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Variation in the *Eucalyptus globulus* Complex Revisited

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Abstract

Patterns of variation in the *Eucalyptus globulus* Labill. complex are reassessed by combining capsule measurements from an earlier study with recent collections, mainly of subspecies *globulus*. Four groups of populations are apparent and can be ascribed to the four subspecies *maidenii*, *pseudoglobulus*, *bicostata* and *globulus*. Intergrade populations between the latter three subspecies are widespread and mainly occur in the Otway Ranges and west Gippsland. There is a continuum in capsule morphology between the three-fruited subspecies, *pseudoglobulus* and *bicostata*. Subspecies *globulus* intergrades with these three-fruited intermediates. Three-fruited intergrade populations occurring north and south of the range of core *pseudoglobulus* can be differentiated and probably represent intergrades between *pseudoglobulus* and *bicostata* and between *pseudoglobulus* and *globulus* respectively. Reports of *bicostata* in the Furneaux Group and southern Victoria are thus probably erroneous and result from convergence in capsule morphology. The previously described taxon *E. stjohnii* (R. T. Bak.) R. T. Bak. is part of the continuum between subspecies *pseudoglobulus* and *bicostata*, but closer to *pseudoglobulus*. Populations phenotypically intermediate between and significantly different from *globulus* and the three-fruited intergrades are highly variable and occur in western Tasmania, on the northern end of Flinders Island, in the Otway Ranges and in west Gippsland. An isolated population on Rodondo Island is highly variable and has closest affinities to *pseudoglobulus* despite being within the geographical range of core *globulus*. The population from King Island is intermediate between the Otway phenotype and core *globulus*. The climatic regimes of the subspecies are markedly different and most three-fruited and *globulus* intergrade populations have closer climatic affinities to *pseudoglobulus* and *globulus* respectively. Hypotheses relating to the origin of the pattern of variation in *E. globulus* are discussed.

Introduction

The *Eucalyptus globulus* complex (informal subgenus *Symphyomyrtus*, series Viminales, Pryor and Johnson 1971) is currently divided into four subspecies, *E. globulus* Labill. subspecies *globulus*, *E. globulus* subspecies *bicostata* (Maiden, Blakely, & J. Simm.) Kirkpatr., *E. globulus* subspecies *pseudoglobulus* (Naudin ex Maiden) Kirkpatr. and *E. globulus* subspecies *maidenii* (F. Muell.) Kirkpatr. (Kirkpatrick 1975*a*, 1975*b*, 1975*c*; Chippendale 1988) hereafter referred to only by their subspecific epithets (e.g. *bicostata*). Each of the subspecies has previously been given specific status. A fifth taxon, *E. stjohnii* (R. T. Bak.), R. T. Bak. was previously considered to encompass populations now included

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Table 1. Site details of populations from the 1987 and 1988 CSIRO collections of *E. globulus* used in this analysis

The symbols are those used for the rest of this analysis. The number of trees in the population for which capsule measurements were available are indicated. Populations for which samples were also available from Kirkpatrick's (1975*a*, 1975*c*) collection are indicated (*). The broad geographic region is indicated with 'V' for Victoria or 'T' for Tasmania, otherwise the site is from the Bass Strait Islands

Population	Geographical region	Symbol	Latitude (°S)	Longitude (°E)	Altitude (m)	Sample size
Badgers Creek	West Coast Central (T)	g2	41° 59′	145° 18	10–120	25
Bonnet Point	East Coast South Central (T)	G35	42° 57′	147° 28′	30	3
Blue Gum Hill	East Coast South (T)	G7	43° 05′	146° 42′	150–480	4
Cannon Spur *	Otway Ranges (V)	g6	38° 46′	143° 32′	200	5
Cape Patton	Otway Ranges (V)	g9	38° 40′	143° 48′	130–300	16
Central East Flinders Island *	Furneaux Group	G41	39° 59′	148° 11′	60	1
Central Flinders Island *	Furneaux Group	G31	40° 02′	148° 01′	140–240	8
Central King Island	King Island	G36	40° 00′	144° 00′	80	14
Central North Flinders Island	Furneaux Group	g4	39° 55′	147° 57′	40	5
Clarke Island	Furneaux Group	G27	40° 32′	148° 08′	40	6
Collinsvale	East Coast South Central (T)	G9	42° 50′	147° 12′	135–460	14
Dover	East Coast South (T)	G2	43° 16′	146° 59′	190	6
Ellendale	East Coast South Central (T)	G10	42° 38′	146° 42′	460	5
German Town	East Coast North (T)	G22	41° 34′	148° 12′	400	5
Hedley	South Gippsland (V)	G34	38° 38′	146° 30′	150–180	12
Hobart South *	East Coast South Central (T)	G12	42° 56′	147° 17′	70–350	4
Jamieson Creek	Otway Ranges (V)	g8	38° 36′	143° 54′	200	7
Jeeralang North	South Gippsland (V)	g16	38° 19′	146° 33′	220–460	33
Lighthouse, Wilsons Promontory	South Gippsland (V)	G33	39° 08′	146° 25′	60	9
Lonnavale	East Coast South (T)	G4	42° 58′	146° 44′	216	4
Lorne *	Otway Ranges (V)	g10	38° 31′	143° 57′	210	16
Macquarie Harbour	West Coast Central (T)	g1	42° 20′	145° 20′	20	8

Population	Geographical region	Symbol	Latitude (°S)	Longitude (°E)	Altitude (m)	Sample size
Moogara	East Coast South Central (T)	G11	42° 47′	146° 55′	430–450	24
Mt Dromedary	East Coast South Central (T)	G15	42° 43′	147° 09′	300	4
North Cape Barren Island	Furneaux Group	G29	40° 22′	148° 13′	20–60	10
North Flinders Island	Furneaux Group	g5	39° 46′	147° 52′	20–60	5
North Geeveston	East Coast South (T)	G37	43° 08′	146° 57′	200	3
North Maria Island	East Coast Central (T)	G18	42° 37′	148° 05′	10–480	6
Otway State Forest	Otway Ranges (V)	g7	38° 45′	143° 26′	100–240	22
Parker Spur *	Otway Ranges (V)	g11	38° 49′	143° 34′	130–160	13
Pepper Hill	East Coast North (T)	G25	41° 38′	147° 51′	540	10
Port Davey	West Coast South (T)	g3	43° 16′	145° 55′	20	6
Recherche	East Coast South (T)	G1	43° 30′	146° 53′	40	5
Royal George	East Coast North (T)	G24	41° 52′	147° 59′	560	9
South Arm	East Coast South Central (T)	G13	43° 01′	147° 28′	25	2
South Bruny Island	East Coast South (T)	G6	43° 22′	147° 16′	10–200	7
South Flinders Island *	Furneaux Group	G30	40° 16′	148° 10′	5–20	2
South Geeveston	East Coast South (T)	G5	43° 12′	146° 54′	250	7
South King Island	King Island	G32	40° 00′	144° 00′	20–100	2
St Helens *	East Coast North (T)	G26	41° 16′	148° 18′	120	13
Tarrana *	East Coast South Central (T)	G14	43° 04′	147° 50′	20	5
Tinderbox	East Coast South Central (T)	G8	43° 02′	147° 20′	80	40
West Cape Barren Island	Furneaux Group	G28	40° 24′	148° 00′	20–220	33
Total numbers						438

in *bicostata* and to have taxonomic priority (Hall *et al.* 1970; Pryor and Johnson 1971), but has been included in *pseudoglobulus* by Kirkpatrick (1975*a*, 1975*b*) and Chippendale (1988). Core populations of the four recognised taxa are geographically separated (Figs 1, 4) and are mainly differentiated on reproductive traits (e.g. Kirkpatrick 1975*a*; Chippendale 1988). Subspecies *maidenii* has up to seven fruits per umbel and the smallest capsules in the complex and *globulus* has solitary flowers and the largest capsules. Subspecies *bicostata* and *pseudoglobulus* are three fruited with *pseudoglobulus* having smaller capsules, fewer ribs on the capsules and longer pedicels than *bicostata*.

Morphological studies have shown that geographically extensive zones of clinal intergradation occur between the core areas (Kirkpatrick 1971, 1975*a*, 1975*c*). However, the taxonomic affinities of populations outside of the core areas are often difficult to determine and important outlying populations on the west coast of Tasmania and King Island were not included in Kirkpatrick's study. The resolution of these taxonomic problems and a more detailed assessment of the variation patterns in this complex are now required because of increasing interest in *E. globulus* by tree breeders (Volker and Raymond 1989; Borralho *et al.* 1992). *E. globulus* is grown worldwide for pulpwood production in temperate zones, particularly subspecies *globulus* because of its generally superior growth and pulp properties (e.g. Volker and Orme 1988; Volker and Raymond 1989; Borralho *et al.* 1992).

