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Genetic parameter estimates and parental selection in *Eucalyptus longirostrata* and *Corymbia henryi* populations tested in South Africa

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Abstract

The sub-tropical species, *Eucalyptus longirostrata* (formerly *E. punctata* var *longirostrata*) and *Corymbia henryi* were investigated as alternative species for growth on the Zululand coastal plain in South Africa. Provenance/progeny trials were established in 2001 at two sites, namely, Nyalazi and Kwambonambi. The seed material purchased from the Commonwealth Scientific and Industrial Research Organization in Australia in 2000 included six provenances of *E. longirostrata* and five provenances of *C. henry*i. Six-year diameter at breast height measurements were completed in 2007. Individual narrow-sense heritability coefficients for diameter growth varied from 0.30 to 0.58 for both species, with heritabilities being higher at the drier

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Nyalazi site. Heritabilities and breeding values were calculated prior to making selections in field. A total of 143 selections were made in the *E. longirostrata* trials, and 113 in the *C. henryi* trials during 2008. Predicted gains for the next generation range from 2.8 cm (20%) to 6.1 cm (61%) increase in diameter for *E. longirostrata*, and 3.4 cm (23%) to 5.4 cm (49%) increase for *C. henryi*, depending on site and selection scenario. Provenance differences were evident in *E. longirostrata* at both sites; however, there were no significant differences between the *C. henryi* provenances of Australian origin. The top families of both species performed better than the hybrid controls at the Nyalazi site, indicating that both *E. longirostrata* and *C. henryi* are viable alternative species for successful growth on the drier sites of the Zululand coastal plain.

Key words: tree breeding, genetic parameters, heritability, genetic gains, BLUP, selection.

Introduction

The Zululand coastal plain is one of South Africa's major commercial plantation forestry areas. The region has become based on clonal forestry, generally favouring *E. grandis* and its hybrids with certain other *Eucalyptus* species. However, *E. grandis* is susceptible to various diseases and is not particularly drought tolerant. As such, it has serious limitations under the sub-tropical conditions in Zululand as a pure species (GARDNER, 2000).

In an effort to search for alternative species for successful growth on the Zululand coastal plains, the Institute for Commercial Forestry Research (ICFR) established a series of site-species interaction trials during 1992. Results from these trials, based on growth, disease resistance and pulping properties, showed that *E. longirostrata* was one of the top performing pure species at the southern, highly productive site and, on the drier, more marginal site, *C. henryi* performed very well (DARROW, 1995; GARDNER et al., 2001). Site-species interaction trials established in 1996 in northern Zululand and Maputaland, on sites considered too hot and dry for optimum growth of *E. grandis*, confirmed the potential of both species. Results indicated that these species have good growth, fibre and wood chip production on moderately dry sites on the Zululand coastal plain, are adaptable to a wide range of soil conditions and, due to these characteristics, may become increasingly valuable alternative species in dry, sub-tropical Zululand (GARDNER et al., 2007; GARDNER and LITTLE, 2009). Based on these results, comprehensive provenance/progeny trials of *E. longirostrata* and *C. henryi* were established by the ICFR at two sites in 2001.

Height measurements and survival assessments were undertaken in 2002, one year after planting (SWAIN and OSCROFT, 2003). Initial survival at Nyalazi was excellent (over 98%) for both species, and Kwambonambi had approximately 85% survival for both species. Diameter at breast height (dbh) measurements were completed in all trials at 45 months of age, with additional disease assessments in the *C. henryi* trials at 57 months of age, after a range of stem diseases were noted in these trials (SWAIN and OSCROFT, 2008). Surprisingly, there was very little disease at the dry Nyalazi site, the most notable disease being Botryosphaeria canker, but at very low infection rates. Botryosphaeria canker was more prevalent at the wetter Kwambonambi site but, although noticeable throughout the trial, only caused damage to a few families. These families were from different provenances, so it does not appear that there are any provenance differences with regard to susceptibility to this disease in Zululand. Thus, it appears that *C. henryi* is more susceptible to disease on wetter sites than on dry sites. There was very little disease noted in the *E. longirostrata* trials.

