EUCALYPTUS NITENS GENETIC PARAMETERS*

M. G. HAMILTON† and B. M. POTTS
School of Plant Science and Cooperative Research Centre for Forestry,
University of Tasmania, Private Bag 55, Hobart, Tasmania, 7001, Australia.

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ABSTRACT

Eucalyptus nitens (Deane et Maiden) Maiden 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. Parameter estimates from control-pollinated progeny trials were 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 mating type our average parameter estimates are likely to be robust. In open-pollinated trials, average heritabilities for growth traits (e.g., $\overline{h}^2_{op}$= 0.26 for diameter) were generally lower than those for wood property traits (e.g., $\overline{h}^2_{op}$ = 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., cellulose content and pulp yield). For most traits, inter-site genetic correlations were, on average, positive and strong (e.g., $\overline{r}_g$ =0.70 for diameter) but some weak individual estimates were observed. 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. Estimates of genetic parameters for solidwood traits were also uncommon in the literature.

Keywords: growth; wood property; tree architecture; fitness; standard genetic parameter; heritability; additive genetic coefficient of variation; genetic correlation; *Eucalyptus nitens*.

INTRODUCTION

The area planted in *Eucalyptus nitens* has expanded considerably over the past decade, particularly in Australia (total plantation area was c. 143 000 ha in 2005;

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† Corresponding author: Matthew.Hamilton@utas.edu.au

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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 have been reported in the literature for a wide range of traits.

Estimates of genetic parameters are properties not only of biological traits but also 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 to examine patterns of genetic (co)variation within and between trait categories (Falconer & Mackay 1996), simulate breeding strategies (e.g., Borralho & Dutkowski 1998; Pilbeam & Dutkowski 2004), develop optimal selection indices (Cotterill & Dean 1990; Ponzoni & Newman 1989; Schneeberger *et al*. 1992), and predict breeding values and response to selection. 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 published and unpublished reports. 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 as necessary (e.g., some intertrait correlations with branch size were inverted because trees with large branches were assigned a high score in one study and a low score in others). Where repeated estimates of a parameter from the same trial were available, 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). 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 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 were also calculated but not presented, as they were based on a smaller number of estimates and 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. Furthermore, where individual-site estimates of a parameter were available, pooled multiple-site estimates were excluded.

RESULTS

Heritabilities and Additive Genetic Coefficients of Variation

Estimates of heritability were highly variable in most traits (e.g., $h^2_{op} = 0.00$ to 0.78 for diameter and $h^2_{op} = 0.00$ to 1.00 for pilodyn penetration; Table 1). A relatively large number of estimates of heritabilities and additive genetic coefficients of variation were available for growth traits, basic density, and pilodyn penetration (a trait commonly assessed as an indirect measure of wood density), reflecting the relative ease of measurement and economic importance of these traits (Tables 1 and 2).

The average heritability for diameter was similar for OP ($\bar{h}^2_{op} = 0.26$) and full-sib CP progeny trials ($\bar{h}^2_{cp} = 0.24$) but higher for pollen-mix CP trials ($\bar{h}^2_{pm} = 0.39$; Table1). The mean heritability for diameter from OP trials was lower than those for other measures of growth (e.g., $\bar{h}^2_{op} = 0.40$ for basal area and 0.39 for volume). However, when average heritabilities for diameter were calculated from the same OP trials used to calculate mean heritabilities for other growth traits they were also relatively high (e.g., $\bar{h}^2_{op} = 0.40$ for diameter from 12 of the 13 trials used to calculate the mean heritability for basal area). This result suggests that these differences between trait averages were principally due to trial differences as opposed to differences in growth trait heritabilities *per se.* 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).

