GENETIC PARAMETERS AND GENOTYPE-BY-ENVIRONMENT INTERACTIONS FOR BASIC DENSITY, PILODYN PENETRATION AND STEM DIAMETER IN *EUCALYPTUS GLOBULUS*

A. Muneri[1,3] & C. A. Raymond[1,2]

[1)] CRC for Sustainable Production Forestry, GPO Box 252-12, Hobart TAS 7001 Australia
[2)] CSIRO Forestry and Forest Products, GPO Box 252-12, Hobart TAS 7001 Australia
[3)] Current Address: Queensland Forest Research Institute, PO Box 631, Indooroopilly QLD 4068 Australia
Author for Correspondence: Carolyn Raymond, CSIRO Forestry and Forest Products, GPO Box 252-12, Hobart TAS 7001 Australia, Phone: 03 6226 7948, Fax: 03 6226 7901, Email: Carolyn.Raymond@ffp.csiro.au

Received January 13, 2000; accepted October 20, 2000

ABSTRACT

Genetic parameters for basic density, pilodyn penetration and stem diameter were estimated using open-pollinated progeny from 70 families collected from across the natural distribution of *Eucalyptus globulus*. Six populations (subraces) were sampled: West Otways, Strzelecki Ranges, Furneaux Islands, King Island, north east Tasmania and south east Tasmania. Data from three sites were analysed to determine the degree and practical importance of genotype by environment interactions.

Basic density was under strong genetic control (individual, narrow-sense heritability ranging from 0.67 to 1.00) whilst both diameter and pilodyn penetration were under low to moderate genetic control (h^2 ranging from 0.16 to 0.33 and 0.13 to 0.27 respectively). Genetic correlations between basic density and pilodyn penetration were strong (–0.60 to –1.16) but no relationship was found between basic density and stem diameter. Subraces ranked differently for basic density and pilodyn penetration indicating differences in the relationship between pilodyn penetration and basic density and raising questions about the usefulness of pilodyn for general screening.

Although genotype by environment interaction was detected for diameter and basic density it is not considered to be a serious problem for breeding programs. For diameter, the interaction was caused by three families from the West Otway subrace. For basic density, the interaction was caused by 13 families spread across all subraces except King Island. However, the genetic correlations for basic density between sites were moderate to strong.

Key words: *Eucalyptus globulus*, stem diameter, wood properties, basic density, pilodyn, heritability, genetic correlations, genotype by environment interaction

INTRODUCTION

Eucalyptus globulus is widely planted in southern Australia, predominantly for kraft pulping. A breeding objective for kraft pulping of temperate eucalypts developed by GREAVES *et al.* (1997) identified tree volume and basic density as the two most economically important traits for breeding, followed by kraft pulp yield. Breeding programs in southern Australia currently include these wood properties in their breeding objective but little information is available about the degree of genetic control of the wood properties, or how this varies across sites.

Previous studies of genetic variation in *E. globulus* in southern Australia have concentrated on estimating genetic parameters for tree diameter (VOLKER *et al.* 1990; BORRALHO *et al.* 1995) using trials based on the CSIRO Australian Tree Seed Centre collection (GARDINER & CRAWFORD 1987, 1988) of more than 600 open-pollinated families. The few published studies of genetic parameters for wood properties in *E. globulus* have used a limited range of seedlots or sites but indicate that heritabilities for wood properties are higher than those for growth traits (BORRALHO *et al.* 1992, 1993; COTTERILL & BROLIN 1997; DEAN *et al.* 1990; MACDONALD *et al.* 1997). As plantations of *E. globulus* cover a wide range of environmental conditions, families may be expected to differ in their performance across sites. Determining the size and practical importance of genotype by environment interactions (GEI) is critical for designing tree breeding programs and making decisions about plantation establishment.

The wood property of interest for this study was basic density, which is defined as the mass of oven-dry wood per unit green volume of wood and is a critical

© ARBORA PUBLISHERS

quality trait for both production of pulp and paper and for sawn timber. Two methods for assessing basic density were used in this study: removing wood increment cores from each tree and determining their basic density, and using a pilodyn to assess density indirectly on standing trees.

The presence of GEI will reduce the rate of progress possible in a breeding program. Studies of GEI in other temperate eucalypt species have largely been restricted to tree growth but have indicated a wide range of different patterns of interaction; from very strong, geographically based interactions in *E. delegatensis* (GARNIER-GERE *et al.* 1995), to relatively small and inconsistent interactions in *E. regnans* (RAYMOND *et al.* 1997). As wood properties are generally under much stronger genetic control than tree growth it may be expected that the magnitude and patterns of GEI may differ from those observed for growth traits.

GEI may be caused by two factors: different variances between the sites, or changes in the ranking of genotypes across sites. The significance and practical importance of GEI may be assessed in a number of ways, starting with significance of the interaction term in an across site analysis of variance. However, the statistical significance of the interaction term does not provide information on the practical importance of the interaction to a breeding program. SHELBOURNE (1972) proposed that if the ratio of the interaction component of variance to the genetic component of variance was greater than 0.5 then the interactions were considered to be a threat to the rate of genetic progress in a breeding program. Another way of examining the importance of GEI is to calculate the genetic correlations between pairs of sites for each trait (BURDON 1977). If correlations are large, then GEI would be expected to have little impact on the rate of progress. Alternatively, the data can be examined to determine whether any geographic patterns are present or whether the interactions are due to particular sites or families. If only a few families are causing the interaction, the potential problem caused by GEI may be avoided by not including these families in the breeding population.

Each of the above approaches was used to examine genotype by environment interactions for wood density, pilodyn penetration and tree diameter using data from three open-pollinated progeny trials of *E. globulus*. As only three sites were available for analysis it was not feasible to undertake more sophisticated analyses of GEI such as joint regression analysis (FINLAY & WILKINSON 1963).