This paper reports on the six-year dbh measurements completed in 2007, as well as the estimated genetic parameters and genetic gain predictions from the six-year measurements. Provenance and family mean comparisons are discussed, and two parental selection scenarios, based on estimated breeding values, are presented.

Materials and Methods

Genetic material and field design

Seed from six provenances of *E. longirostrata* and five provenances of *C. henryi* was purchased from the Commonwealth Scientific and Industrial Research Organization (CSIRO) in 2000. Details of the provenance origins are provided in *Table 1*. The two species are not represented by the complete natural distribution of these species, but rather all the seedlots that were available at the time, *i.e.* 50 *E. longirostrata* maternal families and 43 *C. henryi* maternal families, with each provenance represented by only 5 to 12 families. Two provenance/progeny trials of each species were established at Nyalazi and Kwambonambi in Zululand, and a Breeding Seed Orchard (BSO) for each species was established at Teza. The site at Kwambonambi was considered the most favourable site for growth in terms of rainfall. Trial details, site information and details of the controls used are provided in *Table 2*. Dependent on the number of families included in each trial, the field design was either a balanced or unbalanced lattice design, with each family represented in eight tree line-plots replicated four times. The spacing and stocking varied slightly depending on the specific spacing used by the landowner (*Table 2*).

The species controls (*E. grandis*) and clonal controls (*E. grandis* TAG 14 and *E. grandis* hybrid clones, *i.e.* *E. grandis* x *E. calmaldulensis* clone (GC); *E. grandis* x *E. urophylla* clone (GU); and *E. grandis* x *E. tereticornis* clone (GT)) were planted around the outside of the trials in 3 x 8 rectangular plots, with the inner six trees being measured. This layout was used to prevent inter-species competition between the controls and the provenances within the trial, nevertheless still providing a comparative measure of the different controls with the *E. longirostrata* or *C. henryi* material. The *C. henryi* Zululand bulk (ex ICFR site-species trials SGE 32 and 34 in Zululand) was included as an internal control in the body of the *C. henryi* trials (*Table 1*). It is important to recognise that the wild, unimproved material from Australia used in this trial series is being compared to the external con-

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Table 1. – Provenance origins of *Eucalyptus longirostrata* and *Corymbia henryi* included in South African provenance/progeny trials.

Provenances (ex Australia)	CSIRO seedlot no.	Latitude (S)	Longitude (E)	Altitude (m a.s.l.)	Number of mother trees
E. longirostrata:					
NNW Chinchilla, QLD [1]	16008	26°22'	152°22'	330	5
Barakula, QLD	20404	26°19'	150°41'	300	10
Starkvale Creek, QLD	20007	25°20'	145°20'	450	10
var Mount Moffat, QLD	19702	25°05'	148°05'	730	10
Coominglah SF [2], QLD	19312	24°48'	150°48'	480	5
Blackdown Tableland, QLD	20008	23°46'	149°04'	900	10
C. henryi:					
Myrtle Creek SF A, NSW [3]	20419	29°12'	153°01'	50	8
Myrtle Creek SF B, NSW	19468	29°09'	152°09'	50	10
Bungawalbin SF, NSW	19749	29°04'	153°04'	60	5
Braemar SF, NSW	19750	29°02'	152°02'	90	6
Ewingar SF, NSW	16899	29°01'	152°01'	520	10
Zululand bulk, RSA [4]	-	28°42'	32°08'	50	12

[1] Queensland.
[2] State Forest.
[3] New South Wales.
[4] Seed ex-ICFR site-species trials SGE 32 and SGE 34.

trols which are either: *a)* improved, pure species seedlots which have undergone at least one generation of improvement for growth, *b)* an *E. grandis* clone, selected for superior growth, or *c)* hybrid clones, bred and selected for growth and adaptability in Zululand. The data for the external controls were analysed separately, as these controls were not included in the experimental design of the trials.

The BSOs at Teza comprised eight tree line-plots, replicated six times. The seedlings at Teza were planted with 3 g Hydrogel/1 ℓ water per plant; those at Nyalazi with 2 g Hydrogel/2 ℓ water per plant and 320 g Agrofert; those at Kwambonambi with 1 ℓ water per plant and 220 g 5.2.0 only.

