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P.D. Kube, N.M.G. Borralho, I. Bail, W.N. Tibbets, and R. McConnochie

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ABSTRACT

The genetic control of diameter growth of *Eucalyptus nitens* was studied in open pollinated progeny trials in Australia and New Zealand. A total of 42,582 progeny from 370 native forest mother trees were grown on 29 different sites. The pooled regional heritabilities in Tasmania, Victoria and New Zealand were 0.33, 0.32 and 0.20 respectively. The genetic correlations between Victoria and Tasmania, and Victoria and New Zealand were 0.71 and 0.89, respectively. This suggests that transfer of genetic material and breeding information between regions should be effective. Family by site variance, within and across regions, was significant but low, and accounted for 3 to 5% of total variation. In the few trials where measurements were taken at different ages, a very high age to age genetic correlation was observed.

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INTRODUCTION

Eucalyptus nitens (Deane & Maiden) Maiden is an important cool-temperate hardwood plantation species in Australia (Tasmania and Victoria) and New Zealand. Pulpwood is the main product, although there is interest in using this species for sawn timber and reconstituted products. Currently in Australia there is approximately 48,000 ha of *E. nitens* in plantations, and an annual planting rate of about 7,000 ha. In New Zealand there is about 8,000 ha of plantation with an annual planting rate of about 5,000 ha. Plantation areas are expanding in both Australia and New Zealand.

Studies of the genetic variation in *E. nitens* began in the mid 1970's. Early work concentrated on provenance variation. There have been studies of the genetic variation of growth between provenances in Victoria (pederick 1979, 1985), Tasmania (Kube 1993), New Zealand (King and Wilcox 1988), and South Africa (Purnell and Lundquist 1986, Stanger 1991). Genetic parameters for growth traits in *E. nitens* have been published (King and Wilcox 1988, Woolaston *et al.* 1991, Whiteman *et al.* 1992, Hodge *et al. 1995)* but these were based on only one or a few sites. Genetic parameters across broad geographic regions have not been calculated.

A comprehensive analysis of the genetic control of growth in *E. nitens* is an important prerequisite for breeding value prediction. This analysis is especially important when selection and deployment trees covers diverse sites and regions. In particular, an assessment of the magnitude of additive, plot, genotype by site, and error variances and covariances is required (Jarvis *et al.* 1995). In this study the genetic control of growth across a wide range of sites in Australia and New Zealand is examined. Genetic parameters are calculated and the importance of genotype-environment interactions are investigated.

MATERIALS AND METHODS

Genetic material

Collections of *E. nitens* genetic material used in this study were done between 1971 and 1985. Four collections were made independently by different organisations. These were Victorian Department of Conservation and Natural Resources (144 families between 1971 and 1981), Kylisa Seeds (146 families between 1982 and 1985), CSIRO Tree Seed Centre (36 families in 1976), and North Forest Products (44 families in 1980).

The genetic material consisted of 42,582 open pollinated progeny from 370 native forest mother trees. Most mother trees were randomly selected from the central Victorian provenances (Toorongo, Macalister and Rubicon) in roughly equal proportions (see Pederick 1979 for definition of provenances). Other provenances (Errinundra, Southern NSW, and Northern NSW) were poorly represented in the trials, and were excluded from this analysis. Families from the Christmas Creek and Tanjil Bren populations (Toorongo provenance) were also excluded. They are now classified as *E. denticulata* (Cook and Ladiges 1991), and have shown significantly poorer growth than core *E. nitens* from Victoria and southern NSW (Pederick 1979). However populations likely to be intermediate between *E. nitens* and *E. denticulata* on the Toorongo Plateau could not be identified and may have been included.

Trial establishment and assessment

Progeny were planted on 29 sites in Tasmania, Victoria and New Zealand. Trials were established independently by seven organisations between 1976 and 1990, and covered a wide range of soil types, rainfalls and altitudes (Table 1). Consequently growth rates varied considerably between sites. Most were on good to fair sites although some were on sites that would not normally be used for *E. nitens* plantations (trials 13, 15, 16 and 17). All trials were cultivated prior to planting and received fertiliser following planting. Spacing for all trials was in the vicinity of 1000 trees per ha but sites 23 and 24 were thinned to about 300 trees per ha prior to assessment by thinning four tree plots to single tree plots.

