

Hybridization and clinal variation
in some Tasmanian eucalypts

by

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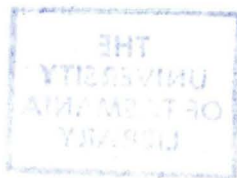
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DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university and contains no copy or paraphrase of material previously published or written by another person, except where due reference is made in the text.

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Abstract

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Summary

This thesis comprises two sections. In the first, a multivariate approach is adopted in a population survey of variation in the sub-alpine species *E. gunnii*. As taxonomically defined by Pryor and Johnson (1971) this species encompasses a diverse assemblage of populations and comprises two sub-species, spp. *gunnii* and ssp. *archeri*, often given specific status. The present study indicates that *E. gunnii* is a polymorphic species comprising a multidimensional clinally varying series of highly differentiated populations. This is summarized by classification of populations into 5 main phenetic groups which are geographically concordant and more or less correspond to the taxonomic perception of the complex. Progeny trials indicate that these phenetic groups are genetically defined yet represent a continuum. In part, population differentiation appears to result from the interaction of multi-character clines paralleling at least two major habitat gradients.

Whilst considerable differentiation occurs between disjunct stands, a large portion of the variation occurs in more or less continuous stands on the Central Plateau. In this area, the two sub-species are parapatric and major independent clines are associated with increasing exposure to the alpine environment and the transition between sub-species. A detailed investigation of these clines is undertaken and reciprocal progeny trials suggest natural selection is a major factor in their maintenance. In addition it is shown that parallel clines in flowering time have the potential to retard gene flow along these clines. The origin of these clines and variation in the complex is addressed and it is suggested both primary differentiation and introgression are important determinants of the variation pattern and population differentiation. Gene exchange with surrounding *Eucalyptus* species may be an important evolutionary stimulus, the effects of which are probably accentuated in small, marginal isolates.

The evolutionary role of hybridization is further examined in two separate studies in the second section of the thesis. The argument is developed that in addition to the release of variability, interspecific hybridization may be of significance as a means of actually dispersing genes or coadapted gene combinations where the adaptive response is limited by restricted seed dispersal. Supportive data are firstly presented from a study of a rare naturally occurring F_1 hybrid between *E. obliqua* and *E. pulchella* which is believed to have arisen by recent migration of *E. obliqua* pollen into the range of *E. pulchella*. Evidence from progeny

trials and the natural occurrence of a second generation of hybrid saplings lends credence to the hypothesis that species could invade suitable sites within the range of another potentially interbreeding species by long distance pollen migration, followed by back-selection to the coadapted gene combinations of the pollen parent from a segregating hybrid swarm. Further evidence is presented from a detailed study of the genetic and competitive interaction of two closely related species *E. risdonii* and *E. amygdalina*. A genetic analysis of a hybrid swarm is undertaken and barriers to hybridization are examined in terms of reproductive capacity, seedling vigour and flowering time. The competitive interaction of the two species and hybrids is investigated by a comparison of mortality, vegetative regeneration and seedling recruitment following wildfire. The data presented indicate a marked fitness differential at the species boundary and suggest that *E. risdonii* should be expanding its range. This is supported by a demographic study of boundary and pure species stands. The dispersal potential of *E. risdonii* is examined and data suggest that hybridization may contribute significantly to the flow of *E. risdonii* genes into the range of *E. amygdalina* and to the invasion by *E. risdonii* of suitable sites within the range of *E. amygdalina*. This is discussed in the broader context of species migration and invasion following shifts in the competitive interaction between species.

PART 1

Variation in the *Eucalyptus gunnii*-*archeri* complex.

CHAPTER 1

Variation in the *Eucalyptus gunnii*-*archeri* complex1. Variation in the adult phenotype1.1 Introduction

Geographic variation is a common feature of many widely distributed species (see Gould and Johnston 1972; Endler 1977 and references cited therein). This is exemplified by many northern hemisphere forest tree genera (e.g. Stebbins 1950; Grant 1958; Steinhoff and Andresen 1971; Fung and Wright 1972; Ledig and Fryer 1972; Smouse and Saylor 1973a; Sterne and Roche 1974; Wright 1976; Adams 1977; Hamrick 1979; Givnish 1981; Guries and Ledig 1982) where clinal variation and intergradation are common. In such cases restricted sampling may result in the proliferation of a wide array of species or subspecies classifications, whereas intensive sampling has often demonstrated that variant populations form a graded series, being linked by a complex pattern of clines (Jain and Bradshaw 1966; Phillips *et al.* 1973).

This is certainly the case in *Eucalyptus*. While many species appear well defined and distinct, others exhibit considerable variability, and intergradation between recognized taxa is common (see Pryor and Johnson 1971, 1981 and references cited therein). In many cases recognized taxa appear as extremes of genetic continua or as clinal arrays (e.g. Pryor 1957a, 1959a, 1962; Jackson 1960a; Green 1969a; Pryor and Johnson 1971; Kirkpatrick 1974, 1975a; Gillison 1976; Phillips and Reid 1980). Geographic variation appears the norm and has been demonstrated for a wide range of morphological, physiological and chemical characteristics in such species as *E. camaldulensis* (e.g. Pryor and Byrne 1969; Banks and Hillis 1969; Burley *et al.* 1971; Karshon 1972), *E. globulus* (Kirkpatrick 1975a), *E. obliqua* (e.g. Green 1971; Brown *et al.* 1976; Pederick 1976), *E. ovata* (e.g. Simmons 1974; Clucas and Ladiges 1979; Ladiges *et al.* 1981), *E. pauciflora* (e.g. Pryor 1957a; Harwood 1980), *E. viminalis* (e.g. Pryor 1959b, 1962; Ladiges and Ashton 1974; Phillips and Reid 1980), *E. caesia* (Hopper and Burgman 1983; Moran and Hopper 1983) and many others. Evenly graded clinal variation may be exhibited where stands are continuous, although clines are frequently stepped and where major disjunctions are involved, geographic races are often distinguished (Pryor and Johnson 1971). Nevertheless, geographic isolation appears unnecessary for differentiation, and local steep clines over short distances have been reported in continuous populations (e.g. Pryor 1957a; Barber and Jackson 1957;

Jackson 1960a; Ladiges 1976; Phillips and Reid 1980; Harwood 1980). This is clearly seen in *E. urnigera*, where Barber and Jackson (1957) suggest strong selective forces maintain marked local differentiation despite considerable gene flow.

Adaptive differentiation appears to be a major determinant of the pattern of variation and genetic differentiation within species as a response to local habitat heterogeneity has been shown for many, obviously adaptive, characters. These include frost resistance (e.g. Pryor 1957a; Ashton 1958; Thomas and Barber 1974a & b; Green 1969a; Eldridge 1969, 1972; Paton 1972, 1981; Pederick 1976; Harwood 1980), drought resistance (e.g. Ladiges 1974, 1976), photosynthetic parameters (e.g. Thomas and Barber 1974a & b; Slatyer 1977a,b & c, 1978; Slatyer and Ferrar 1977), growth rate (e.g. Pryor 1957a; Ashton 1958; Brown *et al.* 1976), temperature responses (e.g. Eldridge 1969; Green 1969a; Paton 1980) and tolerance to high soil pH (Ladiges and Ashton 1977; Anderson and Ladiges 1978, 1982). In addition, morphological or anatomical differentiation is common, frequently paralleling gradients in altitude (e.g. Barber 1955; Pryor 1957a; Barber and Jackson 1957; Jackson 1960a; Larsen 1965; Eldridge 1969, 1972; Green 1969b; Brown *et al.* 1976; Phillips and Reid 1980), moisture availability (e.g. Ladiges and Ashton 1974; Kirkpatrick 1976) or continentality (e.g. Pryor and Byrne 1969; Kirkpatrick 1975a). Strong environmental gradients have been shown to cause simultaneous clinal variation in many characters resulting in gross phenotypic differentiation, and considerable taxonomic confusion (e.g. Pryor 1957a; Green 1969b; Jackson 1960a). Moreover, *Eucalyptus* species frequently exhibit weak reproductive isolation (e.g. Brett 1938; Jackson 1958; Pryor 1951a, 1952, 1976; Pryor and Johnson 1971) and secondary intergradation is often implicated in contributing to the variability and the continuity between species (e.g. Brett 1938; Pryor 1951a,b, 1955a,b, 1959a,b, 1976; Pryor and Johnson 1971, 1981; Kirkpatrick 1971, 1976, 1977a; Parsons and Kirkpatrick 1972; Hopper *et al.* 1978; Drake 1980).

The present investigation concerns the pattern and origin of variation within *E. gunnii* (*sensu* Pryor and Johnson 1971), the Tasmanian endemic cider gum. As taxonomically defined by Pryor and Johnson (1971) this species encompasses a diverse assemblage of populations and comprises two subspecies, *ssp. gunnii* and *ssp. archeri*, often given specific status (Blakely 1934; Brett 1938; Jackson 1965; Hall and Brooker 1972; Curtis and Morris 1975). In addition, forms previously described as *E. divaricata* (Brett 1938) are currently included in the subspecies *gunnii* (Curtis 1956; Pryor and Johnson

1971). This study concerns the clinal nature of the variation within the *E. gunnii*-*archeri* complex and in particular, the relationship between the two taxa *E. archeri* and *E. gunnii* in an area of parapatry. The specific objective of this chapter is to describe the pattern of variation in adult morphology. This is followed by a study of genetic variation in seedlings grown in a common environment (Chapter 2) and a report of reciprocal progeny experiments along the major environmental gradients (Chapter 3). The problem of the origin of the clines within the *E. gunnii*-*archeri* complex is addressed in Chapter 4.

1.2 Affinities and Historical Taxonomy

E. gunnii and *E. archeri* show close affinities to several Tasmanian species (*E. urnigera*, *E. morrisbyi*, *E. perriniana* and *E. cordata*) which together comprise the group locally referred to as the 'Alpine White Gums' (Jackson 1965). In the latest revision of the genus by Pryor and Johnson (1971), these species are placed in the Subseries *Cordatinae* (Subgenus *Symphyomyrtus*; Section *Maidenaria*; Series *Viminales*). The close phylogenetic relationship of the Tasmanian endemics *E. gunnii*, *E. archeri*, *E. urnigera* and *E. morrisbyi* is recognized and, along with the mainland species *E. glaucescens*, they comprise the superspecies *Gunnii*.

E. gunnii Hook f. was first described by Hooker (1844) from specimens obtained by R.C. Gunn (Marlborough, near Lake Echo). The species had been known to the colonists of Tasmania for some time, being colloquially referred to as the "Cider Tree." This name emanated from the refreshing sap collected from this species by shepherds and stockmen. Anxious to observe this renowned species in its native habitat, Hooker made a specific excursion to the centre of the island during his stay in Hobart as part of the 1843 Antarctic Expedition. Benthams (1866) description of *E. gunnii* basically follows Hooker (1844), but encompasses a similar Victorian eucalypt recorded near the summit of the Baw Baw Mountains. *E. gunnii* is figured by Mueller (1879) and he notes *E. acervula* as a synonym. His composite description resulted in the subspecies *E. gunnii* Hook f. var. *ovata* (synonymous with *E. ovata* Labill) and var. *acervula* being split from *E. gunnii* (Deane and Maiden 1901). Deane and Maiden (1899) had previously proposed *E. gunnii* Hook f. var. *glauca* to include mainland forms subsequently recognized as *E. perriniana* F.V.M. (Maiden 1917) and *E. glaucescens* Maiden and Blakely (Maiden 1933). Rodway (1903) and Baker and Smith (cited in Brett 1938) had previously concluded that *E. gunnii* was

distinct from *E. perriniana* and the latter authors considered *E. gunnii* was endemic to Tasmania.

Further restriction of the range of variation encompassed by *E. gunnii* Hook f. followed the recognition of a new species, *E. archeri* Maiden and Blakely (Maiden 1933) from specimens collected by W.H. Archer in 1848 from the Western Mountains and by the Rev. H. Rupp from Mt. Barrow and previously included in *E. gunnii* (Maiden 1917; Rodway 1918). The Western Mountains do not correspond to a specific location and Brett (1938) considers this reference to mean the Western Tiers. He notes that material collected from the latter locality closely match the type. Maiden (1933) considered *E. archeri* to differ from *E. gunnii* in being strictly glabrous in all characters (cf. glaucous *E. gunnii*), in the yellow-green leaves and in the smaller sessile buds and fruits. Concurrent descriptions of *E. gunnii* and *E. archeri* were first published by Blakely (1934). *E. glaucescens*, *E. gunnii*, *E. perriniana* and *E. urnigera* were grouped in Blakely's series *Globulares*. Another species, *E. irbyi* Baker and Smith, grouped along with these species and found only at Alma Tier and Interlaken (Tasmania) is considered by later authors (Brett 1938; Curtis 1956) to be of hybrid origin (*E. gunnii* x *E. dalrympleana*). Blakely considered *E. archeri* to have closer affinities with the endemic Tasmanian yellow gums *E. vernicosa* Hook f., *E. subcrenulata* Maiden and Blakely and *E. johnstonii* Maiden [later treated as cline forms (Jackson 1960a) or subspecies (Pryor and Johnson 1971) of *E. vernicosa*] and together they were assigned to a different series. Mueller (1879) had previously treated *E. vernicosa* as a dwarf form of *E. gunnii* and Jackson (1960a) notes this was probably due to a resemblance between *E. vernicosa* and *E. archeri*. He expands further on this topic suggesting convergence and parallelisms in the variation pattern of the yellow gums (*E. vernicosa* cline forms) with that in the *E. gunnii* group. The alpine species *E. archeri* is noted as resembling the *subcrenulata-parvula* region of the *E. vernicosa* cline whereas lower altitude forms of both groups remain distinct. Nevertheless Jackson (1960a) considers the real affinities of *E. archeri* are with members of the *E. gunnii* group.

In taxonomic works after Blakely (e.g. Brett 1938; Curtis 1956; Hall *et al.* 1970; Pryor and Johnson 1971; Hall and Brooker 1972; Curtis and Morris 1975) *E. archeri* is considered as having a greater affinity with the alpine white gum species, particularly *E. gunnii*. In fact, it was the extent of the relationship of *E. gunnii* and *E. archeri* and the specific status of *E. archeri* which appeared to be in doubt. Brett (1938) maintained specific status for both. However Barber (1955) treats the glaucousness difference

emphasized by Maiden (1933) as an adaptive, clinally varying character of both juvenile and adult *E. gunnii* and Jackson (1960a) suggests that *E. archeri* was probably a green dwarf form of *E. gunnii*. Curtis (1956) treats *E. archeri* as a green variant of *E. gunnii* but in a revised edition of her work (Curtis and Morris 1975) describes *E. archeri* as a species "...resembling *gunnii* but not glaucous in any part (except occasionally very slightly on the juvenile leaves)." Hall and Brooker (1972) refer to *E. archeri* at the specific level, but comment that Pryor and Johnson (1971) anticipate subspecific status.

While there is considerable variation in the main characters used to define and discriminate the two forms by different authors, there appears general consensus on differences in habit, glaucousness, juvenile leaf shape, adult leaf thickness, peduncle and pedicel length and capsule shape. However, it appears clear from the taxonomic works cited that as more specimens of *E. gunnii* and *E. archeri* are examined, the more difficult they become to distinguish.

Brett (1938) further restricted the variation encompassed in *E. gunnii* Hook f. by raising to specific rank variants found on open flats on the northern and eastern shores of the Great Lake, at Miena and skirting St. Patrick's Plain. This variant was described as *E. divaricata* McAuley and Brett, but subsequent authors (Curtis 1956; Penfold and Willis 1961; Hall et al. 1970) obviously include this species in *E. gunnii* Hook f. and Pryor and Johnson (1971) note it as a minor variant of *E. gunnii* ssp. *gunnii*. The main differences between *E. divaricata* and *E. gunnii* according to Brett's descriptions included the divaricating branching pattern and increased glaucousness (extending onto branchlets, buds and fruits) of *E. divaricata* as well as fruit shape differences. The fruit of *E. divaricata* were described as cylindroid to sub-urceolate in shape whereas those of *E. gunnii* ranged from hemispherical or campanulate to ovoid-truncate. Brett's cited locations for *E. gunnii* included Middlesex Plain below Cradle Mountain, Alma Tier and Mt. Arrowsmith. The population at Middlesex Plain was later referred to by Barber (1955) as comprising types 'intermediate' in glaucousness between forms on the northern scarp of the Western Tiers (i.e. *E. archeri* Curtis and Morris 1975; Hall and Brooker 1972) and forms around Breona on the edge of Great Lake (i.e. Brett's *E. divaricata*).

The affinities given by Brett for *E. divaricata* imply similarity with *E. gunnii* and *E. urnigera* Hook f. Affinities between *E. gunnii* and *E. urnigera* had previously been suggested by Blakely (1934). Barber (1955) also considers them closely related and suggests *E. urnigera* should be considered a geographical subspecies replacing *E. gunnii* on the southern mountains. However, the specific rank of these two species has remained undisputed (e.g. Blakely 1934; Curtis 1956; Hall and Gray 1973; Pryor and Johnson 1971; Curtis and Morris 1975).

It is apparent from the taxonomic history that *E. gunnii* (sensu Pryor and Johnson 1971) is a highly variable taxon. Three recognizable variants are recorded in the literature corresponding to:-

(i) *E. gunnii* ssp. *archeri* (i.e. *E. archeri* Maiden and Blakely) and within *E. gunnii* ssp. *gunnii*

(ii) *E. divaricata* McAuley and Brett

and (iii) *E. gunnii* as described by Brett (1938).

The existence of other variants was confirmed in a preliminary survey of the superspecies *Gunnii* (Potts 1978) and the present study constitutes a more intensive analysis of the variation within and between the two taxa *E. gunnii* and *E. archeri*. For the purposes of presentation, *E. gunnii* (sensu Pryor and Johnson 1971) will be referred to as the *E. gunnii*-*archeri* complex. Where either taxa is being specified, reference will be made to *E. gunnii* or *E. archeri*, and this will occur when assignment to either taxa is unambiguous.

1.3 Ecology and Distribution of the *E. gunnii*-*archeri* Complex*

The superspecies *Gunnii* (sensu Pryor and Johnson 1971) comprises species occupying alpine or sub-alpine habitats, with the exception of *E. morrisbyi*. *E. morrisbyi* is restricted to two small stands in lowland habitats in south-eastern Tasmania (Risdon and Cremorne) and the main population at Calverts Hill (Cremorne) occurs near the coast just above sea level (up to 100 m). The geographical distribution of the other Tasmanian endemics (*E. archeri*, *E. gunnii* and *E. urnigera*) is indicated in Fig. 1.1. In general, these endemic species are usually confined to soils developed from igneous parent material (normally Jurassic dolerite) and appear to be restricted to regions of between 800 mm and 2000 mm annual rainfall mainly in central areas of the island. This group appears to be adapted to relatively fertile soils

* sites mentioned are detailed in Table 1.1 and shown in Figs. 1.2 and 1.3.

and is replaced by the *E. vernicosa* group on the less fertile sites of the pre-carboniferous fold province in the west of the island (Jackson 1960a). However, there is considerable overlap in geographical distribution and both groups occur on the mountains in the south-east of the island.

In terms of the principal occurrence of each species, *E. urnigera*, *E. gunnii* and *E. archeri* form a geographical series (Fig. 1.1). *E. urnigera* achieves maximum development on the mountains in the south-east of the island, such as the Mt. Wellington Range and the Mt. Field Plateau. The main occurrence of *E. gunnii* is on the upper slopes and plateau of the central massif of ^{the} island, particularly the Central Plateau. Populations assigned to *E. archeri* occur along the northern scarp of the Central Plateau (along the Western Tiers) as well as on several of the north-eastern mountains. Major fault grabens isolate the highland areas of the Central Plateau, the Ben Lomond plateau (NE) and the Mt. Field-Wellington Ranges. However, populations ascribed to these species transcend these major habitat disjunctions. Small disjunct stands of *E. urnigera* extend as far north as Alma Tier on the south-eastern edge of the Central Plateau and *E. gunnii* extends as a series of small isolated populations through the Lake St. Clair-Mt. King William area, as far south as the base of the Mt. Anne-Eliza Plateau, Mt. Field and Snug Plains. *E. archeri* and *E. urnigera* are allopatric and distinct forms of *E. gunnii* and *E. archeri* do not co-occur. In contrast, *E. urnigera* and *E. gunnii* may occur together but are ecologically ~~separated~~. *E. gunnii* occupies the poorly drained marshy sites whereas *E. urnigera* occurs on the better drained slopes, often in association with *E. coccifera*. This is clearly exemplified in the Broad River Valley (Mt. Field) and at Jimmy's Marsh (Alma Tier). Both species may occur in close contact, and where they do, the boundary between stands is usually sharp and specific integrity is maintained except for the occurrence of occasional intermediates (suspected hybrids). Nevertheless, some continuity between these species appears to occur through several allopatric populations sampled in this study (i.e. Snow Hill and Scrummys' Marsh-Alma Tier).

The habitat in which *E. gunnii* is most commonly found is relatively open and defined by poor soil drainage and cold temperatures. The interaction of *E. gunnii* with surrounding eucalypt species appears best explained by its ability to better tolerate this combination of factors, as well as a lower tolerance of summer drought. *E. gunnii* is no doubt one of the most frost-tolerant eucalypt species. Based on the minimum survival temperature in Britain, *E. gunnii* is ranked along with the other Tasmanian species

E. vernicosa, *E. subcrenulata* and *E. coccifera* (Martin 1948; Barber 1955; Marien 1979; Evans 1980; Anon. 1982) and Evans (1980) also suggests *E. archeri*. The cold tolerance of *E. gunnii* is graphically emphasized by Hooker (1844) in the initial description of the species after he witnessed the devastating effects of the great frost of 1837. *E. gunnii* was noted to be almost uninjured whereas surrounding species and eucalypts even at lower elevations were completely killed. On the Central Plateau (Figs. 1.2 and 1.3), *E. gunnii* is found skirting the edges of 'frost hollows', lake edges or on poorly drained valley flats (Fig. 1.4). The topography of the Central Plateau is essentially 'stepped' due to the development of sub-aerial erosion surfaces following periods of geological uplift (Davies 1959). Davies (1959) recognizes six main erosion surfaces, of which three:- the St. Clair (730-820 m), lower Plateau (915-1065 m) and higher Plateau (1190-1340 m) surfaces, are of particular relevance. *E. gunnii* often forms extensive open woodlands on the inverted tree line in the rock basin depressions on the lower Plateau surface, particularly between 1000 and 1100 m. These depressions collect cold air drainage from high grounds and are subject to intense radiation frosts. Meteorological records (1972) from Miena and Shannon, both situated near the edge of such depressions, indicate an average frost frequency of over 200 per year, with up to 130 per year recorded as heavy. The general problem of the exclusion of *E. gunnii* and other eucalypt species from these 'frost hollows' is discussed by Jackson (1973). He considers the exceptional frosts occurring every 50 to 100 years are sufficient to kill all mature eucalypts in the frost hollows. The incidence of moderate frosts and competition with surviving tussock grass or sedge communities is then sufficient to restrict colonization. In addition, in the absence of the buffering effect of an overhead canopy, temperatures may be more extreme and frosts more intense in microhabitats normally suitable for seedling establishment.

E. gunnii is replaced on the better drained slopes at high altitudes by *E. coccifera* and lower altitudes by *E. delegatensis*, *E. pauciflora* and *E. dalrympleana* (e.g. Fig. 1.4). On the southern slopes of the Central Plateau, in areas below 960 m and particularly where rainfall becomes limiting, *E. gunnii* is only encountered sporadically being generally restricted to poorly drained river courses where during winter it is subject to frequent flooding. At these lower altitudes, particularly on the St. Clair surface, it is replaced by *E. rodwayi* as the species tolerant

of poor soil drainage (Jackson 1973). On these sheltered lower altitude forest sites (e.g. <1000 m) *E. gunnii* may attain heights of up to 30 m (Fig. 1.5) and is frequently found emergent above a dense wet sclerophyll understory dominated by *Leptospermum lanigerum*. However, with increasing altitude and exposure, the tree height is reduced and in the open woodlands the trees (12-20 m) exhibit a marked divaricating branching pattern (hence *E. divaricata*) (Fig. 1.6). At its higher altitudinal limit a variant of *E. gunnii* may extend with *E. coccifera* onto extremely exposed sites as a mallee or stunted (4-5 m) single stemmed tree. These forms are found where *E. gunnii* populations generally confined to the lower Plateau surface extend onto the lip of the exposed higher Plateau surface (e.g. Liawenee; Fig. 1.7).

Populations of *E. gunnii* occurring south of the Central Plateau are at relatively low altitudes (850-600 m) and are usually on the peaty podzolic soils developed on button grass (*Gymnoschoenus sphaerocephalus*) plains. In the majority of these populations *E. gunnii* rarely exceeds 4-5 m in height and often exhibits a mallee habit. This is most likely a result of the high fire frequency associated with the sedge community (Jackson 1968). *E. gunnii* extends westward, through the Lake St. Clair-Cradle Mt. region (e.g. Pelion Plains, Middlesex Plains) to the basalt plains south of St. Valentines Peak, near Guilford (660 m). In the latter area, small stands of *E. gunnii* 15-25 m high, follow stream or rainforest margins or form open woodlands with such species as *E. delegatensis* and *E. rodwayi*. The habitat of *E. gunnii* on Middlesex Plains near Cradle Mt. is similar although at a slightly higher altitude. Both populations occur on peaty soils developed above Tertiary basalt bedrock in high rainfall areas (approx. 2000 mm/year). The *E. gunnii* at Middlesex Plains is replaced by the yellow gums on the Precambrian metamorphic rocks at higher altitude.

E. archeri usually occurs as a mallee or small tree on talus slopes at or above the upper altitudinal limit of sub-alpine *E. delegatensis*-*E. dalrympleana* forests on the Western Tiers and north-eastern mountains (c.a. 1000-1200 m; Figs. 1.4 and 1.8). It is generally confined to high rainfall areas (>1200 mm/year) and may extend into sub-alpine mixed forest with temperate rainforest species (e.g. *Nothofagus cunninghamii*). In competition with rainforest species the survival of eucalypts depends on fire maintaining an open disclimax vegetation (Gilbert 1958; Jackson 1968, 1973). In the absence of fire, particularly in high rainfall, sheltered areas, eucalypts are unable to regenerate beneath the closed forest canopy and are eliminated within a single generation resulting in the development of the rainforest climax. However *E. archeri* generally occurs over shrubberies of wet sclerophyll and

rainforest species where talus slopes naturally maintain fairly open vegetation. Nevertheless, examples of tall, overmature *E. archeri* (20-30 m) protruding above a dense rainforest canopy can be found.

On the Western Tiers, *E. archeri* occurs near Great Lake (Brett 1938; Hall and Brooker 1972; Curtis and Morris 1975), and similar populations have been located as far west as Western Bluff. The populations west of Projection Bluff are isolated from *E. gunnii* on the Central Plateau by extensive sedge- and heath-lands developed on the higher Plateau surface west and north of Lake Augusta. *E. archeri* (i.e. forms with green adult foliage) occupies a distinctive habitat and extends along the Western Tiers on a shelf of exposed carboniferous sediments overlain with dolerite talus, directly beneath steep dolerite escarpments (Figs. 1.4 and 1.8). The habitat occupied by these forms is characterized by high rainfall and the dolerite scarps afford shelter from the westerly storms. The steep escarpments result in the early loss of sun and even in summer the habitat may be shaded by mid-afternoon. Insolation is further reduced by extensive cloud cover which differentially accumulates along the Western Tiers as opposed to southern areas of the Central Plateau. This effectively results in a rainfall gradient across the Central Plateau with precipitation declining rapidly toward the south-east (Fig. 1.9). In this area, *E. archeri* occurs on fairly wet sites and is replaced by the snow gum *E. coccifera* at higher altitudes and on better drained sites. At the northern end of Great Lake on topographically sheltered sites, a variant of the *E. gunnii-archeri* complex extends over the scarp of the Western Tiers with *E. coccifera*. Populations classified as *E. archeri* and *E. gunnii* are more or less continuous in this area, being linked by this variant which is both geographically and morphologically intermediate. Similarly, variants of the *E. gunnii-archeri* complex occur further west in the Upper Mersey Valley-Walls of Jerusalem area which are difficult to assign to either taxa. These populations occur at relatively high altitude (1000-1150 m) with *E. coccifera* and occasionally *E. subcrenulata*, but again only on topographically sheltered and poorly drained sites. Populations were located at the immediate outflows of glacial lakes such as Lake Ball (LB), Lake Charles (LC), and Lake Myrtle (LM). A population with close affinities to *E. archeri* was also located near the summit of Mt. Roland (MR), north of the Western Tiers, growing with a variant of the *E. nitida-coccifera* complex. No population belonging to the *E. gunnii-archeri* complex has as yet been found on another isolated peak, Quamby Bluff, immediately north of Projection Bluff.

Populations classified as *E. archeri* are found on the NE mountain block and are isolated from the Central Plateau populations by the graben of the Central Midlands. Populations have been recorded from Mt. Barrow (MB, Brett 1938) and Ben Lomond (BL, Curtis and Morris 1975) and specimens in the Tasmanian Herbarium have been collected by Prof. W.D. Jackson from Mt. Maurice (MM) and Ben Nevis (BN). In the course of this study populations belonging to this complex have also been located on the nearby Mt. Saddleback (SD) and Mt. Victoria (MV), although no population was found on Mt. Arthur. These north-eastern populations occur as series of small populations isolated on mountains rising above an extensive sub-alpine plateau (e.g. Diddieum - Mathinna Plains plateau - approximately 800 m).

On these mountains, particularly Mt. Barrow, Ben Lomond (Fig. 1.10) and Ben Nevis, the habitat occupied by *E. archeri* is very similar to that described for populations on the Western Tiers, growing on talus slopes at the tree-line with, or just above a sub-alpine *E. delegatensis* forest. However, *E. archeri* is the tree-line species on these mountains as *E. coccifera*, the tree-line species on the other dolerite capped mountains in the rest of the island, is absent. The closest occurrence of *E. coccifera* is on Snow Hill in the Eastern Tiers, where it occurs with a variant of *E. gunnii*. However, the Eastern Tiers are isolated from the NE mountains by the large valley formed by the South Esk and St. Pauls Rivers. On several mountains such as Mt. Barrow, Ben Nevis and Mt. Saddleback, populations may extend onto the better drained talus slopes which would normally be occupied by *E. coccifera*. The Mt. Victoria population, the most easterly site, is an anomaly in several respects. Firstly, while the adult foliage of trees from the other NE populations is typically green or at most subglaucous (e.g. Ben Nevis), the Mt. Victoria population contained trees which were quite glaucous, a characteristic of *E. gunnii*. Secondly, it occurs on a button grass plain, on the Ulna Plain (800 m), at the base of Mt. Victoria and is separated from the tree-line by a dense rainforest. The peaty podzolic soils and topography of this site are similar to that frequently occupied by low altitude forms classified as *E. gunnii* in the south-east of the island.

1.4 Methods

Sampling Sites

The sampling strategy adopted for this study represented a compromise between four major objectives. These were:-

- (i) to examine the nature of the variation between contiguous populations classified as *E. archeri* and *E. gunnii* on the Central Plateau;
- (ii) to examine the variation within a more or less continuous population of *E. gunnii* over an altitudinal gradient on the southern end of the Central Plateau;
- (iii) to obtain a broad perspective of the variation pattern within the *E. gunnii-archeri* complex as a whole; and
- (iv) to determine the affinities of several outlying anomalous populations (e.g. Mt. Victoria, Snow Hill and Mt. Roland).

With these aims an attempt was made to sample populations over the full geographical and ecological range of the complex.

Population locations are indicated in Figs. 1.2 and 1.3 and further site and sample particulars given in Table 1.1. The transition from *E. archeri* to *E. gunnii* north of Great Lake was examined in the same area in which Barber (1955) had previously demonstrated a cline in the glaucousness of adult and juvenile foliage. Eight populations were sampled along a 32 km north-south transect from morphs which would classify as *E. archeri* beneath Projection Bluff to morphs classified as *E. gunnii* around the edge of Great Lake (Pine Lake transect - P₁, P₂, P₃, P₄, P₅, Br, SB and SL; Fig. 1.3). Several other sites from the northern end of Great Lake were sampled including a small plain at the head of the Liffey River (LR) and several sites on the NE side of Great Lake (PN, NE and PH; Fig. 1.3).

The other major transect studied in detail extended in an east-west direction on the southern end of the Central Plateau and paralleled gradients in exposure and rainfall (Southern Plateau transect - LH, SL, Pf and A₁; Figs. 1.2 and 1.3). This transect encompasses the altitudinal extremes of *E. gunnii* on the Central Plateau including the high altitude mallee variant occupying the extremely exposed lip of the higher Plateau surface above

Liawenee (LH), forms representative of the extensive woodland population developed at a lower level around Great Lake (e.g. SL) and variants found on low altitude forest sites (e.g. Pf, A₁). For the main geographical survey, all known populations on the north-eastern mountains were sampled as well as a wide range of populations in the south and west. The choice of sampling sites was defined by both the scattered disjunct distribution pattern as well as accessibility. Morphological data were available for 37 populations, with a complete data set collected for 551 individuals. Most ecological and geographical extremes in the complex are represented. Samples of *E. subcrenulata* and *E. urnigera* were also collected for comparison with these populations. The *E. subcrenulata* sample comprised a total of 20 trees, one half of which were collected from Lake Charles (parapatric with population LC) and the other from Cradle Mountain. Two samples of *E. urnigera* were included, one from the northernmost population of this species on Alma Tier (parapatric with population AH) and the other was a pooled sample from previous collections on the southern mountains (Potts 1978). The latter sample included 5 trees from each of 4 sites (Mt. Wellington - 640 and 1000 m, Mt. Field near Lake Fenton - 1020 m and Mt. Dromedary - 750 m) and encompassed a large portion of the phenotypic diversity in southern populations of this species.

Sampling of Trees

For each population, trees were sampled from a representative area, where possible following a transect line and avoiding adjacent individuals. The length of the transect varied depending on tree density and population size. The number of individuals sampled per population ranged from a minimum of 6 to a maximum of 26 (Table 1.1). An attempt was made to sample 20 individuals per population and this is achieved for the Southern Plateau and Pine Lake transects and most of the NE mountains (17 out of 37 populations). However, it was not possible to maintain a consistent sample size as many inaccessible populations were collected on walking trips with limitations on time and space.

A problem encountered in the sampling was in delimiting the *E. gunnii*-*archeri* complex where obvious hybridization with parapatric *Symphyomyrtus* species (*E. dalrympleana*, *E. subcrenulata*, *E. rodwayi* and *E. brookerana*) occurred. The criteria adopted basically followed that used by Kirkpatrick (1973) and Smouse and Saylor (1973a) which was to exclude obvious F₁ types or those more similar to the other species. Trees exhibiting slight deviation toward another species were retained in the sample. As seed was required sampling was biased toward trees with readily accessible capsules.

Sun leaves and capsules were collected from several areas of the crown. Where necessary trees were climbed or pruners used, and in several extreme cases trees were felled. At the time of collection, the glaucousness grade of each mother was assessed using the criteria in Table 1.2. Glaucousness is most pronounced on actively expanding foliage and fades on older foliage (Barber 1955). It was therefore necessary to carefully inspect samples collected out of the growing season and assign scores on the basis of the maximum glaucousness observed. Trees from the Pine Lake and Southern Plateau transects were sampled in autumn when growth had ceased, but most were labelled and scored for glaucousness during spring while monitoring their flowering behaviour.

Significant variation in leaf shape and size occurs within the crown of eucalypts associated with shading (e.g. Ladiges and Ashton 1974), seasonal (e.g. Pryor 1957a) and ontogenetic effects which makes random sampling of leaves impractical. In alpine species such as *E. gunnii-archeri* where growth usually ceases during winter, seasonal variation is particularly marked. Leaves increase in size and become more lanceolate toward the peak of the growing season. In *E. gunnii-archeri*, leaves expanded at the beginning or end of the growing season are smaller with a change in shape corresponding, to varying degrees, to a cyclic reversion to the leaf shape exhibited by an earlier ontogenetic phase (Potts 1978). In addition, similar differences are found between exposed and lee sides of the tree at high altitudes. Accordingly, sampling was stratified by collecting foliage from the northern side of the tree, with sun leaves near branch ends being subjectively chosen for measurement from an area of maximal summer growth. This generally corresponded to the region where internode and intranode expansion was greatest. The relative difference observed between trees at this point is usually retained throughout the seasonal cycle (Potts 1978). Developmental (e.g. Green 1969b) and some seasonal (e.g. Ladiges and Ashton 1974) variation also occurs in reproductive characters. However, as noted by Kirkpatrick (1975a) these generally exhibit less phenotypic plasticity than vegetative characters. Where possible large numbers of capsules were collected to ensure adequate seed samples. Three mature umbels were subjectively chosen for measurement from the centre of the range from each tree and a single central capsule from each inflorescence was measured. The morphometric character set from each tree comprised the average of measurements from usually 5 leaves and 3 inflorescences.

Characters Scored

The morphometric characters scored from each tree are indicated in Fig. 1.11 and Table 1.3 and comprise 6 leaf and 9 inflorescence measurements. This suite of measurements, along with glaucousness, includes the majority of characters emphasized in the taxonomic literature as well as those considered important in an initial survey of the *Gunnii* group (Potts 1978). Leaf dimensions were recorded either by hand or using a HP91111A graphics tablet interfaced with an HP9825A micro-computer. The majority of leaves were measured by digitizing which involved using photocopies of leaves made on a Konshiroku U-Bix U3 photocopier. Tests on this photocopier indicated no image distortion. Extensive comparisons were made between samples measured manually and by digitizing. There was no significant (or consistent) difference between either method in univariate (ANOVA) or multivariate (MANOVA) tests. In addition, the deviation between methods was demonstrated to be of a similar magnitude as that between two different workers measuring the same data manually or by digitizing, or a single worker replicating the same set of measurements. The measurement error in all of these cases was trivial when compared to the difference between populations. Digitized results are thus directly comparable with manual measurements. In view of both the rapidity with which data can be accumulated and the reduced opportunity for experimental error arising from data transfer, this technique offers considerable benefit for morphometric studies.

The dimensions scored from each inflorescence were measured to the nearest 0.1 mm using vernier callipers. Valve position (VPOS) and size (VSIZ) indices were derived by assigning each capsule measured a score from 1 to 4 and averaging scores. Valve position relative to the capsule rim was scored as insert (1), level (2), slightly exsert (3) and markedly exsert (4). Similarly, valve size classes correspond to membranous (1), intermediate (2), woody (3) and large thick woody (4) valves. In both indices the highest category was rarely used, but was included so as to differentiate samples from *E. subcrenulata* and *E. dalrympleana* if necessary; both of which usually have large exsert woody valves (4,4). The disk level (DISK) was measured from the capsule rim using the slide end of the vernier callipers. The capsule dimensions - rim width (RIM W), maximum width (MAX W), distance to the widest point (PT.MAX W) and capsule length (CAP.L), were considered the minimum combination of dimensions necessary to differentiate the wide array of capsule shapes observed in this complex (e.g. campanulate, ovoid-truncate, cylindrical, urceolate, barrel shape). The urceolate capsule shape which mainly occurs in *E. urnigera* is occasionally encountered in populations of

the *E. gunnii-archeri* complex and appears to be a result of the disk being excessively sunken and thus these forms can be differentiated on this character. Where sides of the capsule were initially parallel, the distance to the widest point was scored from the rim to the point of deflection. This differentiated conic and cylindrical shapes, both of which would result in the rim width and the maximum capsule width being equivalent.

Statistical Analysis

The description of the complex pattern of morphological variation and environmental response in the *E. gunnii-archeri* complex necessitated the measurement of a wide range of characters. While variation in specific characters or dimensions may be of particular interest, it is clearly the pattern of gross phenotypic variation which is important. Assessment of the variation pattern is thus dominated by the use of multivariate techniques. Multivariate techniques have been widely utilized in the study of geographical variation or hybridization in forest tree genera (e.g. Namkoong 1966; Smouse and Saylor 1973a, b; Gordon 1976 and many others), including *Eucalyptus* (e.g. Clifford and Binet 1954; Kirkpatrick *et al.* 1973; Kirkpatrick 1975a, 1976, 1977a; Gillison 1976; Phillips and Reid 1980; Ladiges *et al.* 1981).

The multivariate approach adopted in this study mainly utilizes principal component analysis (PCA, e.g. Seal 1966), canonical correlations analysis (CANCORR, e.g. Cooley and Lohnes 1971; Phillips *et al.* 1973), canonical variates analysis (CVA, e.g. Rao 1952; Seal 1966), multivariate analysis of variance (MANOVA, e.g. Bartlett 1947; Rao 1952) and Mahalanobis' distance ($\sqrt{D^2}$; e.g. Rao 1952; Seal 1966; Goodman 1972; Orloci 1978). Tests for both the homogeneity of the covariance matrices and the significance of eigen values obtained from CVA follow Seal (1966). The 95% confidence limits set on group centroids in the CVA ordinations represent $\bar{x} \pm 1.96/\sqrt{n}$ (Phillips *et al.* 1973). As suggested by Phillips *et al.* (1973), coefficients of the canonical variates have been weighted by the corresponding within groups standard deviation of each variable in order to detect those variables having the greatest influence on the canonical variate. Where the objective is population discrimination or relationship CVA and $\sqrt{D^2}$ have been employed. CVA effectively transforms population centroids to a space in which the pooled within groups dispersion is a hypersphere and then independent canonical axes are sequentially aligned in the direction of maximum group

dispersion (Rempe and Weber 1972). The variation between centroids is thus considered in relation to the magnitude and direction of variation within groups and the distance between centroids is measured in terms of generalized as opposed to Euclidean distances (Phillips *et al.* 1973). Canonical axes are calculated such that the first vector accounts for the maximum variation between the transformed group centroids. The second vector is independent of the first, and accounts for the maximum possible proportion of the residual variation and so on. PCA is used when examining variation - (1) between individuals independent of *a priori* groupings, (2) between group centroids independent of the within groups variability, or (3) the within groups variability. All PCA's have been performed using the correlation matrix. As an adjunct to the ordinations presented, classification of group centroids using Mahalanabis' distance as a dissimilarity measure was performed. The clustering methods (CLUSTAN) used were single linkage (Sokal and Sneath 1963), average linkage (Sokal and Michener 1967) and Ward's method (Ward 1963). Detailed discussions of the multivariate techniques and terminology used herein are to be found in Rao (1952), Seal (1966), Blackith and Reyment (1971), Rempe and Weber (1972), Phillips *et al.* (1973) and Orloci (1978). Variation along the main canonical variates was related to facets of environmental variation by univariate and multiple regression against altitude, rainfall, latitude and longitude. The significance of regressions was tested by analysis of variance (ANOVA) and for multiple regressions, the significance of the partial regression coefficient for each independent variate was tested using the t-test and redundant variates were sequentially eliminated in a stepdown manner. The geographical coordinates and altitude of each site was determined from the 1:100000 TAS MAP (Lands Dept., Hobart) series and the mean annual rainfall values were interpolated from a contoured meteorological map (Met. Bureau 1980). Geographical coordinates correspond directly to universal grid references taken from the TAS MAP series.

Flowering Phenology

A study of variation in flowering time between populations along the Pine Lake and Southern Plateau transects (Fig. 1.3) was undertaken over two seasons from 1979 to 1981. A subset of the populations (Pf,SL,LH,SB,Br,P₃,P₂, and P₁) were surveyed in the first season by recording the proportion of trees flowering in a random sample of between 20 and 50 trees per population. Permanent transects of 20 trees were established in the second season (usually those sampled from the morphometric survey) at all the previous sites as well as P₄ and P₅. Microhabitat variation was examined at the exposed site above Liawenee (LH) in a small scale survey involving 6 trees from 7 sites. Sites were located over a steep topographic transition from the lower plateau to the higher plateau surface (see Fig. 1.12) and basically represented 5 exposed and 2 sheltered locations. Sites were scored at monthly intervals over the flowering period (i.e. Nov 1979-May 1980; Oct. 1980-May 1981). Observations indicated that out-of-season flowering was insignificant. During the second season, a crude estimate of the intensity of flowering for each tree was obtained from subjective scores of the percentage of flowers on the tree relative to the abundance of potential flowers (i.e. buds, flowers and young fruit). This allowed the peak and mean flowering time of each tree to be estimated.

1.5 Results

Analysis of Herbarium Material

Variation in specimens classified as *E. archeri* (n=36), *E. gunnii* (n=47) and *E. urnigera* (n=17) in the Tasmanian Herbarium were initially examined to assess the morphological continuity between these closely related taxa. Due to the difficulty in handling specimens only a subset of the characters used in the main morphometric survey were measured. These included LL, LW, LWP, PET, PEDU, CAP.W and the distance from the base of the pedicel to the capsule rim (CAP.L + PEDI) (see Fig. 1.11).

MANOVA indicated a highly significant difference in morphology between taxa ($P \leq 0.001$) with *E. urnigera* specimens distinct from both *E. gunnii* and *E. archeri* (Tables 1.4 and 1.5). *E. gunnii* and *E. archeri* specimens were more similar, yet their centroids are significantly different (MANOVA; $P < 0.001$), differing mainly in capsule width (Table 1.4). The relationship between taxa was summarized using canonical variates analysis (CVA) based on 7 morphometric characters. The transformed taxa means resulting from CVA

are plotted in Fig. 1.12. The first canonical axis separates *E.urnigera* from *E. gunnii* and *E. archeri* and is mainly weighted by capsule, peduncle and lamina length (Table 1.6). *E. archeri* and *E. gunnii* specimens are separated on the second canonical axis which is dominated by capsule width (MAX.W) (Table 1.6). Differences in capsule morphology between the two taxa have been consistently emphasized in the literature (e.g. Blakely 1934) and the difference in herbarium specimens corresponds with variation from the sessile squat (e.g. campanulate shape) capsules of *E. archeri* to the pedicelate, more elongate types (e.g. cylindrical to ovoid-truncate shape) types of *E. gunnii*. Nevertheless, in the space defined by the CVA ordination (Fig. 1.12), in which taxa discrimination is maximized, there is considerable overlap between *E. gunnii* and *E. archeri*, with no apparent morphological discontinuity between specimens.

Field

Phenetic Variation Between Populations

Significant differences ($P < 0.001$) between populations were obtained for all morphometric characters (Table 1.3) and populations exhibit greatest differentiation for LAMTH, PEDI, LWP, LL, PET.L and CAP.L. Bivariate plots of population means (Appendix 1) show the complex nature of the variation pattern, with characters exhibiting continuous and often correlated variation. Populations recorded as *E. archeri* (e.g. P₁, P₂, BL, MB) and *E. gunnii* (e.g. SL, Br, SB, MS, Al and AH) in the literature are differentiated along several univariates (e.g. PEDI, LAMTH) as well as on a range of bi-variate comparisons (e.g. RIM.W/CAP.L, PEDI/RIM W, RIM W/MAX.W; Appendix 1). Many of these characters are recorded as diagnostic of the two species. However when the full range of variation in the complex is considered, continuity is apparent in all cases.

Variation in Glaucousness

Northern populations, including those recorded as *E. archeri* in the literature, are usually dominated by trees with green adult foliage (GLAUC=0), although occasional subglaucous (GLAUC=1) trees may be encountered (e.g. BN) (Fig. 1.13; Table 1.1). The maximum development of glaucousness occurs in open woodland populations skirting frost hollows on the lower Plateau surface, particularly on the southern end of the Central Plateau (e.g. Shannon Lagoon; Fig. 1.13). The foliage of trees in these populations is covered with a thick layer of non-structural cuticular wax (particularly in spring) which extends onto young stems, buds and fruits. This gives an intense glaucous appearance to the foliage which contrasts markedly with that of the northern green variants. The intensity of glaucousness in

populations declines radially at varying rates from this area (Fig. 1.13). Contiguous populations at higher and lower altitudes (e.g. PF and LH) are less glaucous and peripheral southern, eastern and western populations comprise individuals of intermediate glaucousness. Occasionally sub-glaucous individuals are encountered in these populations, but only rarely do green and glaucous individuals co-occur (e.g. SH, MV, P₃, P₄, P₅). Nevertheless populations exhibiting extreme levels of glaucousness are more or less continuous on the Central Plateau and are clinally linked through a series of geographically intermediate populations (i.e. Pine Lake Transect; Table 1.1; Fig. 1.13; Barber 1955). These intermediate populations (P₃, P₄, P₅) contain both green or sub-glaucous individuals as well as those scored as glaucous (Table 1.1), although the latter trees are usually less glaucous than those in the more southern populations (e.g. SL, SB).

Variation in Reproductive Characters

Virtually all individuals sampled possessed three-flowered inflorescences, with higher numbers (up to 7) only rarely encountered and then usually associated with hybridization with species from the series *Ovatae* (e.g. *E. rodwayi*). Despite conservatism in inflorescence structure, populations exhibited marked differentiation involving both size and shape of components of the inflorescence. Individual peduncle lengths varied from 1 to 16 mm and pedicels ranged from completely absent to a maximum of 5.7 mm, with population means ranging from 4.0 to 8.6 mm for peduncle length and 0.1 to 2.3 mm for pedicel length. A geographical cline was evident in both characters, with pedicel and peduncle length increasing toward the south-east (Appendix 1). This is partly correlated with variation in altitude and the major variation in both characters occurs along the southern Plateau transect (Appendix 1). The inflorescence becomes more compressed and is held closer to the stem with increasing altitude (Fig. 1.14). However, geographical variation in pedicel length in particular, also corresponds to an inherent difference between populations classified as *E. archeri* and *E. gunnii*. Capsules of *E. archeri* populations tend to be sessile while those of *E. gunnii* are usually pedicellate, a distinction emphasized in the original description by Blakely (1934). Over all populations, the variation is continuous, although along the Pine Lake transect there is a stepped decrease in pedicel length corresponding to the rapid altitudinal transition from populations around Great Lake (e.g. Br) to higher altitude sites near Pine Lake (P₃, P₄ and P₅). Capsule size as measured by the maximum capsule diameter (MAX.W) clinally increases along a geographical gradient from west to east ($P < 0.001$; Fig. 1.15) with the largest capsules occurring in populations on the NE mountains (e.g. MB

and BN) and Eastern Tiers (SH). This geographical cline is modified by altitude, with increasing exposure decreasing capsule size (e.g. SV vs. PP and MS; SB and SL vs. LH; A1 vs. AH; P₁ vs. P₂). Populations differed significantly in capsule shape as measured by the ratios RIM W/MAX.W, - RIM W/CAP.L and PT.MAX.W/CAP.L (Appendix. 1), with continuous variation from campanulate or conic types through ovoid-truncate or cylindrical types to elongate barrel shapes. A geographically diverse set of populations (MV, MM, BN, RR, BD and SV) and *E. gunnii* populations on the southern end of the Central Plateau (e.g. SB and SL) represent respective end points of this continuum. This continuum in capsule shape is associated (possibly causally) with a trend toward deeply sunken disks (e.g. Appendix 1) and membraneous valves.

Population variation in reproductive characters was summarized using CVA which yielded 7 significant eigen values of which the first three accounted for 73% of the total variation between centroids. The corresponding eigen vectors are shown in Table 1.7 and population means are plotted in Fig. 1.16. Regression analyses indicate that these three independent directions of variation are, over all sites, uniquely associated with variation in latitude (CV₁), longitude (CV₂) and altitude (CV₃) (Table 1.8). CV₁ is dominated by capsule (CAP.L) and pedicel (PEDI) length contrasted against valve size (VSIZ) and differentiates populations with pedicellate capsules and small valves from those with shorter, sessile capsules and more woody valves. It describes a major latitudinal cline within the complex, differentiating southern and northern populations. However, at a local level, it also differentiates populations along the southern Plateau transect describing a morphological series involving a general reduction in umbel and capsule size associated with the altitudinal transition from the tall sub-alpine forest forms (e.g. Pf, A1) to the stunted high altitude form (LH) (Fig. 1.14). Populations classified as *E. archeri* are differentiated from this high altitude form along the second axis. The second axis (CV₂) is dominated by both measures of capsule width (RIM W and MAX.W) and separates populations with broad and narrow capsules of similar length, representing a difference in capsule size and shape. The longitudinal cline described by CV₂ mainly reflects the increase in capsule size toward the east (e.g. Fig. 1.15). The third axis (CV₃) describes residual variation associated with a more complex capsule shape change, and separates populations exhibiting barrel and conic shaped capsules of similar length and width. Variation along this axis is highly correlated with altitude, representing a shift from ovoid-truncate or conic capsules with level disks at low altitudes to sunken disks and barrel shaped capsules at higher

altitudes. In particular, the southern and north-western *E. gunnii* populations (e.g. RR,SV,MS,BD, PF and A1) are differentiated from the higher altitude central populations (e.g. SB and SL) in this respect.

Populations classified as *E. archeri* are clearly differentiated from the central *E. gunnii* populations on reproductive characters. However, when the complete geographical range of the complex is examined, populations form a continuous morphological series involving the interaction of at least three independent clines.

Variation in Vegetative Characters

In contrast to the reproductive characters, the main variation in all vegetative characters except curvature was associated ($P < 0.001$) with variation in altitude. Leaf dimensions decrease with increasing altitude while leaf thickness increases. CVA of the 6 leaf characters resulted in all eigen values being significant although the two largest accounted for 75% of the variation between centroids. Standardized eigen vectors corresponding to the two largest eigen values are given in Table 1.9 and population means are plotted in Fig. 1.17. High values of CV_1 result from a decrease in leaf dimensions and an increase in lamina thickness (LAMTH) whereas high values along the CV_2 result from a relative increase in LWP, LAMTH and CURV. The regressions of CV_1 on both altitude and latitude were significant ($P < 0.001$ and $P < 0.05$ respectively). However multiple regression analysis indicated that the correlation with latitude was mainly a result of co-variation with altitude ($P < 0.001$) arising from a general shift in the complex toward the tree-line habitat in the north and north-east. CV_1 describes clinal variation in leaf morphology associated with increasing exposure to the alpine environment and altitude alone accounts for 41% of the variation. Populations along the Southern Plateau transect are clearly differentiated on this vector which varies clinally between altitudinal extremes (LH and A₁). CV_2 describes residual variation which is independent of altitude and over all sites is unrelated to geographical position or rainfall. However, for sites on the Central Plateau, it defines a clear geographical cline in leaf morphology linking populations classified as *E. archeri* on the northern scarp of the Western Tiers to the southern populations classified as *E. gunnii*.

More intensive sampling was undertaken along a local exposure gradient (2 km) from the open woodland and frost hollow sites around the edge of Liawenee Moor to the high altitude exposed sites on the upper Plateau surface (Fig. 1.14). This sampling indicated local steepening of the cline

in leaf morphology along the southern Plateau transect was directly associated with a rapid topographical transition between erosion surfaces. The stepped nature of the landscape results in geographically extensive stands being stabilized at a similar adaptive level. The most extreme high altitude variants occur as stunted trees or mallees, scattered in the alpine shrubbery near or on the margin of the high altitude populations. These forms are characterized by reduced internode and intranode expansion and small ovate-elliptical leaves resembling the leaf shape normally expressed in the ontogenetically 'intermediate' phase. Occasionally individuals are encountered which are reproductively mature, yet only bear the 'juvenile' leaf type. The retention of the 'juvenile' or 'intermediate' type of foliage to the reproductive phase in these marginal sites is not a consequence of recent regeneration and some of the larger stems have been aged at 50 to 150 years. High altitude variants on the Western Tiers (e.g. P₃, P₄, P₅, NE) and on mountains such as Mt. Saddleback (SD) and Mt. Roland (MR) differ from high altitude southern forms (LH) in that the adult leaf shape is usually fully expressed. The latter population appears to be on the most exposed site.

Total Morphometric Analysis

Population Ordination

CVA of the full set of 15 morphological characters resulted in 11 significant eigen values and major trends could be recognized along the first three. These together accounted for 68% of the variation between centroids and the corresponding vectors are given in Table 1.10 and population means plotted in Fig. 1.18.

The major direction of morphological differentiation in the complex (CV₁; 40%) is associated with variation in altitude ($P < 0.001$; Table 1.8) and is typified by the clinal series of populations along the southern Plateau transect. CV₁ is dominated by pedicel (PEDI) and petiole (PET.L) length, lamina thickness (LAMTH) and valve size (VSIZ) (Table 1.10). A significant portion of the morphological difference between populations classified as *E. archeri* and *E. gunnii* is no doubt related to *E. archeri* generally occupying higher altitude sites than the vast majority of *E. gunnii* populations. Variation along CV₁ and a shift toward the *E. archeri* phenotype occurs with increasing exposure to the alpine environment, with a decrease in pedicel and capsule length and an increase in lamina thickness. However the difference between populations classified as *E. archeri* and *E. gunnii* is not simply an extension of variation trends associated with altitude as inferred

by Jackson (1960a).

The second canonical variate (CV_2 ; Figs. 1.18 and 1.19) describes a unique direction of morphological variation which, over all sites, appears to be independent of altitude, rainfall and geographic position (Table 1.8). However it clearly differentiates populations on the basis of glaucousness (Fig. 1.20) and on a local scale is associated with the transition from the open woodland habitat on the edge of 'frost hollows' around Great Lake to the alpine shrubbery and mixed forest habitat on the northern scarp of the Western Tiers. Populations from these habitats (e.g. SL,SB and MC,P₁,P₂ respectively) are the extremes of a phenetic continuum which is typified by the clinal series of populations along the Pine Lake transect (Fig. 1.19). The main differentiation with respect to CV_2 and glaucousness appears confined to the higher altitude populations. This could arise for instance with a pertinent habitat gradient being only defined for this complex, or its effects only manifest, in the high altitude region of the exposure gradient.

CV_2 is mainly weighted by LWP, LAMTH, RIM.W contrasted against CAP.L and PEDI which corresponds to the character combination given most weight in the literature (Appendix 1) and the herbarium analysis (Table 1.6) in discriminating *E. gunnii* and *E. archeri* morphs. However Figs. 1.18, 1.19 and 1.20 clearly indicate that populations classified as *E. archeri* and *E. gunnii* represent extremes of a phenetic cline involving parallel variation in morphology and glaucousness. The continuity between these taxa is further demonstrated in Fig. 1.21 by the continuous distribution of individuals along the morphological cline differentiating populations along the Pine Lake transect. Geographically intermediate populations are dominated by intermediate phenotypes and do not comprise varying mixtures of distinct morphs (i.e. *E. archeri* + *E. gunnii*). This cline is partly repeated on the western end of the Central Plateau from the Walls of Jerusalem (i.e. TH,LB) southward to Lake Myrtle (i.e. LM,LC) (Fig. 1.18). However, the latter populations are differentiated from intermediates north of Great Lake along CV_3 (Fig. 1.18). CV_3 separates the north-western populations from those in the centre and east of the island and defines an independent morphological cline from the St. Valentines Peak population, through the Cradle Mountain and upper Mersey Valley samples to populations on the Central Plateau. This vector is mainly weighted by LAMTH, PEDU, MAX.W and DISK contrasted against LW.

Virtually an identical assessment of the variation pattern was obtained by PCA of the group centroids (Fig. 1.22). This differs from the previous

analysis in that distances between populations are measured in terms of standardized Euclidean as opposed to generalized distances. The vectors defining the major directions of variation are more easily interpreted than in CVA and in Fig. 1.22 the characters used in the analysis have been simultaneously ordinated in the space defined by the objects, allowing a concise summarization of the variation pattern. Scores for each character represent the correlation coefficient between the character and the principal component (see Orloci 1978). Ordination in this manner clearly indicates the characters most closely associated with the major axes of variation and the proximity of objects to characters is indicative of the positive effect of characters in placing the object. It can be readily seen for example that variation along PC_1 associated with a decrease in altitude results from high values of PEDI, PEDU, CAP.L, PET.L and LL and low values of LAMTH. Similarly, variation along PC_2 in the direction of the *E. archeri* populations involves high values for VSIZ, VPOS, MAX.W, RIM W, LL, PET.L and LWP, but low values of DISK and PT.MAX.W. The morphological cline differentiating the north-western populations (PC_3) involves a decrease in MAX.W, RIM W, DISK and LAMTH and a relative increase in LW and LWP.

The inclusion of the glaucousness score along with the morphometric characters in a CVA resulted in the major axis of variation accounting for 57% of the variation between populations and being completely dominated by glaucousness (Fig. 1.23). Nevertheless, the three major directions of clinal variation previously described were recovered with similar population rankings and vector interpretations. The only difference was that the greatest phenetic differentiation occurs along the Pine Lake transect, with altitudinal differentiation (CV_2 , 17%) becoming of secondary significance. Populations with green adult foliage which would classify as *E. archeri* form a distinct cluster in this ordination as do the populations of intermediate glaucousness north of Great Lake (Fig. 1.23). These latter populations are differentiated from other populations of intermediate glaucousness and appear as a fairly coherent group.

Population Classification

The ordination studies strongly suggest that populations comprising the *E. gunnii*-*archeri* complex are highly differentiated yet comprise a morphological continuum. This was confirmed by two additional lines of evidence. Firstly, plexus diagrams (based on the 15 variable CVA shown in Fig. 1.18) in which all populations between which the Mahalanobis' distance did not exceed the $P < 0.01$ level of significance were linked, resulted in a

complete fusion of the main core of the complex. However several populations, peripheral to the main morphological continuum such as MC, LH, SV and SP remained unlinked. Secondly, single linkage clustering did not find distinct morphological groups. Populations north of Great Lake (P_1 to Br) as well as on Mt. Roland (MR), Mt. Saddleback (SD) and Ben Lomond (BL) appear as a fairly similar assemblage, but the dendrogram is characterized by chaining. While recognizing the continuous and clinal nature of phenetic variation within the complex, it was nevertheless desirable, for the pragmatic purpose of summarization, to partition the complex into equatable phenetic units. To this end, the classification from Wards' minimum variance clustering was used to identify clusters which can be conceived as broad reference points in a multidimensional morphological continuum.

The dendrogram from the classification based on the 15 morphometric characters and the glaucousness score is shown in Fig. 1.24 and this classification was stable when subject to iterative relocation. The geographical distribution of populations at the 5 cluster level is indicated in Fig. 1.25 and there is clearly reasonable congruence between geographic location and phenotype. This is indicative of a significant correlation ($P < 0.001$) between geographic and phenetic distance ($\sqrt{D^2}$) throughout the complex which, at least partly, reflects a similarity of habitat with geographic proximity. The main phenetic clusters represent northern ('*E. archeri*', 1; 'Pine Lake intermediates', 2), central ('*E. divaricata*', 3), north-western ('NW *E. gunnii*', 5) and southern ('southern *E. gunnii*', 4) morphs. Similarly there is close correspondence between clusters and the perception of taxa in the literature. One of the northern clusters (1) corresponds to *E. archeri*, the central cluster (3) to *E. divaricata*, and the southern (4) and north-western (5) clusters, together appear to encompass Brett's (1938) *E. gunnii*.

A similar classification was obtained using only morphological characters (Figs. 1.26 and 1.27). With the exception of the 'Pine Lake intermediates' (cluster 2; Fig. 1.24) the clusters recognized in the previous classification (Fig. 1.24) are reasonably well defined on morphological criteria alone. The nearest neighbourhood relationships and the morphological classification (Fig. 1.26) indicate that the 'Pine Lake intermediate' populations (Fig. 1.24) are morphologically more similar to the local *E. archeri* populations (P_1 and P_2) than populations from any other cluster. As such, the 'Pine Lake intermediate' cluster (Fig. 1.24) is perhaps best considered as glaucous forms of *E. archeri*. The populations in the '*E. archeri*' cluster (Fig. 1.24) are mainly grouped on the basis of green adult

foliage, yet it is clear from the morphological classification (Fig. 1.26) and Figs. 1.17, 1.20 and 1.23 that the Mt. Maurice (MM) and Mt. Barrow (MB) populations are morphological outliers. In the morphological classification, (Fig. 1.26) these two populations are grouped in a minor fifth cluster (cluster 5 ; Fig. 1.26) along with several others (LB,OP and MV). An examination of the minimum spanning tree based on Fig. 1.18 and the nearest neighbourhood relationships indicates that morphologically, these populations lie intermediate between populations in the '*E. archeri*' and 'NW *E. gunnii*' clusters. The geographical distribution of populations in this cluster to some extent parallels the distribution of the '*E. archeri*' cluster (Fig. 1.27) and using average linkage clustering, these NE populations link much earlier to the '*E. archeri*' populations. While the Mt. Victoria population is a geographical anomaly (Fig. 1.25) due to its glaucousness, in terms of morphology its closest affinities are with neighbouring populations on Ben Nevis and Mt. Maurice.

Character Correlations

A degree of concordance in the pattern of variation of reproductive and vegetative characters is evident from Figs. 1.16 and 1.17. The major axes of variation in both sets differentiate populations along the southern Plateau transect and both second axes describe clinal variation along the Pine Lake transect. Concordance in the variation pattern was examined by canonical correlations analysis, a technique which simultaneously transforms two sets of variates so as to maximize the correlation between specific linear combinations of each set. Subsequent pairs of vectors are derived using the same criteria, but are chosen to be orthogonal and uncorrelated with previously derived vectors. The correlation between pairs of transformed vectors is thus maximized while correlations among pairs are eliminated.

Canonical correlations and coefficients for the first two pairs of canonical variates are given in Table 1.11 and population values for each pair are plotted in Fig. 1.28. The correlation between the first pair of canonical variates was highly significant ($P < 0.001$) indicating a strong relationship in the pattern of variation in reproductive and vegetative characters. This pair of variates describes a morphological series associated with a parallel response in both character sets to variation in altitude. This involves a decrease in lamina and petiole length and an increase in lamina thickness with increasing altitude which is paralleled by a decrease in both pedicel and capsule width. The second canonical correlation was not quite statistically significant due to a low number of

degrees of freedom, but this pair of vectors is of interest in describing parallel variation in reproductive and vegetative characters along the Pine Lake transect.

The parallel variation in vegetative and reproductive characters is of particular significance in view of the fact that at the univariate level there is virtually no significant correlations between character sets within populations (Table 1.12a). Correlations between characters in the pooled within groups matrix are maintained in the absence of markedly differing selective forces and most likely indicate developmental or pleiotropic relationships. At this level many characters appear strongly correlated, forming what are considered by Olson and Miller (1958) as functionally related groups. For example, in the vegetative character set, LL, LWP, PET.L and CURVE are highly correlated suggesting developmental interdependence associated with variation in general leaf length. In contrast, lamina width (LW) and thickness (LAMTH) vary independent of the leaf length measures. Variation between populations involves parallel variation in many characters which, within populations, are independent (Table 1.12a). For example, the degree of glaucousness is independent of all morphological characters within populations, yet between groups is significantly correlated ($P < 0.001$) with variation in a number of vegetative (e.g. CURV, LAMTH) and reproductive (e.g. PEDI, RIM.W, VSIZ and VPOS) characters. Such characters are possibly selectively linked or alternatively exhibit a common plastic response to environmental variation.

The pattern of variation within and between populations was compared for vegetative and reproductive character sets by PCA. The first three vectors from each analysis is given in Table 1.13 as well as the angles between vectors derived from comparable within and between populations analyses (see Blackith and Reymont 1971). The principal axes derived from the pooled within population correlation matrices indicate the major directions in which variation is canalized within populations. While there are obvious similarities between vectors derived from the within and between population matrices, a comparison of the angles between these vectors indicates that the major directions of variation do not coincide. Differentiation between populations appears to be more than an extension of the pattern of variation within populations and seems to involve additional components. Concordant character variation between populations may be partly a consequence of developmental or pleiotropic relationships between some characters (e.g. PET.L, LL, LWP, etc.) and thus the result of variation in a single biological trait. Nevertheless, a large component appears to be a result of parallel variation in biologically independent character complexes.

Phenetic convergence in the *E. gunnii*-*archeri* complex

A similarity between *E. archeri* and the Tasmanian yellow gums (*E. vernicosa* cline forms), has been noted (Blakely 1934; Jackson 1960a) and some of the specimens in the Tasmanian Herbarium collected from Mt. Roland and classified as *E. subcrenulata* bear close affinities to the *E. gunnii*-*archeri* complex. In addition, the affinitive relationships given by Brett (1938) for *E. divaricata* suggests that this form lies intermediate between *E. gunnii* and *E. urnigera*. During the course of this study, two populations in particular, Snow Hill (SH) and Scrummies Marsh (A₁), were noted to exhibit morphological affinities to *E. urnigera*. Accordingly, the similarity of populations and the continuity of the *E. gunnii*-*archeri* complex with both *E. subcrenulata* and *E. urnigera* was examined.

Samples of both southern and northern (i.e. Alma Tier) *E. urnigera* as well as *E. subcrenulata* were included with the 37 population samples from the *E. gunnii*-*archeri* complex and the variation between populations was analysed using CVA. Only 13 of the 15 morphometric characters (excluding CURVE and PT.MAX.W) were used in the analysis as the full character set was not available for the sample of southern *E. urnigera*. The first two canonical variates accounted for 67% of the variation between populations and clearly differentiated *E. urnigera* and *E. subcrenulata* samples from populations of the *E. gunnii*-*archeri* complex (Fig. 1.29). *E. urnigera* populations are distinct and separated from the *E. gunnii* complex along CV₁ which is dominated by reproductive characters and represents a significant increase in peduncle and pedicel length, maximum capsule width and disk level (i.e. disk becomes more sunken) in *E. urnigera*. The *E. subcrenulata* sample is also distinct from the *E. gunnii*-*archeri* continuum being mainly differentiated (CV₂) on the basis of a greater lamina thickness and maximum capsule width, and large, woody exsert valves. This is in the same direction in which previous analyses (Tables 1.7, 1.9, 1.10, 1.11 and 1.14) indicated that populations classified as *E. archeri* were differentiated from the *E. gunnii* populations. All populations comprising the *E. gunnii*-*archeri* complex were significantly ($P < 0.001$) different from the *E. urnigera* and *E. subcrenulata* samples (Fig. 1.29). However, the northern populations and in particular those on the Western Tiers (P₁, P₂, MR, LB) tend more toward the *E. subcrenulata* phenotype whereas the 'southern *E. gunnii*' and '*E. divaricata*' populations tend toward the *E. urnigera* phenotype (Figs. 1.29, 1.30).

The ordination of individual trees along CV_1 and CV_2 (Fig. 1.29) shows virtually no overlap between *E. urnigera* and *E. gunnii-archeri* point swarms. Where *E. urnigera* and *E. gunnii* are parapatric on the south-eastern mountains (e.g. BD, SP), they are morphologically and ecologically distinct and intermediate phenotypes are only encountered as rare, sporadic individuals. Nevertheless, on the south-eastern edge of the Central Plateau, on Alma Tier, populations of both species exhibit phenetic convergence. The northern population of *E. urnigera* is distinct from the sample from the southern mountains and clearly tends toward the *E. gunnii* phenotype due mainly to a reduction in capsule, pedicel and peduncle size. The population of *E. gunnii* growing around the same marsh (AH) remains morphologically distinct, yet a nearby population (at the lower altitudinal limit for *E. gunnii* in this area) on Scrummies Marsh (A_1) is dominated by intermediate phenotypes (Fig. 1.29). The Scrummies Marsh population is approximately 1.5 km from the nearest *E. urnigera*, although several abnormal phenotypes which were thought to be possible hybrids were found closer ($\approx .5$ km). In terms of soil drainage, which appears to be the main ecological factor differentiating the habitats occupied by the two species in this area, the poorly drained Scrummies Marsh site was more similar to a *E. gunnii* habitat. Similar, but less marked, convergence was apparent in the Snow Hill (SH) population on the Eastern Tiers, immediately east of Alma Tier but separated by the Midlands graben disjunction. In contrast to the Scrummies Marsh site, this population, in places, extends onto better drained sites which resemble those occupied by *E. urnigera* elsewhere. Morphologically this population is more similar to the southern *E. gunnii* populations than the northern *E. urnigera* and no *E. urnigera* has as yet been located in this area.

The sample of *E. subcrenulata* is significantly different ($P < 0.001$) from the northern *E. gunnii-archeri* populations. However, there is some overlap at the individual level (Fig. 1.30). Some trees, particularly in populations on the Western Tiers and Mt. Roland tend toward the *E. subcrenulata* phenotype and in the space defined by the ordination in Fig. 1.30 overlap the *E. subcrenulata* distribution. Nevertheless, these individuals were distinct from the *E. subcrenulata* phenotype on several diagnostic characteristics not assessed in the analysis. Firstly, *E. subcrenulata* specimens often retain a membranous outer operculum to a late stage in bud development, a characteristic not encountered in *E. gunnii-archeri* samples. Secondly, the buds of *E. subcrenulata* differ from those of the *E. gunnii-archeri* complex in being more rugose, frequently distinctively ridged and with a

wider, flattened peduncle. And finally, the juvenile and adult foliage of the yellow gum complex is glabrous and generally the leaf surface is more shiny than comparable glabrous foliage of *E. archeri*. The few individuals which overlap morphologically with *E. subcrenulata* would not classify with *E. subcrenulata* on these additional criteria, with most possessing either subglaucous adult or juvenile (coppice) foliage. Where members of the yellow gum complex are associated with, or at least in the same geographical area as, populations of the *E. gunnii*-*archeri* complex (e.g. Lake Charles (LC), Cradle Mountain, Mt. Field and Snug Plains (SP)) they are clearly differentiated. *E. subcrenulata* extends onto the western end of the Central Plateau and scattered populations regularly occur south of Mt. Jerusalem. The eastward extension of *E. subcrenulata* onto the Central Plateau as yet remains to be fully ascertained. The only confirmed location of *E. subcrenulata* on the eastern portion of the Central Plateau is a small isolated pocket discovered recently by Mr. A.M. Gray near the southern end of Great Lake (on Miena Hill). However, in view of the fact that a similar isolated occurrence has also recently been located further east on the Eastern Tiers, near Snow Hill (Dr. M. Brown, pers.comm.) more scattered populations may yet be located in this area. While the adult morphology of some individuals in the populations sampled north of Great Lake superficially resembles that of *E. subcrenulata*, typical *E. subcrenulata* does not occur in or has not yet been located within 20 km of these populations.

Flowering Phenology

A cline in flowering time parallels the morphological continuum between *E. archeri* and *E. gunnii* populations on the Central Plateau (Figs. 1.19, 1.32). Populations of *E. gunnii* around Great Lake (i.e. SL, SB and Br) flower up to two months earlier than *E. archeri* populations (e.g. P₁ and P₂) and the periods of peak flowering are clearly separate. The cline in flowering time, as with the cline in reproductive characters (Fig. 1.16), is locally steepened over a 1 km transition from the Breona (Br) to Mickey's Creek (P₅) stands. This step corresponds to a rapid topographical transition from the lower Plateau to the upper Plateau erosion surfaces and would represent a major barrier to pollen flow along the morphological cline. Flowering in intermediate populations (P₃, P₄ and P₅) is coincident with the stands classified as *E. archeri*. Within populations along the Pine Lake transect, the correlation of flowering time with glaucousness or morphology was not significant, indicating that variation in flowering time between individuals from the same site is independent of phenotype.

Variation in flowering time of a similar magnitude also occurs along the southern Plateau transect with the '*E. divaricata*' populations around Great Lake corresponding to the '*E. divaricata*' cluster flowering significantly earlier in the growing season than populations at lower (Pf) and higher altitude (LH). The high altitude mallee forms near Liawenee flower approximately a month later than contiguous populations on the lower Plateau surface. Variation in flowering phenology along a local exposure gradient in this area indicated that flowering is delayed on the more exposed higher altitude sites (Fig. 1.14), which suggests that the stepped cline along the Pine Lake transect is at least partly a response to variation in altitude. Paradoxically, the difference in flowering phenology between the open woodland sites around Great Lake (SL, SB and Br) and the lower altitude tall forest site at Pensford (Pf) involves the reverse trend. The population at Pensford flowers later than the former populations and overlaps with more distant high altitude stands. Concurrent observations on other 'southern *E. gunnii*' populations (SP, BD, A₁) suggest this trend is widespread with the low altitude, southern forms flowering later in the growing season than the central '*E. divaricata*' populations. Populations at Pensford (Pf) and Shannon Lagoon (SL) are separated by approximately 4 km and occur at the base and top of a 200 m rise from St. Patricks Plains to Barren Plains (Fig. 1.14). These sites are linked by a continuous stand of *E. gunnii* and observations on the intervening stand indicated that a sharp boundary, rather than a gradation, occurred between early and late flowering forms 0.7 km over the lip of Barren Plains.

The pattern of variation in flowering time in the complex appears to be partly explained by an underlying cline in the actual rate of bud development, which increases with decreasing altitude. Most buds are initiated in mid-summer and in the Pensford population these flower late the following season whereas at higher altitudes, development is retarded and buds do not flower until the third growing season. In the '*E. divaricata*' populations buds flower early in the third season but an even longer period of development seems to be required at higher altitudes resulting in flowering late the third season. The Pensford population usually only retains the bud crop of a single season whereas higher altitude populations generally accumulate two seasons' buds in the crown. While the underlying rate of bud development may only differ slightly between the Pensford and Shannon Lagoon sites, this may have a marked effect on the flowering time possibly due to the cessation of development during the winter months. However this exposure trend does not account for the late flowering of the low altitude '*E. archeri*' population (P₁).

1.6 Discussion

This study indicates that the taxa described as *E. archeri* and *E. gunnii* represent extremes of a morphological continuum and internally encompass a broad array of morphologically differentiated populations. Phenetic variation within the complex involves a multidimensional clinal pattern arising from the interaction of at least several major multi-character clines which appear to be varying in response to differing facets of the environment. For example, the main variation in reproductive characters involves independent geographic clines, with pedicel and capsule length increasing southward and capsule width increasing toward the east. A degree of parallelism in the geographic pattern of variation in several Tasmanian species is apparent in these respects. Kirkpatrick (1975a) reports a general increase in the incidence of pedicellate individuals of *E. globulus* toward the south of its Tasmanian range and capsule size increases in the south-east in the *E. vernicosa* complex (Jackson 1960a), the Tasmanian snow gum *E. coccifera* (Shaw 1982) and the present study also suggests *E. urnigera*. The climate of Tasmania is dominated by a prevailing westerly airstream which results in a major east-west climatic gradient across the island with more clement conditions in the east. This parallelism may reflect a common response to climatic variation (e.g. Ladiges and Ashton 1974) although it may be significant that Davies (1974) suggests the south-east provided a forest refugia during the Pliestocene glacials. The main differentiation in the complex, however, appears to result from the interaction of two main multi-character clines which seem to parallel independent habitat gradients. These gradients involve variation in a complex set of factors associated with firstly, variation in exposure to the alpine environment and secondly a transition in the sub-alpine region from the open woodland to the mixed eucalypt/rainforest habitat.

Altitudinal gradients are a common cause of phenetic differentiation within *Eucalyptus* (e.g. Pryor 1957a; Barber and Jackson 1957; Jackson 1960a; Kirkpatrick 1975a; Phillips and Reid 1980) and usually involve parallel variation in numerous characters resulting in marked differentiation. A common response in most species is for a reduction in tree height to be coupled with a decrease in leaf size and an increase in lamina thickness. The altitudinal cline on the southern end of the Central Plateau in particular, bears marked similarities to that described by Jackson (1960a) in the *E. vernicosa* complex. For instance, the direction of change in capsule shape in the transition from the *subcrenulata* to the *vernicosa* cline forms involves a similar trend to that observed with altitude in the *E. gunnii*-

archeri complex (Fig. 1.14). In addition, the expression of the 'juvenile' or 'intermediate' foliage type in the high altitude form above Liawenee appears indicative of a general trend and has been observed (at the upper altitudinal limits) in *E. coccifera* (Potts, unpubl.), *E. urnigera* (Thomas and Barber 1974a) and *E. vernicosa* (Jackson 1960a; Barber 1965). These parallelisms provide circumstantial evidence for a common, possibly adaptive, morphological response to altitude. However, there is no doubt that this morphological variation would be paralleled by important anatomical (e.g. Jackson 1960a) and physiological (e.g. Pryor 1957a; Ashton 1958; Slatyer and Ferrar 1977; Slatyer 1977a,b,c, 1978) differences more readily associated with fitness.

Barber (1955) similarly suggests that the cline in glaucousness, between the '*E. archeri*' and '*E. divaricata*' populations around Great Lake is adaptive and cites parallel clines in both *E. coccifera* and *E. delegatensis* as evidence. He notes that glaucousness in a wide range of species increases in environments subject to greater frost activity and that non-glaucous types are usually associated with temperate rainforest species in higher rainfall areas as opposed to open sclerophyll vegetation. In this respect in particular he notes a similarity between the cline in the *E. gunnii-archeri* complex and that in *E. urnigera* (Barber and Jackson 1957). The latter cline involves an increase in glaucousness with a transition from the closed low altitude forest environment (560-670 m) to the open alpine habitat (900-1050 m). Barber and Jackson (1957) demonstrated high selective coefficients associated with this character in *E. urnigera* with a complete clinal transition in the frequency of glaucous individuals occurring over an altitudinal change of about 200 m (approx. 1 km ground distance). Disruptive selection appeared to maintain this cline despite a 5-10% reproductive loss through reciprocal immigration or segregation of lethal genotypes along the cline. Thomas and Barber (1974a and b) suggest this cline is maintained by a balance between opposing selective forces. The high reflectance of glaucous leaves in the photosynthetically active and infra-red wavelengths resulted in a reduced photosynthetic potential under low light intensities in the closed forest environment. However, glaucousness appears advantageous in the highly insolated alpine habitat in reducing transpiration and damage to the photosynthetic system by lowering leaf temperatures. This accords with other observations in *Eucalyptus* (e.g. Cameron 1970) and other forest tree genera (Fung and Wright 1972) for an increase in cuticular wax in areas of high insolation. In the present study, the majority of non-glaucous populations occur in high rainfall areas where insolation may be limiting due to a combination of factors

including increased cloud cover, topography (e.g. Fig. 1.19) and associated vegetation. Thomas and Barber (1974a) further suggest glaucousness is of adaptive significance in reducing low temperature damage to wet leaves by allowing supercooling. However this is not confirmed in the later work of Paton (1972,1981) and Harwood (1980, 1981), and Paton (1981) suggests that, genetically and physiologically, frost sensitivity and glaucousness are unrelated. Ecologically it is difficult to separate these alternatives as apparently more frost prone and open habitats frequently co-occur.

