

Genetic characterisation of a *Eucalyptus nitens* base breeding population in South Africa

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Summary

The measurement and statistical analysis of data from eight *Eucalyptus nitens* trials established in the summer rainfall forestry region of South Africa during the 1980s and 1990s, have enabled the characterisation of the Institute for Commercial Forestry's breeding population. Provenance testing showed that the more northerly New South Wales (Australia) *Eucalyptus nitens* provenances of Barren Mountain and Barrington Tops are distinctly better suited to the summer rainfall areas of South Africa than the southern New South Wales provenances and the Victorian provenance, Penny Saddle. Generally, the species was not badly affected by *Coniothyrium* canker. High Type B genetic correlations for all sites pairs, except one comparison, ranged from 0.75 to 0.99 for dbh, indicating very little, or no, genotype-environment interaction for diameter at

breast height for the genotypes tested in this study. Narrow sense heritability coefficients ranged from 0.01 to 0.34, indicating that the species generally exhibits sufficient breeding opportunity for improvement of diameter growth. High genetic correlations of greater than 0.90 between diameter measurements at 52 to 62 months after establishment and diameter measurements at 94 or 113 months were found, indicating that selections can be reliably made at five or six years.

Predicted genetic gains were highest in the trials at Goedehoop and Arthur's Seat, with increases in diameter at breast height of 3.07 cm (17.1%) and 3.17 cm (20.7%), respectively, at full rotation.

Keywords: *E. nitens*, genetic parameters, heritability, genetic correlations, genotype-environment interaction, predicted gain

Introduction

Historically, *Eucalyptus grandis* has been the most important hardwood species for the South African forestry industry. However, increasing demand by the mining timber sector during the early 1900s and by the pulp and paper industry in the 1980s, led to the expansion of hardwood forestry into colder areas, often at altitudes exceeding 1 400 m and prone to frosts and snow, which are not suitable for growth of *E. grandis* (Darrow 1994). *Eucalyptus nitens* has become important on such high altitude, temperate sites in the summer rainfall forestry regions of South Africa, grown originally for mining timber, but more recently for pulp and paper production, as demands have changed. Plantation

areas of *E. nitens* in South Africa currently cover approximately 46 600 ha (Germishuizen, pers comm¹).

In its natural habitat in Australia, *E. nitens* occurs between 600 and 1200 m elevation in disjunct populations in the Victorian alps, eastern Victoria and southern New South Wales (NSW). Two small populations are also found at Barrington Tops and Ebor/Barren Mountain in northern NSW, at altitudes of up to 1600 m. Rainfall is moderate to high, ranging in distribution between summer maxima in northern NSW to winter maxima in eastern Victoria. Thus there are a wide range of provenances available for testing for suitability to growth in the summer rainfall regions of South Africa. Landscapes vary from undulating tablelands to mountain slopes, where the species prefers the less exposed positions (Boland et al. 1992).

Generally in South Africa, *E. nitens* appears ideally suited to colder areas with a mean annual temperature (MAT) greater than 14°C for optimal growth (Swain and Gardner 2003). The species is clearly unsuccessful in warmer areas and should only be planted on sites with a MAT less than 16°C (Swain and Gardner 2003). At the warmer end of the MAT range, mean annual precipitation (MAP) should be at least 950 mm, while 825 mm is sufficient at the cooler end of its range (Swain and Gardner 2003). Although *E. nitens* is classified as frost tolerant, it is not as frost-hardy as *E. macarthurii* (Darrow 1994, 1996) and thus should not be planted in low landscape positions where extreme frosts are likely to occur. Provenance differences for growth under different climatic conditions have been found in Institute for Commercial Forestry Research (ICFR) site-species

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interaction trials. Ebor and Barren Mountain appear to be the most cold tolerant of the *E. nitens* provenances tested in South Africa (Gardner 2001) and seem to tolerate strong winds and exposure to chill very well, as long as the sites fall within the recommended MAT range. Tallaganda provenance showed the most drought and frost tolerance, although Ebor tolerates lower temperatures without frost better than Tallaganda (Darrow 1996, Gardner 2001). The diverse range of Australian provenances, the varying performance of these provenances in South African site-species trials and the disparate array of South African forestry sites, indicate that the presence of genotype by environment interaction (GEI) is a possibility in *E. nitens* populations in South Africa, and should be investigated further.

Eucalyptus nitens is recognised as the most snow tolerant, or snow hardy, of the Cold Tolerant Eucalypts (CTEs) grown in South Africa, and has clearly demonstrated good resistance to damage by all but the heaviest of snowfalls (Gardner and Swain 1996, Kunz and Gardner 2001). Currently, there is no suitable alternative commercial species to *E. nitens* on sites prone to moderate frost and heavy snows. The species is, however, very sensitive to fire. The species has good kraft pulping properties (Clarke 2000) and dissolving pulp yields ranging from 45.5 to 51.5%, over a range of sites (Clarke 1995, Clarke et al. 1999).

Provenance/progeny trials for *E. nitens* seedlots imported from Australia were established by the South African Department of Forestry during the 1980s. The ICFR took over these trials in 1989 and established additional trials at the end of the 1980s and early 1990s to determine which Australian provenances are best suited to South

African summer rainfall growing conditions, and to identify seedlots which could be included in a tree improvement programme to selectively improve this species.

This paper uses the results from the range of trials to characterise the *E. nitens* population from a genetic perspective and to identify provenance differences for growth. Estimates of variances and narrow sense heritabilities were calculated as this information is fundamental to determining breeding potential of the population under consideration, to designing breeding strategies and is used for purposes of selection of superior families and individuals (White 1987, Falconer and Mackay 1996). The potential gains estimated from such calculations are important to funders of the *E. nitens* tree improvement programme, as these indicate whether investments in the breeding programme are justified. Genetic correlations for both juvenile-mature and trait-trait measurements were estimated, as the former is a very useful measure of which of the earlier measurements is the best predictor of top individuals and seedlots at full rotation (van Buijtenen 1992), whilst the latter correlation indicates whether an increase in one measured trait will positively or negatively affect another measured trait, if at all (Cotterill and Dean 1990, Falconer and Mackay 1996).

The existence of GEI in this population was explored, as the presence of GEI will influence the breeding strategy on how the population should be managed, i.e. as discrete populations for specific environments in the presence of GEI (Squillace 1969) or by the exclusion of unstable genotypes (Kanzler 2002). The knowledge obtained from this study will inform the development of the breeding programme for the next generation of trials such that gains are maximised over a range of sites.

