

**Population variation and conservation
status of a rare Tasmanian endemic,
*Eucalyptus cordata***

B. M. POTTS

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Population variation and conservation status

of

a rare Tasmanian endemic,

Eucalyptus cordata

by

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Tasmanian Forest Research Council Inc.

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Summary

An attempt was made to verify and sample all populations of *E. cordata* indicated on herbarium sheets (e.g. EUCLIST), in the literature, or from current workers. Twenty-nine separate populations of this rare Tasmanian endemic have been located. Populations range in size from single individuals to over 5000 individuals, but only 3 populations exceed 500 individuals. The average size of the remainder is less than 200. Extensive data on adult morphology, floristic composition and environmental characteristics were collected from 21 of the populations. In addition, a progeny trial comprising the 21 populations, representatives of related species, and putative natural hybrids collected from stands of *E. cordata* was grown in a glasshouse.

There is highly significant differentiation in adult and seedling morphology amongst populations of *E. cordata*. This variation has a strong genetic basis, and is strongly associated with climatic factors (e.g. mean annual rainfall) that vary across the geographic range of the species. Analyses indicate that the species can be split into two relatively well-defined morphs that are more or less geographically concordant. These morphs are distinctly different in the angularity of both the adult and seedling stem; but they differ significantly in numerous other characters. A taxonomic revision of the species is thus proposed with the recognition of two subspecies.

The two morphs are mainly differentiated along a water availability/drainage gradient. This gradient is evident at both the broad climatic and microhabitat level with the angular stemmed morph occurring on the cooler, higher rainfall, and often waterlogged, western sites. There are also marked differences in site floristics between morphs. However, the compositional variation is continuous whereas the pattern of phenetic differentiation between populations appears stepped in both a geographic and ecological space. Variation between populations within each subspecies shows weaker correlation with ecological factors. The small, relict eastern populations show the greatest affinity to other related species in the *Cordatinae* and are believed to be the more primitive. However, several of the eastern populations are clearly deviant and appear to be introgressed with genes of *E. viminalis*. Most populations of *E. cordata* are genetically isolated due to the insular distribution pattern and hybridisation with surrounding species may have a significant impact on the genetic variability within populations.

E. cordata clearly warrants classification as rare, although this survey suggests that the species in general is not currently endangered. Nevertheless, specific populations may be at risk through small population size or disturbance and in terms of a cross-classification of the genetic and ecological diversity, the current reservation system is not satisfactory. Nearly 50% of the *E. cordata* populations occur on private land; the rest occur in State Reserves or on Crown land. At least 5 of the populations have been markedly disturbed through agricultural development and are under threat. The 'eastern' morph is well reserved with the larger stands relatively undisturbed and secure in State Reserves (Perpendicular Mountain in the Maria Island National Park and Cape Queen Elizabeth in the Bruny Neck Game Reserve). In contrast, the 'western' morph is unreserved and many of the populations are disturbed and at risk through agricultural development. The main stronghold of the 'western' morph, and the species in general, occurs in State forest on Snug Tiers.

Specific recommendations (summary)

Recommendation 1

All authorities responsible for the management of Crown Land on which *E. cordata* occurs should be notified immediately and management policies adopted to ensure these populations and suitable buffer zones remain undisturbed, or do not receive further disturbance through human activities.

Recommendation 2

A reserve should be established encompassing the stands of *E. cordata* in State forest on Snug Tiers.

Recommendation 3

Negotiations should be commenced with A.N.M. on the management of the *E. cordata* stand at Moogara and possibly to establish a reserve of more formal status. Recommended management includes the immediate removal of *Pinus radiata* from surrounding areas in which *E. cordata* regeneration occurs and later population expansion through planting of local *E. cordata*.

Recommendation 4

A reserve should be established on Brown Mountain to include the summit and to encompass the population with affinities to *E. cordata* (Bc).

Recommendation 5

The population of *E. cordata* on Chimney Pot Hill (CP) should be accorded reservation status.

Recommendation 6

The degree of threat to the *E. cordata* populations on private land should be closely monitored and liaison with land-owners maintained to minimize any future threat to these populations.

Recommendation 7

Some level of reservation should be given to the area on Meredith Tier which includes the population MT and the nearby population of the endemic *E. barberi*.

Chapter 1 Introduction

Eucalyptus cordata (heart-leaved silver gum) is a regional endemic confined to the southeast of Tasmania. It is placed in the informal Subseries *Cordatinae* (Subgenus *Symphyomyrtus* ; section *Viminales*) by Pryor and Johnson (1971). It is broadly grouped with other endemics such as *E. gunnii*, *E. morrisbyi* and *E. urnigera* as well as with mainland species such as *E. pulverulenta* and *E. cinerea* (Pryor and Johnson 1971). Affinities to *E. urnigera* (Mueller 1880; Brett 1938) and *E. pulverulenta* (Mueller 1880; Baker 1902; Maiden 1913; Hall and Brooker 1972) have been specifically noted. *E. cordata* is planted widely as an ornamental. It is usually homoblastic and the persistent, highly glaucous, cordate juvenile foliage is a distinctive feature of the species (Hall and Brooker 1972).

Eucalyptus cordata is considered a rare and endangered species by Pryor (1981) and is listed as a vulnerable species by Fry and Benson (1986). The necessity for a detailed study of this rare species was recognized early by Brett (1938) and more recently emphasized by Pryor (1981). Detailed genetic and ecological studies are essential for the development of strategies for the short and long term conservation of species (e.g. Halloran 1985; Frankel and Soulé 1981; Moran and Hopper 1987). In particular, a knowledge of the genetic diversity over the full geographical range of species is a major prerequisite (Moran and Hopper 1987), as is an understanding of the genetic variability in relation to the ecology of the species (Pederick 1985). A population survey was thus undertaken to fully evaluate the genetic resource and to provide a basis for the development of a conservation strategy for *E. cordata*.

This study attempted to locate and verify all known occurrences of *E. cordata* and to provide sufficient information for the assessment of its conservation status in terms of the principles of genetic conservation as detailed by Frankel and Soulé (1981). The approach adopted was to detail -

- (1) the distribution and conservation status of populations
 - (2) the genetic diversity within the species
 - (3) the ecological diversity within the species
 - (4) the association of patterns of genetic and ecological variability
- and
- (5) the taxonomic affinities and evolutionary trends in the species.

During the survey it also became apparent that a taxonomic revision of the species was necessary.

The "phenetic" as opposed to "genetic" approach (*sensu* Brown and Moran 1981) was used to evaluate the genetic resource. A multivariate approach was adopted to assess phenotypic variability; the phenotypic space was defined by morphometric characters measured from field-sampled adults as well as glasshouse-grown seedlings. Heritabilities, and hence genetic variance components, of traits were not directly quantified as family identity was not retained in the progeny trial. Nevertheless, the progeny trial undertaken provided a clear indication of the genetic component underlying the variation between populations.

The heritability of adult characters in *Eucalyptus* is not readily estimated as many years are required for reproductive maturity and, due to ontogenetic effects such as heteroblasty, vegetative characters at different stages in the life cycle are not necessarily directly comparable. The inheritance of morphometric characters in *Eucalyptus* has been mainly studied using interspecific hybrids (e.g. Pryor 1957a, 1976; Cauvin *et al.* 1987; Tibbits 1988) where the majority of characters exhibit intermediate inheritance. Nevertheless, within species, a strong association between variation in adult phenotype and genetically based variation in the phenotype of glasshouse-grown seedlings is the norm in *Eucalyptus*, at least at the population level (e.g. Pryor 1957b; Barber and Jackson 1958; Phillips and Reid 1980; Ladiges and Ashton 1974; Shaw *et al.* 1984; Potts and Reid 1985b; Wiltshire and Reid 1987). This strong association has been demonstrated in *E. gunnii*, a species closely related to *E. cordata* (Potts and Reid 1985b). Variation between families within populations of *E. gunnii* was significant for virtually all seedling morphometric and growth characters (Potts and Reid 1985b), which is indicative of significant components of heritable, additive genetic variation. In addition, reciprocal transplant trials with *E. gunnii* also indicated significant genetic variation at the population level (Potts 1985). There were significant environmental and/or population x environmental components to the phenotypic variation in most growth or size related characters but these components were virtually negligible in other characters such as components of leaf shape and glaucousness.

Environmental or ecological diversity amongst populations of *E. cordata* was both directly and indirectly assessed. For direct measures of environmental variables, the sites were either assigned to relatively coarse categories (e.g. drainage) or, as in the case of macro-climatic variables, a climatic model was used to estimate site values from the geographic position and altitude. An alternative, and possibly more satisfactory approach, was to use floristic similarity as an indirect measure of relative distance between sites in environmental/ecological space. An estimate of the similarity of selective environments is thus obtained which should be relatively independent of estimates of phenetic or genetic similarity. The indirect floristic approach assumes historical effects are small and that there is a strong association between floristic and ecological similarity. This assumption is fundamental to indirect gradient analysis (*sensu* Whittaker 1967); an approach widely accepted and used to identify environmental gradients through ordination of floristic or compositional data (e.g. Austin and Cunningham 1981; Minchin 1983, 1987; Bowman and Kirkpatrick 1984; Faith *et al.* 1987). This indirect approach is appealing as it allows the integration of macro- and micro-habitat variation as well as temporal effects in the assessment of ecological similarity.

Chapter 2 Methods

2.1 Distribution and sampling sites

An attempt was made to verify and sample populations of *E. cordata* from all locations indicated on herbaria sheets (Tasmanian and Melbourne Herbaria; EUCLIST [Nov. 1983] Chippendale and Ledek 1984), in the taxonomic literature (Rodway 1918; Blakely 1934; Brett 1938; Hall and Brooker 1972) and from current workers.

The locations of populations sampled are indicated in Fig. 2.1 (see also Appendix 1), and further site and sample details are given in Table 2.1. Several populations verified were not included in the phenetic study as they were either located after analyses were complete (Be, PB and CP2- Table 2.1) or had been recently burnt (i.e. BR, CH2, CH3 and SR - Table 2.1).

2.2 Environmental and stand characteristics

At each site, the environmental and stand characteristics indicated in Table 2.2 were recorded from the central region of each stand. In addition, the land tenure was determined and the degree of disturbance of each stand was assessed in terms of fire (fire scars, estimated time since last fire), human (e.g. selective logging, clearing, tracks) and other disturbance (e.g. stock or insect damage, introduced weeds). The times since the last fire were obtained from records or estimates of the age of coppice resprouts of *E. cordata* or proteaceous shrubs in the vicinity. Soil pH was measured using a CSIRO field pH kit from samples taken from the top 5 cm at 3 random locations within the stand and values averaged. Slope and aspect were measured using a clinometer and a compass. Demographic attributes of the stand including the presence of germinants and seedlings, the reproductive (abundance of capsules and flowers) and vegetative vigour, and the pattern of distribution of *E. cordata* within the local geographical area were noted. Estimates of the population size were obtained from either direct counts or approximated by subsampling and extrapolating to the estimated area covered by the population.

2.2.1 Bioclimatic profile

Estimates of climatic parameters for each site were obtained from the climatic model BIOCLIM developed by H. Nix, M. Hutchinson and J. Busby (Busby 1984; Busby 1986). Using geographic location (latitude and longitude) and altitude, monthly rainfall and minimum and maximum temperatures are estimated from climatic surfaces fitted to data measured at meteorological stations. These rainfall and temperature estimates are then used to derive 12 selected climatic variables (Table 2.2) for each site which are believed to characterize annual, seasonal, and extreme components of the climate important to plant growth. Estimated values for these 12 variables at each of the 21 sites sampled (see Appendix 4) were used to derive a species climatic profile. Using point altitudes, estimated on a 0.1° latitude/longitude grid for Tasmania, areas with similar climatic values were then identified and a

climatically defined geographical range for the species was derived.

2.3 Floristics

The percentage foliage cover and mean height of all woody species and large sedges (*Gahnia*, *Lepidosperma*, *Dianella*, *Lomandra*, and *Diplarrena*) were scored within 5 quadrats randomly located in central regions of each *E. cordata* population. Where plants were locally distributed as small, high density patches, the central region of up to 5 patches was sampled. Following Bowman and Kirkpatrick (1984), a 5 x 5m quadrat was used for those species more than 5m tall and a 2 x 2m quadrat located randomly within the larger quadrat was used for those less than 5m tall. In all cases, only eucalypt species were eligible for scoring in the 5 x 5m quadrats. The percentage cover of bracken (*Pteridium esculentum*), other ferns, grass, other graminoids, herbs, moss, litter, rock and bare ground were estimated for 1 x 1m quadrats randomly located within each of the 2 x 2m quadrats. Percentage cover values from each of the 5 quadrats were averaged to provide site values.

2.4 Sampling of Individuals

In general, an attempt was made to randomly sample 10 mature individuals from a central, representative area from each population. In large populations, a transect line was followed and adjacent individuals avoided. If the population was locally distributed in high density patches, individuals from a range of patches were sampled. However, in many cases, low population numbers necessitated virtually all mature individuals in the stand being sampled regardless of position, and in 5 populations less than 10 mature individuals were located. Putative hybrids were found in many of populations. These were sampled for hybrid studies, but following Potts and Reid (1985a), obvious F1 types or those more similar to the other species were excluded from the population sample if randomly encountered.

Herbarium specimens of all individuals sampled were collected and have been lodged with the Tasmanian Herbarium. In addition, sun leaves and capsules were sampled from several areas of the crown of each individual for measurement and seed collection. *E. cordata* is generally homoblastic and the typical petiolate and lanceolate 'adult' leaf type is only rarely produced. Accordingly, for consistent comparison between phenotypes, three typical leaves of the 'juvenile' type (opposite and sessile) were chosen from an area of maximal summer growth on capsule bearing branches. To account for the few cases where the 'adult' leaf type was expressed in upper regions of the crown, the most 'adult' type leaf was also sampled from each individual.

2.5 Adult morphology

Variation in adult phenotype amongst populations of *E. cordata* was examined using the morphometric characters indicated in Table 2.3. These leaf and capsule characters correspond to those used by Potts and Reid (1985a, 1985b) to examine variation in species closely related to *E. cordata*, and details of their measurement are given therein. Glaucousness of the adult foliage (0 green - 4 highly glaucous) and the shape of the young stem (0 round - 4 markedly quadrangular with costa) were assessed on a 5 point scale.

2.6 Progeny trial

Variation amongst populations as assessed from field sampling natural populations may compound main and interaction effects of environmental, ontogenetic and genetic components of variation. Accordingly, an indication of the magnitude of genetic differentiation amongst populations was obtained using a progeny trial in which open-pollinated *E. cordata* seedlings were grown in a common glasshouse environment.

Populations of closely related species in the same Subseries *Cordatinae* (*E. gunnii* subsp. *gunnii* and subsp. *archeri*, *E. urnigera*, *E. morrisbyi*, *E. glaucescens*, *E. perriniana*, *E. pulverulenta*, and *E. dalrympleana*) as well as *E. viminalis*, *E. vernicosa* subsp. *johnsonii*, *E. ovata*, *E. brookerana* and *E. globulus* (see Pryor and Johnson 1971) were also incorporated in the trial in order to examine the affinities of the *E. cordata* populations, aid with the identification of hybrids, and to provide a context in which to assess the variation within *E. cordata*. A population sample of trees collected from Meredith Tier (MT) was included. This population was recorded as the northern most population of *E. cordata* in Brown *et al.* (1983), but following sampling is believed to be of hybrid origin (*E. cordata* x *E. barberi* or *E. gunnii* x *E. barberi*) and too deviant to be included within *E. cordata* (see Appendix 3). A subsample of the *E. cordata* population on Brown Mt. (Bu) comprising 4 selected trees developing adult foliage and showing slight affinities toward *E. urnigera-morrisbyi* was also included.

Each population was represented by pooled samples of open pollinated seed from up to 10 trees and population details are given in Table 2.4. A total of 21 *E. cordata*, 12 *E. gunnii*, 1 *E. morrisbyi*, 4 *E. urnigera*, 4 *E. glaucescens*, 2 *E. perriniana* populations were included. The remaining species were represented by trees sampled from a range of sites. Single tree progenies from all putative hybrids collected and pure species controls were grown simultaneously, with the main trial but were grouped into family lots adjacent to, but not included, in the main experimental design.

Seedlings from the main trial were arranged in a randomized complete block design comprising 20 blocks with each population of *E. cordata* (incl. MT and Bu), *E. morrisbyi*, and *E. globulus* represented once per block. Pairs of the other populations and species were allocated population positions within the randomized block design and one of either pair randomly allocated to a block position. This design resulted in a replication of 20 seedlings for

each *E. cordata* population and species samples of *E. morrisbyi* and *E. globulus*, and 10 seedlings for the other population or species samples. The randomized block was surrounded by an edge row comprised of linearly replicated blocks of 5 seedlings of the *E. gunnii* populations - SH, MA, SP and MV and these extra seedlings were included in the population sample analysed. Unfortunately, seedling mortality during the trial was relatively high, mainly due to fungus attack which differentially affected the 'eastern' populations of *E. cordata*. Nevertheless, all populations planted were represented in the final scoring although the number of replicates per population varied markedly (4 to 17 for the *E. cordata* populations; Table 2.4).

Seedlings were grown in individual plastic bags filled with potting mix under an 18 h photoperiod (natural light was supplemented with a mixed incandescent and florescent light source of approx. 10Wm^{-2}). A quarter strength Aquasol nutrient solution was applied weekly. Seedling height (Ht), number of nodes expanded (NODES) and number of laterals (with more than 1 node fully expanded) were scored after 3 months and one cotyledon and a second node leaf (cots. = node 0) were removed for measuring. After 5 months, a fifth and tenth node leaf were also removed and other characters scored.

The full suite of characters scored from the seedlings is indicated in Table 2.5. Scoring of ordered multistate characters was achieved by comparison with standards and using either a 5 (0-4) or 3 (0-2) point scale. The 3 classes used to assess the colour differences, presumably arising from variation in anthocyanin development, on the undersurface of cotyledons (ANTHcot) and seedling leaves (ANTH2u, ANTH5u, ANTH10u) follow Wilcox (1982) - viz. 0 none (undersurface green), 1 intermediate (e.g. green with a tinge of purple) and 2 purple. Anthocyanin development and the density of large oil glands on the upper surface of the leaves (OILGL2, OILGL5, OILGL10) were assessed from dried, pressed leaves (there is no marked change in these characters between fresh and dry material). As with the adult leaves, the leaf dimensions indicated in Fig. 2.2. were digitized from photocopies of dried specimens following Potts and Reid (1985b).

2.7 Statistical analysis

2.7.1 Morphometric data

Differentiation amongst populations was examined in the univariate case using analysis of variance (ANOVA - model 11; Sokal and Rohlf 1981). Variance components attributable to between (σ_p) and within (σ_w) population effects were estimated using the GENSTAT macro HIERANOVA which uses Gower's (1962) algorithm for the estimation of variance components in non-orthogonal hierarchical analyses of variance. The percentage of the total variability ($\sigma_t = \sigma_p + \sigma_w$) attributable to each level was then calculated for each character. Multivariate comparisons of populations were undertaken using multivariate analysis of variance (MANOVA) and discriminant analysis (also termed canonical variates analysis; Phillips *et al.* 1973). The latter method partitions

the variation between population centroids in discriminatory space into unique maximum variance directions of differentiation, termed discriminant functions or canonical variates. The importance of characters in these discriminant functions was summarized by plotting character vectors in the 2 dimensional discriminant space, the length and direction of which were defined by the corresponding weightings of the characters on the standardized discriminant functions. The transformation into discriminatory space results in the pooled within populations dispersion being a unit hypersphere (Rempe and Weber 1972) and the distances between populations are Mahalanobis' generalized distances (Mahalanobis 1936). The discriminatory functions are linear combinations of the original variables which maximize the difference between populations. The test of the significance of the eigen value corresponding to each discriminant function is given by Seal (1966). The ordination of population centroids in the reduced subspace defined by the main discriminant functions effectively summarizes the Mahalanobis' distances between populations and the 95% confidence circle set on group centroids has a radius of $1.96/\sqrt{N}$, where N is the number of replicates in the population (Phillips *et al.* 1973).

Populations were classified using Average Linkage (i.e. UPGMA) and Single Linkage clustering (Sneath and Sokal 1973). These classifications were agglomerative and hierarchical and used the Mahalanobis' distance (D) as the dissimilarity measure. The Mahalanobis' distance between two populations was indirectly calculated as the euclidean distance between their centroids in the space defined by the full suite of discriminant functions (Phillips *et al.* 1973; McPherson pers. com.). The test for the significance of the Mahalanobis' distance follows Rao (1952).

A discriminant analysis using step-wise backward elimination of characters was used to identify redundant variables and determine the optimal subset of discriminating characters necessary to fully describe the pattern of population differentiation. All variables for which greater than 0.1% of the within-groups variance was not accounted for by other variables (i.e. 'tolerance') were initially forced into the analysis. Partial F values were then calculated and characters for which the partial F value was not significant at the 0.05 probability level were sequentially eliminated from the analysis. Partial F values of the remaining variables were recalculated following each elimination. This procedure was repeated until all variables remaining in the analysis had significant partial F values, indicating a unique and significant contribution of each remaining variable to the discrimination of populations.

Discriminant analyses and MANOVA's were performed using the DISCRIMINANT and principal components analyses (see Appendix 4) of correlation matrices performed using the FACTOR subprograms of SPSS^x (SPSS Inc. 1986). Cluster analyses and the calculation of the Mahalanobis' distance from discriminant scores were performed using the CLUSTER subprogram of the same package.

ANOVA and the multivariate methods used assume residuals are normally distributed and that sample variances are homogeneous. However, while moderate departures from these assumptions can be tolerated in univariate (Sokal and Rohlf 1981) and discriminant (Lachenbruch 1975) analyses, an attempt was made to optimize these criteria at

the univariate level by data transformation. The replication was insufficient to extend these tests to the multivariate level. The homogeneity of variance assumption was tested using Cochran's C test and trends in the relationship between the sample mean and variance were examined through plotting. The normality of the distribution of pooled residuals was tested by measuring the skewness (g_1) and the kurtosis (g_2) of the distribution of pooled residuals. Following Sokal and Rolf (1981) the significance of the departures of g_1 and g_2 from the normal distribution values of 0 was tested using a 2-tailed t-test. As the sample size (N) was greater than 100, standard errors for these statistics are approximately $\sqrt{6/N}$ and $\sqrt{24/N}$ respectively. All variables used in analyses were treated as potentially continuous and tests were performed using the 21 *E. cordata* populations. In the few cases where isolated abnormal seedlings occurred in population samples and were clearly hybrids or backcrosses with other species, these were excluded from all analyses (except for populations PR and HF where such individuals were the norm). Following the transformations indicated in Tables 2.3 and 2.5, pooled residuals were normally distributed and variances homogeneous for the majority of characters used in the analysis of the *E. cordata* populations ($P < 0.01$). Pooled residuals were calculated using MINITAB (Ryan *et al.* 1985) and sample statistics computed and homogeneity of variances examined using the CONDESCRIPTIVE and MANOVA subprograms respectively of SPSS^x.

2.7.2 Floristic data

The floristic relationship of stands was examined on the basis of the compositional similarity of associated tree (excluding *E. cordata*), shrub and large sedge understorey species. Following Minchin (1987), stands were ordinated using the non-linear technique of non-metric multidimensional scaling (NMDS). This technique was applied to the Kulczynski dissimilarity matrix calculated from percentage cover scores which were standardized so species have equal maxima (see Faith *et al.* 1987). NMDS derives an ordination of the sites, in a specified number of dimensions, such that the distances between sites-points has the best possible monotonic (rank-order) fit with the input dissimilarities. Details of this approach are summarized in Bowman and Minchin (1987). Starting configurations for the initial 'global' NMDS analyses were derived from detrended correspondence analysis (DCA; Hill and Gauch 1980) using DECORANA (Hill 1979a) and 19 randomly generated starting configurations, and the solution with minimum stress selected. Separate 'global' NMDS ordinations were performed in one to four dimensions and a suitable dimensionality selected following Bowman and Minchin (1987).

Data entry and manipulation were performed, and site-by-species ordered tables produced, using ECOPAK (Minchin 1986). The NMDS ordinations were performed using KYST (Kruskal *et al.* 1973). Sites and species were classified by Two-way Indicator Species Analysis using the programme TWINSpan (Hill 1979b). The classification was based on presence/absence (c.f. % cover for NMDS) of only species present in two or more sites.

2.7.3 Environmental, floristic and phenetic correlates

Several approaches were adopted to investigate the relationship between patterns of environmental, phenetic and floristic variation. Bivariate plots were inspected and correlation and linear regression coefficients calculated between population means and environmental factors. In addition, environmental trends in the morphometric ordinations were examined using rotational correlation analysis.

Rotational correlation is a technique which finds the vector (rotated axis) in the ordination space which is such that the projections (scores) of sites on this vector are maximally correlated with the value of a given variable (Bowman and Minchin 1987). This method is analogous to multiple regression and is a useful approach for fitting vectors into a multi-dimensional space. The correlation between a vector and the fitted vector indicates the goodness-of-fit of, for example, an environmental variable into the ordination space. The cosine of the angles with the dimensions defining the configuration indicate the direction of the fitted vector. Vectors were standardized to unit length so that in a 2-dimensional plot of a multi-dimensional space, the deviation of the length of the fitted vector from unity indicates the extent the vector dips into other dimensions.

The technique was used to fit vectors into ordination (phenetic or floristic) space and to detect clinal patterns of character variation in geographical space. In addition, in the floristic ordination, the projections (scores) of the sites on to environmental vectors exhibiting strong correlations to the ordination space were computed and used as the floristically determined positions of stands along the given environmental gradient. This indirect method of the positioning sites along environmental gradients (i.e. indirect gradient analysis) may be an advantageous approach where the time scale over which environmental gradients operate do not permit their direct measurement (e.g. rare drought or frost events) or, as in the present study, where only crude, direct measures of an environmental gradient are available.

Rotational correlation analyses were performed using a version of PROFIT (Chang and Carroll 1968), modified to link with the ecological data base system ECOPAK (Minchin 1986). The linear option was used which will detect monotonic trends, even when there is a large curvilinear component.

Table 2.1 Location and characteristics of populations of *E. cordata*.

The table indicates population codes, universal grid references, the number of individuals for which a full morphological data set was available, estimates of the population size, land tenure, the average height (m) and percentage of individuals developing, and mean percentage, of adult or intermediate type foliage.

LOCATION	CODE	UNIVERSAL		NUMBER OF		APPROXIMATE LAND	AV. TREE	ADULT FOLIAGE	
		GRID REFERENCE		INDIVIDUALS	POPULATION	TENURE	HEIGHT	%	Mean
		E/W	N/S	SAMPLED	SIZE		(m)	Indiv.	%
Perpendicular Mt.(top)	Pt	5933	52766	10	300+	State Reserve	2.8	0	0
Perpendicular Mt.(low)	Pl	5930	52765	10	200	State Reserve	2.9	0	0
Prosser River	PR	5691	52881	4	6	Private	1.3	0	0
Hellfire Bluff	HF	5766	52683	10	150	State Reserve	2.0	0	0
Bluestone Tier	BT	5652	52932	10	55	Crown Land	1.8	0	0
Bream Creek	BC	5687	52614	10	65	Private	1.9	0	0
Hospital Creek	HC	5673	52660	10	150	Flora Reserve	2.9	0	0
Cape Queen Elizabeth	QE	5345	52109	10	1000	Game Reserve	1.7	0	0
Square Mountain	SM	5506	52695	9	200	Private	2.7	0	0
Electrona	El	5200	52335	10	110	Private	5.9	0	0
Snug Plain	SP	5120	52317	10	5000+	State Forest	3.2	0	0
Falls Hill	FH	5128	52320	5	30	State Forest	3.7	0	0
Herringback (top)	H1	5113	52383	10	300	Private	5.1	0	0
Herringback (low)	H2	5119	52385	10	300	Private	4.2	0	0
Chimney Pot Hill	CP	5225	52476	10	500	H.C.C.	2.8	0	0
Leslie Road	LR	5177	52431	10	200	Private	4.8	0	0
Combes Hill	CH	5140	52442	10	800	Private	5.3	0	0
Mt. Lloyd	ML	4958	52572	10	150	Private	7.9	30	1.5
Moogara	Mo	4930	52613	10	100	Private	15.8	10	0.2
Tarrana	Ta	5714	52319	6	85	Private	3.1	0	0
Brown Mountain	Bc	5428	52837	7	150	State Forest	3.3	50	3.8
Burdons Razorback	BR	5671	52640	-	1	Private	-	0	0
Combes Hill	CH2	5134	52432	-	300	Private	-	0	0
Combes Hill	CH3	5136	52438	-	300	Private	-	0	0
Summerleas Road	SR	5220	52461	-	10	Private	-	0	0
Chimney Pot Hill 2	CP2	5221	52479	-	60	Private	-	0	0
Betts' Road	Be	5166	52440	-	2	Private	-	0	0
Penguin Island	Pe	5301	52001	-	200	State Reserve	4.5	40	1.2
Pony Bottom Creek	PB	5737	52712	-	40	State Forest	-	-	-
Meredith Tier *	MT	5763	53301	10	30	State Forest	-	-	-

*not *E. cordata* see Appendix 2

Table 2.2 Environmental and stand characteristics recorded from each population.

CHARACTER CODE	DESCRIPTION
LAT	Latitude (degrees) 1, 2
LONG	Longitude (degrees) 1, 2
ALT	Altitude (m) 1, 2
ASPECT	Site aspect measured to the closest octant
SLOPE	Slope of site (degrees) 1, 2
ROCKTYPE	bed rock type (jurassic dolerite, permian mudstone)
SOILTYPE	Soil type class (sand; sandy loam; loam; clay loam; clay; peat)
SOILDEPTH	Soil depth class 1, 2 [1 shallow (<10cm) 2 medium (10-50cm) 3 deep (≥50cm)]
PH	pH of the top 5cm soil layer ¹
DRAINAGE	Site drainage class (1 excessive 2 free 3 impeded) 1, 2
TOPPOS	Topographic position ¹ (1 ridge 2 hilltop 3 cliff slope 4 upper slope 5 mid slope 6 lower slope 7 plain/plateau)
WIND	Wind exposure (1 sheltered 2 medium 3 exposed) 1, 2
POPSIZE	Population size class derived from estimates of the number of individuals ¹ with lignotuber size ≤21 cm (1 ≤10 2 ≤100 3 ≤200 4 ≤300 5 ≤1000 6 >1000)
DISTURBANCE	Human disturbance class ¹ (1 undisturbed 2 slight disturbance evident, having very little impact on population 3 severely disturbed, including large portion of population possibly lost through clearing)
LASTFIRE	Estimated time since last fire (years) ¹
EUCS	Number of associated eucalypt species
HYBRIDS	Relative frequency of putative natural hybrids in population ¹ (0 none 1 rare one or two observed 3 frequently encountered)
DISTRIBUTION	Localized pattern of distribution ¹ (1 extensive 2 localized high density patches 3 scattered at low density 4 rare/sporadic individuals)
Synthetic climatic variables (BIOCLIM)	
MNANTEMP	annual mean temperature (°C) 1, 2
MINMINTEMP	minimum temperature of the coldest month (°C) 1, 2
MAXMAXTEMP	maximum temperature of the hottest month (°C)
TEMPRANGE	annual temperature range (MAXMAXTEMP - MINMINTEMP) (°C) ²
TEMPWETQ	mean temperature of the wettest quarter (3 months) (°C)
TEMPDRYQ	mean temperature of the driest quarter (3 months) (°C)
MNANRAIN	annual mean precipitation (mm) 1, 2
RAINWETM	precipitation of the wettest month (mm)
RAINDRYM	precipitation of the driest month (mm)
RAINRANGE	annual precipitation range (RAINWETM - RAINDRYM) (mm) 1, 2
RAINWETQ	precipitation of the wettest quarter (mm)
RAINDRYQ	precipitation of the driest quarter (mm)
ClimPC1	composite climatic variable from PCA of 12 BIOCLIM variables 1, 2 (contrasts rainfall+ and temperature- variables; see Appendix 4, Table 2)

¹ = fitted into floristic ordination space (Fig. 5.1)

² = fitted into phenetic space (Fig. 4.7)

Code	Character description	Untransformed		F value Trans- 20,169 formation		% Variance	
		Mean	s.d.			Between	Within
LL	Lamina length (mm)	56.4	18.23	21.7	log 10(X)	69.6	30.4
LW	Lamina width (mm)	51.2	13.04	29.8	log 10(X)	76.0	24.0
LWP	length from lamina base to widest point (mm)	21.3	6.74	5.2	ratio LWP/LL	31.8	68.2
BASE	Degree of lobing when leaf base is cordate (mm)	4.2	2.07	16.0	log10(1+X)	62.4	37.6
APEX	Measure of the degree of indentation of the leaf apex when leaf apex is emarginate (mm)	0.6	0.65	3.5	log10(1+X)	21.7	78.3
				Leaf Average		52.3	47.7
PEDU	Peduncle length (mm)	6.5	2.01	5.0	log 10(X+1)	30.9	69.1
CAPL	Capsule length (mm)	10.3	1.65	16.4	log 10(X)	61.7	38.3
PEDI	Pedicel length (mm)	0.2	0.48	3.9	log10(1+X)	20.7	79.3
RIMW	Capsule rim width (mm)	9.9	1.72	15.7	log 10(X)	61.0	39.0
MAXW	Maximum capsule width (mm)	10.9	1.73	18.7	log 10(X)	64.9	35.1
PTMW	Distance from capsule rim to maximum capsule width (mm)	3.0	0.84	4.3	none	36.8	63.2
DISK	Disk level (mm)	2.1	0.63	4.9	none	30.1	69.9
VSIz	Relative valve size (1 membranous - 4 woody)	2.6	0.75	11.1	none	52.7	47.3
VPOS	Relative valve position (1 insert - 4 exsert)	1.8	0.51	3.4	none	20.7	79.3
				Reproductive Average		42.2	57.8
				Leaf + Reproductive Average		45.8	54.2
GLAUC	Foliage glaucousness (0 green - 4 highly glaucous)	3.9	0.32	20.0	none	67.7	32.3
STSHAPE	Stem shape (0 round - 4 markedly quadrangular)	1.4	1.71	92.2	none	90.9	9.1
				Grand Average		50.0	50.0

GLAUC	Foliage glaucousness (0 green - 4 highly glaucous)	3.9	0.32	20.0	none	67.7	32.3
STSHAPE	Stem shape (0 round - 4 markedly quadrangular)	1.4	1.71	92.2	none	90.9	9.1

Table 2.4 Populations used in the progeny trial.

The locations, code, universal grid reference, altitude, the number of females used for the pooled seed sample, the total number of seedlings for which a full data set of 28 variables was available and the percentage of putative hybrid seedlings in each sample are indicated. The percentage of hybrids combines data from the main trial and seedlings left growing in the initial germination pots. The relative frequency of hybrids in natural stands of *E. cordata* (HYBRIDS - Table 2.2) is indicated. Unless otherwise indicated, the number of females pooled for each seedlot is at least five.

LOCATION	CODE	UNIVERSAL GRID REFERENCE E/W	ALTITUDE (m) N/S	NUMBER FEMALES POOLED (N)	NUMBER SEEDLINGS SCORED	% PUTATIVE HYBRID SEEDLINGS	HYBRIDS NATURAL STAND (0-2)	
E. cordata								
Perpendicular Mt.(top)	Pt	5933	52766	340	10	9	0 (25)	1 7
Perpendicular Mt.(low)	Pl	5930	52765	240	10	4	0 (26)	0
Prosser River	PR	5691	52881	100	4	10	90 (20) 5, 6	1 6
Hellfire Bluff	HF	5766	52683	270	10	7	81 (21) 5, 6	2 5, 6
Bluestone Tier	BT	5652	52932	350	10	7	5 (19) 5	0
Bream Creek	BC	5687	52614	120	10	6	35 (23) 5	2 5, 9
Hospital Creek	HC	5673	52660	240	10	5	5 (19) 7	1 5
Cape Queen Elizabeth	QE	5345	52109	100	10	6	5 (21) 5	1 5 or 6
Square Mountain	SM	5506	52695	370	9	9	0 (16)	0
Electrona	El	5200	52335	140	6	10	0 (19)	0
Snug Plain	SP	5120	52317	560	10	14	0 (26)	0
Falls Hill	FH	5128	52320	660	5	13	0 (31)	0
Herringback (top)	Ht	5113	52383	680	10	10	20(21)7	1 7
Herringback (low)	Hi	5119	52385	560	10	12	0 (20)	2 13
Chimney Pot Hill	CP	5225	52476	430	4	11	0 (19)	0
Leslie Road	LR	5177	52431	250	10	9	0 (23)	0
Combes Hill	CH	5140	52442	640	10	16	0 (31)	0
Mt. Lloyd	ML	4958	52572	500	10	17	0 (29)	0
Moogara	Mo	4930	52613	460	10	13	0 (23)	0
Tarrana	Ta	5714	52319	150	4	10	0 (23)	0
Brown Mountain	Bc	5428	52837	710	9	9	0 (24)8	2 5, 8
E. gunnii-archeri								
Projection Bluff(high)	PB	4776	53807	1100	10	4	0 (20)	
Pine Lake	P3	4760	53775	1150	10	6	0 (10)	
Shannon Lagoon	SL	4805	53513	1050	10	6	0 (13)	
Liawenee	LH	4682	53619	1150	10	4	0 (9)	
Snug Plains	SPg	5133	52330	600	10	30	0 (43)	
Snow Hill	SH	5693	53592	950	10	24	14 (42)9	
Jimneys Marsh	AT	5037	53375	1010		8	0 (28)	
Guildford	SV	3955	54168	660		3	10 (21)9	
Mt. Victoria	MV	5687	54228	790		21	15 (41)10	
Mt. Arthur	MA	5208	54283	500		29	0 (46)	

continued

LOCATION	CODE	UNIVERSAL		ALTITUDE	NUMBER	NUMBER	% PUTATIVE	HYBRIDS
		GRID REFERENCE		(m)	FEMALES	SEEDLINGS	HYBRID	NATURAL
		E/W	N/S		POOLED	SCORED	SEEDLINGS	STAND
					(N)			(0-2)
E. morrisbyi								
Calverts Hill	CH	5428	52453	80		16	7 (30) ⁵	
E. urnigera								
Mt. Wellington	MW			1000		5	0 (33)	
Herringback Range	HBku	5116	52383	610		6	0 (17)	
Jimneys Marsh	ATu	5037	53375	1010		9	0 (23)	
Wombat Moor	WM					7	0 (11)	
E. glaucescens								
Guthaga (13287 ¹)	GIG					8	25 (24) ¹¹	
Mt. Baw Baw	GIBB					8	4 (24) ¹¹	
Mt. Tingi Ringi(12455 ¹)	Glc					2	11 (18) ¹¹	
St. Gwinear (13273 ¹)	Gld					6	5 (21) ¹¹	
E. perriniana								
Hungry Flats	Tper			540		6	0 (10)	
Mainland ²	Mper			1200-800		10	0 (13)	
E. pulverulenta								
Ornamentals	Pui				3	4		
E. dalrympleana								
Central Plateau	Dal					5	0 (13)	
E. viminalis								
Cape Pillar/MM	Vim					7	0 (18)	
E. globulus								
Pooled	Glob					16	0 (29)	
E. johnstonii								
Herringback Range	John	5119	52385	560	4	9	31 (26) ¹²	
E. ovata								
Sandfly	Ov				5	6	0 (33)	
E. brookerana								
Bream Creek	Br				3	18	0 (28)	
Others								
Meredith Tier ³	MT	5763	53301	460	11	9	47 (18)	
Brown Mountain ⁴	Bu	5119	52385	560	4	12	0 (23)	

¹ CSIRO collection numbers

² Pooled from mainland seed sources (see Wiltshire and Reid 1987)

³ hybridized population (either *E. gunnii* x *barberi* or *E. cordata* x *barberi*)

⁴ selections from *E. cordata* population developing adult foliage

⁵ x *viminalis*/*dalrympleana*

⁶ introgressed populations

⁷ x *globulus* Ht = possible backcrosses onto pure female; HC = possible F1

⁸ 2 seedlings with emarginate apices similar to *E. urnigera*

⁹ x *E. ovata*/*brookerana*

¹⁰ x *E. rodwayi*

¹¹ x unknown

¹² x *cordata*; possible backcrosses onto pure female

¹³ x *E. vernicosa* subsp. *johnstonii*

Table 2.5 Seedling character codes, descriptions, grand means and standard deviations for untransformed data.

The transformations optimizing homogeneity of variances and the normality of residuals criteria and applied in all analyses are shown. The variables used in the calculation of canonical variates and Mahalanobis' distances between populations in analyses of the 21 *E. cordata* populations alone (cord), with closely related species (total), and the variables remaining in the step-down discriminant analysis of the 21 *E. cordata* populations (step-down) are indicated.

Code	Character description	Transformation	Analysis		
			cord	step -down	total
<u>Cotyledonary characters</u>					
COTPET	Cotyledon petiole length (mm)	none	+	+	+
COTL	Cotyledon length (mm)	none	+		+
COTW	Cotyledon width (mm)	none	+	+	+
COTAP	Cotyledon apex measure (mm)	none	+	+	+
ANTHcot	Anthocyanin pigmentation [0 none (green) - 2 red/purple]	none	+	+	+
<u>Seedling leaf characters</u>					
2nd node leaf					
LL2	Lamina length (mm)	none	+		+
LW2	Lamina width (mm)	none	+		+
LWP2	Distance from lamina base to widest point (mm)	ratio LWP2/LL2	+		+
ANTH2u	Anthocyanin pigmentation on abaxial surface 0 green - 2 red/purple	none			+
OILGL2	Oil gland density 0 none - 4 many	none			+
<u>Juvenile leaf characters</u>					
5th node leaf (cots = 0)					
LL5	Lamina length (mm)	none	+		+
LW5	Lamina width (mm)	none	+		+
LWP5	Distance from lamina base to widest point (mm)	ratio LWP5/LL5	+	+	+
BASE5	Basal measure (mm)	log 10(X+1)	+	+	+
ANTH5u	Anthocyanin pigmentation on abaxial surface 0 green - 2 red/purple	none			+
OILGL5	Oil gland density 0 none - 4 many	none	+	+	+
10th node leaf					
PET10	Petiole length (mm)				
LL10	Lamina length (mm)	none	+	+	+
LW10	Lamina width node 10(mm)	none	+	+	+
LWP10	Distance from lamina base to widest point - node 10(mm)	ratio LWP10/LL10	+	+	+
BASE10	Basal measure - node 10 (mm)	log 10(X+1)	+	+	+
APEX10	Apex measure - node 10 (mm)	-1/(X ² +1)	+	+	+
ANTH10u	Anthocyanin under 10th node leaf 0 green - 2 red	none			+
OILGL10	Oil gland density 0 none - 4 many (assessed over all leaves)	none	+		+
ANTHmid	Anthocyanin on midrib (adaxial surface)				

continued

Code	Character description	Transformation	Analysis		
			cord -down	step	total
CREN	CRENULATE Lamina MARGIN 0 straight - 2 crenulate	none	+	+	+
PETmax	Maximum petiole length (mm)	none			+
<u>Stem characters</u>					
HT	Height at 3 months (cm)	none	+	+	+
NODES	Number of nodes expanded at 3 months	\sqrt{X}	+		+
PROPLAT	Proportion of axillary buds on main stem developing laterals with > 1 node fully expanded	$\arcsin\sqrt{p}$	+	+	+
RUGOSE	STEM RUGOSENESSE 0 smooth - 2 rugose	none	+	+	+
STSHAPE	STEM SHAPE 0 round - 4 square	none	+	+	+
ANTHstem	Anthocyanin pigmentation on stem 0 green - 4 red	$\log 10(X+1)$	+	+	+
INTER10	Internode length measured across node 10 (mm)	none	+	+	+
INTRAmx	Maximum intranode length (mm)	none			+
INTRA10	Intranode length 10th node (mm)	none			
<u>Others</u>					
GLAUC	Seedling glaucousness 0 green - 4 highly glaucous	X^3	+	+	+

Figure 2.1 The distribution of verified (•) and unverified (o) sites of *E. cordata*. Population codes are detailed in Table 2.1. (PA= Port Arthur)

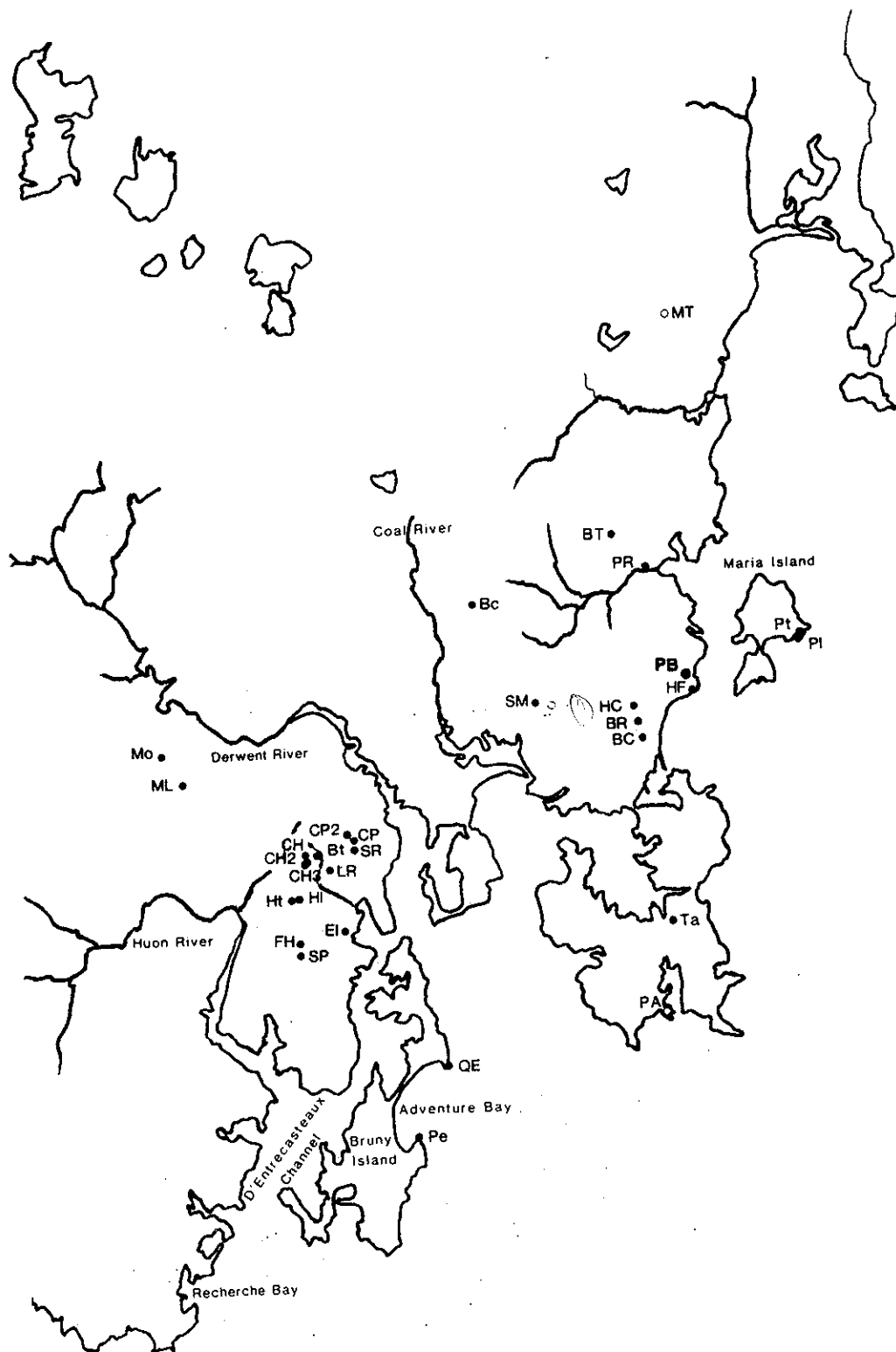
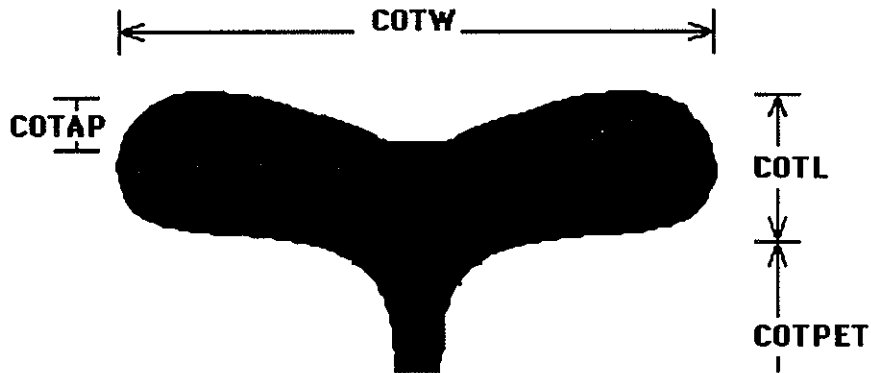
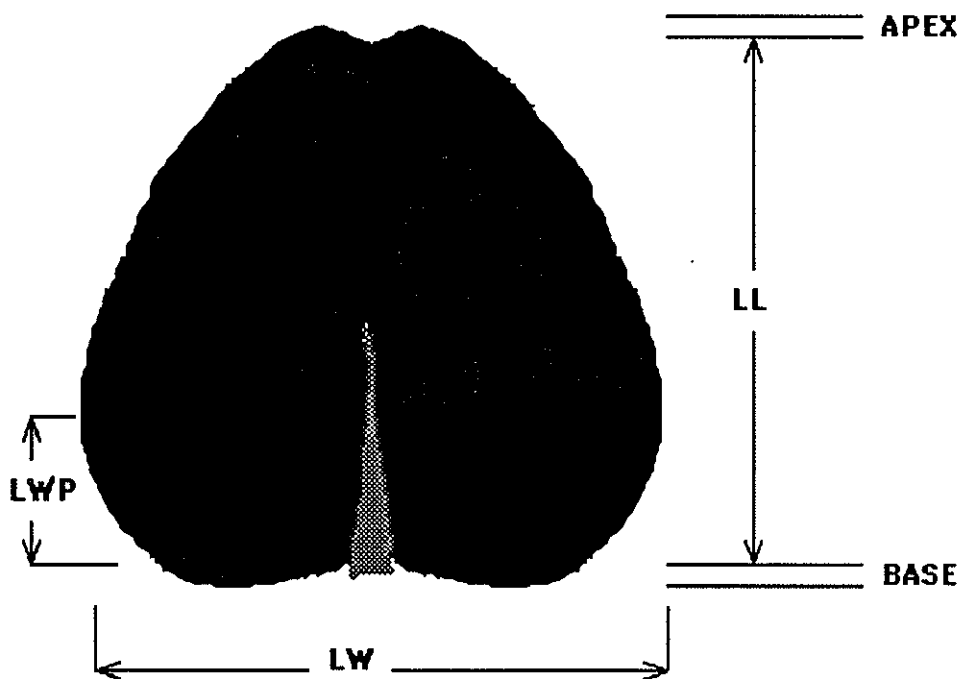


Figure 2.2 (a) Cotyledon and (b) adult and seedling leaf dimensions measured (not to scale).

