

REVIEW OF *EUCALYPTUS NITENS* GENETIC PARAMETERS

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ABSTRACT

Eucalyptus nitens is a significant plantation species in temperate regions of the world, with breeding occurring in Australia, Chile, South Africa and New Zealand. We reviewed published genetic parameters from over 100 field trials and calculated average values for key growth, wood property, tree architecture and fitness traits. Average heritabilities for growth traits (e.g. $\bar{h}_{op}^2=0.26$ for diameter) were generally lower than those for wood property traits (e.g. $\bar{h}_{op}^2=0.51$ for basic density). However, this trend was reversed in average additive genetic coefficients of variation (e.g. $CV_a=13.3\%$ for diameter and 4.5% for basic density). Inter-age genetic correlations for stem diameter ranged from 0.68 to 1.00 but were not available for important wood property traits (e.g. basic density, cellulose content and pulp yield). The few inter-site genetic correlations reported were on average positive and strong (e.g. $\bar{r}_g=0.70$ for diameter). The average genetic correlation between diameter and basic density was -0.27. Few estimates of genetic correlations for pulp yield (or cellulose content) with diameter and basic density were available. Parameter estimates from control-pollinated progeny trials were also

rare. However, numerous parameter estimates were available from open-pollinated progeny trials for several traits, such as diameter and wood basic density, suggesting that for this cross type our average values are likely to be robust standard parameter estimates.

INTRODUCTION

The area planted to *Eucalyptus nitens* (Dean et Maiden) Maiden has expanded considerably over the past decade, particularly in Australia (total plantation area was c. 143,000 ha in 2005; Parsons *et al.* 2006) and Chile (c. 140,000 ha in 2004; INFOR 2004). The majority of these plantations are managed for the production of pulpwood but there is increasing interest in producing solidwood products from plantation-grown *E. nitens* (INFOR 2004; Kube & Raymond 2005).

Estimates of genetic parameters such as narrow-sense heritability (h^2), the additive genetic coefficient of variation (CV_a), and inter-site, inter-age and inter-trait genetic correlations are required for breeding research and the design and implementation of breeding strategies (Falconer & Mackay 1996; Houle 1992; Koots *et al.* 1994). Accordingly, estimates of these parameters are reported in the literature for a wide range of traits.

Estimates of genetic parameters are properties not only of biological traits but of the populations, environments, methods of measurement, sampling protocols and assumptions in analyses used to determine them (Falconer & Mackay 1996; Koots *et al.* 1994). However, averages of independent estimates of genetic parameters are used by breeders (1) in simulation studies (e.g. Borralho & Dutkowski 1998; Pilbeam & Dutkowski 2004), (2) to provide accurate starting values for mixed model restricted maximum likelihood (REML) analyses (Gilmour *et al.* 2002), (3) to examine patterns of genetic (co)variation within and between trait categories (Falconer & Mackay 1996), (4) to develop optimal selection indices (Cotterill & Dean 1990; Ponzoni & Newman 1989; Schneeberger *et al.* 1992), (5) in genetic analyses when the estimation of precise genetic parameters using other approaches is not possible or computationally complex, and/or (6)

to predict response to selection in, or breeding values for, unmeasured traits (e.g. harvest-age traits from selection-age traits, traits at one site from those assessed at another or hard-to-measure traits (e.g. objective traits) from easy-to-measure traits (e.g. selection traits; Falconer & Mackay 1996)). The principal aims of this study were to collate estimates of *E. nitens* genetic parameters, examine trends in these data and calculate average genetic parameters (sometimes referred to as standard genetic parameters; Cotterill & Dean 1990) for growth, wood property, tree architecture and fitness traits.

