ESTIMATES OF GENETIC PARAMETERS AND GENETIC GAINS FOR GROWTH TRAITS OF TWO *EUCALYPTUS UROPHYLLA* POPULATIONS IN ZULULAND, SOUTH AFRICA

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Abstract

In South Africa, *Eucalyptus urophylla* is an important species due to its disease tolerance to fungal diseases like *Crysoporthe austroafricana* and the *Coniothyrium* sp. cankers. It is mainly planted as a parental species in a hybrid combination with *E. grandis*. Generally, the *E. grandis* x *E. urophylla* hybrid has better disease tolerance and higher wood density than pure *E. grandis.* The current strategy is to maintain large breeding populations of both parental species in order to provide improved elite selections for hybrid crosses on a regular basis. With this in mind, two *E. urophylla* populations, consisting of five provenance/progeny trials, were established in the subtropical region of Zululand. The aims of this study were firstly to determine the magnitude of genotype by environment interaction of *E. urophylla* in Zululand; secondly to estimate genetic parameter and

correlations for DBH, height and volume; and lastly to identify selections to advance the current breeding population as well as to hybridise with *E. grandis*.
Results indicated that genotype by environment interaction effects would be practically negligible for growth in Zululand and a single breeding population will therefore be appropriate. In general, all growth traits were under low to moderate genetic control, with narrow sense heritabilities ranging between 0.14 and 0.48 for volume. The genetic correlations between growth traits were high (0.98 and 0.99 for DBH-volume). This is an indication that DBH is a sufficient growth measure to use in *E. urophylla* breeding programmes. BLUP estimates indicated that a selection scenario of 200 individuals will generate genetic gains of 44.7% over the population mean. The estimated gains for the top 50 individuals that could potentially be used as hybrid parents to cross with *E. grandis* was 59.8% over the population mean.

Keywords

E. urophylla; genetic parameters; genetic correlations; genetic gains

Introduction

The *Eucalyptus* genus is now being planted worldwide in order to keep up with the demand for wood and fibre. *Eucalyptus urophylla* is one of the eucalypt species that has increased in popularity, especially in humid and sub-humid tropical climates of Africa, Latin America, Southern China and South-East Asia (Eldridge et al. 1993). In some countries *E. urophylla* is deployed as a pure species, but it is better known as an important hybrid partner and is commonly crossed with other eucalypt species to produce progeny that often exhibit remarkable hybrid vigour for growth (Hodge and Dvorak 2015).

In the subtropical regions of South Africa, namely Zululand, *E. urophylla* serves as a very important parental species in a hybrid combination with *E. grandis* Hill ex Maiden to produce fast-growing clonal plantations for the pulp industry. *Eucalyptus urophylla* is especially more tolerant to fungal diseases like *Crysoporthe austroafricana* and the *Coniothyrium* sp than pure *E. grandis* in Zululand (Retief and Stanger 2009). Generally, the *E. grandis* x *E. urophylla* hybrid has better disease tolerance and higher wood density than pure *E. grandis* (Retief and Stanger 2009, Hodge and Dvorak 2015). The current breeding strategy is to maintain and improve large breeding populations of both parental species in order to provide elite selections for hybrid crosses on a regular basis. With this in mind, two *E. urophylla* populations were established in Zululand. A total of five trials were established and included a total of 219 families from 17 provenances.

In order to develop the best hybrid breeding strategy for these *E. urophylla* populations in Zululand, it is important to determine the genetic correlation, the magnitude of genotype by environment interaction (GxE) and estimates of genetic parameters of economically important traits. In this case, tree growth (height, diameter at 1.3 m [DBH] and volume) was identified as the most important trait.

Estimating genetic correlations between the three growth traits could provide information to improve the cost effectiveness of the breeding programme. A good correlation between traits will provide the opportunity to measure fewer traits and make the programme more cost effective.

Various levels of GxE have been reported for *E. urophylla* (Mori et al. 1990, Wei and Borralho 1998, Hodge and Dvorak 2015). Mori et al. (1990) for example, have reported losses in volume of 26.7% due to GxE. It is therefore important to determine the magnitude of GxE for the two *E. urophylla* populations in Zululand in order to set up a breeding population and selecting environmentally stable genotypes.

Some information on genetic parameters for growth traits of *E. urophylla* is available. In general, growth of *E. urophylla* has been reported to be under low to moderate genetic control with narrow-sense heritabilities ranging between 0.11 and 0.41 in China (Wei and Borralho 1998), 0.1 and 0.31 in Vietnam (Kien et al. 2009), and 0.15 on average across 5 countries (Hodge and Dvorak 2015). However, the population structure and environmental factors of these studies are different to the ones in our study, and it's important to investigate the genetic parameters of *E. urophylla* in Zululand for hybrid breeding using this species.