MATERIAL AND METHODS

This study was based on removal of 12 mm diameter bark-to-bark increment cores using a motor driven coring machine which leaves a 22 mm hole through the tree. As we did not wish to kill the sampled trees we were restricted to sampling only those sites where trees were sufficiently large. The minimum diameter over bark at breast height (DBHOB) for sampled trees was set at 15 cm. Three trials provided suitable material and were sampled: Massy Greene in Tasmania and Mt Worth and Flynn in Victoria (Table 1). The Massy Greene trial was established using 5 replicates, each containing 25 incomplete blocks of 24 open-pollinated families in two-tree line plots. The Victorian trials have 5 sublines based on geographic groupings of seedlots. Each subline has 20 randomised complete blocks of 39 to 47 open-pollinated families, planted as single tree plots. Each subline was planted as a distinct unit and separated from other sublines by a minimum of 100 m. Two families in each subline were *E. globulus* control seedlots which were planted in all sublines. Data were collected from these control families in each subline and used to determine differences due to subline location within site.

The study aimed to sample as much of the natural range of the species as possible. Using the race classification of JORDAN *et al.* (1994) and pilodyn information from a study by MACDONALD *et al.* (1997), six

Table 1. Location, rainfall and elevation for each site.

Trial	Massy Greene	Mt Worth	Flynn
Location	Tasmania	Victoria	Victoria
Owner	North Forest Products	Australian Paper Plantations	Australian Paper Plantations
Latitude (South)	41° 05'	38° 16'	38° 13'
Longitude (East)	145° 54'	146° 02'	146° 16'
Elevation (m)	120	380	60 - 80
Rainfall (mm)	1130	1200	700
Age (years)	7	8	8

Table 2. Number of families sampled within subrace and seedlot locality. The bold figures indicate the total number of families from each subrace.

Subrace number and name		Locality	Number of families
2	West Otways	Cannan Spur	6
		Otway State Forest	6
		Parker Spur	8
			20
5	Srzelecki	Bowden Road	4
		Jeerlang	3
		Jeerlang North	8
			15
6	Madalya Road (Gippsland)	Madalya Road	**5**
9	Furneaux	Central Flinders Island	4
		Central North Flinders Island	2
		North Flinders Island	2
		South Flinders Island	2
			10
11	NE Tasmania	Royal George	**5**
16	SE Tasmania	North Maria Island	5
			5
22	King Island	Central King Island	5
		South King Island	5
			10

races were selected to represent a wide range of pilodyn penetration - King Island for high penetration; Furneaux, South Eastern Tasmania and North Eastern Tasmania for intermediate penetration; and West Otways and Strzelecki for low penetration. Seventy families (Table 2) representing 15 collection areas (seedlot localities as defined by JORDAN *et al.* (1994)) and representing seven subraces (according to a new racial classification of DUTKOWSKI *et al.* (1997)) were selected across these six races.

To reduce potential sources of bias in the study we selected families on the basis that they occurred at each site and little emphasis was placed on family growth. Six trees were sampled per family, with sampling commencing in the first replicate. The first 6 acceptable trees (unforked, straight and greater than 15 cm DBHOB) in each family were sampled.

Two methods for assessing basic density were used: removing bark-to-bark increment cores using a motor-driven corer and using a pilodyn. The location for sampling and numbers of samples required had previously been determined in an extensive study of within-tree variation across multiple sites by RAYMOND and MUNERI (2000).

A pilodyn is a hand-held instrument which fires a flat-nosed steel striker pin into a tree with a fixed force (COWN 1981). The depth of penetration of the pin can be read directly from the scale on the instrument and has been shown to be strongly negatively correlated with wood density at the point of sampling (GREAVES *et al.* 1996; RAYMOND & MACDONALD 1998). A window is cut into the bark of the tree and the pilodyn pin fired directly into the wood. The advantages of using a pilodyn is that it is fast and non-destructive. However, pilodyn penetration is not as good a predictor of whole tree density as disc or core samples and the repeatability of pilodyn readings around the stem may be variable (RAYMOND & MACDONALD 1998).

Each tree was measured for DBHOB and two pilodyn penetration readings were taken from the west side of the tree at 1.3 m above ground following results from studies by GREAVES *et al.* (1996) and RAYMOND and MACDONALD (1998). A bark-to-bark core was extracted at 1.1 m, following the sampling recommendations of RAYMOND and MUNERI (2000). Basic density was determined using the water displacement method. To minimise seasonal effects, all trials were sampled in late winter and early spring, prior to active growth commencing. The trials were sampled consecutively, with all sampling done within a five week

© ARBORA PUBLISHERS

period.

Estimation of genetic parameters

To determine whether the restriction on tree size had resulted in a biased sample, the distribution of diameters of the cored trees was compared to the diameters of all available trees within the selected families at each site using data from the last complete diameter assessment of the trials (ages 4 or 5). Visual comparison of the histograms of tree sizes indicated no systematic bias (results not presented here).

The two Victorian trials, Mt Worth and Flynn, were sampled across 5 sublines with families being nested within sublines. Subline effects for all traits were calculated using data from the two control families and fitting the following model, in matrix notation:

$$\mathbf{y}_c = \mathbf{X}_1\mathbf{c} + \mathbf{X}_2\mathbf{s} + \mathbf{e} \quad [1]$$

where $\mathbf{y}_c$ is the vector of individual tree observations for the control families, **c** is a vector of fixed control family effects, **s** is a vector of fixed subline effects and $\mathbf{X}_1$ and $\mathbf{X}_2$ are incidence matrices for the fixed effects. Analyses of variance indicated a significant difference ($p < 0.05$) between sublines for diameter at Flynn and pilodyn penetration at Mt Worth, suggesting the need to adjust the relevant data. As the sublines had been established by grouping seedlots by geographic region, the subrace effect was confounded with the subline and replicate within subline effects. If the data had been adjusted for differences between the control families and subsequently analysed it would not have been possible to separate the subrace and replicate within subline effects in the analysis. To overcome this problem the two control families were defined as a new subrace (subrace 1) and in the subsequent analysis the model was structured so that all other data were fitted as deviations from subrace 1.