METHODS

Estimates of within-genetic-group narrow-sense heritabilities, genetic correlations (inter-age, inter-site and inter-trait), variance components and progeny trial means for *E. nitens* growth, wood property, tree architecture and fitness traits were collated from the published and unpublished literature. Where analogous characteristics were deemed to have been assessed across studies, common trait names and indicative units of measurement were allocated and correlation estimates were inverted (i.e. positive correlations were made negative and *vice versa*) as necessary. Where repeated estimates from the same trial were available for a parameter, only one was retained (generally from the most recent assessment). Where possible, variance component and heritability estimates were standardised assuming a coefficient of relationship within open-pollinated families of 0.4 to account for an assumed selfing rate of 30% (Falconer & Mackay 1996; Griffin & Cotterill 1988). In cases where this was not possible, data were excluded from analyses. The additive genetic coefficient of variation expressed as a percentage (i.e. the square root of the additive genetic variance divided by the mean multiplied by 100; Houle 1992) was calculated for each trait and trial where the requisite information was available. The genetic groups fitted in the analyses undertaken to calculate genetic parameters varied within the reviewed literature but were generally those defined by Pederick (1979) or Dutkowski *et al.* (2001).

For each trait, or combination of traits, arithmetic mean (i.e. average) heritabilities, additive genetic coefficients of variation and genetic correlations were calculated.

Parameter means weighted by the square-root of the number of families used to calculate independent estimates were also calculated but not presented, as they were based on a smaller number of independent estimates and, in any case, not appreciably different to arithmetic means. For diameter, separate arithmetic means were calculated for data sourced from open-pollinated (OP), full-sib control-pollinated (CP) and pollen-mix CP progeny trials. Age of assessment was not taken into consideration in the estimation of inter-site and inter-trait correlations (i.e. inter-age correlations were assumed to equal one). Where the effect of site was confounded with the effect of trait, genetic correlations were excluded from analyses. Combined-site estimates were also excluded where individual-site estimates of a parameter were available.

RESULTS

Heritabilities and additive genetic coefficients of variation

Independent estimates of heritability were highly variable in most traits (e.g. $h_{op}^2=0.00$ to 0.78 for diameter and $h_{op}^2=0.00$ to 1.00 for pilodyn penetration; Table 1). A relatively large number of independent estimates of heritabilities and additive genetic coefficients of variation were available for growth traits, basic density and pilodyn penetration, reflecting the ease of measurement and economic importance of these traits (Tables 1 and 2).

The average heritability for diameter was similar for OP ($\bar{h}_{op}^2=0.26$) and full-sib CP progeny trials ($\bar{h}_{cp}^2=0.24$) but higher for pollen-mix CP trials ($\bar{h}_{pm}^2=0.39$; Table1). The mean heritability for diameter from OP trials was lower than those for other measures of growth (e.g. $\bar{h}_{op}^2=0.40$ for basal area and 0.39 for volume). However, average heritabilities for diameter when calculated from subsets of trials in common with those used to calculate mean heritabilities for other growth traits were also relatively high (e.g. $\bar{h}_{op}^2=0.40$ for diameter from 12 trials in common with those used to calculate the

mean heritability for basal area). Average additive genetic coefficients of variation for diameter were similar for OP ($CV_a=13.3\%$) and pollen-mix CP trials ($CV_a=12.8\%$) but lower for full-sib CP trials ($CV_a=8.6\%$; Table 2).

Average heritabilities for wood property traits (e.g. $\bar{h}_{op}^2=0.51$ for basic density) were generally higher than those for growth traits (e.g. $\bar{h}_{op}^2=0.26$ for diameter; Table 1).

However, the opposite was true for additive genetic coefficients of variation (e.g. $CV_a=13.3\%$ for diameter and 4.5% for basic density; Table 2). Average heritabilities for tree architecture traits were low to moderate (e.g. $\bar{h}_{op}^2=0.04$ for forks to 0.28 for stem straightness) and those for fitness traits varied widely (e.g. $\bar{h}_{op}^2=0.00$ for *Mycosphaerella* damage on adult foliage to 1.05 for a measure of frost resistance). Mean additive genetic coefficients of variation for tree architecture and fitness traits were generally based on a small number of independent estimates and were highly variable.

