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Genetic Variation of Physical and Chemical Wood Properties of *Eucalyptus globulus*

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Abstract

This study considered the degree of genetic variation for diameter (DBH), basic density (BD), predicted pulp yield (PPY), fibre length (FL), microfibril angle (MFA) and cellulose content (CC) amongst eight subraces of *Eucalyptus globulus* growing in a field trial in NW Tasmania. There were significant subrace effects for BD, FL and CC. This variation affected the relative profitability of the subraces for pulp production. On average, the most profitable subraces (on NPV/ha over the base population mean) were Strzelecki Ranges ($862.04), Western Otways ($657.80) and Strzelecki Foothills ($576.81). The genetic control (heritability) of variation in DBH, FL and MFA was moderate ($0.15 < h^2 < 0.27$), while control for BD, PPY and CC was high ($h^2 > 0.40$). Genetic correlations between growth and wood properties were not statistically significant, except for DBH-MFA (–0.86). Most genetic correlations amongst wood properties were outside the parametric space (< -1 or > 1), but there were significant correlations between BD-MFA (–0.70) and PPY-CC (0.82). The empirical response

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to selection on an index based on a pulp wood objective (which included volume and basic density) resulted in a gain of 4.3% for DBH, 7.9% for BD and marginal changes for all other traits, with a net impact in profit of $1,270/ha. However, future profit calculations will need to consider the effect of FL, MFA and CC on the economics of wood processing to fully evaluate the economic impact of breeding.

Key words: BLUP, racial variation, heritability, genetic correlations, breeding, profit.

Introduction

Eucalyptus globulus Labill is the foremost pulpwood eucalypt in temperate regions, and it is widely planted in Spain, Portugal, Chile, Australia and South Africa, with an estimated total estate of over 2 million ha (DOUGHTY, 2000; POTTS *et al.,* 2004). Previous research has shown that there is considerable genetic variation in *E. globulus* for multiple traits (e.g., DUTKOWSKI and POTTS, 1999), and wood properties are no exception (MUNERI and RAYMOND, 2000; MIRANDA *et al.,* 2001a; MIRANDA *et al.,* 2001b). Furthermore, considerable gain for commercial plantations can be obtained exploiting the genetic variation within natural populations of *E. globulus*.

Tree breeding has evolved simultaneously with the forest industry. Breeding programs have progressed from improving mostly growth and form (e.g., THULIN, 1957; BANNISTER, 1959) to tailoring genetic material towards end-products requirements (e.g., BORRALHO *et al.,* 1993; GREAVES *et al.,* 1997; APIOLAZA and GARRICK, 2001). The direction of genetic progress for a breeding program is dictated by its breeding objective; i.e., by the linear combination of traits and their relative economic importance (HAZEL, 1943; PONZONI, 1986; GODDARD, 1998). The current breeding objective for *Eucalyptus globulus* in Australia includes volume (VOL [m³/ha]), basic density (BD [kg/m³]) and pulp yield (PY [%]), where all traits are considered at rotation age. This objective is based on economic modelling of a vertically integrated pulp production industry (GREAVES et al., 1997).

Breeding objectives are periodically updated, reflecting changing economic circumstances, new knowledge about industrial processes and incorporation of additional industrial systems to be served by material from the breeding program (APIOLAZA and GREAVES, 2001). Additional processes under consideration for *E. globulus* are paper production, sawn timber, veneers and reconstituted wood. The closer one gets to final products, the greater the influence of wood properties on the economics of the process (RAYMOND and APIOLAZA, 2004). There are many other wood properties that either provide extra information on objective traits (i.e., may act as selection criteria) or influence products not considered by the current breeding objective. Cellulose content (CC [%]), calculated as grams of cellulose per mass of wood, is considered to be a reliable predictor of pulp yield in *E. nitens* (KUBE et al., 2001; RAYMOND and SCHIMLECK, 2002). Microfibril angle (MFA [degrees]) measures the angle of the miscelles (aggregations of microfibrils) with respect to the longitudinal access of the cells. The smaller the angle the greater the tensile strength of the fibre and the smaller its shrinkage (BOOTLE, 1983). Fibre length (FL [mm]) measures the total length of wood fibres, which represent 66% of the wood tissue (MIRANDA et al., 2001a). In general terms, final users will want to increase VOL, BD, PY and CC, and to reduce MFA (Dr Bruce Greaves, personal communication). These traits may be either included in alternative objectives, or to be considered in the deployment phase objective. The latter is an objective used only for the production populations (e.g. seed orchards or clonal propagation systems), which includes extra traits as well as non-additive genetic effects.