The aims of this study were therefore to (1) determine the magnitude of genotype by environment interaction of *E. urophylla* for the Zululand region; (2) to estimate genetic parameters and correlations for DBH, height and survival; and (3) to identify selections to advance the current breeding population as well as to hybridise with *E. grandis*.

Materials and methods

Breeding material

The first *E. urophylla* breeding material was imported during 1988-1990. Open-pollinated seed was collected from randomly selected trees located in 17 provenances in Indonesian islands. A total of 219 families from these provenances were imported and established in two populations (PE023 and PV042) across five sites. The parent trees of these families were situated at an altitude range between 175 – 1050 meters above sea level (m.a.s.l.). **Table 1** gives a breakdown of all the *E. urophylla* provenances that were established in trials.

Table 1: Provenance data of two *Eucalyptus urophylla* populations (PE023 and PV042) established in five provenance/progeny trials in Zululand

Provenance	No. of families	Year of import	Lat. S	Long. E	Alt. (m.a.s.l.)	Trial series
Egon	18	1988	8° 38'	122° 35'	515	PE023
Lewotobi	16	1988	8° 31'	122° 45'	398	PE023
Mandiri	5	1988	8° 15'	122° 45'	415	PE023
Wuko	4	1988	8° 33'	122° 33'	830	PE023
Ilwaki1	4	1990	7° 54'	126° 26'	490	PV042
Ilwaki2	28	1990	7° 52'	126° 27'	515	PV042
Mareke Arnau	28	1990	7° 49'	126° 10'	300	PV042
Telemar	6	1990	7° 54'	125° 58'	200	PV042
Carbutu	8	1990	7° 56'	125° 53'	175	PV042
Rotus Uhak	37	1990	7° 39'	126° 29'	350	PV042
Old Uhak	6	1990	7° 36'	126° 37'	215	PV042
Lalikki	9	1990	7° 42'	126° 21'	220	PV042
Apui	10	1990	8° 17'	124° 40'	1050	PV042
Wai Kui	10	1990	8° 14'	124° 44'	580	PV042
Pintumas	15	1990	8° 19'	124° 31'	550	PV042
Dalaki	6	1990	8° 31'	124° 05'	430	PV042
Baubillatung	9	1990	8° 20'	124° 02'	285	PV042

Table 2: Site and trial information of five *Eucalyptus urophylla* provenance/progeny trials in Zululand

	PE023A	PE023B	PV042A	PV042B	PV042C
Longitude	32° 13' E	32° 21' E	32° 04' E	32° 17' E	31° 58' E
Latitude	28° 31' S	28° 15' S	28° 35' S	28° 01' S	28° 42' S
M.A.P. (mm)	1128	995	984	852	1103
Altitude (m.a.s.l)	24	47	87	37	61
Major soil type	Fw35	Fw1210	Hu2200	Ct1100	Ct1100
Effective rooting depth (m)	1.2	1.51	1.51	1.51	1.0
Planting date	11/1988	11/1988	03/12/1991	26/01/1992	26/03/1992
Replications	4	4	8	8	6
Plot size	1x8 tree line	1x8 tree line	1x5 tree line	1x5 tree line	1x5 tree line
Number of families	43	20	130	68	162

Trial establishment and measurements

Two *E. urophylla* populations, consisting of two and three trials respectively (PE023A&B and PV042A&B&C), were established in Zululand. The sites generally have deep sandy soils. Mean annual temperature (M.A.T.) is 21^{o}C at all sites, and the mean annual precipitation (M.A.P.) ranged from 852 mm to 1128 mm (**Table 2**). Each trial was planted in a randomised complete block design (R.C.B.), replicated between four and eight times across each site. Each family was planted in a line plot where the families of the same provenance had been grouped together within each replication ("sets within replications"). Tree planting spacing was 3 m x 2.5 m in all trials. Trial measurements were scheduled at mid-rotation (3 - 4 years) and at rotation age (7-8 years). Measurements were not available at all ages for all trials. Growth traits namely: height in metres and DBH in centimetres were taken and under bark tree volume was calculated using the following equation as described by Zhou and Liang (1991):

$$\text{Volume} = 0.00002618(\text{DBH})^2(\text{height})$$

Statistical analysis

Standardisation of data

Forest trees often display heterogeneous variances for growth traits where a strong relationship between the mean of the trait and its phenotypic and genetic variances are seen. This relationship is such that the field trials with bigger trees will have larger phenotypic and genetic variances than the field trials with smaller trees even if the trials are at the same age (Hodge and Dvorak, 2012). In order to deal with this situation, White et al. (2007) recommend data standardization prior to ANOVA, variance component analysis, or multi-site mixed model analysis. Standardization of data will homogenize variances that