Genetic correlations

Independent estimates of inter-age genetic correlation for diameter ranged from 0.68 to 1.00 from ten single-site estimates with an initial assessment age of three to six years (Dutkowski 2004; Kube *et al.* 2001; Raymond 1995; Woolaston *et al.* 1991; see also Greaves *et al.* (1997b) and Volker (2002) for combined-site estimates). However, only three of these independent estimates ($r_g=0.79, 0.98$ and 1.00 ; Kube *et al.* 2001) were between ages approximating selection age (six years) and harvest age (12 years).

Independent estimates of inter-age genetic correlation for height were generally lower than those for diameter, ranging from 0.48 to 0.80 from four estimates with an initial assessment age of two to four years (Dutkowski 2004). Only one estimate of inter-age genetic correlation for frost damage in plantations was present in the literature ($r_g=0.69$ between age one and four years; Tibbits & Hodge 2003) and no estimates for important wood property traits, such as basic density, pulp yield and cellulose content, were reported.

Mean inter-site genetic correlations were positive and strong for most traits. However, independent estimates of inter-site correlations were highly variable for diameter (Figure 1) and notably weak for extractives content ($r_g=0.16$ to 0.55) and fibre coarseness ($r_g=-0.22$ to 0.00 ; Table 3).

Genetic correlations among growth traits were generally strong (e.g. $\bar{r}_g=0.99$ between basal area and volume from three independent OP trial estimates; Tibbits & Hodge 1998). However, the mean genetic correlation between height and diameter was only 0.58 from 15 estimates (Alvear & Prado 1993; Dutkowski 2004; Greaves *et al.* 1997b; Ipinza *et al.* 1998; Johnson 1996; Whiteman *et al.* 1992).

The mean genetic correlation between basic density and pilodyn penetration was -0.90 from four OP trial estimates (Dutkowski 2004; Gea *et al.* 1997a; Kube & Raymond 2002c; Tibbits & Hodge 1998). A small number of independent estimates of genetic correlation between different measures of branching (e.g. between branch angle and branch size; $r_g=-0.20$ and 0.85), stem bification (e.g. between ramicorns and forks; $r_g=1.00$) and frost damage (e.g. between frost damage in plantations and leaf sample artificial freeze test results (T50); $r_g=0.37$) were also present in the literature (Johnson 1996; Tibbits & Hodge 2003; Whiteman *et al.* 1992).

Independent estimates of genetic correlation between fitness and growth traits were generally strong. For example, the mean genetic correlation between frost damage in plantations and basal area was -0.75 from two independent estimates (Tibbits & Hodge 2003) and the one available estimate of the genetic correlation between *Chrysophtharta bimaculata* (Chrysomelid leaf beetle) damage and diameter was -0.93 (Raymond 1995). However, the only available estimate of the genetic correlation between leaf sample artificial freeze tests results (T50) and growth (basal area) was just -0.04 (Tibbits & Hodge 2003).

The average genetic correlation between diameter and basic density was -0.27 and that between diameter and pilodyn penetration was 0.49 (Table 4). The mean genetic

correlation between diameter and cellulose content was 0.56, comparable with the one available estimate of that between basal area and pulp yield ($r_g=0.63$). The only available estimate of the genetic correlation between basic density and pulp yield was 0.42. However, cellulose content is considered a reliable predictor of pulp yield (Kube *et al.* 2001; Raymond & Schimleck 2002) and corresponding independent estimates of the genetic correlation between basic density and cellulose content were highly variable with a mean of -0.07. Only a small number of independent estimates of genetic correlation between fibre dimension traits (e.g. between fibre coarseness and fibre length $\bar{r}_g = -0.11$ from two estimates; Kube *et al.* 2001) and other pulpwood traits were present in the literature.

Independent estimates of genetic correlations among solidwood traits (Raymond 2000) were uncommon in the literature (Table 4). However, the average genetic correlation between diameter and form (straightness) was 0.53 and that between gross shrinkage (core volume) and basic density was -0.57. The direction of the genetic correlation between branch size and diameter was not clear, as independent estimates ranged from -0.51 to 0.26. Other independent estimates of genetic correlations among solidwood traits included those between decay and basic density ($r_g=-0.30$), branch size and forks ($r_g=0.11$), branch size and form ($r_g=-0.17$ and 0.70) and form and forks ($r_g=0.24$; Johnson 1996; Kube & Raymond 2001; Whiteman *et al.* 1992).