The largest ever population collection of subspecies *globulus* and intergrade populations was recently undertaken by the CSIRO from over 42 localities (Gardiner and Crawford 1987, 1988). Genetic material from this collection will constitute base breeding populations in many countries and has been established on numerous sites throughout Australia. In the present study the phenetic affinities of samples in this collection are examined within the framework of Kirkpatrick's (1975*a*, 1975*c*) initial data and the patterns of variation in the complex are re-assessed. This study forms a foundation for detailed studies of the pattern and scale of genetic diversity currently being undertaken.

Methods

Collection Sites

The sites sampled in Kirkpatrick's (1975*a*, 1975*b*, 1975*c*) initial study and those sampled more recently by the CSIRO's Tree Seed Centre (Gardiner and Crawford 1987, 1988) and from additional collections near Hobart are shown in Fig. 1. Trees sampled during these surveys were geographically classified into populations (within approximately 10 km). Details of the new collections are given in Table 1. The CSIRO collection gave a more detailed coverage of subspecies *globulus* (see Table 1 and Fig. 1). Measurements from 96 populations (954 individuals) were available from Kirkpatrick's initial study, encompassing a large proportion of the geographical range of the four subspecies of *E. globulus*. Full details of these populations are given in Kirkpatrick (1973) and the symbols used for these sites in the present study are given in the Appendix. Measurements were made from photographs of specimens of a key population, Rodondo Island (p1), which was sampled, but not measured, by Kirkpatrick (1973). Where the same population was collected by both Kirkpatrick and the CSIRO, samples were pooled.

Morphological and Climatic Characters

The morphometric characters indicated in Table 2 and figured in Kirkpatrick (1975*c*) were measured from capsule samples and herbarium specimens from the CSIRO collection where available. Dimensions were recorded from up to five umbels per tree and the number of capsules/umbel were recorded from up to 45 umbels per tree. The climatic parameters listed in Table 3 were derived using the program EPLUS (Tasmanian Forestry Commission, unpublished) from climatic surfaces estimated by ESOCLIM (H. A. Nix, J. P. Busby, M. F. Hutchinson and J. P. McMahon unpublished).

Statistical Analyses

The mean of each morphological character was calculated for each tree and used for all subsequent analyses. The morphological variables were transformed (Table 2) to optimise within

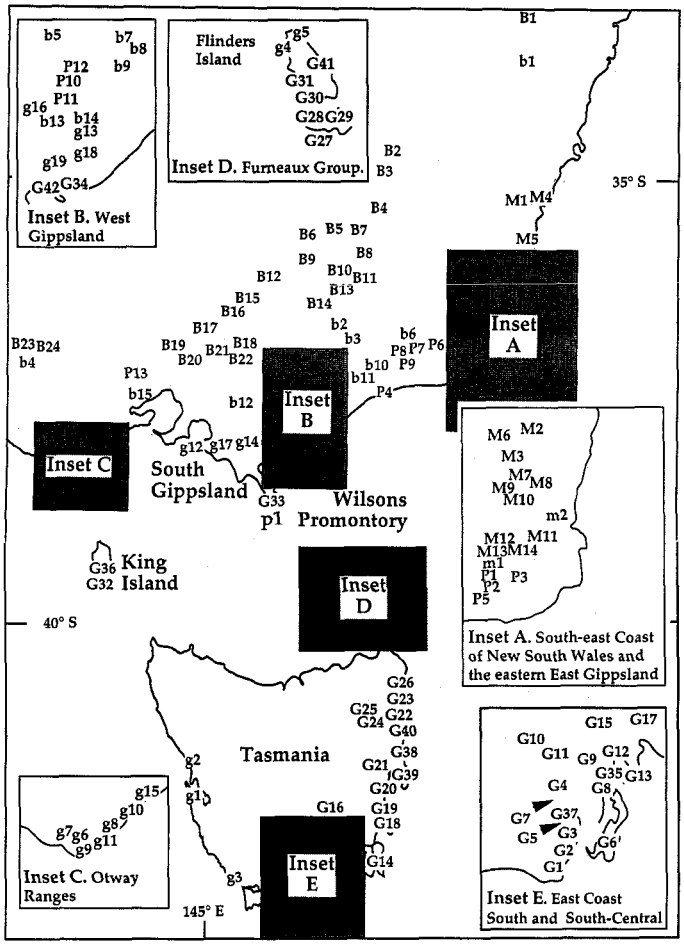

Fig. 1. The location of populations of the *Eucalyptus globulus* complex sampled in Tasmania and south-eastern Australia. Population symbols are detailed in Table 1 or Appendix.

population normality and to remove the association between the population means and variances at the univariate level. To minimise any differences arising from sampling methods and times between collections, the measurements in the CSIRO collection of each variable were adjusted after transformation by adding the differences between the grand means of populations common to both collections. Before this adjustment, significant differences ($P < 0{\cdot}05$) occurred between the two collection for only two of the variables (rib and pedu) each of which contributed little to the final classification. For each variable, comparisons were made with one-way analysis of variance between populations within the whole data set, between populations within the CSIRO collection, between the core populations of the subspecies *bicostata*, *globulus* and *pseudoglobulus* (as defined below) and between populations in Kirkpatrick's original collection. In order to reassess Kirkpatrick's (1975*a*) subspecific classification, multivariate comparisons were undertaken using discriminant analysis to differentiate all populations (from both Kirkpatrick's and CSIRO's data sets) which contained more than five trees. Discriminant analysis determines independent vectors weighted according to the variability between populations relative to the variability within populations and in so doing creates a multi-dimensional space which best discriminates between populations (see Sokal and Rohlf 1981 pp. 683–685). An analysis of the combined data set was

Table 2. Morphological traits measured on wild populations

Transformations, transformed variable names and F values from analyses of variance of the transformed variables between all populations ('All') and between subsamples of the cores of *globulus*, *bicostata* and *pseudoglobulus* used to classify the trees in the CSIRO collection ('subspp.') are shown. 95 % ranges of each morphological variable for each subpecies core are calculated as back transformed values of the transformed means ± 2 standard deviations. Characters excluded from the multivariate analysis of all sites are indicated (*)

Character	Transformation	Variable name	F value		95% range of subspecies cores			
			subsp. $df = (2, 297)$	all $(df = (121, 1268)$				
Number of capsules per umbel	ln	n_caps	2749·0	223·5	5·0–7·7	2·4–3·4	2·9–3·1	1–1·4
Capsule diameter (mm)	ln	cap_dia	1710·9	138·6	6·6–11·6	8·7–13·7	13·7–20·2	19·3–28·3
Capsule height (mm)	square root	cap_ht	932·1	61·5	6·6–10·9	8·3–12·6	12·1–18·4	14·0–21·9
Number of ribs per capsule	none	rib	873·9	50·7	0–1·6	0–2·2	1·4–3·2	3·1–7·2
Peduncle length (mm)	ln	pedu	112·0	26·7	9·3–20·7	2·0–11·7	1·1–7·1	0·6–5·6
Proportion of pedicellate capsules	square root	pediprop	120·2	20·1	0·28–1	0·1–1	0·01–0·02	0·16–0·46
Disc height (mm)	square root	disc_ht	105·8	28·7	0–0·1	0·0–0·7	0·1–3·5	0–2·6
Height of the calycine ring (mm)*	none	lncal	125·4	—	0–0·2	0·1–0·7	0·3–1·8	0·1–1·3
Leaf length (mm)*	ln	ll	101·1	—	173–425	192–400	216–533	181–356
Leaf width (mm)*	ln	lw	39·4	—	23–48	17–49	22–57	22–48

Table 3. Estimated climatic parameters for core populations of the subspecies of *E. globulus*

The range of each parameter is listed under 'climatic envelopes' for each subspecies core with the bold letters indicating subspecies groupings based on Tukey's Method (SAS 1988) (e.g. for twmq *maidenii* and *bicostata* have **a**'s and *globulus* **b**, this means that the mean of *bicostata* and *maidenii* are not significantly different for this variable, but are larger than and differ significantly from *globulus*). *F* values from analyses of variance between subspecies cores of each variable are listed. All *F* values are highly significant ($P < 0{\cdot}0001$), except rann and rdrym which are significant ($P < 0{\cdot}05$)