As discussed by Pryor and Johnson (1971), the ecological specificity of most *Eucalypt* species results in the species range being partitioned into a series of closely circumscribed geographically isolated stands. This pattern of distribution is similar to that observed in many forest tree species (e.g. Fung and Wright 1972; Gordon 1976). A large number of the *E. gunnii*-*archeri* populations sampled represent small isolated stands separated from each other by large habitat disjunctions. Estimates of gene flow in *Eucalyptus* (e.g. Barber 1965; Pryor 1976) are in accord with the generally accepted view of leptokúrtic gene flow patterns in plants (see Ehrlich and Raven 1969; Levin and Kerster 1974 and cited references). Rare long distance dispersal between these disjunct populations may be significant in the introduction of novel genes. However, the importance of gene flow in opposing disruptive selection and differentiation would be negligible. Nevertheless, while many of these isolated populations appear as outliers and differ significantly from their geographically nearest neighbours, considerable phenetic variation also occurs in the virtually continuous populations on the Central Plateau. Furthermore, considerable phenetic divergence frequently occurs in continuous stands over relatively short distances (Figs. 1.14 and 1.19) and directly parallels environment change. This is particularly so of the exposure cline which is locally stepped in direct response to rapid topographical transitions between erosion surfaces. Marked local differentiation appears to be maintained over extremely short distances and significant differences over a distance of 50 meters were observed at the Liawenee site between samples differing in degree of exposure.

In view of the large genetic component demonstrated to underlie the observed phenetic variation in the following chapter, it is possible that where the topographic transition is steep, gene flow may be responsible for the local smoothing and displacement of clines. A net migration of genes would be expected both down-slope and, due to the prevailing westerly airstream, eastward. Downslope migration of seed, for example, may account for the smoothing of the exposure cline over the steep altitudinal

transition from Breona (Br) to the Mickey's Creek (P₅) site. Furthermore, if variation in flowering time proves to have a genetic basis, asymmetric gene flow, bias toward the east, could account for the displacement of the flowering time boundary between Shannon Lagoon (SL) and Pensford (Pf) over the lip of Barren Plains.

Differences in flowering time within these continuous stands would reinforce isolation by distance and has the potential to retard pollen flow along the morphological continuum. Marked differences in flowering time between contiguous populations were observed and were associated with rapid topographic variation and paralleled local steepening in the morphological cline (Figs. 1.12 and 1.17). McNeilly and Antonovics (1968) consider flowering time variation is one of the simplest mechanisms of reducing gene flow and similarly found significant differences in flowering time between adjacent locally differentiated mine and pasture populations of *Agrostis tenuis* and *Anthoxanthum odoratum*. These authors note that differences in flowering may be the result of direct adaptation to local ecological conditions, or have evolved as a consequence of gene flow, specifically as an isolating mechanism (i.e. Wallace Effect; Grant 1966, 1971). It is generally accepted that isolating mechanisms may be selected to reduce gametic wastage arising from hybridization and the disruptive effect of gene flow. Mayr (1963) maintains this will occur only during secondary intergradation. However, many authors consider this a mechanism for *in situ* primary speciation (e.g. Fisher 1930; Barber 1965; Grant 1966; Endler 1977; Caisse and Antonovics 1978). This is discussed by Barber (1965) in relation to an environmental gradient inducing simultaneous clinal variation in a large number of genes. He maintains that as the cline steepens a greater number of individuals or gametes, differing in an increasing number of selectively correlated alleles, will disperse into unfavourable environments, thus increasing the selective pressure for a reduction in gene flow. However, as Crosby (1970) points out, selection against hybridization is a second-order event and as such is likely to be less effective than the direct selection processes commonly encountered. Levin (1970a) suggests selection for reproductive isolation arising from mis-mating is more likely to occur in animals than plants, and that a reduction in gene flow in plants is more likely to arise as a by-product of competition for pollinators. Furthermore, Barber (1965) also argues that selection against reproductive loss will diminish where density-dependent selection is important, as is the case in many forest tree genera. Nevertheless, marked differences in flowering time between closely related *Eucalyptus* species have been recorded (e.g.

Barber 1965; Pryor 1976; Ashton 1981a; Drake 1980). However, as noted by Sterne and Roche (1974) selection frequently involves variation in whole character complexes arising from the same environmental factor affecting several characters. As such, it is quite likely that phenetic variation in response to a marked environmental gradient may also be paralleled by adaptive variation in facets of the reproductive biology. This appears to be the case in the present study where gene flow is potentially restricted along the cline as a secondary consequence of a response of the reproductive biology to local ecological conditions. Variation in flowering time appears to result from genetic or plastic differences in the rate of bud development along the exposure cline. A common trend in *Eucalyptus* is for the seasonal onset and peak of flowering to be delayed with increasing altitude, with a wave of flowering occurring from warmer to colder sites (e.g. van Loon 1966; Ashton 1975; Griffin 1980). The heritability of these differences is unknown, but in northern hemisphere species, genetic variation in the reproductive phenology is well documented (see Sterne and Roche 1974).

In the more or less continuous stands of *E. gunnii-archeri* on the Central Plateau, the stepped nature of the landscape results in geographically extensive populations being stabilized at a similar adaptive level and marked differences on morphology and flowering time may occur over relatively short distances. In addition, the displacement of *E. gunnii-archeri* from the better drained slopes between erosion surfaces by other *Eucalyptus* species results in only a limited area of suitable habitat at intermediate exposure levels, and the corresponding reduction in population density is also equivalent to a partial barrier to gene flow (Endler 1977). Phenotypes intermediate in both morphology and flowering time between these adaptive modes are thus less frequently encountered and channels for gene flow are reduced. This particularly applies to morphs recognized by Brett (1938) as *E. divaricata* which form extensive populations of similar morphology on the lower plateau surface, and which are differentiated on flowering time from populations at higher and lower altitudes. Such parallel adaptive variation in the reproductive phenology may not be significant where extensive populations are distributed along shallow environmental gradients. However, it may be of importance, whether genetic or plastic, under conditions of local genetic divergence such as described by Jain and Bradshaw (1966), particularly where the habitat is of small size and susceptible to genetic swamping. Endler (1977) notes the effect of a partial barrier on a gradient model is to increase differentiation and to "attract" steps. He suggests this latter property may be a significant factor in establishing concordance of independent multi-genic clines as all clines with null points sufficiently near the barrier will form

steps at the barrier. In this respect, a steepening of a cline involving a character which incidentally affects gene flow will thus tend to locally increase differentiation in other characters which in turn may result in a strengthening of the barrier to gene flow with feedback eventually resulting in reproductive isolation. This contrasts with previously described mechanisms for parapatric speciation (e.g. Barber 1965; Grant 1966, 1971; Endler 1977; Caisse and Antonovics 1978) involving character displacement and thus reverse clines, where gametic loss is the primary stimulus for the evolution of reproductive isolation. A reduction in gene flow along a cline arising from parallel direct selection of facets of the reproductive biology is theoretically unnecessary for parapatric differentiation or speciation (e.g. Endler 1977; Caisse and Antonovics 1978). Nevertheless it is probably common (e.g. McNeilly and Antonovics 1968; Allard 1970; Levin 1978b) and may be significant in enhancing the rate of divergence and speciation, and may possibly form a foundation for the evolution of more stable reproductive isolating mechanisms.

Table 1.1 Population codes, phenetic class, grid reference, altitude, number of individuals per sample and percentage of trees classified as green or sub-glaucous (i.e. GLAUC=0 or 1). The phenetic classes correspond to those recognized at the conclusion of Chapter 1 (i.e. Fig. 1.24) and correspond to '*E. archeri*' (1), 'Pine Lake intermediates' (2), '*E. divaricata*' (3), 'southern *E. gunnii*' (4) and 'NW *E. gunnii*' (5). Grid references (1 unit=1 km) are based on the 1:100,000 TASMAP series.

POPULATION	PHENETIC GRID REFERENCE				ALTITUDE (m)	N	% GLAUC=0/1
	CODE	CLASS	E/W	N/S			
Projection Bluff low	P1	1	476	5883	980	20	100
Projection Bluff high	P2	1	477	5381	1100	20	100
Pine Lake 1	P3	2	476	5378	1150	20	75
Pine Lake 2	P4	2	477	5377	1140	20	40
Mickey's Creek	P5	2	476	5375	1150	20	20
Breona	Br	3	475	5374	1040	20	0
South Brandum	SB	3	474	5368	1040	20	0
Shannon Lagoon	SL	3	480	5351	1050	20	0
Liawenee	LH	3	468	5361	1150	20	0
Scrummies Marsh	A1	4	504	5335	930	20	0
Jimmy's Marsh	AH	3	504	5340	1010	10	0
Pensford	PF	4	484	5349	960	20	0
Middlesex Plains	MS	5	416	5400	760	8	12
Pencil Pine Creek	PP	5	411	5400	870	6	0
St. Valentines Peak	SV	5	396	5417	660	10	60
Mole Creek	MC	1	446	5391	1140	10	100
Mt. Rufus	RF	4	428	5334	1050	6	0
Broad River	BD	4	466	5278	830	9	0
Trapper's Hut	TH	5	438	5373	1130	10	0
Lake Ball	LB	5	442	5370	1150	9	0
Lake Charles	LC	5	437	5363	1070	10	0
Lake Myrtle	LM	5	434	5364	1030	10	0
Pelion Plains	OP	5	420	5369	960	10	0
Liffey River	LR	2	477	5380	980	10	60
Mt. Roland	MR	1	440	5410	1120	20	100
Ben Lomond	BL	1	553	5404	1230	20	100
Mt. Barrow	MB	1	534	5417	1200	20	100
Ben Nevis	BN	1	553	5417	1140	20	100
Mt. Maurice	MM	1	549	5426	1000	20	100
Mt. Saddleback	SD	1	563	5417	1180	18	100
Mt. Victoria	MV	5	569	5423	790	20	30
Snow Hill	SH	4	569	5359	950	26	19
Snug Plains	SP	4	513	5233	600	16	6
Repulse River	RR	5	461	5289	760	6	0
Poatina Highway	PH	2	488	5371	1080	6	50
Poatina Inlet	PN	3	486	5368	1040	6	0
NE Plateau	NE	2	485	5372	1120	15	0

Table 1.2 Field glaucousness classes

0	-	all foliage green
1	-	slight glaucousness on newly expanded foliage (not persistent)
2	-	moderately intense glaucousness on young foliage
3	-	as (2) but lightly extending onto young stems
4	-	intense glaucousness on young growth, extending onto stems and buds, but not persistent on older leaves, buds and fruits
5	-	as (4) but persistent on older leaves, buds and fruits.

Table 1.3 Character codes, descriptions, grand means (\bar{X}), standard deviations (SD) and F ratios for population differences (n=551). All F ratios are highly significant (P<0.001).

Code	Character description	Grand		F _{36,514}
		\bar{X}	SD	
LL	lamina length (mm)	71.6	12.76	14.6
LW	lamina width (max.) (mm)	19.3	3.78	6.6
LWP	length to the widest point (mm)	28.8	5.67	16.3
PET.L	petiole length (mm)	18.1	4.09	12.9
LAMTH	lamina thickness (mm)	0.36	0.06	19.8
CURV	curvature (mm)	2.4	1.44	6.2
PEDU	peduncle length (mm)	5.8	1.86	7.8
CAP.L	capsule length (mm)	7.0	0.94	10.1
PEDI	pedicel length (mm)	0.6	0.70	16.9
RIM.W	capsule rim width (mm)	5.7	0.74	7.6
MAX.W	maximum capsule width (mm)	6.3	0.64	7.6
PT.MAX.W	distance to maximum capsule width (mm)	2.1	0.88	5.4
DISK	disk level (mm)	1.0	0.46	6.3
VSIZ	relative valve size	1.6	0.55	6.6
VPOS	relative valve position	1.6	0.51	5.6

Table 1.4 Character means (\bar{X}) and standard errors (SE) for herbarium material classified as *E. archeri* (n=36), *E. gunnii* (n=47) and *E. urnigera* (n=17). The probability levels for F values for both the difference between all three taxa (Fa,g,u) and the difference between *E. archeri* and *E. gunnii* (Fa,g) are indicated. All measurements are in mm. (NS=not significant, *=P<0.05, **=P<0.01, ***=P<0.001).

	<i>E. archeri</i>		<i>E. gunnii</i>		<i>E. urnigera</i>		Fa,g,u	Fa,g
	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	(2,97)	(1,81)
LL	66.5	1.80	68.6	1.85	77.9	3.83	**	NS
LW	19.5	0.79	18.8	0.58	21.2	1.16	NS	NS
LWP	24.1	0.84	24.1	0.76	24.1	1.39	NS	NS
PET.L	18.0	0.79	17.9	0.72	23.0	1.37	***	NS
PEDU	5.3	0.33	5.3	0.30	13.5	1.15	***	NS
MAX.W	5.9	0.20	4.7	0.21	6.2	0.96	***	***
CAP.L & PEDI	6.7	0.14	6.8	0.10	14.3	0.29	***	NS

Table 1.5 Mahalanobis' distances ($\sqrt{D^2}$) between taxa centroids based on herbarium material.

	<i>E. archeri</i>	<i>E. gunnii</i>
<i>E. gunnii</i>	1.67	
<i>E. urnigera</i>	5.07	4.52

Table 1.6 Standardized canonical variates derived from CVA of herbarium data. The relative magnitude (%) of the corresponding eigen value is indicated.

	CV ₁ (86%)	CV ₂ (14%)
LL	-0.42	-0.24
LW	-0.06	0.14
LWP	0.31	-0.03
PET.L	-0.14	0.06
PEDU	-0.31	0.03
PEDI+CAP.L	-0.73	-0.23
MAX.W	0.29	0.93

Table 1.7 Standardized canonical variates derived from CVA of the reproductive characters (see Fig. 1.16). The relative magnitude (%) of the corresponding eigen values is indicated.

	CV ₁ (44%)	CV ₂ (19%)	CV ₃ (10%)
PEOU	0.14	0.28	0.16
CAP.L	0.45	-0.19	-0.28
PEDI	0.76	-0.23	0.57
RIM.W	0.07	0.47	0.20
MAX.W	-0.02	0.52	-0.22
PT.MAX.W	-0.11	0.21	-0.53
DISK	-0.01	0.07	-0.19
VSIZ	-0.43	-0.36	-0.40
VPOS	0.04	0.41	0.05

Table 1.8

The regression of the main canonical variates derived from CVA of (a) reproductive (Table 1.7), (b) vegetative (Table 1.9), (c) vegetative and reproductive (Table 1.10) and (d) vegetative+reproductive+glaucousness, character sets against the environmental variates - longitude (E/W), latitude (N/S), altitude (ALT) and mean annual rainfall (RAIN) (n=37). The significance of each univariate regression coefficient (β) is indicated as well as the significance of each partial coefficient (β^1) in the multiple regression. The significance of the multiple regression is indicated and where the step-down procedure retained more than a single variate, the significance of the partial coefficients in the step-down equation is also shown. The percentage of the variance accounted for by significant regressions is shown in brackets. (- = not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

Dependent Phenetic Variate		E/W	Environmental Variate N/S	ALT	RAIN	Multiple Regression
(a) Reproductive Characters (9)						
CV ₁ (44%)	β	-	*** (29)	*(11)	-	
	β^1	-	***	-	-	** (32)
CV ₂ (19%)	β	*** (36)	-	-	-	
	β^1	***	-	-	-	*** (38)
CV ₃ (10%)	β	-	-	*** (27)	-	
	β^1	-	-	***	-	** (28)
(b) Vegetative characters (6)						
CV ₁ (53%)	β	-	*(11)	*** (41)	-	
	β^1	-	-	***	-	*** (42)
CV ₂ (22%)	β	-	-	-	-	
	β^1	-	-	-	-	-
(c) Vegetative and reproductive characters (15)						
CV ₁ (40%)	β	-	** (19)	*** (34)	-	
	β^1	-	-	***	-	*** (39)
CV ₂ (17%)	β	-	-	-	-	
	β^1	-	-	-	-	-
CV ₃ (9%)	β	-	-	*(15)	*** (19)	
	β^1	-	*	***	-	*** (44)
step-down equation	β^1	*	**	***	excl.	*** (42)
(d) Vegetative, reproductive and glaucousness (16)						
CV ₁ (57%)	β	-	*** (28)	*(11)	-	
	β^1	-	***	-	-	*** (34)
CV ₂ (17%)	β	-	-	*** (25)	-	
	β^1	-	-	***	-	** (29)
CV ₃ (5%)	β	** (14)	-	** (17)	*** (23)	
	β^1	-	*	***	-	*** (48)
step-down equation	β^1	**	***	***	excl.	*** (46)

Table 1.9 Standardized canonical variates derived from CVA of the vegetative characters (see Fig. 1.17). The relative magnitude (%) of the corresponding eigen values is indicated.

	CV ₁ (53%)	CV ₂ (22%)
LL	-0.10	0.07
LW	-0.26	0.05
LWP	-0.30	0.68
PET.L	-0.52	0.04
LAMTH	0.75	0.67
CURV	-0.07	0.27

Table 1.10 Standardized canonical variates derived from CVA of vegetative and reproductive characters (see Fig. 1.18). The relative magnitude of the corresponding eigen value is indicated.

	CV ₁ (40%)	CV ₂ (17%)	CV ₃ (9%)
LL	0.10	0.21	-0.16
LW	0.19	0.11	-0.43
LWP	0.17	0.54	0.13
PET.L	0.36	0.13	0.12
LAMTH	-0.58	0.31	0.48
CURV	-0.12	0.22	0.01
PEDU	-0.08	0.11	0.45
CAP.L	-0.22	-0.39	0.07
PEDI	0.49	-0.26	0.13
RIM.W	0.18	0.45	0.02
MAX.W	-0.03	0.16	0.25
PT.MAX.W	-0.00	0.10	0.11
DISK	-0.12	-0.11	0.40
VSIZ	-0.31	0.06	-0.18
VPOS	0.02	0.06	0.20

Table 1.11 Canonical correlations and vectors for the first two canonical variate sets relating vegetative and reproductive characters (n=37).

	1.	2.
Canonical Correlation ($\sqrt{\lambda}$)	0.87	0.73
Significance:	0.001	0.083
<u>Vegetative characters (CV₁)</u>		
LL	0.56	0.34
LW	-0.12	-0.34
LWP	-0.05	-1.33
PET.L	0.40	-0.54
LAMTH	-0.45	-0.34
CURV	-0.52	-0.35
<u>Reproductive characters (CV₂)</u>		
PEDU	0.07	-0.33
CAP.L	-0.28	-1.03
PEDI	1.06	0.43
RIM.W	0.96	-0.80
MAX.W	-0.62	1.01
PT.MAX.W	0.35	-0.57
DISK	-0.58	0.99
VSIZ	-0.16	-0.19
VPOS	-0.44	-0.52

Table 1.12 Significant correlation coefficients calculated (a) pooled within populations (d.f.=513), and
(b) between population means (d.f.=35) (- = NS; * = P<0.05, ** = P<0.01, *** = P<0.001)

(a) Pooled within populations

	LL	LW	LWP	PET.L	LAMTH	CURV	PEOU	CAP.L	PEDI	RIM.W	MAX.W	PT.MAX.W	DISK	VSIZ	VPOS
LW	-														
LWP	*** 0.73	-													
PET.L	*** 0.41	-	*** 0.36												
LAMTH	-	-	-	-											
CURVE	-	-	*** 0.35	* 0.14	-										
PEOU	-	** 0.20	-	-	*-0.15	-									
CAP.L	-	-	-	-	-	-	*** 0.41								
PEDI	-	-	-	-	-	-	*** 0.33	*** 0.23							
RIM.W	-	-	-	-	-	-	-	* 0.17	-						
CAP.W	-	-	-	-	-	-	-	*** 0.42	-	*** 0.78					
PT MAX.W	-	-	-	-	-	-	-	*** 0.41	-	***-0.32	-				
DISK	-	-	-	-	-	-	* 0.18	*** 0.45	** 0.19	** -0.20	-	*** 0.46			
VSIZ	-	-	-	-	-	-	-	-	-	*** 0.44	*** 0.30	***-0.28	***-0.29		
VPOS	-	-	-	-	-	-	*-0.14	***-0.31	-	*** 0.36	-	***-0.46	***-0.61	*** 0.48	
GLAUC	-	-	-	-	-	-	-	-	-	-	-	-	-	*-0.15	-

(b) Between population means

	LL	LW	LWP	PET.L	LAMTH	CURV	PEOU	CAP.L	PEDI	RIM.W	MAX.W	PT MAX.W	DISK	VSIZ	VPOS
LW	* 0.36														
LWP	*** 0.90	* 0.34													
PET.L	*** 0.80	** 0.47	*** 0.85												
LAMTH	*-0.39	** -0.51	*-0.35	***-0.54											
CURVE	*** 0.63	-	*** 0.63	** 0.44	-										
PEOU	** 0.42	-	** 0.43	*** 0.58	*-0.41	-									
CAP.L	-	-	-	** 0.46	*-0.38	-	*** 0.77								
PEDI	* 0.35	-	-	*** 0.58	***-0.68	-	*** 0.75	*** 0.69							
RIM.W	** 0.48	-	* 0.35	* 0.35	-	** 0.49	-	-	-						
MAX.W	* 0.36	-	-	-	-	** 0.42	* 0.35	** 0.48	-	*** 0.89					
PT MAX.W	-	-	-	-	-	-	-	*** 0.60	-	-	-				
DISK	-	-	-	-	-	-	** 0.49	*** 0.73	*** 0.53	-	-	*** 0.72			
VSIZ	-	-	-	-	* 0.41	* 0.35	*-0.37	***-0.56	** -0.46	-	-	*-0.40	***-0.43		
VPOS	-	-	-	-	-	* 0.40	-	***-0.52	*-0.38	** 0.50	-	***-0.68	***-0.66	*** 0.66	
GLAUC	-	-	-	-	***-0.53	** -0.49	-	* 0.34	*** 0.57	***-0.55	*-0.39	* 0.36	* 0.38	***-0.61	***-0.53

Table 1.13 The first three eigen vectors (% Trace) derived from PCA of the pooled within and between populations correlation matrices derived from: (a) vegetative and (b) reproductive character sets. The angles ($^{\circ}$) between vectors derived from within and between groups analyses are also given.

(a) Vegetative characters

	WITHIN (d.f.=518)			BETWEEN (d.f.=35)		
	PC ₁ (38%)	PC ₂ (17%)	PC ₃ (17%)	PC ₁ (59%)	PC ₂ (25%)	PC ₃ (9%)
LL	0.60	0.02	-0.04	0.50	0.15	-0.05
LW	-0.02	0.79	0.38	0.28	-0.53	0.79
LWP	0.56	0.05	-0.02	0.50	0.17	-0.03
PET.L	0.38	0.12	0.48	0.50	-0.07	-0.14
LAMTH	-0.10	-0.52	0.78	-0.29	0.57	0.57
CURV	0.42	-0.29	-0.15	0.32	0.59	0.17

ANGLES BETWEEN VECTORS ($^{\circ}$)

	WITHIN		
	PC ₁	PC ₂	PC ₃
BETWEEN			
PC ₁	24	68	88
PC ₂	69	151	83
PC ₃	96	75	49

(b) Reproductive characters

	WITHIN			BETWEEN		
	PC ₁ (32%)	PC ₂ (25%)	PC ₃ (13%)	PC ₁ (48%)	PC ₂ (27%)	PC ₃ (11%)
PEDU	0.19	0.30	0.55	0.35	0.26	-0.39
CAP.L	0.31	0.45	-0.05	0.44	0.22	0.00
PEDI	0.17	0.20	0.66	0.36	0.09	-0.55
RIM.W	-0.30	0.50	-0.17	-0.06	0.62	0.08
CAP.W	-0.09	0.58	-0.33	0.10	0.58	0.32
PT.MAX.W	0.43	0.06	-0.19	0.36	-0.11	0.55
DISK	0.45	0.12	-0.16	0.41	-0.03	0.25
VSIZ	-0.35	0.26	0.10	-0.34	0.19	0.19
VPOS	-0.48	0.03	0.20	-0.37	0.32	-0.18

ANGLES BETWEEN VECTORS ($^{\circ}$)

	WITHIN		
	PC ₁	PC ₂	PC ₃
BETWEEN			
PC ₁	25	68	82
PC ₂	113	27	90
PC ₃	81	84	150



Fig. 1.1. The geographical distribution of *E. archeri*, *E. gunnii* and *E. urnigera* (modified from Jackson 1965). Species occupy suitable habitats within the area indicated.

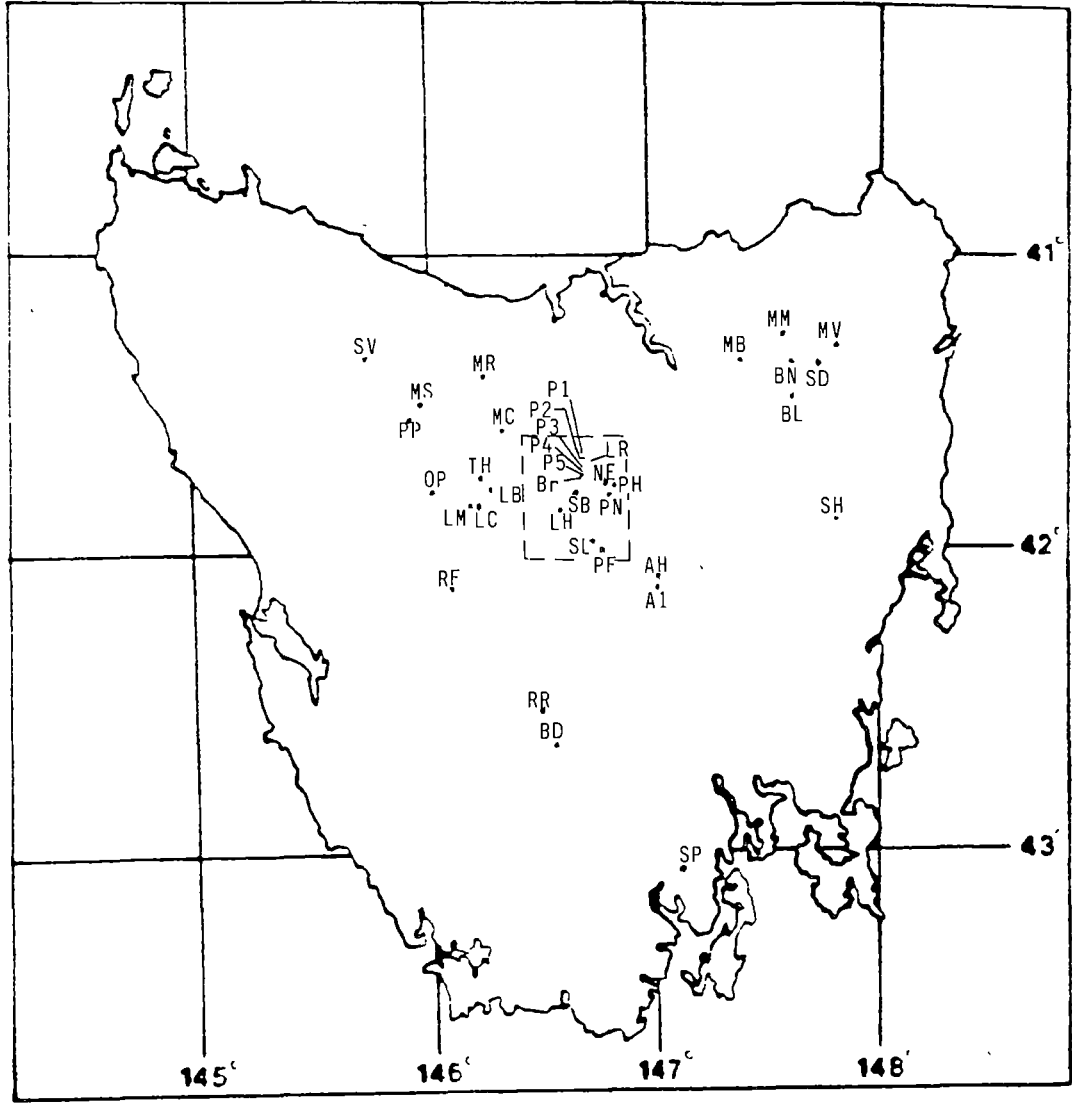


Fig. 1.2. Location of sampling sites. Population codes are detailed in Table 1.1. Insert is expanded in Fig. 1.3.

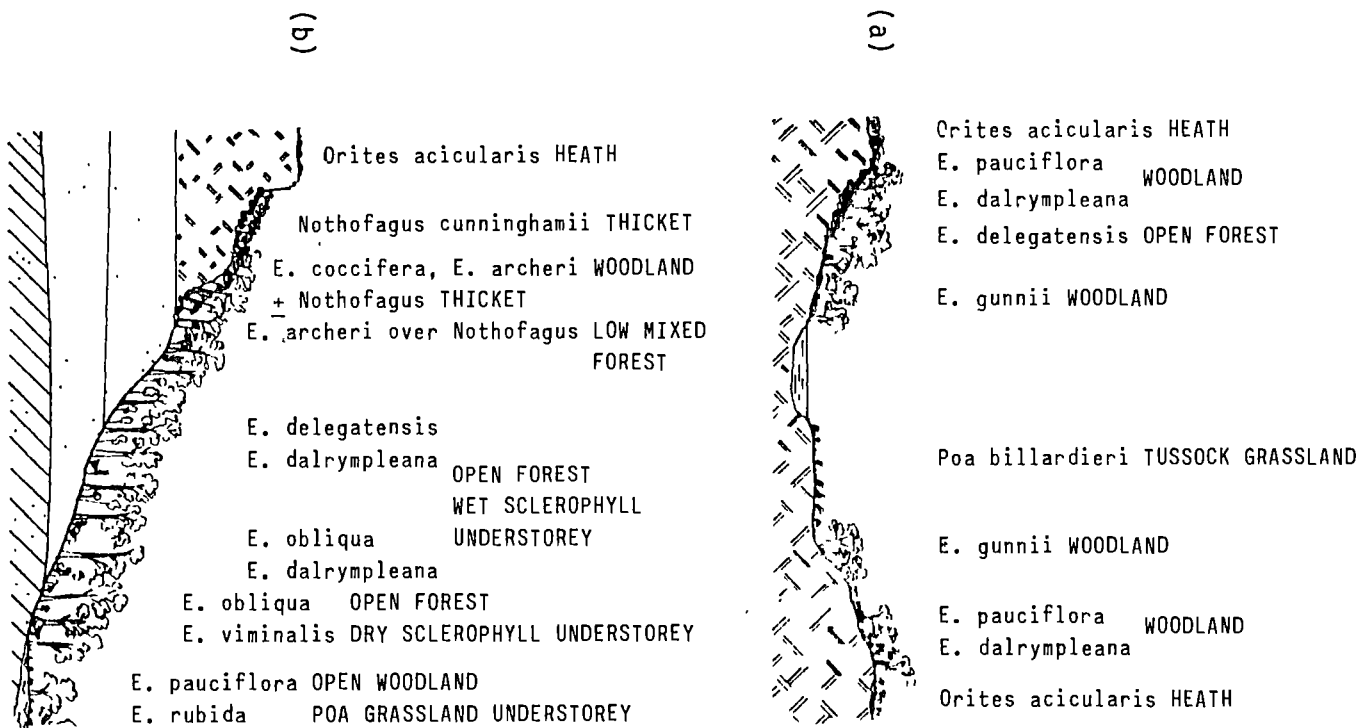


Fig. 1.4. Idealized profiles of the vegetation on (a) the lower Plateau surface (*E. gunnii* habitat) and (b) the northern scarp of the Western Tiers (*E. archeri* habitat) (modified from Jackson 1973).



Fig. 1.5 Low altitude forest form of *E. gunnii* at Pensford (Pf, 960 m).



Fig. 1.6 *E. gunnii* from near Shannon Lagoon (SL, 1050 m). This is typical of the form and habitat of the extensive *E. gunnii* populations around Great Lake. This form was described by Brett (1938) as *E. divaricata*.

(a)



(b)



Fig. 1.7 (a) Stunted tree and (b) mallee variant of *E. gunnii* from the high altitude site near Liawenee (LH, 1150 m).

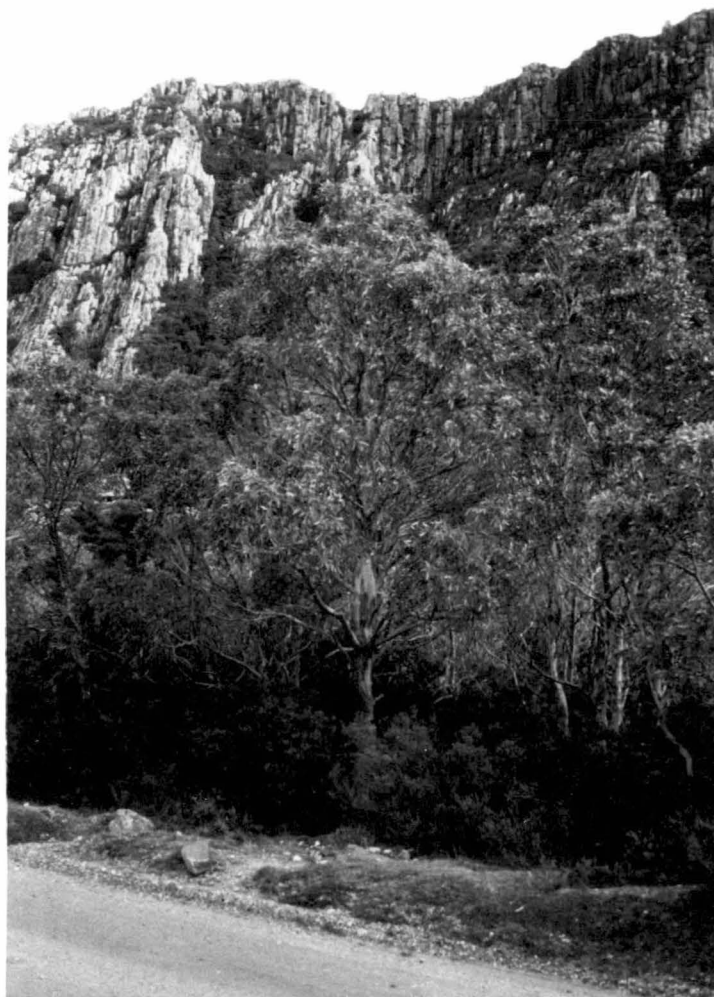


Fig. 1.8 *E. archeri* habitat on the northern scarp of the Western Tiers, near Projection Bluff (P₂, 1140 m).



Fig. 1.10 *E. archeri* habitat on Ben Lomond (BL, 1230 m).

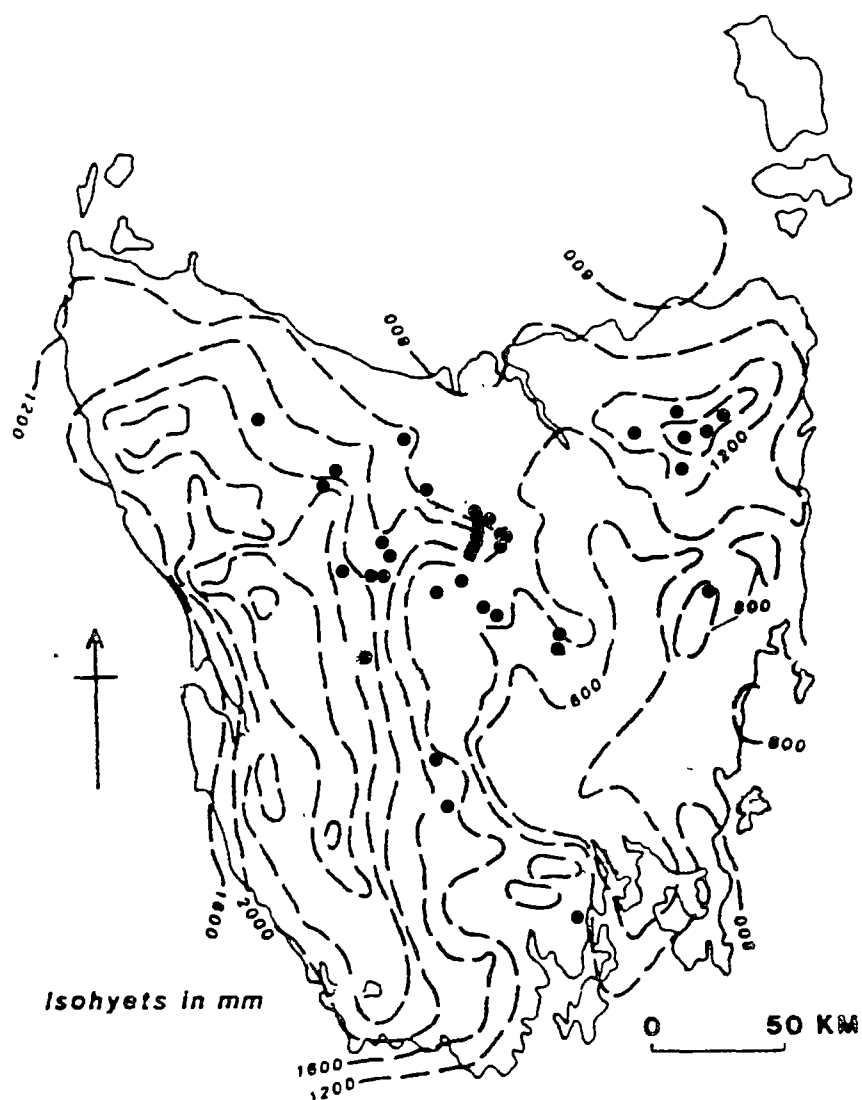


Fig. 1.9. Mean annual rainfall (mm). The distribution of sites sampled for the population survey is indicated (●).

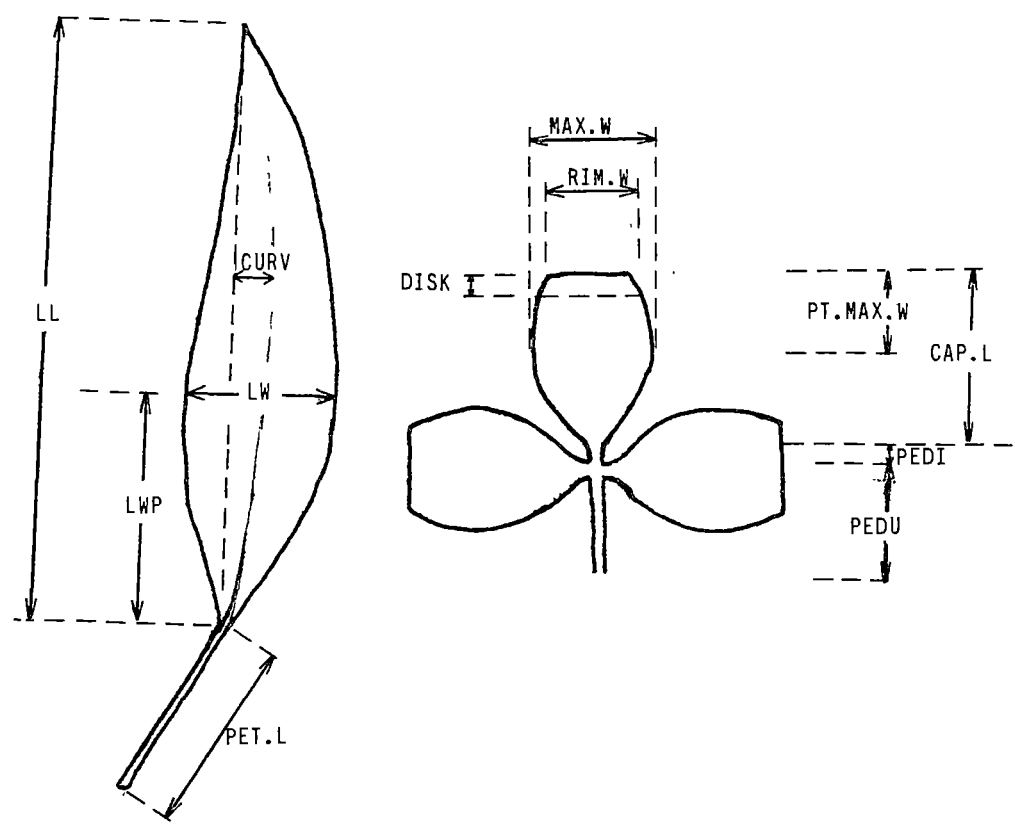


Fig. 1.11. Morphometric characters scored from adult leaves and inflorescences. Codes correspond to characters listed in Table 1.3.

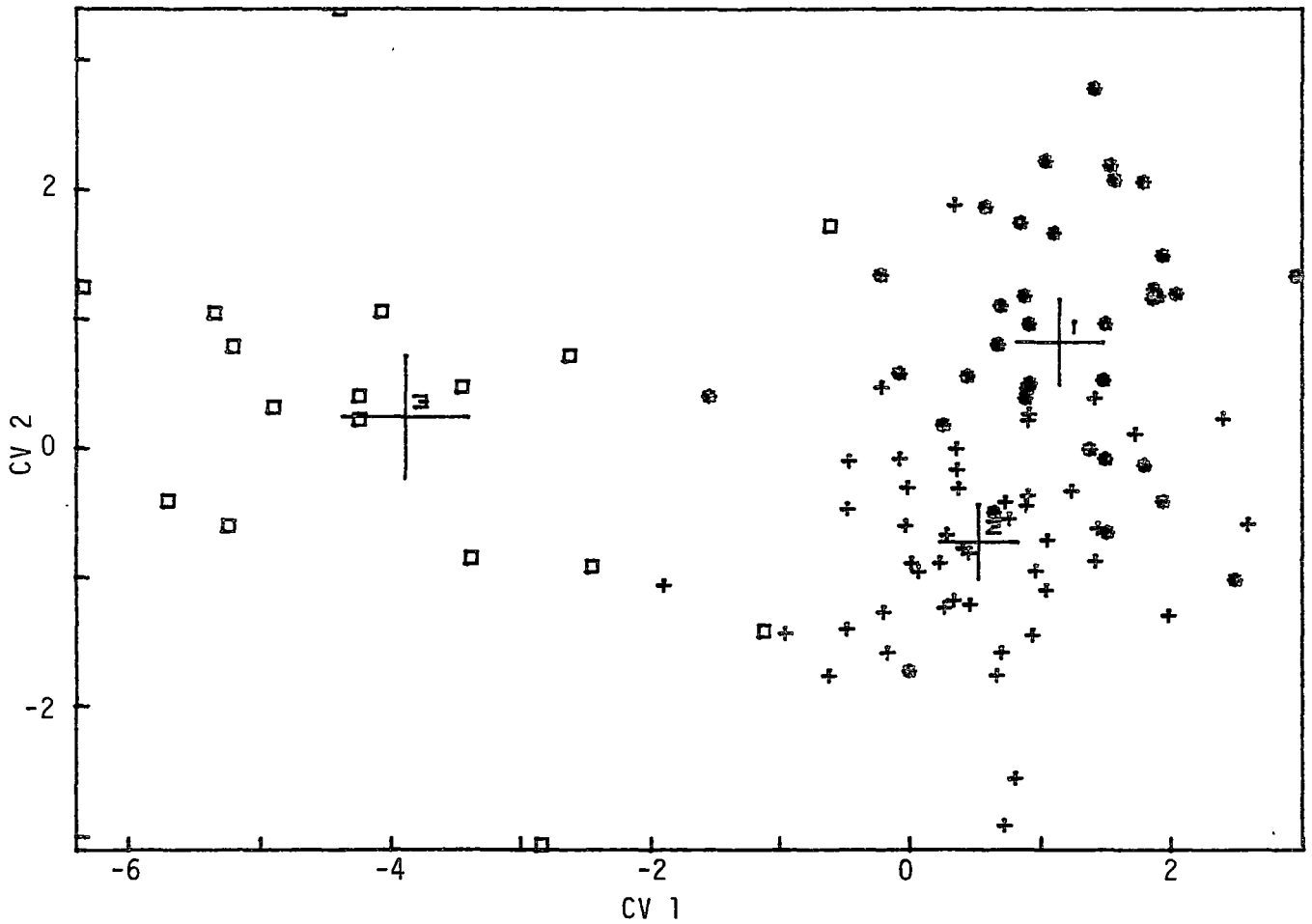


Fig. 1.12. CVA of herbarium material. Individual scores and taxa means on the first and second canonical axes (see Table 1.6) for *E. archeri* (*,1), *E. gunnii* (+,2) and *E. urnigera* (□,3). The 95% confidence limits for the group centroids are indicated.

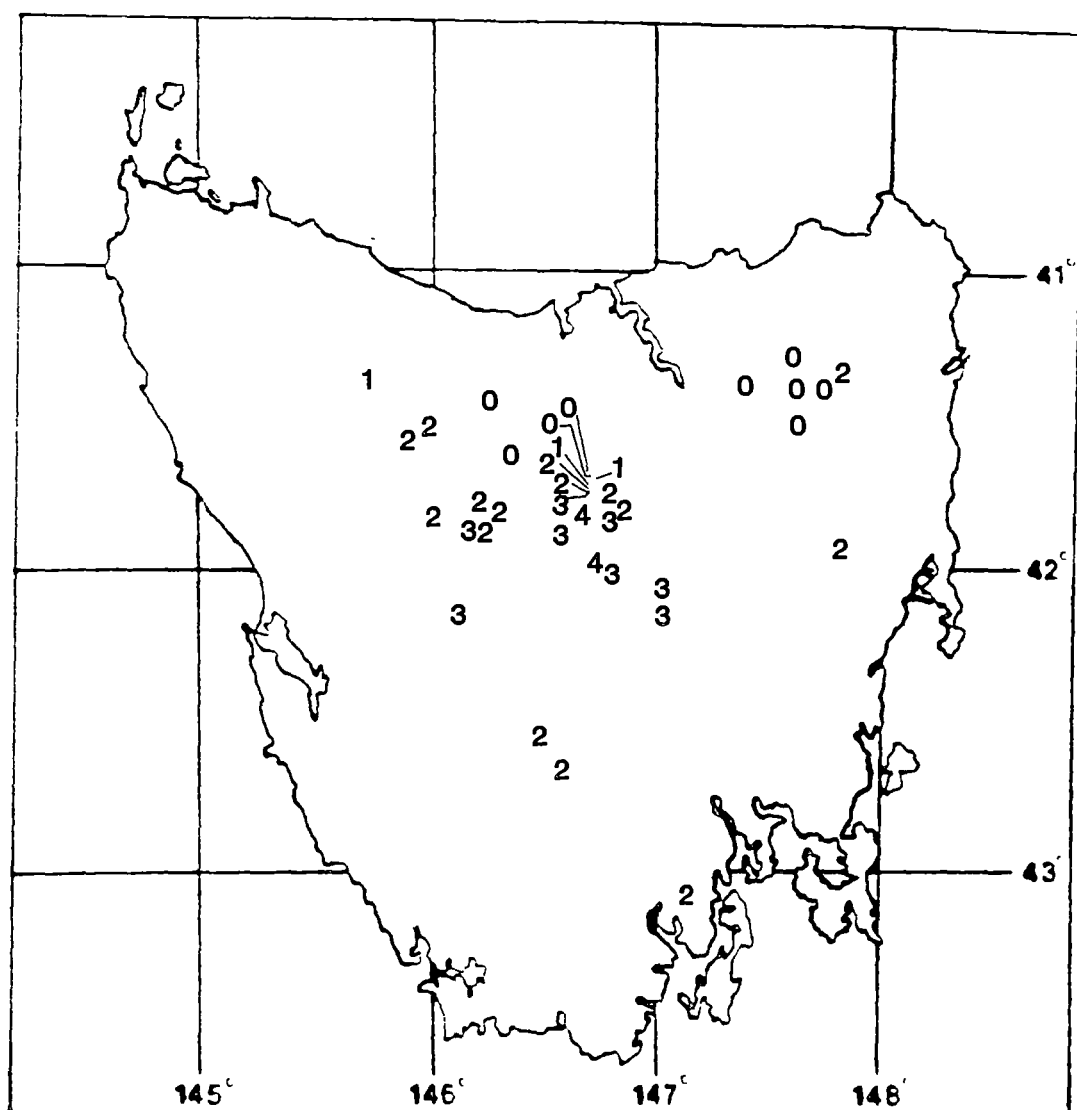


Fig. 1.13. Geographical variation in glaucousness (GLAUC). Values correspond to the average glaucousness score rounded to the nearest integer (0=green, 4=highly glaucous). Population locations correspond to Fig. 1.2.

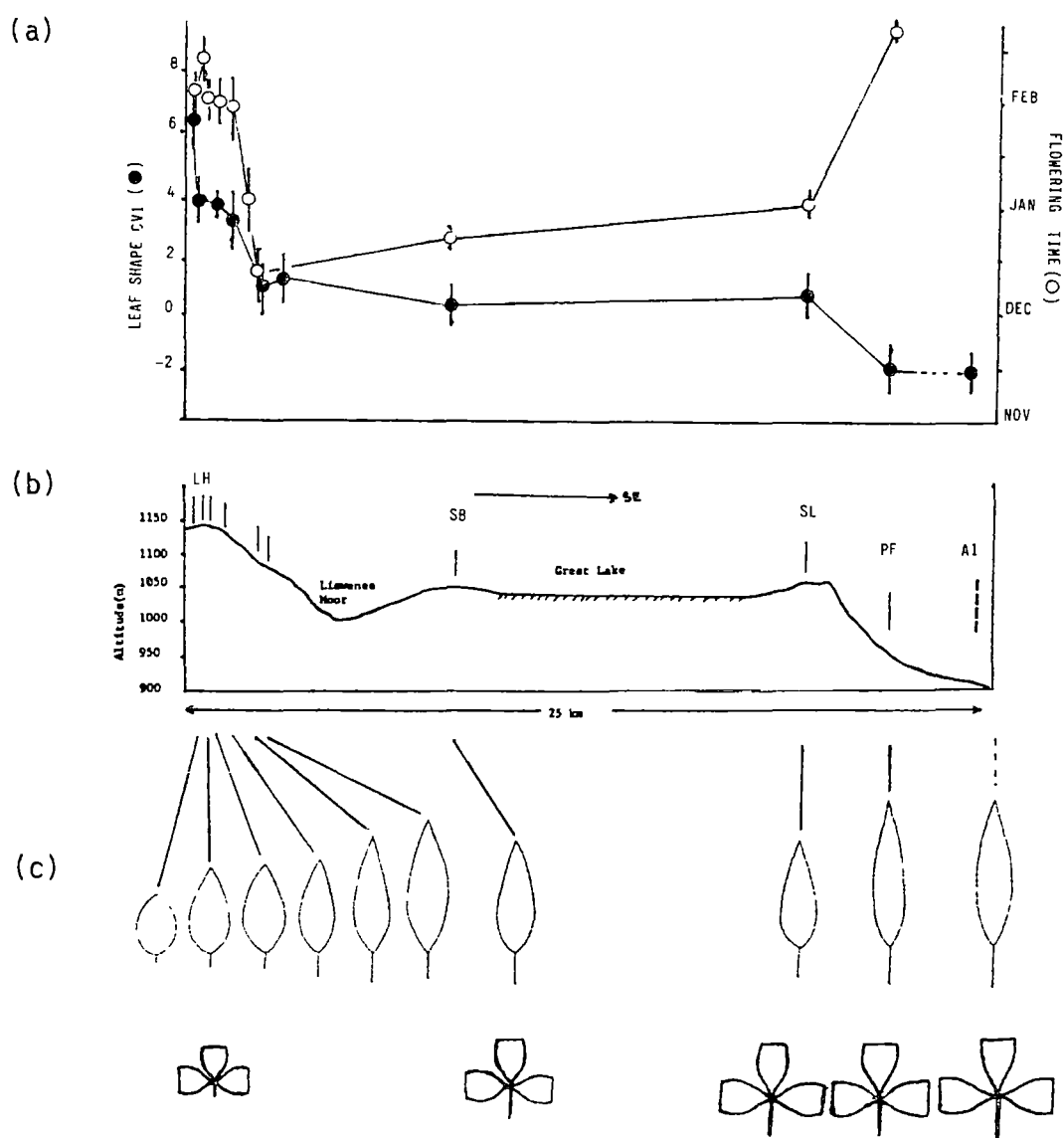
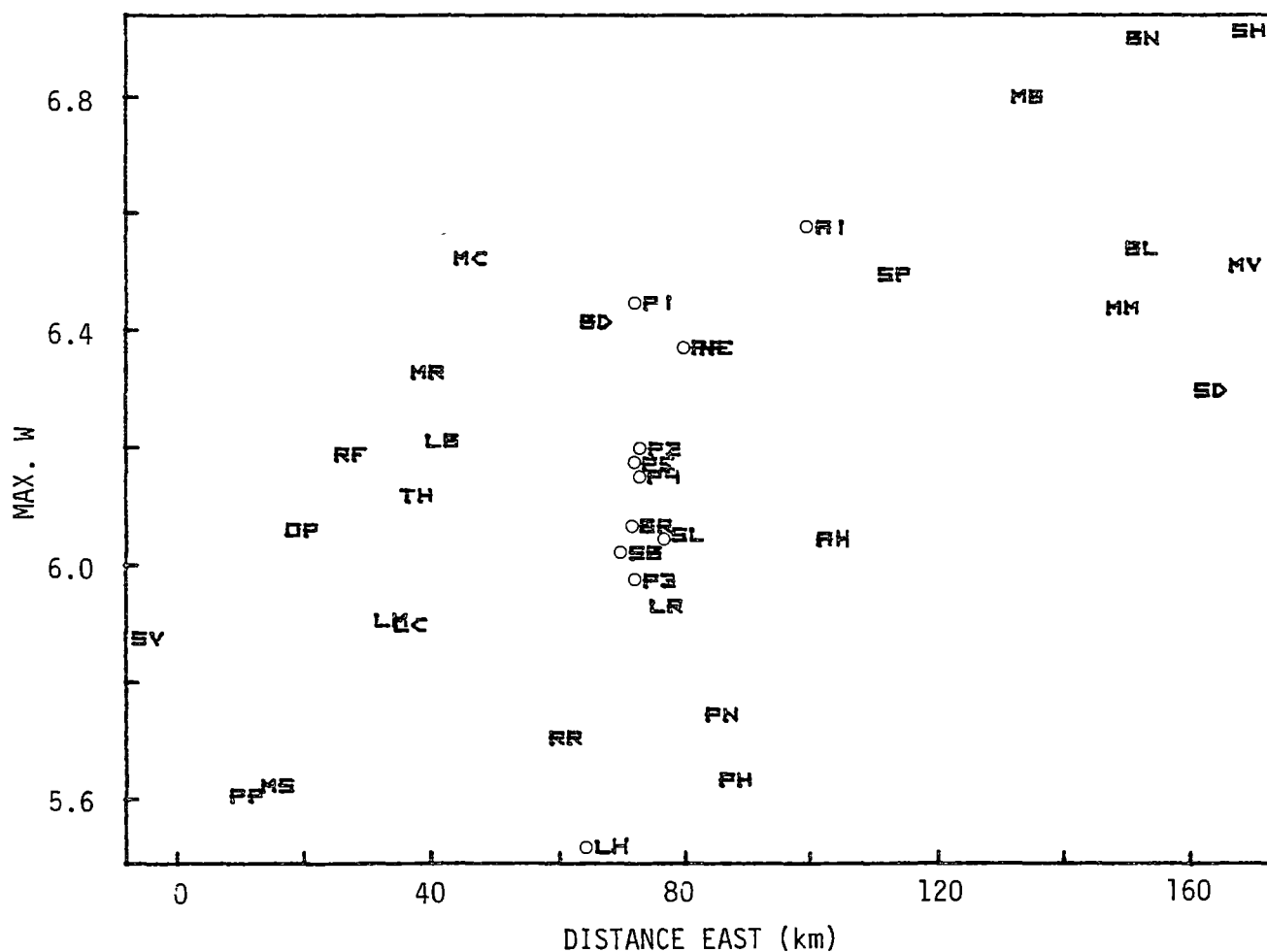


Fig. 1.14. Variation along the southern Plateau transect. (a) Population means and 95% C.L. for CVI derived from CVA of the 5 leaf dimensions (excluding LAMTH) (●) and mean (\pm SE) flowering time in the 1980 season (see Fig. 1.31, ○), (b) topographic cross section, (c) leaf and inflorescence ideograms based on character means.



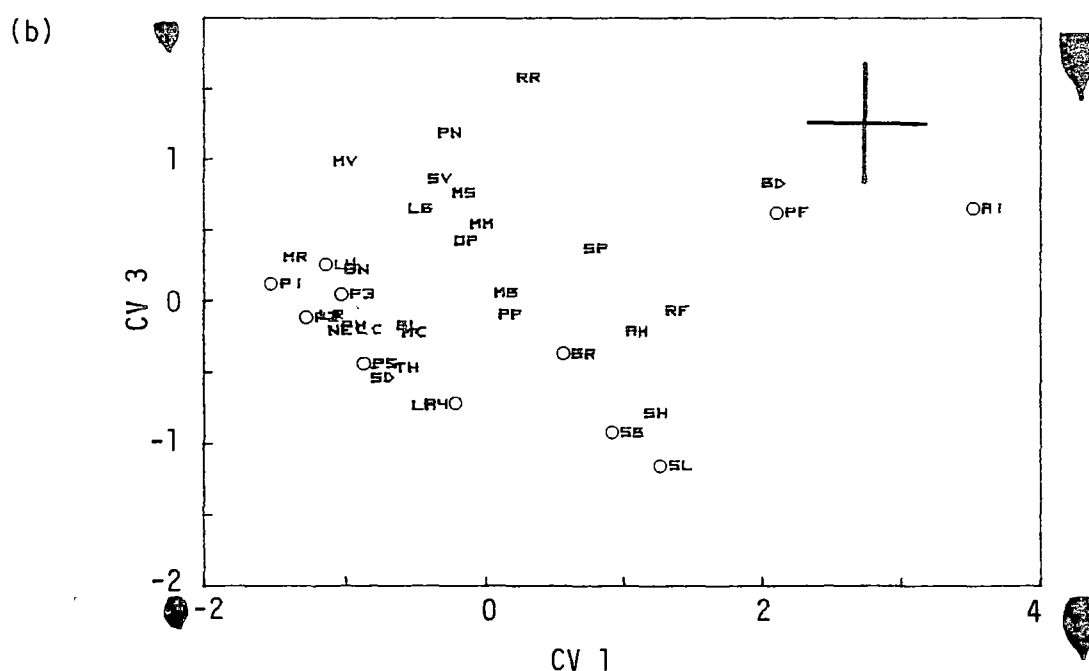
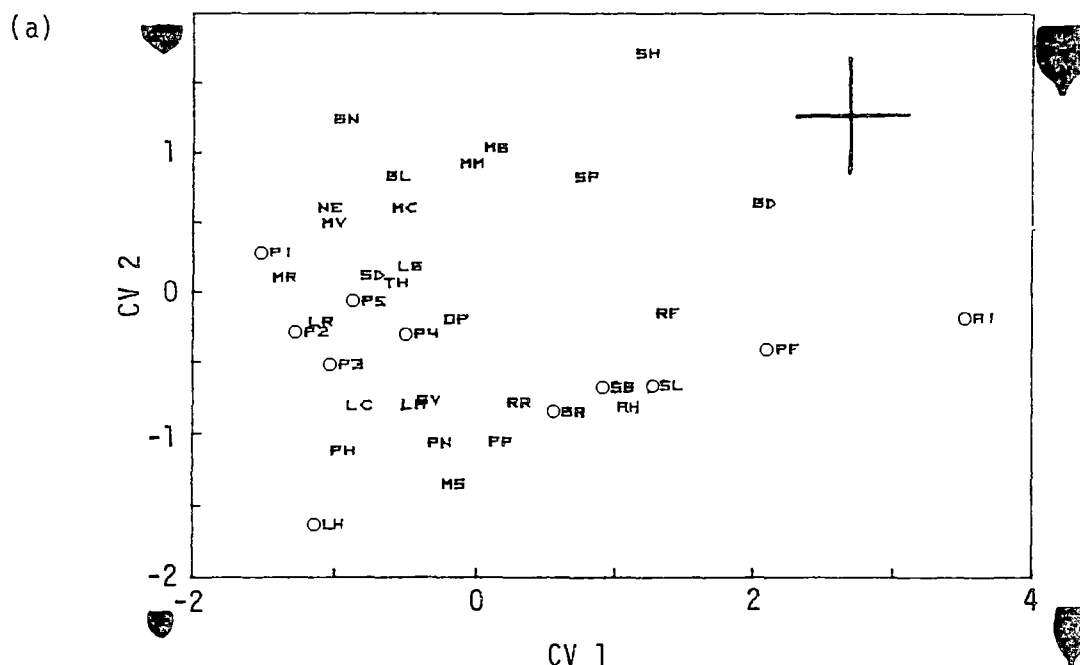


Fig. 1.16. CVA of reproductive characters. Population means on the first three canonical variates (CV_1 , CV_2 and CV_3 ; Table 1.7). The 95% confidence limits are based on $n=20$ and populations along the Pine Lake and southern Plateau transects are marked (0). Ideograms indicate the major variation trends described by each axis.

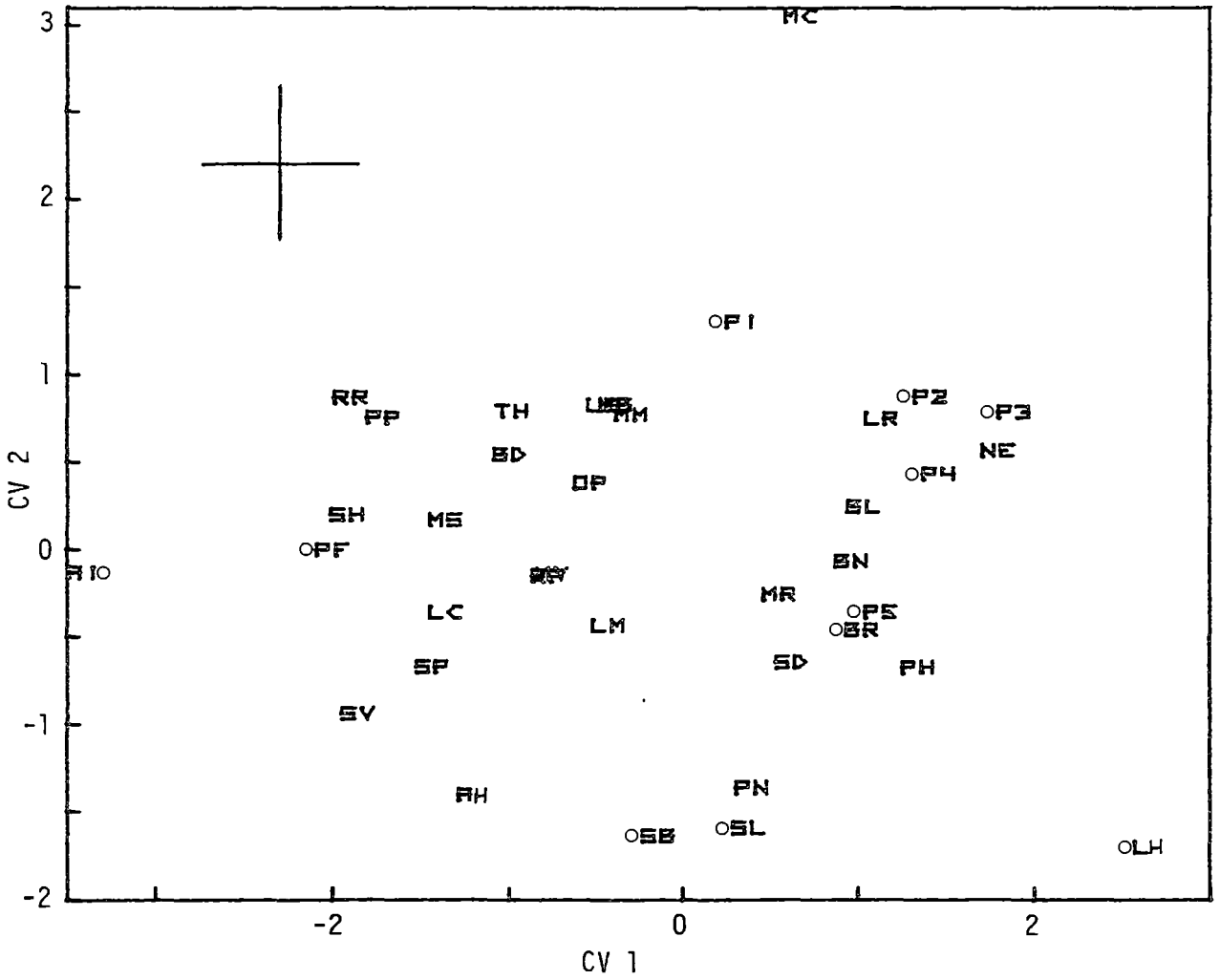


Fig. 1.17. CVA of vegetative characters. Population means on the first two canonical variates (CV₁ and CV₂; Table 1.9). The 95% confidence limits are based on n=20 and populations along the Pine Lake and southern Plateau transects are marked (0).

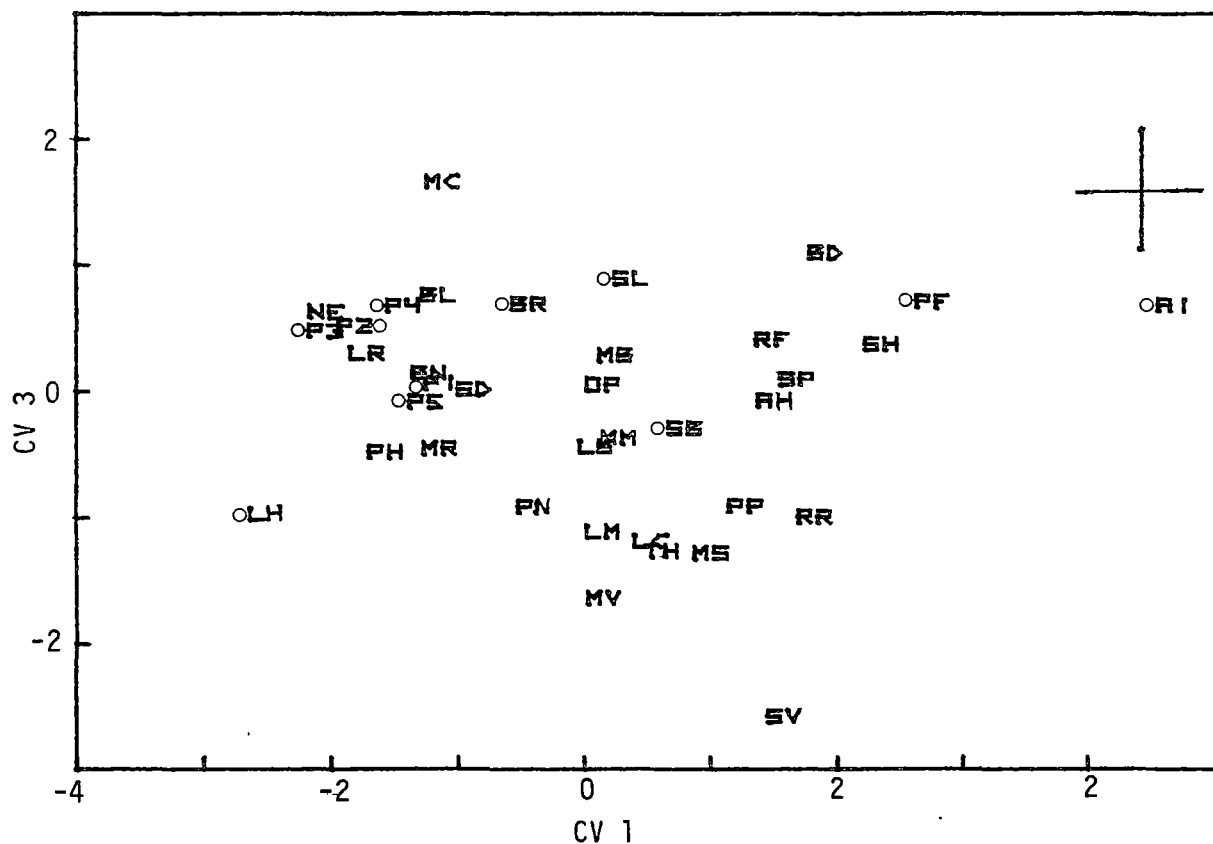
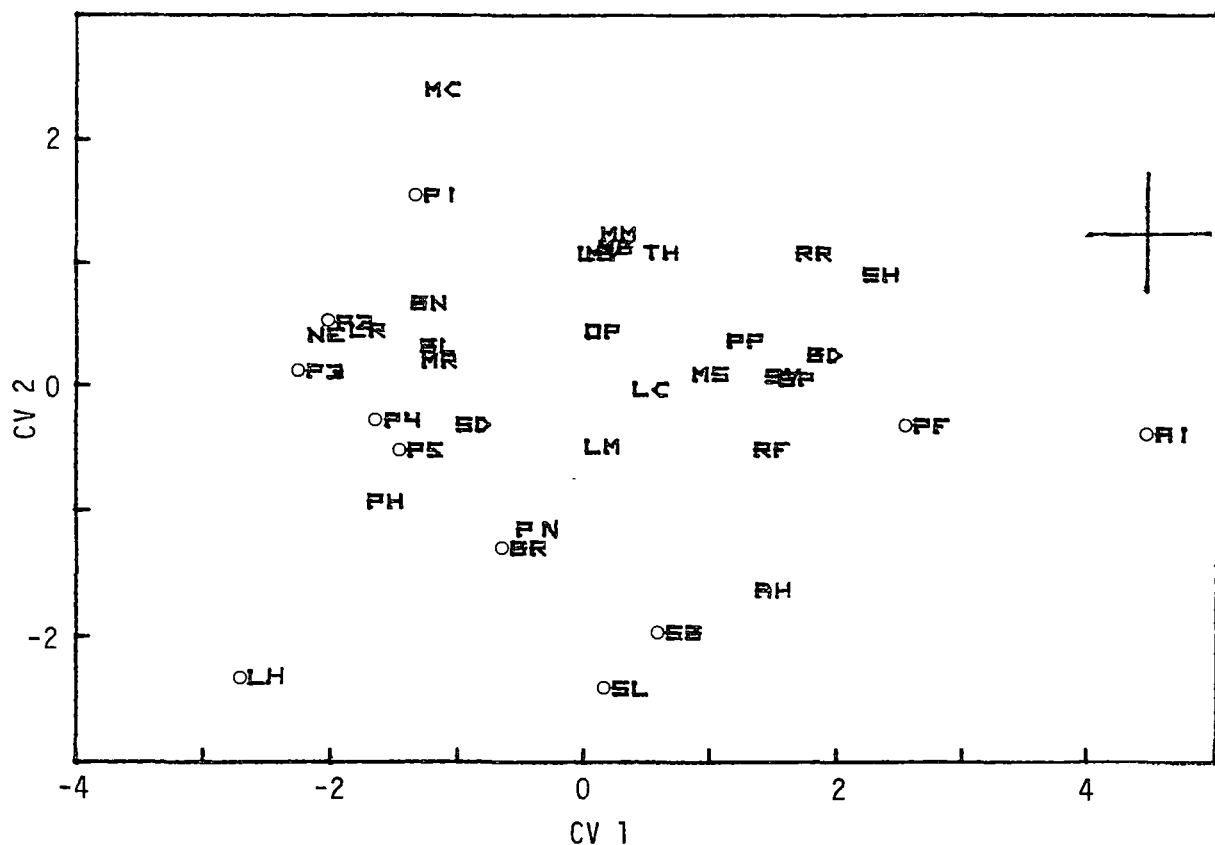


Fig. 1.18. CVA of the 15 morphometric characters. Population means on the first three canonical variates (CV_1 , CV_2 and CV_3 ; Table 1.10). The 95% confidence limits are based on $n=20$ and populations along the Pine Lake and southern Plateau transects are marked (0).

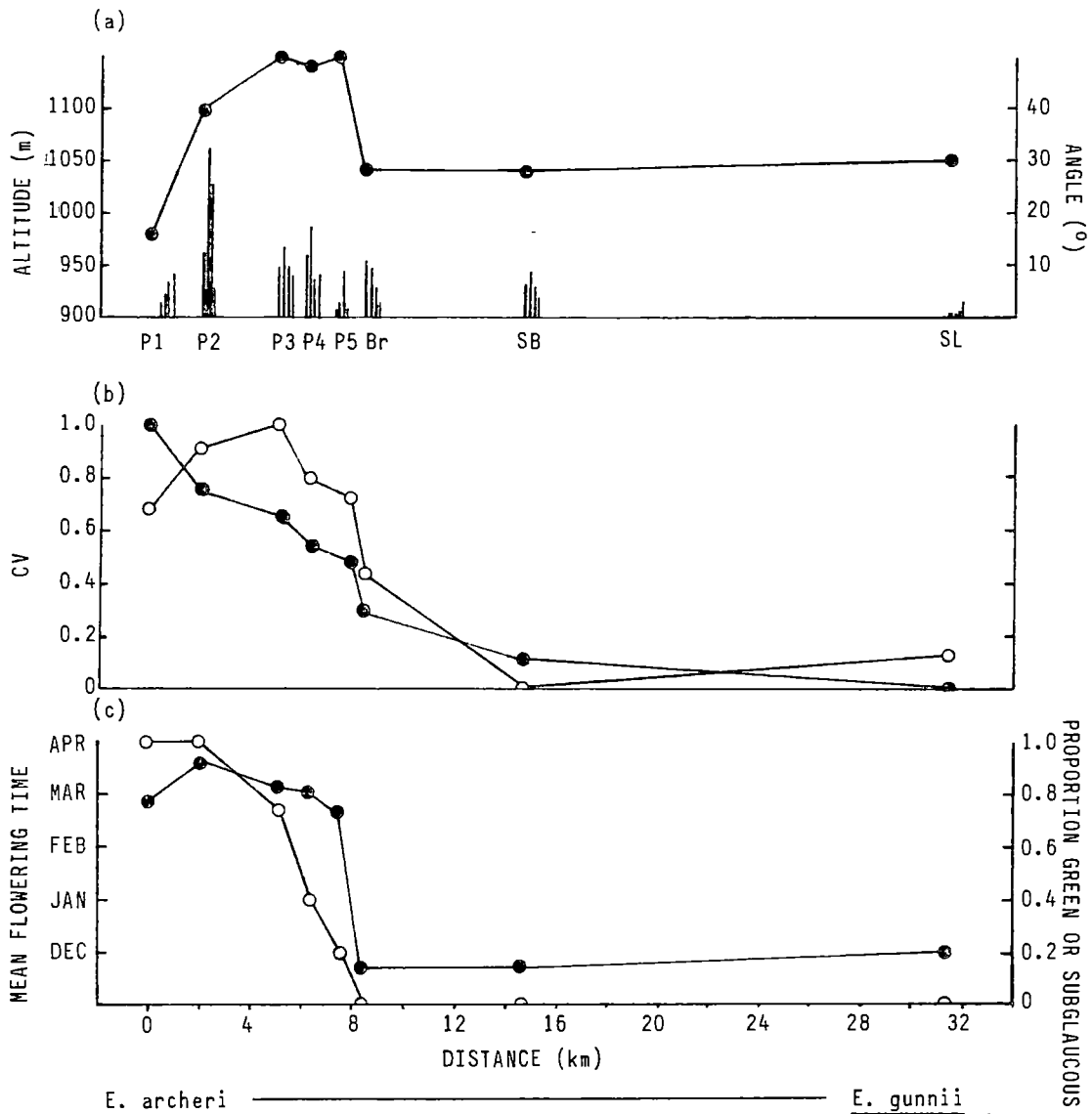


Fig. 1.19. Environmental and phenetic variation along the Pine Lake transect.

(a) Variation in altitude (●) and horizon cut-off angles (°) taken from NW, W, SW and S bearings.

(b) Variation in CV1 (○) and CV2 (●), derived from CVA of the 15 morphometric characters (see Table 1.10; Fig. 1.18). Values are standardized to have a range of 1.

(c) Variation in the proportion of individuals classified as either green (GLAUC=0) or subglaucous (GLAUC=1) as opposed to glaucous (GLAUC=2,3 or 4) (○) and the mean flowering time in the 1980 season (●) (see Fig.1.31).

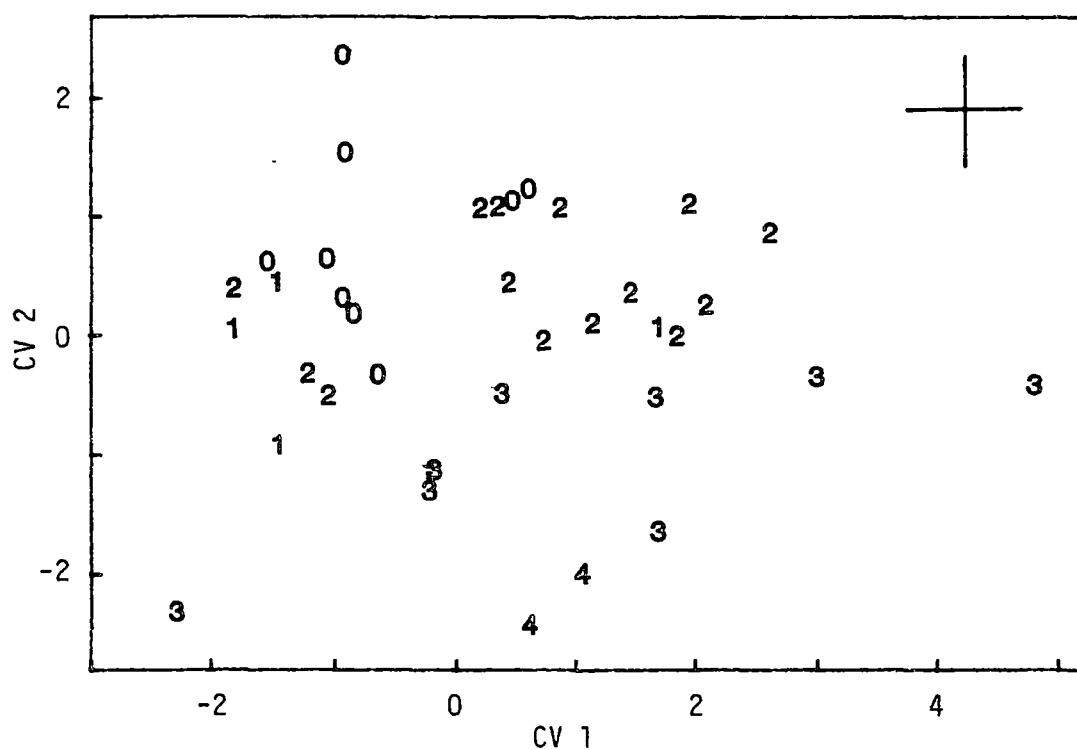


Fig. 1.20. Variation in glaucousness in relation to the main directions of morphometric differentiation. CV_1 and CV_2 are derived from CVA of 15 morphometric characters (see Fig. 1.18; Table 1.10). Population glaucousness values correspond to the average glaucousness score (GLAUC) rounded to the nearest integer (0=green, 4=highly glaucous).

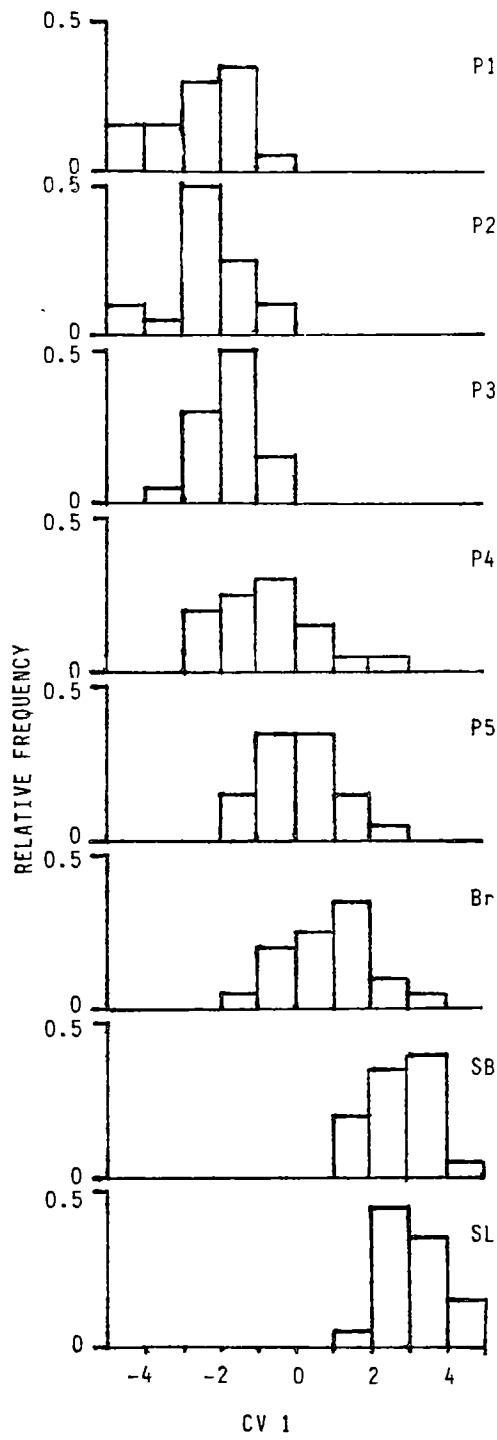


Fig. 1.21. Relative frequency histograms of individual scores along the main morphological cline differentiating populations along the Pine Lake transect. CV1 (70%) is derived from CVA of the 15 morphometric characters using only populations along the Pine Lake transect.

