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GENETIC VARIATION IN GROWTH, STEM STRAIGHTNESS AND WOOD PROPERTIES IN *EUCALYPTUS DUNNII* TRIALS IN NORTHERN NEW SOUTH WALES

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ABSTRACT

Eucalyptus dunnii provenance-family trials planted at two contrasting sites in north-eastern New South Wales (NSW) and containing 219 seedlots were assessed for growth and form at age-6½ years. Wood basic density and collapse of sample cores from a subset of the seedlots at one site were also assessed. Volume was more than four times greater at the warmer coastal site compared with the cooler, higher altitude site. Highly significant differences occurred among provenances for volume and stem straightness only at the coastal site. Provenance differences for wood basic density and collapse were not significant. Better provenances for growth at the coastal site were from southern (Moleton-Kangaroo River) and northern (NSW border ranges) populations. A *Eucalyptus grandis* seedling seed orchard seedlot included in the trials was inferior to *E. dunnii* for both growth and stem form.

Variation between families-within-provenances was significant for all traits assessed at each site. Individual tree heritability estimates were low to moderate for volume and stem straightness (0.14 to 0.28) but moderate to high for the wood properties (0.42 to 0.75). Phenotypic correlations between traits were generally low but favourable. Genetic correlations between traits ranged from low to high and were generally favourable but the magnitudes of the standard errors on most of these were very large and, for most, exceeded the value of the estimate. Interactions between provenance and site were significant for volume but not for stem straightness. Family by site interactions were significant for both of these traits. However, about 30 % of families did show stability for volume and 11 families ranked in the top 20 % at both sites.

Key words: *Eucalyptus dunnii*, growth rate, basic density, heritability, genetic variation, genetic correlation.

INTRODUCTION

Eucalyptus dunnii Maiden (Dunn's white gum) is a tall forest tree whose natural occurrence is mainly limited to two small disjunct populations. These are located in the Moleton–Kangaroo River area of New South Wales (NSW), Australia, north-west of Coffs Harbour (30 °S), and in the Border Ranges of NSW and Queensland (about 28 °S) (see Figure 1). In natural stands it occurs primarily on the margins of rainforests and has a preference for fertile basaltic or alluvial soils between 400 m and 650 m altitude (BENSON & HAGER 1993).

As an exotic, *E. dunnii* has demonstrated adaptability to a wide range of soil types of good depth and moderate to high fertility (HERBERT 1994). Thus it has gained favour as a plantation species in several countries over the past 10–15 years. In particular, it is viewed as an alternative to the widely-planted *E. grandis*, being better adapted than the latter to slightly drier and/or more frost prone sites (DARROW 1994, CABI 2000, JOHNSON & ARNOLD 2000). Trials in south central China have shown *E. dunnii* to be a promising plantation species for some summer rainfall areas which are also subject to winter frosts (MANNION & ZHANG 1989, WANG *et al.* 1999, ARNOLD & LUO 2003). In South Africa, it grows well on drought-prone high-veldt areas (SWAIN & GARDNER 1997, SWAIN 2001). In cooler areas of southern Brazil and in parts of Argentina, *E. dunnii* is seen to have potential for wide establishment due to high growth rates and reasonable wood qualities for pulp production (PEREIRA *et al.* 1986, MARCÓ & LOPÉZ 1995).

In Australia, trial plantings on coastal sites in northern NSW during the 1970s and 1980s showed *E. dunnii* to have high growth rates and often excellent stem form with fine branching. In several species trials on fertile ex-forest sites *E. dunnii* equalled or outgrew 'traditional' plantation eucalypts such as *E. grandis* and *E. pilularis* by age 15–18 years (JOHNSON & STANTON 1993). Such results helped to prompt larger scale planting of *E. dunnii* in northern NSW and south–east Queensland from 1994 onwards. To date more than 10,000 ha have been established (WOOD *et al.* 2001),

