Quantitative Genetics of *Eucalyptus globulus:* Affinities of Land Race and Native Stand Localities

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Abstract

Genetic variation was examined in a *Eucalyptus globulus* base population collection comprising 276 seed lots from 12 Australian localities and four land races developed in Europe and South America. Thirty variables collected over a 4-year period from four field trials in Argentina representing growth, relative bark thickness, tree form, transition to adult foliage and pilodyn penetration were used to determine the quantitative genetic affinities of the populations. The patterns of quantitative genetic differentiation were summarised using canonical discriminant and cluster analyses. Tasmanian and Victorian native stand localities were clearly genetically different. Land race samples were variable but generally had closer affinities to native stand localities from southern Tasmania. Portuguese selected full sibs families were the fastest growing, even faster than OP progeny with the same parents presumably due to inbreeding depression after partial selfing. Many native stand localities were superior in growth to land race material. The only consistent genetic difference found between land race and native stand material was in tree form at two sites. The generally better form of land race samples is most likely due to artificial selection. Large gains in both growth and wood density can be simply achieved by using material from appropriate native provenances.

Key words: Eucalyptus globulus, genetic diversity, geographic variation, land race, provenances.

Introduction

Eucalyptus globulus ssp. *globulus* is the major pulpwood species grown in temperate regions of the world, with more than 1.7 million hectares planted (Tibbits *et al.,* 1997). This subspecies is a native of Tasmania and coastal regions of south-eastern Australia (Jordan *et al.,* 1994). The gene pool is highly differentiated across this geographic range (Dutkowski and Potts, 1999) as well as on a local scale (Jordan *et al.,* 2000). The subspecies also intergrades with *E. globulus* ssp. *bicostata* and *E. globulus* ssp. *pseudoglobulus* over extensive areas of continental Australia (Jordan *et al.,* 1994) and some of these intergrade populations are important components of breeding programs (Dutkowski and Potts, 1999; Jones *et al.,* 2001).

While *E. globulus* is native to Australia, major land races can now be found on most continents, but their exact origin is generally unknown and many are believed to be derived from a narrow genetic base (Poynton, 1979; Eldridge and Griffin, 1990; Eldridge *et al.,* 1993). *Eucalyptus globulus* ssp. *globulus* was the first eucalypt to be widely known outside of Australia (Jacobs, 1981). Plantings of this species were well established in southern Europe and Northern Africa by the mid 1800's (Penfold and Willis, 1961; Jacobs, 1981). Nowadays, it is the main eucalypt species cultivated in Portugal and Spain (Tibbits *et al.,* 1997). *E. globulus* was introduced into Chile in 1823 (Navarro and Vecchi, 1920; Jacobs, 1981) and an extensive forest base was rapidly developed in the early 1900's in the vicinity of Lota (VIII Region, Bío-Bío) (Bernath, 1940). In Argentina, *E. globulus* was the first eucalypt introduced in 1857 (Penfold and Willis, 1961; INTA, 1995). Although the species is only a minor component of the eucalypt estate in Argentina (Eldridge *et al.,* 1993), there is now increasing interest in expanding this estate (Lopez *et al.,* 1997).

Genetic improvement of *E. globulus* ssp. *globulus* commenced in the late 1960's with small breeding programs in Portugal and Australia, but most programs commenced in the late 1980's or early 1990's (Orme, 1977; Tibbits *et al.,* 1997). A main focus of early programs was the screening of a major provenance collection undertaken in 1975 to 1976 (Orme, 1977; Volker and Orme, 1988). By the late 1980's, major breeding programs for the pulp and paper industry had commenced in many countries around the world, such as Australia (Tibbits *et al.,* 1997), Chile (Vergara and Griffin, 1997), Portugal (Araújo *et al.,* 1997) and Spain (Vega Alonso *et al.,* 1994). The overseas programs were either based on selections derived from land races or more recent introductions of Australian native stand seed collections undertaken, for example, by Orme (1977) (e.g. Portugal – Almeida *et al.,* 1995; Miranda *et al.,* 2001) or the CSIRO Australian Tree Seed Centre (Gardiner and Crawford, 1987; 1988) (e.g. Chile – Infante and Prado, 1991; China – Zang *et al.,* 1995; Portugal – MacDonald *et al.,* 1995; Spain – Vega Alonso *et al.,* 1994; Soria *et al.,* 1997). In many cases, native stand re-introductions are seen as a way to more rapidly improve the genetic quality of plantations (Eldridge *et al.,* 1993) and new base population material is being screened for merging with land race selections (e.g. Araújo *et al.,* 1997; Vergara and Griffin, 1997).

The rate of germplasm exchange between breeding and deployment programs around the world is increasing. It is therefore important to know the origin and characteristics of land race material and how it compares with native stand provenances. *E. globulus* ssp. *globulus* land race material subject to varying levels of artificial selection have been compared to unselected native stand provenances in trials in many countries (Australia – Volker and Orme, 1988; Chile – Infante and Prado, 1991; China – Zang *et al.,* 1995; Portugal – Almeida *et al.,* 1995; Spain – Vega Alonso *et al.,* 1994). A key issue is whether such land races have differentiated from native stand material under the influence of natural or artificial selection in their new environment.

We examine the pattern of variation in a new collection of native stand seed lots of *E. globulus* ssp. *globulus* and intergrade populations grown in 4 Argentinian trials. We also deter-

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mined the quantitative genetic affinities and relative performance of land race selections from Portugal, Spain, Chile and Argentina in the same trials.

Materials and Methods

Plant material

A *E. globulus* ssp. *globulus* base population established on 4 sites in the Buenos Aires Province, Argentina was evaluated. The trials initially included 14,925 trees from 276 seed lots. 222 open pollinated (OP) seed lots were from a range wide collection of native stands in Australia that was undertaken by Kylisa Seeds Pty Ltd in 1993 to 1994 (*Figure 1; Table 1*). These seed lots are independent of those evaluated in early trials in other countries (see Introduction), although most of the collection localities were the same. The 10 seed lots from King Island were provided by the CSIRO Australian Tree Seed Centre. Land races from Portugal, Spain, Chile and Argentina were also represented as OP or control pollinated full-sib (FS) families, or commercial bulk collections. The Portuguese land race was represented by OP and FS families from a SOPORCEL clonal seed orchard. The Spanish land race was represented by OP families from selected trees in Asturias (Northern Spain) and a bulk sample which was a commercial seed lot from Huelva (south-western Spain). The Chilean land race was represented by three different bulk samples from the VIII Region, Bío-Bío, two commercial bulks from the Angol area and one from a seed production area at Roble Huacho where trees had been selected at an intensity of approximately 1 in 4. The Argentinian land race was represented by a commercial bulk from the Miramar region and 7 OP families collected from trees, mass selected for growth and form in a commercial plantation near Claromecó. The two last regions are in the traditional *E. globulus* ssp. *globulus* planting zone, which is south-east of the Buenos Aires Province.

