GENETIC PARAMETERS FOR DIAMETER, BASIC DENSITY, CELLULOSE CONTENT AND FIBRE PROPERTIES FOR *EUCALYPTUS NITENS*

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ABSTRACT

Genetic parameters were estimated for stem diameter, basic density, fibre length, fibre coarseness and cellulose content from 12-year-old *Eucalyptus nitens* progeny trials in Tasmania. Heritability for diameter averaged 0.19 at 6 years, 0.38 at 12 years, and 0.45 for the diameter increment between 6 and 12 years. Heritability for basic density, fibre length and cellulose content averaged 0.70, 0.58 and 0.79 respectively and differed significantly between sites. Heritabilities for fibre coarseness were highly variable and correlations between sites low. There were favourable genetic correlations between diameter/cellulose (0.79), diameter/fibre length (0.37) and cellulose/fibre length (0.54). There were adverse genetic correlations between basic density/diameter (–0.57) and basic density/cellulose (–0.45). Genetic correlations between fibre length/density were variable (0 to 0.75). There was no significant genotype by environment interaction for diameter and fibre length. For basic density and cellulose content, interactions were significant but small.

Key words: *Eucalyptus nitens,* genetic parameters, stem diameter, basic density, cellulose content, fibre properties

INTRODUCTION

Eucalyptus nitens (Deane & Maiden) Maiden is used as a hardwood plantation species in cool-temperate regions in Australia (Tasmania and Victoria), Chile, South Africa and New Zealand. The global plantation area was about 150,000 ha in 1995, and was projected to increase to 220,000 ha by 1999 (TIBBITS *et al.* 1997). *E. nitens* is used for pulpwood although plantations of this species are now being grown for veneer, sawn timber and reconstituted products (NEILSEN & PINKARD 2000).

Improving both productivity and product quality of plantations is a goal of research, and tree improvement in particular. Historically, improving productivity has been the main priority. This is reflected by the emphasis on growth in early genetic improvement studies for this species (PEDERICK 1979; KING & WILCOX 1988; WOOLASTON *et al.* 1991; WHITEMAN *et al.* 1992). The importance of quality was recognised through tree form in these studies, but it has not been until recently that wood properties have become an integral part of *E. nitens* breeding programs (GEA *et al.* 1997; TIBBITS & HODGE 1998).

Wood properties are now widely recognised as important to end product value and overall profitability. Relationships between wood properties and profitability of kraft pulp production are well documented (DEAN *et al.* 1990; BORRALHO *et al.* 1993; GREAVES *et al.* 1997), and all studies have found increased basic density and pulp yield to be important. For cold caustic soda, production relationships are less well defined however the important wood properties appear to be low density and long fibre length (BANHAM *et al.* 1995; JONES & RICHARDSON 1999). Relationships between wood properties and paper quality are more complex, sometimes antagonistic and less well defined (RAYMOND & GREAVES 1997). Some paper properties appear to require thin walled fibres and low density wood while other paper properties require the opposite (ARBUTHNOT 1991; KIBBLEWHITE *et al.* 1998). These studies have indicated that improvements to pulping profitability will not necessarily improve all paper properties.

This study calculates the genetic parameters of traits important for wood fibre production in *E. nitens*. Estimates are made of heritability, genetic and phenotypic correlations, and magnitude of genotype by environment interaction. Traits studied are diameter, basic density, cellulose content, fibre length, and fibre coarseness. Data for wood properties are based upon

recently developed non-destructive sampling methods (KUBE & RAYMOND 2001; MUNERI & RAYMOND 2001; RAYMOND & MUNERI 2001). Cellulose content is used as an indicator of pulp yield. Measuring pulp yield directly is expensive and requires relatively large wood samples, and recent studies have shown cellulose content to be a reliable predictor of pulp yield in *E. nitens* (WALLIS *et al.* 1996; KUBE & RAYMOND 2001).

MATERIALS AND METHODS

Trial establishment and assessment

The genetic material consisted of open pollinated progeny from 40 native forest families from the Toorongo Plateau in the central highlands of Victoria. Mother trees were growing as a pure stand in an open forest and stem diameters ranged from 35 to 110 cm. This location is described in PEDERICK (1979).

Progeny trials were established in 1984 on three sites in northern Tasmania, all with good soil fertility and good productivity (Table 1). Stocking at planting was 1100 trees ha^{-1} (3 m by 3 m spacing). The trial design was a randomised complete block with single tree plots and 16 replications per site. Survival at ages 6 and 12 years was 87 % and 81 % respectively.

All trees were measured for diameter at breast height (1.3 m) at 6 and 12 years. Wood properties measured were basic density, fibre length, fibre coarseness and cellulose content. Wood samples were taken at 12 years using two 12 mm diameter bark to bark cores at a height of 0.9 m. One core was used to measure basic density, fibre length and fibre coarseness; and the second used to measure cellulose content. Core sampling at this height has been shown to be a reliable predictor of whole tree values of basic density (KUBE & RAYMOND 2001; RAYMOND & MUNERI 2001), fibre length and fibre coarseness (MUNERI & RAYMOND 2001) and cellulose content (KUBE & RAYMOND 2001). Trees less than 10 cm diameter were excluded from diameter and wood property assessments. Trees of this size were all strongly suppressed with no diameter increment between ages 6 and 12, and had atypical wood properties. These trees were found to inflate error variances.