Data for each trial were analysed using the model:

$$\mathbf{y} = \mathbf{X}_1\mathbf{r} + \mathbf{X}_2\mathbf{b} + \mathbf{Z}_1\mathbf{f} + \mathbf{e} \quad [2]$$

where **y** is the vector of individual tree data for basic density, pilodyn penetration and diameter, **r** is a vector of fixed subrace effects, **b** is a vector of fixed replicate effects, **f** is a vector of random family effects nested within subrace, **e** is the vector of residuals and $\mathbf{X}_1$, $\mathbf{X}_2$, and $\mathbf{Z}_1$, are incidence matrices relating the observations to the effects in the model.

To test the significance of genotype by environment interaction the following model was fitted:

$$\mathbf{y} = \mathbf{X}_1\mathbf{r} + \mathbf{X}_2\mathbf{b} + \mathbf{X}_3\mathbf{s} + \mathbf{X}_4\mathbf{c} + \mathbf{Z}_1\mathbf{f} + \mathbf{Z}_2\mathbf{i} + \mathbf{e} \quad [3]$$

where **s** and **c** are respectively vectors of fixed site and subrace by site interaction effects, and **i** is a vector of random family by site interaction effect. $\mathbf{X}_3$, $\mathbf{X}_4$ and $\mathbf{Z}_2$ are the incidence matrices for these effects, and other symbols are the same as those in Equation 2.

For all models, the best linear unbiased estimates (BLUEs) of subrace effects and best linear unbiased predictors (BLUPs) of family means were estimated using REML in GENSTAT. All variance components, genetic parameters and their standard errors were estimated using ASREML (GILMOUR *et al.* 1998).

Individual narrow-sense heritabilities were calculated, assuming a coefficient of relatedness of 0.4 (VOLKER *et al.* 1990) as:

$$h^2 = \frac{\sigma_f^2}{r(\sigma_f^2 + \sigma_e^2)} \quad [4]$$

for the single site analysis and,

$$h^2 = \frac{\sigma_f^2}{r(\sigma_f^2 + \sigma_i^2 + \sigma_e^2)} \quad [5]$$

for combined sites analysis, and where r is the coefficient of relatedness, σ_f^2 is the between family variance component, σ_i^2 family by site interaction variance and σ_e^2 is the error variance.

Genetic correlations were estimated between all traits within each site and between sites for each trait.

$$r_G = \frac{cov(f_1,f_2)}{\sqrt{\sigma_{f1}^2\,\sigma_{f2}^2}} \quad [6]$$

where cov (f_1,f_2) is the family covariance between traits 1 and 2, or sites 1 and 2. Phenotypic correlations between traits were estimated on an individual tree basis for each site.

Genotype by environment interaction

The practical importance of the genotype by environment interaction was evaluated by examining:

- whether the interaction terms were significant in the across-site analysis of variance,
- potential causes due to differing variances or changes in rankings. Subraces and families that contributed most to site interaction were identified on the basis of rank changes (MATHESON & RAYMOND

1984). The ranking of each subrace and family for all traits were calculated for each site as well as across the three sites. Mean rank deviation was estimated as the sum of the absolute rank deviation from the across site rank divided by the number of sites,

- the ratio of the variance components for the interaction term and families to determine whether it was greater than 0.5 (SHELBOURNE 1972),
- genetic correlations between the sites (BURDON 1977).

To explore potential causes for the observed site by family interaction the data were subdivided in several ways:

- Geographic groups of subraces by State – Victoria versus Tasmania with the Bass Strait Islands included in the Tasmanian group
- The most interactive subrace based on average rank deviations was deleted
- The most interactive families were sequentially deleted.

RESULTS

Site differences

Sites differed significantly for all three traits, with Mt Worth having the largest trees but the lowest basic density (Table 3). In contrast, the other site in Victoria, Flynn, had the smallest trees and a significantly higher basic density than the other two sites.

Subrace effects

Subraces differed significantly for both basic density and pilodyn penetration at each site but differences between the subraces were not significant for diameter at Mt Worth or Flynn. Ranking of subraces (Table 3) for diameter varied considerably across sites but as there were no significant differences between subraces for two of the sites these differences are not considered important.

Ranking of subraces for basic density and pilodyn penetration (Table 3) were largely stable across the sites. The Strzelecki subrace ranked highest for basic density at each site and King Island ranked lowest. However, the top ranked subrace for pilodyn penetration (based on the smallest degree of penetration) at each site was NE Tasmania, which ranked 3rd, 4th or 5th for density. The Royal George locality of the NE Tasmania subrace also had the lowest pilodyn penetration at Massy Greene in the study of JORDAN *et al.* (1998). However, at the other four sites in Jordan's study, Royal George ranked intermediate for pilodyn penetration. When all data for basic density and pilodyn penetration in the current study are plotted together (Figure 1) there appears to be a strong and consistent relationship between density and pilodyn penetration. However, if data for each site are compared separately (Table 3, Figure 2) a different pattern emerges. NE Tasmania ranked highest for pilodyn penetration (lowest penetration) at all sites but is intermediate for density. Both measures of wood density identified King Island as having the lowest density at each site but results for the other subraces are not as clear. If the results for King Island were not included at Mt Worth, there would appear to be no relationship between the subrace means for basic density and pilodyn penetration. Similarly, at Flynn there appear to be two distinct groups of subraces, with the five subraces having mean densities above 530 $kg \cdot m^{-3}$ showing no significant difference in mean pilodyn penetration. These results suggest that the subraces have different relationships between density and pilodyn penetration.

