

Genetic Variation in the Juvenile Leaf Morphology of *Eucalyptus globulus* Labill. ssp *globulus*.

B. M. Potts and G. J. Jordan

Cooperative Research Centre for Temperate Hardwood Forestry and Department of Plant Science, University of Tasmania, G. P. O. Box 252C, Hobart, Tas. 7001, Australia.

E-mail: B.M.Potts@plant.utas.edu.au

Abstract

The patterns of genetic variation in the length and shape of juvenile leaves of *Eucalyptus globulus* ssp *globulus* are described. Significant additive genetic variation occurred within populations for all traits. Leaf length was more heritable ($h^2 = 0.34$) than most leaf shape traits ($h^2 = 0.19-0.34$). Significant genetic differences also occur between populations in both leaf length and shape with the strongest differentiation occurring in leaf length. There were strong intra- and interpopulation genetic correlations amongst most of the leaf traits. Height and volume at two years of age were genetically independent of leaf length, but within populations, faster growth was genetically correlated with increased basal lobing and a shift of the widest point closer to the leaf base. The intra- and interpopulation genetic correlations were markedly different for some pairs of traits. Leaf length was genetically independent of the height of transition from the juvenile to the adult leaf form within populations, yet genetic differences between populations were highly correlated. Growth was more highly genetically correlated with different facets of leaf shape within populations than between populations. It is argued that correlated selection is the most likely cause of correlated genetic variation between populations when traits are genetically independent within populations.

Introduction

Many *Eucalyptus* species are heteroblastic, producing juvenile and adult leaves differing markedly in morphology and anatomy (Johnson 1926; Pryor 1976). The size and shape of juvenile leaves in particular are important taxonomic characters in *Eucalyptus* (Pryor 1976) with closely related species being differentiated by these traits (e.g. Phillips and Reid 1980; Potts and Reid 1985b; Wiltshire *et al.* 1991). Due to their early ontogenetic expression, these traits are also widely used in studies of hybridisation (e.g. Pryor 1951; Potts and Reid 1985a) and intraspecific variation (e.g. Burley and Hans 1980; Phillips and Reid 1980; Potts and Reid 1985b; Wiltshire *et al.* 1992). The degree to which they are determined by genetic, ontogenetic (e.g. Wiltshire and Reid 1992) and environmental (e.g. Metcalfe *et al.* 1991) effects is of considerable evolutionary and taxonomic interest and, coupled with the adaptive significance of genetic differences (e.g. Thomas and Barber 1974; Givnish 1979), is important in explaining the diversity of leaf morphology in *Eucalyptus*.

Differences in juvenile leaf morphology between eucalypt species have been shown to be under strong genetic control and artificial interspecific F₁ hybrids are more or less intermediate in these traits (e.g. Pryor 1957a; Potts and Reid 1985a; Cauvin *et al.* 1987; Tibbits 1988), although dominance may contribute (e.g. Mergen *et al.* 1966; Pilipenka 1969). While there have been many studies of intraspecific variation in juvenile leaf length and shape in the genus, few have examined the inheritance of these differences (e.g. Potts 1985; Tibbits 1988). Associations have been reported at the population level between juvenile leaf length or shape and other traits such as precocity of transition to the adult leaf form (e.g. Wiltshire *et al.* 1992) and growth rate (e.g. Pryor 1957b; Potts 1985; Potts and Jackson 1986). However, in such cases, it is difficult to determine whether the variation in leaf morphology is adaptive *per se* or simply arises from genetic correlation with trait(s) more closely related to fitness. We address these issues in a study of the quantitative genetic variation in juvenile leaf length and shape in *E. globulus* ssp. *globulus*. The scale and pattern of genetic variation in juvenile leaf morphology within this taxon are examined and estimates of the heritability of these traits and their correlations with early growth rate and precocity of vegetative phase change are obtained.

Eucalyptus globulus ssp. *globulus* is the focus of our genetic research because of its worldwide importance in plantation pulpwood production. It is markedly heteroblastic with elliptic-ovate, glaucous, opposite, sessile and stem clasping juvenile leaves (Fig. 1) and lanceolate, falcate, green, alternate and petiolate adult leaves (Boland *et al.* 1985). The natural distribution of ssp. *globulus* can be broadly divided into (1) a taxonomically homogenous core zone in eastern Tasmania where it has a more or less continuous distribution in coastal areas, (2) a taxonomically more diverse zone of intergradation with mainland subspecies (King Island, the Furneaux Group and southern Victoria) and (3) isolated, apparently relict populations in western Tasmania (Fig. 2; Kirkpatrick 1975; Jordan *et al.* 1993). The present study is based on a trial established from a large population collection of ssp. *globulus* and extends studies of the pattern of variation of adult morphology in wild populations (Jordan *et al.* 1993) and growth (Jordan *et al.* in press; Potts and Jordan submitted) in this taxon.

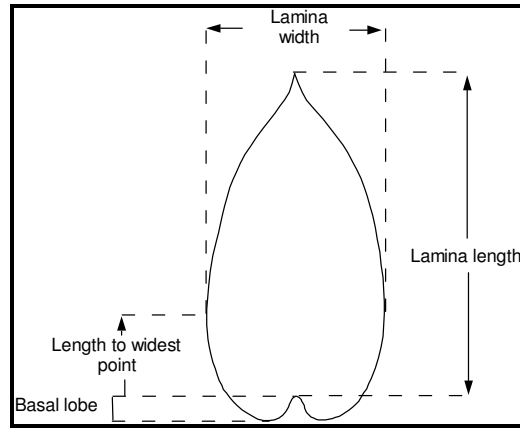


Figure 1. A typical *E. globulus ssp globulus* juvenile leaf showing the traits measured.

Material and Methods

Seed Provenances and Field Trial

Open-pollinated seed lots were collected from throughout the geographical range of *ssp globulus* and populations intergrading with mainland subspecies (Fig. 2; Table 1). Full locality details are given by Jordan *et al.* (1993, in press) and Potts and Jordan (submitted). The trees in the collections were grouped into 52 localities (within approximately 10 km diameter), and regions (within about 100-150 km) (Table 1). Only the 45 localities with four or more families (Table 1) were used in this analysis. In some localities more than one population was sampled. These were classed as sites (within about 1-3 km radius) within localities.