Basic density was defined as oven-dry wood mass per unit volume of green wood, and was measured using the water displacement method (TAPPI 1989). Between 5 and 13 trees per family per site were randomly sampled (average of 8). Following an initial analysis, 11 trees were excluded due to high residuals (greater than 3 standard deviations from mean). These trees had low diameters, very little diameter increment between 6 and 12 years, and very high density. The total number of trees and range of values in the final data set are shown in Table 2.

Fibre length and fibre coarseness were measured using a Kajaani FS200 fibre analyser. When density measurements were completed, cores were macerated using a sodium hydroxide and peracetic acid digestion. Length-weighted average fibre lengths were used to place greater emphasis on uncut fibres. These measurements are produced routinely by the Kajaani FS200. Samples from Gog and Kamona were assayed on the same machine whilst those from Dial were assayed in a different laboratory. Five trees were randomly sampled per family per site. A total of 7 fibre coarseness records were discarded due to very high residuals (all had very high fibre coarseness). The total number of trees sampled and the range of values are shown in Table 2.

Crude cellulose content (g cellulose per dry mass wood) was measured using the method of WALLIS *et al.* (1997). Wood cores were dried at 27 °C, fragmented in a disc pulveriser, and ground in a Wiley mill with a 1 mm mesh. Non-cellulosic compounds were solubilized by digestion in diglyme and hydrochloric acid and the cellulose residue collected by filtration, washed and dried. Duplicate samples were assayed for 25 % of samples as a general check on accuracy. An initial analysis was done (fitting the model shown below) to identify outliers, on which a second set of duplicate samples were done. In total 45 samples were identified as outliers and repeated. Sample trees were the same as those used for fibre measurements (5 per family per

Table 1. Location and description of field sites.

	Dial	Gog	Kamona
Latitude (South)	41° 10'	41° 29'	41° 08'
Longitude (East)	146° 04'	146° 23'	147° 40'
Altitude (m)	100	300	160
Rainfall (mm/year)	1060	1200	1150
Mean max. temp. warmest month (° C)	22.3	21.8	23.4
Mean min. temp. coolest month (° C)	3.8	2.4	2.5
Parent material	mudstone	basalt	granite

Table 2. Description of data used in analyses.

	Trait	Min.	Mean	Max.	SD	*n*
D_6	Dbh age 6 (cm)	4.3	11.9	24.1	3.4	1159
D_{12}	Dbh age 12 (cm)	10.1	21.1	40.4	6.0	1160
D_{INC}	Dbh increment 6 to 12 (cm)	0.6	9.2	21.0	3.7	1158
BD	Basic density, core ($kg \cdot m^{-3}$)	362	451	568	31	841
CELL	Cellulose, core (% $kg \cdot kg^{-1}$)	38.0	41.5	45.4	1.4	545
FL	Fibre length, core (μm)	535	720	890	63.3	503
FC	Fibre coarseness, core ($\mu g \cdot m^{-1}$)	34.0	55.5	77.5	6.84	497

site), with 42 additional samples included to obtain data on trees with outstanding growth.

Estimation of genetic parameters

Variances, covariances, correlations and errors for each site and each trait were estimated simultaneously by fitting multivariate multisite models. Multivariate analyses use information more efficiently and can improve the precision of genetic parameters when selected subsets of data are used (DIETERS *et al.* 1999). An example of their use is shown and discussed in APIOLAZA & GARRICK (2001). Multivariate-multisite models allow all genetic correlations to be calculated directly, and use appropriate variance-covariance matrices for each site. These models treat measurements on different sites as different traits. Analyses were done using ASREML (GILMOUR *et al.* 1999), and the model fitted was:

$$Y = \mu + SITE + REP(SITE) + FAM(SITE) + e$$

where Y is a vector of data for each trait; μ is the mean for each trait; *SITE* are the site effects for each trait fitted as a fixed factor; *REP(SITE)* are the within site replicate effects for each trait fitted as a fixed factor; *FAM(SITE)* are the within site family effects for each trait fitted as a random factor; and e is a vector of residuals for each trait. Full inter-trait and inter-site variance and covariance matrices were fitted for the family and residual effects.

A second model was fitted to determine the importance of genotype by environment interactions and to estimate genetic correlations and heritabilities when data was pooled across sites. Error variances for each trait were all similar and therefore adjusting to a constant error variance was not considered necessary. The analysis was also done using ASREML and the model fitted was:

$$Y = \mu + SITE + REP(SITE) + FAM + FAM.SITE + e$$

where Y, μ, *SITE*, *REP(SITE)* and e are as previously defined; *FAM* are the across site family effects for each trait fitted as a random factor; and *FAM.SITE* are the site by family interaction effects for each trait fitted as a random factor. The model term *FAM* included an inter-trait variance and covariance matrix pooled across sites.

The traits analysed were diameter 6 years, diameter 12 years, diameter increment between 6 and 12 years, basic density, cellulose content, fibre length and fibre coarseness. For the multivariate-multisite model, ASREML would not converge when more than four traits were analysed simultaneously and therefore the analyses were done in stages. In total seven models with different combinations of traits were fitted. Heritabilities, genetic correlations and their standard errors were calculated by ASREML. The coefficient of relationship used in heritability calculations was 0.4 which assumes a selfing rate of approximately 30 % (GRIFFIN & COTTERILL 1988).