Trials established by each organisation were designed to have families replicated across sites, but there were no coordinated efforts to ensure genetic links across different organisations. However there were sound links between most trials because all organisations sourced their material from the same collections. In addition, the policy of free distribution of seedlots followed by the Department of Conservation and Natural Resources resulted in some seedlots being used by all organisations. Of the 370 families represented, 51% were established on five or more sites and 66% were on three or more sites.

Most trials were were randomised complete block designs, with varying numbers of trees per plot and blocks (Table 1). The number of families in each trial varied from 27 to 175, and the number of trees ranged between 233 and 3381. Trials 14, 15, 16, and 17 had families nested in sublines. Each trial had four sublines linked by 6 control seedlots. The controls were two *E. nitens* open pollinated family seedlots, and two bulked seedlots of *E. globulus* and *E. regnans*.

The only trait included in this analysis was diameter at breast height (dbh) over bark. Assessment ages ranged between 2 and 16 years although 80% of trials were between 4 and 9 years old (Table 1). Trees were excluded from the analysis if they had more than one leader below breast height, or were damaged by physical or biological agents such that the mean for those damage classes was substantially below the trial mean. No more than 2% of trees were excluded from any trial after applying these criteria.

Table 1: Description of *Eucalyptus nitens* trial sites and trial designs.

Trial no.[1]	Location	Local number	Owner[2]	Region	Lat. (° ' S)	Long. (° ' E)	Alt. (m)	Rainfall (mm)	Year planted	Age (years)	Trial design[3]	No. reps.	Trees per plot	No. fam.	No. trees
1	Dial Range	RP252/3	FT	Tas	41 10	146 03	100	1060	1984	6	RCB	16	1	33	480
2	Gog Range	RP252/4	FT	Tas	41 29	146 23	300	1200	1984	6	RCB	16	1	33	446
2	Kamona	RP252/5	FT	Tas	41 08	147 40	150	1150	1984	6	RCB	16	1	33	424
4	Meunna	RP252/7	FT	Tas	41 05	145 29	250	1610	1988	5	RCB	4	20	30	2110
5	Winkleigh		BT	Tas	41 17	146 50	160	955	1989	5	RCB	10	5	31	1376
23	Huntsman SO	81/04.4	NFP	Tas	41 43	146 37	480	1100	1982	6	RCB	8	1	27	233
24	Hampshire SO	81/04.1	NFP	Tas	41 17	145 44	540	1536	1984	7	RCB	17	1	27	459
25	Hampshire Ext.	81/04.3	NFP	Tas	41 17	145 44	540	1536	1981	6	RCB	14	1	80	895
26	Hampshire Farm	81/04.2	NFP	Tas	41 14	145 47	460	1536	1984	6	RCB	24	1	48	824
27	Massy Greene	86/01.2	NFP	Tas	41 05	145 54	145	990	1986	4	RCB	22	1	173	2759
28	Huntsman 86	86/01.4	NFP	Tas	41 43	146 35	430	1100	1986	6	RCB	20	1	175	3309
29	Hunstman 82	81/04.5	NFP	Tas	41 43	146 37	420	1100	1982	6	RCB	3	9	33	792
6	Narbethong	EUC436	CFTT	Vic	37 32	145 36	770	1200	1975	6	RICB	3	8	41	881
7	Powelltown	EUC435	CFTT	Vic	37 50	145 36	600	1480	1975	6	RICB	6	8	41	1806
8	Toolangi	EUC439	CFTT	Vic	37 30	145 27	620	1200	1978	16	RICB	8	8	44	1453
9	Powelltown	EUC438	CFTT	Vic	37 50	145 45	600	1480	1978	16	RICB	4	8	46	787
10	Jeeralang	VRD26	APL	Vic	38 28	146 30	600	1200	1978	9	RCB	5	8	35	1143
11	Silver Creek	VRD28	APL	Vic	38 18	146 16	160	970	1986	4	RCB	40	1	94	3351
12	Silver Creek	VRD29	APL	Vic	38 18	146 20	106	910	1986	4	RCB	40	1	94	3247
13	Flynn	VRD30	APL	Vic	38 13	146 40	80	730	1986	4	RCB	40	1	94	3381
14	Mt Worth	VRD41	APL	Vic	38 16	146 02	380	1180	1988	6	RCB-S	20	1	87	1731
15	Flynn	VRD42	APL	Vic	38 13	146 46	80	680	1988	6	RCB-S	20	1	85	1511
16	Glencoe	VRD43	APL	Vic	38 13	147 04	90	620	1988	6	RCB-S	20	1	82	1579
17	Stockdale	VRD44	APL	Vic	37 62	147 10	80	700	1988	6	RCB-S	20	1	82	1499
18	Tostaree	EUC441	CFTT	Vic	37 47	148 11	20	880	1992	2	RICB	10	3	38	1103
19	Kuark	EUC442	CFTT	Vic	37 35	148 43	250	1100	1992	2	RICB	10	3	39	1138
30	Rotoaira	R1830/3	NZ FRI	NZ	39 04	175 45	700	900	1978	8	RCB	36	1	79	2389
31	Longwood	S420/4	NZ FRI	NZ	46 15	167 47	100	1500	1978	8	RCB	27	1	41	773
32	Kaingaroa	R1977	NZ FRI	NZ	38 10	176 40	230	1500	1979	6	RCB	30	1	77	1954