The objective of this project is to provide insights on the degree of variation amongst natural populations of *E. globulus* for physical (basic wood density, fibre length, and micro fibril angle) and chemical (pulp yield and cellulose content) wood properties and their relationship with growth. This research also offers a first approximation for the degree of additive genetic control (heritability), the genetic association (genetic correlations) between these traits and the expected response to selection.

Materials and Methods

The study was based on an open pollinated progeny test at West Ridgley in North Western Tasmania (for details see MACDONALD *et al.,* 1997). The trial was established in 1989 and included families from the CSIRO 1987-88 base population collection. The test has an incomplete block design, with 451 families in 5 replicates, with 17 incomplete blocks each, using two-tree row plots. Although West Ridgley contains material from 22 subraces, sampling focused on eight subraces (as defined by DUTKOWSKI and POTTS, 1999) already sampled for wood density and growth in trials at Massy Greene, Mt Worth and Flynn (MUNERI and RAYMOND, 2000).

In 2000, all 2662 surviving trees were assessed for diameter over bark (DBH [cm]) and 188 trees were sampled for wood properties. The latter represented 35 families from 8 subraces, choosing mostly one, and only a few times two, tree per plot. Three increment cores (at around 1.1 m height) were taken from each tree. The first one was used to estimate basic density using the water displacement method. This core was then macerated to determine average core fibre length (FL [mm]). The second core was analysed to determine pith to bark variation for density and microfibril angle (MFA [degrees]) using SilviScan (EVANS *et al.,* 2000). The third core was used to estimate predicted pulp yield (PPY [%]) using Near Infra-Red Analysis (NIRA) and cellulose content (CC [%]) from a laboratory digest (RAYMOND and SCHIMLECK, 2002).

The most generic model equation used in the trial was:

$$y = Xf + Z_1b + Z_2p + Z_3a + e \qquad \text{Equation 1}$$

where y is the vector of phenotypic observations, f is the vector of fixed effects (subrace and replicate), b is the

vector of random incomplete block effects, p is the random vector of plot effects, a is the vector of random additive genetic effects and e is the vector of random residuals (environmental and non-additive effects). X, Z_1, Z_2 and Z_3 are design matrices linking the phenotypic observations with the fixed and random effects.

The expected value and dispersion matrices, assuming a multivariate normal distribution (MVN) are:

$$\begin{bmatrix} y \\ b \\ p \\ a \\ e \end{bmatrix} \sim MVN \left(\begin{bmatrix} Xf \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} V & Z_1B & Z_2P & Z_3G & R \\ BZ_1' & B & 0 & 0 & 0 \\ PZ_2' & 0 & P_0 & 0 & 0 \\ GZ_3' & 0 & 0 & G & 0 \\ R & 0 & 0 & 0 & R \end{bmatrix} \right) \quad \text{Equation 2}$$

where $B = \sigma_b^2 I$, $P = \sigma_p^2 I$, $G = \sigma_a^2 A$ and $R = \sigma_e^2 I$, I is an identity matrix, 0 is a null matrix and A is the numerator relationship matrix for the trees. In addition, σ_b^2 is the incomplete block variance, σ_p^2 is the plot variance (only fitted for DBH), σ_a^2 is the additive genetic variance and σ_e^2 is the residuals variance. The A matrix was modified to take into account 30 % average selfing in *E. globulus* (DUTKOWSKI *et al.,* 2001).

This model was fitted for each trait using ASReml (GILMOUR *et al.,* 2002), testing significance of both fixed effects with a Wald test, and random effects using a Likelihood Ratio Test (LRT). The analyses of all traits started with the full model equation, but the final model was fitted after dropping non-significant random effects (*Table 1*).

Table 1. – Factors included in the analysis and number of observations for each trait. An x indicates the inclusion of the factor in the final model for a trait. The number of observations for wood properties varies because of problems processing a few wood cores.