Genetic parameter estimates

Heritabilities for both diameter and pilodyn penetration (Table 4) were low at Mt Worth and Flynn and moderate at Massy Greene. In contrast, heritability estimates for basic density were high for all sites, ranging from 0.67 for Massy Greene to 1.00 for Flynn. Heritability estimates for diameter at Mt Worth and Flynn were lower than those previously published for the same species of 0.17 to 0.35 (DEAN *et al.* 1990; VOLKER *et al.* 1990; BORRALHO *et al.* 1995; MACDONALD *et al.* 1997; JORDAN *et al.* 1998). For density, the heritability estimates are at the higher end of those reported previously (ranging from 0.44 to 0.80; BORRALHO *et al.* 1992, 1993; COTTERILL & BROLIN 1997; DEAN *et al.* 1990) whilst the pilodyn results are lower than other published results (range 0.16 to 0.57; DEAN *et al.* 1990; JORDAN *et al.* 1998; MACDONALD *et al.* 1997). However, the structure used for defining provenances or races varied between studies and may have influenced the heritability estimates obtained.

Genetic correlations (Table 5) between diameter and basic density were small, ranging from zero at Massy Greene to –0.44 at Flynn, and within the range of previously published estimates (range –0.46 to –0.08; BORRALHO *et al.* 1992; DEAN *et al.* 1990). The respective phenotypic correlations (Table 5) were also small, indicating no strong relationship between tree size and basic density for this species.

Estimated genetic correlations between diameter and pilodyn penetration present a mixed picture. Both the genetic and phenotypic correlations were small and non significant for Massy Greene and Mt Worth. At Flynn,

© ARBORA PUBLISHERS

Table 3. Subrace BLUEs, standard deviations for individual tree data (SD) and rankings for diameter (cm), basic density (kg/m^3) and pilodyn penetration (mm). Site means and standard deviations are given together with ranges for both subrace BLUEs and family BLUPs. Low pilodyn readings are ranked high for ease of comparison with density.

Trait	Subrace	Massy Greene			Mt Worth			Flynn		
		Mean	(SD)	Rank	Mean	(SD)	Rank	Mean	(SD)	Rank
Diameter	West Otways	23.0	(3.9)	2	25.8	(4.6)	1	19.7	(2.6)	1
	Strzelecki	22.1	(3.2)	4	22.0	(4.2)	7	17.0	(2.4)	6
	Madalaya Road	23.7	(3.9)	1	24.2	(5.2)	6	16.7	(2.3)	7
	Furneaux	21.2	(3.0)	5	24.4	(4.2)	5	18.7	(2.3)	3
	NE Tasmania	18.7	(2.7)	7	24.5	(3.1)	4	17.5	(1.9)	5
	SE Tasmania	20.1	(3.7)	6	24.7	(3.6)	3	18.7	(2.1)	4
	King Island	22.6	(4.1)	3	25.1	(5.1)	2	19.6	(2.6)	2
	Site mean (SD)	21.8 (3.7)			24.0 (4.6)			18.5 (2.4)		
	Range for subrace BLUEs	18.7–23.7			22.0–25.8			16.7–19.7		
	Range for subrace BLUPs	19.8–23.6			22.7–25.4			17.5–19.1		
Density	West Otways	469	(33)	6	465	(31)	3	554	(31)	3
	Strzelecki	504	(37)	1	474	(30)	1	571	(37)	1
	Madalaya Road	487	(34)	2	463	(33)	4	559	(34)	2
	Furneaux	481	(36)	4	468	(33)	2	533	(32)	5
	NE Tasmania	485	(41)	3	455	(32)	5	538	(28)	4
	SE Tasmania	471	(44)	5	442	(27)	6	504	(32)	6
	King Island	428	(35)	7	423	(34)	7	489	(33)	7
	Site mean (SD)	473 (42)			460 (35)			543 (41)		
	Range for subrace BLUEs	428–504			423–474			489–571		
	Range for subrace BLUPs	436–500			420–491			473–581		
Pilodyn	West Otways	12.1	(2.1)	5	13.5	(1.9)	5	10.0	(1.2)	3
	Strzelecki	10.9	(1.3)	2	12.8	(1.5)	2	9.8	(1.3)	2
	Madalaya Road	10.9	(1.4)	2	13.2	(1.5)	3	10.2	(1.0)	4
	Furneaux	11.6	(1.7)	4	13.7	(1.4)	6	10.8	(0.9)	5
	NE Tasmania	10.4	(1.5)	1	12.4	(1.4)	1	9.8	(1.0)	1
	SE Tasmania	12.1	(1.6)	5	13.3	(1.1)	4	11.5	(1.0)	6
	King Island	13.5	(2.0)	7	15.3	(2.0)	7	12.1	(1.4)	7
	Site mean (SD)	11.8 (1.9)			13.2 (1.7)			10.3 (1.4)		
	Range for subrace BLUEs	10.4–13.5			12.4–15.3			9.8–12.1		
	Range for subrace BLUPs	10.1–12.4			12.9–13.8			10.2–10.8		

the genetic correlation between diameter and pilodyn penetration was strong and positive indicating that larger genotypes had deeper penetration of the pilodyn pin. However, all three genetic correlations fell within the wide range previously reported, ranging from –0.07 (JORDAN *et al.* 1998) to 1.24 (DEAN *et al.* 1990).

Genetic correlations between basic density and pilodyn penetration properties were strongly negative for all sites, ranging from –0.60 for Massy Greene to –1.16 for Flynn and consistent with the strong negative genetic correlation reported by DEAN *et al.* (1990). The respective phenotypic correlations were smaller, ranging from –0.35 to –0.45.

Genotype x Environment interaction

The across-site analyses of variance (Table 6) indicated that the subrace by site interaction term was not significant for any trait. However, the family by site interaction term was significant for diameter and basic density but not for pilodyn penetration. The difference in the results for the analyses of density and pilodyn penetration is disturbing in that the family by site interaction is significant for density but not for pilodyn.

