BURCZYK, 1992). These two trends suggest that the genetic efficiency of the seed orchard considered as a mating unit was increasing. However, significant temporal variation in male strobili production was observed for the studied orchard (BURCZYK and CHAŁUPKA, 1997). Those findings suggest, that despite little temporal changes in outcrossing rates, the outcross mating patterns (contamination, parental contribution, pollen dispersal) may vary in time, resulting in a variable genetic composition of the progeny produced in different years. Since selfing in conifers seems relatively constant, and usually accounts for less than 10% of effective fertilizations, it might be more interesting for future studies to focus on the temporal variation of outcross mating patterns both in natural and seed orchard populations.

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Genetic Control of Growth Traits of *Eucalyptus urophylla* S. T. BLAKE in South East China

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Abstract

Data from five thinned *E. urophylla* progeny trials in south east China were used to estimate the genetic parameters heritability, age-age correlations and Type B correlations for DBH and height from age 1 to 5 years. Heritabilities ranged between 0.11 and 0.41 for DBH, and between 0.12 and 0.49 for HT. Heritability increased with age. Age-age correlations for DBH and height were generally very high; effective early selection could be made as early as 12 months. High Type B correlations and low family-by-fertiliser interaction for both DBH and height suggested that genotype-by-environment interaction should not be important for this species in the

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region of the trials.

Key words: heritability, age-age correlation, Type-B correlation, genotype-by-environment interaction, genotype-by-fertiliser interaction, REML, *Eucalyptus urophylla.*

FDC: 165.3; 181.525; 232.1; 237.4; 561.1/.2; 176.1 *Eucalyptus urophylla;* (510).

Introduction

Eucalypts are becoming increasingly important in southern China for fuel wood, mining timber, leaf oil, fibreboard and pulpwood (QI, 1989; ELDRIDGE *et al.,* 1993). Approximately 670000 ha of plantation have been established in South China with a current planting rate of 50000 ha annually (WANG, 1991; LIU *et al.,* 1996). The productivity, however, has reportedly been low (6 m^3/ha to 10 m^3/ha), in part due to inadequate seed resources and poor silvicultural operations (TURNBULL, 1981; LIU *et al.,* 1996). In order to improve this, several research programs, carried out by the National Research Projects (QI, 1989) and international cooperative programs (MANNION and WEI, 1989; BROWN, 1994), began in the 1980s. Since this time, a wide range of species and provenance trials has been established. Results show *Eucalyptus urophylla* S. T. BLAKE is one of the most promising species (MANNION and WEI, 1989; PEGG and LI, 1989; WANG, 1989; BAI, 1994).

Currently, the information on genetic parameters for *E. urophylla* is very limited and confined to tests in Brazil and Indonesia (MORI *et al.,* 1990; KURINOBU *et al.,* 1996; NIRSATMANTO *et al.,* 1996). The aim of this paper is to estimate genetic and phenotypic parameters and their age trends in five *E. urophylla* progeny trials in the Guangxi Zhuang Autonomous Region in south east China, and discuss some implications for the development of appropriate breeding strategies for this species in China.

Material and Method

Location and trial description

The data sets used in this study are from five trials established in three series (denoted locally as 46, 54 and 77) under the China-Australian Program for Technical Cooperation. Series 46 includes three trials located at Dongmen State Forest Farm (labelled as 46D), Weidu State Forest Farm (46W) and Qinlian State Forest Farm (46Q). Series 54 and 77 include only one trial each, both at Dongmen. All trials are in the Guangxi Zhuang Autonomous Region of south east China (*Table 2*).

Series 46 was established at three sites in an attempt to test the importance of genotype-by-environment interaction in *E. urophylla.* The experimental sites at Dongmen and Weidu are typical of most of inland Guangxi forest estate with red lateritic clay loam soils. The site at Qinlian is distinct. The soil is sandy, with poor water retention, and lower organic matter, nitrogen, phosphorus and potassium. Being just 20 km away from the sea, it is also where more serious damage from typhoons occur. This site is typical of most of the coastal area of Guangdong and Guangxi. All sites have a rainfall above 1200 mm and experience distinct dry autumn/winter and wet spring/summer seasons.

The experimental design is a randomised complete block with single tree plots with 30, 40 or 42 replications (*Table 2*). In trials 46D and 77, however, families were assigned to sets. At 46D, 100 families were randomly divided into two sets with 50 families each, within set families were then randomly planted. At trial 77, a similar procedure was followed with 200 families and 4 sets of 50 families each. Therefore an initial analysis of 46D and 77 included a set effect.