Character	Transformation	variable name	climatic envelopes *maidenii*	*pseudoglobulus*	*bicostata*	*globulus*	*F* value between subspecies *df* =(3, 88)
annual temperature range (°C)	inverse	tspan	21·2–26·6 **a,b**	20·2–25·2 **b**	21·8–29·0 **a**	15·0–20·0 **c**	148·4
mean temperature of the warmest quarter (°C)	square	twmq	16·0–20·3 **a**	17·6–19·5 **a**	16·3–20·7 **a**	12·9–18·5 **b**	39·9
coefficient of variation of rainfall	ln	rcvar	11·2–21·9 **b**	10·5–13·9 **c**	14·1–35·8 **a**	10·9–38·1 **b**	32·7
mean precipitation of the warmest quarter (mm)	square root	rwmq	200–310 **a**	120–246 **b**	110–274 **b,c**	125–250 **c**	17·6
mean precipitation of the coldest quarter (mm)	ln	rclq	171–270 **b**	111–319 **b**	214–511 **a**	138–387 **b**	13·8
mean temperature of the coldest quarter (°C)	none	tclq	4·5–10·5 **b**	6·6–9·6 **b**	4·1–7·6 **a**	5·2–10·3 **b**	11·5
mean annual temperature (°C)	none	tann	10·4–15·5 **a,b**	12·1–14·3 **a**	10·2–14·0 **b,c**	8·9–14·1 **c**	10·0
mean precipitation of the dryest month (mm)	none	rdrym	43–63 **a,b**	33–75 **a**	29–72 **a,b**	38–73 **b**	3·3
mean temperature of the wettest quarter (°C)[A]	square root	twetq	7·3–19·2 **a**	7·2–15·7 **b**	4·1–17·5 **d**	5·4–13·7 **c**	28·1
mean temperature of the dryest quarter (°C)[A]	cube	tdryq	5·5–17·1 **c**	9·6–18·8 **b**	6·3–20·7 **a**	9·5–18·3 **b**	22·8
mean precipitation of the wettest month (mm)[A]	ln	rwetm	81–117 **b**	51–120 **b**	73–181 **a**	59–147 **b**	9·1
mean annual precipitation (mm)[A]	loge	rann	757–1053 **a,b**	490–1114 **b**	632–1430 **a**	572–1303 **b**	4·7

[A] Excluded by the stepwise discriminant procedure.

performed on all the variables indicated in Table 2 except the height of the calycine ring (lncal), leaf length (ll) and leaf width (lw). These last three variables were considered by Kirkpatrick (1973) to differentiate subspecies*bicostata* and *pseudoglobulus* but Kirkpatrick (1975*a*, 1975*c*) demonstrated that these subspecies were adequately differentiated on reproductive traits alone. The significance of the variation between populations in our samples for these three variables was low and it was not possible to measure these variables on the CSIRO populations consistently with Kirkpatrick's measurements. For comparison, Kirkpatrick's original data set alone was similarly analysed using all the variables. Scores on the discriminant functions of all individuals were derived and then population means of these scores were calculated. The relative importance of the major variables in differentiating populations in the discriminant space were summarised by vectors indicating the direction of variation in the discriminant space. The lengths of the vectors were proportional to the univariate F values between populations, and the directions were determined by the standardised canonical coefficients. Populations were classified using average linkage clustering (Sneath and Sokal 1973) of these mean scores. The distances between populations are thus Mahalanobis' distances (Phillips *et al.* 1973). The variation within each population within the two-dimensional space discriminating subspecies was calculated as the variance of the euclidean distances of individuals from the group centroid.

Climatic parameters were transformed as for morphological variables. Multivariate comparisons between subspecies cores were undertaken using discriminant analysis after four largely redundant variables (see Table 3) were excluded using stepwise discriminant analysis. Scores on the resulting discriminant functions were then calculated for all populations. Analyses of variance, stepwise and canonical discriminant analyses and cluster analyses were calculated using the GLM, STEPDISC, DISCRIM and CLUSTER procedures, respectively, in the statistical package SAS (SAS 1988).

The capsule morphology of each individual tree within the CSIRO data set was compared with the capsule phenotype of core populations of the subspecies *globulus*, *pseudoglobulus* and *bicostata*, in order to assess the nature of the variability within these populations, and the geographical distribution of trees with capsules matching the phenotypes of these subspecies. A data set was constructed containing ten individuals from each of ten populations from each of the cores as defined from the classification of the total data set (group G in Fig. 3 for *globulus*, group B for *bicostata* and group P for *pseudoglobulus*). Only populations from Kirkpatrick's (1975 *a*, 1975*c*) data set were chosen and preference was given to populations also in Kirkpatrick's subspecies cores (see the Appendix). Following Potts and Reid (1983), the generalised distance (Mahalanobis's distance) of each individual tree in the CSIRO collection from the centroid of the cores of each subspecies and its significance were calculated according to equations 5·1 and 5·2*b* in Orlóci (1978). Separate variance–covariance matrices were used for comparisons with each subspecies to account for differences in variance/covariance structure. Only the three most discriminatory capsule morphology variables (capht, capdia and ribs) were used in these analyses.

Results

Variation Throughout the Range of the Complex

Results of the univariate analyses of variance are given for each morphological variable in Table 2. All variables showed highly significant ($P < 0{\cdot}0001$) differences between populations and subspecies. The variables ncaps, capdia, capht and rib, in that order, showed the greatest discrimination between populations and subspecies, except that populations within the CSIRO collection were most differentiated by capdia and rib.

The population mean scores along the two major discriminant functions derived from the analysis of the combined data set are shown in Fig. 2*a*. Ninety-two percent of the variation amongst populations is summarised by this ordination, with 85 % explained by the first discriminant function. Increasing scores along the first discriminant function are primarily determined by decreasing numbers of capsules per umbel (ncaps) and increasing capsule diameter (capdia). Most populations fall into three groups along this axis with populations classified as subspecies *maidenii* (seven small capsules per umbel) and *globulus* (large single capsules) by Kirkpatrick (1975*a*) at either extreme, with predominantly three-fruited populations, including Kirkpatrick's core populations of subspecies *bicostata* and *pseudoglobulus*, intermediate. These three fruited populations show a well defined

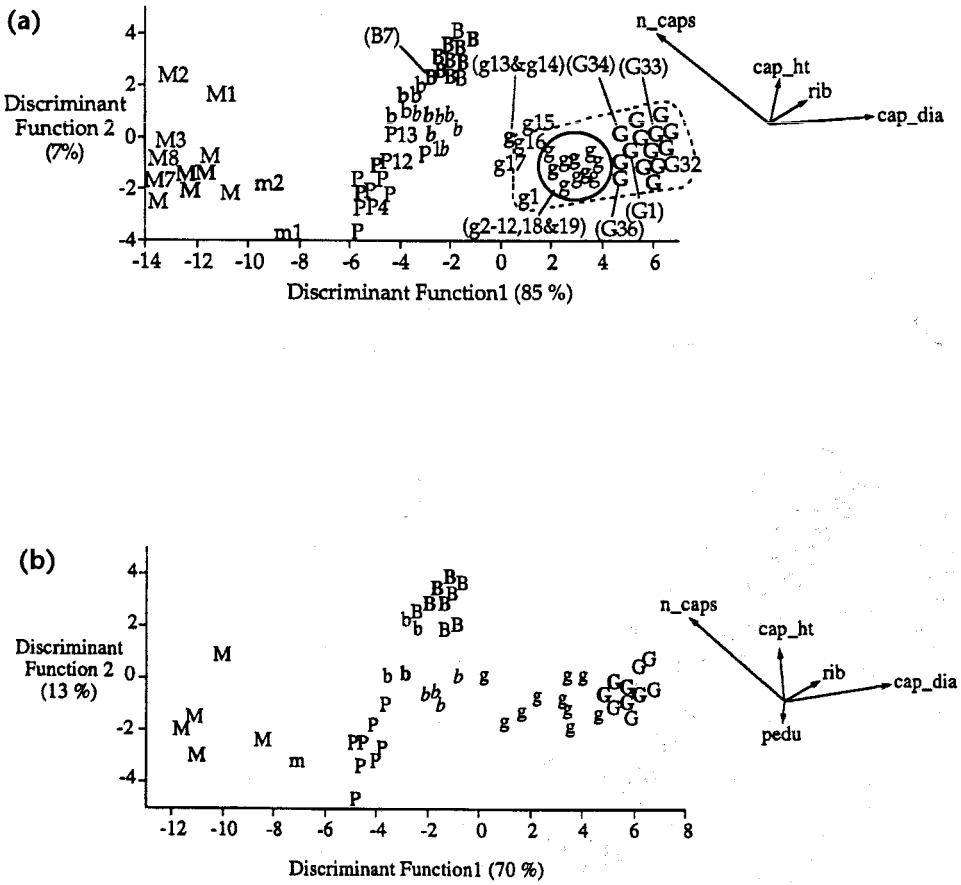

Fig. 2. Plots of population mean scores on discriminant functions derived from analysis of the *Eucalyptus globulus* complex using (*a*) the seven capsule variables indicated in Table 2 and the whole data set, and (*b*) all variables on only Kirkpatrick's (1975*a*, 1975*c*) data set. The proportion of multivariate variation between populations explained by each axis is shown. The labels correspond to the groups shown in Fig. 3 (**bold** type indicates multiple occurrence of the same symbol), except some key populations which are identified by the population symbols from Fig. 1. The vectors on the right hand side indicate the significance of the major variables in differentiating populations and their direction of variation in the discriminant space. The dashed line indicates the range of variation encompassed by the CSIRO collection and three-fruited intergrade populations (group *b*) south of the range of *pseudoglobulus* are labelled with italics.

morphological series in a direction slightly oblique to the second discriminant function with a tight group of subspecies *bicostata* populations at one extreme and a group including the type locality of *E. pseudoglobulus* near the other extreme.

