Genetic variation in growth of *Eucalyptus grandis* grown under irrigation in south-eastern Australia

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Summary

Within- and between-provenance variation in growth, to age 4.5 y, of *Eucalyptus grandis* Hill ex Maiden was investigated in three irrigated provenance-family trials at two localities (Shepparton and Koorlong) in northern Victoria. These trials contained 47 *E. grandis* seedlots representing both natural stand provenances and planted stands including seed orchards and plus-trees selected in plantations.

Height growth was poor to mediocre, with site averages being 1.4–2.4 m y^{-1}. There was significant provenance variation in some growth traits at each site. Material selected in plantations at Loxton, South Australia, and material from a seed orchard at Coffs Harbour, New South Wales, generally showed the best growth across sites.

At all three sites there were significant differences between families for various growth traits. Estimates of individual-tree heritability for growth traits ranged from very low (0.08) to moderate (0.21). With data combined from all sites, both provenance and family-within-provenance differences proved significant for most traits. In contrast, site by provenance and site by family-within-provenance interactions for growth traits were not significant.

The results are discussed in terms of the importance of provenance selection for *E. grandis* and the opportunities for genetic improvement in the species through within-provenance selection.

Keywords: provenance trials; genetic variation; tree breeding; *Eucalyptus grandis*; Victoria

Introduction

Eucalyptus grandis is one of the eucalypts most widely planted around the world. In Australia, strong interest developed in planting this species in the late 1960s and early 1970s, and the Australian Paper Mills Company (APM) began establishing plantations in the Coffs Harbour region of New South Wales (NSW). However, this interest faded and APM's plantations were subsequently sold in the mid-1970s to State Forests of NSW (Matheson *et al.* 1996). More than 10 y later, field trials conducted by the Shell Company of Australia identified *E. grandis* as the best eucalypt available for establishment of fast-growing pulpwood plantations over a wide range of coastal Queensland sites (Cromer *et al.* 1991). Though few plantations of the species were subsequently established, renewed interest in plantations of the species since the late 1990s has resulted in thousands of hectares being established in north-eastern NSW and south-eastern Queensland (Wood *et al.* 2001). In addition, *E. grandis* is one of the key parent species from which hybrid eucalypts are currently being developed for a wide range of site types in Australia (Harwood and Arnold 1999).

Early provenance trials of *E. grandis* in Australia were established in 1972 near Coffs Harbour, NSW, in Wedding Bells State Forest (SF) and in Wild Cattle Creek SF by the then Forestry Commission of NSW to test seed collected from sources across a wide altitudinal and latitudinal range (Burgess 1988). Further provenance trials were established in 1982 at Wedding Bells SF and at Peachester near Nambour in Queensland (Burgess 1988). More recently, several *E. grandis* trials have been established under irrigation in the southern Murray-Darling Basin (MDB), outside the species' natural range. At Loxton, South Australia, Land Energy Pty Ltd established a provenance trial in collaboration with Golden Choice Ltd in 1988 as part of an effluent water re-use plantation (Arnold *et al.* 1996). In 1991, CSIRO initiated an irrigated trial at Dubbo, NSW, to test 40 family seedlots collected from natural stands as part of an inbreeding study (Burgess *et al.* 1996).

These earlier Australian trials, along with numerous others in temperate and subtropical environments overseas, have shown some of the most productive *E. grandis* provenances to be those from the northern coastal part of NSW around Coffs Harbour (Burgess 1988; CABI 2000). However, in any one plantation environment there are typically also other provenances from geographically wide-ranging and disparate parts of the species' natural range that tend to perform well (CABI 2000). In addition, significant and marked differences in growth have often been noted between seedlots of the species obtained within one small geographic area (Matheson and Mullin 1987; Burgess 1988; Eldridge *et al.* 1993; Arnold *et al.* 1996; CABI 2000).