Materials and methods

Field trials

One hundred and sixty-five *E. nitens* seedlots were imported from Australia by the South African Department of Forestry during the 1980s, representing seedlots from eight provenances in NSW and Victoria i.e., Ebor, Barrington Tops, Barren Mountain, Badja, Tallaganda, Glenbog, Bendoc and Penny Saddle. These seedlots were established in four series of provenance/progeny trials on two sites for each trial series. **Table 1** provides details of the sites where the trials were established, as well as trial design information. **Table 2** provides information on the origins of the provenances represented in the trials. Details of seedlots allocated to each site can be found in Swain et al. (1998). The majority of seedlots are represented at both sites within each trial series, but the seedlots vary considerably between the different trial series. As early results from the E88/05 and E88/06 trial series indicated that there were significant differences between seedlots collected from two different areas within the Barrington Tops provenance area in Australia (Stanger 1991), a further comprehensive collection was done at Barrington Tops, and a fifth trial series (E88/07) established in South Africa in 1992, including 56 new imports from Australia. All trials were planted at a spacing of 2 x 3 m, with an initial planting density of 1667 stems per hectare. Trees were established in line plots of 5 to 10 trees. Controls in the first four trial series (E88/01 to E88/06) included 17 landrace seedlots collected from South African *E. nitens* plantations (**Table 2**), and an improved bulk from a private breeding programme was included in the E88/05 and E88/06 trial series (M1278). The E88/07 trial series included top performing *E. nitens* families from the first four trial series, 2nd generation selections from the then

Table 1: Site and trial information of five *Eucalyptus nitens* provenance/progeny trial series in South Africa. MPU = Mpumalanga province, KZN = KwaZulu-Natal province, MAP = Mean Annual Precipitation, MAT = Mean Annual Temperature, latt = lattice

Trial no.	Location	Latitude (S)	Longitude (E)	Altitude (m)	MAP (mm)	MAT (°C)	Soil depth (mm)	Planting date	No. of seedlots	Trial design	No. of reps	No. trees/plot
E88/01	Jessievale, MPU	26° 15' 20.02"	30° 31' 29.48"	1706	873	14.5	850	08/12/1982	42	6x7 latt	10	10
	Amsterdam, MPU	26° 8' 36.02"	30° 43' 7.39"	1691	864	14.8	1200	14/12/1982	36	6x6 latt	10	10
E88/03	Daspoort, MPU	26° 13' 13.30"	30° 39' 55.75"	1618	874	14.8	1000	18/01/1985	49	7x7 latt	8	6
	Helvetia, MPU	25° 34' 8.44"	30° 18' 23.81"	1646	789	15.6	1000	19/03/1985	49	7x7 latt	8	6
E88/05	Woodstock, MPU	26° 23' 25.75"	30° 41' 14.15"	1578	867	14.4	1000	11/02/1988	141	2(8x9) latt	6	6
E88/06	Babanango, KZN	28° 18' 27.37"	31° 4' 57.43"	1338	780	16.6	1000	29/03/1988	92	2(7x8) latt	9	5
E88/07	Goedehoop, MPU	26° 10' 28.94"	30° 39' 30.69"	1737	884	14.4	1000	01/12/1992	100	10x10 latt	4	8
	Arthur's Seat, MPU	26° 18' 4.46"	30° 37' 33.15"	1645	871	15.2	1000	14/12/1992	100	10x10 latt	4	8

New Zealand Forestry Research Institute (NZFRI), selections from a site-species trial in Lesotho and two *E. grandis x nitens* (*E. GxN*) hybrids.

Table 2: Origins of *Eucalyptus nitens* provenances and control seedlots established in five South African provenance/progeny trial series over eight sites. MPU = Mpumalanga province, KZN = KwaZulu-Natal province, NSW = New South Wales, VIC = Victoria, SA = South Africa, NZFRI = New Zealand Forestry Research Institute, *E. GxN* = *E. grandis x nitens* hybrid.

Trial no.	Location of trials	Provenances/Control	Latitude (S)	Longitude (E)	Altitude (m)		
E88/01	Jessievale, MPU Amsterdam, MPU	Tallaganda, NSW	35°48'	149°31'	1280		
		Barren Mountain, NSW	30°23'	152°28'	1460		
		Badja, NSW	36°00'	149°36'	1300		
		Penny Saddle, VIC	37°47'	146°16'	900		
		Woodbush, SA (landrace)	23°35'	29°59'	1780		
E88/03	Daspoort, MPU Helvetia, MPU	Barrington Tops (Mt Carson), NSW	30°57'	151°30'	Unknown		
		Barren Mountain, NSW	30°23'	152°28'	1250-1560		
		Badja, NSW	36°10'	149°31'	880-1300		
		Penny Saddle, VIC	37°47'	146°16'	900		
		Belfast, SA (landrace)	25°39'	30°02'	1880		
		Perdestal, Jessievale, SA (landrace)	26°14'	30°31'	1750		
E88/05 E88/06	Woodstock, MPU Babanango, KZN	Ebor, NSW	30°29'	152°24'	1560		
		Tallaganda, NSW	35°49'	149°30'	1180-1450		
		Badja, NSW	36°01'	149°34'	880-1240		
		Glenbog, NSW	36°38'	149°24'	900-1200		
		Barrington Tops, NSW	31°55'	151°30'	1450		
		Bendoc, VIC	37°12'	145°52'	790-1040		
		Nelshoogte, SA (landrace)	25°48'	30°47'	1450		
		<i>E. nitens</i> improved bulk (M1278)	-	-	-		
		E88/07	Goedehoop, MPU Arthur's Seat, MPU	Barrington Tops (Kholwa Fire Trail), NSW	31°38'	151°30'	1200-1300
				Barrington Tops (Mt Carson), NSW	31°55'	151°30'	1450
Badja, NSW	35°59'			149°34'	1100-1200		
Glenbog control (Family 37209 & 37224)	36°38'			149°24'	900-1200		
Ebor controls (Families 37255, 37650 & 37651)	30°29'			152°24'	1560		
NZFRI (2 nd generation selections ex New Zealand)	-			-	930		
Thaba Putsoa (selections ex abandoned species trial, Lesotho)	-			-	-		
Perdestal, Jessievale, SA (landrace)	26°14'			30°31'	1750		
<i>E. GxN</i> natural hybrid M, SA	-	-	-				
<i>E. GxN</i> hybrid H, SA	-	-	-				

Data collection and statistical analyses

Trials were routinely measured for height, using expandable height rods, at one or two years after establishment, and at approximately three, six and nine years after establishment for diameter at breast height (dbh), using diameter tapes. Final measurements of the trials were done at 101 months in the E88/01 trial series, 110 and

94 months in the E88/03 Daspoort and Helvetia trials, respectively, 76 and 110 months in the E88/05 and E88/06 series, respectively, and at 113 months in the E88/07 series. Rotation age height measurements were done at 113 months in the E88/07 series. Following the presence of *Coniothyrium* canker (formerly *Coniothyrium zuluense*, now *Teratosphaeria zuluense*) being noted in some of the trials, the E88/01 and E88/03 series were scored for the presence of lesions on the stem, indicating possible infection by *T. zuluense*, at 101 months and 86 months respectively. Although commercial stands of *E. nitens* appear not to be particularly susceptible to this stem disease, as is *E. grandis*, symptoms can appear in areas of high rainfall and optimal growth (FABI 2000). A subjective scoring system of 0 to 2 was used, where 0 indicated no lesions or sign of disease; 1 indicated the presence of some lesions and 2 indicated marked signs of the disease. The disease scores were analysed both at a provenance and individual seedlot level.

Each site in a trial series was analysed separately in order to obtain single-site genetic parameter estimates. Statistical analyses were conducted using SAS[®] Institute Inc. Software 9.2 (2002-2008). To test for normality for dbh, residuals were plotted against fitted values. None showed any detectable trends or patterns and it can therefore be said that the condition $\varepsilon_{ijklm} \sim \text{iid}(0, \sigma^2)$ were met for these data, and the standard ANOVA assumptions are valid. Provenance and family means were calculated for all sites individually using Proc GLM, as this procedure is recommended for unbalanced designs (Hettasch et al. 2007). Significant replication effects were corrected for and F-statistics were calculated to test for significant differences among families and provenances. Comparisons for differences between treatments were made using

Fisher's test for Least Significance Differences (LSD) for $\alpha = 0.05$, as this test allowed for expression of more differences than tests such as Student-Newman-Keuls (SNK) multiple range test. Provenance means for both dbh and survival were calculated in order to provide information to South African growers on which seed to import from Australia until the South African breeding programmes could provide sufficient quantities of improved seed within the country.