(a) COTYLEDON



(b) LEAF

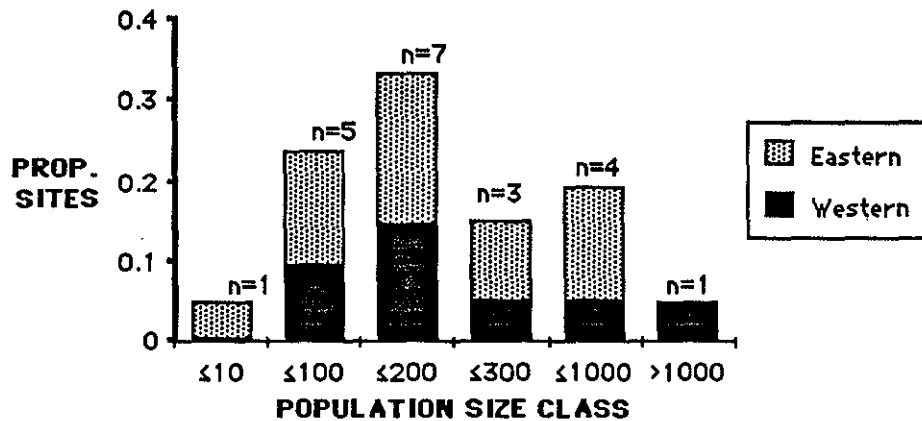


Chapter 3 Distribution and ecology

3.1 Distribution

All sites of *E. cordata* verified during this survey are indicated in Figure 2.1 and Table 2.1. Twenty-nine¹ separate populations have been located, ranging in size from single individuals to stands of over 5000 (average approximately 440; Fig. 3.1). In terms of population size, the main stronghold of the species is clearly the sub-alpine area around Snug Tiers (SP; Table 2.1), although populations in other areas, particularly the Derwent Valley (e.g. Ml and Mo), may have been more extensive prior to agricultural development.

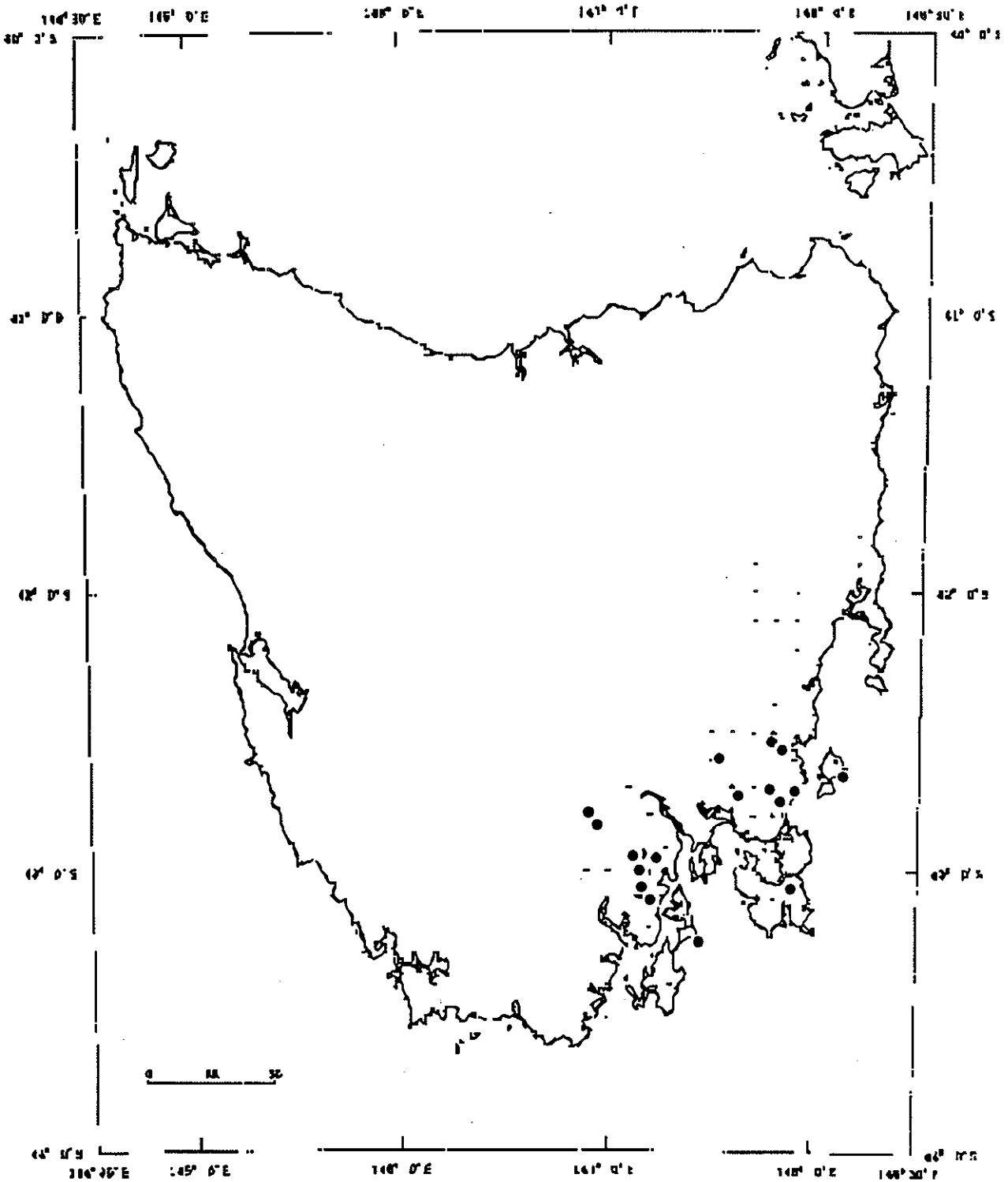
Figure 3.1 The proportion of *E. cordata* populations in each size class.
The classification of populations into 'eastern' and 'western' forms follows Fig. 4.11 (n=21).



The species is confined to the southeast of Tasmania where its distribution closely follows the limits of the southeastern glacial refuge (*sensu* Davies 1974). Its distribution is patchy and the suppressed and scattered nature of many of the small, insular populations is suggestive of a relict distribution pattern. The distribution of areas of similar climate to sites occupied by *E. cordata* is also relatively localized (Fig. 3.2). However, the distribution of *E. cordata* in these areas is clearly incomplete as comparable microhabitats are extensive within the predicted climatic zone. Populations are concentrated in two main geographic areas, viz. the Mt. Wellington Range in the west and the general vicinity of Prossers Sugarloaf in the east, which are separated by a major lowland disjunction between the Derwent and Coal Rivers. However, populations also occur on Bruny and Maria Islands, both of which would have been continuous with the Tasmanian mainland during glacial periods.

¹ Eight additional 'western' populations have recently been located near Chicks Perch (see Appendix 1).

Figure 3.2 The distribution of sites predicted by BIOCLIM as climatically suitable for *E. cordata* (- or +). Sites used to define the climatic envelope are indicated (●).



The geographical range of *E. cordata* has been previously indicated by Jackson (1965), Hall and Brooker (1972), Kirkpatrick and Backhouse (1980) and Brown *et al.* (1983). The northern-most population indicated in the latter work (Meredith Tier - MT) could not be included within *E. cordata* and although the population on Brown Mountain (Bc) deviates in the direction of the closely related species (e.g. *E. urnigera* or *E. morrisbyi*), it has closest affinity to *E. cordata* and has been included in this study (see Appendix 3). The southern extension of the range of *E. cordata* onto the southern end of Bruny Island and south of Southport in the Recherche Bay area as indicated by Jackson (1965) could not be verified despite an extensive search. The bioclimatic prediction (Fig. 3.2) suggests climatically suitable areas for *E. cordata* exist near Dover and Southport, but to date no stands have been located west or south of the Huon Valley. The type locality of *E. cordata* was believed to be Recherche Bay (Hooker 1856; Maiden 1913; Hall and Brooker 1972). However, this is incorrect as investigations (see Appendix 3) have shown that the type locality is Penguin Island which lies off Fluted Cape on Bruny Island (Pe Fig. 2.1). This locality could account for the record on the southern end of Bruny Island (Jackson 1965) and, while not included in the data defining the climatic envelope of *E. cordata*, an occurrence in the appropriate grid cell was predicted (Fig. 3.2).

Other populations of *E. cordata* no doubt exist and the areas of most likely occurrence can be predicted from Fig. 3.2. In particular, there is a high probability further populations occur in the general vicinity of Mt. Wellington (including Snug Plains) and Prossers Sugarloaf. Furthermore, the predicted occurrence and unverified reports suggest that further populations of *E. cordata* may occur on Tasman Peninsula.

3.2 Ecology

The geographic range of *E. cordata* transgresses Gentilli's (1972) moist subhumid cool to humid cool climatic zones and its climatic profile is given in Table 3.2. Populations occur over an altitudinal range from near sea-level (Pe 40m) to 710 m (mean= 374 m; n=21). There is a two-fold difference between sites in estimates of the mean annual rainfall (689 to 1408 mm) and the average minimum temperature in the coldest month ranges from 0.5 to 3.4 °C (Table 3.1). The synthetic rainfall and temperature variables form two sheaves of vectors which vary nearly at right angles across the geographical range of *E. cordata* (Fig. 3.3). Site rainfall increases toward the southwest whereas temperatures increase toward the southeast of the species range. The latter trend is a direct reflection of the tendency for site altitude to increase toward the northwest of the species range (Fig. 3.3). Geographical position and altitude are used to estimate, and are integrated in, the synthetic climatic variables. The aspect, slope and topographic position of sites vary widely (Fig. 3.4) and there is no trend for changes in altitude, aspect, topographic position or slope of the site to be associated. There is a marked trend for *E. cordata* to occur on poorer drained sites with increasing altitude, but with decreasing rainfall there is a shift to drier microhabitats. Populations mainly occur on medium to deep clay-loam soils (Fig. 3.4), ranging in pH from 6.0 to 7.0 and derived from Jurassic dolerite bed rock. The populations at Electrona (EI) and Cape Queen Elizabeth (QE) are the

only exceptions, both occurring on a Permian mudstone bedrock. Soils are usually well to poorly drained, although several eastern populations (HF, QE, Pt and TA) occur on shallow soils on relatively steep, excessively drained sites (Fig. 3.4). Populations usually occur on sheltered or moderately exposed sites (Fig. 3.10), although populations on the summits of Perpendicular Mountain, Falls Hill, Herringback Range and Cape Queen Elizabeth are more exposed. The latter population occurs as a pure stand on an exposed, dry cliff line 100m above sea-level (see Appendix 2).

Stands of *E. cordata* are rarely pure (Fig. 3.5) and the pure stands at Moogara (Mo), on the top of Perpendicular Mountain (Pt), on Cape Queen Elizabeth (QE) and Penguin Island (Pe not included in analysis) are exceptions. The main eucalypt species associated with *E. cordata* are *E. pulchella* (57% of sites), *E. globulus* (43%), *E. obliqua* (38%), *E. delegatensis* (29%) and *E. viminalis* (24%) (Fig. 3.6). Occasional associates include *E. coccifera* (10%), *E. tenuiramis* (10%) and (less than 5%) *E. rubida*, *E. urnigera* and *E. johnstonii*. In the east, *E. cordata* often occurs as a stunted mallee (1-2m), understorey species scattered (Fig. 3.5) beneath dry, open, lowland woodland dominated by *E. pulchella* with occasional *E. globulus* (Fig. 3.6). However, with increasing altitude and rainfall in the west there is a shift toward greater cover and site dominance by *E. cordata* (Fig. 3.5 and 3.3) and co-occurrence with species more commonly associated with wetter (e.g. *E. obliqua*) or sub-alpine habitats (*E. delegatensis*, *E. johnstonii*, *E. urnigera* and *E. coccifera*). It is only in these wetter sites that *E. cordata* achieves the tree habit (e.g. Leslie Road, LR; Mt. Lloyd, ML and Moogara, Mo). In many cases, particularly in the west of its range, *E. cordata* tends to replace surrounding eucalypt species on poorer drained wetter sites dominated by the sedge, *Gahnia grandis* (e.g. SP, LR, Mo, ML, SM, Bc, CP and HI).

Table 3.1 The bioclimatic profile of *E. cordata* (n=21).

Variable codes are detailed in Table 2.2.

SYNTHETIC

CLIMATIC			MIN	PERCENTILES		MAX
VARIABLE	MEAN	S.D.	VALUE	25	75	VALUE
MNANTEMP	10.0	1.47	7.8	8.5	11.2	11.9
MINMINTEMP	2.2	0.95	0.5	1.4	2.9	3.4
MAXMAXTEMP	20.0	1.51	17.7	18.4	21.1	22.2
TEMPRGE	17.8	0.71	16.9	17.3	18.1	19.4
TEMPWETQ	9.7	2.58	5.5	8.3	11.8	13.0
TEMPDRYQ	14.0	1.48	11.8	12.5	15.3	16.0
MNANRAIN	989	214.9	689	855	992	1408
RAINWETM	97	20	73	85	98	133
RAINDRYM	63	12.8	45	55	62	89
RAINRGE	34	6.7	25	30	39	46
RAINWETQ	276	58.5	212	240	279	388
RAINDRYQ	205	41.8	152	181	201	289

Figure 3.3 The pattern of geographical variation of environmental factors amongst sites of *E. cordata*.

The phenetic and floristic classification follows Table 7. 1 and variables are detailed in Table 2.2.

(* = floristically derived estimates; PC1,5 and 6 are PCA axes derived from the total analysis of adult and seedling characters discussed in section 4.3)

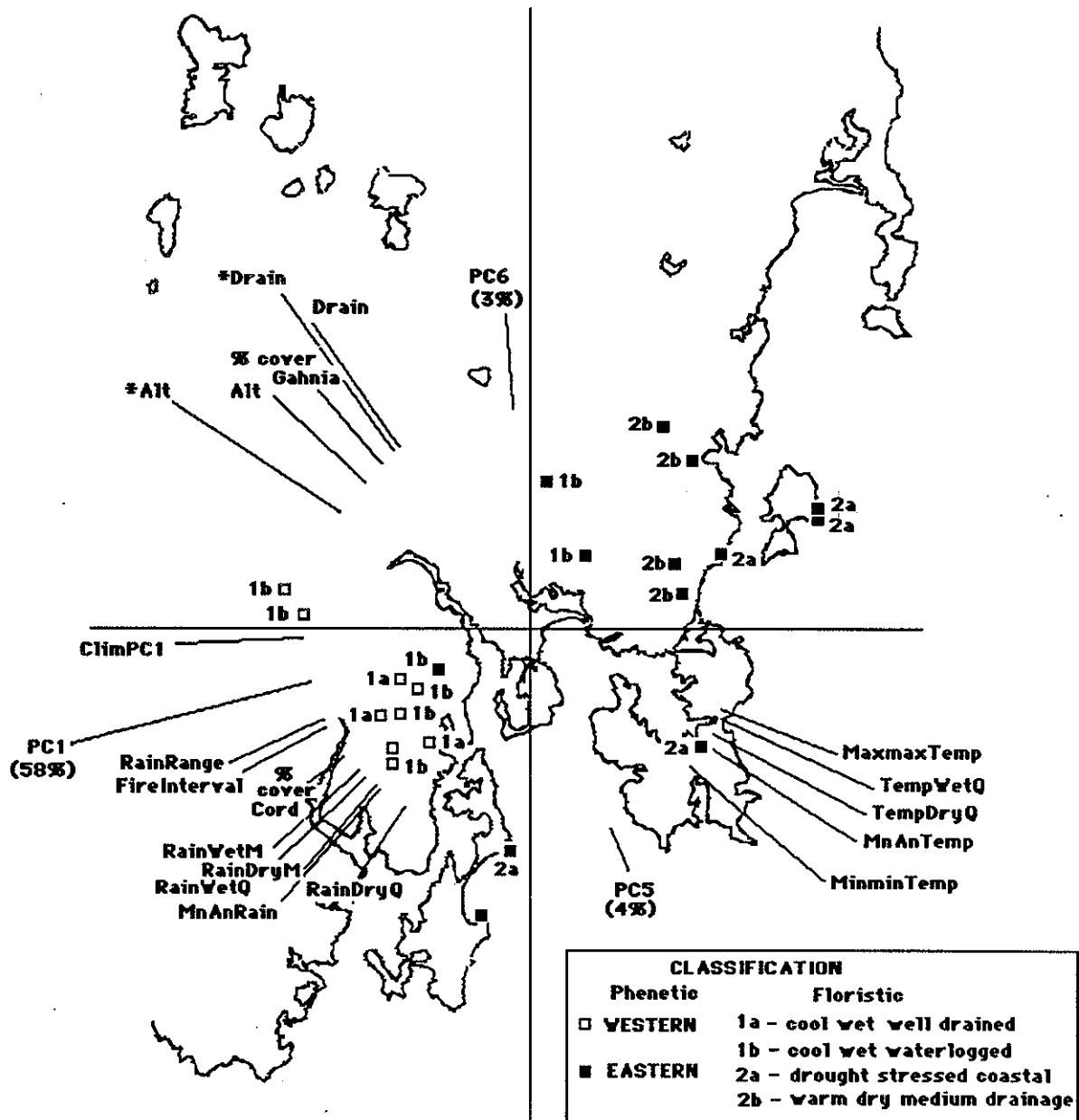


Figure 3.4 The proportion of *E. cordata* sites in the (a) topographic position, (b) slope, (c) aspect, (d) soil depth, (e) drainage and (f) wind exposure categories indicated (n=21).

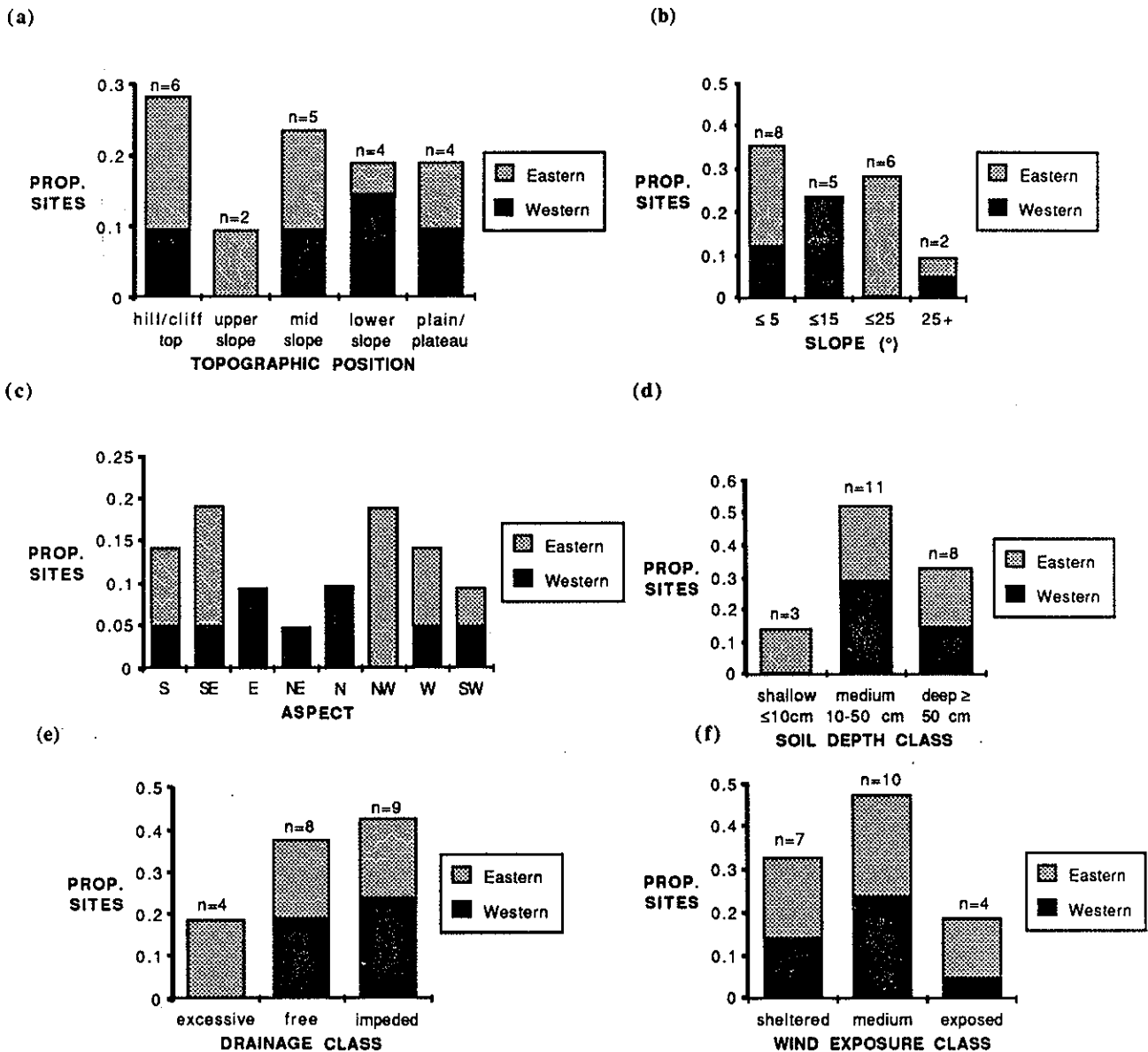
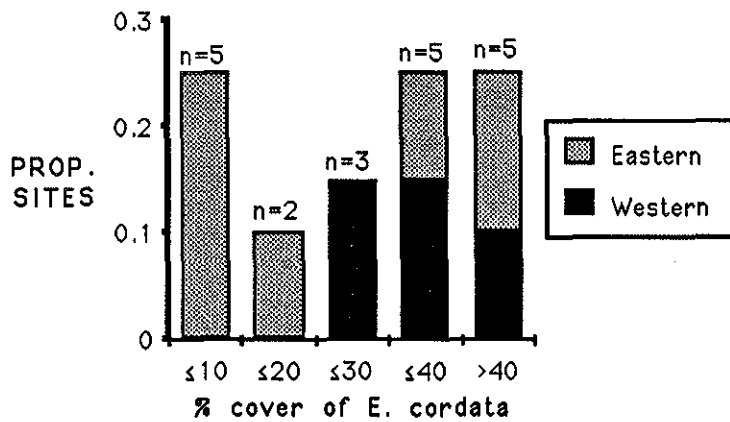


Figure 3.5 The proportion of *E. cordata* populations in the categories of (a) the percentage cover and (b) cover relative to the total cover of all eucalypts (n=20).

(a)



(b)

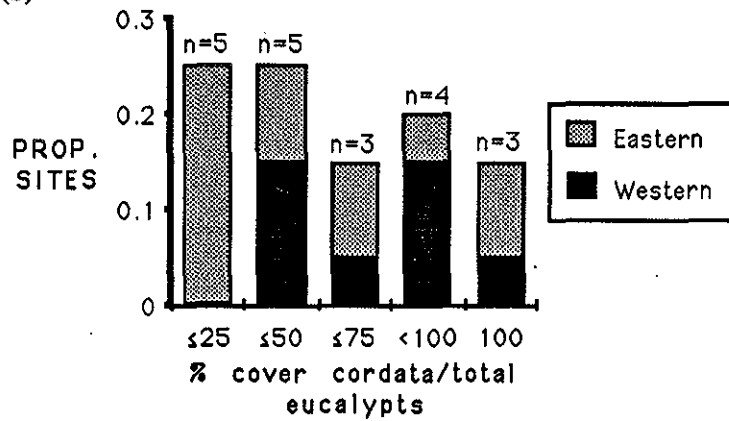
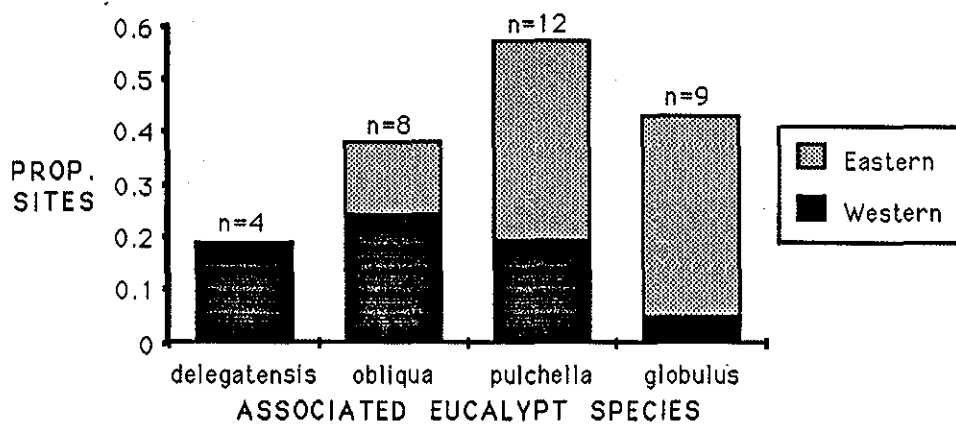


Figure 3.6 The proportion of *E. cordata* populations in which the eucalypt species indicated co-occur with *E. cordata*.



Chapter 4 Phenotypic and genetic variation amongst populations

4.1 Adult phenotype

Population mean values for the 16 adult morphometric characters studied are shown in Appendix 5. Variation between population means was highly significant ($P < 0.001$) for all of the characters studied (Table 2.3), with STSHAPE, LW, LL, GLAUC, MAXW, CAPL, BASE and RIMW (in decreasing order) showing the highest F values. The percentage of the total variability ($\sigma_t = \sigma_p + \sigma_w$) of each character attributable to the between (σ_p) and within (σ_w) population variance components are given in Table 2.3. While the distribution of variability differed widely between characters (σ_p/σ_t 20.7% - 90.9%), on average the interpopulation component of the variability in adult morphology is high, accounting for 50% of the total variation. Leaf and reproductive character sets are more or less comparable with an average of 52.3% and 45.8% respectively of the variability attributable to the interpopulation component.

The differentiation between populations was summarized by discriminant functions analysis using the full set of 16 morphometric characters, which yielded 11 significant ($P < 0.01$) eigen values, the first 3 of which accounted for 81% of the total variation between population centroids. Population centroids are shown in the space defined by these three discriminant functions in Fig. 4.1, and vectors indicate the importance and direction of variation of the major discriminating characters. There was very little redundancy in the morphological data set and only one character (APEX) was excluded from the step-down discriminant analysis.

The major axis (CV1) accounts for 63.7% of the interpopulation variation and is dominated by stem shape (STSHAPE), but also reflects differentiation in capsule (CAPL and MAXW) and leaf (LL, LW and BASE) size (Appendix 5). Populations with markedly angular stems and large leaves and capsules have positive values along CV1 and are separated from those with round stems and smaller leaves and capsules along this axis. The second and third axes mainly describe independent directions of variation amongst the eastern populations. The second axis (Fig. 4.1a) identifies the population from Hellfire Bluff (HF) as an outlier due to its reduced glaucousness and narrow leaves (see Appendix 5 - GLAUC, LW/LL). The third axis mainly reflects residual variation in leaf shape and describes clinal variation between the round stemmed populations separating those with narrow leaves such as Pe, Pt and PR from the broad leaved populations such as Bc and SM (Fig. 4.1b and Appendix 5). The type population from Penguin Island (Pe) has the narrowest leaves of all populations of *E. cordata* (Appendix 5 - LW/LL). This population also has a high frequency of individuals developing adult foliage (Table 2.1) and while all leaves measured were sessile, the narrow leaves may be a result of the leaves being ontogenetically more mature.

In the space defined by the ordination (Fig. 4.1), populations tend to form two relatively discrete clusters with only the population at Leslie Road (LR) intermediate. The two main groups of populations are consistently recovered using a variety of clustering techniques (e.g. average and single linkage - Fig. 4.2) and character combinations with the population LR consistently grouping with the populations with angular stems. These results strongly indicate a natural grouping of populations into two main morphs as indicated in Fig. 3.3. These morphs are geographically concordant and more or less correspond to eastern (round stemmed) and western (angular stemmed) variants. With the exception of the populations near Chimney Pot Hill (e.g. CP), these morphs are separated by a major lowland disjunction between the Derwent and Coal Rivers and the D'Entrecasteaux Channel (Fig. 3.3). The population on Chimney Pot Hill is one of the most eastern populations on the west side of this disjunction yet its morphology is typical of the eastern group (i.e. round stems, small leaves and capsules - Fig. 4.1 and Appendix 5). Moreover, within a localized area south of Mt. Wellington (Kingborough) there is considerable variation amongst populations and disjunct populations transgressing the full range of variation along CV1 occur within 20 km (i.e. CP, LR, El, Ht, FH, SP, CH and HI - Fig. 4.1). While the populations LR, El and Ht have closest affinities to other western populations (Fig. 4.2), they clearly deviate in the direction of the eastern populations because stem angularity is not well developed (STSHAPE) and the leaves are smaller than other populations in the western group (e.g. LL - Appendix 5).

The major component of differentiation between populations is accounted for by this grouping of populations. Nevertheless, in the discriminant space there is considerable differentiation amongst populations within each of these main groups, particularly the 'eastern' populations. This is reflected in the high dimensionality of the discriminant solution (11 significant eigen values) and the second and lower discriminant functions mainly separate eastern populations along unique directions of differentiation. Based on the significance of the Mahalanobis' distance between populations, only 4 out of a total of 231 pairs of comparisons were not significantly different ($P > 0.05$). Furthermore, with few exceptions all populations were highly significantly different ($P < 0.001$) from their nearest neighbour in the discriminant space and this is indicated in the single linkage dendrogram in Fig. 4.2b. This dendrogram clearly shows that the populations on Brown Mountain (Bc) and Hellfire Bluff (HF) are outliers, although they have closest morphological affinities to the eastern populations (Figs. 4.1 and 4.2). The population on Hellfire Bluff (HF) is unique as the adult foliage was not fully glaucous (GLAUC = 3) whereas in all other populations except Bc, the foliage of virtually all individuals sampled was highly glaucous (GLAUC = 4). The population on Brown Mountain (Bc) also deviates from other eastern populations on several reproductive characters (e.g. PEDU, CAPL, PEDI, PTMAXW and DISK - Appendix 5), the combination of which suggests variation in the direction of the closely related species *E. urnigera* or *E. morrisbyi* (Fig. 4.3).

4.2 Seedling phenotype

Population mean values for the 28 seedling characters examined are shown in Appendix 5 and ANOVA indicates significant differences ($P < 0.05$) amongst population mean values for all characters. Progenies were grown in a common glasshouse environment and these results indicate marked genetic differentiation amongst populations. However characters vary widely in the percentage of their total variability attributable to the interpopulation variance component (i.e. the intra-class correlation coefficient for populations, t_p - Lawrence 1982) which ranges from 2.1 to 87%, with STSHAPE, RUGOSE, LW10, GLAUC, COTL, CREN, COTW, LL10 and BASE10 (in decreasing order) showing the highest values. Over all seedling characters, the mean percentage attributable to the interpopulation component is 23% which is less than half the comparable estimate derived from adult characters scored from natural populations (50%, Table 2.3). Clearly, a large portion of the variation in seedling characters lies within populations, although with family identity not retained it is not possible to determine whether this is due to heritable between family within population effects or nonheritable sources.

For the population mean, there is a strong correlation between comparable seedling and adult characters (Fig. 4.4), indicating a large heritable component to the variation in adult morphology between populations. Furthermore, the grouping of populations defined on the basis of adult morphology is similar, but even more distinct, based on the seedling characters (Figs. 4.5 and 4.6), and there is even little overlap at the individual level (Fig. 4.5b). As in the adult analysis, stem shape (STSHAPE) is the main character weighting the discriminant function separating the two groups of populations in the seedling analysis (Fig. 4.5) and is contrasted against the degree of rugoseness of the seedling stem (Fig. 4.5; see also RUGOSE Appendix 5). Positive variation along the seedling CV1 (Fig. 4.5) toward the western, angular stemmed group also involves an increase in leaf size (e.g. LL10 and LW10 - Appendix 5). The western populations LR, EI and Ht deviate toward the eastern populations on both adult and seedlings characters (Fig. 4.1 and 4.5). However, while LR tended to be intermediate in the adult ordination (Fig. 4.1), it is clearly grouped with other western populations on seedling characters (Fig. 4.6), supporting the adult classification (Fig. 4.2).

With the set of seedling characters studied there are significant differences between virtually all populations, indicating marked genetic differentiation within *E. cordata*, not only between, but also within the major population groupings. For example, the significance of the Mahalanobis' distance between populations using only variables retained in the step-down discriminant analysis (see Table 2.5) indicated that virtually all populations were significantly different from each other. Only 7 (see Fig. 4.6b) out of a total of 210 comparisons (3%) were not significant ($P < 0.05$) and 86% of comparisons were highly significantly different ($P < 0.001$). As suggested from the adult samples, there was greater genetic differentiation amongst eastern populations of *E. cordata* than amongst the western group of populations. Lower order discriminant functions mainly differentiated amongst the eastern populations, and in the dendograms in Fig. 4.8 the vast majority of western populations fuse prior to even the first fusion of the eastern populations. Further, separate discriminant functions analyses of each set of populations indicated not only much greater total variability amongst the eastern populations (i.e. sum of the

eigen values for the eastern group was 15.5 compared to 6.1 for the western group), but much higher dimensionality of the genetic variation. For example, significant ($P < 0.001$) variation between populations occurred along six discriminant functions in the eastern analysis compared with only two for the western analysis.

The main axis of genetic variation (CV1) amongst western populations is in the direction of the eastern populations and orders the western populations as in Fig. 4.5. By contrast, the main discriminant function in the eastern analysis separates populations PR and HF from other eastern populations mainly on the basis of narrow leaves and reduced glaucousness (e.g. Fig. 4.5 and Appendix 5). This variation is in the direction of *E. viminalis*, a *Symphyomyrtus* species widespread throughout the geographical range of *E. cordata* and occurring in the vicinity of 50% of the eastern populations including PR and HF. Some of the seedlings from both of these populations fall within the envelope encompassed by the other eastern *E. cordata* populations in Fig. 4.5b and would classify as *E. cordata*, although the majority of seedlings from these populations lie outside this envelope. These deviant seedlings are intermediate between the eastern *E. cordata* and *E. viminalis* and are probably hybrids. This is also reflected in the deviant adult morphology of the population from Hellfire Bluff (HF - Fig. 4.2b). However, while the adult morphology of the Prosser River sample varies slightly in the direction of *E. viminalis* (e.g. increased pedicel length, relatively narrow, small leaves; Appendix 5), it is no more deviant than several of the more typical eastern populations (e.g. Pt and TA - Fig. 4.2b). In seedling morphology, these two populations and the population from Brown Mountain are clearly outliers from the main core of eastern populations (Fig. 4.6b). The population from Brown Mountain (Bc), which varied in the direction of *E. urnigera* or *E. morrisbyi* on reproductive characters, also exhibits some juvenile characteristics such as small broad leaves with an emarginate apex (APEX10, LL10, LW10 and LWP10 - Fig. 4.6) which again, in combination, is consistent with variation in the direction of at least some morphs of *E. urnigera* (see Barber and Jackson 1957; Thomas and Barber 1974) or *E. morrisbyi*.

4.3 Total variation

In order to integrate adult and seedling character sets (only compatible at the population level) yet maintain the advantage of operating in a discriminatory space within each set, the full suite of discriminant functions from the separate analyses were combined. The euclidean distances between populations in the space so defined were calculated and used as the overall measures of population dissimilarity. The principal component analysis (PCA) using the variance-covariance matrix were calculated across the full set of discriminant functions using GENSTAT. The PCA did not weight population values by the number in each group as does discriminant functions analysis.

The ordination of populations along the first two axes derived from this analysis is shown in Fig. 4.7 and the single and average linkage classifications of populations are shown in Fig. 4.8. The first PCA axis (57.7%) clearly separated 'eastern' and 'western' populations whereas the next three axes were primarily involved in

separating outliers from the main core of 'eastern' populations (Axis 2 [9.5%] - PR, HF; Axis 3 [5.9%] - Bc; Axis 4 [4.1%] - TA). The first two axes from this analysis were dominated by a virtual equal weighting of the corresponding discriminant functions from adult and seedling analyses where as other components involved more complex weightings. For the original adult and seedling characters maintained in the step-down discriminant analyses (e.g. Tables 2.3 minus APEX, Table 2.5) and selected ratios, the directions of vectors fitted by rotational correlation analysis into the space defined by the first 6 axes from this PCA (accounting for 84% of the total variation in the space defined by the 36 discriminant functions) are shown in Fig. 4.7.

An increase along axis 1 in the direction of the 'western' form is mainly associated with an increase in seedling and adult stem angularity but also reflects an increase in capsule size (RIMW, MAXW and CAPL) and adult and seedling leaf size (e.g. LL, LL10 and LW10) and to some extent cotyledon width (COTW). The separation of populations PR and HF from other 'eastern' populations along the second axis is mainly associated with a decrease in adult and seedling glaucousness (GLAUC), lamina base (BASE and BASE5) and lamina width (LW, LW/LL, LW10 and LW/LL10) and an increase in the redness of the seedling stem (ANTHST) (Figure 4.7). The Brown Mountain population (Bc) is separated from other eastern populations along axis 3 mainly due to an increase in PTMAXW, DISK, LWP, APEX10 and decrease in COTAP and VPOS, the combination of which is consistent with variation in the direction of *E. urnigera* or *E. morrisbyi*. The Tarrana population (TA) is separated from other eastern populations along axis 4 due to an increase in VSIZ and a decrease in ANTHCOT and RUGOSE. However, the morphological outliers differentiated on the second, third and fourth axes clearly have closest affinities to, and classify with, the eastern populations (Fig. 4.8). The single linkage dendrogram (Fig. 4.8b) indicates that the distances between these populations and their nearest neighbours are only slightly greater than the distance between the closest neighbours from 'western' and 'eastern' populations. Furthermore, the distance by which these outlying populations deviate from the majority of the 'eastern' core populations is less than the majority of distances between 'western' and 'eastern' populations.

4.4 Environmental correlates

Significant geographical trends or clines were apparent for many of the morphometric characters examined, with linear, or at least monotonic, trends being detected for 12 of the 15 adult and 13 of the 18 seedling characters (Fig. 4.9 - only those variables remaining in the step-down discriminant analyses were examined; seedling Table 2.5; adult Table 2.3 minus APEX). Most of the differentiation in adult and seedling variables is broadly aligned with longitude, although several variables vary orthogonally to the main sheaf of vectors, varying in an approximate north/south direction (e.g. LWP, ANTHcot, PEDU, COTW, COTAP, BASE5 and RUGOSE). However, the variables broadly aligned with latitude tend to show less differentiation between populations (F values in Fig. 4.9) and the correlations between the fitted vector and the variable tend to be less, indicating strength of the association with geographical position is weaker than for vectors aligned with longitude.

Environmental vectors were fitted by rotational correlation analysis into the ordination space defined by the first 6 dimensions of the PCA of seedling and adult discriminant scores shown in Fig. 4.7. Only the environmental variables indicated in Table 2.2 were fitted and, where the correlation between the fitted vector and the environmental variable was significant ($P < 0.05$), its direction in the space defined by the first two morphometric axes is indicated in Fig. 4.7. Significant morphological variation occurred along most of the environmental variables examined and a substantial proportion of the morphological variation in *E. cordata* can be related to variation in geographical position (LAT & LONG), climatic (e.g. MNANRAIN, MINMINTEMP, MNANTEMP, RAINRANGE), environmental (e.g. DRAIN, ALT, FIREINT) and floristic (e.g. *DRAIN, *ALT, %COV DRY/T and %COV CORD) variables (Fig. 4.7). None of the fitted environmental vectors were closely aligned with the first or fourth axes of the ordination and most dipped into other dimensions; many toward the 5th axis (e.g. SLOPE, SOILDEPTH, WINDEXP, MNANRAIN and TEMPRANGE). Only the first, fifth and 6th axes showed significant trends in geographic space. (Fig. 3.3).

The vectors most closely aligned to the first axis of the ordination were longitude (LONG - 120° ; $r = 0.93$), the vector describing floristic variation related to altitude (i.e. indirect estimate of site exposure to the alpine environment *ALT - 59° ; $r = 0.79$), mean annual rainfall (MNANRAIN - 60° ; $r = 0.78$) and the climatic index (ClimPC1 63° ; $r = 0.84$). Nevertheless, morphological variation along these and several other vectors (ALT, *DRAINAGE, RAINRANGE, MINMINTEMP, MNANTEMP, TEMPRANGE) compounds differences between 'eastern' and 'western' populations of the species, resulting in their separation to varying degrees. Longitude was the only fitted vector along which there was no overlap of populations of either form, although in the morphological space variation in this direction was clearly clinal (Figure 4.10a). However the vector of best fit of the first PCA axis into geographical space varied in a WSW direction (i.e. 13.5° from west; $r = 0.86$; Fig. 3.3) and when viewed in this direction the variation was stepped (Fig. 4.10b). There was a gentle, 90 km, cline occurring within the eastern populations toward the west then a rapid morphological change occurring over a distance of approximately 11 km from the 'eastern' Chimney Pot Hill population (CP) through the lowland 'western' populations at Electra (EI) and Leslie Road (LR) to the Combes Hill population (CH) (Fig. 4.10b).

Percentage rock cover (%ROCK - 146° ; $r = 0.62$) and slope (SLOPE 122° ; $r = 0.53$) were the only fitted vectors aligned in the direction of the second axis and, while the fit was relatively poor, this reflects the tendency for the introgressed populations PR and HF to occur on steeper, rockier sites than other 'eastern' populations. The only fitted vector aligned with the third axis was the percentage cover of *Gahnia grandis* (%GAHNIA 149°); the fit was poor ($r = 0.62$) yet reflected the abnormally high cover (87%) of this sedge beneath the morphologically outlying stand on Brown Mountain. This high cover is atypical for the eastern populations and the sedge, while common beneath 'western' stands, occurs in only 3 other stands of 'eastern' *E. cordata* (CP, PI and SM), and then the cover is relatively low.

The fifth PCA axis (3.6%) weakly varies in a southeasterly direction across the species range (Fig. 3.3) and tends to simultaneously separate coastal (+) and inland (-) 'eastern' populations as well as differentiate locally high (+)

and low (-) altitude populations within each group. Several environmental vectors are aligned in a similar direction to the 5th axis with mean annual rainfall (MNANRAIN 39°; $r=0.88$) and wind exposure (WIND 35°; $r=0.47$) increasing, temperature range (TEMPRANGE 138°; $r=0.66$) and soil depth (SOILDEPTH 146°; $r=0.46$) decreasing, and the understorey floristics shifting toward higher altitude and drought tolerant components with increasing values along the 5th PCA axis (*ALT 136°; $r=0.78$ and *DRAINAGE 140°; $r=0.74$ -see Fig. 5.4). This axis seems to describe morphological variation along an environmental gradient associated with increasing exposure to wind and drought in coastal or higher altitude environments and, although the fit of WIND and SOILDEPTH vectors into the morphometric space was not significant, these two vectors were the most closely aligned with the 5th axis. The alignment of morphometric variables with this axis suggests that variation along the 5th axis in the direction of increasing exposure is associated with a decrease in pedicel (PEDI 145°; $r=0.84$) and peduncle (PEDU 133°; $r=0.81$) length, cotyledon width (COTW 135°; $r=0.84$), anthocyanin content (ANTHcot 135°; $r=0.91$) and seedling growth rate (HT 148°; $r=0.58$). Reduction in peduncle and pedicel length and seedling growth rate with increasing exposure to the alpine environment has been similarly noted in the closely related species *E. gunnii* (Potts and Reid 1985 a, b). Furthermore, the significant geographic trends apparent for 4 of these characters (PEDU, COTW, ANTHcot and HT; Fig. 4.9) which increase in a northwesterly direction across the range of the species, are no doubt partly a consequence of this gradient. However, while morphological variation is detectable along this environmental gradient, the extent of differentiation between populations is small (3.6%) when compared to variation along the first axis (57.7%).

Of all the environmental variables fitted into the 6 dimensional morphological space, only latitude is closely aligned (30°) to the sixth axis. The sixth axis mainly describes geographical variation within the 'eastern' populations separating the southern populations CP, QE and TA from more northern 'eastern' populations. However, the differentiation between these populations only accounts for 2.8% of the total variation between population centroids.

Table 4.1 Grand means and standard deviations of untransformed seedling characters for the 21 *E. cordata* populations.

The F ratios for the difference between populations based on transformed values are indicated (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$) along with the percentage of variance between and within populations based on variance component estimates.

VARIABLE CODE	GRAND		F 20,186	% VARIANCE	
	Mean	s.d.		between	within
COTPET	2.38	0.622	2.45 ***	13.0	87.0
COTL	2.87	0.640	6.78 ***	36.7	63.3
COTW	7.34	0.092	6.58 ***	35.5	64.5
COTAP	0.35	0.184	2.97 ***	17.4	82.6
LL2	23.54	0.352	2.27 **	11.8	88.2
LW2	11.05	0.207	2.10 **	10.4	89.6
LWPTLL2	0.39	0.005	1.88 *	8.6	91.4
LL5	36.33	0.526	2.64 ***	14.7	85.3
LW5	27.89	0.444	2.77 ***	16.0	84.0
BASE5	1.27	0.070	2.69 ***	15.4	84.6
LWPTOLL5	0.34	0.004	1.32 *	2.1	97.9
LL10	42.28	0.661	6.28 ***	33.5	66.5
LW10	37.07	0.590	8.43 ***	43.9	56.1
BASE10	2.39	0.099	5.26 ***	29.6	70.4
APEX10	0.09	0.011	3.64 ***	21.5	78.5
LWPTLL10	0.32	0.004	2.80 ***	16.9	83.1
HT	32.48	0.432	3.22 ***	18.4	81.6
NODES	8.82	0.087	1.84 *	7.9	92.1
RUGOSE	2.30	0.063	14.26 ***	57.2	42.8
STSHAPE	2.27	0.111	69.47 ***	87.4	12.6
GLAUC	3.77	0.039	7.89 ***	41.5	58.5
ANTHSTEM	0.62	0.054	2.41 **	12.6	87.5
CREN	1.34	0.045	6.65 ***	36.5	63.5
INTER10	41.22	0.722	1.78 *	7.5	92.5
ANTHCOT	1.31	0.053	3.01 ***	17.0	83.0
OILGL5	0.89	0.049	2.10 **	10.1	89.9
OILGL10	2.24	0.063	2.05 **	10.6	89.4
PROPLAT	0.19	0.012	4.10 ***	23.9	76.1
			MEAN	23.0	77.0

Figure 4.1 Discriminant function analysis of adult characters.

Ordination of population centroids along the three major discriminant functions (CV1 -3) derived from analysis of the 16 adult characters indicated in Table 2.3. Populations are grouped into (o) eastern and (•) western forms based on the classification in Fig. 4.2a. The 95% confidence circle is based on average N.