In 1993–1994, three provenance-family trials of *E. grandis* were established across a range of effluent-irrigated sites in south-eastern Australia to evaluate seedlots from both natural-stand provenances and from selections in planted stands and tree improvement programs. The objectives of these trials included: (i) assessment of the performances of provenances and families-within-provenances in economically important traits in *E. grandis* grown under (effluent) irrigation in south-eastern Australia; and (ii) identification of families and provenances which offer the best

Table 1. Climatic parameters for the three *Eucalyptus grandis* provenance–family trial sites established in 1993–1994 and the climatic requirements for *E. grandis* plantations

Parameter	Koorlong	Shepparton	Requirements for viable plantations[a]
Mean annual rainfall (mm)	293	563	700–2500
Average water supplied from irrigation per year (mm)	825	700	
Sum of rainfall plus irrigation (mm)	1118	1263	
Mean annual temperature (°C)	16.8	15.1	14–25
Mean maximum temperature hottest month (°C)	32.0	30.0	25–34
Mean minimum temperature coldest month (°C)	4.3	3.1	3–16
Absolute minimum temperature (°C)	–5.7	–6.2	> –8
Annual evaporation (mm)	2150	~1380	Not specified

[a] Source of data: Booth and Pryor (1991)

potential for future genetic improvement. This paper reports on variation between and within provenances for growth to age 4.5 y in these trials. The significance of genotype x environment interactions for growth traits across the three trial sites is also reported.

Methods

Trial sites and layouts

In December 1993–January 1994, *E. grandis* provenance-family trials were established at three sites in Victoria — two close to Koorlong near Mildura and one near Shepparton. Climatic parameters for these sites are provided in Table 1. At all sites, tree spacing was 3 m between rows and 2 m between trees within rows.

The two sites near Koorlong (site A, 34°20'4.4"S, 142°04'36.9"E; and site B, 34°20'9.0"S, 142°04'17.2"E, both about 30 m asl) are located within a 105-ha hardwood plantation, drip-irrigated with effluent water. The effluent comprises primary-treated domestic and industrial wastewater from the Mildura/Irymple region. The soil at trial site A at Koorlong is free-draining with a deep sandy loam (30–60 cm deep) overlying a clay formation. Trial site B at Koorlong has a heavier clay loam soil. Prior to establishment the soils at both sites were relatively alkaline (pH 8.0–8.5 at 20 cm depth). Site preparation consisted of ripping planting lines to 60 cm depth and treating planting lines with pre-emergent herbicides.

The trial at the Shepparton site (36°19'13.5"S, 145°23'25.1"E and 113 m asl) is within a property belonging to Goulburn Valley Water. The trial is trickle-irrigated with primary-treated domestic and industrial effluent water from the Shepparton/Mooroopna region. Soils are grey-brown clay loams at 0–15 cm overlaying yellow-grey medium and heavy clays to 200 cm. The clay subsoils are dense and intractable, and not a good medium for tree root development. Soil analysis revealed a mean pH of 6.6 at the soil surface (0–25 cm). Deeper profiles, 25–200 cm, had a pH of 7.5–8.3. Site preparation involved ripping to a depth of 60 cm followed by the application of gypsum at a rate of 5 t ha^{-1}.

Seedlots

The three trials involved a total of 47 seedlots representing 15 different provenances of *E. grandis* and 6 seedlots representing a single provenance of *E. saligna* (Table 2). These included both single mother-parent open-pollinated seedlots (i.e. individual family) and multiple-parent bulked seedlots. When the trials were established the provenance of *E. saligna* was believed to be *E. grandis*. It was obtained from Blackdown Tableland, Queensland, an area where the distributions of the two species overlap. Though the populations in this area of central eastern Queensland are sometimes considered intermediate, as they can be difficult to assign to either species, the adult phenotypes from seed obtained from these populations tend to segregate clearly towards either *E. grandis* or *E. saligna* (CABI 2000).

Three of the 15 *E. grandis* provenances were from planted stands that were contributing to genetic improvement programs. One was from a South African clonal seed orchard, and was brought into Australia in the mid-1970s. The second came from a seedling seed orchard established near Coffs Harbour by the Forestry Commission of NSW in the mid-1970s. The third came from parent trees identified from intensive phenotypic selection at age 4.5 y in a 20-ha irrigated *E. grandis* plantation at Loxton, South Australia, which had been established using a seedlot comprising bulked seed from at least 30 parent trees in Wedding Bells SF. Each of these three sources were represented only as multiple-parent bulked seedlots. Not all seedlots were represented at all sites (Table 2).