Trial 54 contained 42 blocks, with 12 of them being used as a fertilisation trial. This involved three treatments: no fertiliser, P20:K30 (Phosphorus 20 kg/ha and potassium 30 kg/ha), and N (nitrogen) 100:P50:K50 kg/ha. The section used as fertilisation trial will be used to test the effect of family-by-fertiliser interaction.

A heavy thinning was conducted, to about one half of the original stocking at trial 46D and 77 and to about one third of the original stocking in trial 54, on the basis of tree size. This was conducted soon after the third year measurement at 46D, nine months after the first year measurement at trial 54, and four months after the third measurement at 77.

Diameter at breast height (DBH) in centimetres and height (HT) in meters were measured in all surviving trees annually, at each trial.

Table 1. – Details of provenance origin and number of families included in five *E. urophylla* progeny trials in China.

Seedlot	Provenance	Latit.	Longit.	Alti. (m)	No. of families 46D	46W	46Q	54	77
79	Upper Ulanu River, Alor, IND	8°20’S	124°27’E	500	23	11	9	1	
12960	34 km N of Soe, Timor, IND	8°30’S	126°00’E	1250				2	
13011	Mt. Lewotobi, Flores Island, IND	8°32’S	122°47’E	500				35	
13243	Republic of the Congo	0°00’	100°00’W	0				6	
14531	Mt. Egon, Flores Island, IND	8°38’S	122°27’E	515	34	18	20	19	
14532	Mt. Lewotobi, Flores Island, IND	8°31’S	122°45’E	398	30	15	15	3	
var	Seed Orchard, Aracruz, BRZ	19°48’S	48°17’W	30				3	
Dongmen	Seed Production Area, PRC	22°23’N	107°30’E	200	13	6	6	19	24
17564	Mandiri, Flores Island, IND	8°15'S	122°58'E	410					18
17565	Mt. Lewotobi, Flores Island, IND	8°32'S	122°48'E	375					48
17566	Wukoh, Flores island, IND	8°35'S	122°35'E	375					2
17567	Egon, Flores Island, IND	8°38'S	122°27'E	450					82
17568	Kalabahi, Alor, IND	8°19'S	124°40'E	700					1
17569	Apui, Alor, IND	8°16'S	124°50'E	800					2
17570	Bangat, Flores Island, IND	8°38'S	122°27'E	330					3
17571	Wairteban, Egon, IND	8°38'S	122°27'E	525					4
17572	Iling Gele, Egon,IND	8°37'S	122°27'E	600					8
17573	Andelan, Egon, IND	8°36'S	122°28'E	725					4
17574	Jawaghar, Egon, IND	8°36'S	122°28'E	550					4

Table 2. – Details of *E. urophylla* progeny trials 46D, 46W, 46Q, 54 and 77.

	46D	46W	46Q	54	77
Latitude, longitude	22°15'N 107°40'E	23°40'N 109°12'E	21°50'N 109°05'E	22°15'N 107°40'E	22°15'N 107°40'E
Altitude	150m	80m	50m	150m	150m
Soil	Red lateritic clay loam	Red lateritic clay loam	Sandy	Red lateritic clay loam	Red lateritic clay loam
Annual rainfall (mm)	1213	1376	2000	1213	1213
Annual average temperature(°C)	21.3	20.7	22.0	21.3	21.3
Site preparation	ripped	ploughed	trenched	ripped	ripped
Previous vegetation	*E. citrodora*	*E. exserta*	*E. exserta*	bamboo	bamboo
Planting date	17/05/1988	26/05/1988	05/05/1988	04/05/1989	04/05/1990
Fertiliser (kg/ha)	N100:P50:K50	N100:P50:K50	N100:P50:K50	various	N100:P50:K50
No. replication	30	30	30	42	40
Spacing	3x2m	3x2m	3x2m	3x2m	3x2m
No. of families	100	50	47	90	200

Genetic material

All families in the five trials were from open-pollinated seed collected in native stands, seed prodoction areas or seed orchard, as detailed in *table 1.* There were 100, 50, 50, 90 and 200 families included in trials 46D, 46W, 46Q, 54 and 77, respectively. The same 50 families were planted across 46D, 46W and 46Q, with three families missing at 46Q due to the lack of seedlings. There were 15 families in common between trial 54 and the 46 series. However, there were no common families between trial 77 and the other trials. Two entries in Trial 54 were excluded from the analysis because one was a hybrid between *E. urophylla* and *E. grandis,* and another was an unpedigreed bulk seedlot of 15 mother trees. The seedlots from the Dongmen land race were collected from plus-trees selected for growth and tree form in various experiments such as provenance trials, seed production areas, or plantations (PEGG, 1984).