Estimation of genetic parameters

Estimates of variance components and narrow sense heritabilities were calculated for the individual sites. Controls were removed from the data before the variance components were estimated using Restricted Maximum Likelihood Method (REML) (Patterson and Thompson 1971) and the VARCOMP procedure in SAS[®] Institute Inc. Software 9.2 (2002-2008), with the following model:

$$y_{ijklm} = \mu + R_i + B_{j(i)} + P_k + f_{l(k)} + e_{ijklm},$$

where y_{ijklm} = individual phenotypic observation for the trait of the l^{th} seedlot/family within provenance k in the j^{th} block within replication i , μ = overall mean, R_i = i^{th} replication effect (fixed), $B_{j(i)}$ = block (within rep) effect (fixed), P_k = provenance effect (fixed), $f_{l(k)}$ = seedlot/family effect within provenance (random) and e_{ijklm} = random error effects.

Additional analyses were done ignoring the effect of provenance, as selections were actually made for best individuals and seedlots irrespective of, or across, provenances. The model was adjusted accordingly.

When the genetic parameters for half-sibs were calculated, a coefficient of relationship (cr) of 0.33 was used. This was based on the assumption that full-sibs do occur in

matings from open-pollination, and at least some inbreeding is assumed to occur in natural stands (Squillace 1974, Verryn 1993). The ICFR have accepted the assumptions stated above and standardised on a coefficient of relationship of 0.33 when calculating genetic parameters for growth traits in *E. nitens*. Therefore, the additive genetic variance was estimated as:

$$\hat{\sigma}_A^2 = \hat{\sigma}_f^2 / 0.33$$

where σ_f^2 is the seedlot/family variance.

Single-site narrow sense individual heritability (h^2) and within-family (h_{wf}^2) heritability estimates were calculated, respectively, for all traits using the formulae (Falconer and Mackay 1996):

$$h^2 = \frac{1}{0.33} \hat{\sigma}_f^2 / \hat{\sigma}_{phen}^2$$

and

$$h_{wf}^2 = \frac{(1 - 0.33)h^2}{1 - (0.33h^2)},$$

where σ_{phen}^2 is the phenotypic variance. Initially provenance effects were included in the heritability estimations. Estimations were then repeated excluding provenance effects, as final selections were made in top performing families across provenances.

Genotype by environment interaction

Type B genetic correlations were estimated for dbh, both nested within provenance and excluding provenance effects, to give an indication of any potential genotype by environment interaction (GEI). Where two traits are measured on different individuals within genetic groups, for example a genetic correlation between trees of the same family grown in different environments, the correlation can be designated a Type B

genetic correlation. A Type B genetic correlation (r_{Bg}) of 0.67 is the level at which the GEI variance represents 50% of the total additive variance, and is the point where it is postulated that the GEI variance may be a cause for concern among tree breeders (Shelbourne 1972). Type B correlations at the family level (r_{Bg}) were estimated for all possible site pairs as follows (Burdon 1977):

$$r_{Bg} = \frac{\sigma_f}{\sigma_f^2 + \sigma_{site*f}^2}$$

The variance components were estimated using PROC MIXED in SAS[®] Institute Inc. Software 9.2 (Copyright © 2002-2008 SAS Institute Inc.), as it was not possible to directly estimate the site x family covariance for family nested within provenance using the VARCOMP/CORR procedures in SAS with this dataset. The only restrictions on the site comparisons were that the sites being paired should have at least 15 families in common (Kanzler and Hodge 2000). As there were 20 seedlots in common across all the E88/01, E88/03 and E88/05 trials, and 16 in common across the E88/03, E88/05 and E88/06 trials, correlations were carried out on all site pair combinations except the E88/07series.

Combined site analysis

A combined site analysis was done on 71 seedlots (numbers 1 to 34840) to determine overall performance of these common families across the range of sites and environments represented over the trial series. Only these seedlots were included in the comparison, as they were present on at least four sites. The E88/07 trial series at Arthur's Seat and Goedehoop had very few families in common with the earlier trial

series, and were therefore excluded from the combined site analysis. Significant site effects were corrected for.

Juvenile-mature and trait genetic correlations

Juvenile-mature genetic correlations (r_{g12}) were estimated at all sites using the following formula:

$$r_{g12} = \frac{cov_{12}}{\sqrt{var_1 \times var_2}}$$

Where cov_{12} = the family covariance of the trait at age 1 and age 2, var_1 = the family variance of the trait at age 1 (similarly for age 2). Standard errors were calculated according to Becker (1992).

Predicted genetic gain

The potential genetic gain to be obtained through selection varies according to the heritability of the trait under consideration, the present phenotypic variation for that trait in the population and the intensity of selection. Gains in dbh were predicted for the progeny of each trial as if selection was applied by roguing the poorest 30% of the families from each trial, then leaving the best tree per plot of the remaining 70% families standing, followed by bulking of seed from the top 15 to 36 families in each trial. This was done using the formula (Verry et al. 2000):

$$\Delta G = 0.5(\Delta G_f) + 0.5(\Delta G_m), \text{ where}$$

$$\Delta G_f \text{ and } \Delta G_m = 0.5 \left[SI_b \times cr \times \frac{\sigma_A^2}{\sigma_f} \right] + \left[SI_{wf} \times \frac{(t-1)}{t} \times (1-cr) \times \frac{\sigma_A^2}{\sigma_{wf}} \right],$$

and the predictions are the predicted genetic gains from female and male selection in a population, respectively. (ΔG = predicted genetic gain or response to selection, ΔG_f = predicted genetic gain from female selection, ΔG_m = predicted genetic gain from male selection, SI_b = selection intensity between/among female or male families, respectively, cr = coefficient of relationship, σ_A^2 = additive genetic variance, σ_f = standard deviation among families, SI_{wf} = selection intensity within female or male families, respectively, within plots, t = number of trees per plot, and σ_{wf} = standard deviation within families). The selection intensity for male and females differed as, in addition to roguing and thinning, the top 15 to 36 families would be selected to make up bulk seed. Male and female selection intensities between/among families and within families within plots were determined using the standardised selection intensity tables of Becker (1975).

Results and discussion

Provenance performance

There were significant differences between Australian provenances for dbh at all sites ($p < 0.0001$). **Tables 3** and **4** present provenance comparisons for dbh and percentage survival for the five *E. nitens* trial series. The more northern New South Wales (NSW) provenance of Barren Mountain performed significantly better ($p < 0.05$) than the southern NSW provenances of Tallaganda and Glenbog, and the Victorian provenances of Penny Saddle and Bendoc, at all sites excepting Helvetia. Barren Mountain was not included at Goedehoop and Arthur's Seat. This provenance also performed significantly better ($p < 0.05$) than the more southern NSW provenance of Badja at three of the six sites where it was included. Generally, the more northern NSW provenances of Barren Mountain and Barrington Tops performed better than the southern *E. nitens*

Table 3: Final mean diameter at breast height (dbh) (with percentage survival in brackets) for *Eucalyptus nitens* provenances and controls in four trial series over six sites in South Africa. Treatment means for dbh which do not differ significantly from each other bear the same letter of the alphabet