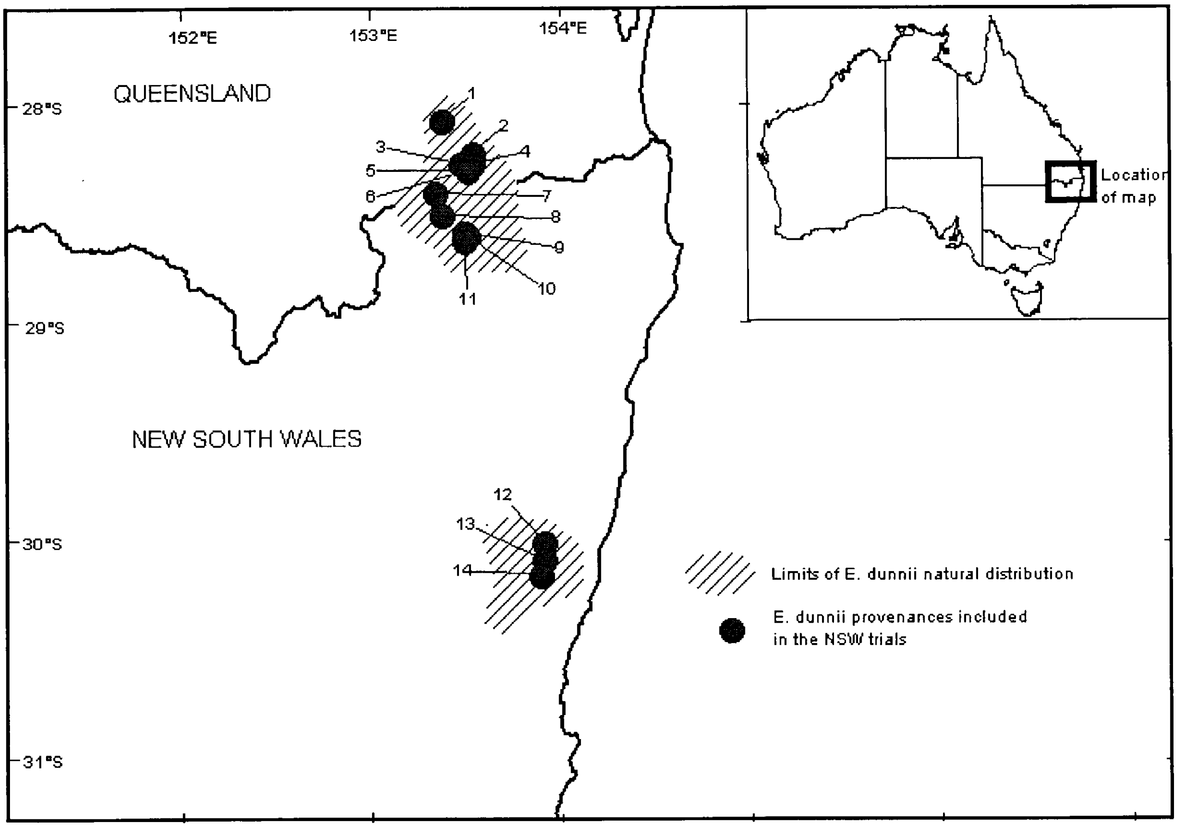

Figure 1. Geographic location of the 14 *E. dunnii* provenances represented in the provenance-family trials at Boambee and Megan in northern New South Wales along with the approximate geographic limits of *E. dunnii*'s natural distribution (provenances are referenced by their ID number to parameters provided in Table 2).

much of which is on higher altitude sites (>500 m asl), or on lower-lying creek flats prone to frost.

Kraft pulping studies in Uruguay have shown wood from 4-year-old plantation-grown *E. dunnii* can give higher yields of pulp than wood from *E. grandis*, with a higher tensile strength and some superior paper making properties (BACKMAN & DE LEON 1998). Plantation-grown timber of *E. dunnii* may be suited for a range of solid wood applications but more research is need in this area. Logs from young trees under 10 years old have a reputation in South Africa for end splitting badly and are not recommended for use there as mining timber (STANGER 1993). However, plantation-grown *E. grandis* logs are also subject to severe end splitting (*e.g.* MALAN 1979), and efforts have been made for many years in South Africa to reduce this problem through breeding and silviculture, with some success. Sawing and drying trials of young (14-year-old) *E. dunnii* trees from a Victorian plantation showed its timber to be well suited to appearance grade products; that sawing distortion was within acceptable limits; and that seasoning collapse encountered in some boards was not an insurmountable problem (WASHUSEN 1995). Studies on 9 to 25 year-old plantation grown logs from northern NSW have indicated that the species produces timber of a strength and hardness acceptable for a range of end-uses (DICKSON *et al.* 2003).

Substantial genetic variation in wood quality and in growth has been observed between individual trees of *E. dunnii* (see JOHNSON & ARNOLD 2000, SWAIN 2001, DICKSON *et al.* 2002). As both of these characteristics are widely recognised as important to product value and overall plantation profitability (KUBE *et al.* 2001), such variation can lead to a wide range in log values. Simultaneously, however, this variation also provides the potential for improvement of wood qualities through tree breeding.

Because of increasing interest in planting *E. dunnii* in north-eastern NSW, provenance-family trials were planted at two sites in northern NSW, in early 1995. This project was a cooperative initiative by CSIRO and State Forests of NSW. The aims of the trials included:

- assessment of provenance and family performance with respect to economically important traits;
- identification of provenances and families which

offer the greaest potential for ongoing genetic improvement; and

- comparison of the growth and form of *E. dunnii* with that of *E. grandis* seed orchard stock.

Early results (age-39 months) for growth in these trials have been reported by JOHNSON & ARNOLD (2000). The aims of this current study are to report on growth and stem straightness in both of these trials, and wood properties (basic density and collapse) from one of these trials, at 6½ years of age. It is the first study to examine genetic variability of wood quality traits and correlations of these traits with growth in *E. dunnii* grown in Australia.