[1] Trial numbers allocated in this study.

[2] FT = Forestry Tasmania, BT = Boral Tasmania, NFP = North Forest Products, CFTT = Centre for Forest Tree Technology, APL = Amcor Plantations, NZ FRI = New Zealand Forest Research Institute.

[3] RCB = randomised complete block, RICB = randomised incomplete block, RCB-S = randomised complete block within sublines.

Statistical analysis

The model used in the analysis of each trial was, in matrix notation:

$$y = Xb + Z_u u + Z_p p + e$$

where y is the vector of individual tree observations for dbh, b is the vector of fixed block effects, u is the vector of individual and parental tree breeding values, p is the vector of random plot effects, and e is the vector of residuals. The terms X, Z_u and Z_p are incidence matrices relating effects to terms in the model (replicates, tree and plot respectively). Provenances were initially included for some trials (4, 13 and 14), but they were not significant and were removed.

Trial data was combined for regional analyses where regions were arbitrarily defined as Tasmania, Victoria, and New Zealand. In this analysis the model was:

$$y = Xb + Z_u u + Z_p p + Z_i i + e$$

where b is the vector of fixed block within site effects, i is the vector of random family by site interaction terms within a region, Z_i is the incidence matrix for these effects, and the other symbols are the same as those used above. There was a wide range in error variances between trials. Therefore values were divided by the phenotypic standard deviation for each trial in analyses combining data from different trials. Trials 5, 23, 24, 26 and 29 were excluded from the combined analyses because the data appeared aberrant. Reasons for excluding each of these trials are discussed in greater detail in the next section.

Variance components, heritibilities, and the standard error of heritabiities were calculated using the program DFREML (Meyer 1991a) which assumes half-sib families. The simplex procedure of Nelder and Mead (1965) was used to reach convergence, with a stopping criteria for the variance of the function values in the simplex (-2log$L$) set at 10^{-7}. An outcrossing rate of about 70% is usually assumed in natural stands of eucalypts, and the appropriate coefficient of relationship is r = $^1/_{2.5}$ (Griffin and Cotterill 1988). Therefore heritabilities and standard errors were subsequently adjusted.