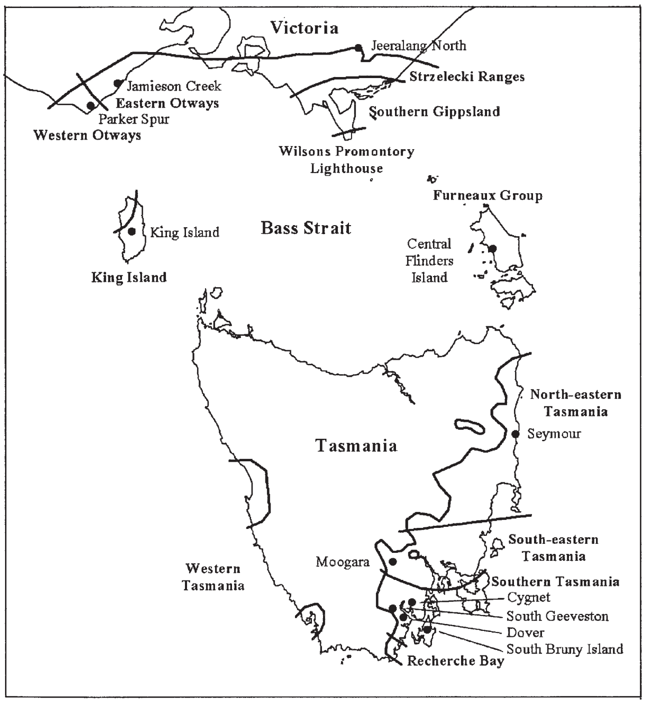

Fig. 1. – Map of south-east Australia showing seed collection localities and the races of *Eucalyptus globulus* ssp. *globulus* as defined by DUTKOWSKI and POTTS (1999).

The trials comprised 15 replicates of sets of 20 (4x5 trees) or 25 (5x5 trees) families. Families were allocated to sets based mainly on geographic provenance with a view to later conversion of the trials to seed orchards. Replicates of each set were randomly arranged throughout the trial and families within each set were randomly arranged in single tree plots. A double external buffer row was planted to minimise edge effects within the trials. Site conditions for all trials were similar and characterised by low altitude, uniform rainfall and fertile soil. The sites are identified as BALC, BOSC, MANU and VOCA and details are summarised in *table 2*. At each site, the soil was ploughed and ripped, a pre-emergent herbicide applied and planting undertaken at 3 m x 3 m spacing. Growth rates were best at the higher rainfall sites of BOSC and VOCA (*Table 3*). Survival was high in all sites (88% to 96%) and best at BALC and BOSC.

Table 1. – The provenance of *Eucalyptus globulus* ssp. *globulus* families and allocation in the four Argentinian trials. The race of DUTKOWSKI and POTTS (1999) is given when localities were comparable with their study, latitude (Lat.) and longitude (Long.) of the native stand collecting localities are given as well as the number of seed lots (families or bulks) at each trial site and across all sites. All the native stand families were derived from open pollinated seed lots (OP) whereas the land race samples included OP families, full-sib families (FS) or bulk seed collections.

		Lat.	Long.	Trials				
Provenance	Race			BALC	BOSC	VOCA	MANU	Total
Parker Spur	Western Otways	38° 47'	143° 35'	30	27	30	26	30
Jamieson Creek	Eastern Otways	38° 36'	143° 53'	21	19	21	19	21
Jeeralang North	Strzelecki Ranges	38° 20'	146° 31'	30	29	30	30	30
South Bruny Island	Southern Tasmania	43° 22'	147° 17'	10	9	10	10	10
Cygnet		43° 08'	147° 06'	23	22	23	23	23
Dover bulk	Southern Tasmania	43° 16'	147° 00'	-	-	1	-	1
Central Flinders Island	Furneaux	40° 04'	148° 00'	36	34	38	34	38
Dover	Southern Tasmania	43° 16'	147° 00'	24	21	24	23	24
South Geeveston	Southern Tasmania	43° 11'	146° 53'	4	4	4	4	4
Central King Island	King Island	39° 53'	143° 59'	10	7	10	9	10
Moogara	South-eastern Tasmania	42° 47'	146° 53'	23	21	23	23	23
Seymour	North-eastern Tasmania	41° 40'	148° 17'	10	7	10	9	10
Portugal OP				21	12	28	19	28
Portugal FS				6	6	10	10	10
Spain bulk				1	1	-	-	1
Spain OP				-	-	2	2	2
Argentina bulk				-	-	1	-	1
Argentina OP				-	-	7	7	7
Chile bulks				1	1	3	2	3
TOTAL				250	220	275	250	276

Table 2. – Location, soil, climate details, year of establishment and number of families in each trial.

	Trials			
	BALC	BOSC	MANU	VOCA
Latitude	37° 45'	38° 39'	37° 53'	38° 28'
Longitude	58° 17'	59° 04'	59° 56'	59° 06'
Altitude (m)	133	13	210	49
Soil	Clay loam	Sandy loam	Clay loam	Loam
pH	5.9	6.1	6.1	6.7
Organic matter (%)	6.5	5.9	5.6	3.5
Annual rainfall (mm)	908	1008	850	930
Annual average temperature (°C)	13.5	14.0	13.3	13.4
Absolute minimum (°C)	-5.4	-3.3	-5.8	-4.0
Year of establishment	1995	1995	1996	1996
No. of families	250	220	250	275

Table 3. – Phenotypic means for all traits assessed from each trial and respective units. Abbreviations used for the variables are described in text. Variables with a superscript (1) were logit transformed for analysis and means backtransformed for presentation.