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

	Indicative unit	No.of estimates	Mean	Min	Max	Relevant references (numbers refer to Reference list)
Growth traits						
Basal area	cm^2	13	0.40	0.10	0.86	6, 23, 28, 48, 49
Basal area (under bark)	cm^2	3	0.75	0.43	1.38	48
Diameter – OP trials	cm	79	0.26	0.00	0.78	1, 6, 8, 9, 13, 14, 18, 21, 22, 23, 27, 28, 31, 32, 33, 35, 36, 37, 43, 50, 51, 52, 53, 54
Diameter – Full-sib CP trials	cm	23	0.24	0.02	0.55	8, 9, 22, 23, 50
Diameter - Pollen-mix CP trials	cm	14	0.39	0.00	0.98	9
Diameter increment (ages 6 to 12)	cm	3	0.45	0.35	0.53	37
Height	m	19	0.23	0.06	0.72	1, 8, 9, 18, 27, 28, 48, 52, 53
Productivity (survival × BA91)	cm^2	2	0.33	0.21	0.44	49
Volume	m^3	13	0.39	0.01	1.30	1, 18, 23, 24, 48
Mean*				**0.30**		
Wood property traits						
Bark thickness relative to diameter	mm/cm	1	0.78			23
Cellulose content	%	5	0.67	0.37	1.05	20, 31, 33, 35, 37
Decay (cross-sectional area after artificial wounding)	cm^2	1	0.13			51
Decay (in second core)	%	1	0.38			33
Decay (incidence of heart-rot decay)	Present	2	0.44	0.24	0.63	31
Decay (incidence of heart-rot discolouration)	Present	2	0.13	0.04	0.21	31
Decay (incidence of wounding decay)	Present	1	0.60			31
Decay (incidence of wounding discolouration)	Present	1	0.20			31
Decay (longitudinal extension after artificial wounding)	m	1	0.17			51
Density (basic)	kg/m^3	16	0.51	0.11	0.96	6, 7, 9, 13, 20, 21, 31, 33, 35, 37, 48
Density (basic) differential	kg/m^3	1	0.32			33
Extractives (methanol soluble)	%	4	0.73	0.22	1.29	31, 33

continued over leaf

TABLE 1–*cont.*

	Indicative unit	No.of estimates	Mean	Min	Max	Relevant references (numbers refer to Reference list)
Fibre coarseness	mg/m	2	0.49	0.39	0.58	37
Fibre length	mm	3	0.58	0.25	0.80	7, 37
Gross shrinkage (core, Kube method)	%	5	0.39	0.23	0.61	21, 33, 35
Gross shrinkage (core, average diameter)	mm	2	0.20	0.11	0.28	21
Gross shrinkage (core, volume)	%	2	0.42	0.37	0.47	21
Lignin content	%	2	0.39	0.30	0.48	20
Microfibril angle	°	1	0.53			33
Pilodyn penetration	mm	13	0.35	0.00	1.00	9, 13, 14, 18, 17, 22, 23, 31, 32, 48, 50
Pulp yield	%	8	0.50	0.03	0.79	6, 15, 48
Shrinkage (core, score)	Score	2	0.08	0.02	0.14	21
Mean*			**0.45**			
Tree architecture traits						
Branch angle (flat = high score)	Score	2	0.22	0.11	0.32	28, 52, 53
Branch retention (branches on lower 1.5 m)	Count	1	0.21			52, 53
Branch retention (dead branches on lower 1.5 m)	Count	1	0.14			28
Branch size	Score	6	0.12	0.04	0.25	28, 31, 32, 33, 52, 53
Branching habit (“good = high score)	Score	2	0.20	0.20	0.20	13, 14
Forks	Count	1	0.04			28
Form (malformation)	Score	2	0.05	0.05	0.05	14
Form (straightness)	Score	5	0.28	0.20	0.44	13, 14, 28, 48, 52, 53
Ramicorns	Count	1	0.05			28
Mean*			**0.17**			
Fitness traits						
Diameter increment† (*C. bimaculata*)	cm	1	0.59			43
Frost (relative conductivity –5.5°C)	RC	1	0.34			50
Frost (relative conductivity –7.0°C)	RC	1	1.02			50
Frost (relative conductivity –8.5°C)	RC	1	1.05			50
Frost (T50)	°C	2	0.68	0.37	0.99	49
Frost damage (plantations)	%	4	0.19	0.00	0.44	9, 23, 49

continued over leaf

TABLE 1–*cont.*

	Indicative unit	No.of estimates	Mean	Min	Max	Relevant references (numbers refer to Reference list)
Insect damage	%	1	0.45			9
Insect damage (*C. bimaculata*)	Score	1	0.48			43
Mycosphaerella damage – Adult	%	1	0.00			8
Mycosphaerella damage – Juvenile	%	1	0.21			8
Survival	%	2	0.21	0.01	0.41	49
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 after defoliation damage by *Chrysophtharta bimaculata* (Chrysomelid leaf beetle)

‡ No explanation of the difference between malformation and straightness was provided by 14 (Gea, McConnochie, Hong & Shelbourne 1997).