The population mean scores along the two major discriminant functions derived from the analysis of Kirkpatrick's (1975*a*, 1975*c*) data set using all the variables in Table 1 are shown in Fig. 2*b*. The trends apparent in this analysis are essentially the same as in Fig. 2*a*, except that the *globulus* intergrade populations (group g) merge with populations almost exactly intermediate between *pseudoglobulus* and *bicostata*.

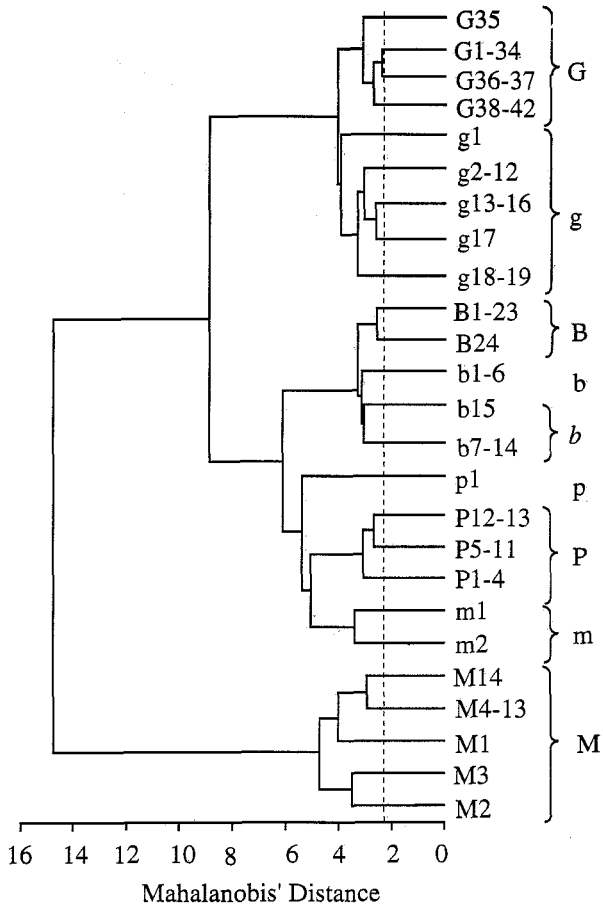

Fig. 3. Dendrogram derived from average linkage clustering of populations of the *E. globulus* complex. The analysis was based on Mahalanobis's distances derived from discriminant analysis of the seven capsule variables and the dashed line indicates the level at which the dendrogram has been truncated. Symbols are the population labels from Fig. 1. Groups of populations discussed in the text are defined by the large brackets.

The multivariate variation in capsule morphology in the complex is summarised in the dendrogram in Fig. 3. Four major groupings are apparent, corresponding to the four subspecies. These groups are robust, since similar groupings to these were generated by both the analysis of Kirkpatrick's data set alone using more variables and analysis of the

combined data set excluding the primary discriminating variable (ncaps). Four key groups of populations which more or less retain their integrity in all analyses are indicated by capital letters in Fig. 3. These four key groups contain virtually all the core populations of the subspecies designated by Kirkpatrick (1975*a*), and were used to define the cores of these subspecies. Each of the cores include populations from or near the type localities (see Kirkpatrick 1975*a*; *globulus* G1, *bicostata* B7, *pseudoglobulus* P4 and *maidenii* M7 & M8). Group G is subspecies *globulus*, group M is subspecies *maidenii*, group B is subspecies *bicostata* and group P is subspecies *pseudoglobulus*. These core groupings form the extremities of variation along the two discriminant functions in Fig. 2. The other populations are intermediate between the subspecies cores in this two dimensional discriminant space and have been designated the lower case letter of the subspecies to which they have closest affinity in capsule morphology (g2–19 referred to as *globulus* intergrades, b1–15 referred to as three-fruited intergrades, m1–2 referred to as *maidenii /pseudoglobulus* intergrades). Several populations are differentiated in capsule morphology from the core and intermediate populations and are considered to be outliers. These are three northern populations with affinities to *maidenii* (M1–3), the Macquarie Harbour population (g1) which has affinities to *globulus*, and the Rodondo Island population (p1) which has closest affinities to *pseudoglobulus* (Fig. 3).

The core of subspecies *globulus* (G1–42 in Fig. 1) occurs through eastern Tasmania, King Island, most of the Furneaux Group and on and near Wilson's Promontory. The core of subspecies *pseudoglobulus* (P1–13) occurs in East Gippsland with some populations in West Gippsland. The core of subspecies *bicostata* (B1–24) occurs in a broad band inland of the Great Dividing Range in Victoria and the southern half of New South Wales. The core of subspecies *maidenii* (M4–14) occurs near the south east coast of New South Wales.

Subspecies *maidenii* appears to be the most distinct of the subspecies in the dendrogram in Fig. 3, but *maidenii /pseudoglobulus* intergrades (m1 and m2) occur near the only area where these two subspecies are contiguous (e.g. Cann River region; Fig. 1). However, these intermediate populations are fewer (Fig. 2) and more localised (Fig. 1) than three-fruited intergrades (group b) or *globulus* intergrades (group g). There is continuous variation from subspecies *pseudoglobulus* through populations P12 and P13, and then the group b populations to *bicostata* (Fig. 2). The group b populations consistently cluster with core *bicostata* (group B) on capsule morphology (Figs 2*a* and 3), but using all of Kirkpatrick's variables are more intermediate between *pseudoglobulus* and *bicostata* (Fig. 2*b*). The Lerderderg Gorge population (P13), which is the type locality of *E. stjohnii*, groups with core *pseudoglobulus* populations (Fig. 3), although it is clearly part of the continuum between *pseudoglobulus* and *bicostata* (Fig. 2). A large group of populations (group g) with smaller capsules, fewer ribs (more *bicostata*-like), and a higher frequency of multi-fruited umbels per tree than *globulus*, classify with *globulus* but clearly intergrade with the three-fruited intergrades (Fig. 2). The population from central King Island (G36) classifies with core *globulus* (Fig. 3) but is intermediate between the Otway intermediates and core *globulus* (Fig. 2). The two individuals from southern King Island (G32) were more typical of core *globulus* (Fig. 2). The *globulus* intermediates (group g) occur in several geographically isolated regions. All populations sampled in the Otway Ranges (g6–11, g15), two populations on northern Flinders Island (g4–5), all populations on the west coast of Tasmania (g1–3) and many in west Gippsland (g12–14, g16–19) are of this phenotype.

The three-fruited intergrade populations (group b) are also geographically intermediate between *pseudoglobulus* and either *bicostata* or the *globulus* intergrades (group g) (Fig. 1), except for one northern population (b1). There are geographically contiguous clines in Gippsland radiating from *pseudoglobulus*, through three-fruited intergrades (group b), northward into *bicostata* and southward into *globulus* (inset B; Fig. 1). Populations of the intermediate group b which are geographically intermediate between *pseudoglobulus* and

the *globulus* intergrades (group g) also deviated phenotypically in the direction of *globulus* (designated group *b* in Fig. 2*a*). The difference between the group b populations to the north (b1–5) and south (b6–15) of the *pseudoglobulus* range is relatively subtle when compared to the variation between groups. However, these intermediates can be differentiated on capsule morphology (MANOVA, $P < 0{\cdot}001$), with only a 12% overlap of individual trees occurring along the discriminant function differentiating these two groups. The southern group b trees have larger capsules (capdia, capht), longer peduncles (pedu), lower discs (discht) and a greater proportion of pedicellate capsules (pediprop) than the northern trees, although capdia and pediprop are the main discriminators. The phenotypically outlying population on Rodondo Island (p1) is an enigma as it is disjunct from the distribution of *pseudoglobulus* (to which it has closest affinities) and falls within the geographic range of *globulus* and intergrades (group g).