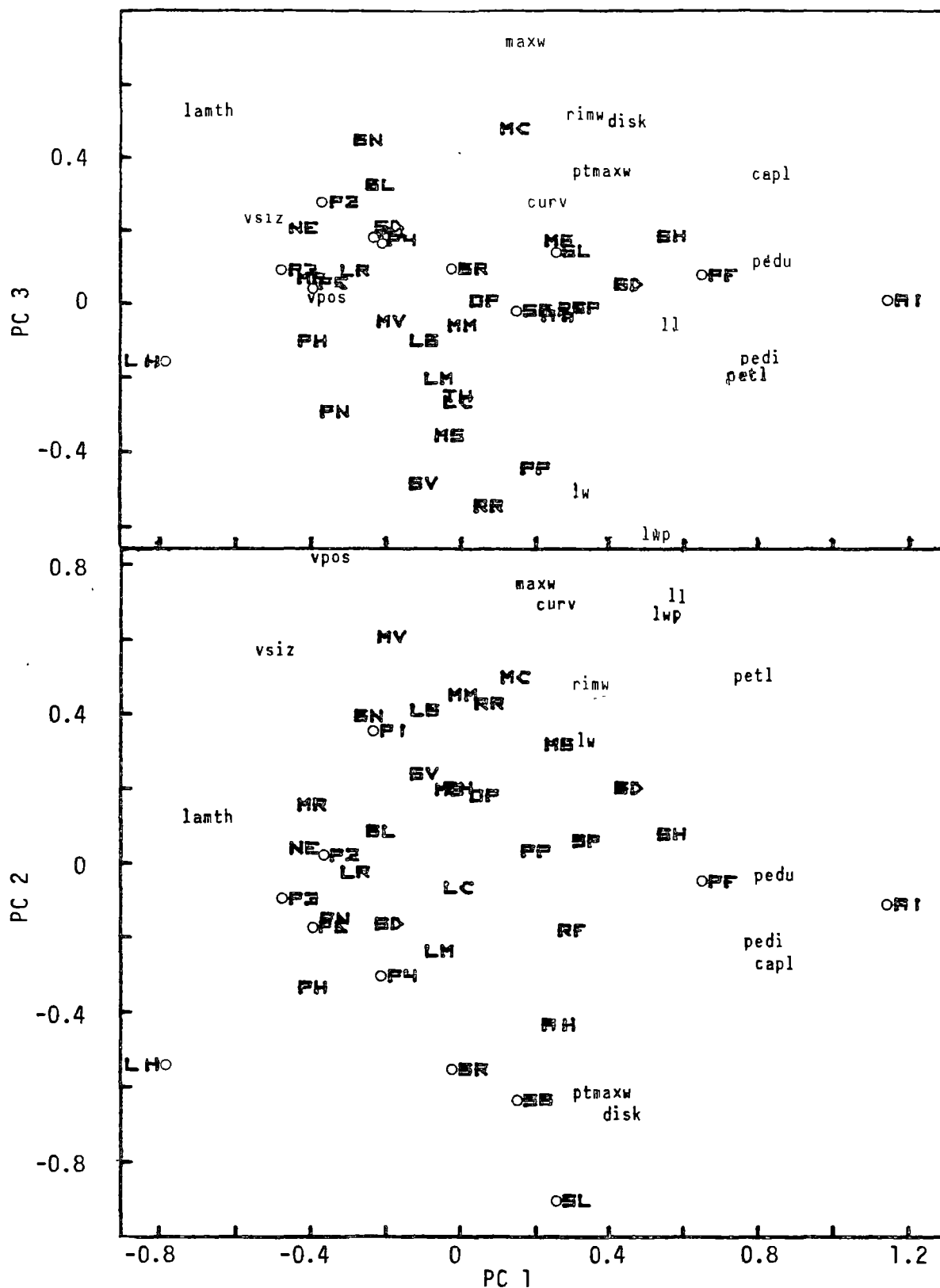


Fig. 1.22. PCA based on population means for the 15 morphometric characters. Population values are plotted for the first three PC's and the characters are ordinated in the same space with values corresponding to their correlation coefficient with the respective principal component. Populations along the southern Plateau and Pine Lake transects are indicated (o).

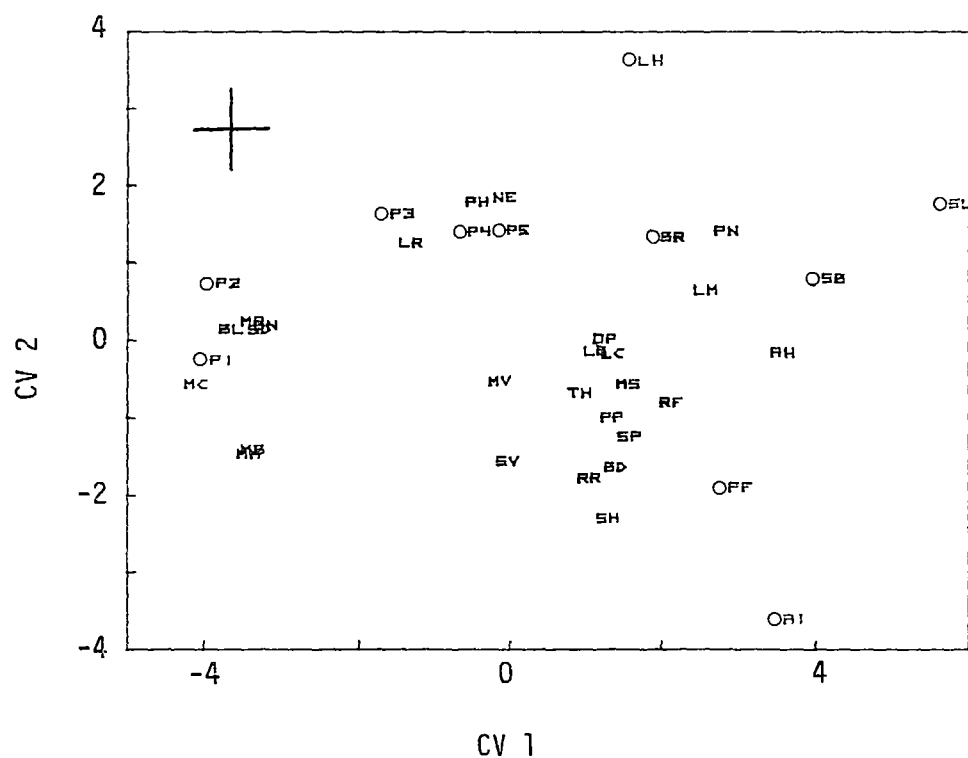


Fig. 1.23. CVA of the 15 morphometric character and glaucousness. Population means on the first two canonical variates (CV_1 and CV_2). The 95% confidence limits are based on $n=20$ and populations along the Pine Lake and southern Plateau transects are marked (0).

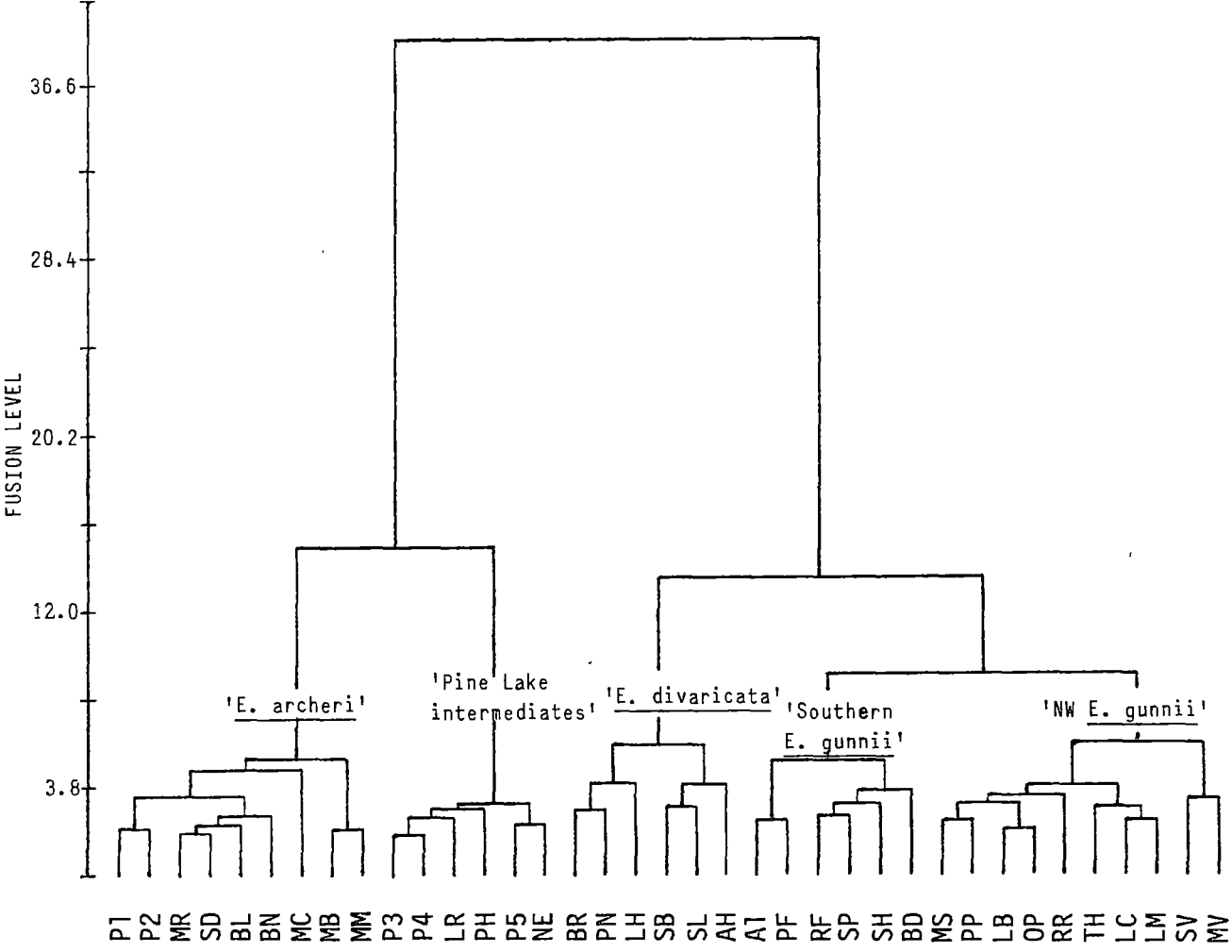


Fig. 1.24. Dendrogram from Ward's minimum variance clustering of populations based on the 15 morphometric characters and the glaucousness score.

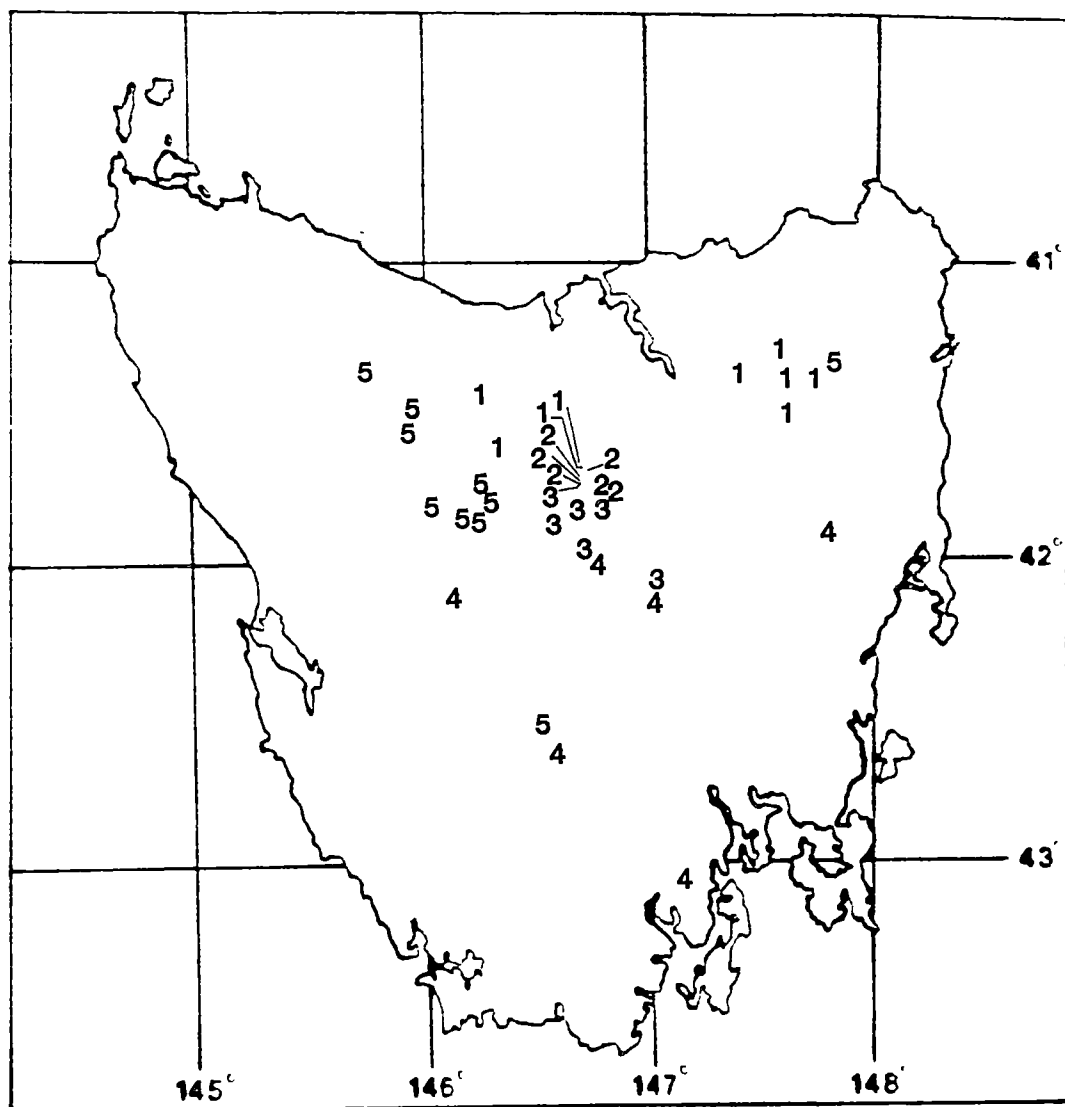


Fig. 1.25. Geographical distribution of the clusters defined at the 5 group level by the Ward's minimum variance classification shown in Fig. 1.24. Populations are grouped into phenetic classes corresponding to '*E. archeri*' (1), 'Pine Lake intermediates' (2), '*E. divaricata*' (3), 'southern *E. gunnii*' (4) and 'NW *E. gunnii*' (5).

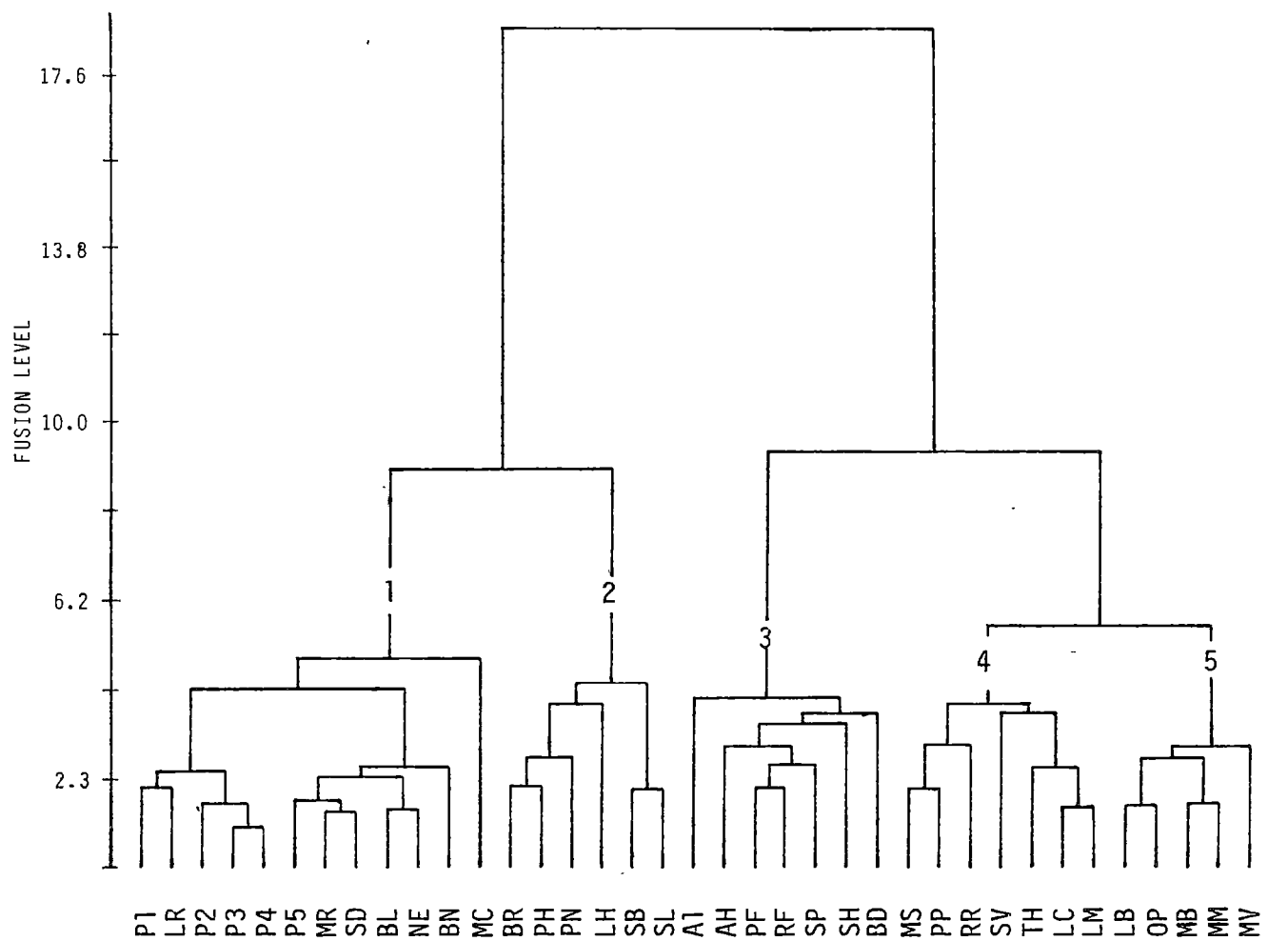


Fig. 1.26. Dendrogram from Ward's minimum variance clustering of populations based on the 15 morphometric characters.

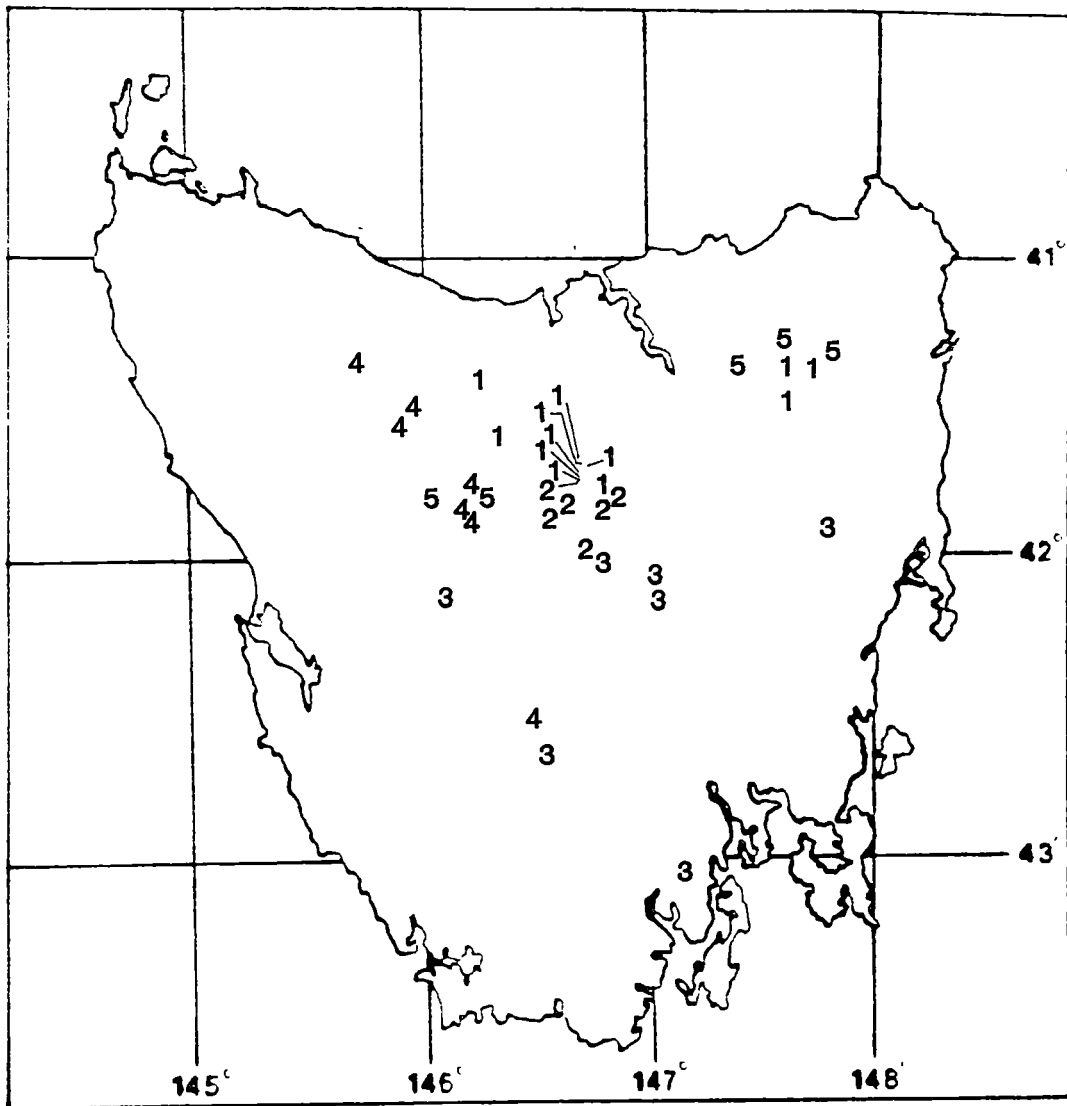
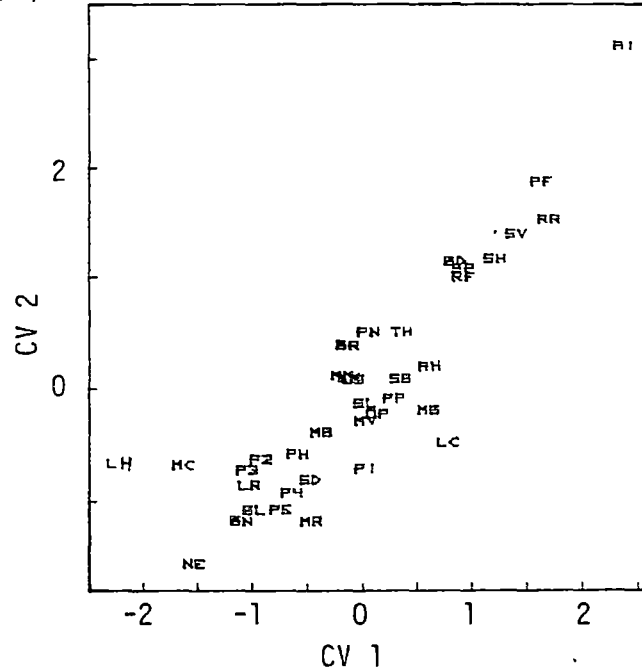


Fig. 1.27. Geographical distribution of the clusters defined at the 5 group level by the Ward's minimum variance classification shown in Fig. 1.26. Populations from cluster 5 are morphologically intermediate between clusters 1 and 4.

SET 1



SET 2

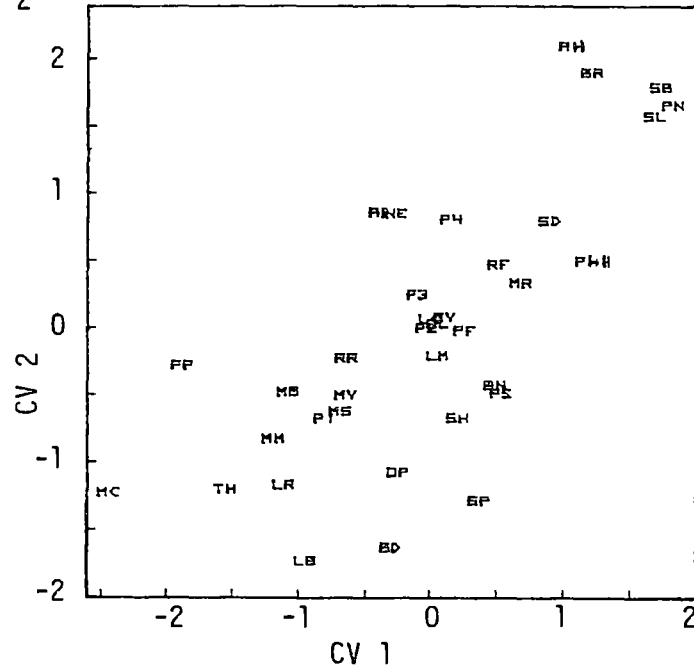


Fig. 1.28. Population means on the first two pairs of canonical variates derived from canonical correlations analysis of reproductive and vegetative character sets ($n=37$). Axes are weighted indices composed of vegetative (CV 1) and reproductive (CV 2) characters and sets 1 and 2 correspond to the first and second canonical correlations given in Table 1.11 respectively.

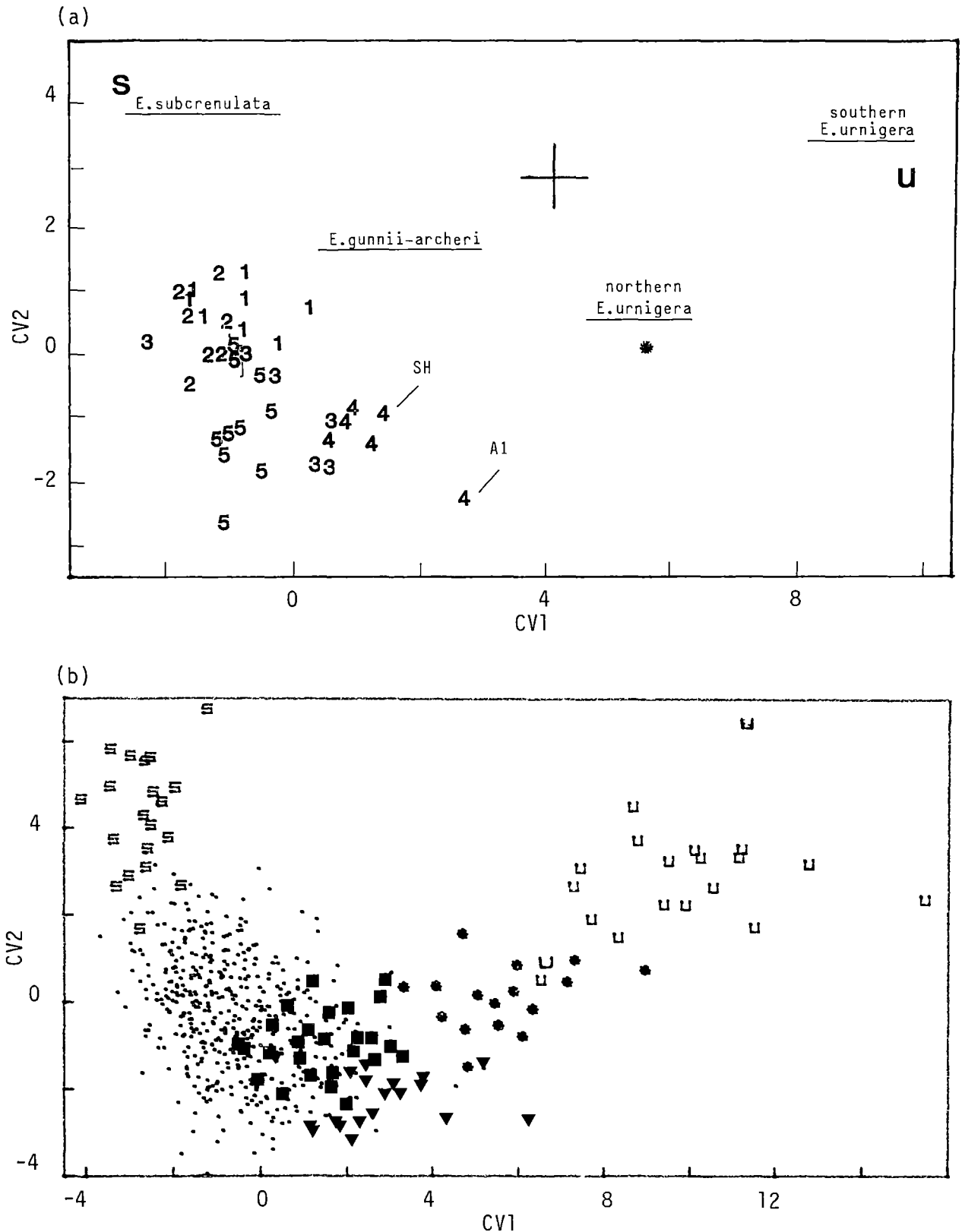


Fig. 1.29. CVA of populations of the *E. gunnii-archeri* complex, *E. subcrenulata* and *E. urnigera*. (a) Population means and (b) individuals of *E. subcrenulata* (s); *E. urnigera* (*=Alma Tier; u=southern mountains) and *E. gunnii-archeri*. In (a) the *E. gunnii-archeri* populations are grouped into phenetic classes corresponding to '*E. archeri*' (1), 'Pine Lake intermediates' (2), '*E. divaricata*' (3), 'southern *E. gunnii*' (4) and 'NW *E. gunnii*' (5) (Fig. 1.24) whereas in (b) individuals are indicated by dots with the exception of the Snow Hill (■) and Scrummies Marsh (▼) populations.

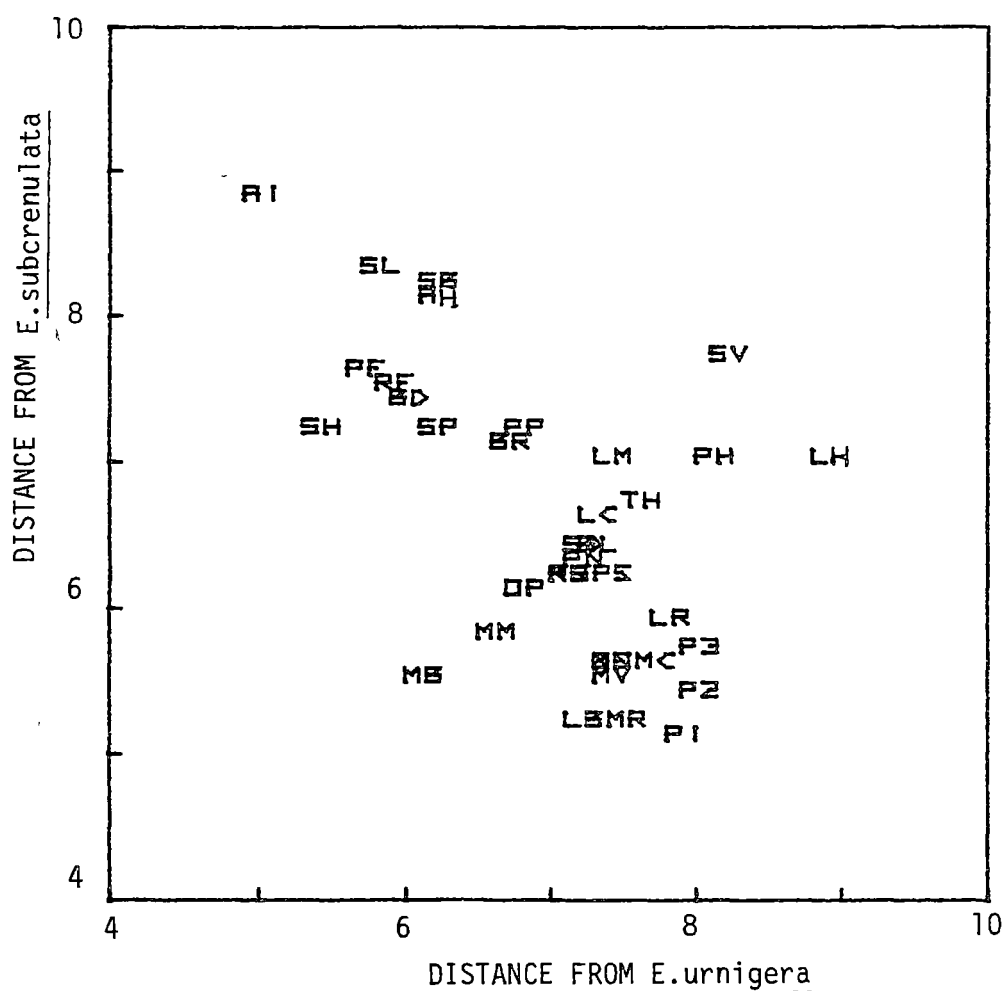


Fig. 1.30. Mahalanobis' distance of the *E. gunnii-archeri* populations from *E. subcrenulata* and *E. urnigera* (Alma Tier) samples. Population codes are detailed in Table 1.2.

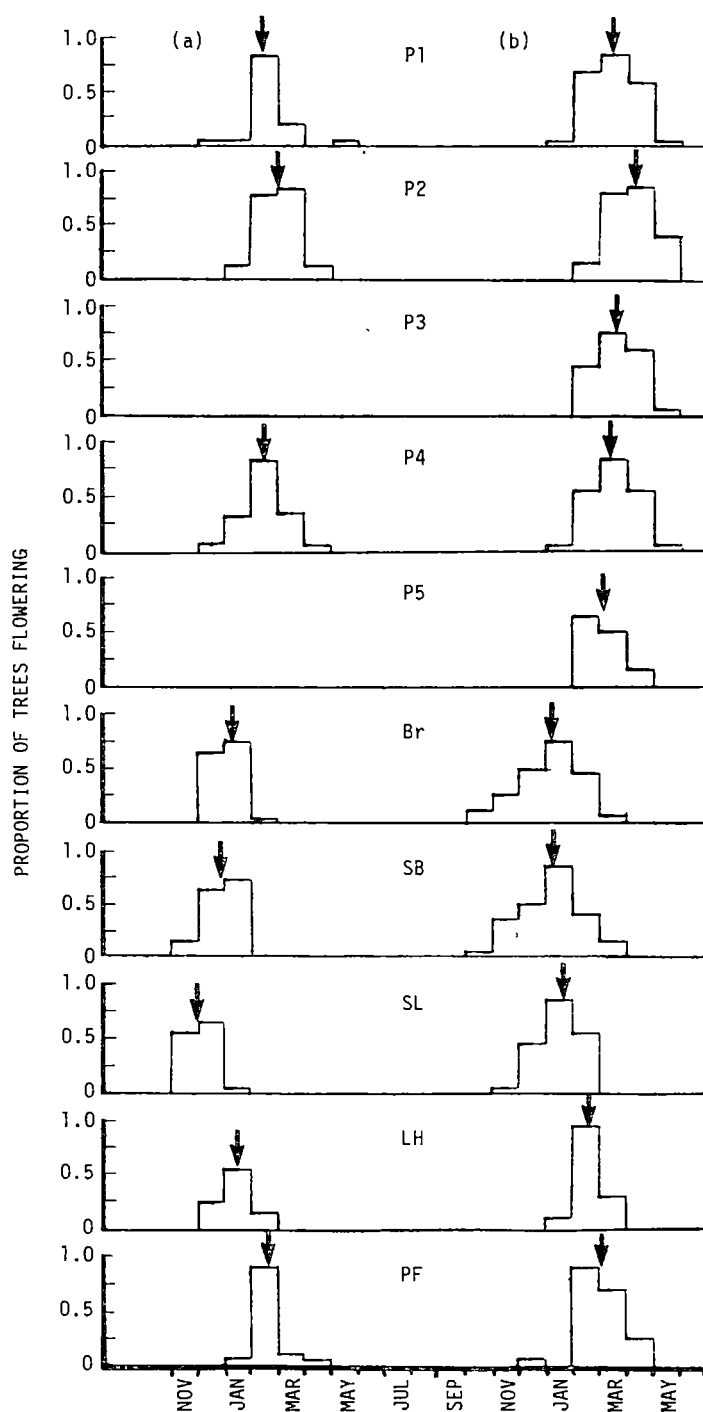


Fig. 1.31. The proportion of trees observed flowering in (a) 1979/80 and (b) 1980/81 growing season. The mean of each distribution is indicated (↓).

Variation in the *Eucalyptus gunnii*-*archeri* complexII. Variation in the seedling phenotype2.1 Introduction

Marked differentiation in the adult phenotype was demonstrated between populations of the *E. gunnii*-*archeri* complex in the previous chapter. A large portion of this phenetic variation was associated with differences in habitat and it is suggested that at least a component of the variation is adaptive. However, it is necessary to clearly differentiate between phenetic variation due to a plastic response to environmental heterogeneity (e.g. Bradshaw 1965, 1974; Wu and Jain 1978) as opposed to genetic differentiation and evolutionary divergence (e.g. Turesson 1922; Clausen *et al.* 1940; Jain and Bradshaw 1966). In *Eucalyptus*, as with most forest tree genera (see Sterne and Roche 1974; Wright 1976; Hamrick 1976), estimates of the genetic component associated with variation in the adult phenotype rests, by necessity, on comparisons of seedling characters in open pollinated progenies (e.g. Pryor 1957a; Green 1971; Ladiges and Ashton 1974; Kirkpatrick 1975a; Gillison 1976; Slatyer and Ferrar 1977; Clucas and Ladiges 1979; Phillips and Reid 1980; Ladiges *et al.* 1981). In many *Eucalyptus* species, including *E. gunnii*-*archeri*, this involves a comparison of the pattern of variation in completely different life history phases associated with marked heteroblastic variation.

This chapter reports on variation between populations in seedling growth and phenotype when open pollinated *E. gunnii*-*archeri* progenies are grown in a common environment. In addition, the degree of genetic variation underlying differences observed in the adult phenotype is examined. Results are presented from two separate progeny trials. The first involves two year old seedlings from seven populations and concentrates on variation along the southern Plateau transect as well as representative populations classified as *E. gunnii*-*archeri*. The second trial involves a larger number of populations and individuals and concentrates on variation along the phenetic continuum between *E. gunnii* and *E. archeri* as well as between the northern *E. gunnii*-*archeri* populations.

2.2 MethodsTrial 1

Populations used in the first progeny trial as well as the number of mothers and total number of seedlings for which a full data set was available are given in Table 2.1. Seedlings used in this trial were part of a larger

trial discussed by Potts (1978) involving a broad survey of the superspecies *Gunnii*. Seedlings were initially grown in a semi-random design in F.H. 408 (3.8 x 7.5 cm) paper pot strips under glasshouse conditions and natural photoperiod. These were later transferred outdoors and after 10 months were repotted into 17 x 19 cm cans filled with potting mix. Outdoors, seedlings were arranged into 4 randomized blocks, watered regularly and supplied with $\frac{1}{4}$ strength Aquasol solution once every two weeks. These seedlings were scored in March 1979 for the characters listed in Table 2.2 and later transferred to the experimental gardens discussed in Chapter 3. Three leaves were collected from consecutive nodes generally commencing at node 20 (cotyledons = 0). In all cases, the leaves collected were expanded outdoors in the same growing season. The thickness of each leaf was recorded when removed using a spring loaded micrometer and the leaf dimensions shown in Fig. 2.1 were digitized from photocopies of pressed leaves in the same manner as described in Chapter 1. Leaf dimensions (including LAMTH) for each seedling represented the average measurements from the 3 leaves. Scoring of multistate characters was achieved by comparison with standards.

Trial 2

The second trial was designed with two main objectives. These were, firstly, to examine in detail seedling variation along the continuum between *E. gunnii* and *E. archeri*, (i.e. Pine Lake transect) and secondly, to assess genetic variation in seedlings' characters between northern populations of the complex. Populations used in this trial and the number of seedlings for which the full data set was available are indicated in Table 2.3. Each population was represented by 10 families grown from open pollinated seed collected from individuals sampled in the survey of adult variation (Chapter 1) and where possible, selected to evenly encompass the full geographical area sampled at each site. An estimate of the variability within each family was required for trees along the Pine Lake transect (see Chapter 4) and thus an attempt was made to grow 18 seedlings from each mother selected from these populations. Only 6 seedlings per mother were grown for other populations. However, due to mortality, a maximum of 150 and 50 seedlings per population respectively were scored and where possible, these were equally distributed amongst families.

A maximum of 50 well filled seeds from each mother was weighed and then germinated on germination pads under continuous light. The light was provided by a mixed florescent-incandescent source and the temperature held at 22°C. The germination was monitored daily and the seedlings planted were usually the first to germinate. Seedlings were planted into 6 blocks of F.H.

(5 x 7.5 cm) paper pot strips. Each block, consisting of 420 pots, was mounted in a wooden tray over a 3-4 cm layer of gravel and filled with potting soil. Blocks were treated as comprising 10 rows of 40 pots with each population from the Pine Lake transect represented three times and the remaining populations once per row, resulting in 40 site positions. These positions were allocated over rows using a latin square design for the first 40 rows, half of which was repeated for the last 20 rows. Seedlings from each mother were randomly allocated to population positions within this arrangement and each block comprising 400 seedlings was surrounded by an edge row. The seedlings were grown in a glasshouse under an 18 hour photoperiod and after two months, a $\frac{1}{4}$ strength Aquasol nutrient solution was applied weekly. The natural photoperiod was extended using a mixed florescent-incandescent light source.

The seedlings were scored for the characters listed in Table 2.4, with the final scoring and leaf collections occurring 6 months after planting. A single leaf was collected from each of the 9th, 10th, 11th and 15th leaf pairs (cotyledons = 0) and the dimensions shown in Fig. 2.1 measured as previously described. Leaf dimensions used in the morphometric analyses for each seedling represent the average of measurements taken from the 9th, 10th and 11th node leaves.

Statistical techniques utilized in the analysis of both trials have been described in Chapter 1. Population differentiation in the qualitative characters was tested using the chi-squared test of association (Table 2.9) and results presented as the relative frequency of key classes or as mean values (Fig. 2.4). The relationship between seedling and adult characters was investigated at the univariate and multivariate level, the latter involving the comparison of sets of seedling and adult characters by canonical correlations analysis (e.g. Gillison 1976). The seedling phenotype for each mother was estimated from the mean value of its offspring. Morphometric data for mothers used in Trial 1 were collected previous to this study (Potts 1978) and only include 13 of the 15 morphometric characters (excluding CURVE, VPOS and VSIZ) used in Chapter 1. The full adult data set was available for the 70 mothers used from Trial 2.

2.3 Results

Genetic differentiation between populations

Trial 1

A partition of the variation in seedling characters (Table 2.5) indicates that in a common environment a large component (68-95%) is accounted for by variation between progenies. The major source of genetic variation between progenies is a result of significant ($P < 0.001$) differences between taxa (i.e. *E. archeri* and *E. gunnii* populations) and between populations within taxa (Table 2.5). However, significant variation in most characters was evident between progenies within populations which, assuming random mating within populations, directly reflects significant differences in the genotype of trees from the same site.

The major component of variation in most cases is associated with differences between *E. archeri* and *E. gunnii* populations. This is clearly shown by the CVA of populations based on either the full suite of seedling characters (Table 2.6; Fig. 2.2) or leaf dimensions alone (Table 2.7; Fig. 2.3). In the space defined by the ordination in Fig. 2.2, populations form two discrete clusters with virtually no overlap in the distribution of individual seedlings of either taxa. The Mahalanobis' distances between populations (Table 2.8) indicate greater genetic differentiation in seedling characters between populations of either taxa than between populations classified as the same taxa. For the *E. gunnii* populations, this contrasts with the adult phenotype, where morphological differentiation along the southern Plateau transect (e.g. LH vs Pf) was more comparable with that between extreme populations along the Pine Lake transect (e.g. P₁ vs SL) (Table 2.8b; Figs. 1.18, 1.22). However estimates of population dissimilarity based on the total adult character set (i.e. including glaucousness; Fig. 1.23; Table 2.8a), and from which the classification given in Fig. 1.24 is based, are strongly correlated ($r = 0.87$; $P < 0.001$) with estimates of dissimilarity based on genetic differences in the seedling phenotype (Table 2.8). Despite significant, genetically based variation in the seedling phenotype (which within the *E. gunnii* populations was measured across extremes of the altitudinal range (600-1150 m), the genetic differentiation between populations in most seedling characters appears to be relatively small when compared to the variation between the taxa *E. gunnii* and *E. archeri* (Table 2.5; Figs. 2.2 and 2.3).

The character weightings on the canonical axis which differentiates *E. archeri* and *E. gunnii* populations in Fig. 2.2 (see Table 2.6) indicate that the main differences between *E. archeri* and *E. gunnii* populations involve parallel variation in glaucousness (Table 2.9; Fig. 2.4o), stem verrucae (Table 2.6; Fig. 2.4q), leaf shape and thickness (Table 2.6; Figs. 2.4a-f and 2.3), and growth rate (e.g. Figs. 2.4g,h). The juvenile leaf shape of *E. archeri* seedlings differs markedly from that of the *E. gunnii* populations (Fig. 2.3) and a similar difference in leaf shape is noted between green and glaucous forms of *E. urnigera* (Barber and Jackson 1957). In the *E. gunnii-archeri* complex, as in many *Eucalyptus* species, leaves in the juvenile phase are opposite and sessile and the transition to the adult phase involves a continuous change, with leaves becoming alternate, more lanceolate and petiolate. The frequency of seedlings developing intranodes and petioles differs significantly between taxa (Table 2.9; Fig. 2.4r) with *E. gunnii* populations retaining the juvenile phase later in both a developmental (i.e. node of transition) and temporal sense. However, within *E. gunnii* this varies clinally with altitude with the higher altitude populations (LH and SL) retaining the juvenile phase longer than low altitude forms (Pf and SP). This is not a result of differences in the rate of node expansion (Fig. 2.4k; Table 2.9) and represents genetic differences between populations in ontogenetic development. The difference in leaf shape between *E. gunnii* and *E. archeri* populations is not directly a result of measuring 'intermediate' type leaves in *E. archeri* as differences of a similar magnitude were observed using seedling leaves from the 5th node (Potts 1978).

The main differences between populations within taxa involves parallel trends associated with altitudinal variation and this is described by the second canonical axes in both Fig. 2.2 and Fig. 2.3. Variation in leaf dimensions within taxa (Figs. 2.4a-f) appear to mainly relate to changes in juvenile leaf size whereas variation in juvenile leaf characters between *E. gunnii* and *E. archeri* appear to involve an actual shape change (Fig. 2.3). Several characters vary clinally with altitude, and these are generally associated with extension growth such as internode length (Fig. 2.4n), leaf size (Figs. 2.4a-c and 2.3) and as noted previously, the development of the intranode and petiole. Furthermore, growth rate as measured by seedling height (Fig. 2.4g) and stem diameter (Fig. 2.4h) decreases with increasing altitude and apical dominance is less pronounced in higher altitude populations (Fig. 2.4l). The relative differences in seedling height accord with the relative height of the mature trees, with the obvious exception of the population at Snug Plains (SP). The Snug Plains population consists

of mallees with stems less than 2 m high whereas its seedlings are, on the average, the tallest of the populations examined. This suggests that the mallee habit displayed by many of the low altitude populations on button-grass plains is a result of environmental modification, most likely due to frequent burning of the button-grass habitat. The degree of red colouration of the young stems (ANTH) due to the presence of anthocyanins (see Barber 1956; Sharma and Crowden 1974) clinally increases with decreasing altitude (Table 2.9; Fig. 2.4p) and reaches maximum expression in the closed low altitude forest site at Projection Bluff (P_1). A steep cline occurs between contiguous low (P_1) and high (P_2) altitude sites at Projection Bluff with an increase in the frequency of green stemmed seedlings from 2.9% to 29.1% over 2 km ground distance. Wilcox (1982) describes variation in anthocyanin content of the undersurface of seedling leaves which is polymorphic and Barber (1965) considers variation in the anthocyanin content of young expanding leaves in both *E. urnigera* and *E. dalrympleana* to be also polymorphic. However, in the present study the variation was continuous with seedlings mainly varying in the intensity of red colouration on the young stem. Lignotuber development is least in the populations from the mixed eucalypt/rainforest habitat beneath Projection Bluff (P_1 and P_2) and greatest in the population from the open woodland, 'frost hollow' habitat (SL) (Fig. 2.4j). This is in accordance with the trend noted in other species (e.g. Ladiges and Ashton 1974; Ashton 1981b) for an increase in lignotuber development in areas prone to frequent drought and fire such as "open-forest, woodlands and 'tree' heath environments." The progeny trials discussed in Chapter 3, clearly indicate that the open woodland habitat (SL) is the most environmentally stressful for seedling establishment and the probability of seedling survival following initial establishment is the lowest whereas it is greatest at the Projection Bluff site (P_2).

These results clearly indicate that marked genetic differentiation is maintained within continuous stands and this may occur over relatively short distances between contiguous populations (e.g. Pf and SL; P_1 and P_2). Significant differentiation occurs along the southern Plateau transect (LH, SH, Pf) with most characters varying clinally with altitude. Not all characters show this clinal trend and several have optima in the centre of the altitudinal gradient (e.g. glaucousness, Fig. 2.4o; lignotuber development, Fig. 2.4j). This appears to be fairly common (e.g. Ashton 1958; Phillips and Reid 1980) and in many cases is possibly the result of interaction with a secondary environmental gradient (e.g. Fig. 1.18), although at a multivariate level, this must be clearly distinguished from artifacts

of the analytical technique (e.g. Austin and Noy-Meir 1971). Similar genetic variation with altitude to that observed has been described in a taxonomically diverse range of *Eucalyptus* species (e.g. Pryor 1957a; Barber 1955, 1965; Barber and Jackson 1957; Jackson 1960b; Green 1969a; Eldridge 1972). The genetic response to variation in altitude involves correlated variation in a large number of characters. For the examples discussed by Barber (1965) it is suggested independent acts of selection as opposed to pleiotropic gene action is the major cause of correlation. In the present study there is some evidence that pleiotropic gene action may partly explain the correlated response in several characters. For example, within populations, there are significant positive ($P < 0.01$) correlations between measures of growth rate (e.g. HT and DIA) and characters associated with leaf size (e.g. LL and LW). This suggests variation in the latter characters may be partly a pleiotropic effect of variation in general growth rate which appears to universally decrease at high altitudes (e.g. Pryor 1957a; Barber and Jackson 1957; Ashton 1958; Jackson 1960b; Hamrick 1976) as well as in many other ecologically extreme habitats (Parsons 1968c). Nevertheless, characters such as lamina thickness (LAMTH) and anthocyanin intensity (ANTH), within groups, appear to vary relatively independently of each other and the growth measures, which suggest correlated variation with altitude, are a result of these characters being selectively linked.

Trial 2

As in Trial 1, the majority of the genetic variation in seedling characters is distributed between populations (Table 2.10) and this is summarized in the canonical variate ordinations shown in Figs. 2.5 and 2.6 based on the total (Table 2.11) and seedling leaf (Table 2.12) data sets respectively. The minimum variance clustering of populations derived from the adult samples (Fig. 1.24) accounts for a major component of the variation between populations (Table 2.10). Significant differences between clusters were observed in all seedling characters (Table 2.13) which indicates that the clusters recognized in Chapter 1 (Fig. 1.24) are genetically defined. All clusters are well represented in this trial with the exception of the 'southern *E. gunnii*' cluster which only includes the Snow Hill (SH) population. Nevertheless, similar genetic differences between more representative populations of this cluster (e.g. SP and PF) and populations from the '*E. divaricata*' and '*E. archeri*' clusters were shown in Trial 1.

Pine Lake transect

Populations assigned to the '*E. archeri*' and '*E. divaricata*' clusters are markedly differentiated on adult (e.g. Figs. 1.18 and 1.23) and seedling (e.g. Figs. 2.2, 2.3, 2.5, 2.6; Table 2.13) characters. Nevertheless, seedlings grown from populations sampled along a geographical continuum between extreme populations on the Central Plateau (i.e. Pine Lake transect, P₁ to SB) clearly indicate that these populations form a clinal series with the *E. divaricata* and *E. archeri* morphs representing extremes of a genetic continuum (Figs. 2.5, 2.6, 2.7, 2.8, 2.9). This clinal trend is slightly offset in one of the geographically intermediate populations (P₄; Figs. 2.5 and 2.6) possibly due to this site being more sheltered than its immediate neighbours (P₃ and P₅). The main canonical vector describing this cline (Fig. 2.7) accounts for 77% of the variation between these populations and mainly contrasts lamina length (LL) and glaucousness (GLAUC) against the distance to the widest point (LWP). The continuous nature of the variation along this vector is shown in Fig. 2.7 and it is clearly seen that the cline involves a gradual change in phenotype as opposed to the frequency of distinct morphs. Phenotypes intermediate between the *E. archeri* and *E. divaricata* morphs are common and dominate fairly extensive, transitional populations north of Great Lake. Furthermore, intermediate populations extend beyond this area of parapatry (Figs. 2.5 and 2.6) also occurring as disjunct stands in the upper Mersey Valley region (TH, LC, LB and LM). However these western populations vary in a clinal manner from those north of Great Lake (Figs. 2.5 and 2.6), a trend also evident in the adult phenotype (Figs. 1.18 and 1.23).

Variation in non-structural, waxy glaucousness (see Barber 1955; Hallam and Chambers 1970) is a prominent feature of this cline and has been previously described for field samples of both juvenile and adult foliage (Barber 1955; Chapter 1). The data presented in Table 2.17 indicate that these clines have a genetic basis and there is a strong correlation ($r = 0.87$; $P < 0.001$) between the maternal and progeny mean glaucousness score. Glaucousness on both adults and juveniles reaches maximum intensity in the '*E. divaricata*' populations around Great Lake and seedlings from these trees were virtually all highly glaucous (e.g. SL - Table 2.9, Fig. 2.40; SB - Table 2.3, Fig. 2.9). Seedlings from '*E. archeri*' mothers (e.g. P₁ and P₂) were usually subglaucous, even from trees with green adult foliage, with only 2.7% classified as green (GLAUC = 0). The cline in glaucousness along the Pine Lake transect involves the gradual increase in the intensity, persistence and distribution of waxy glaucousness

on the seedling. Variation in the intensity is associated with the changes in structure and density of cuticular tube wax as exemplified in the scanning-electron micrographs in Figs. 2.10 and 2.11 which is similar to that reported in other species (e.g. Hall *et al.* 1965; Hallam and Chambers 1970; Cameron 1970). The intense glaucous appearance results from clusters of long wax rodlets or tubes whereas the cuticle surface of green or subglaucous forms appears smooth or the wax is deposited as flat flakes (Fig. 2.10). Hall *et al.* (1965) note that in *E. urnigera* the rodlets are deposited over the flat flakes and the varying grades of glaucousness correspond to changes in the proportion of the two types of wax which differ in their chemical structure. The cline in glaucousness along the Pine Lake transect differs from that described in *E. urnigera* (Barber and Jackson (1957) in that extreme morphs are less differentiated and the cline is less steep. The *E. archeri* seedlings rarely exhibit the shiny appearance and smooth cuticle of the green forms of *E. urnigera* (Fig. 2.10; Potts 1978).

The genetic mechanisms controlling the expression of glaucousness in *Eucalyptus* is not fully known, although most workers consider that the inheritance of glaucousness is probably relatively simple, but multifactorial, and is affected by modifiers (Barber 1955, 1965; Barber and Jackson 1957; Paton 1981). Barber (1955) reports a fully glaucous *E. gunnii* mother from Breona giving a fairly sharp segregation of green and glaucous seedlings, with some variation in the glaucousness which suggests modifiers were segregating as well as a major gene. He suggests the cline in glaucousness along the Pine Lake transect may involve a clinal change in the frequency of alleles at at least two loci. In the majority of progenies examined in the present trial (from 70 mothers) variation in glaucousness grade within progenies was continuous, unimodal and suggestive of the cline involving variation in genes modifying the expression of glaucousness (possibly polygenes) as opposed to a major gene controlling the presence or absence of wax. This contrasts with the steep cline in *E. urnigera* where segregation is often fairly sharp which suggests the cline may primarily involve major genes, although minor genes are obviously also involved. It has been suggested (Phillips 1979) that this contrast may reflect a basic adaptive difference in the genetic control of character variation between topocline as opposed to steep ecocline situations (e.g. Stebbins 1950; Grant 1971).

Genetic differentiation between isolated populations on the NE mountains

The populations of the *E. gunnii-archeri* complex on the NE mountains comprise small disjunct populations with the majority (BL, MB, SD and BN) occupying the tree-line habitat on isolated mountain peaks. However the populations on Mt. Maurice (MM) and Mt. Victoria (MV) occupy different lower altitude sites. The similarity in habitat as opposed to geographical proximity is reflected in the degree of genetic divergence of these isolated populations. The tree-line populations from widely separated mountain peaks appear relatively similar in seedling phenotype (Figs. 2.5, 2.6 and 2.12) and clearly differentiated from the lower altitude sites (MM and MV). With the exception of the Mt. Victoria population, these north-eastern populations form a clinal series with a relative increase in leaf length with decreasing exposure (Figs. 2.6 and 2.12). The phenotype of the Mt. Maurice population appears to be an extension of this clinal trend (Figs. 2.5, 2.6 and 2.12). On the other hand, the population on the low altitude marsh at the base of Mt. Victoria is unique, for this area, in its habitat as well as for seedling and adult morphology (e.g. Figs. 1.25 and 2.12). It is mainly differentiated from the other NE population on the degree of glaucousness and leaf morphology. The seedling leaves of this population are the narrowest in the complex (as measured by $\log LL/LW$; Figs. 2.6 and 2.13) while the seedlings are usually glaucous and comparatively late in the development of the petiole and intranode (Table 2.3). This contrasts with the normal trend in the complex for narrower leaves to be associated with a decrease in glaucousness (Fig. 2.13) and the earlier development of the petiole and intranode (e.g. MM, SV; Table 2.3).

The Mt. Victoria population is the smallest population in the NE mountains and its divergence could be explained in terms of drift. However this is unlikely for several reasons. Firstly, small disjunct stands of a similar population size also occur in the upper Mersey Valley (e.g. TH, LB and LM), yet divergence between these populations was not as marked as between the NE populations (e.g. Figs. 2.5 and 2.6). While this may reflect several factors such as similarity of habitat, geographical proximity or less time since isolation, it provides circumstantial evidence against drift alone being a major factor in population differentiation. Secondly, populations occupying habitats in other areas which superficially appear similar to the Mt. Victoria site (e.g. SP, LM) are glaucous which suggests this character is of selective advantage in such habitats. However, comparable populations do not exhibit the narrow juvenile leaf shape.

The most likely explanation for the unique characteristics of the Mt. Victoria population involves both adaptation to a specific habitat as well as gene exchange with the surrounding low altitude species, particularly *E. rodwayi* (series *Ovatae*). *E. rodwayi* has narrow-green juvenile leaves and a number of suspected *E. rodwayi* x *E. gunnii* hybrids were excluded from the population sample. Progenies grown from these suspected hybrids segregated a broad spectrum of phenotypes ranging from glaucous-broad to green-narrow leaved forms. This suggests hybridization is actively occurring in this population and it is quite likely that introgression of *E. rodwayi* genes into the population has contributed to its differentiation from neighbouring populations. As noted previously (Chapter 1.3), *E. rodwayi* replaces *E. gunnii* at lower altitudes as the species tolerant of poor soil drainage and in the NE highlands, it forms extensive populations on other poorly drained areas at a similar altitude to the Mt. Victoria site. In terms of altitude, this site appears marginal for the *E. gunnii*-*archeri* complex, although the severity of the site may be accentuated by local cold air drainage from the slopes of Mt. Victoria. Nevertheless, it is possible that the observed hybridization is a consequence of genetic invasion of the site by genes of the more widespread species *E. rodwayi* and heralds ecological replacement. *E. dalrympleana* may also prove to be implicated and hybrids with *E. gunnii* have been reported (e.g. *E. irbyi*, Curtis 1956; Pryor and Johnson 1971; Marien and Thibout 1979).

Correlation between the adult and seedling phenotype

In order to assess the degree to which variation in the adult phenotype reflected either environmental or genetic effects, the correlation between variation in the adult and seedling phenotypes was examined by comparison of individual characters as well as canonical correlations analysis of various sets of adult and seedling characters (e.g. Gillison 1976). Estimates of the parental seedling phenotype are based on the mean value of their progeny. In the present study this is not directly equivalent to the maternal breeding value (see Falconer 1960), being confounded with a genetic component associated with non-random mating.

Trial 1

A large portion of the variation in seedling values is associated with covariation in the comparable adult character (e.g. LAMTH, LL, LW, LWP, L.L.PET; Table 2.14). The highest correlation occurs for lamina thickness (LAMTH; $r = 0.9$; Fig. 2.14) suggesting a large genetic component to the

variation observed in the adults which is particularly significant in view of the high weighting given to this character along the major directions of variation in adult morphology (Table 1.10). Canonical correlations analysis of adult and seedling leaf character sets resulted in two significant canonical correlations (Table 2.15) which describe parallel variation in two independent directions (Fig. 2.15) and indicates a close relationship between variation in adult and juvenile leaf characters. The relationship between reproductive and seedling leaf character sets was weaker, with only one significant canonical correlation ($\sqrt{\lambda} = 0.75$; $P < 0.001$). This pair of canonical vectors described a similar arrangement of phenotypes as depicted in Fig. 2.15a, with pedicel and peduncle length and capsule width characters being the most highly weighted reproductive characters. Canonical correlations analysis based on the full set of seedling and adult characters resulted in two significant canonical correlations ($P < 0.001$) and the corresponding pairs of canonical vectors are given in Table 2.16 and individuals are ordinated in the space defined by each pair in Fig. 2.16. The first pair of canonical vectors describe variation in seedling phenotype which parallels altitudinal variation in the adult phenotype similar to that of the main direction of phenetic variation in the complex (i.e. CV_1 ; Fig. 1.18). The second pair of vectors (Fig. 2.16b) describe parallel variation in juvenile and adult phenotypes associated with differentiation between *E. gunnii* and *E. archeri* populations on the Central Plateau which is comparable with the second major direction of variation in the complex (i.e. CV_2 ; Fig. 1.18).

Pine Lake Transect (Trial 2)

Analyses based on the 70 trees from the Pine Lake transect similarly indicate a close relationship between clinal variation in the adult phenotype and genetically based variation in the seedling phenotype at both a univariate (Table 2.17) and multivariate level (Table 2.18; Fig. 2.17). Canonical correlations analysis of a range of seedling and parental character sets, in each case, yielded only a single significant canonical correlation and which directly described parallel clinal variation between the '*E. divaricata*' and '*E. archeri*' morphs. This is exemplified by the strong canonical correlation ($\sqrt{\lambda} = 0.93$; $P < 0.001$) between the full adult and seedling data sets (Table 2.18) depicted in Fig. 2.17 which is indicative of the trend obtained in other analyses. Trees from transitional populations (P_5 , P_4 , P_3) are clearly intermediate in both the adult and juvenile phenotype (Fig. 2.17). Clinal variation in adult phenotype along the Pine Lake transect (Figs. 1.18, 1.19 and 1.20) is thus directly correlated with a genetically based cline in the seedling phenotype.

2.4 Discussion

These analyses clearly indicate that parallel, genetically based, variation in the seedling phenotypes underlies the two major phenetic clines in the *E. gunnii*-*archeri* complex along the southern Plateau and Pine Lake transects (e.g. Figs. 1.18, 1.19, 1.20, 1.21, 1.22 and 1.23). Moreover, there is a significant correlation ($P < 0.001$) between the Mahalanobis' distances between populations determined from both adult and seedling character sets (Trial 1, $r = 0.87$, $P < 0.001$; Trial 2, $r = 0.57$, $P < 0.001$). This suggests a correspondence between phenetic and genetic similarity, with population differences as assessed from field samples of the adult phenotype generally reflecting the degree of genetic differentiation in the seedling phenotype. Populations at the geographical margins of the distribution (e.g. MV, SV) appear as genetic outliers to the main nucleus of the complex in both seedling (e.g. Figs. 2.5, 2.6 and 2.13) and adult analyses. Specific exceptions to this trend occur, involving both apparent convergence and divergence. For example, in a relative sense, populations along the southern Plateau transect appear more differentiated in the adult as opposed to the juvenile phenotype. In contrast, populations from Mt. Roland (MR) and Mt. Saddleback (SD) appear similar in adult morphology (Figs. 1.24 and 1.26) yet are clearly differentiated on seedling characters (Fig. 2.5). These anomalies could arise with a large environmental component to variation in adult characters and represent the result of phenotypic canalization, or alternatively arise from ontogenetic variation in the degree of genetic differentiation. In favour of the latter hypothesis, long term studies (e.g. Jackson 1960b; Barber 1965) indicate a large genetic component to phenetic variation in adult characters in *Eucalyptus*. In addition, ontogenetic variation in the degree of differentiation between populations has been reported (Jackson 1960b) and this is exemplified at the species level in the examples cited by Barber (1965). Closely related species may possess similar adult foliage and reproductive characters yet differ considerably in their juvenile phase (e.g. *E. viminalis* and *E. rubida*). In other species the reverse applies (e.g. *E. urnigera*, *E. morrisbyi* and *E. gunnii*). High pollen migration rates may mask genetic differentiation in the natural population resulting in convergence of progenies (e.g. Hamrick 1976). This may be significant in continuous stands where clines are steep (e.g. Br to P₅). However in much of the present study this is unlikely to be important, particularly over large areas where clines are shallow and population samples widely spaced or between disjunct stands due to gene flow limitations (see Chapter 8).

This study indicates that *E. gunnii* (*sensu* Pryor and Johnson 1971) is a polymorphic species comprising a multi-dimensional clinally varying series of highly differentiated populations. This multi-dimensional variation is summarized by classification of populations into 5 main phenetic groups which more or less correspond to morphs recognized in the literature as *E. archeri* and *E. divaricata*, their intermediates; and within *E. gunnii* (*sensu* Brett 1938); north-western and southern forms (Fig. 1.24). These phenetic groups are shown to be genetically differentiated. Nevertheless, when the full range of the species is examined, both geographically continuous and isolated populations form a clinal series with no discontinuity apparent between morphs. In part, population differentiation appears to result from the interaction of multi-character clines paralleling at least two major habitat gradients. These relate to a complex set of factors associated with variation in firstly exposure to the alpine environment and secondly a transition from the open woodland to the mixed eucalypt/rainforest habitat. *E. divaricata* and *E. archeri* morphs represent extremes of a genetic continuum and on the Central Plateau appear clinally differentiated mainly with respect to the latter habitat gradient whereas '*E. divaricata*' and the 'southern *E. gunnii*' morphs are differentiated on the former. All morphs appear as extensions of the same gene pool and the inclusion of *E. archeri* as a subspecies of *E. gunnii* by Pryor and Johnson (1971) accords with their taxonomic treatments of *E. pauciflora* (see Pryor 1957a; Green 1969b), *E. vernicosa* (see Jackson 1960a) and *E. globulus* (see Kirkpatrick 1974). For parity it is suggested that a more equitable and comprehensive partition of the ecological and geographical variation in the complex could be achieved by additional recognition of '*E. divaricata*', 'intermediates', 'north-western' and 'southern' morphs as subspecies or varieties of *E. gunnii*. While the recognition of 'cline-form' as a taxonomic category is against current conventions, the clinal nature of the variation between these morphs suggests they would be better conceived as 'cline-forms' of *E. gunnii*. This is analogous to the conception by Pryor (1957a) and Jackson (1960a) of the pattern of variation in *E. pauciflora* and *E. vernicosa* respectively.

Table 2.1 Populations used in Trial 1. For each population, the number of mothers and total number of seedlings for which the full data set was available are indicated. Site locations are given in Table 1.1 and Figs. 1.2 and 1.3.

Population		Code	Number of Mothers	Total Number of Seedlings
<i>E. archeri</i>				
Ben Lomond	(1230m)	BL	6	68
Projection Bluff low	(980m)	P ₁	6	71
Projection Bluff high	(1100m)	P ₂	6	55
<i>E. gunnii</i>				
Liawenee	(1150m)	LH	6	81
Shannon Lagoon	(1050m)	SL	6	58
Pensford	(960m)	Pf	6	67
Snug Plains	(600m)	SP	5	62
Total			41	462

Table 2.2 Description of characters scored from seedlings in Trial 1.
The leaf dimensions measured are shown in Fig. 2.1.

<u>Quantitative</u>	
<u>Code</u>	<u>Description</u>
1. LL	lamina length (mm)
2. LW	lamina width (mm)
3. LWP	length to the widest point (mm)
4. BASE	basal measure (mm)
5. EMARG	emarginate apex measure (mm)
6. LAMTH	lamina thickness (mm) measured using a spring loaded micrometer
7. INTER	distance between the 20th and 22nd nodes. Where leaf pairs were alternate this was taken from the bottom leaf of the lower node to the top leaf of the upper node (cm)
8. LLINTRA	maximum intranode length (cm)
9. LLPET	maximum petiole length (cm; usually = 0)
10. REL.L.L.L.	the length of the longest lateral relative to the total seedling height (X/Ht) (ratio)
11. Pr.LAT	the number of laterals (>1NE) developed as a proportion of the potential number (i.e. X/2NE) (ratio)
12. HT	seedling height (cm)
13. NE	number of leaf pairs expanded on the main stem (cotyledons = 0)
14. DIA	stem diameter measured at the cotyledonary node, at right angles to the cotyledons (cm)
15. (L-D)/D	lignotuber development expressed as the difference between DIA (14) and a similar measurement taken across the lignotubers at the cotyledonary node, relative to stem diameter (see Ladiges and Ashton 1974)
16. Nos.Lig	number of lignotubers
<u>Ordered Multistate</u>	
17. GLAUC	degree of glaucousness (0 green - 5 marked glaucousness extending onto stems and old leaves)
18. ST. VERR	the density of verrucae (oil glands) on the seedling stem (0 smooth - 5 highest density)
19. ANTH	the development of red pigmentation (anthocyanin) on the seedling stem (0 green - 5 deep red over most of the newly expanded stem)

Table 2.2 Description of characters scored from seedlings in Trial 1.
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6. LAMTH	lamina thickness (mm) measured using a spring loaded micrometer
7. INTER	distance between the 20th and 22nd nodes. Where leaf pairs were alternate this was taken from the bottom leaf of the lower node to the top leaf of the upper node (cm)
8. LLINTRA	maximum intranode length (cm)
9. LLPET	maximum petiole length (cm; usually = 0)
10. REL.L.L.L.	the length of the longest lateral relative to the total seedling height (X/Ht) (ratio)
11. Pr.LAT	the number of laterals ($>1NE$) developed as a proportion of the potential number (i.e. $X/2NE$) (ratio)
12. HT	seedling height (cm)
13. NE	number of leaf pairs expanded on the main stem (cotyledons = 0)
14. DIA	stem diameter measured at the cotyledonary node, at right angles to the cotyledons (cm)
15. (L-D)/D	lignotuber development expressed as the difference between DIA (14) and a similar measurement taken across the lignotubers at the cotyledonary node, relative to stem diameter (see Ladiges and Ashton 1974)
16. Nos.Lig	number of lignotubers
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17. GLAUC	degree of glaucousness (0 green - 5 marked glaucousness extending onto stems and old leaves)
18. ST. VERR	the density of verrucae (oil glands) on the seedling stem (0 smooth - 5 highest density)
19. ANTH	the development of red pigmentation (anthocyanin) on the seedling stem (0 green - 5 deep red over most of the newly expanded stem)

Table 2.3 Populations used in Trial 2. The number of mothers and total number of seedlings for which the full data set was available, the percentage of seedlings developing petioles and intranodes, and classified as green or subglaucous (classes 0 to 2) are indicated for each population. Cluster codes correspond to Fig. 1.24 (i.e. 1 = '*E. archeri*'; 2 = 'Pine Lake intermediates'; 3 = '*E. divaricata*'; 4 = 'southern *E. gunnii*'; 5 = 'NW *E. gunnii*'; * = Pine Lake transect).

Population	Code	Cluster	Number of mothers	Number of seedlings	Percentage developing		% green or subglaucous (Classes 0-2)
					Petioles	Intranodes	
*Projection Bluff	P ₁	1	10	102	47.1	52.9	81.4
*Projection Bluff	P ₂	1	10	122	54.9	39.3	73.8
*Pine Lake	P ₃	2	10	136	22.1	15.4	16.1
*Pine Lake	P ₄	2	10	123	32.5	23.6	21.1
*Mickey's Creek	P ₅	2	10	127	21.3	18.1	9.4
*Breona	Br	3	10	135	8.8	6.6	1.4
*South Brandum	SB	3	10	128	9.4	10.9	1.6
Mole Creek	MC	1	9	49	51.0	46.9	59.2
Mt. Roland	MR	1	10	47	36.2	10.6	17.0
Trapper's Hut	TH	5	10	50	38.0	28.0	4.0
Lake Ball	LB	5	7	27	44.4	18.5	3.7
Lake Charles	LC	5	10	39	38.5	20.5	7.7
Lake Myrtle	LM	5	9	45	42.2	35.6	15.6
St. Valentines Peak	SV	5	10	48	81.3	68.8	8.4
Middlesex Plains	MS	5	10	49	59.2	42.9	2.0
Snow Hill	SH	4	10	49	57.1	53.1	14.3
Ben Lomond	BL	1	10	42	40.5	45.2	59.5
Mt. Saddleback	SD	1	10	50	26.0	22.0	38.0
Mt. Maurice	MM	1	10	50	72.0	48.0	82.0
Ben Nevis	BN	1	10	50	42.0	30.0	62.0
Mt. Barrow	MB	1	10	46	41.3	21.7	30.3
Mt. Victoria	MV	5	10	50	46.0	26.0	22.0
Total			215	1565			

Table 2.4 Description of characters other than leaf dimensions scored from seedlings in Trial 2. The leaf dimensions measured are the same as in Fig. 2.1 and listed in Table 2.2.

<u>Code</u>	<u>Description</u>
HT	seedling height at 6 months (mm)
GLAUC	degree of glaucousness (0 green - 4 marked glaucousness extending onto stems and old leaves; \equiv classes 4 + 5, Table 2.2)
Petiole *	presence (1)/absence (0) of petiole at 6 months
Intranode *	presence (1)/absence (0) of an intranode at 6 months
SQST	stem shape (0-3; round = 0, distinctly angular = 3)

* These characters were also scored for the 10th leaf pair (cotyledons = 0).

Table 2.5 Components of variation in seedling characters from Trial 1. Estimates of the variance within progenies (σ_W^2 ; d.f.=421), between trees (i.e. progenies) within populations (σ_F^2 , d.f.=34), between populations within taxa (σ_P^2 ; d.f.=5) and between taxa (σ_T^2 ; d.f.=1; i.e. *E. gunnii* vs *E. archeri*) expressed as a percentage of the total variance ($\sigma_G^2 = \sigma_W^2 + \sigma_F^2 + \sigma_P^2 + \sigma_T^2$). The percentage of the overall variance between populations (σ_{P+T}^2) and families (σ_{F+P+T}^2) relative to the total variance between families and seedlings respectively (i.e. $\sigma_{P+T}^2 / (\sigma_{P+T}^2 + \sigma_F^2)$; $\sigma_{F+P+T}^2 / (\sigma_{F+P+T}^2 + \sigma_W^2)$) are given as well as selected variance ratios and their significance (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). See Table 2.2 for explanation of characters.

Character	Percentage of total variance (σ_G^2)				F ratios			Percentage of variance	
	Between taxa	Between populations within taxa	Between mothers within populations	Within progenies	σ_T^2	F ratios	σ_F^2	Percentage of variance	
	(σ_T^2 / σ_G^2)	(σ_P^2 / σ_G^2)	(σ_F^2 / σ_G^2)	(σ_W^2 / σ_G^2)	σ_P^2	σ_F^2	σ_W^2	σ_{P+T}^2	σ_{F+P+T}^2
					(1,5)	(5,34)	(34,421)	$\sigma_{P+T}^2 + \sigma_F^2$	$\sigma_{F+P+T}^2 + \sigma_W^2$
LL	84.0	14.4	1.2	0.4	5.8	12.2***	3.1***	94.8	91.7
LW	24.9	64.6	7.0	3.5	0.4	9.2***	2.0**	89.4	80.8
LWP	97.0	2.0	0.8	0.21	49.1***	2.4	3.6***	96.1	94.1
BASE	95.9	3.3	0.52	0.26	28.5**	6.4***	2.0***	97.3	92.7
EMARG	95.3	3.0	1.0	0.8	32.2**	3.1*	1.2	95.0	81.2
LAMTH	97.3	1.7	0.6	0.4	57.1***	3.1*	1.4	98.2	92.5
LL/LW	96.1	2.7	1.0	0.2	36.2***	2.5*	5.0***	94.7	94.5
HT	62.1	34.8	2.3	0.8	1.8	15.0***	2.9***	94.4	90.7
DIA	45.0	36.5	13.4	5.1	1.2	7.4***	2.8***	73.9	77.5
LLINTRA	62.0	19.5	12.1	7.0	3.2	3.0*	1.9**	68.6	68.7
LLPET	77.7	18.1	2.3	1.9	4.3	7.7***	1.3	92.5	76.8
(L-D)/D	74.5	19.5	4.7	1.7	3.8	4.1**	2.8***	86.8	82.3
Pr.LAT	0.5	79.7	12.8	7.0	0.0	32.5***	1.6*	84.0	74.9
REL.L.L.L.	55.2	31.2	8.1	5.5	0.4	19.3***	1.5*	81.3	68.8
INTER	24.7	63.6	7.7	4.0	0.4	8.3***	1.9**	88.2	79.1
NE	86.9	6.0	4.5	2.3	14.5*	1.2	2.1***	80.1	75.6

Table 2.6 Standardized canonical variates derived from CVA of the total seedling character set from Trial 1 (see Fig. 2.2).

	CV ₁ (77%)	CV ₂ (14.6%)
LL	-0.02	-0.05
LW	-0.12	-0.01
LWP	-0.28	0.00
BASE	-0.25	-0.05
EMARG	0.02	-0.01
GLAUC	0.73	-0.07
ANTH	-0.03	-0.01
ST.VERR	-0.29	-0.16
HT	0.25	-0.45
DIA	0.13	0.05
NOS.LIG	-0.17	-0.01
LLINTRA	-0.08	0.02
LLPET	0.00	-0.07
NE	-0.10	0.28
INTER	0.01	0.03
LAMTH	-0.23	0.22
REL.L.L.L.	0.17	-0.03
Pr.LAT	-0.11	0.02
(L-D)/D	0.06	0.80

Table 2.7 Standardized canonical variates derived from CVA of seedling leaf characters from Trial 1 (see Fig. 2.3).

	CV ₁ (78.6%)	CV ₂ (10.2%)
LL	0.14	0.53
LW	-0.19	0.62
LWP	-0.68	-0.51
BASE	0.63	-0.23
EMARG	0.28	0.15

Table 2.8 Generalized distances between populations used in Trial 1 based on adult (*italics*) and seedling characters for (a) total (i.e. Table 2.6 vs 1.10 + GLAUC), and (b) leaf character (i.e. Table 2.7 vs 1.9) sets.