MATERIALS AND METHODS

Trial sites

Two provenance-family trials of *E. dunnii* were established in early 1995 on contrasting sites on State Forest land in the Coffs Harbour area of northern NSW. One site, Boambee, is a low altitude, mild temperature coastal ex-hardwood plantation site (Table 1). The other, Megan, is a higher-altitude, colder, ex-pasture site near Dorrigo. Soils at both sites were classified as Yellow Podzolics. Additional site and soil details for these trials are provided in Table 1.

Seedlots

Both trials contain seedlings raised from 219 open-pollinated (family) seedlots collected from individual *E. dunnii* trees in 21 natural stands from the species' range (Table 2). These 21 stands were chosen to provide reasonable coverage of the species' natural geographic range, given a constraint of limited seed availability (see Figure 1). Seed availability in its natural stands is generally quite limited as *E. dunnii* is a very shy seeding species (CABI 2000). Attempts to collect seeds from many stands were unsuccessful due to the absence of seeds. Nonetheless, the stands from where seeds were obtained for inclusion in these trials provided a reasonable coverage of its range. On account of the close proximity of some of the 21 stands to others, those from within 2 minutes latitude and 50 m altitude of each other were combined to be regarded as single provenances for the purposes of data analyses. Thus, the *E. dunnii* material included in the trials was considered to represent 14 provenances, numbered from north to south (see Table 2).

Within each stand sampled, the parent trees from which seed was collected were of 'good–average' quality and located at least 100 m apart from one another.

One control seedlot of *E. grandis* was also included in the trials. This was a bulk mix of seed collected from more than 20 of the 42 superior families (from an original 104), retained in State Forests' Wedding Bells seedling seed orchard, near Coffs Harbour, after thinning at age-12 years.

Trial design

The 220 seedlots in each trial were represented by six replicates of 4-tree row plots. Trees were spaced at 3.0 m (between rows) by 2.4 m (within rows). Both trials were incomplete block (ICB) designs with one-dimensional blocking (columns) within replicates.

Establishment

Seedlings were germinated and grown for a month in a glasshouse, then dibbled into Hiko V93 cells (up to 160 seedlings per family) and placed outside under high shade. When the seedlings were approximately 10 cm tall, they were moved to holding areas in full sunlight to grow on and then harden (JOHNSON & ARNOLD 2000).

The Megan site had been cleared previously for grazing. A small section that carried regenerating wattle and low natural forest regeneration was cleared. The rest of the site carried pasture, which was burnt and sprayed with Glyphosate in November 1994. The site was cultivated using a winged ripper to rip planting lines 30–50 cm deep, close to the contours. The planting lines were sprayed with residual weedicide (Simazine at 12 litres · ha^{-1}) in mid-December 1994.

The Boambee site carried considerable debris after the clear-felling of the previous 40-year-old *E. grandis* plantation. This was pushed into wind-rows and burnt in spring 1994. A winged ripper pulled by a crawler tractor ripped planting lines to a 50–60 cm depth between the *E. grandis* stumps. Regrowth of woody weeds was sprayed with Glyphosate herbicide in December 1994.

The trials were hand planted in February 1995. Within a month of planting, each seedling at both sites received one 20 g Langley Tree Tablet (N 20 % : P 4.4 % : K 8.2 % : S 6.0 %) which was buried at a depth of 10 cm at a distance of about 15 cm from each seedling.

At two years of age, growth over most of the Megan trial was noticeably retarded compared with trees in routine plantings nearby, and a supplementary application of 100g di-ammonium phosphate fertiliser per tree was made in November 1997, along with strip spraying of Glyphosate herbicide along the tree rows. Early growth at Boambee was substantially better than at Megan and by age-4 years a selective thinning was necessary. The best 2 trees per 4-tree row plot were retained in this thinning, as judged subjectively on tree volume and stem and branch form. The Megan trial had not been thinned at the time of the assessment reported here.

Assessments

In May 2001 (at age-75 months) all living trees in the best-growing 5 of the 6 replicates at Boambee, and in the best 4 of the 6 replicates at Megan, were assessed for diameter at a height of 1.3 m (DBH) and total height (HT). Heights were measured using Vertex electronic heighting instruments. Stem straightness (STR) was also assessed at this age, but only on trees in the Megan trial, using a subjective 6-point score. Score 6 was assigned to trees whose stem (excluding the top 1 m of new growth) was essentially completely straight. Score 1 was used for badly kinked or otherwise deformed stems that had no potential of being merchantable. Scores of 2, 3, 4 and 5 represented gradations of stem straightness between these extremes. Stem straightness in the Boambee trial was scored, using a similar scale, in an earlier assessment (age-39 months) as reported by JOHNSON & ARNOLD (2000), and thus was not reassessed at 75 months. Data for *STR* from that earlier Boambee assessment were used in the analyses reported here.

To examine variation and obtain genetic parameters for wood properties, a non-destructive sampling program involving removal of bark-to-bark increment cores at a height of 0.9 m above ground was carried out in the Boambee trial. The sample height of 0.9 m was used for this study as an earlier study had shown that the density of cores taken from this height could provide a reliable prediction ($r^2 = 0.88$) of whole whole-tree basic density (CSIRO and State Forests of NSW unpublished data).