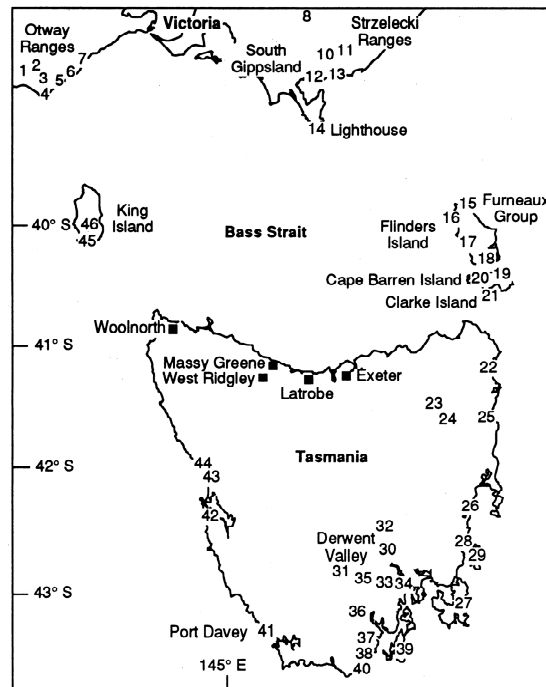


Figure 2. Map of localities and trial site. The symbols are from Table 1.

Table 1. Regions and localities with codes and number of families used here.

The codes follow Jordan *et al.* (in press), so one number code (9) is missing, since this locality had too few trees.

Region	Locality	Code	Number of families
Mainland Australia			
Otway Ranges	South West Lavers Hill	1	6
	Otway State Forest	2	43
	Cannan Spur	3	21
	Parker Spur	4	56
	Cape Patton	5	18
	Jamieson Creek	6	7
	Lorne	7	16
Gippsland	Jeeralang North	8	50
	Madalya Road	10	8
	Bowden Road	11	5
	Port Franklin	12	4
	Hedley	13	12
	Lighthouse, Wilsons Promontory	14	16
Bass Strait Islands			
Furneaux Group	North Flinders Island	15	12
	Central North Flinders Island	16	13
	Central Flinders Island	17	23
	South Flinders Island	18	12
	North Cape Barren Island	19	10
	West Cape Barren Island	20	34
	Clarke Island	21	6
King Island	South King Island	45	9
	Central King Island	46	23
Tasmania			
East Coast North	St Helens	22	11
	Pepper Hill	23	10
	Royal George	24	9
	German Town	25	5
East Coast Central	Mayfield	26	5
	Tarrana	27	5
	Triabunna	28	9
	North Maria Island	29	7
Derwent Valley	Mt Dromedary	30	4
	Ellendale	31	4
	Moogara	32	26
	Collinsvale	33	5
	Hobart South	34	10
East Coast South,	Jericho	35	10
	Blue Gum Hill	36	4
	South Geeveston	37	7
	Dover	38	5
	South Bruny Island	39	7
	Recherche Bay	40	4
West Coast	Port Davey	41	6
	Macquarie Harbour	42	8
	Little Henty River	43	11
	Badgers Creek	44	10

Seedlings grown from the seed lots were planted by North Forest Products at Massy Greene near Burnie in northern Tasmania in July 1989 (Fig. 2). This trial followed a resolvable incomplete block design (Patterson and Williams 1976). Five replicates each contained all 600 families (including four fillers). Each replicate contained 24 incomplete blocks of 25 families in two-tree contiguous plots. Full trial details are presented by Jordan *et al.* (in press) and Potts and Jordan (submitted).

Morphological and Growth Traits

Trees were sampled at 18 months of age (January 1991) from four of the five replicates (giving a maximum of 8 replicates per family). A typical juvenile leaf was taken from the main stem of each tree at approximately 1 m height. For the few trees (mainly from the Lighthouse population) which had changed, or were changing to adult foliage at 1m, typical juvenile leaves were collected lower down. The length of the lamina, the width, the length to the widest point and the length of the basal lobing were digitised from photocopies of each fresh leaf, as indicated in Fig. 1.

Total height, diameter at breast height and height to vegetative phase change were measured on the same trees in July 1991. Phase change was taken as the height of the first petiolate leaf on the main stem (usually several decimetres above the first alternate leaves). The height of phase change of trees which had not changed to adult foliage in 1991 were measured in 1992 and 1993. By 1993, 98 % of trees had undergone vegetative phase change. For the purposes of this study, the height to phase change of the remainder was set at the height in 1993 plus 0.5 m. This occurred in only 49 (1.3 %) of the observations.

Statistical Methods

The following traits were calculated from the leaf measurements, LL (transformed lamina length), LW (transformed relative leaf width), LWP (transformed relative length to the widest point) and BASE (transformed relative length of the basal lobe), as detailed in Table 2. The transformations eliminated the correlation between family means and variances, and optimised the normality assumptions of discriminant and regression analyses.

Table 2. Variables used in this analysis.

Variable name	Symbol	Value
Transformed lamina length	LL	$\ln(\text{lamina length})$
Transformed relative width	LW	$\ln(\text{leaf width/lamina length})$
Transformed relative length to widest point	LWP	$\sqrt{(\text{length to widest point/lamina length})}$
Transformed relative base length	BASE	$\sqrt{(\text{length of basal lobe/lamina length})}$
Transformed height to phase change	HTPC	$\ln(\text{height to phase change})$
Transformed height	HT	$(\text{height at two years})^2$
Transformed volume	VOL	$\sqrt{(1/3 \text{ area} \times \text{height})}$

Variance Components and Family Means

Variance components attributable to each level of the geographic and experimental hierarchies were estimated for each leaf trait (LL, LW, LWP, BASE). The model of analysis included plots within family, family within locality, locality within region, region and the design effects of incomplete blocks and replicates. Due to computing limitations, the analysis was undertaken in several stages. Within plot and between plot variance components and generalised least squares (GLS) means for families were estimated for each trait from individual tree data using a model in which the effects of families and replicates within the trial were treated as fixed, and the effects of incomplete blocks within replicates and between

plots within families were random. Family within localities variance components were estimated from analyses based on plot means.

Variance components for levels of the geographical hierarchy were estimated using GLS family means as the units. Except where stated, these analyses excluded the highly atypical Lighthouse locality (14 in Fig. 2), and pooled the small West Coast regions. Locality within region and region components were estimated using only localities containing two or more families and regions containing two or more localities. The site within locality component was estimated separately using only sites with two or more families, and localities with two or more sites. This stratum was excluded from the full analysis since its inclusion caused gross design imbalance (Table 3). Components, their standard errors and GLS means of fixed effects were estimated using the REML and VCOMPONENTS directives of Genstat V (Genstat 1991) or the REML option of the VARCOMP procedure of SAS (SAS 1990). The significance of components was tested by the likelihood ratio test (McCullagh and Nelder 1989, pp 476-478).