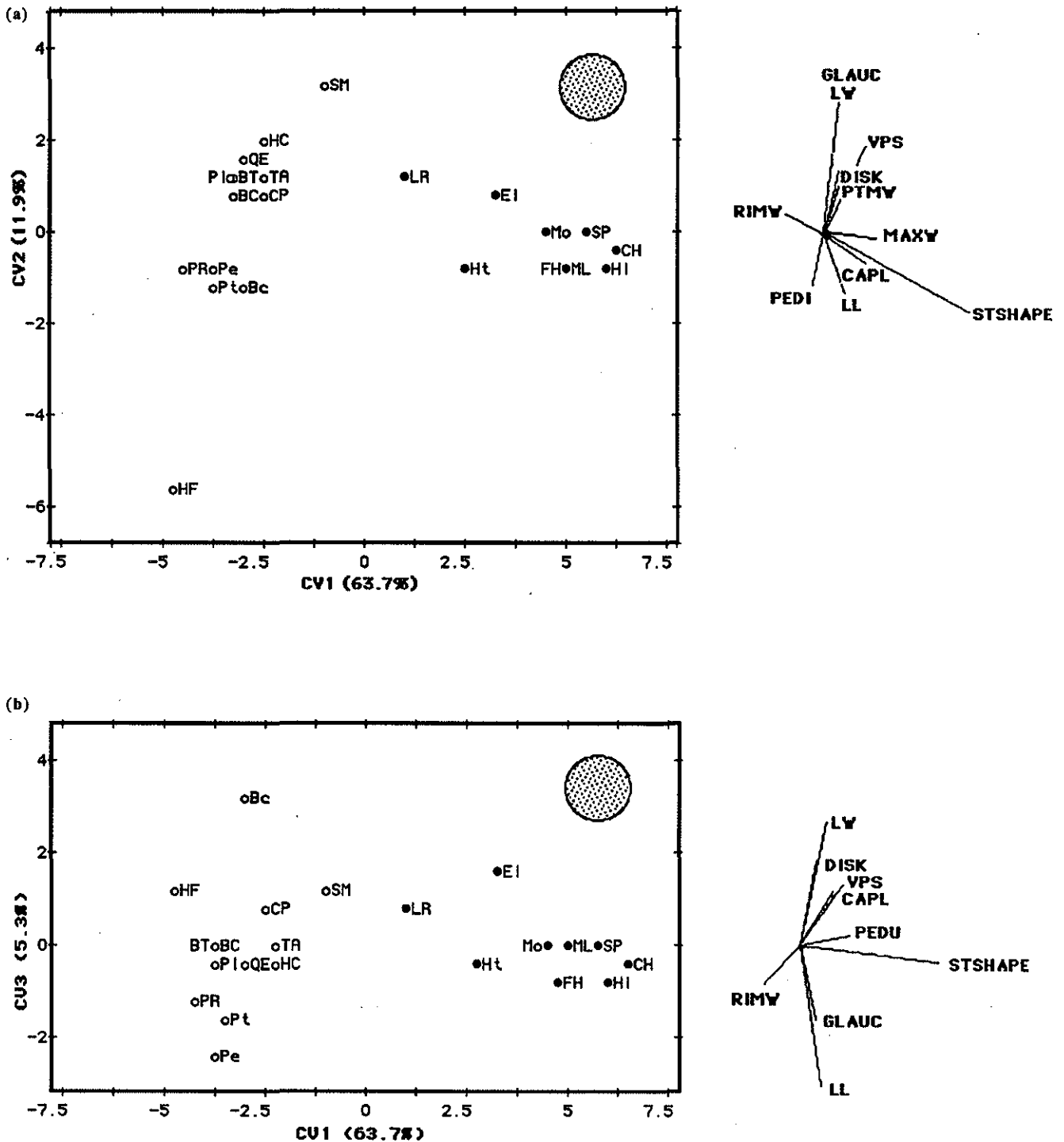
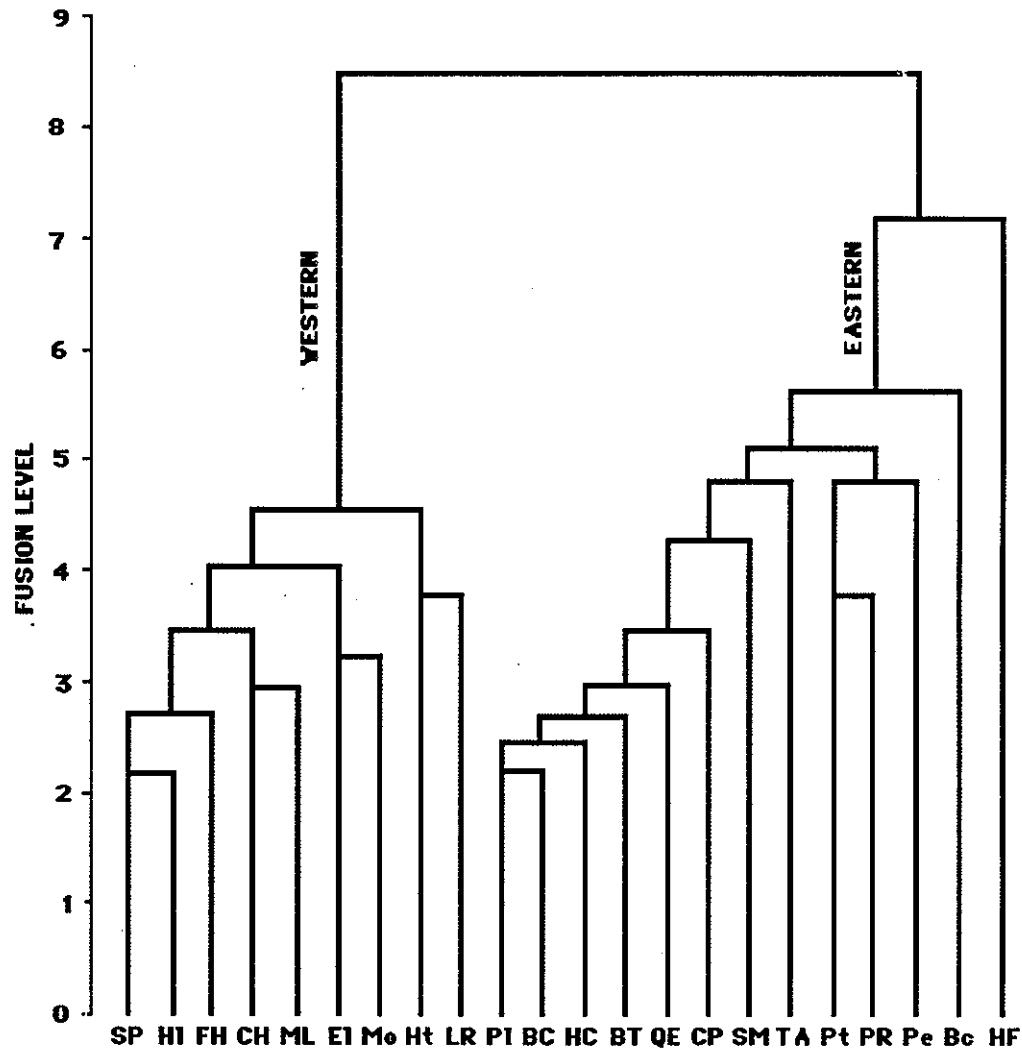


Figure 4.2 (a) Average linkage and (b) single linkage classifications of populations.

The Mahalanobis' generalized distance was the dissimilarity measure and was calculated using the 16 morphological characters indicated in Table 2.3.

(a) Average Linkage



(b) Single Linkage

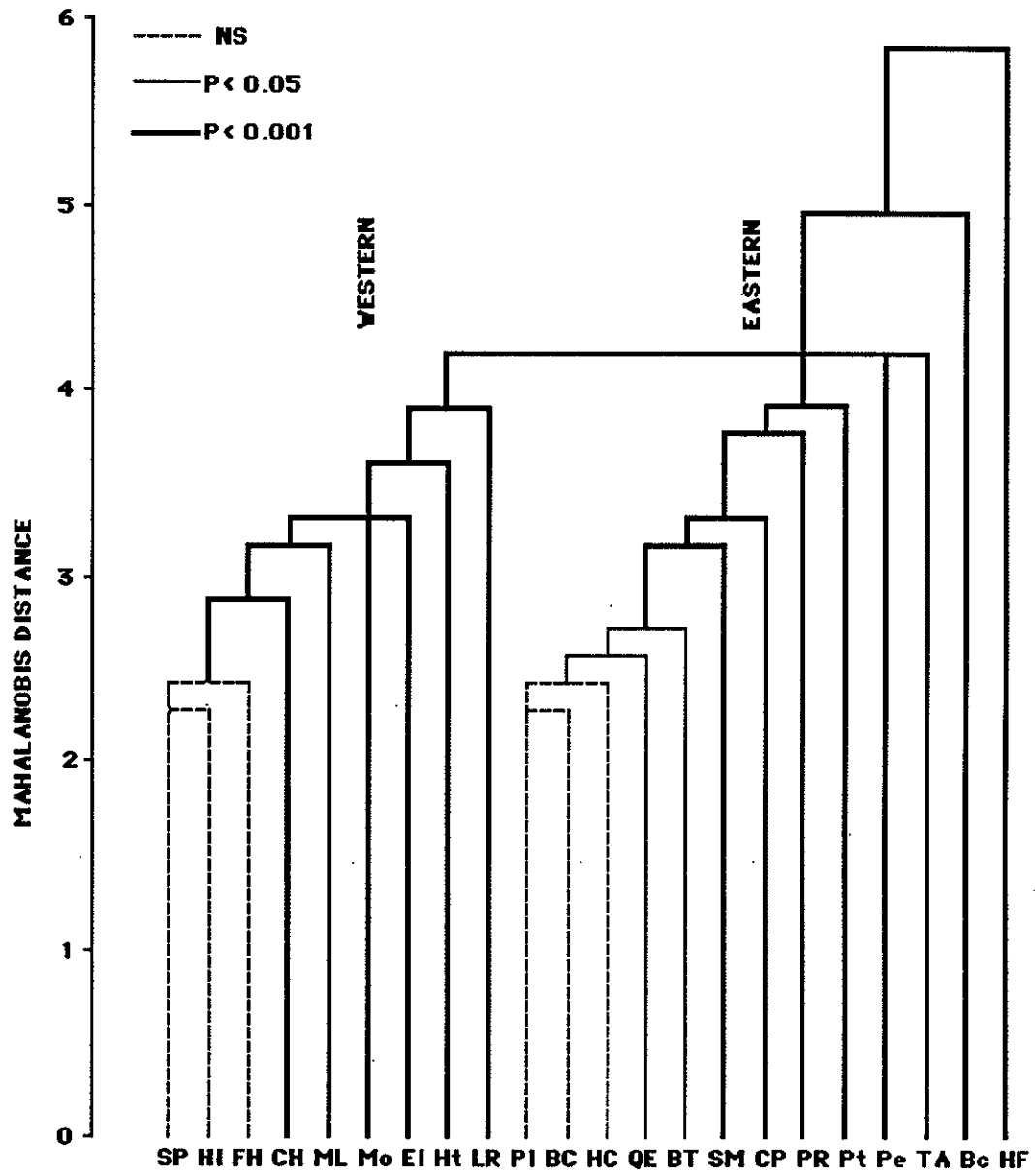


Figure 4.3 Representative capsules from populations of *E. cordata*, closely related species, *E. globulus* and the artificial F1 hybrid *E. globulus* x *cordata*.

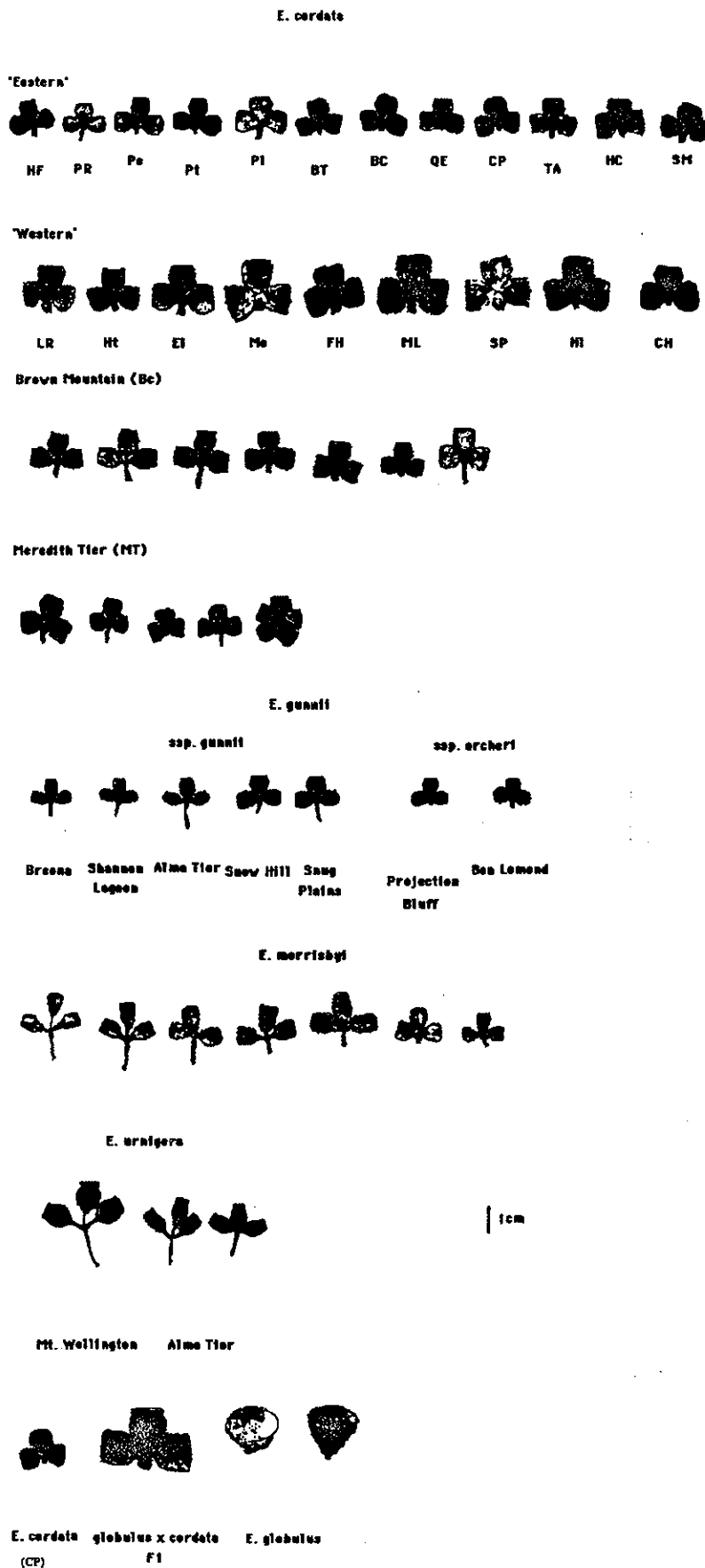


Figure 4.4 Regression between population means for comparable seedling and adult characters.

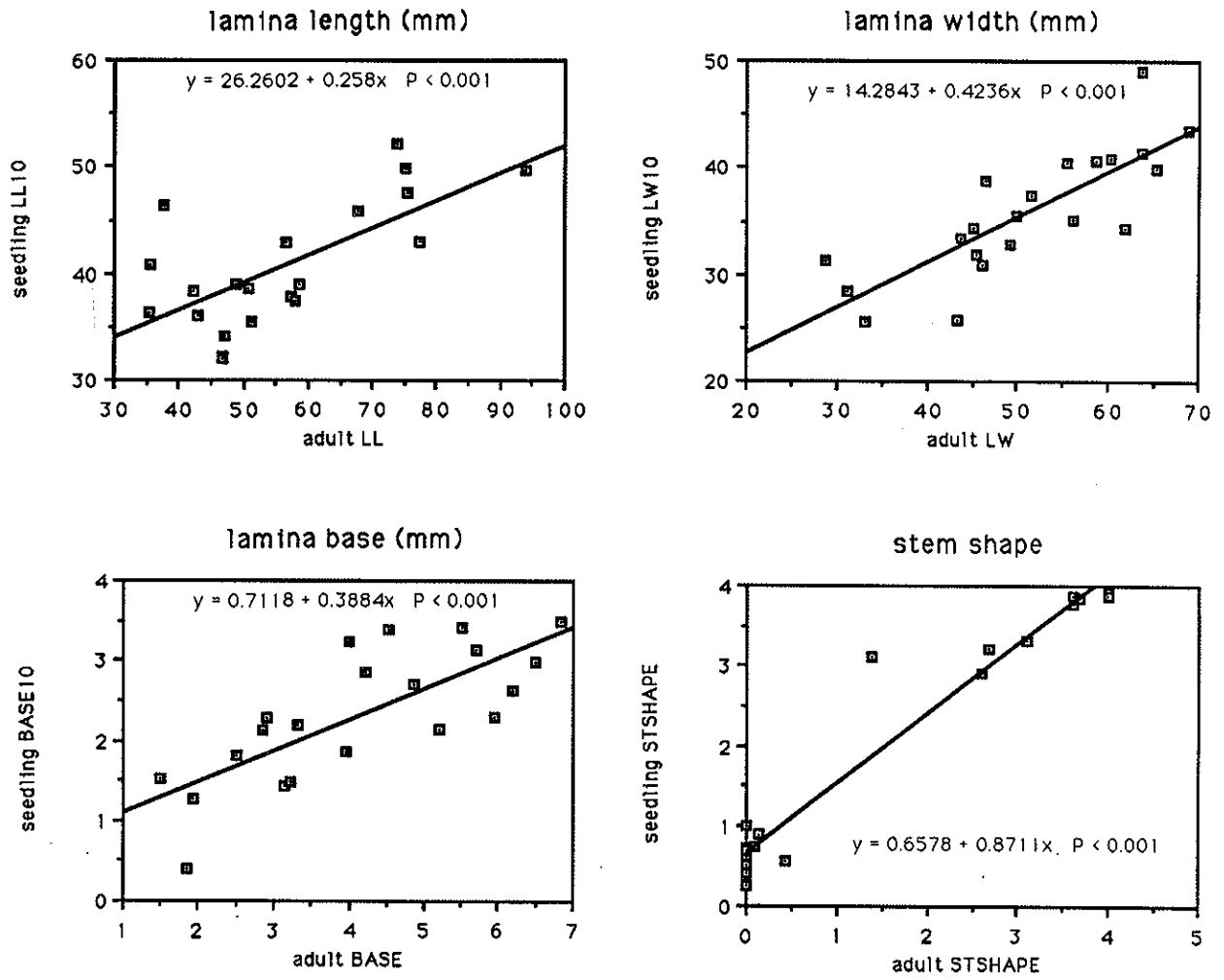
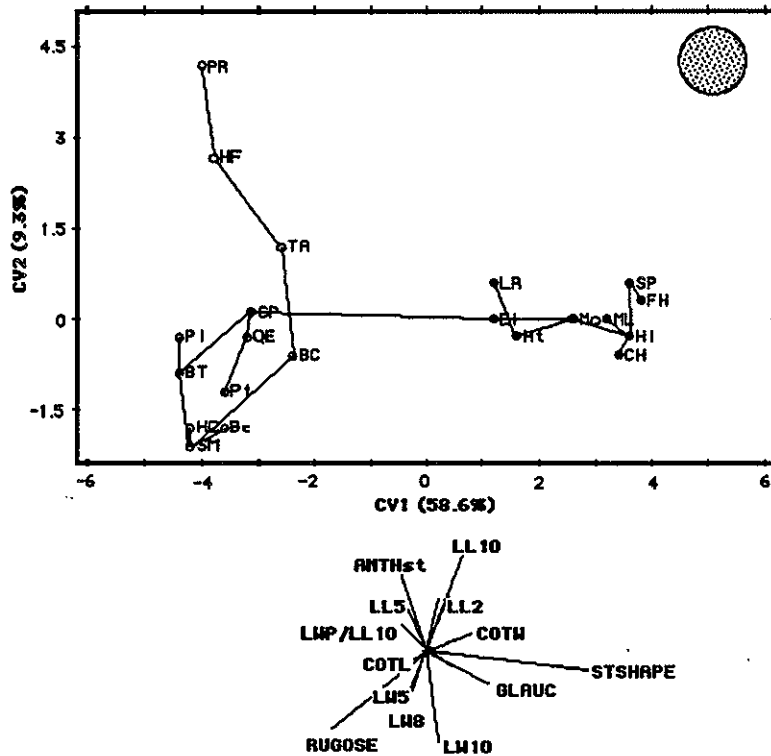


Figure 4.5 Discriminant function analysis of seedling characters.

Ordination of population centroids along the first two discriminant functions (CV1 and CV2) derived from analysis of the 28 seedling characters indicated in Table 2.5. Populations are grouped into (o) eastern and (●) western forms based on the classification in Fig. 4.2a. The minimum spanning tree and 95% confidence sphere for the centroids (based on the average N) are shown in (a) and individuals and population centroids are plotted in (b) (E = 'eastern', W = 'western' and 3 = PR 4 = HF).

(a)



(b)

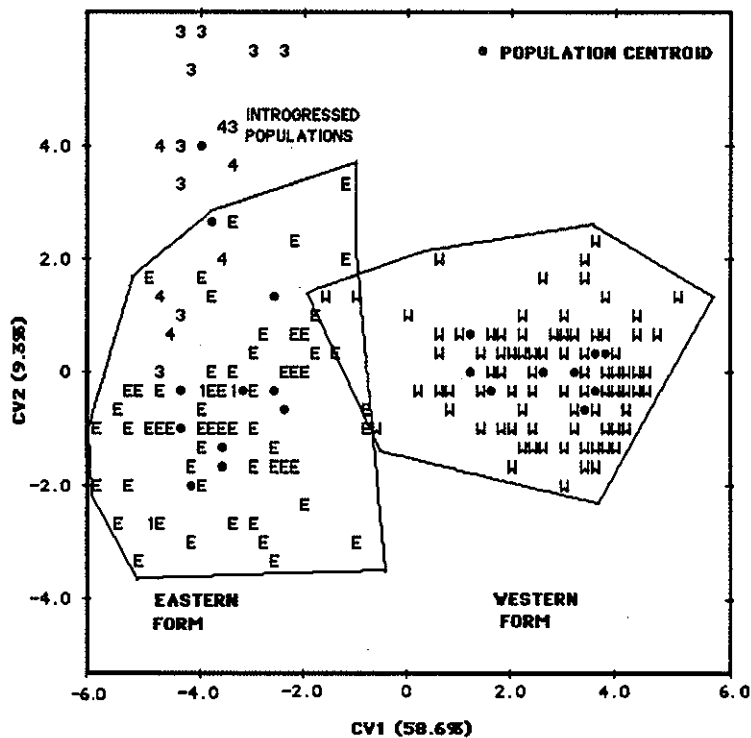
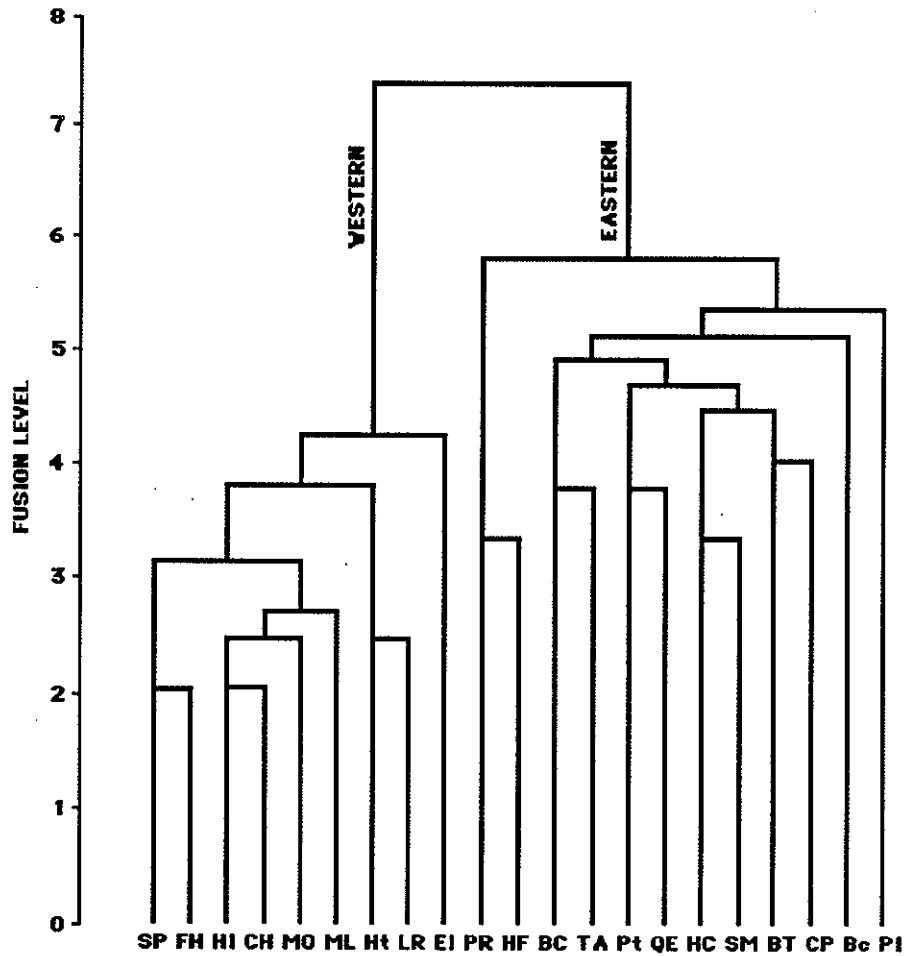


Figure 4.6 (a) Average and (b) single linkage classifications of populations based on seedling characters.

The Mahalanobis' distance was the dissimilarity measure and was calculated using the 28 morphological characters indicated in Table 2.5.

(a) Average Linkage



(b) Single Linkage

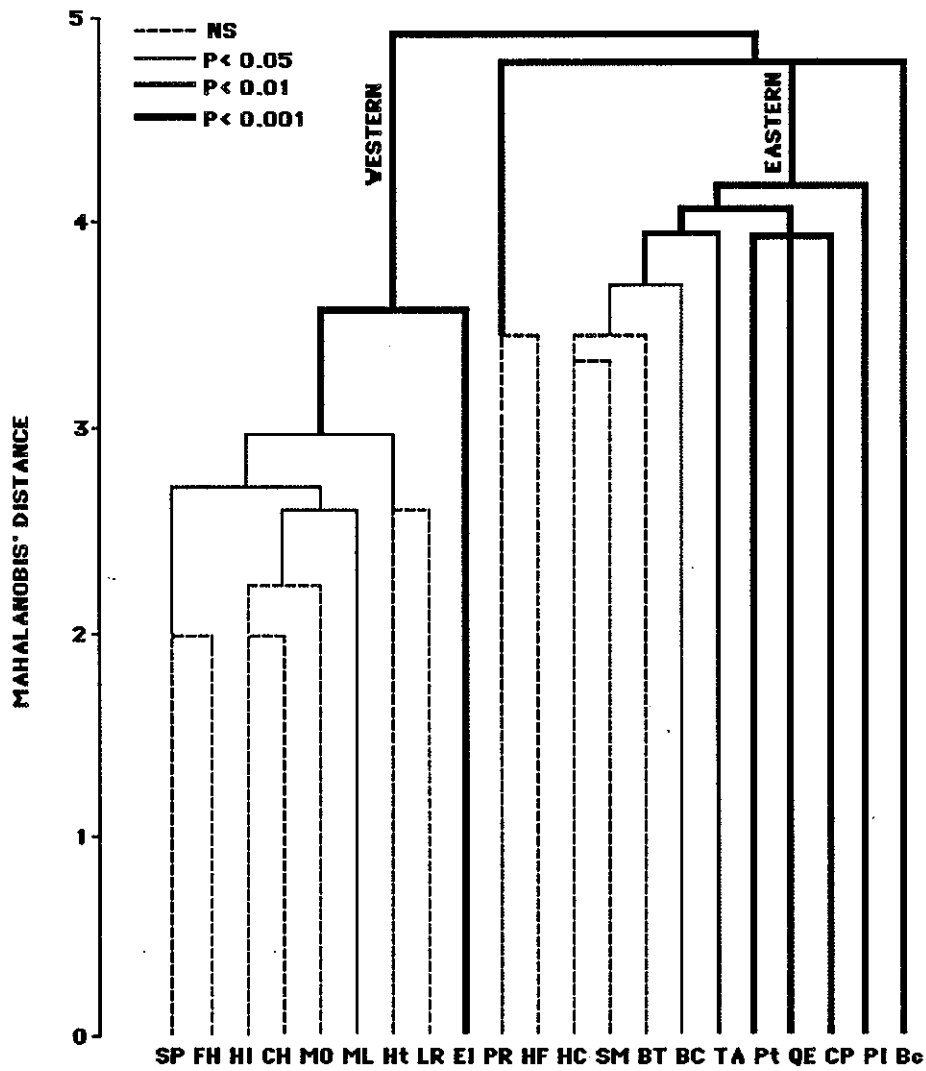


Figure 4.7 PCA ordination of populations based on combined seedling and adult discriminant scores.

The direction of vectors fitted by rotational correlation analysis into the space defined by the first 6 axes of the PCA are indicated for adult and seedling characters. Deviation of the vector length from unity (STSHAPE approx. 1) indicates the extent vectors dip into other dimensions and the relative fit of the vectors (r) into the ordination is indicated by their width.

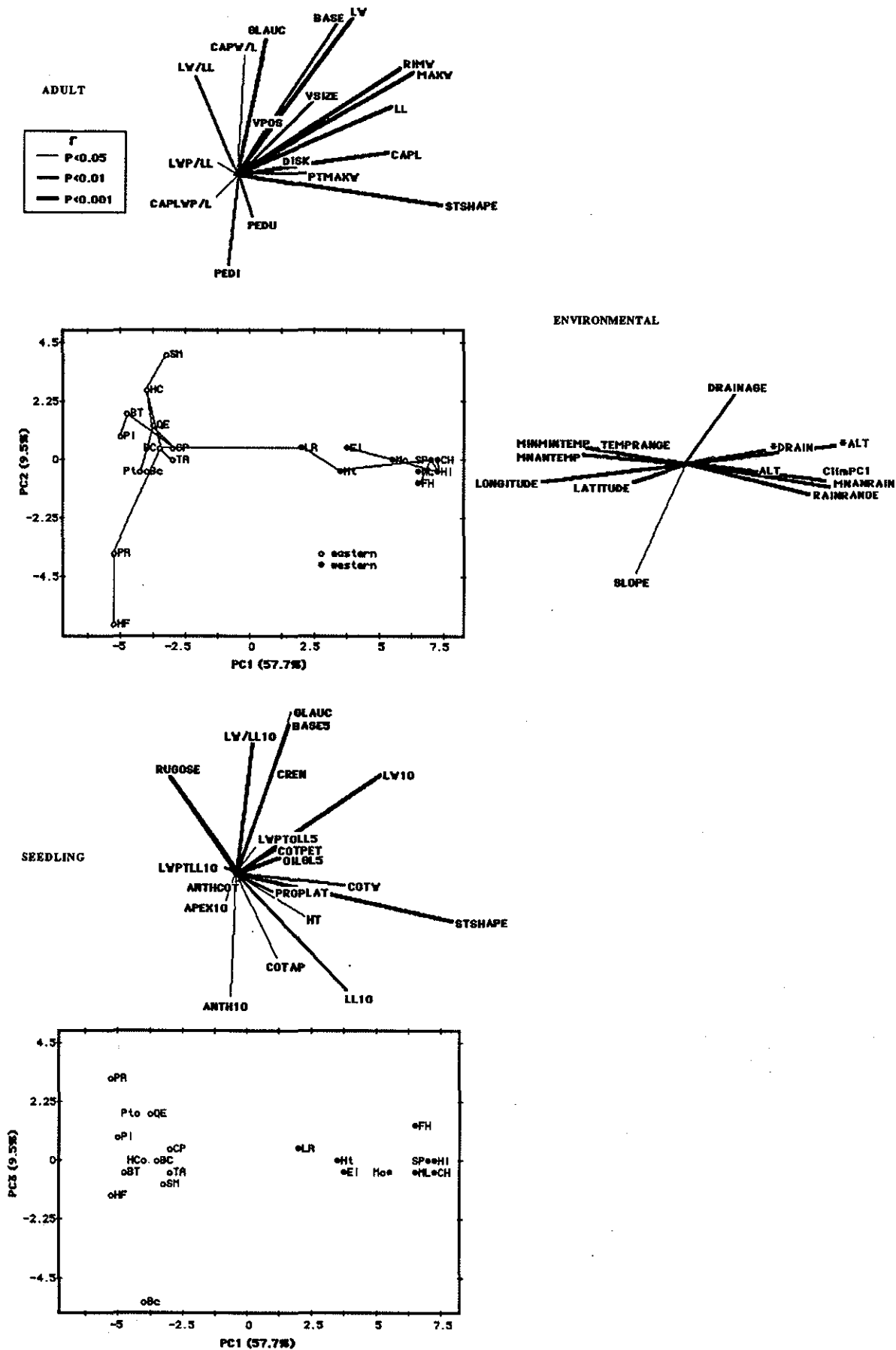
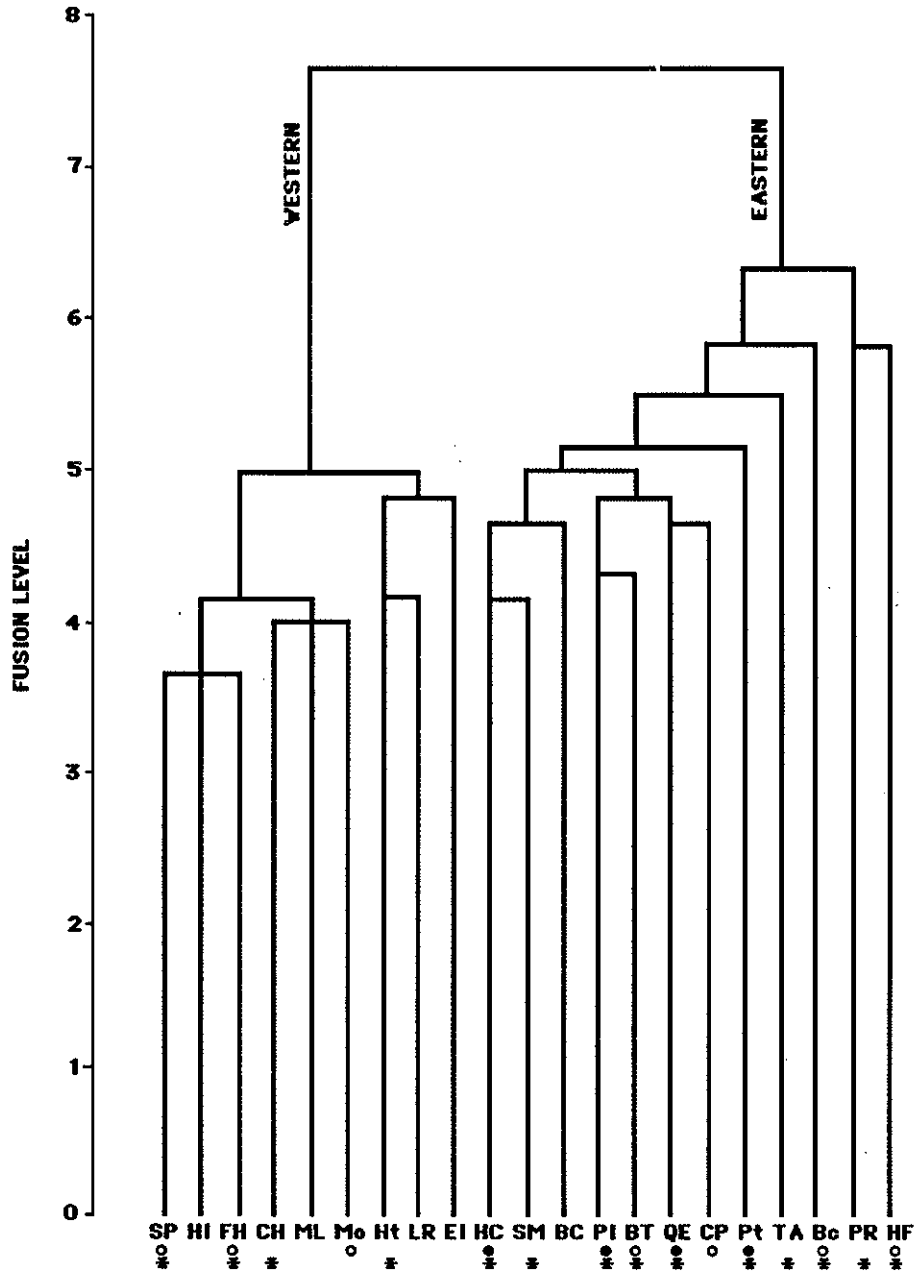


Figure 4.8 (a) Average linkage and (b) single linkage classifications of populations based on seedling and adult characters.

The dissimilarity measure was the euclidean distance between populations calculated using scores on adult and juvenile discriminant functions. [• high conservation status (State, Flora or Game Reserve); o located on crown land or state forest or in the case of Mo ANM seed reserve; * relatively undisturbed]

(a) Average linkage



(b) Single linkage

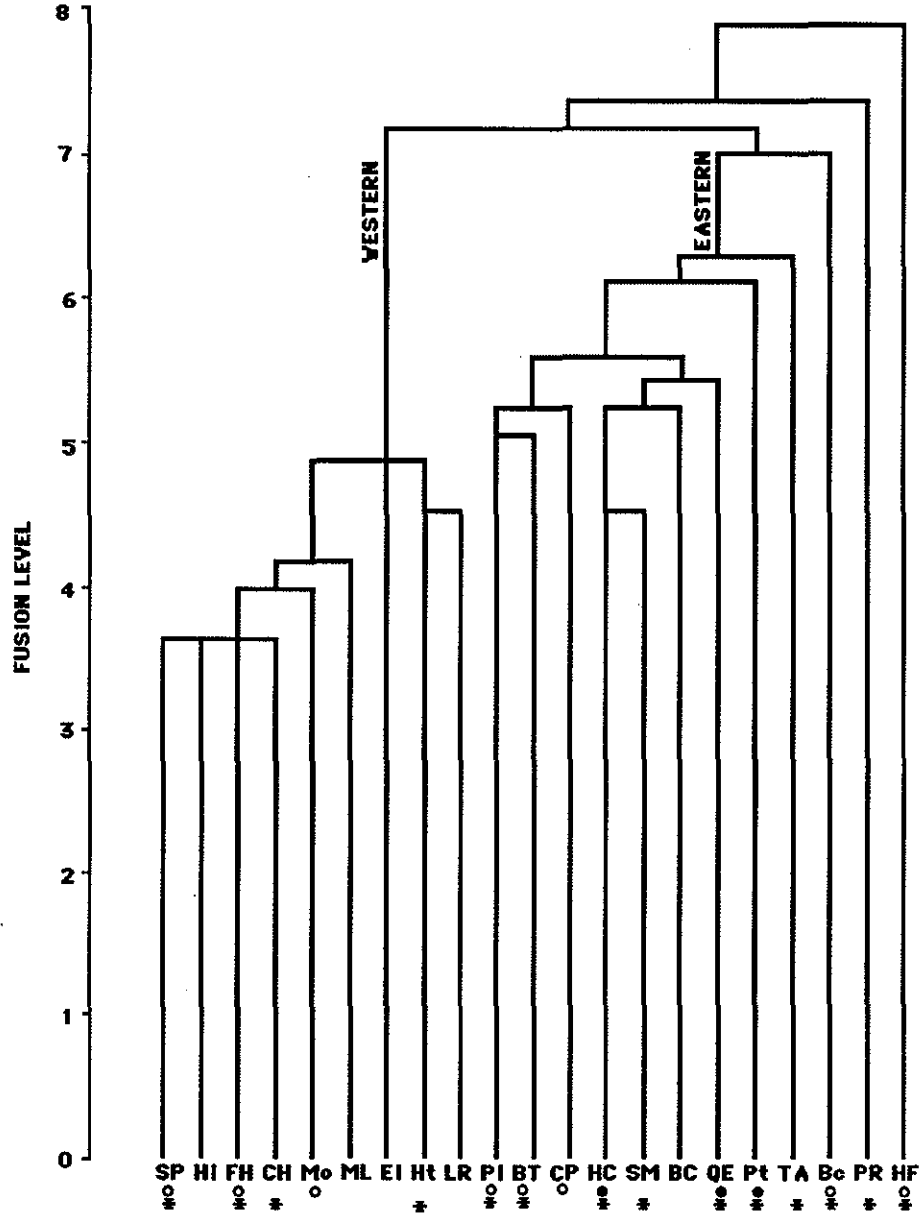


Figure 4.9 Directions of clinal variation in adult and seedling characters.

The direction and significance of the fit of morphometric vectors fitted in to the geographic space by rotational correlation analysis. Character codes are detailed in Tables 2.2 (Adult -upper case) and 2.5 (Seedling - lower case). Population differentiation is significant ($P < 0.001$) for all characters and the length of the vector is proportional to the F-value (except for PC1, PC5 and PC6 which are principal components from section 4.3).

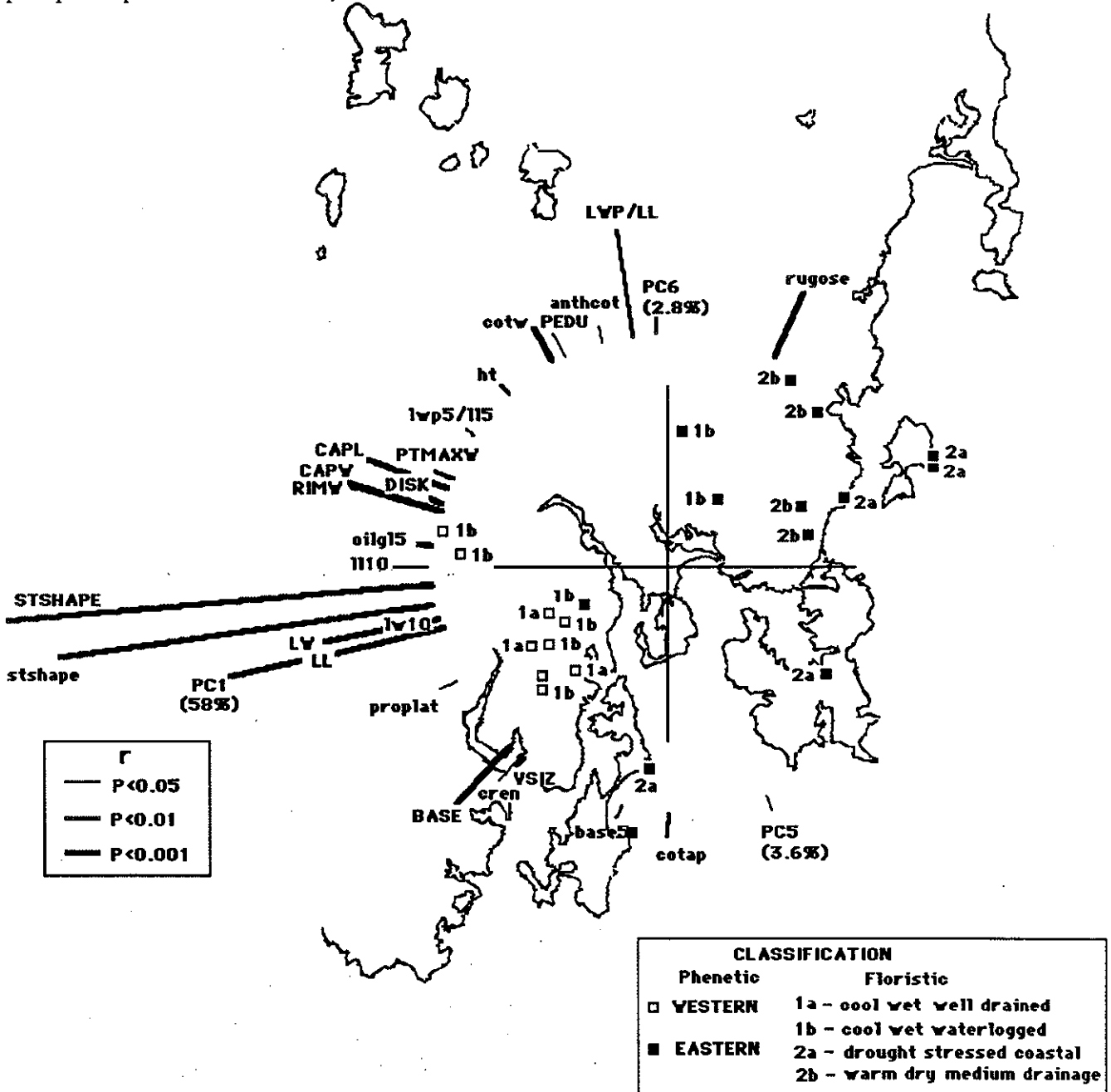
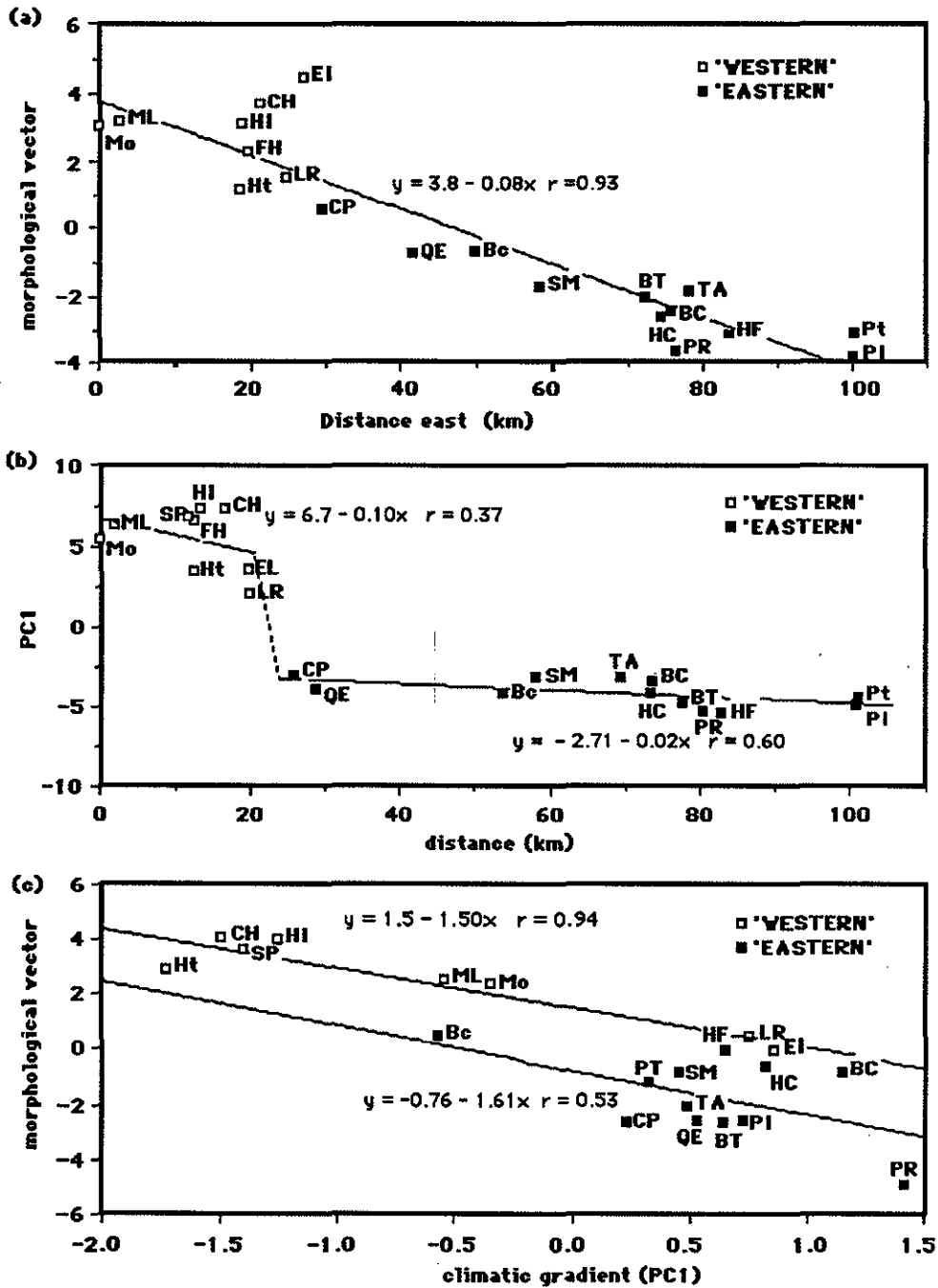


Figure 4.10 Pattern of phenetic variation associated with geographic and climatic gradients.

(a) Longitude and (c) the climatic index fitted into the 6 dimensional phenetic space (see Fig.4.7) and (b) PC1 from Fig. 4.7 fitted into geographical space.



Chapter 5 Floristic variation amongst populations

5.1 General site floristics

A total of ninety-seven species were recorded with *E. cordata* and the species are listed in order of decreasing frequency of occurrence in Appendix 6. Only seven species (*Pultenaea juniperina*, *Leptospermum scoparium*, *Lomatia tinctoria*, *Callistemon pallidus*, *Eucalyptus pulchella*, *Gahnia grandis* and *Acacia verticillata*) were common to more than 40% of the stands of *E. cordata*. Forty percent of the species occurred on only one (5%) and fifty eight percent on only two (10%) sites. The mean cover of *E. cordata* was 27.4 % whereas only three associated species had a mean cover greater than five percent (*Gahnia grandis* 20.8%, *Eucalyptus pulchella* 13.5%, *Pultenaea juniperina* 7.3%). The total cover of understorey species (growth form ≤ 7) beneath stands of *E. cordata* ranged from 10.4% to 118% (mean 62.5%). The understorey richness ranged from 5 to 16 species (mean 9.3 species), but the two most abundant species at each site accounted for 30 to 92% of the total cover (mean 66.5%).

5.2 Site ordination: indirect gradient analysis

The two-dimensional NMDS ordination shown in Fig. 5.1 (stress= 0.21) was accepted as an adequate representation of the pattern of floristic variation amongst the 20 sites of *E. cordata*. The floristic variation shown in the ordination is strongly related to geographic and topographic position, and seems to mainly reflect the interaction of two nearly orthogonal environmental gradients, both of which appear to be independently related to site water relations. The compositional change running approximately 25° to axis one is related to broad-scale climatic variation associated with increasing rainfall and decreasing temperatures toward the west (Fig. 5.1 - ClimPC1, MNANRAIN). The BIOCLIM (MnAnRain) and the composite climatic (ClimPC1) vectors are broadly aligned in this direction (Fig. 5.1), and the decreasing temperature is partly a consequence of an increase in the altitude of sites of *E. cordata* toward the northwest of the species range (Fig. 3.3). The climatic gradient results in a compositional change from species generally associated with lowland, dry sclerophyll (e.g. *Eucalyptus pulchella*, *Eucalyptus globulus*, *Astroloma humifusum*, *Bursaria spinosa*) to those generally associated with medium altitude, wet sclerophyll vegetation (e.g. *Cassinia aculeata*, *Acacia riceana*, *Eucalyptus delegatensis*, *Eucalyptus obliqua*). Superimposed, but relatively independent of this compositional change is floristic variation arising from localized variation in site drainage (or drought stress) which in the ordination runs at nearly right angles to the climatic gradient (Fig. 5.1). Fitted vectors for topographic position (TOPOG), drainage (DRAIN), wind exposure, percent rock cover and soil depth were aligned in this direction, although the fit of the latter three variables was not significant (Fig. 5.1). The angles between the vectors fitted by rotational correlation into the floristic ordination for MNANRAIN or CLIMPC1 and DRAINAGE are 84.2° and 70°, and between MNANRAIN or CLIMPC1 and TOPOG, 97° and 87° respectively.