DISCUSSION

Heritabilities and additive genetic coefficients of variation

The average heritability for diameter was probably the most precise estimate of this parameter for growth in OP trials, because it was derived from a large number of independent estimates and there was evidence that sites used to estimate average heritabilities for other growth traits were not representative of this larger sample. Potts *et al.* (2004) reported a similar average heritability for diameter in *E. globulus* ($\bar{h}_{op}^2=0.28$ for diameter from 22 OP trials), a closely related species (Brooker 2000).

Average heritabilities for wood property traits were generally higher than that for diameter, indicating that wood properties are under stronger additive genetic control than growth. However, average additive genetic coefficients of variation for wood properties were relatively small suggesting that response to selection in these traits may be limited, due to relatively low additive genetic variation, despite their high heritabilities (Houle 1992).

Differences among cross types (i.e. OP, full-sib CP and pollen-mix CP) in the average heritability and additive genetic coefficient of variation for diameter were almost certainly partly caused by differences in the populations and environments represented in each trial type. However, it is also possible that the assumptions of 30% selfing and no inbreeding depression in the analyses of *E. nitens* OP progeny trial data were not valid and contributed to these differences. For example, Hardner & Tibbits (1998) found that diameter exhibited significant inbreeding depression. In contrast, Volker (2002) found little or no direct evidence of inbreeding depression but did identify disparities between OP and CP genetic parameter estimates. However, both of these studies were based on relatively small sample sizes and further research into the extent and effect of inbreeding is required before the costs and benefits of OP versus CP trials can be meaningfully compared.

The generally low heritabilities observed in tree architecture traits were probably partly due to high levels of measurement error in the subjective methods used to assess them. However, the moderate additive genetic coefficients of variation in these traits indicated that selection within populations could nonetheless result in appreciable genetic gains. High independent estimates of heritability for some fitness traits provided evidence that breeding could also be utilised to improve the fitness of *E. nitens* in specific environments (e.g. sites prone to disease, frost or insect attack).

Genetic correlations

It was not possible to predict the optimal selection age for any trait, given the limited number of independent estimates of genetic correlations between early-age and harvest-age assessments. However, independent estimates of inter-age genetic correlations for diameter were generally strong suggesting that selection for this trait could be undertaken across a wide range of ages with little reduction in genetic gain. Interestingly, independent estimates of inter-age genetic correlations for height were in most cases weaker than those for diameter, possibly due to the generally younger age of initial assessment (two to four years) and correspondingly greater influence of establishment effects on height measurements.

Although strong average inter-site genetic correlations were observed for most traits, some weak independent estimates for growth traits, extractives content and fibre coarseness were identified suggesting that genotype-by-environment interaction in these traits may be of consequence between some sites (Burdon 1977). Regionalisation of large plantation estates might be necessary for breeding and deployment purposes if rapid improvement of these traits is to be achieved across all site types (Namkoong *et al.* 1988).

The generally strong genetic correlations observed among growth traits other than height indicated that selection for any one of these traits would result in a highly correlated response to selection in the others. Similarly, the strongly negative average correlation between basic density and pilodyn penetration suggested that pilodyn penetration is a good predictor of basic density.

Although inter-trait genetic correlations between fitness and growth traits were generally strong, only correlations from sites at which genetic variation in fitness traits were strongly expressed were reported in the literature. It is likely that some of the weak independent estimates of inter-site genetic correlation for diameter (Figure 1) were due to

differences in exposure to stressors, such as frost or insect attack, between sites and corresponding differences in the effect of resistance genes on growth.