(a)							
	BL	P ₁	P ₂	LH	SL	PF	SP
BL	X	2.7	2.3	7.0	9.8	7.3	5.6
P ₁	2.1	X	1.8	7.4	10.1	7.2	5.9
P ₂	2.0	1.7	X	6.7	9.8	7.3	6.1
LH	5.1	5.3	4.3	X	5.2	6.1	5.4
SL	7.8	8.3	7.2	3.3	X	5.0	5.6
PF	6.4	6.8	5.7	2.6	2.8	X	3.0
SP	6.3	6.3	5.4	2.4	2.8	2.4	X
(b)							
	BL	P ₁	P ₂	LH	SL	PF	SP
BL	X	2.0	1.1	2.9	2.2	3.1	2.8
P ₁	1.4	X	1.5	4.2	3.0	2.9	3.1
P ₂	0.8	1.0	X	3.2	2.7	3.5	4.1
LH	2.5	3.0	2.4	X	2.6	5.3	4.4
SL	3.3	3.8	3.4	1.4	X	3.0	2.2
PF	2.2	2.5	2.2	1.1	1.8	X	1.3
SP	2.5	2.6	2.5	1.3	1.7	0.9	X

Table 2.9 Percentage of seedlings in each population developing an intranode (LLINTRA#0), developing a petiole (a = LLPET#0; b = between the 20th and 22nd leaf pair), with green or subglaucous foliage (GLAUC = 0 and 1) as well as green (ANTH = 0) and smooth (ST.VERR = 0) stems. The significance the Chi-squared (χ^2) test for independence of population or taxa (*E. gunnii* vs *E. archeri*) and character class is given (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

Character	Population							χ^2	χ^2
	BL	P ₁	P ₂	LH	SL	Pf	SP	popul.	taxa
n	68	71	55	81	56	67	62		
INTRA	80.9	88.7	65.5	34.6	39.3	70.1	91.9	***	***
PET (a)	79.4	66.2	81.8	6.2	1.8	50.7	64.5	***	***
(b)	16.2	12.7	18.2	0	0	3	0	**	***
GLAUC (green or subgl.)	45.6	70.4	34.5	0	0	0	1.6	***	***
ANTH (green stem)	17.6	2.8	29.1	40.7	23.2	11.9	14.5	***	
ST.VERR (smooth)	0	0	0	13.6	10.7	28.4	0	***	***

Table 2.10 Components of variation in seedling characters from Trial 2. Estimates of the variance within progenies (σ_W^2 ; d.f.=1351), between trees (i.e. progenies) within populations (σ_F^2 ; d.f.=192), between populations within clusters (σ_P^2 ; d.f.=17) and between clusters (σ_T^2 ; d.f.=4; clusters are shown in Table 2.2) are given expressed as a percentage of the total variance ($\sigma_G^2 = \sigma_W^2 + \sigma_F^2 + \sigma_P^2 + \sigma_T^2$). The percentage of the overall variance between populations (σ_{P+C}^2) and families (σ_{F+P+T}^2) relative to the total variance between families and seedlings respectively (i.e. $\sigma_{P+T}^2 / \sigma_{P+T}^2 + \sigma_F^2$; $\sigma_{F+P+T}^2 / \sigma_{F+P+T}^2 + \sigma_W^2$) are indicated as well as selected variance ratios and their significance NS = not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). See Table 2.4 and Fig. 2.1 for explanation of characters (CV₁ = main canonical vector given in Table 2.11 and shown in Fig. 2.5; PCa & b = first (1) and second (2) PC's derived from PCA (TOT/CORR) of total (a) and seedling leaf (b) data sets

Character	Percentage of total variance (σ_G^2)				F ratios			Percentage of variance	
	Between clusters	Between populations within clusters	Between mothers within populations	Within progenies	F ratios			$\frac{\sigma_{P+T}^2}{\sigma_{P+T}^2 + \sigma_F^2}$	$\frac{\sigma_{F+P+T}^2}{\sigma_{F+P+T}^2 + \sigma_W^2}$
	(σ_T^2 / σ_G^2)	(σ_P^2 / σ_G^2)	(σ_F^2 / σ_G^2)	(σ_W^2 / σ_G^2)	$\frac{\sigma_T^2}{\sigma_P^2}$	$\frac{\sigma_P^2}{\sigma_F^2}$	$\frac{\sigma_F^2}{\sigma_W^2}$		
					(4, 17)	(21, 192)	(213, 1351)		
LL	79.5	17.6	2.2	0.7	4.5*	7.9***	3.1***	93.0	87.3
LW	78.1	16.3	4.1	1.5	4.8**	4.0***	2.8***	87.2	89.1
LWP	85.5	12.3	1.6	0.5	7.0**	7.6***	2.9***	94.2	87.9
BASC	93.1	5.3	1.0	0.5	17.4***	5.1***	2.0***	95.5	85.7
EMARG	69.8	20.2	6.9	3.1	3.5*	2.9***	2.2***	81.2	74.7
LL/LW	84.6	11.9	2.2	1.2	7.1**	5.3***	1.9***	92.0	95.6
IIT	84.6	9.6	3.6	2.2	8.8***	2.7***	1.6***	86.9	71.4
CV ₁	95.3	3.8	0.5	0.2	25.1***	8.1***	2.1***	99.4	97.9
PCa 1	90.4	8.4	0.9	0.3	10.7***	9.5***	2.7***	99.1	97.6
PCa 2	88.5	8.4	2.2	0.9	10.5***	3.8***	2.5***	93.8	87.4
PCb 1	83.9	13.9	1.6	0.6	6.0**	8.5***	3.0**	94.3	88.2
PCb 2	87.6	8.9	2.6	1.0	9.9***	3.4***	2.6***	90.2	84.1

Table 2.11 Standardized canonical variates derived from CVA of seedling characters from Trial 2 (see Fig. 2.8).

	CV ₁ (50.4%)	CV ₂ (24.3%)
LL	-0.33	0.67
LW	-0.04	0.23
LWP	0.58	-0.54
BASE	-0.32	-0.36
EMARG	-0.06	0.03
GLAUC	-0.60	0.25
PET	0.05	0.04
INTRA	0.18	-0.00
HT	0.00	-0.01
SQST	0.21	0.09

Table 2.12 Standardized canonical variates derived from CVA of seedling leaf characters from Trial 2 (see Fig. 2.6).

	CV ₁ (53.3%)	CV ₂ (21.4%)
LL	-0.35	0.61
LW	-0.20	0.29
LWP	-0.26	-0.71
BASE	-0.87	-0.18
EMARG	0.11	0.10

Table 2.13 Cluster statistics for seedlings in Trial 2. Seedlings were pooled on the basis of the adult population classification presented in Fig. 1.24. (a) The percentage of seedlings classified as green or subglaucous (i.e. GLAUC = 0 to 2), developing a petiole or intranode after 6 months and with round stems (i.e. SQST = 0). (b) Character means (SE) and the significance of the F-test for the difference between clusters. The results of the multiple range test (Student - Newman - Keuls procedure; see Sokal and Rolf 1969) for differences between cluster means are indicated by lines linking homogeneous means. Character codes are detailed in Table 2.4.

Character	' <i>E. archeri</i> '	'Pine Lake intermediates'	' <i>E. divaricata</i> '	'southern <i>E. gunnii</i> '	'NW <i>E. gunnii</i> '		
	(1)	(2)	(3)	(4)	(5)		
(a)	n	558	386	264	49	308	χ^2 cluster
% green or subglaucous	61	16	2	14	9		***
% presence of petiole	47	25	9	57	51		***
% presence of intranode	38	19	9	53	35		***
% round stem (SQST = 0)	8	18	32	6	12		***
(b)						F ratio (4,1560)	Homogeneous means (low+high)
LL	23.1 (0.20)	21.7 (0.21)	19.1 (0.19)	26.2 (0.87)	25.3 (0.34)	22 (***)	3 2 1 <u>5</u> 4
LW	21.5 (0.16)	22.5 (0.18)	22.8 (0.20)	27.8 (0.60)	23.7 (0.26)	40 (***)	1 <u>2</u> <u>3</u> 5 4
LWP	10.7 (0.10)	9.8 (0.10)	7.8 (0.09)	11.5 (0.38)	10.9 (0.15)	105 (***)	3 2 1 <u>5</u> 4
BASE	0.4 (0.02)	0.5 (0.02)	1.1 (0.04)	0.7 (0.07)	0.42(0.02)	144 (***)	<u>1</u> <u>5</u> <u>2</u> 4 3
EMARG	0.11(0.008)	0.12(0.011)	0.21(0.015)	0.32(0.048)	0.14(0.012)	19 (***)	<u>1</u> <u>5</u> <u>2</u> 3 4
HT	193 (1.7)	212 (2.0)	223 (2.5)	232 (6.8)	211 (2.3)	34 (***)	1 <u>5</u> <u>2</u> <u>3</u> <u>4</u>

Table 2.14 Correlation coefficients (r; d.f.=38) between adult and seedling characters for trees from Trial 1. Correlations significantly different from zero are indicated (*, P<0.05; **, P<0.01; ***, P<0.001).

Seedling Characters	Adult characters											
	Vegetative								Reproductive			
	LL	LW	LWP	PET.L	LAMTH	PEDU	CAP.L	PEDI	RIM W.	MAX.CAP.W	PT.MAX	DISK
LL	*** 0.61	-0.23	*** 0.60	*** 0.52	0.18	0.02	0.02	-0.27	*** 0.51	* 0.40	0.10	-0.21
LW	** 0.41	** 0.41	** 0.42	0.27	** -0.49	* 0.34	0.12	0.13	0.02	0.08	0.00	-0.10
LWP	*** 0.52	* -0.31	*** 0.52	** 0.45	* 0.36	-0.10	-0.02	* -0.39	*** 0.53	* 0.38	0.10	-0.24
LLPET	*** 0.55	* -0.31	*** 0.63	*** 0.64	0.04	0.03	0.11	-0.24	* 0.35	0.29	0.06	-0.18
LAMTH	-0.17	** -0.41	-0.25	-0.29	*** 0.90	*** -0.59	* -0.32	*** -0.54	0.22	0.07	-0.15	-0.21
BASE	-0.19	*** 0.52	-0.19	-0.19	*** -0.63	* 0.35	0.05	** 0.42	*** -0.43	-0.28	-0.09	0.04
EMARG	-0.28	*** 0.61	-0.18	-0.23	*** -0.53	0.23	-0.09	0.29	** -0.40	* -0.34	-0.22	-0.06
GLAUC	-0.25	** 0.46	-0.25	-0.18	*** -0.60	* 0.33	0.09	*** 0.51	*** -0.52	* -0.38	0.02	0.17
ANTH	*** 0.53	-0.10	** 0.41	** 0.40	-0.13	0.25	0.22	0.00	0.26	0.20	-0.02	-0.17
RUGOSE	0.19	-0.11	0.18	0.15	0.28	-0.05	-0.07	*** -0.53	** 0.41	* 0.33	-0.18	* -0.37
HT	** 0.41	0.27	* 0.39	** 0.45	*** -0.71	*** 0.56	0.26	** 0.46	0.02	0.06	0.09	0.00
DIA	* 0.32	0.01	0.26	* 0.35	** -0.44	* 0.39	0.11	** 0.48	0.08	0.08	-0.02	-0.13
LLINTRA	* 0.36	-0.24	0.22	0.26	0.03	0.12	0.29	-0.19	0.28	* 0.32	0.08	-0.13
NE	-0.07	0.30	-0.15	-0.06	* -0.36	0.24	0.10	* 0.39	-0.16	-0.16	-0.09	0.06
INTER	*** 0.54	0.13	*** 0.54	** 0.42	*** -0.50	** 0.47	0.30	* 0.37	0.01	0.03	* 0.35	0.08
REL.L.L.L	** -0.43	-0.06	* -0.39	* -0.33	-0.11	-0.09	-0.01	0.19	** -0.48	-0.27	0.07	0.24
Pr.LAT	0.00	-0.09	-0.05	0.08	-0.02	-0.01	-0.17	0.06	-0.04	-0.06	-0.20	-0.01
(L-D)/D	-0.12	0.07	-0.18	-0.01	* -0.36	0.25	0.22	* 0.36	-0.17	-0.07	0.05	-0.05

Table 2.15 Significant canonical correlations and vectors relating seedling and adult leaf character sets for trees from Trial 1 (n = 41).

	<u>Canonical correlation</u>	
	SET 1	SET 2
Canonical correlation ($\sqrt{\lambda}$)	0.93	0.78
Significance	(P<0.001)	(P<0.001)

	<u>Canonical vectors</u>	
	Adult characters	
LL	0.09	0.27
LW	-0.16	0.03
LWP	-0.16	0.45
PET	0.19	0.44
LAMTH	0.97	0.25

	<u>Seedling characters</u>	
LL	-0.82	0.07
LW	-0.08	0.12
LWP	0.98	0.74
BASE	0.21	-0.09
EMARG	-0.24	-0.33
LAMTH	0.73	-0.62

Table 2.16 Significant canonical correlations and vectors relating seedling and adult character sets for trees from Trial 1 (n = 41).

	<u>Canonical correlation</u>	
	SET 1	SET 2
Canonical correlation ($\sqrt{\lambda}$)	0.98	0.98
Significance	(P<0.001)	(P<0.001)

	<u>Canonical vectors</u>	
	Adult characters	
LL	0.41	0.52
LW	-0.12	-0.00
LWP	-0.45	0.14
PET	-0.30	0.22
LAMTH	0.63	0.64
PEDU	-0.36	-0.05
CAP.L	0.39	0.11
PEDI	0.21	-0.09
RIM.W	-0.08	0.11
MAX.W	-0.17	-0.01
PT.MAX.W	-0.33	0.05
DISK	0.11	-0.36

	<u>Seedling characters</u>	
LL	1.03	-1.77
LW	-0.65	0.48
LWP	-1.31	1.97
BASE	0.60	0.03
EMARG	-0.01	-0.38
GLAUC	-0.18	0.10
ANTH	0.38	0.21
ST.VERR.	-0.30	-0.09
HT	-1.36	0.71
DIA	-0.17	0.09
NOS.LIG	-0.12	-0.00
LLINTRA	0.33	-0.32
LLPET	0.20	0.15
NE	0.98	-0.52
INTER	0.56	-0.02
LAMTH	0.68	0.68
REL.L.L.L.	-0.16	-0.13
Pr.LAT	0.11	0.01
(L-D)/D	-0.27	0.14

Table 2.17 Correlation coefficients (r; d.f.=68) between adult and seedling characters based on trees from the Pine Lake transect (Trial 2). Correlations significantly different from zero are indicated (* P<0.05; ** P<0.01; *** P<0.001). Explanation of seedling characters CV₁, PCa₁, PCa₂ and PCb₁ is given in Table 2.10. Canonical variates presented as adult characters correspond to the first and second vectors derived from the 15 (Table 1.10; Fig. 1.18; CVA02 1 & 2) and 16 (Fig. 1.23; CVA01 1 & 2) variable CVA's of adult populations presented in Chapter 1.

Seedling Characters	Adult characters								Canonical variates			
	Leaf											
	LL	LW	LWP	PET.L	LAMTH	CURVE	LL/LW	GLAUC	CVA01 1	CVA01 2	CVA02 1	CVA02 2
LL	0.12	*-0.29	0.17	0.05	*** 0.41	* 0.29	* 0.24	***-0.45	***-0.46	** 0.33	***-0.40	0.02
LW	***-0.39	* 0.26	***-0.42	-0.08	-0.14	***-0.38	***-0.56	*** 0.47	0.17	** -0.35	* 0.28	0.03
LWP	0.22	** -0.38	* 0.30	0.13	*** 0.51	*** 0.39	** 0.37	***-0.65	***-0.58	*** 0.52	***-0.56	0.06
PETIOLE	** 0.32	*-0.24	* 0.30	** 0.34	** 0.32	*** 0.45	*** 0.40	***-0.63	***-0.32	*** 0.45	***-0.48	-0.08
BASE	*-0.24	*** 0.41	** 0.37	-0.01	***-0.52	** -0.31	***-0.45	*** 0.70	*** 0.63	***-0.53	*** 0.62	-0.03
EMARG	** -0.35	** 0.31	** -0.38	-0.02	** -0.32	** -0.31	***-0.47	*** 0.44	** 0.36	** -0.32	** 0.35	0.12
GLAUC	***-0.44	*** 0.46	***-0.54	-0.17	***-0.45	***-0.50	***-0.58	*** 0.87	*** 0.53	***-0.61	*** 0.61	-0.02
INTRANODE	*** 0.51	-0.20	** 0.38	** 0.33	0.20	*** 0.50	*** 0.49	***-0.60	-0.17	*** 0.50	***-0.33	0.12
HT	** -0.31	** 0.38	***-0.41	-0.15	*-0.29	** -0.32	***-0.43	*** 0.44	* 0.24	***-0.42	* 0.26	-0.16
SQST	*** 0.44	** -0.36	*** 0.40	0.23	** 0.34	** 0.36	*** 0.50	***-0.53	** 0.33	*** 0.44	** -0.32	0.06
CV ₁	*** 0.44	***-0.48	*** 0.53	0.17	*** 0.53	*** 0.51	*** 0.59	***-0.87	***-0.60	*** 0.65	***-0.66	0.04
PCa 1	** 0.37	***-0.44	*** 0.43	0.18	*** 0.53	*** 0.48	*** 0.51	***-0.78	***-0.58	*** 0.59	***-0.61	0.03
PCa 2	***-0.46	*** 0.44	***-0.56	-0.08	** -0.38	***-0.44	***-0.66	*** 0.71	*** 0.44	***-0.54	*** 0.50	0.01
PCb 1	0.15	** -0.35	* 0.24	0.06	*** 0.50	* 0.30	* 0.30	***-0.58	***-0.57	*** 0.44	***-0.52	0.04
LL/LW	** 0.37	***-0.43	*** 0.45	0.11	*** 0.43	*** 0.52	*** 0.59	***-0.70	***-0.50	*** 0.53	***-0.50	0.01

Seedling Characters	Reproductive									
	PEDU	CAP.L	PEDI	RIM.W	MAX.W	PT.MAX.W	DISK	VSIZ	VPOS	MEAN FLOWERING TIME
LL	-0.09	*-0.25	** -0.36	0.02	-0.09	0.02	*-0.27	* 0.24	0.16	*** 0.42
LW	0.20	0.20	0.17	0.07	0.05	-0.19	-0.03	-0.19	-0.12	** -0.35
LWP	-0.17	** -0.38	***-0.46	0.08	-0.08	-0.00	** -0.34	** 0.37	* 0.26	*** 0.62
PETIOLE	*-0.29	** -0.36	** -0.32	-0.05	-0.12	0.18	-0.21	* 0.26	0.14	*** 0.51
BASE	* 0.25	*** 0.40	*** 0.53	-0.02	0.10	-0.06	** 0.31	** -0.38	*-0.24	***-0.67
EMARG	0.13	0.20	** 0.31	0.16	0.19	*-0.25	0.05	-0.13	-0.01	***-0.39
GLAUC	0.21	** 0.34	** 0.38	-0.08	0.04	-0.16	0.21	***-0.45	*-0.24	***-0.68
INTRANODE	-0.09	-0.12	-0.22	0.14	0.13	0.17	-0.07	** 0.32	0.08	*** 0.51
HT	0.13	0.15	0.17	-0.16	-0.08	-0.07	0.07	-0.16	-0.07	***-0.42
SQST	0.07	-0.18	-0.07	0.14	0.01	0.08	-0.08	*** 0.46	0.22	*** 0.52
CV ₁	-0.22	***-0.41	***-0.47	0.08	-0.06	0.12	*-0.27	*** 0.48	* 0.29	*** 0.76
PCa 1	-0.20	** -0.38	***-0.47	0.06	-0.08	0.10	*-0.30	*** 0.42	* 0.25	*** 0.70
PCa 2	* 0.24	** 0.31	** 0.35	0.02	0.08	-0.20	0.10	** -0.32	-0.18	***-0.60
PCb 1	-0.15	** -0.34	***-0.46	0.05	-0.10	0.00	** -0.33	** 0.32	0.23	*** 0.46
LL/LW	-0.22	** -0.34	***-0.39	-0.02	-0.10	0.15	-0.18	** 0.32	0.21	*** 0.48

Table 2.18 The relationship between adult and seedling phenotype for trees sampled along the Pine Lake transect. Significant canonical correlation ($\sqrt{\lambda}$) and vectors derived from separate canonical correlations analysis of seedling and adult character sets. Codes correspond to characters listed in Tables 1.3 and 2.4.

	SET 1	SET 1
Canonical correlation ($\sqrt{\lambda}$)	0.93	0.87
Significance	($P < 0.001$)	($P < 0.001$)
	<u>Adult character set</u>	
LL	0.14	0.32
LW	-0.11	-0.23
LWP	0.10	0.18
PET	0.10	0.11
LAMTH	-0.05	0.26
CURV	-0.04	0.07
PEDU	0.05	0.05
CAP.L	-0.03	-0.26
PEDI	-0.07	-0.32
RIM.W	-0.21	-0.01
MAX.W	0.01	-0.11
PT.MAX.W	0.19	0.29
DISK	-0.05	0.02
VSIZ	0.04	
VPOS	0.06	
GLAUC	-0.77	
	<u>Seedling character set</u>	
LL	-0.31	-0.71
LW	-0.05	-0.08
LWP	0.20	0.94
BASE	-0.16	0.15
EMARG	-0.18	-0.44
GLAUC	-0.71	-0.35
PETIOLE	0.13	0.16
INTRANODE	-0.01	-0.06
HT	0.06	-0.06
SQST	0.06	0.07

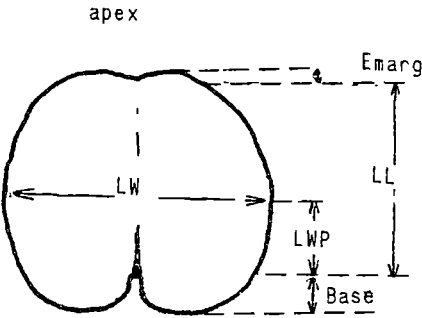


Fig. 2.1 Juvenile leaf measurements. Codes correspond to those in Table 2.2.

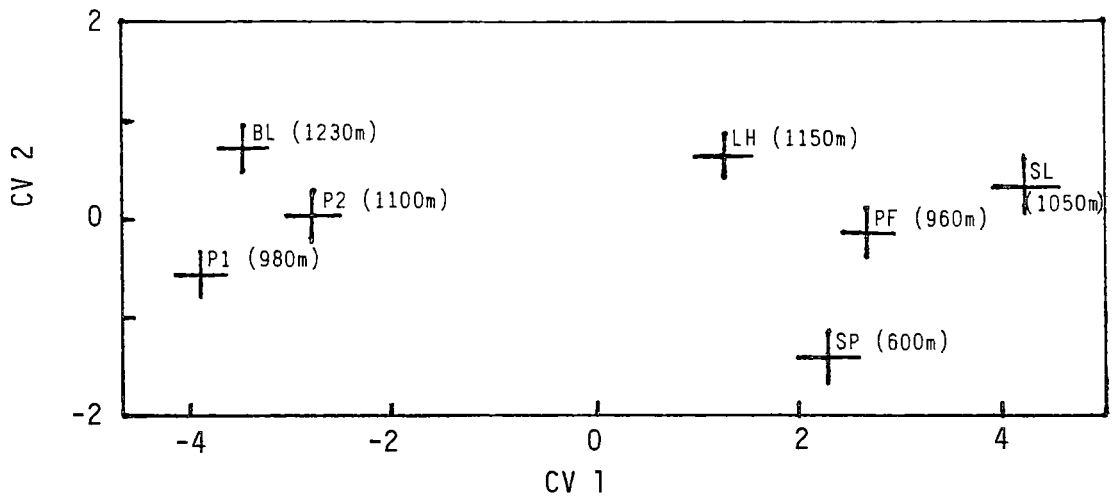


Fig. 2.2 CVA of the full seedling character set from Trial 1. Population centroids and their 95% confidence limits are plotted on CV1 and CV2 (see Table 2.6). Population codes are given in Table 2.1.

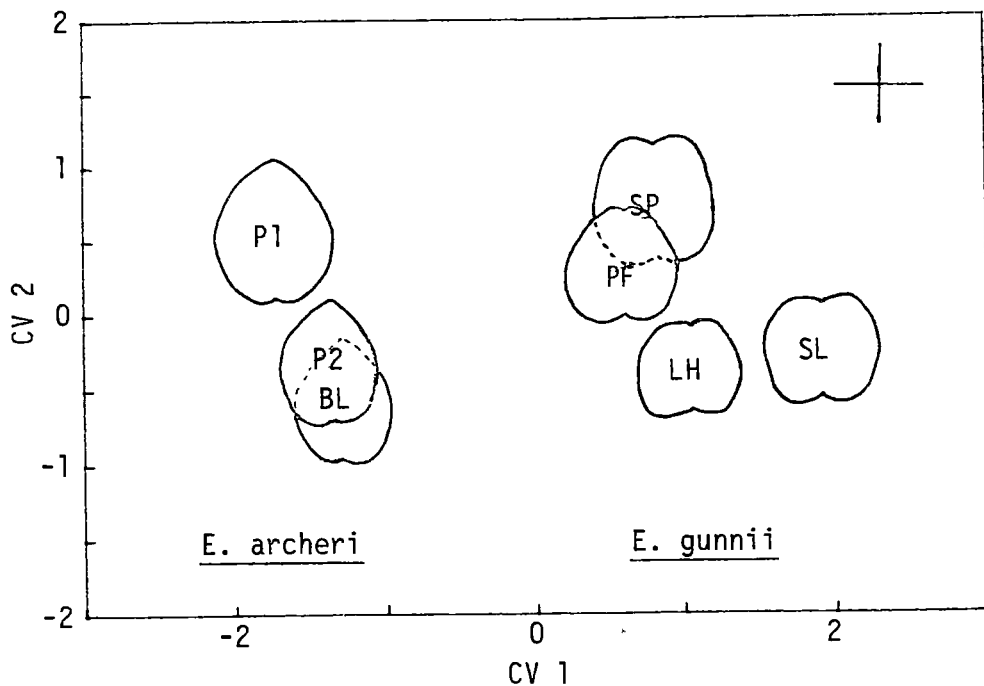


Fig. 2.3 CVA of seedling leaf dimensions (Trial 1; Table 2.7). Population codes (see Fig. 2.2) are centred on the centroid and leaf ideograms based on character means are shown. The 95% confidence interval is based on the minimum N.

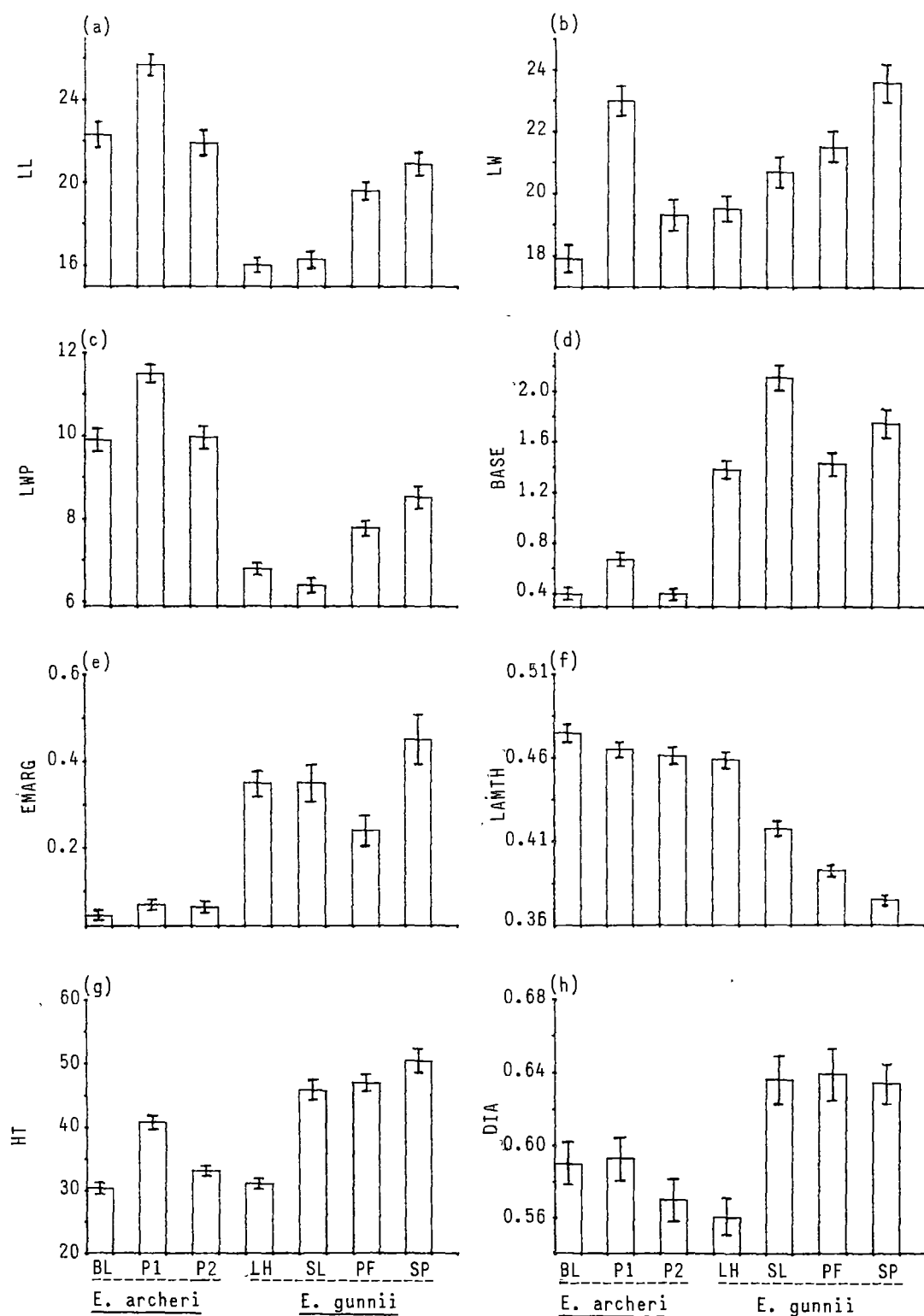


Fig. 2.4 Population means (\pm SE) for :-

(a) LL (b) LW (c) LWP (d) PERF (e) EMARG (f) LAMTH (g) HT (h) DIA (i) NOS.LIG. (j) (L-D)/D (k) NE (l) REL.L.L.L. (m) LLINTRA (n) INTER (o) GLAUC (p) ANTH (q) ST.VERR and (r) PETIOLE. Character descriptions are given in Fig. 2.1 and Table 2.2. Continued next page.

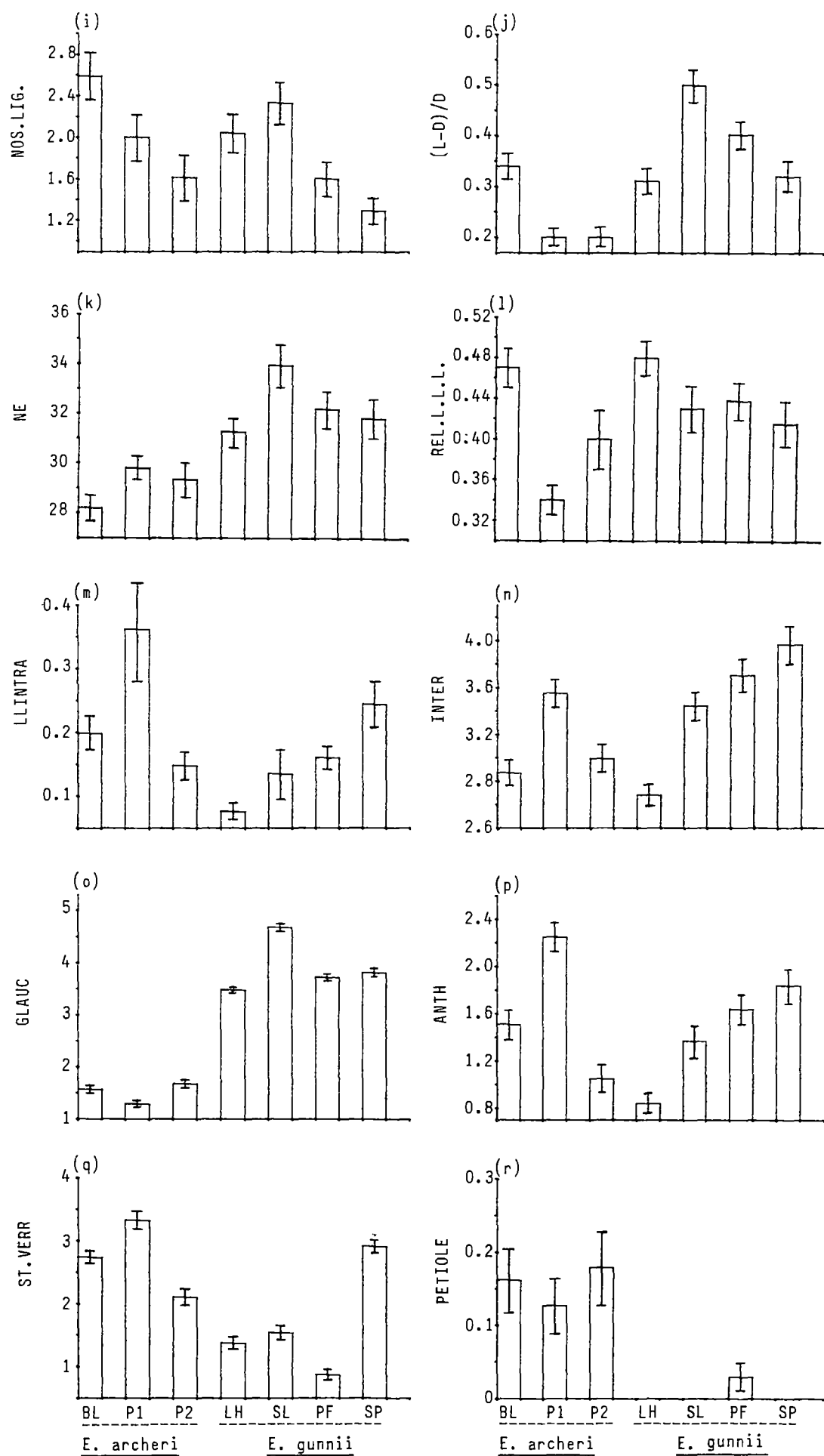


Fig. 2.4 Continued.

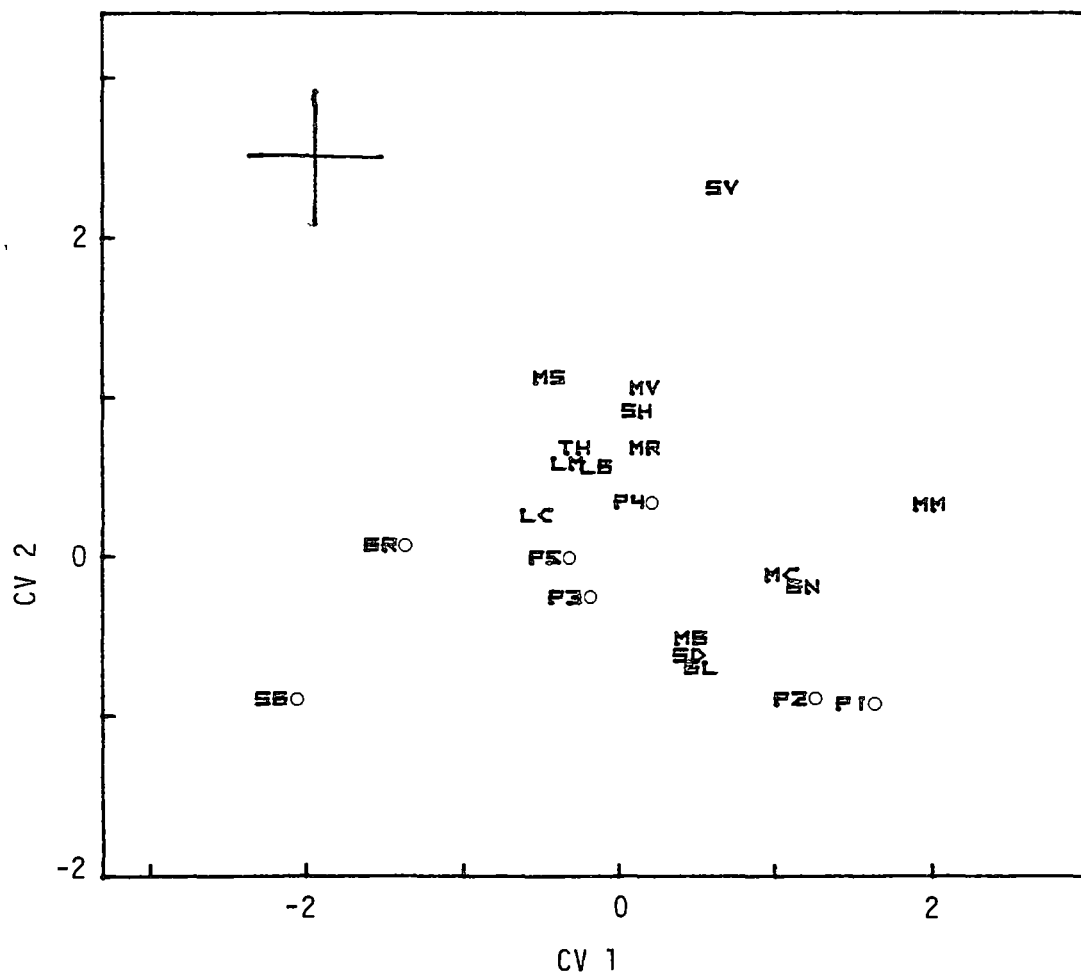


Fig. 2.5 CVA of the full seedling character set from Trial 2 (see Table 2.11). Population centroids are indicated and population codes are given in Table 2.3. The 95% confidence interval is based on the minimum N and populations on the Pine Lake transect are marked (o).

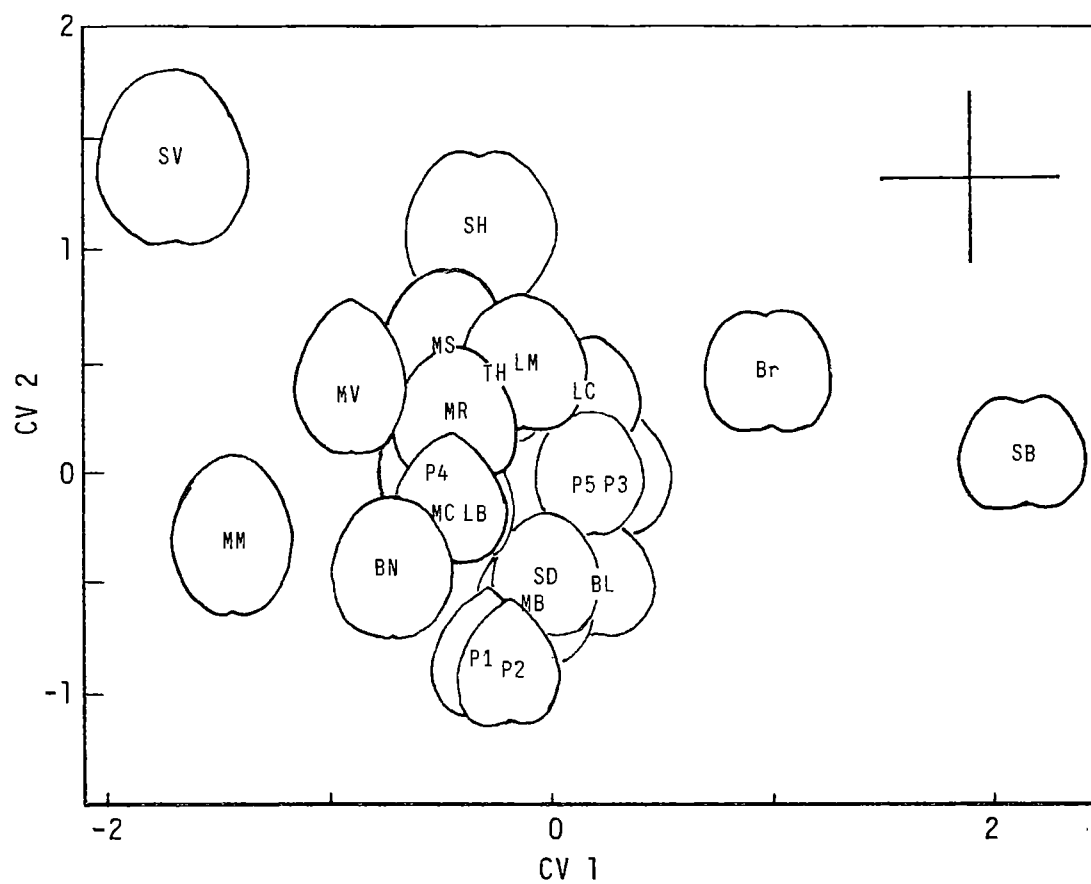


Fig. 2.6 CVA of seedling leaf dimensions for the *E. gunnii* - *archeri* populations in Trial 2 (see Table 2.12). Population codes (see Table 2.3) are centred on the centroid and leaf ideograms based on character means are shown. The 95% confidence interval is based on the minimum N.

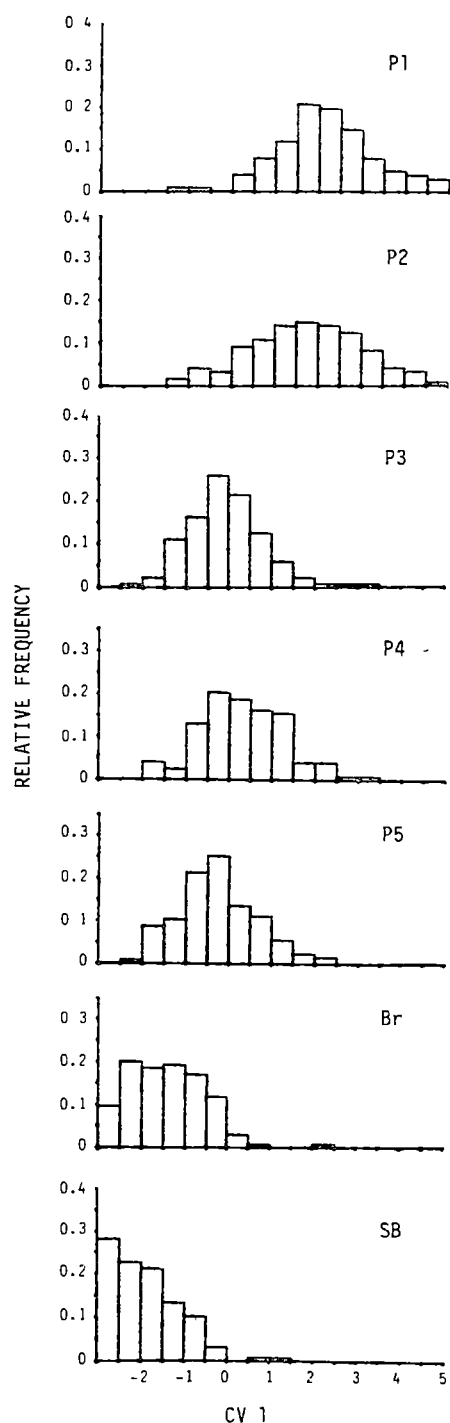


Fig. 2.7 Relative frequency histograms of CV1 scores for populations along the Pine Lake transect (Trial 2). CV1 was derived from CVA of the full seedling character set (e.g. Table 2.11) and accounts for 77% of the variation between transformed centroids of the 7 populations.

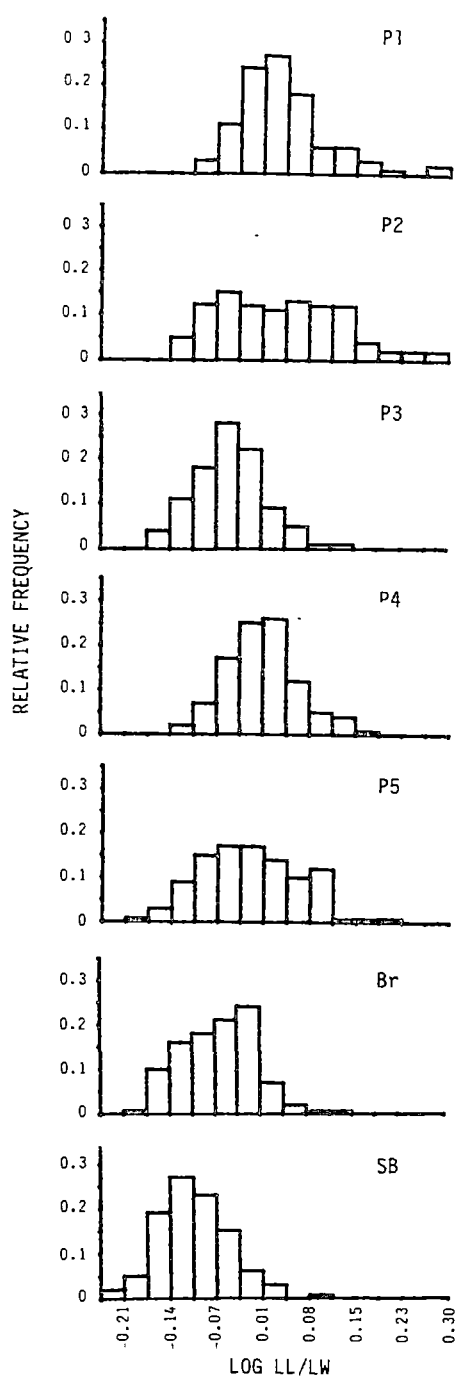


Fig. 2.8 Relative frequency histograms of log LL/LW scores for populations along the Pine Lake transect (Trial 2).

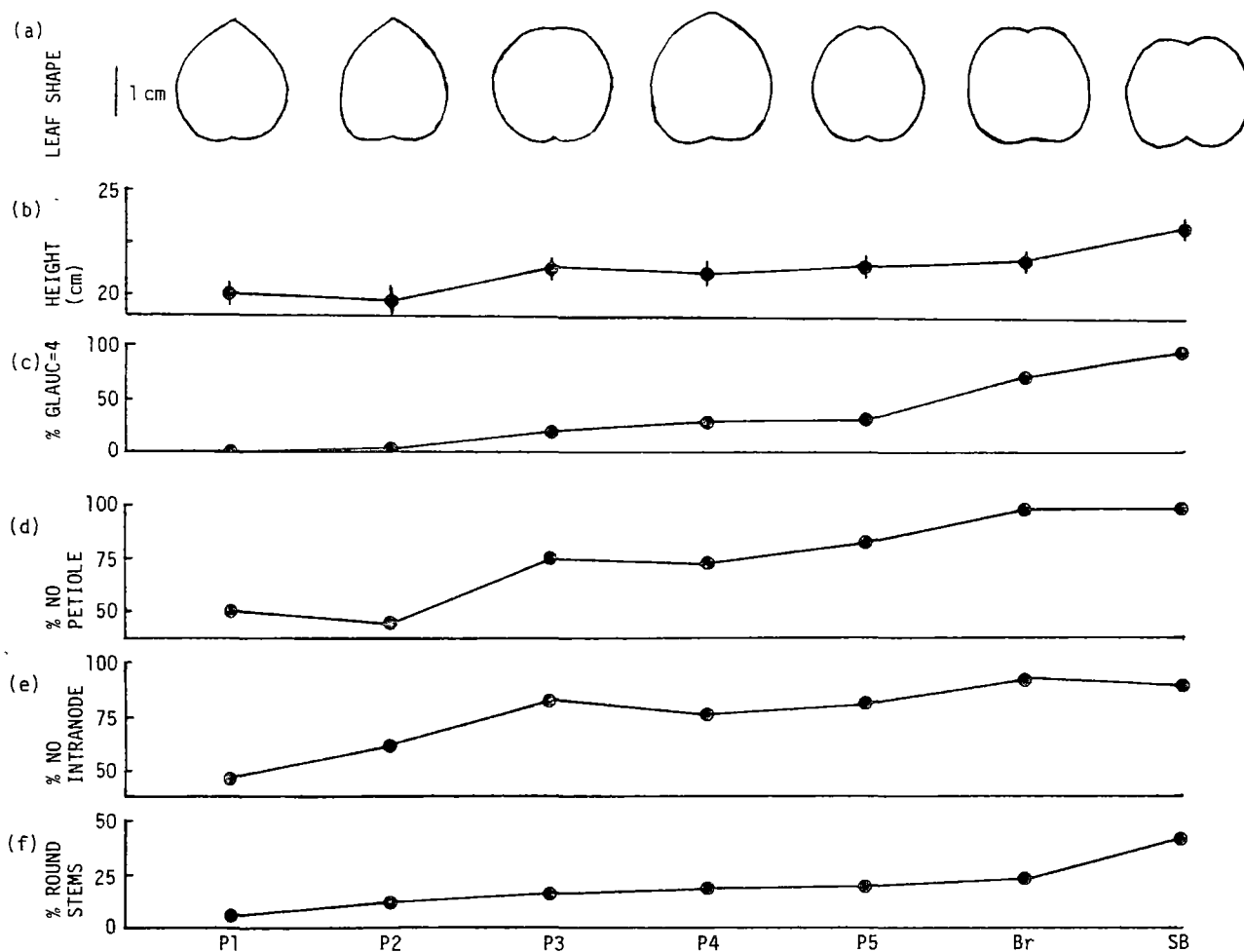


Fig. 2.9 Character variation along the Pine Lake transect. Variation in (a) leaf shape (ideograms based on character means), (b) mean height \pm SE (cm), (c) glaucousness (% GLAUC=4), the percentage of seedlings (d) not developing petioles, (e) not developing intranodes and (f) with round stems (SQST=0).

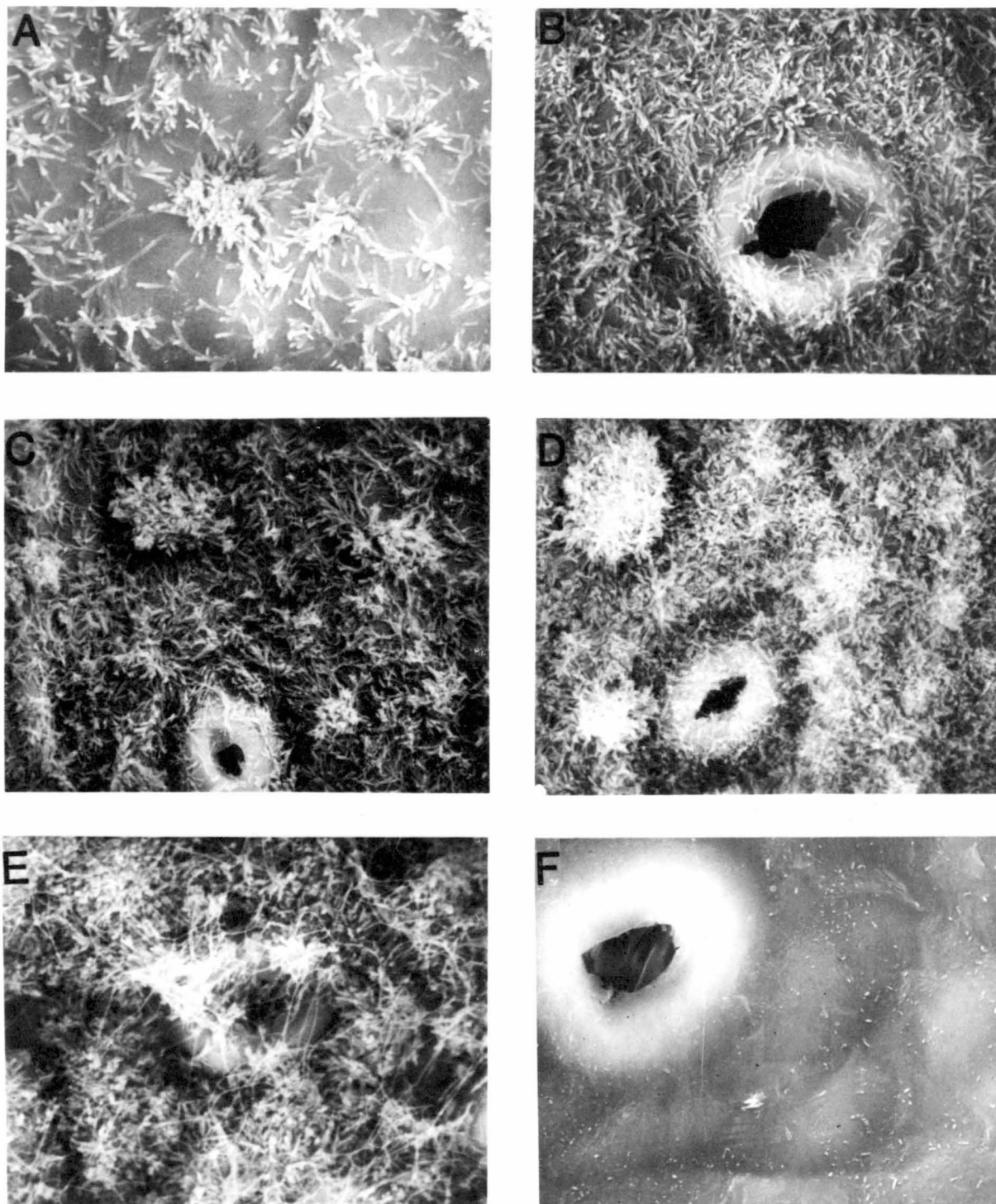


Fig. 2.10 Scanning electron micrographs of the adaxial surface of newly expanded seedling leaves ($\times 2000$) showing variation in structural features of the wax layer associated with the sequence of glaucousness grades encountered in Trial 1. (A) *E. archeri* (P_1 ; GLAUC=1), (B) *E. archeri* (P_1 ; GLAUC=2), (C) *E. archeri* (BL; GLAUC=3), (D) *E. gunnii* (LH; GLAUC=4), (E) *E. gunnii* (SL; GLAUC=5), (F) *E. johnstonii* (GLAUC=0).

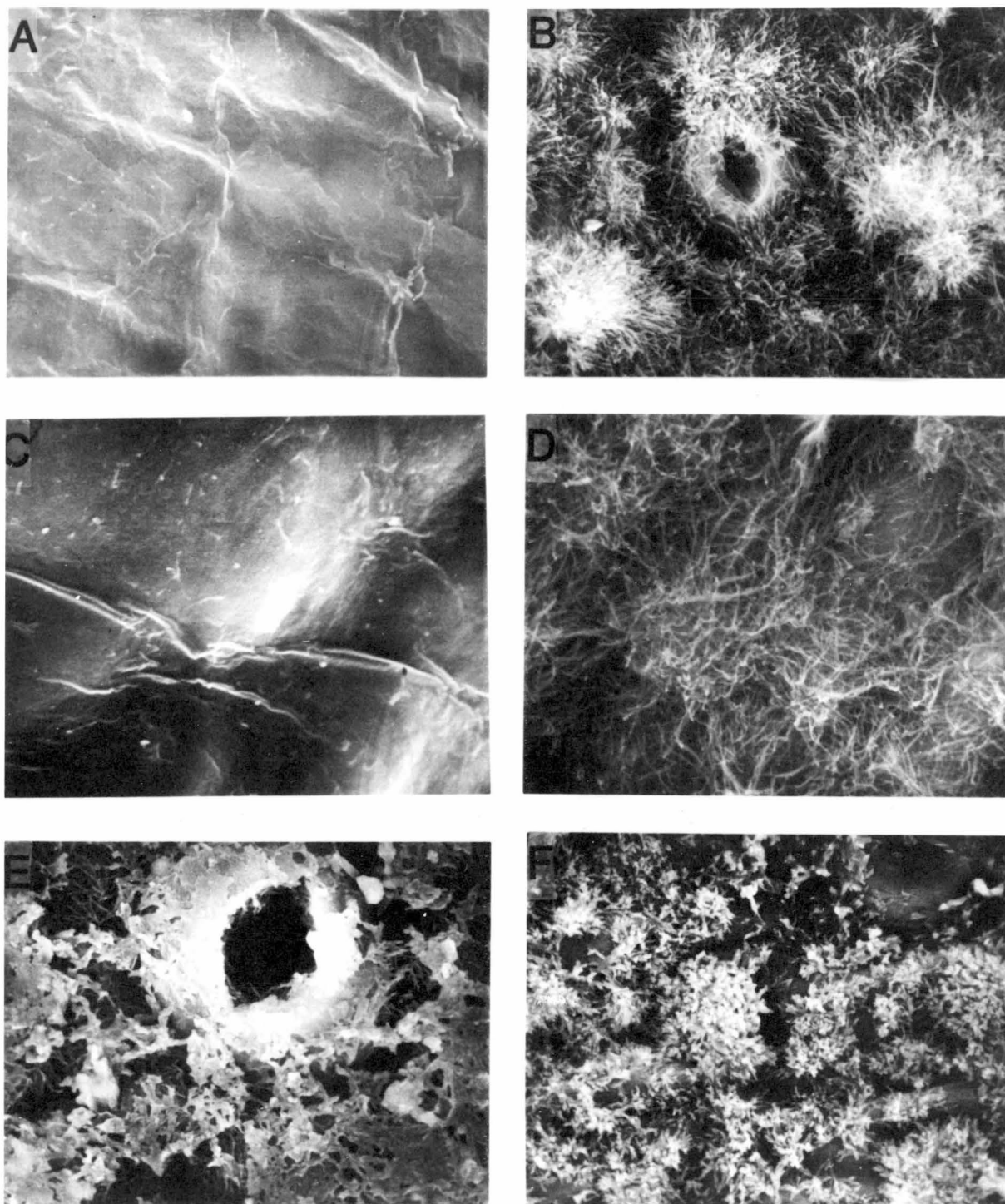


Fig. 2.11 Scanning electron micrographs of leaf and stem surfaces ($\times 2000$). Adaxial surfaces of newly expanded leaves of *E. urnigera* showing extreme glaucousness grades (A) low altitude green form (GLAUC=0), (B) high altitude glaucous form (GLAUC=5). Stem surfaces of (C) *E. archeri* (P_1 ; GLAUC=1) and (D) *E. gunnii* (SL; GLAUC=5) seedlings. Structural changes associated with the decrease in intensity of glaucousness between (F) newly expanded and (E) old leaves of *E. urnigera* (GLAUC=5; adaxial).

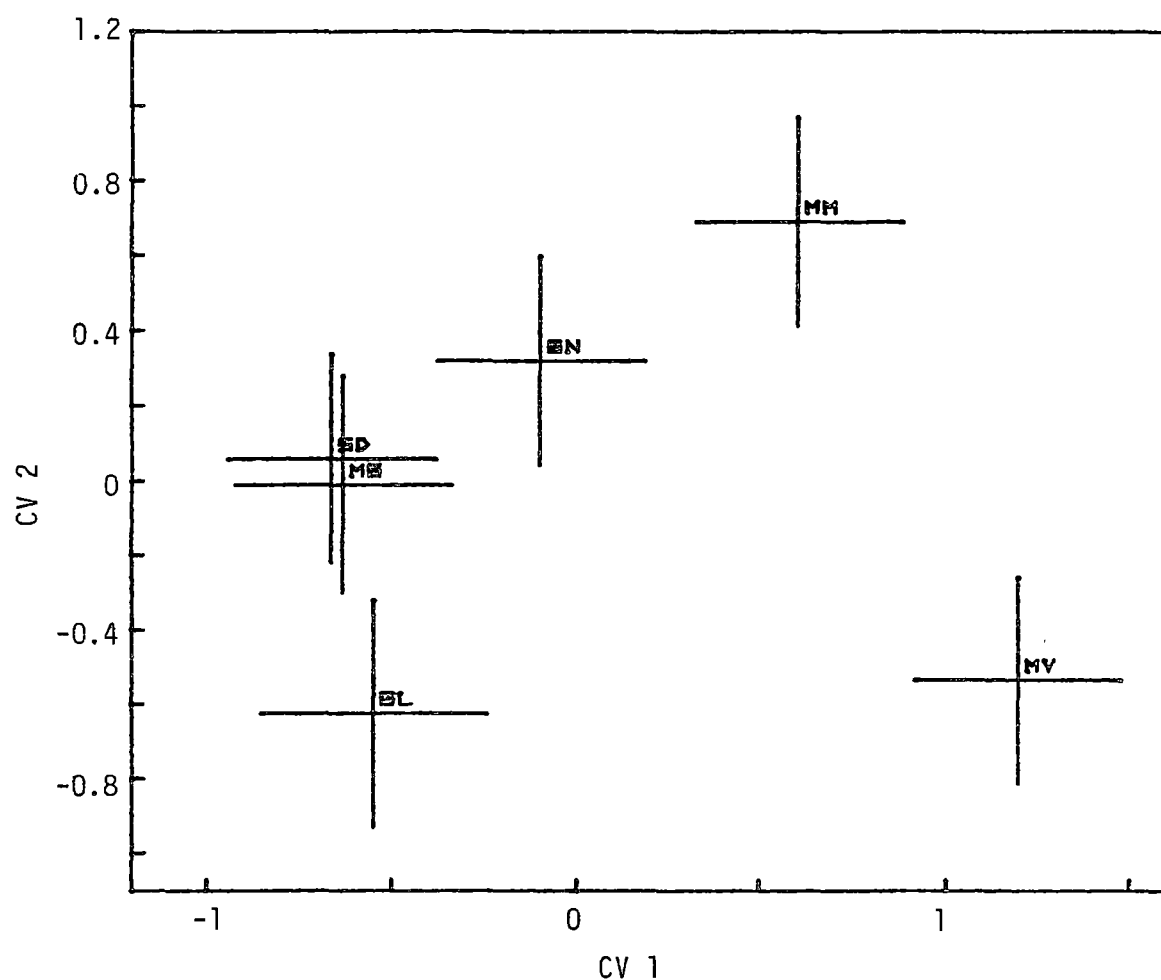


Fig. 2.12 CVA ordination of populations on the NE mountains (Trial 2). The CVA was based on the full seedling character set (e.g. Table 2.11) and the population centroids and their 95% confidence limits are shown. (MV=Mt. Victoria; BL=Ben Lomond; MB=Mt. Barrow; SD=Mt. Saddleback; BN=Ben Nevis; MM=Mt. Maurice).

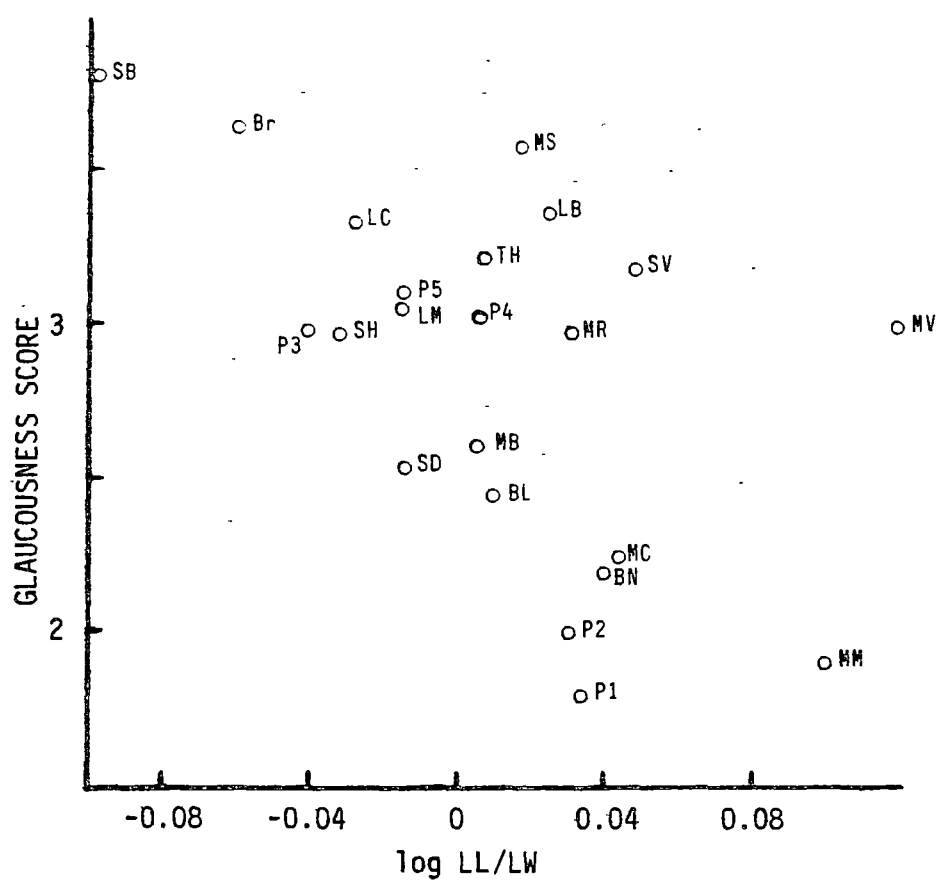


Fig. 2.13 The mean glaucousness score plotted against the mean log LL/LW (Trial 2).

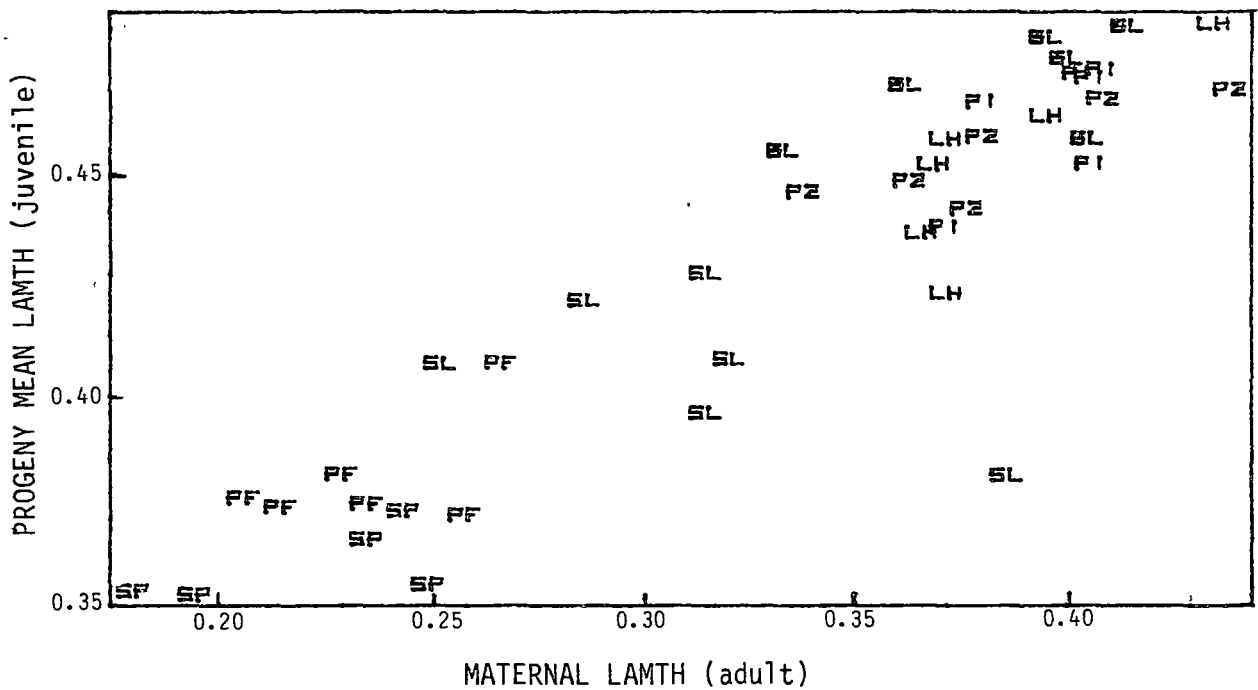


Fig. 2.14 Progeny mean lamina thickness (LAMTH: mm) plotted against the maternal value for trees in Trial 1 ($r=0.90$; $P<0.001$). Adult leaves were measured dried whereas seedling leaves were scored when fresh. The population code for each tree is indicated and corresponds to those given in Table 2.1.

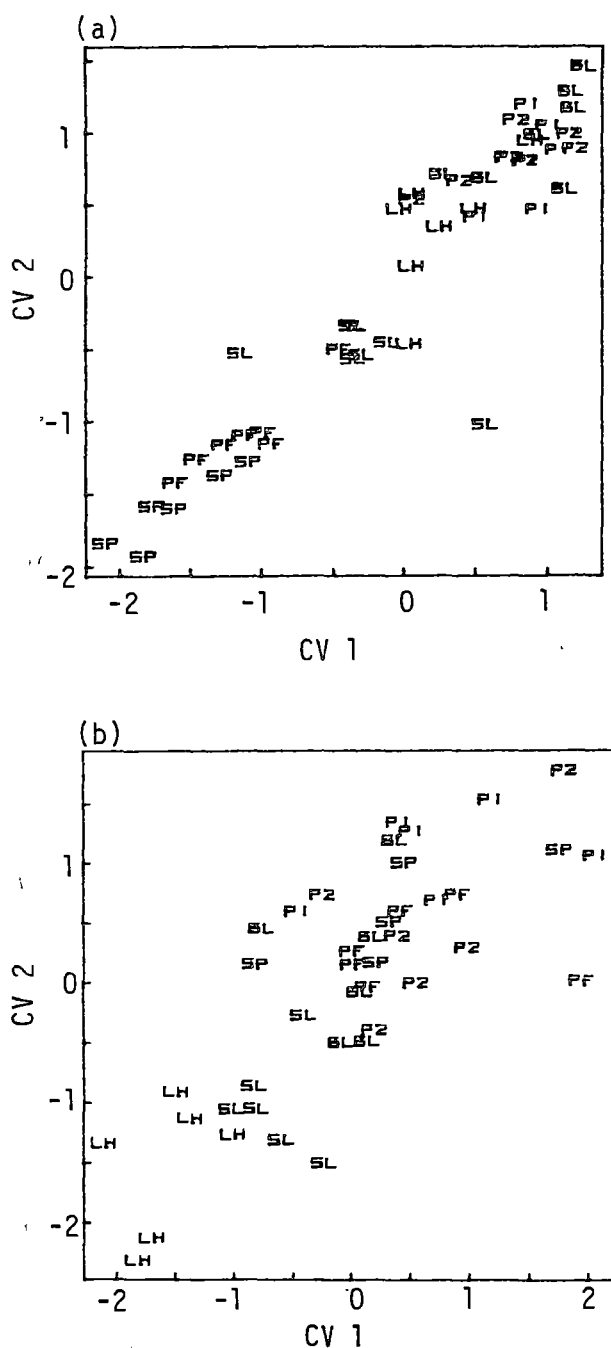


Fig. 2.15 The relationship between the adult and seedling leaf characters (Trial 1). Maternal scores on the first two pairs of canonical variates derived from canonical correlations analysis of seedling and adult leaf character sets (see Table 2.15; $n=41$). Individual trees are plotted using their population codes as given in Table 2.1. Each pair of vectors represents independent maximizations of the canonical correlation between character sets. (a) 1st pair, $r=0.93$; (b) 2nd pair, $r=0.78$.

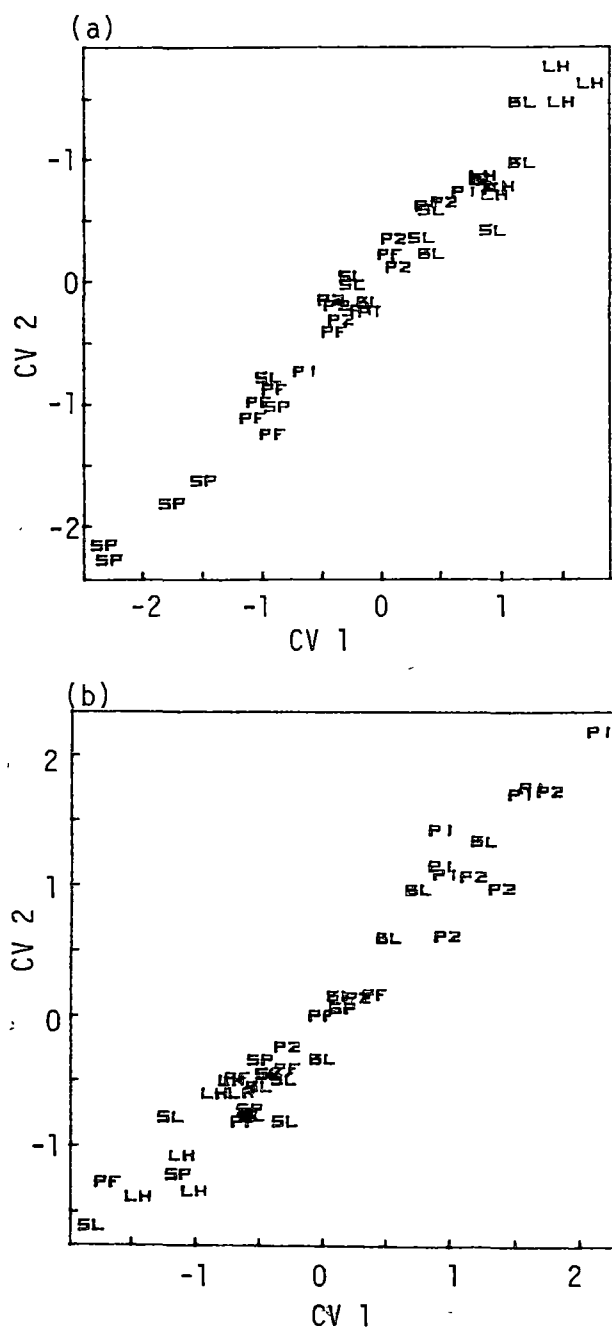


Fig. 2.16 The relationship between the adult and seedling phenotype (Trial 1). Maternal scores on the first two pairs of canonical variates derived from canonical correlations analysis of seedling and adult character sets (see Table 2.16; $n=41$). Individual trees are plotted using their population codes as given in Table 2.1. (a) 1st pair, $r=0.98$; (b) 2nd pair, $r=0.98$.

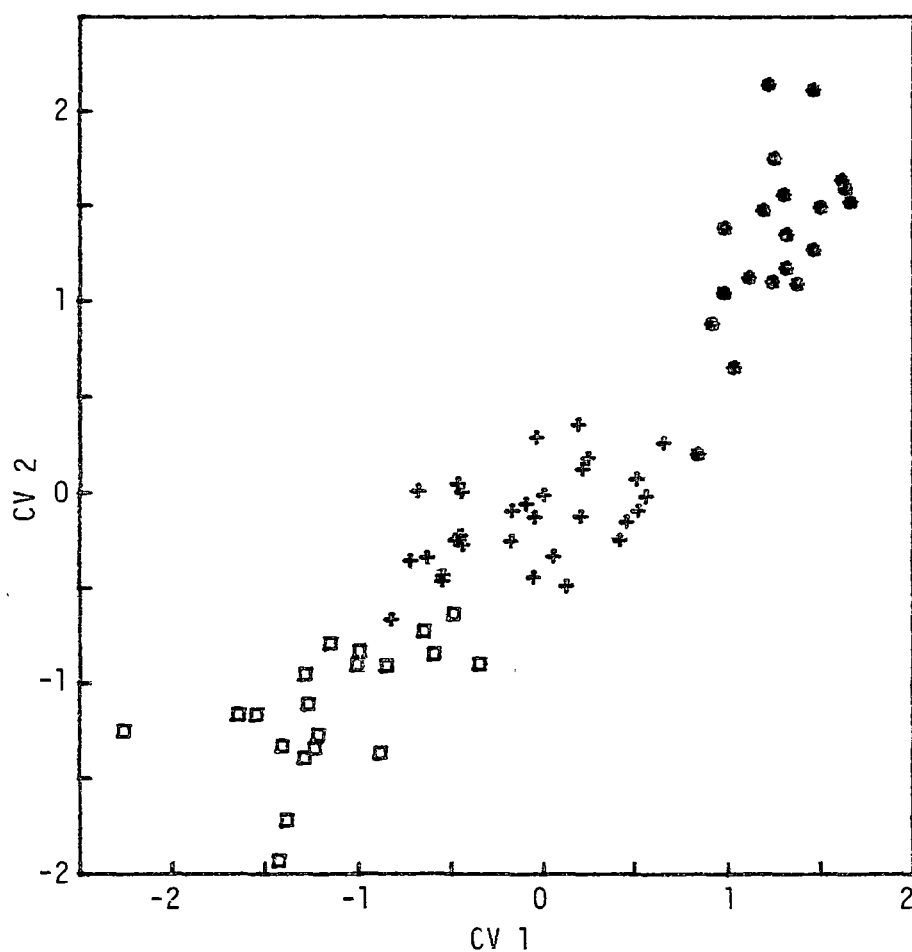


Fig. 2.17 The relationship between the adult and seedling phenotype for trees along the Pine Lake transect (Trial 2). Maternal scores on the single pair of canonical vectors corresponding to the only significant canonical correlation, obtained between seedling (CV2) and adult (CV1) character sets (see Table 2.18; $n=70$). Individual trees are grouped on a population basis into *E. archeri* (•; P1, P2), 'intermediate' (+; P3, P4, P5) and *E. divaricata* (□; Br, SB) types.

Variation in the *Eucalyptus gunnii*-*archeri* complexIII. Reciprocal transplant trials3.1 Introduction

In the previous chapters two major genetically based clines are demonstrated to occur in the more or less continuous stands of *E. gunnii*-*archeri* on the Central Plateau. These multi-character clines appear to parallel independent habitat gradients and encompass a large portion of the variation in the *E. gunnii*-*archeri* complex. A north-south cline (Pine Lake transect) occurs between populations classified as *E. archeri* and *E. gunnii* ('*E. divaricata*' form) and is associated with the transition from a sub-alpine, mixed eucalypt/rainforest habitat on the northern scarp of the Western Tiers to the open woodland habitat bordering the extensive 'frost hollows' on the lower Plateau surface. Interacting with this cline is another major cline associated with variation in exposure to the alpine environment which achieves maximum expression along an altitudinal gradient running east-west (southern Plateau transect). This transect encompasses populations which represent phenetic extremes of this cline within the *E. gunnii*-*archeri* complex as well as the clinal transition between forms classified as *E. divaricata* and *E. gunnii* by Brett (1938).

The present chapter reports the results of reciprocal progeny trials established near the extremes of each major cline. These trials provide an indication of the selective differential between extreme morphs as well as a biological assay of site characteristics. In addition, the relative magnitude of the plastic response in a range of morphological characters is assessed.

3.2 Methods

Two year old seedlings from Trial 1 (Chapter 2) were transplanted (April, 1979) into four experimental gardens at the Liawenee (LH, 1150 m), Shannon Lagoon (SL, 1050 m), Pensford (PF, 960 m) and Projection Bluff (P₂, 1100 m) sites (Fig. 1.3). Six populations were included in the trial representing *E. archeri* (P₁, P₂) and *E. gunnii* ('*E. divaricata*' LH, SL and 'southern *E. gunnii*' PF, SP morphs see Fig. 1.24). Site particulars are given in Tables 1.1 and 2.1. Populations LH and PF are taken as extremes of the altitudinal gradient along the southern Plateau transect and the *E. archeri* populations (P₁, P₂) and SL represent extremes of the north-south cline (i.e. Pine Lake transect) (see Figs. 1.18 & 1.23). At

each site 12 seedlings from each population were planted in two 6 x 6 latin squares placed end to end and surrounded by an edge row. Seedlings were planted 1 m apart and as far as possible each mother was represented once per square being randomly assigned to a population position. Each garden was fenced and the only site treatment involved the removal of shrub cover where necessary (i.e. P₂ and LH).

Characters scored

Over the first two growing seasons (1979-80, 1980-81) the gardens were inspected at monthly intervals. Assessments of survival and growth were made regularly over a four year period (to April 1983). Seedlings appearing dead at the time of scoring were classified as such regardless of whether later regeneration occurred from lignotuber or epicormic buds. Height was measured from ground level to the maximum vertical height of the living portion of the plant. Stem diameter (September 1981) was measured at the cotyledonary node (see Table 2.2). Height and stem diameter were expressed as the increment from the corresponding measure prior to planting. The basal area (December 1982) of each surviving seedling was estimated from the diameter at 10 cm above ground level of all living stems.

Estimates of the percentage of the leaf area damaged by frost were obtained approximately two months after planting following the method of Ashton (1958). For each leaf, the fraction of leaf area killed was estimated to the nearest quarter and the total damage estimated from the number of leaves in each category. Prior to planting seedlings had been hardened outdoors at Hobart. A similar approach was adopted in estimating the percentage of the leaf area expanded over the 1980-81 growing season which was lost through direct insect grazing or due to necrosis, although in this case single leaf estimates were made to the nearest half. At the time of scoring (September 1981), the number of leaves on lignotuberous shoots as opposed to the main stem were recorded and the percentage of leaves occurring on lignotuberous shoots was used as an estimate of the relative vigour of the main stem and as an indication of seedling form. The percentage of leaf area lost from the 1979-80 season's growth due to insect grazing was subjectively evaluated. Seedlings were scored for the presence or absence of a petiole or intranode (February 1981) and later (September 1981) the maximum intranode length and corresponding internode length were measured. A single representative leaf from the area of maximum summer growth (see Section 1.4) was collected (September 1981) from each

seedling and the dimensions indicated in Fig. 2.1 as well as petiole length (PET) were measured by digitizing (see Section 1.4). The glaucousness grade of each progeny was scored on a 5 class scale from green or very lightly subglaucous (0) to highly glaucous leaves and stems (4).

Insect collections

In order to obtain estimates of the relative abundance and composition of the phytophagous insect fauna at each site, insects were collected from the foliage of mature *E. gunnii-archeri* trees surrounding each garden over the 1979-80 (November-April) and 1980-81 (January and February) growing seasons. Samples were collected using an insect net and taking 25 sweeps of the foliage, involving at least 10 adult trees at each site. The bias associated with this sampling method is discussed by Morrow (1977). Collections were sorted into species groups and tentatively identified by Dr. J. Madden (Faculty of Agric.; Uni. of Tas.) and only species known to be phytophagous were included in the survey.

Statistical analysis

Growth and morphometric data were subjected to ^{two-way} analysis of variance with deaths treated as missing values. In the latter stages of the trial, this obviously biases the growth results as differential mortality is also a manifestation of the treatment effects. For the growth results the between squares as well as row and column effects within squares were removed from the error. In most cases, although significant, these effects were relatively small and were not taken into account in the analysis of the morphometric data. Frequency data were tested by the χ^2 test for association. For the purpose of testing frequency data, populations were pooled into '*E. archeri*' ($P_1 + P_2$), '*E. divaricata*' (LH + SL) and 'southern *E. gunnii*' (PF + SP) types ($n=24$) due to the low number of replicates in each population. While this grouping of populations corresponds to the phenetic classification (Figs. 1.24 and 1.25), populations form a clinal series (e.g. LH, SL, PF, SP; Figs. 2.2 and 2.3) and there are clearly significant genetic differences between populations within each grouping.