In the climatically drier region, local floristic variation in the direction of increasing water availability is mainly associated with a change from excessively drained (DRAIN = 1), steep, wind exposed microhabitats to sheltered, moderately drained (DRAIN = 2) sites, and more-or-less corresponds to the environmental difference between exposed coastal and inland sites. Increasing drought stress is associated with an increase in the occurrence and cover of *Banksia marginata*, *Casuarina stricta*, *Exocarpos cupressoides*, *Pultenaea daphnoides*, *Lepidosperma laterale* and *Lomatia tinctoria* (see photos Appendix 2). On relatively wetter sites (DRAIN = 2), the occurrence and cover of *Leptospermum scoparium*, other eucalypt species [*E. pulchella* (e.g. Fig. 5.1) and *E. viminalis*], *Goodenia ovata* and *Callistemon pallidus* increases (e.g. BT - Appendix 2). In the climatically wetter region, however, variation along the second gradient in the direction of increasing water availability is mainly associated with a transition from moderate to poorly drained microhabitats (Fig. 5.1). Poorer drainage results in increasing understorey cover, decreasing understorey diversity, and increasing cover of *Gahnia grandis* (e.g. Fig. 5.1), *Leptospermum scoparium* and *Bauera rubiodes* (e.g. Ht, El versus SP, Bc - Appendix 2). However, it is the increasing dominance of the understorey by the sedge *Gahnia grandis* which is most notable. The cover of this sedge exceeds 50% on many of the waterlogged sites and on Snug Plain and Brown Mountain its cover reaches 78 and 87 percent respectively.

On the drier moderately drained sites in the east, the dominance of the site by *E. cordata* relative to other eucalypt species decreases, as does the plant height and the size of the *E. cordata* population (Fig. 5.1). The percentage cover of *E. pulchella* increases and the stands are generally comprised of scattered mallees beneath the *E. pulchella* canopy (Fig. 5.1). There is little floristic difference between areas occupied by *E. cordata* and the surrounding vegetation. Of the populations in the climatically warmer and drier area, it is only on the more exposed coastal sites on Maria Island (Pt), Cape Queen Elizabeth (QE) and Penguin Island (Pe) that *E. cordata* achieves full site dominance (cf. other eucalypt species). These are the largest of the 'eastern' populations and the distributional pattern described is consistent with the majority of 'eastern' *E. cordata* populations being relicts, possibly of a colder environment.

5.3 Site and species classification

The ordination suggests that stands of *E. cordata* varied more-or-less continuously in floristic composition and the TWINSpan classification was used to summarise this compositional continuum. With some minor subjective re-allocation of species the two-way TWINSpan classification of sites and species is shown in Table 5.1, and with the re-allocation of the Electrona site, the geographical distribution of the four group classification (Fig. 5.2) is indicated in Fig. 3.3. The primary dichotomy broadly separates sites into wet and dry sclerophyll floristic groups (Table 5.1, Fig. 5.2). Within the dry sclerophyll group, populations may be further separated into dry, coastal or wetter, inland floristic groups (Table 5.1). As previously noted, the coastal sites are characterized by the absence of the less drought tolerant, dry sclerophyll species (e.g. Table 5.1) and the presence of *Casuarina stricta* and *Banksia marginata* (Fig. 5.2). The classification of sites is more-or-less concordant with the position of sites in the ordination in Fig. 5.1, despite the use of qualitative as opposed to quantitative abundance information. The only

major discrepancy is the site at Electrona (El), which the TWINSpan classification suggests has closest floristics affinities to the population at Leslie Road (LR). The Electrona site is anomalous in several respects, being the lowest altitudinal occurrence of the 'western' form as well as occurring on Permian mudstone. It contains both low altitude as well as well-drained floristic components and in these characteristics shows affinities to both LR and Ht. Based on the NMDS result the Electrona site was re-allocated to the well-drained wet sclerophyll floristic group (Fig. 5.2).

In summary, the *E. cordata* sites may thus be classified on the basis of their floristics into dry, coastal (exposed, dry, excessively drained - drought stressed), dry sclerophyll (warm, dry, moderately drained), well-drained wet sclerophyll (cool, wet, well-drained) and waterlogged wet sclerophyll (cool wet poorly drained) floristic/environmental groups which are differentiated on a combination of broad-scale climatic and localised microhabitat variation.

5.4 Relationship between patterns of floristic and phenetic variation

The indirect gradient analysis indicates that the populations of *E. cordata* vary along at least two major ecological gradients, which independently vary across the range of *E. cordata* (e.g. Fig. 3.3 and 5.1). Furthermore, the ordination indicates marked differences in floristic composition between the majority of 'eastern' and 'western' populations. The majority of populations with the 'eastern' morphology occur with species commonly associated with lowland dry sclerophyll vegetation, and occur in the dry coastal or dry sclerophyll floristic groups (Fig. 5.2 - group 2). In contrast, the 'western' morph is confined to populations in well drained or poorly drained wet sclerophyll floristic groups (Fig. 5.2 - group 1). However, the floristic variation amongst populations is relatively continuous which contrasts with the discontinuous morphological differentiation between populations. This is clearly seen in Fig. 5.3a where there is a compositional continuum along the vector differentiating 'eastern' and 'western' morphs (i.e. PC1 - Fig. 4.7) when it is fitted by rotational correlation into the floristic ordination. Thus in both an ecological (floristically defined - Figs. 5.1 and 5.3a) and geographical space (i.e. Fig. 4.11) the pattern of phenetic differentiation between populations of *E. cordata* appears stepped as opposed to gradational, despite gradational environmental continuity.

Ecological continuity between populations of either morph was also apparent along directly (CLIMPC1 - Fig. 4.10c) or indirectly (floristically defined) measured climatic (e.g. *CLIMPC1 - Fig. 5.3 b) and drainage (*DRAIN - Fig. 5.3 c) gradients. The populations with the 'western' morph occur at one extreme of a complex ecological gradient which mainly compounds variation due to increasing altitude, poorer drainage and higher, and more reliable, rainfall. Minor spatial (Fig. 4.10a,b) or climatic (Fig. 4.10c and 5.3b) disjunctions were not associated with marked phenetic differentiation and were transgressed by populations of one or other morph. Regression analyses indicate a tendency for the direction of phenetic variation within each morph to be parallel and slightly convergent along the climatic gradient (Fig. 4.10c and 5.3b), and the 'eastern' populations clearly converge toward

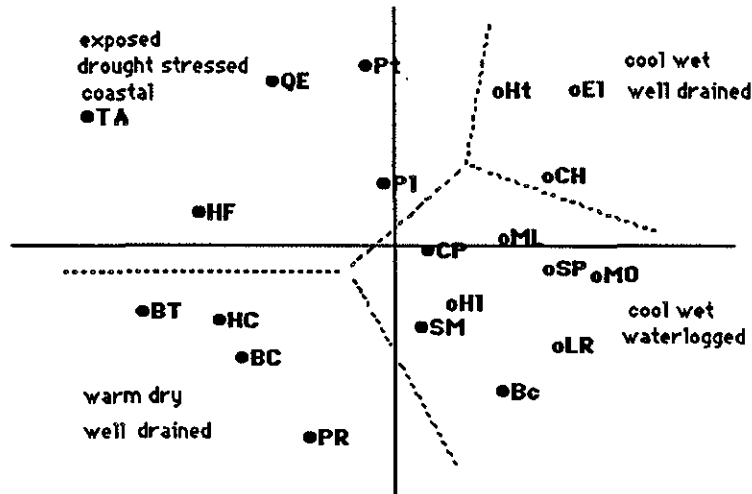
the 'western' morph along the drainage gradient (Fig. 5.3 c). However, the convergent trends along the drainage (Fig. 5.3c) or climatic (4.10c and 5.3b) gradients clearly do not account for the large difference in grand means and are insufficient to explain the large phenetic difference between morphs.

The floristic composition of the 'eastern' populations on Perpendicular Mountain (Pl), Chimney Pot Hill (CP), Small Mountain (SM) and Brown Mountain (Bc) is most similar to the 'western' populations (reflected in the presence of *Gahnia grandis*), and the latter three sites were floristically classified with the poorly drained 'western' sites (Fig. 5.3 and 5.1). The population on Brown Mountain is a morphological outlier, and the morphology of populations SM and CP deviates little in the direction of the 'western' populations. Of the 'western' populations, Ht, LR and El vary most in morphology in the direction of the 'eastern' populations. The floristics indicate that Ht and El occur on the driest of the 'western' sites, which could explain their deviation toward the 'eastern' morph. However, such deviation is not apparent in the only other 'western' population not occurring on a waterlogged site (CH) and the other 'western' population which deviates toward the 'eastern' morph (LR) occurs on a poorly drained site (Fig. 5.1).

The ordination distances between sites in Fig. 5.1 suggests that the compositional change associated with nearly 50 km of geographical and climatic variation may be only marginally greater than that resulting from localized microhabitat variation in drainage and exposure. Furthermore, the ordination suggests much greater floristic variation amongst 'eastern' than 'western' populations of *E. cordata*. This accords with the greater phenetic and genetic differentiation amongst 'eastern' stands and suggests much greater environmental heterogeneity amongst the more geographically wide-spread 'eastern' populations of *E. cordata*. The populations with the 'eastern' morphology occupy ecological habitats ranging from exposed, drought prone coastal to higher altitude waterlogged sites. However, while there is considerable floristic differentiation between these sites, once the difference between 'eastern' and 'western' populations has been removed, only a very small proportion of the residual morphological variability in the species can be directly related to variation in an environmental gradient. For example, it is not until the fifth PCA axis of the total analysis (e.g Section 4.3) that morphological variability was detected within the 'eastern' populations which could be associated with increasing exposure to the coastal environment (i.e the difference between the dry coastal and dry sclerophyll floristic groups), and even then this variation only accounted for 3.6% of the total morphological differentiation.

Figure 5.1 NMDS floristic ordination of *E. cordata* sites.
The glyphs in b correspond to the drainage index score.

(a)



(b)

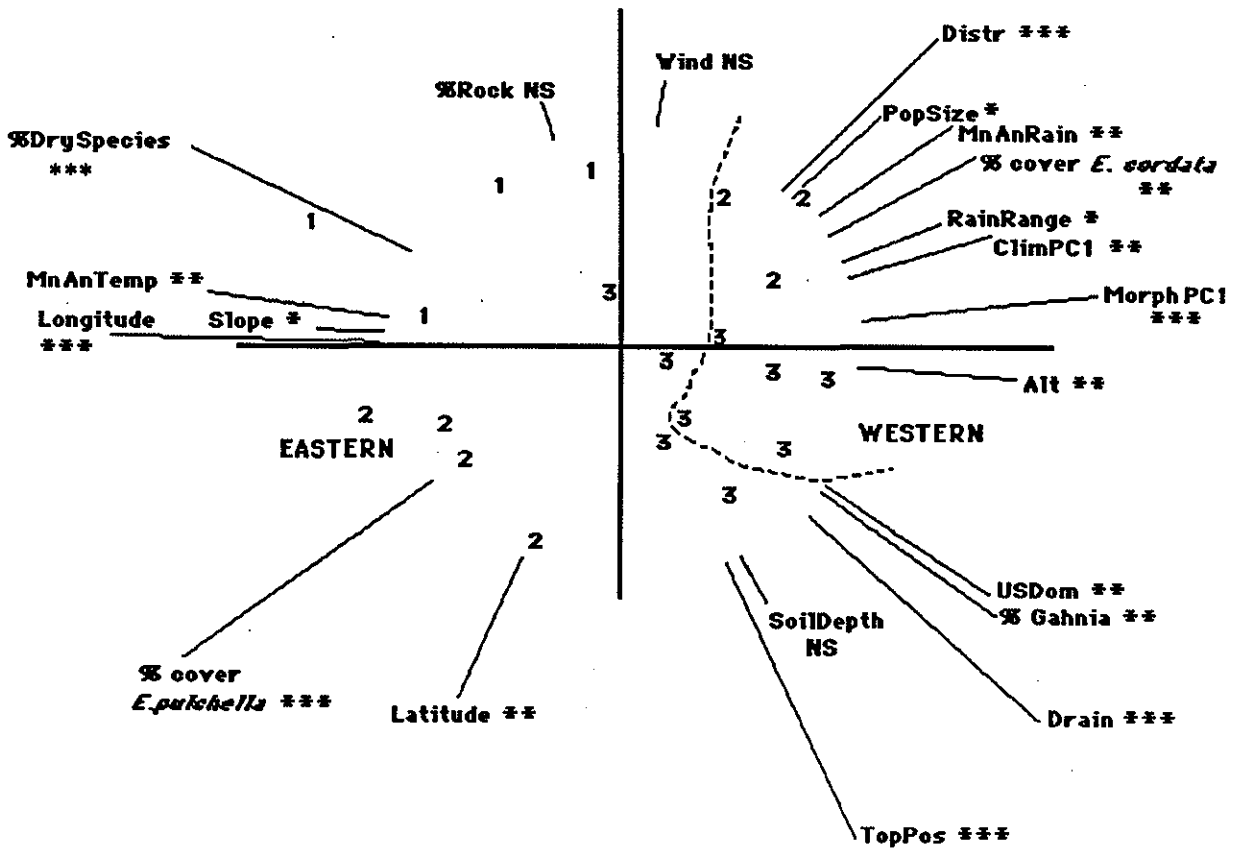


Figure 5.2 Twinspan classification of sites of *E. cordata*

Indicator species are indicated for each dichotomy. The geographical distribution of the 4 groups indicated is plotted in Fig. 3.3.

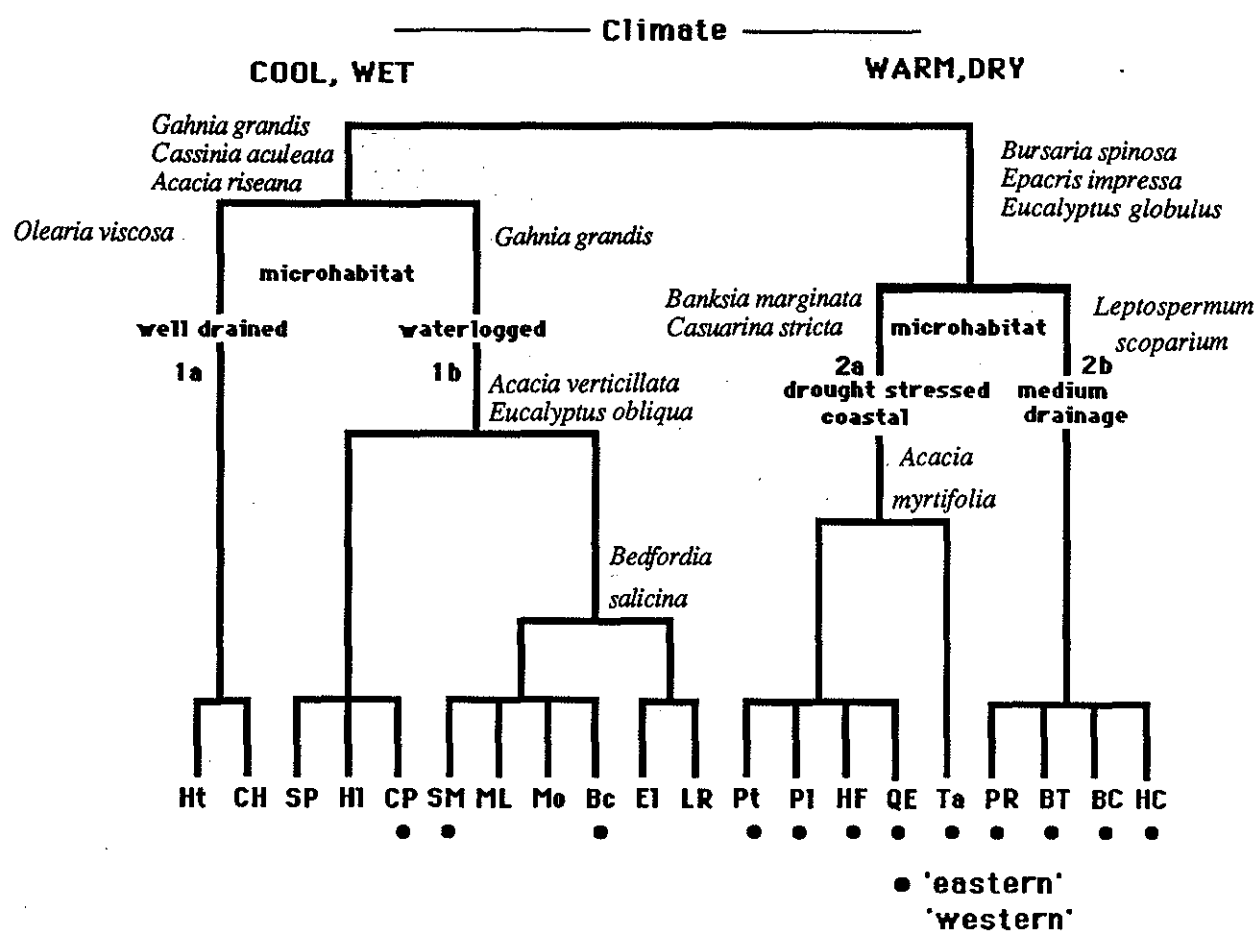


Figure 5.3 Relationship between phenetic and floristic variation amongst populations of *E. cordata*.

(a) PC1 (Fig. 4.7) fitted into the 2 dimensional NMDS floristic space. Floristically derived (b) climatic (CLIMPC1- Table 2.2) and (c) drainage gradients fitted into the 6 dimensional phenetic space (Fig. 4.7). Vectors were fitted using rotational correlation analysis. Regression lines and equations and correlation coefficients for each morph are indicated.

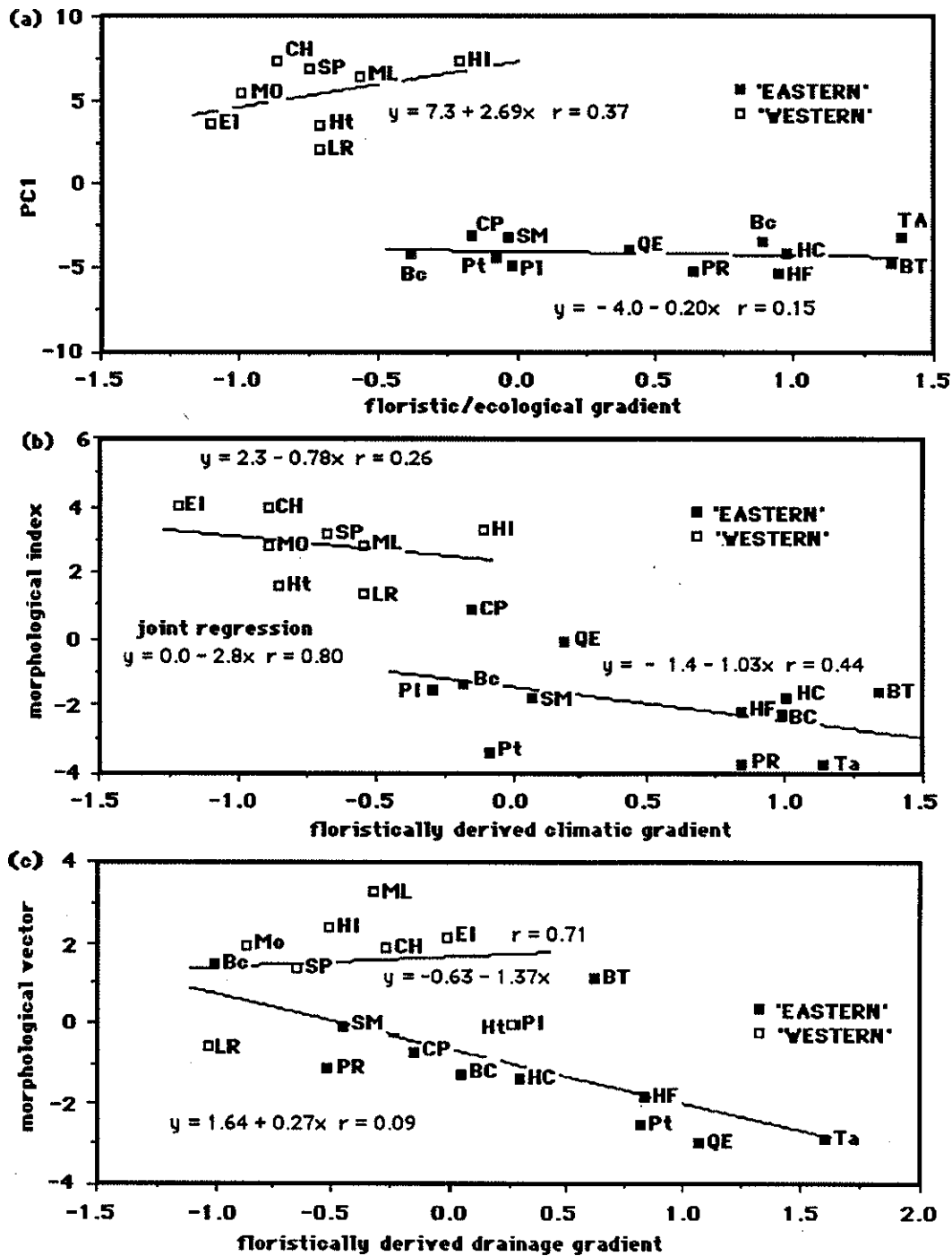


Table 5.1 Species and stand classification as derived from TWINSpan.

Indicator species are in bold lettering.

	Ht	SPCP	MLBc	LR	PIQE	PRBC
	CH	HI	SMMO	EI	PtHFTA	BTHC
	STAND GROUP					
	1a	1b	2a	2b		
Spyridium sp.	••	•-----	-----	-----		
Westringia angustifolia	••	•-----	-----	-----		
Bedfordia salicina	••	••-----••	-----•	-----		
Gonocarpus teucrioides	••	••-----	-----•	-----		
Olearia viscosa	••	-----•	•-----	-----		
Acacia riceana	••	-----••	-----	-----		
Coprosma hirtella	•	-----••	-----	-----		
Notelaea ligustrina	•	-----•	-----	-----		
Olearia floribunda	•	•-----••	-----	-----		
Olearia myrsinoides	•	••-----	-----	-----		
Senecio linearifolius	•	•-----	-----	-----		
Bauera rubioides	---	••-----	-----	-----		
Daviesia ulicina	---	•-----	-----	-----		
Gahnia grandis	---	••••••••	•-----	-----		
Hibbertia procumbens	---	•-----	-----	-----		
Eucalyptus delegatensis	---	••-----	-----	-----		
Coprosma quadrifida	---	-----••	-----	-----		
Eucalyptus dalrympleana	---	-----•	-----	-----		
Acacia verticillata	•	-----••••	•-----	-----•		
Lepidosperma elatius	---	-----••	-----	-----•		
Eucalyptus obliqua	---	-----••••	•-----	-----		
Banksia marginata	---	•-----•	•••-----	-----		
Pultenaea daphnoides	•	-----•	•••-----	-----		
Hibbertia riparia	---	-----•	•-----	-----		
Pultenaea gunnii	---	-----•	•-----	-----		
Eucalyptus tenuiramis	---	-----•	•-----	-----		
Exocarpos cupressiformis	---	•-----	•••-----	-----		
Pimelea nivea	•	-----	•••-----	-----		
Casuarina stricta	---	-----	•••-----	-----		
Veronica formosa	---	-----	•-----	-----		
Lepidosperma laterale	---	-----	•••-----	-----		
Helichrysum scutellifolium	---	-----	•••-----	-----		
Astroloma humifusum	---	-----	•••-----	•-----		
Cyathodes glauca	---	•-----	-----	•-----		
Diplarrena moraea	---	•-----	-----	•-----		
Persoonia juniperina	•	-----	-----	•-----		
Eucalyptus pulchella	---	•••-----	•••-----	••••		
Olearia phlogopappa	•	-----	•-----	-----		
Acacia genistifolia	---	-----	•••-----	•-----		
Acacia myrtifolia	---	-----	•-----	•-----		
Epacris impressa	---	-----	•••-----	•••-----		
Lomandra longifolia	---	-----	•••-----	•••-----		
Acacia stricta	---	-----	•-----	•-----		
Beyeria viscosa	---	-----	•-----	•-----		
Eucalyptus globulus	---	•-----	•••-----	•••-----		
Acacia dealbata	---	-----	•-----	•-----		
Bursaria spinosa	---	-----	•••-----	•••-----		
Eucalyptus viminalis	---	-----	•-----	•-----		
Goodenia ovata	---	•-----•	•-----	•••-----		
Correa reflexa	---	•-----	-----	•-----		
Leptospermum lanigerum	---	•-----	•-----	•-----		
Callistemon pallidus	••	••-----	•-----	•••-----		
Dianella tasmanica	••	•-----	•-----	•-----		
Leptospermum scoparium	---	••••••••	•-----	•••-----		
Pultenaea juniperina	••	••••••••	•••-----	•••-----		
Lomatia tinctoria	••	••••••	•••-----	•-----		

Chapter 6 Taxonomic treatment of *E. cordata*

6.1 Introduction

Analyses indicate that populations currently included within *E. cordata* form two phenetic groups that are more or less geographically concordant, being comprised of populations with predominantly western and eastern distributions, and differing in habitat characteristics. The discreteness of the two major morphs within *E. cordata* is examined in this chapter and the major characters discriminating the morphs are determined. A taxonomic revision of *E. cordata* is proposed with the recognition of two subspecies. The degree of differentiation amongst populations of *E. cordata* is also compared with the variation amongst and within closely related species. The affinities and evolution of the two subspecies of *E. cordata* are addressed.

6.2 Morphological differentiation

Individuals were initially assigned as 'eastern' or 'western' morphs on the basis of the population classification in Fig. 4.8. The difference between the two morphs was then examined using univariate ANOVA and discriminant function analysis. The discriminant analyses were used to-

- (1) examine the differentiation and continuity between morphs at the individual level
- (2) determine the smallest set of characters necessary to optimally differentiate morphs and
- (3) provide a re-classification based on individual (as opposed to population) phenotype.

For each morph, the univariate means and 95% confidence limits for all seedling and adult characters are indicated in Table 6.1. As expected from the population analyses, the two morphs are highly significantly different on the majority of characters. Seedlings of the two morphs differ ($P < 0.05$) in all characters except GLAUC, CREN, OILGL5, ANTHcot, APEX10 and NODES and adults differ in all characters except LWP/LL, APEX and PEDI.

The differentiation of the two morphs is summarized by the discriminant functions and ideograms indicated Fig. 6.1. The morphs are clearly differentiated using the full adult and seedling character sets (Fig. 6.1 a and c). In each case stem shape is the main discriminating character, although characters relating to capsule size (i.e. CAPL, RIMW and VPS) are also highly weighted in the adult analysis. There are several intermediate populations (El, Ht and LR) and, at the individual level, there are also intermediate phenotypes. However, while there is continuous phenotypic variation along all discriminant functions, intermediate phenotypes are relatively rare and there is only minor overlap of the two groups at the individual level. Even when the main discriminating variable, stem shape (STSHAPE), is excluded and the two morphs are compared on the basis of leaf and capsule dimensions alone (Fig. 6.1b), they are still significantly different and there is still relatively little overlap of the distributions.

There is good congruence between the population and individual classifications, and individuals can be relatively accurately classified into morphs based on population locality alone. Using all characters, the level of mis-classification is only 3.2% in the adult population (Table 6.2 -1a) and 0.5% in the seedling population (Table 6.2 - 2a). The mis-classification in each case is virtually confined to individuals from the intermediate populations EI, Ht and LR (Table 6.3). These populations are variable for stem shape although mis-allocated individuals were generally intermediate in phenotype. A low percentage of individuals in each population have round or intermediate stem shapes and thus classifying as the 'eastern' morph whereas the majority of individuals classify as the 'western' morph on this characteristic (Table 6.3). The separation of either adults or seedlings when only dimensional data is utilized (Morph- Table 6.3) is not as discrete, although the level of mis-classification is still relatively low (e.g. adult 8.0% Table 6.2 -1b; seedlings 13.8% Table 6.3 - 2b).

Step-down discriminant analyses indicate that optimal differentiation of the two morphs of *E. cordata* is possible with only a small sub-set of characters (Table 6.2). Capsule length (CAPL), distance from the rim to maximum width of the capsule (PTMW) and stem shape (STSHAPE) all contribute significantly to differentiate adults of each morph (Table 6.2-1a), although stem shape (STSHAPE - Table 6.2) is the prime discriminating characteristic. Using only these subsets of characters the change in the level of mis-classification from using the full data set is virtually negligible (Table 6.2). There is also good association between stem shape and other morphological differences at the individual level. Ninety-two percent of adults were classified as the same morph using either stem shape or leaf and capsule dimensions. In a comparable classification, 97% of seedlings were classified as the same morph; all seedlings from the 'western' populations were similarly classified, but 5% of the round-stemmed seedlings were classified as the 'western' morph using seedling leaf and form dimensions (i.e. Table 6.2 - 2b). Only 4.7% of angular stemmed adults had the leaf and capsule morphology of the 'eastern' morph whereas 10.8% of round stemmed adults were mis-classified. The latter atypical combinations of a round stem shape with the relatively large leaves and capsules of the 'western' morph mainly occur in 'eastern' populations on the wetter sites (e.g. CP, SM, HC and BC - Table 6.3; Fig. 5.1). These atypical character combinations also occur in the seedling classification (Table 6.3) and are indicative of convergence toward the 'western' morph which occurs along the drainage gradient (see Section 5.4).

6.3 Taxonomic affinities and evolution

Populations of *E. cordata* and closely related species are classified on the basis of their seedling phenotype in Fig. 6.2. There is a reasonable agreement between the taxonomic and phenetic classification. The 'western' populations of *E. cordata* group together and populations are classified into taxonomic groups in the majority of cases (e.g. *E. gunnii*, 'eastern' *E. cordata* and *E. glaucescens*; *E. urnigera* is an exception). However, in both the average linkage (Fig. 6.2) and single linkage dendrograms, most of the 'eastern' populations are linked with the populations of *E. gunnii*, *E. urnigera* and *E. morrisbyi* before they link with the 'western' *E. cordata* populations. The degree of differentiation in seedling characteristics within *E. cordata* is thus relatively large when compared to

the difference amongst and within other closely related Tasmanian species. However, this high level of differentiation in the seedling phenotype is not unique to the *E. cordata* populations and is comparable with, for example, the degree of differentiation between green and glaucous morphs of *E. urnigera* (e.g. HB versus AT and WM - Fig. 6.2).

Thus in seedling morphology the 'eastern' morph of *E. cordata* has closer affinities to other species in the Subseries *Cordatinae* than it does to the 'western' morph and it is most similar to glaucous forms of species such as *E. gunnii*, *E. urnigera* and *E. morrisbyi* (Fig. 6.3). This similarity is directly attributable to stem shape; the stem shape of the 'western' morph is not found in any of the other species in the *Cordatinae*, where the species have round, or at most slightly angular, stems. Within the series *Viminales*, similar markedly quadrangular stems with costa are otherwise confined to the subseries *Neglectinae* and *Globulinae*. The populations currently included within *E. cordata* could thus be polyphyletic, with the 'western' populations being derived by neoteny from the *Globulinae*. In fact, Jackson (1965) places *E. cordata* with the blue gum group and Sharma's (1974) classification of the Tasmanian eucalypts using anthocyanin, peroxidase and other protein data, places *E. cordata* closer to *E. globulus* than the Tasmanian *Cordatinae* species. However, there are several taxonomic anomalies in her classification and sample sizes and localities are not given. The 'western' morph clearly deviates in the direction of the *Globulinae* (e.g. *E. globulus*), but this is not marked (e.g. Fig. 6.3) and is mainly attributable to stem shape. The larger leaves and capsules of the 'western' morph also represents variation in the direction of *E. globulus*. However, the juvenile leaf shape of the species in the Superspecies *Globulus* (e.g. *E. globulus*), while superficially similar, is significantly different from the juvenile leaf of the 'western' morph and the capsule and bud morphologies are distinctly different (e.g. Fig. 4.3 - capsules).

The 'western' morph has closer morphological affinities to the *Cordatinae* than the *Globulinae* species (e.g. *E. globulus* Fig. 6.3), and when stem shape is not considered, it is morphologically continuous with the 'eastern' morph. While there are subtle shape differences (e.g. Figs. 4.3 and 6.1), the weightings of leaf and capsule characters in the discriminant functions (Table 6.2 1b) are all positive indicating that the morphs are mainly separated on the size of the lamina and capsule (e.g. Figs. 4.3 and 6.1). The morphological continuity and the existence of several populations which are "polymorphic" for stem shape would strongly suggest that the 'eastern' and 'western' morphs are sister taxa. Furthermore, several lines of evidence suggest that the 'western' morph was derived from ancestral populations of the 'eastern' morph and not *vice versa*. Firstly, the 'eastern' morph has closer affinities to other near relatives in the *Cordatinae*. All other species in this subseries have round stems which suggests that this is the ancestral condition in *E. cordata*. Secondly, the 'eastern' morph has a much broader geographical distribution (Fig. 3.3) and exhibits much greater divergence between populations than the 'western' morph (Chapter 4). Thirdly, the small size and suppressed and scattered nature of many stands of the 'eastern' populations are indicative of a relict distribution pattern. An identical set of population characteristics has been detailed for *E. caesia* in Western Australia (Hopper *et al.* 1984; Hopper *et al.* 1983; Moran and Hopper 1983; Hopper and Burgman 1983) and would also apply to the *E. risdonii-tenuiramis* complex in Tasmania. These species all have a similar insular distribution pattern, and in both *E. caesia* and *E. cordata* evolution appears to be

in the direction of increasing size of reproductive and vegetative organs. In each species, new subspecies appear to have evolved in a restricted portion of the range of a more widespread and variable ancestral form; suggesting that local differentiation in, and expansion from, small allopatric populations may be a common mode of speciation in the genus.

Quadrangular stems with costa occur in all sections of the *Symphyomyrtus*, with the possible exception of the *Adnataria*. Species differing markedly in stem characteristics occur in many series (e.g. *SEC*, *SIP*, *SIT*, *SIV*, *SLE*, *SLI*, *SLO*, *SNE*, *SPI*; codes follow Pryor and Johnson 1971) and even in the same superspecies (e.g. *Tereticornis*, *Pyriformis*, *Dumosa*, *Clelandii*, *Merrickiae*, *Griffithsii* and *Tereticornis*), which would suggest that in an evolutionary sense stem characteristics are relatively mobile. While the stem shape of the 'western' morph is unique in the *Cordatinae* and is not found in the the closely related *Viminalinae*, similarity with the *Globulinae* species may be a result of parrallel evolution. For example, it is possible that this stem shape may be of adaptive value for the mechanical support of large juvenile leaves. Nevertheless, it is also possible that this stem characteristic was initially derived through ancient introgression of genes from a *Globulinae* species or ancestor. *E. globulus* and *E. cordata* grow in close geographical proximity in southern Tasmania and while it is rarely associated with 'western' populations, it occurs with many of the 'eastern' populations (Fig. 3.6). The two species have been artificially hybridised yielding a vigorous F2 (Chapter 7) and, while currently rare, putative natural hybrids were located during this survey (Chapter 7). An hypothesis of introgressive hybridisation is not inconsistent with the proposed taxonomic treatment of *E. cordata*, but further work is required to test these alternative hypotheses.

6.4 Taxonomic status

With significant genetic, habitat and distributional differences between populations dominated by either morph, coupled with the relative rarity of intermediate phenotypes and populations, separate taxonomic treatment of these two major morphs of *E. cordata* is clearly warranted. These morphs are mainly differentiated on stem shape, but also differ in other morphological and growth differences (see Fig. 6.1). The adult and seedling morphology of the two morphs are relatively discrete and the association between differences in morphology and stem shape is relatively consistent both at the population and individual level. The level of differentiation between these morphs is taxonomically significant and the degree of continuity is minor when compared to that frequently encountered, and currently taxonomically acceptable at both the specific and subspecific level within the genus (e.g. see Pryor and Johnson 1971; Phillips and Reid 1980; Bramwells and Whiffin 1984; Potts and Reid 1985b). A taxonomic revision of *E. cordata* is thus proposed with the recognition of a new subspecies. The morphology of the holotype and isotypes of *E. cordata* (e.g. Fig. 6.4 and 6.5) and samples collected from the type locality clearly match the 'eastern' morph; the mean of their discriminant scores lying close to the grand mean for the 'eastern' morph (Fig. 6.1). The 'eastern' morph therefore corresponds to *E. cordata* as originally described by Labillardière (1806) and is thus by taxonomic convention *E. cordata* subsp. *cordata*. The angular stemmed 'western' morph thus requires formal taxonomic description as a new subspecies.

Table 6.1 Character means and 95 percent confidence intervals of samples of 'eastern' and 'western' morphs.

The F values and probabilities for the difference between morphs are indicated ('western' -seedling N=114 adult N=85; 'eastern' seedling N=76 adult N=102). Character codes are detailed in Tables 2.3 and 2.5 and where necessary values have been back-transformed.

(NS = not significant; $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

	'eastern' morph			'western' morph				
	Lower	mean	Upper	Lower	mean	Upper	F VALUE	PROBABILITY
	limit		limit	limit		limit		
SEEDLING CHARACTERS								
COTPET	1.0	2.3	3.5	1.2	2.5	3.7	7.2	**
COTL	16	2.5	3.5	1.9	3.1	4.4	51.1	***
COTAP	-0.1	0.3	0.6	0.0	0.4	0.7	17.4	***
LL2	12.1	21.3	30.5	14.7	24.4	34.1	16.8	***
LW2	4.7	10.4	16.0	5.9	11.7	17.6	8.0	**
LL5	18.9	32.8	46.7	24.6	38.1	51.5	29.8	***
LW5	13.7	26.4	39.2	17.9	29.7	41.4	13.6	***
BASE5	-0.1	1.0	3.4	0	1.3	4.3	5.8	*
LL10	22	36.2	50.4	28.3	45.7	63.2	66.5	***
LW10	17.9	32.7	47.5	26.9	41.1	55.3	56.5	***
BASE10	0.2	1.7	5.3	0.7	2.7	7.0	22.1	***
APEX10	0	0.2	0.5	0	0.1	0.3	1.9	NS
HT	17.6	29.3	41.1	20.7	33.4	46.1	12.7	***
NQDES	5.8	8.5	11.6	6.6	8.7	11.2	0.0	NS
RUGOSE	1.1	2.9	4.8	0.9	1.8	2.8	120.8	***
STSHAPE	-0.7	0.7	2.0	2.4	3.6	4.7	1036	***
GLAUC	2.9	3.8	4.4	3.4	3.9	4.4	3.5	NS
ANTHSTEM	-0.5	0.3	2.0	-0.3	0.5	2.3	5.4	*
CREN	0.1	1.3	2.6	0.4	1.5	2.6	3.6	NS
INTER10	15.6	37.6	59.5	25.4	44.3	63.2	19.6	***
ANTHCOT	-0.4	1.3	2.9	-0.1	1.3	2.8	0.3	NS
OILGL5	-0.4	0.9	2.2	-0.6	0.9	2.4	0.4	NS
OILGL10	0.2	2.1	4.0	0.8	2.4	4.0	4.9	*
COTW	4.3	6.6	8.9	5.4	7.9	10.3	48.6	***
PROPLAT	0.0	0.1	0.6	0.0	0.1	0.6	1.2	NS
LWP/LL10	0.2	0.3	0.5	0.2	0.3	0.4	5.4	*
ADULT CHARACTERS								
LL	29.9	46.9	73.6	44.1	68.7	107	132.3	***
LW	28.9	44.6	68.7	43.3	59.4	81.5	102.6	***
LWP/LL	0.3	0.4	0.5	0.3	0.4	0.5	2.0	NS
BASE	1.0	3.1	7.6	2.3	5.0	10.0	53.7	***
APEX	-0.3	0.5	2.0	-0.2	0.5	1.9	0.3	NS
PEDU	3.1	5.7	10.0	3.8	6.7	11.5	15.0	***
CAPL	7.51	9.2	11.2	9.2	11.5	14.4	213.6	***
PEDI	-0.3	0.2	0.8	-0.4	0.2	1.3	0.5	NS
RIMW	6.8	8.8	11.5	8.8	11.1	14.0	151.2	***
MAXW	8.0	9.8	12.0	9.9	12.2	15.2	205.8	***
PTMW	1.5	2.7	4.0	1.5	3.3	5.2	26.5	***
DISK	0.7	1.8	2.9	1.11	2.4	3.6	40.6	***
VSZ	0.9	2.3	3.6	1.8	3.0	4.2	64.9	***
VPS	0.7	1.8	2.8	0.9	1.9	3.0	6.8	*
GLAUC	3.4	3.9	4.5	3.8	4.0	4.2	5.5	*
STSHAPE	-0.4	0.1	0.56	1.0	3.2	5.3	785.5	***

Table 6.2 Classification functions and standardized discriminant function coefficients.

For classification of individuals, the transformed character values (see Tables 2.3 or 2.5) are substituted into the classification functions for each morph and a case is assigned to the morph for which the function yields the highest value. Individuals from PR and HF were excluded from the initial analysis but in virtually all cases classified with the 'eastern' form (see Table 6.4).

1. Adult analyses

(a) step-down from all adult characters

(identical classification results were obtained using all variables)

	<u>Classification functions</u>		Discriminant Function
	Eastern	Western	
CAPL	550.5	600.4	0.50
PTMW	-11.5	-12.9	-0.23
STSHAPE	-1.0	4.4	0.89
(CONSTANT)	-249.9	-305.0	

Population grouping Predicted group membership

Eastern	100%	0%
Western	7%	93%

PERCENT OF "GROUPED" CASES CORRECTLY CLASSIFIED = 96.8%

(b) step-down from adult leaf and capsule dimensions

	<u>Classification functions</u>		Discriminant Function
	Eastern	Western	
LL	130.4	142.1	0.41
BASE	10.3	16.2	0.31
CAPL	240.2	270.6	0.50
MAXW	261.7	281.6	0.33
(CONSTANT)	-358.1	-434.4	

Population grouping Predicted group membership

Eastern	92%	8%
Western	8%	92%

PERCENT OF "GROUPED" CASES CORRECTLY CLASSIFIED: 92.0%

(c) Stem shape alone

	<u>Classification functions</u>	
	Eastern	Western
STSHAPE	0.1	5.6
(CONSTANT)	-0.7	-9.5

Population grouping Predicted group membership

Eastern	100%	0%
Western	9%	91%

PERCENT OF "GROUPED" CASES CORRECTLY CLASSIFIED: 96.0%

continued

2. Seedling analyses

(a) all seedling characters

Population	Predicted group membership	
grouping		
Eastern	100%	0%
Western	1%	99%
PERCENT OF "GROUPED" CASES CORRECTLY CLASSIFIED = 99.5%		

(b) seedling leaf and form dimensions only

Population	Predicted group membership	
grouping		
Eastern	88%	12%
Western	15%	85%
PERCENT OF "GROUPED" CASES CORRECTLY CLASSIFIED = 86.2%		

(c) step-down from all seedling characters (excluding NODES and HT)

	<u>Classification functions</u>		Discriminant Function
	Eastern	Western	
RUGOSE	5.90	3.48	-0.34
STSHAPE	1.66	9.50	0.95
(CONSTANT)	-10.1	-20.95	

Population	Predicted group membership	
grouping		
Eastern	99%	1%
Western	1%	99%
PERCENT OF "GROUPED" CASES CORRECTLY CLASSIFIED = 99.1%		

(d) Stem shape alone

	<u>Classification functions</u>	
	Eastern	Western
STSHAPE	1.8	9.6
(CONSTANT)	-1.3	-17.9

Population	Predicted group membership	
grouping		
Eastern	99%	1%
Western	4%	96%
PERCENT OF "GROUPED" CASES CORRECTLY CLASSIFIED: 97.1%		

Table 6.3 Percentage of individuals in each population classified as the 'eastern' morph.

Adults and seedlings were classified using discriminant scores derived from step-down analyses of the total (Total) and morphological (Morph - excluding STSHAPE, RUGOSE and GLAUC) data sets and stem shape alone (STSHAPE). Three isotypes of *E. cordata* from the Paris herbarium have also been included.

-----Percentage 'Eastern' morph-----							
Population classification		-----ADULT-----			-----SEEDLING-----		
		Total	Morph	STSHAPE	Total	Morph	STSHAPE
Pt	100	100	100	100	100	100	100
Pl	100	100	100	100	100	100	100
PR	100	100	100	100	90	50	100
HF	100	100	100	100	86	43	100
BT	100	100	100	100	100	100	100
BC	100	100	90	100	100	83	100
HC	100	100	80	100	100	60	100
QE	100	100	100	100	100	83	100
SM	100	100	67	100	100	78	100
CP	100	100	90	100	100	64	100
Bc	100	100	86	100	100	100	100
TA	100	100	100	100	100	100	100
Pe	100	100	100	100			
Isotypes	100	100	100	100			
(P)							
El	0	10	10	20	0	10	30
SP	0	0	0	0	0	7	0
FH	0	0	0	0	0	8	0
Ht	0	20	40	30	10	70	10
Hi	0	0	0	0	0	0	0
LR	0	30	10	30	0	33	11
CH	0	0	0	0	0	0	0
ML	0	0	0	0	0	12	0
Mo	0	0	10	0	0	15	0

Figure 6.1 Differentiation of morphs within *E. cordata*.

The distributions of individuals along discriminant functions separating the two morphs of *E. cordata* are indicated. Discriminant functions were derived from analysis of (a) all adult characters, (b) only adult leaf and capsule dimensions (c) all seedling characters and (d) seedling form and leaf dimensions only. Individuals were grouped into morphs based on the population classification in Fig. 4.8. Typical stems (and cross-section; neither to scale), capsules, buds and adult and seedling leaves of each morph are shown. The mean discriminant score of each morph, the type population (Pe) and 3 isotypes from the Paris Herbarium are indicated in (a).

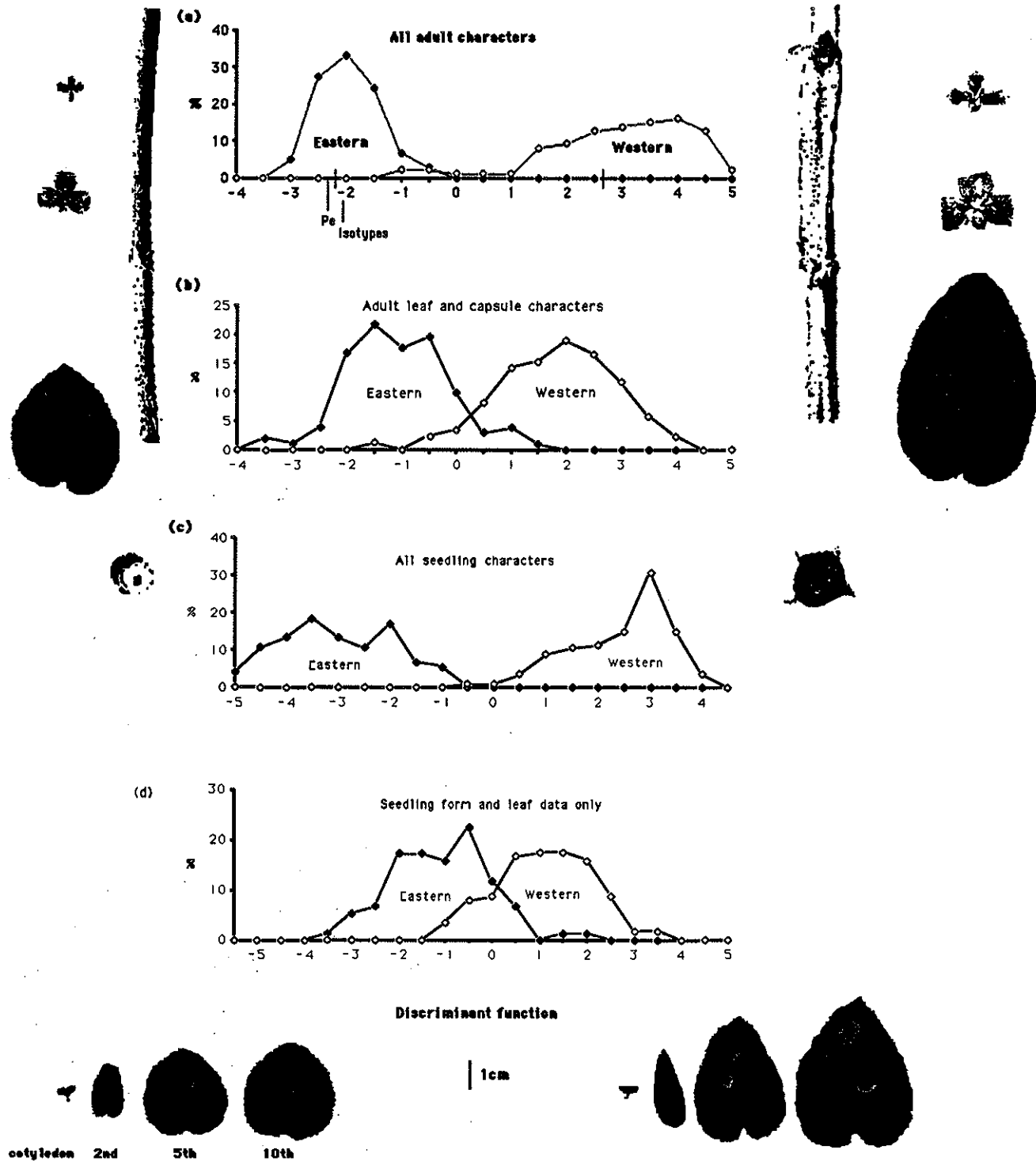


Figure 6.2. Average linkage dendrogram of populations of *E. cordata* (C), *E. gunnii* (G or A), *E. urnigera* (U), *E. morrisbyi* (M) and *E. glaucescens* (Gl).
The dissimilarity measure was the Mahalanobis' distance calculated for the total suite of seedling characters (see Table 2.5). Population codes are detailed in Table 2.4.