Trait	N	rep	subrace	iblock	plot	tree
DBH	2662	x	x	x		x
BD	188	x	x			x
PPY	184	x	x			x
FL	169	x	x			x
MFA	173	x	x			x
CC	184	x	x			x

The heritability (h^2), or degree of additive genetic control, was calculated for each trait using:

$$h^2 = \frac{\sigma_a^2}{\left(\sigma_a^2 + \sigma_e^2 \right)}$$

This assumes that predicted breeding values are adjusted by replicate, subrace and incomplete block before selection.

Additive genetic covariance components ($\sigma_{a_{12}}$) and genetic correlations (r_g) between two traits were obtained from bivariate analyses:

$$r_g = \frac{\sigma_{a_{12}}}{\sqrt{\sigma_{a_1}^2 \sigma_{a_2}^2}}$$

where $\sigma_{a_1}^2$ and $\sigma_{a_2}^2$ are the additive genetic variances for traits 1 and 2. Bivariate models extend equations 1 and 2, where each of the vectors now contains values for two

traits and the covariance matrices are $B = \Sigma_\oplus B_0$, $P = \Sigma_\oplus P_0$, $G = A \otimes G_0$, and $R = \Sigma_\oplus R_0$. Now B_0, P_0, G_0 and R_0 are matrices of dimension 2×2 containing the variances for each trait and the covariance between traits; $\Sigma_\oplus$ and $\otimes$ are the direct sum and direct product operations respectively.

While the current *E. globulus* breeding objective traits includes volume, basic density and pulp yield, selection is currently carried out based on stem diameter and core basic density (KERR *et al.,* 2002). A selection index I [\$/ha] was obtained maximising the correlation between selection criteria and genetic-economic value using:

$$I = G_{ss}^{-1} G_{so} w$$

where G_{ss} and G_{so} are the additive genetic covariance matrices for selection criteria (DBH and core BD), and between selection criteria and objective traits (VOL, BD and PY) respectively, and w is the vector of economic weights (see *Table 2*) estimated by GREAVES *et al.* (1997). The overall breeding values used in the calculations included both subrace effects and additive genetic effects.

In principle, it is possible to estimate algebraically the correlated response to selection on *I* for non-objective traits (FL, MFA and CC). However, given the low precision of the estimated genetic correlations (see results and discussion section), it was preferred to obtain an empirical response to selection as the difference between the population mean and the top 10% based on index value.

Results and Discussion

Subrace differences

Differences between subraces means were significant for BD, FL and CC (see *Table 3*). The magnitude of the differences between the best and worst subrace can be as high as 33 % for growth (DBH), 15 % for physical (FL and MFA) and 9 % for chemical (CC) wood properties. In terms of average pulp productivity (BD*PPY in kg pulp/m^3), Strzelecki Ranges is the best, while King Island is the worst subrace, mostly reflecting differences on BD. However, King Island can partially compensate for this with additional growth, making it on average the third highest producer of pulp per ha (Results not shown). The subrace rankings for BD are similar to those presented by (MUNERI and RAYMOND, 2000), while the significant differences for FL are consistent with the findings of MIRANDA *et al.* (2001a).

Figure 1 presents the subrace distribution of economic values for individual trees, which summarises the breeding values for DBH, BD and PPY. During the early 1990s planting of King Island stock in Australia was quite popular due to its higher growth rate; however, concerns about its low basic density prompted industry to switch to mainland stock (mostly from the Strzelecki and Otways areas; POTTS *et al.,* 1999). It is clear that, in financial terms, the superiority of Strzelecki Foothills, Strzelecki Ranges and Eastern Otways for a pulp wood breeding objective at the West Ridgley site is consistent with that decision. When selecting the top 10 % of trees (22 out of 224 including parents and progenies), which is

Table 2. – Additive genetic variances (σ_a^2), genetic correlations (r_g) and economic weights (w) used for the construction of the selection index.

| | Unit | σ_a^2 | w | Correlations (r_g) | | | | |
				DBH	core BD	VOL	BD	PY
DBH	Cm	5.15		1	0	0.95	0	0
core BD	kg/m³	516.63		0	1	0	1	0.15
VOL	m³/ha	3183.86	12.56					
BD	kg/m³	516.63	23.77					
PY	%	1.057	279.59					

Table 3. – Subrace means for diameter at breast height (DBH), basic density (BD), predicted pulp yield (PPY), fibre length (FL), microfibril angle (MFA), cellulose content (CC) and index value (I). There are significant (P < 0.05) differences between subraces for BD, FL and CC[§]. All traits were assessed at age 11 years.