Statistical analysis

Statistical analysis was conducted in three stages. Firstly, each trial was analysed separately to estimate genetic parameters at each site, hence confounding the genotype-by-environment interaction (GEI) with the family effect. Secondly, data from Series 46 and 54 were pooled, and the importance of family-by-site interaction was tested. Also in trial 54 the family-by-fertiliser interaction was investigated. Thirdly, correlations between measurements at different ages was analysed for each trial and across series 46 and 54. The single site analysis at 46D and 77 was based on the following generalised linear mixed models:

$$y = Xb + W_1 s + W_2 set + Za + e \tag{1}$$

and in the remaining trials as:

$$y = Xb + Ws + Za + e \tag{2}$$

where y is the vector of observed DBH or HT at each sites, b is the vector of fixed block effects, s is a vector of random provenance effect, a is vector of additive genetic effects for individual trees, and set is the vector of set effect. X, W_1, W_2, and Z are known incidence matrices. In trials 46D and 77, the Chi-square ratio test (MCCULLAGH and NELDER, 1989), comparing maximum likelihood from model (1) and (2), showed that set effect was not significant and was subsequently dropped from the model (1). Results are therefore based on model (2) only. The significance test for provenance effect was also conducted by the same method at 0.05 level. Since selective thinning and mortality occurred at all sites, estimates were based on a multivariate REML analysis which eliminated the effect of the removal of the smaller trees (WEI and BORRALHO, 1998). Therefore all parameters reported in this study were free of bias from selective thinning.

For the pooled analyses, and the family-by-fertiliser interaction analysis at trial 54, the model was:

$$y = Xb + W_1 s + W_2 fs + Za + e \tag{3}$$

where y is a vector of DBH or HT at all four sites for each age, and fs is a vector of the effect of GEI (family-by-site, and family-by-fertiliser, respectively). Before conducting the pooled analyses, data was standardised by multiplying it by the ratio of phenotypic standard deviation from the pooled data to the phenotypic standard deviation from each site; this eliminates the effect of heterogenous genetic variances across different sites (VISSCHER *et al.,* 1991). The significance for provenance or GEI effect was tested by the Chi-square ratio test (MCCULLAGH and NELDER, 1989), comparing maximum likelihood from the models including and excluding the term being tested.

In order to further investigate the GEI, genetic correlations between sites were also estimated based on multivariate REML analysis, by treating measurements from different sites as different traits based on model (2).

For the estimation of age-age correlation, a multivariate analysis on model (2) was conducted, treating measurements at different ages as different traits.

Estimates of variance and covariance components were conducted using VCE program, a quasi-Newton REML algorithm based on exact first derivations (GROENEVELD, 1996). Though isozyme analysis by HOUSE and BELL (1994) and RAPD and AFLP markers analysis by GAIOTTO *et al.* (1997) found that the outcrossing rate at natural *E. urophylla* stands was around 0.9, with inbreeding occurring at natural stands. This made the assumption of complete half-sib relationship of open-pollinated families invalid. A genetic relationships of 1/3 (GAIOTTO *et al.,* 1997), therefore, was assumed in the individual model (2), for open-pollinated families. Within-provenance heritability at a single site was estimated as:

$$h_1^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_a^2 + \hat{\sigma}_e^2} \tag{4}$$

where $\hat{\sigma}_a^2$ and $\hat{\sigma}_e^2$ are the estimates of additive genetic and residual variances, respectively; and across sites or family-by-fertiliser interaction analysis as:

$$h_2^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_a^2 + \hat{\sigma}_{fs}^2 + \hat{\sigma}_e^2} \qquad (5)$$

where $\hat{\sigma}_{fs}^2$ is the estimate of variance due to family-by-environment.

A ratio (s^2) of variance due to provenance effect over the phenotypic variance was also estimated in a single site as:

$$s_1^2 = \frac{\hat{\sigma}_s^2}{\hat{\sigma}_a^2 + \hat{\sigma}_s^2 + \hat{\sigma}_e^2} \qquad (6)$$

where $\hat{\sigma}_s^2$ was the variance due to the provenance effect; and across sites or family-by-fertiliser analysis as:

$$s_2^2 = \frac{\hat{\sigma}_s^2}{\hat{\sigma}_a^2 + \hat{\sigma}_s^2 + \hat{\sigma}_{fs}^2 + \hat{\sigma}_e^2} \qquad (7)$$

Age-age correlation (r) was estimated as:

$$r = \frac{\hat{\sigma}_{ij}}{\hat{\sigma}_i \hat{\sigma}_j} \qquad (8)$$

where $\hat{\sigma}_{ij}$ is the estimate covariance between ith and jth year for DBH or HT, $\hat{\sigma}_i$ and $\hat{\sigma}_j$ are the square-root of variances at ith and jth years, respectively. $\hat{\sigma}_i$, $\hat{\sigma}_j$ and $\hat{\sigma}_{ij}$ were referred to phenotypic or genetic (co)variances corresponding to the phenotypic or genetic correlations.