will be used together in the linear model. It will also eliminate any spurious GxE (Burdon 1977, Eisen and Saxon 1983). The standardization for the analysis of this paper was performed as described by Hodge and Dvorak (2012). First, the coefficient of variation was calculated for each replication for each growth trait. The mean coefficient of variances (CV_y) for each family-site-trait combination was also calculated. The phenotypic observations were then standardized in each replication to a mean = 100, and standard deviation = 100 x CV_y using PROC STANDARD in SAS (SAS Institute 2002). This is equal to dividing all observations by the phenotypic standard deviation (SD), as recommended by White et al. (2007), followed by adding a constant (100%) and multiplying by a constant (100 x CV_y). The population mean for the growth trait can therefore be interpreted as 100%, and the associated variances and SD are the same size relative to mean as in the raw data. Predicted breeding values and all variance components can thus be directly interpreted as percentage gain (above or below 100%) without back-transformation or rescaling.

Family-site variance components and genetic parameters

Variance components analyses were done using SAS (SAS Institute 2002). The following variance components analyses were conducted for each family and each site where it was tested:

- Single-trait analyses for the three growth traits (height, DBH, and volume).
- Multiple-trait analyses for the three growth traits at a single-age were used to estimate genetic parameters for each trait, and genetic correlations among traits.

The linear model for all the analyses was the same as described by Hodge and Dvorak (2012):

$y_{ijklm} = \mu + E_i + R(E)_{ij} + P_k + PE_{jk} + F(P)_{kl} + F(P)E_{jkl} + e_{ijklm}$

Where,

y_{ijklm} = phenotypic observation of the $ijklm^{th}$ tree

μ = overall mean

E_i = fixed effect of the i^{th} trial

$R(E)_{ij}$ = fixed effect of the j^{th} replication nested in the i^{th} trial

P_k = random effect of the k^{th} provenance

$E[P_k]$ = 0

$Var[P_k] = \sigma^2_{prov}$

PE_{jk} = random interaction of the k^{th} provenance and the i^{th} trial

$E[PE_{jk}] = 0$

$Var[PE_{jk}] = \sigma^2_{pe}$

$F(P)_{kl}$= random effect across sites of the l^{th} family in the k^{th} provenance

$E[F(P)_{kl}] = 0$

$Var[F(P)_{kl}] = \sigma^2_{f(p)}$

$F(P)E_{jkl}$= random interaction of the l^{th} family in the k^{th} provenance and the i^{th} trial

$E[F(P)E_{jkl}] = 0$

$Var[F(P)E_{jkl}] = \sigma^2_{f(p)e}$

e_{ijklm} = random error associated with the $ijklm^{th}$ tree

$E[e_{ijklm}] = 0$

$Var[e_{ijklm}] = \sigma^2_e$

Phenotypic variance within-provenance (σ^2_{phen}) was estimated as follows:

$$\hat{}^2_{phen} = \hat{\sigma}^2_{f(p)} + \hat{}^2_{f(p)e} + \hat{}^2_{e}$$

Narrow-sense heritability within provenance ($h^2_{f(p)}$) was estimated as:

$$h^2_{f(p)} = \frac{3\hat{\sigma}^2_{f(p)}}{\hat{}^2_{phen}}$$

In addition, narrow-sense heritability for family (excluding provenance effect) was estimated as:

$$h^2_f = \frac{3\hat{\sigma}^2_f}{\hat{}^2_{fam\ phen}}$$

Where,

$$\hat{}^2_{fam\ phen} = \hat{\sigma}^2_f + \hat{}^2_{fe} + \hat{}^2_{e}$$

A certain amount of inbreeding and/or percentage full-sibs does occur among open-pollinated families. The covariance among open-pollinated families would therefore typically be higher than one-quarter of additive genetic variance (Squillace 1974). Thus a coefficient of 3 instead of 4 was multiplied by the family variance in the calculation of heritability. Dieters et al. (1995) found that using 3 as a coefficient gives better agreement between parameter estimates from open and controlled pollinated populations of the same genetic material.

The amount of provenance variation was estimated as follows:

$$P^2 = \frac{\hat{}^2_{prov}}{\hat{}^2_{phen}}$$

This way, provenance variation (P^2) can directly be compared to additive genetic variation ($h^2_{f(p)}$ and h^2_f) (Hodge 2012). Standard errors of P^2 and of $h^2_{f(p)}$ and h^2_f were estimated using the standard errors of $\hat{}^2_{prov}$, $\hat{}^2_{f(p)}$ and h^2_f respectively, and treating $\hat{}^2_{phen}$ as a constant according to Dickerson's approximation (Dickerson 1969).