In Trials 14, 15, 16 and 17, families were nested within sublines. Individual tree measurements were adjusted for subline and replicate effects before the calculation of variance components. First, subline effects were calculated, using the following model:

$$yc = Xs + Z_1 r + Z_2 c + e$$

where yc is the vector of individual observations for the control seedlots only, s is the fixed subline effects, r is the random replicate within subline effects and c is the random control seedlot effects. The terms X, Z_1 and Z_2 are incidence matrices for the fixed and random effects (sublines, replicates, and control seedlot respectively). After all data were adjusted for subline effects, replicate within subline effects were calculated using the following model:

$$y = Xr + Zf + e$$

where y is the vector of individual observations for all trees, f is the random family effects, and r is the random replicate within subline effects. The REML procedure on GENSTAT 5 was used for these calculations.

Pair-wise genetic correlations between sites and regions, and age to age correlations were calculated using DFREML (Meyer 1991a). This uses a bivariate REML analysis (Schaeffer *et*

al. 1978, Meyer 1991a) to calculate variance and covariance components, with covariances estimates based on the information from relatives across sites. Convergence was determined using the same procedure as that in the univariate analyses. Genetic correlations were calculated between regions, and for pairs of sites (across all regions) for which there were more than 15 families in common. Plot effects were removed from the bivariate model due to computing limitations. Standard errors of genetic correlations were calculated according to Falconer (1989).

RESULTS AND DISCUSSION

Variance components and heritabilities

Additive variance appeared strongly related to tree size, and generally increased in proportion to mean tree diameter (Table 2 and Figure 1a). Trial 26 fell slightly below this trend, but was known to have had unusual establishment methods which would affect tree growth and the expression of genetic differences.

The relationship between error variance and mean tree size was less clear. Although error variance appeared to also increase in proportion to tree size, several trials did not conform to this trend (Table 2 and Figure 1b). Trials 23 and 24 had very low error variances and this was probably due to within plot culling where the original four trees per plot were reduced to a single tree. A possible explanation for other error variances being below the trend is that error variance is greatly influenced by local environmental conditions. Site and age (or tree size) effects are confounded in this data set, and it is known that error variance can vary considerably from site to site. Therefore the exact change in error variance relative to additive genetic variance probably cannot be seen in this data set.

Plot variance, a measure of family by block interaction, could only be estimated in trials with multiple tree plots. Plot variances were generally small, accounting for between 1 and 11% of total variation (Table 2). The only exception was trial 5, where plots accounted for 25% of total variation. Such a high value is likely to indicate errors in recording seedlot identities for some plots.

Individual trial heritabilities ranged between 0.08 and 0.59 (Table 2). Standard errors were between 0.03 and 0.18, with most being less than 0.1. There was no apparent relationship between mean dbh of the trial and heritability (Figure 1c). Some of the extreme values are likely to be biased. Trial 5 (h^2 = 0.08) was a progeny trial of a small number of second generation selections, and the additive genetic variance may be reduced due to selection. Heritabilities for trials 23 and 24 (h^2 = 0.51 and 0.59 respectively) are probably inflated due to the reduction in error variance after within plot culling. For other extreme values (trials 13 and 14) there was no obvious explanation, even after close examination of the data. However despite this apparent wide range of heritibilities, only trials 6 trials (numbers 5, 13, 14, 26, 28 and 31) were significantly different at 5% level from the average heritability (0.31).

Figure 1: Relationships between mean diameter of trial and (a) additive genetic variance, (b) error variance, and (c) heritability. Data points indicate the code each trial (see Table 1).