Result and Discussion

Growth performance

Table 3 presents the growth performance at the five trials. The most outstanding feature is the rapid growth during the first two years, with an apparent decline by year five. Annual increments for DBH and HT were usually around 4.5 cm and 5 m during the first two years, respectively, dropping to around 1 cm in DBH and 1 m in HT at age five. Relatively slow growth in the first year at 46D, 46W and 77 was probably caused by serious drought conditions after planting in these sites.

Though average HT at 54 was three meters greater than that at 46D at five years, DBH was almost the same at both trials. This may be due to the different stocking densities caused by the thinning with fewer trees (558 stems/ha) at 46D than at 54 (1016 stems/ha). It is known that thinning has a strong effect on DBH but has little effect on height growth in *E. regnans* (West and Osler, 1995).

Provenance merit

Growth of different provenances, based on their best linear unbiased predictors, in trials 46D and 54 at 5 years old and in trial 77 at 4 years are given in *figure 1*. The Aracruz seedlot (Brazil) from clonal seed orchard (var) and the seedlots 14532,

Table 3. – Overall means and standard deviations (s.d.) for DBH (cm) and HT (m) from year 1 to 5 in *E. urophylla* progeny trials in south east China.

Trial		DBH by year					HT by year				
		1	2	3	4	5	1	2	3	4	5
46D	mean	2.22	7.00	8.68	11.03	13.81	2.79	7.64	10.82	13.06	15.86
	s.d.	1.16	1.95	2.22	1.64	2.13	0.82	1.61	1.97	1.49	1.88
46W	mean	1.83		8.96			1.83		8.96		
	s.d.	0.91		2.33			0.54		1.96		
46Q	mean	1.24					1.24				
	s.d.	0.82					0.46				
54	mean	4.59	8.80	10.71	12.55	13.50	5.72	10.79	13.50	17.36	18.72
	s.d.	1.92	1.95	2.06	2.69	3.17	1.83	1.98	1.89	2.54	2.94
77	mean		6.5	8.2	11.4		2.7	8.8	11.7	15.5	
	s.d.		1.84	2.09	2.09		0.81	1.77	1.89	1.95	

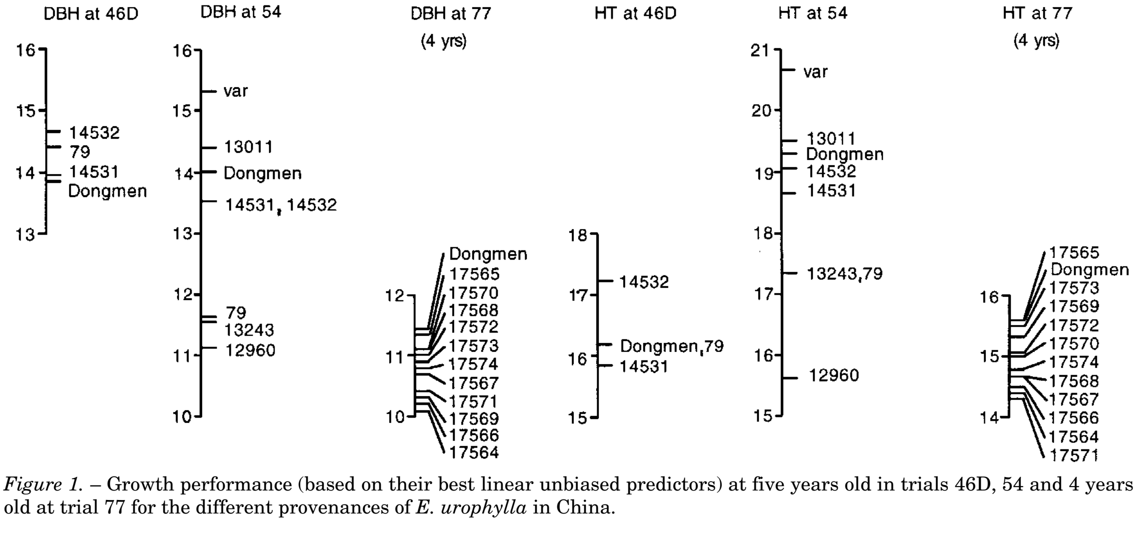

Figure 1. – Growth performance (based on their best linear unbiased predictors) at five years old in trials 46D, 54 and 4 years old at trial 77 for the different provenances of *E. urophylla* in China.