Trial design

The two Koorlong trials and the one at Shepparton each comprised five complete replicates with rows and columns within replicates providing two-dimensional blocking within replicates. The seedlots in each trial were represented as 4-tree row plots in each replicate. Seedlots were not grouped by provenances in the field designs.

Culture

The Shepparton trial was irrigated at an average rate of 7.0 ML ha^{-1} y^{-1}. The two Koorlong trials received irrigation at rates ranging from 5.1 to 9.4 ML ha^{-1} y^{-1}. Post-establishment weed control was limited to slashing every 2–3 mo until canopy closure adequately suppressed weed growth.

Assessment

All surviving trees were assessed in mid-1998, at about 4.5 y of age, for height and diameter. Heights were measured to the nearest 0.1 m

Table 2. Details of the *Eucalyptus grandis* and *E. saligna* seedlots established in the trials at Koorlong and Shepparton

CSIRO seedlot no.	Species	Number of parent trees[a]	Location	Provenance details			No. of multiple-parent bulked seedlots and single mother-parent open-pollinated seedlots					
				Latitude	Longitude	Altitude	Koorlong A		Koorlong B		Shepparton	
				(S)	(E)	(m asl)	Bulked	Single	Bulked	Single	Bulked	Single
11159	*E. grandis*	4	Mt George, NSW	31°50'	152°00'	300	1	0	1	0	0	0
11996	*E. grandis*	6	Bulahdelah, NSW	32°25'	152°10'	200	1	0	1	0	1	0
15120	*E. grandis*	10	Lake Cathie, NSW	31°32'	152°52'	10	1	0	1	0	1	0
15632	*E. grandis*	8	Woondum, Qld	26°17'	152°48'	100	1	0	1	0	1	0
16435	*E. grandis*	8	Wedding Bells SF, NSW	30°09'	153°07'	120	1	4	1	4	0	5
16437	*E. grandis*	15	Wahau Trig, NSW	30°05'	153°01'	300	1	5	1	5	0	6
16439	*E. grandis*	12	Orara SF, NSW	30°11'	153°08'	3	1	0	1	0	0	0
16442	*E. grandis*	–	Bruxner Park, NSW	30°14'	153°05'	200	0	5	0	5	0	6
16454	*E. grandis*	–	Pine Creek SF, NSW	30°24'	153°00'	150	0	6	0	6	0	5
16447	*E. grandis*	–	Langleys Rd, Coffs Harbour, NSW	30°13'	152°56'	630	0	6	0	6	0	6
18277	*E. grandis*	–	Bellthorpe, Qld	26°52'	152°42'	400	0	6	0	6	0	6
ERA-1[b]	*E. grandis*	>10	Boambee, NSW	30°18'	153°03'	60	0	0	0	0	1	0
ERA-2[b]	*E. grandis*	100	Loxton, SA — plantation selects	34°26'	140°36'	30	1	0	1	0	0	0
18146	*E. grandis*	>24[c]	Coffs Harbour seedling seed orchard (SFNSW)	30°08'	153°07'	100	1	0	1	0	1	0
17803	*E. grandis*	Bulked[d]	Clonal seed orchard — Pretoria, South Africa	–	–	–	1	0	1	0	0	0
18229	*E. saligna*	–	Blackdown Tableland, Qld	23°50'	149°05'	880	0	6	0	6	0	6
				Total number of seedlots: (i) single parent tree			38		38		40	
				(ii) multiple-parent bulked seedlots			10		10		5	
				Total number of provenances			14		14		12	

[a]Number of seed parent trees contributing to the bulk seedlot
[b]Seedlots ERA-1 and ERA-2 were not obtained through CSIRO
[c]The Coffs Harbour seedling seed orchard seedlot comprised a multiple-parent bulked seedlot made up of seed from 3 to 4 parent trees of each of the 24 families in the State Forests of NSW seed orchard at the time of collection
[d]This seedlot consists of an imported multiple-parent bulk seedlot from a clonal seed orchard (number of parent trees uncertain) in South Africa

using height poles, and diameters at breast height (1.3 m) over bark (DBH) were measured to the nearest 0.1 cm with diameter tapes.

Analyses

The software package DataPlus (Williams *et al.* 1997) was used to pre-process the data and screen for incorrect entries and outlying values. Extreme outliers were excluded from the analyses.