As GEI may be caused by scale differences between sites it was essential to check that the standard deviations and residual variance for each site are relatively

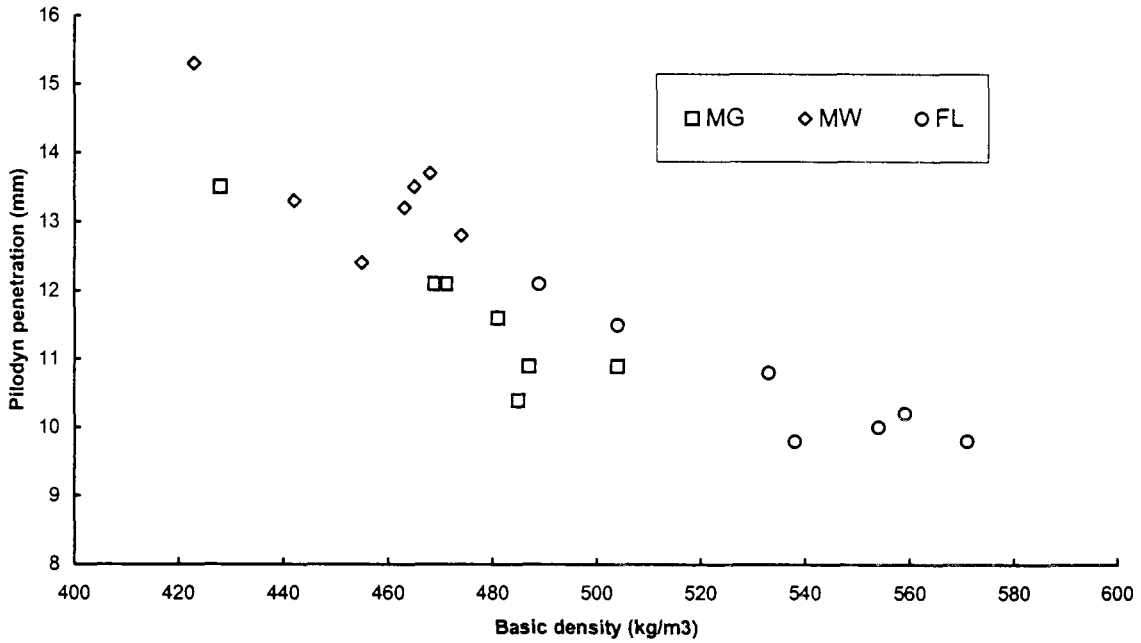


Figure 1. Plot of subrace means for pilodyn penetration versus basic density across all three sites. (MG=Massy Greene, MW=Mt Worth and FL=Flynn).

homogeneous. Standard deviations (Table 3) and residual variance components (Table 4) were very similar across sites for basic density and pilodyn. The range in residual variance for diameter was greater but still well within the ten-fold range considered acceptable by PATTERSON and SILVEY (1980).

Another cause of GEI is changes in ranking of genotypes across sites. Table 3 indicates that ranking of the subraces changed considerably for diameter but that rankings were relatively constant across sites for both basic density and pilodyn penetration. Families also changed rankings across sites for each trait.

Variance components obtained from the combined analysis (Table 7) indicated that the family by site interaction term accounted for more than twice the family variance for diameter, but was only one third of the size of the family component of variance for basic density. Heritability estimate for diameter and basic density (0.06 and 0.63 respectively) were lower than the individual site estimates (Table 4) due to the presence of genotype by site interaction. Genetic correlations between sites (Table 8) were moderate to strong for basic density and pilodyn penetration but generally moderate to low for diameter. The two Victorian sites showed the strongest genetic correlation for diameter but weakest correlation for basic density.

Subdividing the data into groups on a geographic basis yielded different results for diameter and density.

Table 4. Variance components and heritabilities (standard error) for diameter (cm), basic density ($kg \cdot m^{-3}$) and pilodyn penetration (mm) at each site

Trait	Genetic parameters	Massy Greene	Mt. Worth	Flynn
Diameter	Family variance	1.55	1.09	0.346
	Residual variance	10.39	17.40	5.069
	Heritability ± s.e.	0.33 (0.11)	0.15 (0.12)	0.16 (0.10)
Basic density	Family variance	338.98	343.67	428.27
	Residual variance	930.32	643.31	641.05
	Heritability ± s.e.	0.67 (0.13)	0.87 (0.16)	1.00 (0.15)
Pilodyn	Family variance	0.304	0.145	0.068
	Residual variance	2.461	2.481	1.250
	Heritability ± s.e.	0.27 (0.10)	0.14 (0.11)	0.13 (0.11)

© ARBORA PUBLISHERS

Table 5. Genetic correlations (standard error) and phenotypic correlations (below diagonal) between diameter, basic density and pilodyn penetration at each site

Site	Trait	Diameter	Basic density	Pilodyn
Massy Greene	Diameter		0.00 (0.21)	0.18 (0.27)
	Basic density	0.09		–0.60 (0.17)
	Pilodyn	–0.02	–0.35	
Mt. Worth	Diameter		–0.22 (0.34)	0.04 (0.58)
	Basic density	0.03		–1.06 (0.20)
	Pilodyn	0.11	–0.45	
Flynn	Diameter		–0.44 (0.25)	0.85 (0.33)
	Basic density	–0.07		–1.16
	Pilodyn	0.16	–0.42	

Table 6. Across-site analysis of variance.

Source of variation	Degrees of freedom	Mean squares		
		Diameter	Basic density	Pilodyn
All sites				
Site	2	3476.73**	899584**	995.6**
Replicate within sites	174	19.00**	2707**	3.3*
Subrace	7	105.40**	50749**	73.5**
Subrace by site	13	24.90	1681	2.4
Family	64	19.70**	5609**	4.9*
Family by site	126	15.30**	1282**	2.2
Residual	933	11.00	738	2.1

* $p < 0.05$, ** $p < 0.01$

Table 7. Variance components and heritabilities (standard error) for diameter, basic density and pilodyn for combined data from Massy Greene, Mt. Worth and Flynn.