		Trials			
Variable	Unit	BALC	BOSC	MANU	VOCA
DBH2	cm	6.6	8.6	5.5	7.7
DBH3	cm	9.2	11.6	8.2	10.7
DBH4	cm	11.2	14.8	-	-
ADFO^1	proportion	0.29	0.26	0.36	0.46
HT1	cm	126	149	-	-
HT2	cm	494	504	421	537
FORM	point 1 – 4	2.9	2.0	2.6	2.5
FORK^1	proportion	0.25	0.48	-	-
PILO	mm	12.6	12.9	-	-
BARK	% of DBH	8.0	8.6	-	-

Measurements

Trees were assessed for growth, pilodyn penetration, bark thickness, tree form and the timing of the transition to adult foliage (*Table 3*). Over bark diameter (cm) was measured at breast height (1.3 m) at 2 (DBH2), 3 (DBH3) and 4 (DBH4) years after planting. Total height (cm) was measured at 1 (HT1) and 2 (HT2) years. Assessments were made of the proportion of adult foliage at 2 years (ADFO) and form (FORM) at 3 or 4 years. ADFO and FORM were subjectively assessed using a 4-point scoring system. ADFO was scored from 0 (no adult foliage) to 1 (complete adult foliage) using the classes 0, 0.33, 0.66 and 1 at BALC and BOSC; and classes 0, 0.33, 0.5 and 1 at MANU and VOCA. FORM was assessed from 1 (worst) to 4 (best) at 4 years at BALC and BOSC and 3 years at MANU and VOCA. The bark thickness (mm) (BTHI) and pilodyn penetration (mm) (PILO) were assessed from trees at BALC and BOSC at 4 years of age following the procedure of MacDonald *et al.* (1997), except only one measurement was taken per tree. Pilodyn penetration is an indirect measure of wood basic density because they are inversely related (Greaves *et al.,* 1996). The variable BARK used for analysis is the percentage of DBH4 that was bark for each individual tree and it was estimated as:

$$\text{BARK} = 20 * \text{BTHI} / \text{DBH4}$$

The presence or absence of forks at 2 years (FORK) was also assessed at BALC and BOSC, approximately 2 months after light hail damage.

Analyses

The general sets of data used for analysis were from all those trees that were alive at the measurement. At one site (MANU) approximately 25% of trees suffered cow damage at an early age and were excluded from analysis. Binomial (FORK) and proportion traits (ADFO) were transformed to a logit scale before analysis to achieve normality of residuals and backtransformed after analysis for presentation.

Family least-square means for all variables were calculated for each individual site. Spatial analysis (Costa e Silva *et al.,* 2001), undertaken with ASREML, was used to calculate family means because of the partial confounding of provenance with the original design units. The original design units (sets) were thus not included in the model. The significance of the differences between locality means were tested with a one-way ANOVA based on these family least-square means, and *a posteriori* comparisons of locality means undertaken with the Tukey test. This analysis was undertaken with the GLM procedure of SAS (SAS version 8), specifically testing differences between: a) native stand localities; b) Portugal OP and FS using only families where the parents were common to both cross types; and c) land race versus native stand OP families.

Principal component analyses were performed on groups of variables representing the same trait to summarise the main component of variance among provenance means. As in Dutkowski and Potts (1999), the first principal component from each analysis was used to derive synthetic traits (italics in the text indicates a synthetic trait) to summarise the variation in growth, diameter, adult foliage, pilodyn penetration, form, fork and bark thickness. Variables and trials used in the calculation of each synthetic trait are showed in *table 5*. Principal component analyses were based on the correlation matrix derived from locality means and undertaken using the PROC PRINCOMP procedure of SAS. The geographic trends in variation for the synthetic traits *growth, adult foliage, form, forking, pilodyn* and *bark thickness* were then visualised by plotting provenance values on maps showing their geographic position.

In order to summarise the overall differentiation between provenances in multivariate space, a discriminant analysis based on family means for 30 variables was undertaken using PROC DISCRIM of SAS. Only 204 OP families from the 13 provenances present in all four trials were used. Scores on the significant discriminant functions were calculated and provenance means plotted in the space defined by the 2 major discriminant functions. UPGMA clustering was also used to summarise the overall quantitative genetic relationships amongst provenances. The clustering was based on the Euclidean distance amongst provenances in the space defined by the 7 significant discriminant functions and was undertaken using the PROC CLUSTER procedure of SAS.

Results and Discussion

Differences among native stand localities

The differences between native stand localities were significant for all variables analysed (*Table 4*). The highest F values were generally for BARK and FORM. For all synthetic traits shown in *figure 2*, the first principal component (PC1; see *Table 5*) summarised positively correlated variation in trait means across trial sites. *Adult foliage, pilodyn* and *bark thickness* explained more than 90% of the total variation amongst localities means, indicating that locality performance was highly stable across sites and thus the genotype by environment interaction was low. Locality performance was also relatively consistent for other traits, such as *growth, diameter, form* and *forking* where the percentage of variation explained ranged from 72% to 88% (see *Table 5*). For comparable synthetic traits, Dutkowski and Potts (1999) reported percentage of correlated variation of locality performance consistently lower than the present study, suggesting that there is less locality x environment interaction in our study than evident in their Tasmanian trials.

Highly significant differences between localities occurred for both diameter and height growth in all of the Argentinian

Table 4. – F-ratio (*F*) and probability (*p*) of no difference between groups from univariate ANOVAs for each variable. The analyses were based on family least square means and compared the 11 native stand localities ($F_{10,\ 190\ \text{to}\ 212}$), Portuguese open pollinated (OP) and full-sibs families (FS) which share common parents ($F_{1,\ 9\ \text{or}\ 10}$), and land race and native stand OP families ($F_{1,\ 213\ \text{to}\ 263}$). Variable codes are detailed in text.