Individual conical tree volumes (dm^3) were calculated using the formula

$$V = Ht \times (3.14\, DBH^2 / 4) / 3 ,$$

where V is individual-tree volume in dm^3; DBH^2 is the diameter at breast height over bark (dm) squared; and Ht is tree height (m).

Analyses of trial data from each site for each of DBH, height and volume were based on the linear model

$$Y_{ijklm} = \mu + R_i + X_{j(i)} + Y_{k(i)} + P_l + F_{m(l)} + e_{ijklm} ,$$

where Y_{ijklm} is the plot mean of the mth family within provenance l in the kth column within replicate i and the jth row within replicate i; μ represents the overall mean; R_i represents the effect of the ith replicate; $X_{j(i)}$ represents the effect of the jth row within replicate i; $Y_{k(i)}$ represents the effect of the kth column within replicate i; P_l represents the effect of the lth provenance; $F_{m(l)}$ represents the effect of the mth family which is nested within provenance l; e_{ijklm} represents the residual error with a mean of zero.

Analyses of variance were carried out in two stages. The first stage involved mixed model analyses using the REML procedure of the GENSTAT software package, for which seedlots and replicates were treated as fixed effects while both rows-within-replicates and columns-within-replicates were treated as random. For the second stage, seedlot means estimated from this first stage were then analysed, using the ANOVA procedure in GENSTAT, according to a nested treatment structure (families nested within provenances). The outputs from the two stages were then combined to produce composite analyses of variance tables for testing the significance of provenance and family-within-provenance effects, following procedures described by Williams and Matheson (1994). The data used for these analyses of variance computations excluded all the *E. saligna* material.

Separate REML analyses were used to obtain means for all families (i.e. *E. grandis* and *E. saligna*), adjusted for replicate, row-within-replicate and column-within-replicate effects (REML means), along with the standard errors of differences between means[1] (SEDs) included in the trials. REML analyses were also used to provide adjusted means for provenances.

Heritabilities

Heritability represents the degree to which a character is influenced by genetics as compared to environment. High heritability indicates that individual phenotypes are indicative of their genotypes (Schmidt 1994). Here, heritability parameters were estimated separately for each trial site for traits that showed significant family-within-provenance variation.

Appropriate variance components for computation of heritabilities were obtained by mixed-model analyses following procedures described by Williams and Matheson (1994). These analyses were conducted using GENSTAT's REML procedure. Only materials representing true single-mother-parent open-pollinated *E. grandis* seedlots were included in these analyses (i.e. all multiple-parent bulked seedlots and all the *E. saligna* seedlots were excluded from the data used for estimating heritabilities).

The mean family-within-provenance variance components in each trial were used to estimate the within-provenance individual tree heritabilities (denoted h^2) following Williams and Matheson (1994, Chapter 6) as

$$h^2 = 1/r \times (\sigma_f^2 / \sigma_P^2) ,$$

where r = coefficient of relationship; σ_f^2 = variance between families within provenances; σ_P^2 (phenotypic variance) = $(\sigma_f^2 + \sigma_m^2 + \sigma_t^2)$; σ_m^2 = variance between plots; σ_t^2 = variance between trees within plots.

The coefficient of relationship (r) used in computation of the individual-tree heritabilities for these open-pollinated *E. grandis* families was taken as 0.40, rather than the value of 0.25 for half-sib families. Previous studies have shown that open-pollinated *E. grandis* families from natural stands generally carry a degree of inbreeding resulting from selfing and neighbourhood inbreeding, and thus are not true half-sibs (Eldridge *et al.* 1993; Burgess *et al.* 1996); the coefficient of 0.4 reflects this. Standard errors for the heritability estimates were calculated according to Becker (1984).