Table 3. Hierarchical partitioning of variance of leaf size and shape parameters for *Eucalyptus globulus* ssp. *globulus*. Estimates of variance components (s^2), their standard errors and the percentages of the total variation attributable to each level are given for each component. Analyses were undertaken using all localities indicated in the text but excluding three abnormal localities (Port Davey, Mt. Dromedary and Lighthouse). Individual narrow-sense heritability estimates and their 95% confidence intervals, and ranges in locality GLS means (backtransformed) are also shown.

Component	----- LL -----		----- LW -----		----- LWP -----		---- BASE ----	
	s^2	(%)	s^2	(%)	s^2	(%)	s^2	(%)
	($\times 10^4$)		($\times 10^4$)		($\times 10^4$)		($\times 10^4$)	
Region	37.5 \pm 21	14.3	7.7 \pm 4.6	5.1	0.33 \pm 0.25	9.2	0.24 \pm 0.15	2.0
Locality within region	11.5 \pm 4.3	4.3	2.2 \pm 1.4	1.5	0.05 \pm 0.13	0.1	0.03 \pm 0.06	0.3
Family within locality	29.0 \pm 3.6	11.1	23.0 \pm 2.4	15.4	1.76 \pm 0.47	4.9	1.31 \pm 0.18	11.0
Between plots	0.3 \pm 0.4	0.1	0.0	0.0	0.00	0.0	0.03 \pm 0.02	0.3
Error (within plots)	183.9 \pm 4.3	70.2	112.2 \pm 2.3	74.9	31.73 \pm 0.72	88.9	9.42 \pm 0.02	79.2
Site within locality	0.3 \pm 1.9	0.1	2.2 \pm 1.9	1.5	0.19 \pm 0.28	0.5	0.10 \pm 0.13	0.8
Heritability	0.37		0.34		0.19		0.29	
(confidence interval)	(0.27 - 0.49)		(0.21 - 0.46)		(0.10 - 0.29)		(0.29 - 0.40)	
Locality range	66 - 89		34 - 44		11 - 17		6 - 9	

Heritabilities

Heritabilities were estimated for each trait with a derivative-free restricted maximum likelihood method (DFREML) as implemented by Meyer (1991) following an individual tree model in the following manner (see Yu *et al.* 1993; Borralho and Wilson 1994; Potts and Jordan submitted). Additive (s_a^2) and error (s_e^2) variances were estimated by optimising the model -

$$y = \mathbf{X}_1 b + \mathbf{X}_2 L + \mathbf{Z} a + e$$

using the simplex algorithm. y is the vector of individual observations, a is a vector of unobservable additive genetic effects, b is a vector of fixed effects for incomplete blocks and L is a vector of fixed locality effects, \mathbf{X}_1 , \mathbf{X}_2 and \mathbf{Z} are design matrices linking effects to observations and e is a vector of residuals. Locality generalised least squares (GLS) means were also estimated with this model. Individual narrow-sense heritabilities (h^2) were calculated as -

$$h^2 = s_a^2 / (s_a^2 + s_e^2).$$

These estimates used 1869 individuals from the 12 localities not classified as remnant by Potts and Jordan (in press). 95% confidence limits were derived from a quadratic approximation to the likelihood function and are asymmetrical. Heritabilities of specific pairs of traits were compared with the likelihood ratio test (McCullagh and Nelder 1989, pp 476-478). The male parent was coded as unknown so individuals within a family were treated as having a half-sib relationship (i.e. genetic correlation $r = 0.25$), however the coefficient of relatedness was adjusted to 0.4 to reflect the mixed mating system in *Eucalyptus* (e.g. Griffin and Cotterill 1988; Volker *et al.* 1990; Potts and Jordan submitted).

Classification of Localities

Localities with at least four families were compared with discriminant analysis (Phillips *et al.* 1973) of family GLS means. Scores on the discriminant functions of all families and population means of these scores were calculated. The relative importance of the major variables in differentiating populations were summarised by vectors in the direction of variation in the discriminant space and proportional in length to the univariate F values between populations. Localities were classified using average linkage clustering (Sneath and Sokal 1973) of their mean scores. The distances between localities are thus Mahalanobis' distances (Phillips *et al.* 1973). Specific contrasts between localities were undertaken with multivariate analyses of variance (MANOVA) using type III sum of squares using family GLS means as the units (see Jordan *et al.* in press).

Correlations Between Traits

Components of covariation for pairs of traits for both the family within locality (intrapopulation) and locality (interpopulation) effects were calculated as follows (see Kelly 1993). Plot means were calculated after traits had been standardised to a grand mean of zero and standard deviation of 1. Variance components for each trait (s_a^2 and s_b^2), and the sum of the two traits of interest (s_{a+b}^2), were estimated using the REML option of the VARCOMP procedure of SAS (SAS 1990). The statistical model included incomplete blocks treated as a fixed effect and locality and family within locality effects as random effects. The covariance component (s_{ab}) was estimated from the equation -

$$s_{a+b}^2 = s_a^2 + s_b^2 + 2(s_{ab}).$$

Genetic and locality correlations were estimated as

$$r = s_{ab} / \sqrt{s_a^2 s_b^2}.$$

Approximate standard errors for intrapopulation genetic correlations were calculated following Falconer (1986, p. 285) using heritability and standard error estimates derived from DFREML. Genetic correlations were considered significant when they differed from zero by more than twice the standard error. Pearson's correlation coefficients were calculated amongst locality GLS means (interpopulation phenotypic correlations) and amongst residuals after the removal of the locality effect (intrapopulation phenotypic correlations).

Correlations with Environmental Parameters

Relationships between locality GLS means of leaf form traits with climatic traits were investigated with univariate, quadratic and multiple regression analyses weighted by the

inverse of the variance of each GLS mean. The weighting compensates for differences in sample sizes and variabilities (PROC REG in SAS 1990). Canonical redundancy analysis was undertaken to determine the proportion of the variation in the set of leaf traits which could be explained by climatic variables using PROC CANCORR in SAS (1990). A wide range of climatic parameters (see Jordan *et al.* 1993; plus average daily radiation adjusted for cloudiness) were estimated using the program EPLUS (Tasmanian Forestry Commission, unpublished) from climatic surfaces estimated by ESOCIM (H. A. Nix, J. P. Busby, M. F. Hutchinson and J. P. McMahon unpublished; Hutchinson 1991), and transformed to optimise the assumptions of the analyses. The extreme Lighthouse, Mt Dromedary and Port Davey localities were excluded.