Data collection and statistical analysis

Diameter at breast height (dbh) was measured in both the *E. longirostrata* and *C. henryi* trials at Nyalazi and Kwambonambi at 76 months of age. Dead or missing trees and runts were removed from the dataset before analysis. Statistical analysis was conducted using SAS® Institute Inc. Software 9.1.3 (Copyright © 2002–2003 SAS Institute Inc.).

To test for normality for dbh, residuals were plotted against fitted values at each site. None showed any detectable trends or patterns. It can therefore be said that the conditions that $\varepsilon_{ijl} \sim$ iid $(0, \sigma^2)$ have been met for these data, and the standard ANOVA assumptions are valid. To test the significance of effects for provenances and families, an F test was carried out, based on the GLM SAS procedure. Comparisons between provenance and family means were made using Student-Newman-Keuls test at the 5% significance level.

The generalised linear mixed model used for the eight tree line-plot analysis was

$$y_{ijl} = \mu + rep_i + fam_j + (rep*fam)_{ij} + \varepsilon_{ijl}$$

where y_{ijl} = mean for the trait of the l^{th} tree in the i^{th} replication and j^{th} family, μ = overall mean, rep = i^{th} replication effect, i = 1,…4, fam = j^{th} family effect, rep*fam = interaction between the i^{th} replication and j^{th} family (plot effect), ε_{ijl} = random error associated with i^{th} replication, j^{th} family and l^{th} tree where $\varepsilon_{ijl} \sim$ iid $(0, \sigma^2)$.

Since the trial was unbalanced due to the number of surviving trees and the unequal number of families per

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Table 2. – Trial and site information of the *Eucalyptus longirostrata* and *Corymbia henryi* provenance/progeny trials and Breeding Seed Orchards (BSOs). External controls included for each trial are shown.

Locality	Planting date	Latitude (S)	Longitude (E)	Altitude (m a.s.l.)	MAP[1] (mm)	MAT[2] (°C)	Soil depth (mm)	Trial design (No. of families)		Spacing (stems/ha)	External controls
Provenance/progeny trials:								*E. longirostrata*	*C. henryi*		*Species/Clone*
Erlandson Estate, Nyalazi	30/08/01	28°13.4'	32°20.0'	20	972 *	21.9	> 1200	6x6 triple lattice (36)	5x7 unbalanced lattice (34)	2.5 x 2.6 m (1538)	*E. grandis* ex Sabie, GU[3] A, *E. grandis* ex Zululand, *E. grandis* ex 7 Oaks, GC[4], *E. grandis* TAG 14, GT[5]
Salpine, Kwambonambi	23/08/01	28°34.1'	32°12.6'	70	1091	21.6	> 1200	6x6 triple lattice (36)	5x7 unbalanced lattice (34)	2.2 x 2.7 m (1638)	*E. grandis* ex Sabie, GU A, *E. grandis* ex Zululand, *E. grandis* ex 7 Oaks, GC, *E. grandis* TAG 14, GU B
BSOs:											
Teza, Kwambonambi	16/08/01	28°30.7'	32°08.1'	60	980	21.8	> 1200	6x6 triple lattice (36)	5x7 unbalanced lattice (33)	2.4 x 3.0 m (1388)	-

[1] Mean annual precipitation.
[2] Mean annual temperature.
[3] GU = *E. grandis* x *E. urophylla* clone.
[4] GC = *E. grandis* x *E. camaldulensis* clone.
[5] GT = *E. grandis* x *E. tereticornis* clone.

* Actual annual rainfall for Nyalazi differed markedly from site MAP (Mean annual precipitation) since the trial was planted in August 2001:

Year :	2001	2002	2003	2004	2005	2006	2007	*Site MAP*
Rainfall (mm) :	853.8	536.1	563.8	894.8	614.4	947.6	585.0	972

provenance, the SAS procedure MIXED with the REML method was employed to estimate variance components. Proc MIXED does not allow the variance component estimates to be negative and produces best linear unbiased predictions (LITTELL et al., 1996).