3.3 Results

Seedling growth and mortality

Significant differences ($P < 0.001$) in the number of surviving seedlings were evident between sites and between populations pooled over sites (Table 3.1). The latter results from high, differential mortality of *E. archeri* (P_1 and P_2) seedlings at the *E. gunnii* sites (LH, SL and PF; Table 3.2), the main causes of which are discussed later. In contrast there is no evidence of differential mortality at the *E. archeri* site (P_2). For surviving seedlings, the environmental component to variation in growth characteristics is large (e.g. Ht. 1981, 1982, 1983, Δ Ht 1981, 1982, 1983; Δ DIA; BASAL AREA; Table 3.3). Population differences in growth rate, noted in Chapter 2, are partly maintained, although the population x site interactions are highly significant ($P < 0.001$) after the initial establishment phase, due partly to a tendency for populations to grow comparatively better at sites most similar to their site of origin. This is exemplified by the average height (Fig. 3.1) and diameter (Fig. 3.2) increments, average height (Fig. 3.3) and basal area (Figs. 3.4 and 3.5) of surviving seedlings.

The habitats at either extreme of the Pine Lake transect (P_2 vs SL) are clearly differentiated on the severity of the environment for seedling establishment (Table 3.1). The open woodland site on the edge of the 'frost hollow' at Shannon Lagoon (SL) is the most severe of all sites for establishment, regardless of seedling genotype (Table 3.2). Survival is even less than at the highest altitude site (LH) and by the third year, virtually all seedlings from populations P_1 , P_2 and SP were dead as well as 50% or more of the seedlings from the remaining *E. gunnii* populations (LH, SL and PF; Table 3.2). This contrasts with the Projection Bluff site (P_2) where after 4 years only two seedlings were dead. There is evidence for strong selection against the *E. archeri* seedlings at the Shannon Lagoon site, with the elimination of the P_1 seedlings in particular being the most rapid (Table 3.2). While there is greater survival of seedlings from the local population at the Shannon Lagoon site (SL-1982, 1983; Table 3.2), this is not significant, and in terms of survival and growth, there is no evidence for a selective response differentiating the *E. gunnii* populations - LH, SL and PF, at this site.

While the probability of seedling survival is greatest at the *E. archeri* site (P_2), the growth of surviving seedlings is generally greater at the Pensford site, except for population P_1 (e.g. Figs. 3.1, 3.4 and 3.5; Table 3.5). The growth of the *E. gunnii* populations - SL, PF and SP, at the

E. archeri site, is significantly reduced when compared to their relative performance at the Pensford site (PF) (Figs. 3.1, 3.2, 3.3, 3.4 and 3.5). At the *E. archeri* site there is clearly a trend for seedlings from the Shannon Lagoon site to exhibit the poorest growth (Figs. 3.1, 3.2, 3.4 and 3.5), although no significant difference between the *E. archeri* (P_1 and P_2) and other populations (PF, SP and LH) is apparent. Nevertheless, in both survival and growth, the *E. archeri* seedlings are clearly more competitive at their local site (P_2) than at any other (Figs. 3.1, 3.2, 3.3, 3.4 and 3.5; Table 3.2).

The difference in seedling mortality between sites at the altitudinal extremes (LH vs PF) is ~~not significant, although there is a~~ trend for survival to be greater at the highest altitude site (LH; 1981, 1982; Table 3.1). This mainly results from high differential mortality of the *E. archeri* (P_1 and P_2) seedlings at the Pensford site over the 1981 winter (Tables 3.2 and 3.4). Nevertheless, the Pensford (PF) and Liawenee (LH) sites are clearly differentiated in terms of productivity (Table 3.4) and for all populations except LH, there is a significant reduction in the stem diameter increment at the Liawenee (LH) site (Fig. 3.2). In addition, the relative magnitude of the reduction in height (Figs. 3.1 and 3.3) and basal area (Figs. 3.4 and 3.5) is significantly less for LH than for the other *E. gunnii* populations - SL, PF and SP. At the Liawenee site, there is a tendency, although not significant, for a greater mortality of the low altitude *E. gunnii* seedlings (PF and SP; Table 3.2). Furthermore, the surviving seedlings (PF and SP) are less vigorous than seedlings from higher altitude sites (LH and SL; Figs. 3.1, 3.2, 3.4 and 3.5). The basal area of surviving seedlings from the Liawenee population is significantly greater than either of the *E. archeri* populations (P_1 and P_2 ; Figs. 3.4 and 3.5) and the latest scoring indicates a greater mortality of *E. archeri* seedlings at this site ($P < 0.01$; April 1983; Table 3.2). These results clearly suggest the highest altitude population is most competitive, if not at a selective advantage, at its own site. It also performs comparatively well at the *E. archeri* site (PB; e.g. Figs. 3.2, 3.3 and 3.4) but is surpassed in growth at the low altitude site at Pensford by the *E. gunnii* populations - SL, PF and SP, which are rapidly dominating surviving seedlings from all other populations (i.e. P_1 , P_2 and LH; Figs. 3.1, 3.2, 3.3, 3.4 and 3.5). While there is some indication of greater basal area of the Pensford seedlings at their local site (Figs. 3.4 and 3.5), this is not significant nor evident for other growth measures (Figs. 3.1, 3.2 and 3.3). To date there is no evidence for a difference in survival or growth between the *E. gunnii* populations - SL, PF and SP, at the Pensford site. The data^{that} suggest the Shannon Lagoon

population (SL) is competitive with populations from both higher (LH) and lower (PF) altitudes at their local site. However, rather than resulting from a broad environmental range, this is more likely to reflect the intermediate status of the population on the exposure cline and suggests a degree of concordance between morphology and the physiological response.

In terms of the growth of surviving seedlings, sites broadly rank in the order Pensford (PF), Projection Bluff (PB), Shannon Lagoon (SL) and Liawenee (LH) (Figs. 3.2, 3.3 and 3.4), with the best growth generally occurring at the low altitude site at Pensford (PF). At the highest altitude (LH) and open woodland (SL) sites, there is effectively a reduction in seedling height due to the death of all or part of the main stem on many seedlings and subsequent regeneration from lignotuberous or epicormic buds. This mainly resulted from the cumulative effects of frost (Fig. 3.6), drought (Tables 3.5 and 3.6) and insect predation (Figs. 3.7 and 3.8), the effects of which were frequently differential and varied between sites (Table 3.3). Reduced vigour of the main stem and a shift toward the lignotuberous multistemmed habit was most apparent at the latter sites, particularly Liawenee (Fig. 3.9). In contrast, at the low altitude site at Pensford, new growth was virtually confined to axillary buds on the main stem. These plastic differences in apical dominance and tree height, accord with the difference in canopy height and habit between high (LH) and low (PF) altitude sites and while genetic differences between populations are in a similar direction (e.g. Figs. 24g,1 and 3.1), there is clearly a large environmental component to both height and habit (Table 3.3). In view of the extreme nature of the open woodland habitat it is quite likely the divaricating branching pattern of the '*E. divaricata*' form (Fig. 1.6) may be partly a result of crown damage and frequent regeneration from epicormic buds.

Frost Damage

Frost damage was first observed on plants one to two weeks after planting following a cold snap with below freezing temperatures accompanied by high winds and snow. Frost sensitivity was assessed two months after planting (July 1979) during which time minimum temperatures ranging from -3.8 to -6°C were recorded (i.e. P_2 -4°C , LH -4°C , SL -6°C , PF -3.8°C).

Significant differences ($P < 0.001$) in the proportion of leaf area damaged were apparent between sites and populations (Table 3.3). The greatest frost damage occurred at the high altitude (LH) and frost hollow (SL) sites. At all sites *E. archeri* (P_1 and P_2) seedlings received

significantly ($P < 0.001$) greater damage than those of *E. gunnii* (LH, SL, PF and SP) (Fig. 3.5). Few seedlings were killed (Table 3.2) and where damage was heavy seedlings recovered from lignotuber or epicormic buds. Similarly, differences in frost sensitivity between green (i.e. *E. archeri*) and glaucous forms of *E. gunnii* have been reported (Lacaze 1962) and results are consistent with Barber's (1955) suggestion that the green or subglaucous forms are selected against in the more frost prone habitats. However, the work of Harwood (1980) and Paton (1981) suggests this may not be a direct result of variation in glaucousness *per se* as suggested by Thomas and Barber (1974a) (see Section 1.6). The greatest frost damage observed in the open woodland site at Shannon Lagoon was indicative of a general trend for lower minimum temperatures to be recorded at this site (Table 3.7). While the differences in minimum temperatures were frequently not large, observations on several frosts indicate frost intensity is less at the *E. archeri* site. It is also significant that maximum temperatures are usually highest at the frost hollow site (SL; Table 3.7) indicating seedlings are subject to greater temperature extremes than at other sites.

Drought Damage

Over the two summers in which the gardens were regularly monitored (1979-80, 1980-81), significant differences ($P < 0.001$) were observed between sites in the frequency of seedlings showing signs of drought damage (Table 3.5). A large amount of damage occurred over both summers at the Shannon Lagoon site but was negligible at other sites. The open nature of the habitat at Shannon Lagoon (Fig. 1.6) results in full exposure to both the late afternoon sun and the dessicating effects of hot, dry NW winds. In both years water stress was apparent by the beginning of February (Table 3.6), whereas early in the season seedlings exhibited relatively vigorous growth. Drought damage was differential, with *E. archeri* seedlings appearing less drought tolerant (1979-80; Table 3.6). Xylem water potential readings taken from seedlings in the Pensford gardens (March 1981) indicated the *E. archeri* seedlings are significantly ($P < 0.001$) less resistant to water loss than *E. gunnii* seedlings (Table 3.8), although stomatal resistance readings were not available to allow full interpretation of these results (see Section 6.3). For the *E. archeri* seedlings, death from water stress in the 1979/80 summer was not associated with the degree of frost damage the previous winter and thus water stress appears to

represent a separate selective effect against the *E. archeri* seedlings in this habitat (see Section 1.6). There is some evidence to suggest that different facets of the selective environment are limiting the growth of *E. archeri* seedlings at the different *E. gunnii* sites. For example, drought was clearly not the cause of the *E. archeri* deaths at Pensford which occurred in winter (Table 3.9). Furthermore, these deaths did not appear to be the direct result of frost damage and their cause is unclear. Nevertheless, it is possible they were associated with fungal attack or waterlogging as the Pensford site in particular, is subject to frequent winter flooding.

Insect damage

Sampling of adult trees and observation on seedlings in the experimental gardens indicate sites are highly differentiated with respect to the local phytophagous insect fauna (Fig. 3.10; Table 3.10). Differences between sites were both qualitative and quantitative with large differences occurring in the relative abundance of Coleoptera (leaf eating; mainly Chrysomelidae and Scarabidae) and Homoptera (sap suckers; mainly Psyllidae) insects (Table 3.10). Phytophagous insect activity is more prominent at higher altitudes in terms of insect abundance and damage (Figs. 3.7, 3.8 and 3.10; Table 3.10). This is particularly so of the highest altitude site (LH) where continuous heavy grazing (mainly by a single *Trachymelid* species) of seedlings and adults resulted in considerable loss of leaf area (Figs. 3.7 and 3.8; Table 3.10) and damage to apices. These observations contrast with those of Burdon and Chilvers (1974b) for *E. pauciflora* where the amount of damage by leaf grazing insects decreased with increasing altitude.

The significance of phytophagous insects as a major selective force in *Eucalyptus* ecology is well recognized (e.g. Burdon and Chilvers 1974a; Morrow 1977; Springett 1978) and is affirmed in this study where insect grazing appears to be a major factor limiting seedling growth (Figs. 3.7 and 3.8; Table 3.10). Estimates of the proportion of leaf area lost from a single season's growth through direct insect grazing is large at several sites (PB, LH) and exceeds losses associated with leaf necrosis arising from a variety of factors (e.g. drought, frost, fungal and other forms of insect {e.g. cocoon} damage) (Fig. 3.8). The low level of phytophagous insect activity at the Pensford site (Figs. 3.7, 3.8 and 3.10; Table 3.10) may partly account for the generally high growth rates at this site (Table 3.5).

There is some evidence of host specificity at the subgenera or species level in *Eucalyptus* (see Pryor 1952; Burdon and Chilvers 1974a; Morrow 1977; Springett 1978, and references cited therein) and the present study suggests that host preference may extend to the population level and be a significant factor in the competitive interaction between genotypes within a single species. This is exemplified by differential grazing of seedlings from specific populations at both the Projection Bluff and Liawenee sites (Table 3.3; Figs. 3.7 and 3.8). At the Projection Bluff site in particular, intense preferential grazing of seedlings from the Shannon Lagoon population (Fig. 3.8), and often extending to 90% defoliation, appears to be the main reason for the poor growth of this population at the *E. archeri* site (Figs. 3.1, 3.2, 3.4 and 3.5). In addition to preferential grazing, there is limited evidence for population preference by some psyllid species. For instance one species (*Eucalyptel* sp.) which occurred in large numbers at the Projection Bluff site in the 1980-81 season appeared to exhibit a preference for *E. gunnii* seedlings, particularly those from the Liawenee population (Table 3.11). In terms of co-evolution of plant host and predator, it may be significant that the relative abundance of Homoptera insects is least at the Liawenee site (Table 3.10; Fig. 3.10). Differential predation may represent a simple primary effect (e.g. the presence or absence of secondary compound) or alternatively involve a complex variety of causes associated with the interaction of several factors (e.g. plant form, drought, nutrition, etc.) (see Springett 1978). Nevertheless, these results suggest that variation in the phytophagous insect fauna over the range of species may well be a significant factor in site adaptation and population differentiation.

Genetic and plastic components to variation in morphological characters

A partition of the components of variation in morphological characters is given in Table 3.12. A large component of the variation in many characters is associated with genetic differences between populations (e.g. PET, BASE, EMARG, LL/LW, LL/LWP, CV1, PC₂, GLAUC; Table 3.12). This contrasts with the large plastic response exhibited by most growth measures (e.g. Ht 1981-1983, Δ Ht 1981-1983, Δ DIA, Basal Area; Table 3.3) as well as inter- and intranode length (Table 3.12). Virtually all variation in the seedling glaucousness score was associated with genetic differences between populations with site and interaction components negligible (Table 3.12). This is particularly significant in view of the ecological and taxonomic importance of this character in the *E. gunnii-archeri* complex.

The largest plastic response in leaf characters occurs in measures related to lamina size (LL, LW and LWP) whereas variation in characters reflecting leaf shape (e.g. EMARG, BASE, LL/LW, LL/LWP) is predominantly genetic. For example, 93% of the total variation in the length to breadth ratio (LL/LW) is directly associated with genetic differentiation between populations, with even the interaction (population x site) component only comprising 2.7% of the total variation and only just significant ($P < 0.05$; Table 3.12). Variation in lamina size and shape appears most clearly separated by PCA (Table 3.13; Fig. 3.11) in which the first component mainly reflects lamina size (PC_1 , 55%), whereas later components mainly incorporate facets of lamina shape (PC_2 , 30%; PC_3 , 12%). ANOVA (Table 3.12) clearly demonstrates that a remarkably low level of plasticity is associated with leaf shape components. In contrast, there is a large plastic component to leaf size, although the population and interaction components are still highly significant ($P < 0.001$). This mainly reflects genetic differences in leaf size between the '*E. divaricata*' and 'southern *E. gunnii*' seedlings (Fig. 3.11). Similar conclusions are evident from CVA (Table 3.13) although the interpretation of vectors is less clear cut.

Plasticity in leaf size appears to be mainly associated with plant vigour with both leaf size and plant vigour decreasing at the Liawenee and Shannon Lagoon sites. The main influence of the environment on leaf shape appears to be through a retardation of the temporal rate of ontogenetic development. The transition from the juvenile to adult foliage involves a continuous sequence with leaves becoming narrower (i.e. lanceolate), isobilateral, opposite and petiolate with maturity. The frequency of plants exhibiting mature characteristics such as intranodes or petioles is significantly less at both the Liawenee and Shannon Lagoon sites (Table 3.14). Again, this appears to be associated with plant vigour, although only partly through the developmental reversion associated with regeneration from lignotubers or epicormic buds, as similar significant trends are evident when only undamaged plants are considered (Table 3.14). As noted previously for other characters, genetic variation in ontogenetic development occurs in a similar direction to the plastic response (Table 3.14; Figs. 2.4 and 2.9). Seedlings from sites in which the general expression of mature characters is environmentally delayed (LH, SL), genetically retain the juvenile foliage type longer than other populations ('*E. archeri*' and 'southern *E. gunnii*'). In this respect, the trends observed in Chapter 2 are clearly exemplified at the Pensford site where despite a comparable growth rate, the seedlings from the Shannon Lagoon population

retain the juvenile foliage longer and thus to a greater height than either of the 'southern *E. gunnii*' populations. Furthermore, despite a slower growth rate, only a small proportion of the *E. archeri* seedlings have retained the juvenile foliage. Where the growth of the *E. archeri* and 'southern *E. gunnii*' seedlings is comparable (e.g. P₂) a lower proportion of *E. archeri* seedlings retain the juvenile foliage (Table 3.14). There is clearly a significant trend from the '*E. archeri*', 'southern *E. gunnii*' to the '*E. divaricata*' morphs for a successive increase in ontogenetic retention of the juvenile foliage. This exemplifies a significant feature of the variation within the complex demonstrating genetically based variation in 'developmental plasticity' (see Bradshaw 1965).

3.4 Discussion

These results indicate a large plastic response in characters which are influenced by or reflect plant vigour (e.g. internode length, lamina size, height, habit) and large treatment effects are frequently reported for such characters in *Eucalyptus* (e.g. Clucas and Ladiges 1979; Davidson and Reid 1980). In contrast, other characters such as glaucousness and those associated with leaf shape exhibit relatively little environmental modification and this is also evident in the data of Clucas and Ladiges (1979). The plasticity in leaf size supports the previous suggestion (Section 2.3) that genetic differentiation in juvenile leaf size along the altitudinal cline may be partly a pleiotropic effect of genetic variation in growth rate. However, a large portion of the variation in adult and seedling leaf characters reflects variation in leaf shape which is particularly significant in differentiating '*E. divaricata*' and '*E. archeri*' morphs.

The growth and mortality data presented suggest a close adaptive response of the *E. gunnii*-*archeri* populations to the local environment. This is a common feature in *Eucalyptus* (Pryor 1959b, 1976; Pryor and Johnson 1971) and is well recognized at the species (e.g. Moore 1959; Parsons and Specht 1967; Parsons 1968a, 1969a; Lamb and Florence 1973; Ashton *et al.* 1975; Ashton 1976, 1981a) and population (e.g. Pryor 1957a, 1976; Barber and Jackson 1957; Barber 1955, 1965; Ladiges and Ashton 1974; Anderson and Ladiges 1982; and many others) level. Differences in fitness are demonstrated between extreme morphs along the major clines on the Central Plateau suggesting selection is a major factor in maintaining genetic differentiation in this more or less

continuous population. Further supportive evidence includes the fact that the clines appear correlated with variation in habitat as well as a degree of parallelism being evident in the variation pattern shown by other species (Barber 1955; Chapter 1). For example, Barber (1955) cites parallel variation in glaucousness in both *E. coccifera* and *E. delegatensis* on the Western Tiers as evidence for the cline in glaucousness between the '*E. archeri*' and '*E. divaricata*' morphs being adaptive. Similarly, samples of *E. coccifera* taken from the same sites as *E. gunnii-archeri* suggest that a parallel reduction in leaf size occurs with increasing exposure, although this parallel response was not evident for other characters (e.g. flowering time; Potts, unpubl.).

Differences in fitness are associated with integrated facets of the local selective regime, including biotic and abiotic factors. Drought and frost sensitivity appear to be the main factors restricting the '*E. archeri*' morph and there is clearly strong selection against this form in sites currently occupied by the *E. gunnii* populations. On the other hand, selection against the glaucous *E. gunnii* seedlings in the *E. archeri* habitat appears to be less intense, although the *E. archeri* seedlings are most competitive in their own habitat. Selection against the *E. gunnii* populations when growing at alien sites appears less than observed for the *E. archeri* populations, although altitudinally extreme morphs are clearly at a competitive disadvantage when grown at their opposite extreme. As also noted in several other species (e.g. *E. pauciflora*, Pryor 1959a; *E. vernicosa*, Jackson 1960b), the high altitude seedlings retain their slow growth rate at low altitudes and are thus unable to compete with faster growing low altitude forms. In the present case, no clear data are available for the demise of the low altitude variant at the highest site. However Pryor (1959a) suggests slow growth at higher altitudes may be advantageous in confining growth to a shorter, frost-free growing period, and several authors (e.g. Paton 1972; Marien 1979) allude to an association between growth rate and frost sensitivity. However initial observations on frost damage at the beginning of the trial indicate a trend for the highest altitude population to be more frost-sensitive than lower altitude populations (e.g. SL, PF and SP). Although not marked, this trend is consistent with the work of Harwood (1980) on *E. pauciflora* where frost resistance may increase in low altitude sites subject to cold air drainage ('frost-hollows'). In addition, preliminary data on *E. gunnii* (Potts, unpubl.) suggests that damage by freezing temperatures is accentuated under waterlogged regimes which, due to the trend toward more waterlogged sites at lower altitudes, could partly account for a high

level of frost resistance being maintained in low altitude populations. While an increase in frost resistance with increasing altitude is commonly observed (e.g. Ashton 1958; Thomas and Barber 1974; Marien 1979; Phillips and Reid 1980) this relationship may be markedly displaced by other environmental considerations (present study; Paton 1972; Harwood 1980). In view of the known complexity of the pre-conditioning process (e.g. Harwood 1980; Paton 1981) further work is clearly required on the genotype-site interaction for a full ecological interpretation of the low temperature response of this species.

A degree of similarity is evident in the selective response of populations from the same phenetic cluster (i.e. '*E. archeri*', '*E. divaricata*' and 'southern *E. gunnii*') and to some degree, the intensity of selection against a population in an alien habitat accords with the degree of genetic differentiation (as shown in Fig. 2.2) from the local population. However, while variation in adult or seedling morphology may be associated with variation in fitness, there is no direct evidence as to whether the characters examined are adaptive *per se* or merely associated with other, perhaps physiological, characters more closely related to fitness. In addition, comparative estimates of fitness are based on the vegetative response and represent partial fitness values (Johnson 1976) corresponding to a specific, relatively short phase in the life cycle of the species. Nevertheless, it is likely that with time, increasing competition ^{in the experimental gardens} will accentuate the trends already evident.

Table 3.1 Seedling deaths in experimental gardens. The number of dead seedlings (a) at each site (n=72) and (b) from each population pooled over all sites (n=48). The significance of the χ^2 test for association is indicated (NS = not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

	1979 (NOV)	1980 (MCH)	1981 (SEPT)	1982 (MAY)	1983 (APRIL)
(a) Site					
P ₂	0	0	1	2	2
LH	4	4	7	15	20
SL	1	21	26	51	58
PF	0	1	18	20	22
	NS	***	***	***	***
(b) Population					
P ₁	2	9	17	24	28
P ₂	2	7	14	19	20
LH	0	0	3	9	13
SL	0	2	4	8	10
PF	1	4	6	11	13
SP	0	4	8	17	18
	NS	*	***	***	***

Table 3.2 Seedling deaths in experimental gardens (n=12). The significance of the χ^2 test for association between mortality and cluster type is indicated (a) '*E. archeri*' vs '*E. divaricata*' vs 'southern *E. gunnii*', (b) '*E. divaricata*' vs 'southern *E. gunnii*'. (NS = not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

	1979 (NOV)	1980 (MCH)	1981 (SEPT)	1982 (APRIL)	1983 (APRIL)
Site: Projection Bluff (P ₂)					
Population					
P ₁	0	0	0	0	0
P ₂	0	0	1	1	1
LH	0	0	0	1	1
SL	0	0	0	0	0
PF	0	0	0	0	0
SP	0	0	0	0	0
(a)	NS	NS	NS	NS	NS
(b)	NS	NS	NS	NS	NS
Site: Liawenee (LH)					
P ₁	1	1	2	4	7
P ₂	2	2	3	4	4
LH	0	0	0	1	1
SL	0	0	0	1	1
PH	1	1	1	2	3
SP	0	0	1	3	4
(a)	NS	NS	NS	NS	*
(b)	NS	NS	NS	NS	NS
Site: Shannon Lagoon (SL)					
P ₁	1	8	8	12	12
P ₂	0	5	6	10	11
LH	0	0	2	6	9
SL	0	2	2	5	7
PF	0	3	4	7	8
SP	0	3	4	11	11
(a)	NS	**	*	**	*
(b)	NS	NS	NS	*	NS
Site: Pensford (PF)					
P ₁	0	0	7	8	9
P ₂	0	0	4	4	4
LH	0	0	1	1	2
SL	0	0	2	2	2
PF	0	0	1	2	2
SP	0	1	3	3	3
(a)	NS	NS	*	**	**
(b)	NS	NS	NS	NS	NS

Table 3.3 Components of variation in growth characters. The percentage of the total variance ($\sigma_T^2 = \sigma_E^2 + \sigma_P^2 + \sigma_{P.E}^2 + \sigma_S^2 + \sigma_R^2$) attributed to site (σ_E^2), population (σ_P^2), interaction (site x pop.; $\sigma_{P.E}^2$), systematic sources within sites (σ_S^2 ; block + row + column) and residual (σ_R^2) effects. The significance of each component is indicated (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). The degrees of freedom for the full design are indicated, but due to mortality orthogonality is not maintained for the majority of characters (see Table 3.2).

Character	EFFECTS				
	Site (σ_E^2)	Population (σ_P^2)	Site x Pop. ($\sigma_{P.E}^2$)	Systematic (σ_S^2)	Residual (σ_R^2)
	d.f.=3	d.f.=5	d.f.=15	d.f.=84	d.f.=80
HEIGHT					
April 1979 (start)	4.0	88.1***	1.9	4.1***	1.9
Mch. 1980	12.3**	77.7***	2.9	4.6***	2.5
Sept. 1981	79.0***	10.4***	6.5***	2.5*	1.7
May 1982	72.9***	16.1***	8.0***	2.2***	0.7
April 1983	70.6***	18.4***	8.4***	1.7**	1.0
Δ HEIGHT					
Mch. 1980	24.8	25.7*	29.3***	10.6	9.7
Sept. 1981	54.0***	36.8***	5.3***	2.4**	1.5
May 1982	82.7***	6.9***	7.7***	2.0***	0.6
April 1983	75.9***	10.3***	8.5***	4.4***	0.8
Δ DIA Sept. 1981	69.8***	12.9**	9.7***	4.5*	3.1
Basal Area Dec. 1982	77.5***	9.6**	7.8***	2.7	2.4
% Frost Damage (1979)	26.3***	63.6***	6.0***	2.1	2.0
% Insect Damage (1981)	65.5***	15.3***	13.9***	3.2*	2.1
% Necrotic (1981)	14.1	53.3***	19.0**	7.7	5.9
% TOTAL DAMAGE (1981)	58.1***	13.1***	20.4**	4.8	3.5
% LEAVES LIG/TOT (1981)	71.3***	12.2***	11.1***	3.3*	2.2
TOT LEAVES(1981)	10.0*	70.2***	11.0***	5.2*	3.6

Table 3.4 Site means (\bar{X}), standard errors (SE) and number of seedlings (n) for height (cm; $\Delta Ht80$, $\Delta Ht81$, $\Delta Ht82$, $\Delta Ht83$) and stem diameter (cm; ΔDIA 1981) increments from measurements prior to planting (April 1979; Chapter 2) and basal area (cm²; 1982).

Site		$\Delta Ht80$	$\Delta Ht81$	$\Delta Ht82$	$\Delta Ht83$	ΔDIA 81	Basal Area 1982	Total Basal Area
P ₂	\bar{X}	2.0	8.8	16.0	25.9	0.35	0.75	51.0
	SE	0.54	1.11	1.96	2.11	0.031	0.57	
	n	70	69	68	68	68	70	
LH	\bar{X}	0.4	-3.4	-3.8	-5.3	0.24	0.46	26.2
	SE	1.19	1.82	2.17	2.37	0.022	0.047	
	n	72	65	57	49	65	54	
SL	\bar{X}	2.5	-2.6	-14.2	4.9	0.32	0.70	14.7
	SE	0.59	3.53	7.26	8.66	0.031	0.139	
	n	49	46	21	14	46	15	
PF	\bar{X}	2.9	18.6	43.7	66.8	0.55	2.92	148.9
	SE	0.3	1.95	4.9	7.8	0.041	0.330	
	n	70	58	51	49	53	51	

Table 3.5 Percentage of plants at each site exhibiting drought damage in March 1980 and 1981.

Site	1980 March	1981 March
P ₁	0	0
LH	0	2.9
SL	45.8	18.1
PF	5.7	1.4
	***	***

Table 3.6 The total number of dead seedlings at the beginning and end of the 1979-80 and 1980-81 summers at the Shannon Lagoon garden (SL). The number of seedlings exhibiting drought damage in January, February and March of each summer is indicated.

	TOTAL DEATHS		DROUGHT DAMAGE			TOTAL DEATHS		DROUGHT DAMAGE		
	1979	1980	1980			1980	1981	1981		
	NOV	MARCH	JAN	FEB	MARCH	DEC	MARCH	JAN	FEB	MARCH
P ₁	1	8	0	4	7	7	8	0	2	2
P ₂	0	5	0	5	5	5	6	0	2	2
LH	0	0	0	2	6	1	2	0	0	1
SL	0	2	0	3	3	1	3	0	2	2
PF	0	2	0	2	6	3	5	0	1	2
SP	0	3	0	3	6	1	4	0	4	4

Table 3.7 Minimum and maximum temperatures ($^{\circ}\text{C}$) recorded near experimental gardens (+ = missing observation).

Site	6/3/79 to 27/4/79	27/4/79 to 5/5/79	5/5/79 to 26/6/79	26/6/79 to 2/11/79	2/11/79 to 26/11/79	26/11/79 to 28/12/79	28/12/79 to 13/1/80	13/1/80 to 5/2/80	5/2/80 to 5/3/80	5/3/80 to 3/4/80	15/10/80 to 13/11/80	13/11/80 to 13/1/80	13/1/80 to 12/2/80	12/2/80 to 12/3/80
P ₂ min	-1.0	-2.0	-4.0	-3.5	-5.0	-2.0	-1.0	0.0	-3.0	-3.5	-4.0	-1.0	-1.5	-0.8
max	22.0	15.0	9.0	21.0	23.5	26.0	32.0	32.0	+	26.0	23.0	32.0	30.0	26.0
LH min	-1.0	-4.0	-3.5	-4.0	-3.0	-2.0	-2.0	-1.0	-4.0	-2.5	-4.5	-2.0	-2.0	-0.8
max	18.0	16.0	11.0	21.0	24.0	30.5	36.0	30.0	28.0	25.0	29.0	36.0	38.0	29.0
SL min	-3.5	-6.0	-5.0	-4.0	-4.5	-2.0	-3.0	-2.0	-4.0	-4.0	-5.0	-3.0	-5.0	-2.0
max	24.0	18.0	13.0	22.7	25.0	+	33.0	+	23.0	27.0	26.5	33.0	34.0	30.0
PF min	-2.0	-3.8	-3.0	-2.5	+	+	-2.0	0	+	-2.0	+	-2.0	+	+
max	21.0	16.0	12.5	18.0	+	+	33.0	26.0	+	25.0	+	33.0	+	+

Table 3.8 Mean water potential (mP) of small shoots taken from seedlings at the Pensford garden in March 1981. Population samples were grouped both spatially and temporally and the difference between populations with the block effect removed from the error was highly significant ($P < 0.001$). (LDS.05=0.236 for $n=9$). (τ one abnormally high reading excluded).

Population	n	\bar{X}	SE
τP_1	10	-0.86	0.109
P_2	12	-1.10	0.117
LH	12	-1.35	0.157
SL	10	-1.39	0.148
PF	10	-1.25	0.093
SP	9	-1.40	0.147

Table 3.9 Seedling mortality at the Pensford garden over the 1981 winter.

Population	Number of dead seedlings		Mortality over the 1981 winter (%)
	March	September	
P_1	0	7	58.3
P_2	0	4	33.3
LH	0	1	8.3
SL	1	2	9.1
PF	1	1	0
SP	2	3	10.0
	NS	***	***

Table 3.10 Summary of insects collected from adult trees and observed (1980-81) on seedlings in the experimental gardens. Abundance data refer to the number of individuals collected or observed.

Adult samples	P ₁	LH	SL	PF
Mean abundance of Coleoptera per sample (SE)	6.9(2.4)	15.1(2.9)	4.3(1.8)	2.5(1.0)
Mean abundance of Homoptera per sample (SE)	10.0(1.9)	4.5(1.3)	10.1(3.4)	7.1(1.2)
Number of Coleoptera species	8	4	9	7
Number of Homoptera species	10	8	7	8
Total number of species	18	12	16	15
Shannon-Weiner Diversity Index	2.46	1.28	1.95	2.28

Experimental Gardens

Mean percentage of leaf area eaten on new growth - 1979-80	19.5	6.7	1.3	3.9
1980-81	21.1	18.2	4.4	0.9
Abundance of Homoptera per seedling	10.0	0.4	3.9	0.6
Abundance of Coleoptera per seedling	0.0	0.4	0.1	0
Proportion of plants on which Homoptera observed	0.86	0.15	0.37	0.22
Proportion of plants on which Coleoptera observed	0.00	0.19	0.04	0.00

Table 3.11 Infestation by an unidentified psyllid species (*Eucalyptel* sp.) at the Projection Bluff garden over the 1980-81 season. The total abundance of psyllids per plant (summed over the period November to March), the proportion of plants infested, the heaviest infestation on any one plant and the mean (SE) abundance per plant at the time of maximum infestation (January 1981) are indicated.

Population	Total number/ plant	Proportion of plants infested	Heaviest infestation	Mean abundance (SE) (Jan.)
P ₁	1.8	42	8	1.2 (0.38)
P ₂	4.6	100	11	3.5 (0.90)
LH	25.6	100	54	22.7 (4.19)
SL	10.2	100	26	7.1 (2.45)
PF	9.7	100	30	10.5 (2.57)
SP	7.8	75	14	7.7 (2.66)

Table 3.12 Components of variation in morphological characters. The percentage of the total variance ($\sigma_T^2 = \sigma_E^2 + \sigma_P^2 + \sigma_{E.P}^2 + \sigma_R^2$) attributed to site (σ_E^2), population (σ_P^2), interaction ($\sigma_{E.P}^2$) and residual effects (σ_R^2). The residual component includes systematic sources of variation (cf. Table 3.3; block, column and row effects). CV1 and 2 and PC1,2 and 3 are canonical variates and principal components derived from the analysis of the leaf characters shown in Table 3.13 and Fig. 3.11. The residual degrees of freedom associated with the leaf characters and the significance of the treatment effects are indicated (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

Character	EFFECTS			
	Site (σ_E^2) d.f.=3	Population (σ_P^2) d.f.=5	Site x Pop. ($\sigma_{E.P}^2$) d.f.=15	Residual (σ_R^2) d.f.=220
LL	48.4***	37.6***	11.2***	2.7
LW	54.6***	36.0***	6.4**	3.0
LWP	41.8***	45.5***	9.5***	3.3
PET	21.7**	60.3***	14.1***	4.0
BASE	14.1*	78.2***	3.5	3.9
EMARG	20.5	63.2***	3.9	12.2
LL/LW	3.3	92.7***	2.7*	1.3
LL/LWP	22.9	45.5***	20.4*	11.2
CV1	6.6**	87.2***	4.8***	1.4
CV2	59.3***	27.8***	10.1***	2.8
PC1	59.3***	28.3***	8.9***	3.4
PC2	2.7	89.5***	4.4	3.4
PC3	14.3	62.7**	7.5	15.4
INTER	67.5***	27.0***	3.8**	1.7
INTRA	71.0***	19.0***	6.8**	3.2
GLAUC	3.3*	87.63***	4.1	5.0

Table 3.13 Standardized eigen vectors derived from CVA and PCA (Fig. 3.11) of leaf characters scored from experimental gardens. Each site-population was treated as a separate group in the CVA whereas any grouping structure was ignored in the PCA (TOT CORR).

	CV1 (60%)	CV2 (27%)	PC1 (55%)	PC2 (30%)	PC3 (12%)
LL	0.71	0.67	0.53	-0.36	0.05
LW	-0.69	0.39	0.56	0.18	-0.14
LWP	0.03	-0.61	0.51	-0.38	0.25
BASE	0.02	-0.10	0.33	0.56	-0.59
EMARG	0.15	0.09	0.16	0.62	0.75

Table 3.14 The proportion of seedlings with petioles and intranodes for (a) the total number of surviving, and (b) undamaged seedlings. Cluster types correspond to '*E. archeri*' (P_1 and P_2), '*E. divaricata*' (LH and SL) and 'southern *E. gunnii*' (PF and SP). The significance of the χ^2 test for association is indicated (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

	(a) TOTAL			(b) UNDAMAGED		
	PETIOLE	INTRANODE	N	PETIOLE	INTRANODE	N
Projection Bluff (P_2)						
$P_1 + P_2$	0.91	0.65	23	0.90	0.71	21
LH + SL	0.04	0.04	24	0.08	0.08	13
PF + SP	0.50	0.42	24	0.57	0.48	21
<u>TOTAL</u>	0.48	0.37	71	0.58	0.47	55
	***	***		***	***	
Liawenee (LH)						
$P_1 + P_2$	0.32	0.05	19	0.86	0.14	7
LH + SL	0.04	0.13	24	0.05	0.14	21
PF + SP	0.30	0.43	23	0.36	0.57	14
<u>TOTAL</u>	0.21	0.21	66	0.29	0.29	42
	*	**		***	*	
Shannon Lagoon (SL)						
$P_1 + P_2$	0.30	0.10	10	1.00	0.33	3
LH + SL	0.05	0.05	19	0.06	0.00	17
PF + SP	0.53	0.35	17	0.64	0.43	14
<u>TOTAL</u>	0.28	0.17	46	0.38	0.21	34
	**	*		***	*	
Pensford (PF)						
$P_1 + P_2$	0.67	0.63	24	0.75	0.50	12
LH + SL	0.05	0.27	22	0.05	0.29	21
PF + SP	0.65	0.45	20	0.68	0.47	19
<u>TOTAL</u>	0.45	0.45	66	0.44	0.40	52
	***	NS		***	NS	
Between gardens	***	***		**	***	

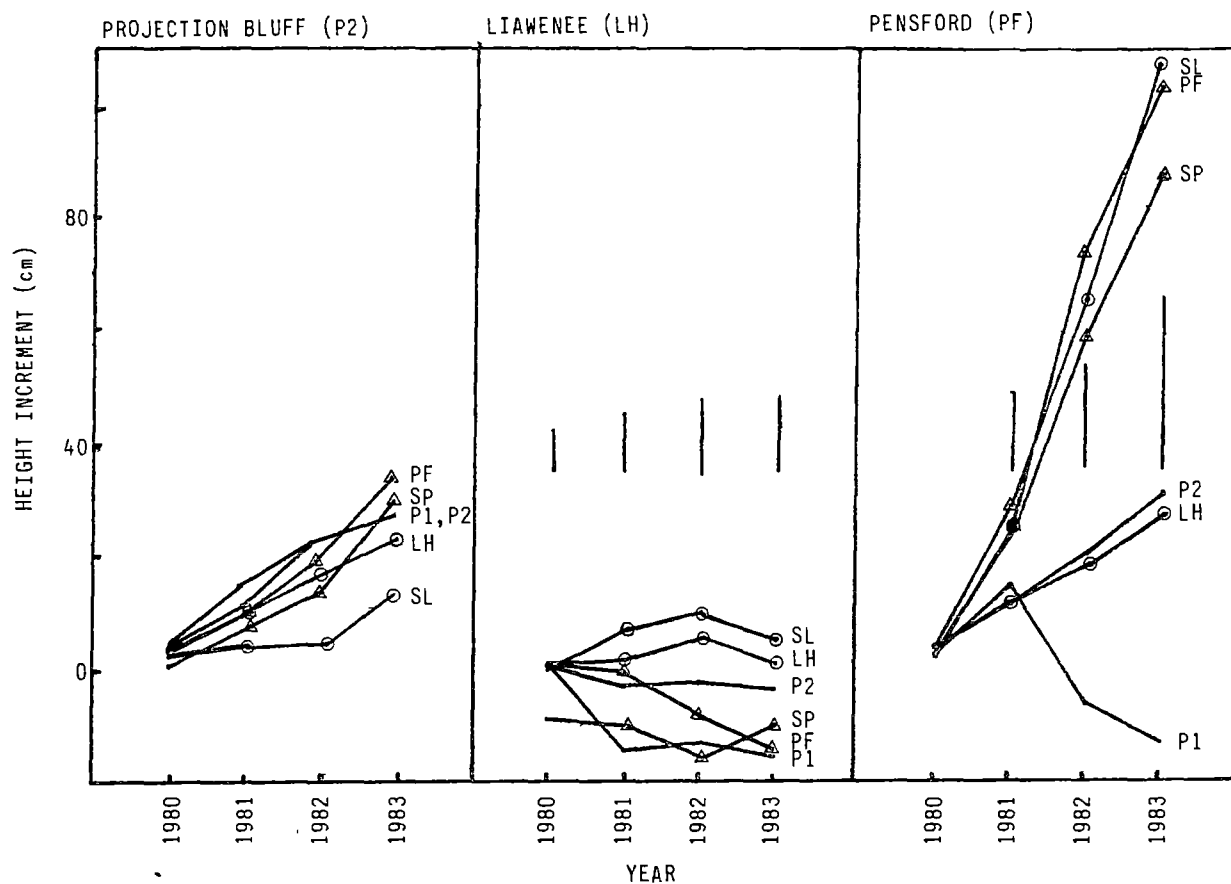


Fig. 3.1 Mean height (cm) increments for '*E. archeri*' (•, P1 and P2), '*E. divaricata*' (○, LH and SL) and 'southern *E. gunnii*' (Δ, PF and SP) populations in experimental gardens are indicated. Increments are calculated from height prior to planting and where the ANOVA for the difference between populations is significant, the LSD_{0.05} (based on $n=12$) is shown. Data are not present for the Shannon Lagoon population due to the low replication in the later phase of the trial.

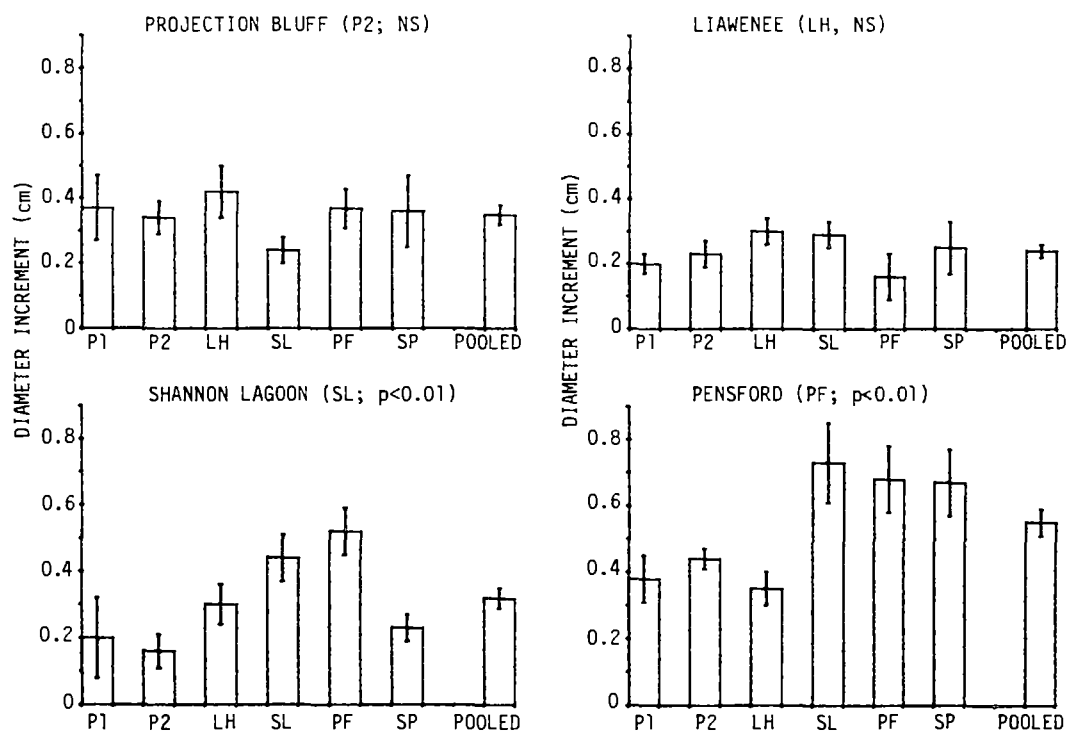


Fig. 3.2 Mean (\pm SE) diameter increment (cm; Sept. 1981; 29 months after planting) for surviving seedlings in experimental gardens. The significance of the difference between populations at each site is indicated.

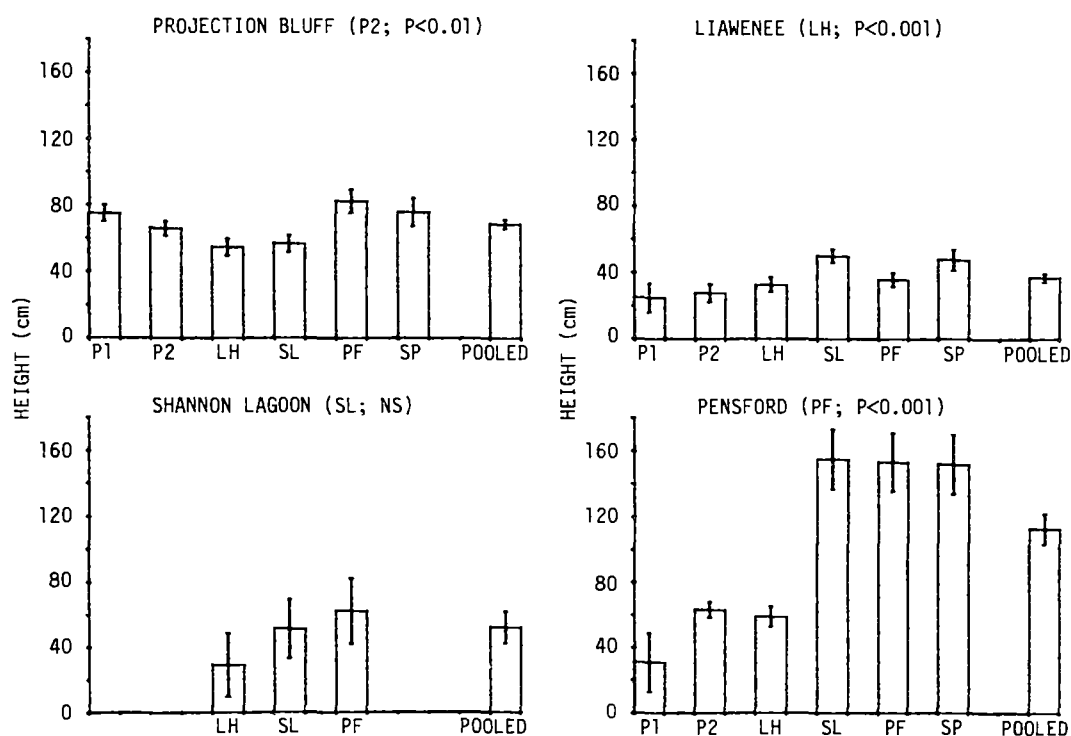


Fig. 3.3 Mean (\pm SE) height (cm) of surviving seedlings 4 years after planting in experimental gardens. The significance of the difference between populations at each site is indicated. All populations for which $n < 3$ are excluded.

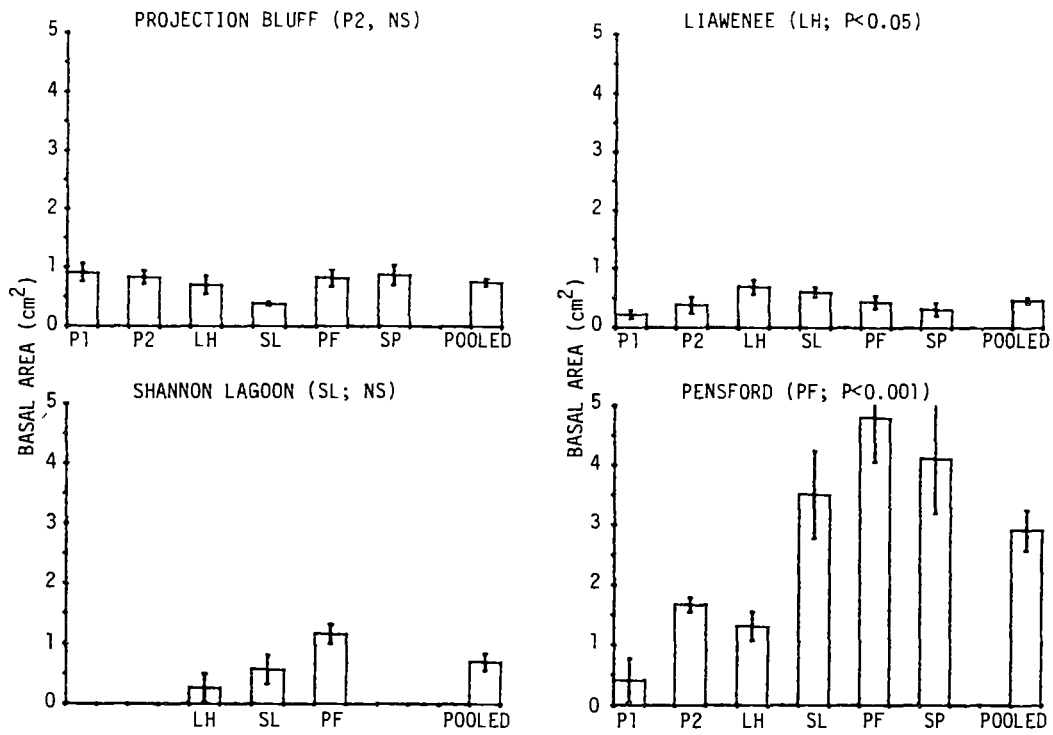


Fig. 3.4 Mean (\pm SE) basal area (cm²) of surviving seedlings 43 months after planting in experimental gardens. The significance of the difference between populations at each site is indicated.

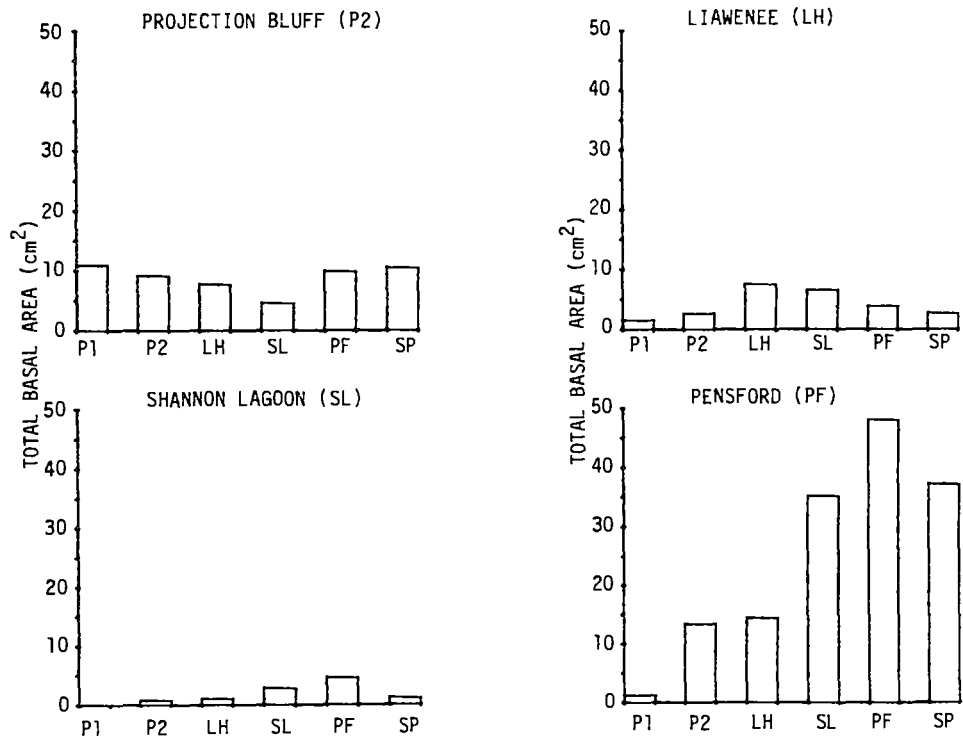


Fig. 3.5 Total basal area (cm²) of each population 43 months after planting.

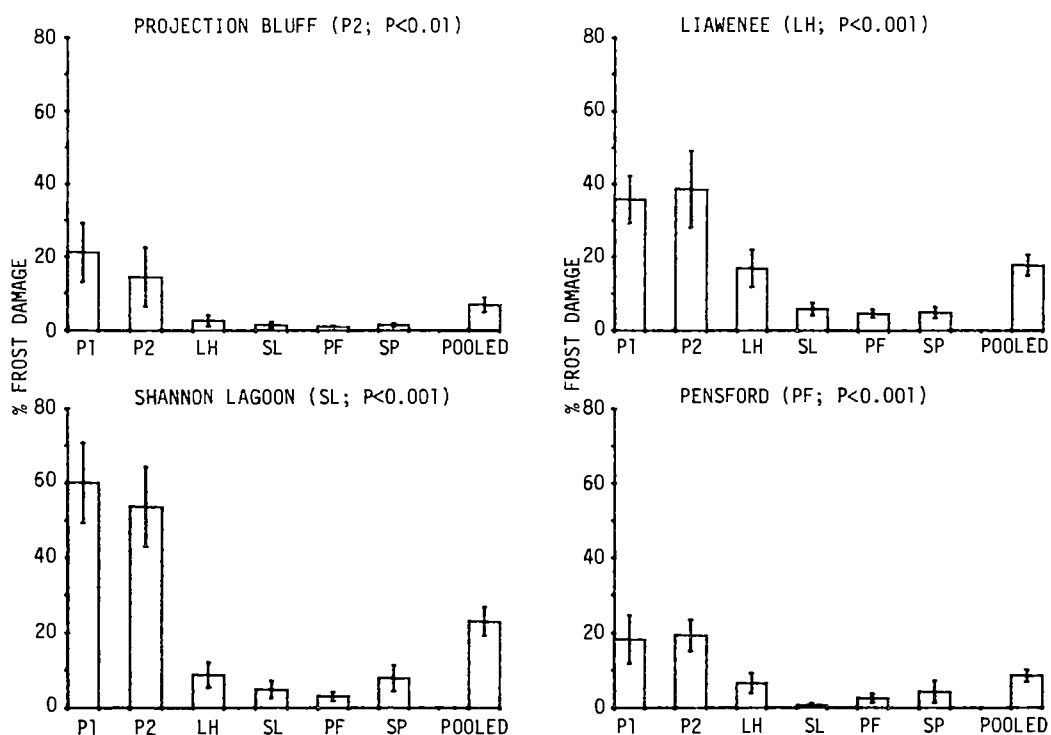


Fig. 3.6 Mean (\pm SE) percentage of leaf area damaged by frost 2 months after planting. The significance of the difference between populations at each site is indicated.

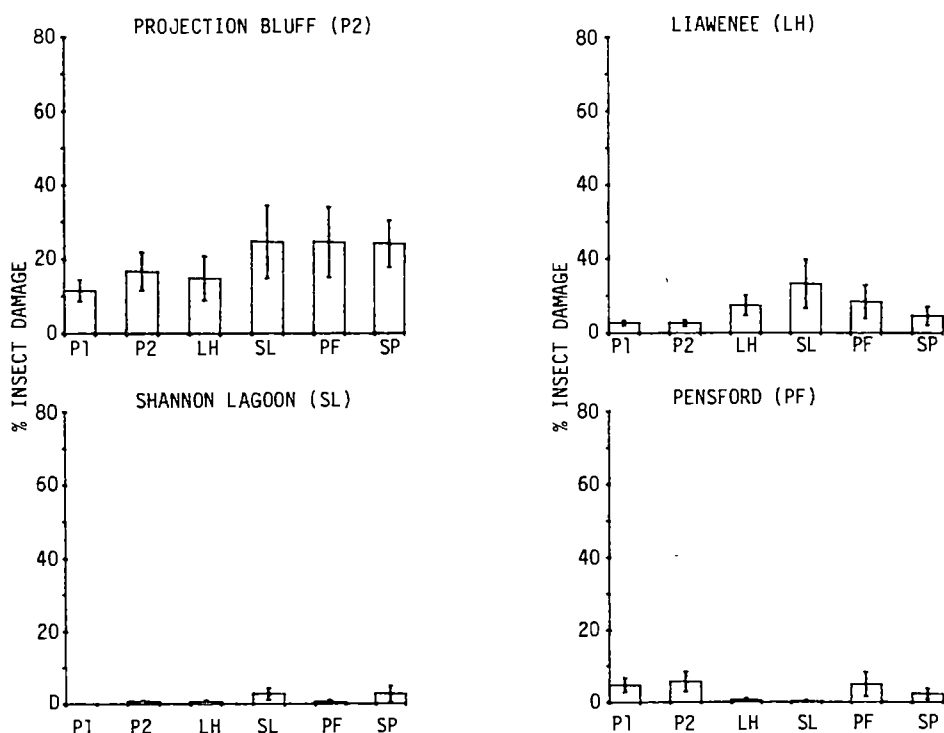


Fig. 3.7 Mean (\pm SE) of the estimated percentage of leaf area expanded in the 1979-80 growing season lost through insect grazing.

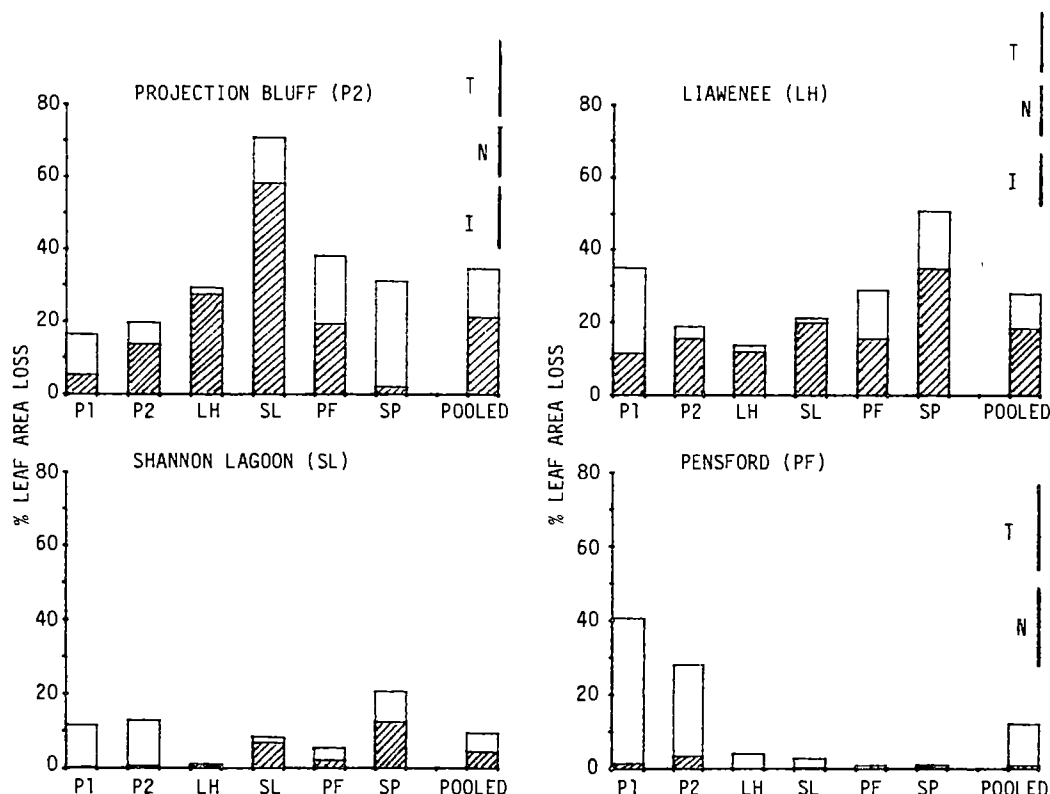


Fig. 3.8 Mean percentage of leaf area expanded in the 1980-81 growing season which was lost through insect grazing (cross-hatched) or necrosis. LSD.05 (based on $n=12$) for the total (T), in insect grazed (I) and necrotic damage (N) are indicated for comparison between populations.

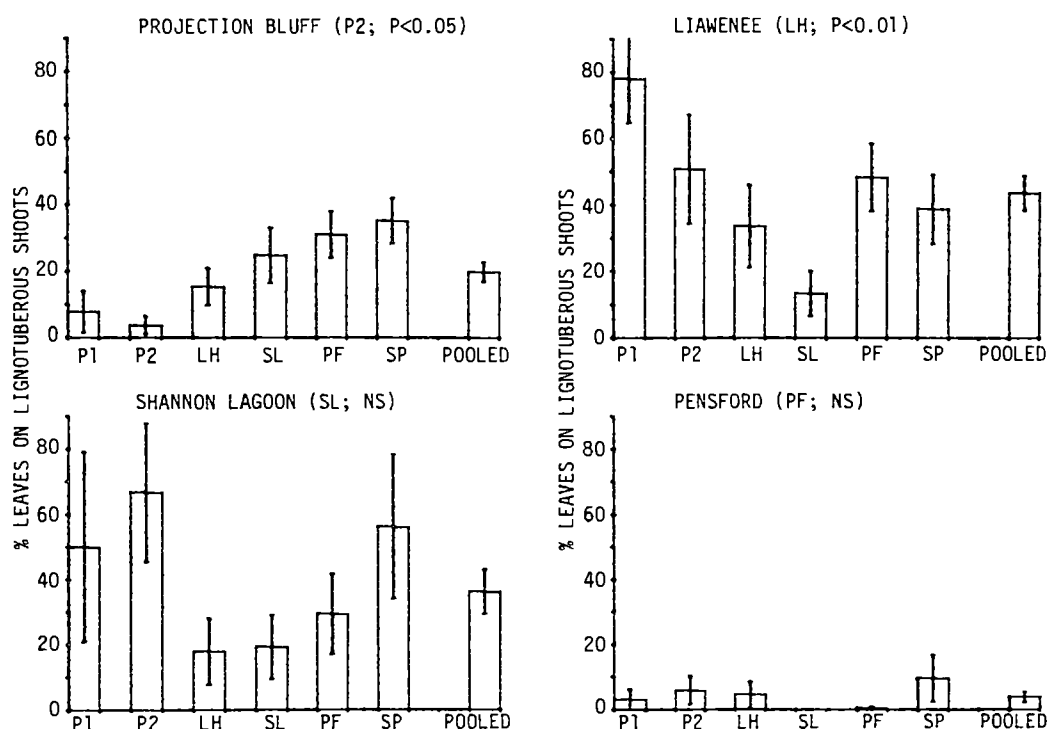


Fig. 3.9 The mean (\pm SE) percentage of the total number of leaves expanded in the 1980-81 season which occur on lignotuberous shoots. The significance of the difference between populations at each site is indicated.

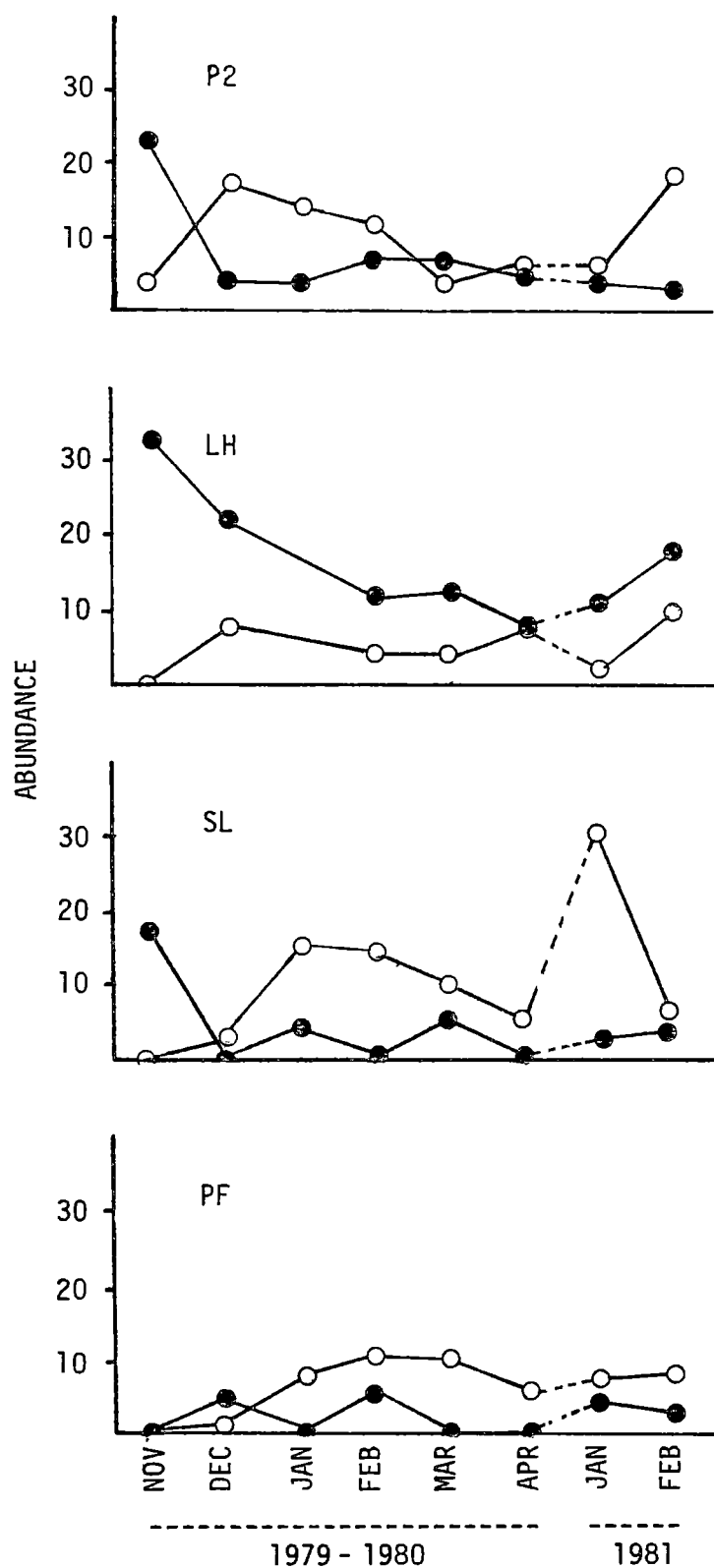


Fig. 3.10 Abundance of Coleoptera (●; leaf eating) and Homoptera (○; sap sucking) insects in samples collected from adult foliage at each site.

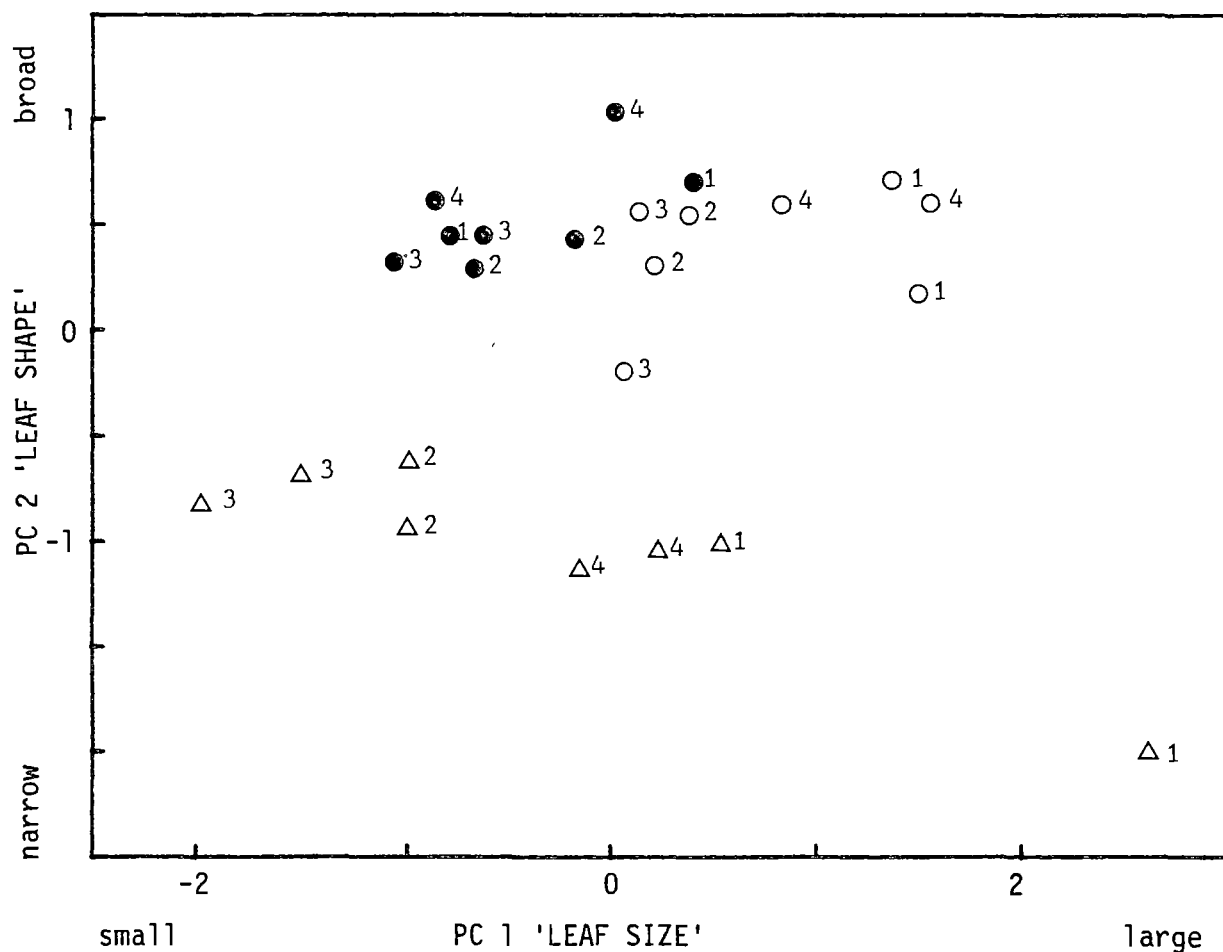


Fig. 3.11 PCA ordination based on seedling leaf characters (Table 3.13) showing the '*E. archeri*' (P₁, P₂; Δ); '*E. divaricata*' (SL, LH; ●) and 'southern *E. gunnii*' (PF, SP; ○) populations means from the experimental gardens (Projection Bluff, P₂ -1; Liawenee, LH -2; Shannon Lagoon, SL -3; Pensford, PF -4). PC1 and PC2 describe variation mainly associated with leaf size and leaf shape respectively.

Variation in the *Eucalyptus gunnii*-*archeri* complexIV. The origin of variation4.1 Introduction

Despite marked differentiation, the *E. gunnii*-*archeri* populations on the Central Plateau form a genetic continuum. Multi-character clines are demonstrated within this continuum between morphs classified as *E. archeri* and *E. gunnii* (i.e. ssp. *archeri* and ssp. *gunnii*, sensu Pryor and Johnson 1971) and between altitudinal extreme variants within *E. gunnii*. The genetic differentiation associated with these clines encompasses a large portion of the variation in the *E. gunnii*-*archeri* complex and the taxonomic perception of this variation has extended to two (e.g. Curtis and Morris 1975) and even three (Brett 1938; *E. archeri*, *E. divaricata* and *E. gunnii*) species. In view of the extent of differentiation and possible partial barriers to gene flow along these clines, their origin is of particular significance and pertains directly to theories of the speciation process.

Consideration of the origin of the clines on the Central Plateau essentially involves two main alternatives - primary or secondary intergradation (e.g. Endler 1977). Primary intergradation implies transitional populations are intermediate between the two extremes of a genetic continuum arising from adaptive differentiation in parapatry. Alternatively, extreme populations have differentiated in allopatry and transitional populations are the result of secondary contact and introgression. It is clearly important to attempt to differentiate these alternatives if only to clarify phylogenetic and taxonomic relationships. This is particularly so of the continuum between morphs previously classified as *E. archeri* and *E. gunnii*. These morphs are usually allopatric, the *E. archeri* morph being generally confined to small disjunct populations near the tree-line of northern mountains whereas the *E. gunnii* (i.e. '*E. divaricata*', 'southern *E. gunnii*' and 'NW *E. gunnii*') morphs are more widespread. Only on the Western Tiers are populations of these morphs parapatric, and in this area intermediates are widespread. The demonstration that this continuum had arisen in parapatry would clearly attest to the significance of disruptive selection in the evolution of major multi-character clines, a step away from parapatric speciation. On the other hand, if the continuum is the result of secondary intergradation, while the nature of the interaction between gene pools would provide fundamental evidence on the degree of reproductive isolation and hence specific status of the taxa involved, the

phylogeny of the *E. archeri* taxa would require careful consideration. Indeed, the continuity between *E. archeri* and *E. gunnii* is fundamental to linking *E. archeri* to the remaining endemic alpine white gum species (superspecies *Gunnii*, *E. urnigera* and *E. morrisbyi*).

The difficulty in distinguishing primary and secondary intergradation from the genetic structure of a population is well recognized (e.g. Anderson 1949, 1953; Barber and Jackson 1957; Mayr 1963; Jackson 1960a,b; Parsons and Kirkpatrick 1972; Hieser 1973; Endler 1977; Millar 1983). Increased variability in transitional, intermediate populations is frequently taken as indicative of hybridization and introgression (e.g. Anderson 1949, 1953; Stebbins 1950; Mayr 1963; Grant 1971). However, with the acceptance of the mechanism of parapatric speciation (see Endler 1977) it is clear that this phenomenon is not restricted to secondary intergradation. Stepped clines may evolve along environmental gradients or across ecotones in the absence of physical barriers (cf. Mayr 1963). In such cases Endler (1977) notes that for a single locus, an increase in variance is expected in the area of maximum slope of a cline based solely on the binomial sampling variance. Similarly Barber and Jackson (1957) argue that a similar peak in variability may develop in parapatry in a region of great ecological change where simultaneous clinal variation occurs at a number of loci. Anderson (1953) cites several criteria (included in Table 4.1) as favouring an introgressive origin. In terms of the structure of introgressed populations Anderson (1953) stresses the loose association of most variables into complexes (cf. Barber and Jackson 1957) and the coherence of parental characters. These criteria form the basis of the method of 'extrapolated correlates' developed by Anderson (1949, 1953; see also Hatheway 1962; Goodman 1966) for the detection of introgression. In contrast, Clifford (1954) emphasizes the need for knowledge of the variability of individual progenies in addition to the variability of the field population. However it could be argued (e.g. Barber and Jackson 1957; Barber 1965; Endler 1977) that the majority of these phenomena are not restricted to secondary intergradation, but may also arise in parapatry as a prelude to parapatric speciation.

In a similar manner, smooth intergradation may result from either primary or secondary intergradation. Mayr (1963) considers the development of smooth or highly variable zones of intergradation following secondary contact will depend upon several factors including the degree

of differentiation and incompatibility of the two gene complexes and whether or not the hybrid belt is sufficiently ancient to permit secondary stabilization. Depending on the degree of incompatibility, hybridization may be a transitory prelude to the development of complete reproductive isolation (e.g. Mayr 1963; Bigelow 1965; Remington 1968). At the other extreme any genetic perturbation may be small and from a pragmatic viewpoint extremely difficult to detect (e.g. Smouse and Saylor 1973a). A peak in the variability of progenies of intermediate phenotypes (initially FI's) would be expected following initial hybridization (e.g. Clifford 1954). However, this peak would decay with introgression and under centripetal selection, intermediates may rapidly approach a level of genetic stability comparable with allopatric populations.

In the absence of strong secondary evidence (e.g. palaeontological, biogeographical, selective coefficients, etc.), there are clear difficulties in deciding the origin of either smooth or highly variable clines and this difficulty extends to cases of allopatric intermediate populations (e.g. Parsons and Kirkpatrick 1972). However regardless of whether extreme morphs have differentiated in allopatry or parapatry, there is generally little dispute as to the hybrid origin of specific individuals in the more extreme cases. In *Eucalyptus*, hybrids are most frequently encountered as sporadic intermediate phenotypes along species boundaries or as localized hybrid swarms often associated with site disturbance (natural or unnatural) (Brett 1938; Pryor 1951b, 1955a,b, 1959a, b, 1976; Jackson 1958; Hopper *et al.* 1978). The confidence to be placed on evidence of natural hybridization (see Gottlieb 1972) depends on the demonstration of some or all of a large number of criteria (see Anderson 1953; Hopper *et al.* 1978 - Table 4.1). However where a number of characters are involved, phenotypic segregation and intermediacy in progenies from intermediate adults, and a sporadic occurrence in the proximity of parental species is usually taken as sufficient evidence of hybridity *per se* (e.g. Clifford 1954; Pryor 1950, 1952, 1976; Pryor and Johnson 1962).

In the present chapter a genetic analysis of populations is undertaken and the status of the zones of intergradation investigated. Population variability is examined for adult (Chapter 1) and seedling (Chapter 2) samples. In addition, the genetic stability of intermediate phenotypes is assessed by a comparison of the variability in progeny from mothers transgressing the phenetic continua. The significance of gene exchange with other potentially interbreeding *Symphomyrtus* species

is addressed and the effect of the Pleistocene climatic perturbations on the distribution and migration of the *E. gunnii-archeri* populations is discussed.

4.2 Methods

Population variability

The comparison of population variability was approached by examining 'overall variability' as well as variability along particular vectors (e.g. PC's) or characters which define specific clinal patterns and differentiate extreme morphs. In the present case, comparisons of 'overall variability' were made using the generalized variance ($|V|$) as suggested by Sokal (1965) and successfully utilized by Goodman (1968) and Soulé (1972). The generalized variance is estimated from the determinant of the sample dispersion matrix, and for two variables is given by:- $|V| = V_1.V_2 (1-r^2)$ where V_1 and V_2 are the variances and r the correlation between the two variables (Phillips *et al.* 1973). This extends to the multivariate case where

$$|V| = |R|\mu^p$$

where R is the corresponding correlation matrix and μ is the geometric mean of the p variances (Kowal 1971). The determinant of the correlation matrix $|R|$ effectively accounts for the redundant component of variation in μ , although there are difficulties in the interpretation of generalized variances as they confound aspects of character correlation and variation (see Phillips *et al.* 1973). In addition Sokal (1965) and Kowal (1971) note pragmatic difficulties when correlation matrices are singular or nearly so. Accordingly, as well as calculating $|V|$, both $|R|$ and the geometric mean of the variances μ were examined. The generalized variance was standardized to be directly comparable with μ (i.e. $|V|^{1/p}$).

Adult samples (Chapter 1)

Generalized variances were calculated for several character sets including:-

(a) 13 morphometric characters ($|V|_{13}$; Table 1.3, excluding VSIZ and VPOS).

(b) a 9 variable subset of (a) excluding one of a pair known to be associated with a high within population correlation coefficient (e.g.

Table 1.12) or suspected of being developmentally related ($|V|_9$; using LL, LW, PET, LAMTH, PEDU, CAPL, PEDI, RIMW and PT.MAX.W.), and (c) a subspace defined by the first 5 PC's ($|V|_{PC_5}$) derived from PCA (TOT. CORR) of a 10 character subset (as (b)+LWP) which together accounted for 82% of the total variation.

The original data were subject to logarithmic transformation which eliminated or at least reduced correlations between the means and variances (e.g. Dow 1976) and then standardized by the grand standard deviation. Generalized variances are tabulated as $\ln|V|$ and following Goodman (1968) approximate standard errors for $\ln|V|$ are given as $\sqrt{2p/n-1}$ where p is the number of characters and n the number of individuals. Generalized variances were not calculated for groups where $n-1 < p$. All estimates of overall variability indicated a similar trend ($P < 0.001$; $r = 0.67 - 0.87$), including estimates based on the average coefficient of variation (Soulé 1972).

Principal component analysis based on the 15 morphometric characters (Table 1.3) was used to summarize variation between individuals ($n=551$) ignoring any a priori grouping structure (TOT, CORR). Population means and variances were then calculated along vectors which maximally differentiated between the '*E. archeri*' and '*E. divaricata*' morphs (PC_2) and between extremes of the altitudinal cline (PC_1). This was repeated using only individuals from populations along the Pine Lake transect ($n=160$).