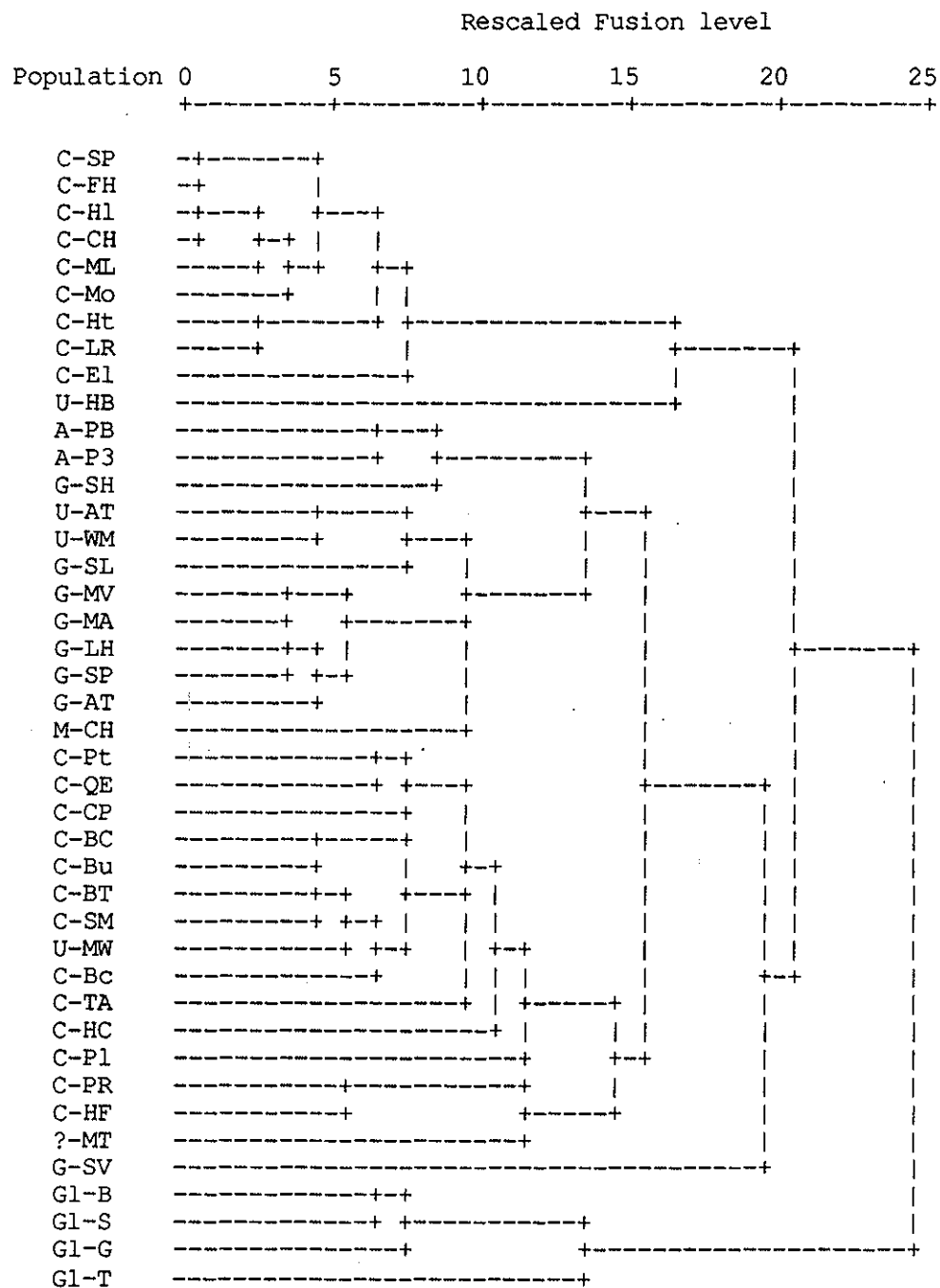


Figure 6.3 Average linkage dendrogram (a) and ordination of taxa on the first two discriminant functions derived from analysis of seedling characters.

(a)

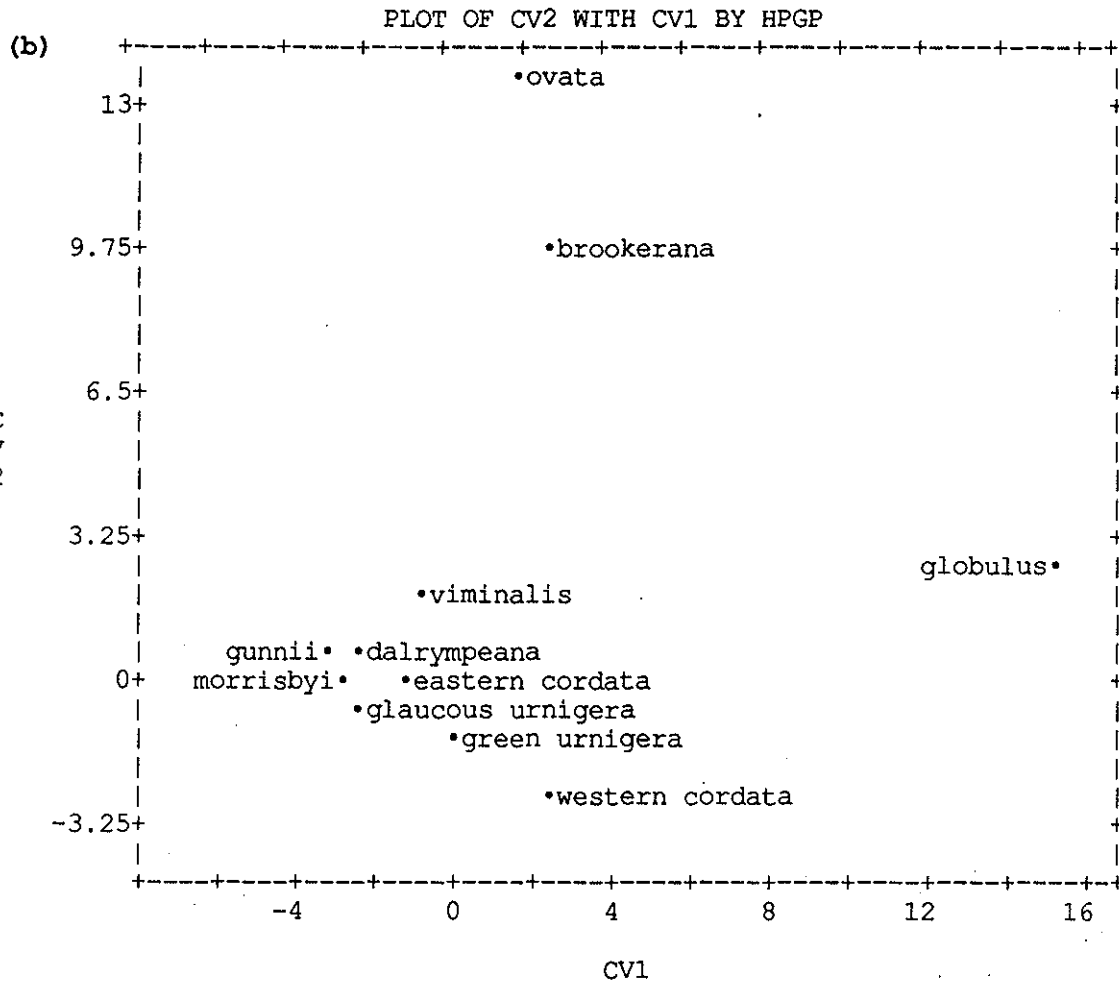
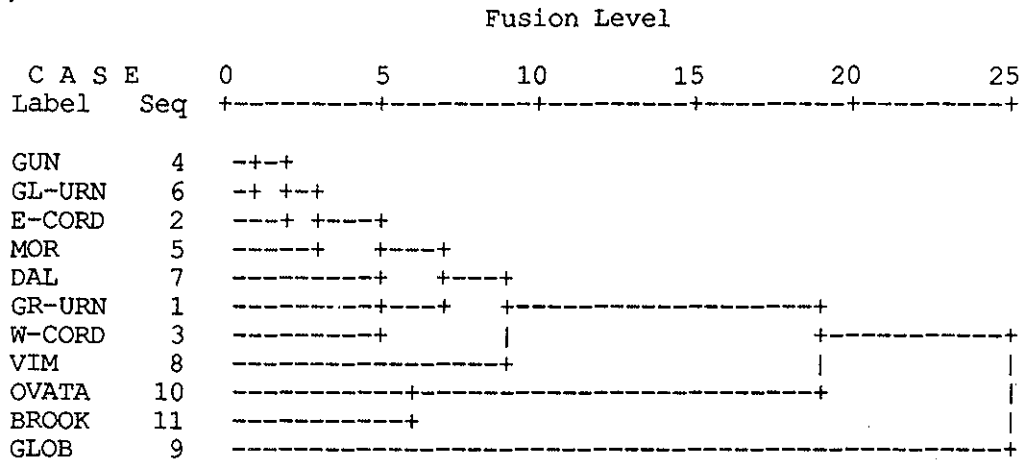
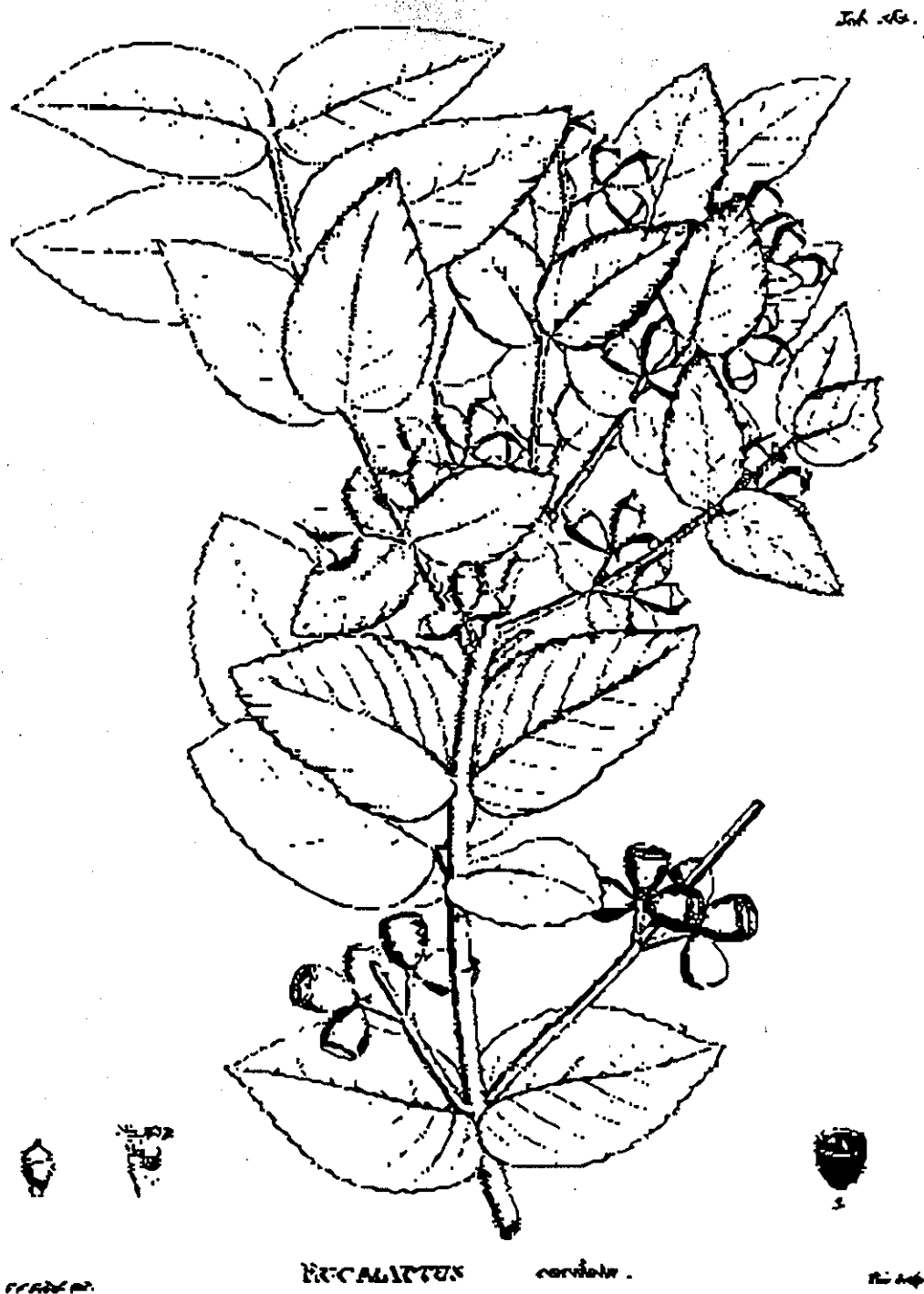
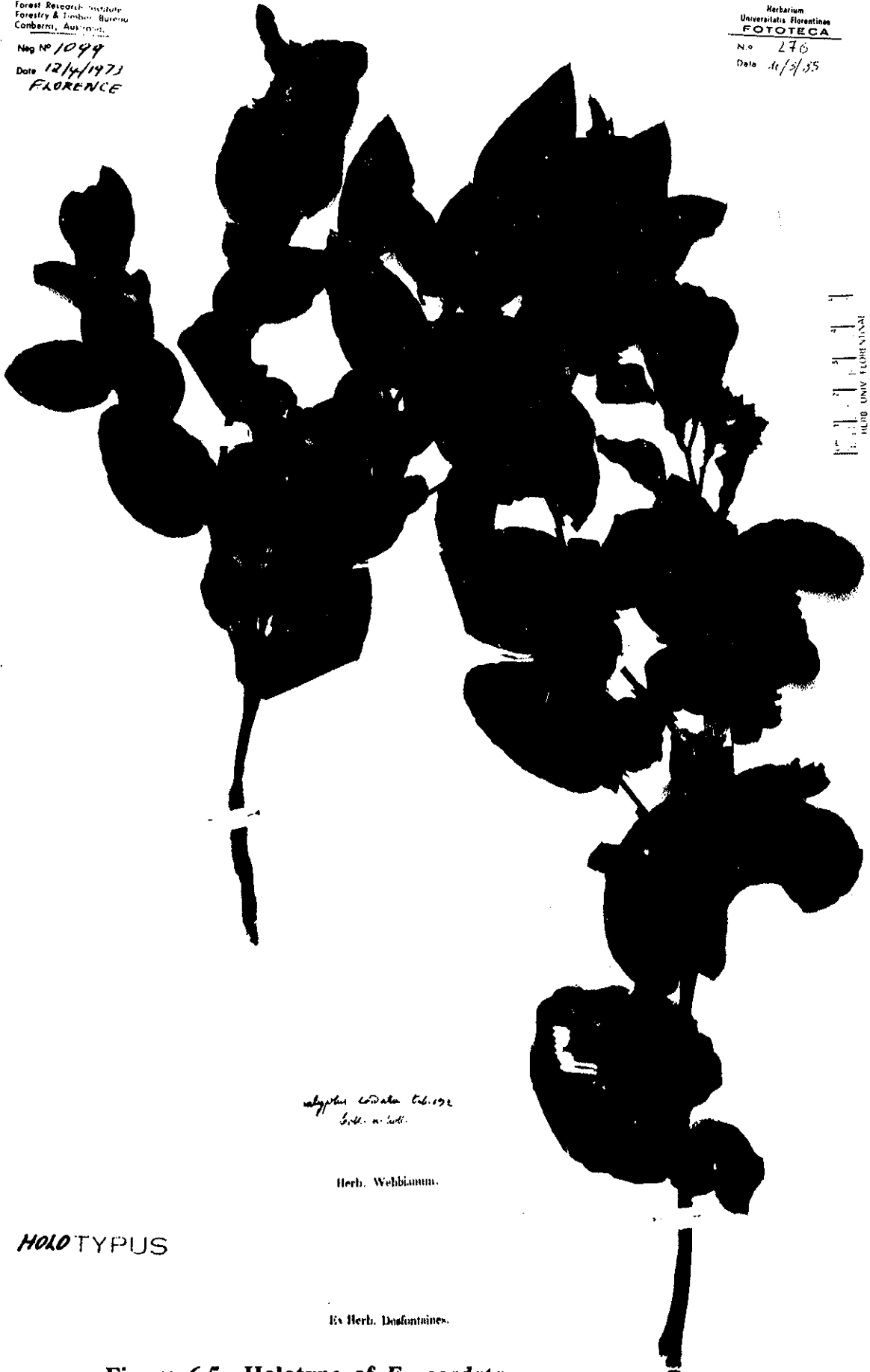


Figure 6.4 *E. cordata* as figured by Labillardière in *Novae Hollandiae Plantarum Specimen* in 1806.



Forest Research Institute
Forestry & Timber Bureau
Conberra, Australia
Neg No 1099
Date 12/4/73
FLORENCE

Herbarium
Universitatis Florentinae
FOTOTECA
No 276
Date 11/3/55



HOLO TYPUS

Figure 6.5 Holotype of *E. cordata*.

Chapter 7 Conservation status and recommendations

7.1 Introduction

For effective species conservation, the importance of *in situ* preservation of viable populations across the full ecological and genetic range of a species is well recognized (Halloran 1985; Frankel 1982; Moran and Hopper 1983, 1987; Hopper *et al.* 1982; Namkoong 1984). Of prime concern is the maintenance of the maximum amount of genetic diversity (e.g. Hopper *et al.* 1982; Halloran 1985; Moran and Hopper 1987) and populations of sufficient size to ensure not only the preservation of short-term fitness, but long-term evolutionary flexibility (Frankel 1982; Frankel and Soulé 1981; Giplin and Soulé 1986; Ledig 1986; Burgman *et al.* 1988). Where possible, natural ecological processes should be maintained and human interference minimized (Halloran 1985).

The conservation status of *E. cordata* is assessed in relation to these considerations. The present chapter assesses the degree of disturbance, reservation status and size of populations of *E. cordata* in relation to the phenetic and ecological diversity within the species. Controlled environment studies indicate that a large genetic component underlies the phenetic variability amongst adults in natural populations of the species. Based on the results in chapters 4 and 5, the phenetic and ecological diversity within the species was broadly summarized by the two-way classification of populations indicated in Fig. 7.1. The integration of ecological diversity into a two-way classification has the potential to allow additional genetic diversity associated with, for example, physiological adaptations, to be captured. It is also possible to identify, and preserve, atypical phenotype/environment combinations. In addition, the long-term potential for the maintenance of genetic variability is enhanced by the preservation of the extant genetic variability across as wide a range of differing environments as practical. This follows from Namkoong's (1984) recommendation to manage population units to encourage increased genetic diversity. While this strategy has particular relevance for *ex situ* gene conservation of high value species, indirect genetic management by ecological means has been suggested for *in situ* conservation of lower value species.

7.2 Disturbance

The majority (70 %) of the populations of *E. cordata* are relatively free of human disturbance (Fig. 7.1). However, disturbance increases with increasing proximity to Hobart and nearly fifty percent of the 'western' populations have been markedly disturbed (Fig. 7.2), mainly due to land clearing or road works. In contrast, eighty-two percent of the 'eastern' populations are relatively undisturbed with only populations at Bream Creek (BC) and on Chimney Pot Hill (CP and CP2) being markedly disturbed. Land clearing has probably reduced the size of populations at the base of the Herringback Range (HI), Leslie Road (Photo - Appendix 2), Moogara (Photo - Appendix 2), Mt. Llyod (photo - Appendix 2) and possibly Electra (EI), Bett's Road (Be) and Bream Creek (BC). In six of these cases, contiguous land has been cleared for agricultural purposes whereas the Moogara population is on the edge of an A.N.M. *Pinus radiata* plantation. The trees are in a small patch around which the

Figure 7.1 Summary of the ecological and phenetic diversity and conservation status of populations of *E. cordata*.

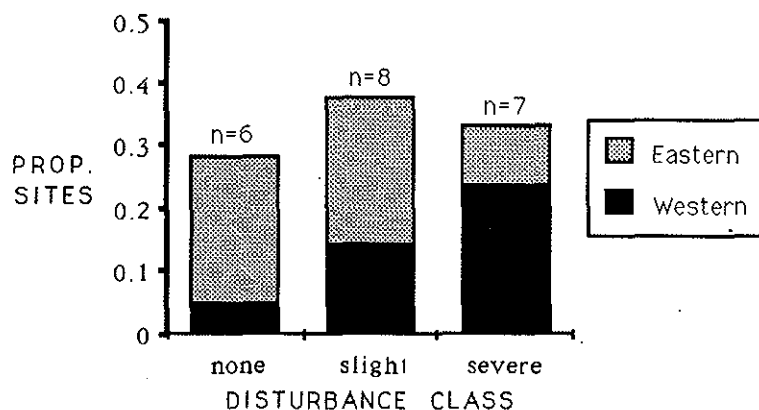
Populations are classified into phenetic and ecological groups on the basis of the phenetic and floristic classifications in chapters 4 and 5 respectively. The degree of disturbance, reservation status and estimates of the effective population size at the time are indicated. Sites not included in analyses (plain text) have been classified on the basis of stem shape and using indicator species from the TWINSpan classification (Fig. 5.2). Estimates of the number of breeding individuals in each population at the time of sampling are indicated (estimates of total population sizes are given in Table 2.1) and subscripts indicate: 1 relatively undisturbed 2 located on crown land or in state forest (Mo = A.N.M seed reserve) 3 state, flora or game reserve.

PHENETIC DIVERSITY		ECOLOGICAL DIVERSITY			
		cool wet		warm dry	
		well drained	waterlogged	well drained	drought stressed coastal
PHENETIC DIVERSITY	outliers		Bc _{1,2} <50 (MT) ₂ <20	PR ₁ <10	HF _{1,3} <50
	non-existent		CP ₂ <20 SM ₁ <50 SR ₁ <20 CP ₂ <20	BT _{1,2} <50 BC <50 HC _{1,3} <50 BR ₁ 1 PB _{1,2} <20	Pt _{1,3} <100 Pl _{1,3} <50 QE _{1,3} >500 Ta ₁ <20 Pe _{1,3} * <100
	intermediates		CH ₁ <100 SP _{1,2} >500 HI <200 ML <50 Mo ₂ <50 FH _{1,2} <20 Be ₂ 2 CH ₂ ₁ <20 CH ₃ ₁ <20	non-existent	
			Ht ₁ <100 EI <100		

surrounding native forest has been completely cleared and which is virtually surrounded by plantation. However, in the immediate vicinity of this patch considerable seedling regeneration of *E. cordata* has occurred in areas planted with *Pinus radiata*. While further investigation is necessary, it is possible that the population of *E. cordata* independently collected by Brett and Rodway from Brown Mountain near Port Arthur, and which could not be re-located during this survey, may have been lost through land clearing. Minor disturbance of populations at Snug Plains, Pony Bottom Creek, Hospital Creek and Square Mountain has occurred through the construction of vehicle tracks and some of the *E. cordata* near the trig site on the summit of Hellfire Bluff has been slashed to provide a sight-line.

Forty-five percent of populations (Pt, Pl, PR, QE, SM, El, CP, CH, CH2, CH3, SR, Pe and PB) had been recently burnt when sampled. In most cases, only patches of the population had been burnt and reproductively mature individuals could usually be located. However, all reproductively mature stems had been killed in several of the populations, resulting in the population being comprised solely of young, immature lignotuberous shoots at the time of sampling (e.g. CH2, CH3, SR). The invasion of stands by introduced species has not been marked and even in sites adjacent to agricultural development, invasion has been minimal and confined to the periphery.

Figure 7.2 The disturbance class of populations of *E. cordata*.



7.3 Reservation status

Fifty percent of the *E. cordata* populations occur on private land; the rest occur in State Reserves or on Crown Land (Fig. 7.1). The 'eastern' populations are well reserved, and at least some populations in each of the three major habitat categories (Fig. 7.1) are either secure in State Reserves or occur on crown land and can be readily protected in management plans. Four of the six populations occurring in drought stressed coastal habitats and

including the largest stands of the 'eastern' form (Perpendicular Mountain, Cape Queen Elizabeth) and the type locality (Penguin Island) are undisturbed and secure in State Reserves. However, populations of the 'eastern' morph occurring on relatively waterlogged sites are the least well preserved, although the two larger populations which occur on Chimney Pot Hill and Brown Mountain are on crown land. The population on Square Mountain is within 500m of State forest.

In contrast to the 'eastern' form, populations of the 'western' morph are poorly reserved. None of the populations are currently secure in State Reserves. However, the main stronghold of the 'western' form occurs in State forest at Snug Plains (SP and FH) and a proposal for the reservation of *E. cordata* within a land management plan for the area is currently being considered. While the population at Moogara occurs on private land owned by Australian Newsprint Mills (A.N.M.), the importance of the site is recognized and the population is preserved as a "seed reserve". The three 'western' populations which deviate toward the 'eastern' morph (Ht, El and LR) occur on private land. These populations are of scientific interest as they may provide the evolutionary link between 'eastern' and 'western' morphs. The rugged topography is likely to result in little disturbance of the population on the summit of Herringback Range (Ht) in the immediate future. However, the lowland populations of the 'western' morph at Electrona (El) and Leslie Road (LR) are not secure, and a house has been recently built within a 100m of the latter population. While the three populations on Combes Hill (CH, CH2 and CH3) occur on private land, they occur in relatively undisturbed forest away from areas of development and they are under no immediate threat.

7.4 Genetic considerations

Conservation of a species such as *E. cordata* with an insular population structure is dependent on the viability of its component populations. Both the short-term fitness and the long-term evolutionary potential of isolated populations is believed to depend to a large extent on the maintenance of sufficient genetic diversity within populations, which is a function of the effective population size. The effective, or breeding, population size is the actual population size modified by factors such as the breeding system, population structure and gene flow (Franklin 1980; Frankel and Soulé 1981; Frankel 1982; Burgman *et al.* 1988). Short-term fitness is believed to depend on avoiding the deleterious effects of inbreeding arising through the loss of heterozygosity. With decreasing population size and increasing inbreeding, selection is unable to prevent the fixation of deleterious recessive alleles through genetic drift. The maintenance of heterozygosity is important as fitness within and between populations is often correlated with heterozygosity (Frankel and Soulé 1981; Ledig 1986), although to date quite variable results have been obtained for forest tree genera (e.g. Ledig *et al.* 1983; Ledig 1986). Long-term evolutionary flexibility is believed to depend on maintaining sufficient genetic variability in the population, and relatively large population sizes are required for the loss of genetic variability through drift to be counter-balanced by the gain from mutation.

7.4.1 Generation time

Brown and Moran (1981) assume that the time scale for concern for forest species is of the order of 100 generations, although Frankel and Soulé (1981) suggests 1000 years. In eucalypts such as *E. cordata* in which individuals are mainly of the mallee habit, it is difficult to estimate the age of individuals and determine the generation time. Individuals usually are comprised of numerous lignotuberos stems from a lignotuber and while stems may be aged, it is virtually impossible to accurately estimate the age of the lignotuber. In *E. cordata* many of the lignotubers were over one metre diameter suggesting great antiquity. Central wood samples from large lignotubers of other species (less than 2m diameter) have been dated younger than 200 years (Wellington *et al.* 1979). Nevertheless, the individuals are probably much older (see Lacey 1983; Noble 1982) and wood samples taken from a lignotuber of the closely related species, *E. gunnii*, on Snug Plains have been dated upto 540 years (Head and Lacey 1988 - their specimen is erroneously cited as *E. coccifera*). Moran and Hopper (1983) suggest the generation time of the mallee *E. caesia* may be several hundred or even a thousand years. Large clumps (up to 15m across) of the mallee, *E. pendens*, with identical genotype have also been reported suggesting a single clonal individual of great age (Moran and Hopper 1987).

Estimates of the time for generation replacement are further complicated by overlapping generations as is the case in *E. cordata* and most eucalypt species. Species such as *E. regnans* with non-overlapping generations appear to be the exception in the genus. Such species tend to be confined to the wetter forests (mixed or wet sclerophyll) and regenerate from seed released following intense wildfire which completely kills the adult stand. The frequency distribution of fire intervals, and hence the generation time of these eucalypt species, is estimated by Jackson (1968) assuming a mean of 100 (wet sclerophyll) to 200 (mixed forest) years. Over-lapping generations would tend to increase the level of inbreeding (Frankel and Soulé 1981) thus necessitating a larger actual population size to compensate (Frankel 1982).

7.4.2 Population size

Based on empirical animal breeding results, an effective population size of 50 is considered the minimum to counteract the short-term effects of inbreeding (Frankel and Soulé 1981), and Namkoong (1984) suggests that for many plant species the minimum is between 20 and 50. Brown and Moran (1981) have shown that a population size of 70 would be theoretically sufficient to maintain half the heterozygosity under neutrality over 100 generations. A much larger population size is necessary to ensure long-term evolutionary adaptability. Several authors suggest a minimum population size of 500 is necessary to maintain a long term viable population (Franklin 1980; Frankel and Soulé 1981), and for forest trees Namkoong (1984) suggests a range from a few hundred to a few thousand trees is sufficient.

There are clearly difficulties in readily defining effective population sizes in natural populations (cf. the number of reproductively mature individuals) and the relevance of these often quoted figures to the real world has been

questioned (e.g. Moran and Hopper 1987 and Burgman *et al.* 1988). Nevertheless, there is little doubt that the predominantly outbreeding eucalypts (see Moran and Bell 1983) maintain relatively high genetic loads of deleterious recessive alleles. While the outcrossing rate of *E. cordata* is unknown, plants have been successfully obtained following selfing of *E. cordata* (Cauvin *et al.* 1987), although the yield was only one fifth the yield following open pollination. Marked inbreeding depression in seed set, germination, growth and survival have been reported in closely related species and these effects are often manifest very early in the life cycle (e.g. Potts *et al.* 1988; Potts and Cauvin 1988). However, it is possible that high genetic loads of deleterious genes can be maintained in small eucalypt populations at little cost if the effects of inbreeding occur in early stages of the life cycle (see also Ledig 1986). This would be particularly relevant in genera such as *Eucalyptus* where density-dependent selection is believed to be important (Barber 1965; Ledig 1986) and the deleterious effects could be further buffered with differential maternal resource-allocation (e.g. Griffin *et al.* 1987).

In general, the mean level of genetic diversity within populations is lower in eucalypt species distributed as small disjunct populations than wide spread, more continuously, distributed species (see data in Brown and Moran 1981; Fripp 1982 and Moran and Hopper 1987). Nevertheless, within the eucalypt species no relationship between population size and genetic diversity or heterozygosity has been demonstrated to date (Moran and Hopper 1983; Moran and Hopper 1987). In fact small marginal or peripherally isolated populations of forest-tree genera are often found to exhibit levels of variability comparable with large, central populations (Potts and Reid 1985b; Moran and Hopper 1987). Moran and Hopper (1987) suggest that species may have intrinsic levels of genetic diversity determined more by long-term evolutionary history than recent phenomena such as the current population size. This is exemplified by the marked difference in the phenetic variability between eastern and western peripheral isolates of the Tasmanian endemic *E. gunnii* (Potts and Reid 1985b). This trend was believed to be associated with a reduction of variability in founder populations in areas colonized since deglaciation in the west and a concentration of variability in many low altitude relict populations in the east. The high variability in many of the relict populations of the species was believed to be at least partly a result of interspecific hybridisation with surrounding species. Accordingly, Moran and Hopper (1987) consider that the success of conservation strategies may ultimately depend on the relative roles of selection, genetic drift and gene flow in determining genetic diversity patterns.

Estimates of the effective size of the *E. cordata* populations are complicated by the vegetative regeneration of plants from lignotubers. Old, well-established plants may bear reproductively immature stems due to recent vegetative regeneration from fire. The estimates of the population size given in Table 2.4 are for the number of plants which are not seedling nor saplings (lignotuber diameter ≤ 21 cm) and do not correspond to the current size of the breeding population. In all cases, the current breeding population is less than the estimated population size. In several cases the discrepancy was marked due to a large proportion of the population having been recently burnt. However, unless there is a change in fire regimes, this state is likely to persist and at least the relative distribution of the number of breeding individuals in populations given in Fig. 7.1 may be realistic for the species.

In total, there are probably at least 11,000 individuals (not seedlings nor saplings) of *E. cordata* in natural populations with populations sizes ranging from 1 to over 5000 individuals (Table 2.1). While the 'western' morph is relatively localized and there are fewer populations, it is the more common morph, accounting for approximately 60% of individuals. Examined superficially, the total number of "potentially" reproductively mature individuals appears to be above the limit for maintaining evolutionary viability. However, with the insular distribution pattern, the species can not be considered a panmictic unit (see section 7.1.3); rather, the viability of the component populations must be assessed individually. The approximate number of breeding individuals in each population at the time of sampling are indicated in Fig. 7.1. Nearly 40% of the populations of *E. cordata* contain 20 or less, and 75% contain 50 or less breeding individuals; numbers at which inbreeding and genetic drift may be important. The problem of inbreeding would be further accentuated as these estimates would be near the upper limit for the effective population size, but with unknown levels of inbreeding and population structure Namkoong (1984) suggests that such figures could be approximately halved. If, however, fire was prevented from recurring until the regenerating coppice reached reproductive maturity, only four populations (PR, BR, SR and Be) would have effective population sizes of less than twenty. In at least one population from each morph (Snug Plains and Cape Queen Elizabeth) the current effective population size should be sufficient to ensure long-term evolutionary flexibility. However, long-distance gene flow between neighbouring populations may enhance the evolutionary potential of some populations by inflating their effective population size.

7.4.3 Gene flow

The relatively small populations of *E. cordata* are localised and isolated from their nearest neighbour by an average of 9.2 km (range = 0.32 - 36.5 km) and the average distance between all populations is 44.8 km. Estimates of gene-flow parameters recently derived for *E. risdonii* (Potts and Reid 1988) suggest an approximation of the standard deviation for total gene-flow in *E. cordata* may be in the order of 50 m which, following Barton and Hewitt (1985), suggests a moderately strong barrier to gene flow between populations of *E. cordata* may be of the order of 5 km (100σ). This is the maximum distance Ashton and Sandiford (1988) reported interspecific hybrids of *E. regnans* occurred from a source and estimates for *E. risdonii* (Potts and Reid 1988) suggest 8.2 km would be a moderately strong barrier to pollen dispersal. With many of the populations (particularly in the east) occurring as scattered undershrubs beneath a taller eucalypt canopy, with a relatively low reproductive output to attract pollinators, even this distance may be an over-estimation. The rate of gene exchange between populations separated by more than 5 km can thus be considered virtually negligible, which suggests the majority of the populations of *E. cordata* are completely geographically isolated from genetic input from the rest of the gene pool (Fig 7.3). The barrier arising from geographical isolation may be further accentuated by differences in flowering time between 'eastern' and 'western' populations (Fig. 7.4). These considerations imply that the species is comprised of at least 15 genetically independent lineages (Fig. 7.3), many of which are already relatively highly differentiated. Low level gene-flow, in a stepping-stone manner, may occur between populations within the few major groups of populations which occur in relatively close geographical proximity (see Fig. 7.3). However, there is a strong correlation between geographical and phenetic distance which suggests the genetic impact of such

Figure 7.3. Single linkage dendrogram indicating the geographic distance between nearest neighbour populations of *E. cordata*.

Populations which may be potentially linked by gene flow (at least in a stepping stone manner) are indicated assuming either a distance of 2 km or 5 km between nearest neighbours constitutes a significant barrier to gene flow (see text). The estimated population size and the phenetic group (● eastern ; ○ western) of each population is shown.

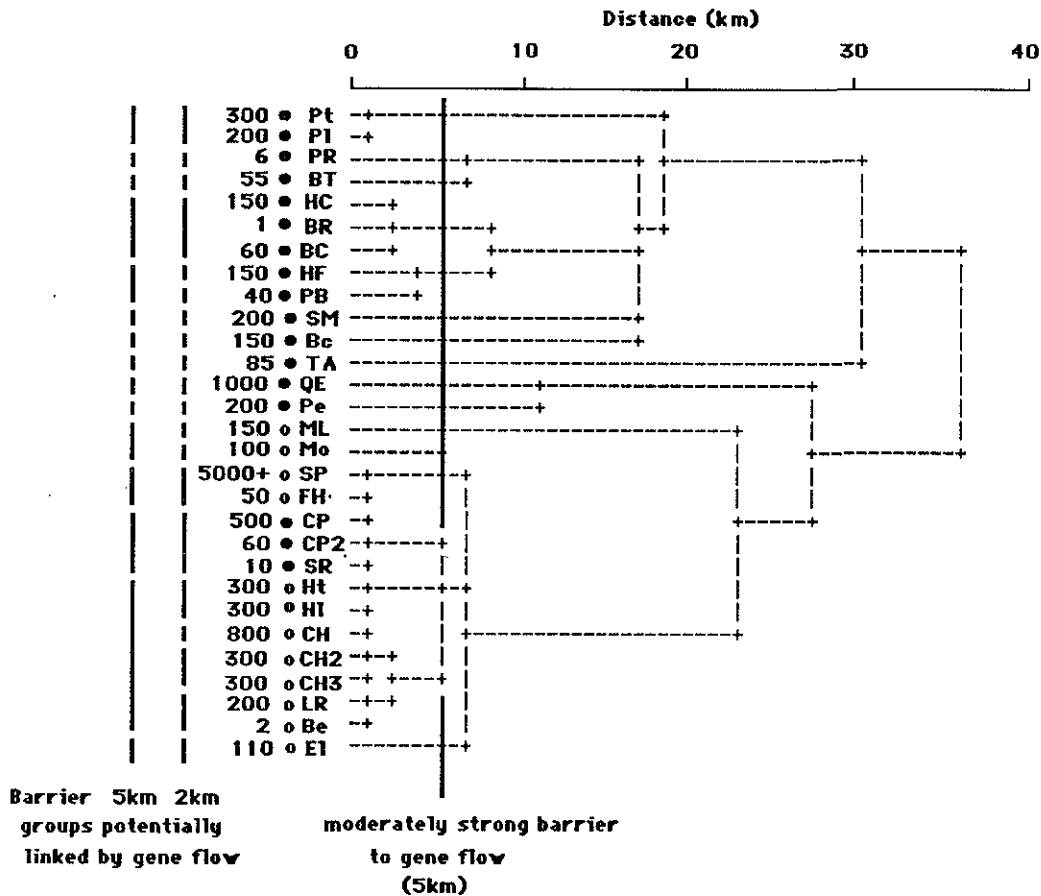
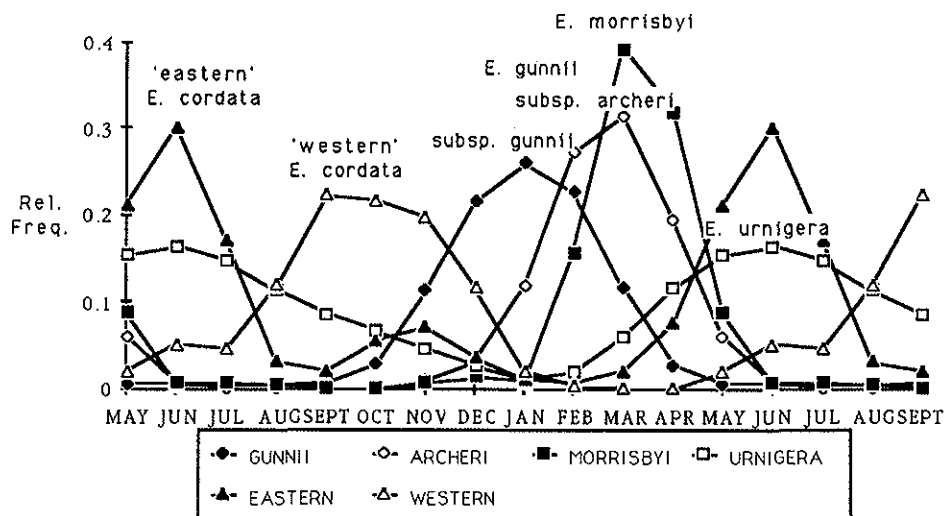
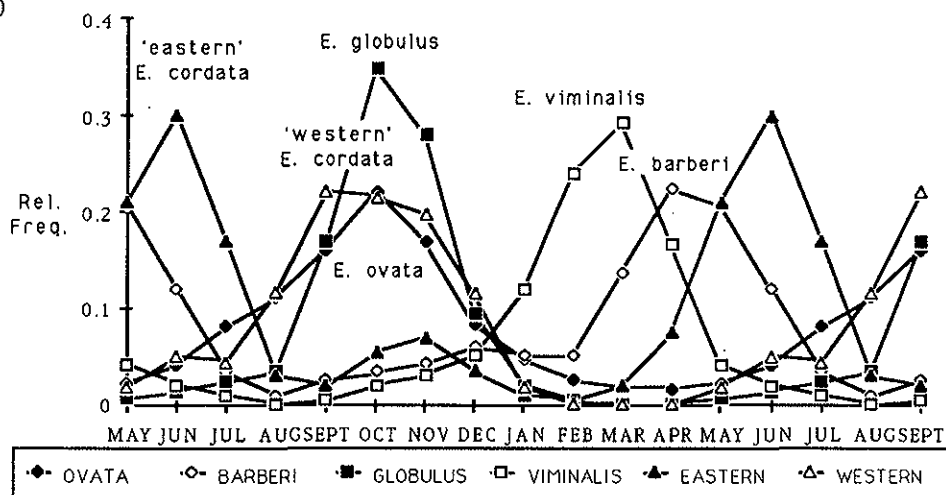


Figure 7.4 Generalised flowering time curves for *E. cordata* and (a) other Tasmanian *Cordatinae* species and (b) associated *Symphyomyrtus* species. The curves represent the relative frequency distribution of flowering time events as recorded from field notes and herbarium specimens (including EUCALIST; *E. urnigera* data provided by M. Savva).

(a)



(b)



immigration may be relatively small. Nevertheless, the effective size of the small populations, particularly south-east of Mt. Wellington (e.g. [CP2, CP and SR] and [Ht, HI, CH, CH1, CH2 and Be]) is probably expanded by interpopulation gene-flow, increasing the long-term viability of the small populations comprising these complexes. A relatively high level of gene-flow might also be expected amongst the separate stands of *E. cordata* on Snug Plains, which in most cases are separated by about 1-2 km (see Appendix 1) and for the purposes of conservation, the *E. cordata* in this area (SP) can be effectively treated as a single population.

Current gene exchange between populations of the 'eastern' and 'western' form is unlikely. The least distance between populations dominated by different morphs is 5.2 km (LR to SR). The closest 'western' population, Leslie Road (LR) is variable in stem shape, but this is also the case for the populations at Electrona (EI) and on the top of Herringback Range (Ht) which are separated by 12.8 and 13.2 km respectively from the nearest 'eastern' population. Closer 'western' populations (e.g. HI and CH) show no such variability suggesting continuing gene-flow is unlikely to be a factor contributing to the convergence of LR, EI and Ht toward the 'eastern' morph.

7.4.4 Interspecific hybridisation

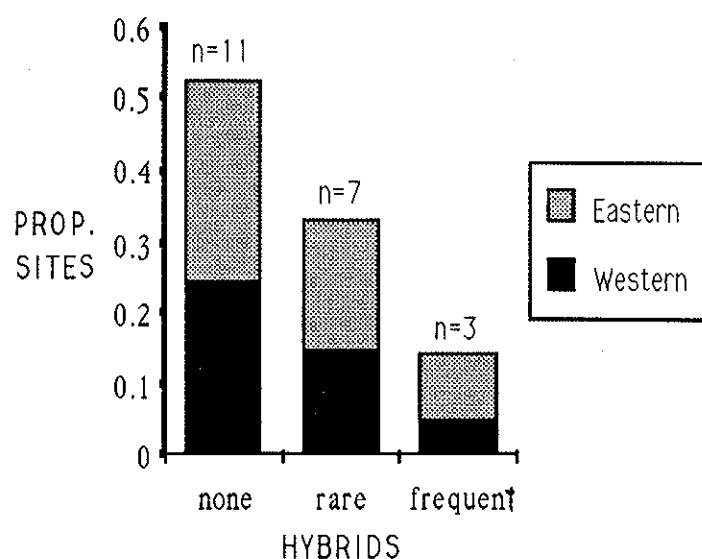
The effects of interspecific hybridisation are rarely considered in genetic conservation, yet in many outbreeding genera such as *Eucalyptus*, where reproductive barriers between species are weak (e.g. Potts *et al.* 1987; Griffin *et al.* 1988), hybridisation with co-occurring species may have an important genetic impact.

E. cordata has been successfully artificially hybridised with several species which often occur in the general vicinity of natural populations. Artificial hybrids of *E. cordata* have been obtained using pollen of *E. gunnii*, *E. dalrympleana* and *E. ovata* (Cauvin *et al.* 1987) and successful hybrids have been produced using *E. cordata* pollen and females of *E. ovata* and *E. morrisbyi* (B. Potts unpubl.). *E. globulus* and *E. cordata* have also been successfully hybridised using both species as females (Max Gilbert pers. com. - *E. globulus* from ornamental in St. David's park ; *E. cordata* from Summerleas Road) and during this survey, a vigorous F2 was grown from one of the original artificial F1 hybrids grown in the Tarrana Forest Reserve. Recent attempts at this cross have failed when *E. globulus* was used as the female whereas outcrosses with *E. globulus* pollen were successful (Potts and Cauvin 1988) which suggests at least a partial barrier to the cross when *E. globulus* is used as the female. However, there does not appear to be strong post-mating barriers to hybridisation of *E. cordata* females (see also Potts *et al.* 1987) and the flowering time of *E. cordata* overlaps several of the *Symphyomyrtus* species which occur in the same general geographical area as *E. cordata* (Fig. 7.4).

The frequency of putative interspecific hybrids in open pollinated progenies grown from the *E. cordata* populations is given in Table 2.4. In most cases, the individuals classified as hybrids were believed to be F1 hybrids on the basis of their morphology and their occurrence as occasional outliers in progenies from pure parents. Putative F1 hybrids with either *E. viminalis*, *E. ovata* or *E. globulus* occurred in progenies from 25% of *E. cordata* populations examined. These are all 'eastern' populations (i.e. BT, BC, HC and QE - Table 2.4 and Pe) occurring in the drier parts of the species range which is reflected in the significant correlation between percentage of hybrids and the climatic variables (*PC1 clim and *MNANRAIN) indicated in Table 7.1. The percentage of hybrids in progenies was also associated with a decreasing cover of *E. cordata* relative to other *Symphomyrtus* species, and increasing cover of the *Monocalyptus* species, *E. pulchella* (Table 7.1). Hybridization does not occur between the two different subgenera and the latter association reflects the tendency for populations growing beneath the canopy of *E. pulchella* to be the small, scattered and suppressed populations having low relative cover.

Interspecific hybrids have become established and grown to maturity in nearly 50% of natural populations of *E. cordata*, although hybrids were common in only about 10% of populations (Fig. 7.5). Notably, there was a significant positive correlation between the percentage of putative F1 hybrids in the progeny and the frequency of putative hybrids in the natural population (Table 7.1). However, there was no association between the frequency of putative hybrids in the natural population and any of the variables examined (Table 7.1). There was no association between site disturbance and hybridisation, clearly indicating that hybridisation is a natural phenomenon. Considerable hybridization between *E. cordata* and *E. johnstonii* does occur on a markedly disturbed site at the base of the Herringback Range (HI), but more extensive hybridisation occurred in several undisturbed stands. The *E. cordata* population at Pony Bottom Creek (PB) flowers synchronously with an associated eucalypt

Figure 7.5 The occurrence of putative hybrids in natural populations of *E. cordata*.



(which is possibly a variant of *E. barberi*) and there appears to be a hybrid swarm between the two populations. Abnormal seedlings believed to be backcrosses to an *E. cordata* x *globulus* hybrid occurred in progeny from the population on the summit of Herringback Range. A single abnormal tree, which progeny tests suggests is an *E. cordata* x *globulus* hybrid was found in this population. The nearest stands of *E. globulus* were several kilometres from the site and this hybrid is possibly an example of long-distance pollen dispersal. While further work is required, the available evidence suggests that interspecific hybridisation may have a marked genetic impact on these small, isolated populations. In the case of both the Prosser River and Hellfire Bluff populations, although a small percentage resembled typical 'eastern' *E. cordata*, the majority of seedlings lay outside the phenetic range acceptable for *E. cordata* and were intermediate between *E. cordata* and the co-occurring *E. viminalis*. These populations are clearly deviant (Chapter 4) and they are believed to be the genetic remnants of populations of *E. cordata* which have been introgressed by the surrounding *E. viminalis*, nearly to the point where they may be considered phantom hybrid populations (e.g. Parsons and Kirkpatrick 1972; Potts and Jackson 1986).

These results strongly suggest that in species with insular population structures such as *E. cordata*, the genetic diversity within populations (and hence, evolutionary future), particularly of the smaller populations, may be determined more by hybridisation with surrounding potentially interbreeding species than interaction with the remainder of the species' gene-pool. The rate of interpopulation gene exchange can not readily be directly assessed, but with the large disjunctions between most of the *E. cordata* populations, this must be negligible (section 7.4.3). There is little doubt that in many of the *E. cordata* populations, the level of gene flow between populations would be far exceeded by the level of F1 interspecific hybridisation (i.e. 2-35 %). Furthermore, there are ample examples of advanced generation hybridisation in the natural populations to suggest that effective gene exchange does occur. This conclusion is also supported by work on localized (e.g. *E. risdonii* - Potts and Reid 1988), regional (*E. gunnii* - Potts and Reid 1985b) and wide-spread eucalypt species (e.g. *E. regnans* - Ashton 1981b; Ashton and Sandiford 1988).

In terms of conservation, interspecific hybridisation clearly has the potential to increase the within-population genetic diversity and therefore must affect both the short- and long-term fitness of populations. It has been suggested that in contrast to classical ideas, in genera such as *Eucalyptus* with weak reproductive barriers, hybridisation may result in a dramatic release of variability during population bottlenecks and may be an integral part of the process of population extinction (Potts and Jackson 1986). The boundaries of small eucalypt populations are often blurred by hybridization (Pryor and Johnson 1971) and during extinction the nucleus of the stand may contract to the point where selection is unable to counter-balance the effects of pollen swamping from surrounding, more abundant species. However, the importance of this variability to gene pool conservation may vary and will depend on several factors including the species combination (see Griffin *et al.* 1988), effective population size (affecting drift), rate of gene flow from other areas of the gene pool and the relative direction and magnitude of selection involved. On the one hand, the influx of variability provided by interspecific hybridization may be advantageous, and Kirkpatrick (1976) suggests slow gene exchange with contiguous species may be one

Table 7.1 Factors associated with the level of interspecific hybridisation in stands of *E. cordata*.