13011 and 17565 from Mt. Lewotobi in Flores Island (Indonesia) were clearly superior. The superiority of Mt. Lewotobi provenance for growth has been reported at other trials in Guangdong and Hainan in China and elsewhere in the world (PEGG *et al.,* 1987; ZHOU and LIANG, 1991; LIANG *et al.,* 1994; LUZ *et al.,* 1996). Seedlots from plus-trees selected in Dongmen were intermediate in trial 46 and better than average in trial 77. Provenances showed similar ranking at 46W and 46Q for DBH and HT at younger ages.

Although the differences in DBH and HT growth between provenances were statistically significant in all trials, the magnitudes of these difference in trial 46D, 46W, 46Q and 77 appears not to be important in practice. PEGG and LI (1989) also concluded there was 'no sound reason for restricting tree improvement work to a particular provenance' based on a provenance trial in Dongmen which included similar provenances as in this study. NGULUBE (1989) also found no significant difference among provenances for HT in Malawi, although 12 provenances from Flores, Alor, Lemobata Timor islands were included. In an international *E. urophylla* provenance trial no superior provenance could be singled out, except for the provenances from high elevation which consistently performed worst (VERCOE and CLARKE, 1994). The larger provenance effects in trial 54 was the result of provenances from a seed orchard at Aracruz in Brazil, which was clearly superior, and the seedlots from the Republic of Congo (13243) and the high-elevation Timor (12960) and Upper Ulanu River in Alor Island (79), which were much poorer. Except for the Alor (which was just represented by one family) and Timor provenances (high-elevation of 1250 m), all other were not from native base populations and results are distinct. Excluding these provenances, the variation was small and similar to that of other trials.

Table 4. – Estimates of additive genetic variance (σ^2_a), variance due to provenance effect (σ^2_s), residual variance (σ^2_e), and phenotypic variance (σ^2_p), within provenance heritabilities (h_l^2 ± approximate s.e.), and provenance repeatability (s_l^2 ± approximate s.e.) for cumulative diameter at breast height (DBH) in *E. urophylla* progeny trials in China.

Trial	Age	DBH		HT	
		h_l^2 ± s.e.	s_l^2 ± s.e.	h_l^2 ± s.e.	s_l^2 ± s.e.
46D	1	0.14 ± 0.02	0.01 ± 0.01	0.17 ± 0.03	0.02 ± 0.01
	2	0.17 ± 0.03	0.00 ± 0.01	0.22 ± 0.02	0.00 ± 0.01
	3	0.22 ± 0.03	0.00 ± 0.01	0.24 ± 0.02	0.00 ± 0.01
	4	0.23 ± 0.03	0.00 ± 0.01	0.27 ± 0.02	0.01 ± 0.01
	5	0.26 ± 0.04	0.00 ± 0.01	0.29 ± 0.03	0.03 ± 0.02
46W	1	0.12 ± 0.07	0.02 ± 0.01	0.14 ± 0.07	0.03 ± 0.01
	3	0.23 ± 0.10	0.00 ± 0.01	0.23 ± 0.10	0.01 ± 0.02
46Q	1	0.11 ± 0.07	0.04 ± 0.04	0.12 ± 0.08	0.06 ± 0.05
54	1	0.23 ± 0.03	0.09 ± 0.04	0.29 ± 0.04	0.12 ± 0.05
	2	0.28 ± 0.03	0.13 ± 0.05	0.38 ± 0.06	0.13 ± 0.06
	3	0.34 ± 0.03	0.13 ± 0.06	0.44 ± 0.06	0.14 ± 0.06
	4	0.38 ± 0.04	0.14 ± 0.06	0.46 ± 0.07	0.18 ± 0.07
	5	0.41 ± 0.04	0.14 ± 0.06	0.49 ± 0.07	0.18 ± 0.07
77	1			0.17 ± 0.04	0.02 ± 0.01
	2	0.19 ± 0.03	0.03 ± 0.01	0.18 ± 0.07	0.02 ± 0.01
	3	0.21 ± 0.04	0.03 ± 0.01	0.20 ± 0.07	0.03 ± 0.01
	4	0.23 ± 0.04	0.04 ± 0.01	0.23 ± 0.07	0.03 ± 0.01

Heritabilities for single sites

In *E. urophylla,* DBH and HT appears to be under moderate to strong genetic control in all trials (*Table 4*). The heritability estimates ranged between 0.14 and 0.41 for DBH, and 0.12 to 0.49 for HT. These agree well with the few estimates that have been reported for *E. urophylla* (MORI *et al.,* 1990; KURINOBU *et al.,* 1996; NIRSATMANTO *et al.,* 1996), and seem to be somewhat higher than that found in temperate eucalypts (eg. VOLKER *et al.,* 1990; BORRALHO *et al.,* 1992b). This suggests that selection for growth traits in *E. urophylla* can be effective even when based on phenotypic selection. Indirect evidence of that can be seen by the better performance of Aracruz and Dongmen land races.