Family variance was estimated as, $\sigma^2_F = 0.33\sigma^2_A$ where σ^2_A is the additive genetic variance. Additive variance was calculated as 3 times the family variance, considering the possible effect of family relationship and the presence of full-sibs within the open-pollinated families (SQUILLACE, 1974). Narrow sense individual heritability (h^2) and within-family (h^2_{wf}) heritability was calculated for each site, using the formulae (SQUILLACE, 1974; FALCONER and MACKAY, 1996):

$$h^2 = \frac{1}{0.33}\sigma^2_F / \sigma^2_P$$

$$h^2_{wf} = \frac{(1-r)h^2}{1-(r.h^2)}$$

where σ^2_P is the phenotypic variance component and r is the coefficient of relationship. Standard errors of observed and genetic variance components, as well as heritabilities were estimated according to Dickerson's approximation (DICKERSON, 1969). Families and individuals with the highest BLUP ranking, regardless of provenance effects, were assumed to be the most desirable trees in the population. Consequently, a family plus within family selection strategy was followed for both species based on BLUP predictions, in conjunction with a critical visual phenotypic assessment in field, conducted for the purposes of disease incidence and stem form assessment.

Predicted genetic gains and selection

The potential genetic gain to be obtained through selection will vary depending on the heritability of the trait under consideration, the phenotypic variation present for that trait in the population and the intensity of selection. The predicted genetic gain was estimated when selection was applied according to two scenarios;

1. Realistic – Best tree per plot of the top 70% of families in the population.

Based on family mean and BLUP ranking for each species at both sites, 28% of the poor families were rogued from the *E. longirostrata* trials, and 26% from the *C. henryi* trials. Of the remaining families, the best tree per plot of eight trees was then selected to remain. Genetic gains were predicted, according to VERRYN et al. (2000) (adapted):

$$\Delta G = \left[SI_b \times r \times \frac{\sigma^2_A}{\sigma_F} \right] + \left[SI_w \times \frac{(t-1)}{t} \times (1-r) \times \frac{\sigma^2_A}{\sigma_{wf}} \right]$$

where ΔG = predicted genetic gain or response to selection, SI_b = selection intensity between/among families, r = coefficient of relationship, σ^2_A = additive genetic variance, σ_F = standard deviation among families, SI_w = selection intensity within families, t = number of trees per family, and σ_{wf} = standard deviation within families.

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2. Selected – Direct selections made from the population, based on BLUP predictions and in-field phenotypic assessments. Genetic gains were predicted as described by FALCONER and MACKAY (1996):

$$\Delta G = ih^2 \sigma_p$$

where ΔG = genetic gain or response to selection, i = selection intensity, h^2 = narrow-sense heritability estimate, and σ_p = phenotypic standard deviation. Selection intensities between/among families and within families were determined using the standardised selection intensity tables of BECKER (1984).

Results and Discussion

The GLM analysis revealed significant differences among provenances and families, according to site and species (*Table 3*), indicating the possibility of increasing growth performance through selection of the more productive provenances and families.

Provenance performance

The Mount Moffat provenance of *E. longirostrata* performed significantly worse ($p < 0.05$) for dbh than NNW Chinchilla and Starkvale Creek at Nyalazi, and significantly worse ($p < 0.05$) than all other provenances at Kwambonambi (*Table 4*). No significant differences ($p > 0.05$) for dbh were observed between the Australian provenances of *C. henryi* at both sites, although the Bungawalbin State Forest and Braemar State Forest provenances performed significantly worse ($p < 0.05$) than the South African *C. henryi* bulk at Nyalazi and Kwambonambi, respectively (*Table 4*).

Family performance

Even though there were no significant differences between the top ten families presented in *Table 4*, significant differences were still evident between the best and worst performing families in each trial ($p < 0.0001$; *Table 3*). The BLUP rank was based on the BLUP prediction of the family breeding value for backward selection.

As anticipated, the hybrids bred for the specific site (*i.e.* GUs at the wetter Kwambonambi site and GCs and GTs at the drier Nyalazi site) performed well. However, at the drier Nyalazi site, the top six *E. longirostrata* families and the top two families of *C. henryi* performed better than all the hybrid controls (*i.e.* GT, GC and GU A) for dbh. Furthermore, the top ten unimproved families of both species outperformed all the pure *E. grandis* controls at this site (*Table 4*). This indicates that both *E. longirostrata* and *C. henryi* have good potential as viable alternative species for successful growth on dry sites of the Zululand coastal plain. The hybrid controls also performed better than the *E. grandis* controls at this dry site, probably due to the fact that low rainfall is limiting to the growth of *E. grandis* (DARROW, 1995).