Average heritabilities for wood property traits (e.g., $\overline{h}^2_{op} = 0.51$ for basic density) were generally higher than those for growth traits (e.g., $\overline{h}^2_{op} = 0.26$ 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., $\overline{h}^2_{op} =$ 0.04 for forks to 0.28 for stem straightness) and those for fitness traits varied widely (e.g., $\overline{h}^2_{op} = 0.00$ 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 highly variable and generally based on a small number of estimates.

Genetic Correlations

Estimates of inter-age genetic correlations for diameter ranged from 0.68 to 1.00 from 10 single-site estimates with an initial assessment age of 3 to 6 years (G.W.Dutkowski unpubl. data; Kube *et al.* 2001; Raymond 1995; Woolaston *et al.* 1991; *see also* Greaves, Borralho, Raymond, Evans & Whiteman (1997) and Volker (2002) for pooled multiple-site estimates). However, only three of these estimates ($r_g = 0.79$, 0.98, and 1.00; Kube *et al.* 2001) were between ages approximating selection age (6 years) and harvest age (12 years). 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 2 to 4 years (Dutkowski unpubl. data). For basic density, Greaves, Borralho, Raymond, Evans & Whiteman (1997) estimated inter-growth-ring genetic correlations, as a measure

TABLE 2–The mean, minimum (Min), and maximum (Max) of 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.

	No. of estimates	Mean	Min	Max	Relevant references (numbers refer to Reference list)
Growth traits					
Diameter – OP trials	59	13.3	0.0	30.4	9, 14, 32, 36, 37, 50
Diameter – Full-sib CP trials	22	8.6	1.8	23.9	9, 50
Diameter - Pollen-mix CP trials	14	12.8	0.0	33.1	9
Diameter increment	3	22.6	19.8	26.3	37
Height	10	11.3	6.1	18.8	9
Mean*		**12.4**			
Wood property traits					
Cellulose content	3	2.5	2.0	2.9	37
Density (basic)	7	4.5	1.5	6.4	9, 37
Fibre coarseness	2	6.5	6.0	6.9	37
Fibre length	3	4.8	3.8	5.3	37
Pilodyn	11	5.1	0.0	10.1	9, 31, 32, 50
Mean*		**4.7**			
Tree architecture traits					
Branch size	2	5.0	4.7	5.3	32
Branching habit (“good” = high score)	2	12.5	12.5	12.6	14
Form (malformation) †	2	6.5	4.3	8.7	14
Form (straightness) †	2	14.1	13.5	14.7	14
Mean*		**9.5**			
Fitness traits					
Frost (relative conductivity –5.5°C)	1	1.3			50
Frost (relative conductivity –7.0°C)	1	3.0			50
Frost (relative conductivity –8.5°C)	1	8.8			50
Frost damage (plantations)	3	13.8	0.0	26.0	9
Insect damage	1	35.4			9
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.

† No explanation of the difference between malformation and straightness was provided by Gea, McConnochie. Hong & Shelbourne (1997)

of inter-age genetic correlations. They reported pooled multiple-site estimates of 0.83 or greater among annual growth rings laid down in years 3 to 7. However, estimates for other important wood property traits, such as pulp yield and cellulose content, were not reported in the literature and only one estimate of inter-age genetic correlation for frost damage in plantations was available (r_g=0.69 between age 1 and 4 years; Tibbits & Hodge 2003).

Mean inter-site genetic correlations were generally positive and strong (Table 3). However, individual estimates of inter-site correlations were highly variable for diameter (Fig. 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., =0.99 between basal area and volume from three OP trial estimates; Tibbits & Hodge 1998).

TABLE 3–The mean, minimum (Min), and maximum (Max) of 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.

	No. of estimates	Mean	Min	Max	Relevant references (numbers refer to Reference list)
Growth traits					
Diameter	106	0.70	–0.15	1.14	20, 27, 29, 31, 32, 35, 36, 37, 54
Diameter increment (ages 6 to 12)	3	1.07	0.98	1.13	37
Height	6	0.94	0.16	1.18	27
Mean*		**0.73**			
Wood property traits					
Cellulose content	4	0.85	0.77	0.91	21, 31, 35, 37
Density (basic)	5	0.77	0.67	0.92	20, 21,31, 35, 37
Extractives (methanol soluble)	3	0.41	0.16	0.55	31
Fibre coarseness	3	–0.07	–0.22	0.00	37
Fibre length	3	1.26	1.19	1.36	37
Gross shrinkage (core, Kube method)	4	0.89	0.56	1.01	20, 35
Gross shrinkage (core, volume)	1	0.86			20
Pilodyn	4	0.91	0.79	0.99	31,32
Mean*		**0.74**			
Tree architecture traits					
Branch size	2	0.72	0.63	0.80	31, 32
Form (straightness)	3	0.78	0.62	0.93	29
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.