In order to determine the genetic (excluding provenance effect and within provenance) or provenance correlations of the same trait expressed on two sites as described by Burdon (1977), type B genetic (r_{Bg} and $r_{Bg(p)}$) and provenance (r_{Bprov}) correlations were estimated as follows:

$$r_{Bg} = \frac{\hat{}^2_f}{(\hat{\sigma}^2_f + \hat{}^2_{fe})}$$

$$r_{Bg(p)} = \frac{\hat{}^2_{f(p)}}{(\hat{\sigma}^2_{f(p)} + \hat{}^2_{f(p)e})}$$

$$r_{Bprov} = \frac{\hat{}^2_p}{(\hat{\sigma}^2_p + \hat{}^2_{pe})}$$

Type B correlation measures GxE that is due to rank changes across environments. This correlation over multiple sites can range between zero and one. An $r_b = 1$ indicates a perfect correlation between performance in different environments.

A genetic coefficient of variation (GCV) ignoring the provenance effect, and secondly within provenance was calculated as follows:

$$GCV_f = 100^* \frac{\hat{f}}{\bar{x}}$$

$$GCV_{f(p)} = 100^* \frac{\hat{f}(p)}{\bar{x}}$$

Where $\bar{x}$ = the trait mean. The GCV expresses the additive genetic standard deviation in terms of percent, and gives an estimation of how much genetic improvement could be made in a trait (Hodge and Dvorak 2012).

Genetic correlations between traits (DBH-height, DBH-volume and height-volume) were also calculated using SAS at the family, family within provenance and provenance levels respectively.

Across-site variance components and provenance BLUPs

An across-site analysis was done for each trial series using the variable volume. Proc mixed in SAS (SAS Institute 2002) was used to conduct the multiple-trait analysis. Fixed and random effects in the models were the same as defined above. Site-site correlations at the family and provenance level (and standard errors) were estimated directly from the SAS output. These analyses were also used to produce provenance, family and individual estimates using best linear unbiased predictions (BLUPs) for volume at each trial series.

Results

Growth results

Mean DBH, height, volume per tree and survival for each provenance in each trial series are presented in **Table 3**. Provenance and families within each provenance effects were significant ($p<0.05$) in all the trial series in terms of standardised tree volume (**Table 4**). Although significant, the range in mean DBH for provenances in the PE023 trial series was small. The top performing provenance in the PE023 trial series was Lewotobi (mean DBH = 13.8 cm), and the worst performing provenance was Mandiri (mean DBH = 13.3 cm). A bigger range between provenances was detected in the PV042 trial series where Apui and Wai Kui provenances performed the best (mean DBH = 16.3 cm and 16.0 cm respectively) and Old Uhak the worst (mean DBH = 12.6 cm). Overall, the survival rates of all provenances were relatively good (between 72.9% and 93.6%).

Growth trait correlations and genetic parameters

In order to examine the provenance and genetic correlations between the three different growth traits (height, DBH and volume), genetic parameter analyses were performed. The analysis was done for individual trials and each trial series combined. These results are presented in **Table 5**. Overall, there were very strong genetic correlations between the various growth traits. The best provenance and genetic correlations were detected between DBH and volume and ranged from 0.97 to 1.00 for all the analyses performed. The genetic correlation between height and DBH ranged from 0.71 to 1.00, and between height and volume from 0.78 to 0.99. Provenance correlations between all three growth traits were very similar to genetic correlations at the PV042 trial series. However, provenance correlations between the three growth traits could in most cases not be

Table 3: Mean growth (DBH, height and volume) and survival of two *Eucalyptus urophylla* populations (PE023 and PV042) established in Zululand

Trial series	Provenance	Age (years)	Trials	DBH (cm)	Height (m)	Volume (m^3)	Survival (%)
PE023	Wuko	4	2	13.7±2.8	13.9±1.8	0.0863±0.042	78.5±41.0
	Egon		2	13.7±3.3	14.0±2.2	0.0893±0.047	88.1±30.5
	Lewotobi		2	13.8±2.9	14.6±2.0	0.0925±0.043	87.0±31.8
	Mandiri		2	13.3±2.8	14.2±1.9	0.0822±0.039	90.9±33.7
PV042	Baubillatung	7	3	14.5±3.4	16.5±3.3	0.1196±0.068	75.1±44.4
	Dalaki		3	14.9±3.6	17.2±3.2	0.1323±0.076	81.8±38.5
	Lalikki		3	14.4±3.3	17.0±3.2	0.1218±0.068	81.7±38.9
	Mareke Arnau		3	12.9±3.3	16.2±3.5	0.0952±0.064	75.8±43.5
	Wai Kui		3	16.0±3.9	17.5±3.3	0.1548±0.090	84.5±38.1
	Apui		3	16.3±4.0	17.5±3.6	0.1626±0.092	72.9±44.6
	Ilwaki1		2	13.5±3.4	16.1±3.8	0.1056±0.057	93.6±25.4
	Ilwaki2		3	14.1±3.5	16.4±3.6	0.1145±0.071	79.7±39.8
	Pintumas		3	14.7±3.8	16.4±3.6	0.1253±0.081	81.0±38.8
	Telemar		3	14.3±3.1	17.1±3.4	0.1191±0.069	79.5±40.1
	Carbutu		3	14.7±3.6	17.3±4.1	0.1289±0.074	75.1±43.6
	Rotus Uhak		3	14.8±3.3	17.2±3.2	0.1278±0.069	85.2±36.6
	Old Uhak		3	12.6±3.2	15.6±3.1	0.0888±0.058	78.3±43.1