Figure 4 shows the variation within populations in the two-dimensional space discriminating subspecies (Fig. 2*a*) in relation to the geographical position of populations. Centres of high

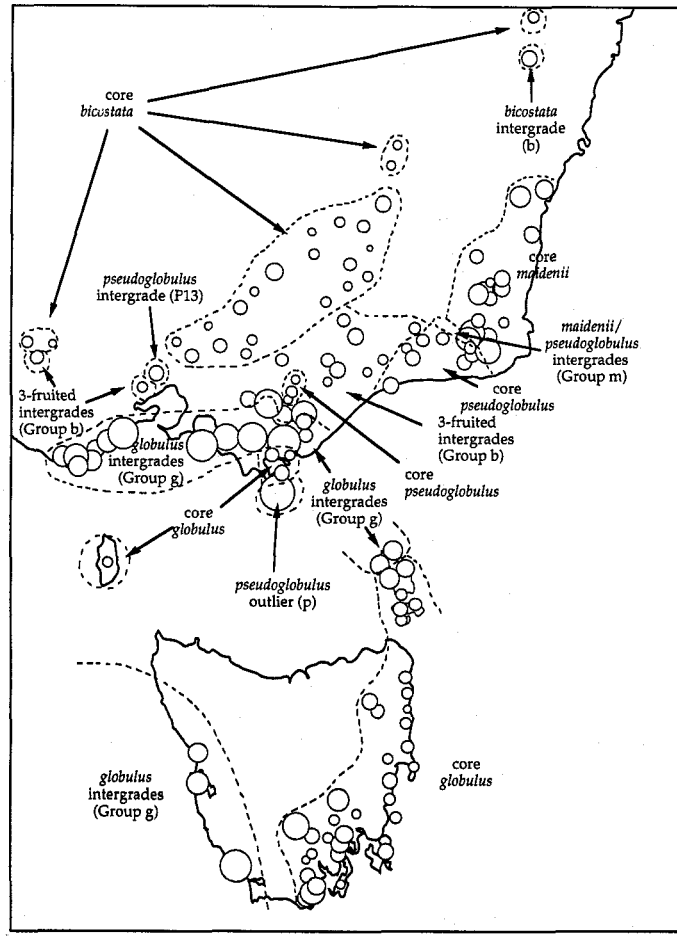

Fig. 4. The within population variability in capsule morphology in relation to geographical location. The area of the circle is proportional to the variation within each population. The dotted lines indicate the limits of core populations of the four subspecies.

within population variability occur in regions of intergradation between subspecies in south and west Gippsland, the Otway Ranges and in the zone of intergradation between *maidenii* and *pseudoglobulus* in the Cann River area. Variation near the zone of intergradation on north Flinders Island is higher than elsewhere in the Furneaux Group. Intermediate and variable populations in these regions of intergradation tend to show continuous varation between the core phenotypes, rather than mixtures of distinct morphs. However, the intermediate mean position between *maidenii* and *pseudoglobulus* of the Yowaka Valley sample (m2; located in the core region of *maidenii*) is the result of a single tree phenotypically similar to *pseudoglobulus* among otherwise normal *maidenii*. The core *globulus* populations in south Gippsland are considerably less variable than nearby intergrade populations. High levels of variation also occur in western Tasmania, particularly in the Port Davey population (g3). Apart from these centres of variability, most populations from the cores of each subspecies are markedly uniform in capsule morphology (Fig. 4), although *maidenii* appears to be the most variable subspecies. High variability was detected in three of the core *globulus* populations from eastern Tasmania (Dover G2, Spring Hill G16 and Ellendale G10).

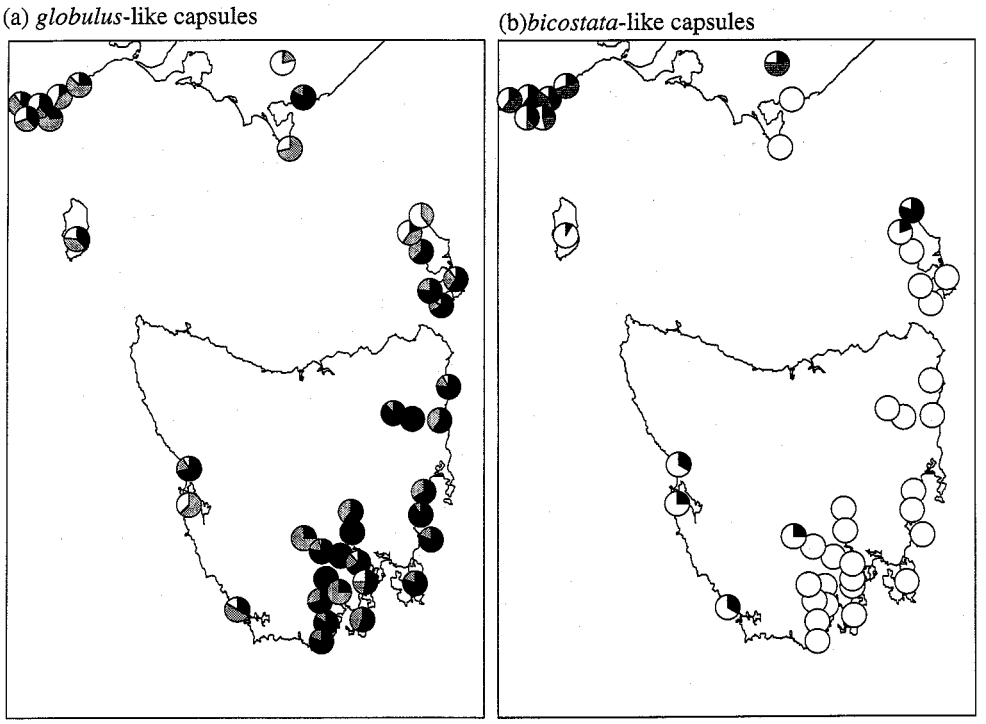

Fig. 5. The proportions of trees of *E. globulus* in CSIRO populations matching ($P > 0{\cdot}05$; shaded), significantly different from ($0{\cdot}001 < P < 0{\cdot}05$; stippled) or highly significantly different from ($P < 0{\cdot}001$; white) the capsule morphology of subspecies (*a*)*globulus* and (*b*) *bicostata*. Populations with fewer than three trees have been excluded.

Variation Within the CSIRO Collection

Figures 5*a* and *b* show, on a geographic basis, the proportions of trees sampled per population which match the capsule phenotype of the cores of subspecies *globulus* and *bicostata* respectively. At least half of the trees sampled in each population in eastern Tasmania (except Ellendale, G10, and North Geeveston, G37), in the Furneaux group

(except for north Flinders Island), in the Badgers Creek population in western Tasmania (g2), and at Hedley in south Gippsland (G34) fall within the multivariate 95% confidence interval of core samples of *globulus* (i.e. they match the *globulus* phenotype at the $P > 0{\cdot}05$ level) (Fig. 5*a*). Trees differing highly significantly from the *globulus* phenotype ($P < 0{\cdot}001$) are rare in south-eastern Tasmania and there is a general decline north and westwards in the frequency of trees with capsules matching the *globulus* phenotype ($P > 0{\cdot}05$). However, the *globulus* phenotype does clearly cross Bass Strait and the majority of trees in populations from the Furneaux Group (except the two north Flinders Island samples) and at Hedley (G34) are of this phenotype. Trees matching the *globulus* phenotype are also found in the Badgers Creek (g2) and Port Davey (g3) populations on the west coast of Tasmania, although 20 and 33% respectively of the trees measured were highly significantly different ($P < 0{\cdot}001$). Most trees in the other populations differed significantly ($P < 0{\cdot}05$) from the *globulus* phenotype. In the remaining western Tasmanian population (Macquarie Harbour, g1) none of the trees measured matched the *globulus* phenotype and one third differed highly significantly. The Jeeralang North population in west Gippsland (g16) has rare trees matching the *globulus* phenotype, but otherwise the trees differ highly significantly. The Lighthouse population (South East Point) on Wilson's Promontory (G33) which precociously develops flowers and adult foliage in field trials (unpubl. data), classifies as *globulus* (Fig. 3) on capsule morphology, but all the trees differ significantly ($P < 0{\cdot}05$) from the core *globulus* phenotype. About one third of the trees in the Otway Ranges (g6–9) and King Island populations (G32 and G36) match the core *globulus* phenotype and about one third are highly significantly different. In the two northern Flinders Island populations (g4 and g5) 40 and 60% respectively of trees differ highly significantly from the *globulus* phenotype, and the sample of g5 contains no trees which match the *globulus* phenotype.