Fifty families in the trial were selected at random and from 5 trees in each of these families (*i.e.* 250 trees in total), one 12 mm diameter sample core was taken at 0.9 m height in September 2001. Green volumes for all cores were measured using the water displacement method, and basic densities calculated after drying at 105 °C (see TAPPI 1985).

In addition, collapse was also assessed in each core. Collapse is a defect that may develop in drying, which appears as irregular and abnormal shrinkage caused by buckling and crushing of cell walls. It can be reversed or 'recovered' by steam reconditioning (BROWN *et al.* 1952), where as volumetric shrinkage is not reversed by such treatment. After drying at 105 °C, bands of very high shrinkage were observed in the cores. Steam reconditioning of the cores for one hour led to almost full recovery, indicating that these bands were due to collapse and not volumetric shrinkage (CHAFFE 1985, KUBE *et al.* 2001). The percentage of maximum collapse evident in each core was then estimated from the equation:

$$COL = \{(D_R - D_C)/D_R\} * 100$$

where: COL = maximum collapse expressed as a percentage, D_C = minimum tangential diameter of the core (excluding central pith area) after drying at 105 °C, D_R = minimum tangential diameter of the core following steam reconditioning for 1 hour.

Data analyses

Trees deemed to be very stunted (<2.5 cm *DBH*) or severely damaged (*e.g.* broken tops – $DBH \geq 10$ cm and HT <3.0 m) were deleted from the data set for each trial before analysis of growth and form traits. Overall, fewer than 1.0 % of living trees were deleted for these reasons from either trial. Tree volume (*VOL*, in m^3), was calculated for trees in both trials using a volume equation developed for *E. dunnii* by COETZEE & NAICKER (1999):

$$\log10(VOL) = -4.5084 + 2.1209*\log10(DBH) + 0.8414*\log10(HT)$$

where: VOL = under bark tree volume in m^3 to 5 cm tip diameter; DBH = diameter at breast height (1.3 m) in cm over bark; HT = total tree height in m; log10 = common logarithm (base 10).

Analyses of variance were carried out on plot mean data based on the following linear model:

$$Y_{ijkl} = \mu + R_i + B_{j(i)} + P_k + F_{l(k)} + e_{ijkl}$$

where: Y_{ijkl} is the plot mean of family l within-provenance k in incomplete block j within replicate i; μ represents the overall mean; R_i represents the effect of replicate i; $B_{j(i)}$ represents the effect of incomplete block j within-replicate i; P_k represents the effect of provenance k; $F_{l(k)}$ represents the effect of family l which is nested within-provenance k; e_{ijkl} represents the residual error with a mean of zero.

Computations of provenance means and analyses of variance were carried out using the GLM Procedure in SAS (SAS INSTITUTE 1992). For these analyses, provenances and replicates were regarded as fixed effects while families-within-provenances and blocks-within-replicates were regarded as random. The TEST option in the RANDOM statement of PROC GLM was used to obtain appropriate tests of hypotheses for these mixed model analyses of variance and to provide the

Table 1. Site details for the northern NSW *E. dunnii* provenance-family trials established in 1995.

Location	Latitude	Longitude	Alt. (m asl)	Mean annual rainfall (mm)	Geology	Soil classification	Soil pH	Aspect/slope	Prior land cover
Boambee Boambee State Forest near Coffs Harbour	30°18′	153°03′	60	1900	Shale, colluvium	Yellow Podzolic Gn2.51[1]	4.5–5.5	Generally S; 2–9 degrees	1950s *E. grandis* plantation
Megan Wild Cattle Creek State Forest near Megan (Dorrigo area)	30°17′	152°47′	730	1600	Devonian argillites, slates and siliceous greywackes	Yellow Podzolic Gn2.24[1]	5.0–6.0	Variable, generally S and W; 7–9 degrees	Mostly unimproved pasture; some natural forest regeneration in far N section

[1] Soil classification according to NORTHCOTE (1979).

Table 2. Details of provenances included in the two *E. dunnii* provenance-family trials established in 1995 in northern NSW.

Provenance number	Provenance name	Latitude	Longitude	Altitude (m)	CSIRO seedlot numbers	No. of families
1	Spicers Peak SF, Qld	28°04′	152°24′	675	16895, 17865, 17911	28
2	Teviot Falls, Qld	28°13′	152°32′	360	17914	12
3	Koreelah SF, NSW (1)	28°16′	152°28′	625	17915	9
4	Headgate Rd, Koreelah, NSW	28°16′	152°32′	625	18735, 18737, 18757	31
5	Koreelah SF, NSW (2)	28°18′	152°30′	575	17917	10
6	Bald Knob, NSW	28°18′	152°30′	660	18738	7
7	Acacia Creek, NSW	28°24′	152°20′	685	17920, 18756	23
8	Beaury SF, NSW	28°30′	152°22′	560	18736	11
9	Yabbra SF, NSW	28°35′	152°29′	565	17909, 18263	22
10	Haystack East Sect, Yabbra SF, NSW	28°36′	152°30′	550	18739	12
11	Yabbra Plains Rd, NSW	28°37′	152°29′	500	18264	12
12	18 km NNW Moleton, NSW	30°00′	152°54′	600	18734	7
13	Kangaroo River SF, NSW	30°05′	152°54′	420	17922	12
14	Moleton, NSW	30°09′	152°53′	500	18740, 18758	23
15	*E. grandis* – Wedding Bells Seed Orchard	30°09′	153°06′	105	C 86.01[1]	Bulk mix of >20 families