		Native stand localities		Portugal OP vs. FS		Land race vs. native	
Trials	Variable	*F*	*p*	*F*	*p*	*F*	*p*
BALC	DBH2	5.5	0.0000	0.1	0.7137	2.2	0.1429
	DBH3	4.3	0.0000	9.8	0.0106	1.5	0.2152
	DBH4	3.5	0.0003	2.6	0.1408	1.4	0.2357
	ADFO	8.8	0.0000	1.7	0.2275	5.2	0.0231
	HT1	3.8	0.0001	0.7	0.4147	4.0	0.0471
	HT2	5.9	0.0000	0.3	0.6008	0.3	0.5759
	FORM	11.8	0.0000	0.8	0.4057	9.6	0.0022
	FORK	2.5	0.0066	0.1	0.7080	0.1	0.7973
	PILO	11.2	0.0000	1.5	0.2530	0.2	0.6505
	BARK	27.3	0.0000	1.1	0.3214	0.2	0.6567
BOSC	DBH2	8.3	0.0000	1.0	0.3534	1.6	0.2102
	DBH3	4.4	0.0000	2.0	0.1881	0.9	0.3380
	DBH4	3.0	0.0016	1.5	0.2556	1.6	0.2078
	ADFO	15.7	0.0000	3.7	0.0856	1.0	0.3278
	FORK	4.6	0.0000	0.1	0.7511	1.1	0.3060
	HT1	13.1	0.0000	0.8	0.3842	0.9	0.3319
	HT2	10.1	0.0000	2.2	0.1760	0.0	0.8811
	FORM	13.1	0.0000	2.4	0.1537	1.9	0.1714
	PILO	7.0	0.0000	4.1	0.0724	0.1	0.7825
	BARK	13.4	0.0000	0.0	0.9678	0.1	0.7903
MANU	DBH2	10.7	0.0000	0.6	0.4505	0.7	0.4022
	DBH3	5.0	0.0000	0.1	0.7545	1.5	0.2203
	ADFO	9.2	0.0000	5.5	0.0444	0.2	0.6275
	HT2	10.8	0.0000	0.2	0.6415	1.0	0.3200
	FORM	7.9	0.0000	0.3	0.5860	0.0	0.8513
VOCA	DBH2	9.4	0.0000	1.0	0.3404	0.0	0.8861
	DBH3	7.2	0.0000	1.6	0.2397	0.1	0.7765
	ADFO	11.0	0.0000	4.9	0.0505	6.7	0.0103
	HT2	15.0	0.0000	0.0	1.0000	0.2	0.6267
	FORM	16.2	0.0000	0.2	0.6785	23.6	0.0000

Table 5. – The percentage of variation explained by the main principal component summarising positive correlated variation between the same trait measured at the various sites and ages. The higher the principal component (PC1), the greater is the means across sites and ages for each trait. These principal components were used to derive synthetic traits that summarised the variation in each trait (see *Figure 1, Table 7*). The more variation explained by the synthetic trait (PC1), the more consistent the locality performed across sites and ages (less genotype x environment or genotype x age interaction).

Synthetic trait	Number of trials	Variable used	Age in years	% explained by PC1
adult foliage	4	ADFO	2	95.5
pilodyn	2	PILO	4	94.2
bark thickness	2	BARK	4	92.7
growth	2	DBH & HT	2 & 3	87.6
diameter	4	DBH	3 & 4	81.9
form	2	FORM	3	79.5
forking	2	FORK	2	71.8

trials at all ages (*P*<0.001), except for DBH4 at BOSC (*P*<0.01) (*Table 4*). The best growth was obtained from native stand seed lots collected from Victoria (Parker Spur, Jamieson Creek, Jeeralang North), South Geeveston and Central Flinders Island whereas the slowest growing localities were from Central King Island, South Bruny Island and Moogara (*Figure 2a* and *Table 6*). Similar rankings were found for 2 and 4 year growth data from the CSIRO 1987/1988 seed collections in trials in Tasmania (JORDAN *et al.,* 1994; DUTKOWSKI and POTTS, 1999) and Chile (INFANTE and PRADO, 1991; PRADO and ALVEAR, 1993), which indicates the general stability of this geographic pattern. The main inconsistency across collections arises in the performance of seed lots collected from King Island. It was generally the slowest growing native stand locality in the Argentinian trials, and also performed poorly in other studies (INFANTE and PRADO, 1991; JORDAN *et al.,* 1994). However, King Island was the best performing provenance reported by VOLKER and ORME (1988) and KUBE *et al.* (1995) from an earlier collection. Such differences may be due to variation in the exact location that the seed is sampled on the island. For example, DUTKOWSKI and POTTS (1999) showed large differences in the growth of collections from South and Central King Island in the CSIRO 1987/1988 collection. This difference may be due to sampling more remnant trees in farmland in the southern sample. Open-pollinated progeny from such isolated trees exhibit poorer growth compared with those from trees in more dense stands (BORRALHO and POTTS, 1996) due to lower outcrossing rates (HARDNER *et al.,* 1996). In our case, seed originated from the relatively isolated, remnant trees suggesting that their open-pollinated progeny would exhibit some degree of inbreeding depression, that is severe in *E. globulus* ssp. *globulus* (HARDNER and POTTS, 1995; LOPEZ *et al.,* 2000). Nevertheless, the possibility of genotype x environment interactions causing the variable performance of King Island can not be discounted. For example, SORIA *et al.* (1997) report relatively better growth of King Island and Western Tasmanian families in trials in the north of Spain compared with those in the drought prone (TORO *et al.,* 1998), south-west of Spain. King Island is known to be relatively drought susceptible (DUTKOWSKI, 1995).

The native stand localities also differed in the timing of the ontogenetic transition from the opposite, sessile and highly glaucous juvenile leaves to the typical alternate, petiolate green adult leaves (*P*<0.001; *Table 4*). Localities exhibiting early transition to adult foliage, and hence having a greater proportion of adult foliage in the canopy at age 2 years, were from Cygnet, localities from Victoria, and Central Flinders Island (*Figure 2b*). Trees from Seymour, in North-eastern Tasmania, retained their juvenile foliage much later than all other localities tested (*Figure 2b*). Similar trends were also reported by DUTKOWSKI and POTTS (1999) and JORDAN *et al.* (2000), where localities from the North-eastern Tasmanian race were shown to retain their juvenile foliage and those from the Eastern and Western Otways and Furneaux races exhibited early transition.