Heritabilities increased from 1 year up to 5 years. This was most apparent in trials 46D and 54. For example, the heritability estimate for DHB at 5 years in trial 46D was almost double that at 1 year (h^2 = 0.14 to 0.26). However, heritabilities seem to reach a plateau after age three in all trials. For instance, in trial 46D the heritabilities remained reasonably stable between three and five years, ranging between 0.22 and 0.26 for DBH, and between 0.24 and 0.29 for HT. This is more apparent for HT in trial 54 where heritability varied only slightly during the last three years from h^2 = 0.44 at 3 years to 0.49 at age 5 years.

Estimates of heritability were generally stable across the 46 trial series and 77, despite imbalance in family distribution and number of families across trials. The only exception was trial 54, which gave higher heritabilities. This may have been caused by the much earlier selective thinning at this trial, which enabled genetic variance being expressed better at a more favourable environment (COTTERILL and DEAN, 1988), and a faster grow rate, in particular at the early stage. This could be also the result of better genetic discrimination on more fertile sites (EISEMANN and NIKLES, 1983; DHAKAL *et al.,* 1996; HAAPANEN, 1996).

As expected, provenance effects were unimportant, accounting for less than 5% of total phenotypic variance and being negligible in trial 46 series and 77 (*Table 4*). The higher proportion in trial 54 was due to the selected land races and wider range of provenances. When provenances from Timor Island, Brazil and Congo were excluded from the analysis, the proportions in this trial were reduced to the same as trial 46 series and 77. This result further confirms that specific selection of provenances at least from low-elevation Alor and Flores islands would not contribute much to the genetic progress in *E. urophylla.*

Heritabilities from pooled analysis

Heritability estimates from pooled across-sites data, which only included trials 46 series and trial 54, showed that growth is under moderate genetic control. Heritability estimates ranged between 0.13 at 1 year and 0.23 at 5 years for DBH, and between 0.17 at 1 year and 0.24 at 5 years for HT (*Table 5*). They also showed a similar increasing pattern over time as observed in the single site analysis. However, the estimates of heritability for both DBH and HT were lower than those from single sites.

It seems that DBH and HT have different responses to the interaction effect (*Table 5*), with DBH being somewhat more interactive than HT. The proportion of variance due to the GEI effect was usually higher in DBH than in HT, and genetic

Table 5. – Estimates of within-provenance heritabilities (h_2^2 ± s.e.), proportion of variance due to provenance effect, and the ratio of variance due to GEI effect (σ^2_{fs}) over family variance ($\hat{\sigma}^2_f = \frac{1}{4}\hat{\sigma}^2_a$) for DBH and HT in *E. urophylla* from year 1 to 5, based on across-sites analysis of trial series 46 and 54.

Trait	Estimates	Age (year)				
		1	2	3	4	5
DBH	$h_2^2 \pm s.e.$	0.13 ± 0.02	0.14 ± 0.02	0.18 ± 0.03	0.20 ± 0.03	0.23 ± 0.03
	$s_2^2 \pm s.e.$	0.10 ± 0.03	0.16 ± 0.04	0.16 ± 0.04	0.15 ± 0.04	0.15 ± 0.04
	$\hat{\sigma}^2_{fs}/\hat{\sigma}^2_f$	0.44	0.73	0.59	0.60	0.54
HT	$h_2^2 \pm s.e.$	0.17 ± 0.03	0.20 ± 0.03	0.23 ± 0.03	0.23 ± 0.04	0.24 ± 0.04
	$s_2^2 \pm s.e.$	0.11 ± 0.04	0.14 ± 0.06	0.14 ± 0.05	0.17 ± 0.06	0.19 ± 0.07
	$\hat{\sigma}^2_{fs}/\hat{\sigma}^2_f$	0.33	0.52	0.46	0.54	0.58

Table 6. – Genetic correlations between four testing sites for DBH and HT in *E. urophylla*.