At Kwambonambi, the most favourable site for growth, the two GU hybrid controls outperformed all *E. longirostrata* families (*Table 4*). This was not surprising, as these GU hybrids were bred for these site conditions. However, two *C. henryi* families from Myrtle Creek B performed better than the two GU hybrids, and several *C. henryi* families outperformed the GC hybrid control (*Table 4*). Although some of the top *E. longirostrata* and *C. henryi* families outperformed the *E. grandis* controls at Kwambonambi, this is not really a relevant comparison, as pure *E. grandis* has been replaced by hybrid clones on a commercial scale on these high productivity sites.

Growth and survival for both species throughout the trial series has been better at Kwambonambi than at the drier Nyalazi site, which was anticipated, based on mean annual precipitation (MAP) alone (*Table 2*). It should be noted however, that during the first two years following establishment of the Nyalazi trials, the site received significantly lower annual rainfall (<565 mm)

Table 3. – Analysis of variance for diameter at breast height at 76 months of age, at two sites, in *Eucalyptus longirostrata* and *Corymbia henryi* South African provenance/progeny trials. d.f. = degrees of freedom.

Site	Species	Source of Variation	d.f.	Sum of squares	Mean Square	F Value	*P*-value
Nyalazi	*E. longirostrata*	Replication	3	71.920	23.973	2.04	0.1069
		Provenance	5	462.994	92.599	7.88	<0.0001
		Family	30	2072.910	69.097	5.88	<0.0001
		Error	804	9449.737	11.753		
	C. henryi	Replication	3	61.014	20.338	1.95	0.1194
		Provenance	5	167.229	33.460	3.22	0.0070
		Family	28	1820.075	65.003	6.25	<0.0001
		Error	835	8690.106	10.407		
Kwambonambi	*E. longirostrata*	Replication	3	12.066	4.022	0.21	0.8870
		Provenance	5	1042.128	208.426	11.07	<0.0001
		Family	30	1714.927	57.164	3.04	<0.0001
		Error	1020	19203.222	18.827		
	C. henryi	Replication	3	60.085	20.028	1.22	0.3025
		Provenance	5	278.255	55.651	3.38	0.0049
		Family	29	2454.388	84.634	5.14	<0.0001
		Error	942	15509.918	16.465		

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than the site average (972 mm) (*Table 2*). These exceptionally dry conditions clearly impacted on growth at this site, yet also provided an opportunity to further investigate the drought tolerance of these two species.

Genetic parameters

Individual heritability coefficients (h^2) obtained for *E. longirostrata* and *C. henryi* at 76 months for dbh, varied from 0.30 to 0.58, according to site quality (*Table 5*).

Table 4. – Provenance performance of *Eucalyptus longirostrata* (a), *Corymbia henryi* (d), and external controls (c) at 76 months of age at two sites, ranked for dbh (cm). The ten top-performing families of *E. longirostrata* (b) and *C. henryi* (e) are shown, including the BLUP ranking. Provenance and family means grouped by the same letter for dbh are not significantly different (Student-Newmans-Keuls test, $\alpha = 0.05$).