Genotype x environment interactions

The data (plot means) from the two trials at Koorlong and the one at Shepparton, excluding all *E. saligna* data, were pooled for combined analyses across sites to examine the significance of genotype x environment interaction effects for *E. grandis*. These analyses were based on the linear model

$$Y_{hijklm} = \mu + S_h + R_{i(h)} + X_{j(h.i)} + C_{k(h.i)} + P_l + S_h \times P_l + F_{m(l)} + S_h \times F_{m(l)} + e_{hijklm} ,$$

where Y_{hijklm} is the plot mean at the hth site of the mth family within the lth provenance in the kth column within replicate i and the jth row within replicate i; μ represents the overall mean; S_h represents the effect of the hth site; $R_{i(h)}$ represents the effect of the ith replicate within site h; $X_{j(h.i)}$ represents the effect of the jth row within replicate i at site h; $C_{k(h.i)}$ represents the effect of the kth column within replicate i at site h; P_l represents the effect of the lth provenance; $S_h \times P_l$ represents the site x provenance interaction effect; $F_{m(l)}$ represents the effect of the mth family which is nested within provenance l; $S_h \times F_{m(l)}$ represents the site x family interaction effect; e_{hijklm} represents the residual error with a mean of zero.

For these analyses, sites, replicates-within-sites and provenances were treated as fixed effects, while rows-within-replicates, columns-within-replicates and families-within-provenances were treated as random effects.

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[1]The standard error of the difference between means provides a basis for judging the significance of the difference(s).

Table 3. Provenance means (and rankings within site) for tree height, diameter at breast height over bark (DBH) and conical tree volume at age 4.5 y in the *E. grandis* trials at three sites in Victoria

CSIRO seedlot no.	Provenance	Koorlong A Height (m)	(rank)	DBH (cm)	(rank)	Volume (dm^3)	(rank)	Koorlong B Height (m)	(rank)	DBH (cm)	(rank)	Volume (dm^3)	(rank)	Shepparton Height (m)	(rank)	DBH (cm)	(rank)	Volume (dm^3)	(rank)
11159	Mt George, NSW	6.0	(13)	6.3	(10)	7.2	(11)	7.8	(5)	8.5	(2)	16.4	(7)	–		–		–	
11996	Bulahdelah, NSW	6.5	(9)	5.8	(14)	5.7	(13)	7.7	(7)	7.9	(7)	14.8	(8)	10.9	(6)	9.8	(4)	28.1	(4)
15120	Lake Cathie, NSW	6.9	(3)	7.0	(2)	8.9	(3)	7.8	(3)	8.0	(5)	17.1	(2)	10.7	(10)	9.3	(9)	24.5	(10)
15632	Woondum, Qld	6.7	(7)	6.9	(5)	8.7	(6)	7.1	(11)	7.9	(7)	13.7	(12)	11.2	(1)	10.0	(1)	29.0	(1)
16435	Wedding Bells SF, NSW	6.5	(10)	6.6	(6)	8.1	(9)	7.0	(13)	7.6	(13)	13.5	(13)	10.6	(11)	9.3	(10)	24.2	(11)
16437	Wahau Trig, NSW	6.5	(11)	6.3	(10)	8.1	(10)	7.1	(12)	7.2	(14)	13.2	(14)	10.7	(8)	9.2	(11)	24.6	(9)
16439	Orara SF, NSW	5.8	(14)	5.0	(15)	4.3	(15)	6.4	(15)	6.4	(15)	10.8	(16)	–		–		–	
16442	Bruxner Park, NSW	6.9	(4)	6.6	(6)	8.9	(4)	7.3	(10)	7.7	(12)	13.7	(11)	11.0	(5)	9.8	(2)	28.3	(2)
16454	Pine Creek SF, NSW	6.9	(5)	6.6	(6)	8.6	(7)	7.8	(4)	7.9	(7)	16.5	(5)	11.2	(1)	9.7	(6)	27.7	(5)
16447	Langleys Rd, Coffs Harbour, NSW	6.3	(12)	5.9	(13)	6.8	(12)	7.6	(9)	7.7	(10)	14.6	(10)	10.8	(7)	9.4	(8)	25.5	(7)
18277	Bellthorpe, Qld	6.7	(8)	6.4	(9)	8.2	(8)	7.6	(8)	8.0	(5)	16.4	(6)	10.7	(9)	9.1	(12)	23.9	(12)
ERA-1[a]	Boambee, NSW	–		–		–		–		–		–		11.1	(3)	9.5	(7)	26.1	(6)
ERA-2[a]	Plantation selects, Loxton, SA	7.7	(1)	7.7	(1)	12.4	(1)	8.0	(1)	8.7	(1)	18.8	(1)	–		–		–	
18146	Coffs Harbour seedling seed orchard	7.6	(2)	7.0	(2)	10.0	(2)	8.0	(1)	8.1	(4)	17.0	(4)	11.1	(3)	9.8	(2)	28.1	(3)
17803	CSO, Pretoria, South Africa	6.9	(6)	7.0	(2)	8.9	(5)	7.7	(6)	8.2	(3)	17.1	(3)	–		–		–	
18229	*E. saligna*, Blackdown Tableland, Qld	4.9	(15)	6.0	(12)	5.7	(14)	6.8	(14)	7.7	(11)	14.8	(9)	10.1	(12)	9.7	(5)	25.4	(8)
Site means		6.5		6.4		9.7		7.4		7.7		15.1		10.7		9.5		27.3	
SED (average) for provenance means		0.53		n.s.		n.s.		0.56		n.s.		n.s.		0.37		n.s.		2.92	