There was strong evidence of an adverse (i.e. negative) genetic correlation between growth and basic density, based on the average genetic correlations of diameter with basic density and pilodyn penetration. In contrast, all independent estimates of genetic correlation between basic density and cellulose content were favourable (i.e. positive). However, the strength and direction of the genetic correlation between pulp yield (or cellulose content) with growth was not clear given the low number and highly variable nature of independent estimates. More robust estimates of correlations among these key pulpwood traits (Borrallho *et al.* 1993; Greaves *et al.* 1997a) are required if the economic worth of genetic gains made through index selection are to be maximised in pulpwood breeding programmes (Ponzoni & Newman 1989; Schneeberger *et al.* 1992). Fortunately, more estimates of these genetic correlations are likely to be published in coming years as indirect measures of pulp yield and cellulose, such as near infrared reflectance spectroscopy (Schimleck *et al.* 2000), are more broadly utilised by breeders.

Although based on a small number of independent estimates, some trends in average genetic correlations among solidwood traits were evident. Average genetic correlations between diameter and form (straightness) and between gross shrinkage and basic density were favourable. However the direction of the genetic correlation between other potentially important solidwood traits, such as that between branch size and diameter, were not clear despite the presence of multiple independent estimates in the literature. Historically, assessment of solidwood selection traits has not been routinely undertaken in many breeding programmes due to a focus on pulpwood traits. However, substantial areas of *E. nitens* are now being managed for the production of veneer and/or sawn timber (Kube & Raymond 2005). Estimates of genetic parameters for solidwood traits are likely to become more prevalent in the literature assuming resources devoted to solidwood breeding increase in line with the expansion of solidwood plantations.

CONCLUSION

Despite the low number of independent estimates available for many genetic parameters, the average values presented in this study are likely to represent more reliable and generally applicable parameter estimates than those derived from individual analyses. Average genetic parameters for some traits, such as diameter and wood basic density in OP trials, were derived from a relatively large number of independent estimates and are likely to be particularly robust. This study also revealed inconsistencies among independent estimates of genetic correlations between key pulpwood selection traits and highlighted a lack of information relating to genetic correlations among solidwood traits. The average genetic parameters presented should be combined with relevant unpublished independent estimates and up-dated as additional advanced-generation data becomes available.

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Table 1. The mean, minimum (Min) and maximum (Max) of independent estimates of heritability for growth, wood property, tree architecture and fitness traits. Data are from open-pollinated progeny trials unless otherwise stated.

	Indicative unit	Number of estimates [†]	Mean	Min	Max
Growth traits					
Basal area	cm ²	13 ^{bnqyz}	0.40	0.10	0.86
Basal area (under bark)	cm ²	3 ^y	0.75	0.43	1.38
Diameter - OP trials	cm	79 ^{abcdefghijklmnopqrstuvwxyzδε}	0.26	0.00	0.78
- Full-sib CP trials	cm	23 ^{demnα}	0.24	0.02	0.55
- Pollen-mix CP trials	cm	14 ^e	0.39	0.00	0.98
Diameter increment (age 6 to 12)	cm	3 ^w	0.45	0.35	0.53
Height	m	19 ^{adeipqyzδ}	0.23	0.06	0.72
Productivity (survival x BA91)	cm ²	2 ^z	0.33	0.21	0.44
Volume	m ³	13 ^{ainoy}	0.39	0.01	1.30
Mean*			0.30		
Wood property traits					
Bark thickness relative to diameter	mm cm ⁻¹	1 ⁿ	0.78		
Cellulose content	%	5 ^{lruvw}	0.67	0.37	1.05
Decay (cross-sectional area after artificial wounding)	cm ²	1 ^β	0.13		
Decay (in second core)	%	1 ^u	0.38		
Decay (incidence of heart-rot decay)	Present	2 ^r	0.44	0.24	0.63
Decay (incidence of heart-rot discolouration)	Present	2 ^r	0.13	0.04	0.21
Decay (incidence of wounding decay)	Present	1 ^r	0.60		
Decay (incidence of wounding discolouration)	Present	1 ^r	0.20		
Decay (longitudinal extension after artificial wounding)	m	1 ^β	0.17		
Density (basic)	kg m ⁻³	16 ^{bcefkrlruvwy}	0.51	0.11	0.96
Density (basic) differential	kg m ⁻³	1 ^u	0.32		
Extractives (Methanol soluble)	%	4 ^{ru}	0.73	0.22	1.29
Fibre Coarseness	mg m ⁻¹	2 ^w	0.49	0.39	0.58
Fibre length	mm	3 ^{cw}	0.58	0.25	0.80
Gross shrinkage (core, Kube method)	%	5 ^{kuv}	0.39	0.23	0.61
Gross shrinkage (core, average diameter)	mm	2 ^k	0.20	0.11	0.28
Gross shrinkage (core, volume)	%	2 ^k	0.42	0.37	0.47
Lignin content	%	2 ^l	0.39	0.30	0.48
Microfibril angle	°	1 ^u	0.53		
Pilodyn penetration	mm	13 ^{efgijmnrtyα}	0.35	0.00	1.00
Pulp yield	%	8 ^{bhy}	0.50	0.03	0.79
Shrinkage (core, score)	Score	2 ^k	0.08	0.02	0.14
Mean*			0.45		