Estimation of genetic gains

Genetic gains were estimated under different selection strategies to demonstrate the impact of adverse correlations between some traits on potential gains. Five different selection strategies were evaluated (see Table 7) and these were as follows: select for diameter only (index 1); selection for basic density only (index 2); selection for cellulose content only (index 3); selection for fibre length only (index 4); and selection using weights for diameter, basic density and cellulose content to maximise profit from kraft pulp production (index 5). The weights used in index 5 approximate those given in GREAVES *et al.* (1997) when converted to standard deviation units.

Individual tree breeding values were calculated for diameter (12 years), basic density, fibre length and cellulose content using an individual tree model in ASREML. For each tree, index values were calculated using the following selection index:

$$I = BV_D \cdot W_D/\sigma_D + BV_{BD} \cdot W_{BD}/\sigma_{BD} + BV_{FL} \cdot W_{FL}/\sigma_{FL} + BV_{CELL} \cdot W_{CELL}/\sigma_{CELL}$$

where I is a unitless index value; BV_D, BV_{BD}, BV_{FL}, and BV_{CELL} are, respectively, breeding values for diameter, basic density, fibre length and cellulose content; σ_D, σ_{BD}, σ_{FL}, σ_{CELL} are additive genetic standard deviations for these traits; and W_D, W_{BD}, W_{FL}, and W_{CELL} are economic weights for each trait. The weights describe the relative importance of a standard deviation unit of each trait.

For each index, the selected population consisted of 60 trees from a population of 1160, or 5 %. This represents the intensity of selection required for a clonal seed orchard where 20 clones are required with the restriction that no family be represented by more than two individuals. Breeding values for each trait were then calculated for the selected trees and expressed as percentage gain of the unselected population.

RESULTS

Site differences

There were statistically significant differences between sites for all traits (Table 3). Growth rates are projected to be 21, 23 and 25 $m^3 \cdot ha^{-1} \cdot year^{-1}$ at rotation age (15 years) for Dial, Gog and Kamona respectively. Basic density, cellulose content and fibre coarseness were highest at Gog, where density was nearly 3 % higher, cellulose content 7 % higher and fibre coarseness 9 % higher than the average of the other sites. Differences in pulp yield between the best and poorest sites are projected to be 2.2 % using relationships in KUBE & RAYMOND (2001). Fibre length was significantly shorter at Dial Range (difference of approximately 14 %), however the assays for this site were done in a different laboratory, and therefore these differences may not be true site differences.

Table 3. Trait means for each site.

Trait	Dial	Gog	Kamona	SED[1]
D_6 (cm)	10.3	10.2	14.8	1.6
D_{12} (cm)	20.3	22.8	25.2	3.1
D_{INC} (cm)	10.0	12.6	10.3	1.9
BD ($kg \cdot m^{-3}$)	447	477	457	15
CELL (% $kg \cdot kg^{-1}$)	40.3	43.0	41.3	0.7
FL (μm)	653	767	763	34
FC ($\mu m \cdot m^{-1}$)	51.0	58.1	55.0	4.0

[1] Standard error of difference, probability of a larger value = 0.05.

Heritability

Individual site heritabilities for diameter at 6 years (Table 4) were low to moderate (0.12 to 0.29), but had increased substantially by 12 years (0.32 to 0.45). At 12 years, differences in heritability between sites were less than those at 6 years. In a combined site analysis, heritabilities for diameter at 6 and 12 years were 0.17 and 0.39 respectively (Table 4), and were almost identical to the average of the individual site heritabilities.

Individual site heritabilities for basic density were high to very high, ranging from 0.50 to 0.96 (Table 4). Estimates varied significantly across sites, with Gog having higher heritability than the other sites. This difference was primarily due to differences in the additive genetic variance across sites. In a combined site analysis the heritability for basic density was 0.51 (Table 4) which was less than the average for individual sites (0.70). Genotype by environment interaction was present for this trait (discussed below) and the different heritabilities presumably represent a shift of additive genetic variance to family by site variance.

Cellulose content also had high to very high individual site heritabilities, ranging from 0.52 to 1.00 (Table 4). As with basic density, estimates across different sites varied significantly, with one site (Dial) having a significantly lower heritability. This was primarily caused by a lower additive genetic variance at that site. Differences in error variance between sites may have been caused by differences in laboratory techniques. The Kamona site was the final site to be done and laboratory equipment and operator skills were improved. As for basic density, the heritability for cellulose content in a combined site analysis was less than the average for individual sites (0.56 compared to 0.79, Table 4) which is presumably caused by significant genotype by environment interaction.

Fibre length had moderate to very high individual site heritabilities, with estimates ranging from 0.25 to 0.80 (Table 4). The low heritability at Dial was due to a much lower additive genetic variance and a higher error variance at that site. However fibre lengths for this site were measured in a different laboratory and the low heritability may be due to this. In a combined site analysis the heritability for fibre length was slightly lower than the average of individual sites (0.46 compared with 0.58, Table 4) however these differences are not statistically different.

Fibre coarseness had variable heritabilities with values being moderately high at two sites, but zero at the third site (Table 4). In a combined site analysis the heritability was low (0.07) and not significantly different from zero (Table 4). Fibre coarseness has been

Table 4. Variance components (±standard error) and heritabilities (±standard error) for diameter at breast height (Dbh), basic density, cellulose content, fibre length and fibre coarseness.