SED = standard error of the difference between means.
[a]Seedlots ERA-1 and ERA-2 were not obtained through CSIRO

Results

Survival and growth

Good survival was obtained in both Koorlong trials (about 85%) and at Shepparton (>90%), and there were no significant differences in survival between either provenances or families within provenances. The best growth was obtained at Shepparton, where tree height and volume at age 4.5 y averaged 10.7 m and 27.3 dm^3 respectively (Table 3). At Koorlong, average height growth was at least 30% less than at Shepparton, with average heights in the two trials at 4.5 y being only 6.5 m and 7.4 m. At all three sites, insect damage was relatively light (<10% defoliation in any one year) and was thus unlikely to have significantly reduced growth.

Provenance variation

Provenance variation was significant ($P < 0.05$) for height in the Koorlong trials and for volume at Shepparton. In both Koorlong trials, the Loxton plantation select provenance performed best for all growth traits (Table 3). Other provenances that performed well for growth in the same two trials included Lake Cathie, Coffs Harbour seed orchard and the South African seed orchard. The poorest *E. grandis* provenance for height, DBH and volume in both Koorlong trials was Orara SF.

At Shepparton, the Woondum provenance ranked best for all growth traits. Others that performed similarly there included Bruxner Park, Buladelah and Coffs Harbour seed orchard. The poorest *E. grandis* provenances at Shepparton were Bellthorpe and Wedding Bells (ranked 11th and 12th for volume respectively). The Lake Cathie provenance, which performed well at Koorlong, grew relatively poorly at Shepparton, ranking only 10th by volume.

The Blackdown Tableland provenance of *E. saligna* grew poorly relative to all the *E. grandis* provenances in the Koorlong A trial, and was generally amongst the poorest *E. grandis* provenances in the other two trials.

Family-within-provenance variation

There were significant differences between families within provenances in height, DBH and volume at Koorlong A and Shepparton. At Koorlong B, only volume differed significantly between families within provenances. The ranges in the family means for tree volume were 17.0–33.2 dm^3, 8.2–29.6 dm^3 and 3.3–13.2 dm^3 at Shepparton, Koorlong B and Koorlong A respectively.

In all three trials, the better families for volume came from a wide range of provenances. The top 10 families for volume at Shepparton represented five provenances, which themselves ranged from superior (Bruxner Park, ranked second for volume) to poor (Bellthorpe, ranked last for volume). At Koorlong A, the top 10 families also represented five provenances, and at Koorlong B, six provenances.

Growth of the individual families of *E. saligna* relative to the *E. grandis* families varied markedly between sites. At Koorlong A, the six *E. saligna* families were all in the poorest 30% of families by volume. In contrast, the same families at Shepparton varied widely in growth performance from superior to poor — two were comparable to the 10 best individual *E. grandis* families for volume and one ranked among the best four. The poorest *E. saligna* family at Shepparton, however, ranked among the poorest four *E. grandis* families for volume.