Trial		46W	46Q	54
46D	DBH	0.68 ± 0.11	0.66 ± 0.12	0.70 ± 0.06
	HT	0.82 ± 0.05	0.90 ± 0.03	0.86 ± 0.03
46W	DBH		0.60 ± 0.17	0.70 ± 0.09
	HT		0.75 ± 0.10	0.99 ± 0.01
46Q	DBH			0.62 ± 0.13
	HT			0.63 ± 0.14

correlations between testing sites were correspondingly lower in DBH (*Table 6*).

SHELBOURNE (1972) proposed a rule of thumb to judge the importance of GEI in selection programs. If the ratio of the variance due to GEI over family variance is larger than 0.5, selection efficiency would be seriously affected if GEI effect is ignored. In this study, the ratio was generally lower than 0.5 in both DBH and HT. Correspondingly, genetic correlation between pairs of sites were generally higher than 0.60 for DBH and 0.70 for HT (*Table 6*). This might suggest that GEI effects are not practically important for growth at least for the Guangxi region. However, given the limited number of sites and the young age at 46Q and 46W, the low values of GEI here should be interpreted cautiously.

The results on GEI from this study differ substantially from those of MORI *et al.* (1990) who found highly significant GEI effect across four sites in Brazil, and ratios of coefficient of variation due to GEI over the coefficient due to genetic effect of 10 and 2, for DBH and HT respectively. In such case, ignoring the effect of GEI will reduce the expected genetic gain by 27%. By contrast, NIRSATMANTO *et al.* (1996) found genetic correlations between two sites to be around 0.8 for both DBH and HT, concluding that genetic gains using selection indices on single sites and across sites were similar.

Heritabilities from fertiliser trial

Family-by-fertiliser interaction (FFI) effect was generally not significant for either DBH or HT in *E. urophylla* (*Table 7*), despite the significant growth response from the application of fertiliser. The proportion of variance due to FFI over family variance was below 0.5 for DBH and HT from 2 to 5 years (*Table 7*). This result was consistent with findings from a two-year old *E. grandis* family trial in South Africa (VAN WYK and FALKENHAGEN, 1984). Thus, genotype-by-fertiliser interaction in *E. urophylla* does not seem to be important based on one trial at Dongmen State Forest Farm.

It is interesting to note the decline of the ratio of variance due to FFI effect over family variance with age, in particular

Table 7. – Estimates of within-provenance heritabilities (h_2^2 ± s.e.), proportion variance due to provenance effect (s_2^2 ± s.e.), and the ratio ($\hat{\sigma}^2_{ff}/\hat{\sigma}^2_f$) of variance due to family-by-fertiliser interaction effect over family variance ($\hat{\sigma}^2_f = \frac{1}{4}\sigma^2_a$) for DBH and HT in *E. urophylla* from year 1 to 5 in trial 54.

Trait	Estimates	Age (year)				
		1	2	3	4	5
DBH	h_2^2 ± s.e.	0.14 ± 0.03	0.26 ± 0.03	0.34 ± 0.03	0.38 ± 0.03	0.41 ± 0.03
	s_2^2 ± s.e.	0.11 ± 0.02	0.14 ± 0.03	0.15 ± 0.03	0.14 ± 0.03	0.14 ± 0.03
	$\hat{\sigma}^2_{ff}/\hat{\sigma}^2_f$	0.73	0.38	0.24	0.16	0.18
HT	h_2^2 ± s.e.	0.19 ± 0.04	0.27 ± 0.03	0.39 ± 0.05	0.39 ± 0.04	0.43 ± 0.05
	s_2^2 ± s.e.	0.16 ± 0.06	0.16 ± 0.05	0.17 ± 0.05	0.17 ± 0.05	0.17 ± 0.05
	$\hat{\sigma}^2_{ff}/\hat{\sigma}^2_f$	0.99	0.31	0.11	0.12	0.07

during the first two years (*Table 7*). This was caused by the diminishing effect of the fertiliser which was applied at age 1.

It is also interesting to note that heritabilities for DBH and HT at different ages estimated from this smaller data set, including only 12 blocks (*Table 7*) were similar to those from using whole trials, including 42 blocks (*Table 4* and *5*), especially at later ages. This suggests that fertiliser effects were mostly accounted for by the blocking, and that little interaction was present.

Correlations between ages

Very strong genetic correlations between early and late growth were apparent across all trials. Genetic correlations ranged between 0.70 and 0.99 for DBH, and between 0.67 and 1.00 for HT (*Table 8*). Correlations between pairs of ages later than the first year were close to one, ranging between 0.90 and 1.00 for DBH, and between 0.87 and 1.00 for HT. High genetic correlations between early and later growth in this study are consistent with findings in other eucalypt species (van Wyk, 1990; Borralho *et al.,* 1992a; Lambeth *et al.,* 1994).