Results

Partitioning of Variation in Leaf Length and Shape

Most of the total phenotypic variation in juvenile leaf traits occurred within families (70.3 - 88.9% between plot + error; Table 3). However, significant differences occurred between families within localities ($P < 0.001$) and between regions (LL and LW $P < 0.001$; LWP $P < 0.01$; BASE $P < 0.05$) for all traits, and between localities within regions for transformed lamina length (LL $P < 0.001$) and relative leaf width (LW $P < 0.05$). Differences between families within localities, between localities within regions and between regions accounted for between 4.9 to 15.4%, 0.3 to 4.4% and 2.0 to 14.3% of the variation, respectively (Table 3). Variation between sites within localities (i.e. between populations within 10 km of each other) was less than 3% of the total variation and only significant ($P < 0.05$) for transformed lamina length. The variance components were similar when the geographic races of Jordan *et al.* (in press) were used instead of regions.

Geographic Distribution of Leaf Form and Classification of Localities

Discriminant analysis indicated that 40% of the differentiation between localities occurred along the first discriminant function, which was dominated by transformed lamina length (Fig. 3). The second discriminant function (33%) mainly differentiates four atypical localities, Lighthouse, Wilsons' Promontory, (14), Port Davey (41), Mt Dromedary (30) and Port Franklin (12), from this continuum on the basis of aspects of leaf shape. There was some separation of the Victorian and Bass Strait Island geographic regions along the second discriminant function (Fig. 3). The Furneaux Group (15-21) and Western Tasmanian localities except Port Davey (42-44) were differentiated from the Gippsland localities on this axis, with the Otway localities intermediate. The Gippsland localities had wider leaves, smaller basal lobes, and greater length to the widest point than the Furneaux Group localities, with the Otway Ranges intermediate for these traits (Fig.5).

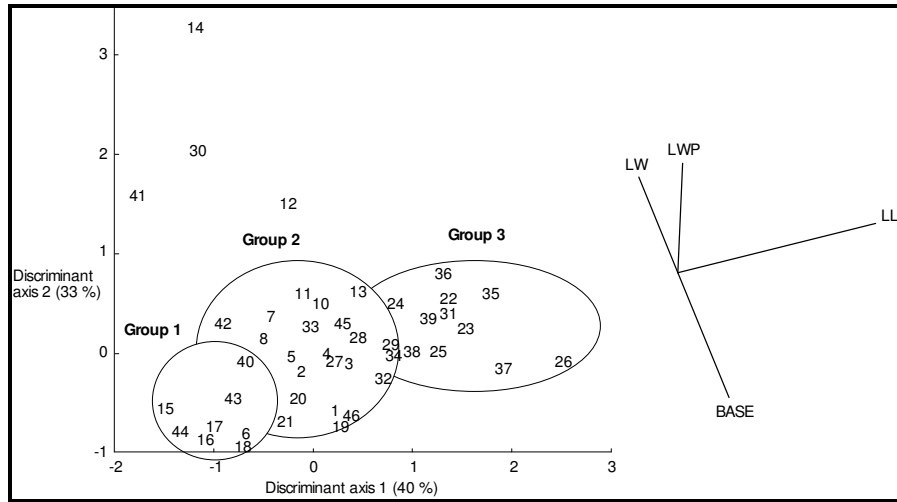


Fig. 3. Locality mean scores on the first two axes produced by the discriminant analysis of family mean scores for leaf form traits (LL, LW, LWP and BASE). The symbols are according to Table 1. The vectors on the right hand side indicate the magnitude and direction of variation of the leaf traits (see text).

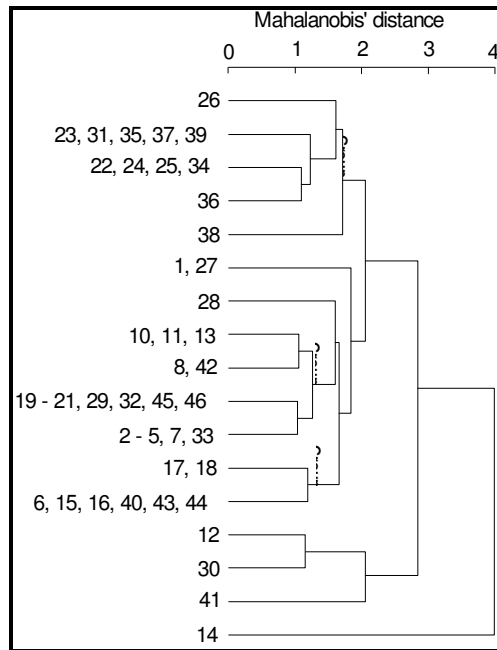


Fig. 4. Average linkage cluster analysis locality mean scores on all axes produced by the discriminant analysis of family mean scores for leaf form traits (LL, LW, LWP and BASE). The symbols are according to Table 1.