Subrace	DBH (cm)	BD (kg/ton)	PPY (%)	FL (mm)	MFA (°)	CC (%)	I ($NPV/ha)
King Island	24.27 a	458.86 c	51.75 a	0.74 ab	15.93 a	42.20 ab	-231.16 bc
Southern Tasmania	20.76 a	486.54 abc	52.04 a	0.81 a	17.95 a	42.78 a	-160.74 b
South-Eastern Tasmania	20.27 a	484.49 bc	51.96 a	0.75 ab	18.83 a	41.89 ab	-671.88 c
North-Eastern Tasmania	18.21 a	486.26 abc	50.51 a	0.68 b	19.55 a	40.19 b	-1267.41 d
Flinders Island	21.08 a	485.22 abc	50.98 a	0.74 ab	16.28 a	41.89 ab	-163.88 b
Strzelecki Foothills	21.24 a	518.67 ab	50.79 a	0.78 ab	16.02 a	41.84 ab	576.81 a
Strzelecki Ranges	20.62 a	531.90 a	51.29 a	0.75 ab	17.15 a	42.19 ab	862.04 a
Western Otways	23.07 a	495.33 abc	52.21 a	0.78 a	17.06 a	43.39 a	657.80 a
Overall mean	21.53	491.60	51.57	0.76	17.21	42.20	0

[§] Same letter within a trait indicates that subraces are not significantly different at α = 0.05.

a common sampling intensity in breeding programs, only four subraces are represented: Strzelecki Ranges (12 trees), Western Otways (6 trees), Strzelecki Foothills (3 trees) and King Island (1 tree).

Nevertheless, it is important to highlight that subrace profitability will depend on the industrial process tailored by the breeding program. There are indications that *E. globulus* solid wood products may benefit of lower wood density (making drying the wood easier); a situation that could favour subraces like King Island (Peter Volker, personal communication).

Genetic parameters

Estimated genetic parameters are presented in *Table 4*. Heritabilities were low to moderate for DBH, FL and MFA (but not significantly different from zero for the last two), and high for BD, PPY and CC. Genetic parameters for DBH and BD are in the range of those previously published elsewhere (e.g., MUNERI and RAYMOND, 2000). The genetic correlations are associated with very large standard errors. Genetic correlations between growth (DBH) and all wood properties were non-significantly different from zero, except for DBH-MFA (r_g = −0.86). There were high significant correlations for BD-CC (r_g = 0.61) and PPY-CC (r_g = 0.82). The correlation BD-MFA was non-significant, while estimates for correlations BD-PPY, BD-FL, PPY-FL, PPY-MFA, FL-MFA and MFA-CC were outside the parameter space (although tested significant), probably due to the small sample size for wood properties (see *Table 1*). *Figure 2* presents a scatter matrix of the overall breeding values for all individuals with wood property measurements, predicted using univariate analyses and accounting for

subrace differences. The scatter matrix confirms the results for the significant genetic correlations (BD-CC and PPY-CC), with the slopes of the linear regressions being close to the correlation values. However, it does not support the high values of genetic correlations outside the parameter space, indicating potential convergence problems in the analyses for those traits.

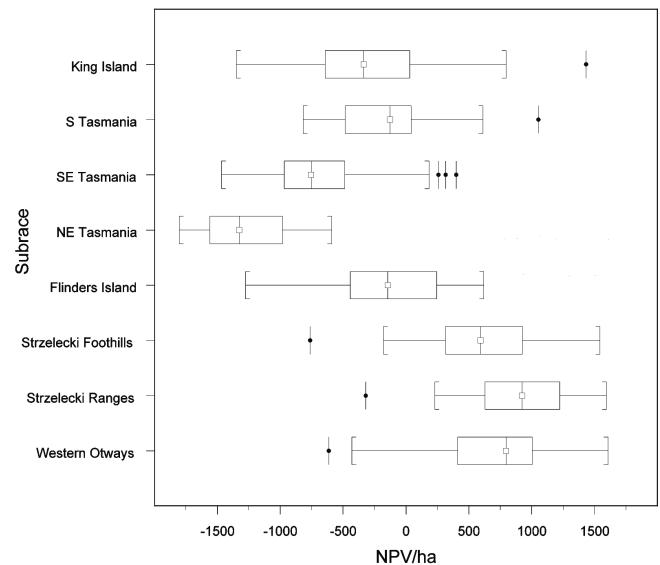The level of additive genetic variation in the population is presented as the coefficient of variation (*Table 4*),

Figure 1. – Distribution of economic values in each subrace. The box plots display the median value (−□−), interquartile range (IQR, the box), values no more than 1.5 IQR beyond the quartiles (vertical lines) and outliers (−•−) for each subrace.

to allow comparisons between traits. There is more additive variation to be exploited within subraces for growth (11%) than for wood properties (<9%). Despite this, given the higher heritabilities for wood properties, similar responses to selection would be expected for both growth and wood properties.

