \boldsymbol{G}_{op}$

$G_u = \boldsymbol{A} \otimes \boldsymbol{G}_{ou}$

A = numerator relationship matrix,

G_{ou} = variance-covariance matrix for the additive genetic effect,

G_{op} = variance-covariance matrix for the plot effect,

R_{oj} = residual covariance matrix for tree j,

$\otimes$ = Kronecker product,

$\oplus$ = direct sum.

Approximate standard errors of variance ratio estimates follow NELDER and MEAD (1965). Heritability estimates obtained from the analysis of survival were in a binomial scale and had to be converted to the liability scale for comparison across trials using the following relationship (OLAUSSON and RÖNNINGEN, 1975; MCGUIRK, 1989):

$$h_L^2 = h_{0/1}^2 \frac{p(1-p)}{z^2} \qquad (4)$$

where $h^2_{0/1}$ is the heritability on the observed binominal scale, h^2_L is the heritability for survival on the underlying (liability) scale, p is the incidence of survival in the trial, and z is the height of the ordinate at the threshold corresponding to the incidence in that trial. The average sib relationship amongst open-pollinated sibs was assumed to be $\frac{1}{2.5}$ (similar to values reported used by VOLKER *et al.,* 1990 and HODGE *et al.,* 1995), thus heritabilities on the liability scale were adjusted for related mating as:

$$h_{op}^2 = \frac{2.5}{4} . h_L^2 \qquad (5)$$

where h^2_{op} is the heritability adjusted for open-pollinated progeny. Phenotypic correlations were corrected from the binomial to liability scales, using the following formula (OLAUSSON) and RÖNNINGEN, 1975):

$$r_L = r_{0/1} \cdot \left[\frac{p_A(1-p_A)}{z_A^2}\right]^{\frac{1}{2}} \left[\frac{p_B(1-p_B)}{z_B^2}\right]^{\frac{1}{2}} \qquad (6)$$

where $r_{0/1}$ and r_L are the phenotypic correlation between binomial trait A and B calculated on the binomial and the liability scale, respectively, p_A and p_B are the incidence of the traits, and z^2_A and z^2_B are the height of the threshold on the liability scale for traits A and B, respectively. Genetic correlations, as shown by OLAUSSON and RÖNNINGEN (1975), are equivalent on the binomial and underlying scales. Phenotypic correlations between survival and growth, where one of the traits is binomial and the other is phenotypically continuous, also needed to be converted to the liability scale (OLAUSSON and RÖNNINGEN, 1975):

$$r_L = r_{0/1} \cdot \left[\frac{p_A(1-p_A)}{z_A^2}\right]^{\frac{1}{2}} \qquad (7)$$

where trait A is assumed to be binomial trait, $r_{0/1}$ and r_L are the phenotypic correlations calculated on the binomial and liability scale, respectively, p_A is the incidence of binomial trait A, and z^2_A is the height of the threshold on the liability scale for trait A. Genetic correlations between survival and growth are also expected to be invariable between the binomial and liability scales (OLAUSSON and RÖNNINGEN, 1975).

Results and Discussion

Overall means of survival and diameter and their standard deviation are given in *table 1*. Survival was very high in most of the northern Tasmanian trials, ranging between 88% at West Ridgley to 96% at Exeter. On the other hand, survival at 5 years at Meunna (also in Tasmania) was only 46%. This trial had a history of severe frosting, especially the initial 2 years after establishment and intense weed competition (PETER KUBE, Forestry Tasmania, pers. communication), with mortality in the first and second years of 17% and 35% respectively. Survival was generally lower in Western Australia and Portugal than in Tasmania. The major cause of mortality in the Western Australian and Portuguese trials was likely to be drought (GREG DUTKOWSKI, Bunnings Tree Farms and Rui

Sousa, pers. communication). The lowest survival in Western Australia was at Busselton, where only 47% of seedlings planted survived to age four, but survival at Bridgetown was very good (91%). The lowest survival in Portugal was at Ameixoeira, with 62%, and at Nave Redonda with 81%.