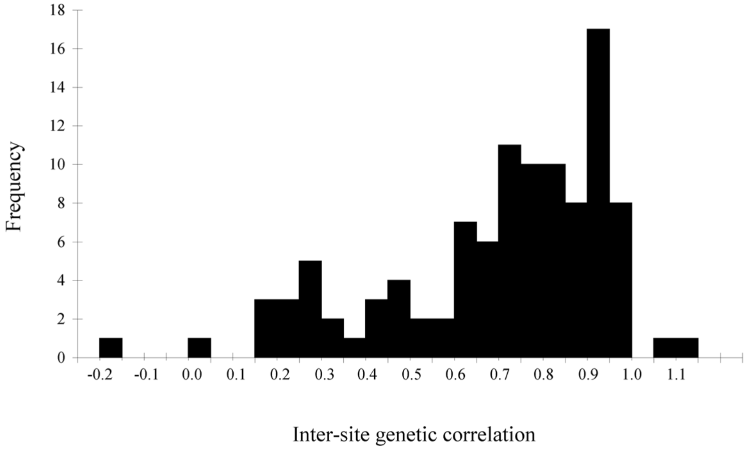

FIG. 1–Estimates of inter-site genetic correlation for diameter from open-pollinated trials.

However, the mean genetic correlation between height and diameter was only 0.58 from 15 estimates (Alvear & Prado 1993; Dutkowski unpubl. data; Greaves, Borralho, Raymond, Evans & Whiteman 1997; Ipinza *et al.* 1998; Johnson 1996; Whiteman *et al.* 1992).

The mean genetic correlation between basic density and pilodyn penetration was –0.90, derived from four OP trial estimates (Table 4). Estimates of inter-trait genetic correlations between different measures of branching (e.g., between branch angle and branch size; r_g = –0.20 and 0.85; Johnson 1996; Whiteman *et al.* 1992), stem bification (e.g., between ramicorns and forks; r_g =1.00; Johnson 1996), and frost damage (e.g., between frost damage in plantations and leaf sample artificial freeze test results [T50]; r_g =0.37; Tibbits & Hodge 2003) were also present in the literature.

Estimates of genetic correlations between fitness and growth traits were generally strong. For example, the two available estimates of the genetic correlation between frost damage in plantations (damaged trees were given a high score) and basal area were –0.58 and –0.91 (Tibbits & Hodge 2003), and the one available estimate of the genetic correlation between *Chrysophtharta bimaculata* (chrysomelid leaf beetle) damage (affected trees were given a high score) 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

TABLE 4–The mean, minimum (Min), and maximum (Max) of 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.

	No. of estimates	Mean	Min	Max	Relevant references (numbers refer to Reference list)
Cellulose content					
Pulpwood traits					
Density (basic)	5	–0.07	–0.53	0.37	20, 33, 34, 35, 37
Diameter	5	0.56	0.25	0.86	20, 33, 34, 35, 37
Extractives (methanol soluble)	1	–1.00†			33, 34
Fibre coarseness	2	0.02	–0.19	0.22	37
Fibre length	3	0.38	–0.13	0.86	37
Solidwood traits					
Branch size (thin = high score)	1	0.46†			33
Decay (in second core)	1	0.39†			33
Gross shrinkage (core, Kube method)	1	0.56†			33, 35
Microfibril angle	1	0.34†			33
Density (basic)					
Pulpwood traits					
Diameter	10	–0.27	–0.79	0.08	9, 13, 20, 21, 31, 33, 34, 35, 37
Extractives (methanol soluble)	1	1.00†			33, 34
Fibre coarseness	2	0.22	0.11	0.33	37
Fibre length	3	0.19	–0.17	0.75	37
Pilodyn	4	–0.90	–1.11	–0.71	9, 13, 31, 48
Pulp yield	1	0.42			34, 48
Solidwood traits					
Branch size (thin = high score)	1	0.37†			33
Decay (in second core)	1	–0.30†			33
Form (straight = high score)	1	0.10†			13
Gross shrinkage (core, Kube method)	1	–0.79†			33, 35
Gross shrinkage (core, volume)	2	–0.57	–0.71	–0.42	21
Microfibril angle	1	–0.63†			33