[1] The seedlot C86.01 was supplied by State Forests of NSW.

expectations of means squares, F ratios and probabilities for the appropriate tests. Provenance means were estimated as Least Squares Means (LSMEANS) from these analyses.

Within-provenance individual tree heritabilities (h_i^2) were calculated using the REML procedure in GENSTAT (PAYNE *et al.* 1987), following procedures described by WILLIAMS *et al.* (2002). For these mixed-model analyses the fixed and random effects were assigned as above and the *E. grandis* control seedlot (Provenance 15) was excluded from the data sets. Heritability values were estimated as follows:

$$h_i^2 = \frac{1}{r} \times \frac{\sigma_f^2}{\sigma_P^2}$$

where: r = coefficient of relationship, σ_f^2 = variance between families-within-provenances, σ_P^2 = phenotypic variance = $(\sigma_f^2 + \sigma_m^2 + \sigma_l^2)$, σ_m^2 = variance between plots, σ_l^2 = variance between trees within plots.

The coefficient of relationship (r) used in computation of individual tree heritabilities was assumed to be 0.4, rather than the value of 0.25 often used for half-sib families. Open-pollinated *E. dunnii* families from natural stands, like those of many other eucalypt species, are generally assumed to carry a degree of inbreeding resulting from selfing and neighbourhood inbreeding, and thus would not be true half-sibs (ELDRIDGE *et al.* 1993; BURGESS *et al.* 1996).

Genetic correlations between traits were calculated from variances and covariances obtained using a mixed model analyses carried out at the individual tree stratum using the MIXED procedure in SAS (SAS INSTITUTE 1992), following methodologies described by WILLIAMS *et al.* (2002). Phenotypic correlations were calculated using the CORR procedure in SAS (SAS INSTITUTE 1992).

Standard errors for the heritability and genetic correlation estimates were calculated according to BECKER (1984). To determine the significance of genotype × environment (i.e. provenance × site; and, family × site) interaction effects for volume and stem straightness, plot mean data from the two trials were pooled for a combined analysis across sites using the GLM procedure in SAS. The *E. grandis* material in both trials was also omitted from this analysis. The linear model given above was expanded to include a site effect; a provenance by site interaction; and a family-within-provenance by site interaction. Sites, replicates, provenances and provenances by sites were treated as fixed effects and family-within-provenance, site by family-within-provenance and block-within-replicate effects were treated as random.

RESULTS

Growth and stem straightness

The number of trees assessed and analysed in 5 replicates at Boambee was 93.2 % of full stocking (i.e. 2 trees remaining per row plot following the thinning in 1999). The "missing" trees were accounted for by windthrow, previous mortality, and a few damaged or stunted trees eliminated prior to analyses. At Megan there was 90.6 % of the full stocking in the analyses. Most of the missing trees had died in the first year, with a small number of surviving stunted trees and others damaged severely through loss of leaders in wind.

The mean tree volume at Boambee (236.5 dm^3) was 4.75 times that at Megan (49.7 dm^3) (Table 3). Stem straightness at both sites was very good. Differences between provenances at Megan were not statistically significant for these traits (p = 0.06 and 0.19 respectively) but they were at Boambee ($p < 0.01$, Table 4). However, it is important to note that the selective thinning carried out in the Boambee trial prior to the age-75 month assessment, which was carried out at an equal intensity within each family row plot, will have reduced within family variances resulting in greater power to detect significant differences at that site.

The best-ranking provenances for volume included 8 (Beaury SF), 10 (Haystack East, Yabbra) and 11 (Yabbra Plains Rd) at both sites. Trees from 6 (Bald Knob) and 14 (Moleton) grew well at Boambee, the latter with above average stem straightness.

As a group, the provenances from the species' southern-most population were not distinctly different from the northern provenances, for either mean tree volume or stem straightness (Table 3). However, material of Queensland origin (Provenance numbers 1 and 2) ranked poorly for mean tree volume at both sites. Provenance 1 (Spicers Peak SF) was especially poor at Boambee, and 2 (Teviot Falls) was poor at Megan, although both did show above average mean stem straightness. The Wedding Bells *E. grandis* grew very poorly at Megan with a mean tree volume less than half of the trial mean, and the worst stem straightness at that site. At Boambee *E. grandis* had a mean tree volume about 90 % of the trial average and by far the poorest stem straightness.