Progeny variability (Chapter 2)

The analysis of progeny variability is based on the trials discussed in Chapter 2 and was mainly confined to juvenile leaf shape. Variation in juvenile leaf shape is a major feature of population differentiation in the *E. gunnii-archeri* complex, differentiating *E. archeri* and *E. gunnii* (especially '*E. divaricata*' morphs). Furthermore, several potentially interbreeding species frequently occurring sympatric with the *E. gunnii-archeri* populations (e.g. *E. rodwayi* and *E. dalrympleana*) were generally clearly distinguished from the *E. gunnii-archeri* populations by narrower juvenile leaves. Variability in juvenile leaf shape was restricted to comparisons of $\log LL/LW$ which differentiated extreme morphs along the Pine Lake transect and was highly correlated ($P < 0.001$) with more complex multivariate descriptors of leaf shape and general phenetic differentiation. The variance in $\log LL/LW$ was calculated for all populations in both Trial 1 and Trial 2 (see Chapter 2) and the variation within populations partitioned into between and within progeny components. For each population, the significance of the difference between progeny means and variances were

tested and populations were compared for differences in total and pooled within-progeny variances. In addition, means and variances were calculated for individual progenies from populations along the geographical continuum between '*E. archeri*' and '*E. divaricata*' morphs (i.e. Pine Lake transect) and following the approach of Clifford (1954), progeny variances were plotted against the mean. A similar approach was adopted for populations in Trial 1 using the main vector defining the altitudinal cline along the southern Plateau transect (i.e. CV₂ - Table 2.6; Fig. 2.2). Generalized variance estimates for populations in Trial 1 were obtained in the same manner as previously described, and for populations in Trial 1 these were based on the quantitative characters indicated in Table 2.2. Extraneous adult and seedling data utilized are obtained from data or analyses presented in Chapters 1 and 2 respectively. All significance tests for comparisons of univariate variances are based on Bartlett's test for homogeneity of variances (e.g. Sokal and Rolf 1969).

4.3 Results

Pine Lake Transect

Population Variability

The variability in adult morphology differs significantly ($P < 0.01$) between populations along the geographical continuum between '*E. archeri*' and '*E. divaricata*' morphs (Fig. 4.1). There is a general peak in variability in geographically intermediate populations due to greater variability in the high altitude '*E. archeri*' (P_2) and several intermediate populations (P_3 and P_4 ; Fig. 4.1A,B). This is not a result of obvious bimodality (Fig. 1.21) nor does it correspond to areas of marked steepening in character clines (e.g. Fig. 4.2). Similar conclusions are apparent when estimates of overall variability are compared (Figs. 4.1, 4.3; Table 4.2). Furthermore, separate analyses suggest the peak in variability in these populations results from greater variability in reproductive as opposed to vegetative characters (Figs. 4.1 and 4.4), particularly in populations P_2 and P_4 .

Analyses of juvenile leaf shape ($\log LL/LW$) similarly indicate significant differences between populations for both the total ($P < 0.01$) and pooled within-progeny variances (Figs. 4.5 and 4.6; Table 4.3). With the exception of population P_2 , the peaks in variability do not coincide with those for adult morphology. A portion of the difference in

variability between these populations can be attributed to an overall residual association between the mean and standard deviation as indicated in Fig. 4.6. Nevertheless there are clearly marked increases in variability in populations P_5 and P_2 arising mainly from significant differences between progenies (Table 4.3) which suggests maternal heterogeneity. Similarly, Fig. 4.6B suggests the degree of glaucousness is most variable in the intermediate population P_4 , which is clearly more variable than its immediate neighbours (P_3 and P_5).

These results indicate high levels of variability for a range of characters in several geographically intermediate populations, although the peaks for each character do not all coincide. For example, populations P_2 and P_4 exhibit the greatest variability in reproductive characters and P_5 is consistently uniform (e.g. Figs. 4.3 and 4.4). However while seedling glaucousness is relatively variable in P_4 (Fig. 4.6) seedling leaf shape is comparatively uniform (Figs. 4.5 and 4.6). In contrast, P_5 exhibits relatively little variability in adult vegetative or reproductive characters yet is highly variable in seedling leaf shape.

Progeny variability

Populations differ significantly ($P < 0.05$) in the pooled within-progeny variability in juvenile leaf shape (Table 4.3). This could be expected solely on the basis of greater maternal heterogeneity (e.g. P_2 and P_5 ; Table 4.2), although the variability is not evenly distributed. There are significant differences in the variability of progenies from populations P_1 ($P < 0.05$), P_2 ($P < 0.01$) and P_5 ($P < 0.05$) due to the abnormally high variability in several progenies (Fig. 4.7). With a single exception, there is no indication of increased variability in intermediate progenies as would be expected following recent hybridization (Fig. 4.7). Several of the more narrow leaved *E. archeri* (P_1 and P_2) progenies are highly variable and there is clearly a trend within these populations for the narrow leaved progenies to be the more variable. This could result from the general trend for earlier maturation in *E. archeri* seedlings with the more variable narrow leaved progenies being in a phase of rapid ontogenetic change in leaf shape. However, comparisons of intranode and petiole development and leaf shape variation between the 10th and 15th nodes suggests that for these populations this does not effectively account for the significant differences in variability between these populations (e.g. P_1 vs P_2) or the abnormally high variability in specific progenies. There is a tendency for mothers of intermediate morphology (i.e. CV_2 ; Fig. 1.18) to produce the more variable progenies (Fig. 4.8). However this is

not marked and these results indicate that the vast majority of intermediate phenotypes are genetically stable, with levels of variability comparable to that observed in the progenies of extreme phenotypes.

Increased progeny variability may confound a variety of effects including maternal heterozygosity, degree of outcrossing and heterogeneity in the pollen environment. However, the fact that the vast majority of trees from the same population and encompassing a wide range of flowering times (Fig. 4.9) produce uniform progenies would argue strongly against outcrossing being a significant factor in the high level of variability exhibited by several progenies (Fig. 4.3). Furthermore, there is no obvious evidence of hybridization with other *Symphyomyrtus* species which could markedly affect leaf shape or character variation in general. All populations along this transect with the exception of the low altitude *E. archeri* population (P_1) are well isolated from any major source of alien pollen, being only associated with *Monocalyptus* species with which interbreeding does not occur (e.g. Pryor 1976). This would suggest that abnormally high progeny variability in leaf shape is a direct result of maternal heterozygosity in factors directly affecting leaf shape and which are inherent within the *E. gunnii-archeri* gene pool. It is possible ^{that} the highly variable progeny in population P_5 (Fig. 4.7) were from an F_1 hybrid between extreme morphs from a different population. However this is not supported by any segregation in other characteristics (e.g. glaucousness) and due to the high variability between progenies within this population (Fig. 4.7; Table 4.3) is more likely to have arisen from the crossing of extreme morphs occurring in the same population.

Character associations

The independence of characters both within populations and progenies would argue strongly against recent secondary intergradation (e.g. Anderson 1939, 1949, 1953). For example, there is no association between progeny variability in leaf shape and glaucousness, and progenies apparently segregating for leaf shape are not those exhibiting high variability in glaucousness. Furthermore, progenies which are highly variable in leaf shape or glaucousness are few and widely distributed. Single progenies from each of SB, Br, P_4 and P_2 exhibit abnormally high levels of variability in glaucousness, although the high variability in population P_4 is a result of relatively high variation in 5 progenies. There is no evidence to suggest characters are retained in 'parental' combinations in intermediate populations as would be expected following

recent secondary intergradation. Within intermediate populations (P_2 , P_3 and P_5) there is no correlation between flowering time, fruit shape (PC1; Fig. 4.1C) and adult leaf shape (PC1; Fig. 4.1C) or glaucousness. Furthermore based on maternal means, there is no 'parental' association between adult morphology, juvenile leaf shape and seedling glaucousness (e.g. Figs. 4.10 and 4.11). All data indicate a completely random association between developmentally independent characters in intermediate populations. In contrast within the *E. archeri* populations (P_1 and P_2) there is a strong correlation between juvenile leaf shape and seedling glaucousness with mothers tending toward the *E. gunnii* leaf shape being the more glaucous (e.g. Fig. 4.10; $P < 0.001$). However, 'parental' combinations of characters are not evident for other characters (e.g. Fig. 4.5). These results indicate that while character clines differentiating '*E. archeri*' and '*E. divaricata*' morphs are more or less parallel (Fig. 4.2) they are independent and do not closely coincide nor do peaks in variability as may be expected in the early stages of secondary intergradation.

Southern Plateau transect

In contrast to the phenetic continuum along the Pine Lake transect, there is no significant difference in variability between populations along the main vectors defining the altitudinal cline (Fig. 4.1; Southern Plateau Transect). Furthermore, in terms of overall variability, the Shannon Lagoon population (SL) which is intermediate with respect to the altitudinal cline, is less variable than populations at either extreme. There is no marked increase in overall variability in the extreme population on Scrummies Marsh (A1; Figs. 4.1, 4.3, 4.4, 4.12, 4.13; Table 4.2) which, as discussed in Chapter 1, tends phenetically toward the local *E. urnigera* as well as being in the general proximity to areas of hybridization with both *E. dalrympleana* and *E. rodwayi*. On the other hand, the low altitude population at Pensford (PF) appears the most variable (Figs. 4.1, 4.3, 4.4, 4.13 and 4.14; Table 4.2), particularly when vegetative and reproductive characters are examined separately. The magnitude of the reduction in $|V|$ when all characters are examined simultaneously (Fig. 4.3) suggests relatively high correlation between vegetative and reproductive characters. A range of hybrids with *E. dalrympleana* were encountered along the stand boundary at this site and while it is possible that gene exchange with *E. dalrympleana* has contributed to an increase in overall variability in adult morphology

at this site, there was no indication of hybridization in the progenies examined (Fig. 4.14; Table 4.4).

Progeny trials including populations LH, SL and PF, as well as the geographically isolated population SP (Trial 1, Chapter 2) indicate no significant differences in the total variability in seedling leaf shape ($\log LL/LW$) between populations, although significant differences ($P < 0.01$) were observed between progenies at altitudinally extreme sites (i.e. LH and SP; Table 4.4). Similarly, the difference in variability between populations along the main vector defining the altitudinal cline (CV_1 ; Fig. 2.5; Table 2.6), was not significant although there are significant differences between progenies within populations (Table 4.4).

Differentiation between progenies increases with altitude which could be explained by greater microhabitat variation in relation to factors directly associated with the altitudinal cline (e.g. exposure) at higher altitudes. A similar, but a non-significant trend was apparent in adult morphology (Fig. 4.1a,c) and accords with data presented in Fig. 1.14 indicating significant phenetic differentiation over short distances along exposure gradients at the high altitude site (LH). However, in terms of overall variability, the reverse trend appears to be the case in both adult and seedling samples (Table 4.4). Differences in variability between progenies were insignificant (except SP - CV_1 ; Table 4.4) and Fig. 4.14 clearly shows no indication of segregation in intermediate progenies. These results coupled with the demonstration of selective differentials along this cline (Chapter 3) strongly argue for spatially varying selective forces being the prime cause of phenetic differentiation along the southern Plateau transect.

General patterns of population variability

Adult phenotype

'Overall variability' (i.e. $|V|$) tends to increase in populations toward the eastern limits of the distribution (Figs. 4.3, 4.12, 4.13; Table 4.2). The small, isolated populations in the north-eastern (i.e. MB, BN, MM and MV) and eastern (i.e. SH) mountains are in general the most variable populations in the complex. This trend is mainly a result of variability in vegetative characters (Fig. 4.15), although variability in reproductive characters is high in specific populations (e.g. BL, MB, SH and SP; Fig. 4.16). The population on Mt. Saddleback (SD) is an obvious exception and was noted as being phenotypically uniform when collected. In addition, the site was also relatively homogeneous and the population was fairly isolated

from any potentially interbreeding species. In the latter respect, this population contrasts with many of the highly variable eastern populations (e.g. BN, MV and SH) where field evidence and progeny trials indicate active hybridization with other parapatric *Symphyomyrtus* species. The data suggest low levels of variation in leaf and reproductive characters in the small disjunct western populations (e.g. TH, LB, LC, LM, OP, MS and SV; Figs. 4.15 and 4.16). Smaller sample sizes were generally collected in western populations and it is possible that lower variability is partly a result of transgressing relatively less microhabitat variation. However in several cases (e.g. RR, TH, LB and LM) the majority of mature trees at the site were collected and the sample accurately reflects the variability of the population. The overall variability in most disjunct eastern populations appears to be higher than for the majority of samples from the large continuous stands on the Central Plateau (e.g. Figs. 4.12, 4.13; Table 4.2). However, there are significant differences in variability amongst these central populations and the variability in reproductive characters in several populations north of Great Lake (P_2 , P_4 and Br) is amongst the highest observed (Fig. 4.4).

Progeny variability

There is some correspondence between variable adult morphology and variability in either seedling leaf shape or glaucousness (Fig. 4.6). For example, high variability in adult morphology is associated with comparatively high variability in juvenile leaf shape in populations MB, P_2 , BN and MV (Fig. 4.6a). However, seedlings from the Snow Hill (SH) population appear to be relatively uniform in leaf shape but are abnormally variable in glaucousness grade (Fig. 4.6b) with sporadic green variants (8%) occurring amongst predominantly glaucous seedlings. The Mt. Victoria population is highly variable in adult morphology (Figs. 4.3, 4.4, 4.13, and 4.14; Table 4.2), seedling glaucousness (6% green; Fig. 4.7a) and juvenile leaf shape (Figs. 4.5, 4.6a). The high variability in both progenies and adults in this population clearly supports the previous suggestion (Section 2.5) that gene exchange is occurring with parapatric species (mainly *E. rodwayi*) and has possibly been a significant factor in population divergence. In contrast to the trend in adult morphology, several populations in the upper Mersey Valley are relatively variable in seedling leaf shape and glaucousness (Fig. 4.6, LC, LM).

The genetic interaction of the *E. gunnii-archeri* populations with other *Symphomyrtus* species

The convergence of the *E. archeri* adult phenotype toward *E. subcrenulata* noted previously (Fig. 1.29) was further investigated by a comparison of *E. subcrenulata* and *E. gunnii-archeri* seedlings. This was aimed at specifically testing the hypothesis that introgression of *E. subcrenulata* genes into the *E. gunnii-archeri* complex may have contributed to population divergence and increased variability in reproductive characters in several populations along the geographical continuum between *E. archeri* and *E. gunnii*. Convergence in adult morphology toward *E. subcrenulata* is greater in the *E. archeri* populations on the Western Tiers (e.g. P₁, P₂, P₃ and MC) than those from the NE mountains (e.g. MM, SD, BL, BN). Furthermore, sporadic individuals with capsules similar to *E. subcrenulata* but normal in other characters were encountered in populations on the Western Tiers (e.g. P₁, P₂, P₃, P₄, MC) and Mt. Roland (MR). The north-eastern limit of *E. subcrenulata*, and the Tasmanian yellow gums in general, is on the Eastern Tiers near Snow Hill, and coincides with that for the snow gum, *E. coccifera*. Neither of these species are known to occur on the NE mountains which suggests that any present day or pre-historic gene exchange between *E. gunnii-archeri* populations in this area and the yellow gum gene pool would be minimal. While populations of *E. gunnii-archeri* on the Western Tiers and *E. subcrenulata* are allopatric, they are closest to the present day eastern limits of the main *E. subcrenulata* distribution (see Chapter 1) which is in the upper Mersey Valley - Walls of Jeruselum area. Populations sampled from this area (TH, LB, LC and LM) are thus closest to *E. subcrenulata* and the population at Lake Charles (LC) was parapatric and *E. subcrenulata* also occurs on Mt. Roland (MR). Nevertheless the CVA ordination in Fig. 4.17 indicates that these populations are less similar to *E. subcrenulata* in seedling phenotype than north-eastern populations and the *E. archeri* populations (P₁, P₂ and MC) on the Western Tiers. Similarly plots of individual seedlings in the space defined by this ordination (Fig. 4.18) show no evidence for gene exchange between *E. subcrenulata* and the *E. gunnii-archeri* at Lake Charles and both seedling and adult phenotypes remain distinct. Sporadic hybrids between *E. subcrenulata* and *E. gunnii-archeri* have been reported (Jackson 1960a) and several rare intermediate phenotypes were collected from the Lake Charles area, but progeny trials failed to provide any evidence for their being of hybrid origin, although there is some possibility of gene exchange occurring on Mt. Roland (Fig. 4.18).

The occurrence of seedling phenotypes tending toward *E. subcrenulata* in populations on the NE mountains (e.g. MM, MB, BL, SD), clearly indicates that their occurrence is not contingent upon proximity to *E. subcrenulata*. As with adult morphology, convergence toward the *E. subcrenulata* phenotype is in a similar direction to that differentiating *E. archeri* from *E. gunnii* seedlings and is apparent in leaf and stem shape, growth rate and glaucousness. However seedlings of *E. subcrenulata* are generally differentiated from those of *E. archeri* in all being green (GLAUC=0), usually square stemmed, slower growing and developing intranodes and petioles at much later nodes. Furthermore, similar seedling phenotypes may arise from hybridization with other species. For example, hybridization was suspected to be occurring with *E. brookerana* on Snow Hill on the basis of adult morphology, but as noted by Ladiges *et al.* (1981) the seedlings of the latter species have similarities to those of *E. subcrenulata* (e.g. square stems, glabrous, etc.).

On the present evidence it appears unnecessary to evoke a hypothesis of introgression to account for convergence of the *E. archeri* phenotype toward *E. subcrenulata*. These results suggest such genes may inherently reside in the *E. gunnii-archeri* gene pool and convergence is most likely a result of parallel evolution. Furthermore it is unlikely '*E. archeri*' has closer phylogenetic links with the yellow gum complex (*E. vernicosa*, *E. subcrenulata* and *E. johnstonii*) and all analyses indicate closer similarity and continuity with the *E. gunnii* populations. The adaptive significance of many of the convergent features (e.g. glaucousness, growth rate) have been discussed (Chapters 1 and 2) and many of the phenetic differences between *E. archeri* and *E. gunnii* are in the same direction differentiating green and glaucous forms of *E. urnigera* (Barber and Jackson 1957).

The majority of populations in the widespread stands of *E. gunnii-archeri* on the Central Plateau are geographically isolated from other potentially interbreeding species. Hybridization is generally only significant at the lower altitude sites where populations are parapatric with *E. dalrympleana* or *E. rodwayi*. In such cases hybridization is generally confined to the stand margins and in larger stands appears to have only a small effect on variability (e.g. PF, A1), possibly being counter-balanced by gene flow from central regions or the nucleus of the stand. This contrasts with the situation in several small marginal isolates (e.g. MV, SH) where the swamping effect of pollen inflow from larger, surrounding stands of other potentially interbreeding species may partly account for the high variability in many of the eastern populations.

This clearly appears to be the case at Mt. Victoria and is probably accentuated by the ecologically marginal nature of this site. However active hybridization is occurring on Ben Nevis (BN) involving a stunted high altitude variant of *E. dalrympleana* (Fig. 4.19) and while obvious hybrids were excluded from this sample, adult leaves of this population deviate in the direction of *E. dalrympleana* on several characters (e.g. LWP/LL, CURVE). As noted, hybridization was also observed on Snow Hill although the situation appears to be more complex. Individuals with greater than 3 fruits per umbel were sporadically encountered as well as occasional green variants which were not always associated with a high number of capsules per umbel. Progenies grown from green 7 fruited variants segregated for glaucousness, and in one case, additional segregation in leaf shape, was suggestive of a *E. gunnii* x *E. brookerana* hybrid combination. However several progenies from mothers showing no signs of hybridism also produced occasional green variants. While this could be indicative of backcrossing or an advanced stage of introgression, the segregation in glaucousness in otherwise normal progenies is similar to that encountered in *E. urnigera* (Barber and Jackson 1957). In view of the high variability of this population its genetic structure clearly warrants further investigation in terms of hybridization and microhabitat variation.

4.4 Discussion

The genetic structure of populations along the Pine Lake transect indicates that the phenetic continuum between the '*E. archeri*' and '*E. divaricata*' morphs is not a result of recent secondary intergradation. This is indicated by the genetic stability and widespread distribution of intermediate phenotypes, the independence of character clines and general absence of strong character associations in intermediate populations, and the failure of peaks of variability to clearly coincide in intermediate populations. The hypothesis of neutral secondary contact can be excluded on the basis of the results and discussion presented in Chapter 3, although the intensity of selection on different characters or at different sites may differ markedly. In this respect, the general increase in reproductive as opposed to vegetative characters in several geographically intermediate populations on the Western Tiers may be significant. However there is no clear evidence from the genetic structure of the populations to differentiate between partial stabilization of a zone of secondary intergradation

as opposed to primary parapatric differentiation.

The high level of variability observed in several intermediate populations could arise by hybridization and introgression followed by partial stabilization. However, this would also be expected in an area of steep clinal variation purely on the basis of gene flow, regardless of the origin of the cline. The significance of gene flow on variability would increase with proximity to steps in the cline, markedly increasing the variability in the seedling population. Nevertheless, for characters closely related to fitness, provided gene flow is not excessive, strong centripetal, density dependent selection (e.g. Barber and Jackson 1957; Barber 1965) may rapidly re-establish homogeneity in the adult population. This could explain discrepancies where populations exhibit comparatively greater variability in seedling as opposed to adult characters. However this does not account for a large portion of the variability in seedlings being distributed between progenies (e.g. P_5 and P_2), nor explain the reverse case (e.g. P_4). Local microhabitat heterogeneity may also affect population variability, although neither of the more variable populations (e.g. P_2 and P_4) were from obviously heterogeneous habitats.

The influence of the last Pleistocene glacial on distribution and evolution in the *E. gunnii*-*archeri* complex

The current distribution and variation pattern of the *E. gunnii*-*archeri* populations appear to be best explained by consideration of both historical and ecological factors. The effect of the Pleistocene glacial cycles and in particular the Last Glaciation on the distribution and composition of the current Tasmanian vegetation is well recognized (e.g. Davies 1974; Macphail and Jackson 1978; Macphail and Peterson 1975; Macphail 1979, 1980; Kirkpatrick and Brown, 1984). The effect of these glacial cycles was two-fold involving habitat perturbation as well as the periodic removal of a major barrier to migration. The latter arose by the formation of a land-bridge to the Australian mainland following lowered sea-levels during glacial periods. Little is known of the sequence of *Eucalyptus* evolution or invasion although Jackson (1965) suggests wholly endemic groups and relic distributions of species with mainland affinities indicate periods of isolation and reciprocal invasion during the Pleistocene. The high endemism in the superspecies *Gunnii* and the current distribution pattern strongly suggest this group to be an early component of the *Eucalyptus* flora.

The glacial cycles would have seen populations of alpine and sub-alpine species isolated on high ground during interglacials, expand and coalesce

during periods of glaciation (Kirkpatrick and Brown, 1984). For the Last Glacial it is estimated that temperatures were about 5°C lower than present (Davies 1974; Macphail 1979; Kiernan *et al.* 1983) with the tree-line near the present sea-level on the west coast, rising to 400-500 m above the present sea-level on the east coast (Macphail 1979) which accords with the trend in the current tree-line (Kirkpatrick 1982). The main areas available for *Eucalyptus* forest would have been in the east and south-east (Davies 1974; Fig. 4.20). Davies (1974) considers the distribution pattern of many of the *Eucalyptus* species (e.g. *E. tenuiramis*, *E. risdonii*, *E. pulchella*, *E. morrisbyi*, *E. urnigera*, *E. globulus* and *E. cordata*) indicates confinement to a south-eastern Glacial refugia. The major rise in temperatures between c.a. 12,000-10,000 B.P., accompanied by rising precipitation resulted in expansion of arboreal taxa across Tasmania and upslope onto mountains (Macphail and Peterson 1975; Macphail 1979). Species such as *E. gunnii*-*archeri* pre-adapted to alpine or sub-alpine habitats would have closely followed the retreat of glacial and periglacial zones, and the rugged Tasmanian topography would ensure habitat discontinuity and range fragmentation. It is unlikely ^{that} the numerous small populations of sub-alpine eucalypts, isolated at relatively low altitudes on hill tops and mountains throughout Tasmania (particularly in the south-east), represent anything but remnants of a much larger and in many cases continuous Glacial distribution. At lower altitudes peripheral isolates are left stranded on high ground, whereas at high altitudes migration into new terrain would be hindered by rugged topography, favouring colonization from 'founder' populations. Large depletions of the gene pool may occur, and many species of particularly limited distribution (e.g. *E. perriniana*, *E. morrisbyi* and *E. cordata*) may be relics of a glacial selective regime having no modern day analogue.

Consideration of the possible Glacial distribution of the *E. gunnii*-*archeri* populations and possible migration routes following deglaciation provides a unified theory to account for the present day distribution and variation pattern of the complex. During the Last Glacial the area on the Central Plateau currently occupied by the *E. gunnii*-*archeri* populations was either glaciated or subject to periglacial activity (Banks 1973; Davies 1974; Fig. 4.20). However *E. gunnii* was probably widely distributed in the south-eastern Glacial refugia and the 'southern *E. gunnii*' populations most likely represent the remnants of this distribution. Nevertheless, the isolated occurrences of populations on the north-eastern mountains and in the far north-west (e.g. SV) provides strong circumstantial evidence for a separate widespread northern distribution, isolated from the southern

populations by a large expanse of unsuitable high-moor habitat (Fig. 4.20). A western distribution is unlikely on the basis of climatic and geological considerations and a post-Glacial migration route from the south would not effectively account for the low altitude disjunctions in the far north-west (e.g. SV; 660 m) nor the isolated populations north of the Western Tiers (e.g. MR). The existence of a widespread northern population would partly explain the phenetic affinities between populations in the far north-west, upper Mersey Valley and on the north-east mountains (Figs. 1.25, 1.26, 1.27 and 1.28). Furthermore, there is evidence for an eastern disjunction between northern and southern floras which would probably have been maintained by low tree-lines coupled with a marked rainshadow creating a 'glacial-arid' environment directly east of the Central Plateau (Macphail and Jackson 1978; Colhoun 1978). This is supported by the absence from the north-eastern mountains of other sub-alpine species (e.g. *E. coccifera*, *E. subcrenulata*, *E. johnstonii* and *E. urnigera*) which frequently occur on the same mountains as *E. gunnii* in the south or west. Indeed, it is the marked absence of *E. coccifera*, the normal tree-line species on dolerite-capped mountains in other areas, which suggests post-glacial migration from the south or west accounting for these isolated north-eastern populations of *E. gunnii*-*archeri* is unlikely. The closest occurrence of *E. coccifera* is in the Eastern Tiers with a population of 'southern *E. gunnii*' (SH). Kirkpatrick and Brown (1984), similarly suggest the absence of particular endemic plants toward the north may be a result of remoteness from Glacial refugia rather than unsuitability of the environment and cite *E. tenuiramis* and *E. pulchella* amongst examples. This suggests habitat disjunction between northern and southern floras at least during the Last Glacial which may have acted as a barrier to invasion from mainland species as well as retarded radiation from areas of possible speciation in the south-east.

Biogeographical evidence strongly suggests the continuum between the '*E. archeri*' and '*E. divaricata*' morphs over the Western Tiers is a result of secondary intergradation and that extreme morphs differentiated in allopatry. The more extreme climatic regime along the Western Tiers, the higher Plateau surface and further west would essentially suggest a suture-zone (Remington 1968) between southern and northern floras. Intermediate populations north of Great Lake (P_3 , P_4 and P_5) as well as populations in the upper Mersey Valley (TH, LB, LM, LC) clearly occur in the more youthful and, due to glaciation, possibly more ecologically disturbed habitats than extreme morphs. In terms of the criteria outlined by Anderson (1953) this would clearly favour a hypothesis of secondary

intergradation. Furthermore, there is strong evidence to suggest that sites currently occupied by extreme morphs would have been spatially continuous with similar glacial habitats. For example, the northern scarp of the Western Tiers drops sharply to the coastal plain and any sub-alpine northern population following a retreating tree-line in the vicinity of the Western Tiers would have been subject to an "*E. archeri*" environment. The disjunct occurrences of '*E. archeri*' populations in this area (e.g. Western Bluff-MC, Mt. Roland-MR) more isolated from a southern source suggest such a northern Glacial population may have existed. There is no doubt that the colonization of the lower Plateau surface around Great Lake would have occurred from the south via the large areas of spatially continuous "*E. divaricata*" habitat on the St. Clair surface (730-820 m) currently dominated by *E. rodwayi*. The early pollen records for the St. Clair surface indicate conditions similar to those now prevailing on the lower Plateau surface (Jackson 1973) and the migration route is supported by relic distributions of both *E. coccifera* and *E. gunnii*.

Macphail (1979) indicates the forests on the Central Plateau are less than 8500 years old which, assuming a generation replacement time of 250 years, suggests the variation patterns in this area have been established in less than 34 generations. If secondary contact occurred as hypothesized, this would have probably been maximal during the climatic optima estimated at ca. 5000-8000 years B.P (Macphail 1979), allowing many generations for selective stabilization. The widespread distribution of allopatric populations and individuals which exhibit some degree of intermediacy or varying combinations of the characters differentiating the '*E. archeri*' and '*E. divaricata*' morphs leave little doubt as to the selective value of intermediate phenotypes. Many characteristics differentiating '*E. archeri*' and '*E. divaricata*' morphs appear to be mobile in an evolutionary sense (e.g. glaucousness, growth rate, leaf thickness, rate of ontogenetic development) explaining allopatric convergence and rapid stabilization. This is exemplified by the convergence of the high altitude '*E. divaricata*' population (LH) toward the '*E. archeri*' adult phenotype (e.g. Figs. 1.16, 1.17, 1.18) although the seedling phenotype is clearly distinct (Figs. 2.2, 2.3). However the high altitude intermediate populations on the Western Tiers (P_3 , P_4 and P_5) have closer affinities to the local '*E. archeri*' populations (P_1 and P_2) and are better conceived as high altitude forms of *E. archeri* (e.g. Fig. 1.26). Nevertheless secondary intergradation could partly account for the distinctive characteristics of these intermediates (e.g. Fig. 1.23, 1.24) and possibly the high

variability in reproductive characters in several populations.

The altitudinal cline along the southern Plateau transect is clearly a result of parapatric adaptive radiation or stabilization of pre-existing clines following migration on to the lower Plateau surface from the south. The occurrence of the 'southern *E. gunnii*' populations at relatively low altitudes on mountains with other sub-alpine species (e.g. *E. urnigera*, *E. coccifera*) strongly suggests these are remnants of a distribution in the south-eastern Glacial refugia and from which the '*E. divaricata*' populations probably evolved. This is particularly significant in view of the phenetic similarities between the 'southern *E. gunnii*' and the other alpine white gum taxa *E. urnigera* (Fig. 1.29) and *E. morrisbyi* (Potts 1978; PF). The full assessment of the variation within the *E. gunnii*-*archeri* complex indicates that the lowland taxon, *E. morrisbyi*, has particularly close phenetic affinities to populations from Snow Hill (SH) and Scrummies Marsh (A1). The taxon *E. morrisbyi* appears to be an extension of clinal trends within the *E. gunnii*-*archeri* complex and has possibly differentiated from a remnant of a glacial distribution of the 'southern *E. gunnii*'. While the affinities between *E. morrisbyi*, *E. urnigera* and 'southern *E. gunnii*' could result from introgression or parallel adaptation, the more likely explanation points to a common ancestor.

This phylogeny suggests that northern and southern *E. gunnii* populations may represent a relatively ancient dichotomy. The general phenetic affinities of the 'NW *E. gunnii*' with the 'southern *E. gunnii*' (e.g. Fig. 1.24) probably result from a similarity of habitat and lack of divergence as opposed to convergence. The affinities of the population at Repulse River (RR) to the 'NW *E. gunnii*' (e.g. Figs. 1.24, 1.25, 1.26, 1.27) is probably more a matter of chance as phenetically this population is an outlier and the small sample (n=6) represented virtually the full complement of mature individuals at this site. The most likely phylogeny of the '*E. archeri*' morph is for it to have differentiated from a northern population, probably independently in the vicinity of the Western Tiers and on the north-eastern mountains. Following the upward migration of the tree-line in the north-east, widespread populations probably occurred at the level (ca. 800 m) of the Diddleum-Mathinna Plains on the extensive sites now occupied by *E. rodwayi*. The Mt. Victoria population is probably a relic of this expansion and has closest morphometric affinities to neighbouring populations on Ben Nevis and Mt. Maurice which suggests selection

for the glaucous morph in the open marshy habitat. It is possible full differentiation of '*E. archeri*' phenotype occurred as a result of parallel adaptation following isolation on their respective mountain peaks. However, similar habitats would have probably occurred on the slopes of the north-eastern block during the Last Glacial. The absence of other sub-alpine species capable of occupying the tree-line habitat in the north-east has possibly been an important evolutionary stimulus for the differentiation of the '*E. archeri*' phenotype and a wider ecological range may partly account for the high variability in many of these populations. This may similarly apply to the Western Tiers and the possibility that the *E. coccifera*-*E. archeri* association in this area is of recent origin requires investigation.

It is suggested that the taxa *E. archeri* and *E. urnigera* have differentiated into comparable sub-alpine habitats possibly from northern and southern populations of ^{an ancestral} *E. gunnii* ^{type} respectively - *E. urnigera* evolving on the dry south-east mountains, *E. archeri* on the wetter northern mountains. The *E. urnigera* and southern populations of *E. gunnii* would have been parapatric in the Last Glacial. It may be significant that speciation appears relatively complete with parapatric populations usually discrete and reproductively isolated by a shift in flowering time and marked divergence in reproductive characters. In contrast when parapatric, *E. archeri* and *E. gunnii* ('*E. divaricata*' form) coalesce both genetically and phenetically, clearly indicating the status of geographical sub-species as given by Pryor and Johnson (1971) is appropriate. The interpretation of the variation pattern in the *E. gunnii*-*archeri* complex presented points to a reticulate mode of evolution involving population divergence, parallel convergence and introgression, and this is possibly a common feature of eucalypt evolution.

Evolution in marginal isolates

The inevitable consequence of large-scale changes in the selective regime and shifts in the flora as typified by the Pleistocene glacial cycles is the isolation of small populations at the ecological and geographical extremes of the species margins. In contrast to the classical concept of marginal populations (e.g. Mayr 1963), marginal or isolated populations of forest-tree genera are often noted as exhibiting levels of variability comparable with central populations (see Libby *et al.* 1969; Tigerstedt 1973; Sterne and Roche 1974). For the *E. gunnii*-*archeri* populations this comparison was not consistent due to a general trend for

an overall decrease in variability in western populations (e.g. Fig. 4.13). It is suggested this partly results from differences between western and eastern marginal isolates and possibly reflects a reduction in variability in 'founder' populations in newly colonized areas (see Mayr 1963) as opposed to a concentration of variability in many eastern relic populations. Hybridization with lowland species appears to be one of the main causes of the high variability in eastern populations (e.g. MV, BN and SH) and appears to be intimately associated with the process of range restriction and extinction. Stebbins (1959) contends that hybridization will be more frequent where species contact in marginal environments, particularly if associated with the opening up of new ecological niches. This is accentuated in marginal isolates where the nucleus of the population may contract to a point where selection is unable to counterbalance high pollen flow from the surrounding, potentially interbreeding species (e.g. Kirkpatrick *et al.* 1973; Levin 1978c). This may eventually result in the formation of phantom hybrid populations (e.g. Pryor 1951b; Parsons and Kirkpatrick 1972; Kirkpatrick *et al.* 1973) and even the assimilation of the genetic remnants of a species into the gene pool of the invading species (e.g. Harlan and de Wet 1963). In contrast, Kirkpatrick (1976) suggests slow gene-exchange with contiguous species may be a means by which a small, isolated population may retain evolutionary flexibility. The genetic variability and differentiation may then depend on species' composition and interbreeding potential of contiguous species.

Ecologically marginal populations, particularly peripheral isolates, play a central role in theories of range extension and evolutionary theory (e.g. Mayr 1963; Levin 1970b; Soulé 1973; Sterne and Roche 1974 and cited references) and are attributed a major role in bursts of adaptive radiation (Gould and Eldridge 1977). The combined effects of isolation, population size (e.g. Mayr 1963) and atypical or catastrophic (e.g. Lewis 1962) selective regimes make the probability of extinction high. Nevertheless, Levin (1970b) notes that "major shifts in the adaptive mode and successful expansion from refugia are of sufficient frequency to render the species border an area of very active speciation." Mayr (1963) stresses the potential for a 'genetic revolution' associated with a loss of variability in 'founder' populations. However, Levin (1970b) also emphasizes that a similar genetic perturbation may arise in marginal populations following hybridization disrupting developmental homeostasis which may serve as a stimulus for quantum evolution. In view of the high variability and deviant nature of many lower altitude peripheral isolates in the *E. gunnii*-*archeri* complex

(e.g. SH, MV and BN) it is suggested such populations may play a significant role in differentiation and speciation in *Eucalyptus*. Furthermore, while hybridization may not appear important at the boundary of large populations it may be a significant evolutionary stimulus in small, marginal isolates. This may be accentuated by the effects of drift associated with the small effective population size (see Moran and Hopper 1983).

The present study further suggests that *Eucalyptus* populations retain a large store of potential phenetic variation associated with developmental plasticity. Large differences are demonstrated between populations in both the physiological and chronological period over which the juvenile form is retained (e.g. Chapters 2 and 3) and observations suggest the actual rate of transition to the adult foliage type may also vary considerably. For example, increasing altitude along the southern Plateau transect results in a genetically based retention of the juvenile foliage. Furthermore, at the most exposed site (Liawenee) occasional individuals are found bearing capsules in the juvenile leaf phase. Neotenic processes (retention of the juvenile form of ancestors, in extreme cases into the reproductive phase) may allow rapid and potentially large differentiation of the 'adult' phenotype with the minimum of genetic restructuring, and Barber (1965)^{that} suggests this process may have been a significant factor in eucalypt evolution. As demonstrated in Chapter 3, and also noted in other species (Davidson *et al.* 1983), the juvenile or intermediate phase is often retained longer in extreme environments of exposure and drought. Flowering may occur during these phases suggesting the potential for the rapid formation of variants by neoteny and subsequent adaptation.

Acceptance of the phylogeny discussed requires a knowledge of the potential of populations to migrate as a continuous front and through discontinuous habitats by a stepping-stone process. Nevertheless, the foregoing discussion has made the assumption that the potential for *Eucalyptus* invasion, particularly through a pre-established flora, is relatively limited. In the following chapters data are presented to suggest that seed migration in *Eucalyptus* is limited and hybridization may be significant as a migration mechanism where reproductive barriers are weak.

Table 4.1 Criteria given by Hopper *et al.* (1978) as constituting evidence for natural hybridization (see Anderson 1953; Pryor and Johnson 1962; Hopper 1977a).

- (1) Intermediate morphology of suspected hybrids.
- (2) Phenotypic segregation in hybrid progeny.
- (3) Occurrence of hybrids in sympatric parental stands.
- (4) Close agreement in morphology, between suspected and experimentally synthesized hybrids.
- (5) Occurrence of hybrids in disturbed or relatively youthful habitats.
- (6) Impaired reproductive capabilities of hybrids relative to parental individuals (i.e. F_2 breakdown).
- (7) Occurrence of interspecific pollen exchange by indiscriminant vectors in sympatric parental stands.

Table 4.2: The logarithm of the generalized variance ($\ln|V|$) and approximate standard error (SE) calculated for subsets of 9 and 13 morphometric characters. Populations were excluded if $n-1 < p$. (*=Pine Lake transect; †=southern Plateau transect).

Population Code	9 Characters		13 Characters	
	$\ln V _9$	SE	$\ln V _{13}$	SE
*P ₁	-11.4	0.95	-21.8	1.37
*P ₂	-11.2	0.95	-17.1	1.37
*P ₃	-11.1	0.95	-19.6	1.37
*P ₄	- 9.7	0.95	-17.0	1.37
*P ₅	-11.6	0.95	-22.0	1.37
*Br	- 8.9	0.95	-18.4	1.37
*SB	-11.7	0.95	-21.0	1.37
†*SL	-14.2	0.95	-24.7	1.37
† LH	-10.3	0.95	-21.0	1.37
† A1	-12.5	0.95	-21.0	1.37
† PF	- 9.2	0.95	-19.8	1.37
SV	-15.7	2.00		
MC	-13.7	2.00		
TH	-14.8	2.00		
LC	-23.4	2.00		
LM	-18.3	2.00		
OP	-15.0	2.00		
LR	-17.4	2.00		
MR	- 9.9	0.95	-17.2	1.37
BL	- 9.7	0.95	-19.9	1.37
MB	- 6.9	0.95	-15.8	1.37
BN	- 7.4	0.95	-15.1	1.37
MM	- 7.6	0.95	-17.1	1.37
SD	-14.2	1.06	-28.1	1.37
MV	- 8.5	0.95	-14.9	1.37
SH	- 5.3	0.72	-11.1	1.04
SP	- 9.2	1.13	-18.3	1.63
NE	-14.1	1.29	-24.6	1.86

Table 4.3: Partition of the variation in seedling leaf shape (log LL/LW) into total, between progenies and pooled within progenies components for each population in Trial 2. The significance of the F ratio for the difference between progenies within each population is indicated (A) as well as the significance (B) of Bartlett's test for the equality of progeny variances within populations (NS=not significant; * P<0.05; ** P<0.01; ***=P<0.001).

Population Code	Variance (x 10 ³)			F Ratio	Prob. ^A	Prob. ^B equal variances
	Total	Within Progenies	Between Progenies			
P ₁	4.48	4.20	7.23	1.7	NS	*
P ₂	8.99	5.38	53.88	10.0	***	**
P ₃	3.55	3.48	4.56	1.3	NS	NS
P ₄	3.45	3.45	3.40	1.0	NS	NS
P ₅	5.79	4.30	25.10	5.8	***	*
Br	3.62	3.45	6.02	1.7	NS	NS
SB	3.15	3.02	4.75	1.6	NS	NS
MC	7.94	4.50	20.42	4.5	***	-
MR	5.49	6.13	2.83	0.5	NS	-
TH	3.91	3.91	5.11	1.3	NS	-
LB	4.86	2.70	11.49	4.3	*	-
LC	5.99	4.17	10.14	2.4	*	-
LM	5.90	4.61	13.75	3.0	*	-
SV	5.45	4.88	8.78	1.8	NS	-
MS	3.25	2.27	7.09	3.1	**	-
SH	4.42	5.39	0.84	0.2	NS	-
BL	3.66	4.07	1.99	0.5	NS	-
SA	5.01	3.44	3.23	0.9	NS	-
MM	7.11	6.81	8.41	1.2	NS	-
BN	9.74	8.40	13.67	1.6	NS	-
MB	6.94	4.88	15.16	3.1	**	-
MV	10.09	4.14	39.86	9.6	***	-

(- insufficient replication).

Table 4.4: (a) Partition of the variation in seedling leaf shape ($\log LL/LW$) and CV_2 (Fig. 2.2; Table 2.7) following Table 4.3 for the *E. gunnii* populations from Trial 1. (b) The logarithm of the generalized variance ($\ln|V|$) and its approximate standard error, the standardized generalized variance ($|V|^{1/p}$) and the geometric mean of the variances (μ) calculated for the set of 13 quantitative characters listed in Table 2.6. The total number of mothers and seedlings are given in Table 2.1.

(a)

Population Code	Variance (x 10 ³)			F Ratio	Prob. ^A	Prob. ^B equal variances
	Total	Within Progenies	Between Progenies			
log LL/LW						
LH	3.61	2.95	13.30	4.5	**	NS
SL	3.84	3.78	4.38	1.2	NS	NS
PF	3.79	3.75	4.32	1.2	NS	NS
SP	4.76	3.91	17.57	4.5	**	NS
CV ₂ (Variance x 1)						
LH	1.25	0.96	5.44	5.7	***	NS
SL	1.52	1.25	4.30	3.5	**	NS
PF	1.11	1.00	2.42	2.4	*	NS
SP	0.97	0.88	2.56	2.6	*	*

(b)

	<u>ln v </u>	<u>SE</u>	<u> v ^{1/p}</u>	<u>μ</u>
LH	-14.4	0.33	0.33	0.71
SL	-13.9	0.46	0.34	0.73
PF	-12.6	0.39	0.38	0.77
SP	-10.6	0.43	0.44	0.88

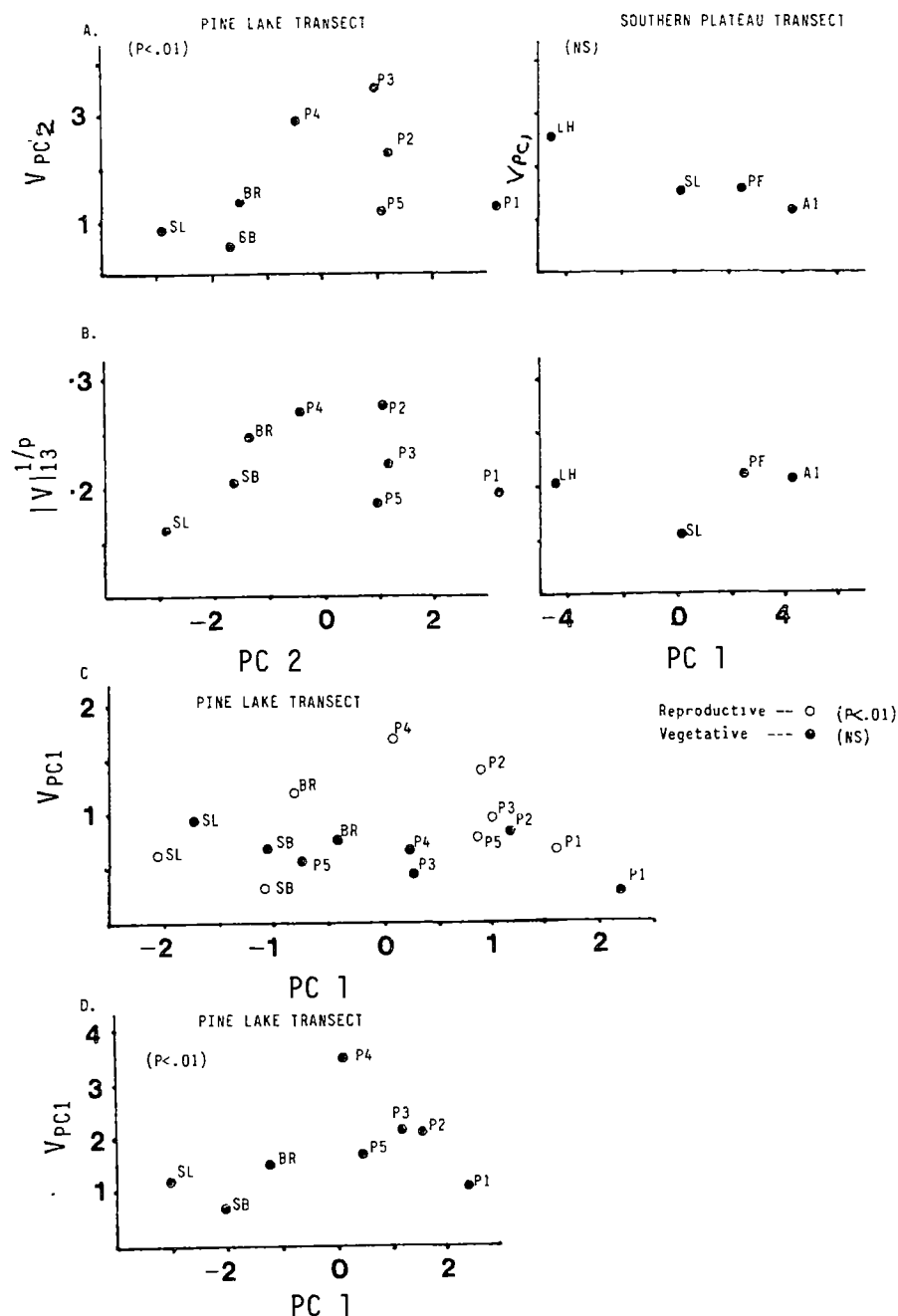


Fig. 4.1 (A) Population variances (V_{PC1}), (B) standardized generalized variances ($|V|_{13}^{1/p}$; Table 4.1) plotted against the mean value on PC₁ (southern Plateau transect) or PC₂ (Pine Lake transect) derived from PCA (TOT CORR, ALLGRPS) of 13 morphometric characters. (C) Population variances (V_{PC1}) plotted against the mean value along PC₁ derived from separate PCA's (TOT CORR for Pine Lake transect populations only) of reproductive (p=7; excl. VALPOS, VALSZ), vegetative (p=6) and (D) total (p=13) character sets.

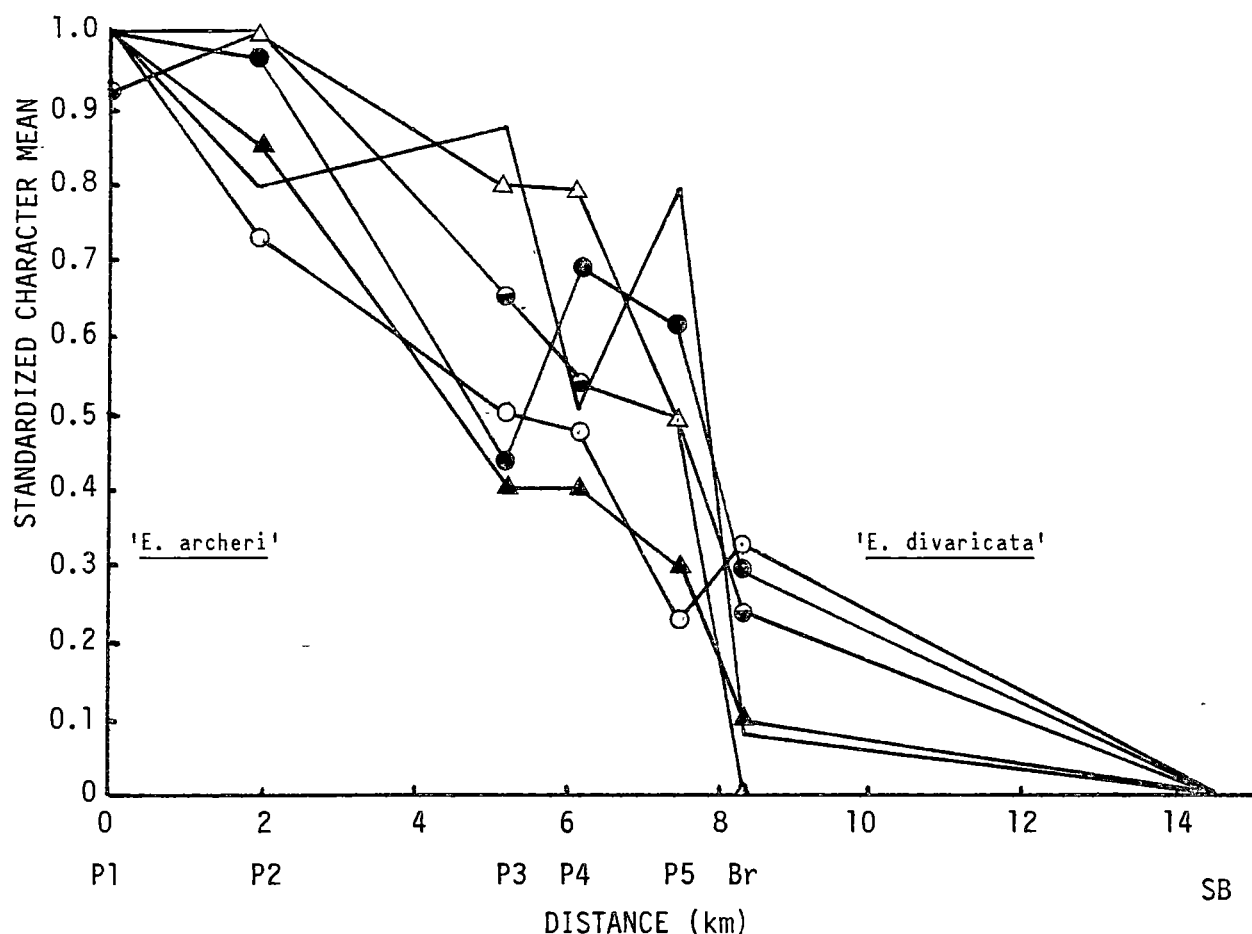


Fig. 4.2 Mean glaucousness score (seedling ▲; adult Δ), seedling leaf shape (i.e. $\log LL/LW$ ●), value on PC_1 derived from vegetative (○, as Fig. 4.1B) and reproductive (•, as Fig. 4.1B) characters and flowering time (⊙) for populations along the Pine Lake transect ($P_1 \rightarrow SB$). Means have been standardized to have a range of 1.

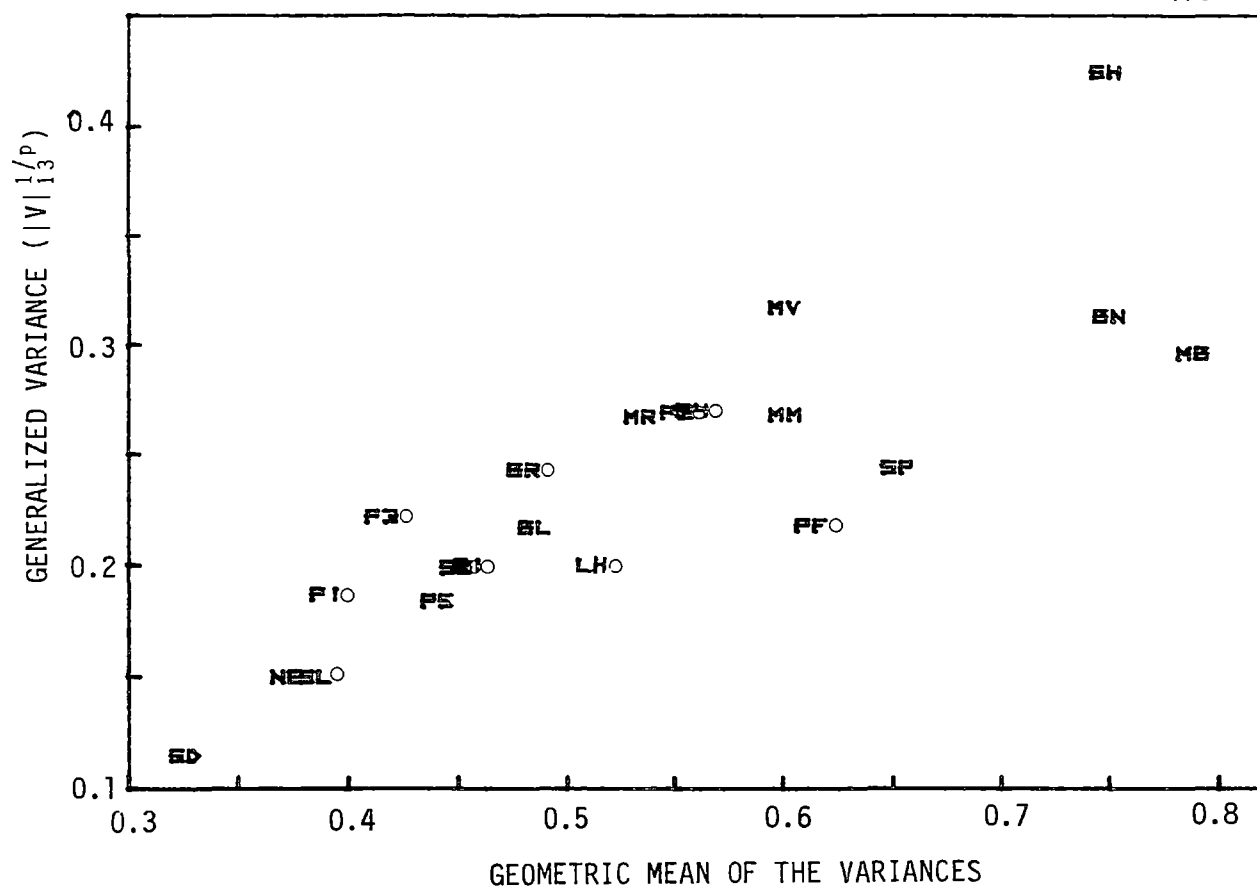


Fig. 4.3 Standardized generalized variance ($|V|_{13}^{1/p}$) derived from 13 morphometric characters plotted against the geometric mean of the variances (μ).

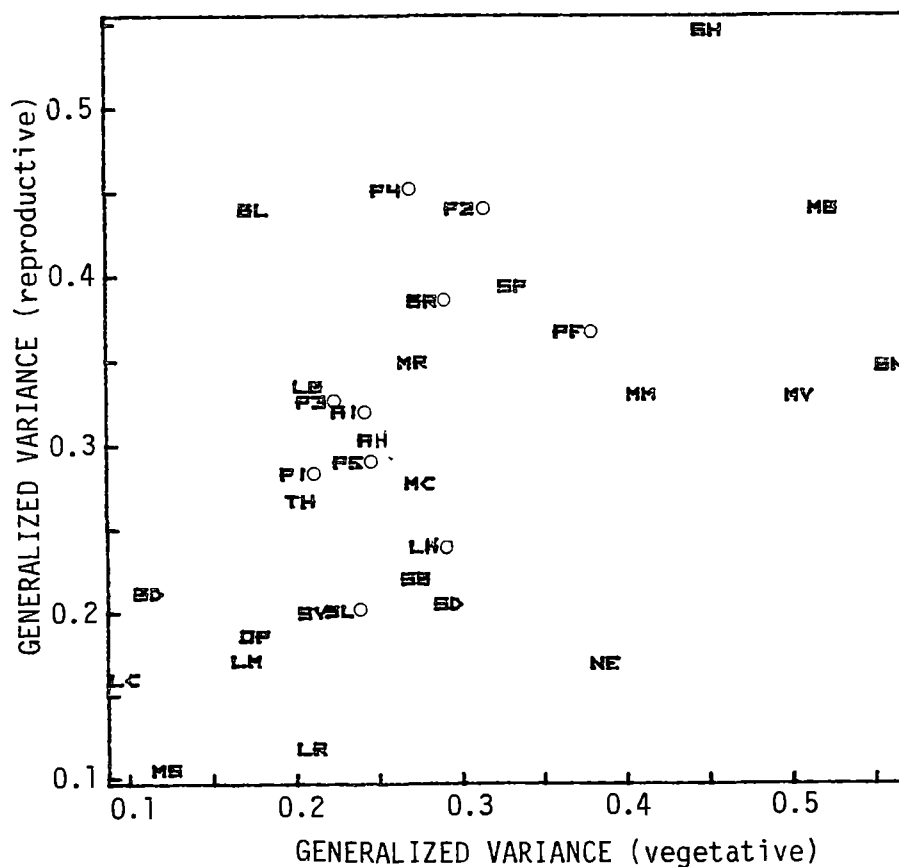


Fig. 4.4 Standardized values of the generalized variance ($|V|^{1/p}$) for reproductive ($p=7$) and vegetative ($p=6$) character sets.

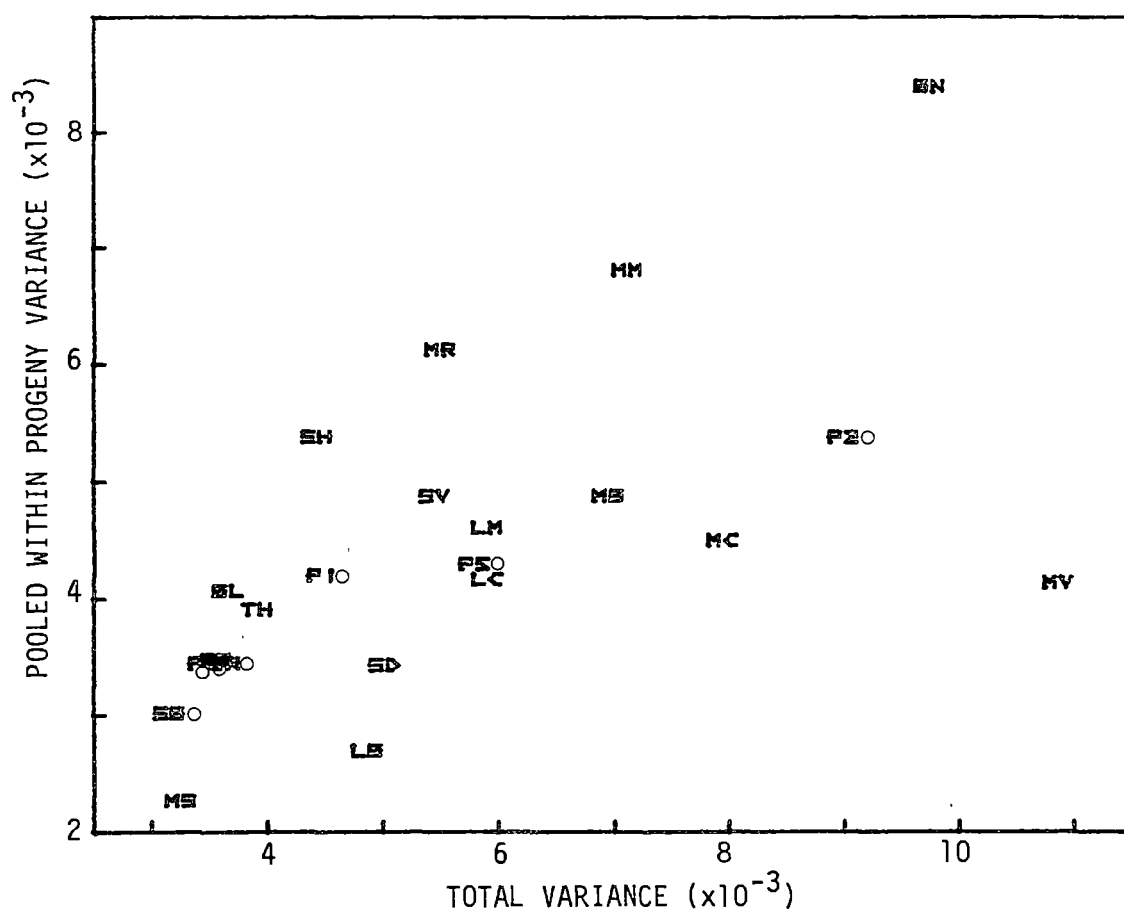


Fig. 4.5 Pooled within progeny variance plotted against the total variance for seedling leaf shape ($\log LL/LW$) for populations in Trial 2.

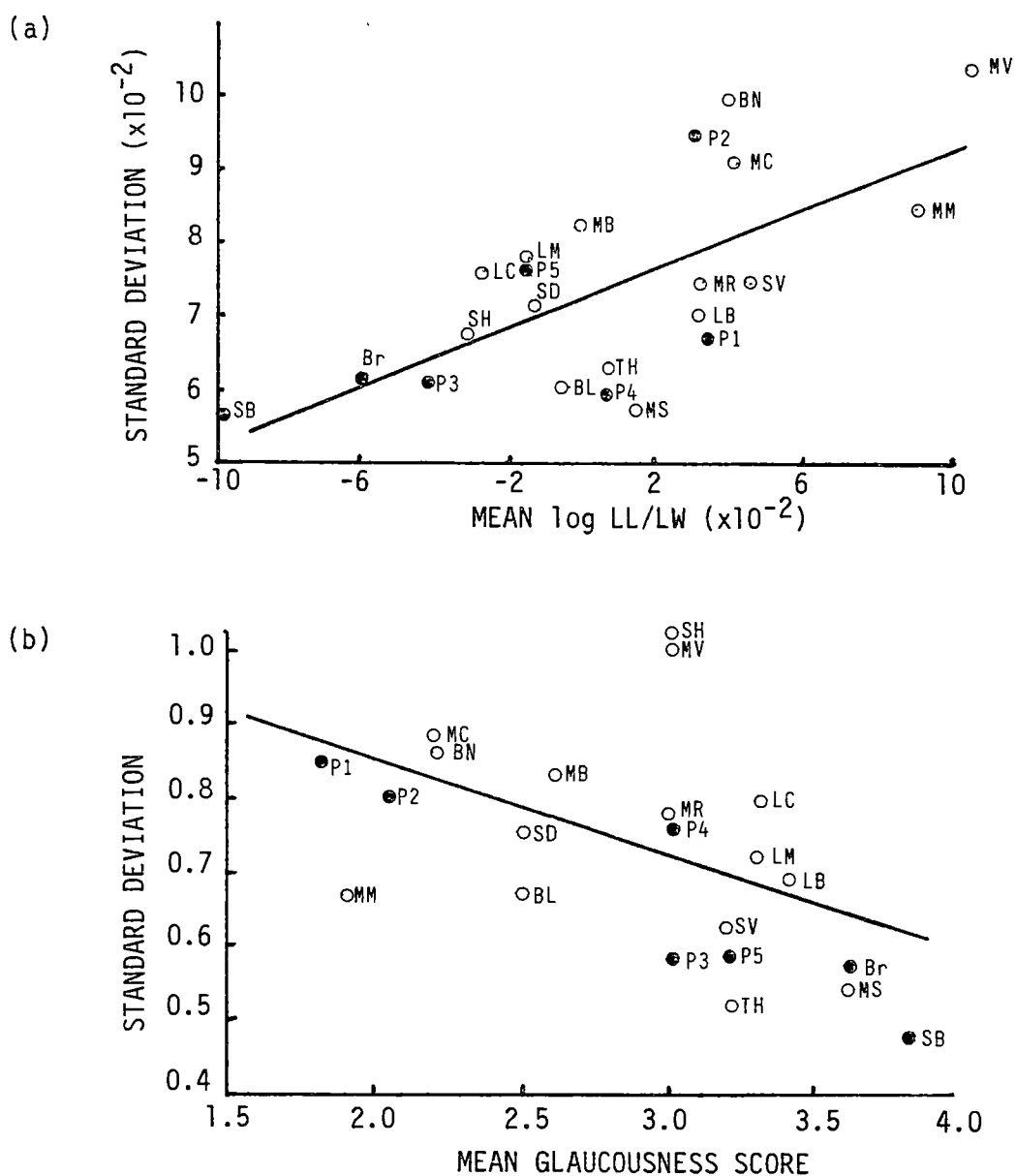


Fig. 4.6 Standard deviation (SD) plotted against the population mean for (a) seedling leaf shape ($\log LL/LW$) and (b) seedling glaucousness scores. The perpendicular deviation from the regression line is indicative of the relative variability following removal of the dependence upon the mean. Populations along the Pine Lake transect are marked (●).

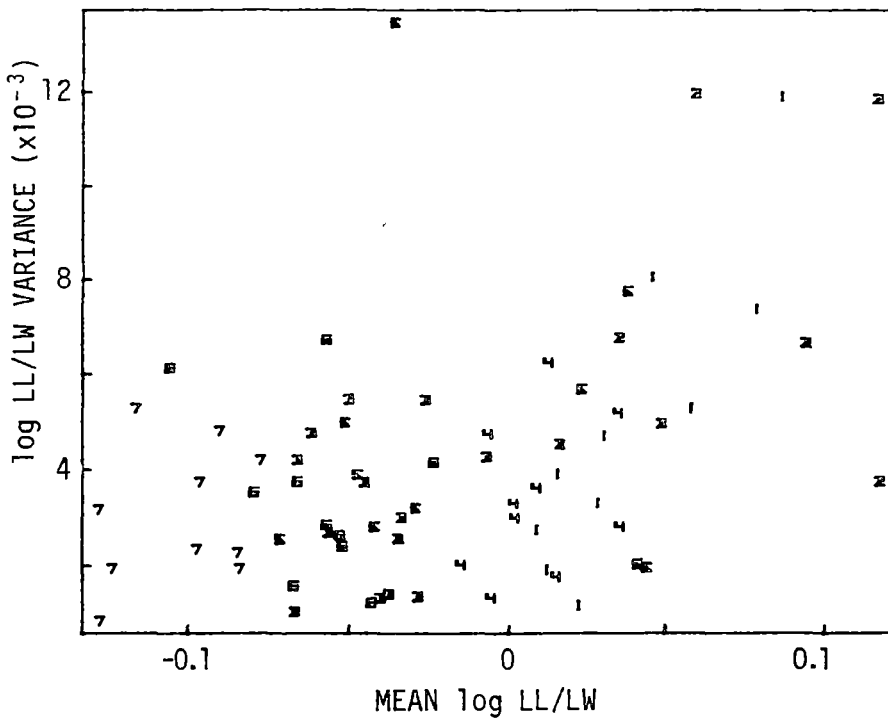


Fig. 4.7 . Progeny variance (V_x) plotted against the mean value for seedling leaf shape (i.e. log LL/LW) (presentation follows Clifford (1954)). Numbers correspond to the rank order of the population from which the progenies were obtained along the Pine Lake transect {'*E. archeri*' ($P_1=1$; $P_2=2$); 'Pine Lake Intermediates' ($P_3=3$; $P_4=4$; $P_5=5$); '*E. divaricata*' ($Br=6$; $SB=7$)}.

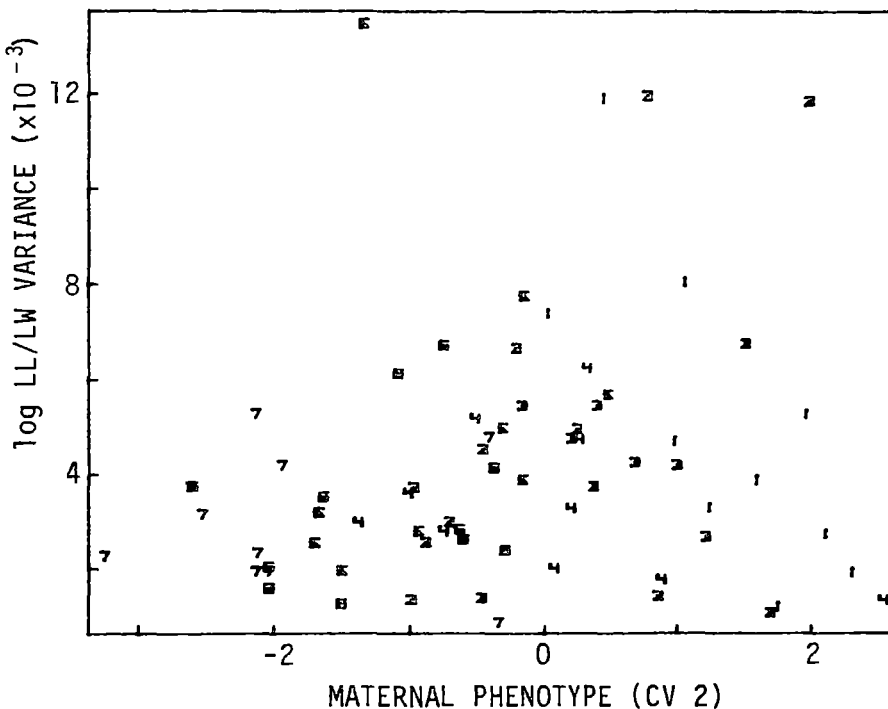


Fig. 4.8 Progeny variance (V_x) in seedling leaf shape (i.e. log LL/LW) plotted against the maternal phenotype score (i.e. CV_2 ; Fig. 1.18; Table 1.10).

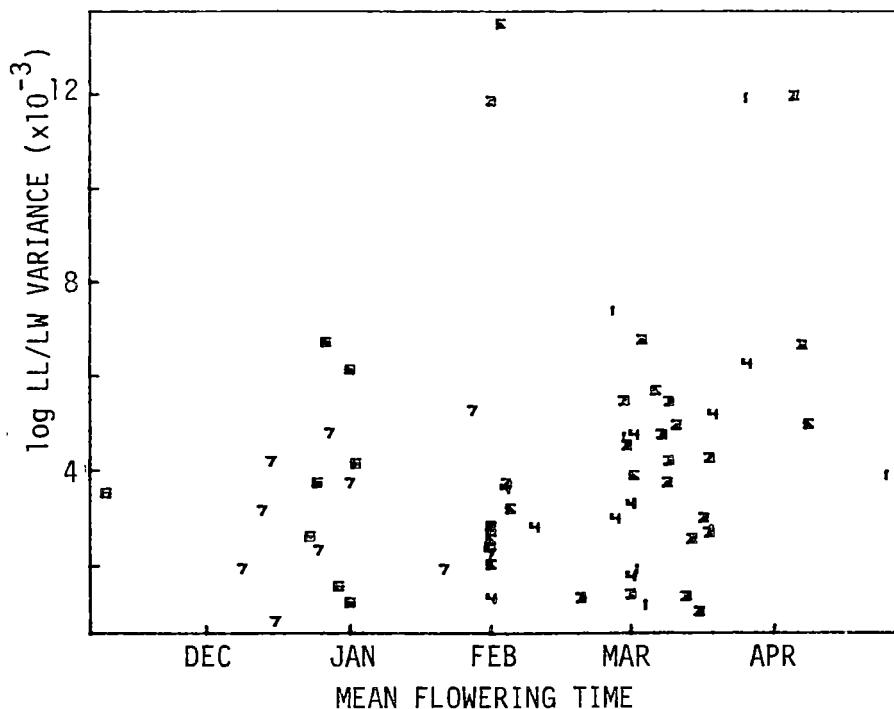


Fig. 4.9 Progeny variance (V_x) in seedling leaf shape (i.e. $\log LL/LW$) plotted against the maternal mean flowering time (see Chapter 1). Codes correspond to that used in Fig. 4.7.

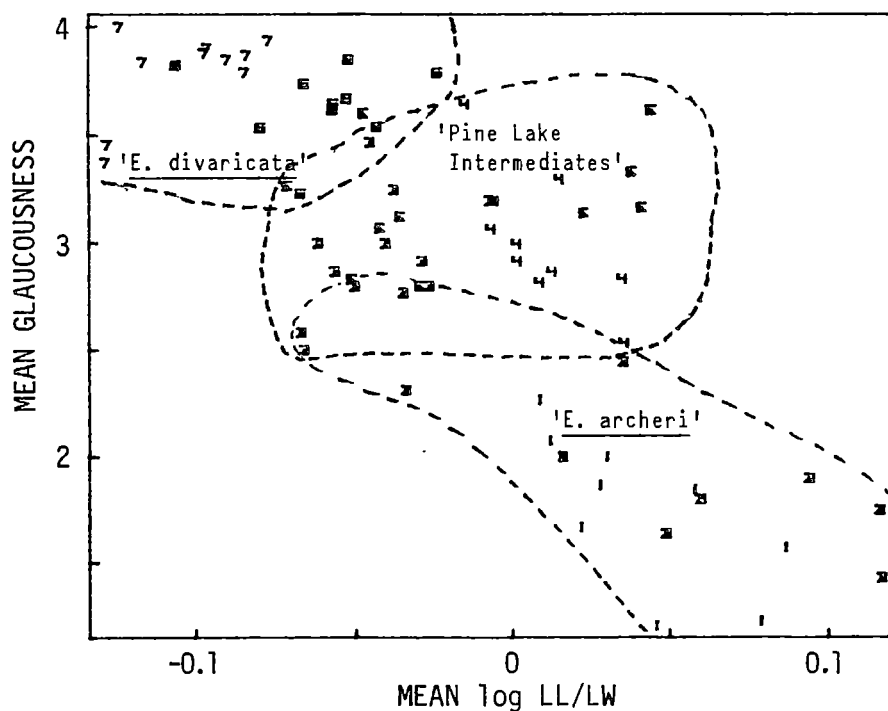


Fig. 4.10 Mean seedling glaucousness score plotted against mean leaf shape (i.e. $\log LL/LW$) for progenies from the Pine Lake transect. Codes correspond to those used on Fig. 4.7.

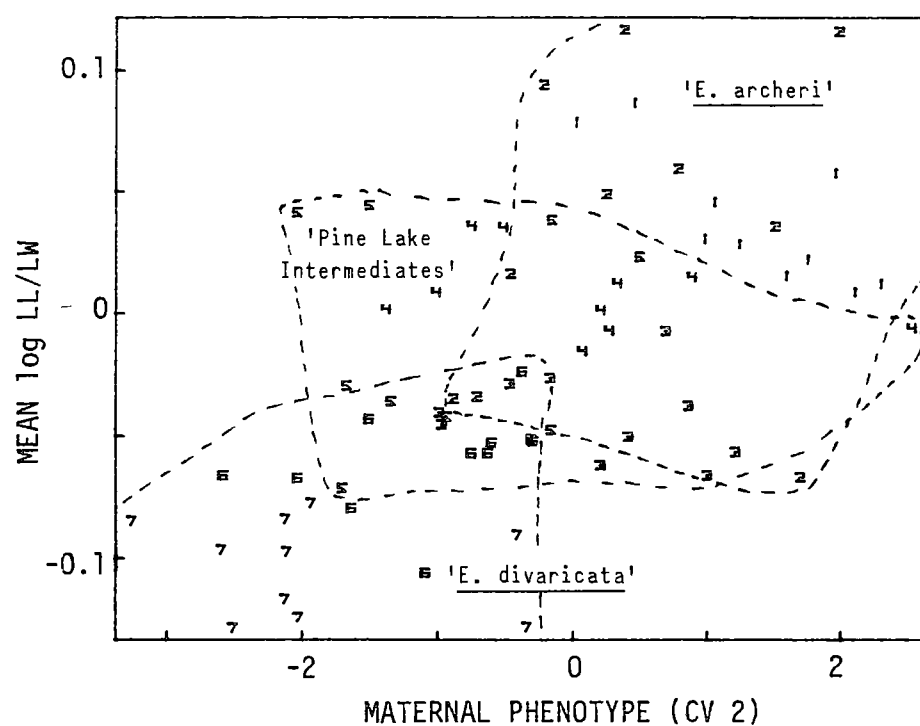


Fig. 4.11 Mean seedling leaf shape (i.e. $\log LL/LW$) plotted against the maternal phenotype score (i.e. CV2; Fig. 1.18; Table 1.10). Codes correspond to those used in Fig. 4.7.

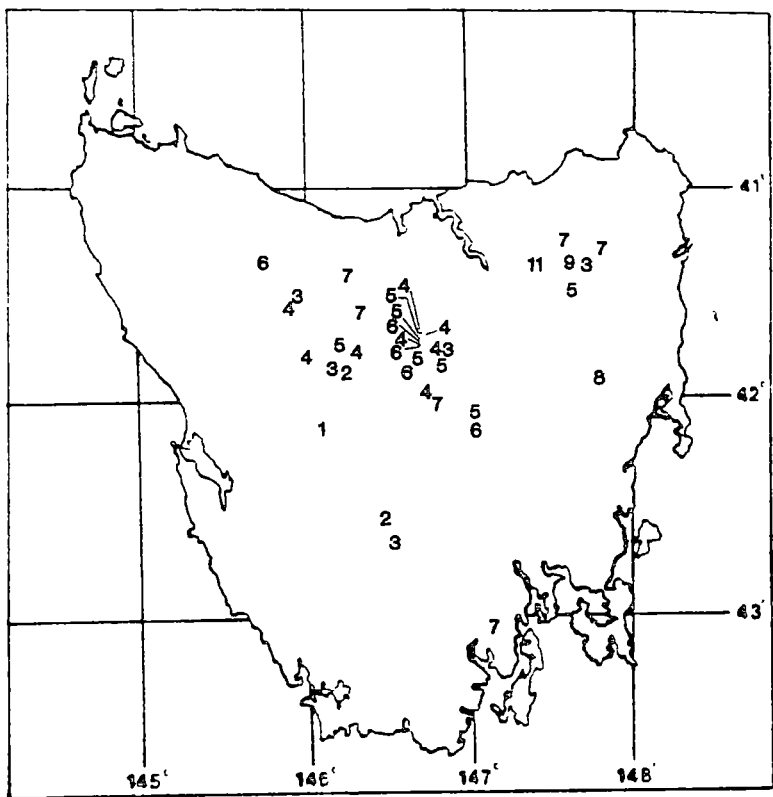


Fig. 4.12 Standardized values of the generalized variance (i.e. $|V|_{PC5}^{1/p} \times 10^{-1}$) calculated in the space defined by the first 5 PC's (c) which accounts for 82% of the total variation between individuals. Values have been rounded to the nearest integer.

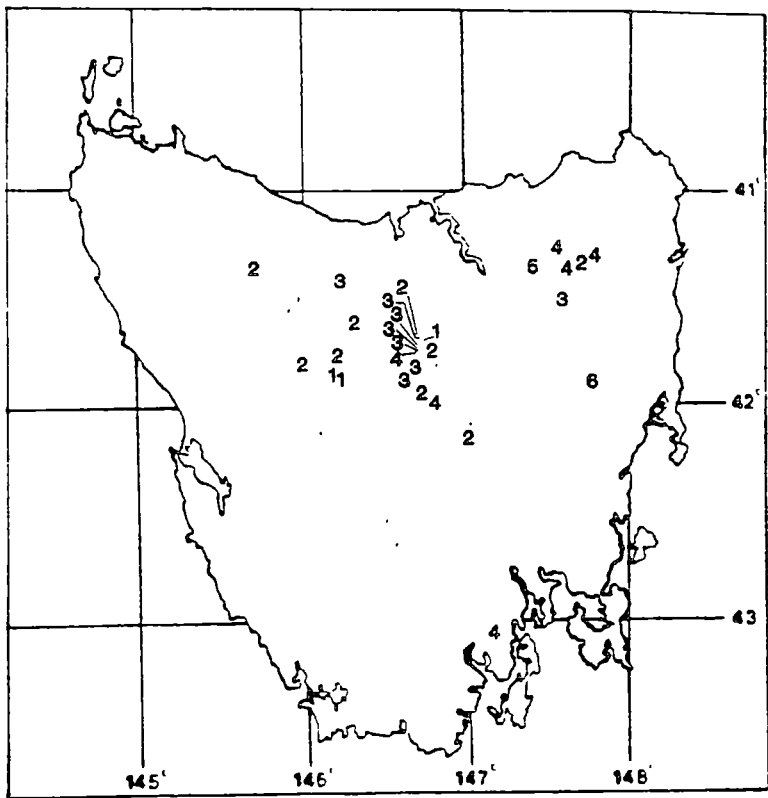


Fig. 4.13 Standardized values of the generalized variance (i.e. $|V|_9^{1/p} \times 10^{-1}$; b) rounded to the nearest integer. Populations with $n-1 < p$ have been excluded.