The table indicates the value and significance (two-tailed) of Kendall's rank correlation coefficient between the relative frequency of hybrids in the natural stand (HYBRIDS - Table 2.2) and in open pollinated progenies (see Table 2.4) and the site variables indicated. Variable codes are detailed in Table 2.2 and variables preceded with an asterisk are floristically defined estimates (see Chapter 5). (ns not significant; * $P < 0.05$; ** $P < 0.01$)

	-----HYBRIDIZATION-----							
					(excluding PR and HF)			
	FIELD		PROGENY		FIELD		PROGENY	
LASTFIRE	0.02	ns	-.10	ns	0.04	ns	-0.02	ns
POPSIZE	0.03	ns	-0.31	ns	0.14	ns	-0.17	ns
No. associated								
- <i>Symphyomyrtus</i> species	0.22	ns	0.29	ns	0.16	ns	0.29	ns
- <i>Eucalyptus</i> species	-0.08	ns	0.20	ns	-0.09	ns	0.12	ns
DISTURBANCE	0.00	ns	0.05	ns	0.07	ns	0.25	ns
DISTRIBUTION	-0.15	ns	-0.48	*	-0.12	ns	-0.44	ns
Understory richness	-0.24	ns	-0.09	ns	-0.29	ns	-0.09	ns
Relative cover of <i>E. cordata</i>								
-relative to <i>Symphyomrytus</i> spp.	-0.27	ns	-0.51	**	-0.16	ns	-0.41	*
-relative to other <i>Eucalyptus</i> spp.	-0.02	ns	-0.37	*	0.11	ns	-0.28	ns
% cover of <i>E. cordata</i>	-0.11	ns	-0.30	ns	-0.04	ns	-0.19	ns
% cover of <i>E. pulchella</i>	0.23	ns	0.56	**	0.10	ns	0.54	*
PC1 geog (see fig. 3.3)	-0.26	ns	-0.37	*	-0.17	ns	-0.25	ns
ALT	-0.12	ns	-0.38	*	-0.06	ns	-0.31	ns
*ALT	-0.26	ns	-0.43	*	-0.18	ns	-0.40	*
*DRAINAGE	-0.06	ns	-0.19	ns	-0.01	ns	-0.23	ns
*MNANRAIN	-0.35	ns	-0.56	*	-0.33	ns	-0.51	**
*CLIMPC1 (see fig. 5.1)	-0.20	ns	-0.48	**	-0.23	ns	-0.48	*
Hybrids in progeny	0.60	**			0.57	**		

means by which small relict populations may retain evolutionary flexibility. On the other hand, depending on the selection coefficients, hybridization may simply increase the genetic load on the population with no obvious genetic impact (e.g. Wiltshire and Reid 1987) or, with extensive introgression, result in complete genetic degradation (Potts and Reid 1985b; Potts and Jackson 1986) such as may have already occurred in several of the *E. cordata* populations. In this respect Pryor (1951) compares the two relict species *E. glaucescens* and *E. perriniana* of similar sub-alpine distribution. Populations of *E. glaucescens* appeared to be undergoing introgressive invasion by the surrounding *E. viminalis* whereas there was no trace of hybridisation in the small relict stands of *E. perriniana* (see also Wiltshire and Reid 1987). Extinction or range restriction may thus occur by simple competitive displacement or involve the more complex introgressive displacement.

There can be little doubt that *E. cordata* is a relict species and that at least in parts of its range, the populations are probably facing eventual extinction due to natural competitive exclusion by co-occurring eucalypt species. This is particularly so for the small 'eastern' populations on well drained, dry sclerophyll forest sites (e.g. BT, BC, HC, BR, PB, HF and PR) where the species occurs as scattered undershrubs beneath the *E. pulchella* canopy, and the reproductive loading of the plants is low when compared to surrounding species. These are the main populations in which hybrids occurred in open-pollinated progenies (Table 7.1), and while natural hybrids are not always associated with these populations (Table 7.1), hybrid swarms exist (e.g. PB) and possibly extensive introgression has possibly occurred in several of these populations (e.g. HF and PR).

7.5 Conservation status

E. cordata is a rare Tasmanian endemic with a regional (*sensu* Moran and Hopper 1987) geographical distribution but, in contrast to previous assessments (e.g. Pryor 1981; Fry and Benson 1986), this survey suggests that as a species, *E. cordata* is not currently endangered or threatened. Following the categories of Leigh et al. (1984), *E. cordata* thus clearly warrants a conservation status of "R". This category includes species which are rare but not currently considered endangered or vulnerable and are represented by a relatively large population in a very restricted area or by small populations spread over a wide range or some intermediate combination. The majority of *E. cordata* populations (70%) are currently relatively free of human interference, and there is no evidence that major loss of the genetic resource has occurred since European settlement. Nearly fifty percent of the populations located are either secure in State Reserves or occur on Crown Land where conservation policies can be readily implemented. The effective population size of over 50% of the population appears to be sufficient to maintain short-term fitness and the size of at least one population of each morph would appear sufficient for long term evolutionary adaptability to be maintained. Nevertheless, at present the species is not adequately conserved and the current reserve system does not cover the full range of genetic and ecological diversity in the species. Thus there is an urgent need for the implementation of a specific conservation strategy to ensure that the conservation status of this rare species is not degraded.

At least five of the populations have been markedly disturbed and are under threat of further disturbance and many of the populations required to conserve the full ecological and genetic diversity in the species occur outside reserves. The larger populations of the 'eastern' morph (Perpendicular Mountain, Cape Queen Elizabeth and Penguin Island) are undisturbed and occur in relatively secure State Reserves. However, no population of the 'western' subspecies is officially reserved although the main stronghold of this subspecies (and of the species) on Snug Plains occurs in State forest and a proposal for its reservation within a land management plan is currently being prepared. In addition, several populations of specific scientific interest have been identified, several of which are outliers (e.g. PR, HF and Bc) and these require some level of reservation.

7.6 Recommendations

The distribution of genetic variability and the population structure of *E. cordata* is very similar to that described for the rare Western Australian eucalypt, *E. caesia* (Hopper *et al.* 1982; Moran and Hopper 1983, 1987), and in both instances the optimum strategy for *in situ* conservation is prescribed by the effective populations sizes and the distribution of the genetic diversity (Moran and Hopper 1983). Each species has a disjunct distribution pattern with many of the populations at, or below, the often quoted minimum population size for conservation, in which case, the whole population should be retained wherever possible (Moran and Hopper 1983). In addition, both species show strong patterns of geographical differentiation such that a large component of the variability is distributed between as opposed to within populations. In such cases, the strategy for optimum *in situ* conservation is to maximize the size of individual populations and to safeguard an adequate range and as many populations as possible (Frankel 1982; Moran and Hopper 1983). Accordingly, populations encompassing the full genetic and ecological diversity of the species should be accorded some level of reservation, or at least included in management plans to avoid future disturbance. Where resources are limiting, priority should be toward the larger and least disturbed of the populations.

Adoption of the major recommendations listed below in order of decreasing priority should ensure optimal conservation of *E. cordata*. Due to the limited number and generally small size of the populations, and with a large number of the populations occurring on Crown Land, this can be achieved with the allocation of minimal resources. Adequate conservation should be possible without acquisition of populations on private land although, with suitable liaison with private property owners, there is no reason why, at least in the short-term, all populations of this species can not be preserved with minimal disturbance. This is important in order to maintain the individual components of the population complexes previously identified south-east of Mt. Wellington. The short and long term fitness of the populations comprising these complexes is increased beyond that expected on the basis of population size by virtue of potential links through gene-flow with other populations. *Ex situ* conservation is unnecessary, although a plantation using progenies grown for the present study was established on private land in 1985 with support from Greening Australia. Nevertheless, genetic management of several of the disturbed populations which have been reduced in size by land clearing would be genetically beneficial, and would

enhance awareness of conservation. This management would simply involve expansion of populations through re-planting of contiguous areas with seed collected from the same population. For example, it is possible to establish local *E. cordata* along fence lines at both Electrona and Leslie Road permitting the effective size of these populations to be increased.

SPECIFIC RECOMMENDATIONS

Recommendation 1

All authorities responsible for the management of Crown Land on which *E. cordata* occurs should be notified immediately and management policies adopted to ensure these populations and suitable buffer zones remain undisturbed, or do not receive further disturbance through human activities.

Specific biological management of *E. cordata* is not recommended, although a relatively low fire frequency should be maintained where possible. Little specific information is available on the response of the species to fire. It is unlikely to differ greatly from that described for *E. risdonii* (e.g. Potts 1986), although observations indicate that the time for coppice to reach reproductive age may be greater. As most stems will be killed to ground level by fire and a low percentage of lignotuberous individuals will be killed, it is preferable if fire coincides with full reproductive loading of the population to maximize seedling establishment and prevent fire attrition of the population. Post-fire coppice in the population on Chimney Pot Hill has not reached reproductive maturity after eight years, and the reproductive loading on the majority of the coppice which regenerated after fires in 1967 (e.g. Snug Plains) is still low. There also appears to be a difference between the subspecies in the time to reach reproductive maturity with both coppice and seedlings of the 'eastern' form maturing earlier. A system of patch burning is recommended by Hopper *et al.* 1983, and this appears to be already naturally occurring in the drier areas of the range of *E. cordata*. However, the fire frequency in the drier areas, particularly where *E. cordata* occurs in *E. pulchella* forest is possibly too high, favouring co-occurring tree species.

Reserved areas covered by this recommendation include Perpendicular Mountain (Pt and Pl), Hospital Creek (HC), Cape Queen Elizabeth (QE), and Penguin Island (Pe). State cabinet has approved Hellfire Bluff (HF) for a State Reserve status but the reserve has not yet been declared. Managers of these areas should be aware of the exact location of populations. The health of the populations should be monitored and where possible records of factors affecting populations such as fire history, pests etc. should be maintained.

Unreserved populations on Crown or Council Land covered by this recommendation are Snug Plains (SP and FH), Bluestone Tier (BT), Chimney Pot Hill (CP - H.C.C), Pony Bottom Creek (PB), Brown Mountain (Bc) and Meredith Tier (MT - deviant population), several of which are specifically addressed in the following recommendations. All of the populations on Crown land are in State forest and consequently are the responsibility of the Forestry Commission.

Recommendation 2

A reserve should be established encompassing the stands of *E. cordata* in State Forest on Snug Plains.

Reservation of the *E. cordata* in this area must be given highest priority; this area is the stronghold of the species, and the population is of the 'western' form which is not currently reserved. The area is currently mainly used for fire-wood collection and the areas encompassed by *E. cordata* are relatively small and are of minimal commercial value.

Additional impetus for the establishment of a reserve in this area is the nearby occurrence of an outlying stand of the endemic eucalypt *E. gunnii*. This population of *E. gunnii* is one of the faster growing provenances of the species despite its fire induced mallee habit, and the population differs genetically from more northern populations of the species (Potts and Reid 1985 a and b). The population is the most south-easterly and one of the lowest altitudinal occurrences of the species. Snug Plains is also the only known area where the closely related endemics *E. cordata*, *E. urnigera* and *E. gunnii* co-occur.

Recommendation 3

Negotiations should be commenced with A.N.M. on the management of the *E. cordata* stand at Moogara possibly to establish a reserve of more formal status.

The *E. cordata* at Moogara is again of the 'western' form and this is the major locality at which *E. cordata* occurs as a tree. The tree form is no doubt partly a result of fire protection and such protection should continue. The stand has been reduced in size and is surrounded by *Pinus radiata* plantation. However, there is considerable regeneration of *E. cordata* in the surrounding plantation. It is recommended that immediate steps be taken to remove the *Pinus radiata* immediately surrounding this stand, including all areas in which *E. cordata* regeneration has occurred. Such action will allow buffering of the main stand from invasion and the effective size of the population to be markedly increased when the regeneration matures. The size of this population should also be extended by planting to allow a total of 1-2000 mature trees. This planting should be possible with very little loss of productive *Pinus* plantation and could be either undertaken simultaneously with the initial clearing or after the first cutting of the *Pinus* plantation. Adjacent areas should be planted using only seed derived from the Moogara population. Seed should be collected from a large number of mature individuals and planted as close as practical to a single tree-plot random block design. The randomization of families in this manner is a standard approach to minimize inbreeding in seed orchards.

Recommendation 4

A reserve should be established on Brown Mountain to include the summit and to encompass the population with affinities to *E. cordata* (Bc).

The population on Brown Mountain (Bc) is very important from an evolutionary and taxonomic viewpoint because while it has closest affinities to the 'eastern' subspecies of *E. cordata*, it is an outlier and deviates toward the closely related species. It is the highest altitudinal occurrence of the 'eastern' form of *E. cordata* and occurs on a poorly drained site; a habitat type poorly reserved in the 'eastern' form. This reserve would also encompass a geographically outlying population of the endemic snow gum, *E. coccifera*.

Recommendation 5

The population of *E. cordata* on Chimney Pot Hill (CP) should be accorded reservation status.

This locality is the most western occurrence of the 'eastern' subspecies. Although the population is traversed by several rough vehicle tracks, it is relatively large, and occurs on a water-logged site. The population is not only important from a biogeographical viewpoint, but reservation is necessary to ensure the full combination of ecological and phenotypic diversity within *E. cordata* is preserved. This population is on land managed by the Hobart City Council as part of the Hobart water catchment and with cooperation suitable management should be possible to ensure the preservation of this population.

Recommendation 6

The degree of threat to the *E. cordata* populations on private land should be closely monitored and liaison with land-owners maintained to minimize any future threat to these populations.

Negotiations should be commenced with a view to ensuring some level of protection for the population of *E. cordata* which occurs on private land near Electrona (El). This population is important as it is one of the few polymorphic, intermediate populations of the species and it occurs on mudstone, which is rare for *E. cordata*. It occurs at the lowest altitude and on one of the driest sites of the 'western' populations. Of the three intermediate populations, this site most warrants attention as the degree of variability in stem shape is greatest and it is less threatened than the Leslie Road site. While of low priority, some level of protection of the populations of *E. cordata* on the summit of Herringback Range (Ht) and on Combes Hill (CH) would be beneficial. These populations are not likely to be threatened in the near future. However, if the opportunity arises, or if other proposals are being considered, reservation of these populations would be of value in consolidating the conservation

of the 'western' subspecies of *E. cordata*. For example, the population on Combes Hill is relatively large and is close to the boundary of the Wellington Range Reserve, and if the opportunity arises through land sale, extension of the reserve to include *E. cordata* may be justified.

Recommendation 7

Some level of reservation status should be given to the area on Meredith Tier which includes the population MT and the nearby (approx. 500 m eastward) population of the endemic *E. barberi*.

Further investigation is required to determine the exact affinities of the population on Meredith Tier. Nevertheless, the population is clearly unique (Figure 6.2) and may be a rare example of a natural hybrid swarm between either *E. gunnii* or *E. cordata* and *E. barberi*.

References

- Ashton, D. H. (1981a). Fire in tall open forests (wet sclerophyll forests). In 'Fire and the Australian Biota.' (Eds A. M. Gill, R.H. Graves, and I. R. Noble.) pp. 339-66. (Australian Academy of Science: Canberra.)
- Ashton, D. H. (1981b). The ecology of the boundary between *Eucalyptus regnans* F. Muell. and *E. obliqua* L'Hérit. in Victoria. *Proc. Ecol. Soc. Aust.* 11, 75-94.
- Ashton, D. H., and Sandiford, E. M. (1988). Natural Hybridisation between *Eucalyptus regnans* F. Muell. and *E. macrorhyncha* F. Muell. in the Cathedral Range, Victoria. *Aust. J. Bot.* 36, 1-22.
- Austin, M. P., and Cunningham, R. B. (1981). Observational analysis of environmental gradients. *Proc. Ecol. Soc. Aust.* 11, 109-119.
- Baker, R. T., (1902). On *Eucalyptus cordata*, Labill., and its cognate species. *Aust. Assoc. Adv. of Sci.*, IX, 344-348.
- Barber, H.N., (1965). Selection in natural populations. *Heredity* 20, 551-72.
- Barber, H.N., and Jackson, W.D. (1957). Natural selection in action in *Eucalyptus*. *Nature, Lond.* 179, 1267-9.
- Barton, N. H., and Hewitt, G. M. (1985). Analysis of hybrid zones. *Ann. Rev. Ecol. Syst.* 16, 113-148.
- Bentham, G. (1867). 'Flora Australiensis: A description of the plants of the Australian Territory'. (Lovell Reeve & Co., London.)
- Blackith, R. E. and Reyment, R. A. (1971). 'Multivariate Morphometrics'. (Academic Press: London.)
- Blakely, W. F. (1934). 'A Key to the Eucalypts'. (The Workers Trustees: Sydney.)
- Bowman, D. M. J. S., and Kirkpatrick, J. B. (1984). Geographic structure of stands of *Eucalyptus delegatensis* R. T. Baker on dolerite in Tasmania. *Journ. Biogeog.* 11, 427-437.
- Bowman, D. M. J. S., and Minchin, P. R. (1987). Environmental relationships of woody vegetation patterns in the Australian monsoon tropics. *Aust. J. Bot.* 35, 151-69.
- Bramwells, H. W., and Whiffin, T. (1984). Patterns of Variation in *Eucalyptus siberoxylon* A. Cunn. ex Woolls. 1 Variation in Adult Morphology. *Aust. J. Bot.* 32, 263-81.
- Brett, R. C. (1938). A survey of the *Eucalyptus* species in Tasmania. *Pap. & Proc. Roy. Soc. Tas.* 1937, 75-111.
- Brown, M. J., and Bayly-Stark, H. J. (1979). The plant communities of the East Risdon Nature Reserve. *The Tasmanian Naturalist*, 58, 1-11.
- Brown, M. J., Kirkpatrick, J. B., and Moscal, A. (1983). 'An Atlas of Tasmania's Endemic Flora'. (The Tasm. Conservation Trust Inc., Hobart.)
- Brown, A. D. H., and Moran, G. F. (1981). Isozymes and the genetic resources of forest trees. *Proc. Symp. Isozymes North American Forest Trees and Forest Insects.* (Calif. Gen. Tech. Rep. PSW-48USDA.)
- Busby, J. R. (1984). 'Bioclim Users' Manual - version 1.0'. (Bureau of Flora and Fauna: Canberra.)
- Busby, J. R. (1986). A biogeoclimatic analysis of *Nothofagus cunninghamii* (Hook.) Oerst. in south eastern Australia. *Aust. J. Ecol.* 11, 1-7.
- Burns, T. E., and Skemp, J. R. (1961). 'Van Diemen's Land Correspondents.' (Queen Victoria Museum, Launceston.)
- Burgman, M. A., Akcakaya, H. R., and Loew, S. S. (1988). The use of extinction models for species conservation. *Biological Conservation* 43, 9-25.
- Carr, S. G. M., and Carr, D. J. (1976). The French contribution to the discovery of Australia and its flora. *Endeavour* 35 (124), 21-26.
- Cauvin, B., Potts, B. M., and Potts, W. C. (1987). *Eucalyptus* : Hybridation artificielle - barrières et hérédité des caractères. *Annales de recherches silvicoles* 1986. pp. 255-303. (AFOCEL: Paris.)
- Chang, J. J., and Carroll, J. D. (1968). 'How to use PROFIT, a computer program for property fitting by optimizing non-linear or linear correlation'. (Bell Laboratories: U. S. A.)
- Chippendale, G. M., and Ludek, L. J. (1984). EUCALIST: Computerized Date Retrieval System for *Eucalyptus* (Myrtaceae). *Aust. J. Bot.* 14, 147-152.
- Curtis, W. M., and Morris, D. I. (1975). 'The Student's Flora of Tasmania.' Part 1, 2nd Edn. (Government Printer: Tasmania).
- Davies, J. L. (1974). Quaternary Environments. In *Biogeography and Ecology in Tasmania*, ed. W. D. Williams. (W. Junk, The Hague.)
- Faith, D. P., Minchin, P. R., and Belbin, L. (1987). Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69, 57-68.
- Franklin, I. R. (1980). Evolutionary Change in small populations. Chpt. 8. In 'Conservation Biology: An Evolutionary Ecological Perspective.' eds. M. E. Soulé and Wilcox, B. A.. (Sinaur Assoc. Inc.).

- Frankel, O. H. (1982). The role of conservation genetics in the conservation of rare species. In 'Nature Conservation: The Role of Remnants of Native Vegetation', eds. Saunders, Arnold, G. W., Burbidge, A. A. and Hopkins, J. M.. (Surrey Beatty and Sons Pty Limited: Chipping North, Australia.)
- Frankel, O. H., and Soule M. E. (1981). 'Conservation and Evolution.' (Cambridge University Press, Cambridge.)
- Fripp, Y. J. (1982). Allozyme variation and mating system in two populations of *Eucalyptus kitsoniana* (Luehm.) Maiden. *Aust. For. Res.* 13, 1-10.
- Fry, I., and Benson, J. (1986). Australia's Threatened Plants. In 'A threatened species conservation strategy for Australia' (Eds M. Kennedy and R. Burton) pp. 19-35. (Ecofund Australia: Manly.)
- Gentelli, J. (1972). 'Australian Climatic Patterns'. (Nelson, Melbourne.)
- Giplin, M. E., and Soule M. E. (1986). Minimum Viable Populations: Processes of Species Extinction. pp. 19-34. In *Conservation Biology: The Science of Scarcity and Diversity*, ed. M. E. Soule. (Sinauer Associates, Inc. Massachusetts.)
- Gower, J. C. (1962). Variance component estimation for unbalanced hierarchical classifications. *Biometrics* 18, 537.
- Griffin, A. R., Burgess, I. P., and Wolf, L. (1988). Patterns of Natural and Manipulated Hybridisation in the Genus *Eucalyptus* L'Hérit. - a Review. *Aust. J. Bot.* 36, 41-66.
- Griffin, A. R., Moran, G. F., and Fripp, Y. J. (1987). Preferential outcrossing in *Eucalyptus regnans*. *Aust. J. Bot.* 35, 465-75.
- Hall, N., and Brooker, I. (1972). Heart-leaved Silver Gum: *Eucalyptus cordata* Labill. Forest Tree Series No. 53. (Aust. Govt. Publishing Service: Canberra.)
- Halloran, G. M. (1985). Conservation of the genetic resources of Victorian Plants. 'Proc. The State Conservation Strategy Workshop on Genetic Diversity.' (Ed A. M. Brown) pp. 4-20. Tech. Rep. Series No. 11, Resources and Planning Branch. (Department of Conservation, Forests and Lands: East Melbourne.)
- Head, M. J., and Lacey, C. J. (1988). Radiocarbon Age Determinations from Lignotubers. *Aust. J. Bot.* 36, 93-100.
- Hill, M. O. (1979a). 'DECORANA - a FORTRAN program for detrended correspondence analysis and reciprocal averaging'. (Ecology and systematics Section, Cornell University: Ithaca.)
- Hill, M. O. (1979b). 'TWINSPAN - a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes'. (Ecology and systematics Section, Cornell University: Ithaca.)
- Hill, M. O., and Gauch, H. G. (1980). Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42, 47-58.
- Hogg, G. H. (1938). D'Entrecasteaux: An account of his life, his expedition, and his officers. *Pap. & Proc. Roy. Soc. Tas.* 1937, 53-74.
- Hogg, A., and Kirkpatrick, J. B. (1974). The phytosociology and synecology of some Southern Tasmanian Eucalypt Forests and Woodlands. *J. Biogeog.* 1, 227-245.
- Hooker, J. D. (1856). 'The botany of the Antarctic Voyage. Part 3. Flora Tasmaniae.' (Lovell Reeve, London.)
- Hopper, S. D., and Burgman, M. A. (1983). Cladistic and Phenetic Analyses of Phylogenetic Relationships among Populations of *Eucalyptus caesia*. *Aust. J. Bot.* 31, 35-49.
- Hooper, S.D., Cambell, N. A., and Moran, G. F. (1982). *Eucalyptus caesia*, a rare mallee of granite rocks from southwestern Australia. pp. 46-61 In 'Species at risk: Research in Australia', eds. R. H. Groves and W. D. L. Ride. (Australian Academy Science, Canberra.)
- Hooper, S.D., Cambell, N. A., and Caputi, N. (1984). Geographical variation, subspecies discrimination and evolution in fruits, leaves and buds of *Eucalyptus caesia* (Myrtaceae). *Nuytsia* 5, 179-194.
- Hopkins, A. J. H., and Robinson, C. J. (1981). Fire induced structural changes in a Western Australian woodland. *Aust J. Ecol.* 6, 177-88.
- IUCN (1980). 'World Conservation Strategy.' (IUCN: Gland, Switzerland.)
- Jackson, W. D. (1965). Vegetation. In 'Atlas of Tasmania.' (Ed. J. L. Davies.) pp. 30-34. (Lands and Mercury Press, Hobart.)
- Jackson, W. D. (1968). Fire, air, earth, water - an elemental ecology of Tasmania. *Proc. Ecol. Soc. Aust.* 3, 9-16.
- Joppien, R., and Smith, B. (1987). 'The art of Captain Cook's Voyages: The voyage of the resolution and the discovery 1776-1780.' Vol. 3, plate 11 (Oxford University Press, Melbourne.)
- Kantvilas, G. (1983). A brief history of lichenology in Tasmania. *Proc. Roy. Soc. Tas.*, 117: 41-51.
- Kirkpatrick, J. B., and Backhouse, S. (1980). 'Illustrated Guide to Tasmanian Native Trees.' (Mercury-Walch: Hobart.)

- Kirkpatrick, J. B., and Nunez, M. (1980). Vegetation-radiation relationships in mountainous terrain: eucalypt-dominated vegetation in the Risdon-Hills, Tasmania. *J. Biogeography* 7, 197-208.
- Kruscal, J. B., Young, F. W., and Seery, J. B. (1973). 'How to use KYST, a very flexible program to do multidimensional scaling and unfolding.' (Bell Laboratories: U.S.A.)
- Labillardière, J. J., (1800). 'Relation du Voyage à la Recherche de la Pérouse'. (Paris.)
- Labillardière, J. J., (1804-1807). 'Novae Hollandiae Plantarum Specimen'. Vol. 11. (Paris.)
- Lacey, C. J. (1983). Development of large plate-like lignitubers in *Eucalyptus botryoides* Sm. in relation to environmental factors. *Aust. J. Bot.* 31, 105-18.
- Lachenbruch, P. A. (1975). 'Discriminant Analysis'. (Hafner Press: New York.)
- Ladiges, P. Y., and Ashton, D. H. (1974). Variation in some central Victorian populations of *E. viminalis* Labill. *Aust. J. Bot.* 22, 81-102.
- Lawrence, M. J. (1984). The genetical analysis of ecological traits. In 'Evolutionary Ecology - The 23rd Symposium of the British Ecological Society Leeds 1982'. (Ed. B. Shorrocks.) pp. 27-63. (Blackwell Scientific Publications, Oxford.)
- Ledig, F. T. (1986). Heterozygosity, Heterosis, and Fitness in Outbreeding Plants. pp. 77-104. In 'Conservation Biology: The Science of Scarcity and Diversity'. (Ed. M. E. Soulé.) pp. 77-104. (Sinauer Associates, Inc., Massachusetts.)
- Ledig, F. T., Guries, R. P., and Bonefeld, B. A. (1983). The relation of growth to heterozygosity in Pitch Pine. *Evolution* 37, 1227-1238.
- Leigh, J., R. Boden and J. Briggs (1984). 'Extinct and Endangered Plants of Australia'. (Macmillan Co., Sth. Melbourne).
- Maiden, J. M., (1910). Records of the earlier French Botanists as regards Australian plants. *J. Roy. Soc. N.S.W.* 44, 123-155.
- Maiden, J. M. (1913). 'A Critical Revision of the genus Eucalyptus'. Vol. 2: pts 17-19. (Government Printer, Sydney.)
- Maiden, J.M. (1919). Notes on Tasmanian eucalypts. *J. Roy. Soc. N.S.W.* 53, 82-90.
- Mahalanobis, P. C. (1936). On the generalized distance in statistics. *Proc. Nat. Inst. Sci. India* 2, 49-55.
- Minchin, P. R. (1983). A comparative evaluation of techniques for ecological ordination using simulated vegetation data and an integrated ordination-classification analysis of the alpine and subalpine plant communities of the Mt. Field plateau, Tasmania. Ph. D. thesis, University of Tasmania.
- Minchin, P. R. (1986). 'How to use ECOPAK: an ecological database system.' CSIRO Aust. Div. Water and Land Resources, Tech. Memo. 86/6.
- Minchin, P. R. (1987). An evaluation of the robustness of techniques for ecological ordination. *Vegetatio* 69, 89-107.
- Moran, G. F., and Bell, J. C. (1983). Eucalypts. In 'Isozymes in Plant Genetics and Breeding: Part B.' (Eds. S. D. Tanksley and T. J. Orton.) pp. 423-441. (Elsevier Science Publishers, Amsterdam.)
- Moran, G. F., and Hopper, S.D. (1983). Genetic diversity and the insular population structure of the rare granite rock species, *Eucalyptus caesia*. *Aust. J. Bot.* 31, 161-72.
- Moran, G. F., and Hopper, S. D. (1987). Conservation of the Genetic Resources of Rare and Widespread Eucalypts in Remnant Vegetation. In 'Nature Conservation: The Role of Remnants of Native Vegetation.' (Eds D. A. Saunders, G. W. Arnold, A. A. Burbidge, and J. M. Hopkins.) pp. 151-162. (Surrey Beatty and Sons Pty Limited: Chipping North, Australia.)
- Namkoong, G. (1984). A concept of gene conservation. *Silvae Genetica* 33 (160-163).
- Nelson, E. C. (1974). The locations of collection and collectors of specimens described by Labillardière in "Novae Hollandiae Plantarum Specimen": additional notes. *Proc. Roy. Soc. Tas.*, 108: 159-170.
- Nelson, E. C. (1975). The collectors and type locations of some of Labillardière's "Terra Van-Leuwin" (Western Australia) specimens. *Taxon*, 24: 319-336.
- Noble, J. C. (1982). The significance of fire in the biology and evolutionary ecology of mallee *Eucalyptus* populations. In 'Evolution of the Flora and Fauna of Arid Australia'. (Eds W. R. Barker and P. J. M. Greensland.) pp. 153-9. (Peacock Publications: Frewville, S. A.)
- Parsons, J. B., and Kirkpatrick, J. B. (1972). Possible phantom hybrids in *Eucalyptus*. *New Phytol.* 71, 1213-1219.
- Pederick, L. A. (1985). Genetic Resources of Victoria's Eucalypts. Proc. In 'The State Conservation Strategy Workshop on Genetic Diversity.' (Ed A. M. Brown) pp. 21-26. (Tech. Rep. Series No. 11, Resources and Planning Branch. Department of Conservation, Forests and Lands: East Melbourne.)
- Phillips, B. F., Cambell, N. A., and Wilson, B.R. (1973). A multivariate study of geographical variation in the whelk *Dicathais*. *J. Exp. Mar. Biol. Ecol.* 11, 27-69.

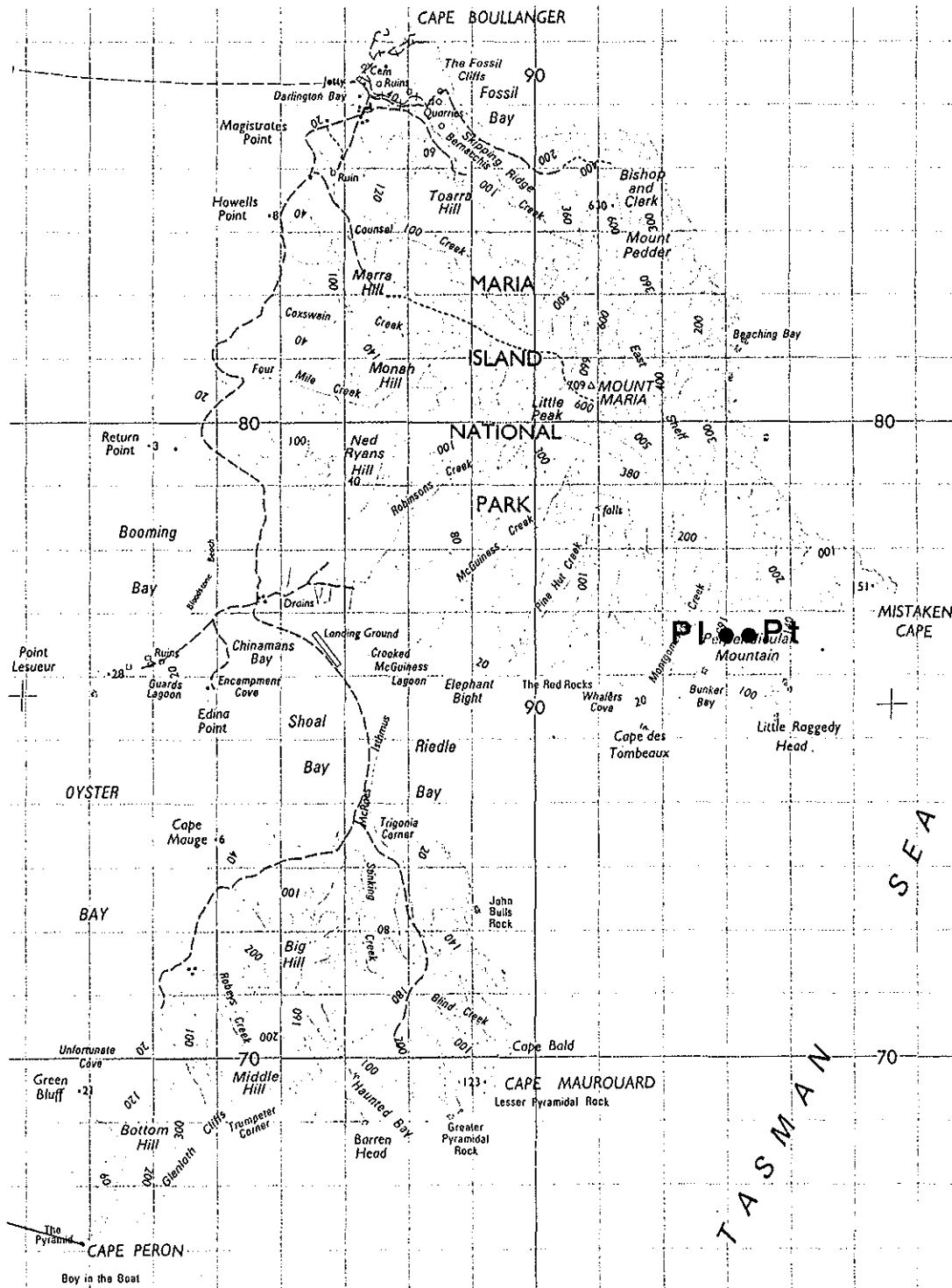
- Phillips, R. L., and Reid, J. B. (1980). Clinal variation between *Eucalyptus viminalis* Labill. and *E. pulchella* Desf. *Aust. J. Bot.* 28, 329-42.
- Pilipenko, F. S. (1969). Hybridisation of eucalypts in the USSR. Akademiya Nauk SSSR. Botanicheski Institut. Trudy 6th Series, Rastanii Zelende Stroitel'Stud No. 9. 5-68. Translated by P. Auckland Ciles, Melbourne.
- Potts, B. M. (1985). Variation in the *Eucalyptus gunnii*-*archeri* complex. 111. Reciprocal Transplant Trials. *Aust. J. Bot.* 33, 687-704.
- Potts, B. M. (1988). The distribution and type locality of *Eucalyptus cordata* Labill. - and historical account. *Pap. Proc. Roy. Soc. Tas.* 122, (in press).
- Potts, B. M. and Cauvin, B. (1988). Inbreeding and interspecific hybridisation of *Eucalyptus*. In 'Proceedings of the International Forestry Conference for the Australian Bicentenary.' (The Australian Forest Development Institute: Albury-Wodonga, Australia.)
- Potts, B. M., and Jackson, W. D. (1986). Evolutionary processes in the Tasmanian high altitude eucalypts. In 'Flora and Fauna of the Alpine Australasia. Ages and Origins'. (Ed. B. Barlow.) pp. 511-527. (CSIRO, Melbourne, Australia.)
- Potts, B. M., Potts, W. C. and Cauvin, B. (1987). Inbreeding and interspecific hybridisation in *Eucalyptus gunnii*. *Silvae Genetica* 36, 194-199.
- Potts, B. M., and Reid, J. B. (1985a). Variation in the *Eucalyptus gunnii*-*archeri* complex. 1. Variation in the adult phenotype. *Aust. J. Bot.* 33, 337-59.
- Potts, B. M., and Reid, J. B. (1985b). Variation in the *Eucalyptus gunnii*-*archeri* complex. 11. The origin of variation. *Aust. J. Bot.* 33, 519-41.
- Potts, B. M., and Reid, J. B. (1988). Hybridization as a dispersal mechanism. *Evolution* 42: 1245-55.
- Pryor, L. D. (1951). A genetic analysis of some Eucalyptus populations. *Proc. Linn. Soc. N.S.W.*, 76, 140-148.
- Pryor, L.D. (1957a). The inheritance of some characters in *Eucalyptus*. *Proc. Lin. Soc. NSW.* 77, 147-155.
- Pryor, L.D. (1957b). Variation in snow gum (*Eucalyptus pauciflora* Sieb.). *Proc. Linn. Soc. N.S.W.* 81, 299-305.
- Pryor, L. D. (1976). 'Biology of the eucalypts'. (Arnold, London.)
- Pryor, L. D. (1981). 'Australian Endangered Species: Eucalypts'. (Australian National Parks and Wildlife Service, Special Publication 5.)
- Pryor, L. D., and Johnson, L. A. S. (1971). 'A Classification of the Eucalypts.' (Aust. Natl. Univ. Press: Canberra.)
- Rao, C. R. (1952). 'Advanced Statistical Methods in Biometric Research'. (John Wiley & Sons: New York).
- Rempe U., and Weber, E. E. (1972). An illustration of the principal ideas of MANOVA. *Biometrics* 28, 235-38.
- Rodway, L. (1918). Tasmanian eucalypts. *Proc. Roy. Soc. Tas.* 1917, 1-20.
- Ryan, B. F., Joiner, B. L., and Ryan, T. A. (1982). 'MINITAB' (Duxbury Press: Boston.)
- Seal, H. L. (1966). 'Multivariate Statistical Analysis for Biologists.' (Methuen and Co.: London).
- Sharma, P. J. (1974). Chemotaxonomy of the genus *Eucalyptus* species. Ph. D. thesis, University of Tasmania.
- Shaw, M.J., Potts, B.M., and Reid, J.B. (1984). Variation within and between the species *Eucalyptus nitida* Hook.f. and *E. coccifera* Hook.f.. *Aust. J. Bot.* 32, 641-54.
- Sokal, R. R., and Rohlf, F. L. (1981). 'Biometry' 2nd edition. (W. H. Freeman: San Fransisco).
- Sneath, P. H. A., and Sokal, P. R. (1973). 'Numerical Taxonomy'. (W. H. Freeman: San Fransisco).
- Stafleu, F. A. (1966). 'Introduction to facsimile edition of Novae Hollandiae Plantarum Specimen (Labillardiere 1804)') *Historiae Naturalis Classica*, Weinheim.)
- Stephens, T. (1882). Note 27. Specimen of *Eucalyptus cordata*. *Proc. Roy. Soc. Tas.*, 1881: iv.
- Stephens, T., (1889). Notes and Exhibits. *Proc. Roy. Soc. Tas.*, 1888: xxxiii.
- SPSS Inc. (1986). 'SPSSx User's Guide'. 2nd Edn. (McGraw-Hill Book Co.: New York).
- Taylor, H. G. (1973). 'The discovery of Tasmania' (Cat and Fiddle Press, Hobart.)
- Thomas, D. A., and Barber, H. N. (1974). Studies on leaf water characteristics of a cline of *Eucalyptus urnigera* from Mt. Wellington, Tasmania. 1. Water repellancy and the freezing of leaves. *Aust. J. Bot.* 22, 501-18.
- Tibbits, W. N. (1988). Germination and Morphology of Eucalypt Progeny from Control Pollinations. *Aust. J. Bot.* (in press).
- Townrow, J. E. S. (1978). *Stipa* L. in Tasmania - historical notes: Taxonomic contributions 1768-1968 and the type locality of *Stipa flavescens* Labill.. *Proc. Roy. Soc. Tas.*, 112, 215-226.

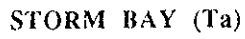
- Triebel, L. A. and Batt, J. C., (1957). 'French exploration of Australia with special reference to Tasmania'. (Tas. Govt. Printer, Hobart)
- Turnbull, J. W. (1977). Exploration and Conservation of Eucalypt Gene Resources. In 'Proceedings of the "Third World Consultation on Forest Tree Breeding, Canberra". (FAO: Rome).
- Wellington, A. B., Polach, H. A., and Noble, J. R. (1979). Radiocarbon dating of lignotubers from mallee forms of *Eucalyptus*. *Search* 10, 282-283.
- Whittacher, R. H. (1967). Gradient analysis of vegetation. *Biol. Rev.* 42, 207-64.
- Wilcox, M. D. (1982). Anthocyanin polymorphism in seedlings of *Eucalyptus fastigata* Deane & Maiden. *Aust. J. Bot.* 30, 501-9.
- Willis, J. H. (1970). 'A Handbook to Plants in Victoria, Vol.1'. (Melbourne University Press: Melbourne).
- Wiltshire, R. J. E., and Reid, J. B. (1987). Genetic variation in the Spinning Gum, *Eucalyptus perriniana* F. Muell. ex Rodway. *Aust. J. Bot.* 35, 33-47.
- Von Mueller, Baron Ferd., (1880). 'Eucalyptographia. A Descriptive Atlas of the Eucalypts of Australia and the Adjoining Islands'. (Trubner and Co., London.)

Appendix 1 POPULATION LOCALITIES

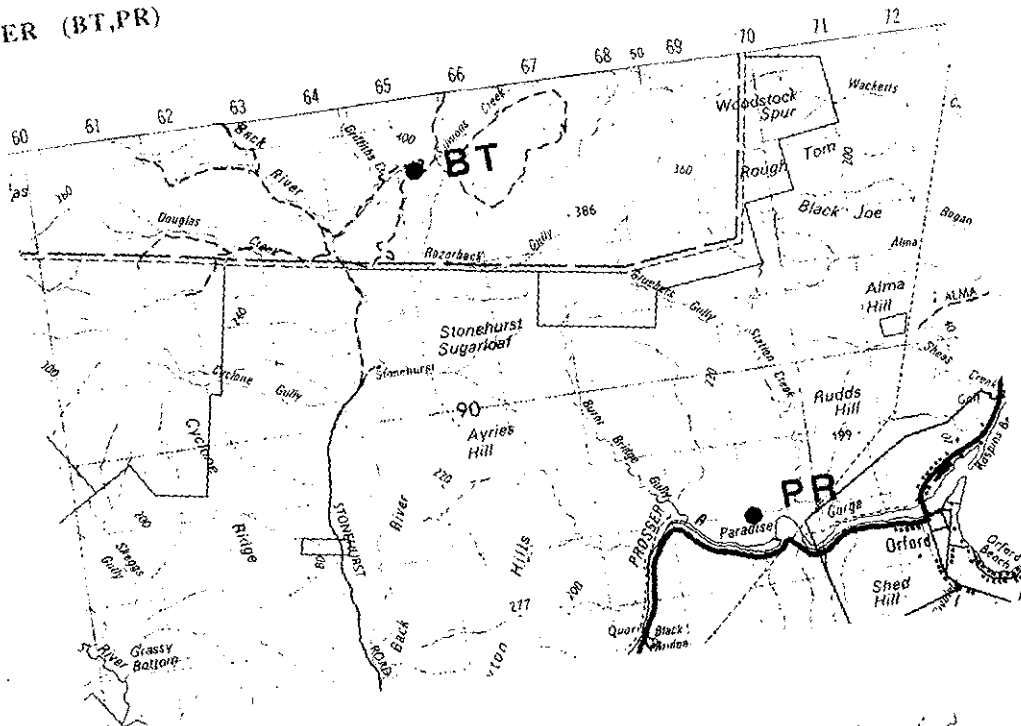
Maps have been reproduced courtesy of TASMAP (1:100,000 Land Tenure or Topographic series).