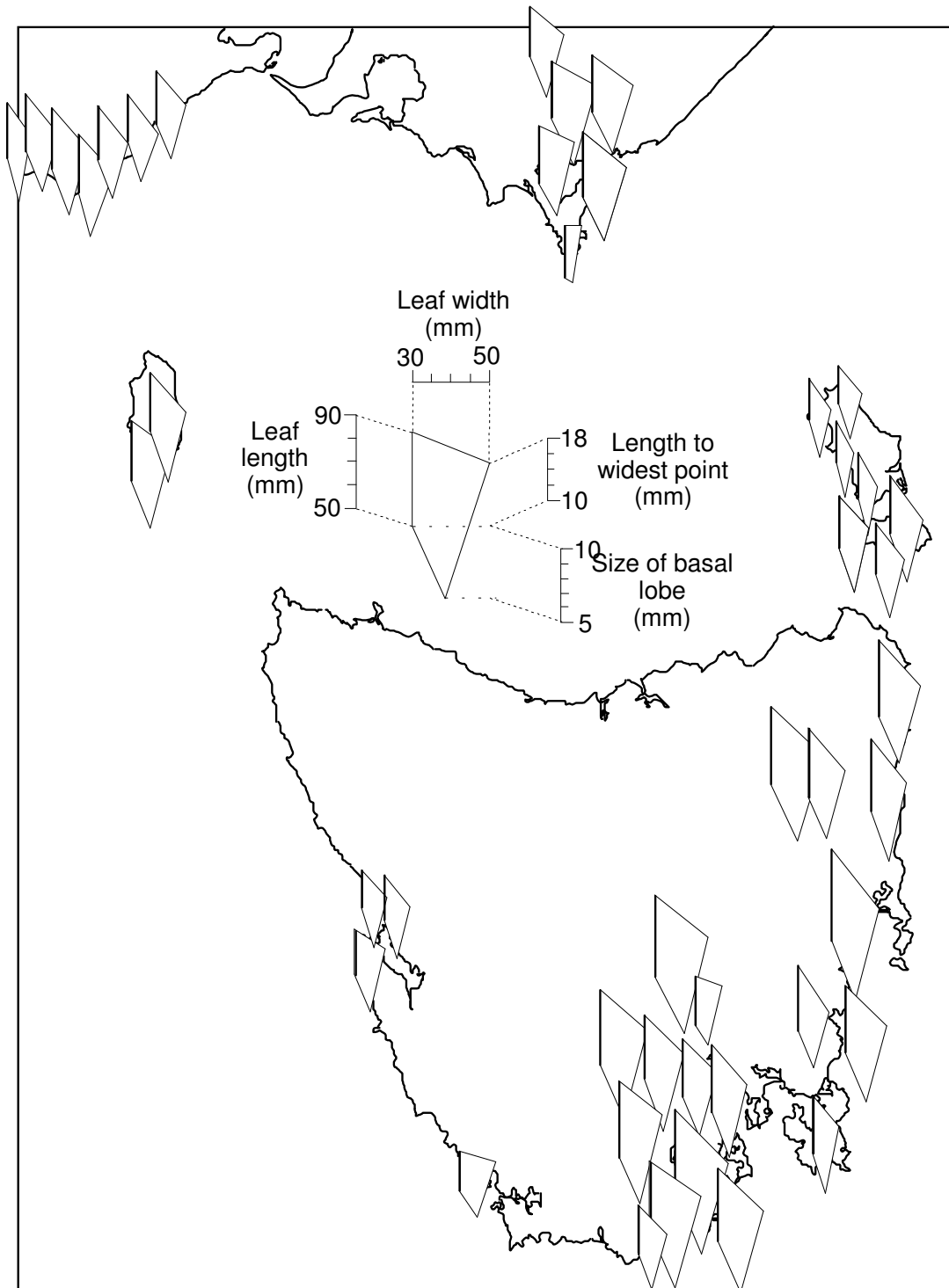


Fig. 5. Locality mean leaf forms. The leaf dimensions are calculated from back transformed values of LL, LW, LWP and BASE.

The four outlying localities in Fig. 3 are also outliers in the cluster analysis (Fig. 4) and the first three are outliers for traits other than leaf form. The Lighthouse population is of mallee habit. Although its capsules are morphologically consistent with the taxonomic core of *ssp globulus* (Jordan *et al.* 1993), its slow growth and precocious vegetative phase change and flowering are unique in *ssp globulus* (Hasan 1993; Potts and Jordan 1993). It has the narrowest juvenile leaves, the smallest basal lobes and greatest relative length to the widest point of any of the localities (Fig. 5). This shape is consistent with deviation towards the adult form and may be related to the precocious change to adult foliage. The Port Davey (41) and Mt Dromedary (30) localities had smaller juvenile leaves than most other localities with relatively small basal lobes, and high relative length to the widest point (Fig. 5). The juvenile leaves of *E. globulus* are normally glaucous, but these two localities produced by far the highest proportions of seedlings with green and/or subglaucous leaves in the collection (Potts and Jordan 1993) suggesting that hybridisation may have caused the deviant leaf morphology.

The cluster analysis (Fig. 4) primarily reflected the continuum in leaf length (Fig. 3) with three main clusters of small- (cluster 1), intermediate- (2) and large- (3) leaf localities. Most of the eastern and southern Tasmanian localities formed a cluster (cluster 3) with high scores on the first discriminant axis (Fig. 3) and long leaves (Fig. 5). The smallest leaved localities (cluster 1) were mainly from the west coast of Tasmania (42-44) and Flinders Island (15-18). A marked morphological cline extends from the Furneaux Group to northern Tasmania with the leaf size of localities from Cape Barren (19, 20) and Clarke Islands (21) intermediate (Figs 3 and 5). This cline does not extend into Victoria (Figs 3 & 5). The most southerly population (Recherche Bay; 40) also has small leaves like the western Tasmanian populations (Figs 3, 4 and 5) and was clearly distinct from nearby populations (37-39) in specific MANOVA contrasts. Most localities from the Otway Ranges (1-7, except 6), Gippsland (8-14) and King Island (45, 46) were intermediate in leaf length and cluster together (cluster 2).

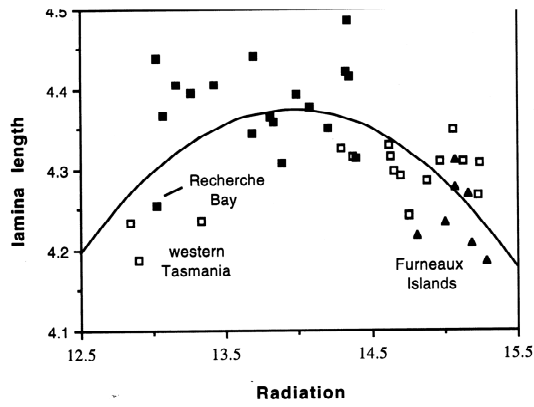
While most differentiation in juvenile leaf morphology could be attributed to differences between geographical regions (Table 3), there were significant differences between localities within the Otway Ranges (MANOVA; $P < 0.01$), the Furneaux Group ($P < 0.001$), East Coast Central ($P < 0.05$) and Derwent Valley ($P < 0.001$) regions, when the three outliers (14, 30 and 41) were removed.