Table 1 (cont.). The mean, minimum (Min) and maximum (Max) of independent estimates of heritability for growth, wood property, tree architecture and fitness traits. Data are from open-pollinated progeny trials unless otherwise stated.

	Indicative unit	Number of estimates [†]	Mean	Min	Max
Tree architecture traits					
Branch angle (flat = high score)	Score	2 ^{qχδ}	0.22	0.11	0.32
Branch retention (branches on lower 1.5 m)	Count	1 ^{χδ}	0.21		
Branch retention (dead branches on lower 1.5 m)	Count	1 ^q	0.14		
Branch size	Score	6 ^{qrtuχδ}	0.12	0.04	0.25
Branching habit	Score	2 ^{fg}	0.20	0.20	0.20
Forks	Count	1 ^q	0.04		
Form (malformation)	Score	2 ^g	0.05	0.05	0.05
Form (straightness)	Score	5 ^{fgqyχδ}	0.28	0.20	0.44
Ramicorns	Count	1 ^q	0.05		
Mean*			0.17		
Fitness traits					
Diameter increment (<i>C. bimaclata</i>) [§]	cm	1 ^x	0.59		
Frost (relative conductivity -5.5°C)	RC	1 ^α	0.34		
Frost (relative conductivity -7.0°C)	RC	1 ^α	1.02		
Frost (relative conductivity -8.5°C)	RC	1 ^α	1.05		
Frost (T50)	°C	2 ^z	0.68	0.37	0.99
Frost damage (plantations)	%	4 ^{enz}	0.19	0.00	0.44
Insect damage	%	1 ^e	0.45		
Insect damage (<i>C. bimaclata</i>)	Score	1 ^x	0.48		
<i>Mycosphaerella</i> damage - Adult	%	1 ^d	0.00		
<i>Mycosphaerella</i> damage - Juvenile	%	1 ^d	0.21		
Survival	%	2 ^z	0.21	0.01	0.41
Mean*			0.42		

* Mean weighted by the number of estimates for each trait. Note that multiple estimates (i.e. those for different traits) from some sites were utilised.

§ Trial assessed prior to and following defoliation damage by *Chrysophtharta bimaclata* (Chrysomelid leaf beetle)

† Estimates were sourced from ^{a)}Alvear & Prado (1993), ^{b)}de Little *et al.* (1992), ^{c)}Dean *et al.* (1990), ^{d)}Dungey *et al.* (1997), ^{e)}Dutkowski (2004), ^{f)}Gea *et al.* (1997a), ^{g)}Gea *et al.* (1997b), ^{h)}Greaves (1997), ⁱ⁾Greaves *et al.* (1997b), ^{j)}Greaves *et al.* (1996), ^{k)}Hamilton *et al.* (2004a), ^{l)}Hamilton *et al.* (2004b), ^{m)}Hardner & Tibbits (1996), ⁿ⁾Hardner & Tibbits (1998), ^{o)}Hodge *et al.* (1996), ^{p)}Ipinza *et al.* (1998), ^{q)}Johnson (1996), ^{r)}Kube (2005), ^{s)}Kube *et al.* (1995), ^{t)}Kube & Dutkowski (2002), ^{u)}Kube & Raymond (2001), ^{v)}Kube & Raymond (2005), ^{w)}Kube *et al.* (2001), ^{x)}Raymond (1995), ^{y)}Tibbits & Hodge (1998), ^{z)}Tibbits & Hodge (2003), ^{a)}Volker (2002), ^{β)}White *et al.* (1999), ^{z)}Whiteman *et al.* (1988), ^{δ)}Whiteman *et al.* (1992) and ^{ε)}Woolaston *et al.* (1991).