The form of trees from the native stand localities differed significantly on all sites (*P*<0.001; *Table 4*). Trees with the best form were from Jeeralang North, Moogara and South Geeveston, whilst trees from Seymour, Jamieson Creek and Central Finders Island had the poorest form (*Figure 2c* and *Table 6*). Localities also differed for early forking, mainly due to hail damage in the two sites assessed (*P*<0.01 at BALC and *P*<0.001 at BOSC; *Table 4*). Trees more susceptible to forking were from South Bruny Island, Jamieson Creek and Central Finders Island localities (*Figure 2d*). The locality with the least forking was Jeeralang North. There was some consistency between good form and low forking at the locality level (e.g. Jeeralang North vs Jamieson Creek and Central Finders Island), although the positive correlation was not statistically significant (*Table 7*). Again there is consistency in the pattern of genetic diversity in form revealed in other studies. In trials established from the Orme collection in Tasmania, trees from King Island, Jeeralang, Geeveston and Uxbridge (i.e. Moogara) had the better average form while those from Seymour clearly had the worst (VOLKER and ORME, 1988). The poor form of the latter locality was noted as being typical of many of the localities on the East coast of Tasmania. Locality level information is not given for a trial established in China from the CSIRO 1987 collection (ZANG *et al.,* 1995). However, the mean form of trees from Eastern Victorian followed by Southern Tasmania

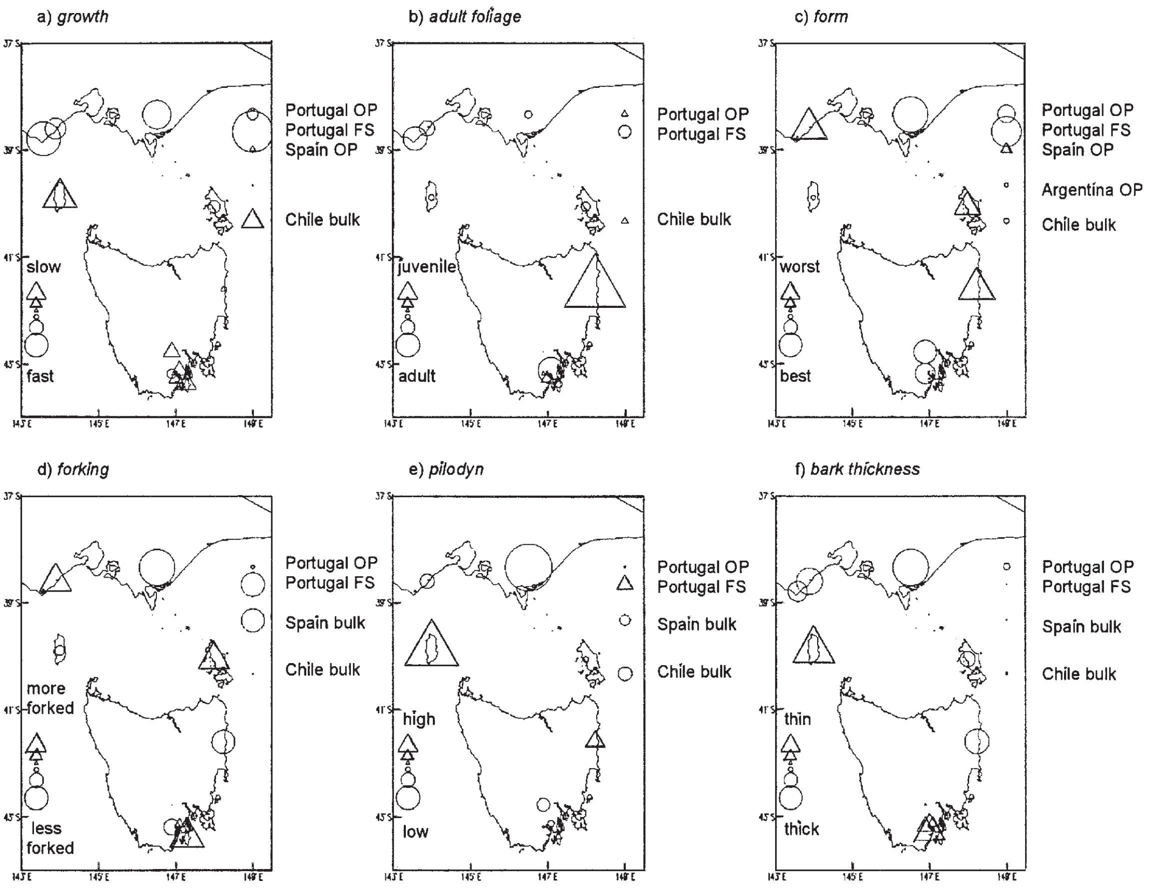

Fig. 2. – Geographic variation in (a) growth, (b) adult foliage, (c) form, (d) forking, (e) pilodyn penetration, and f) relative bark thickness amongst native stand and land race samples of *Eucalyptus globulus* ssp. *globulus*. The provenance means of the first principal component indicated in *table 5* is plotted with large circles representing favourable values and large triangles representing the least favourable values from a breeding perspective.

was the best whereas the average form of trees from Eastern Tasmania and the Bass Strait Islands was the worst.

Pilodyn penetration, an indicator of wood density, differed significantly amongst the native stand localities in both Argentinian trials ($P<0.001$; *Table 4*). Pilodyn penetration was highest in trees from Central King Island followed by Seymour, and lowest in trees from Jeeralang North and Jamieson Creek (*Figure 2e* and *Table 6*). The locality ranking was very similar for the subset of localities in common with those tested in Portugal using wood cores (MIRANDA *et al.,* 2001) and the pilodyn assessment of the CSIRO 1987/88 collection in Tasmania (DUTKOWSKI and POTTS, 1999). In all cases, Jeeralang North had the highest wood density and King Island the lowest. The similarity in locality performance in different countries and across

Table 6. – Locality means for diameter (cm) and tree form (1 = worst, 4 = best) at VOCA age 3, and pilodyn penetration (mm) at BALC age 4 in native stand and land race (*) families of *Eucalyptus globulus* ssp. *globulus* grown in Argentina. Results are presented for these sites as they contained the most land race samples. Provenances grouped by the same vertical line are not significantly different ($P > 0.05$) following the TUKEY test.