There is evidence suggesting that genetic parameters for growth traits are upwardly biased for open pollinated *E. globulus* (Potts *et al.,* 1995). Although the numerator relationship matrix was modified to account for an average selfing, there is variation from family to family on selfing rates or inbreeding depression levels likely to

affect the estimates, thus the correction is only an approximation (Borralho, 1994; Hardner *et al.,* 1996).

Response to selection

Table 5 shows the effect of selection on the selection index:

$$I = 296.68 \, BV_{DBH} + 25.67 \, BV_{BD}$$

where BV_{DBH} and BV_{BD} refer to the overall (including subrace effects) breeding values for DBH and BD respectively. This index emphasises basic density, with an empirical gain of 7.9% on basic density, 4.3% on

Table 4. – Heritabilities (bold diagonal), genetic correlations between traits (below diagonal) and additive coefficients of variation (last column). Standard errors are between parentheses.

	DBH	BD	PPY	FL	MFA	CC	AddCV
DBH	**0.20** (0.04)						11.19
BD	-0.58[†] (0.44)	**0.44** (0.22)					4.67
PPY	-0.16[†] (0.48)	1.08[§] (0.24)	**0.43** (0.22)				2.04
FL	-0.02[†] (0.57)	1.21[§] (0.58)	1.03[§] (0.28)	**0.16**[†] (0.17)			3.74
MFA	-0.86 (0.40)	-0.70[†] (0.41)	-1.11[§] (0.34)	-1.11[§] (0.41)	**0.27**[†] (0.24)		8.36
CC	0.61[†] (0.34)	0.61 (0.25)	0.82 (0.11)	1.12[§] (0.22)	-1.10[§] (0.27)	**0.84** (0.27)	2.99

[†] Parameter is not significant using a Likelihood Ratio Test (P > 0.05).

[§] Correlation is outside the parameter space. Sample size is too small to determine an accurate value.
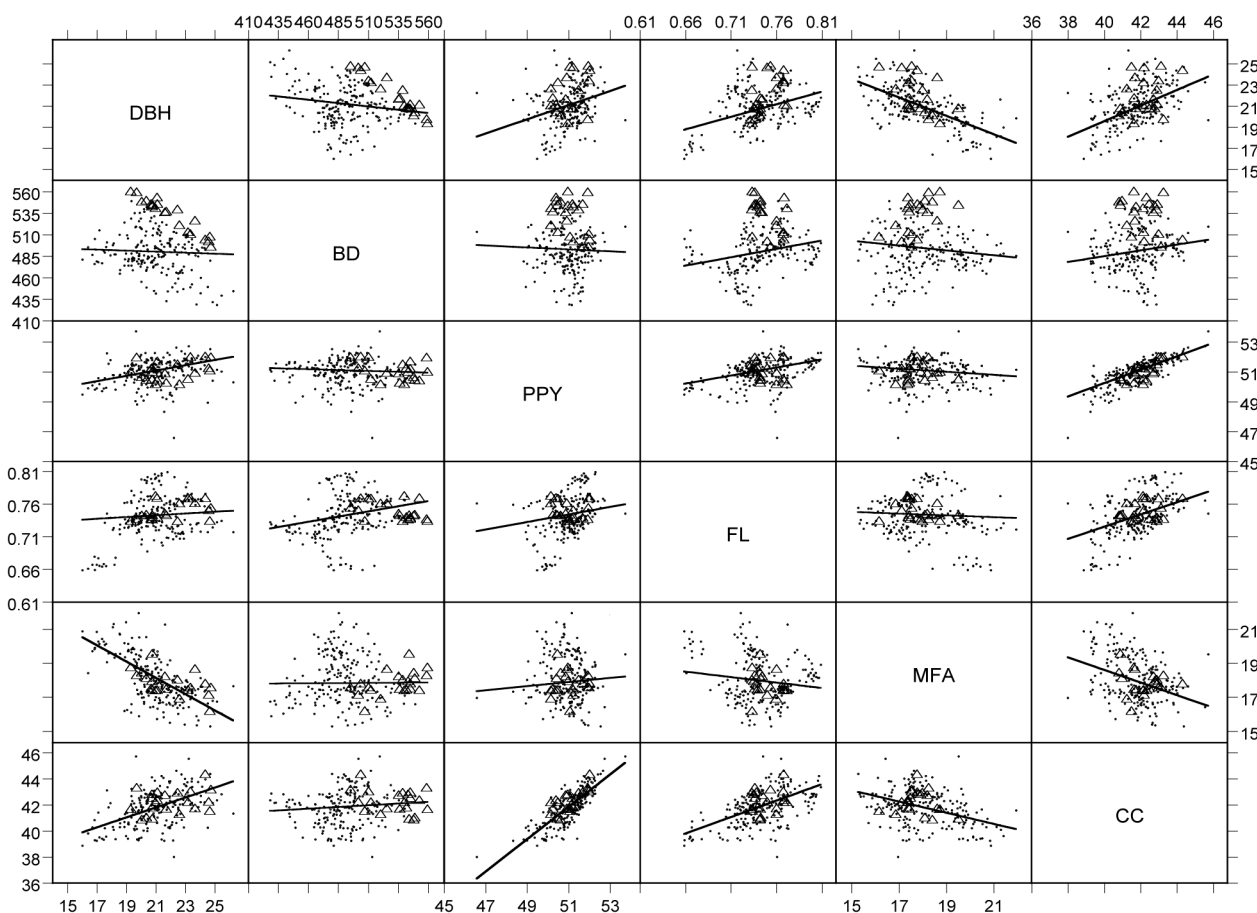