Trait	Site	σ^2_{family}	$\sigma^2_{family.site}$	σ^2_{error}	h^2
Dbh age 6 (cm)	Dial	0.31±0.20		6.23±0.46	0.12±0.08
	Gog	0.82±0.34		6.24±0.48	0.29±0.10
	Kamona	0.81±0.46		11.25±0.91	0.17±0.09
	All sites	0.58±0.21	0.05±0.13	7.8 ±0.35	0.17±0.06
Dbh age 12 (cm)	Dial	4.35±1.54		25.0±1.8	0.37±0.12
	Gog	6.09±2.09		28.0±2.1	0.45±0.13
	Kamona	5.64±2.78		38.6±3.1	0.32±0.12
	All sites	5.56±1.57	0.00	29.9±1.3	0.39±0.10
Dbh increment (cm)	Dial	2.76±0.86		10.39±0.76	0.53±0.14
	Gog	2.49±0.82		10.38±0.83	0.48±0.15
	Kamona	2.02±0.78		10.39±0.76	0.35±0.13
	All sites	2.61±0.71	0.00	10.95±0.48	0.48±0.11
Basic density ($kg \cdot m^{-3}$)	Dial	177± 62		716±63	0.50±0.16
	Gog	374±110		602±55	0.96±0.18
	Kamona	199± 71		587±59	0.63±0.17
	All sites	188± 58	59±26	613±36	0.51±0.13
Cellulose (% $kg \cdot kg^{-1}$)	Dial	0.26±0.12		1.00±0.13	0.52±0.21
	Gog	0.55±0.18		1.05±0.12	0.86±0.20
	Kamona	0.58±0.18		0.81±0.09	1.05±0.21
	All sites	0.37±0.12	0.07±0.06	1.22±0.09	0.54±0.15
Fibre length (μm)	Dial	251±190		2276±297	0.25±0.19
	Gog	667±233		1409±169	0.80±0.21
	Kamona	607±231		1631±194	0.68±0.21
	All sites	502±166	0.00	2199±161	0.46±0.13
Fibre coarseness ($\mu g \cdot m^{-1}$)	Dial	0.0 ±0.0		31.0 ±3.6	0.0 ±0.0
	Gog	6.46±2.80		21.49±2.71	0.58±0.23
	Kamona	4.38±2.34		23.9 ±2.99	0.39±0.13
	All sites	0.95±0.99	0.98±1.43	32.19±0.32	0.07±0.07

found to be an unreliable trait because it does not distinguish between small fibres with thick walls and large fibres with thin walls (ARBUTHNOT 1991; MUNERI & RAYMOND 2001). In this study, genetic correlations for fibre coarseness between sites were zero (Table 6) indicating that a different trait is being measured at each site. Therefore, although it appears there may be some degree of genetic control over the cross sectional dimensions of a fibre the response is highly dependent on the site conditions.

Correlations

There were adverse genetic correlations between diameter/basic density and basic density/cellulose content. Correlations between diameter/basic density were variable across sites but mostly strong. For diameter at 12 years and basic density, values for individual sites ranged from –0.16 to –0.77, and in a pooled analysis the correlation was –0.57 (Table 5). Correlations tended to be more negative at a younger age (–0.72 compared with –0.57 in the combined site analysis). Genetic correlations between basic density and cellulose content were also variable across sites (Table 5). Values ranged from –0.19 to –0.53 and in a pooled analysis the correlation was –0.45.

There were favourable genetic correlations for diameter/cellulose content, diameter / fibre length and fibre length/cellulose content (Table 5). For diameter/ cellulose content, values for individual sites were significantly different, but all were strongly positive. Values ranged between 0.62 and 0.86, and in a pooled analysis the correlation was 0.79. Correlations for fibre length/diameter were variable across sites (–0.20 to 0.49) but in a pooled analysis this correlation was 0.37. Similarly, correlations between fibre length/cellulose

Table 5. Genetic correlations (r_G) with standard errors above diagonal and phenotypic correlations (r) below diagonal.

Site		D_6	D_{12}	*BD*	*CELL*	*FL*	*FC*
Dial	D_6		0.79±0.14	-0.54±0.29	0.73±0.32	-0.20±0.43	0±0
	D_{12}	0.79*		-0.16±0.24	0.86±0.16	0.36±0.34	0±0
	BD	-0.21*	-0.17*		-0.26±0.27	0.75±0.32	0±0
	CELL	0.09	0.23*	0.09		-0.13±0.26	0±0
	FL	-0.14*	0.08	0.23*	0.48*		0±0
	FC	0.19*	0.07	0.01	-0.21*	-0.12	
Gog	D_6		0.98±0.03	-0.66±0.18	0.83±0.14	0.49±0.23	0.18±0.30
	D_{12}	0.87*		-0.77±0.13	0.81±0.12	0.51±0.20	0.12±0.27
	BD	-0.13	-0.12		-0.53±0.18	-0.17±0.22	0.11±0.25
	CELL	0.18	0.35*	0.06		0.86±0.16	0.22±0.25
	FL	0.11	0.26*	0.14	0.45*		0.47±0.24
	FC	0.03	0.06	0.16	0.11	0.22*	
Kamona	D_6		1.00±0.04	-0.94±0.24	0.64±0.24	0.29±0.32	-0.77±0.41
	D_{12}	0.89*		-0.71±0.20	0.62±0.18	0.27±0.26	-0.45±0.33
	BD	-0.02	-0.03		-0.19±0.23	-0.01±0.21	0.33±0.29
	CELL	0.25*	0.40*	0.09		0.41±0.20	-0.19±0.27
	FL	0.26*	0.38*	0.22*	0.49*		-0.68±0.28
	FC	0.17*	0.21*	0.26*	0.00	0.04	
All sites	D_6		0.97±0.02	-0.72±0.14	0.82±0.11	0.34±0.21	-0.20±0.35
	D_{12}	0.82*		-0.57±0.15	0.79±0.10	0.37±0.19	-0.11±0.32
	BD	-0.14*	-0.11		-0.45±0.18	0.15±0.22	0.29±0.32
	CELL	0.14*	0.32*	0.11		0.50±0.16	-0.07±0.33
	FL	0.02	0.14*	0.26*	0.46*		0.39±0.33
	FC	0.00	0.06	0.22*	0.05	0.25*	

* Significantly different at 0.05.

content were highly variable across sites (–0.13 to 0.86) and strongly favourable in the pooled analysis (0.54).