Diameter at VOCA		Tree form at VOCA		Pilodyn penetration at BALC	
Provenance	Mean	Provenance	Mean	Provenance	Mean
*Portugal FS	12.00	*Portugal FS	3.05	Jeeralang N.	11.65
Parker Spur	11.54	*Argentina Bulk	2.93	*Chile Bulks	12.24
Jeeralang N.	11.34	Moogara	2.84	Sth. Geeveston	12.38
Sth. Geeveston	11.17	*Portugal OP	2.81	Jamieson Ck.	12.47
Jamieson Ck.	10.98	*Chile Bulks	2.78	*Spain Bulk	12.48
Cent. Flinders I.	10.91	Jeeralang N.	2.77	Moogara	12.57
*Argentina OP	10.90	*Argentina OP	2.76	Cent. Flinders I.	12.59
*Portugal OP	10.74	Sth. Geeveston	2.66	Cygnet	12.61
*Spain OP	10.68	Cygnet	2.62	Sth. Bruny I.	12.63
Seymour	10.61	Sth. Bruny I.	2.54	Dover	12.68
Dover	10.29	Dover	2.54	*Portugal OP	12.68
Cygnet	10.15	*Spain OP	2.45	Parker Spur	12.81
Sth. Bruny I.	9.97	Parker Spur	2.41	*Portugal FS	12.92
Moogara	9.83	Cent. King I.	2.29	Seymour	13.08
*Chile Bulks	9.31	Cent. Flinders I.	2.16	Cent. King I.	14.03
Cent. King I.	9.18	Seymour	2.14		
*Argentina Bulk	8.65	Jamieson Ck.	2.05		

multiple collections is consistent with low genotype by environment interaction (MACDONALD *et al.,* 1997) and strong genetic structuring of the gene pool for this trait.

Highly significant differences were found amongst *E. globulus* ssp. *globulus* native stand localities for relative bark thickness (*P*<0.001; *Table 4*). Bark was thicker on trees from Jeeralang North, Jamieson Creek and Seymour. By contrast, Central King Island had thin bark, as did localities from Southern Tasmania (*Figure 2f*). The same pattern of genetic differentiation was detected in Tasmanian trials using the CSIRO 1987/1988 seed collection, where localities from Victoria and north-east Tasmania were shown to have the thickest bark (DUTKOWSKI and POTTS, 1999).

While patterns of variation amongst the native stand localities sampled in this study was independent for most of the traits; there was evidence for correlated variation in several cases (*Table 7*). Localities with thicker bark were also those with denser wood, and the faster growing localities had both thicker bark and denser wood (i.e. lower pilodyn penetration). However, while the association of thick bark and dense wood was evident in the larger sample of native stand localities studied by DUTKOWSKI and POTTS (1999), the associations of both traits with increased growth were not evident. The faster growing races of *E. globulus* ssp. *globulus* make the transition to adult foliage earlier (JORDAN *et al.,* 2000), but this trend was not significant amongst the localities in the present study.

Table 7. – PEARSON correlation coefficients amongst native stand locality means for the synthetic traits plotted in *figure 2.* Significant correlations are marked as * 0.01 < *P* < 0.05, ** *P* < 0.01.

Synthetic trait	*growth*	*form*	*adult foliage*	*forking*	*pilodyn*
form	-0.09				
adult foliage	0.19	0.33			
forking	-0.05	-0.50	0.44		
pilodyn	-0.63*	-0.28	-0.27	0.02	
bark thickness	0.78**	-0.29	-0.07	-0.01	-0.61*

The first two dimensions of the discriminant space shown in *figure 3* and the dendrogram in *figure 4* summarise the pattern of differentiation amongst the native stand localities. All localities from Victoria (Jeeralang North, Jamieson Creek and Parker Spur) were differentiated from localities in South-eastern Tasmania. Central Flinders Island was intermediate but had closer affinities to Jamieson Creek and Parker Spur, localities from the Otways Ranges in Victoria. This differentiation was consistent with the results of DUTKOWSKI and POTTS (1999) for quantitative traits and that observed by NESBITT *et al.* (1995) using RAPD markers. Central King Island was an outlier to the south-eastern Tasmanian localities in the present study (*Figure 4*). NESBITT *et al.* (1995) and DUTKOWSKI and POTTS (1999) also reported that King Island localities were outliers, but in the later case with quantitative genetic affinities to western Tasmanian localities not included in the present study. Cygnet clustered with Moogara although both have close affinities to the Southern Tasmanian group of localities (South Bruny Island, Dover and South Geeveston). Cygnet lies near the boundary of the Southern and South-eastern Tasmanian races of *E. globulus* ssp. *globulus* as defined by DUTKOWSKI and POTTS (1999). This locality was not sampled in their study, but its affinities to Moogara, which is classified in the South-eastern Tasmania race, suggests that the boundaries between these two adjoining races may be further south than they indicated. The Seymour population is an outlier in our analysis which is probably a reflection of it being the only representative of the North-eastern Tasmania race in this study.

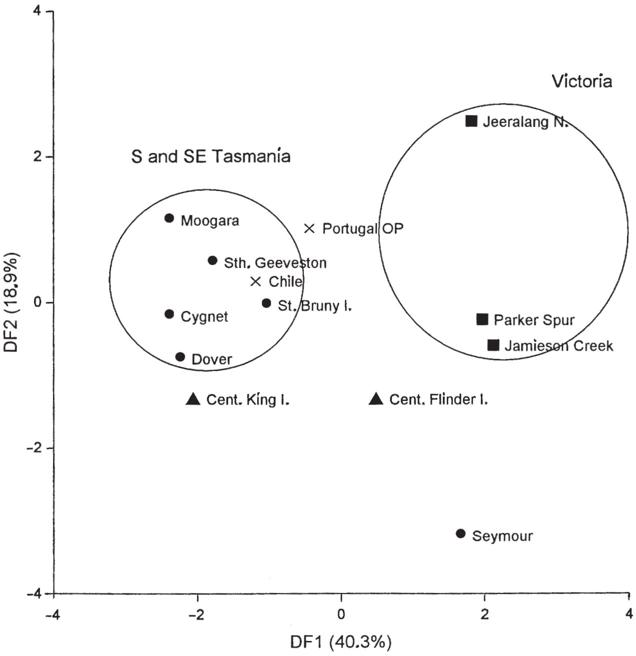

Fig. 3. – *Eucalyptus globulus* ssp. *globulus* provenance means scores on the first two discriminant functions (DF) derived from analysis of growth, form, adult foliage, bark and pilodyn penetration. The localities are from Victoria (■), the Bass Strait Islands (▲), Tasmania (•) and exotic land races (×). The analysis was based on family mean data and the percentage of variation explained by each discriminant function is indicated.