The distribution of trees matching the capsule morphology of core *bicostata* (Fig. 5*b*) more or less complements the comparison with *globulus* phenotypes (Fig. 5*a*). Populations with high proportions of trees matching the *globulus* phenotype have few or no trees matching the *bicostata* phenotype, and *vice versa*. Trees matching ($P > 0{\cdot}05$) the *bicostata* capsule phenotype only occur in the Otway region (g6–10) and Jeeralang North population in west Gippsland (g16) which is mainly a reflection of the intermediate status of these populations. However, other trees with superficial similarity ($0{\cdot}05 > P > 0{\cdot}001$) to the *bicostata* phenotype occur in the Otway Ranges, Jeeralang North, central King Island, western Tasmanian populations, northern Flinders Island and Ellendale (central Tasmania) populations. In the Jeeralang North population (g16), 21% of the trees match the *bicostata* phenotype and 25 % of trees are highly significantly different. In most of the Otway Ranges populations, between one third and one half of the trees match the *bicostata* capsule phenotype while fewer than half the trees are highly significantly different. All the trees in the South Gippsland populations, the Wilson's Promontory lighthouse (G33) and Hedley (G34) are highly significantly different from the *bicostata* phenotype.

The distribution of trees matching the *pseudoglobulus* phenotype is not shown, but no trees in the CSIRO collection match ($P > 0{\cdot}05$) this phenotype. All trees differ highly significantly from the *pseudoglobulus* phenotype except a few trees in Jeeralang North (3%) and two of the Otway Ranges (Cape Patton 6%, Jamieson Creek 14%) populations.

Figure 6 shows the proportions per population of trees with umbels with more than one fruit. A low proportion of trees with at least some multi-fruited umbels are found in most of the core *globulus* populations. However, populations from eastern Tasmania, the Furneaux Group, King Island and south Gippsland are almost entirely one-fruited, although slightly higher proportions of multi-fruited (ncaps > 1) umbels occur in the Ellendale, Spring Hill and North Flinders Island populations. The western Tasmanian, Jeeralang North and Otway Ranges populations have the highest proportions of trees with multi-fruited

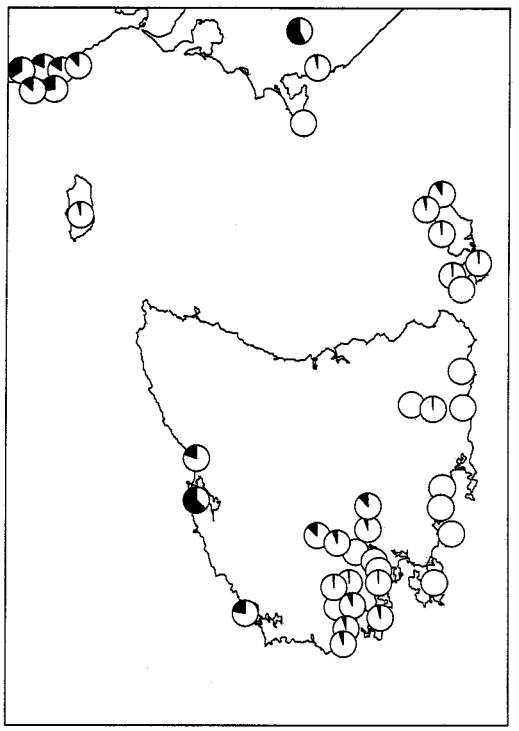

Fig. 6. The population mean proportion of one-fruited umbels per tree (white). Shaded areas represent means of the proportions of umbels with more than one fruit.

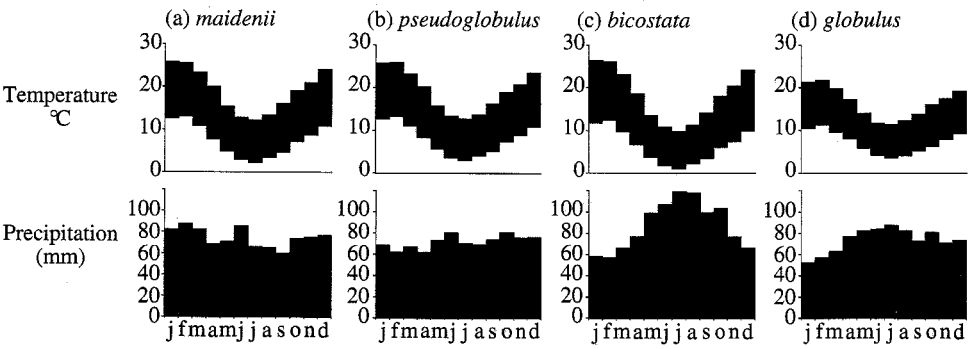

Fig. 7. Mean monthly minimum and maximum temperatures and precipitation for the subspecies cores of *E. globulus*.

umbels, with the Jeeralang North (g16) and Macquarie Harbour (g1) populations being mostly multi-fruited.

Climatic Variation

The annual temperature range (tspan) is the climatic parameter most significant in differentiating subspecies followed by the mean temperature of the warmest quarter (twmq), the coefficient of variation of rainfall (rcvar) and the mean temperature of the wettest quarter

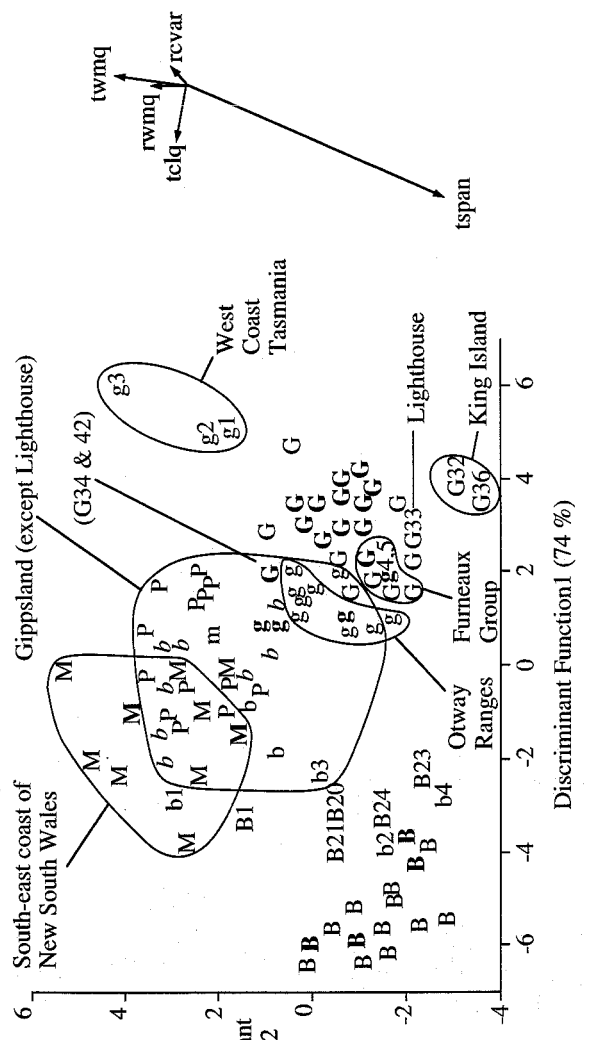

Fig. 8. Discriminant analysis of estimated climatic parameters of populations of *E. globulus*. Population scores are shown on the two major axes of the three dimensional space differentiating the cores of the four subspecies. Population codes follow Fig. 1.

(twetq) (Table 3). The average monthly rainfall and minimum and maximum temperatures of each subspecies are plotted in Fig. 7, and Fig. 8 summarises 94% of the multivariate climatic variation between core populations of the four subspecies. The cores of *globulus*, *bicostata* and *maidenii* are clearly differentiated in their climatic profiles (Fig. 8). There are fewer differences in climate between the cores of *pseudoglobulus* and *maidenii* and, while there is no overlap between core populations when the third discriminant function is considered, the climates of the cores of *pseudoglobulus* and the southern *maidenii* populations are similar.

The climatic transition from core *maidenii* to core *pseudoglobulus* involves a change from a summer rainfall regime to a relatively uniform distribution of rainfall throughout the year (i.e. decreasing rcvar, rwmq and twetq and increasing tdryq; Table 3) (Fig. 7). The transition from core *pseudoglobulus* to core *bicostata* involves significant changes in 9 of the 12 climatic parameters listed in Table 3. This difference basically reflects greater continentality of the climate (more seasonal variation in temperature and rainfall) and greater winter rainfall in core *bicostata* (i.e. decreasing tann, tclq and twetq and increasing tspan, rcvar, rclq, rwetm, tdryq and rann; Table 3). Core populations of *pseudoglobulus* and *globulus* are climatically differentiated on 7 of the 12 climatic parameters (Table 3). Summer temperatures and rainfall are lower in core *globulus* and there is less seasonal variation in temperature and more seasonality in rainfall compared with core *pseudoglobulus* (i.e. decreasing tann, tspan, twmq, rdrym, rwmq, and twetq and increasing rcvar) (Fig. 7). The climate of core *bicostata* is more seasonal in terms of both temperature (tspan) and rainfall (rcvar) than that of core *globulus* with lower winter (tclq) and higher summer (twmq) temperatures and higher winter rainfall (rclq) and a greater diurnal range in temperature (Fig. 7).