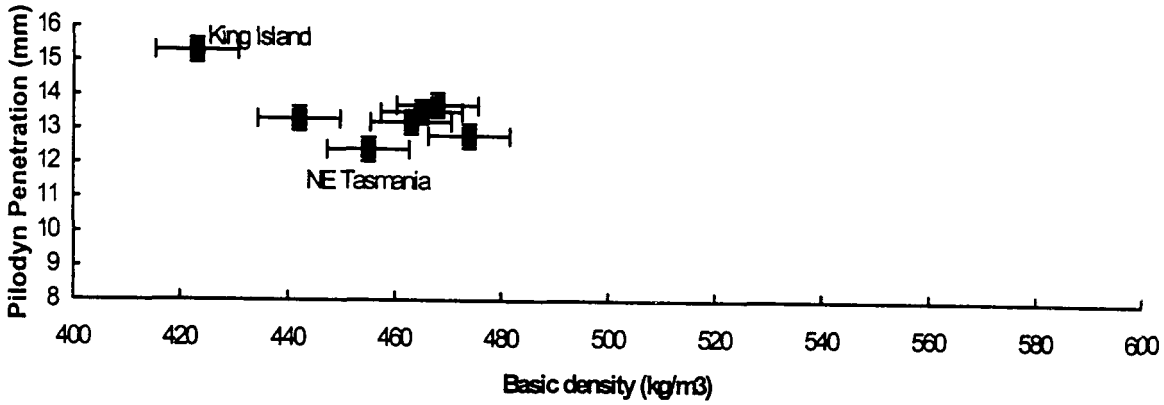
Genetic parameters	Diameter	Basic density	Pilodyn
Family variance	0.31	280.4	0.17
Family by site variance	0.70	99.6	0.21
Residual variance	11.04	740.9	2.13
Heritability (±s.e)	0.06 (0.05)	0.63 (0.11)	0.19 (0.06)

When the Tasmanian subraces were analysed alone, the site by family interaction for diameter became non-significant whilst for the Victorian subraces it remained significant. For density, the geographic grouping did not have any effect, with the site by family interaction remaining significant for both groups.

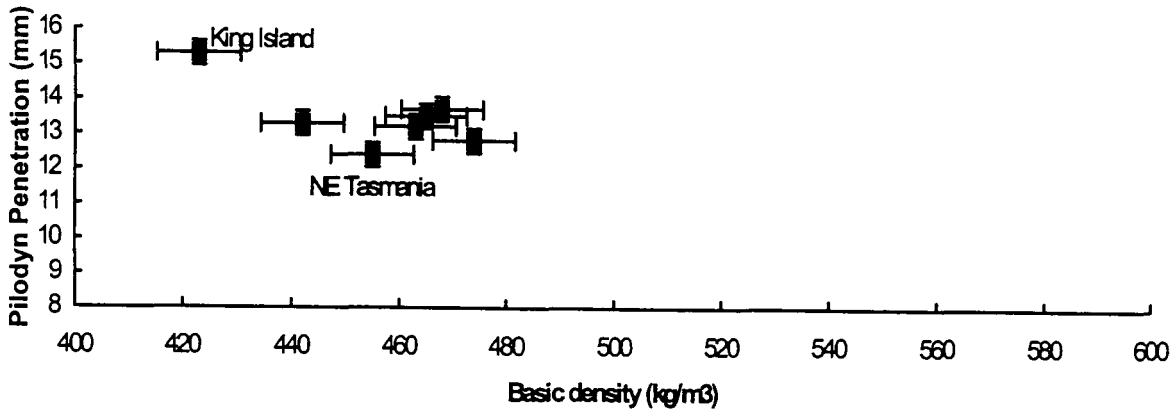
Removal of the most interactive subrace, based on average rank deviations for families within the subrace, also had a large effect on the results of the analysis of variance for diameter but no effect for density. For diameter, the interaction appeared to be due to the West Otways subrace. Further investigation of this subrace indicated that the interaction was being caused by the three families with the greatest average rank deviations. If these families were omitted from the analysis, the site by family effect became non-significant.

The site by family interaction appeared to be more

a.) Massy Greene



b.) Mt Worth



c.) Flynn

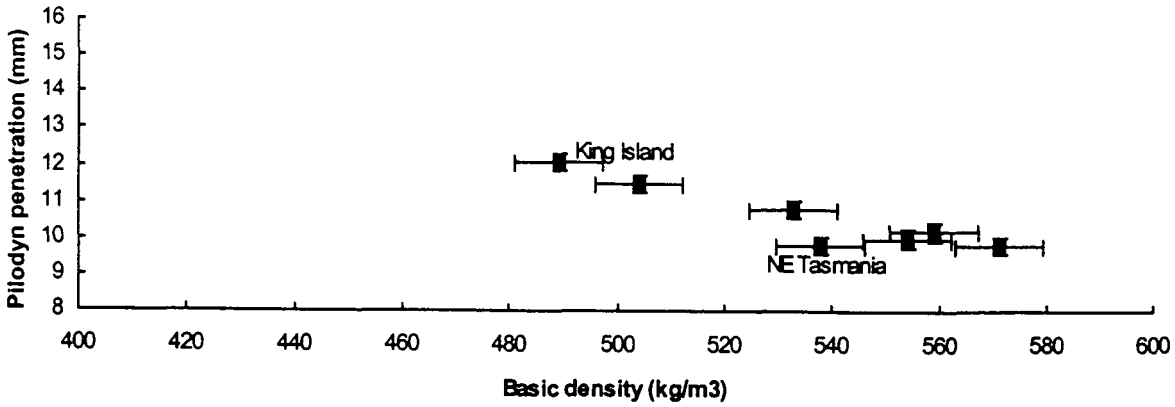


Figure 2. Plot of subrace means (with standard error bars) for pilodyn penetration versus basic density for each site.

© ARBORA PUBLISHERS

Table 8. Genetic correlations (standard error) between sites for diameter, basic density and pilodyn.