Table 4: Analysis of variance table for standardized tree volume of *Eucalyptus urophylla* provenances and families within provenances in two populations (PE023 and PV042) at four and seven years of age respectively

PE023 trial series					
Source	DF	Type III SS	Mean Square	F Value	Pr > F
Trial	1	10821.19	10821.19	6.28	0.0123
Rep(trial)	6	5239.15	873.19	0.51	0.8036
Provenance	3	19646.41	6548.80	3.80	0.0099
Family(provenance)	39	249255.43	6391.16	3.71	<.0001
Trial*provenance	3	21842.96	7280.99	4.23	0.0055
Trial*family(provenance)	16	36572.60	2285.79	1.33	0.1717
PV042 trial series					
Trial	2	22252.84	11126.42	4.33	0.0132
Rep(trial)	19	8859.23	466.28	0.18	1
Provenance	13	1411968.58	108612.97	42.25	<.0001
Family(provenance)	190	2403861.12	12651.90	4.92	<.0001
Trial*provenance	20	279734.16	13986.71	5.44	<.0001
Trial*family(provenance)	167	1522573.01	9117.20	3.55	<.0001

Table 5: Provenance and genetic correlations between three different growth traits (height, DBH and volume) for two *Eucalyptus urophylla* populations (PE023 and PV042) established in Zululand. Error values are the SE. na = SE of a provenance or genetic correlation could not be calculated as the estimate was bounded at the theoretical limit of zero or one

			Provenance correlations (r_{prov})		Family (Provenance) correlations ($r_{g(p)}$)		Family correlations (r_g)	
Trial	Age (years)	Trait	with DBH	with volume	with DBH	with volume	with DBH	with volume
		height	na	na	0.71±0.129	0.78±0.063	0.71±0.132	0.78±0.064
PE023A	4	DBH		na		0.98±0.004		0.98±0.004
		height	1.00(na)	0.99±0.004	0.83±0.073	0.89±0.030	0.83±0.060	0.91±0.025
PE023B	4	DBH		1.00(na)		0.99±0.004		0.98±0.006
		height	na	na	0.83±0.097	0.89±0.067	0.74±0.132	0.89±0.062
PE023A&B	4	DBH		na		0.98±0.012		0.98±0.012
		height	0.88±0.074	0.88±0.075	0.87±0.036	0.88±0.033	0.85±0.032	0.86±0.030
PV042A	7	DBH		0.99±0.001		0.99±0.002		0.99±0.001
		height	0.90±0.070	0.90±0.066	0.92±0.031	0.92±0.031	0.90±0.030	0.89±0.033
PV042B	7	DBH		0.99±0.001		0.99±0.003		0.99±0.001
		height	0.87±0.176	0.91±0.066	0.97±0.007	0.95±0.011	0.92±0.015	0.93±0.015
PV042C	7	DBH		0.98±0.013		0.98±0.005		0.97±0.005
		height	0.95±0.027	0.96±0.021	0.93±0.039	0.91±0.053	0.89±0.031	0.88±0.015
PV042A&B&C	7	DBH		0.99±0.003		0.98±0.015		0.98±0.002

calculated for the PE023 trial series as the estimates were bounded to the theoretical limit of zero.