MARIA (Pt, Pl)

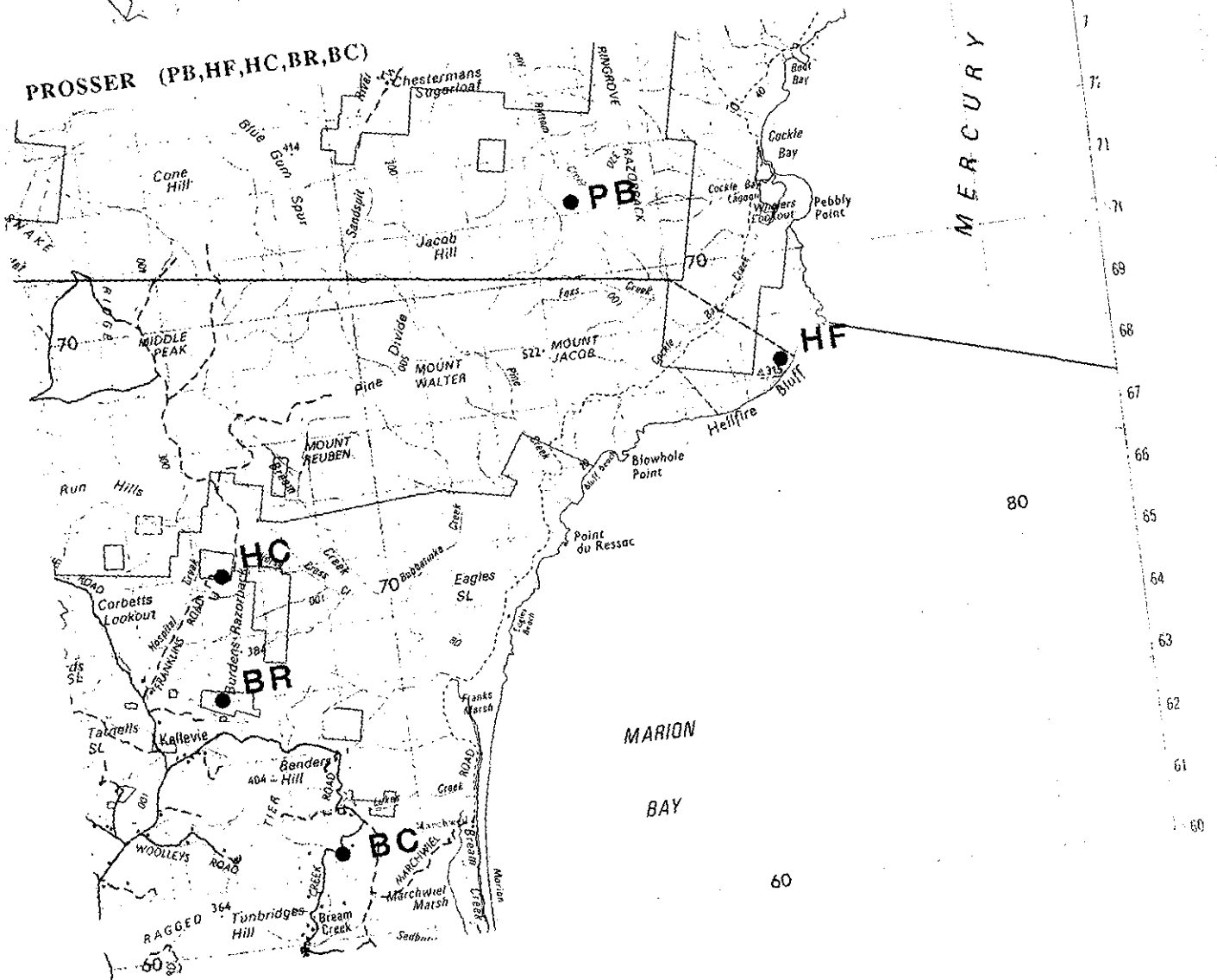




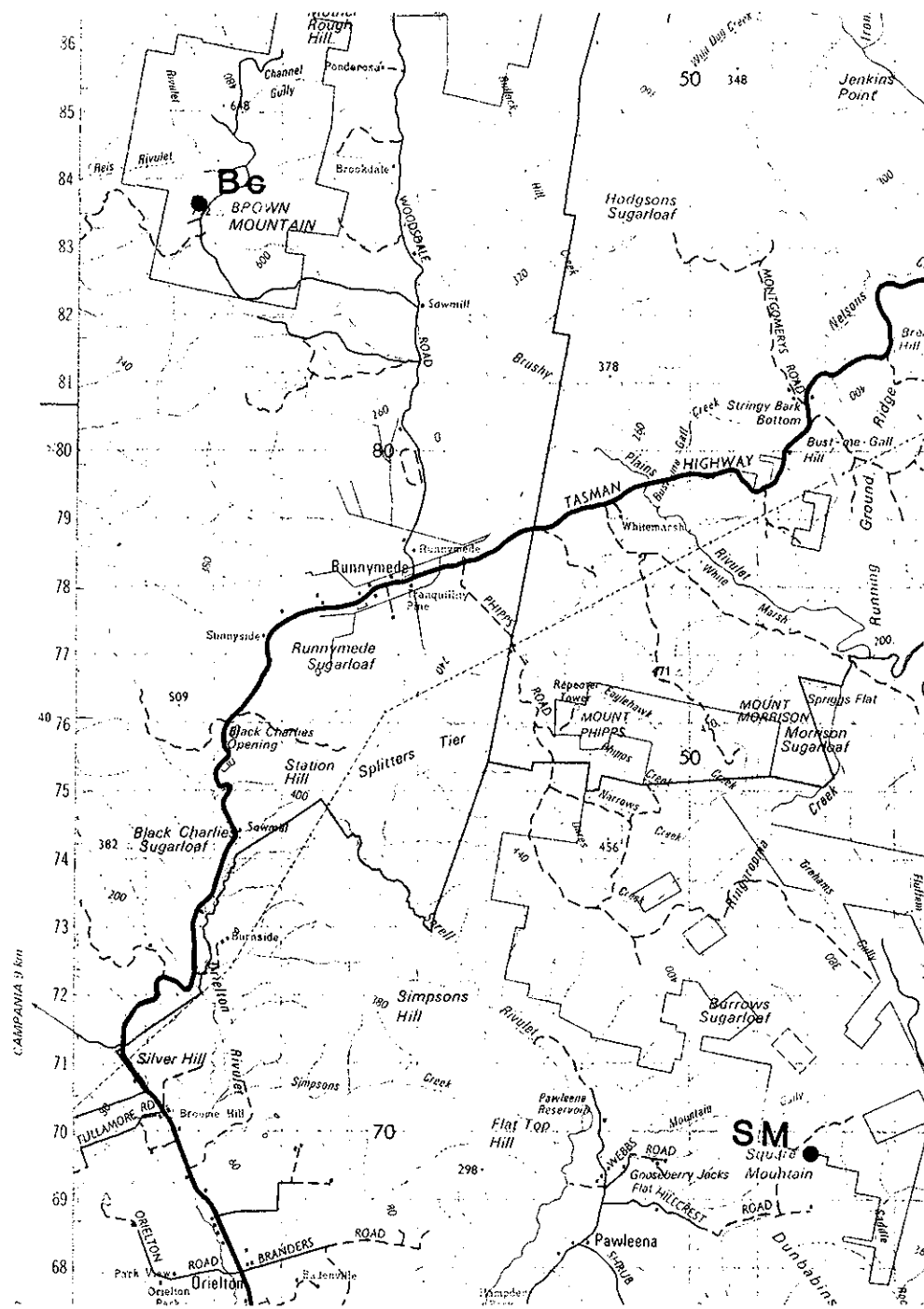
PROSSER (BT,PR)



PROSSER (PB, HF, HC, BR, BC)



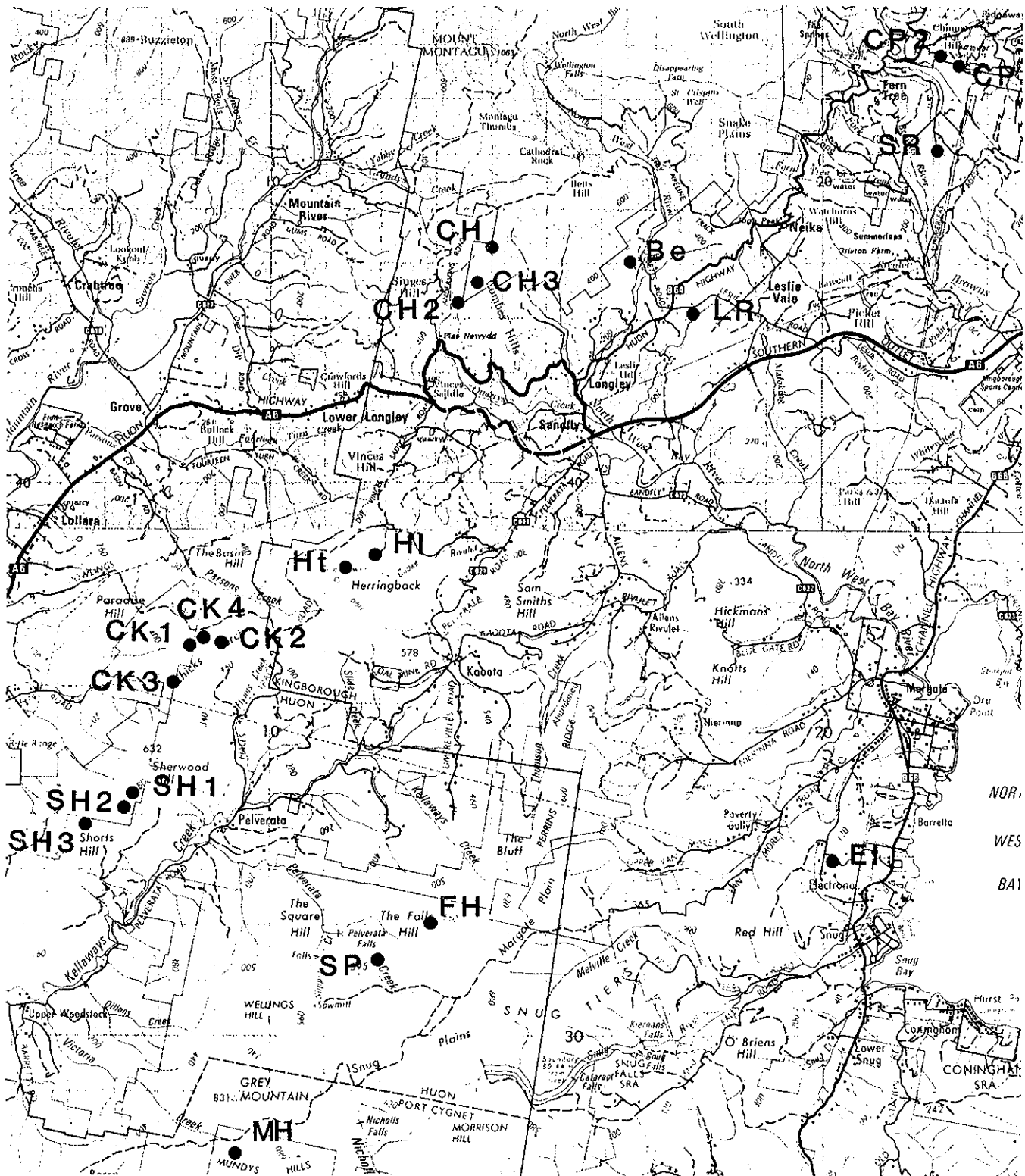
PROSSER (Bc,SM)



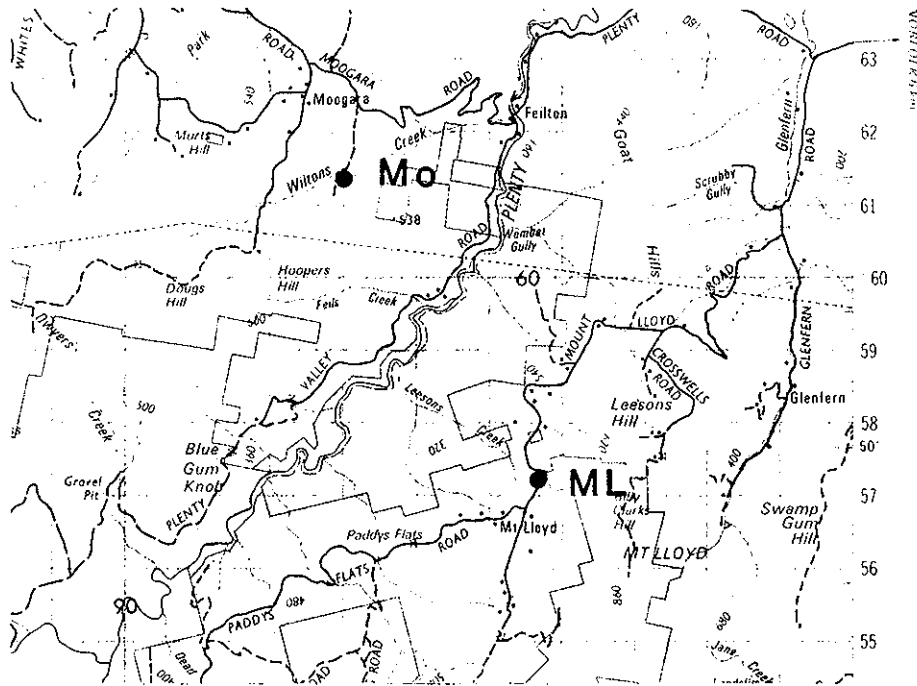
DERWENT (CP2,CP,SR,Be,CH,CH3,CH2,LR)

D'ENTRECASTEAUX

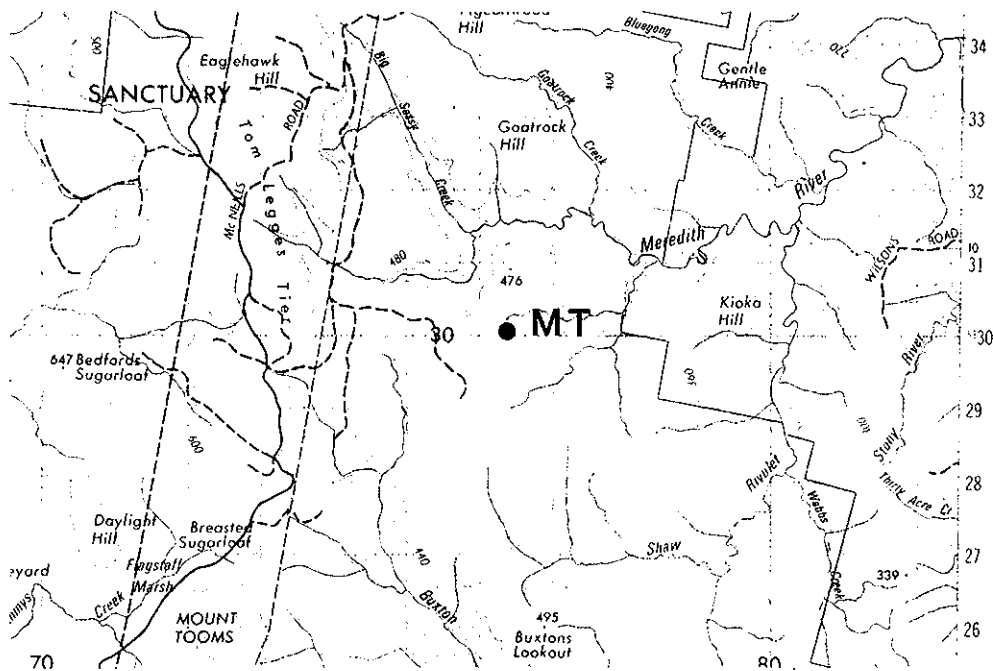
(Ht,HI,EL,FH,SP; recently located populations 12/12/88 = CK1-4 AND SH1-3)



TYENNA (Mo,ML)

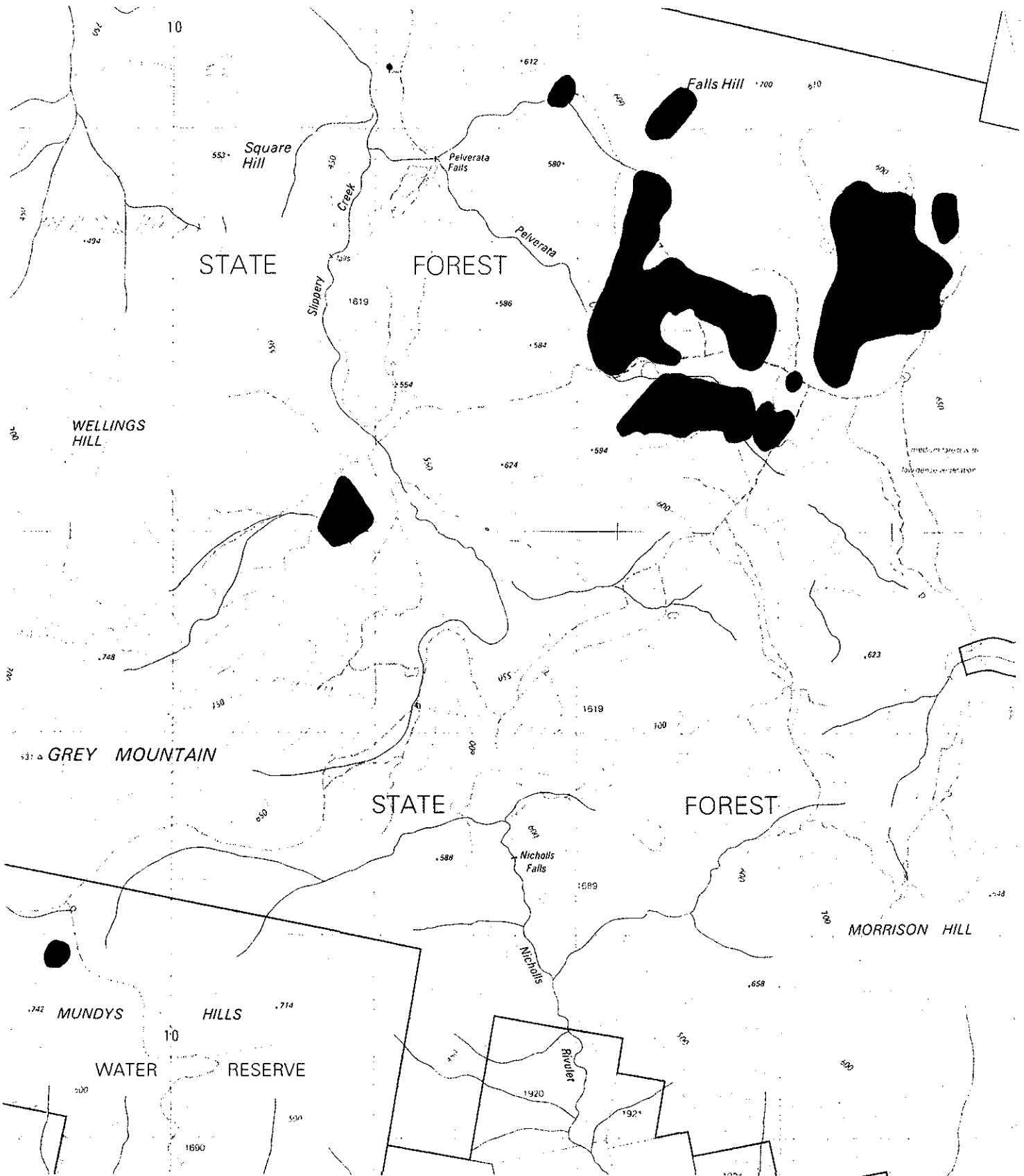


LITTLE SWANPORT (MT)



The distribution of *E. cordata* in State Forest on Snug Tiers (SP,FH)

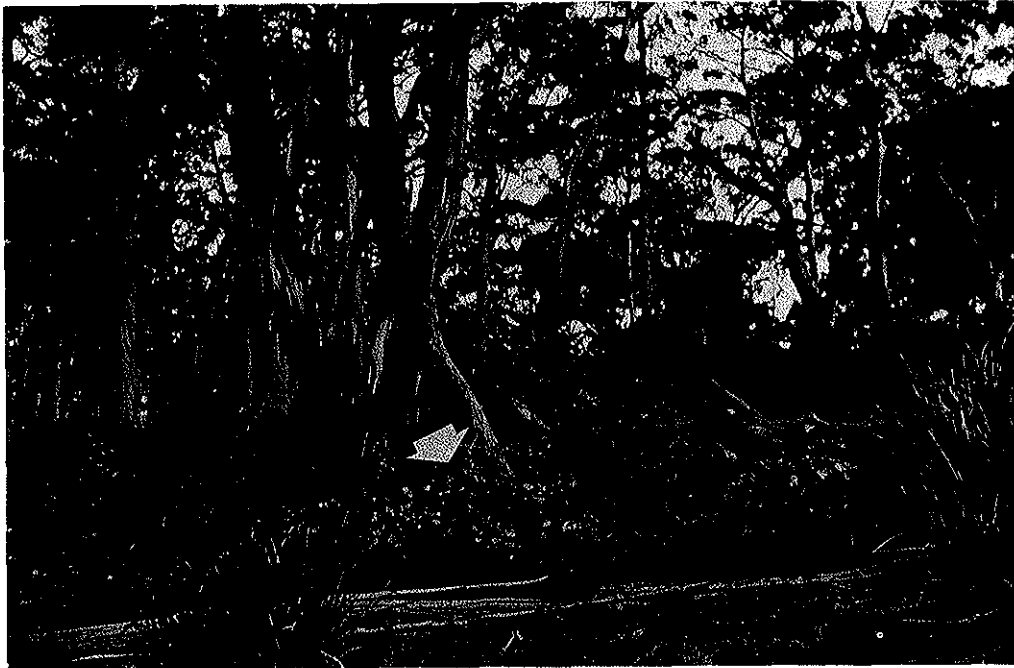
(Data provided courtesy of the Forestry Commission of Tasmania [modified from Davidson 1978]).



Appendix 2 POPULATION PHOTOGRAPHS

'eastern' morph : floristic group 2b

Tarrana (Ta)



Hellfire Bluff (HF) -outlying morph

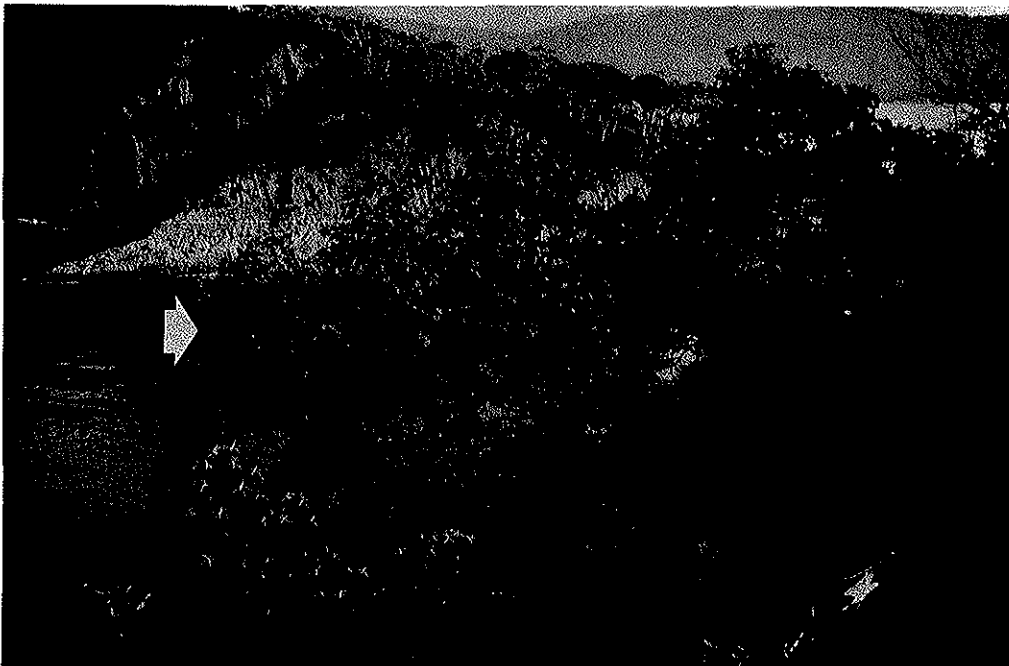


'eastern' morph : floristic group 2b

Cape Queen Elizabeth (QE)



Penguin Island (Pe -type locality)



'eastern' morph : floristic group 2b

Perpendicular Mountain (Pt -summit)



Perpendicular Mountain (Pl)



'eastern' morph : floristic group 2a

Bream Creek (BC)

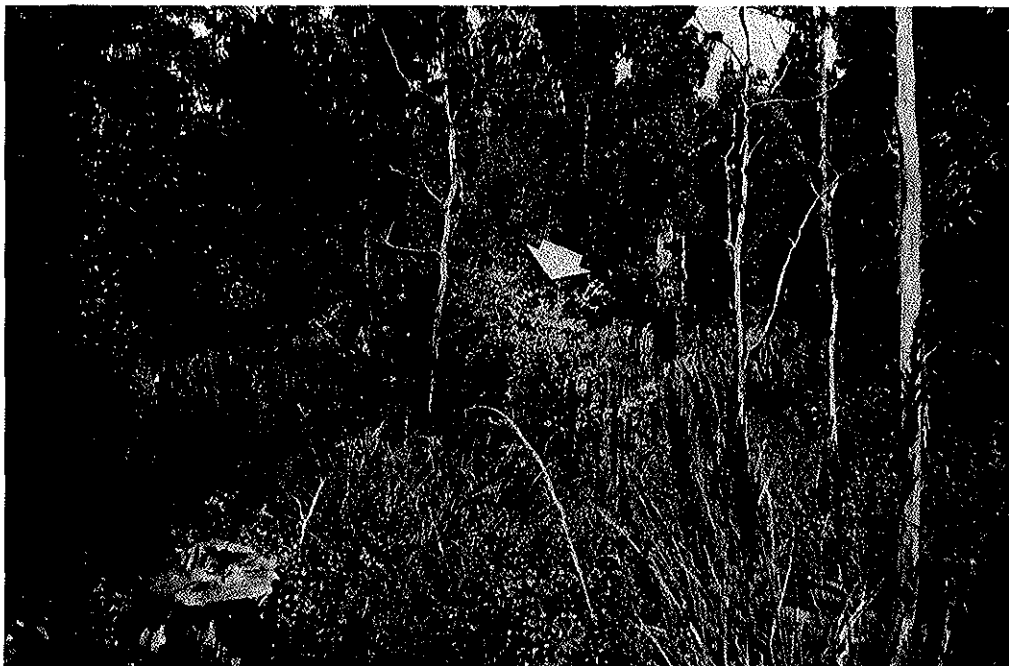


Hospital Creek (HC)



'eastern' morph : floristic group 1b

Small Mountain (SM)



Chimney Pot Hill (CP)



'western' morph : floristic group 1b

Snug Plains (SP)



Mt. Llyod (ML)



'western' morph : floristic group 2b

Moogara (Mo)



'western' morph (intermediate populations) : floristic group 2b

Electrona (El)



Leslie Road (LR)



'eastern' morph outlying population: floristic group 1b

Brown Mountain (Bc)



Meredith Tier MT (not included in *E. cordata*): floristic group 1b



Variation in bark type amongst trees at Moogara (Mo)



Lignotuber development trunk of *E. cordata* at Cape Queen Elizabeth (QE)



Appendix 3 The type locality of *Eucalyptus cordata*.

(extract from Potts 1988)

During the present survey it became apparent that some reports of the distribution of *E. cordata* required clarification and that the type locality previously indicated for the species (Hooker 1856; Bentham 1867; Baker 1902; Maiden 1913; Hall and Brooker 1972) was incorrect. According to Jackson (1965), *Eucalyptus cordata* occurs south of the Huon Valley, in the Recherche Bay area and the type locality of *E. cordata* has been cited as Recherche Bay by numerous authors (Hooker 1856; Bentham 1867; Baker 1902; Maiden 1913; Hall and Brooker 1972). However, failure to locate any populations of *E. cordata* in this area, despite extensive searching, prompted a re-assessment of the evidence for the type locality.

E. cordata was initially collected by Jacques Julien de Labillardière (1800), the botanist and chief scientist on the French expedition under the command of Bruni D'Entrecasteaux sent in search of the ill-fated La Pérouse expedition by the French Constituent Assembly in 1791. The expedition in the ships *la Recherche* and *l'Espérance* was in Australian waters from 1792 to 1793 and visited Tasmania twice during this period (see Maiden 1910; Hogg 1938; Stafleu 1966; Carr and Carr 1976). *E. cordata* was described and illustrated in Labillardière's work on the botany of the voyage, *Novae Hollandiae Plantarum Specimen* in 1806. The locality for *E. cordata* was given as 'capite van-Dieman'; the general locality given for all of his Tasmanian collections (Kantvilas 1983). *E. cordata* was later collected by Joseph Hooker and Ronald Gunn from the 'Huon district' (Hooker 1856) and, in part 3 of his *Botany of the Antarctic Voyage*, Hooker (1856) indicates Labillardière's locality for *E. cordata* to be Recherche Bay. In his *Eucalyptographia*, von Mueller (1880) lists several collectors who located *E. cordata* in the same region as Labillardière (Brown, Hooker, Gunn, Stephens and Abbott), yet Maiden (1913) could find no evidence for this statement.

In a letter to Sir William Hooker, the father of Joseph Hooker, Gunn wrote of an excursion to Recherche Bay in 1838 which enabled him to identify nearly all of Labillardière's Tasmanian species (Dec. 1843; Letter 184, Burns and Skemp 1961). In the same paragraph he mentions *E. cordata*, although no clear indication is given as to whether or not he located this species in the area. There is a specimen of *E. cordata* attributed to Gunn at Kew with the locality given as Recherche Bay, although the specific code given (No. 1207) does not correspond to Gunn's code for *E. cordata* (No. 1071). This specimen has been inspected and is clearly *E. cordata* with the morphology similar to that found in the western populations of *E. cordata*. However, the specimen is not annotated in Gunn's handwriting, is undated and does not have one of Gunn's coded collecting labels which is atypical for Gunn's specimens. This specimen is on the same herbarium sheet as a specimen collected by Gunn from near the Huon River (30/10/1839) and may have originated from this collecting trip. Furthermore, in discussing Labillardière's collections in later correspondence (Letter 185, Burns and Skemp 1961) Gunn notes - "*Eucalyptus cordata* [Lab.] t.152. Is my own No 1071 - a species I never saw except in the Country South of Hobart Town."

Where Gunn located species at Recherche Bay, this was clearly indicated in the letter and the latter comment

probably refers to the area immediately south of Hobart. The specimens sent to Baron von Mueller by Abbott (MEL104507 and MEL104504) were from Huon Road (North-West Bay). However, there is one specimen sent to him by T. Stephens from Recherche Bay (MEL 104502 - left specimen). At the time, with von Mueller preparing his *Eucalyptographia*, there was considerable interest in this 'rare species' and the belief that Recherche Bay was the type locality was widely held (Stephens 1882, 1889) -

"..... this interesting tree, discovered and described long ago, had been lost to sight for more than forty years. It was originally reported as a denizen of Recherche Bay by the French expedition under Labillardière; and long afterwards, in Sir John Franklin's time, it was found by Sir Joseph Hooker and the late Mr. Ronald Gunn ' in the Huon district ', no precise locality having been recorded. From that time to the present it appears to have eluded the search of botanists; and it was only in October last that, in answer to repeated enquires, specimens were at last obtained from Recherche Bay, but without flower or fruit." (Stephens 1882).

The letter accompanying the specimen read -

"*Eucalyptus cordata* is found at last. ...I received from Recherche Bay a branchlet of a young *Eucalyptus*..., and this was followed by a letter from the finder stating that there was no blossom or any sign of fruit on any of the trees near."

(Stephens to von Mueller, Nov. 1880).

Inspection of this specimen suggests that it is probably not *E. cordata*, but more likely a juvenile of *E. globulus*, which would accord with the noted absence of reproductive material. The juvenile foliage of *E. globulus* resembles the adult foliage of the western populations of *E. cordata*.

The belief that Recherche Bay was the type locality no doubt stemmed from Hookers (1856) original citing, although he gave this locality for many of Labillardière's 'capite van-Diemen' locations. Labillardière was based, and collected extensively in the vicinity of Recherche Bay. He records collecting several species of eucalypts on the shore to the north-east of their anchorage on 23th of April 1792, but no distinguishing remarks on the species collected are given (Labillardière 1800). He later (6th May 1792) records specifically collecting *E. globulus* by felling a tree in order to obtain flowers, and designates the name for the species in his journal. However, he also collected from other areas along the D'Entrecasteaux Channel, including Bruny Island (Townrow 1978) and it is always possible he may have made multiple, unrecorded collections of single species.

Bentham (1867, vol. 3, p. 224) ascribes a specimen of Labillardière's, without flower or fruit, collected from Maria Island to the mainland species, *E. macrocarpa*. In reference to this, Maiden (1913 p. 241) later notes - "Maria Island is off the coast of Tasmania, and I suggest that Labillardière's specimen is *E. cordata*, Labill." Labillardière did not collect on Maria Island, although collections from Maria Island were made later by Leschenault de la Tour, the botanist on the French expedition (1800 - 1804) commanded by Nicholas Baudin (Taylor 1973). Specimens from the Baudin expedition were not described as a whole, but examined at odd intervals by monographers (Maiden 1910). There is strong evidence that Labillardière accessed this collection and used some specimens in his *Novae Hollandiae Plantarum Specimen*, mislabelling the localities (Nelson 1974, 1975; Carr and Carr 1976). The herbarium specimen ascribed to Labillardière by Bentham has not yet

been located. However, it is possible that a specimen of *E. cordata* was collected from the summit of Perpendicular Mountain during the Baudin expedition and has been both misidentified and mistakenly attributed to Labillardière. Nevertheless, this is not a cause of confusion and there is no doubt that Labillardière personally collected *E. cordata*.

Recent findings have revealed that Recherche Bay is not the type locality of *E. cordata*, and it follows there is no solid evidence for its occurrence in the area. In *Relation du Voyage de la Recherche de la Pérouse*, Labillardière specifically records collecting a eucalypt from Penguin Island while the expedition was anchored in Adventure Bay, just prior to the final departure from Tasmania. This island had been previously charted and is clearly named on charts from Captain James Cook's 1777 expedition (Triebel and Batt 1957). Labillardière's (1800; p. 76) description leaves no doubt this eucalypt is *E. cordata* -

"Je recueillis sur l'île aux Pingouins ; un *eucalyptus* de hauteur médiocre, qu' on reconnoitra facilement à ses feuilles opposées, sessiles et glauques;...."

The translation of *glauque* (glaucous) in the english version of his journal (1800) -

".., opposite, sessile leaves, of a whitish green colour, with a slight tint of blue.."

is not as botanically exact as the original and similar, but more severe problems with the translated version have been detailed by Carr and Carr (1976).

The occurrence of *E. cordata* on Penguin Island has recently been verified (14/8/1987) after having escaped the notice of botanists for nearly two centuries. The small island is dominated by *Casuarina stricta* low forest, with some *E. globulus* on the northern aspect, most of which has been recently burnt (March 1986). However, *E. cordata* occurs on the wetter, southern cliff slope which faces Fluted Cape and the majority of the population is unburnt. The population is small, comprising approximately 200 mature individuals, and cannot be missed when following the narrow ridge to the summit of the island, the path presumably taken by Labillardière in 1793. A few individuals are readily accessible from the main ridge suggesting that the type locality can be predicted to within less than 30m. It is even possible that the same individuals have been sampled in the present survey.

Labillardière's holotype (FI, Herb. Webbiana) and isotypes (MEL104513; G; P) of *E. cordata* are consistent with specimens collected from Penguin Island. Moreover, this population is somewhat atypical for *E. cordata* as approximately 40% of reproductively mature individuals had developed a very small proportion (<5%) of adult or intermediate foliage. Such individuals are usually rare in natural populations of *E. cordata*. The opposite and glaucous juvenile type of foliage is usually fully retained through out the life of an individual, although intermediate or adult leaves may occasionally be seen at the top of large trees (Hall and Brooker 1972).

Nevertheless, Maiden (1919) notes -

".....*E. cordata* is one of the few remaining species with homoblastic leaves, I would invite the further attention of collectors to this tree, in order that they may search, especially near the tops, both cultivated

specimens, and trees in their native habitats, for pedicellate, lanceolate leaves. The nearest I have got to this state is in a specimen (2c of Plate 84 C.R.) collected by Labillardière himself."

Specific records of collection can be obtained for some of the 265 specimens described in *Novae Hollandiae Plantarum Specimen* from Labillardière's journal (Labillardière 1800). Along with the example of *E. cornuta* Labill., described by Carr and Carr (1976), the present case attests to the accuracy and detail of his account. Furthermore, due to the limited size of the *E. cordata* population on Penguin Island, the relocation of this type locality may be one of the most exact from this early period of botanical exploration in Australia. In other cases, specific predictions of Labillardière's type localities have been made by integrating population, phenological and distributional data with excursion and anchorage records (e.g. *Stipa* - Townrow 1978). All of the other Tasmanian eucalypts collected and described by Labillardière (1806), viz. *E. ovata* Labill., *E. viminalis* Labill., *E. globulus* Labill. and *E. amygdalina* Labill., are widespread through the areas Labillardière visited (e.g. Kirkpatrick and Backhouse 1980). Specific mention is only made of *E. globulus*, although his numerous references to *E. resinifera* no doubt refer to *E. obliqua*; a species widespread in Tasmania and common in the vicinity of Recherche Bay. When describing *E. ovata*, Labillardière (1806) gives the locality as 'terra van-Leuwin' (Western Australia), the only other area in Australia at which he collected. *E. ovata* is confined to south-east Australia, including Tasmania, and this is one of the species used by Nelson (1974, 1975) to demonstrate that Labillardière accessed other collections as well as confused some of his own collecting localities in specimens described in *Novae Hollandiae Plantarum Specimen*. Nevertheless, many of the location anomalies and other problems associated with Labillardière's works have now been resolved (Nelson 1974 and 1975; Carr and Carr 1976).

It is possible *E. cordata* was also observed during Cook's 1777 visit to Adventure Bay as a recently published sketch by William Ellis from this expedition may feature *E. cordata* (Joppien and Smith 1987). Professor W. D. Jackson (Joppien and Smith 1987; page 630) suggested plants in the foreground of the sketch, on the shore, may be either juvenile *E. globulus* or *E. cordata*. His observations were made prior to the re-discovery of *E. cordata* on Penguin Island. The island is in the immediate vicinity of Cook's anchorage and is the only area known today where *E. cordata* grows near sea-level. In fact the leaf shape, tree form and even the possible adult foliage on one of the top branches (specifically noted by Prof. Jackson) are more consistent with the *E. cordata* in this area than juvenile *E. globulus*.

Additional notes

Several additional anomolous records of *E. cordata* were found which require further comment.

Meredith Tier (MT)

The northern most population indicated in Brown *et al.*(1983) on Meredith Tier (MT) was not included within *E. cordata* and its exact affinities require further investigation. When this population was originally located by F. Duncan, it was regenerating from wildfire and the original specimen collected bore capsules in the juvenile foliage stage. However, when sampled several years later, all reproductively mature individuals had developed adult foliage. The exact affinities of this population are masked by what appears to be extensive hybridization with the nearby *E. barberi*. This population is within the climatic range of *E. cordata* as predicted using the climatic model BIOCLIM (Fig. 3.2). However, the closest and northern most stand of *E. cordata* is on Bluestone Tier (BT) which is over 40 km south of this site. The population on Meredith Tier may have closer affinities to *E. gunnii*, the nearest population of which occurs only 7km away, near Tooms Lake.

Brown Mountain, Port Arthur (PA)

The Port Arthur and Brown Mountain locations noted by Brett (1938) and Rodway (1918) respectively correspond to herbarium specimens (HO 15629-32, 15637-39, 15660-62, 16077) they independently collected from Brown Mountain near Port Arthur. This population was not relocated despite extensive searching. Some of Rodway's specimens (initially labelled *E. globulus* var. *Harrisoni* e.g. HO 16077) from this location were noted as collected from tall trees (100-200') whereas the vegetation in this specific area is low mallee and no stands could be found in taller, wetter forests nearby. Brett's specimen from the same location is annotated as being an *E. globulus* x *cordata* hybrid and that the *E. cordata* in the area was an undershrub growing in association with *E. globulus*. Intermediate or adult foliage occurs on some of these specimens.

In this respect, the resemblance between some of the specimens collected by Rodway and Brett from Brown Mountain and those from the type locality is noteworthy and may account for Brett's (1938) record of hybridization between *E. globulus* and *E. cordata*.

Brown Mountain, Campania (Bc)

The Brown Mountain (Bc) sampled in the present survey occurs near Campania and is no doubt the Brown Mountain and Campania locations given by Brett (1938) and Rodway (1918) respectively. Brett's Port Arthur locality probably corresponds to his specimens from the Brown Mountain near Port Arthur. While individuals developing intermediate type foliage were found in the population on Brown Mountain near Campania (Table 2.1), this mountain is unlikely to have been confused with the locality collected by Rodway or Brett from near

Port Arthur (PA ; see above). The population near Campania is low mallee, there is no *E. globulus* in the vicinity and the specimens do not correspond to samples collected from this population. The population (Bc) showed some affinities to *E. urnigera* and *E. morrisbyi* in capsule shape and juvenile leaf shape, but the majority of individuals developed flowers in the juvenile leaf stage. While this stage is not fully persistent (Table 2.1), it has been included within *E. cordata* for the present survey. In this respect it is significant that Brett (1938) indicates *E. cordata* has affinities to *E. urnigera* and von Mueller (1880) notes:

"Crenulate leaves occur also in *E. urnigera*, and, strange as it may appear, it is to this species that *E. cordata* bears the closest alliance; for although the aged state of *E. urnigera* has scattered long-stalked dark-green and lanceolar-sickle-shaped leaves, more slender elongated and downward more attenuated calyces on conspicuous stalklets with ampler lid and urn-shaped fruits with deeply enclosed valves, yet trees are now known (through Mr. Stephens from "Old Man's Head," a subalpine mountain near Lake Crescent)[no doubt Alma Tier], which to all appearance form a complete transit from *E. urnigera* to *E. cordata*. Moreover Mr. Aug. Oldfield sent many years ago from the middle-regions of Mount Wellington sterile saplings as the young state of *E. urnigera*, the adventitious lower shoots of which can in no way be distinguished in foliage from *E. cordata* and which are also partly pruinous. On the summit of Mount Wellington I collected a state of *E. urnigera*, with all leaves nearly oval and with simply truncate-ovate fruits."

Nelson's Tier

The Nelson's Tier location noted by several authors (Stephens 1889; Blakely 1934; Brett 1938) probably corresponds to the population sampled on the contiguous Square Mountain (SM), although the possibility of other populations in this general locality can not be discounted.

Fisherman's Island

The present day locality of Abbott's specimen collected in 1881 (MEL104503) and labelled 'Fisherman's Island' is unclear. This specimen corresponds to the morphology found in the western populations and does not correspond to samples from Maria (Pt, Pl) or Bruny (QE, Pe) Islands.

APPENDIX 4 Analysis of synthetic climatic variables for sites of *E. cordata*.

Table 1 Differentiation between 'eastern' and 'western' populations.

The table indicates the F value for the difference between morphs, weightings in the step-down discriminant function and mean and standard deviation for each morph for variables retained in the step-down discriminant function.

SYNTHETIC CLIMATIC VARIABLE	F 1,19	Stand. Discrim Function	EASTERN (n=12) Mean	s.d.	WESTERN (n=9) Mean	s.d.
1 MNANTP	11.00 **	-4.64	10.7	1.17	9.0	1.24
2 MINMINTP	10.53 **	5.52	2.7	0.83	1.6	0.72
3 MAXMAXTP	7.89 *	-				
4 TEMPRGE	2.73 NS	-				
5 TEMPWETQ	8.45 **	-				
6 TEMPDRYQ	10.87 **	-				
7 MNANRAIN	22.99 ***	-24.03	855	74.8	1169	211.1
8 RAINWETM	20.05 ***	-				
9 RAINDRYM	14.36 **	-				
10 RAINRGE	28.18 ***	-				
11 RAINWETQ	19.55 ***	14.34	86	6.2	113	19.6
12 RAINDRYQ	11.84 **	9.83	56	5.2	72	14.0

FIGURE 1 Principal components ordination of the *E. cordata* populations based on standardized values of the 12 synthetic climatic variables. PC1 = PC1clim in Table 2.2.
(o = Eastern form • = Western form)

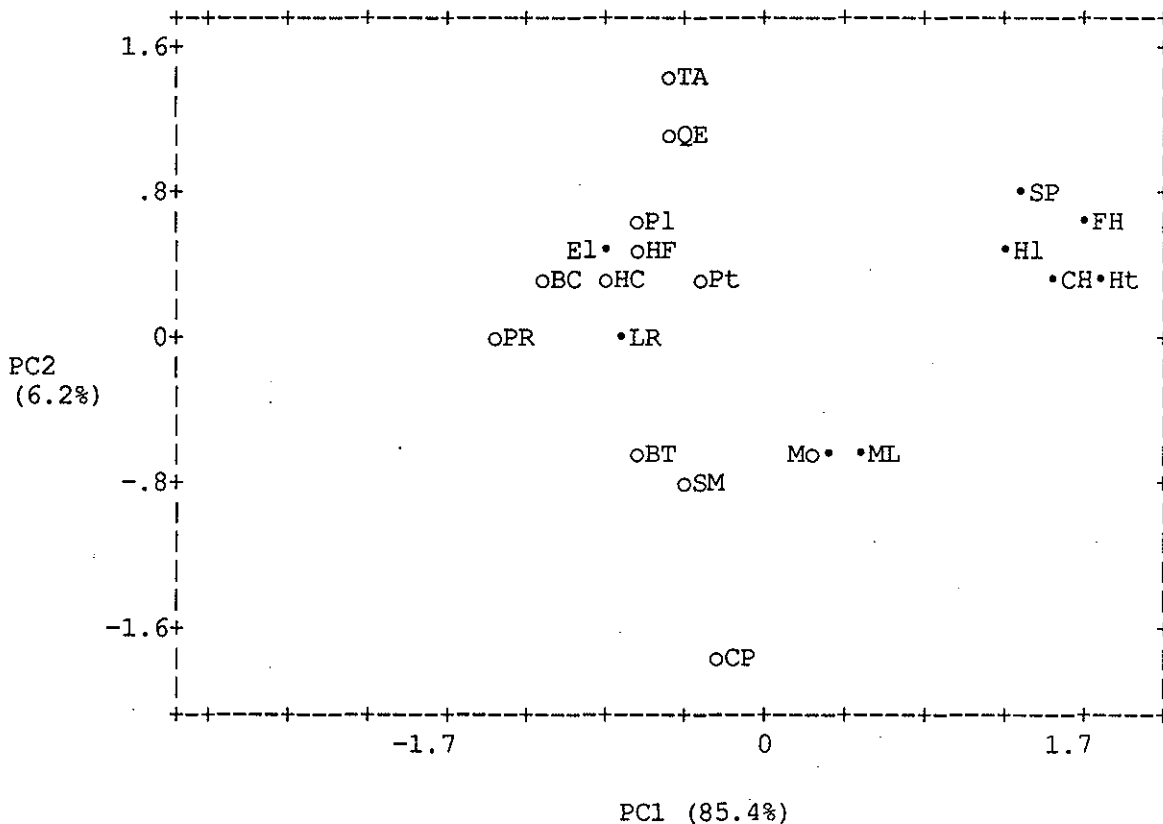


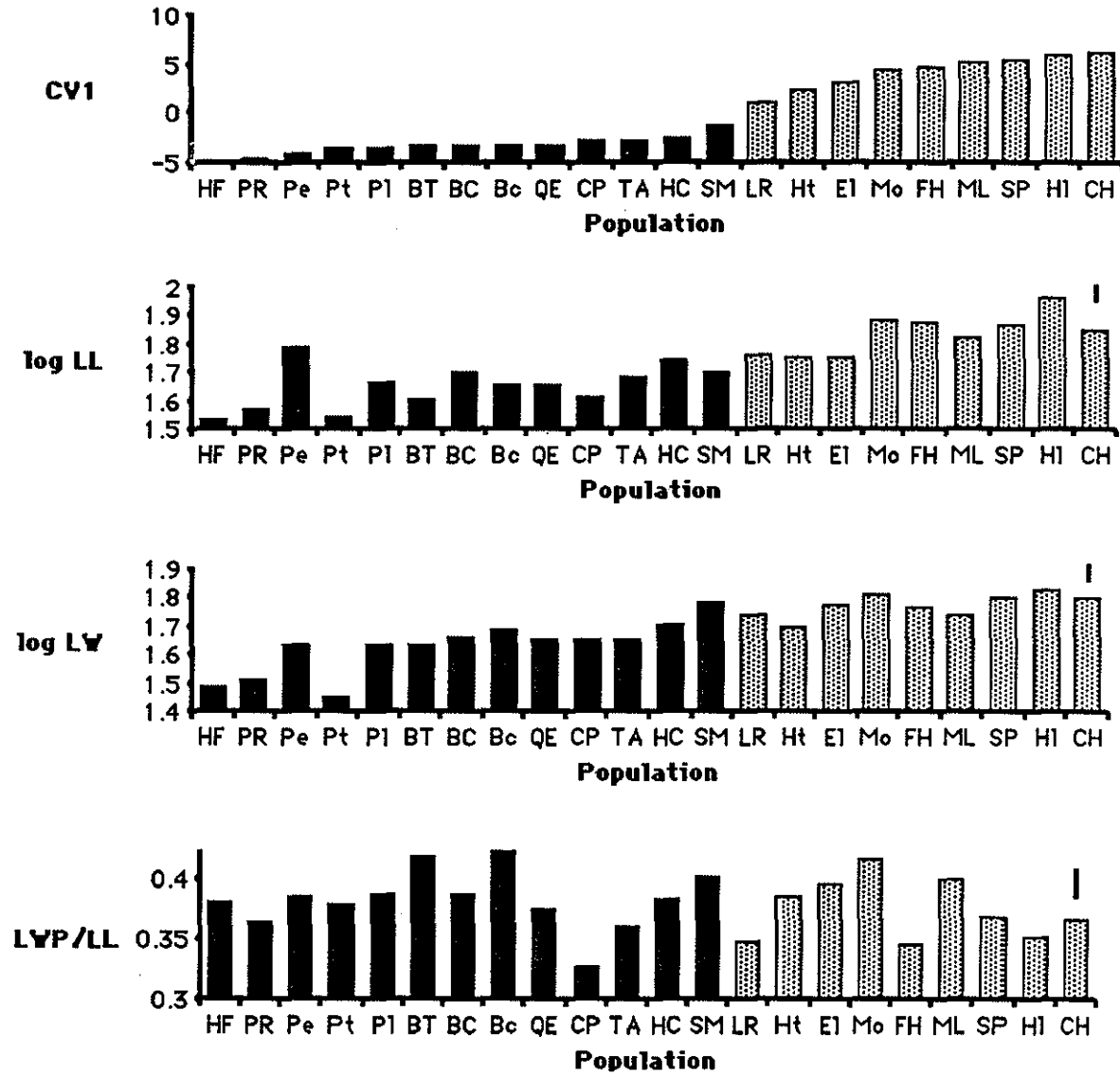
Table 2 Variable weightings on the first two principal components indicated in Figure 1.