Trait	Site	Mt Worth	Flynn
Diameter	Massy Greene	0.12 (0.39)	0.29 (0.37)
	Mt Worth		0.76 (0.44)
Basic density	Massy Greene	0.83 (0.11)	0.91 (0.08)
	Mt Worth		0.46 (0.14)
Pilodyn	Massy Greene	1.37 (0.51)	0.46 (0.42)
	Mt Worth		1.32 (0.76)

complex for the density data as it could not be explained in terms of geographic groups or by removing the subrace with the most interactive families. The family mean data was ranked based on average rank deviation. Examination of this data revealed that families from across most of the subraces appeared in the top group for rank deviations. To determine how many families were contributing to the presence of the family by site interaction, families with the greatest rank deviations were sequentially deleted and the model rerun on remaining data. Thirteen families (18 % of families) were deleted before the interaction became non-significant. These families were distributed across most of the subraces with 3 from the West Otways, 3 from Strzelecki, 2 from Madalya Road, 1 from Furneaux, 2 from NE Tasmania and 2 from SE Tasmania. The only subrace not represented was King Island.

DISCUSSION

Large differences were found between diameter and basic density for the genetic architecture of the traits, the genetic parameter estimates and for the degree of genotype by environment interaction. When the genetic architecture of the traits is examined, the small differences found among the subraces for diameter confirms published results from previous studies in this species based solely on growth data (VOLKER & ORME 1988; DAOQUIN *et al.* 1995; KUBE *et al.* 1995; MACDONALD *et al.* 1997). However, very large differences were found between the subraces for basic density. The within-race heritabilities for diameter were relatively low (range 0.15 to 0.33) and similar to that found in other studies. For basic density the within-race heritability estimates were very high (ranging from 0.67 to 1.00) indicating that wood density is under much stronger genetic control than diameter. The implication of this for assessing patterns of within-species variation are serious in that conclusions drawn for growth data which is under low to moderate genetic control may be totally inappropriate for other traits under much stronger genetic control.

Patterns of genotype by environment interaction for basic density also differed from those observed for tree diameter. Whilst the family by site interaction was significant for both diameter and basic density, the causes of this interaction differed. For diameter, the interaction was caused by only a few families whilst for basic density the interaction was more complex. In terms of practical importance, the genotype by environment interaction for both diameter and basic density would appear to be minor. There was no interaction between the subraces and sites for either trait. For diameter the significant site by family interaction term was due to very few families from a single subrace (West Otways). For density, the site by subrace term was not significant in any across site analyses. Although the site by family interaction term was significant in the analysis of variance, it contributed very little to the overall variation. Genetic correlations between sites were strong, indicating that families which performed well at one site also did well at other sites. Interactive families were found in all subraces except King Island and removal of 18% of the most interactive families yielded a non-significant site by family interaction.

One question that needs resolving is how important is the reduction in heritability due to site by family interaction in a trait of high heritability? The across-site heritability for basic density was lower than that for each individual site but at $h^2 = 0.63$ was still at the high end of the range of heritability values. Potential gains from selection for this trait are thus large, even after accounting for the losses due to the interaction.

Basic density and tree diameter were not strongly correlated at any site, indicating that the two traits are largely independent. The breeding objective currently being used for temperate eucalypts in southern Australia includes both these traits and results from this study indicate that both traits should be included in the selection program as they display very different patterns of variation.

However, the question of the best method for assessing basic density needs to be addressed. When the two methods used in this study (pilodyn penetration or density of increment core samples) were compared, the results were somewhat different. MACDONALD *et al.* (1997) suggested that pilodyn penetration and density should be considered to be the same trait due to the very high genetic correlations reported between the traits. Results of the current study confirmed the high genetic correlation at the family level but found problems with using a pilodyn across different populations. The relationship between density and pilodyn penetration appeared to differ across the subraces. The subrace that ranked highest for pilodyn penetration was found to be intermediate for density. For this to occur, the subraces must differ in the degree of resistance offered to the pin, possibly due to differences in wood anatomy, ring width or within-ring density variation (RAYMOND & MACDONALD 1998). The heritability of pilodyn penetration (range 0.13 to 0.27) was much smaller than that found for density (range 0.67 to 1.00), indicating that selection on pilodyn penetration would be less accurate than selection on density of cores. Given the differences in the heritabilities and the different relationships between pilodyn penetration and density across the subraces, the usefulness of pilodyn in general screening for wood density becomes questionable.

ACKNOWLEDGEMENTS

The able assistance of Andrew MacDonald and Jason Lawson in collecting and processing the wood samples is gratefully acknowledged. Thanks also to those collaborators from Australian Paper Plantations and North Forest Products who kindly let us sample their trees and provided assistance with organising and undertaking this study. Finally, the authors wish to thank Greg Dutkowski for his assistance with selection of seedlots for sampling and both Greg and Nuno Borralho for their interest and comments on this study.

REFERENCES

BORRALHO, N. M. G., COTTERILL, P. P. & KANOWSKI, P. J. 1992: Genetic parameters and gains expected from selection for dry weight in *Eucalyptus globulus* ssp. *globulus* in Portugal. *Forest Science* **38**: 80–94.

BORRALHO, N. M. G., COTTERILL, P. P. & KANOWSKI, P. J. 1993: Breeding objectives for pulp production of *Eucalyptus globulus* under different industrial cost structures. *Canadian Journal of Forest Research* **23**:648–656.

BORRALHO, N. M. G., JARVIS, S. F. & POTTS, B. M. 1995: Multivariate restricted maximum likelihood estimation of genetic parameters for diameter at 3 to 5 years in the *Eucalyptus globulus* base population in Australia. *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. 230–232. Proc. CRC-IUFRO Conf., Hobart Australia, 19–24 February 1995. (CRC for Temperate Hardwood Forestry: Hobart).

BURDON, R. D. 1977: Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. *Silvae Genetica* **26**:168–75.

COTTERILL, P. P. & BROLIN, A. 1997: Improving *Eucalyptus* wood, pulp and paper quality by genetic selection. *In:* Proc. IUFRO Conference on Silviculture and Improvement of Eucalypts., Salvador, Brazil, August 1997. Volume 1: Tree Improvement Strategies pp 1–13.