Heritabilities

Variance components, individual heritabilities and their approximate standard errors for survival at each trial are given in *table 2*. Heritability of survival (h^2_{op}) was moderate to high ranging between 0.19 at Nave Redonda, in Portugal and 0.57 at West Ridgley in Tasmania, and with a mean across all trials of 0.31. The 2 trials most affected by drought (Ameixoeira with 63% survival and Busselton with 42% survival) had consistently lower heritabilities, with h^2_{op} = 0.23 and 0.21 respectively. On the other hand, the trials where the primary cause of mortality was attributed to frost damage (West Ridgley and to a lesser extent Meunna) had higher heritabilities (h^2_{op} = 0.57 and 0.32 respectively), in agreement with previous estimates of heritability for frost damage under controlled conditions (ALMEIDA, 1993) or using electric conductivity in leaf discs in ssp. *globulus* (VOLKER *et al.*, 1995). In the remaining sites in Tasmania and at Bridgetown in Western Australia, where survival was close to 100%, heritabilities were generally high, although for such high levels of incidence, the additive genetic variances are expected to be slightly biased upwards (MERCER and HILL, 1984).

Correlations between Survival at Different Trials

Genetic and adjusted phenotypic correlations of survival across trials are presented in *table 3*. Genetic correlations between survival in Tasmanian trials (bottom right hand corner of *Table 3*) were generally very high, averaging around 0.70, but ranged from 0.16 between Exeter and Meunna, to 0.92 between Massy Greene and Exeter. It is interesting to note that the genetic correlations between Meunna, where severe frost damage was reported, and other Tasmanian trials were generally low, exept for the correlation with West Ridgley (r_g = 0.81) where frost damage was also reported.

The genetic correlation between Bridgetown and Busselton in Western Australia (r_g = 0.39), and between Nave Redonda and Busselton (r_g = 0.40) were comparatively low and would indicate the specific drought conditions at Busselton. Genetic correlations between trials with a history of drought related mortality (e.g. Busselton and Ameixoeira) and trials with a history of frost related mortality (e.g. West Ridgley and Meunna) were, as expected, lower (r_g between 0.16 and 0.27) suggesting that survival ability for frost and survival ability for drought are relatively independent.

Overall, genetic correlations between survival at Western Australia and Tasmania were low, ranging between 0.14 and 0.57 (average 0.33), suggesting that different factors were operating within each region to effect the survival of seedlings. Genetic correlations between Portuguese and Tasmania sites (between 0.16 and 0.78, average 0.42) and between Western Australia and Portuguese sites (between 0.14 and 0.57, average 0.42) were also moderate (*Table 3*).

Correlations between Survival and Growth

Covariance estimates between growth and survival, and the additive genetic (r_g) and phenotypic (r_p) correlations between these 2 traits at each trial are given in *table 4*. The adjusted phenotypic correlations for Massy Greene and Exeter result in values above one. This is likely to be due to the bias associated with the high incidence of survival at these trials. Genetic correlations between growth and survival were consistently positive, ranging between 0.08 at Mumballup and 0.81 at

Table 2. – Main cause of seedling mortality, mean survival (in % units) and estimates of additive genetic (V_a), error (V_e), plot (V_{plot}) and total phenotypic (V_{total}) variances and corresponding heritability on the binomical scale (h^2_B ± s.e.) and heritabilities adjusted to the liability scale and for open-pollination (h^2_{op}) for survival across all trials, at age 4 to 5 years.

Trial	*Cause*	*Survival*	V_a	V_e	V_{plot}	V_{total}	h^2_B	*(s.e.)*	h^2_{op}
Portugal									
Ameixoeira	drought	63	0.044	0.155	0.012	0.210	0.21	(0.10)	0.23
Nave Redonda	drought frost	81	0.021	0.121	0.008	0.151	0.14	(0.03)	0.19
Western Australia									
Mumballup	drought	86	0.036	0.078	0.011	0.125	0.29	(0.06)	0.41
Bridgetown	drought	91	0.025	0.058	0.004	0.087	0.29	(0.06)	0.48
Busselton	drought	47	0.041	0.134	0.014	0.190	0.22	(0.05)	0.21
Tasmania									
Woolnorth		91	0.008	0.046	0.003	0.057	0.14	(0.04)	0.35
West Ridgley	frost	88	0.017	0.048	0.001	0.066	0.26	(0.05)	0.57
Massy Greene		95	0.002	0.029	0.002	0.033	0.06	(0.03)	0.20
Latrobe		91	0.005	0.053	0.002	0.060	0.08	(0.03)	0.20
Exeter		96	0.002	0.026	0.001	0.029	0.07	(0.03)	0.28
Meunna	frost weeds	46	0.052	0.127	0.056	0.235	0.32	(0.10)	0.32

Table 3. – Estimates of between-trial genetic (r_g), above diagonal, and phenotypic (r_L), below diagonal, correlations for survival across all trials. An X denotes that the number of corresponding families represented in each trial was too few, to allow a meaningful correlation.