Overall, growth was under weak to moderate genetic control in both the *E. urophylla* populations. At four years, heritability (h_f^2) for height, DBH and volume was calculated as 0.20, 0.12 and 0.14, respectively (**Table 6**). Higher heritabilities for the three growth traits were calculated at seven years for the PV042 trial series. It must be borne in mind that more families were established in the PV042 trial series, especially at PV042C (162 families). As a result, the variance between families increased and may explain the higher heritabilities (h_f^2=0.60 for volume) reported for PV042C relative to other trial sites. The across site heritability (h_f^2) for height, DBH and volume in the PV042 trial series was estimated at 0.17, 0.30 and 0.26 respectively. As expected, the genetic parameter estimates for heritability (h_f^2) and type B genetic correlation (r_{Bg}) for family without the provenance effect were higher than the heritability ($h_{f(p)}^2$) and type B genetic correlations ($r_{Bg(p)}$) for family within provenance for all three growth traits. This difference was especially evident as P^2 increases. For instance, at the PV042 trial series $h_{f(p)}^2$ was lower than h_f^2 for DBH (0.07 and 0.30) and volume (0.06 and 0.26) across the three sites. Four year results of the PE023 trial series showed that h_f^2 was 0.20 and $h_{f(p)}^2$ was 0.17 for height. Where P^2 could not be calculated for DBH and height, h_f^2 and $h_{f(p)}^2$ are reported as the same (0.12 for DBH and 0.14 for height). The type B genetic correlation for height was higher for the family without provenance effect (r_{Bg} = 0.89) than for the family within provenance effect ($r_{Bg(p)}$= 0.86), but the same for DBH and volume (0.61) in the PE023 trial series. However, in most cases provenance variation (P^2) and type B provenance correlation (r_{Bprov}) could not be calculated for the PE023 trial series due to the insignificance of the provenance effect at the PE023B trial site. Provenance variance was

Table 6: Provenance and genetic parameters for three different growth traits (height, DBH and volume) for two *Eucalyptus urophylla* populations (PE023 and PV042) established in Zululand. Error values are the SE. na = SE of a provenance or genetic correlation could not be calculated as the estimate was bounded at the theoretical limit of zero or one

Trial	Age (years)	Trait	Provenance		Family(provenance)				Family			
			P^2	r_{Bprov}	$h^2_{f(p)}$	$r_{Bg(p)}$	$GCV_{f(p)}$	V_{phen}	h^2_f	r_{Bg}	GCV_f	V_{phen}
		height	na		0.13±0.05		2.85	181.35	0.13±0.06		2.76	180.47
PE023A	4	DBH	na		0.17±0.06		4.99	435.41	0.17±0.06		4.97	435.3
		volume	na		0.18±0.07		10.65	1861.50	0.18±0.07		10.51	1859.02
		height	0.07±0.08		0.17±0.13		3.24	182.29	0.32±0.16		4.53	192.52
PE023B	4	DBH	0.01±0.02		0.18±0.11		5.16	454.64	0.18±0.11		5.23	455.49
		volume	0.03±0.05		0.18±0.12		10.40	1827.44	0.22±0.13		11.71	1857.24
		height	0.01±0.01	na	0.17±0.07	0.86±0.09	3.22	183.23	0.20±0.07	0.89±0.07	3.49	184.87
PE023A&B	4	DBH	na	na	0.12±0.06	0.61±0.20	4.14	442.56	0.12±0.06	0.61±0.21	4.14	442.57
		volume	na	na	0.14±0.07	0.61±0.22	9.21	1865.52	0.14±0.07	0.61±0.21	9.21	1865.52
		height	0.04±0.02		0.14±0.03		3.90	316.98	0.22±0.04		4.91	325.49
PV042A	7	DBH	0.09±0.04		0.18±0.04		5.65	536.14	0.38±0.06		8.58	576.89
		volume	0.09±0.04		0.20±0.04		13.92	2961.96	0.39±0.06		20.25	3171.98
		height	0.07±0.04		0.16±0.05		4.13	314.78	0.31±0.08		5.79	329.42
PV042B	7	DBH	0.18±0.09		0.28±0.08		6.85	497.06	0.70±0.13		11.69	584.67
		volume	0.2±0,09		0.26±0.07		15.30	2745.42	0.67±0.13		26.65	3198.78
		height	0.03±0.02		0.41±0.06		6.61	322.97	0.45±0.07		6.98	327.23
PV042C	7	DBH	0.07±0.03		0.44±0.07		9.01	548.03	0.58±0.08		10.61	579.26
		volume	0.07±0.03		0.48±0.07		22.15	3036.84	0.60±0.08		25.30	3181.83
		height	0.03±0.01	0.59±0.29	0.08±0.03	0.27±0.11	2.95	318.57	0.17±0.04	0.44±0.09	4.26	327.19
PV042A&B&C	7	DBH	0.09±0.04	0.77±0.13	0.07±0.03	0.20±0.12	3.55	535.65	0.30±0.06	0.53±0.09	7.57	579.02
		volume	0.09±0.04	0.76±0.13	0.06±0.03	0.14±0.11	7.43	2954.13	0.26±0.01	0.46±0.09	16.75	3182.93

calculated for the PV042 trial series at seven years of age and was lowest for height (0.03) and the same for DBH and volume (0.09) across the three trials. The r_{Bprov} followed a similar trend with height being the lowest (0.59) and DBH and volume displaying similar r_{Bprov} of 0.77 and 0.76 respectively. The provenance type B correlations were much higher than the type B genetic correlations at this trial series. The $r_{Bg(p)}$ for height, DBH and volume were 0.27, 0.20 and 0.14. When the provenance effect was excluded from the analysis, the type B genetic correlation (r_{Bg}) for height, DBH and volume increased to 0.44, 0.53 and 0.46 respectively. This is an indication that the provenance effect stayed fairly stable across sites and that a combined site analysis can be performed.