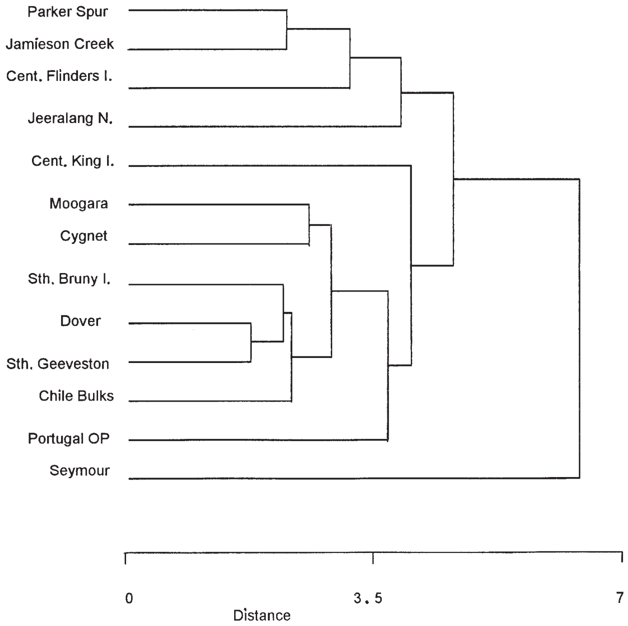

Fig. 4 – Dendrogram from UPGMA clustering of native stand and land race localities of *Eucalyptus globulus* ssp. *globulus.*

Land race differentiation

For the majority of traits, the landrace samples were within the range of variation found for the native stand localities (*Figure 2*). Few significant differences were detected in the specific comparison of native stand and land race families (*Table 4*). The most significant difference involved tree form, which was significantly better in the land race than native stand families on two sites (VOCA *P*<0.001; BALC *P*<0.01). The generally better form of land race samples (*Figure 2c*) was most marked at VOCA, where the land race samples from Portugal, Argentina and Chile had better form than all native stand localities except Moogara (*Table 6*). Spain OP was the exception for the landrace samples as it had only average tree form compared with native stand families (*Table 6*). Better form of Portuguese and Australian open-pollinated seed orchard progeny compared to native stand progeny was found in China, and even the unimproved local Chinese land race had better form than most native stand samples (ZANG *et al.,* 1995). Several authors (e.g. POYNTON, 1979; JACOBS, 1981) have noted the good form of overseas plantations of *E. globulus* ssp. *globulus.* Such better form could simply be a plastic response to the absence of damage by the numerous pests and diseases which have co-evolved with eucalypts in Australia (PRYOR, 1976). However, the present study suggests that the good form in overseas plantations has a genetic basis and is likely to be due to artificial selection. ALMEIDA *et al.* (1995) also reported that land races from Spain, Portugal and USA were more frost tolerant than native provenances of *E. globulus* ssp. *globulus*, and suggested that this is likely to be due to selection after introduction. Such improved frost resistance is similarly reported for the local Chinese land race of *E. globulus* (ZANG *et al.,* 1995).

The growth rate of the individual land races varied markedly (*Figure 2a; Table 6*), in part reflecting their degree of genetic improvement. VOCA was the site where most land race samples were represented and where the most significant differences between all provenances were detected ($P<0.001$). At this site, the open pollinated families from Argentina, Portugal and Spain were only average in their performance and were outperformed by many native stand localities (*Table 6*). This average performance occurred despite the fact that the native trees sampled were effectively unselected whereas the land race parents were selected to varying degrees from even aged plantations on the basis of size and form. In addition, the land race OP seed was not only obtained directly from selected trees in plantations (Argentina, Spain), but from a grafted seed orchard (Portugal). The bulk seed lots used for commercial plantation establishment were the worst of all seed lots tested, except for the native stand seed lots from Central King Island which are likely to be highly inbred (see above). The deleterious impact of inbreeding on the growth of open-pollinated families is no doubt reflected in the superior growth of the Portugal FS families compared with the Portugal OP families (*Figure 2a; Table 6*). Depression in the growth of *E. globulus* ssp. *globulus* open pollinated progeny compared to outcrossed controls is well known (HARDNER and POTTS, 1995; HARDNER *et al.,* 1996; LOPEZ *et al.,* 2000). While this trend was consistent in all cases when we compared the FS and OP progenies from exactly the same parents, the difference was only statistically significant in one case (BALC DBH3; *Table 4*).

The relatively poor growth of the land race OPs compared to many of the native stand localities may be due to selection from a narrow, and probably not the best, genetic base or inbreeding effects (ELDRIDGE *et al.,* 1993). This poor growth performance is also evident at the family level where a high percentage of the top performing families were from native stands. The best performing families at VOCA were from the native stand localities, Parker Spur, Jeeralang North and Jamieson Creek, where 60%, 40% and 29% of families respectively were in the top 25% for growth (DBH3) in the trial. Twenty-five percent of the Portuguese OP families were in the top 25% of families and the top family ranked 6th. Apart from one family from the Argentina OP, no other land race OP family or bulk seed lot was represented in the top 25% of families in the trial. While 80% of the Portuguese full sib families were in the top 25%, the top full-sib family still only ranked 8th in the whole trial.

Seed lots from land race and native localities have been tested in other countries with variable results. At 6 sites in Portugal, the average growth of local seed lots covered the full range of variation observed for a wide range of native Australian localities of *E. globulus* (ALMEIDA *et al.,* 1995). However, one local Portuguese provenance was noted to give the best average performance across all sites. In Yunnan, China, the average tree diameter of seed lots from the unimproved local land race, as well as seed orchards in Tasmania and Portugal, was greater than the native stand provenances (ZANG *et al.,* 1995). However, only the Tasmanian seed orchard seed lots exceeded the native Victorian provenances on height growth. In 14 sites in Spain samples of the local population and clones used as controls, exceeded the average growth of native provenances (SORIA *et al.,* 1997). However, at the family level, it was noted that several Australian families exceed the growth of local controls and would constitute good material for future breeding.