Figure 1a

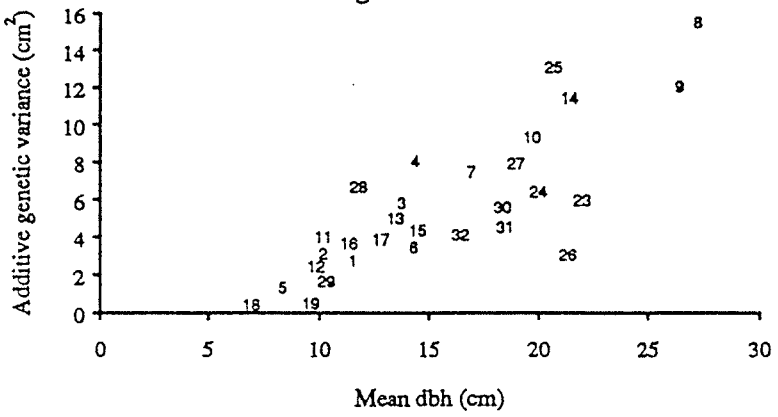

Figure 1b

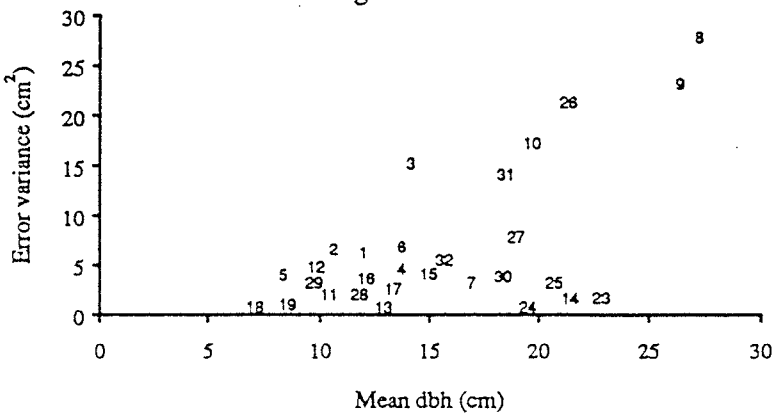

Figure 1c

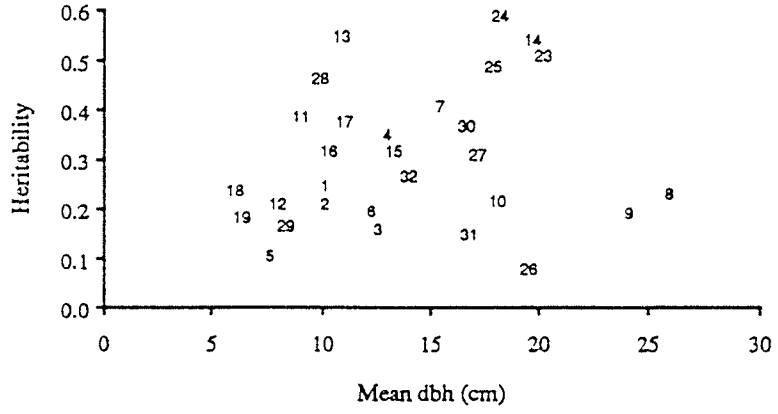

Table 2: Variance components and heritabilities for diameter at breast height on each trial site.