Trial number Site Assessment age	E88/01 Jessievale 101 months		E88/01 Amsterdam 101 months		E88/03 Daspoort 110 months		E88/03 Helvetia 94 months		E88/05 Woodstock 76 months		E88/06 Babanango 110 months			
Provenance	No. of seedlots	dbh (cm) (% survival)	No. of seedlots	dbh (cm) (% survival)	Provenance	No. of seedlots	dbh (cm) (% survival)	No. of seedlots	dbh (cm) (% survival)	Provenance	No. of seedlots	dbh (cm) (% survival)	No. of seedlots	dbh (cm) (% survival)
Barren Mountain	11	17.95 (75.8) a	11	18.49 (76.4) a	Barren Mountain	9	20.24 (81.3) a	8	17.87 (72.5) ab	Barren Mountain	9	15.13 (74.7) ab	3	19.49 (78.9) b
Tallaganda	13	16.48 (72.5) b	6	17.25 (72.7) ab	Barrington Tops	10	20.13 (89.2) a	10	18.39 (72.5) a	BTops ⁴ (Mt Carson)	9	14.66 (73.5) bc	6	20.46 (83.2) a
Badja	15	16.38 (68.3) b	16	16.66 (68.0) bc	Nelshoogte, SA ¹ (l/race) ²	8	17.57 (82.6) bc	8	16.36 (54.9) bcd	Badja	18	14.64 (69.1) bc	9	19.17 (75.6) bc
Woodbush, SA (l/race)	1	15.09 (42.0) c	1	18.90 (66.0) a	Badja	12	16.98 (83.3) cd	13	16.35 (55.1) bcd	Tallaganda	40	14.52 (69.3) bc	31	18.23 (76.2) cd
Penny Saddle	2	14.75 (44.5) c	2	15.15 (33.0) c	Penny Saddle	1	16.22 (85.4) cd	1	17.12 (54.2) abc	Glenbog	28	14.43 (67.9) bcd	20	17.95 (70.0) d
					Belfast, SA (l/race)	3	15.78 (74.3) d	4	15.47 (49.5) cd	Nelshoogte, SA (l/race)	4	14.41 (75.0) bcd	5	18.23 (75.9) cde
					Jessievale, SA (l/race)	4	11.36 (49.5) e	3	15.07 (21.5) d	Ebor	14	14.07 (73.2) cd	7	18.76 (75.6) bcd
										BTops ⁴ (Kholwa FT ⁵)	9	13.96 (69.4) cd	8	18.33 (64.7) cd
										Bendoc	5	13.71 (61.1) d	-	-
Mean		16.78		17.39			18.09		17.19			18.34		14.47
SD³		4.299		5.145			5.298		4.450			4.571		3.279

¹ South Africa;

² Landrace;

³ Standard deviation;

⁴ Barrington Tops;

⁵ Kholwa Fire Trail

provenances of Penny Saddle, Bendoc, Glenbog and Tallaganda. Stand density at final measurement varied between site and provenance, being generally lower at Helvetia and Woodstock. Final stand density of Badja provenance was poor at three of the six sites, yet the provenance did not perform significantly worse for dbh than Tallaganda, which ranked second for dbh at Jessievale and Amsterdam. Survival of Victorian provenance, Penny Saddle, was poor at Jessievale, Amsterdam and Helvetia, but good at Daspoort. Although significant differences still existed between the two different collections of Barrington Tops at Babanango at final measurement ($p < 0.05$), the early measurements of this trial series having prompted the further collection of this provenance and the establishment of the E88/07 trial series, there were no significant differences ($p > 0.05$) between the two different Barrington Tops collections from Mount Carson and Kholwa Fire Trail in either of the subsequent E88/07 trials at Goedehoop and Arthur's Seat.

Table 4: Final mean diameter at breast height (dbh) (with percentage survival in brackets) for *Eucalyptus nitens* provenances and controls in the E88/07 trial series at two sites in South Africa. Treatment means for dbh which do not differ significantly from each other bear the same letter of the alphabet

Trial number Site Assessment age	E88/07 Goedehoop 113 months		E88/07 Arthur's Seat 113 months		
Provenance	No. of seedlots	dbh (cm) (% survival)	Provenance	No. of seedlots	dbh (cm) (% survival)
GxN H	1	20.84 (87.5) a	GxN M	1	18.86 (100.0) a
GxN M	1	20.58 (96.9) a	Thaba Putsoa, Lesotho	3	16.30 (85.4) b
Glenbog control 37209	1	19.66 (87.5) ab	Glenbog controls (37209 & 37224)	2	16.08 (81.3) bc
Barrington Tops (Mt Carson)	15	18.24 (76.3) ab	Badja	26	15.98 (88.0) bc
Badja	26	18.24 (81.0) ab	NZFRI ¹ , New Zealand	11	15.78 (83.5) bc
Thaba Putsoa, Lesotho	3	17.86 (77.1) b	Barrington Tops (Kholwa Fire Trail)	27	14.84 (81.3) bcd
Barrington Tops (Kholwa Fire Trail)	27	17.84 (80.2) b	Ebor controls (37255, 37650, 37651)	3	14.65 (70.8) bcd
Ebor controls (37255 & 37650)	2	17.73 (60.9) b	Barrington Tops (Mt Carson)	15	14.51 (80.0) cd
NZFRI ¹ , New Zealand	13	17.48 (74.8) b	Jessievale, SA ² (l/race) ³	9	11.15 (53.8) e
Jessievale, SA ² (l/race) ³	9	14.59 (55.9) c			
Mean		17.79			15.12
SD⁴		4.790			4.346

¹ New Zealand Forestry Research Institute;

² South Africa;

³ Landrace;

⁴ Standard deviation

The Victorian provenance, Penny Saddle, did not perform as well as several of the other Australian provenances for dbh, except at Helvetia, where this provenance was one of the top performing provenances with Barrington Tops and Barren Mountain. The juvenile leaves of the Victorian provenance displayed susceptibility to leafspot (*Mycosphaerella nobilosa*) and it is likely that the trees at the other three sites never recovered after this early setback. Other authors have found this to be the case in *E. nitens* (Lundquist and Purnell 1987, Hunter et al. 2004) and in *E. globulus* subsp. *bicostata* (Komakech et al. 2009). In Australia, the Victorian provenances are tending towards a winter rainfall maximum with a drier summer and it is interesting that, of the sites in this South African trial series, the disease did not appear to be as prevalent at the Helvetia site, which has slightly lower rainfall than the other sites. This was also found in a South African trial series of *E. globulus* subsp. *bicostata*, where susceptible provenances were less infected at 30 months at two sites with lower rainfall (≤ 900 mm) than sites with higher rainfall (> 950 mm) (Komakech et al. 2009).

ICFR site-species interaction trials have shown that Ebor and Barren Mountain appear to be the most cold tolerant of the *E. nitens* provenances tested, and Tallaganda the most frost and drought tolerant (Darrow 1996, Gardner 2001, Swain 2001). The results of these trials support this to some degree, as Barren Mountain was the top performing provenance at three of the five cold sites at which it was present, i.e., Jessievale, Amsterdam and Daspoort, and performed well at the other cold sites, i.e., Helvetia and Woodstock.

Disease assessments for *T. zuluense* were done in the E88/01 and E88/03 trials and significant provenance differences ($p < 0.05$) were found at three of the four sites (**Table 5**). Although the ranking of the provenances changed over site with respect to presence of the disease, it appears that Badja and Tallaganda were the provenances least affected by the disease. Generally however, with the exception of a few seedlots which had scores of 1.5, i.e., 32097 at Jessievale (ex Barren Mountain), 32079 at Daspoort (ex Badja) and 34832 (ex Barrington Tops), these populations of *E. nitens* do not seem to be badly affected by the canker. This disease seems to have been worse at Amsterdam than at the other three sites (mean score 1.02). Trees of those seedlots which were badly affected at more than one site were rogued from the ICFR trials when the trials were converted to seed orchards (seedlots marked in **Table 8**).