Table 4. Individual tree heritabilities (within provenance) for *E. grandis* at age 4.5 y at three Victorian sites. Heritabilities were estimated only for those traits and sites where differences between families within provenances proved significant ($P < 0.05$)

Trait	Individual-tree heritability ± s.e.		
	Koorlong A	Koorlong B	Shepparton
Height	0.21 ± 0.18	–	0.12 ± 0.10
DBH	0.14 ± 0.14	–	0.08 ± 0.09
Volume	0.12 ± 0.16	0.08 ± 0.13	0.11 ± 0.10

Heritability

Individual-tree heritabilities for each trait were estimated only where family differences were significant (Table 4). Even so, the heritabilities obtained were relatively low and ranged from 0.08 for DBH at Shepparton and for volume at Koorlong B, to 0.21 for height at Koorlong A. The standard errors on four of the heritabilities obtained exceeded the magnitude of the heritability. The other three cases were height at Koorlong A (0.21 ± 0.18) and both height and volume at Shepparton (0.12 ± 0.10 and 0.11 ± 0.10 respectively).

Analyses across sites: genotype x environment interactions

When data from the three sites were combined, provenance differences were significant ($P < 0.05$) for height and volume, and family-within-provenance differences were significant for all three traits. In contrast, environment (trial site) x provenance and environment x family-within-provenance interactions for growth (height, DBH and volume) were not significant. Many of the provenances and families within provenances showed relatively consistent growth performance, relative to site averages, across the three trials.

Discussion

Climatic parameters, excepting rainfall, for the three trial sites are within requirements defined for *E. grandis* by Booth and Pryor (1991) (Table 1). However, even though the irrigation applied at all of the sites overcame any rainfall constraint for plantation development, growth has been only poor to mediocre in these trials. At the best site, Shepparton, average height increment was only about 2.4 m y^{-1}, and at the two Koorlong sites the averages were only 1.4 and 1.6 m y^{-1}. In contrast, Arnold *et al.* (1996) reported an average mean dominant height of 18.7 m to age 5½ y (3.4 m y^{-1}) from an effluent-irrigated *E. grandis* trial near Loxton, South Australia, where the climate is similar to that at Koorlong. In another effluent-irrigated trial near Wagga Wagga, NSW, the average height of *E. grandis* was reported to have reached more than 9.5 m in less than 3 y (>3.2 m y^{-1}) (Myers 1994).

An important factor that has probably constrained growth of the *E. grandis*, at least at Koorlong, is the low to very low daytime humidity typically experienced there over much the growing season. *Eucalyptus grandis* is a sub-tropical species from summer-rainfall climates, and under conditions of low humidity it has a tendency to close its stomata and stop carbon dioxide uptake, even when adequate soil moisture is present (Myers *et al.* 1996). This stomatal response can limit its growth in dry Mediterranean-type environments, such as that at Koorlong, even when irrigation is ample.

Another factor that may have limited growth in the first year or two of these trials was water supply. At Koorlong, on occasional days during the first year, there was insufficient water to keep the trees hydrated. At Shepparton, irrigation problems also limited the water supply to the trial on a few occasions during the first two years.

Alkalinity of the Koorlong soils (pH 8.0 to 8.5) may be another factor contributing to the slower growth there, relative to that at Shepparton. Although *E. grandis* is moderately tolerant of pH in the range 8.0–9.0, best growth is obtained with soil pH closer to 7 (Marcar and Khanna 1997). At Shepparton, which provided the best growth overall of the three sites, soil pH, 6.6 for the surface soil and 7.5–8.3 at deeper levels, was closer to optimum for this species.

Across sites, ‘Plantation select’ material from Loxton and/or the seed orchard material from Coffs Harbour generally grew best. Unimproved natural stand provenances matched the growth of Coffs Harbour seed orchard material only at Shepparton. The reasonably good performance of this latter material across the three trial sites was expected. Its volume growth has generally been similar or superior to that of good natural stand provenances in trials in both Australia and Sri Lanka (Cromer *et al.* 1991; Davidson 1993; Bandara *et al.* 2002).

The material from the Loxton plantation selects was notable for its clearly and consistently superior growth in both trials at Koorlong. It generally also shows superior form in that environment (E.B. Allender, 1999, *pers. comm.*). Clearly the intensive phenotypic selection in the Loxton plantation at around age 4½ y proved very effective in identifying superior parent trees. The worth of intensive selection for genetic improvement of *E. grandis* had been demonstrated previously in Florida. There, four generations of intensive phenotypic selection provided gains of more than 160% in volume and significant increases in stem straightness relative to the first-generation material, all in a period of less than 20 y (Meskimen 1983; Rockwood 1991).