There appeared to be no significant genetic correlations for fibre length/basic density, and fire coarseness and all other traits (Table 5). For fibre length and basic density, correlations were highly variable across sites, ranging from –0.17 to 0.75, and in a pooled analysis not significantly different from zero. Genetic correlations between fibre coarseness and other wood traits formed no pattern with correlations often being completely opposite on different sites.

Phenotypic correlations between diameter at 6 and 12 years were strong, however other relationships were weak (Table 5). The strongest were those between fibre length and cellulose content (r = 0.45 to 0.49), and diameter at 12 years and cellulose content (r = 0.23 to 0.40). There were significant negative correlations between diameter and basic density at two sites, although the relationship was very weak. Phenotypic correlations of fibre coarseness with other traits were not consistent across sites. A positive relationship between fibre coarseness and density could be expected since high density wood usually has thicker cell walls (MALAN *et al.* 1994), however this relationship was always weak and significant on two sites only.

Genotype by environment interaction

There was no significant genotype by environment interaction for diameter at 6 or 12 years. Family by site variance was either zero or extremely low (Table 4) and genetic correlations between sites were very high (Table 6). Similarly, fibre length had no genotype by environment interaction and a very high genetic correlation between sites (Tables 4 and 6).

Genotype by environment interaction for basic density was relatively small but significant. Family by site variance consisted of 6 % of total variation (Table 4), and genetic correlations between sites ranged between 0.67 to 0.92 (Table 6). The interaction appeared to be caused by minor rank changes from many families. Excluding groups of families did not substantially reduce the interaction. At best, dropping the most interactive family reduced the family by site variance to 5 % of total, but dropping other families made very little difference. Scale effects can also cause genotype

by environment interaction, where genetic expression on one site may be much stronger than other sites. However for these data, scale effects contributed very little to this variation. After weighting the data by the site standard deviation, family by site variance reduced by only 0.5 %.

Genotype by environment interaction for cellulose content was also relatively small but significant. Family by site variance consisted of 4 % of total variation (Table 4), and genetic correlations between sites ranged from 0.77 to 0.91 (Table 6). This interaction appears to be mainly caused by scaling effects. After weighting the data by the site standard deviation family by site variance reduced to less than 2 % of total.

Table 6. Genetic correlations (±standard error) between sites.

Trait	Dial-Gog	Dial-Kamona	Gog-Kamona
D_6	1.08 ±0.31	0.59 ±0.43	1.16±0.25
D_{12}	1.09 ±010	0.93±0.13	1.14±0.12
D_{INC}	1.09 ±0.07	0.98 ±0.11	1.13 ±0.11
BD	0.73 ±0.15	0.67 ±0.19	0.92 ±0.11
CELL	0.77 ±0.23	0.91±0.19	0.89 ±0.15
FL	1.22±0.37	1.19 ±0.40	1.36 ±0.29
FC	0	0	-0.22±0.32

DISCUSSION

Comparing genetic parameters

Published heritability estimates for *E. nitens* diameter cover a wide range (0.11 to 0.55) and those from this study fall within that range. Six year diameters are at the bottom end of the range and are comparable to those of WOOLASTON *et al.* (1991), WHITEMAN *et al.* (1992), JOHNSON (1996) and GEA *et al.* (1997). Twelve year diameters are at the upper end of the range and are comparable to some of the basal area estimates of TIBBITS & HODGE (1998). The published information generally confirms the trend of increasing heritability with age.

Reported heritabilities for *E. nitens* basic density also cover a wide range (0.17 to 0.83) and those from this study fall in the mid to upper end of that range (GREAVES *et al.* 1995; GEA *et al.* 1997; TIBBITS & HODGE 1998). As in this study, some very high individual site heritabilities have been reported but estimates tend to be lower in a combined site analysis. The most comprehensive study for *E. nitens* basic density is that of TIBBITS & HODGE (1998) and the combined site heritability from that study (0.43±0.09) is very similar to that from this current study (0.51±0.13). The very high heritability estimate from the Gog site is not without precedent; similar values are reported for *E. globulus* (MUNERI & RAYMOND 2000).

Heritabilities for cellulose content from this study are higher than other published estimates of both cellulose content and pulp yield for eucalypts. For pulp yield, most estimates are in the range of 0.30 to 0.63, although some heritabilities as low as 0.02 have been reported (CLARKE 1990; DEAN *et al.* 1990; BORRALHO *et al.* 1993; TIBBITS & HODGE 1998; RAYMOND *et al.* 2001). Published heritabilities for cellulose content (all for *E. globulus*) cover a similar range, varying from 0.31 to 0.57 (COTTERILL & BROLIN 1997; RAYMOND & SCHIMLECK 2001). The combined site heritability for cellulose content from this study is higher than the combined site pulp yield estimate for *E. nitens* of TIBBITS & HODGE (1998), however differences are not large (0.56±0.15 compared with 0.38±0.08).