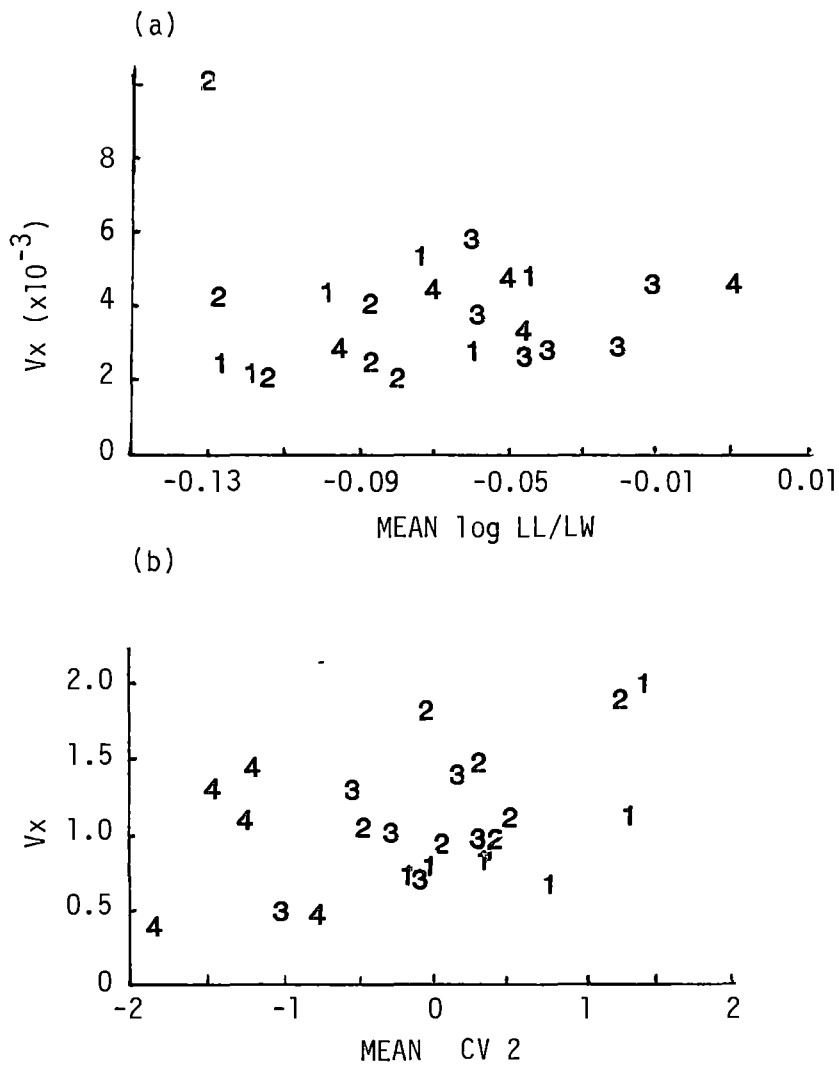


Fig. 4.14 Progeny variance (Vx) plotted against the mean for (a) seedling leaf shape (i.e. log LL/LW) and (b) CV_2 (Fig. 2.2; Table 2.1). Numbers correspond to populations from which progenies were obtained (LH=1; SL=2; PF=3; SP=4; high→low altitude 1→4).

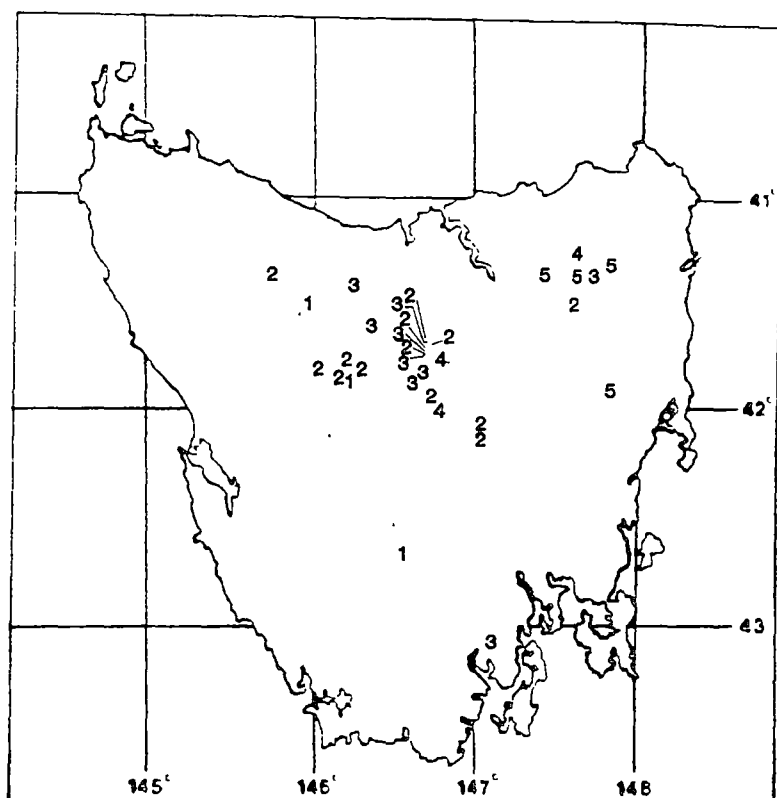


Fig. 4.15 Standardized values of the generalized variance (i.e. $|V|^{1/p} \times 10^{-1}$) calculated for vegetative characters only. Values have been rounded to the nearest integer and populations with $n-1 < p$ have been excluded.

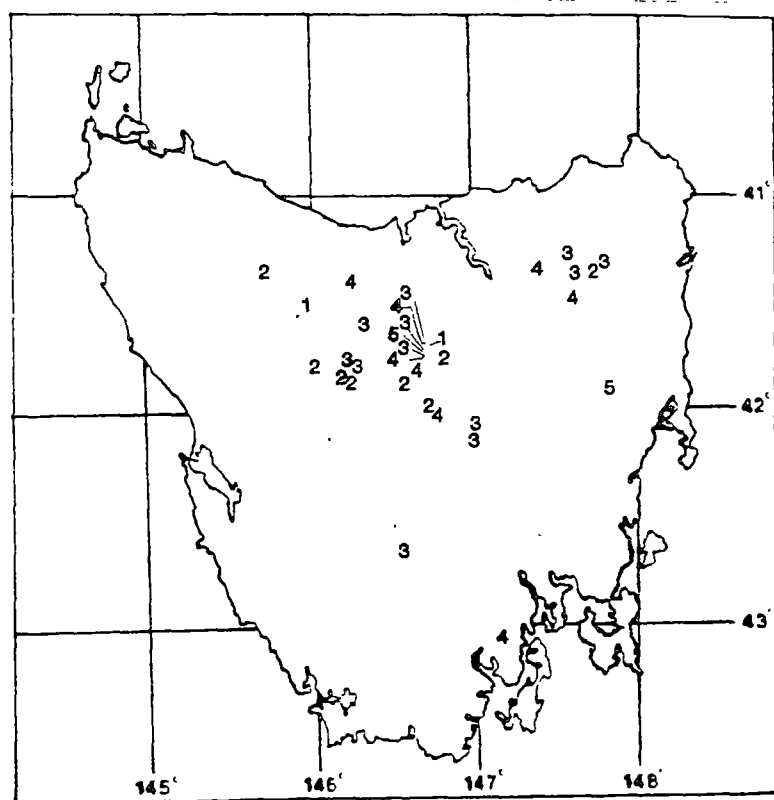


Fig. 4.16 Standardized values of the generalized variance (i.e. $|V|^{1/p} \times 10^{-1}$) calculated for reproductive characters only. Values have been rounded to the nearest integer and populations with $n-1 < p$ have been excluded.

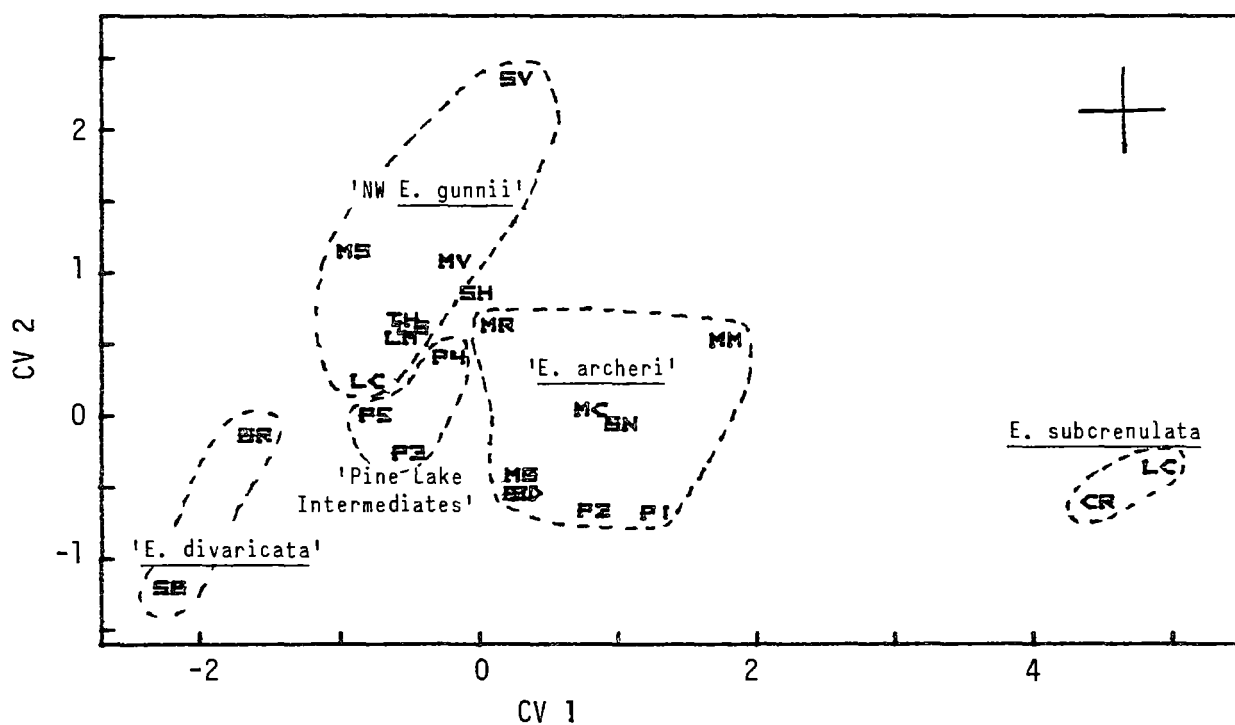


Fig. 4.17 CVA ordination of population centroids of the *E. gunnii-archeri* and *E. subcrenulata* seedling samples. The analysis is based on the seedling characters indicated in Table 2.7 and cluster limits (Fig. 1.24) are indicated.

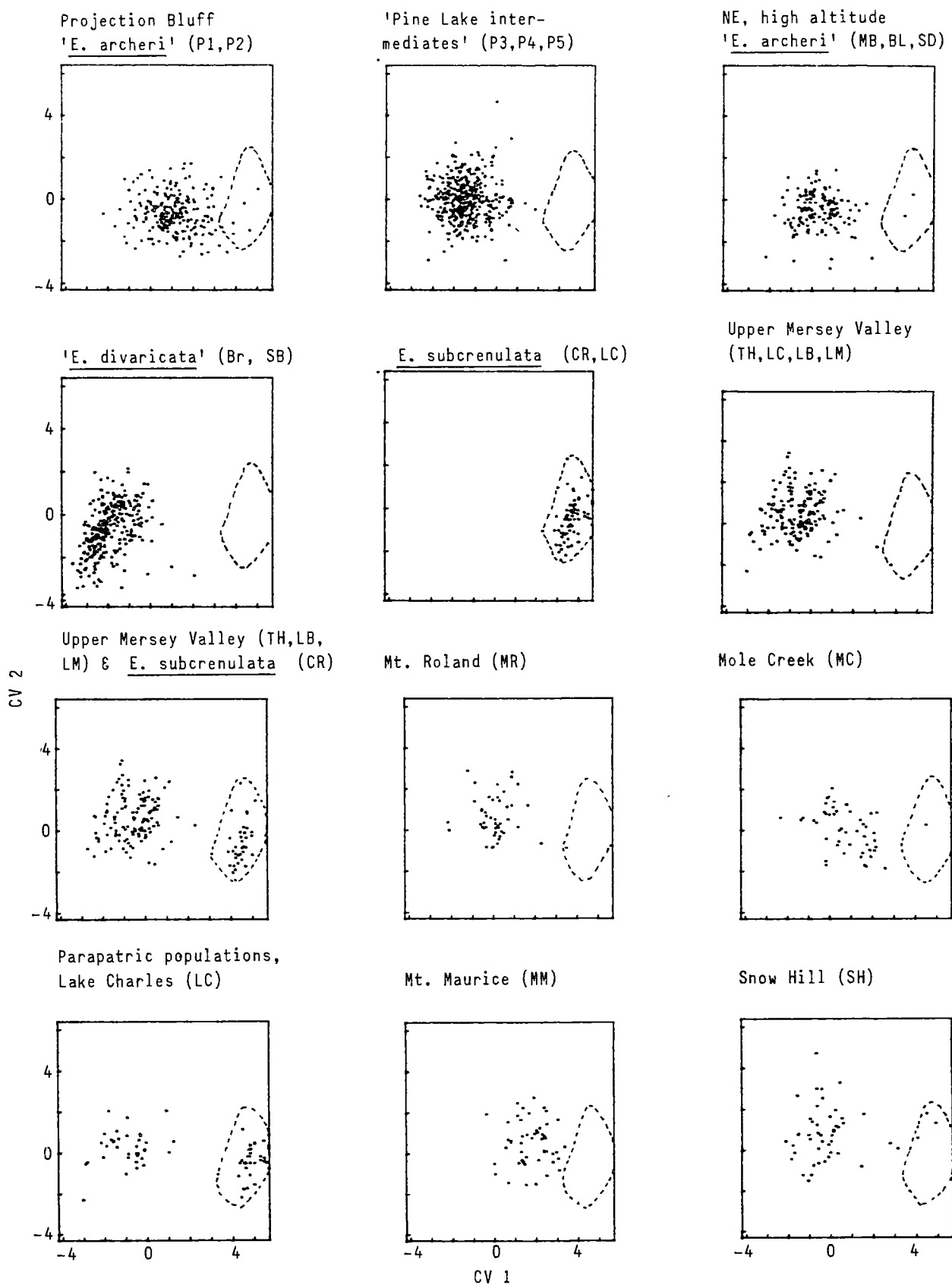


Fig. 4.18 Plots of *E. gunnii-archeri* and *E. subcrenulata* seedlings in the space defined by CV_1 and CV_2 from Fig. 4.17. The outer limit of the distribution of *E. subcrenulata* seedlings [Cradle Mt. (CR) and LC] is indicated.

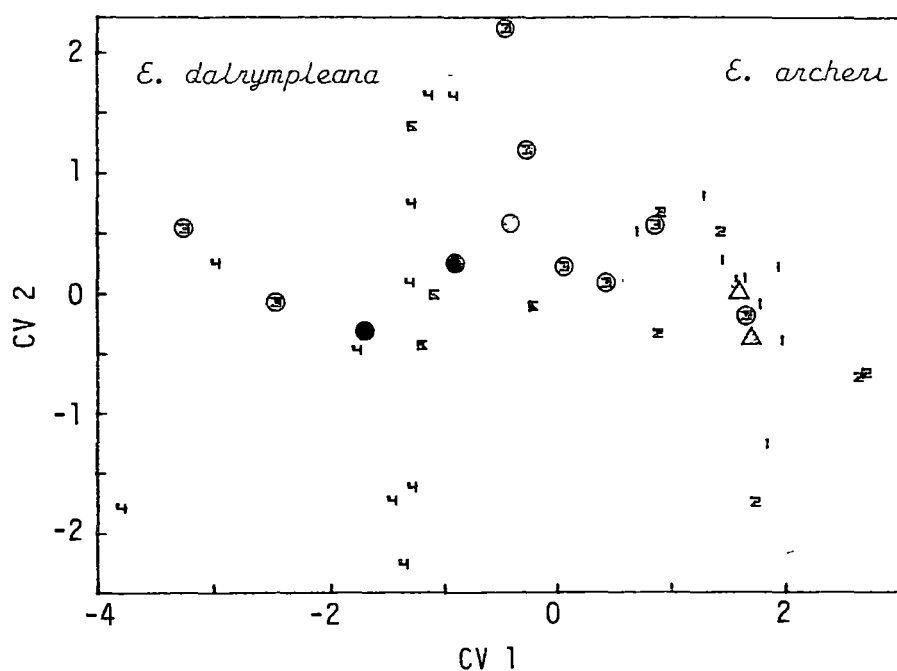


Fig. 4.19. Hybridization between *E. archeri* and *E. dalrympleana* on Ben Nevis. The distribution (numbers) and progeny means (symbols) of *E. dalrympleana* (4,5;●), *E. archeri* (1,2;△) and a suspected hybrid (③;○). Progenies were grown from open pollinated seed collected from trees in the vicinity of the Ben Nevis *E. archeri* population and the CVA was based on 3 seedling leaf characters (LL, LW and LWP).

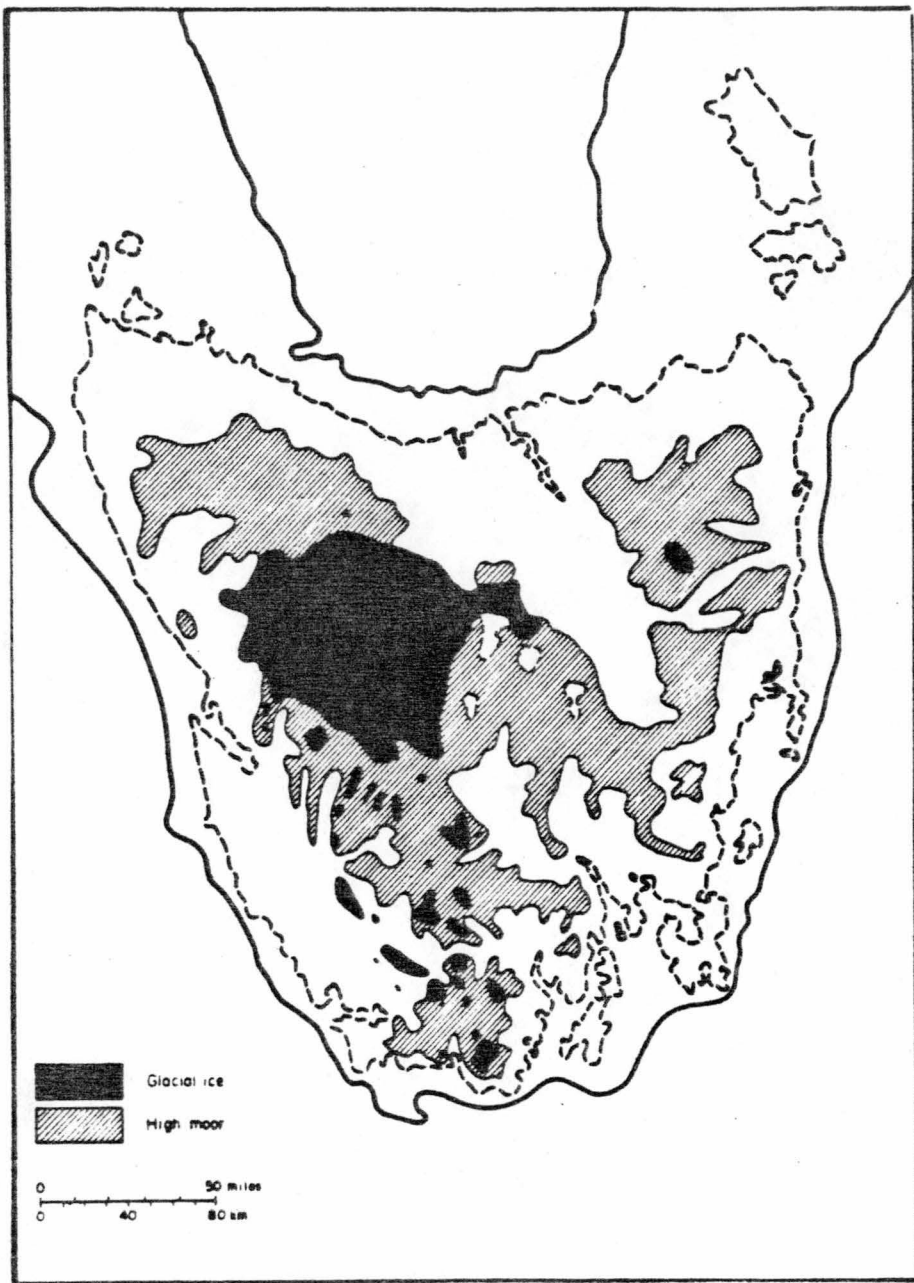


Fig. 4.20 Tasmanian environments at the maximum of the Last Glacial (from Davies 1974). Recent work (Macphail 1979; Kiernan et al. 1983) suggests that the tree-line was probably much closer to the coast in the west than indicated by Davies (1974) and probably rose from near the present sea-level (---) on the west coast to 400-500 m above the present sea-level on the east coast (as indicated).

PART 2

Studies in hybridization

1. Hybridization between *Eucalyptus obliqua* and *E. pulchella*.
2. The dynamics of hybridization between *E. risdonii* and *E. amygdalina*.

CHAPTER 5

Hybridization between *Eucalyptus obliqua* and
*E. pulchella*5.1 Introduction

While strict genetic isolation appears to be maintained at the subgeneric level (taxonomic treatment follows Pryor and Johnson 1971) within the genus *Eucalyptus* (Pryor 1959a, 1976), there seem to be no absolute barriers to interbreeding between species within subgenera. However, the existence of intrinsic mechanisms which prevent or reduce the probability of natural hybridization between parapatric or sympatric species from the same subgenus have been noted (Pryor 1959b, 1976, Barber 1965; Parsons and Rowan 1968; Hopper *et al.* 1978; Rogers and Westman 1979; Drake 1980, 1981a, 1981b, Ashton 1981a).

This is certainly the case with the association of *E. obliqua* (subgenus *Monocalyptus*, series *Obliquae*) with the endemic peppermint species (subgenus *Monocalyptus*, series *Piperitae*, *E. amygdalina*, *E. pulchella* and *E. tenuiramis*) in the lowland sclerophyll forests of south-eastern Tasmania. The ecological preferences of these species (Hogg and Kirkpatrick 1974; Davidson *et al.* 1983) maintain an intricate mosaic distribution, yet despite often intimate contact naturally occurring hybrids between *E. obliqua* and the peppermint species are extremely rare. This is in marked contrast to ecotones between pairs of the *Piperitae* species where hybrids and hybrid swarms are frequently encountered. Reported hybrid combinations between the Tasmanian *Obliquae* and *Piperitae* are few (Curtis and Morris, 1975, *E. pauciflora* X *E. amygdalina*; Jackson 1958, *E. sieberi* X *E. amygdalina*; Pryor 1957b, *E. delegatensis* X *E. coccifera*, *E. delegatensis* X *E. amygdalina*). The only record of *E. obliqua* interbreeding with the *Piperitae* is given by Ashton and Williams (1973, *E. radiata*, Victoria). Again, hybrids are very rare, and in this case '...appear to occur only in areas where *E. obliqua* is already hybridizing with other stringy-barks'.

E. obliqua and *E. pulchella* are the major representatives of the subgenus *Monocalyptus* present on the lowland dolerite hills of south-eastern Tasmania. *E. pulchella* is virtually restricted to this habitat whereas *E. obliqua* exhibits a broad geographic and edaphic range. *E. pulchella* dominates the drier slopes but is replaced by *E. obliqua* on sites with more available moisture. This replacement is typically associated with a transition from north-facing to south-facing aspects. Often the boundary between the two species is sharp and follows the ridges. However, the exact location and width of the ecotone on other aspects is variable and dependent on localized climatic, edaphic and topographic features.

A search of *E. obliqua* and *E. pulchella* forests has to date yielded only two independent sites of possible hybridization involving mature trees. A single mature tree, intermediate in numerous characters between *E. obliqua* and *E. pulchella* and exhibiting a combination of characters rarely encountered, was located at each site. In each case, the proposed mature hybrid was growing on the edge of a shallow gully on a north-facing slope dominated by *E. pulchella*. At the main study site (Fig. 5.1) near Snug Falls, Tas., saplings lying outside the phenotypic range of either species were also present in relatively low frequency and were mainly restricted to the small gully. The absence of such phenotypes in any other comparable section of the forest, as well as the increased phenotypic diversity, strongly suggest these saplings result from either seed or pollen migration from the single mature intermediate tree (H1). A similar pattern of sapling distribution was found in the gully near the second mature intermediate tree.

5.2 Methods

Adult Morphology

Ten mature trees of *E. obliqua* and *E. pulchella* were sampled from the general locality of the putative hybrid (H1) near Snug Falls, Tas.. The sample was representative of the localized phenotypic variation within the parental species. For reasons similar to those of Phillips and Reid (1980), sampling within trees was restricted to fruits and sun leaves typical of the area of peak summer growth. Similar samples were taken from the two mature putative hybrids (H1 and H2). The adult characters measured in this study are shown in Fig. 5.2 and listed in Table 5.1. Measurements from 10 leaves and usually 10 umbels (minimum of 3) were averaged for each tree. Capsule weight was obtained from the weight of a single sample of 10-30 air-dried capsules (usually 30).

Progeny Trial

Open pollinated seed was collected from H1 and three representative trees of *E. obliqua* and *E. pulchella*. Forty-eight seedlings from each *E. obliqua* and *E. pulchella* mother (144 per species) and 96 from H1 were transplanted into veneer tubes filled with potting soil. Progenies were grouped and their relative positions and orientations in the glasshouse rearranged periodically throughout the trial. Seedlings were grown under the natural photoperiod, watered daily and supplied with a liquid nutrient solution twice weekly.

A preliminary scoring of growth rate was made after 7 weeks, with seedling height and number of leaf pairs expanded being recorded. After 11 weeks

seedlings were scored for the growth and discriminating morphological characteristics listed in Table 5.2. The dimensions of a single leaf as well as the internode and intranode length were measured from the fifth and seventh nodes. Where leaf pairs were alternate, the top leaf was chosen for measuring. Scoring of the multistate characters was achieved by comparison with standards. The density of prominent oil glands was scored by holding the fifth leaf in front of a standard lamp (small oil glands cannot be detected using this technique). Not all seedlings had completely expanded the seventh leaf pair at the time of scoring, hence most analyses are restricted to the fifth node data set and the ontogenetic comparison confined to only 220 out of a total of 312 surviving seedlings.

Estimation of Seed Output Parameters

From each of the mothers used in the progeny trial, three samples (each of 30 capsules) were air-dried and seed and chaff extracted. The number and weight of opened capsules and total weight of seed and chaff extracted from each sample were recorded. Prior to imbibition, the distinction between seed and chaff is difficult to determine; however, a random sample of 20 apparently well filled seed was weighed. The total sample of seed and chaff was spread onto thiram-dusted germination pads, placed in a petri dish and deionized water added regularly. Throughout the germination period samples were held in growth cabinets at 22°C in a continuous mixture of incandescent and fluorescent light. Seeds were recorded as germinated when the testa was ruptured and the radicle emerged.

On termination, all ungerminated seed was separated from the chaff and the viability tested by squashing. A seed was classified as still viable if a firm white embryo was extracted. The remaining sample comprising only chaff was dried and weighed. Using the weight of a subsample of 50 chaff particles, the number of chaff particles was estimated. The germination response was examined only for seeds germinating over the initial test period of 50 days using the germinative energy index (GEI, Grose 1963) and germinative capacity GC; number of seeds germinated/total number of viable seeds, Grose 1957). However, a variety of other measures gave similar results.

Statistical Methods

The transformations of the original quantitative variables used are shown in Tables 5.1 and 5.2. Analysis of the data set was by principal components (PCA; Seal 1966), discriminant function (Fisher 1936) and likelihood analysis (Namkoong 1966; Goodman 1967). PCA was also employed in reducing the

dimensionality of specific, biologically related subsets of the original variables. Multiple discriminant function analysis (i.e. Canonical Variates Analysis, Seal 1966) has been widely used in the study of hybridization in *Eucalyptus* (e.g. Clifford and Binet 1954; Kirkpatrick 1977a; Hopper *et al.* 1978). This technique assumes a common variance-covariance matrix, although Lachenbruch (1975) reported it as sufficiently robust to moderate departures from both normality and homogeneity. Despite attempts to optimize homogeneity at the univariate level by transformation, gross heterogeneity in the variance-covariance matrices was apparent between progeny of the parental species.

In cases which obviously violate the assumptions for discriminant analysis, Namkoong (1966) recommended the more general approach of likelihood analysis. Using such techniques intermediate values can arise as a consequence of an individual being equally unlike either species and lying outside the species complex being examined. To negate this problem, Namkoong recommended the use of an ordination in which the generalized distances from the parental species' centroids ($\sqrt{D^2}$) are treated as separate probability functions. Confidence limits for the generalized distance of individuals from a population centroid are given by Orloci (1978). Character sets used in the multivariate analyses presented include, for the adult data, variables 1-13 in Table 5.1 (see Fig. 5.2) and, for the seedling data, those indicated in Table 5.2 in addition to the leaf dimensions 1-7 (PCA, Fig. 5.5) or 1-5 (likelihood analysis, Fig. 5.6) in Table 5.1.

5.3 Results

Adult Morphology

The presumed parents, *E. obliqua* and *E. pulchella* are morphologically distinct in numerous adult characters. Typical adult leaves and fruits of *E. obliqua*, *E. pulchella* and the proposed hybrid are shown in Fig. 5.3 and a summary of the major differences in adult leaf and fruit dimensions is given in Table 5.1. The difference between the two species was highly significant ($P > 0.001$) for all dimensions recorded, with no range overlap occurring for 9 of the 14 dimensions. The proposed hybrids are intermediate between the means of the two species in all but lamina length and the two least discriminating characters, length to the widest point and pedicel length, and lie intermediate and outside the range of either species for maximum lamina width, basal asymmetry, petiole length and disc level. The linear combination of the leaf and fruit dimensions which maximally discriminates the two species was calculated using discriminant analysis, and the ordination along this vector is shown in Fig. 5.4.

This discriminant function describes a direction of gross morphological variation between *E. obliqua* and *E. pulchella* along which, as expected from the univariate results, both proposed hybrids lie intermediate and distinct from either species. Although the proposed hybrids are slightly closer to *E. pulchella*, they lie well within the 95% confidence limits of a hypothetical F_1 distribution centred on a mean of zero and with a standard deviation equivalent to either the minimum or pooled parental standard deviation.

Intermediacy was noted for several characters not measured, including operculum shape and bark type. The thick, fibrous, rough bark of *E. obliqua* is persistent to the secondary branches whereas that of *E. pulchella* is decortivating with an occasional stocking. The proposed hybrids maintain a rough bark on the trunk which is slightly more scaly than in *E. obliqua*; however, the secondary branches and upper crown are decortivating.

Progeny Trial

Seedling morphology

With the exception of the height at 7 and 11 weeks and the lamina thickness of the seventh leaf, all characters differed significantly ($P < 0.001$) between the two pure species, with the mean of the proposed hybrid (H1) progeny lying intermediate. The morphological discontinuity between *E. obliqua* and *E. pulchella* seedlings is portrayed in the principal component and generalized distance ordinations (Figs. 5.5 and 5.6). In the space defined by each ordination the pure species appear as discrete clusters with the progeny of H1 intermediate and highly variable, encompassing the range between the pure species. The first principal component, accounting for 58.7% of the total variation, effectively separated seedlings of either species. Weightings of the characters on this vector were virtually equal with signs as expected given the directions of differences in the univariate means of the two pure species.

Ontogenetic variation

Although neither proposed parental species exhibits the marked heteroblastic development found in many species of *Eucalyptus*, significant ontogenetic differentiation does occur (Fig. 5.7). Most of the characters observed display continuous and, in some cases, correlated variation associated with the transition from the seedling to adult morphology. However, the pattern of ontogenetic development differs between the two species and between characters. For example, the petiole and intranode first develop at a significantly ($P < 0.001$) later node in *E. pulchella* than in *E. obliqua*. The progeny of H1 tends to be

intermediate in this respect. In *E. pulchella* the intranode tends to develop prior to the petiole whereas the converse applies in *E. obliqua*. Most characters examined (Table 5.3) show significant ($P < 0.001$) and usually differential ontogenetic variation between the fifth and seventh nodes, yet at both nodes significant ($P < 0.001$) discrimination between species still occurs. Lamina thickness is an exception, only differentiating the species at the fifth node. The pattern of variation between the fifth and seventh node is an extension of general trends, associated with maturity and, as implied from Fig. 5.7, involves an increase in all characters except lamina width which significantly ($P < 0.001$) decreases.

The ontogenetic stage at which the lamina width starts to decrease varies between the two species. Lamina width significantly ($P < 0.001$) decreases in *E. pulchella* between the fifth and seventh node whereas it increases in *E. obliqua*. This reflects a change in leaf size in *E. obliqua* but a change in shape in *E. pulchella*. The mean of the progeny of H1 shows no significant difference between nodes 5 and 7. A partitioning of the progeny of H1 into leaf shape classes (Fig. 5.8) indicates that individuals tending toward either parental species in leaf morphology display the parental pattern of ontogenetic variation whereas intermediate seedlings display an intermediate response. Similar conclusions are evident from an examination of variation in lamina thickness and the development of the petiole and intranode. The mean of the progeny of the proposed hybrid tree (H1) is therefore not only intermediate between *E. obliqua* and *E. pulchella* in morphology at any particular developmental stage but also intermediate in the manner in which many of these characters vary ontogenetically.

Progeny variability

The progeny of H1 is more variable than progeny from either *E. obliqua* or *E. pulchella* parents in most of the discriminatory characters, particularly those in which the variation between species is significantly greater than that resulting from ontogenetic causes (e.g. lamina length, lamina width and petiole length; Table 5.3). Strong correlations are evident between characters within the progeny of H1 (Fig. 5.9), indicating a tendency for characters to occur in combinations typical of either *E. obliqua* or *E. pulchella*. Many of the character correlations observed in the progeny of H1 are not evident within progenies of either species and involve what could be considered developmentally independent characters. This suggests an underlying genetic as opposed to an allometric or pleiotropic cause. This effect is further accentuated if partial correlations removing the effect of height are used to account for the influence of general plant vigour on the various correlations.

From the previous ordinations (Figs. 5.5 and 5.6, Table 5.4) it is apparent the coherent variation between characters within the progeny of H1 results in a single major direction of phenotypic (and presumably genotypic) variation that lies along the axis discriminating *E. pulchella* and *E. obliqua* seedling clusters. The principal components analysis indicates that 25% of the variability within the progeny of H1 lies in this direction (along PC 1) which is twice that of any other axis. The progeny of H1 shows significantly greater ($P < 0.001$) variation than any other progeny along this axis (Table 5.4). The major principal axis within the progeny of H1 differs only slightly (16°) from the major axis described for the total ordination (Fig. 5.5). There appears to be no single dominant direction of variation other than that pointing toward the proposed parental clusters. The narrow unidirectional spread of the progeny of the proposed hybrid (H1) in the $\sqrt{D^2}$ ordination (Fig. 5.6) clearly indicates that the contribution of any unidentified, markedly different species to the genome of the hybrid or through backcrossing is unlikely. Furthermore, comparison of the range of distance scores along either axis in this ordination confirms that there is a greater diversity of phenotypes within the progeny of H1 compared with the pure species.

Backcrossing

From Figs. 5.5 and 5.6 and Table 5.5 it is evident that the distribution of the progeny of H1 is skewed toward *E. pulchella*. This effect is not a methodological artefact being consistent regardless of the character set or ordination technique used. Furthermore, it is unlikely to result from genetic dominance because of the large character set employed. Inviability of individuals tending toward *E. obliqua* cannot be discounted, but it is unlikely as surviving seedlings of this form are as vigorous as intermediates or those tending toward *E. pulchella* (Table 5.6). Backcrossing of the presumed F_1 hybrid to the surrounding *E. pulchella* is the most likely explanation, although the possibility that the putative hybrid (H1) was not an F_1 must be considered. The only mature *Eucalyptus* in the vicinity of H1 are all pure *E. pulchella* with the nearest *E. obliqua* being nearly 100 m away and the main population over 300 m from the hybrid. There is considerable overlap in flowering times between H1 and the surrounding *E. pulchella* population whereas there is virtually no overlap with *E. obliqua* (Fig. 5.10). The outcrossing rate of *E. obliqua* is estimated at 76% (Brown *et al.* 1975) but is unknown for either *E. pulchella* or H1. If it is assumed that inheritance of all characters is additive, H1 is an F_1 hybrid and all outcrossing is occurring with *E. pulchella*, then the displacement of the

mean of the likelihood index for the hybrid from the parental midpoint would be accounted for by a backcrossing rate of about 65%. Regardless of the rate, virtually all outcrossed seed from H1 will be backcrosses to *E. pulchella*.

The converse does not apply: pollen from H1 will comprise only a small percentage of the pollen environment of *E. pulchella* trees in this population. The *E. pulchella* trees used in the progeny trial were from the immediate vicinity of H1, and of the 129 surviving seedlings only two ($\approx 1.5\%$) could be distinguished as possible backcrosses to the putative hybrid. Many of the deviant *E. pulchella* seedlings shown in Fig. 5.6 appeared to be *E. pulchella* types but were recorded as exhibiting abnormal development or reduced vigour. However, one seedling showing normal growth was considered on the basis of several characters to have affinities toward *E. tenuiramis* (*Piperitae*). This individual probably originated from outcrossing to *E. tenuiramis*, the nearest occurrence of which is c.1.5 km from the study site.

Fitness parameters

Seed Output. Significant differences ($P < 0.001$) between mothers used in the progeny trial are noted for capsule, seed and chaff weight, with the putative hybrid (H1) lying intermediate and being significantly different from mothers of either species. There is no significant difference between mothers in the germination response as measured by GEI or for seed viability. However, the germination capacity (GC) of one *E. pulchella* mother (P2) is significantly ($P < 0.05$) lower than all other mothers. The mothers differ significantly ($P < 0.001$) in the number of viable seeds produced per open capsule, with H1 being lowest (Fig. 5.11). Within the pure species there appears to be a relationship between seed output and capsule size which accounts for the low seed output of one mother from both species (P1,02). However, this is not the case with H1 which would be expected to be intermediate. Relative to the total number of seed produced both the weight of chaff and the estimated number of particles comprising the chaff are significantly ($P < 0.001$) greater for H1 than for either *E. pulchella* or *E. obliqua* (Fig. 5.11). In the subgenus *Monocalyptus*, chaff comprises ovulodes and infertile ovules (Carr and Carr 1962; Boland *et al.* 1980), although the similarity in the shape of ovulodes and ovules does not allow their ready separation. The abnormally high chaff to seed content of H1, particularly when compared with the similarity of the pure species mothers in this respect, indicates the low seed output by H1 may be a consequence of either a greater gametic or zygotic abortion rate or failure of fertilization.

The data therefore suggest a marked reduction in the actual seed output per capsule relative to the potential output in H1 compared with the trees of either parental species. This reduction is accentuated by observations that suggest the actual number of capsules per unit biomass is also less in H1 and appears to be a result of a greater loss of flowers and young fruit than of reduced bud initiation. In terms of seed output, therefore, the purported hybrid (H1) appears to be at an evolutionary disadvantage when compared with the surrounding *E. pulchella* trees and the more distant *E. obliqua*, despite a vigorous vegetative appearance. However, this does not imply that segregates from the hybrid are necessarily at a similar disadvantage.

Seedling Survival and Vigour. No significant differences were observed in seedling mortality between the pure species or hybrid progenies after 7 or 11 weeks. However, the number of seedlings classified as runts differed significantly ($P < 0.001$) between progenies (*E. obliqua* 20%, hybrid 10.5%, *E. pulchella* 6.8%) due mainly to the large number of runts produced by one *E. obliqua* mother. Despite this, the actual number of normal seedlings classified as vigorous did not differ significantly between *E. obliqua* and *E. pulchella* whereas the progeny of H1 contained a significantly higher proportion (*E. obliqua* 55.4%, hybrid 79.1%, *E. pulchella* 62.9%; $P < 0.01$). This is also reflected in a comparison of seedling heights (Table 5.5), although the progeny of H1 is significantly different ($P < 0.001$) only from *E. pulchella*. A partition of the progeny of H1 into F_1 , backcross and parental morphological types indicated a trend within the progeny of H1 for seedlings indistinguishable from the pure species to be the most vigorous (Table 5.5). Furthermore, these seedlings tended to be more vigorous than their counterparts from the pure species, but again the difference was significant ($P < 0.001$) only for *E. pulchella*. Within the *E. pulchella* seedlings, vigour tended to decrease with increasing distance from the species' centroid. It is difficult to ascertain whether this represents a true selective effect against genetic deviants or a pleiotropic effect of reduced vigour *per se* on morphological expression.

5.4 Discussion

The intermediacy and marked genetic segregation in the progeny of the intermediate tree (H1) strongly suggest that it has originated from recent hybridization (possibly F_1) between the two taxa *E. obliqua* and *E. pulchella*. This study constitutes the first substantiated report of hybridization between the ubiquitous species *E. obliqua* and any of the Tasmanian endemic *Piperitae* species.

The rarity of this hybrid combination and indeed that of *E. obliqua* with other Tasmanian species from the series *Piperitae* appears to be partly due to differences in flowering time coupled with varying degrees of spatial and ecological separation. The peak flowering period of *E. obliqua* shows little overlap with that of any of the *Piperitae* species, whereas within the *Piperitae* there is considerable overlap between species (Fig. 5.10). This difference appears indicative of a general response of the *Obliquae* species to flower later in the season than the *Piperitae* species and may explain, at least partly, the lack of natural hybridization between the series (Fig. 5.12). Ecological considerations appear to reinforce these differences, since the *Piperitae* species least separated from *E. obliqua* in peak flowering period (e.g. *E. risdonii* and *E. coccifera*) are those least likely to occur in association with *E. obliqua*. *E. obliqua* most commonly forms ecotones with either *E. amygdalina* or *E. pulchella*, both of which have usually finished flowering before the local *E. obliqua* population commences. However, such barriers may occasionally be broken down by long-distance pollen migration or by seasonal and altitudinal variation in the flowering period which has been noted to occur in *Eucalyptus* species (e.g. Pryor 1956, 1976; van Loon 1966; Ashton 1975, 1981a; Griffin 1980). Nevertheless, hybridization of *E. pulchella* and *E. obliqua* may be further hindered by differences in flower size (Pryor 1956) as well as postzygotic barriers such as the reduced reproductive output of the proposed hybrid (Fig. 5.11). The latter could be explained in terms of genetic breakdown in the F_2 , although it is necessary to distinguish this effect from other factors such as differential pollination and inbreeding.

Although a degree of recombination between morphological characters occurs in hybrid populations and hybrid progenies of *Eucalyptus* (Pryor 1952, 1955a, 1957b, 1958; Ashton 1958), there is a tendency for the coherence of parental combinations (Pryor 1957b; Hartley 1965; Fig. 5.9). The reasons for this coherence include linkage, inviability of extreme recombinants, pleiotropy, allometric relationships and backcrossing (e.g. to *E. pulchella* in this study) (Anderson 1939; Dempster 1949; Clausen and Hiesey 1960; Goodman 1966). The present results do not allow these alternatives to be distinguished but several probably apply to some extent. Coherence, when combined with centripetal selective processes favouring parental types in later stages of the life cycle (Pryor 1951a, 1956, 1976; Hartley 1965; Rogers and Westman 1979), is probably important in maintaining specific identity in *Eucalyptus*. Although parental type segregates were the most vigorous within the present hybrid progeny, the fitness of these hybrid products needs to be assessed under both differing selective and competitive regimes.

Evolutionary Implications

The distribution of single *Eucalyptus* species is frequently discontinuous, with populations being confined to closely circumscribed stands that occasionally exhibit major disjunctions (Pryor and Johnson 1971). The mechanisms involved in the evolution of this distribution pattern are similar to those relating to the origin of the phantom hybrid populations discussed by Pryor (1951b, 1955b), Parsons and Kirkpatrick (1972) and Kirkpatrick *et al.* (1973). Hypotheses pertaining to the origin of both phenomena include: (1) independent parallel evolution; (2) relic distribution following range fragmentation or restriction; (3) seed migration; (4) pollen migration. The last two alternatives imply active genetic invasion, often across considerable expanse of unfavourable habitat, and establishment on a site already occupied by another vegetation type or *Eucalyptus* species (albeit often at the expense of a considerable genetic load). It is proposed that the study site at Snug Falls simulates conditions expected during the initial phase of invasion by long-distance pollen migration. Several cases involving sporadic intermediate phenotypes well within the range of one species have been discussed by Pryor (1951b, 1955b, 1958), Pryor *et al.* (1956) and Ashton and Williams (1973), although greater disjunctions of the putative parental species are involved and the origin of intermediates less obvious than in the present example.

In the present case, it is suggested that the intermediate tree (H1) is an F_1 hybrid having arisen by recent migration of *E. obliqua* pollen into the range of *E. pulchella*. There is evidence of a second generation of hybrid saplings that are also localized and concentrated in a shallow gully on an otherwise dry, north-facing slope dominated by *E. pulchella*. The gully is not so dry as typical *E. pulchella* habitats and tends towards an *E. obliqua* habitat. These hybrid saplings may represent the progenitors of a hybrid swarm, heralding an invasion of a favourable site within the range of *E. pulchella* by *E. obliqua* genes. This is supported by the predominance of intermediate or *E. obliqua*-tending types amongst the natural hybrid saplings in the bottom of the gully, despite a bias toward *E. pulchella* types on the drier slope of the gully (Fig. 5.1) and in the progeny of the intermediate tree due to backcrossing (Table 5.5).

This study lends credence to the hypothesis that species could invade suitable sites within the range of another potentially interbreeding species by long-distance pollen migration, followed by back selection to the coadapted gene combinations of the pollen parent from a segregating hybrid swarm. Where the genetic differentiation between species is relatively small, the probability of deriving the original gene combinations of the

pollen species in the F_2 generation would be fairly high. Nevertheless, even where the phylogenetic distance between the species is relatively large, as in this example, the cohesive processes discussed previously will tend to increase the probability of parental gene combinations being derived by segregation. This concept is exemplified by the fact that 5% of the progeny from the intermediate tree possessed phenotypes similar to the purported pollen parent *E. obliqua*.

However, this is clearly only one possible outcome of long-distance pollen migration. Extinction is the most likely result, particularly where the favourable habitat is of limited size and subject to genetic swamping by pollen and seed from the surrounding species. Another alternative is the selection and stabilization of a hybrid product if the habitat is suited to a combination of the parental characteristics. Which of these alternatives prevails will depend on the size and stability of the selection coefficients favouring the invading genes or gene combinations, as well as chance events. In view of the barriers to interbreeding between *E. obliqua* and *E. pulchella*, this mechanism of migration may not play a major role in the dynamic interaction between these two species. However, there is evidence that it is a potentially effective mechanism of migration which should be given serious consideration, especially where reproductive isolation is incomplete and seed migration limited.

This is investigated further in the following chapters in a study of the genetic interaction between *E. risdonii* and *E. amygdalina*. These species belong to the same series (*Piperitae*) and hybridization between them is much more prevalent than in the present case (see Fig. 5.12).

Table 5.1 Untransformed adult character means and standard deviations for *E. obliqua* and *E. pulchella* samples and data for individual hybrid trees.

Any transformation applied to these characters is indicated as well as the *F* ratio for the difference between species based on the transformed data [$F(1,18)_{0.001}=15.4$]. Numbers correspond to the characters indicated in Fig. 5.2.

	<i>E. pulchella</i> (n=10)		H1	H2	<i>E. obliqua</i> (n=10)		<i>F</i> ratio	Trans- formation
	Mean	s.d.			Mean	s.d.		
Leaf dimensions (cm)								
1 Lamina length	10.02	1.316	14.92	12.73	14.42	1.093	62.0	log(1+)
2 Max. lamina width	0.66	0.073	1.42	1.57	3.50	0.230	1587.3	log(1+)
3 Length to widest point (lwp)	5.79	1.136	6.67	4.72	4.41	0.409	16.6	log(1+)
4 lwp asymmetry	0.07	0.041	0.49	0.42	0.75	0.080	110.3	✓
5 Curvature	0.83	0.247	1.37	0.96	1.71	0.254	56.4	log(1+)
6 Basal asymmetry	0.02	0.015	0.12	0.19	0.54	0.166	219.0	✓
7 Petiole length	0.60	0.057	1.22	1.22	1.81	0.267	394.2	log(1+)
Fruit dimensions (cm)								
8 Peduncle length	0.61	0.212	0.73	0.95	1.17	0.162	36.2	log
9 Pedicel length	0.15	0.037	0.43	0.14	0.34	0.133	26.7	log
10 Capsule length	0.58	0.049	0.75	0.79	0.92	0.109	100.0	log
11 Max. capsule width	0.56	0.028	0.68	0.70	0.78	0.093	63.7	log
12 Max. capsule width - rim width	0.05	0.020	0.10	0.10	0.15	0.040	66.7	log(1+)
13 Disc level	0.02	0.020	0.08	0.08	0.14	0.041	57.5	log(1+)
Capsule weight (mg)	68	10.2	127	154	244	74.6	55.1	

Table 5.2 Description of characters scored from seedlings

The leaf dimensions measured are the same as in Fig. 5.2. Characters used in the seedling principal component analysis (*) and likelihood analysis (+) are indicated as well as any transformation (log, $\log(1+x)$, $\sqrt{}$, \arcsin) applied.

Character defined	Description
<i>Quantitative</i>	
1 Height (Ht)	Seedling height (cm)
2 No. of expanded leaf pairs (NE)	Number of leaf pairs expanded (cotyledons = 0) (*, +, log)
3 Diameter	Stem diameter (cm) measured at the cotyledonary node, at right angles to the cotyledons
4 Leaf angle	Angle ($^{\circ}$) subtended between a single 5th node leaf and the stem (*, +)
5 ^A Proportion of laterals	Number of laterals (>1 NE) developed as a proportion of the potential number, i.e. $X/2 \times NE$ (ratio)
6 ^A Relative length of longest lateral	Length of longest lateral relative to total seedling height, i.e. X/Ht (ratio)
7 ^A Relative position of longest lateral	Relative nodal position of longest lateral, i.e. X/NE ; 0 if no laterals (ratio)
8 Lamina thickness	Lamina thickness ($mm \times 10^2$), measured with a spring-loaded micrometer (*, +, log)
9 Internode	Internode length (cm). When leaf pairs were alternate, taken from top leaf of lower leaf of relevant node (*, +, $\log(1+x)$)
10 Intranode	Intranode length (cm). Distance between points of attachment of paired leaves (opposite leaves=0) (*, +, $\log(1+x)$)
<i>Ordered multistate</i>	
11 Stem verrucae	Density of verrucae (oil glands) on seedling stem (1-5, <i>E. pulchella</i> =1, highest density) (*)
12 Oil glands	Density of oil glands on 5th leaf (1-5, <i>E. pulchella</i> =1, lowest density) (*)

^AUsing principal component analysis (total variance-covariance) these standardized characters were combined into a single compound character that was a comprehensive descriptor of seedling apical dominance (*, +).

Table 5.3 Analysis of variance for species (*E. pulchella* vs. *E. obliqua*) and ontogenetic (fifth vs. seventh node) effects on character variation (x $P < 0.05$; xx $P < 0.01$; xxx $P < 0.001$).

	Species Effect	Ontogenetic Effect	Sp. x Ont. Interaction	Species versus [Ont. + (Sp. x Ont.)] Effects	Increase in discrimination between species with node
	F(1,304)	F(1,304)	F(1,304)	F(1,2)	F(1,1)
lamina l. (1)	2544.7 xxx	3.3	0	36.6 x	1.1
lamina w. (2)	6362.6 xxx	3.2	10.8 xxx	452.3 xx	1.4
lwp (3)	276.1 xxx	17.6 xxx	5.6 x	11.9	1.8
lwpasy (4)	115.9 xxx	22.3 xxx	12.5 xxx	3.3	3.9
curvature (5)	72.9 xxx	18.8 xxx	10.1 xx	2.5	4.3
basal asy. (6)	996.2 xxx	206.3 xxx	236.2 xxx	2.3	8.4
petiole l. (7)	6579.4 xxx	106.0 xxx	123.3 xxx	28.7 x	1.7
lamina thick.	89.1 xxx	23.2 xxx	79.9 xxx	0.9	-26.0
intra.	3540.6 xxx	69.3 xxx	34.0 xxx	34.3 x	1.5
inter.	1489.1 xxx	110.7 xxx	0	13.5	1.1

Table 5.4 Maternal means and variances from the PCA derived from the total standardised data matrix (see Fig. 5.2).

Mother	n	Mean on PC 1	Variance on PC 1	Total variance over all axes	% of the Maternal Variance on PC 1	Ratio of the variances along the two most variable axes
<i>E. obliqua</i>	1 28	-3.7	0.27	6.79	4.07	1.1
	2 41	-3.5	0.57	7.37	7.7	2.2
	3 37	-3.5	0.30	6.47	4.6	1.0
H ₁	77	-0.1	2.12	8.48	25.0	2.3
<i>E. pulchella</i>	1 41	2.6	0.88	6.88	12.8	1.3
	2 46	3.2	0.46	4.57	10.0	1.1
	3 42	3.0	0.54	6.14	8.8	1.1

Table 5.5 Means and s.e. for seedling height (11 weeks) and the number (n) and percentage (%) of seedlings in each phenotypic class from either species and the proposed hybrid.

The progeny from the proposed hybrid was partitioned into parental, F_1 and backcross morphological classes based on the significance of the generalized distance and the likelihood index scores. Parental morphological classes comprise hybrid individuals statistically indistinguishable from the parental centroids. The class partitioning of *E. pulchella* seedlings was based on the significance of the generalized distance of an individual from the *E. pulchella* centroid. Significantly different from the *E. pulchella* centroid at * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. n.s., not significantly different.

	Maternal Type	Progeny type	Seedling ht (cm)		n	%
			Mean	s.e.		
1	<i>E. obliqua</i>	Grand	40.87	1.16	106	
2	Hybrid (H1)	Grand	43.15	0.29	77	
	Morphological class	<i>E. obliqua</i>	47.6	2.82	4	5.2
		Backcross- <i>obliqua</i>	42.6	2.91	11	14.3
		F_1 (intermediate)	42.5	1.81	24	31.2
		Backcross- <i>pulchella</i>	42.4	1.78	28	36.4
		<i>E. pulchella</i>	45.5	1.46	10	13.0
3	<i>E. pulchella</i>	Grand	36.9	0.98	129	
	Morphological class	n.s.	38.94	0.968	102	79.1
		*	32.94	3.46	9	7.0
		**	30.25	1.79	8	6.2
		***	25.1	5.64	10	7.8

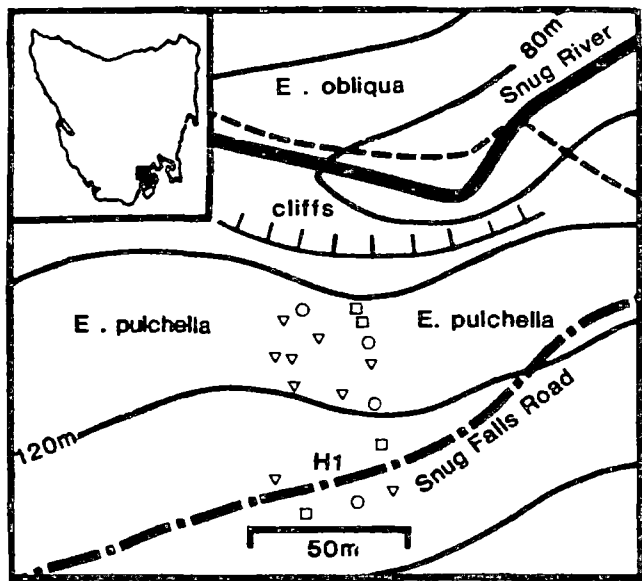


Fig. 5.1. Location of the study area in SE Tasmania (lat. 43°4', long. 147°0'14"). The location of the putative *E. obliqua* \times *E. pulchella* hybrid (H1) is indicated as well as the distribution within the forest of hybrid saplings classified as intermediates (○) or tending toward either *E. obliqua* (□) or *E. pulchella* (Δ) but different from the pure species.

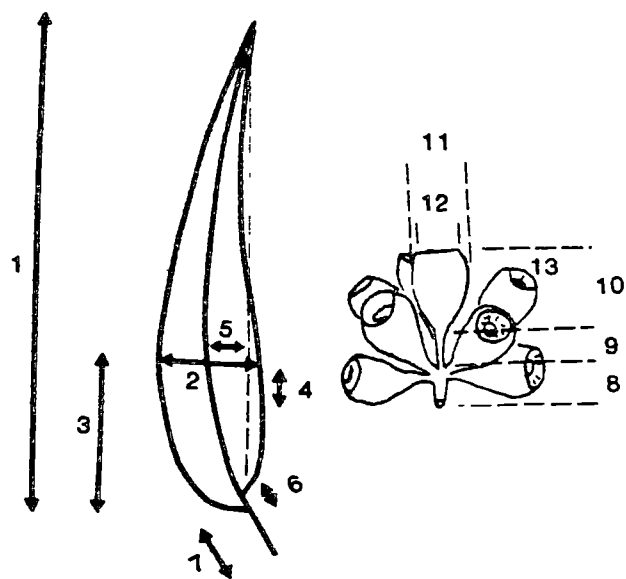


Fig. 5.2. Leaf and fruit measurements taken for the study of adult morphology. Numbers correspond to characters listed in Table 5.1.

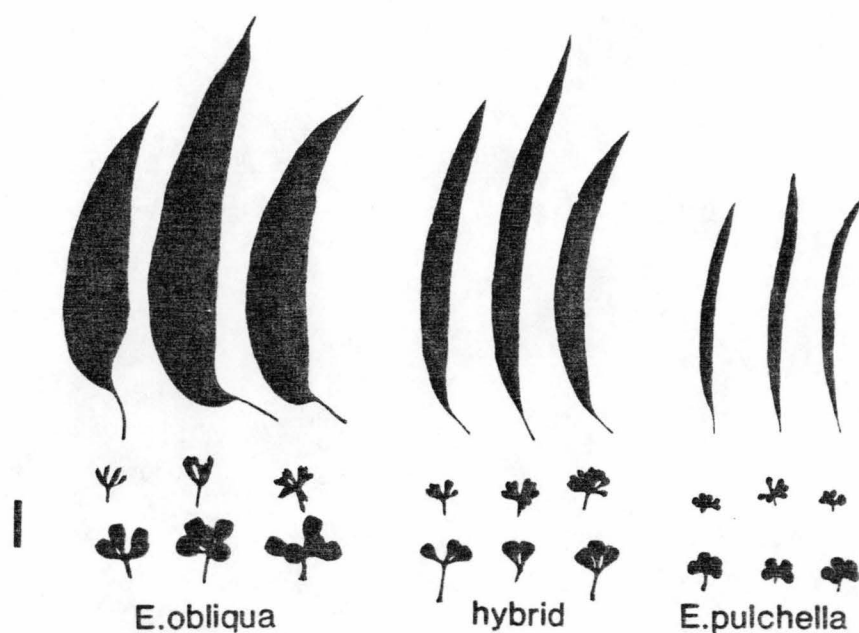


Fig. 5.3. Representative leaf, bud and fruit samples from three *E. obliqua* and *E. pulchella* individuals as well as three samples from the putative hybrid H1. Scale: 2 cm.

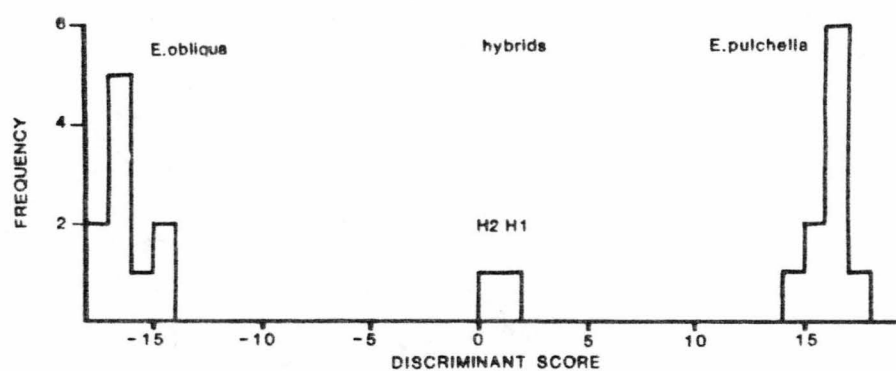


Fig. 5.4. Frequency distribution of scores along the hybrid index derived from discriminant analysis of adult morphological characters.

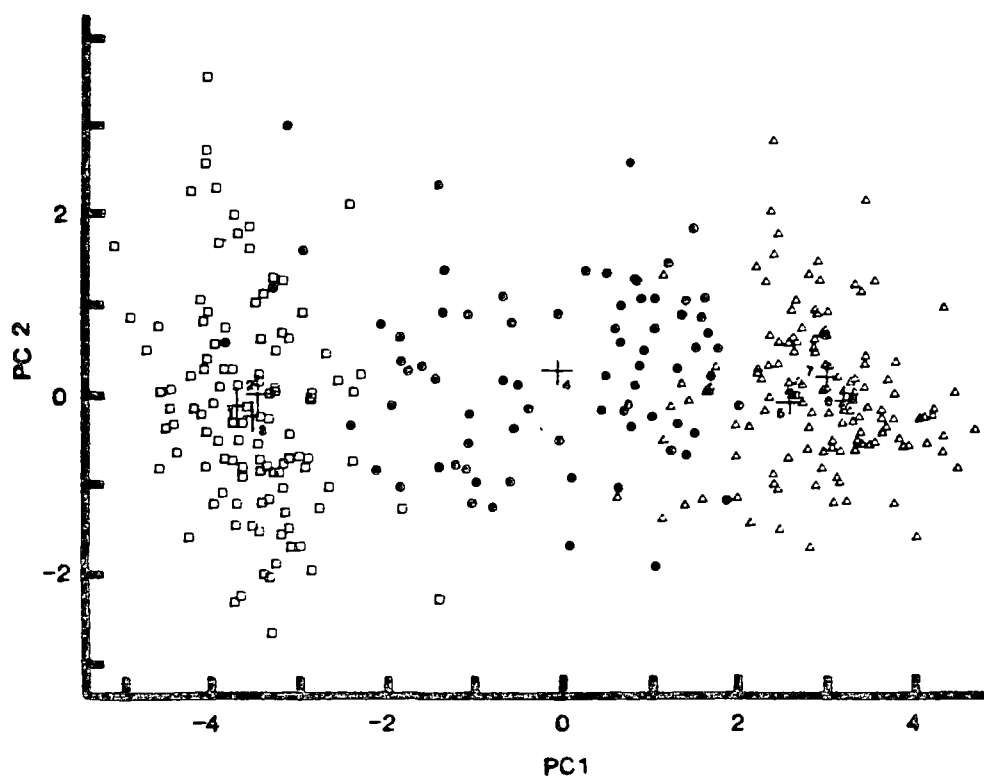


Fig. 5.5. Principal component analysis of seedlings of *E. obliqua* (\square), *E. pulchella* (Δ) and the putative hybrid (\bullet). Means with s.e. bars are shown for individual progenies of *E. obliqua* (1, 2, 3), *E. pulchella* (5, 6, 7) and the hybrid (4).

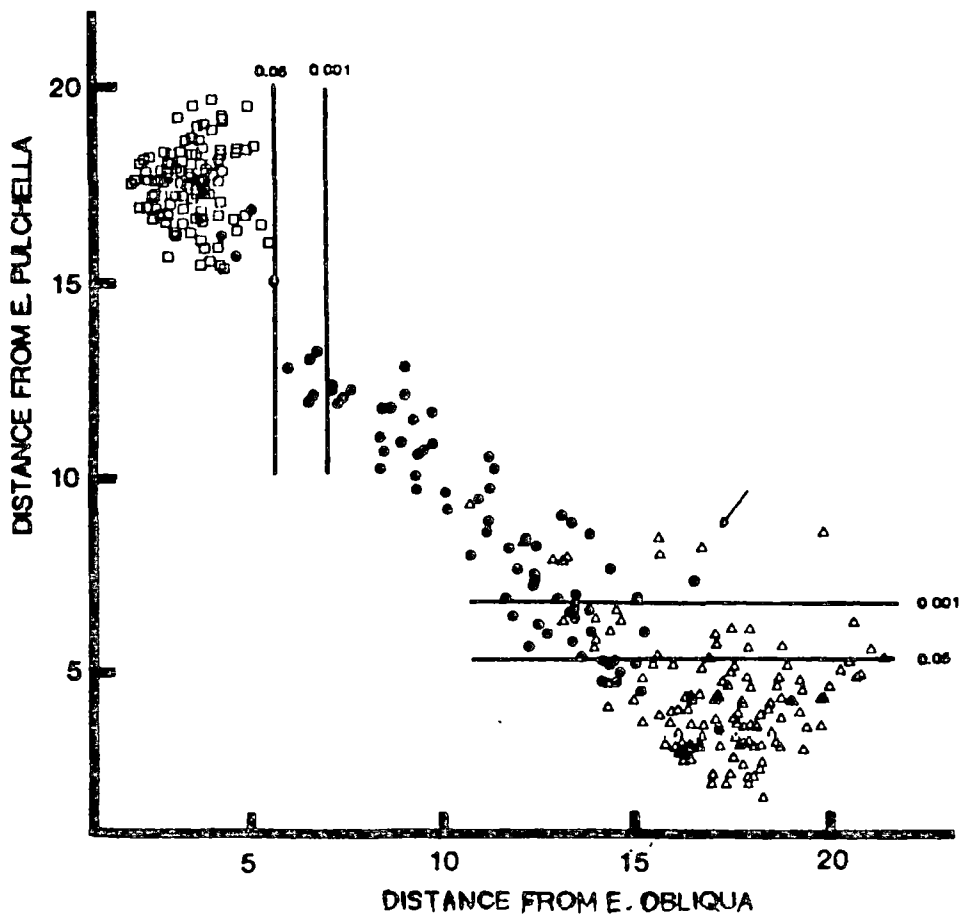


Fig. 5.6. Ordination of seedlings of *E. obliqua* (\square), *E. pulchella* (Δ) and the putative hybrid (\bullet) based on the generalized distance of individuals from *E. pulchella* and *E. obliqua* centroids. Confidence limits based on the significance of the generalized distance are indicated. An abnormal seedling considered to be a *E. tenuiramis* \times *E. pulchella* hybrid is indicated by the arrow.

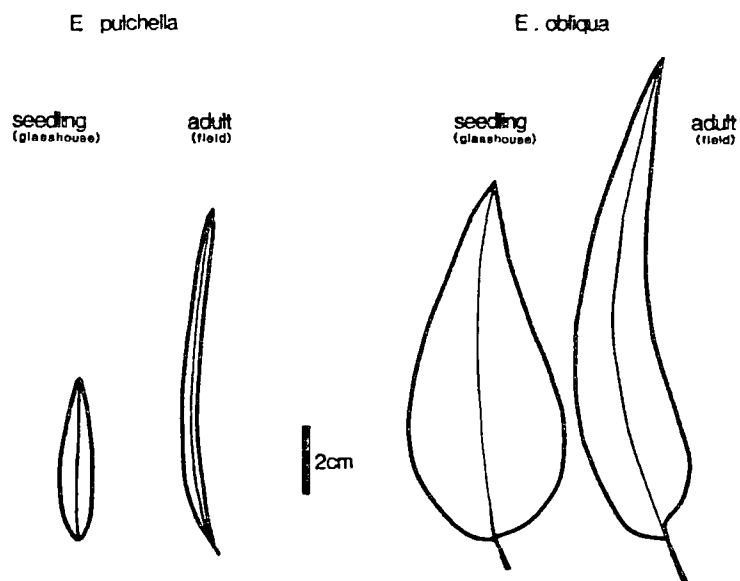


Fig. 5.7. Ontogenetic variation in leaf shape.

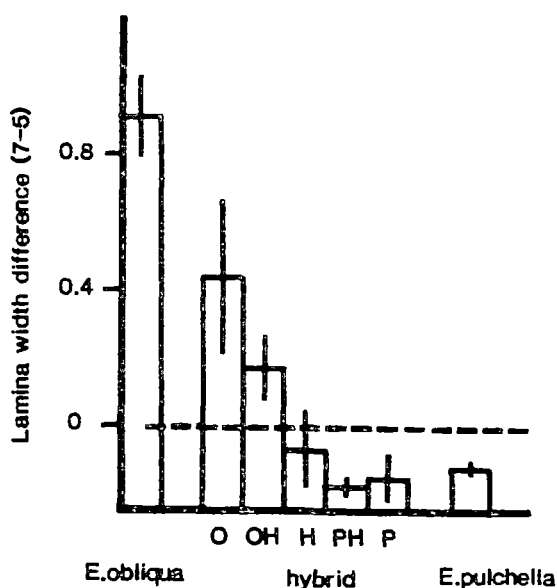


Fig. 5.8. The mean difference (\pm SE) in lamina width between the fifth and seventh nodes in pure species and hybrid progeny. The hybrid progeny is partitioned into morphological classes based on the leaf shape at the seventh node as in Table 5.5.

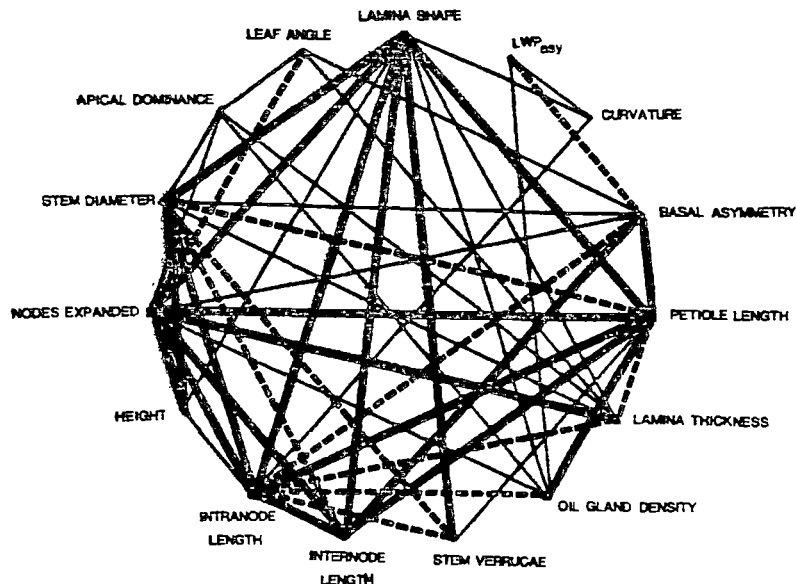


Fig. 5.9. The significant correlation coefficients between seedling characters in the hybrid progeny (d.f. 75). Leaf and node characters are from the fifth node. Lamina shape is derived from principal component analysis (total variance-covariance) of the three lamina dimensions (lamina length, lamina width and length to widest point (lwp) and accounts for 93% of the variation in these variables. Solid line, $P < 0.05$. Dashed line, $P < 0.01$. Thick, solid line, $P < 0.001$.

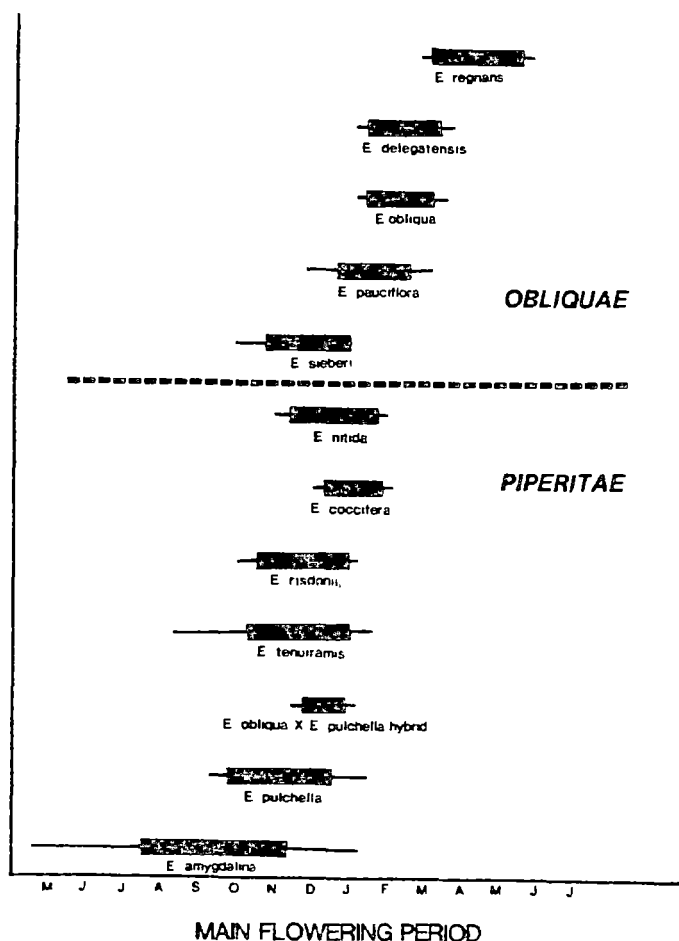


Fig. 5.10. Flowering periods of the Tasmanian *Monocalyptus* species (excl. *E. radiata*). Data represent a generalization of the peak flowering period of typical populations and incorporate field, herbarium and published data. In particular, the flowering periods of *E. obliqua* and most of the *Piperitae* species were assessed over the period 1980-82 during field work in southern Tasmania.

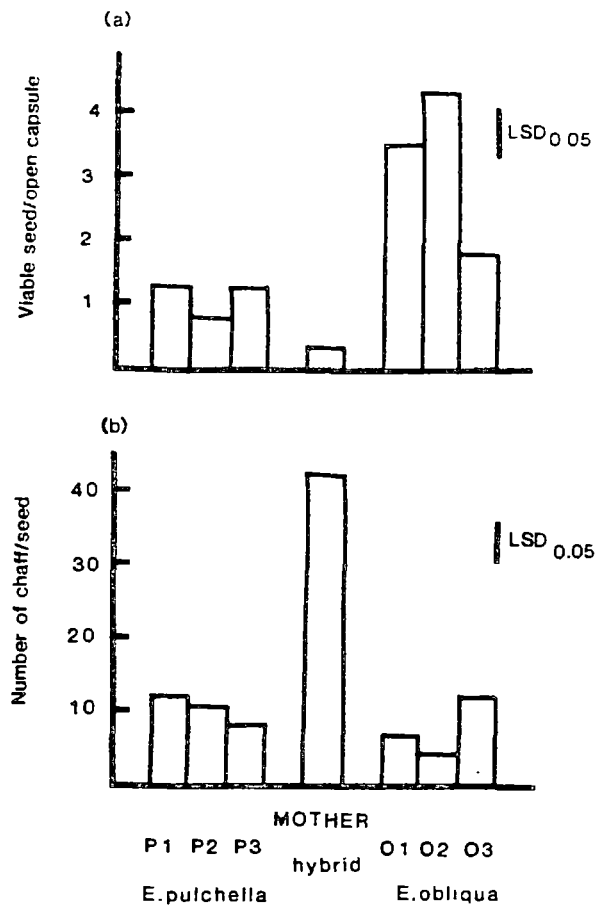


Fig. 5.11. Seed output parameters. Means of each mother for (a) total number of viable seed per open capsule, (b) estimated number of chaff particles produced per seed.

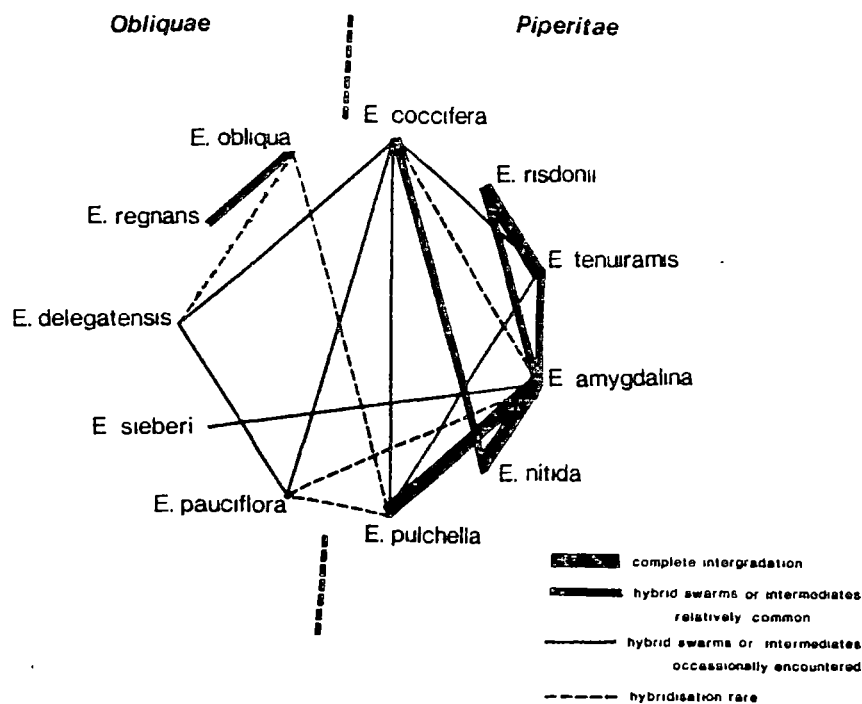


Fig. 5.12. The degree of genetic continuity amongst the Tasmanian *Monocalyptus* species (excl. *E. radiata*). The data are based on extensive field observations as well as progeny testing and published reports.

CHAPTER 6

The dynamics of hybridization between *E. risdonii* and *E. amygdalina*

I. Genetic analysis of a hybrid swarm

6.1 Introduction

The role of hybridization in evolution has been the subject of much discussion (e.g. Epling 1947a,b; Anderson 1949; Anderson and Stebbins 1954; Stebbins 1950, 1959, 1969; Grant 1971; Rollins 1954; Hieser 1949, 1973; Rattenbury 1962; Wagner 1970; Levin 1969, 1970c, 1978a; Raven 1980). The significance of speciation by allopolyploidy is well documented (see Grant 1971), yet as noted by Levin (1978a) the full importance of hybridization at the diploid level is a matter of conjecture. However, most authors agree that hybridization may be an important evolutionary phenomenon, providing populations with enhanced evolutionary flexibility. Hybridization may extend a species' gene pool and hence ecological range by introgression (e.g. Anderson 1949; Harland and de Wet 1963) as well as releasing novel combinations of parental genes or even transgressive gene combinations (e.g. Ehrendorfer 1959; Lewentin and Birch 1966; Stebbins 1969) to be sifted by natural selection. The stabilization of diploid hybrid derivatives may account for the evolution of new lineages and many possible examples are found in the literature (see Anderson and Stebbins 1954; Grant 1971; Gottlieb 1972 and Levin 1978a). However, Gottlieb (1972) notes that it is more difficult to recognize stabilized hybrid entities at the diploid level and the literature contains only a small number of examples relative to examples of allopolyploidy.

The genetic variability released following hybridization may be of little consequence in stable habitats (Stebbins 1969), and even detrimental. In such cases selection may operate to strengthen reproductive isolation and prevent gametic wastage (e.g. Wallace Effect; Grant 1966). Nevertheless, Anderson and Stebbins (1954) argue that the evolutionary significance of hybridization accrues from the release of such variation in times of environmental change. They postulate ^{that} rapid evolution and bursts of novel diversification at various times in the past ~~were~~ the result of hybridization and followed geological, climatic or floristic shifts. Similarly, Epling (1947a,b) had previously suggested that there may be actual selection for the ability to hybridize in changing environments. This concept is developed by Rattenbury (1962) who argues that in an insular forest flora such as New Zealand's, survival of sequential climatic perturbation may

have depended on phases of hybridization, with selection favouring groups which remain interfertile and polymorphic. In addition to the release of variability, the present study suggests interspecific hybridization may be of significance as a means of actually dispersing genes or coadapted gene combinations where the adaptive response is limited by restricted seed dispersal.

While sceptical of many cases of purported introgression, Hieser (1973) suggests that most introgression that does occur appears to be highly localized and to extend only a short distance from the area of active hybridization. Similarly, there is a general trend for active hybridization (i.e. F_1 and hybrid swarms) to be confined to ecotonal areas (see Hopper 1978a and references cited therein). The main hypotheses evoked to explain this distribution include limited physiological tolerance, competitive exclusion and limited gene dispersal. In the latter case, it is proposed that limitations on pollen and seed dispersal would tend to confine hybrids to areas where the parental species grow in close proximity (Epling 1947a; Levin and Kerster 1974; Hopper 1978a,b and Levin 1978b) and this appears the simplest and most likely explanation in many examples.