Figure 2. – Scatter matrix of overall breeding values (including subrace effects) for the traits under analysis. Triangles depict the top 10% of individuals for the selection index and lines provide an indication of correlation between traits. Selected trees are mostly in the centre of the distributions of PPY, FL, MFA and CC, confirming the small responses to selection for those traits.

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Table 5. – Complete and selected population breeding value means. Absolute gain is the difference between complete and selected means. Profit per ha is expressed as difference from the complete population mean.

Population	Traits						
	DBH	BD	PPY	FL	MFA	CC	$/ha
Complete	21.02	493.09	50.97	0.74	18.04	41.78	0
Selected	21.91	532.22	51.00	0.75	17.76	42.19	1270.62
Absolute gain	0.89[a]	39.13[a]	0.03	0.01	-0.28	0.41	1270.62[a]

[a] Gain is statistically significant (P < 0.05)

diameter and marginal changes on all other traits. Considering the economic objective, the predicted profit is significant with an additional $1270.62 per ha obtained above using the average of the population under study. *Figure 2* shows that the selected trees (triangles) are mostly in the centre of the distributions of PPY, FL, MFA and CC, confirming the minor changes on the average of those traits.

Conclusions

The economics of plantations and forest products depend on the combination of multiple traits. Initial selection in most breeding programs has focused on a single trait (usually growth) or a small number of traits without regard for wood properties. Current selection on DBH and BD resulted in marginal changes in other traits for which there is significant genetic variation. Including other wood properties in profit calculation will likely change the trees used for breeding. Profit due to changes of FL, MFA and CC will need to be ascertained to study the impact of changes on these traits on the economics of wood processing.

The significant subrace effects for BD, FL and CC was not only reflected on individual traits, but it also affected the relative profitability of the subraces with respect to the base population mean. On average, the most profitable subraces (on NPV/ha over the base population mean) were Strzelecki Ranges ($862.04), Western Otways ($657.80) and Strzelecki Foothills ($576.81). Therefore, careful selection of subraces (and potentially even collection sites within subrace) will improve profit with little, if any, additional cost.

Despite changes in sampling methods and estimation of wood properties, small sample size remains an issue for the estimation of genetic parameters, especially genetic correlations. If confirmed, the lack of significant correlations amongst growth and most wood properties will facilitate tailoring selection towards alternative objectives without major loss of growth productivity. The reported genetic parameters should ideally be confirmed with a larger sample size and in a controlled pollination situation.

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