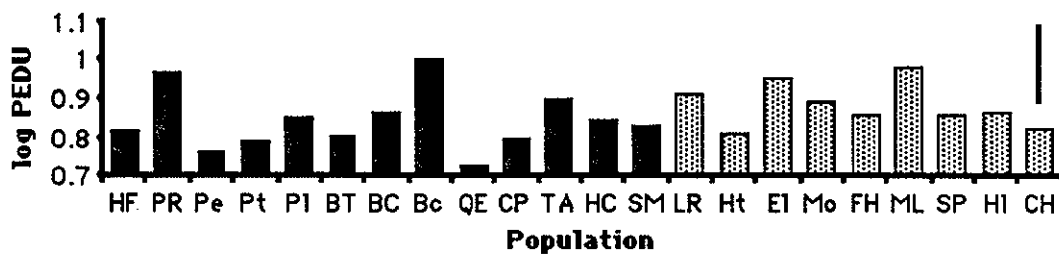
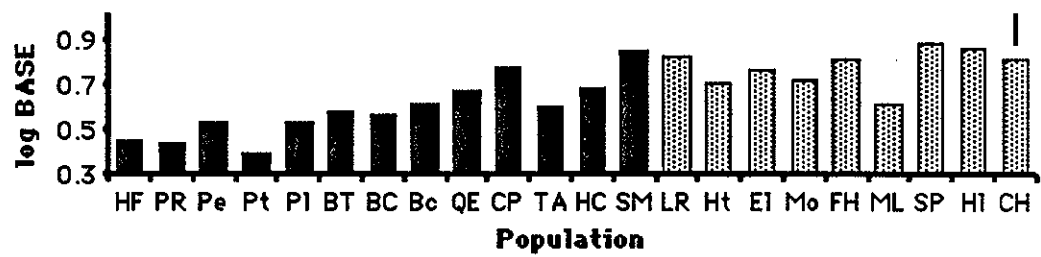
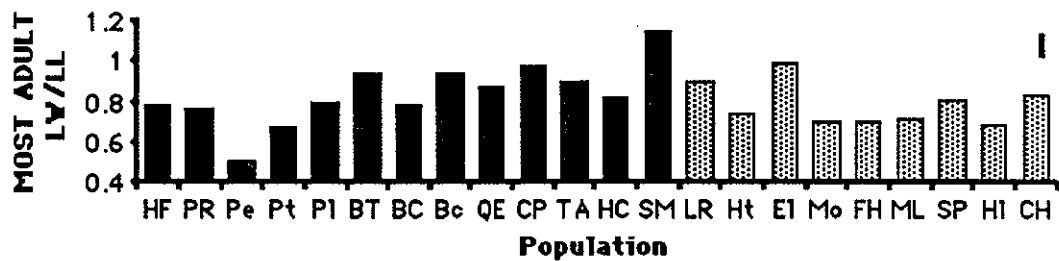
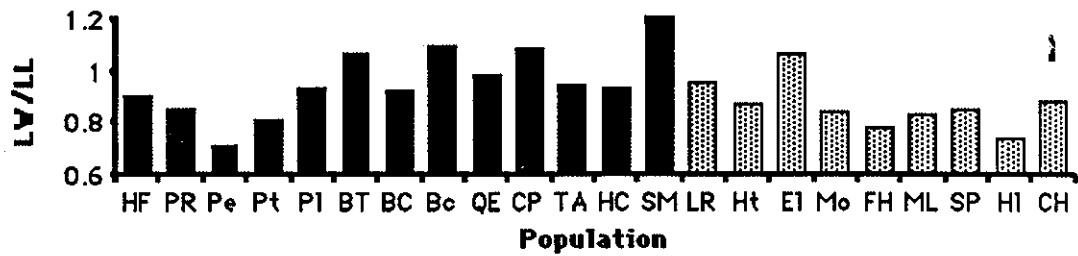
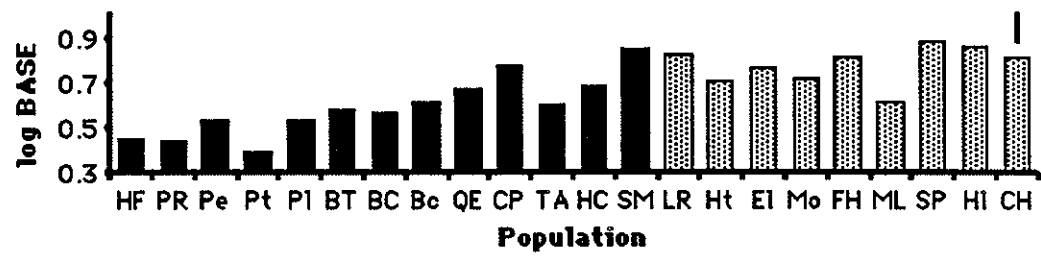
	PC1 85.4%	PC2 6.2%
1 MNANTEMP	-0.93	0.35
2 MINMINTEMP	-0.88	0.41
3 MAXMAXTEMP	-0.96	0.25
4 TEMPRGE	-0.87	-0.03
5 TEMPWETQ	-0.73	-0.01
6 TEMPDRYQ	-0.95	0.32
7 MNANRAIN	0.97	0.22
8 RAINWETM	0.97	0.21
9 RAINDRYM	0.97	0.14
10 RAINRGE	0.90	0.31
11 RAINWETQ	0.98	0.18
12 RAINDRYQ	0.95	0.20

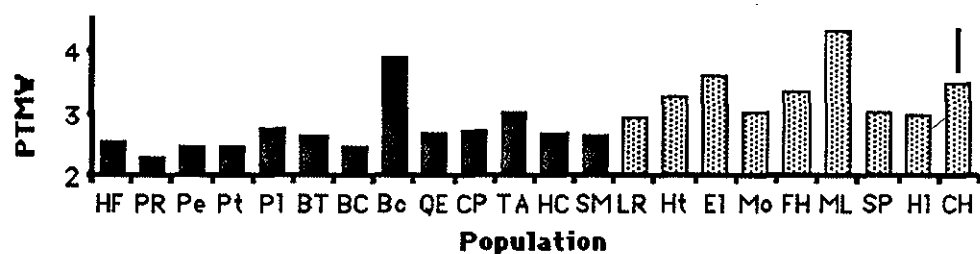
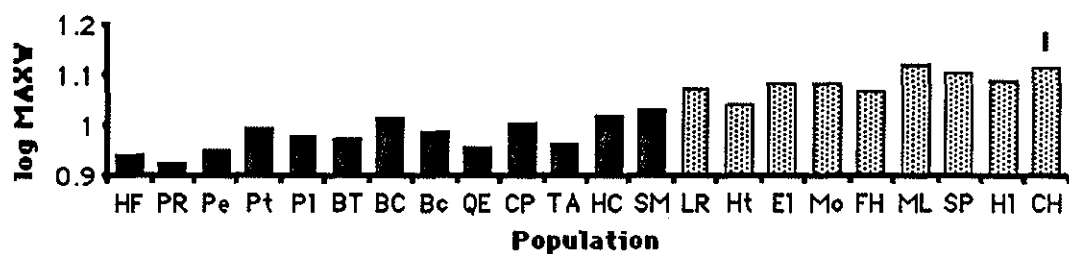
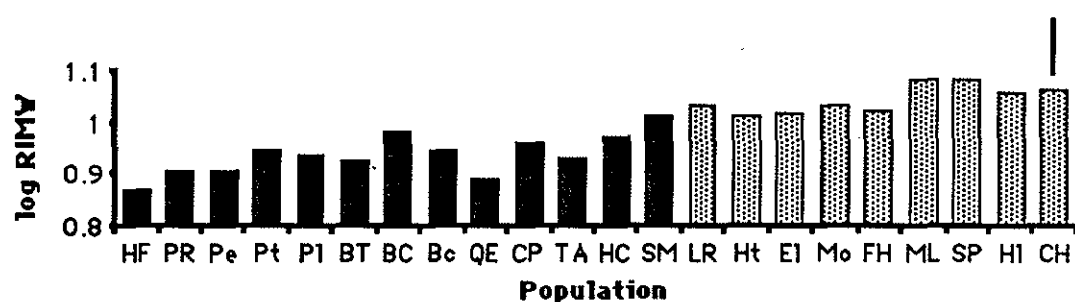
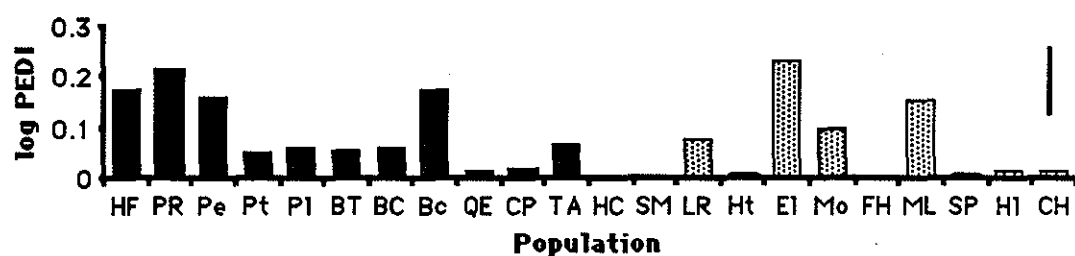
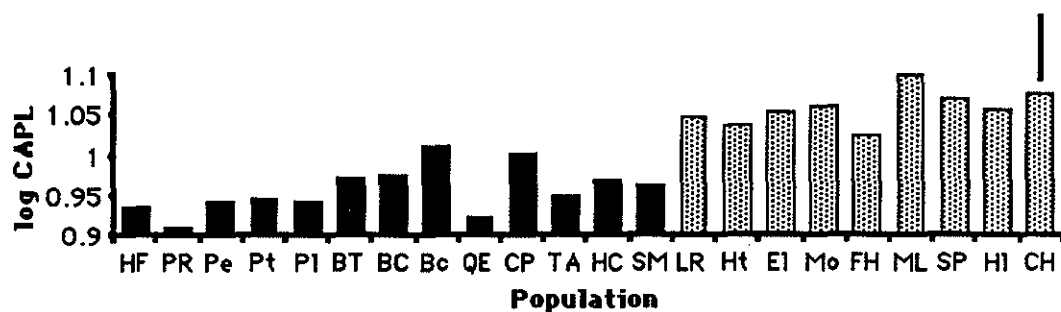
APPENDIX 5 Population means for adult and seedling characters.

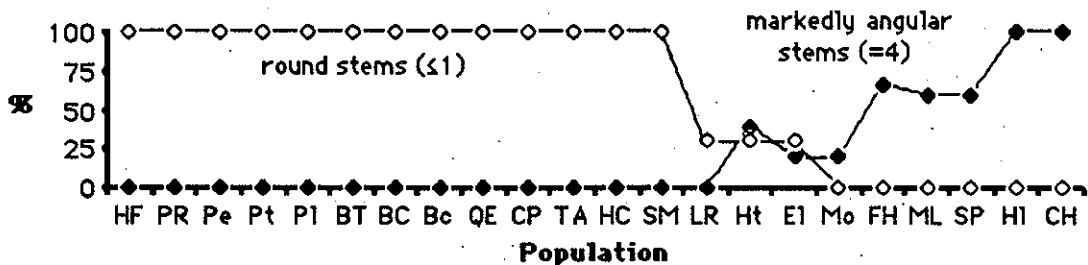
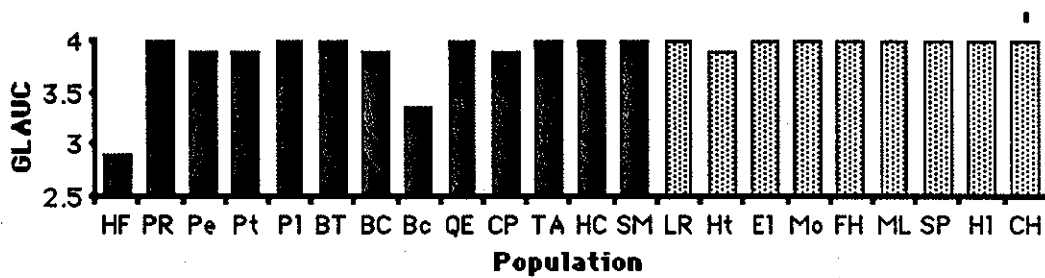
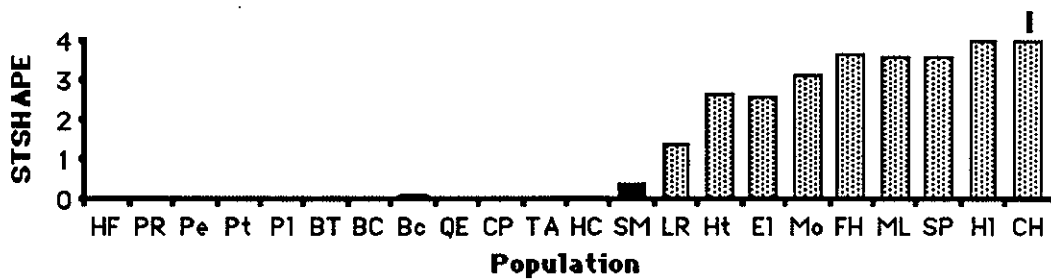
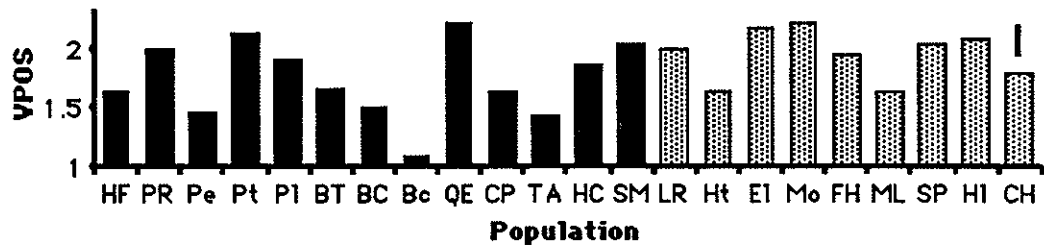
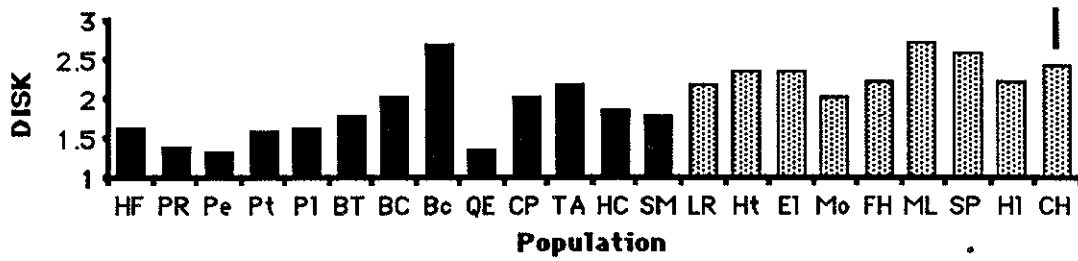
Populations are ranked according to their position along the first discriminant function (CV1) from analysis of either adult or seedling character sets. The bars represent the LSD 0.05 based on n=10.

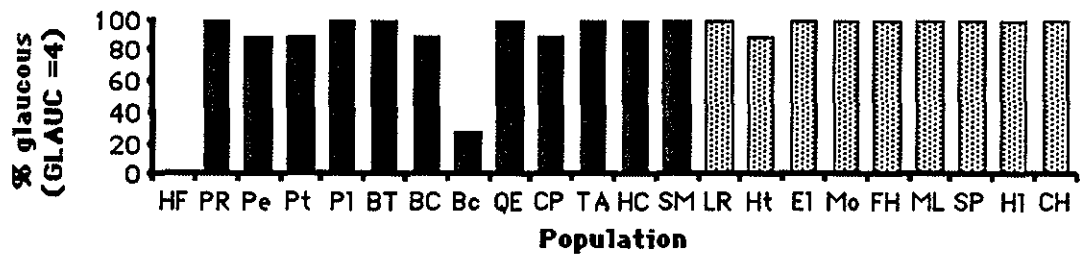
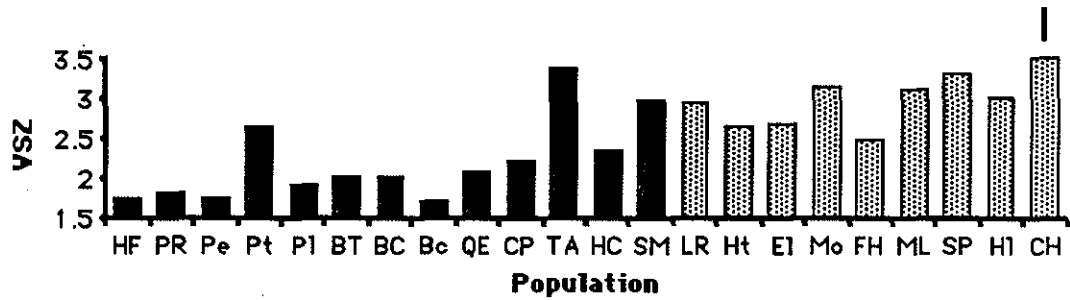
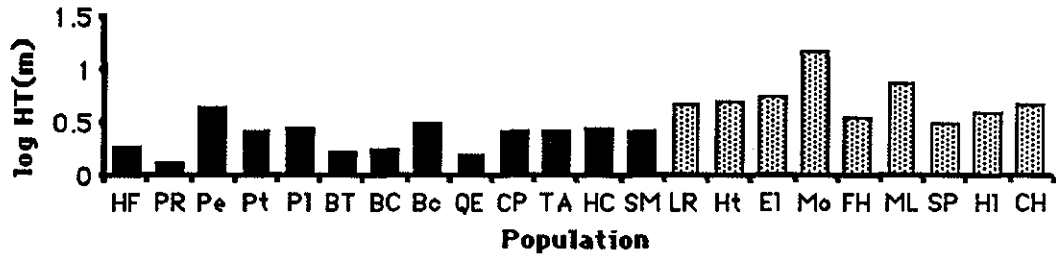
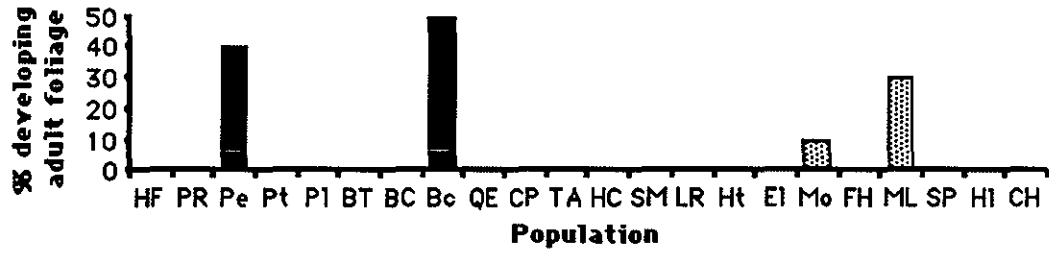
ADULT CHARACTERS



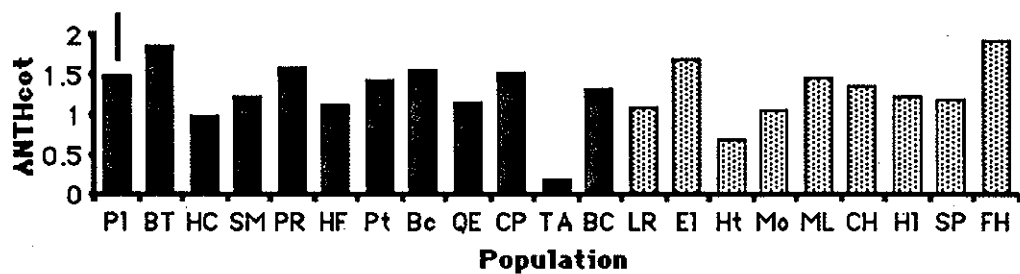
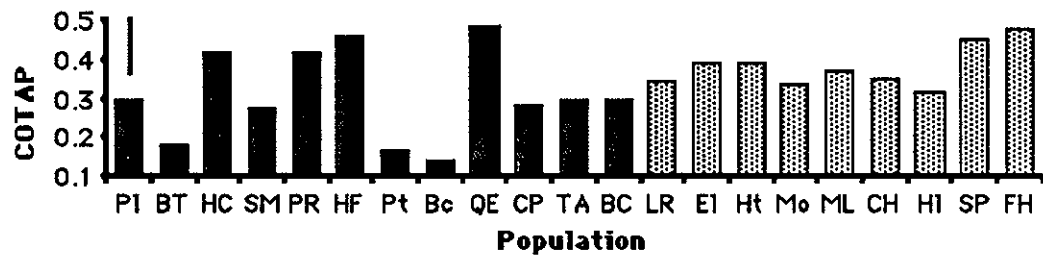
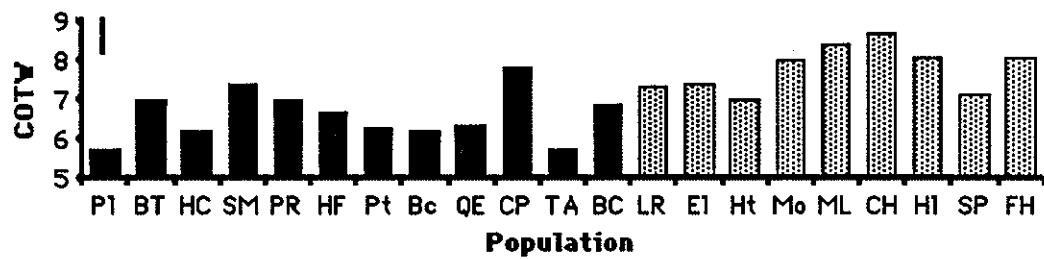
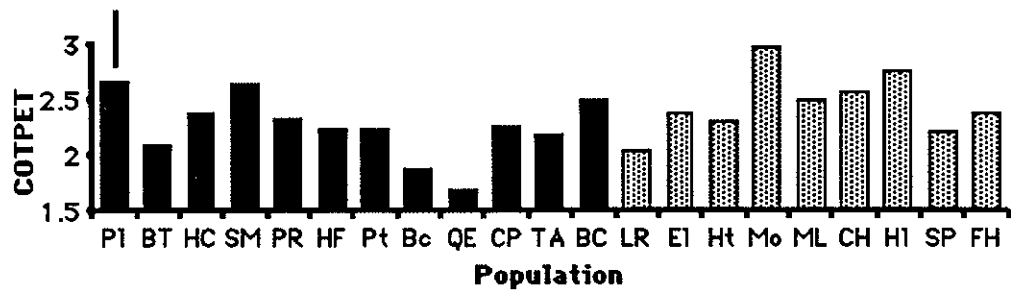
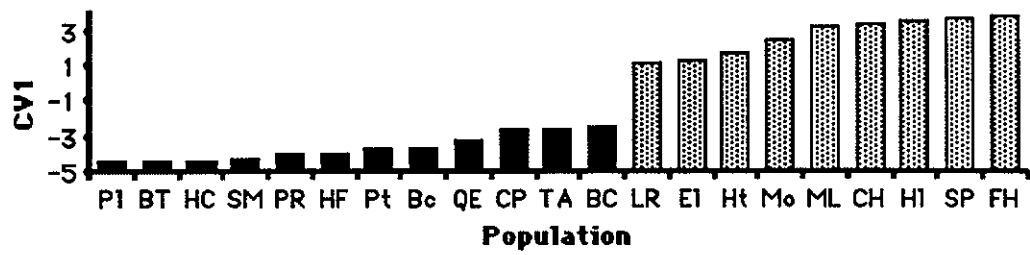


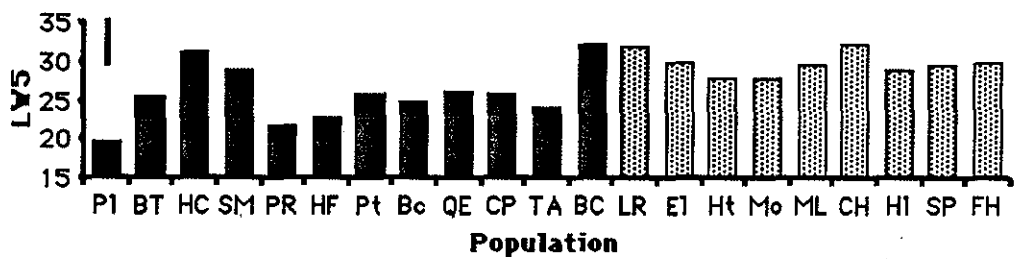
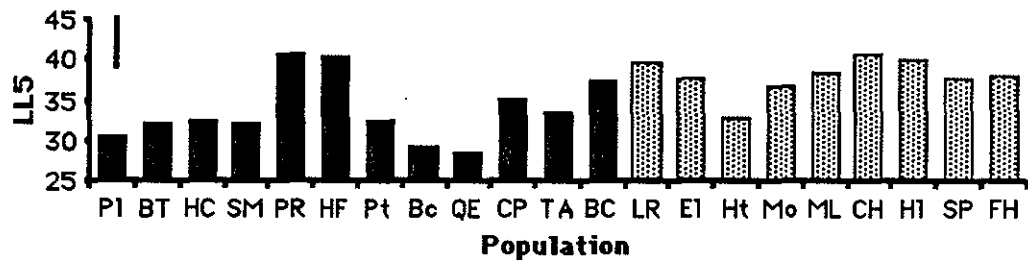
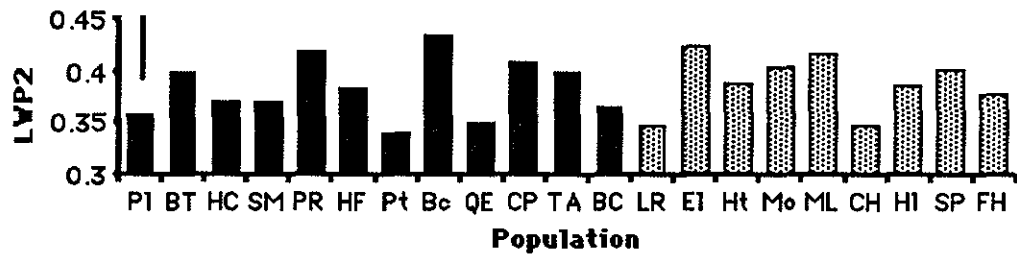
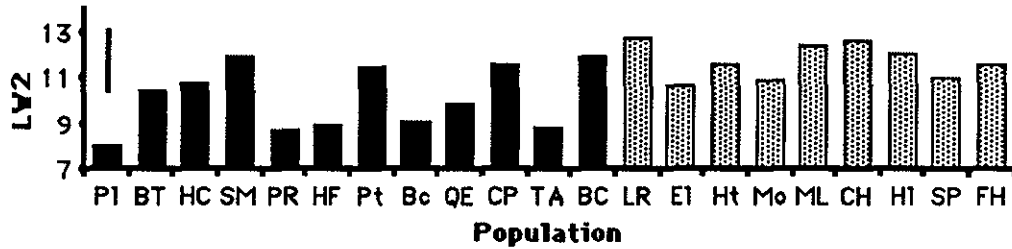
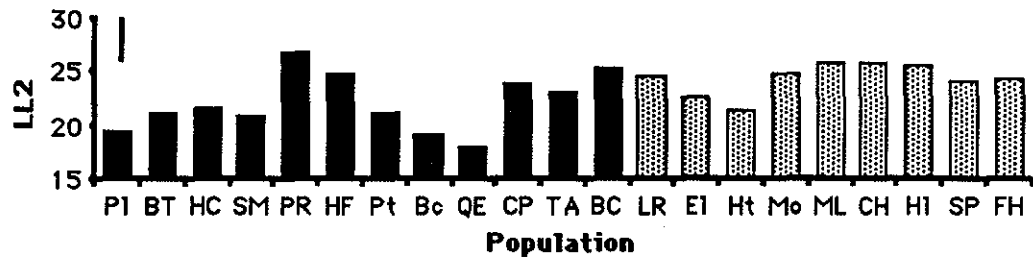


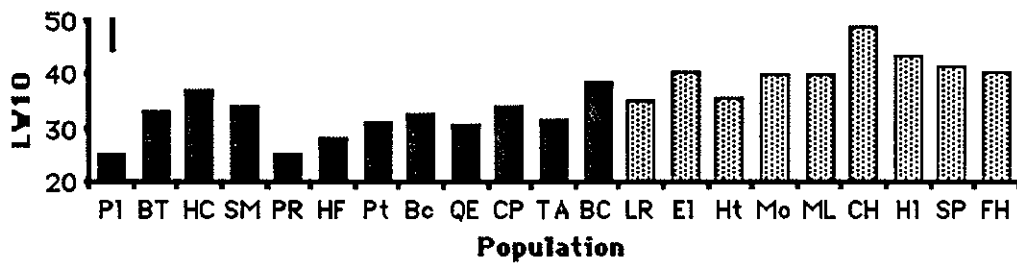
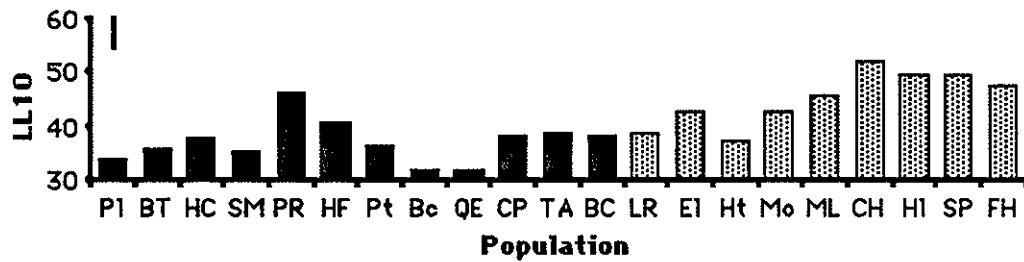
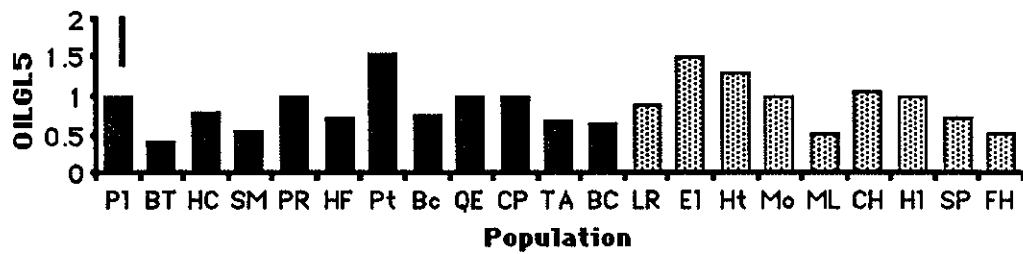
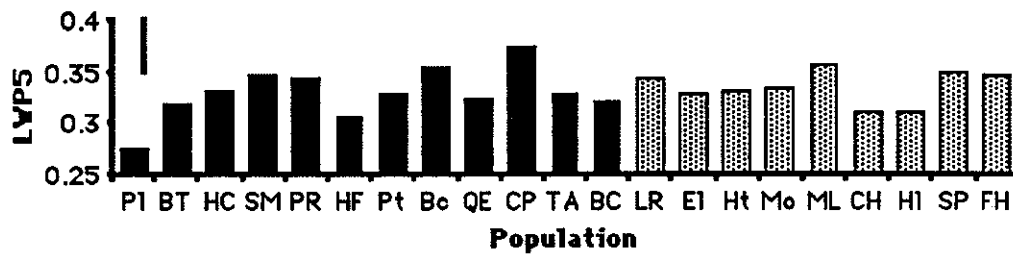
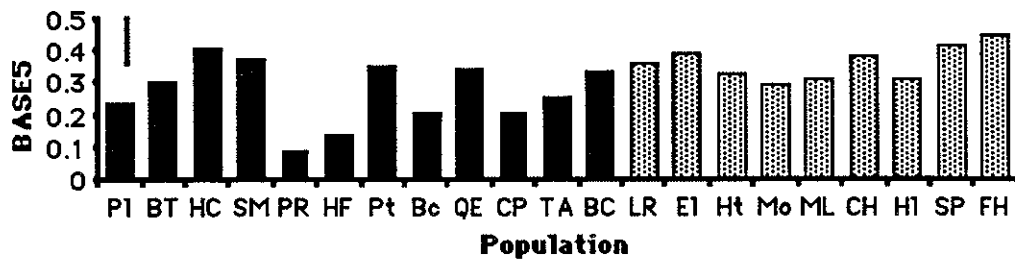


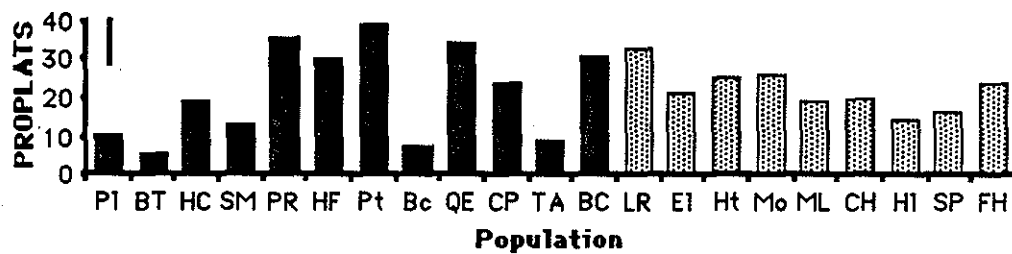
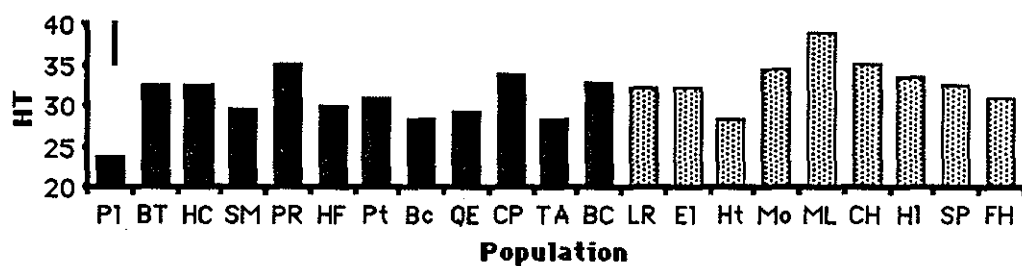
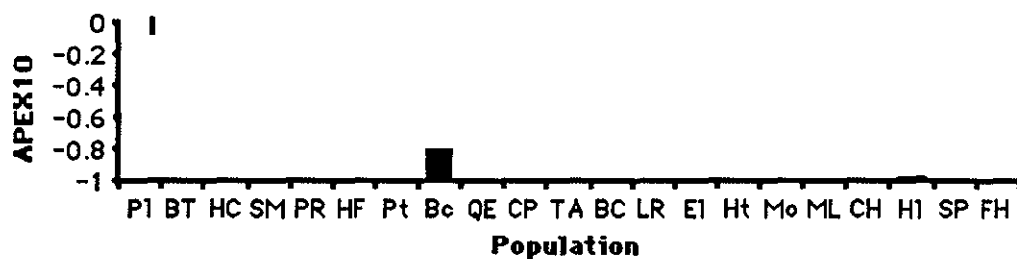
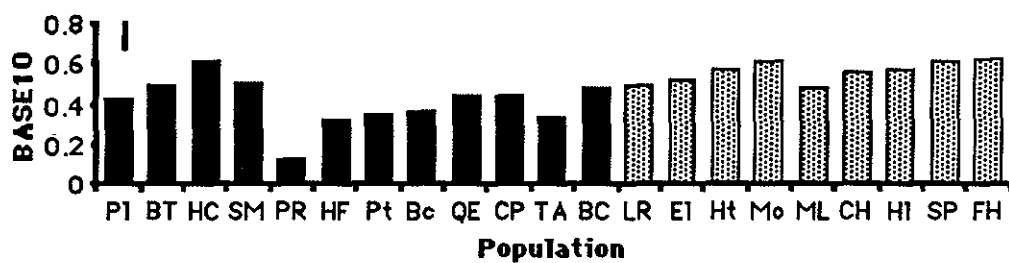
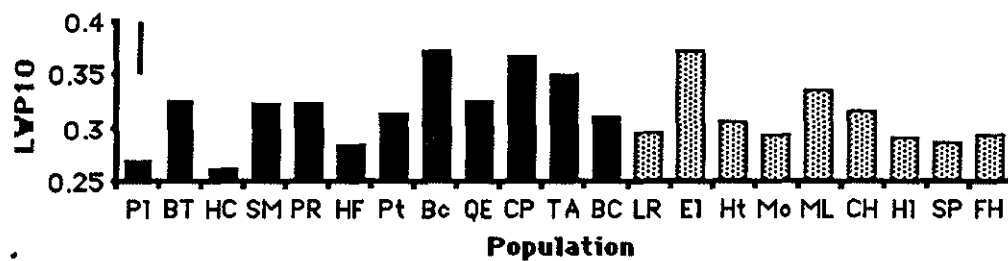


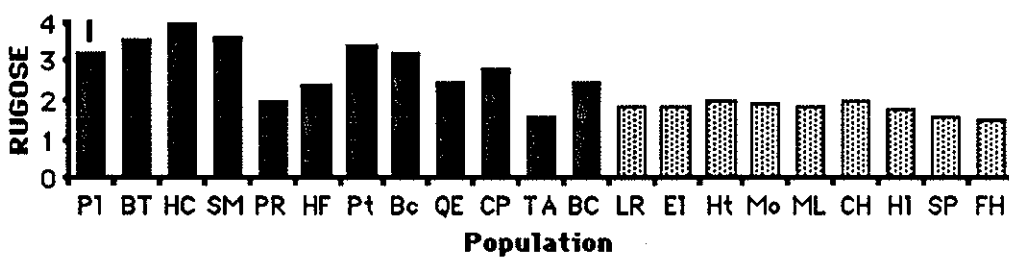
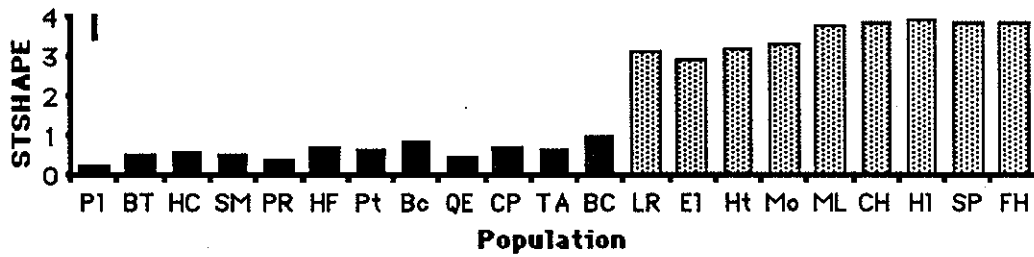
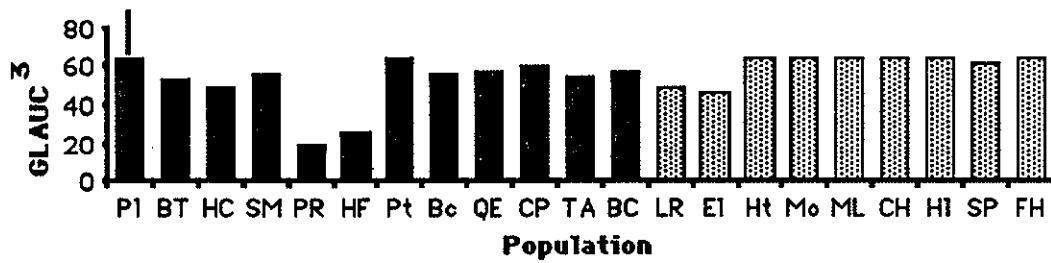
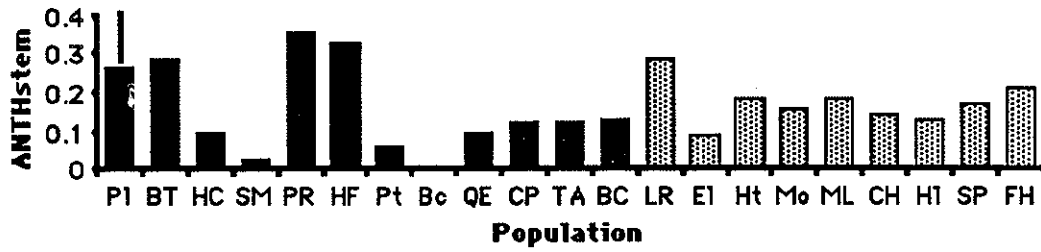
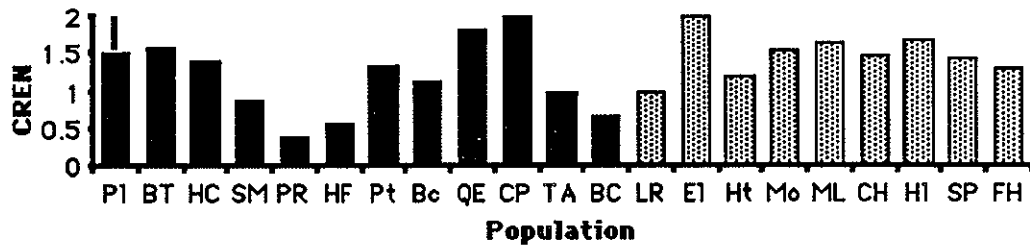
SEEDLING CHARACTERS

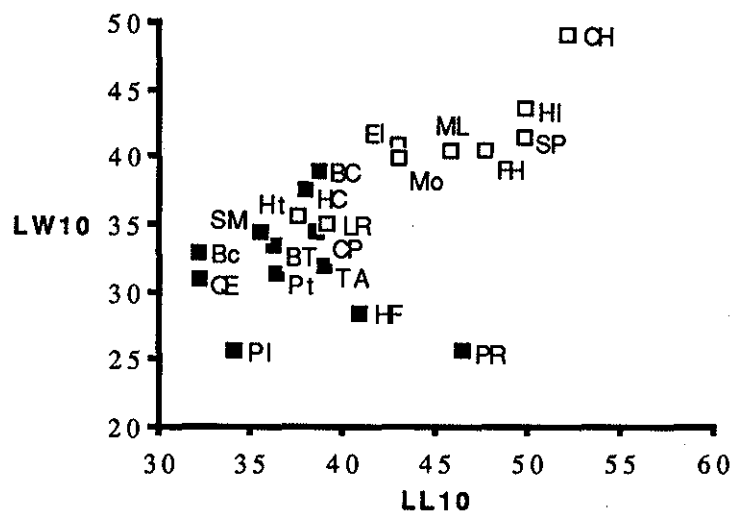
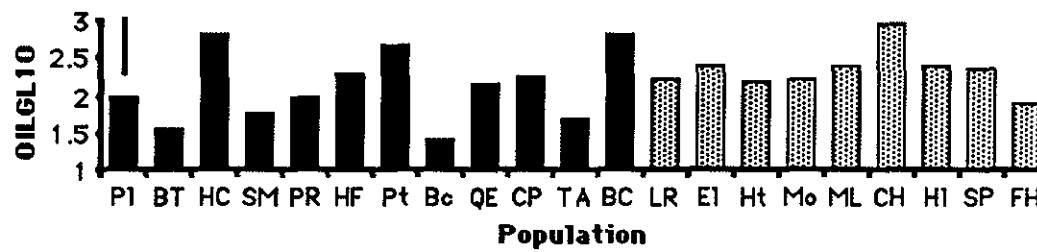
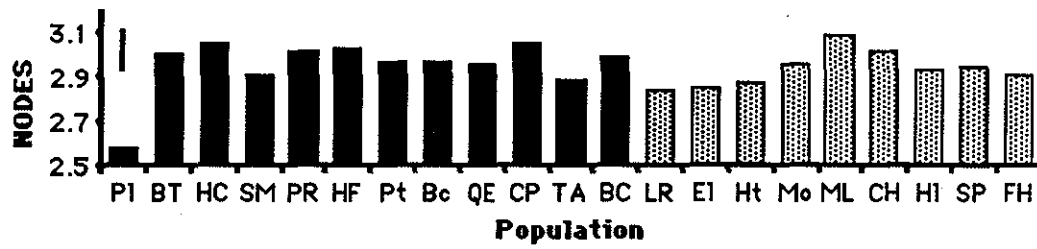












APPENDIX 6 Species associated with *Eucalyptus cordata*.

The species are ranked in order of decreasing frequency of occurrence in sites of *E. cordata*. The table indicates the distribution pattern (DIST.; 0 rare 1 occasional 2 locally abundant 3 widespread 4 widespread and abundant), growth form (GRTH.; 1 monocot 2 herb 3 perennial herb 4 creeper 5 undershrub 6 shrub 7 shrub-small tree 8 tree), whether the species is endemic (END. 1 endemic), the number and percentage of sites at which the species was recorded, and the mean cover of each species. In addition, the abundance class of each species in each site is shown (percentage cover 0 absent + < 0.1 1 ≤ 1 2 ≤ 5 3 ≤ 25 4 ≤ 50 5 ≤ 75 6 ≤ 100) with the sites ranked in order of their score along the main axis of morphological differentiation (PC1 - Fig. 4.7).

GENUS	SPECIES	DIST	END.	GRTH.	Nos. Sites	%	Mean Cover (%)	SITES RANKED ON PC1									
								eastern	-----					westernooo o o ooo		
								HPPBP	HQB	STCL	HEM	MSHC					
								FRI	Tt	Cc	EC	MAP	Rt	IO	LPI	H	
Eucalyptus	cordata	0	1	8	20	100	27.40	33	43	43	33	44	33	33	43	4	
Pultenaea	juniperina	4	0	6	15	75	7.33	20	31	20	00	13	32	13	10	3336	
Leptospermum	scoparium	4	0	6	13	65	3.87	02	22	03	21	13	03	20	02	230	
Lomatia	tinctoria	4	1	6	11	55	1.36	21	20	20	00	02	11	03	01	0022	
Callistemon	pallidus	4	0	6	10	50	1.38	20	01	02	10	30	00	20	20	0212	
Eucalyptus	pulchella	2	1	8	10	50	13.45	44	35	05	00	43	02	00	00	0230	
Gahnia	grandis	4	0	1	9	45	20.75	00	30	00	06	00	30	44	00	54640	
Acacia	verticillata	4	0	7	8	40	2.97	00	30	00	02	03	20	00	02	113000	
Bedfordia	salicina	4	0	7	7	35	0.88	00	00	00	00	10	00	00	23	100+21	
Bursaria	spinosa	4	0	7	7	35	1.27	21	21	21	00	30	00	00	00	000000	
Banksia	marginata	4	0	7	6	30	0.56	00	20	10	01	10	00	10	02	00100	
Cassinia	aculeata	4	0	6	6	30	0.59	00	00	00	00	00	00	00	20	202111	
Dianella	tasmanica	4	0	1	6	30	0.45	00	20	10	00	02	00	01	10	10001	
Epacris	impressa	4	0	5	6	30	0.79	23	21	00	00	10	10	00	00	000000	
Goodenia	ovata	4	0	6	6	30	3.43	00	01	03	03	13	00	00	03	000000	
Eucalyptus	globulus	2	0	8	6	30	1.47	30	22	21	00	00	00	00	00	03000	
Eucalyptus	obliqua	4	0	8	6	30	6.25	00	20	00	00	00	04	00	30	433000	
Acacia	riceana	2	1	7	5	25	0.52	00	00	00	00	00	01	00	02	202001	
Gonocarpus	teucroides	4	0	3	5	25	0.46	00	00	00	00	00	22	10	10	000001	
Pultenaea	daphnoides	2	0	6	5	25	0.41	20	00	20	02	20	00	00	00	10000+	
Astroloma	humifusum	4	0	5	4	20	0.57	20	01	00	02	20	01	00	00	000000	
Bauera	rubiodes	4	0	6	4	20	1.15	00	00	00	00	03	00	00	00	0030230	
Lepidosperma	elatus	4	0	1	4	20	1.87	03	00	00	03	00	02	00	03	00000000	
Olearia	floribunda	4	0	6	4	20	0.25	00	00	00	02	00	00	00	00	010101	
Olearia	viscosa	3	0	6	4	20	0.65	00	00	02	00	00	00	00	00	03001001	
Pimelea	nivea	4	1	6	4	20	0.34	00	20	10	01	10	00	00	02	0000000	
Lomandra	longifolia	4	0	1	4	20	2.00	00	03	03	02	20	02	00	00	00000000	
Eucalyptus	delegatensis	4	0	8	4	20	1.10	00	00	00	00	00	00	00	00	023230	
Acacia	genistifolia	4	0	6	3	15	0.40	20	00	02	00	00	01	00	00	00000000	
Casuarina	stricta	4	0	7	3	15	0.07	00	10	10	01	10	00	00	00	00000000	
Coprosma	hirtella	2	0	6	3	15	0.31	00	00	00	00	00	01	00	00	0000001002	
Correa	reflexa	3	0	6	3	15	0.06	01	00	00	00	00	00	00	00	0000000010	
Exocarpos	cupressiformis	3	0	7	3	15	0.19	10	00	00	00	20	00	01	10	00000000	
Leptospermum	lanigerum	4	0	6	3	15	3.70	00	20	00	00	00	00	00	00	0043000	
Notelaea	ligustrina	4	0	7	3	15	0.07	00	00	00	00	00	00	00	01	0000000010001	
Olearia	myrsinoides	4	0	6	3	15	0.11	00	00	00	00	00	00	00	00	0000000011	
Senecio	linearifolius	4	0	5	3	15	0.16	00	00	00	00	00	00	00	00	1020010	
Spyridium	species	3	0	5	3	15	0.15	00	00	00	00	00	00	00	00	1000101	
Westringia	angustifolia	4	1	6	3	15	0.75	00	00	00	00	00	00	00	00	1000031	
Lepidosperma	laterale	4	0	1	3	15	2.40	00	03	03	00	00	00	00	03	0000000000	

cont. GENUS	SPECIES	DIST	END.	GRTH.	Nos. Sites	% Sites	Mean Cover (%)	SITES RANKED ON PC1 eastern ——— western
							000 0 0 000
								HPPBPHBQBSTCLHEMMSHC
								FRI Tt CcECMAPRt IO LPI H
Acacia	dealbata	2	0	7	2	10	0.83	00010300000000000000
Acacia	myrtifolia	4	0	6	2	10	0.30	00000200002000000000
Acacia	stricta	4	0	6	2	10	0.10	00010001000000000000
Beyeria	viscosa	4	0	7	2	10	0.06	01100000000000000000
Coprosma	quadrifida	3	0	6	2	10	0.12	000000000000000120000
Cyathodes	glauc	4	1	6	2	10	0.06	00010000010000000000
Daviesia	ulicina	4	0	6	2	10	0.07	00000000000100100000
Diplarrena	moraea	4	0	1	2	10	0.70	02000000000300000000
Helichrysum	scutellifolium	2	1	6	2	10	0.27	00002000001000000000
Hibbertia	procumbens	2	0	6	2	10	0.50	000000000200000000030
Hibbertia	riparia	4	0	6	2	10	0.06	00000000001010000000
Olearia	phlogopappa	4	0	6	2	10	0.30	00000001000002000000
Persoonia	juniperina	3	0	6	2	10	0.10	00020000000000000000+
Pultenaea	gunnii	4	0	6	2	10	0.05	00000000001000010000
Veronica	formosa	2	1	6	2	10	0.07	10001000000000000000
Eucalyptus	dalrympleana	4	0	8	2	10	0.45	00000000020000002000
Eucalyptus	tenuiramis	2	1	8	2	10	1.25	00000000003000100000
Eucalyptus	viminialis	4	0	8	2	10	0.08	01010000000000000000
Acacia	melanoxylon	4	0	8	1	5	0.05	00001000000000000000
Acacia	sophorae	2	0	7	1	5	0.02	00000001000000000000
Billardiaria	longifolia	4	0	4?	1	5	0.05	000000000000000000001
Bossiaea	prostrata	4	0	5	1	5	0.01	00000000001000000000
Cassytha	glabella	4	0	4	1	5	0.01	00100000000000000000
Casuarina	littoralis	4	0	7	1	5	0.10	02000000000000000000
Casuarina	monilifera	4	0	6	1	5	0.70	00000000003000000000
Comosperma	volubile	2	0	5	1	5	0.02	10000000000000000000
Correa	alba	2	0	6	1	5	0.05	00001000000000000000
Cyathodes	juniperina	4	0	6	1	5	0.30	30000000000000000000
Dodonaea	viscosa	4	0	7	1	5	0.10	00000002000000000000
Epacris	marginata	2	1	5	1	5	0.25	00002000000000000000
Eriostemon	verrucosus	3	0	5	1	5	0.02	10000000000000000000
Geranium	potentilloides	3	0	2	1	5	0.05	000000000000000000001
Hakea	lissosperma	4	0	7	1	5	0.05	00000000000001000000
Helichrysum	dendroideum	4	0	7	1	5	0.10	00000000000020000000
Helichrysum	obcordatum	4	0	6	1	5	0.20	20000000000000000000
Hibbertia	empetrifolia	3	0	6	1	5	0.05	000000000000000000001
Kunzea	ambigua	2	0	6	1	5	0.30	00003000000000000000
Leptomeria	drupaceae	3	0	6	1	5	0.01	00000000010000000000
Leucopogon	parviflorus	4	0	6	1	5	0.25	00000002000000000000
Melaleuca	squarrosa	4	0	6	1	5	0.30	00000000000030000000
Odixia	achlaena	0	1	6	1	5	0.80	00000300000000000000
Olearia	lirata	4	0	7	1	5	0.05	00100000000000000000
Phebalium	squameum	3	0	7	1	5	0.05	000000000000000000001
Pittosporum	bicolor	2	0	7	1	5	0.05	00000000000001000000
Pomaderris	apetala	4	0	7	1	5	0.02	00000000000000010000
Pultenaea	dendata	3	0	6	1	5	0.10	00000200000000000000
Sphaerolobium	vimineum	4	0	5	1	5	0.05	00000000001000000000
Stylidium	graminifolium	4	0	3	1	5	0.01	00000000001000000000
Tetratheca	glandulosa	3	0	5	1	5	0.05	00000000001000000000
Tetratheca	pilosa	3	0	5	1	5	0.05	00000000000000000100
Viola	hederacea	4	0	2	1	5	0.05	000000000000000000001
Viola	sieberana	4	0	2	1	5	0.01	00000000001000000000

Appendix 7 Arboretum

Seedlings from this study were planted (10/3/85) in a trial on ex-agricultural land near New Norfolk. The only site preparation was the removal or slashing of blackberries and shrubs where necessary and plants had attained sufficient height by 1988 for sheep to be used to reduce the undergrowth.

Location: Glenfern, 14 km SW of New Norfolk. The site is within 5 km of two of natural stands at Mt. Lloyd (ML) and Moogara (Mo).

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