When the genetic coefficient of variation (GCV) was investigated, it was evident that the GCV was lowest for height, intermediate for DBH and highest for volume in all cases. The $GCV_{f(p)}$ for height, DBH and volume was 3.2%, 4.1% and 9.2% respectively in the PE023 trial series. At the PV042 trial series, the $GCV_{f(p)}$ for height, DBH and volume was 2.9%, 3.5% and 7.4% respectively. The $GCV_{f(p)}$ expresses the additive genetic standard deviation (within provenance) in terms of percent. In other words, those trees in the population that have breeding values of one genetic standard deviation above the mean will have 9.2% (in the PE023 trial series) and 7.4% (in the PV042 trial series) more volume growth than the provenance mean (Cornelius 1994). It is clear that there are tremendous opportunities to make genetic gains in this *E. urophylla* population. For instance, if it is possible to identify the trees in the PV042 trial series that have breeding values of two genetic standard deviations above the mean, this would represent 14.8% additional gain above the provenance mean (Hodge and Dvorak 2012).

BLUP and genetic gains

Best linear unbiased predictions were made for provenance (G_{prov}), families within provenance ($G_{fam(p)}$) and individual trees (G_i). Individual tree breeding values (BV) is equal to the sum of the above mentioned predictions. The predictions are expressed in units of percentage gain above the unimproved population mean for volume. For the purpose of this article, only G_{prov} and the range in $G_{fam(p)}$ for the two *E. urophylla* populations are displayed in **Table 7**. Estimations of provenance predictions were calculated to be a theoretical zero at the PE023 trial series. It should be borne in mind that this trial series represents a limited number of only four provenances and the amount of families within provenances ranged between four and 18. In contrast to the PE023 trial series, a big range in provenance predictions was estimated for the PV042 trial series. Predicted gains for Apui and Wai Kui provenances were the biggest at 27.8% and 24.8% respectively. Predicted gains for Old Uhak provenance were the lowest at -25.3%.

In a scenario where the top 200 individuals are selected based on their BV, the average predicted gains are 54.6% more than the population mean. However, such a scenario will drastically reduce the genetic diversity in the population and will only include individuals from 61 families and 7 provenances. An alternative selection strategy would be to select the top 40 individuals from the PE023 population and the top 160 individuals from the PV042 population, but not more than two individuals per family. The estimated gains (44.7%) of this scenario will be less than the first scenario, but a reasonable genetic base (200 individuals from 100 families and 14 provenances) will remain. The genetic diversity in such a breeding population should be sufficient for future breeding, especially if one takes into account that *E. urophylla* only gets utilised as a hybrid parent in making crosses with *E. grandis* in Zululand.

A scenario to construct an elite population, could be to select the top two individuals (based on BV) from the top five families (based on $G_{fam(p)}$) of the five best provenances

Table 7: Predicted gains (%) for provenances (G_{prov}) and families within provenances ($G_{fam(p)}$) of two *Eucalyptus urophylla* populations (PE023 and PV042) in Zululand.

Trial series	Provenance	No. of families	G_{prov}	Range in $G_{fam(p)}$
PE023	Wuko	4	na	-10.7 - 3.4
	Egon	18	na	-12.4 - 19.7
	Lewotobi	16	na	-8.8 - 18.6
	Mandiri	5	na	-12.8 - 9.2
PV042	Baubillatung	9	0.38	-3.1 - 3.6
	Dalaki	6	8.95	-5.4 - 13.2
	Lalikki	9	-0.31	-8.1 - 10.2
	Mareke Arnau	28	-19.9	-9.9 - 6.9
	Wai Kui	10	24.78	-4.5 - 8.1
	Apui	10	27.81	-6.7 - 10.2
	Ilwaki1	4	-14.23	-2.9 - 0
	Ilwaki2	28	-5.89	-7.6 - 7.7
	Pintumas	15	2.1	-12.4 - 7.2
	Telemar	6	-1.51	-1.9 - 1.6
	Carbutu	8	-0.38	-7.5 - 6.6
	Rotus Uhak	37	3.51	-8.7 - 7.4
	Old Uhak	6	-25.31	-6.2 - 2.5

(based on G_{prov}). This scenario would result in 50 selections with an average BV of 59.8% above the population mean.