continued over leaf

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

TABLE 4–*cont.*

	No. of estimates	Mean	Min	Max	Relevant references (numbers refer to Reference list)
Diameter					
Pulpwood traits					
Extractives (methanol soluble)	1	–0.70†			33, 34
Fibre coarseness	3	–0.11	–0.45	0.12	37
Fibre length	3	0.38	0.27	0.51	37
Pilodyn	6	0.49	0.20	0.82	9, 13, 18, 31, 32
Pulp yield	1	0.63*			48
Solidwood traits					
Branch size (thin = high score)	4	–0.09	–0.51	0.26	28, 32, 33, 52
Decay (in second core)	1	–0.03†			33
Forks	1	–0.01			28
Form (straight = high score)	2	0.53	0.50	0.55	9, 28, 52
Gross shrinkage (core, Kube method)	1	0.78†			33, 35
Gross shrinkage (core volume)	2	0.06	–0.13	0.25	21
Microfibril angle	1	0.56†			33

* Correlation between basal area and pulp yield

† Pooled estimate from a multiple-site analysis

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 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 estimates of genetic correlation among fibre dimension traits were present in the literature (e.g., between fibre coarseness and fibre length r_g = –0.68 and 0.47; Kube *et al.* 2001).

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 stem diameter was not clear, as estimates ranged from –0.51 to 0.26. Other estimates of genetic correlations among solidwood traits included those between decay and basic density (r_g = –0.30; Kube & Raymond 2001), branch size and forks (r_g = 0.11; Johnson 1996), branch size and form (r_g = –0.17 and 0.70; Johnson 1996; Whiteman *et al.* 1992), and form and forks (r_g =0.24; Johnson 1996), although some of these traits were not under strong additive genetic control.

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 estimates (Table 1). Potts *et al.* (2004) reported a similar average heritability for diameter in *E. globulus* Labill. ($\bar{h}^2_{op}$ =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 (Table 1), 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 (Table 2) 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 mating types (i.e., OP, full-sib CP, and pollen-mix CP) in the average heritability and additive genetic coefficient of variation for diameter (Tables 1 and 2) were probably due to differences in populations and trial environments. 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 direct evidence of inbreeding depression in OP progeny 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 in *E. nitens* 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 (Table 1) 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 (Table 2) indicated that selection within populations could nonetheless result in appreciable genetic gains. High estimates of heritability for some fitness traits (Table 1) 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 estimates of genetic correlations between early-age and harvest-age assessments. However, 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, 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 (2 to 4 years) and correspondingly greater influence of establishment effects on height measurements.

The generally strong genetic correlations observed among growth traits other than height (Table 4) 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 was strongly expressed were reported in the literature. It is possible that some of the weak estimates of inter-site genetic correlation for diameter (Fig. 1; Table 3) were due to differences in exposure to stressors, such as insect attack or frost, between sites and corresponding differences in the effect of resistance genes on growth (Dutkowski *et al.* 2006; Tibbits & Hodge 2003).

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 (Table 4). In contrast, all 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) and growth were not clear, given the low number and highly variable nature of estimates. More robust estimates of correlations among these key pulpwood traits (Borralho *et al.* 1993; Greaves, Borralho & Raymond 1997) are required if the economic worth of genetic gains made through index selection are to be maximised in pulpwood breeding programmes. Fortunately, more estimates of these genetic correlations are likely to be published in coming years, as indirect measures of pulp yield and cellulose content, such as near infrared reflectance spectroscopy (Schimleck *et al.* 2000), become more broadly utilised by breeders.

Average genetic correlations between diameter and form (straightness) and between gross shrinkage and basic density were favourable (Table 4). However the direction of the genetic correlation between other potentially important solidwood traits, such as that between branch size and diameter, was not clear, despite the presence of multiple 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.

In summary, despite the low number of 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 estimates and are likely to be particularly robust. This study revealed inconsistencies among 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 estimates and up-dated as additional advanced-generation data become available.

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