Table 5: Assessment for *Teratosphaeria zuluense* in four *Eucalyptus nitens* provenance/progeny trials in South Africa. Infection scores: 0 = no lesions, 1 = presence of some lesions, 2 = marked signs of the disease. Scores which do not differ significantly from each other bear the same letter of the alphabet

Trial number	E88/01				E88/03				
	Site	Amsterdam	Jessievale	Daspoort	Helvetia	Amsterdam	Jessievale	Daspoort	Helvetia
Assessment age	101 months	101 months	101 months	86 months	86 months	86 months	86 months	86 months	86 months
Provenance	Disease score	Provenance	Disease score	Provenance	Disease score	Provenance	Disease score	Provenance	Disease score
Penny Saddle	0.8 a	Tallaganda	0.9 a	Jessievale, SA	0.8 a	Nelshoogte, SA	0.7 a		
Badja	1.0 ab	Badja	1.0 ab	Badja	0.9 a	Barren Mountain	0.8 a		
Tallaganda	1.0 b	Woodbush, SA	1.0 ab	Nelshoogte, SA	1.0 a	Badja	0.9 a		
Woodbush, SA ¹	1.0 b	Barren Mountain	1.1 ab	Barren Mountain	1.0 a	Jessievale, SA	0.9 a		
Barren Mountain	1.2 b	Penny Saddle	1.2 b	Belfast, SA	1.0 a	Penny Saddle	0.9 ab		
				Barrington Tops	1.0 a	Belfast, SA	0.9 ab		
				Penny Saddle	1.1 a	Barrington Tops	1.2 b		
Mean	1.02		0.97		0.96		0.91		

¹ South Africa

Family performance

Significant differences existed ($p < 0.05$) between the top seedlots at Amsterdam, Daspoort, Babanango, and between top and bottom performing seedlots at all sites.

Although *E. nitens* is not recommended for areas where the altitude is lower than

1400 m and where MAT is greater than 16 °C (Herbert 1993), the average growth at Babanango (altitude 1325 m and MAT 16 °C) was better than that of the other seven sites, all of which can be described as high altitude sites (**Tables 3 and 4**).

Genetic parameters

Variance components and individual heritability estimates for dbh and height are presented in **Table 6**. Narrow-sense heritabilities ranging from 0.10 to 0.30 are considered intermediate to high, and generally indicate that moderate to good genetic gains can be expected from individual tree selection (Namkoong 1979, Cotterill and Dean 1990). This is the range most commonly found in eucalypts (Cotterill and Dean 1990). On the contrary, heritabilities less than 0.10 are considered low in forestry, resulting in poor genetic gains from selection (Falconer and Mackay 1996). The individual heritability coefficients (h^2) obtained for dbh in *E. nitens* in this study ranged from 0.01 to 0.34 when families were nested within provenance, and from 0.11 to 0.63 for families across provenance, depending on age of trees and site (**Table 6**). With regards to the heritability estimates of family nested within provenance, estimates were highest at Arthur's Seat at all ages ($h^2 \sim 0.27 - 0.34$ for dbh); for families irrespective of provenance, heritability estimates were highest at Daspoort at all ages ($h^2 \sim 0.58 - 0.63$). The site with the lowest heritabilities generally for families nested within provenance was Helvetia ($h^2 \sim 0.01 - 0.08$); whilst Jessievale had the lowest estimates for families across provenance ($h^2 \sim 0.11 - 0.19$). The dbh heritability estimates fell within the intermediate range for eucalypts, with the exception of Jessievale and Helvetia, and compared well with those estimated in previous *E. nitens* studies for dbh: 0.24 (converted from family h^2 of 0.80, King and Wilcox 1988), 0.18 (Whiteman et al. 1992), 0.14 (Johnson 1996), 0.11

Table 6: Variance components and genetic parameters with standard errors for *Eucalyptus nitens* at eight sites in South Africa, for diameter at breast height (Dbh) at different ages. σ^2_A = additive variance, σ^2_f = family variance nested within provenance, σ^2_e = error variance, σ_p = phenotypic standard deviation, σ_{wf} = standard deviation within families, h^2 = heritability of individual values (narrow-sense) for a) family nested within provenance and b) family excluding provenance effects, h^2_{wf} = within family heritability for family nested within provenance

Site (age in months)	σ^2_A	σ^2_f	σ^2_e	σ_p	σ_{wf}	$h^2_{fam(prov)}$	h^2_{fam}	$h^2_{wf(prov)}$
<i>Dbh:</i>								
Jessievale (39)	0.35 ± 0.144	0.12 ± 0.048	6.51 ± 0.163	2.57	2.15	0.05 ± 0.022	0.19 ± 0.052	0.04
Jessievale (101)	1.06 ± 0.464	0.35 ± 0.153	20.99 ± 0.551	4.62	3.84	0.05 ± 0.022	0.11 ± 0.034	0.03
Amsterdam (39)	0.91 ± 0.354	0.30 ± 0.117	6.50 ± 0.243	2.61	2.23	0.13 ± 0.052	0.19 ± 0.062	0.09
Amsterdam (101)	4.06 ± 1.618	1.34 ± 0.534	27.97 ± 1.136	5.41	4.63	0.14 ± 0.055	0.20 ± 0.066	0.10
Daspoort (30)	0.57 ± 0.186	0.19 ± 0.061	3.99 ± 0.123	2.05	1.75	0.14 ± 0.044	0.63 ± 0.141	0.10
Daspoort (60)	1.83 ± 1.912	0.60 ± 0.631	12.52 ± 0.410	3.62	3.10	0.14 ± 0.146	0.63 ± 0.146	0.10
Dasport (110)	3.90 ± 1.348	1.29 ± 0.445	28.48 ± 0.955	5.45	4.66	0.13 ± 0.045	0.58 ± 0.137	0.10
Helvetia (24)	0.16 ± 0.217	0.05 ± 0.023	2.10 ± 0.066	1.47	1.23	0.08 ± 0.032	0.34 ± 0.083	0.05
Helvetia (62)	0.17 ± 0.314	0.05 ± 0.104	10.80 ± 0.418	3.30	2.71	0.02 ± 0.029	0.23 ± 0.073	0.01
Helvetia (73)	0.16 ± 0.390	0.05 ± 0.129	13.80 ± 0.534	3.72	3.06	0.01 ± 0.028	0.21 ± 0.068	0.01
Helvetia (94)	0.20 ± 0.589	0.07 ± 0.194	22.78 ± 0.887	4.78	3.93	0.01 ± 0.026	0.14 ± 0.051	0.01
Woodstock (36)	0.93 ± 0.171	0.31 ± 0.056	3.97 ± 0.093	2.07	1.81	0.22 ± 0.040	0.26 ± 0.044	0.16
Woodstock (76)	1.61 ± 0.368	0.53 ± 0.122	10.81 ± 0.261	3.37	2.89	0.14 ± 0.032	0.15 ± 0.033	0.10
Babanango (35)	1.22 ± 0.236	0.40 ± 0.078	3.65 ± 0.088	2.01	1.81	0.30 ± 0.058	0.32 ± 0.060	0.22
Babanango (62)	3.18 ± 0.662	1.05 ± 0.219	13.65 ± 0.329	3.83	3.36	0.22 ± 0.045	0.28 ± 0.054	0.16
Babanango (110)	4.04 ± 0.886	1.33 ± 0.292	20.98 ± 0.512	4.72	4.10	0.18 ± 0.040	0.25 ± 0.049	0.13
Goedehoop (36)	1.00 ± 0.215	0.33 ± 0.005	3.46 ± 0.010	1.95	1.73	0.26 ± 0.057	0.29 ± 0.060	0.19
Goedehoop (52)	2.35 ± 0.518	0.78 ± 0.171	8.86 ± 0.253	3.10	2.74	0.24 ± 0.054	0.26 ± 0.055	0.18
Goedehoop (77)	3.14 ± 0.733	1.03 ± 0.242	14.11 ± 0.407	3.89	3.40	0.21 ± 0.048	0.21 ± 0.047	0.15
Goedehoop (113)	5.78 ± 1.444	1.91 ± 0.477	24.21 ± 0.760	5.11	4.48	0.22 ± 0.055	0.21 ± 0.053	0.16
Arthur's Seat (36)	1.09 ± 0.224	0.36 ± 0.074	3.02 ± 0.087	1.84	1.66	0.32 ± 0.066	0.39 ± 0.075	0.24
Arthur's Seat (52)	2.68 ± 0.552	0.88 ± 0.182	7.06 ± 0.208	2.82	2.56	0.34 ± 0.069	0.41 ± 0.079	0.25
Arthur's Seat (77)	4.03 ± 0.853	1.33 ± 0.282	11.43 ± 0.344	3.57	3.22	0.32 ± 0.067	0.38 ± 0.074	0.24
Arthur's Seat (113)	5.67 ± 1.275	1.87 ± 0.421	19.50 ± 0.596	4.62	4.12	0.27 ± 0.060	0.30 ± 0.064	0.20
<i>Height:</i>								
Daspoort (17)	0.13 ± 0.038	0.04 ± 0.013	0.59 ± 0.018	0.79	0.70	0.21 ± 0.060	0.69 ± 0.154	0.15
Helvetia (12)	0.03 ± 0.010	0.01 ± 0.003	0.25 ± 0.008	0.51	0.43	0.11 ± 0.031	0.27 ± 0.067	0.08
Babanango (12)	0.03 ± 1.124	0.01 ± 0.002	0.14 ± 0.003	0.39	0.34	0.20 ± 0.041	0.25 ± 0.047	0.14
Goedehoop (113)	4.60 ± 1.057	1.52 ± 0.349	14.37 ± 0.453	3.99	3.57	0.29 ± 0.067	0.30 ± 0.067	0.21
Arthur's Seat (113)	4.65 ± 0.940	1.54 ± 0.310	9.98 ± 0.309	3.39	3.13	0.40 ± 0.082	0.44 ± 0.086	0.31