Genetic Parameters and Correlations with Growth and Phase Change

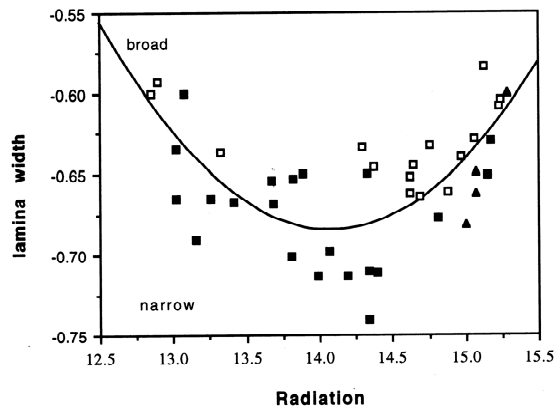
The estimates of individual narrow-sense heritabilities for transformed lamina length (0.37), transformed relative leaf width (0.34) and transformed relative length of the basal lobe (0.29) were significantly ($P < 0.001$) greater than that of relative length to the widest point (0.19), and all were significantly greater than zero (Table 3). This suggests that between 19% to 37% of the variation in leaf traits within localities was due to additive genetic variation.

Tables 4 and 5 show phenotypic and genetic correlations between leaf traits and growth and transformed height to phase change, within and between localities. The phenotypic and genetic correlations were mostly similar both within and between localities. Most intrapopulation phenotypic correlations were significantly greater than zero, although they were mostly weak ($|r| < 0.3$). Significant interpopulation phenotypic correlations occurred between transformed lamina length and both transformed relative lamina width ($r = -0.5$; $P < 0.01$) and transformed height to phase change ($r = 0.64$; $P < 0.001$), transformed relative length of the basal lobe and both transformed relative width of the lamina ($r = 0.52$; $P < 0.01$) and the transformed relative length to the widest point ($r = -0.39$; $P < 0.01$), and transformed lamina width with both transformed two year height ($r = 0.39$; $P < 0.01$) and transformed volume ($r = 0.30$; $P < 0.05$).

(a)



(b)



(c)

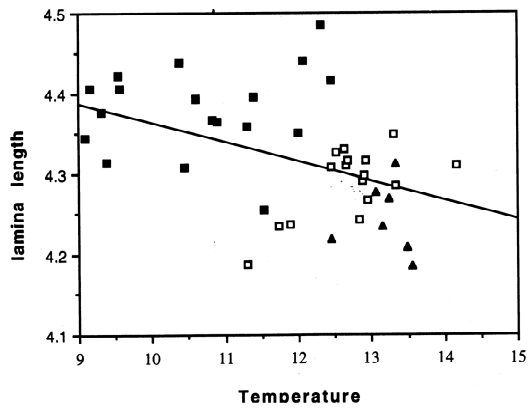


Fig. 6. Plots of locality means for (a) transformed lamina length (quadratic $r^2 = 38\%$) and (b) relative lamina width (quadratic $r^2 = 49\%$) against average daily radiation ($\text{kJ m}^{-2} \text{day}^{-1}$) and (c) transformed lamina length (linear $r^2 = 20\%$) against mean annual temperature ($^{\circ}\text{C}$) for each locality. Closed squares are eastern Tasmanian populations, open squares are mainland, King Island and western Tasmanian populations and triangles are Furneaux Group populations.

Table 4. Phenotypic correlations between leaf traits, growth traits at two years, and height to phase change within and amongst localities.

Pearson's correlations based on residuals (n=2245) and locality means (n=42) are shown. The significances are indicated (n.s. = not significant, * P<0.05, ** P<0.01 *** P<0.001).

Trait	----- Within localities -----				----- Between localities -----			
	LL ¹	LW	LWP	BASE	LL	LW	LWP	BASE
LW¹	-0.32 ***				-0.50 ***			
LWP	-0.10 ***	-0.07 **			0.13 ns	0.17 ns		
BASE	-0.20 ***	0.51 ***	-0.32 ***		-0.47 ***	0.52 ***	-0.39 ***	
HT	0.25 ***	0.05 *	-0.23 ***	0.18 ***	-0.09 ns	0.39 **	-0.00 ns	0.06 ns
VOL	0.27 ***	0.06 **	-0.24 ***	0.22 ***	-0.01 ns	0.30 *	-0.17 ns	0.07 ns
HTPC	0.12 ***	0.14 ***	-0.15 ***	0.20 ***	0.64 ***	-0.25 ns	-0.21 ns	-0.08 ns

¹ LL is transformed lamina length); LW is transformed relative leaf width; LWP is transformed relative length to widest point; BASE is transformed relative length of basal lobe; HT is transformed height; VOL is transformed volume and HTPC is transformed height to phase change.

Table 5. Genetic (additive) and locality correlations between leaf traits, growth traits at two years, and height to phase change.

Data from Port Davey, Lighthouse and Mt Dromedary localities have been excluded.

Trait	----- Genetic correlations \pm se -----				----- Locality correlations -----			
	LL ¹	LW	LWP	BASE	LL	LW	LWP	BASE
LW¹	-0.37 \pm 0.10				-0.62			
LWP	-0.21 \pm 0.13	-0.10 \pm 0.14			0.19	0.98		
BASE	-0.31 \pm 0.11	0.81 \pm 0.04	-0.45 \pm 0.12		-0.78	0.55	0.47	
HT	0.15 \pm 0.10	0.05 \pm 0.11	-0.49 \pm 0.10	0.21 \pm 0.11	-0.20	0.50	0.22	-0.08
VOL	0.09 \pm 0.11	0.16 \pm 0.12	-0.39 \pm 0.13	0.29 \pm 0.12	-0.09	0.25	-0.16	-0.34
HTPC	0.10 \pm 0.12	0.22 \pm 0.12	-0.24 \pm 0.14	0.27 \pm 0.12	0.77	-0.41	-0.11	-0.57

¹ LL is transformed lamina length); LW is transformed relative leaf width; LWP is transformed relative length to widest point; BASE is transformed relative length of basal lobe; HT is transformed height; VOL is transformed volume and HTPC is transformed height to phase change.