Table 2. The mean, minimum (Min) and maximum (Max) of independent estimates of the additive genetic coefficient of variation (expressed as a percentage) for growth, wood property, tree architecture and fitness traits. Data are from open-pollinated progeny trials unless otherwise stated. Indicative units for traits are outlined in Table 1.

	Number of estimates [†]	Mean	Min	Max
Growth traits				
Diameter - OP trials	59 ^{a b d e g h}	13.3	0.0	30.4
- Full-sib CP trials	22 ^{a h}	8.6	1.8	23.9
- Pollen-mix CP trials	14 ^a	12.8	0.0	33.1
Diameter increment	3 ^g	22.6	19.8	26.3
Height	10 ^a	11.3	6.1	18.8
Mean*		12.4		
Wood property traits				
Cellulose content	3 ^g	2.5	2.0	2.9
Density (basic)	7 ^{a g}	4.5	1.5	6.4
Fibre Coarseness	2 ^g	6.5	6.0	6.9
Fibre length	3 ^g	4.8	3.8	5.3
Pilodyn	11 ^{a c e h}	5.1	0.0	10.1
Mean*		4.7		
Tree architecture traits				
Branch size	2 ^e	5.0	4.7	5.3
Branching habits	2 ^b	12.5	12.5	12.6
Form (malformation)	2 ^b	6.5	4.3	8.7
Form (straightness)	2 ^b	14.1	13.5	14.7
Mean*		9.5		
Fitness traits				
Frost (relative conductivity -5.5°C)	1 ^h	1.3		
Frost (relative conductivity -7.0°C)	1 ^h	3.0		
Frost (relative conductivity -8.5°C)	1 ^h	8.8		
Frost damage (plantations)	3 ^a	13.8	0.0	26.0
Insect damage	1 ^a	35.4		
Mean*		12.8		

* Mean weighted by the number of estimates for each trait. Note that multiple estimates (i.e. those for different traits) from some sites were utilised.

[†] Estimates were sourced from ^aDutkowski (2004), ^bGea *et al.* (1997b), ^cKube (2005), ^dKube *et al.* (1995), ^eKube & Dutkowski (2002), ^gKube *et al.* (2001) and ^hVolker (2002).

Table 3. The mean, minimum (Min) and maximum (Max) of independent estimates of inter-site genetic correlations for growth, wood property, tree architecture and fitness traits from open-pollinated progeny trials. Indicative units for traits are outlined in Table 1.

	Number of estimates [†]	Mean	Min	Max
Growth traits				
Diameter	106 ^{a c d e f g i j k}	0.70	-0.15	1.14
Diameter increment (age 6 to 12)	3 ^j	1.07	0.98	1.13
Height	6 ^c	0.94	0.16	1.18
Mean*		0.73		
Wood property traits				
Cellulose content	4 ^{b f i j}	0.85	0.77	0.91
Density (basic)	5 ^{a b f i j}	0.77	0.67	0.92
Extractives (methanol soluble)	3 ^f	0.41	0.16	0.55
Fibre coarseness	3 ^j	-0.07	-0.22	0.00
Fibre length	3 ^j	1.26	1.19	1.36
Gross shrinkage (core, Kube method)	4 ^{a i}	0.89	0.56	1.01
Gross shrinkage (core, volume)	1 ^a	0.86		
Lignin content	1 ^b	0.85		
Pilodyn	4 ^{f g}	0.91	0.79	0.99
Mean*		0.75		
Tree architecture traits				
Branch size	2 ^{f g}	0.72	0.63	0.80
Form (straightness)	3 ^d	0.78	0.62	0.93
Mean*		0.75		

* Mean weighted by the number of estimates for each trait. Note that multiple estimates (i.e. those for different traits) from some sites were utilised.