Heritabilities for fibre length from this study (which ranged from 0.25 to 0.80) tend to be higher than other reported values for eucalypts. Published estimates are all for single sites and vary between 0.30 to 0.54 (DEAN *et al.* 1990; COTTERILL & BROLIN 1997; RAYMOND *et al.* 1998), with the only estimate for *E. nitens* being 0.32 (DEAN *et al.* 1990). For fibre coarseness of eucalypts, published heritabilities vary between 0.03 to 0.40 (COTTERILL & BROLIN 1997; DEAN *et al.* 1990; RAYMOND *et al.* 1998), with the only estimate for *E. nitens* being 0.03 (DEAN *et al.* 1990). However all appear to be based on single sites and probably do not reflect exploitable genetic variation given the poor across site repeatability found in this study.

Published estimates of genetic correlations for eucalypts are highly variable. Those for diameter/basic density are usually negative but range between 0 and -0.6 (CLARKE 1990; DEAN *et al.* 1990; GEA *et al.* 1997; TIBBITS & HODGE 1998; MUNERI & RAYMOND 2000). Individual site estimates from this study were also variable (-0.16 to -0.77) but generally more strongly negative. For diameter and pulp yield of *E. nitens*, published genetic correlations are positive (TIBBITS & HODGE 1998) and those from this study were also positive but were much stronger (0.79±0.10 compared with 0.24±0.12). However for other eucalypts estimates are negative and range from -0.16 to -0.54 (CLARKE 1990; DEAN *et al.* 1990; RAYMOND *et al.* 2001). For basic density and pulp yield, published genetic correlations for eucalypts are either zero or positive and range between 0 and 0.7 (DEAN *et al.* 1990; TIBBITS & HODGE 1998; RAYMOND *et al.* 2001). This study is unique in finding strongly negative correlations between these traits.

There are a number of possible reasons for the

variability in estimates of genetic correlations. Firstly, this may be due to inherent variation between species and populations. Published data suggests species differences may exist (eg. differences between *E. nitens* and *E. globulus*). However, no studies have examined differences between races within a species. Secondly, there appears be variation across sites. This may be related to different amounts of genetic expression on different sites influencing the strength of some correlations. Thirdly, some estimates of genetic correlations are made using small or truncated data sets because wood testing can be relatively costly and this may bias some estimates. Regardless of the reasons for variable genetic correlations, it appears unwise for tree breeders to assume 'standard' correlations when making selections. A safer approach would be to assess a sample of the population to estimate 'true' genetic correlations and apply these to the estimation of breeding values.

Gains from selection

Large simultaneous gains cannot be obtained in all traits due to the negative correlations between basic density and diameter, and basic density and cellulose content (Table 7). Gains in diameter of 20 % are predicted. However, selection for diameter alone will cause a 4 % decline in basic density. Similarly, if selecting for basic density alone an increase of 8 % is predicted, but this will lead to a fall in diameter and cellulose content of 15 % and 2 % respectively. Favourable correlations between diameter and cellulose content results in improved cellulose content for any index with a growth emphasis. Similarly, fibre length will increase under all selection strategies due to favourable correlations with diameter and generally favourable correlations with both density and cellulose content.

Understanding the economic value of each trait is essential for multitrait selection because adverse genetic correlations require 'trade-offs' between traits. This can be demonstrated using the Kraft pulp economic weights of GREAVES *et al.* (1997). Using these weights, it can be shown that the economic gain (expressed as profit per ha) of selecting for diameter, basic density or cellulose content alone (indices 1 to 3 in Table 7) is only half of that when selecting on the Kraft pulp index (index 5 on Table 7). When using this index the gains for diameter, basic density and cellulose content were 13 %, 1 % and 2 % respectively (Table 7). Under this index the largest 'trade-off' in potential gain was in basic density.

Implications for breeding programs

The strong adverse genetic correlation between basic density and diameter is of greatest importance to breeding programs. Selection for diameter alone will result in a decline in basic density and this will compromise the profitability of tree breeding for most enterprises. Therefore it is important that tree breeding programs do two things. Firstly, there must be a sound assessment of the economic importance of basic density, and appropriate economic weights applied. In the preceding section, the economic weights of Greaves *et al.* (1997) have been used but different weights are appropriate for different enterprises (see Borralho *et al.* 1993). Secondly, there should be routine screening for basic density to find good combinations of diameter and basic density (ie. to find 'correlation breakers'). For example, under a different set of economic weights it can be shown that gains of 5 % can be obtained in both diameter and basic density.

Cellulose content, which has been shown to be a reliable indicator of kraft pulp yield (WALLIS *et al.* 1996; KUBE & RAYMOND 2001), is highly heritable. On two sites almost all variation was explained by additive genetic variance. It is also highly correlated with other traits. This study found favourable genetic correlations between growth and cellulose content and this is supported by other studies in *E. nitens* (TIBBITS &

Table 7. Genetic gains for each trait (% of mean value) using different selection strategies.