The core populations of *bicostata* form a well differentiated climatic group (B, B20, B21, B23 & B24), except for the northernmost population from Widden River (B1). The three-fruited intergrades (group b) are spread through the climatic ranges of *bicostata*, *pseudoglobulus* and *maidenii* with the climate of several populations (b3, b5 and b7) intermediate between that of core *bicostata* and core *pseudoglobulus*. Three of the four three-fruited intergrades from closest to the range of core *bicostata* (b2–4) fall more or less within the *bicostata* climatic group, but the climate of the majority of these populations (group b) is closer to that of core *pseudoglobulus*. There is a continuum in the climate of the remaining populations from a group of core *globulus* (G, G32–34, G36 & G42) populations at one extreme through core populations of *pseudoglobulus* (P) to core *maidenii* (M). The *globulus* intergrades (group g) are spread from near the climatic envelope of core *globulus* towards the climatic envelope of *pseudoglobulus*, but the climate of these populations is closer to that of core *globulus*. The intergrade populations on north Flinders Island (g4, g5) are anomalous since their climates are consistent with the climatic range of core populations of *globulus* in the Furneaux group. Morphologically intermediate populations in the vicinity of the Jeeralangs in west Gippsland (b13–15, g16, g18, g19) have climates intermediate between that of core *pseudoglobulus* and core *globulus*. Thus populations which are intermediate between *pseudoglobulus* and *bicostata* in capsule morphology (group b) encompass populations which are spatially and climatically intermediate between *pseudoglobulus* and *bicostata* and those intermediate between *pseudoglobulus* and *globulus*. While the three western Tasmanian populations (g1–g3) have closer morphological affinities to the Otway populations, they are climatically well differentiated from all other populations, although g1 and g2 have closest climatic affinities to the type locality of *globulus* at Recherche Bay (G1).

Discussion

The classification of the whole *E. globulus* complex presented here is generally consistent with that of Kirkpatrick (1975*a*, 1975*c*), with four groups readily ascribed to the same

four subspecies, and intergrade populations mainly occurring in the Otway Ranges and Gippsland (Fig. 1). However, a number of significant differences occur. Kirkpatrick (1975*a*, 1975*c*) identifies *pseudoglobulus* as the central group of the complex, with the other three subspecies intergrading into it. While our analyses of capsule morphology also show continuous variation between *pseudoglobulus* and *bicostata*, *globulus* intergrades with a part of this continuum (Fig. 2*a*, *b*). Subspecies *maidenii* appears to be linked to *pseudoglobulus* but distant from the other subspecies (Fig. 2*a*, *b*), although *maidenii* appears less distinct when the number of capsules per umbel (ncaps) is removed from the analysis. Kirkpatrick (1975*a*) identified a larger group of populations as being core and peripheral *pseudoglobulus* than our analysis. In particular, the west and south Gippsland populations he attributed to *pseudoglobulus* are part of the morphological continuum between *pseudoglobulus* and *bicostata* or *globulus* and, at least on capsule morphology, are closer to *bicostata*, although many are highly variable and climatically most have closer affinities to *pseudoglobulus*. The northern Flinders Island population, which Kirkpatrick (1975*a*) identified as being peripheral *pseudoglobulus* is intergrade *globulus* in our analysis (group g—Fig. 2), with some individuals approaching the capsule morphology of core *bicostata* ($P < 0{\cdot}001$) (Fig. 5*b*) and none similar to core *pseudoglobulus*. This would account for earlier reports for the distribution of *bicostata* (e.g. Kirkpatrick 1971) and recent records further north in the Furneaux Group (West Sister Island; Chippendale 1988). However, intermediates between *globulus* and *pseudoglobulus* would be expected to resemble intermediates between *bicostata* and *pseudoglobulus* in capsule morphology since both should show ribbed capsules of intermediate size. In our analysis, populations classified as core *bicostata* on capsule morphology only occur north of the Great Dividing Range. Kirkpatrick (1975*a*) had core *bicostata* populations extending over the Great Dividing Range which is consistent with the climatic affinities of these populations (b2–4; Fig. 8), although our analyses indicate that the capsule morphology of populations south of the Great Dividing Range deviate from core *bicostata* in the direction of *pseudoglobulus* (Fig. 1).

The subspecies appear to be meaningful taxonomic entities since the cores are relatively uniform (compared to intergrade populations), both within and between populations, and encompass large geographical areas (Fig. 4) of clearly different climates (Fig. 8) whereas intergrade populations (except between *pseudoglobulus* and *bicostata*) are highly variable (Fig. 4). The sample from the type locality of *E. stjohnii* at Lerderderg Gorge (P13) is part of the continuum between subspecies *bicostata* and *pseudoglobulus*, but has closer affinities to core populations of *pseudoglobulus* (Fig. 3). Its phenotype is clearly distinct from other populations in this region (g6–11, g15, b15 in Figs 1 and 2), but it is geographically isolated from core populations of *pseudoglobulus*. Similar phenotypes occur near Glenmaggie in west Gippsland (P12) and may have extended through the region now occupied by Melbourne prior to the clearing of forest. *E. stjohnii* is thus best treated as an intermediate form peripheral to *pseudoglobulus* rather than as a separate subspecies or species.

It is assumed that the ancestral group within the complex was closest to subspecies *maidenii*, because umbels composed of seven small fruits occur in the other members of the subseries *Globulinae* (Pryor and Johnson 1971) which are logical outgroups for the complex. Following the same reasoning, subspecies *globulus* and *bicostata* are likely to have been derived from subspecies *pseudoglobulus* or a morphologically similar ancestor. The intermediate group between these three subspecies (group b in Figs 2 and 3) may be derived from subspecies *pseudoglobulus* and be descended from the common ancestors of subspecies *globulus* and *bicostata* (primary intergrades) or it may be the result of hybridisation (secondary intergrades) between these taxa, or a combination of both. In the case of primary intergradation, differentiation in characters not considered in this study may have occurred, particularly if they have existed in genetic isolation for considerable periods. The climate of the Furneaux Group and other southern areas, such as the Otway Ranges and

Jeeralangs, in which individuals matching the capsule morphology of *bicostata* occur, is markedly different from that of the areas occupied by populations classified as *bicostata* (Fig. 8). Full differentiation of the *bicostata* phenotype probably occurred in the continental climates inland of the Great Dividing Range. The three-fruited intergrades now occurring north of the range of *pseudoglobulus* do not show elevated variability and are probably the remnants of earlier primary or secondary intergradation between *pseudoglobulus* and *bicostata*. It is likely, therefore, that the three-fruited intergrades (group b) have arisen independently at least twice. Forms occurring on the southern slopes of the Great Dividing Range are likely to have been the result of intergradation between *pseudoglobulus* and *bicostata* and forms south of this in West Gippsland are likely to have been the result of intergradation between *pseudoglobulus* and *globulus*. The reasons for the parallel evolution of large capsules in such contrasting climatic environments are unclear.

Despite some phenotypic resemblance to intergrades between *pseudoglobulus* and *bicostata*, the *globulus* intergrades in the Otway Ranges, northern Flinders Island and possibly on the west coast of Tasmania are also likely to be part of the continuum between *globulus* and *pseudoglobulus* (or their intergrades). Such phenotypes and populations would be expected to be phylogenetically and physiologically unrelated to *bicostata*, which is supported by the leaf and calycine ring data of Kirkpatrick (1975*c*), the contrasts in the current climatic regimes (Fig. 8) and the performance of these intermediate populations in field trials (Volker and Orme 1988). Records of *bicostata* in the Furneaux Group, south Gippsland and the Otway Ranges (Kirkpatrick 1971; Chippendale 1988) are thus probably misleading. It is unlikely that the southern occurrences of phenotypes resembling *bicostata* are genetic remnants of a more southern distribution of *bicostata* during glacial periods, although the Bassian Plain would have experienced more continental (due to greater land area) and colder climates with winter rainfall during glacial periods, due to the northward displacement of climatic belts (Bowler 1982).