Wood density is another trait that is important when breeding *E. globulus* ssp. *globulus* for pulpwood (BORRALHO *et al.,* 1993). The average pilodyn penetration of our land race samples was spread across the full range of natural variation (*Figure 2e; Table 6*). Trees from Chile bulks had the lower penetration, Spain bulk was intermediate, and the pilodyn penetration for the Portugal OP and FS families was high. However, in this analysis the difference amongst land race samples was not statistically significant. The only comparison of the wood density of land race and native provenances of *E. globulus* published is that of MIRANDA *et al.* (2001). In this study of 3 trials in Portugal, the land race samples from Spain and Portugal transgressed the full range of variation in average wood basic density observed amongst native provenances. However, there was a trend for the land race samples to be in the higher range of density, but this was not the case in the present study.

Marked, spatially structured genetic differentiation of the native gene pool provides the opportunity to examine the overall genetic affinities and possible origin of selections from the *E. globulus* ssp. *globulus* land races developed on several continents. The patterns of multivariate differentiation amongst provenances are summarised in the ordination in *figure 3* and dendrogram in *figure 4.* Only the Chilean and Portugese land races were sufficiently represented across all trials to allow their inclusion in the analysis. The Chile bulks clearly had close quantitative genetic affinities to localities from the Southern Tasmanian race of *E. globulus* ssp. *globulus.* This affinity is consistent with isozyme studies that show samples from the Chilean land race have greater molecular genetic affinities to southern Tasmania (EATON, 1994). The Portuguese OP sample was somewhat intermediate between Tasmanian and Victorian localities (*Figure 3*). However, it had closest affinities to South Bruny Island, Moogara and South Geeveston (*Figure 3*), and clustered with the southern Tasmanian localities (*Figure 4*).

Quantitative genetic affinities of land race samples of *E. globulus* have been addressed in several other studies. ZANG *et al.* (1995) found that the local Chinese land race from Yunnan province also had close affinities to native localities from southern Tasmania, which is consistent with this area being an early source of seed distributed around the world. However, in comparing the performance of 6 land race samples from Portugal on traits, such as survival, growth, frost tolerance, bark content and wood density, ALMEIDA *et al.,* (1995) notes that they rank across the full distribution of native localities. This result suggests that a broad provenance origin of the Portuguese land race is likely. However, our study suggests that the average affinities of the 12 OP families derived from selections from diverse areas in Portugal (and which were represented in all four trials) lies with native localities from southern Tasmania. A predominantly southern or south-eastern Tasmanian origin of plantations of *E. globulus* ssp. *globulus* in Spain and Portugal is suggested by Orme (1977) based on observation of morphology. This is the core of the distribution of subspecies *E. globulus* ssp. *globulus* (Jordan *et al.,* 1994).

Conclusion

This study demonstrates marked genetic differences between the native localities of *E. globulus* ssp. *globulus*, consistent with previous studies. This genetic differentiation is geographically structured and involves independent variation in many quantitative traits. The spatial patterns of genetic diversity in *E. globulus* ssp. *globulus* are stable, being clearly revealed in independent samples of the native gene pool and expressed under different environments transgressing both northern and southern hemispheres.

The strong geographic structuring of variation in the *E. globulus* ssp. *globulus* native gene pool allows the affinities and potential origin of exotic land races to be examined. The average quantitative genetic affinities of the Chilean and Portuguese land race samples tested in this study lie with populations in the core range of this subspecies in southern Tasmania. However, there is some evidence to suggest that the land races have undergone genetic differentiation for at least one key trait after their introduction into exotic countries, potentially due to historic, or more recent, artificial phenotypic selection. The performance of land race samples from throughout the world for key economic traits varies widely which for growth can, to some extent, be explained by differences in their level of genetic improvement. The present study indicates that some local land race material being used for deployment may be of low genetic quality and clearly emphasises the gains that can be made by the introduction of new material from Australia for both breeding and deployment.

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Parental Environment Effects on Cold Acclimation and Height Growth in Lodgepole Pine Seedlings

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Abstract

Lodgepole pine stands from a number of seed sources were established in different commercial forest environments in northern Sweden in the 1970's as part of the introduction effort of this species. Parental environment effects (aftereffects) were studied in progeny from stands originating from two seed sources (Fireside and Toad River, British Columbia), with each seed source grown in six different Swedish environments. The occurrence of aftereffects on cold acclimation (freezing damage and mortality) and height growth of the progeny was investigated in the greenhouse and freezing chamber. One growing season height and cold acclimation differed significantly among stand sites, though the magnitude of the site effect was relatively small. Seedlings were taller at lower elevations, at higher site indexes and in longer growing degree-days environments. With longer growing degree-days freezing damage was significantly lower in the Fireside origin, but not significantly higher in the Toad River origin. Height and resistance to cold damage were positively correlated in the Fireside origin but not in the Toad River origin. The results suggest that aftereffects could be manipulated to benefit reforestation by choosing the proper combination of genetic materials and environments for seed production. Aftereffects could also constitute a problem for tree breeding, because the environment in which a seed sample is produced could be confounded with its inherent genetic value.

Key words: Seed origin, freezing test, aftereffects, growing degree-day, tree breeding.

Introduction

It is well accepted in tree breeding that establishing seed orchards in more southern or warmer regions usually results in early flowering, higher seed production, heavier seed, and higher seed germination rates (e.g. Schmidtling, 1984, 1987). These types of beneficial effects, known as "aftereffects", are caused by the difference between the original and present environment where the seed is produced. Aftereffects can also influence adaptive traits. Indeed, several studies have shown that Norway spruce (*Picea abies*) raised from seed produced under milder environments grew faster, flushed later in the spring and set buds later in the autumn, had a longer shoot elongation period, and were therefore more sensitive to cold conditions than those of the same genetic composition produced under harsher environments (Bjørnstad, 1981; Johnsen, 1989a and b; Johnsen et al., 1995, 1996; Skrøppa, 1994; Johnsen and Skrøppa, 1996). Aftereffects in *Picea abies* might last for many years (Johnsen, 1989b; Johnsen and Skrøppa, 1996) or possibly indefinitely. Similar observations have been made in *Picea glauca* (Stoehr et al., 1998) and *Pinus sylvestris* (Lindgren and Wang, 1986; Dormling and Johnsen, 1992; Andersson, 1994; Lindgren and Wei, 1994). Aftereffects in

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