Trial code	Location	Region	No. records	No. fam.	Mean dbh (cm)	Additive genetic variance (cm^2)	Plot variance (cm^2)	Error variance (cm^2)	Heritability [1] (± s.e.)
1	Dial	Tas	480	33	10.3	3.6		5.7	0.24 ± 0.09
2	Gog	Tas	446	33	9.9	3.2		6.1	0.21 ± 0.09
3	Kamona	Tas	424	33	13.0	5.3		15.4	0.16 ± 0.08
4	Meunna	Tas	2110	30	13.2	8.1	1.6	4.9	0.35 ± 0.11
5	Winkleigh	Tas	1231	35	7.9	1.2	1.7	4.1	0.11 ± 0.06
23	Huntsman SO	Tas	233	27	20.6	6.1		1.4	0.51 ± 0.18
24	Hampshire SO	Tas	459	27	18.6	6.5		0.4	0.59 ± 0.14
25	Hamsphire Ext.	Tas	895	80	19.3	13.1		3.4	0.50 ± 0.09
26	Hampshire Farm	Tas	824	48	20.0	3.2		21.5	0.08 ± 0.04
27	Massy Greene	Tas	2759	173	17.6	8.0		8.0	0.31 ± 0.04
28	Huntsman 86	Tas	3309	175	10.4	6.8		2.2	0.47 ± 0.05
29	Huntsman 82	Tas	792	33	8.9	1.8	0.9	3.4	0.18 ± 0.10
6	Narbethong	Vic	881	41	12.6	3.7	0.9	7.0	0.20 ± 0.09
7	Powelltown	Vic	1806	41	15.8	7.6	0.5	3.3	0.41 ± 0.09
8	Toolangi	Vic	1453	44	26.1	15.6	1.2	28.0	0.22 ± 0.06
9	Powelltown	Vic	787	46	25.2	12.1	0.3	23.4	0.21 ± 0.08
10	Jeeralang	Vic	1143	35	18.3	9.4	0.1	17.4	0.22 ± 0.06
11	Silver Crk 1	Vic	3351	94	9.5	4.1		2.5	0.39 ± 0.06
12	Silver Crk 2	Vic	3247	94	8.5	2.5		4.9	0.21 ± 0.03
13	Flynn	Vic	3381	94	11.6	4.9		0.5	0.56 ± 0.07
14	Mt Worth	Vic	1731	87	20.0	11.5		1.8	0.54 ± 0.08
15	Flynn	Vic	1511	85	13.6	4.3		4.3	0.32 ± 0.06
16	Glencoe	Vic	1578	82	10.7	4.0		3.8	0.32 ± 0.06
17	Stockdale	Vic	1499	82	11.4	3.7		2.4	0.38 ± 0.07
18	Tostaree	Vic	1103	38	6.3	0.6	0.1	0.9	0.24 ± 0.08
19	Kuark	Vic	1138	39	7.2	0.6	0.2	1.2	0.19 ± 0.07
30	Rotoaira	NZ	2389	79	17.0	5.7		4.0	0.37 ± 0.06
31	Longwood	NZ	773	41	17.1	4.6		14.3	0.15 ± 0.06
32	Kaingaroa 1	NZ	1954	77	14.3	4.3		5.7	0.27 ± 0.06

[1] Heritabilities and standard errors adjusted for a coefficient of relationship of 0.4.

Heritabilities for the pooled analyses in Tasmania and Victoria were very similar but heritability in New Zealand appeared significantly lower (Table 3). The heritability from a combined analysis was 0.28. These values are in the upper limit of the range reported for this species in previous estimates (Woolaston *et al.* 1991, Whiteman *et al.* 1992, Hodge *et al.* 1995). The heritabilities appear to be greater than reported for other eucalypt species growing in Australia, such as *E. globulus* (Borralho *et al.* 1995), and *E. regnans* (Raymond 1995).

Family by site interaction within each region was consistently small, accounting for 2 to 4% of total variance. For all regions combined the relative size of family by site variation was 4% (Table 3). This suggests genotype by environment interaction for growth is small, a result which will be later discussed in the context of genetic correlations.

Table 3: Variance components of standardised data and heritabilities for diameter in each region, and for all regions combined.

Region	Additive genetic variance	Family by site variance	Plot variance	Error variance	Heritability (± standard error)
Tasmania	0.54	0.03	0.10	0.34	0.33 ± 0.04
Victoria	0.50	0.02	0.03	0.44	0.32 ± 0.03
New Zealand	0.32	0.04	0.00	0.63	0.20 ± 0.04
All combined	0.45	0.04	0.05	0.46	0.28 ± 0.03

[1] Heritabilities and standard errors adjusted for a coefficient of relationship of 0.4.

Age to age correlations

Site and age effects can confound the comparison of genetic parameters between trials. For most trials in this study there was no way to separate these effects since trials were only measured once. However multiple measurements were made in a small number of trials (numbers 4, 6, 9, 30 and 32). The genetic correlations between diameter growth at different ages ranged between 0.67 and 0.97 (Table 4). Interestingly, the correlation between age one height and age five diameter was also relatively high. These high values for age to age correlations agree well with previous estimates from *E. globulus* (Borralho *et al.* 1992).

The data suggests that selection when dbh is about 8 cm (probably three to four years old) is an appropriate indicator of growth at later ages. This is encouraging since it indicates that results derived from the current data set will remain valid at later ages.

Table 4: Additive genetic variances, error variances, heritibilities and genetic correlations for early age and late age assessments of diameter.