Migration of phenotypes between Victoria and Tasmania has undoubtedly occurred, and is likely to have been related to the sporadic occurrence of land bridges between Tasmania and Victoria coinciding with large climatic changes (Shackleton and Opdyke 1973; Cann *et al.* 1988). Bathymetry (AUS CHART 422) indicates that two disjunct land connections may have provided opportunities for this migration, one across eastern Bass Strait from north-east Tasmania through the Furneaux Group to South Gippsland east of Wilsons Promontory, and another from north-western Tasmania through King Island to the Otway Ranges near Lorne (g10) and also to South Gippsland west of Phillip Island (g12). The eastern connection almost certainly existed more or less continuously from 40 ka to about 10 ka (Cann *et al.* 1988) and during the numerous previous glacials (Shackleton and Opdyke 1973) with connections through the western route being less frequent and of shorter duration (e.g. Blom 1988). The occurrence of both core *globulus* populations and highly variable *globulus* intergrade populations both on Flinders Island and in south and west Gippsland provides evidence that the eastern route provided a major migration route at some time. The existence of the western migration route is less clear. The means of capsule morphology from two western Tasmania populations (Badgers Creek and Port Davey), and the King Island populations are intermediate between populations from the Otway region and core *globulus* (Fig. 2*a*) but a hybrid origin of the apparently intermediate phenotypes in western Tasmanian cannot be discounted (see below).

Kirkpatrick (1975*c*) favoured a hypothesis of primary divergence to explain the geographically contiguous clines linking the subspecies in this complex, on the basis of the different patterns of geographical variation and the fact that isolation and recontact would have had to occur in three directions if these transition zones are the result of secondary intergradation. However, he noted the possibility that the extant pattern of variation could reflect a combination of both primary and secondary intergradation occurring at different times and amongst different combinations of the subspecies.

It is difficult to explain the occurrence of forms similar to *pseudoglobulus* on Rodondo Island, and to a lesser extent on northern Flinders Island, in between populations of core *globulus* unless secondary intergradation has occurred. It is also difficult to explain the persistence of high variability in the intergrade populations in Gippsland and in the Otway Ranges from the time of primary intergradation in the absence of steep ecological gradients (see Endler 1977). The hypothesis which explains the present data most simply is that full differentiation of the *globulus* phenotype occurred in isolation in Tasmania, this phenotype later migrated northward into Victoria, primarily via an eastern route, where secondary intergradation with three-fruited forms occurred. These southern three-fruited forms were probably the remnants of primary lineage from *pseudoglobulus* leading towards *globulus*. The high variability within the intermediate Otway populations (Fig. 4) is more difficult to explain unless it is the result of historical secondary contact with populations of *globulus* via King Island or through the longer eastern route. The hypothesis that the *globulus* phenotype differentiated in southern Victoria, and three-fruited phenotypes subsequently invaded populations of subspecies *globulus* in the Otway Ranges, west and south Gippsland, the Bass Strait Islands, and perhaps western Tasmania appears less plausible since this requires sympatric/parapatric differentiation of *pseudoglobulus* and *globulus* in the absence of marked environmental differentiation.

There is some indication that the patterns of migration of the subspecies and their intermediates have resulted in distributions that are not in equilibrium with present environmental conditions. This is particularly striking in the case of Bass Strait, where populations with strong *pseudoglobulus* influence are sandwiched between good *globulus* populations. The number of tree generations that have elapsed since the Last Glacial (perhaps as few as 30) and the restricted dispersal abilities of eucalypts suggest that it is possible that the zones of intergradation may still be shifting in response to climate change that took place about 10 000 years ago. The lack of congruence between climate and morphology shown for many of these populations is consistent with this hypothesis.

Hybridisation with other *Symphyomyrtus* species is a possible alternative mechanism for the occurrence of phenotypes diverging from the subspecies cores (e.g. Kirkpatrick *et al.* 1973), particularly in *globulus* in western Tasmania. Controlled pollination studies suggest that hybridisation of subspecies *globulus* with any of the Tasmanian *Symphyomyrtus* species would result in smaller capsules and greater numbers per umbel. However, the difference in flower size between the core *globulus* and most of the other Tasmanian *Symphyomyrtus* species means that normally the F_1 hybrid can only be produced using subspecies *globulus* as the male parent (Potts and Savva 1989; Gore*et al.* 1990). Backcrossing to females of subspecies *globulus* may be possible since F_1 hybrids have intermediate floral morphology. Introgressive hybridisation with related species, such as *E. viminalis* or *E. ovata /brookeriana* may have occurred in the west coast, and several other populations in Tasmania (e.g. Ellendale and Triabunna) (Potts and Jordan 1993). Trees in the Macquarie Harbour population (g1) have a high frequency of multi-fruited umbels, none closely matches the *globulus* capsule phenotype (Fig. 5*a*) and the population is clearly an outlier in the ordinations (Fig. 2). A high frequency of green and subglaucous seedling phenotypes has also been reported in the Macquarie Harbour and Port Davey (g3) populations which is suggestive of hybridisation (Potts and Jordan 1993), although it is possible that the unique climate of the west coast has resulted in selection for atypical phenotypes.

The origins of geographic variation in morphology are difficult to resolve on the basis of phenotypic similarity in reproductive traits since similarity and differences in selection environments and hybridisation may have distorted relationships. Quantitative and molecular genetic studies currently being undertaken may help resolve questions highlighted by this study including which hypothesis best explains the morphological variation pattern in the complex, the genetic basis of this pattern and its congruency with patterns using molecular markers, the significance of hybridisation with other species in the isolated western Tasmanian

populations, and whether current subspecies, particularly *maidenii*, should be elevated back to specific status. In the latter case it is notable that high levels of abnormalities have been recorded in artificial F_1 hybrids between *bicostata* and *globulus* (Potts *et al.* 1992) and genetically based differences in flowering time have been reported amongst provenances of *E. globulus* (Volker *et al.* 1988).

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Appendix

Populations Used in This Study From Kirkpatrick's (1975*a,c*) Study

The symbols used in this study (New Coding) and in Kirkpatrick's study (Old Coding) and the sites used to define subspecies cores for the classification of trees in the CSIRO collections (*) are indicated

Site name	Old coding	New coding	Site name	Old coding	New coding
Widden River*	B1	B1	Burrinjuck*	B3	B2
Wee Jasper	B4	B3	Talbingo*	B5	B4
Mundaroo*	B6	B5	Mullengandra	B7	B6
Tumbarumba	B8	B7	Tooma	B9	B8
Mt Granya	B10	B9	Shelley*	B11	B10
Teapot Creek	B12	B11	Beechworth	B13	B12
Upper Nariel	B14	B13	Tawonga	B15	B14
Whitfield*	B16	B15	Mt Samaria*	B17	B16
Mt Wombat	B18	B17	Mt Buller*	B21	B18
Tallarook	B22	B19	Break O'Day*	B23	B20
Snobs Creek*	B24	B21	Jamieson	B25	B22
Glen Patrick	B26	B23	Amphitheatre	B27	B24

Dover	G1	G2	Esperence*	G2	G3
Hobart South*	G4	G12	Tarrana*	G3	G14
Buckland	G5	G17	Spring Hill	G6	G16
Triabunna*	G7	G19	Mayfield	G8	G20
Lake Leake Road*	G10	G21	Beaumaris*	G13	G23
St Helens	G14	G26	South Flinders Island*	G15	G30
Central Flinders Island*	G16	G31	Bicheno	G11	G38
Coles Bay*	G9	G39	Lagoons*	G12	G40
Central East Flinders Island	G17	G41	Port Franklin	G23	G42
Cannon Spur	G19	g6	Lorne	G20	g10
Parker Spur	G18	g11	Phillip Island	G22	g12
Blackwarry	16	g13	Mardan	18	g14
Breakfast Creek	G21	g15	Loch	19	g17
Bowden Road	G25	g18	Madalya Road	G24	g19
Jenolan	B2	b1	Falls Creek	B19	b2
Omeo	B20	b3	Dawson's Rock	B28	b4
Licola	B29	b5	Gelantipy	6	b6
Peel Gap	B30	b7	Cobannah	B31	b8
Mt Moornap	B32	b9	Bruthen	B33	b10
Deptford	B34	b11	Neerim	20	b12
Jeeralang	17	b13	Willung	15	b14
You Yangs	22	b15	Noorinbee*	1	P1
Cann River*	2	P2	Drummer*	3	P3
Metang*	11	P4	Mt Cann*	4	P5
Goongerah*	5	P6	Murrindal*	7	P7
Dinner Hill	8	P8	Buchan*	9	P9
Seaton*	13	P10	Toongabbie*	14	P11
Glenmaggie	12	P12	Lerderderg	21	P13
Rodondo Island		p1	Weeraguna	M15	m1
Yowaka Valley	M11	m2	Araluen	M1	M1
Numbugga	M4	M2	Lookout	M6	M3
Currowan Creek	M2	M4	Tilba Tilba	M3	M5
Brown Mountain	M5	M6	Tantawangalo	M7	M7
Yurammie	M8	M8	Big Jack Mountain	M6	M9
Rocky Hall	M10	M10	Towamba	M12	M11
Flatback	M13	M12	Kowat	M14	M13
Wroxham	M16	M14			

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