Nyalazi				Kwambonambi			
***a) E. longirostrata* provenances**							
Provenance	**Number of families**	**Dbh (cm)**		**Provenance**	**Number of families**	**Dbh (cm)**	
Coominglah SF	16	11.14	a	Coominglah SF	5	15.44	a
Starkvale Creek	10	10.90	ab	Blackdown Tableland	9	14.34	b
Barakula	4	9.99	abc	Starkvale Creek	10	14.14	b
Coominglah SF	5	9.78	bc	Barakula	4	13.79	b
Blackdown Tableland	9	9.39	c	NNW Chinchilla	2	13.26	b
Mt Moffat	6	8.87	c	Mt Moffat	6	12.01	c
***b) E. longirostrata* top families**							
Provenance origin	**Family**	**Dbh (cm)**	**BLUP rank**	**Provenance origin**	**Family**	**Dbh (cm)**	**BLUP rank**
Starkvale Creek	31	12.90 *	1	Coominglah SF	20	17.26 *	1
Barakula	6	12.60	3	Blackdown Tableland	42	17.10	2
Starkvale Creek	37	12.50	2	Coominglah SF	16	16.30	3
Blackdown Tableland	42	12.48	5	Coominglah SF	18	15.83	4
Starkvale Creek	38	12.19	4	Blackdown Tableland	44	15.78	5
Blackdown Tableland	44	11.97	6	NNW Chinchilla	15	15.43	6
NNW Chinchilla	15	11.83	7	Starkvale Creek	37	15.24	7
Starkvale Creek	35	11.31	9	Barakula	6	15.01	8
Starkvale Creek	33	11.28	8	Starkvale Creek	36	14.92	9
NNW Chinchilla	16	10.78	10	Starkvale Creek	38	14.75	11
Trial mean		9.99		**Trial mean**		13.95	
Std error mean		0.13		**Std error mean**		0.14	
***c)* External controls**							
GT		11.96	a	GU B		18.24	a
GC		10.57	ab	GU A		17.51	a
GU A		10.42	ab	GC		15.86	ab
E. grandis Tag 14		9.97	b	*E. grandis* Tag 14		15.60	ab
E. grandis ex 7 Oaks		9.44	b	*E. grandis* ex Sabie		15.28	ab
E. grandis ex Sabie		9.43	b	*E. grandis* ex 7 Oaks		14.28	b
E. grandis ex Zululand		8.63	b	*E. grandis* ex Zululand		14.21	b
Control mean		10.11		**Control mean**		15.98	
Std error mean		0.21		**Std error mean**		0.31	
***d) C. henryi* provenances**							
Provenance	**Number of families**	**Dbh (cm)**		**Provenance**	**Number of families**	**Dbh (cm)**	
C. henryi bulk	1	11.41	a	*C. henryi* bulk	1	16.20	a
Myrtle Creek A	8	10.79	ab	Myrtle Creek B	10	15.42	ab
Ewingar SF	8	10.36	ab	Myrtle Creek A	8	15.40	ab
Myrtle Creek B	9	10.28	ab	Bungawalbin SF	5	14.75	ab
Braemar SF	3	10.02	ab	Ewingar SF	8	14.47	ab
Bungawalbin SF	5	9.54	b	Braemar SF	3	13.78	b
***e) C. henryi* top families**							
Provenance origin	**Family**	**Dbh (cm)**	**BLUP rank**	**Provenance origin**	**Family**	**Dbh (cm)**	**BLUP rank**
Myrtle Creek A	4	12.57 *	1	Myrtle Creek B	26	18.33 *	1
Myrtle Creek A	3	12.08	2	Myrtle Creek B	23	17.77	2
Myrtle Creek B	27	11.88	3	Bungawalbin SF	30	17.45	3
Braemar SF	36	11.71	4	Myrtle Creek A	4	17.04	4
Myrtle Creek B	26	11.63	5	Myrtle Creek A	7	16.93	5
Ewingar SF	15	11.49	6	Myrtle Creek B	20	16.85	6
Myrtle Creek A	8	11.47	7	Myrtle Creek A	1	16.24	7
C. henryi bulk [1]	40	11.41	8	*C. henryi* bulk [1]	40	16.20	8
Ewingar SF	11	11.39	9	Myrtle Creek A	2	16.02	9
Myrtle Creek B	24	11.35	10	Bungawalbin SF	29	15.73	10
Trial mean		10.33		**Trial mean**		15.00	
Std error mean		0.12		**Std error mean**		0.14	

* No significant difference between provenance means or family means.
SF = State Forest.
[1] No selections were made from this family (used as a control in the main body of the trial).