There were significant differences between families-within-provenances for stem straightness and volume both sites (Table 4). The top-ranking family at Boambee had a mean tree volume 5.4 times greater than that of the poorest *E. dunnii* family, and at Megan the range was even greater. Superior families for volume

Table 3. ***Eucalyptus dunnii*** **provenance means at approximately age 6 ½ years, for tree volume and stem straightness at Megan and for volume, stem straightness, and core density and collapse at Boambee.**

Provenance	Megan			Boambee				
	VOL (dm^3)	Rank by volume	STR[1] (point)	VOL (dm^3)	Rank by volume	STR (point)	Core density ($kg{\cdot}m^{-3}$)	Collapse %
1	48.556	10	3.73	178.8	15	3.54	462.2	17.3
2	39.353	14	3.68	224.9	11	3.75	462.5	16.0
3	56.733	1	3.43	230.1	10	3.31	479.0	12.8
4	50.365	6	3.70	253.8	7	3.62	475.2	13.4
5	47.238	11	3.49	207.0	13	3.64	–	–
6	50.142	7	3.72	264.2	3	3.43	470.9	15.0
7	53.066	4	3.59	252.2	8	3.39	463.0	14.6
8	53.781	2	3.73	257.3	5	3.44	488.1	10.3
9	43.383	12	3.48	231.0	9	3.55	448.0	13.2
10	53.317	3	3.88	261.6	4	3.66	458.8	20.4
11	52.614	5	3.66	284.2	1	3.49	467.4	16.2
12	42.051	13	3.54	187.3	14	3.37	491.3	12.5
13	49.297	9	3.54	256.3	6	3.32	478.7	11.1
14	49.912	8	3.74	267.1	2	3.61	465.1	12.8
15 (*E. grandis*)	22.858	15	3.10	215.1	12	2.67	–	–
Trial mean	49.71		3.66	236.5		3.53	466	14.9
Average S. E. D.	n. s.		0.16	20.9		0.13	n. s.	n. s.

S. E. D. : Standard Error of the Difference between provenance means.
n. s.: means not significantly different ($p < 0.05$).
[1] Stem straightness at Boambee assessed at age 39 months; volume at Boambee and volume and stem straightness at Megan were assessed at 75 months; and core density and collapse at Boambee assessed at 78 months.

originated from a wide range of provenances with the top 40 families at Boambee representing 12 of the 14 provenances. A similar group at Megan represented 13 of the 14 provenances. Families from provenance 1 (Spicers Peak SF) generally had very poor growth at Boambee, with 16 out of 28 families in the worst-ranking 20 % of families in the trial.

Wood properties

Differences between provenances at Boambee for core basic density and for collapse were not significant (Tables 3 and 4). However, differences between families-within-provenances were significant ($p < 0.05$). Family mean core densities varied from 418 to 516 kg m^{-3} and family means for percentage of maximum collapse varied from 5 to 37 %.

Estimates of heritability and correlations

Estimates obtained of individual tree heritability for volume and stem straightness at Megan and for straightness at Boambee were low (0.19, 0.16 and 0.14 respectively), with low standard errors. Whilst the estimate for volume at Boambee was moderate (0.28) (Table 5), this parameter will also have been affected by the within-family thinning carried out there.

Heritabilities for wood properties at Boambee were much higher, with the estimate for basic density being moderately high (0.42) and that for collapse being high (0.75), with low to moderate standard errors.

Favourable significant phenotypic correlations were found for volume with stem straightness at both sites, though the magnitude of this correlation at Boambee was very low (0.09) (Table 5). There were weak to moderate negative correlations for collapse with volume and with core basic density at Boambee (–0.14 and –0.24 respectively), implying that lower collapse is weakly associated with bigger trees and/or higher wood density. The phenotypic correlations of core basic density with volume, density with stem straightness and collapse with stem straightness at Boambee were very low and not significant.

The additive genetic correlation of volume with stem straightness was positive (favourable) and moderate at both sites (Table 5). Genetic correlations of core density with both volume and stem straightness were also moderate and positive (favourable) at Boambee. The genetic correlation of collapse with core basic

Table 4. Mean squares from analyses of variance for plot mean tree volume, stem straightness, core density and collapse of *E. dunnii* at approximately age 6 ½ years in two provenance-family trials in northern NSW.

Site	Source of variation	Volume		Stem straightness[1]		Core basic density		Collapse	
		df	Mean square	df	Mean square	df	Mean square	df	Mean square
Boambee	Provenance	14	73637**	14	1.4901**	12	2051.12 ns	12	51.47ns
	Family-within-provenance	205	14023**	205	0.6016**	37	1692.71**	37	39.89**
	Residual	857	7708	857	0.4093	195	870.34	190	16.60
Megan	Provenance	14	1280.44 ns	14	0.9141 ns		n. a.		n. a.
	Family-within-provenance	205	702.77**	205	0.6791**				
	Residual	615	357.33	615	0.3796				

ns = not significant; * = significant at $0.01<P\leq0.05$; ** = significant at $P\leq0.01$.

n. a.: trait not assessed.