Trials		**Portugal**		**Western Australia**			**Tasmania**					
	No.	11	12	61	62	63	71	72	73	74	75	76
Portugal												
Ameixoeira	11	–	X	0.29	X	X	0.19	0.27	0.42	0.34	0.46	0.16
Nave Reonda	12	X	–	X	0.58	0.40	0.46	0.78	0.39	0.64	0.57	X
Western Australia												
Mumballup	61	0.31	X	–	X	X	0.36	0.14	0.41	0.28	0.31	0.19
Bridgetown	62	X	0.15	X	–	0.39	0.45	0.46	0.50	0.43	0.57	X
Busselton	63	X	0.34	X	0.59	–	0.16	0.18	0.26	0.23	0.31	X
Tasmania												
Woolnorth	71	0.16	0.15	0.18	0.42	0.14	–	0.81	0.79	0.74	0.65	0.50
West Ridgley	72	0.14	0.27	0.12	0.49	0.16	0.69	–	0.75	0.80	0.88	0.81
Massy Greene	73	0.19	0.30	0.27	0.46	0.08	0.84	0.96	–	0.88	0.92	0.19
Latrobe	74	0.21	0.28	0.29	0.52	0.16	0.49	0.96	1.09	–	0.91	0.44
Exeter	75	0.13	0.16	0.24	0.68	0.17	0.37	0.58	1.61	0.98	–	0.16
Meunna	76	0.10	X	0.14	X	X	0.30	0.55	0.08	0.54	0.16	–

Table 4. – Estimates of additive genetic (r_g) and phenotypic correlations in the liability scale (r_L) between diameter, or height*), and survival within each trial, at age 4 to 5 years.

Trial	r_g	r_L
Portugal		
Ameixoeira	0.53	0.32
Nave Redonda*	0.57	0.53
Western Australia		
Mumballup	0.08	-0.70
Bridgetown	0.65	0.69
Busselton	0.43	0.19
Tasmania		
Woolnorth	0.51	0.40
West Ridgley	0.49	0.39
Massy Greene	0.81	1.46
Latrobe	0.70	0.97
Exeter	0.77	1.75
Meunna	0.38	0.12

*) Estimates based on height growth, not diameter.

Massy Greene, and averaging 0.50 across all trials (*Table 4*). This suggests that genes responsible for faster growth are also associated with those enhancing survival after planting. It is likely that this association is due to a direct casual effect with vigorous growth increasing the chance of survival against environmental stresses such as competition or ground frost. This may not be the case for drought however, if high productivity is associated with higher water consumption. The genetic correlation between survival and growth at Mumballup and Busselton, where severe drought conditions were reported was still positive but comparatively lower (r_g = 0.08 and 0.43 respectively). In contrast, in a recent study comparing growth of surviving trees with drought susceptibility, across four trials in Western Australia, DUTKOWSKI (1995) found a consistently negative genetic correlation (r_g between – 0.43 and – 0.05). Although these estimates are likely to be biased due to non-random mortality across families, they clearly suggest that genetic relationship between growth rate and drought resistance is likely to be poor.

Conclusion

The results showed that early survival of ssp. *globulus* was under moderate to high genetic control, with heritabilities ranging between 0.19 and 0.57. However survival at each site could be explained by different factors, with frost, drought and competition likely to be the major causes of mortality in juvenile plantations. The moderate genetic correlations between trials with different histories, suggest that physiological mechanisms used against frost and drought might be controlled, to a large extent, by different genes. Trials with similar history had consistently higher genetic correlations. Genetic correlations between growth and survival were generally high and positive, but ranged from 0.08 to 0.81, indicating that superior genotypes for growth will also have a greater survival ability.