There were strong, positive intrapopulation ($r=0.81$) and interpopulation ($r=0.55$) genetic correlations between transformed relative width and transformed relative length of the basal lobe. Within localities, increased basal lobing is genetically associated with a shift of the widest point closer to the base of the leaf ($r = -0.45$), but the reverse applies among localities ($r=0.47$) (Table 5). The moderate negative intrapopulation genetic and phenotypic correlations between transformed lamina length and the other leaf traits indicates that additive genetic increases in lamina length are associated with a change in shape. Negative genetic and phenotypic correlations with lamina length are similarly evident at the locality level (LL and LW -0.62 and -0.50 ; LL and BASE -0.78 and -0.47 respectively; Table 5). Of particular significance is the contrast between the marked positive interpopulation genetic correlation of the relative position of the widest point with transformed relative lamina width ($r=0.98$) and with transformed relative length of the basal lobe ($r=0.47$) compared to negative intrapopulation genetic correlations (Table 5). Thus genetic differences between localities result in relatively wider leaves being associated with large basal lobes and the widest point

further from the base, whereas only the association of wider leaves with large basal lobes is expected from the genetic correlations within localities.

Within localities, additive genetic variation in growth rate is effectively independent of additive genetic variation in lamina length and relative lamina width ($0 < r < 0.16$) (Table 5). At the locality level, genetic variation in early growth rate and transformed lamina length are still relatively independent ($0 > r > -0.20$). However, genetically based locality effects for fast height growth are positively associated with those for relatively broad leaves ($r = 0.50$), consistent with the significant ($P < 0.05$) phenotypic correlation (Table 4). The moderately strong negative genetic correlation between LWP and early growth rate ($r = -0.49$ with HT and $r = -0.39$ with VOL) within populations is noteworthy. 15% to 24% of the additive genetic variation within locations in two year volume and height respectively can be explained by additive genetic variation in the position of the widest point of the lamina. Genetically faster growing trees at the test site tend to have juvenile leaves with the widest point closer to the base as well as slightly greater basal lobing ($r = 0.20$ and 0.29). Such trends are not evident at the locality level (Tables 4 and 5).

Within localities, the phenotypic ($-0.15 < r < 0.20$; Table 4) and genetic ($-0.24 < r < 0.27$; Table 5) correlations of juvenile leaf traits with transformed height of transition to phase change (HTPC) are relatively weak (Table 5). However, there are marked contrasts between correlations attributable to genetic differences within localities as opposed to between localities for three of the four leaf traits. There is a strong positive interpopulation phenotypic ($r = 0.64$) and genetic ($r = 0.77$) correlation between transformed height to phase change and transformed lamina length, yet within localities these traits are effectively genetically independent ($r = 0.10$). Similarly, the additive genetic correlations of both transformed relative lamina width ($r = 0.22$) and transformed basal length of the basal lobe ($r = 0.27$) with transformed height to phase change are only weakly positive, yet there are relatively strong negative correlations amongst localities ($r = -0.41$ and -0.57 respectively). Genetically based differences between localities for delayed vegetative phase change are thus associated with longer and relatively narrower leaves with reduced basal lobing. This basically reflects an increase in leaf length with little change in other dimensions (Fig. 5).

The Relationships of Leaf Morphology to Climatic Parameters.

Canonical redundancy analysis indicated that 86.6% of the standardised variance in the four leaf traits could be explained by 13 synthetic climatic variables and their squares. Two of the leaf shape traits (transformed relative length to the widest point and transformed relative length of the basal lobes) were poorly described by climatic parameters, either singly or in combination. However, lamina length and relative leaf width showed strong associations with some climatic parameters (Fig. 6). The quadratic regression of radiation (adjusted for rainfall to account for cloud cover) alone explained 38% and 49% of the variation in transformed lamina length and transformed relative width respectively (Fig. 6). The cline from the large-leaved core Tasmanian *ssp globulus* populations, through the intermediate mainland intergrade populations to the small-leaved populations on Flinders Island parallels an increase in radiation (Fig. 6a). The curvilinear response is mainly due to small leaves occurring in western and far southern Tasmanian populations (40, 42-44) which experience low radiation levels (Fig. 6a). Narrower juvenile leaves tend to occur in localities experiencing intermediate levels of radiation (c. $14 \text{ kJ m}^{-2} \text{ day}^{-1}$; Fig. 6b).

Discussion

Variation in Leaf Traits

Most of the phenotypic variation in *E. globulus* ssp *globulus* in the four leaf traits assessed occurs within open-pollinated families (70-89%), consistent with that reported for growth traits (77-80%) in the same trial (Potts and Jordan submitted). However, there are significant levels of additive genetic variation in leaf length and shape within populations of ssp *globulus*. The heritability estimates of transformed lamina length (LL) and two of the three leaf shape traits (LW and BASE) are also comparable with estimates reported for conic volume and height at two ($h^2 = 0.30-0.39$) and four years ($h^2 = 0.26-0.29$). The strongest discriminator between populations in juvenile leaf morphology was transformed lamina length (Fig. 3). The differentiation between populations in transformed lamina length (localities(regions) + regions = 18.6% of the total variation) was clearly greater than in leaf shape traits (2.3-9.3%; Table 3) and growth traits (5.5-9.9%; Potts and Jordan in press), although all of these were statistically significant ($P < 0.05$). Most of the differentiation in transformed lamina length between localities was due to differences between regions (14% of the total; Table 3).

The cline in lamina length in the Furneaux Group (Fig. 6) is of particular interest. Marked differentiation in the length of seedling leaves (Kirkpatrick 1975, p. 25) and a cline in capsule morphology from intergrade to core ssp *globulus* phenotypes have been reported to occur over limited distances on Flinders Island (Jordan *et al.* 1993; Kirkpatrick 1975). However, steps in the cline in juvenile leaf and capsule morphology occur in different parts of the Furneaux Group. The main change in capsule morphology occurs between northern and central Flinders Island (between localities 16 and 17) and is part of a cline in capsule morphology between intergrade populations on the mainland and core populations in Tasmania. In contrast, the main differentiation in juvenile leaf morphology occurs between Cape Barren (19, 20) and Flinders Island (15-18). Flinders Island is the northern end of a cline in lamina length extending from northern Tasmania and is quite distinct from the Victorian intergrade populations in juvenile leaf morphology (Figs 3 & 5).