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Heritability estimates were higher at Nyalazi for both species. Heritabilities ranging from 0.30 to 1.00 are considered high, with resultant good genetic gains following individual tree selection (NAMKOONG, 1979; COTTERILL and DEAN, 1990; FALCONER and MACKAY, 1996). The heritability estimates fell within the normal range for eucalypts and compared well to those estimated for dbh in *E. grandis*; 0.16 to 0.34 (HARRAND et al., 2009) and 0.60 (LOUW, 2006). The heritability estimates in this study were higher than those found in *E. macarthurii* for dbh; 0.03 to 0.14 (NDLOVU, 2009) and *E. camaldulensis*; 0.11 (MAHMOOD et al., 2003). The heritability estimates for the *E. longirostrata* and *C. henryi* trials demonstrate that these populations exhibit appreciable levels of additive variance for dbh. These higher heritability coefficients may be explained by the origin of the provenances which belong to wild, unimproved Australian genetic material. The within-family heritability (h^2_{wf}), representing the regression of an individual's true breeding value on the deviation of its phenotypic value from the family mean is invariably lower than individual heritability for dbh (COTTERILL and DEAN, 1990), as was found in both species (*Table 5*). This statistic is relevant for estimating gains when selecting top individuals from within each family (FALCONER and MACKAY, 1996). Since the heritability estimates are based on a small number of genotypes in these trials, they could not be assumed to be random samples of the species' breeding populations. Therefore the overall averages are not to be considered representative of the populations' approximate means.

Selections and predicted genetic gains

The predicted genetic worth of families and individuals within families was used to rank and select individual trees, in combination with a rigorous phenotypic evaluation for stem form and incidence of disease. This resulted in the selection of 77 and 66 superior *E. longirostrata* individuals at Nyalazi and Kwambonambi respectively, and of 58 and 55 superior *C. henryi* trees at those same sites, respectively. The number of individuals selected per family was dependent on the individual BLUP rank, the family BLUP rank and phenotypic observation of the individuals in the field, with more

Table 5. – Variance components and genetic parameters with standard errors for *Eucalyptus longirostrata* and *Corymbia henryi* at Nyalazi and Kwambonambi for dbh at 76 months of age.

	σ^2_A	σ^2_F	σ^2_e	σ_p	σ_{wf}	h^2	h^2_{wf}
E. longirostrata							
Nyalazi	8.15 ± 2.528	2.71 ± 0.843	11.41 ± 0.599	3.82	4.11	0.58 ± 0.173	0.46 ± 0.022
Kwambonambi	6.34 ± 2.014	2.11 ± 0.671	18.84 ± 0.835	4.58	4.80	0.30 ± 0.096	0.23 ± 0.008
C. henryi							
Nyalazi	6.51 ± 2.018	2.17 ± 0.673	10.30 ± 0.537	3.55	3.83	0.52 ± 0.160	0.42 ± 0.019
Kwambonambi	7.09 ± 2.174	2.36 ± 0.725	16.47 ± 0.759	4.34	4.61	0.38 ± 0.115	0.29 ± 0.010

σ^2_A = additive variance.
σ^2_F = family variance.
σ^2_e = error/residual variance.
σ_p = phenotypic standard deviation.
σ_{wf} = standard deviation within families.
h^2 = heritability of individual values (narrow-sense).
h^2_{wf} = within family heritability.

Table 6. – Predicted gains (ΔG) for dbh (in cm and as a percentage) in the next generation of *Eucalyptus longirostrata* and *Corymbia henryi*, based on two selection scenarios, *a)* Realistic – best tree per plot of eight trees in the top 70% of families, and *b)* Selected – direct selections based on BLUP predictions.

	E. longirostrata		***C. henryi***	
	Dbh ΔG [cm (%)]	Selection intensity	Dbh ΔG [cm (%)]	Selection intensity
***a)* Realistic**				
Nyalazi	6.1 (61%)	SI_b = 2.773 SI_w = 1.550	5.4 (49%)	SI_b = 2.784 SI_w = 1.550
Kwambonambi	5.0 (36%)	SI_b = 2.773 SI_w = 1.550	5.4 (36%)	SI_b = 2.784 SI_w = 1.550
***b)* Selected**				
Nyalazi	4.3 (43%)	1.918	3.7 (36%)	2.023
Kwambonambi	2.8 (20%)	2.023	3.4 (23%)	2.063

ΔG = predicted genetic gain.
SI_b = selection intensity between/among families.
SI_w = selection intensity within families.

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selections allowed for the families with the higher BLUP ranking.

Interestingly, the Starkvale Creek provenance of *E. longirostrata* accounted for 49.4% of all selections at Nyalazi, but only 24.2% at Kwambomambi. Conversely, Coominglah State Forest accounted for 30.3% of all selections at Kwambonambi, but only 11.7% at Nyalazi.