Trial no.	Location	Age (years)	Mean dbh (cm)	Genetic correlation
4	Meunna, Tas	1[1] and 5	0.9[1] and 13.1	0.77
6	Narbethong, Vic	6 and 19	12.5 and 27.1	0.97 ± 0.01
9	Powelltown, Vic	3 and 16	7.4 and 25.2	0.92 ± 0.01
30	Rotoaira, NZ	3 and 8	4.8 and 17.0	0.67 ± 0.07
32	Kaingaroa, NZ	2 and 6	5.6 and 14.3	0.90 ± 0.03

[1] Age 1 measurements at Meunna were for height (in m).

Genetic correlations

Genetic correlations between trials within a region were generally high. Values ranged from 0.40 to 1.00, with an average of 0.81 (Table 5). The standard errors of the correlations (not shown here) ranged between 0 and 0.18, but in most cases were less than 0.1. Trials established with the same seedlots in the same year (these are trials appearing close to the diagonal on Table 5) usually had higher correlations than those of trials established in different years. For example, correlations between trials 14 to 17, 11 to 13, and 1 to 3 had an average of 0.92, whereas correlations between trials 1, 2 and 3 and 25, 27, and 28 had an average of 0.74. Some trials (such as 13, 15, 16, 17) are on sites with relatively low rainfall and infertile soils where *E. nitens* would not be routinely planted. Nevertheless, performance at these sites

still showed very high correlations with more typical *E. nitens* sites. Overall, correlations of less than about 0.75 within a region were uncommon and it appears that genetic merit for growth at any one site will be a reliable indicator at other sites. Correlations less than 0.75 were often based on a relatively small number of families, and therefore these should be viewed with caution.

Table 5: Genetic correlations between sites (upper diagonal) and number of common families between sites (lower diagonal and in italics).

Region		Tas									Vic												NZ		
	Trial	1	2	3	4	23	24	25	27	28	6	7	8	9	10	11	12	13	14	15	16	17	30	31	32
Tas	1		1.00	0.88				0.61	0.49	0.69									0.42	0.47	0.62	0.68			
	2	*31*		1.00				0.91	0.65	0.92									0.30	0.21	0.41	0.69			
	3	*31*	*34*					0.99	0.51	0.91									0.64	0.56	0.49	0.73			
	4	*0*	*0*	*0*															0.73	0.79	0.34	0.77			
	23	*0*	*0*	*0*	*10*		0.58		0.72																
	24	*0*	*0*	*0*	*10*	*27*		1.00	0.80	0.74															
	25	*21*	*21*	*21*	*10*	*8*	*8*		0.76	0.84			0.25	0.02					0.26	-0.15	0.16	0.30			
	27	*21*	*21*	*21*	*18*	*21*	*21*	*70*		0.84			0.20	0.29		0.94	0.71	0.85	0.45	0.18	0.48	0.67			
	28	*21*	*21*	*21*	*18*	*22*	*22*	*70*	*171*							0.82	0.73	0.72	0.53	0.25	0.70	0.74			
Vic	6	*0*	*0*	*0*	*3*	*2*	*2*	*6*	*7*	*7*		0.95	1.00	0.80											
	7	*0*	*0*	*0*	*3*	*2*	*2*	*6*	*7*	*7*	*56*		0.64	0.61											
	8	*0*	*0*	*0*	*4*	*1*	*1*	*22*	*17*	*17*	*12*	*12*		1.00									0.79		0.80
	9	*0*	*0*	*0*	*4*	*1*	*1*	*21*	*16*	*16*	*13*	*13*	*46*										0.99		0.90
	10	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*									0.88	0.94	0.76
	11	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*84*	*84*	*0*	*0*	*0*	*0*	*0*		0.91	0.93							
	12	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*84*	*84*	*0*	*0*	*0*	*0*	*0*	*94*		0.93							
	13	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*84*	*84*	*0*	*0*	*0*	*0*	*0*	*94*	*94*								
	14	*34*	*34*	*34*	*20*	*7*	*7*	*46*	*51*	*51*	*6*	*6*	*5*	*5*	*0*	*2*	*2*	*2*		0.86	0.86	0.86			
	15	*34*	*34*	*34*	*20*	*7*	*7*	*46*	*51*	*51*	*6*	*6*	*5*	*5*	*0*	*2*	*2*	*2*	*89*		0.97	0.91			
	16	*34*	*34*	*34*	*20*	*7*	*7*	*46*	*51*	*51*	*6*	*6*	*5*	*5*	*0*	*2*	*2*	*2*	*89*	*89*		0.94			
	17	*34*	*34*	*34*	*20*	*7*	*7*	*46*	*51*	*51*	*6*	*6*	*5*	*5*	*0*	*2*	*2*	*2*	*89*	*89*	*89*				
NZ	30	*0*	*0*	*0*	*1*	*2*	*2*	*10*	*7*	*7*	*4*	*4*	*14*	*13*	*32*	*0*	*0*	*0*	*2*	*2*	*2*	*2*		0.77	0.63
	31	*0*	*0*	*0*	*0*	*3*	*3*	*7*	*6*	*6*	*1*	*1*	*7*	*6*	*15*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*41*		0.40
	32	*0*	*0*	*0*	*0*	*5*	*5*	*12*	*10*	*10*	*4*	*4*	*14*	*13*	*33*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*75*	*38*	