[†] Estimates were sourced from ^a)Hamilton *et al.* (2004a), ^b)Hamilton *et al.* (2004b), ^c)Ipinza *et al.* (1998), ^d)King & Wilcox (1988), ^e)Kube *et al.* 1995, ^f)Kube (2005), ^g)Kube & Dutkowski (2002), ^h)Kube & Raymond (2002), ⁱ)Kube & Raymond (2005), ^j)Kube *et al.* (2001) and ^k)Woolaston *et al.* (1991).

Table 4. The mean, minimum (Min) and maximum (Max) of independent estimates of inter-trait correlations of pulpwood and solidwood traits with cellulose content, basic density and diameter. Data are from open-pollinated progeny trials. Indicative units for traits are outlined in Table 1.

	Cellulose content			Density (basic)			Diameter					
	Number of estimates †	Mean	Min	Max	Number of estimates †	Mean	Min	Max	Number of estimates †	Mean	Min	Max
Pulpwood traits												
Density (basic)	5 ^{eijkl}	-0.07	-0.53	0.37								
Diameter	5 ^{eijkl}	0.56	0.25	0.86	10 ^{abdegijkl}	-0.27	-0.79	0.08				
Extractives (methanol soluble)	1 ^{ij}	-1.00 [§]			1 ^{ij}	1.00 [§]			1 ^{ij}	-0.70 [§]		
Fibre Coarseness	2 ^l	0.02	-0.19	0.22	2 ^l	0.22	0.11	0.33	3 ^l	-0.11	-0.45	0.12
Fibre length	3 ^l	0.38	-0.13	0.86	3 ^l	0.19	-0.17	0.75	3 ^l	0.38	0.27	0.51
Pilodyn					4 ^{abgm}	-0.90	-1.11	-0.71	6 ^{abcmgh}	0.49	0.20	0.82
Pulp yield					1 ^{jm}	0.42			1 ^m	0.63 [*]		
Solidwood traits												
Branch size (thin = high score)	1 ⁱ	0.46 [§]			1 ⁱ	0.37 [§]			4 ^{fhin}	-0.09	-0.51	0.26
Decay (in second core)	1 ⁱ	0.39 [§]			1 ⁱ	-0.30 [§]			1 ⁱ	-0.03 [§]		
Forks									1 ^f	-0.01		
Form (straight = high score)					1 ^b	0.10 [§]			2 ^{bfn}	0.53	0.50	0.55
Gross shrinkage (core, Kube method)	1 ^{ik}	0.56 [§]			1 ^{ik}	-0.79 [§]			1 ^{ik}	0.78 [§]		
Gross shrinkage (core, volume)					2 ^d	-0.57	-0.71	-0.42	2 ^d	0.06	-0.13	0.25
Microfibril angle	1 ⁱ	0.34 [§]			1 ⁱ	-0.63 [§]			1 ⁱ	0.56 [§]		

* Correlation between basal area and pulp yield.

§ Estimate from an across-site analysis.

† Estimates were sourced from ^{a)}Dutkowski (2004), ^{b)}Gea *et al.* (1997a), ^{c)}Greaves *et al.* (1997b), ^{d)}Hamilton *et al.* (2004a), ^{e)}Hamilton *et al.* (2004b), ^{f)}Johnson (1996), ^{g)}Kube (2005), ^{h)}Kube & Dutkowski (2002), ⁱ⁾Kube & Raymond (2001), ^{j)}Kube & Raymond (2002), ^{k)}Kube & Raymond (2005), ^{l)}Kube *et al.* (2001), ^{m)}Tibbits & Hodge (1998) and ⁿ⁾Whiteman *et al.* (1992).

Figure 1. Histogram of independent estimates of inter-site genetic correlation for diameter from open-pollinated trials.