[1] Stem straightness at Boambee assessed at age 39 months; volume at Boambee and volume and stem straightness at Megan were assessed at 75 months; and core density and collapse at Boambee assessed at 78 months.

Table 5. Genetic correlations ± standard errors (above diagonals), within-provenance, individual-tree heritabilities ± standard errors (along the diagonals) and phenotypic correlations (below the diagonals) among different traits of *E. dunnii* in provenance-family trials at Boambee and at Megan.

Site		Volume	Stem straightness[1]	Density	Collapse
Megan	Volume	0.19±0.04	0.53±0.13	n. a.	n. a.
	Stem straightness	0.34**	0.16±0.04	n. a.	n. a.
Boambee	Volume	0.28±0.07	0.31±0.69	0.55±0.82	0.99±0.55
	Stem straightness[1]	0.09**	0.14±0.05	0.66±0.47	–0.04±0.39
	Density	–0.03^{ns}	0.02^{ns}	0.42±0.21	–0.38±0.61
	Collapse	–0.14*	–0.03^{ns}	–0.24**	0.75±0.17

ns = phenotypic correlation not significant; * = phenotypic correlation significant at $0.01<P\leq0.05$; ** = phenotypic correlation significant at $P\leq0.01$.

n. a.: trait not assessed.

[1] Stem straightness at Boambee assessed at age 39 months; volume at Boambee and volume and stem straightness at Megan were assessed at 75 months; and core density and collapse at Boambee assessed at 78 months.

Table 6. Mean squares from analyses of variance across sites for plot mean tree volume and stem straightness of *E. dunnii* at approximately age 6 ½ years in two family trials in northern NSW.

Source of variation	Volume		Stem straightness	
	df	Mean square	df	Mean square
Site	1	12379311 **	1	5.2553 **
Replicate-within site	3	38075 **	3	4.8388 **
Provenance	13	39017 ns	13	1.5653 ns
Site x provenance	13	31225 **	13	0.5296 ns
Family-within-provenance	205	7931 **	205	0.8182 **
Site x family-within-provenance	502	5497 **	205	0.5553 **
Residual	1456	4307	1462	0.4032

ns = not significant; * = significant at $0.01<P\leq0.05$; ** = significant at $P\leq0.01$.

n. a.: trait not assessed.

[1] Stem straightness at Boambee assessed at age 39 months; volume at Boambee and volume and stem straightness at Megan were assessed at 75 months.

density was low to moderate and negative (–0.38), which is also considered favourable as it indicates higher density is associated with lower collapse. The genetic correlation of volume with collapse was very high and positive (0.99), which is unfavourable. However, the standard error of the genetic correlation estimates were generally large and ranged up to ±0.82 for the correlation of volume with density at Boambee (Table 5).

Genotype × environment interactions

Provenance by site interactions in these trials were significant ($p < 0.01$) for volume but not for stem straightness (Table 6), with some provenances showing moderate to large rank changes for volume between sites. Provenance 3 (Koreelah 1) was the best at Megan for volume but only 10th at Boambee (Table 3).

Family-within-provenance by site interactions were significant ($p < 0.01$) for both volume and stem straightness (Table 6). Seven families showed well above average volume at both sites. More than 60 families were close in ranking and showed relatively stable performance across the sites. Of the 40 top-ranking families at Boambee, 11 were also in the best 40 at Megan.

DISCUSSION

The relatively poor growth of trees at Megan, compared with that at Boambee, was attributed to a combination of factors. Megan is a tableland site with a shallower soil and cooler, drier climate including frequent winter frosts and a shorter growing season than the coastal Boambee site. During the summers of 1995–96 and 1996–97, attack by insects (especially Christmas beetles, *Angloganthus* spp., and sawflies, *Perga* spp.) caused moderate to heavy defoliation at Megan, effectively reducing some of the height increment gained in preceding springs. In contrast, insect attack at Boambee was very light and did not significantly affect the growth of the trees.

Trees from the northern-most provenance of *E. dunnii*'s range (1 – Spicers Peak SF) had relatively poor volume growth in both trials to age-6½ years. However, the three southern provenances (12, 13 and 14, from the Moleton–Kangaroo River area) were variable in ranking for volume at both sites. Two of the southern provenances were intermediate to superior while the other (18 km NNW of Moleton) was poor. Overall, the results indicate that growth potentials of provenances from both the northern and southern populations are similar. This concurs with results from trials in both South Africa (NIXON & HAGEDORN 1984) and China (WANG *et al.* 1999) where provenances from the northern and from the southern populations have also shown similar growth.