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References

ALMEIDA, M. H.: Estudo da variabilidade geográfica em *Eucalyptus globulus* LABILL. Unpublished PhD Thesis, Univeridade Tecnica de Lisboa, Instituto Superior de Agronomia (1993). — BORRALHO, N. M. G.: Heterogeneous selfing rates and dominance effects in estimating heritabilities from open-pollinated progeny. Can. J. For. Res. **24**: 1079–1082 (1994). — BORRALHO, N. M. G., COTTERILL, P. P. and KANOWSKI, P. J.: Genetic control of growth of *Eucalyptus globulus* in Portugal. I. Genetic and phenotypic parameters. Silvae Genet. **41**: 39–45 (1992). — Borralho, N. M. G., Cotterill, P. P. and Kanowski, P. J.: Breeding objectives for pulp production of *Eucalyptus globulus* under different industrial cost structures. Can. J. For. Res. **23**: 648–656 (1993). — Borallho, N. M. G. and Potts, B. M.: Accounting for native stand characteristics in genetic evaluations of open pollinated progeny from a *Eucalyptus globulus* base population. New Forests **9**: (in press) (1995). — Bulmer, M. G.: The Mathematical Theory of Quantitative Genetics. Oxford, Clarendon Press (1980). — Burdon, R. D.: Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. Silvae Genet. **26**: 168–175 (1977). — Chambers, P. G. S.: An examination of the natural variation and genetic control of survival in *Eucalyptus globulus* ssp. *globulus*. Unpublished, Honours Thesis, University of Tasmania (1994). — Dutkowski, G. W.: Genetic variation in drought susceptibility of *Eucalyptus globulus* ssp. *globulus* in plantations in Western Australia. In: Eucalypt Plantations: Improving Fibre Yield and Quality'. (Eds: B. M. Potts, N. M. G. Barralho, J. B. Reid, R. N. Cromer, W. N. Tibbits and C. A. Raymond). pp. 199–203. Proc. CRC-IUFRO Conf., Hobart, 19th to 24th Feb. (CRC for Temperate and Hardwood Forestry, Hobart) (1995). — Falconer, D. S.: Introduction to Quantitative Genetics. 3rd edition. John Wiley and Sons International, New York (1989). — Gianola, D.: Theory and analysis of threshold characters. J. Anim. Sci. **54**: 1079–1096 (1982). — Griffin, A. R. and Cotterill, P. P.: Genetic variation in growth of outcrossed, selfed and open-pollinated progenies of *Eucalyptus regnans* and some implications for breeding strategy. Silvae Genet. **37**: 124–131 (1988). — Groeneveld, E., Kovac, M. and Wang, T.: PEST, a general purpose BLUP package for multivariate prediction and estimation. In: Proc. 4th World Congress of Genetics Applied to Livestock Production. Edinburgh, **13**: 488–491 (1990). — Hardner, C. M. and Potts, B. M.: The influence of mortality and stand age on the estimation of genetic parameters in *Eucalyptus regnans*. In: Eucalypt Plantations: Improving Fibre Yield and Quality'. (Eds: B. M. Potts, N. M. G. Borralho, J. B. Reid, R. N. Cromer, W. N. Tibbits and C. A. Raymond). pp. 208–211. Proc. CRC-IUFRO Conf., Hobart, 19th to 24th Feb. (CRC for Temperate and Hardwood Forestry, Hobart). (1995). — Henderson, C. R.: Best linear unibased estimation and prediction under a selection model. Biometrics **31**: 423–447 (1975). — Hodge, G. R., Volker, P. W., Potts, B. M. Owen, J. V.: A comparison of genetic information from open-pollinated and control-pollinated progeny tests in two eucalypt species. Theor. Appl. Genet., (in press) (1995). — Jarvis, S. F., Borralho, N. M. G. and Potts, B. M.: Implementation of a multivariate BLUP model for genetic evaluation of *Eucalyptus globulus* in Tasmania. In: Eucalypt Plantations: Improving Fibre Yield and Quality'. (Eds: B. M. Potts, N. M. G. Borralho, J. B. Reid, R. N. Cromer, W. N. Tibbits and C. A. Raymond). pp. 212–216. Proc. CRC-IUFRO Conf., Hobart, 19th to 24th Feb. (CRC for Temperate and Hardwood Forestry, Hobart) (1995). — Jordan, G. J., Borralho, N. M. G., Tilyard, P. and Potts, B. M.: Identification of races in *Eucalyptus globulus* ssp. *globulus* based on growth traits in Tasmania and geographic distribution. Silvae Genet. **43**: (1995). — Juga, J. and Thompson, R.: Estimation of bivariate variance components. In: Proc. 4th World Congress of Genetics Applied to Livestock Production. Edinburgh, **13**: 496–499 (1990). — Magnussen, S.: Bias in genetic variance estimates due to spatial autocorrelation. Theor. Appl. Genet. **86**: 349–355 (1993). — Matheson, A. C. and Raymond, C. A.: Effects of thinning in progeny tests on estimates of genetic parameters in *Pinus radiata*. Silvae Genet. **33**: 125–128 (1984). — McGuirk, B. J.: The estimation of genetic parameters for all-or-none and categorical traits. In: 'Evolution and Animal Breeding'. (Eds: W. G. Hill and T. F. C. MacKay). pp. 175–180. CAB International (1989). — Mercer, J. T. and Hill, W. G.: Estimation of genetic parameters for skeletal defects in broiler chickens. Heredity **53**: 193–203 (1984). — Meyer, K.: DFREML. Programs to Estimate Variance Components by Restricted Maximum Likelihood Using a Derivative-Free Algorithm. User Notes, Version 2 (1991). — Nelder, J. A. and Mead, R.: A simplex method for function minimisation. Computer J. **7**: 147–151 (1965). — Olausson, A. and Rönningen, K.: The estimation of genetic parameters for threshold characters. Act. Agr. Scand. **25**: 201–208 (1975). — Potts, B. M., Volker, P. W., Hodge, G. R., Borralho, N. M. G., Hardner, C. M. and Owen, J. V.: Genetic limitations in the exploitation of base populations of *Eucalyptus globulus* ssp. *globulus*. In: 'Eucalypt Plantations: Improving Fibre Yield and Quality'. (Eds: B. M. Potts, N. M. G. Borralho, J. B. Reid, R. N. Cromer, W. N. Tibbits and C. A. Raymond). pp. 217–221. Proc. CRC-IUFRO Conf., Hobart, 19th to 24th Feb. (CRC for Temperate and Hardwood Forestry, Hobart) (1995). — SAS Institute: SAS Procedures Guide. Version 6. 3rd edition. SAS Institute Inc., Cary, NC, USA (1990). — Schaeffer, L. R., Wilton, J. W. and Thompson, R.: Simultaneous estimation of variance and covariance components from multitrait mixed model equations. Biometrics **34**: 199–208 (1978). — Shaw, R. G.: The comparison of quantitative genetic parameters between populations. Evol. **45**: 143–151 (1991). — Volker, P. W., Dean, C. A., Tibbits, W. N. and Ravenwood, I. C.: Genetic parameters and gains expected from selection in *Eucalyptus globulus* in Tasmania. Silvae Genet. **39**: 18–21 (1990). — Volker, P. W., Owen, J. V. and Barralho, N. M. G.: Genetic variances and covariances for frost tolerance in *Eucalyptus globulus* and *Eucalyptus nitens*. Silvae Genet. **44**: (in press) (1995). — Woolaston, R. R., Kanowski, P. J. and Nikles, D. G.: Genotype-environment interactions in *Pinus caribaea* var. *hondurensis* in Queensland, Australia. II. Family x site interactions. Silvae Genet. **40**: 228–232 (1991).

Population Structure in *Gliricidia sepium* (Leguminosae) as Revealed by Isozyme Variation

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Abstract

Gliricidia sepium (Jacq.) Walp. is a woody legume native to seasonally dry sites in Meso-America. It has been introduced to many other parts of the tropics, where it is utilised as a source of fuelwood, living fences, animal fodder and green manure by rural communities. These introductions have, however, been founded on a narrow, or unknown, genetic base, and poor growth performance has been reported at a number of locations. There is, therefore, a need to diversify the genetic base of this species in domestication, and to explore its population structure as a basis for this diversification. Here we report the use of isozyme markers to investigate the distribution of genetic diversity within and among populations of *G. sepium*. Marked differentiation between populations ($F_{ST} = 0.172$) was observed, although most variation occurred within populations. Averaged over all populations, there was a mean number of alleles per locus (A) of 2.0, a mean percentage polymorphic loci (P) of 60% and a mean observed heterozygosity (H_o) of 0.238, values which suggest a rather higher level of genetic diversity than those reported from other comparable species. The values

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