Though results are not presented here, genetic correlation between DBH and HT growth increments were also highly positive at all trials, especially at Trial 54. Both results suggest the same set of genes are involved across the five years. As a result, early selection for growth at age 5 in *E. urophylla* would likely be to seem effective even as early as one year of age.

Conclusion

With current harvesting ages for *E. urophylla* in south east China being six to eight years, the parameters reported here are directly relevant to define selection strategies for the species, in particular regarding the selection age and the use of genotype-by-environment interaction. This study showed that DBH and HT in *E. urophylla* were under moderate to strong genetic control with h^2 increasing with age, from 0.14 at age 1 year to 0.41 at 5 years for DBH, and from 0.12 to 0.49 for HT. These estimates are considerably higher than most estimates reported for temperate eucalypts but consistent with tropical eucalypts. The additive genetic correlations between ages for DBH and HT were near one. Hence, selection as early as 12 months is expected to be effective for growth traits in such short-rotation tree crops.

Results showed little genotype-by-site interactions with less than 5% of total phenotypic variance due to the interaction and a high genetic correlation between sites. Low genotype-by-environment interaction was also confirmed by the significant effect due to family-by-fertiliser interaction in one trial. The low magnitude of genotype-by-environment interaction, or similarly the very high genetic correlations between growth traits across sites, point to the existence of a single selection strategy and breeding objective across coastal and interior areas in the Guangxi region of China. However, results from a wider range of sites and data from older experiments are needed to confirm the results of this study.

Table 8. – Genetic (above diagonal) and phenotypic (below diagonal) correlations in *E. urophylla* for DBH and HT based on pooled data analysis series 46 and 54, and on a single site in trial 77 for age 1 to 5 years.

(a) pooled

	DBH1	DBH2	DBH3	DBH4	DBH5
DBH1		0.84 ± 0.02	0.79 ± 0.02	0.75 ± 0.02	0.70 ± 0.03
DBH2	0.83		1.00 ± 0.01	0.99 ± 0.01	0.98 ± 0.01
DBH3	0.78	0.97		1.00 ± 0.01	0.99 ± 0.01
DBH4	0.74	0.93	0.97		1.00 ± 0.03
DBH5	0.68	0.89	0.94	0.98	

	HT1	HT2	HT3	HT4	HT5
HT1		0.91 ± 0.02	0.82 ± 0.02	0.83 ± 0.02	0.78 ± 0.03
HT2	0.81		0.97 ± 0.01	0.98 ± 0.01	0.95 ± 0.02
HT3	0.74	0.93		1.00 ± 0.01	1.00 ± 0.01
HT4	0.70	0.87	0.94		0.99 ± 0.01
HT5	0.66	0.85	0.91	0.96	

(b) Trial 77

	DBH1	DBH2	DBH3	DBH4
DBH2			0.99 ± 0.00	0.95 ± 0.01
DBH3		0.97		0.98 ± 0.00
DBH4		0.94	0.96	

	HT1	HT2	HT3	HT4
HT1		0.82 ± 0.02	0.74 ± 0.03	0.67 ± 0.04
HT2	0.77		0.98 ± 0.00	0.94 ± 0.01
HT3	0.74	0.93		0.96 ± 0.01
HT4	0.69	0.86	0.91	

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Maximising Genetic Response in Tree Breeding with Constraints on Group Coancestry

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Abstract

This study compares 4 methods to maximize response to selection while minimizing the inbreeding that accumulated over 6 generations of selection. A selection algorithm is described which maximizes the mean estimated breeding value of the selected trees while constraining the average coancestry among them and hence the status effective number of the population. This algorithm resulted in increased selection response, at a lower, target average coancestry level, compared to truncation selection. However the target average coancestry level for each generation is arbitrarily chosen. A variation of the algorithm is described which attempts to maximize response over 12 generations allowing for the decline in genetic variance caused by inbreeding. This leads to faster genetic gain and higher coancestry than typical tree breeding programs.

Once the selection has been carried out, a mate allocation algorithm arranges matings which give each parent the number of offspring required by the selection algorithm and which minimizes inbreeding in the offspring per mating. This delays the appearance of inbreeding by at least one generation but does not alter the long term rate of inbreeding. The combination of the selection and mating algorithms lead to breeding programs requiring less controlled pollinations than truncation selection with random mating and hence reduce the cost of the breeding program.

Key words: selection, coancestry, inbreeding, BLUP.

FDC: 165.6; 165.3.

Introduction

Application of Cochran's optimal rule for selection (Cochran, 1951) in plant and animal improvement implies

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