(pooled estimates, Gea et al. 1997) and 0.39 (Kube and Raymond 2001). However, all sites had heritabilities lower than those found in seven year old *E. nitens* trees in Victoria, Australia; 0.42 (Greaves et al. 1997). The heritability estimates from this South African study were also within the range described by Hamilton and Potts (2008) and

demonstrate that this breeding population of the species exhibits sufficient potential for selections to result in progeny improved for diameter growth.

There was a trend for the individual heritability estimates in this study to decrease with age across sites, with the exception of the Jessievale, Amsterdam and Daspoort sites, where there was no apparent change in estimates with age. With regards to the other sites, differences amongst ages were generally within the standard error of the estimates. Although a similar, if negligible trend was found in *Eucalyptus* hybrid populations in the Congo (Bouvet et al. 2009), this trend is in contrast to previous eucalypt studies in *E. nitens* (Greaves et al. 1997), *E. grandis* (Gapare et al. 2003) and *E. urophylla* (Wei and Borralho 1998, Kien et al. 2009), although older heritabilities in these *E. grandis* and second *E. urophylla* studies were found to have been inflated due to thinning of the trials. As none of the trials in this South African series were thinned during the rotation, being grown as pulpwood stands, the decline in heritability is likely to have occurred at the time when the site was captured and competition between trees set in, resulting in a decrease in variation between trees and a related decrease in heritability. A marked increase in heritability between early and older ages would decrease relative reliability of early selections (Harrand et al. 2009), thus this opposite trend, although unusual, is encouraging for early selection in these *E. nitens* populations. 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 this study (**Table 6**). This statistic is relevant for estimating gains when selecting top individuals from within each family (Falconer and Mackay 1996).

Genotype by environment interaction (GEI)

Type B genetic correlations (r_{Bg}) between pairs of sites at final measurement were high for dbh when provenance effect was ignored, generally ranging from 0.75 to 0.99 (**Table 7**). The exception to this was the correlation between Babanango and Woodstock (r_{Bg} of 0.33). A similar trend was found for correlations estimated using parameters for family nested within provenance, although there were not always sufficient degrees of freedom to successfully perform this calculation for all site pairs (**Table 7**). An r_{Bg} of 1.00 would indicate a perfect correlation between the behaviours of genotypes on both sites and would suggest the complete absence of GEI. The high Type B correlations estimated for most site pairs indicated very little, or no, GEI for dbh for the *E. nitens* genotypes tested over these sites. The low correlations at Babanango and Woodstock are below the level at which GEI may start to be of concern for the breeder (Shelbourne 1972). These two sites are very different from each other in terms of altitude, MAT and MAP, and the presence of GEI between these two sites would not be unexpected. However, as it is unlikely that *E. nitens* will continue to be grown commercially on site types similar to Babanango, it can be assumed that the performance of this breeding population will not be affected by GEI effects on sites in southern Mpumalanga and the Highveld in South Africa. At the two sites where heights were measured, Goedehoop and Arthur's Seat, the r_{Bg} was 0.70 for families across provenance and 0.595 for family within provenance.

Table 7: Type B genetic correlation estimates (r_{Bg}) of *Eucalyptus nitens* provenance/progeny trials at eight sites in South Africa, for all possible site pairs for dbh (and height in brackets) at final measurement age. Results for families nested within provenance are presented above the diagonal and families excluding provenance effects below the diagonal

Site	Jessievale	Amsterdam	Daspoort	Helvetia	Woodstock	Babanango	Goedehoop	Arthur's Seat
Jessievale	-	0.98	*	*	*	*	**	**
Amsterdam	0.95	-	*	*	0.68	*	**	**
Daspoort	0.99	*	-	0.88	*	0.84	**	**
Helvetia	0.99	0.75	0.87	-	*	0.94	**	**
Babanango	*	*	0.84	0.94	0.59	-	**	**
Woodstock	*	0.68	*	*	-	0.33	**	**
Goedehoop	**	**	**	**	**	**	-	0.89 (0.595)
Arthur's Seat	**	**	**	**	**	**	0.80 (0.70)	-

* no variance components for the site combination ** not enough families in common for GEI

Combined site analysis

The lack of GEI, except for the Woodstock-Babanango comparison, allowed for all sites in the E88/01 to E88/06 series to be analysed as one data set. The combined site analysis to determine overall performance of 71 common seedlots (numbers between 1 and 34840) across the range of five sites is presented in **Table 8**. There were significant differences ($p < 0.05$) between seedlots, the top seedlots generally being from Barrington Tops and Barren Mountain, supporting the findings of the provenance analyses (**Table 3**). Based on the performance of the seedlots in this analysis, top families and individuals within families were selected to form the next generation of progeny trials in *E. nitens*.