The magnitude of the variation between the *E. dunnii* provenances for volume was substantial, particularly at Boambee where mean tree volume for the best provenance (11 – Yabbra Plains Road) was approximately 60 % greater than that of the poorest provenance (1 – Spicers Peak SF). At Megan, mean tree volume of the best provenance (3 – Koorelah) was about 45 % greater than that of the poorest (2 – Teviot Falls). Most of the growth results reported to date from other *E. dunnii* trials have shown smaller differences, albeit for only diameter and height parameters. In a trial assessed at age-10 years in the Moji Mirim region of Brazil the two *E. dunnii* provenances (McPherson Range NSW and Urbenville NSW) differed by about only 10 % in height and 5 % in diameter at breast height (PIRES & PARENTE 1986). At a site in Natal the best two provenances for four-year diameter at breast height (Moleton NSW [12.9 cm] and near Coffs Harbour [12.6 cm], possibly collected from the same stand) exceeded growth of the poorest provenance, Bushman Range NSW (11.6 cm), by less than 10 % (NIXON & HAGEDORN 1984). In a series of trials of 10 provenances across two sites in China, variation in diameter at breast height at age-five years between the best and poorest provenances at any one site was as low as 5 % of the trial mean (WANG *et al.* 1999).

Seedlots of many eucalypt species from natural stands often carry a degree inbreeding due to selfing and mating between neighbouring close relatives (ELDRIDGE *et al.* 1993, BURGESS *et al.* 1996). As *E. dunnii* is known to be a particularly shy flowering species (BOLAND 1984, GRACA 1987), there is a strong likelihood that many of the seedlots used in these trials carried a degree of such inbreeding and this may have influenced their growth performance. With *E. grandis* BURGESS *et al.* (1996) found that individual out-crossing rates ('t' values) in natural stand provenances ranged as low as 0.34 and that variation in out-crossing rates between parent trees may have large influences on differences in growth rates among progenies (BURGESS *et al.* 1996).

Although stem straightness also differed significantly between provenances at Boambee, this is of little consequence given the low magnitude of the variation (the range of provenance means for stem straightness was 3.48 to 3.88 at Boambee and 3.43 to 3.88 at Megan) and the species' generally superior stem form. *E. grandis*, a species generally considered to have good stem straightness (CABI 2000), proved inferior to *E. dunnii* for stem straightness in these trials. *E. grandis* was also substantially inferior in volume at Megan and mediocre to poor at Boambee. Winter frosts at Megan were a factor in its relatively poor volume growth there. *E. dunnii* is known to be better adapted than *E. grandis* for sites subject to frequent winter frosts (down to –8 °C) (CABI 2000).

As detailed above, the selective thinning of the Boambee trial at approximately age-four years will have biased some of the results obtained from the 75-month assessment at that site. Separate studies have revealed that such selective thinning of genetic trials can decrease phenotypic variance whilst increasing estimates of genetic variance (MATHESON & RAYMOND 1984). This would almost certainly have contributed to the higher heritability for volume at Boambee than at Megan. In comparison, heritability estimates for stem straightness were similar, and this trait at Boambee was measured prior to the thinning.

The finding that heritabilities for both of the wood traits were much stronger than those for either volume or stem form in *E. dunnii* is generally consistent with results for other eucalypt species (see ZOBEL *et al.* 1983, ELDRIDGE *et al.* 1993, RAYMOND 2000). In contrast, the positive genetic correlation between volume and basic density suggested by this study differs from most of those published for other eucalypts, which have been negative (RAYMOND 2000). However, the standard errors on most of the genetic correlations from the Boambee site, including that for the genetic correlation of volume and basic density (i.e. 0.55±0.82), were very large and further studies are clearly needed to obtain more meaningful and reliable estimates for most of the combinations of traits.

The high positive genetic correlation between collapse and volume found at Boambee (0.99±0.55) is clearly unfavourable. KUBE *et al.* (2001) also found a strong unfavourable genetic correlation (0.78±0.10) between growth (diameter at breast height) and collapse in increment cores from 12-year-old *E. nitens* in Tasmania. Reasons for such unfavourable high correlations are uncertain. They imply that those trees with genetically superior growth are also genetically inclined to produce timber more prone to collapse. Although most collapse can be 'recovered' or reversed by steam reconditioning (BROWN *et al.* 1952), it would be advantageous for such treatment to be unnecessary.

The instability of *E. dunnii* provenance and family growth performance between the environments represented at the two trial sites will not necessarily impose unnecessary complications on the *E. dunnii* improvement programs for northern NSW and adjacent areas. A reasonable proportion of higher ranked families for volume showed either stable performance across the two environments or a strong responsiveness to favourable sites. Such results indicate it might be possible to compose a single advanced-generation breeding population for an improvement program to service such environments, given that the Boambee and Megan trials between them provide a base breeding population that is sufficiently large for high selection intensities to be adopted. Nonetheless, further investigation of genotype by environment interactions along with other genetic parameters will be warranted in a subsequent improved generation of *E. dunnii*, once inbreeding effects inherent in open-pollinated seed from its natural stands have been reduced.

CONCLUSIONS

Even though *E. dunnii* has a relatively narrow natural distribution, the species does contain significant genetic variation for growth, wood basic density and core collapse. The greater proportion of this arises due to differences within rather than between provenances. Favourable genetic correlations between most of the key traits should enable improvement programs to produce faster growing trees that also provide higher quality, more valuable timber.

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