COWN, D. J. 1981: Use of the Pilodyn wood tester for estimating wood density in standing trees – influence of site and tree age. XVII IUFRO World Forestry Conference, Kyoto, Japan, Sept. 1981

DAOQUIN, Z., HUORAN, W. & YINGTIAN, Y. 1995: Performance and selection of a 4-year *Eucalyptus globulus* seedling seed orchard in Yunnan, China. *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. 226–229. Proc. CRC-IUFRO Conf., Hobart Australia, 19–24 February 1995. (CRC for Temperate Hardwood Forestry: Hobart).

DEAN, G.H., FRENCH, J. & TIBBITS, W.N. 1990: Variation in pulp and papermaking characteristics in a field trial of *Eucalyptus globulus.* Appita 44th Annual General Conference, Rotorua New Zealand. April 1990.

DUTKOWSKI, G., POTTS, B. M. & BORRALHO, N. M. G. 1997: Revised racial classification of *Eucalyptus globulus* ssp. *globulus* and the importance of including race in analysis of progeny trials. *In:* Proc. IUFRO Conference on Silviculture and Improvement of Eucalypts. Salvador, Brazil, 24–29 August 1997. Vol. 1:322–329.

FINLAY, K. W. & WILKINSON, G. W. 1963: The analysis of adaptation in a plant-breeding programme. *Australian Journal of Agricultural Research* **14**:742–54.

GARDINER, C. A. & CRAWFORD, D. F. 1987: 1987 Seed collections of *Eucalyptus globulus* subsp. *globulus* for tree improvement purposes. CSIRO Division of Forest Research. Canberra.

GARDINER, C. A. & CRAWFORD, D. F. 1988: 1988 Seed collections of *Eucalyptus globulus* subsp. *globulus* for tree improvement purposes. CSIRO Division of Forestry and Forest Products. Canberra.

GARNIER-GERE, P., RAYMOND, C. A. & ADES, P. K. 1995: Comparison of models for structuring genotype by environment interaction in *Eucalyptus delegatensis* provenance trials *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. 156–162. Proc. CRC-IUFRO Conf., Hobart Australia, 19–24 February 1995. (CRC for Temperate Hardwood Forestry: Hobart).

GILMOUR, A. R., CULLIS, B. R., WELHAM, S. J. & THOMPSON, R. 1998: ASREML computer software, NSW Agriculture.

GREAVES, B. L., BORRALHO, N. M. G., RAYMOND, C. A. &

© ARBORA PUBLISHERS

FARRINGTON, A. 1996: Use of a pilodyn for indirect selection of basic density in *Eucalyptus nitens*. *Canadian Journal of Forest Research* **26**:1643–1650.

GREAVES, B. L., BORRALHO, N. M. G. & RAYMOND, C. A. 1997: Breeding objective for plantation eucalypts grown for production of kraft pulp. *Forest Science* **43**:465–472.

JORDAN, G. J., BORRALHO, N. M. G., TILYARD, P. & POTTS, B. M. 1994: Identification of races in *Eucalyptus globulus* ssp. *globulus* based on growth traits in Tasmania and geographic distribution. *Silvae Genetica* **43**: 292–298.

JORDAN, G. J., DUTKOWSKI, G. W., POTTS, B. M., MACDONALD, A. C., TILYARD, P. & BORRALHO, N. M. G. 1998: Genetic variation in North Forest Products' *Eucalyptus globulus* ssp. *globulus* base population trials. CRC-SPF Technical Report No. 8. 74pp.

KUBE, P. D., MATHESON, A. C., RAYMOND, C. A. & BOOMSMA, D. B. 1995: Provenance variation in *Eucalyptus 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. 245–246. Proc. CRC-IUFRO Conf., Hobart Australia, 19–24 February 1995. (CRC for Temperate Hardwood Forestry: Hobart).

MACDONALD, A. C., BORRALHO, N. M. G. & POTTS, B. M. 1997: Genetic variation for growth and wood density in *Eucalyptus globulus* ssp. *globulus* in Tasmania (Australia). *Silvae Genetica* **46**:236–241.

MATHESON, A. C. & RAYMOND, C. A. 1984: The impact of genotype x environment interactions on Australian *Pinus radiata* breeding programs. *Australian Forest Research* **14**:11–25.

PATTERSON, H. D. & SILVEY, V. 1980: Statutory and recommended list trials of crop varieties in the United Kingdom (with discussion), *J. R. Statist. Soc. A* **143**:219–252.

RAYMOND, C. A., VOLKER, P. W. & WILLIAMS, E. R. 1997: Provenance variation, genotype by environment interactions and age-age correlations for *Eucalyptus regnans* on nine sites in south eastern Australia. *Forest Genetics* **4**:235–251.

RAYMOND, C. A. & MACDONALD, A. C. 1998: Where to shoot your pilodyn: within tree variation in basic density in plantation *Eucalyptus globulus* and *E. nitens* in Tasmania. *New Forests* **15**:205–211.

RAYMOND, C. A. & MUNERI, A. 2000: Non-destructive sampling of *Eucalyptus globulus* and *E. nitens* for wood properties. 1. Basic density. *Wood Science and Technology* (In press).

SHELBOURNE, C. J. A. 1972: Genotype-environment interaction: its study and its implications in forest tree improvement. *In:* Proc. Joint. Symp. For Forest Tree Breeding of Genetics Subject Group and Section 5, Forest Trees of SABRAO. Govt. For. Exp. Sta., Tokyo, B–1(1),1–28.

VOLKER, P. W., DEAN, C. A., TIBBITS, W. N. & RAVENWOOD, I. C. 1990: Genetic parameters and gains expected from selection in *Eucalyptus globulus* in Tasmania. *Silvae Genetica* **39**: 18–21.

VOLKER, P. W. & ORME, R. K. 1988: Provenance trials of *Eucalyptus globulus* and related species in Tasmania. *Australian Forestry* **51**:257–265.