Table 8: Performance of *Eucalyptus nitens* seedlots (numbers 1 to 34840) across five sites in South Africa (Amsterdam, Jessievale, Helvetia, Daspoort and Babanango), as determined by final diameter at breast height (dbh) measurements. Treatment means which do not differ significantly from each other bear the same letter of the alphabet

Rank	Seedlot	Provenance	Dbh	Rank	Seedlot	Provenance	Dbh
1	34838	Barrington Tops	20.51 a	37	32089	Badja	16.91 def
2	32096	Barren Mountain	20.45 a	38	32083	Badja	16.77 def
3	34833	Barrington Tops	19.50 ab	39	31328	Tallaganda	16.73 def
4	34840 ¹	Barrington Tops	19.45 ab	40	31334	Tallaganda	16.69 def
5	34831	Barrington Tops	19.19 abc	42	32078	Badja	16.69 def
6	34832 ¹	Barrington Tops	19.17 abc	42	31329	Tallaganda	16.68 def
7	34835	Barrington Tops	18.94 abc	43	32084	Badja	16.66 def
8	34839	Barrington Tops	18.90 abc	44	26	Nelshoogte, SA	16.58 ef
9	32101	Barren Mountain	18.67 bc	45	32079 ¹	Badja	16.55 ef
10	32099	Barren Mountain	18.63 bc	46	31327	Tallaganda	16.51 ef
11	32091	Badja	18.55 bcd	47	22	Nelshoogte, SA	16.36 ef
12	31339	Tallaganda	18.47 bcd	48	31335	Tallaganda	16.35 ef
13	32087	Badja	18.42 bcd	49	32086	Badja	16.33 ef
14	32100	Barren Mountain	18.41 bcd	50	32085	Badja	16.31 ef
15	32097 ¹	Barren Mountain	18.38 bcd	51	25	Nelshoogte, SA	16.23 ef
16	34836	Barrington Tops	18.25 bcd	52	32076	Badja	16.21 ef
17	34815	Barrington Tops	18.08 bcd	53	31333	Tallaganda	16.20 ef
18	30	Nelshoogte, SA ²	17.91 bcd	54	27	Nelshoogte, SA	16.18 ef
19	32093 ¹	Barren Mountain	17.88 bcde	55	32090	Badja	16.02 ef
20	27832	Tallaganda	17.84 bcde	56	31189	Penny Saddle	15.99 ef
21	32095	Barren Mountain	17.82 bcde	57	40	Belfast, SA	15.93 f
22	32092	Barren Mountain	17.74 bcde	58	28	Nelshoogte, SA	15.90 f
23	32094 ¹	Barren Mountain	17.67 bcde	59	29	Nelshoogte, SA	15.88 f
24	31338	Tallaganda	17.45 cde	60	32081	Badja	15.79 f
25	34837	Barrington Tops	17.41 cde	61	32088	Badja	15.77 f
26	31332	Tallaganda	17.35 cde	62	42	Belfast, SA	15.76 f
27	31337	Tallaganda	17.33 cde	63	24	Nelshoogte, SA	15.69 f
28	34834	Barrington Tops	17.25 de	64	41	Belfast, SA	15.63 f
29	32082	Badja	17.24 de	65	32080	Badja	15.31 fg
30	32102	Barren Mountain	17.19 def	66	31188	Penny Saddle	13.88 gh
31	32119	Woodbush, SA	17.16 def	67	43	Belfast, SA	13.54 h
32	31331	Tallaganda	17.15 def	68	14	Jessievale, SA	12.63 hi
33	31330	Tallaganda	17.02 def	69	1	Jessievale, SA	11.60 ij
34	32098	Barren Mountain	16.96 def	70	2	Jessievale, SA	10.76 j
35	32077	Badja	16.95 def	71	13	Jessievale, SA	10.38 j
36	31336	Tallaganda	16.91 def				
Mean							17.17
SD³							4.802

¹ Some trees of these seedlots showed infection by *T. zuluense*, refer to Table 5; ² South Africa;

³ Standard deviation

Juvenile-mature and trait genetic correlations

Table 9 presents genetic correlations (r_g) for a range of dbh and height measurements at different ages. Mid-rotation (five to six year) dbh measurements were not done at Jessievale and Amsterdam. The trial at Woodstock was converted to a seed orchard

Table 9: Genetic correlations (below the diagonal) and Pearson's phenotypic correlations (above the diagonal) of early measurements of *Eucalyptus nitens* with a range of later measurements at eight trial sites in South Africa. All phenotypic correlations were significant for $p < 0.0001$

Age	Ht1	Dbh3	Dbh6	Dbh94	Ht9
Ht1	-	-	Das 0.63 Bab 0.34	Das 0.59 Hel 0.47	-
Dbh3	Das 0.94 ± 0.016 Bab 0.73 ± 0.012	-	Das 0.84 Hel 0.65 Woo 0.88 Bab 0.76 Goe 0.85 Art 0.88	Jes 0.80 Ams 0.75 Das 0.80 Hel 0.59 Bab 0.72 Goe 0.80 Art 0.80	Goe 0.66 Art 0.62
Dbh6	Das 0.79 ± 0.021 Hel 0.44 ± 0.025 Bab 0.54 ± 0.018	Woo 0.83 ± 0.004	-	Das 0.96 Bab 0.97 Goe 0.93 Art 0.90	-
Dbh9	Das 0.80 ± 0.019 Hel 0.26 ± 0.022 Bab 0.43 ± 0.020	Jes 0.79 ± 0.006 Ams 0.94 ± 0.002 Das 0.93 ± 0.006 Hel 0.75 ± 0.007 Bab 0.73 ± 0.009 Goe 0.83 ± 0.006 Art 0.83 ± 0.007	Das 1.00 ± 0.000 Hel 0.95 ± 0.002 Bab 0.98 ± 0.001 Goe 0.93 ± 0.002 Art 0.91 ± 0.003	-	Goe 0.83 Art 0.82
Ht9	-	Goe 0.62 ± 0.018 Art 0.76 ± 0.014	Goe 0.72 ± 0.013 Art 0.81 ± 0.012	Goe 0.84 ± 0.009 Art 0.96 ± 0.003	-

Ht1 = height at 12 to 17 months; Dbh3 = dbh at 24 to 39 months; Dbh6 = dbh at 52 to 76 months;
 Dbh9 = dbh at 94 to 113 months; Ht9 = height at 113 months;
 Das = Daspoort; Bab = Babanango; Hel = Helvetia;
 Woo = Woodstock; Jes = Jessievale; Ams = Amsterdam;
 Goe = Goedehoop; Art = Arthur's Seat

seven years after establishment, thus age-age correlations at more than seven years are not possible for the latter site. As expected, the genetic correlations became stronger with decreasing differences between age of measurement. The mid-rotation dbh measurements (\approx six year) were highly correlated with the final dbh measurements at nine years ($r_g > 0.90$), and the earlier dbh measurements at \approx three years were also positively correlated with the final dbh measurements ($r_g > 0.72$). This indicates that early selections for seed/vegetative production could be made as early as three years of age in *E. nitens*, although these authors would recommend making selections after four and a half years. These results concur with what has been found in previous *E. nitens*

studies ($r_g \approx 0.99$) (Greaves et al. 1997) and in other eucalypt species such as *E. grandis* ($r_g \approx 0.98$) (Harrand et al. 2009) and *E. urophylla* ($r_g \approx 0.83$) (Kien et al. 2009).

With regards to trait genetic correlations, the early height measurements at 12 months were strongly correlated with the first dbh measurements at three years ($r_g > 0.72$), but the 12 month height measurements were less strongly correlated with the six year dbh measurements ($r_g 0.44 - 0.79$). As the six year and final dbh measurements were highly correlated with the final height measurements in the E88/07 trial series ($r_g > 0.71$ and > 0.83 , respectively), it could be regarded as sufficient to make selections based solely on dbh for growth at six years, as this would represent both dbh and height at full rotation.