Genetic correlations between pairs of sites in different regions were also generally high, but had a greater range of values than those within a region. Values ranged between -0.15 and 0.94, with an average of 0.56 (Table 5). A close examination of pairs of trials with very poor genetic correlations suggests this result may be due to errors in seedlot coding between organisations. For example, trial 25 was linked to trials 14 to 17 by two separate seed collections. Correlations were calculated separately for each collection. For one collection correlations were reasonable to good, and for the other correlations were very poor. A coding error would also explain the very poor correlations of trials 25 to 28, with trials 8 and 9. Given the irregular nature of the overlap between trials these types of errors do not manifest themselves in every trial, and for most pairs of trials, the coding appears accurate. When trial 25 was excluded, the average genetic correlation between pairs of sites in different regions

increased to 0.68. These results suggest correlations between sites in different regions may not be very different from those within a region.

Genetic correlations between pooled data from Tasmania, Victoria and New Zealand (the latter only based on three trials) were high, and in the vicinity of 0.7 (Table 6). Reliable correlations between Tasmania and New Zealand could not be calculated since there were only 11 families in common between these regions. These correlations cover a wide range of site conditions, planting years, and parents and therefore can be considered accurate. This indicates that genotype by environment interactions across regions are present but are probably not large.

Table 6: Genetic correlations and their standard errors between regions (upper diagonal) and numbers of common families between regions (lower diagonal).

Region	Tasmania	Victoria	New Zealand
Tasmania		0.71 ± 0.03	not calc.
Victoria	179		0.89 ± 0.02
New Zealand	11	50	

CONCLUSION

The present study, the most comprehensive carried out for *E. nitens*, showed diameter was under moderate genetic control. Heritabilities for the 29 trials ranged between 0.08 and 0.59. Regional heritibabilities, which were calculated from pooled data, for Tasmania, Victoria and New Zealand were 0.33, 0.32 and 0.20 respectively. When data was pooled across all regions the heritability was 0.31. This value is in the upper limit of the range reported for this species in previous estimates.

Age to age correlations for diameter growth were also high. Of the four trials for which repeated diameter measurements were available, three had genetic correlations greater than 0.90. It appears that diameter measurements made when trees have a diameter of about 8 cm are often a good indicator of later age growth.

Genetic correlations between pairs of sites both within and across regions were generally good. Estimates covered a wide range of values, with an average of about 0.70. Although some pairs of sites appeared to have very low genetic correlations, it is probable that these result from seedlot coding errors and not biological reasons. The genetic correlations calculated using pooled data were 0.71 between Victoria and Tasmania and 0.89 between Victoria and New Zealand. Family by site variance within and across regions was significant but low, comprising 3 to 5% of total variation. The high genetic correlations and low family by site variance suggest diameter growth can be considered as a single trait across most regions in Australia and New Zealand. This implies that *E. nitens* is a very stable species for growth, and indicates breeding information is easily transferable between regions.

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