It is not surprising that the material from Loxton plantation selects grew better than material from the South African seed orchard in both Koorlong trials. Material from early South African orchards has shown disappointing growth relative to that from better natural stand provenances in trials in both South Africa (Darrow 1983) and Florida (Rockwood and Meskimen 1991). The *E. grandis* introduced to South Africa in the late 19th century, upon which their early plantation and breeding programs were based, is thought to have originated from collections from northern NSW or southern Queensland (Burgess *et al.* 1985). In northern NSW, a commonly-used seed collection area for early *E. grandis* base populations sent to other countries was Orara East (Burgess 1988). Some seedlots from this locality have shown inferior performance in a number of trials, including some near Coffs Harbour (Burgess 1988) and the two reported here at Koorlong. Introductions of range-wide collections of *E. grandis* to South Africa in the later part of 20th century have since provided a better genetic base for breeding programs there (CABI 2000).

The overall lack of significant interaction between genotypes (provenances and families within provenances) and environments (trial sites) across the Koorlong A, Koorlong B and Shepparton sites is important to both tree breeders and those involved in plantation establishment. Most provenances and families selected for superior performance at one of these sites should perform relatively consistently across sites. Likewise material identified as mediocre or poor at one site would be expected to perform similarly elsewhere. However, this inference is limited to the range of environments represented by the three trial sites. In a substantially different environment, one could not be confident of consistent relative growth. Significant interactions between *E. grandis* genotypes and environmental factors for growth traits have been reported elsewhere (Burgess 1988; Endo and Easley 1991). For example, Tuckers Knob and Bellinger River provenances (both NSW) have shown consistent performance relative to other natural stand provenances in trials across a broad range of environments in Australia, South Africa and the United States, while Orara East and Orara West provenances (both also NSW) have varied considerably in their relative performance across the same environments (Burgess 1988).

The variation found between families within provenances in the trials reported here was also expected, as considerable variation of this nature has been reported from trials of *E. grandis* in many countries (e.g. Reddy and Rockwood 1989; Endo and Easley 1991; Burgess *et al.* 1996). In a Sri Lankan provenance-family trial, the variation in growth between families within provenances at age 27 mo exceeded most of the differences between provenances (Bandara *et al.* 2002). The second-best family for growth in that trial came from one of the poorest provenances. However, much of the variation among *E. grandis* families from natural stands is often associated with differences in outcrossing rates between their parent trees (Burgess *et al.* 1996), and therefore with different levels of inbreeding amongst progeny.

Even though heritabilities of growth traits were relatively low, there is a good basis for significant genetic improvement in subsequent generations. This is the case for two reasons. Firstly, there are clearly important differences at the provenance level. Secondly, as *E. grandis* can be readily propagated clonally using micropropagation or rooting of stem cuttings, there is substantial potential for Australian *E. grandis* improvement programs to exploit non-additive genetic variance (e.g. see Eldridge *et al.* 1993 and CABI 2000).

Although one of the original aims in establishing the three *E. grandis* trials reported was to evaluate genetic variation in susceptibility and tolerance to defoliating insect pests, it was not possible to do this during the first 4.5 y. However, there has subsequently been substantial defoliation in both Koorlong trials by larvae of autumn gum moth (*Mnesampela privata*). Genetic variation in defoliation, and tolerance and growth response to those events, will be reported separately.

The poor growth of the *E. saligna* material, relative to the average of *E. grandis*, should not be considered indicative of that species' potential at any of the three sites involved in this research. A single natural stand provenance is not an adequate sample of this species, particularly as the variation in growth between provenances within both *E. saligna* and *E. grandis* can far exceed differences between the means of the two species (e.g. Burgess 1988). Provenances of *E. saligna* from latitudes more temperate than that of the provenance included here might well prove better suited to the trial environments.

Conclusions

The choice of provenance had an important effect on growth of *E. grandis* in these effluent-irrigated trials; material from Australian tree improvement initiatives provided some of the best results. Substantial variation between families within provenances creates opportunities for genetic improvement of the species through selection. Such selection could target the best individual trees regardless of their provenance.

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