Index	Relative weights[1]	D_{12}	*BD*	*CELL*	*FL*
1. Diameter only	1 : 0 : 0 : 0	20	-4	3	2
2. Basic density only	0 : 1 : 0 : 0	-15	8	-2	1
3. Cellulose content only	0 : 0 : 1 : 0	17	-3	3	3
4. Fibre length only	0 : 0 : 0 : 1	10	1	2	6
5. Kraft pulp production[2]	3 : 3 : 1 : 0	13	1	2	4

[1] Relative importance of one standard devition gain for D_{12}, *BD*, *CELL* and *FL* respectively.
[2] Economic weights to maximise profit per ha for unbleached kraft pulp production. Taken from GREAVES *et al.* (1997) and converted to standard deviation units.

HODGE 1998). However, contrary to other studies, correlations between cellulose content (or pulp yield) and wood density were found to be weakly negative. Breeding programs that do not select directly for cellulose content will probably make reasonable gains in this trait. The strong favourable correlation between diameter and cellulose content will lead to a correlated response for cellulose irrespective of the weaker adverse correlation with basic density. Data from this study showed that selecting for diameter and basic density alone will deliver 85 % of gains in cellulose content. A similar result is reported by GREAVES *et al.* (1997), where selecting on an index that included diameter and basic density delivered 95 % of economic gains to a kraft pulp producer.

Fibre length is also highly heritable however the nature of genetic correlations is ambiguous in this study. It appears the genetic expression of this trait is sensitive to site, as indicated by different heritabilities and different patterns of genetic correlations across sites. Despite this, it appears that breeding programs can assume fibre length will increase under all selection regimes without directly selecting for this trait (see Table 7).

Fibre coarseness was an unreliable trait in this study. The measure used here (Kajanni fibre coarseness) appeared to be a different trait on different sites. Problems with Kajanni fibre coarseness have been noted in other studies (ARBUTHNOT 1991), and are caused by the confounding of small diameter/thick walled fibres and large diameter/thin walled fibres. Fibre coarseness is an important trait for paper properties (ARBUTHNOT 1991; KIBBLEWHITE *et al.* 1998) and data from this study suggests genetic variation is present. Therefore another low cost and rapid measurement technique is required if this trait is to be exploited in breeding programs.

CONCLUSION

Diameter growth is under moderate genetic control with genetic expression increasing with age. Basic density, cellulose content and fibre length are under strong genetic control. Breeding programs of *E. nitens* have the potential to make gains in these traits. Fibre coarseness measured on the Kajanni fibre analyser is an unreliable trait, presumably due to confounding of small diameter/thick walled fibres and large diameter/thin walled fibres. Favourable genetic correlations were found between diameter/cellulose content, diameter/fibre length and cellulose/fibre length; adverse correlations between diameter/basic density and basic density/cellulose content; and variable correlations between fibre length/basic density. There is evidence that genetic correlations between traits are variable and standard correlations cannot be assumed. Therefore tree breeders should assess wood properties if for no other reason than to estimate genetic correlations for their population and determine the potential for declining wood quality due to adverse genetic correlations.

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REFERENCES

ARBUTHNOT, A. L. 1991: The influence of basic wood density of eucalypts on pulp and paper properties. *In:* 'Symposium on Intensive Forestry: The Role of Eucalypts'. (Ed. A. P. G. Schonau). Proceedings of the IUFRO symposium, P2.02-01 Productivity of Eucalypts, 2–6 September 1991, Durban, South Africa. pp 966–975.

APIOLAZA, L. A. & GARRICK, D. J. 2001. Analysis of longitudinal data from progeny tests: Some multivariate approaches. *Forest Science* **47**:129–140.

BANHAM, P. W., ORME, K. & RUSSELL, S. L. 1995: Pulpwood qualities required for the cold soda pulping process. *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 1-4. Proc. CRCTHF-IUFRO Conf. Hobart, 19–24 February 1995. (CRC for Temperate Hardwood Forestry: Hobart).

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

CLARKE, C. R. E. 1990: The estimation of genetic parameters of pulp and paper properties in *Eucalyptus grandis* Hill ex Maiden and their implication for tree improvement. Master of Science in Agriculture Thesis, University of Natal, Pietermaritzburg, South Africa. 159 pp

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

DEAN, G. H., FRENCH, J. & MADDERN, K. N. 1990: Breeding eucalypts for manufacture of pulp and paper. *In:* Proceedings 23rd Forest Products Research Conference, CSIRO Division of Forestry and Forest Products, Clayton, Victoria. November 1990. Volume II: 5/2, 15 pp.

DIETERS, M. J., JARVIS, S. F. & GILMOUR, A. R. 1999: Multivariate approach to the estimation of genetic parameters. *In:* Proceedings 25th Meeting, Southern Forest Tree Improvement Conference. New Orleans, Louisiana. July 11–14 1999, SFTIC Sponsored Publication No.47. Bowen, M. and Stine, M. (Editors), Louisiana State

University, pp. 54-59.

GEA, L. D., MCCONNOCHIE, R. & BORRALHO, N. M. G. 1997: Genetic parameters for growth and wood density traits in *Eucalyptus nitens* in New Zealand. *New Zealand Journal of Forest Science* **27**:237-244.

GILMOUR, A. R., CULLIS, B. R., WELHAM, S. J. & THOMPSON, R. 1999: ASREML Reference Manual. NSW Agriculture Biometric Bulletin No. 3. NSW Agriculture.

GREAVES, B. L., BORRALHO, N. M. G., RAYMOND C. A. & FARRINGTON, A. 1995: Use of pilodyn for the 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.

GRIFFIN, A. R. & COTTERILL, P. P. 1988. Genetic variation in growth of outcrossed, selfed and open pollinted progenies of *Eucalyptus regnans* and some implications for breeding strategy. *Silvae Genetica* **37**:124-131.