Discussion

Results of our study indicated that GxE effects would be practically negligible for the growth of *E. urophylla* in Zululand. Our results coincide with the relatively high type B correlations (above 0.55) reported by Wei and Borralho (1998), and Hodge and Dvorak (2015) for *E. urophylla*. Nirsatmanto et al. (1996) reported moderate (0.49 for DBH) type B correlations between two sites in Indonesia, but indicated that predicted gains of the selection index across the sites were still greater than those of the indices at each site. One exception was the study done by Mori et al. (1990). They have reported losses in volume of up to 26.7% due to GxE. However, their testing sites were very different from each other in terms of altitude (ranging from 50 to 820 m.a.s.l.) and M.A.T. (ranging from 21^{o}C to 23.6^{o}C). In our study, the Zululand sites are very similar and situated at altitudes between 24 and 87 m.a.s.l. and a M.A.T of 21^{o}C at all sites. It is therefore recommended that only one *E. urophylla* breeding population should be managed for Zululand.

The strong genetic correlation between the various growth traits for *E. urophylla* that was detected in this study was also noted by Hodge and Dvorak (2015). The results of our study confirm that DBH is a sufficient growth measure to use in *E. urophylla* breeding programmes. Diameter is easier and quicker to measure than heights and will make the measurements of breeding trials more efficient.

Low to moderate genetic control for all three growth traits was evident in this study. The heritabilities calculated in this study is consistent with those reported by others. Narrow-sense heritabilities of 0.11-0.41 was reported for China (Wei and Borralho 1998), 0.10 –

0.31 for Vietnam (Kien et al. 2009), 0.10 for Brazil (de Souza et al. 2011) and 0.15 across five countries (Hodge and Dvorak 2015). Other authors have reported that wood quality traits are under more genetic control than growth, and should be considered in the selection process in future. For instance, Greaves et al. (1996) and Wei and Borralho (1997) reported narrow-sense heritabilities for wood basic density of 0.60 and 0.71 respectively. Darrow and Roeder (1983) also reported that *E. urophylla* has higher basic wood density than pure *E. grandis* in South Africa. However, even though growth is under less genetic control than wood quality traits, volume was still identified as the dominant trait in determining the economic benefits in short-rotation species for pulp production and should therefore not be neglected (Wei and Borralho 1999).

At a provenance level, the good growth performance of the Lewotobi and/or Wai Kui provenances in this study agreed with results reported by others (Ngulube 1989, Zhou and Liang 1991, Luz et al. 1996, Wei and Borralho 1998, Kien et al. 2009). One exception was the good growth performance (27.8% gain) of the Apui provenance in our study relative to the study done by Wei and Borralho (1998). Hodge and Dvorak (2015) reported the same trend for the Apui provenance across countries with genetic gains ranging from -13.9% in Brazil to 3.7% in South Africa. The poor growth performance of the Mandiri provenance was evident in this study, as well as in studies done by Wei and Borralho (1998) and Kien et al. (2009), but not in the study done by Ngulube (1989). Ngulube (1989) reported that Mandiri was one of the four best provenances tested in Malawi. The differences in provenance performance at different countries could be due to the large variation in growth between sources from the same provenance (Hodge and Dvorak 2015). This points to the need for intensive provenance sampling and testing in *E. urophylla* to locate productive sources (Hodge and Dvorak 2015).

Overall, the relatively large provenance and family variation in the two *E. urophylla* populations in Zululand provides opportunities for impressive gains through selection and breeding. In order to conserve the genetic diversity of the main *E. urophylla* breeding population, a selection criteria of 200 selections is recommended. The number of selections from each population (PE023 and PV042) should proportionally be the same as the size of each population relative to the size of the two populations combined. In other words, approximately 20% of the selections should come from the PE023 population and 80% from the PV042 population. A maximum of two trees per family is recommended. The estimated gains for this scenario will be 44.7% over the population mean. In order to construct an elite population for hybrid breeding, the selection of the top two individuals from the top five families of the five best provenances is recommended. This scenario would result in 50 selections with an estimated gain of 59.8%. Elite selections could be used to undertake intra- and inter-specific controlled crosses. Progeny from intra-specific crosses could be infused into the breeding population to enhance the genetic pool with superior genotypes. Superior progeny from the inter-specific crosses with *E. grandis* should be incorporated into an *E. grandis x E. urophylla* clonal testing programme in Zululand.

Conclusions

The relatively large provenance and family variation detected for the two *E. urophylla* populations in our study provides an adequate source to select for genetic gains and to maintain genetic diversity for hybrid and pure species breeding. We also conclude from this study that a single *E. urophylla* breeding population should be sufficient for Zululand due to the relatively low levels of GxE and that only DBH can be used as a growth measure in *E. urophylla* breeding programmes.

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