These selections will be grafted into clonal seed orchards which will produce elite seed for the establishment of advanced generation breeding populations in these species, as well as for commercial seed production. The selected trees will also remain in a breeding seed orchard format once the poorer trees have been thinned from the existing trials, providing opportunities for rapid seed production and testing of protocols for macrocuttings in these species.

The predicted genetic gains, described as an increase in dbh (cm) and a percentage increase, were estimated according to two selection scenarios (*Table 6*). The predicted gain ranged from 2.8 cm (20%) to 6.1 cm (61%) increase in dbh for *E. longirostrata*, and 3.4 cm (23%) to 5.4 cm (49%) for *C. henryi*, and was noted to be higher for both species, using both scenarios, at Nyalazi. The gains for the Realistic scenario (based on the best tree per plot of the top 70% of families in the population) were generally greater than for the Selected scenario (based on direct selections made from the population using BLUP prediction). This was unanticipated as the number of selections was less in the Selected scenario than the Realistic and, theoretically, selection intensity increases with a decreasing number of selections, resulting in greater gain (FALCONER and MACKAY, 1996). However, it is possible for the realised gain from a seed orchard such as that described in the Realistic scenario to be greater than that of the Selected scenario. This is because the Realistic scenario comprises every tree from the Selected scenario, as well as additional superior trees from the top ranking families, due to the selection of the best tree per plot. Therefore, a greater number of superior individuals are included in this Realistic scenario, leading to higher predicted gains. Up to eight superior trees could be selected from the best families in this scenario, and the predicted gains formula used does not take into account the unbalanced number of individuals selected per family (VERRYN et al., 2007).

Conclusions

Significant provenance differences exist in the *E. longirostrata* material tested in these trial series, and it was concluded that the Mount Moffat provenance is not suitable for establishment on the Zululand coastal plains. However, as there were no significant differences between the Australian provenances of *C. henryi* at both sites, it appears that provenance does not play a role in this species under sub-tropical growing conditions in South Africa. The potential which both these species have shown in the provenance/progeny trials is likely to be further realised in the next generation of tree improvement in South Africa. Underlying population parameters are unlikely to represent the natural distribution of these species, as small samples make representative conclusions difficult. Subsequent to the establishment of these trials, further seedlot collections of both species have been done, and future testing would be more representative of the relative performance of the provenances and families, as well as the level of genetic control in the natural distribution of these species.

Both species have a potentially important role to play in commercial afforestation of the drier sites on the Zululand coastal plain. *Eucalyptus longirostrata* is able to hybridise with species such as *E. grandis*, and thus also has potential as a hybrid partner on these and other sites. In contrast, *C. henryi* is not able to hybridise with species such as *E. grandis*, which indicates that *C. henryi* only has potential as a pure species in South Africa, unless it is hybridised with other species from its subgenus, such as *C. torelliana* (LEE, 2007).

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Changes in Genetic Diversity of Whitebark Pine (*Pinus albicaulis* Engelm.) Associated with Inbreeding and White Pine Blister Rust Infection

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Abstract

We investigated the association of inbreeding and infection by the introduced disease white pine blister rust (caused by the fungus *Cronartium ribicola* J. C. Fisch) with genetic diversity of whitebark pine (*Pinus albicaulis* Engelm.) by genetically comparing cohorts of different ages in natural stands. Isozyme analysis of bud tissue was used to estimate expected and observed heterozygosity (H_e and H_o), and Wright's fixation index (F_{is}) for three age cohorts (seedling, young, and mature), sampled from 14 sites in British Columbia, Oregon, Idaho, and Montana. Comparison of genetic diversity parameters among cohorts within a site was used to assess the extent and persistence of inbreeding with age, while comparisons of parameters among sites within a cohort were used to assess the impact of the disease on genetic diversity. Significant evidence of inbreeding ($F_{is} > 0$) was found in all age cohorts. When sites were stratified by level of blister rust infection, differences in F_{is} and H_o among cohorts were only significant when level of infection was low. A significant negative association was found between level of blister rust infection and H_o in the mature cohort. This suggests that when differential selection due to blister rust is weak, more heterozygous individuals may be favored; however, more

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