JOHNSON, I. G. 1996: Growth and form of *Eucalyptus nitens* progenies in New South Wales and selection strategies for a seedling seed orchard. *Australian Forestry* **59**:162-170.

JONES, T. G. & RICHARSON, J. D. 1999: Relationships between wood and chemi-mechanical pulping properties of New Zealand grown *Eucalyptus nitens* trees. *Appita Journal.* **52**:51-56.

KIBBLEWHITE, R. P., RIDDELL, M. J. C. & SHELBOURNE, C. J. A. 1998: Kraft fibre and pulp qualities of 29 trees of New Zealand grown *Eucalyptus nitens*. *Appita Journal* **51**:114-121.

KING, J. N. & WILCOX, M. D. 1988: Family tests as a basis for the genetic improvement of *Eucalyptus nitens* in New Zealand. *New Zealand Journal of Forest Science* **18**:253-266.

KUBE, P. D. & RAYMOND, C. A. 2001: Predicting whole tree basic density and pulp yield using wood core samples in *Eucalyptus nitens*. *Appita Journal* **55** (in press).

MALAN, F. S., MALE, J. R. & VENTER J. S. M. 1994: Relationships between the properties of eucalypt wood and some chemical, pulp and paper properties. *Paper Southern Africa*. February 1994: 6-16.

MUNERI, A. & RAYMOND, C. A. 2000: Genetic parameters and genotype by environment interactions for basic density, Pilodyn penetration and diameter in *Eucalyptus globulus*. *Forest Genetics* 7:321-332

MUNERI, A. & RAYMOND, C. A. 2001: Non destructive sampling of *Eucalyptus globulus* and *E. nitens* for wood properties. II. Fibre length and coarseness. *Wood Science and Technology* **35**:41-56.

NEILSEN, W. A. & PINKARD, E. A. 2000: Developing silvicultural regimes for sawlog and veneer production from temperate eucalypt plantations in Tasmania. *In:* The Future of Eucalypts for Wood Products. Proceedings of an IUFRO Conference, March 19 to 24, 2000, Launceston, Tasmania, Australia. pp 335-348.

PEDERICK, L. A. 1979: Natural variation in shining gum (*Eucalyptus nitens*). *Australian Forest Research* **9**:41-63.

RAYMOND, C. A. & GREAVES, B. L. 1997: Developing breeding objectives for kraft and cold caustic soak (CCS) pulping of eucalypts. *In:* Timber management towards wood quality and end-product value. Proc. CTIA/IUFRO International Wood Quality Workshop. Quebec City, August 1997. pp IV 27-34.

RAYMOND, C. A., BANHAM, P. W., & MACDONALD, A. C. 1998: Within tree variation and genetic control of basic density, fibre length and coarseness in *Eucalyptus regnans* in Tasmania. *Appita Journal* **51**:299-305.

RAYMOND, C. A. & MUNERI, A. 2001: Non destructive sampling of *Eucalyptus globulus* and *E. nitens* for wood properties. I. Basic density. *Wood Science and Technology* **35**:27-39.

RAYMOND, C. A. & SCHIMLECK, L. R. 2001: Development of near infrared reflectance analysis calibrations for estimating genetic parameters for cellulose content in *Eucalyptus globulus*. *Canadian Journal of Forest Research* (in press).

RAYMOND, C. A., SCHIMLECK, L. R., MUNERI, A. & MICHELL, A. J. 2001: Genetic parameters and genotype-by-environment interaction for predicted pulp yield and pulp productivity in *Eucalyptus globulus*. *Forest Genetics* **8**:213-224.

TAPPI (1989). Basic density and moisture content of pulpwood. TAPPI no. T258 om-98.

TIBBITS, W. N., BOOMSMA, D. B. & JARVIS, S. 1997: Distribution, biology, genetics, and improvement programs for *Eucalyptus globulus* and *E. nitens* around the world. Proc: 24th Biennial Southern Forest Tree Improvement Conference, Orlando, Florida USA. June 9-12 1997. pp 81-95.

TIBBITS, W. & HODGE, G. 1998: Genetic parameters and breeding value predictions for *Eucalyptus nitens* wood fibre traits. *Forest Science* **44**:587-598.

WALLIS, A. F. A., WEARNE, R. H. & WRIGHT, P. J. 1996: Analytical characteristics of plantation eucalypt woods relating to kraft pulp yield. *Appita Journal* **49**:427-432.

WALLIS, A. F. A., WEARNE, R. H. & WRIGHT, P. J. 1997: New approaches to rapid analysis of cellulose in wood. *In:* Proceedings of the International Symposium on Wood and Pulping Chemistry, Montreal, June 1997. Vol 1, C3, 1-4.

WHITEMAN, P. H., DEAN, C. A., DORAN, J. C. & CAMERON, J. N. 1992:. Genetic parameters and selection strategies for *Eucalyptus nitens* (Dean and Maiden) in Victoria. *Silvae Genetica* **41**:77-81.

WOOLASTON, R., WHITEMAN, P. H., & CAMERON, J. N. 1991: Genetic analysis of four year diameter measurements for *Eucalyptus nitens* growing across three sites in Victoria Australia. *In:* 'Symposium on Intensive Forestry: The Role of Eucalypts'. (Ed. A. P. G. Schonau). Proceedings of the IUFRO symposium, P2.02-01 Productivity of Eucalypts, 2-6 September 1991, Durban, South Africa. pp 361-370.