Variation in facets of leaf morphology are associated with variation in climate between locations. There is a trend for lamina length to decrease in sites experiencing higher temperatures (e.g. Fig. 6c), and, with the exception of the west coast populations (40, 42-44), greater radiation (Fig. 6a). Givnish (1979) proposes that the overall resource cost to the plant per unit photosynthetic area is less for large leaves than small leaves. However, the adaptive value of small leaves in water-stressed, waterlogged or nutrient-poor environments has been long recognised (e.g. Givnish 1979). Thus variation in water stress arising through high temperatures and high radiation may be a major cause of the genetic differences in juvenile lamina length between localities of ssp *globulus*. In particular, the major cline from northern Tasmania through the Furneaux group is associated with increasing radiation and increasing temperatures (Fig. 6). A curvilinear response of lamina length to soil moisture has been hypothesised, with lamina length initially increasing as water-stress decreases, but then decreasing in saturated soils due to anoxia and leaching of the soils (Givnish 1979). The small leaved localities on the west coast of Tasmania (42-44) and Recherche Bay (40), which cause the curvilinear response observed here are certainly in areas of low radiation, and high rainfall and soil moisture. The west coast localities are, however, also on bedrock of inherently low soil fertility, which is also expected to favour decreased lamina length (Givnish 1979).

Genetic correlations

Strong intrapopulation and interpopulation genetic correlations of the leaf traits with other leaf traits and traits such as growth rate and vegetative phase change (Tables 4 and 5)

may have influenced the evolution of population differences in leaf morphology. Such correlations are common amongst morphological traits (e.g. Sokal 1978; Zeng 1988; Merila and Gustafsson 1993) and, coupled with the levels of additive genetic variation in populations, these correlations are key factors in the morphological response to selection and drift (Lande and Arnold 1983; Clarke 1987; Zeng 1988; Houle 1991). In the present case, transformed lamina length is negatively genetically correlated within populations with all of the shape traits. Thus selection to decrease lamina length, for example, would be expected to also increase any of the leaf shape traits (Falconer 1986). These correlations are most likely pleiotropic through either genetic coding for multiple traits or developmental constraints.

The marked discrepancies between intrapopulation and interpopulation phenotypic and genetic correlations for several character combinations (Tables 4 and 5) are of considerable interest. Zeng (1988) predicted that a high intrapopulation correlation should be always associated with a high interpopulation correlation of the same sign, but low intrapopulation correlations could be paired with a relatively wide range of interpopulation correlations. This response was also predicted by Sokal (1978), and conforms with several empirical studies (Zeng 1988). In the present study, strong genetic correlations amongst leaf traits within populations tend to be amplified at the population level (Table 5) which is consistent with other studies (see Thorpe 1976 and Zeng 1988). However, this does not appear to be the case for the genetic correlations between the leaf and other traits. Some traits which are relatively strongly genetically correlated within populations, such as the growth traits (HT and VOL) with transformed relative position of the widest point (LWP) and transformed relative basal lobing (BASE) (Table 5), are poorly correlated or correlated in a different direction across populations. Similarly, traits which are effectively genetically independent within populations did (e.g. LL and HTPC) or did not (e.g. LL and VOL) co-vary between populations. Evolution may be constrained in the short term by intrapopulation genetic correlations (e.g. Clarke 1987; Zeng 1988), but Zeng (1988) considers that in the long-term correlated responses depend more on correlated selection. Certainly, the present data suggests that some interpopulation genetic correlations appear to have developed despite currently adverse intrapopulation genetic correlations (e.g. HTPC and BASE; HT and LWP; Table 5).

Interpopulation covariation may arise through common genetic control (pleiotropy or linkage) or from independently controlled characters responding similarly to geographic variation in selection pressures (Thorpe 1976). In the present case, it may be possible to determine which cases applies when marked discrepancies between intra- and interpopulation correlations exist. One of the most important discrepancies is between lamina length and vegetative phase change. These traits are effectively genetically independent within populations, yet genetic differences between populations are strongly positively correlated (Table 5). The simplest explanation for this relationship is that small juvenile leaves and early transition to adult foliage are favoured by one environmental factor (e.g. high radiation levels; Fig. 6). However, the response could also be due to the characters responding to different selective forces which have the same patterns of geographic variation (Thorpe 1976). The adaptive significance of the differences between adult and juvenile leaves of *E. globulus* is unclear, but there is evidence that adult leaves of *Eucalyptus globulus* may be better adapted to water stress (Chalmers 1992), so that early phase change may be favoured in water stressed environments. Thus, we propose that water stress may favour both smaller juvenile leaves and early phase change (i.e. correlated selection). Within populations early phase change is also weakly genetically associated with narrower leaves with less basal lobing (i.e. a leaf shape closer to the adult form). However, amongst populations the trend is reversed (Table 4), perhaps partly because these shape traits are negatively correlated with leaf length.

Growth rate and juvenile lamina length are genetically independent both at the intra- and interpopulation level. However, growth rate does seem to be genetically and selectively correlated with facets of leaf shape. Within populations, growth rate at the test site is

positively genetically correlated with relative basal lobing and negatively with the relative length to the widest point (Table 5). In contrast, genetic differences between localities in growth rate (particularly height) are positively correlated with genetic differences in lamina width but relatively independent of differences in basal lobing and position of the widest point. While the intrapopulation genetic correlations amongst the leaf traits are complex, one explanation for this response is that in localities where selective regimes favour genes for fast growth at the test site, the selective environment has also favoured wider leaves with less basal lobing and the widest point further from the base. The lack of intrapopulation correlation between growth and lamina width would argue against a direct causal effect.

General Discussion

The present study highlights the discrepancies which may occur between intra- and interpopulation genetic correlations. The correlations of genetic differences between populations for several pairs of traits suggests either correlated selection or pleiotropy. Intrapopulation genetic correlations between traits complicates the interpretation of multivariate patterns of variation. However, where traits are genetically independent within populations but genetic differences between populations are strongly associated, then there is strong evidence for parallel independent selection. Such correlated selection appears to have occurred between lamina length and vegetative phase change, and between growth rate and leaf shape. In contrast, there appears to be no marked genetic association between lamina length and growth rate. Introgression could explain such correlated patterns of variation, but this is unlikely to be a major factor as significant genetic correlations would also be expected within hybridising populations, at least in early generations (Grant 1979; Biscoe *et al.* 1994). The complex pattern of variation within the *E. globulus* complex, particularly on the Furneaux Group of islands, may result from historical migration patterns (see Jordan *et al.* 1993) superimposed upon adaptive clines in response to extant environments. Research into the phylogeny of these populations based on chloroplast and nuclear DNA, and other morphological traits presently being undertaken may resolve this issue. However, it is important to establish the adaptive basis of the patterns of phenotypic variation in wild populations and the association of quantitative traits with fitness. The families used in the present study have been planted widely in Australia and overseas and there is the opportunity to examine genetic correlations between morphological traits and fitness surrogates (e.g. growth rate, survival, flower production) across a wide range of environments.

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