Predicted genetic gains

The predicted genetic gains from the trials, following roguing, thinning and bulking of the top 15 to 36 families from each trial, are described both as an increase in dbh (cm) and percentage improvement over the trial mean (**Table 10**). The predicted gains ranged from 0.29 cm (1.7%) increase in dbh at Helvetia at 94 months to 3.17 cm (20.7%) increase at Arthur's Seat at 113 months. Due to the low selection intensity in the trials with the larger number of families, highest genetic gains will be achieved by using seed obtained from the E88/07 trials at Goedehoop and Arthur's Seat and the E88/05 trial at Babanango. It should be noted however, that the predicted gains for Helvetia and Woodstock are for 94 and 76 months, respectively, and would be expected to increase with age. With regards to trial series, the progeny of the E88/07 series should produce the best growth of the five series. The gains predicted from these trials are low to intermediate, but additional gains should be recognised in terms of improved

survival/stocking, as is common with improved material. The predicted gains were calculated using the conservative family nested within provenance heritabilities, as provenance could otherwise inflate estimates if not accounted for. Family selection intensities were used, disregarding nesting within provenances.

Table 10: Predicted gains for dbh (cm) in the next generation of *Eucalyptus nitens* from eight provenance/progeny trials in South Africa. Selection intensity between families (SI_b) comprises two parts which are used to predict gains incrementally i.e., i) accounts for selection due to 30% roguing and ii) accounts for female selection when bulking the top 15 to 36 families of the remaining families

Trial sites: age at measurement ¹	$h^2_{fam(prov)}$ ± SE	Selection Intensity between families (SI_b)		Selection Intensity within families (SI_w)	Predicted gain in dbh (cm) (% gain)
		i) For 30% roguing	ii) For bulk composition (nos. in bulk)		
E88/01 Jessievale: 101 months	0.05 ± 0.022	0.466	0.777 (top 15)	1.539	0.99 (6.2%)
E88/01 Amsterdam: 101 months	0.14 ± 0.055	0.493	0.216 (top 36 ²)	1.539	1.25 (7.4%)
E88/03 Daspoort: 113 months	0.13 ± 0.045	0.497	0.826 (top 16)	1.267	2.05 (11.4%)
E88/03 Helvetia: 94 months	0.01 ± 0.026	0.497	0.826 (top 16)	1.267	0.29 (1.7%)
E88/06 Woodstock: 76 months	0.14 ± 0.032	0.474	1.536 (top 15)	1.267	1.55 (10.7%)
E88/05 Babanango: 112 months	0.18 ± 0.040	0.474	1.536 (top 15)	1.163	2.52 (14.0%)
E88/07 Goedehoop: 113 months	0.22 ± 0.055	0.492	1.128 (top 20)	1.424	3.07 (17.1%)
E88/07 Arthur's Seat: 113 months	0.27 ± 0.060	0.492	1.128 (top 20)	1.424	3.17 (20.7%)

$h^2_{fam(prov)}$ = heritability of individual values (narrow-sense) for family nested within provenance

SE = Standard error of h^2

¹ Different ages at time of measurement should be noted

² Poor families were not rogued from this seed orchard before seed was collected

Once actual gains have been measured in progeny trials established from seed collected from these trials, realised heritabilities can be calculated, and it will then be possible to determine whether the estimation of genetic parameters for families nested within provenance was appropriate, or whether the provenance effect should have been ignored.

Conclusions

This study has been invaluable in providing 1st generation benchmarking information on growth, genetic stability across sites, genetic parameters and potential gains in this population of *E. nitens*. Provenance testing at the eight sites has indicated that the more northerly NSW *E. nitens* provenances of Barren Mountain and Barrington Tops are distinctly better suited to growth in the South African summer rainfall region than the southern NSW provenances of Tallaganda and Glenbog, and the Victorian provenances, Penny Saddle and Bendoc. Survival appears to have played a role in provenance performance, as those provenances with better survival at final measurement generally performed better than those with lower survival. Material from Penny Saddle provenance is not recommended for establishment in the summer rainfall areas of South Africa due to its poor performance in most trials, probably due to early susceptibility of the juvenile leaves to leafspot (*M. nobilosa*).

Provenance differences also exist for tolerance to *T. zuluense* (formerly *Coniothyrium* canker), with Badja and Tallaganda appearing to be the provenances least affected by the disease overall. Generally however, the species was not badly affected by the disease at the four sites assessed and the few seedlots which were affected should be removed from existing seed orchards and excluded from selections.

Analyses of the final measurements of the *E. nitens* provenance/progeny trials have identified the top performing seedlots at the eight different sites. The high Type B genetic correlations estimated for all sites pairs indicated very little, or no, GEI for dbh for the *E. nitens* genotypes tested in this study, which implies high genetic stability

across sites. This lack of GEI allowed for a combined site analysis of 71 seedlots to be done, thus identifying the top performing seedlots across five sites. These top seedlots were generally from Barrington Tops and Barren Mountain, supporting the findings of the provenance analyses. Collection of seed from these seedlots will form a good base for progeny testing, although care should be taken to include families from other provenances in order to maintain a broad enough genetic base for advanced generation breeding.

The generally intermediate heritability coefficients (h^2) obtained for *E. nitens* in this study demonstrate that the species exhibits sufficient levels of additive variance for selections to result in progeny improved for diameter growth using conventional breeding strategies. High genetic juvenile-mature correlations of dbh measurements, at 52 to 62 months after establishment, with dbh measurements at 101 or 113 months, have shown that individual tree and family selections can be made as early as five or six years. This suggests that the breeding cycle could be decreased by at least three years, with selections based on growth traits being made for seed or vegetative production after the mid-rotation measurement. This would aid greatly in decreasing the time required to turn over generations in the breeding programme, as well as in the production of improved commercial seed, as flowering in *E. nitens* is slow and erratic (Gardner 2003). Any time gained by early thinning of seed orchards to promote early flowering and subsequent seed production, or by early grafting of elite selections for establishment of Clonal Seed Orchards and seed production will greatly benefit the breeding programme and the South African Forestry Industry. Earlier juvenile-mature correlations, of three year dbh

measurements with full-rotation measurements, are encouraging, and should be investigated further.

Genetic gains predicted from the progeny of these trials ranged according to site, with the highest gains predicted by using seed or vegetative material from the E88/07 trials at Goedehoop and Arthur's Seat and the E88/06 trial at Babanango. Measurement of actual gain achieved in the progeny of these trials will indicate whether the estimation of genetic parameters for families nested within provenance was appropriate in this base breeding population, or whether the provenance effect could be ignored. The realised heritabilities and genetic parameters of future generations will also help inform the presence/absence of non-additive effects between provenances, whether the coefficient of relationship used was correct, and generally indicate whether there are strong digressions from the assumptions made in this benchmarking study.

In summary, this breeding population of *E. nitens* exhibits sufficient variation for dbh between and within seedlots, as well as sufficient levels of additive variance, for significant improvements to be possible using selection of top individuals in top seedlots/families, both within and across provenances. Earlier selections at mid-rotation will shorten the breeding cycle, partially overcoming one of the shortfalls of breeding in this species in South Africa, namely the reticent flowering and resultant delays in seed production of *E. nitens*. Due to this potentially shortened breeding cycle and the genetic stability of the species across sites, these selections and ensuing improved genetic material will result in gains made through the breeding programme being deployed more rapidly commercially.

Acknowledgements

The foresters and research staff at KLF, Mondi Group, Sappi Forests and York Timbers are gratefully acknowledged for their assistance with the establishment and long term maintenance of these trials, many of which have since become seed orchards. The anonymous reviewers of this manuscript are also acknowledged for their useful comments.

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