In *Eucalyptus*, hybridization between species from the same subgenera is relatively common (e.g. Brett 1938; Pryor 1950, 1953, 1959a, 1976; Jackson 1958; Pryor and Johnson 1971, 1981) and, typically, hybrids or hybrid swarms are most frequently encountered in ecotonal areas in association with both parental species (Pryor 1959a, 1976). However, sporadic hybrids or at least intermediate phenotypes are occasionally found some distance from one parent (e.g. Pryor 1951b, 1955b, 1958; Ashton and Williams 1973; Ashton 1981a; Chapter 5). In addition, intermediate (supposed hybrid) populations have been reported isolated from one or occasionally both purported parents and are often interpreted as representing selectively stabilized hybrid entities (termed 'phantom hybrids') (e.g. Pryor 1951b, 1955b, 1959b, 1962; Pryor and Johnson 1971; Parsons and Kirkpatrick 1972; Kirkpatrick *et al.* 1973). Similar phenomena have been reported in other forest tree genera such as *Quercus* (e.g. Tucker and Muller 1956; Forde and Faris 1962; Tucker 1970) and *Pinus* (e.g. Mirov 1967). These populations are often interpreted as the genetic remnants of former more extensive distributions of one or other species, although several authors (e.g. Forde and Faris 1962; Parsons and Kirkpatrick 1972), discuss alternative hypotheses which include remnants of ancestral clines between the two species, long distance dispersal or parallel adaptation and primary differentiation from within a single species' gene pool. However, unless the genesis of the population is observed prior

to stabilization, it is virtually impossible to distinguish between alternatives unless secondary circumstantial biogeographical or palaeontological evidence is available. The problems of testing the hypothesis of hybrid origin and the level of confidence to be placed upon such a judgement are discussed by Gottlieb (1972) and extend to the more general case of distinguishing examples of primary and secondary intergradation from the genetic structure of populations (e.g. Anderson 1949, 1951; Barber and Jackson 1957; Hieser 1973; Endler 1977; Chapter 4).

Studies in natural hybridization or introgression frequently involve a static descriptive approach, without consideration of alternative interpretations (see Gottlieb 1972; Hieser 1973) or the dynamics of the hybridization process. Levin (1978a) considers that major advances in understanding the process will come from experimental analysis of the biology of hybrids and an understanding of gene dispersal. However, plant hybridization studies involving this dynamic approach are few (e.g. Levin 1973; Hopper 1977b and c, 1978 a and b; Drake 1980, 1981a and b). In the present work hybridization between *E. risdonii* and *E. amygdalina* is examined by integrating studies of genetic structure, demography, fitness, regeneration and seedling recruitment. In the foregoing discussion "hybridization" is used in the sense of Stebbins (1959), that is, as "...the crossing between individuals belonging to separate populations which have different adaptive norms," with interspecific hybridization differing only quantitatively, not qualitatively, from hybridization involving lower taxonomic units. This is in the spirit of an ecological species concept of adaptive modes generally applied to temperate forest tree genera (e.g. Burger 1975; van Valen 1976).

E. risdonii and *E. amygdalina* exhibit marked morphological differentiation, yet are closely related being grouped by Pryor and Johnson (1971) in the subseries *Amygdalinae* (subgenus *Monocalyptus*: series *Piperitae*) but in different superspecies. Both species are endemic to Tasmania, but while *E. amygdalina* exhibits both a broad geographic (Fig. 6.1) and edaphic range, *E. risdonii* is of localized distribution and is considered a rare and endangered species (Pryor 1981). It is distributed as a series of small disjunct populations in the dry mudstone hills to the north of the Derwent River near Hobart (Fig. 6.1 and 6.2) and is most closely related to a more widespread species *E. tenuiramis* (Fig. 6.1; Pryor and Johnson 1971;

Sharma 1974). A major phenotypic cline exists between *E. risdonii* and *E. tenuiramis* (Hall and Gray 1975; Potts, unpubl.) which, in addition to other characters, involves the retention of the 'juvenile' foliage type by *E. risdonii*. This cline is through a series of disjunct populations and appears to parallel a water availability gradient and to be an extension of broader clines within *E. tenuiramis*. Brett (1938) suggests *E. tenuiramis* (syn. *E. tasmanica*) may have evolved from *E. risdonii* by the stabilization of hybrid swarms developed with *E. amygdalina*. However, in view of both the current localized distribution of *E. risdonii* and the rarity of species retaining the 'juvenile' foliage in the subgenus *Monocalyptus* (Pryor 1981), it is ~~more than~~ likely *E. risdonii* is a specialized neotenous form of *E. tenuiramis*.

Throughout its entire geographical range, *E. risdonii* is directly associated with *E. amygdalina*. Its distribution is patchy, with the small disjunct populations forming a mosaic within a more or less continuous, widespread population of *E. amygdalina*. *E. risdonii* replaces *E. amygdalina* on apparently drier sites, particularly on the more extreme, dry, north to north-westerly facing aspects (Figs. 6.2 and 6.3. Hybrids between *E. amygdalina* and *E. risdonii* have been previously reported (Brett 1938; Barber 1955; Curtis 1956 and Pryor and Johnson 1971) and are frequently found as isolated individuals scattered along boundaries between the two species. However, in some areas hybrids are widespread and hybrid swarms, or at least local patches of high phenotypic diversity, are encountered. These are not confined to ecotonal areas but are occasionally found some distance from the boundary between the two species.

One such area is the Government Hills at Risdon (Figs. 6.3 and 6.4). In the present study, the genetic and competitive interaction of *E. risdonii* and *E. amygdalina* is examined in this area, concentrating on one of the largest populations of *E. risdonii* in these hills in the area confined within the bounds of the Risdon flora reserve (Fig. 6.3). In this chapter, the genetic structure of a hybrid swarm is analyzed in terms of morphological variation of adults and their progenies, with a view to confirming the suspected hybrid origin of intermediate phenotypes. Barriers to hybridization between these two species are examined in a comparison of seed output parameters of parental and hybrid phenotypes, as well as the vigour of progenies grown under glasshouse and plantation situations. In addition, pre-zygotic barriers to hybridization are investigated in a study of the temporal overlap in flowering of both species and their hybrids from a range of sites.

The genetic analysis of the hybrid swarm was commenced in mid-1979, but the study area was burnt by wildfire in February, 1980. Although genetic analysis of other pertinent sites could not be undertaken, the fire offered a unique opportunity to observe regeneration of the population. The competitive interaction of the two species and hybrids is examined in Chapter 7 by a comparison of mortality, vegetative regeneration, reproductive output and seedling recruitment following the wildfire. These results are used to obtain estimates of the relative fitness of each phenotypic class in boundary regions. The data presented indicate a marked fitness differential at the species boundary and suggest *E. risdonii* should be expanding its range. This is explored further in a demographic study of boundary and single species stands. In addition, the dispersal potential of *E. risdonii* is discussed in Chapter 8, and data are presented which suggest that hybridization may contribute significantly to the flow of *E. risdonii* genes into the range of *E. amygdalina* and possibly to the invasion by *E. risdonii* of suitable sites within the range of *E. amygdalina*.

6.2 Study Sites

The study area is in the Government Hills within the East Risdon Flora Reserve which was established for the protection of a small stand, comprising only a few trees, of a rare *Eucalyptus* species *E. morrisbyi*. This area was the subject of a general ecological study by Kirkpatrick and Nunez (1980) and Nunez (1980) has modelled the solar net radiation input for the same area. Detailed ecological and climatic descriptions of the area are given by these authors.

The present study concentrates on the structure and dynamics of a hybrid swarm developed at the boundary between *E. risdonii* and *E. amygdalina* on the main ridge (Fig. 6.3; sites A, B). Other sites studied include a boundary site on the north slope (Fig. 6.3; site C), well away from the hybrid swarm where hybrids are less diverse and less frequent as well as a range of small patches of abnormal (i.e. non-*E. amygdalina*) phenotypes within the *E. amygdalina* dominated areas along the north-western spur of the main ridge (Fig. 6.3). Hybrids are found scattered all along the boundary of this stand of *E. risdonii* but they are least common along the northern gully boundary and achieve greatest density and complexity in a fairly localized area along the main ridge. The occurrence of sporadic hybrids and occasional hybrid swarms is a typical feature of most *E. risdonii*/*E. amygdalina* stand boundaries and in this respect the area examined is not atypical.

The Government Hills are near Risdon Cove, the first area to be settled by Europeans in Tasmania, and as noted by Kirkpatrick and Nunez (1980) have been subjected to over 170 years of disturbance by European man. The main source of disturbance has been associated with clearing, firewood collection, vehicle tracks and transmission lines. In addition, these hills are located directly across the Derwent River from the Electrolytic Zinc Company Works which prior to 1940 may have affected the area by atmospheric pollution. The actual study site, however, is one of the least disturbed areas in these hills. A rough vehicular track runs along the ridge past the main hybrid swarm but on steeper slopes little visual evidence of disturbance is apparent. The study area is frequently burnt and there has possibly been an increase in the frequency of fires over the last century. Nevertheless, regular firing was probably also maintained prior to European settlement by the Aborigines renowned for their pyric habits (e.g. Jones 1969; Macphail and Jackson 1978). Relics (i.e. middens) of Aboriginal campsites are found throughout the Government Hills.

The study area supports low (3-4 m) mallee type scrub of *E. viminalis* (subgenera *Symphyomyrtus*), *E. amygdalina* and *E. risdonii* on the north slope whereas the more moist southern slopes support taller (≈ 15 m) open *E. amygdalina* forest with *E. viminalis* and *E. globulus* (subgenera *Symphyomyrtus*) in varying proportions. *E. viminalis* was encountered in quadrats and is widely distributed on both northern and southern aspects, but achieves greatest relative cover on the southern slopes. It is most commonly associated with *E. amygdalina*, with which it could be considered to form a mixed stand (*sensu* Pryor 1976). *E. viminalis* may extend into the range of *E. risdonii* but is rare in central regions of *E. risdonii* stands. While hybridization and intergradation is common between most of the Tasmanian *Piperitae* species (Brett 1938; Curtis 1956; Davidson *et al.* 1983), *E. amygdalina* and *E. risdonii* are the only species representative of the *Monocalyptus* breeding group in the Government Hills. The area was burnt by wildfire in February 1980 and was previously last burnt in 1960/1961, with the majority of stems on the northern slope representing twenty year old lignotuberous regeneration.

6.3 Main Selective Forces

Soil water availability as mediated by soil and topographic circumstances is suggested to be the major determinant of species distribution in the study area (Kirkpatrick and Nunez 1980). The distribution of

E. risdonii, for example, was found to be highly correlated with theoretical estimates of both available moisture (-) and the annual net incident radiation (+). This species in general is dominant on extremely dry, steep, north to west facing slopes on shallow soils developed on Permian mudstone (Ferntree Group). *E. amygdalina* is the more mesic species and when parapatric with *E. risdonii* dominates the south facing slopes but extends onto the drier aspects (Edwards 1969; Hamilton 1971; Hogg and Kirkpatrick 1974; Hall and Gray 1975). However, Kirkpatrick and Nunez (1980) note that in the study area "...There appears to be a certain moisture limit below which *E. risdonii* is taller than *E. amygdalina* and above which *E. risdonii* is in the subordinate stratum." No direct physiological data are available on the relative drought tolerance of these two species. Nevertheless, water potential readings taken on grouped samples of a range of phenotypes from the hybrid swarm in mid-March 1981 (Table 6.1) indicate that *E. risdonii* has a significantly greater ($P < 0.01$) resistance to water loss than *E. amygdalina* which in turn exhibits a greater resistance than hybrid phenotypes. No significant difference was obtained between similar samples taken from seedling in an experimental garden, but a similar trend was evident. Although stomatal resistance readings are not available, these results are consistent with the situation described by Sinclair (1980) where the more mesic species is the least capable of controlling the rate of transpiration and thus exhausts its available water during periods of low rainfall.

Whereas *E. risdonii* appears to outcompete *E. amygdalina* on extremely dry, highly insolated sites, its virtual exclusion from the south-facing slopes is probably attributable to a relative lack of insolation (Kirkpatrick and Nunez 1980). This is most likely a consequence of the thick layer of cuticular wax over the surface of adult and seedling leaves of *E. risdonii*, resulting in an intense glaucous appearance, which contrasts markedly with the green leaves of *E. amygdalina*. Similar differences in glaucousness between other species of *Eucalyptus* have been associated with the potential to regenerate in relatively open as opposed to shaded habitats (e.g. Cameron 1970). The adaptive significance of this difference in leaf surface has been investigated in a range of *Eucalyptus* species (e.g. Barber 1955; Barber and Jackson 1957; Thomas 1965; Cameron 1970; Thomas and Barber 1974a and b; Paton 1981; Edwards 1982). The adaptive value of glaucous foliage in environments exposed to high levels of insolation include protection from UV radiation, high temperatures

and extremely high levels of light intensity, and thus involves a reduction in transpiration and temperature inhibition of photosynthesis (Thomas 1965). This advantage must be balanced against a significant reduction in energy absorbed for photosynthesis under low light intensities and large differences in the selective value of this character have been demonstrated within a single species (Barber and Jackson 1957). In all species examined the presence of a cuticular wax layer increased reflectivity by 10-20% of the total incident light, particularly over the photochemically active waveband, and reduced the rate of photosynthesis under non-saturating light intensity levels. Differences in reflectivity of a similar magnitude have been found between *E. risdonii* and *E. amygdalina* (Hamilton 1971). The factors which restrict *E. risdonii* to the driest sites on slopes with high levels of insolation are not clear. However, it is most likely that when sufficient moisture is available *E. amygdalina* achieves a greater growth rate than *E. risdonii*. In addition, it is possible that even on exposed slopes in the absence of fire, under a closed canopy, *E. risdonii* seedlings are unable to compete with *E. amygdalina* seedlings.

Topographic variation within the study area results in a patchy, highly differentiated environment with respect to incident solar radiation (Nunez 1980; Fig. 6.4). Of interest is the sharp ecotone in net radiation at the base, and the shallow gradient across, the north-facing slope of the study area. In addition, there are areas currently occupied by *E. amygdalina* which are subject to levels of insolation comparable to the area occupied by *E. risdonii*. The degree of differentiation varies through time (Nunez 1980; Kirkpatrick and Nunez 1980; Fig. 6.4) with a continuum from a highly differentiated winter habitat to the relatively undifferentiated summer extreme in December. The gross effect of this differentiation when integrated with seasonal variation in rainfall (Kirkpatrick and Nunez 1980; Fig. 6.4) is an environment highly differentiated in terms of moisture availability. This is particularly so for the critical drought period in late summer, with the summation of the water deficit accumulated from November through to March. While the actual amount of available moisture will involve a complex interaction with the type and maturity of the vegetation (e.g. Martin and Specht 1962; Specht 1972; Sinclair 1980), a significant difference in gravimetric water content of samples from the centre of *E. risdonii* and *E. amygdalina* dominated slopes has been recorded (Edwards 1969).

The major determinants of water availability in the study area can thus be summarized in terms of variation in precipitation (temporal) and topography (spatial). However, this will be modified by localized heterogeneity in such factors as soil depth and bedrock fragmentation, although with bedrock type (Permian mudstone) constant throughout the Government Hills, there appears to be only minor variation in actual soil structure. Factors further modifying or interacting with these major gradients are discussed by Kirkpatrick and Nunez (1980). For example, the topographic effect on moisture availability is probably greater than predicted from incident radiation alone due to several factors such as a decrease in soil depth and thus moisture holding capacity on northerly aspects, and direct exposure to hot, dry, north-westerly winds in summer. Nevertheless, stochastic (year to year) and long-term variation in precipitation as well as spatial variation in net radiation interact to produce a spatially and temporally variable selective agent with a large stochastic component. This fluctuating selective mosaic is thus superimposed upon a highly differentiated gene pool. Fire and biotic factors (e.g. insect predation) can be considered secondary selective agents, interacting with water availability, insolation and the vegetation.

6.4 Methods

Adult Morphology

Twenty mature trees of *E. risdonii* and *E. amygdalina* were randomly sampled from the centre of pure stands on northern (Fig. 6.3; site D) and southern (Fig. 6.3; site I) aspects respectively and a sample of 40 mature trees lying outside the normal phenotypic range of either species were randomly collected from the hybrid swarm on the ridge (Fig. 6.3; sites A and B). The relative frequency of these forms in the hybrid zone is discussed in later chapters. Sampling within trees was restricted to inflorescences and sun leaves typical of the area of peak spring/summer growth. The foliage in each tree was assigned a glaucousness ranking from 1 (green) to 5 (highly glaucous), and the morphometric measurements illustrated in Fig. 6.5 were averaged from 3 leaves and one capsule from each of 3 inflorescences per tree. Data were analyzed using principal components analysis (PCA) ignoring taxa grouping (total correlation matrix). Leaf and capsule dimensions were initially treated in separate analyses (Figs. 6.6 and 6.7 respectively) and the variation illustrated by scaled ideograms based on the average character dimensions of individuals in each of 9 equal width classes along the major axis of variation.

Progeny Trial

Open pollinated seed was sown from 4 *E. risdonii*, 5 *E. amygdalina* and 7 hybrid trees (Table 6.2). Two trees each of *E. risdonii* and *E. amygdalina* were sampled from the centre of pure stands (Fig. 6.3; sites D and E respectively) and the hybrid swarm site (Fig. 6.3; sites A and B), although insufficient viable seed was obtained from one of the *E. amygdalina* trees from the hybrid swarm to warrant inclusion in the trial. In addition, two trees from a population of *E. amygdalina* growing on a sandstone substrate south of Hobart (Blackmans Bay) and approximately 5 km from any other *Piperitae* species, were included for comparison with the *E. amygdalina* from the Government Hills. A maximum of thirty seedlings from each mother were grown in 6" vernier tubes filled with potting soil (planted July 1979). Seedlings were grown in a glasshouse under the natural photoperiod, watered daily and supplied with a liquid nutrient solution twice weekly. After 6 months seedlings were scored for the characters listed in Table 6.4 and the dimensions of a single leaf from the 4th and 10th nodes (cotyledons = 0) were recorded as indicated in Fig. 6.5. Where leaf pairs were alternate, the top leaf was chosen for measurement. Scoring of multistate characters was achieved by comparison with standards. The density of prominent oil glands was scored by holding the 10th leaf in front of a standard lamp. Seedling morphological data were analyzed using likelihood analysis (see Chapt. 5.2) based on leaf characters and those characters indicated in Table 6.4 as well as by PCA (total correlation matrix) of seedling leaf dimensions. Where results are presented as standardized (*), values have been adjusted so that the pooled *E. amygdalina* and *E. risdonii* samples have mean values of 0 and 1 respectively.

The criteria used when classifying phenotypes subjectively or statistically using a standardized hybrid index are given in Table 6.3. The statistical classification follows Goodman (1967), with the range between the species' means partitioned about the expected mean values of the F_1 and backcross distributions assuming inheritance is additive. Although this criteria is used for the practical purpose of classification, the genetic history of phenotypes can not be directly inferred from this classification. For example, the backcross phenotype may be derived from either backcrossing or by segregation from an F_1 .

Surviving seedlings from this trial were transplanted, along with seedlings from another trial involving *E. tenuiramis*, into an experimental garden on ex-agricultural land at Richmond, 12 km NE of Hobart, in April 1980.

Seedlings were planted in a semi-random block with a row spacing of 1.5 m. An attempt was made to represent each mother once per row, although variation in the number of surviving seedlings did not permit this to be maintained for all rows. Seedlings were artificially watered only during the first summer (1980/1981), this being necessary to ensure a reasonable establishment rate. Seedling survival results (Table 6.8) are only presented for the following summer (1981/1982) to avoid any artifact due to transplanting. The height and basal area of seedlings in the garden was measured in December 1980, July 1981, and March 1982. Basal area was calculated from stem diameter 10 cm above ground level. The criteria used to classify seedlings from the hybrid progenies into morphological classes for vigour comparisons are given in Table 6.3 and was based on the likelihood index score (see Table 6.4).

The frequency of interspecific - or backcrosses in progenies of pure species' mothers, was assessed from trees used in the present trial, from seedlings grown from mothers used in the germination trial and several trees sampled at a later date from the hybrid zone. The frequency of interspecific - or backcrosses was estimated in each progeny from the frequency of abnormal phenotypes (outliers) subjectively classified as lying outside the normal phenotypic range of that species and resembling the intermediate phenotype (Table 6.3, H). One *E. amygdalina* tree from the hybrid zone was excluded as the possibility of hybridity could not be excluded due to the continuous nature and range of variation displayed in its progeny.

Estimation of Seed Output Parameters

Seed output and germination was examined for a subset of the trees used in the initial morphometric analysis (Fig. 6.9). The choice of trees was dependent on the availability of a sufficient number of capsules and included trees from pure stands of *E. risdonii* (n=9) and *E. amygdalina* (n=7), and a sample from the hybrid zone (n=19) encompassing the full range of phenotypic variation found at this site (Fig. 6.9). From each tree, three samples (in most cases), each of 30 capsules, were air-dried and seed and chaff extracted. The number and weight of open capsules, the total weight of seed and chaff extracted from each sample, and the weight of a random sample of 20 well-filled seeds were recorded. The total sample of seed and chaff was spread onto thiram dusted germination pads, placed in a petri dish and de-ionised water added regularly. Throughout the germination period samples were held in growth cabinets at 22°C in a continuous mixture of incandescent and fluorescent light. Seeds were recorded as germinated when the testa was ruptured and the radicle emerged.

On termination, all ungerminated seed was separated from the chaff and the viability tested by squashing. A seed was classified as still viable if a firm white embryo was extracted. The remaining sample comprising only chaff was dried and weighed. Using the weight of a subsample of 50 chaff particles, the number of chaff particles was estimated. The germination response was examined only for seeds germinating over the test period of 74 days using the mean number of days to germination, the time taken for 50% (T50) and 90% (T90) of the total number of germinated seed to germinate and germinative capacity (i.e. G.C.; the number of seeds germinated/total number of viable seeds, Grose 1957). The results are presented in terms of individual tree means and taxa comparisons made at this level of replication. Trees were partitioned into 5 morphological classes based on the likelihood index scores derived from the 7 morphometric variables indicated in Fig. 6.5 and classified using the criteria described in Table 6.3.

Flowering Phenology

The destruction of the main study site by wildfire in the summer of 1980 necessitated the study of flowering behaviour to concentrate on other unburnt populations in the Government Hills (Fig. 6.3). Permanent transects were established through two pure stands of both *E. risdonii* (3,4) and *E. amygdalina* (1,2), two hybrid swarm sites (8,9) from which samples of both species and hybrids (intermediate class) were scored and three ecotonal sites (5,6,7) from which paired samples of either species were scored. To examine aspect variation within *E. amygdalina* independent of *E. risdonii*, three additional transects (SE-10, Ridge-11, NW-12) were established in the *E. amygdalina* forest on the far northern spur of these hills. Twenty trees from each taxa were scored in each case and generally trees sampled from any one taxa were not adjacent. The length of the transects varied depending upon tree density and ranged from 150-200 m for tall forest sites to 50-100 m for mallee sites.

Transects were scored at monthly intervals (midmonth) from December 1980 to February 1982. The degree of flowering was assessed using 10 x 50 binoculars where individuals could not be examined at eye level. Individuals were classified (absent, 0 - high, 3) according to the density of buds and flowers (relative to crown area) and the intensity of flowering assessed using both an index of the density of flowers relative to crown area (none, 0 - high, 3) and subjective estimates of the percentage of flowers open relative to the total number of flowers, young fruit and buds on

the tree. The use of litter trap and operculum count methods to describe flowering phenology (e.g. Ashton 1975; Loneragan 1979) were not generally applicable in this study as it was necessary to differentiate individuals and taxa from the one area.

The flowering phenology of a taxa stand is described in terms of the number of trees in the sample flowering at each sampling time (for several levels of intensity) and a crude estimate of the intensity of flowering was obtained from the mean of the estimated percentage of open flowers per tree. In addition, two quantitative indices of the interbreeding potential of populations or taxa based on flowering phenology alone were derived from the models described in Appendix 2. An index of assortive mating (S_{jk}) was used to describe the potential for trees from a given taxa stand (maternal group) to receive pollen from trees from an alien stand (pollen donor) as opposed to trees from the same stand. A second index (P_j) was used as an indication of the relative probability of an individual to be pollinated by either *E. amygdalina* or *E. risdonii*. Both indices were calculated over the time period December 1980 to January 1982 for a range of flowering intensities by treating all flowering events involving low bud abundance and flower intensity as not flowering. Data are presented for the case where a flowering event was classified as heavy if the abundance score was greater than one and at least 10% of the buds were in flower. The exclusion of weak flowering trees in the estimation of population values is likely to be more realistic due to pollinator foraging habits (see Levin 1979) and the fact that fruit set was observed to be negligible from weak flowering. The matrix of stand values of S_{jk} (Appendix 2; Table 1) was treated as a dissimilarity matrix and the KIST two-dimensional, local, non-metric scaling (Kruskal 1964a,b; Sneath and Sokal 1973) solution was used to summarize the interbreeding potential of taxa stands (Fig. 6.20). The matrix was split by rows and thus the rank order of distances from a single stand to all others reflects the relative probability of the other stands acting as a pollinating source when only differences in flowering phenology are considered.

6.5 Results and Discussion

The difference in phenotype between *E. amygdalina* and *E. risdonii* can be summarized in terms of variation in leaf and capsule morphology (Table 6.5). The variation in leaf morphology is shown in Fig. 6.6 and described by the first principal component which accounts for 82% of the variation in the total sample. This vector describes the continuum in leaf shape from the

broad, connate leaves of *E. risdonii* to the narrow petiolate leaves of *E. amygdalina*. The samples from the ridge population range in leaf shape between either species with the majority intermediate. The parental species are not as effectively discriminated using capsule morphology, yet are significantly different (MANOVA; $P < 0.001$) with only slight range overlap (Fig. 6.7). The ridge population is again intermediate although showing a slight bias towards *E. risdonii*.

E. risdonii and *E. amygdalina* are further differentiated on several other characters including leaf arrangement, glaucousness and bark type. *E. risdonii* develops an intense waxy glaucousness on the foliage and inflorescence whereas the foliage of *E. amygdalina* is green or at most sub-glaucous. The distribution of glaucous phenotypes relative to leaf and capsule morphology is shown in Fig. 6.8 and it is evident that some recombination of these characters are to be found in the ridge population. The decortivating gum bark type of *E. risdonii* contrasts markedly with the persistent scaly bark of *E. amygdalina*. However, the gum bark type is exhibited in the juvenile or sapling stage of *E. amygdalina*, and the height to which rough bark persists on the trunk of mature trees is variable. This major difference between species is not readily detected when the species are in the mallee habit as is the case with much of the study area. However in forests where the stems are older, hybrids between these two species appear intermediate in this character.

The intermediacy in gross morphology of individuals from the ridge population is illustrated by the PCA (TOT CORR) ordination based on the 7 morphometric variables and glaucousness score (Fig. 6.9). Whereas *E. risdonii* and *E. amygdalina* are usually phenotypically distinct, mature individuals encompassing the complete range in phenotype between these two species can be found in the ridge population. The sample from the ridge of phenotypes deviating from either pure species is highly variable and is dominated by individuals either intermediate or tending toward *E. risdonii* in phenotype. These individuals probably correspond to F_1 and backcross phenotypic groups, in which case there appears to be a noticeable paucity of backcrosses to *E. amygdalina* in the sample. The phenotypes of parents used in the progeny trial are indicated in this ordination for comparison and the hybrid mothers appear to be representative of both the intermediate (F_1 ; H_1 , H_3 , H_5 and H_8) and backcross to *E. risdonii* (H_2 , H_6 and H_9) phenotypic classes. PC_2 (Fig. 6.9) describes residual size variation and separates the *E. amygdalina* mothers used in the progeny trial. The difference between these mothers encompasses a considerable portion of the phenotypic variation

within the species *E. amygdalina*. For example, the two mothers from Tinderbox are typical of forms of *E. amygdalina* growing on soils developed on Triassic sandstone outcrops south of Hobart. This form intergrades into the smaller leaf and fruit forms found growing on soils developed on Permian mudstone north of the Derwent River and exemplified by the Risdon population. This form, in turn, intergrades into a smaller, mallee form growing on particularly dry sites in these areas. This morphological variation in *E. amygdalina* is paralleled by the reduced persistence of rough bark on the trunk and appears to be in the direction of the closely related species *E. pulchella* rather than *E. risdonii*.

Progeny Trial

The hybrid nature of the intermediate mothers is confirmed by their intermediate and highly variable progenies as compared to those of the pure species' mothers. Progenies of the hybrid mothers are intermediate and more variable in the expression of glaucousness and the development of connate leaves and intranodes (Table 6.2). The variability in leaf shape in progenies pooled from mothers of similar adult morphology is illustrated in Fig. 6.10. Using the log LL/LW scale, the inheritance of juvenile leaf shape can be considered additive as Barber (cited by Pryor 1957c) has shown the mean of the *E. amygdalina* and *E. risdonii* F_1 to lie intermediate between the means of either parental species. Pryor (1957c) also indicates that this is the case for several other manipulated F_1 crosses between species with similar differences in juvenile leaf shape. This was confirmed using the 10th node leaf data and leaf samples from 4 F_1 hybrid specimens (Brett's *E. amygdalina* x *E. risdonii* Cross 209) lodged in the Tasmanian Herbarium. The juvenile leaves of the F_1 's are sessile but not connate.

Pooled estimates of the variance in leaf shape within progenies from various mothers are shown in Table 6.6. There is a marked difference between *E. risdonii* and *E. amygdalina* in the variability in leaf shape within individual progenies ($P < 0.001$). This appears to be an inherent statistical difference at the seedling stage but is possibly not retained to later ontogenetic stages (e.g. Fig. 6.10). However, the progenies of mothers from the intermediate morphological class (H_1 , H_3 , H_5 and H_8) are significantly ($P < 0.001$) more variable than either species (Figs. 6.10, 6.11 and 6.12; Table 6.6). Although the variability within progenies of mothers more similar to *E. risdonii* (H_2 , H_6 , H_9) is significantly less ($P < 0.001$) than for intermediate mothers, they are still statistically more variable ($P < 0.001$) than the *E. risdonii* progenies. Similar results are obtained when the total seedling morphological data are considered by the use of the likelihood

index (Fig. 6.12; Table 6.6). Moreover, it is apparent that progenies from mothers of either species are more variable ($P < 0.001$) in the vicinity of the hybrid zone than those from more distant and virtually pure species' stands. These mothers were chosen as morphologically representative of either species and showed no obvious signs of hybridization. The increase in variability with proximity to the hybrid swarm is particularly marked in *E. amygdalina*. However, the high variability in the mallee *E. amygdalina* mother (A_3) is partly due to variation not in the direction of *E. risdonii* and is associated with the abnormally early development of a relatively large petiole and the alternate leaf arrangement.

The peak in variability in progenies from mothers of intermediate phenotype strongly suggests heterozygosity and genetic segregation. These may include F_1 's as several progenies contain a wide array of phenotypes and include seedlings statistically indistinguishable from both *E. risdonii* and *E. amygdalina*. However, given that open pollinated seed has been used in the trial, differing levels of heterogeneity in the pollen environment of the various mothers may distort estimates of the actual magnitude of genetic segregation. Nevertheless, these results constitute substantial evidence for the highly variable ridge population having arisen by hybridization between *E. amygdalina* and *E. risdonii*. This population represents a hybrid swarm which is at least several generations old and probably consists of segregate, backcross and F_1 individuals.

A large heritable component underlies the phenotypic variation observed in adult morphology. The adult leaf shape as measured by $\log LL/LW$, for example, is strongly correlated with the mean value of the seedling leaf shape (Fig. 6.13). This is indicative of the close relationship shown in Fig. 6.14 between variation in the adult phenotype and genotypic variation between progenies. The relative similarity (as measured by the likelihood index) of each mother to the centroid of either species is maintained when accessed by either the adult phenotype or mean value of the likelihood scores of its progeny. However, the hybrids appear closer to *E. risdonii* when the comparison is based on seedling data, which could be due to either heteroblastic development or backcrossing to *E. risdonii*.

The Frequency of Interspecific crosses and Backcrosses

The distribution of leaf shapes in seedlings from intermediate class mothers is skewed toward *E. risdonii* and there appears to be a deficiency of F_1 types (Fig. 6.10). Similarly, the distribution of likelihood index scores in the pooled progenies from intermediate class mothers (Fig. 6.15) indicates a mode in phenotypes intermediate between a hypothetical F_1 and

E. risdonii phenotype. If additive inheritance along this index is assumed, then this mode is centred on the mean value (.75) expected for the $F_1 \times E. risdonii$ backcross distribution. The most likely explanation of this bias is that intermediate mothers are predominantly outcrossing to *E. risdonii* types.

The bias toward *E. risdonii* phenotypes in these progenies is indicative of a predominantly unidirectional flow of genes by pollen migration from *E. risdonii* into the hybrid swarm and surrounding *E. amygdalina*. This is confirmed by two additional lines of evidence. Firstly there is a significantly greater proportion of outliers recorded as possible F_1 hybrids in progenies of *E. amygdalina* than *E. risdonii* mothers from both the hybrid swarm and pure stands at Risdon (Table 6.7). The proportion of such phenotypes was significantly greater in mothers from the hybrid swarm than those from pure stands for both species. Secondly direct observations on the distribution of hybrids established away from the hybrid swarm and ecotonal areas indicates the frequency of sporadic hybrids is greater in areas dominated by *E. amygdalina* than *E. risdonii*.

Seedling Survival and Vigour

No significant differences were observed in seedling mortality between the pure species and hybrid progenies grown under glasshouse conditions or during establishment in the experimental garden (1980/1981). However, over the following year there was a significant (X^2 ; $P < 0.001$) difference in mortality, as well as the proportion of seedlings classified as healthy, in the experimental garden (Table 6.8). This resulted from a significantly greater susceptibility to drought by *E. amygdalina* seedlings from the Blackmans Bay site, and is indicative of marked genetic differentiation within *E. amygdalina* between populations developed on mudstone and sandstone substrates. The majority of deaths over this period were a result of drought with most deaths or drought damage occurring in mid-February 1982 following several days of high temperatures and strong, hot north-westerly winds. No significant difference in mortality was observed between the Risdon *E. amygdalina*, *E. risdonii* or hybrid progenies over this period. In addition, there was no difference in either mortality or the proportion of healthy seedlings between morphological classes in progenies from intermediate mothers.

No significant difference in basal area or height was evident between progenies after two years' field growth calculated from either surviving seedling (Fig. 6.16) or only those classified as healthy. However, there is

a trend within the pooled progenies from intermediate mothers for morphologically intermediate seedlings to be less vigorous than those tending toward *E. risdonii* (H_1 March 1982; Fig. 6.16b; $P < 0.05$). This differentiation within the pooled progenies of the intermediate hybrid mothers was not significant under glasshouse conditions in the initial scoring.

In general, these data indicate no dramatic difference in seedling survival or vigour between hybrid progenies and those of either parental species from the same area. There was a tendency for hybrid progenies to be taller than parental progenies from the same locality after initial growth in the glasshouse (1 vs 3 vs 6; Fig. 6.16a), but this was not obvious after two years in the experimental garden. Differences in vigour between phenotypic classes within the hybrid progenies may be accentuated in the future when competition between individuals intensifies. However, the present trend indicates parental types, particularly those tending toward *E. risdonii*, may out-compete intermediate phenotypes.

Seed Output and Germination

Significant differences ($P < 0.001$) between trees were noted for capsule, seed and chaff weight, which were highly correlated ($P < 0.01$) with differences in adult morphology (Table 6.9a). The intermediate capsule size of the hybrids is associated with intermediate seed and chaff size (Fig. 6.17). The only differences in the germination response between trees was in germinative capacity ($P < 0.05$) and seed viability ($P < 0.05$). However, no significant difference was obtained between trees from the different morphological classes. The measures of germination rate (i.e. T50, T90 and mean time to germination) were correlated with morphology ($P < 0.05$), with seeds of *E. risdonii* (T50=34 days) tending to germinate later than those of *E. amygdalina* (T50=23 days). This trend was evident, but not significant when morphological classes were compared (Fig. 6.18d). The morphological classes differ significantly ($P < 0.001$) in the number of viable seed produced per open capsule (Fig. 6.18b) which can partly be accounted for by differences in capsule size (Table 6.9). However, in the case of both *E. amygdalina* and the *E. amygdalina* backcross class, this is also associated with a marked reduction in apparent fertility as expressed by the estimated number of chaff particles (ovulodes and aborted ovules; see Chapt. 5) per seed (Fig. 6.18c). The parental species differ significantly ($P < 0.001$) in fertility with the hybrids (F_1 morphological types) not significantly different from *E. amygdalina* in the number of viable seeds per capsule (Fig. 6.18b) or per mass of chaff and seed (Fig. 6.18a). The hybrid classes differ significantly ($P < 0.05$) from each

other in the number of viable seed per open capsule. Hybrids similar to either parent do not differ significantly from parental types, although hybrids similar to *E. amygdalina* tend to be less fertile than *E. amygdalina* (Figs. 6.18b and c). This does not reach significance, due partly to the low number of replicates in this hybrid class.

Capsule weight accounts for 40% of the variation between individuals in the number of viable seeds produced per open capsule. Once the effect of capsule size is removed (i.e. by partial correlations; Table 6.9b), differences in viability and the number of chaff per seed both account for significant proportions of the remaining variation (24% and 13% of the total respectively). In the present case, there appears to be an upper limit to the number of viable seed produced per capsule which appears linearly related to capsule weight (Fig. 6.17b). This constraint could arise due to an interdependence of capsule, locule and ovule size. An increase in capsule size results in an increase in seed and chaff size as well as an increase in the number of both seed and chaff per capsule (Table 6.9a) which suggests these factors are to some extent developmentally linked and in the absence of any secondary effect (e.g. predation, abortion, genetic incompatibility, differential pollination) could exhibit intermediate inheritance. However, some recombination between these factors is apparent (e.g. seed weight and capsule size; Fig. 6.17a). Seed, chaff and capsule weight all exhibit marked consistency between replicates from individual trees. In particular, both the weight of seed and chaff appear particularly stable at the individual level, being unaffected by the number of seed or chaff produced per capsule when the joint correlation with capsule weight is removed (Table 6.9b).

Flowering Phenology

The total number of trees in each sample observed to flower at least once is indicated in Table 6.10 and the proportion of trees flowering in each taxa at each sampling period is shown in Fig. 6.19. *E. amygdalina* and *E. risdonii* are separated in the time of peak flowering by two to three months (Fig. 6.19). The greatest intensity of flowering in *E. risdonii* is in early to mid-summer, peaking in December, whereas *E. amygdalina* in this area flowered mainly in late winter to early spring, peaking in August. The flowering of *E. amygdalina* is spread over a longer period than that of *E. risdonii*, possibly due to both lower temperatures during the flowering period as well as a greater difference in peak flowering time between individuals.

The flowering cycle of *E. risdonii* is more synchronized both within and between geographically separate populations (Figs. 6.20 and 6.21). From these data, as well as observations from the previous year and herbarium specimens, flowering within *E. risdonii* appears relatively constant. The flowering during autumn and winter by *E. risdonii* mainly involves buds which failed to flower prior to the cessation of growth in late summer. Within an individual, the earliest initiated buds tend to flower first and occasionally flowering within umbels may be unsynchronized with buds and mature fruits occurring in the one umbel. The flowering cycle of *E. amygdalina* is less clear and longer records are required to fully elucidate the cycle. The peak in summer as well as winter in *E. amygdalina* (Fig. 6.19) results from a low proportion of summer flowering individuals which, in most cases, flowered only weakly or not at all during the winter peak. However several individuals were observed to flower for 12 of the 15 months, exhibiting both a summer and winter peak. Based on the present data, flowering in *E. amygdalina* appears to be variable with either summer or winter flowering forms, with less than 2% of the individuals exhibiting an intermediate period of peak flowering. This is partly a result of the cessation of vegetative growth which seems to occur in both species during late summer, possibly due to water stress developed from the accumulation of the summer water deficit. The difference in flowering phenology between the two species is also reflected in the time at which bud initials are first apparent. In both species, newly initiated buds are generally apparent on an individual immediately after peak flowering, although in some cases, some lag may occur or initiation may fail to occur. Trees continue to initiate buds for one to two months and some *E. risdonii* may be found still initiating buds in winter.

There is considerable overlap in flowering period between species when the total number of trees flowering is considered (Fig. 6.19a). However, when the intensity of flowering is taken into account the two species differ markedly (Figs. 6.19b and c; Tables 6.11 and 6.12). The potential for interbreeding between stands is summarized in the non-metric scaling ordination (Fig. 6.20) of stands based on the assortive mating index scores ($S_{j,k}$; Appendix 2). Differences in flowering phenology between stands appear to confer a significant ($P < 0.001$; Table 6.11) potential for reproductive isolation between *E. risdonii* and *E. amygdalina* which, on the average, is not apparent between intraspecific stands. However, stands of both species appear to differ in the potential for hybridization with interspecific stands

(e.g. Table 6.13; Figs. 6.20 and 6.21), although flowering between *E. risdonii* stands appears more synchronized than between *E. amygdalina* stands (e.g. Figs. 6.20 and 6.21). In *E. amygdalina* this stand variation can be partly attributed to differences between trees from different areas (i.e. pure species, ecotonal and hybrid zone stands; e.g. Appendix 2, Table 2 - Pj; $P < 0.05$; Figs. 6.20 and 6.21). Ecotonal stands (5,6 and 7) differ from hybrid zone (8,9) and pure species (1,2) stands in having a low proportion of individuals flowering in the summer of 1980 (Fig. 6.21). Over the period studied, flowering in ecotonal stands of *E. amygdalina* overlapped the least with that of *E. risdonii*, which suggests a greater inherent potential for reproductive isolation from *E. risdonii*.

Allopatric (pure species) stands of *E. amygdalina* thus appear to exhibit a greater inherent potential for hybridization than parapatric stands. The two parapatric hybrid zone stands located on the ridges are an exception, with flowering being more similar to the pure species sites on the SE slopes (Fig. 6.20). This may partly account for the higher proportion of hybrids at these sites. Concurrent observations were also made on allopatric *E. amygdalina* populations south of the Derwent River, growing on soils developed from Triassic sandstone. The peak flowering period of these stands was later than populations in the Government Hills (October-November) and they thus exhibited a greater overlap with *E. risdonii*. It is difficult to ascertain whether these differences are due to character displacement (i.e. Wallace Effect; Grant 1966) or are a direct consequence of some secondary factor (e.g. Chapter 1; Levin 1970a). Variation between localities at Risdon is not only associated with different species' composition (or genetic structure), but involves an aspect transition from moister SE slopes (pure stands), ridge sites (hybrid swarm) to dry NW slopes (ecotonal). Evidence from a similar transect in the absence of *E. risdonii* (Fig. 6.22) tentatively suggests that the differences between stands from SE and NW slopes may be partly a response of *E. amygdalina* to the more extreme, drier conditions on the NW slope. However, in this case, results are confounded with a marked reduction in both vegetative and reproductive vigour of individuals on the NW slope which was not as apparent in other areas (Table 6.10) and which may affect estimates of the flowering period.

The magnitude of the genetic component associated with differences in flowering phenology between populations is unknown. Nevertheless, genetic variation in flowering time within *Eucalyptus* species has been noted (e.g. Eldridge 1970) and there is strong circumstantial evidence that there is a large genetic component at least to the differences between *E. amygdalina* and *E. risdonii*. This includes the fact that differences in flowering

phenology were maintained between paired samples taken along transects (thus removing the effect of site variation). In addition, observations from ornamental plantings of the two species also suggest differences are at least partially maintained. As a group, hybrids which are intermediate in morphology (F_1 types) between *E. risdonii* and *E. amygdalina* tend to be intermediate in their flowering behaviour (Fig. 6.19; Tables 6.11 and 6.13). Hybrids morphologically similar to one or other of the parents, although not scored, were noted to tend toward the parental flowering behaviour.

Ecotonal and hybrid zone stands of either species can be considered to be equally close to a source of interspecific pollen and it is perhaps significant that hybrids are found in the latter stands where the models of flowering behaviour predict a greater propensity for hybridization. In addition, the proportion of interspecific hybrids expected in outcrossed seed of *E. amygdalina* and *E. risdonii* based on the assortive mating index ($S_{j,k}$) and summed over all boundary sites is .17 and .18 respectively. This suggests equal probability for hybridization, although when only ecotonal sites are considered (Table 6.11) there appears a bias in favour of *E. risdonii* pollinating *E. amygdalina*. The deviation from equal probability of hybridization as noted in the progeny trial (Table 6.7; 0.13 and 0.01 respectively) could arise due to several factors including site variation in flowering phenology, differences in the success rate of reciprocal crosses, and a greater abundance of *E. risdonii* pollen during flowering. In support of the latter proposal, there was a significantly greater ($P < 0.001$) proportion of *E. risdonii* trees classified as having flowered heavily at least once over the sampling period. Furthermore, the larger flowers of *E. risdonii* may release a greater amount of pollen than flowers of *E. amygdalina*.

Table 6.1. Mean water potential (mP) of small shoots taken from *E. risdonii*, *E. amygdalina* and hybrid phenotypes. The hybrids were partitioned into intermediate (H) phenotypes or those similar to either *E. amygdalina* (AH) or *E. risdonii* (RH) (see Table 6.3). Samples were grouped both spatially and temporally and the difference between samples of either species was significant ($P < 0.01$; paired 't' test).

Phenotype	n	\bar{X}	SE
<i>E. risdonii</i> (R)	6	-1.85	.104
Hybrids (RH)	3	-1.56	.101
" (H)	6	-1.47	.052
" (AH)	3	-1.44	.088
<i>E. amygdalina</i> (A)	6	-1.65	.094

Table 6.2. The location and phenotypic class of mothers used in the progeny trial and the number of seedlings in each progeny. The percentage of glaucous (i.e. non-green - class 1) and connate seedlings in each progeny is indicated as well as the percentage of seedlings which had developed intra-nodes or petiolate leaves at the time of scoring.

Mother	Site	N	% glaucous seedlings (i.e. non- green classes 2-5)	% connate seedlings 4th node	10th node	% seedlings developing Intra- node	Petiole
<i>E. risdonii</i>							
R ₁	hybrid swarm	30	100	100	100	0	0
R ₂	" "	28	100	100	100	0	0
R ₃	pure stand	29	100	100	100	0	0
R ₄	" "	30	100	100	100	0	0
RH hybrids							
H ₂	hybrid swarm	30	53	87	100	0	0
H ₆	" "	30	47	73	90	0	0
H ₉	" "	30	53	93	93	0	0
H hybrids							
H ₁	hybrid swarm	30	47	57	73	23	7
H ₃	" "	19	58	95	79	16	0
H ₅	" "	30	20	23	20	20	7
H ₈	" "	30	73	50	63	13	0
<i>E. amygdalina</i>							
A ₁	Blackmans Bay	26	0	0	0	65	30
A ₂	" "	30	0	0	0	33	53
A ₃	hybrid swarm	30	0	0	0	97	100
A ₄	pure stand	30	0	0	0	100	87
A ₅	Risdon "	30	0	0	0	97	93

Table 6.3. Criteria used when classifying phenotypes subjectively or statistically using a hybrid index.

Phenotype	Code	Subjective Criteria	Statistical Criteria (after Goodman 1967)	
			Hypothetical Mean	Range
<i>E. risdonii</i>	R	pure species	1	>.875
Backcross- <i>E. risdonii</i>	RH	lying outside range of the pure species but closer to <i>E. risdonii</i>	.75	.875-.625
Intermediate	H	equally unlike either pure species (F ₁ type hybrid)	.5	.625-.375
Backcross- <i>E. amygdalina</i>	AH	lying outside the range of the pure species but closer to <i>E. amygdalina</i>	.25	.375-.125
<i>E. amygdalina</i>	A	pure species	0	.125>
<i>E. viminalis</i>	V	pure species		

Table 6.4. Description of characters scored from seedlings. The leaf dimensions measured are the same as in Fig. 6.6 (†=used in likelihood analysis).

Code	Description
1. Ht.	Seedling height (cm)
2. NE	Number of leaf pairs expanded (cotyledons = 0)
3. Dia.	Stem diameter measured at the cotyledonary node, at right angles to the cotyledons (mm)
4. Pr. Lat.	The number of laterals (>1NE) developed as a proportion of the potential number (i.e. X/24 NE) (ratio) †
5. LAMTH	Lamina thickness, measured using a spring-loaded micrometer (mm) †
6. L4-10	Distance between the 4th and 10th nodes (cm)
7. Bark	The number of nodes above the cotyledons with bark developing.
8. St. Verr.	The density of verrucae (oil glands) on the seedling stem (1-5; <i>E. amygdalina</i> - highest) †
9. Oil Glands	The density of oil glands on the 10th leaf (1-3; <i>E. risdonii</i> - highest) †
10. Glauousness	The intensity of waxy glauousness on the upper leaves (1-5; <i>E. risdonii</i> - highest) †
11. Intranode	Presence/absence of an intranode (where present, the node of first development was recorded.
12. Petiole	Presence/absence of a petiole (where present, the node of first development was recorded.

Table 6.5. Adult character means (cm) for *E. amygdalina* (n=20), *E. risdonii* (n=20) and hybrid swarm (n=40) samples. The F ratio for the difference between pure species samples is indicated. Characters correspond to those illustrated in Fig. 6.5. (***) = $P < 0.001$).

	<i>E. amygdalina</i> (n=20)	<i>E. risdonii</i> (n=20)	Hybrids (n=40)	F (1,38)	
Peduncle length (PL)	0.83	1.10	1.07	15	***
Capsule length (CL)	0.82	1.03	0.94	43	***
Capsule width (CW)	0.66	0.91	0.76	126	***
Lamina length (LL)	9.05	3.74	5.44	449	***
Lamina width (LW)	0.91	3.39	1.97	928	***
Length to the widest point (LWP)	3.82	0.89	1.83	650	***
Petiole/connate (P/C)	0.97	-1.35	0.02	1202	***

Table 6.6 Pooled within progeny variances estimated for standardized log LL/LW (see Fig. 6.12) and likelihood index (see Fig. 6.15) scores. The significance of the χ^2 test for heterogeneity of variances between progenies is indicated. (NS=not significant, *= $P < 0.05$, **= $P < 0.01$, ***= $P < 0.001$).

Maternal Class	Number of Mothers	d.f.	Log LL/LW Variance	χ^2 HET	Likelihood Index Variance	χ^2 HET
1. <i>E. risdonii</i>	4	114	.003	NS	.003	***
centre (R_3, R_4)	2	58	.003	*	.002	NS
hybrid swarm (R_1, R_2)	2	56	.003	*	.004	NS
2. <i>E. amygdalina</i>	4	112	.024	**	.020	*
Blackmans Bay (A_1, A_2)	2	54	.014	NS	.012	NS
Risdon (A_4, A_5)	2	58	.034	NS	.027	NS
hybrid swarm (A_3)	1	29	.019	-	.049	-
3. H hybrids (H_1, H_3, H_5 and H_6)	4	105	.068	NS	.056	NS
4. RH hybrids (H_2, H_6, H_9)	3	87	.011	**	.013	**

Table 6.7. The percentage of outliers recorded as possible F_1 hybrids (or similar backcrosses) in open pollinated progenies from typical *E. amygdalina* and *E. risdonii* mothers. The pure stand sites were both approximately 100 m from the boundary and hybrid zone. The number of seedlings and mothers used in the assessment are indicated in parenthesis.

Site	<i>E. risdonii</i>	<i>E. amygdalina</i>
1. Isolated pure stand	N/A	0% (184,2)
2. Pure species' stands at Risdon	0% (312,6)	1.9% (155,6)
3. Hybrid zone	1.3% (223,6)	12.9% (62,4)

Table 6.8. Proportion of established seedlings surviving the summer of 1981/82 at the Richmond experimental garden.

	Number of seedlings alive (July 1981)	Proportion alive (March 1982)	Proportion classified as healthy (March 1982)
<i>E. amygdalina</i>			
Tinderbox (A_1, A_2)	39	.64	.26
Risdon (A_3, A_4, A_5)	64	.92	.78
Pooled	103	.82	.58
<i>E. risdonii</i>			
margin (R_1, R_2)	35	.94	.86
centre (R_3, R_4)	46	.89	.85
Pooled	81	.91	.85
Hybrids			
Intermediates (H_1, H_2, H_5, H_8)	84	.96	.88
Backcross - <i>E. risdonii</i> (H_2, H_3, H_9)	63	.86	.78
	147	.92	.84

Table 6.10. The number of trees from each taxa stand (n=20) observed to flower as well as flower heavily at least once over the sampling period. The frequency of individuals with no mature capsules (scored December 1980) in each sample is indicated. Site locations are shown in Fig. 6.3.

Stand type	Location	Number of trees flowering	Number of trees flowering heavily	Number of trees without mature capsules
1. <i>E. amygdalina</i>				
Pure (1)	1	20	19	2
Pure (2)	2	19	15	2
Ecotone (1)	5	20	17	2
Ecotone (2)	6	16	12	3
Ecotone (3)	7	16	12	3
Hybrid Zone (1)	8	18	14	7
Hybrid Zone (2)	9	16	11	11
Pure (SE)	10	20	17	1
Pure (Ridge)	11	16	10	3
Pure (NW)	12	8	1	9
2. <i>E. risdonii</i>				
Pure (1)	3	18	10	3
Pure (2)	4	19	15	2
Ecotone (1)	5	19	15	5
Ecotone (2)	6	20	17	2
Ecotone (3)	7	20	18	2
Hybrid Zone	8	19	18	4
Hybrid Zone	9	18	17	5
3. Hybrids				
Hybrid Zone 1	8	19	13	7
Hybrid Zone 2	9	16	11	10
Ecotone (2) (n=26)	6	-	-	17

Table 6.11. Mean and its 95% confidence range of the index of assortive mating values ($S_{j,k}$) for intra- and inter-specific stand combinations. Values were calculated using the angular transformation of the stand values (Appendix 2; Table 1) and back transformed.

Local Stand Type	Alien Stand Type					
	<i>E. amygdalina</i>			<i>E. risdonii</i>		
	\bar{X}	95% C.L.	N	\bar{X}	95% C.L.	N
<i>E. amygdalina</i>	.45	(.41-.50)	42	.21	(.18-.25)	49
<i>E. risdonii</i>	.19	(.15-.22)	49	.50	(.47-.53)	42

Table 6.12. Mean values of P_j scores. P_j scores are calculated for (a) all flowering events, and (b) only heavy flowering events. Values are indicative of the probability of receiving *E. amygdalina* as opposed to *E. risdonii* pollen.

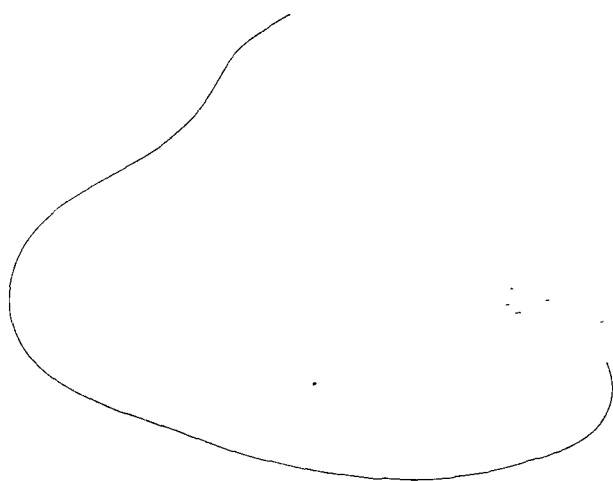
	(a)	(b)
<i>E. amygdalina</i>		
Pure Stands (n=40)	.60	.71
Ecotonal (n=60)	.64	.80
Hybrid Zone (n=40)	.61	.67
<i>E. risdonii</i>		
Pure Stands (n=40)	.34	.29
Ecotonal (n=60)	.32	.22
Hybrid Zone (n=40)	.27	.19
Hybrids (H) (n=40)	.50	.47

Table 6.13. Area means for the stand values of the assortive mating index ($S_{j,k}$; Appendix 2 - Table 1) for comparisons of the type indicated. (0 = no interpopulation crosses in the outcrossed seed from the maternal stand; 0.5 = random mating; P = pure species stands; Ec. = ecotonal stands; H.Z. = stands from hybrid zones).

Alien Stand Type (paternal)							
<i>E. amygdalina</i>				<i>E. risdonii</i>			hybrid
P.	Ec	H.Z.	P.	Ec	H.Z.	H.Z.	
Local Stand Type (maternal)							
<i>E. amygdalina</i>							
P.	.49	.39	.40	.24	.26	.13	.24
Ec	.44	.50	.35	.17	.21	.09	.28
H.Z.	.63	.46	.55	.3	.34	.22	.35
<i>E. risdonii</i>							
P.	.35	.13	.33	.49	.59	.56	.39
Ec	.25	.09	.25	.42	.51	.51	.31
H.Z.	.23	.07	.22	.40	.51	.51	.30
hybrid	.48	.44	.45	.43	.53	.49	.45

E. tenuiramis*E. risdonii**E. amygdalina*

Fig. 6.1. Geographical distribution of *E. risdonii*, *E. tenuiramis* and *E. amygdalina*. These species occupy suitable sites within the geographical area indicated (from Jackson 1965).



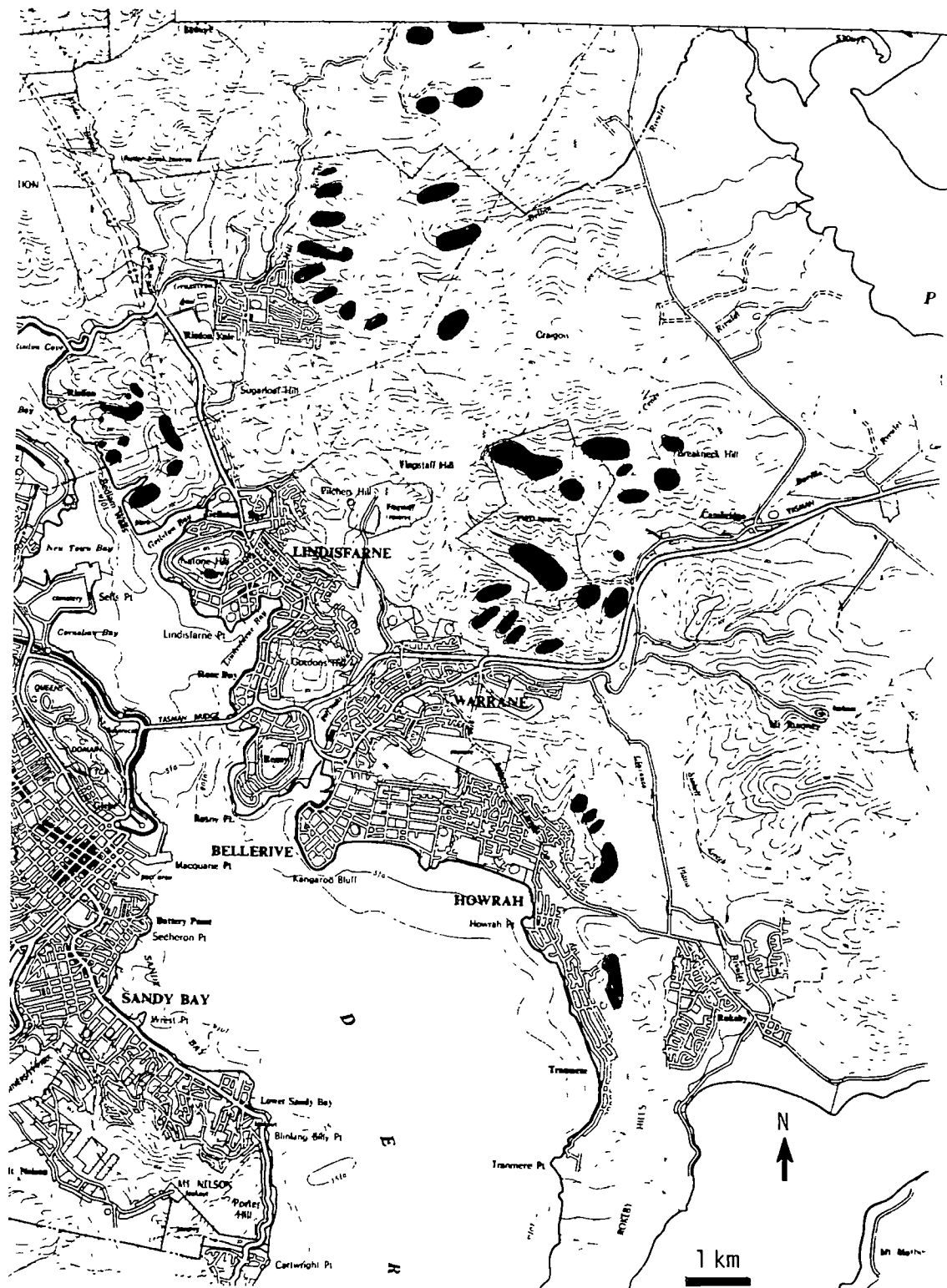


Fig. 6.2. The mosaic distribution pattern of *E. risdonii*. *E. risdonii* is restricted to the geographical area indicated, with the exception of several populations located just outside the northern limit of the map. It is confined to Permian mudstone substrates within this area and generally occupies steep highly insolated slopes. Distribution data was obtained from either aerial photographs or ground survey.

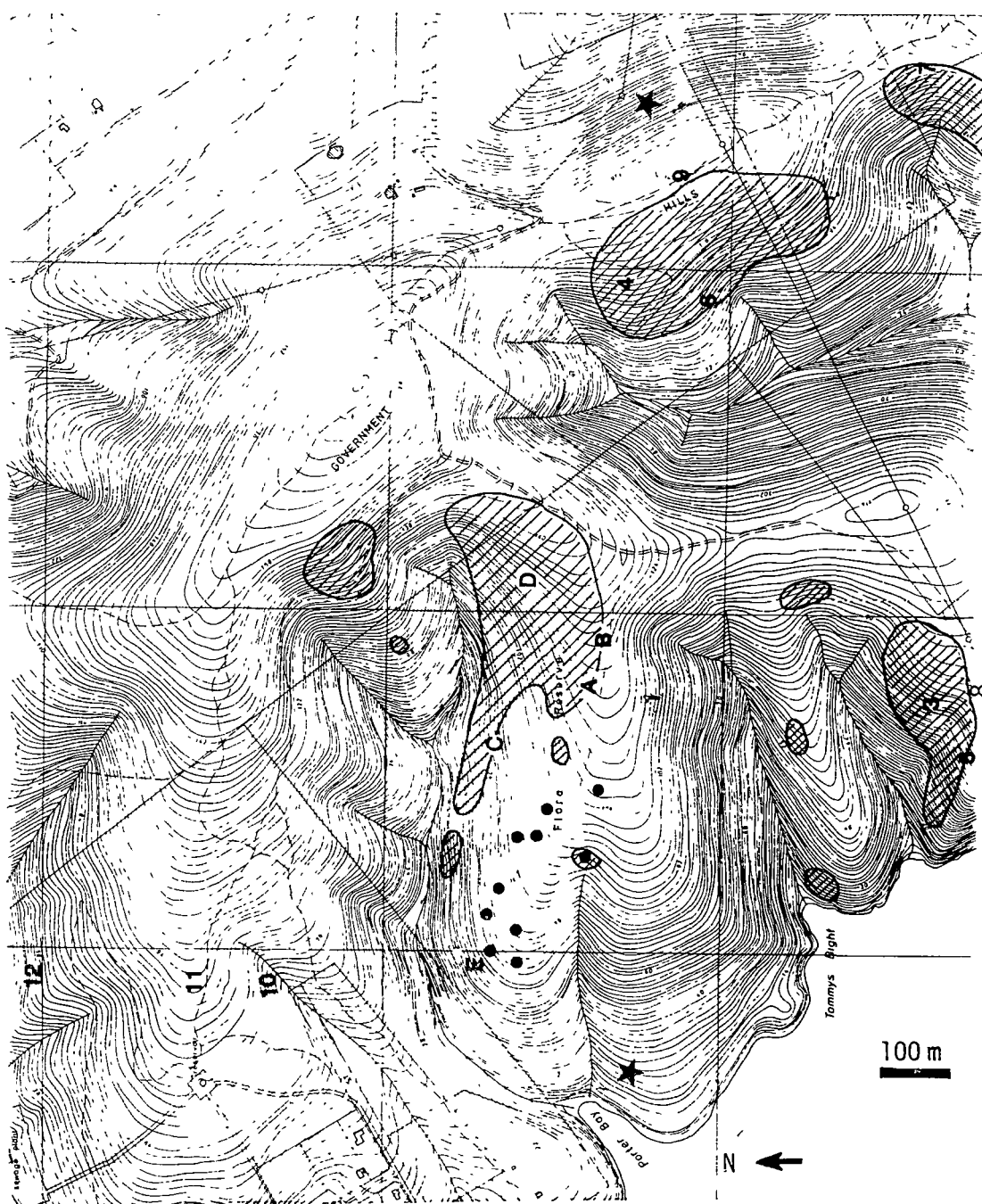


Fig. 6.3. The distribution of *E. resdonii* (cross-hatched) in the study area in the Government Hills, near Risdon. The sites sampled for the demographic survey (Chapter 7) are indicated and include the hybrid swarm (A and B), ecotone (C) and pure *E. resdonii* (D) and *E. amygdalina* (E) stand sites. Numbers correspond to sites sampled during the survey of flowering time (Chapter 6) and the SW and SE corners of the study area used by Nunez (1980; Fig. 6.4) are indicated (*). Dots indicate the location of small, isolated patches of high phenotypic diversity within the range of *E. amygdalina* which are discussed in Chapter 8 (i.e. Fig. 8.3). Sample site 2 was located approximately 100 m south of site 8.

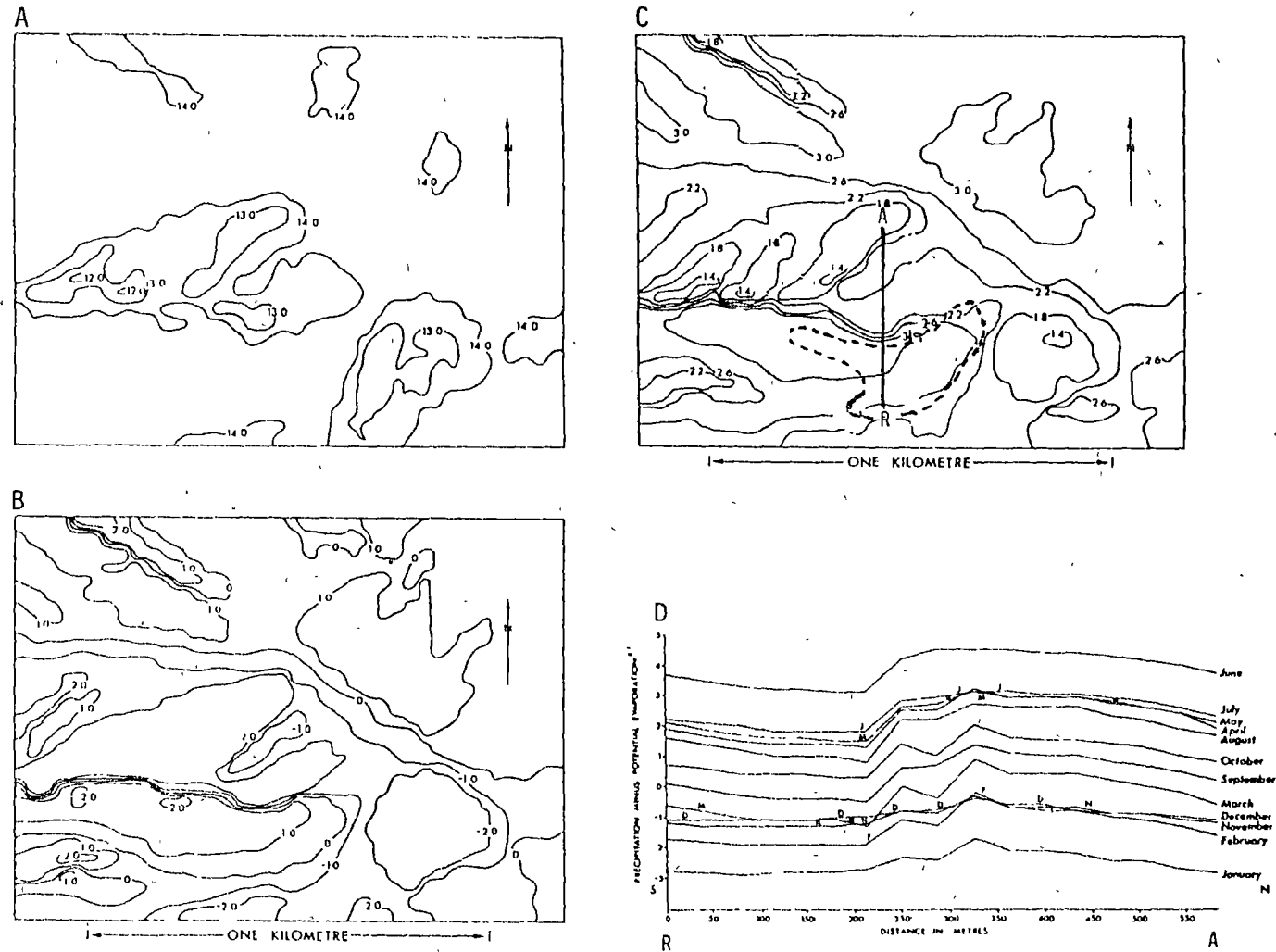


Fig. 6.4. Estimated mean daily net radiation incident on a unit surface ($\text{MJ m}^{-2} \text{day}^{-1}$) in (A) December and (B) June and (C) the yearly net radiation incident on a unit surface ($\text{MJ m}^{-2} \text{year}^{-1} \times 10^3$) for the study area (from Nunez 1980). (D) Monthly variation of precipitation minus potential evaporation 0.7 (cm) along the transect indicated in (C) (from Kirkpatrick and Nunez 1980). The location of the SE and SW corners of the area surveyed by Nunez (1980) are indicated in Fig. 6.3 and the boundary of the main *E. rusdonii* population is indicated in (C).

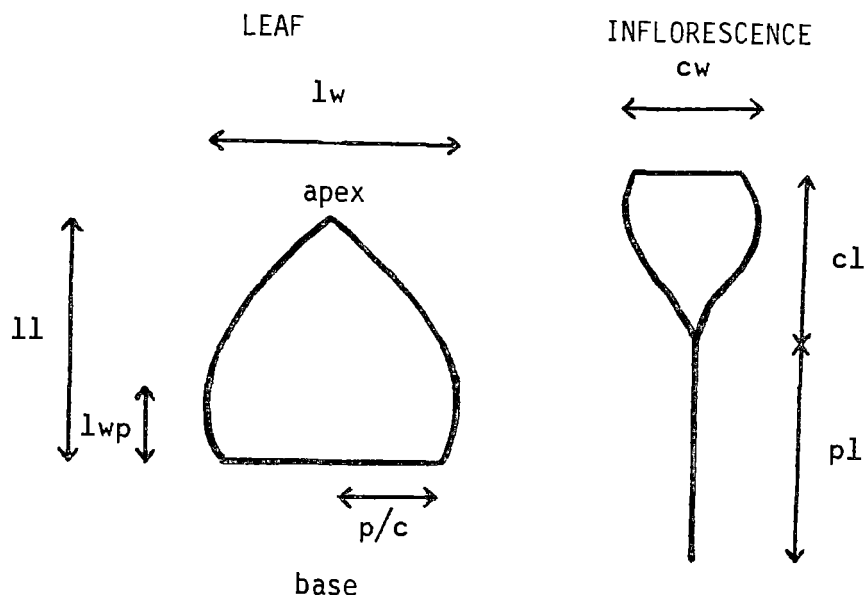


Fig. 6.5. Morphometric characters scored from adult *E. risdonii*, *E. amygdalina* and hybrid samples. P/C was a composite character with positive values describing petiole length and negative values describing the distance over which opposite leaves were joined. The petiolate and connate leaf conditions are mutually exclusive.

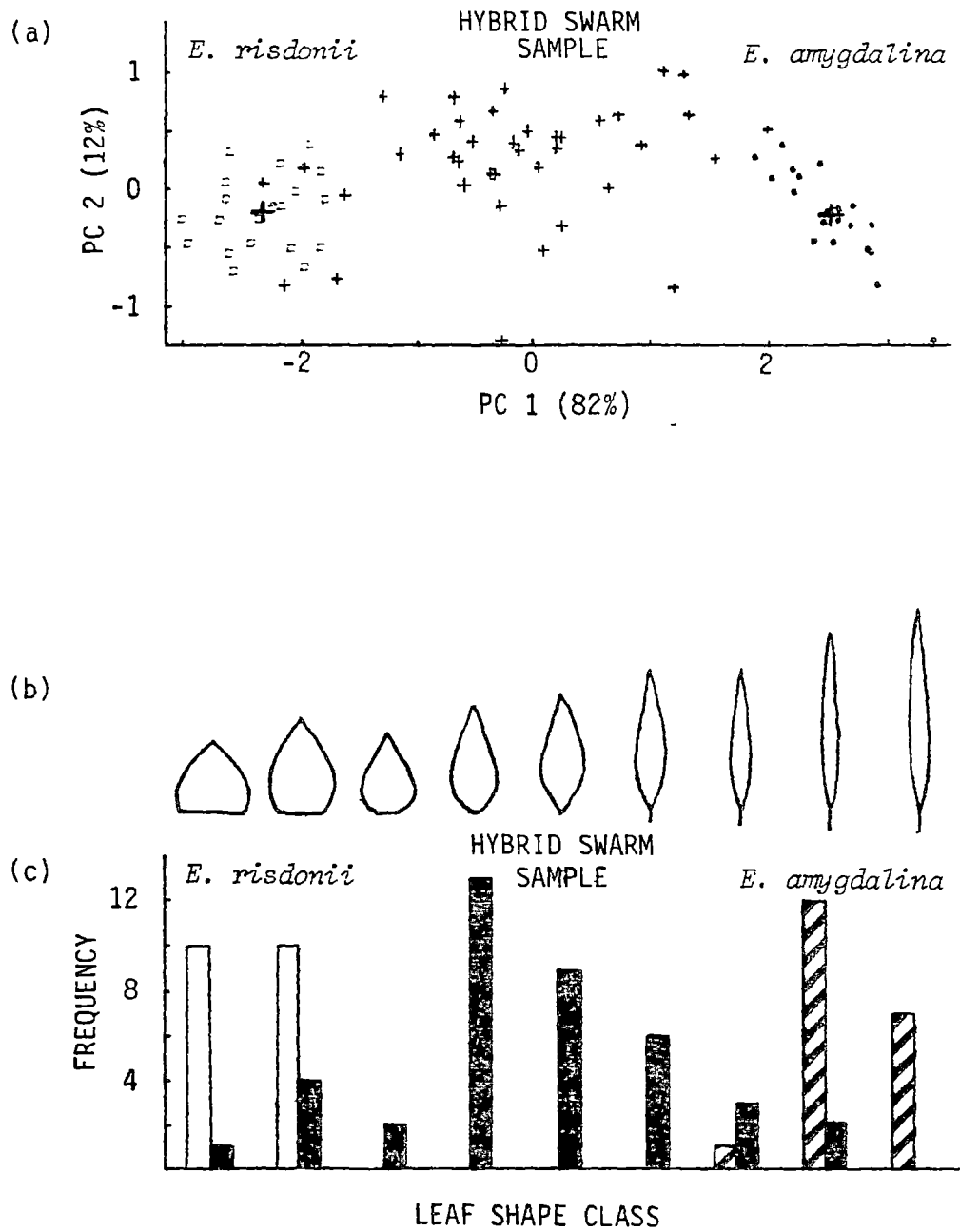


Fig. 6.6. Continuous variation in leaf morphology between *E. risdonii* and *E. amygdalina*.

- (a) PCA ordination of *E. risdonii* (\square), *E. amygdalina* ($*$) and hybrid (+) individuals.
- (b) Representative leaf idiograms of the continuum described by PC_1 .
- (c) Frequency histogram showing the number of individuals in each leaf shape class for *E. risdonii*, *E. amygdalina* and hybrid swarm samples.

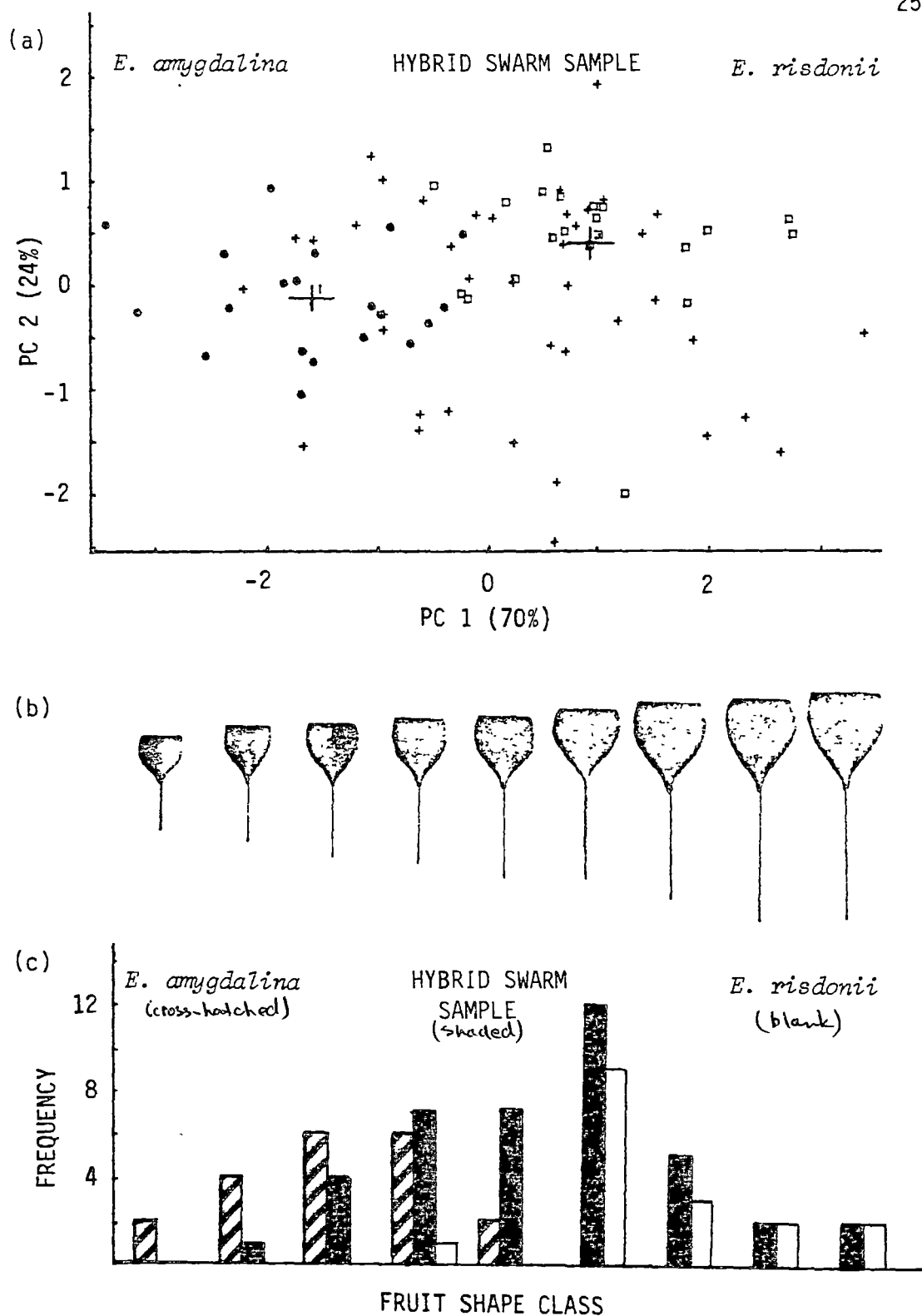


Fig. 6.7. Continuous variation in capsule morphology between *E. risdonii* and *E. amygdalina*.

- (a) PCA ordination of *E. risdonii* (\square), *E. amygdalina* (*) and hybrid (+) individuals.
- (b) Representative capsule idiograms of the continuum described by PC₁.
- (c) Frequency histogram showing the number of individuals in each capsule size class for *E. risdonii*, *E. amygdalina* and hybrid swarm samples.

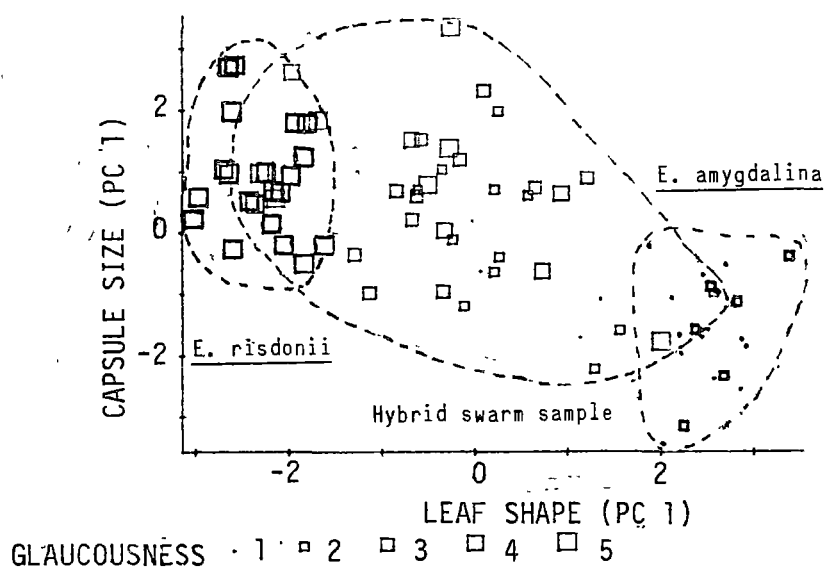


Fig. 6.8. Variation in leaf shape (PC_1 ; Fig. 6.6), capsule size (PC_1 ; Fig. 6.7) and degree of glaucousness. The degree of glaucousness is represented by the size of the glyph as indicated (1 = green; 5 = high glaucous). Dotted lines indicate the limits of *E. risdonii*, *E. amygdalina* and hybrid samples.

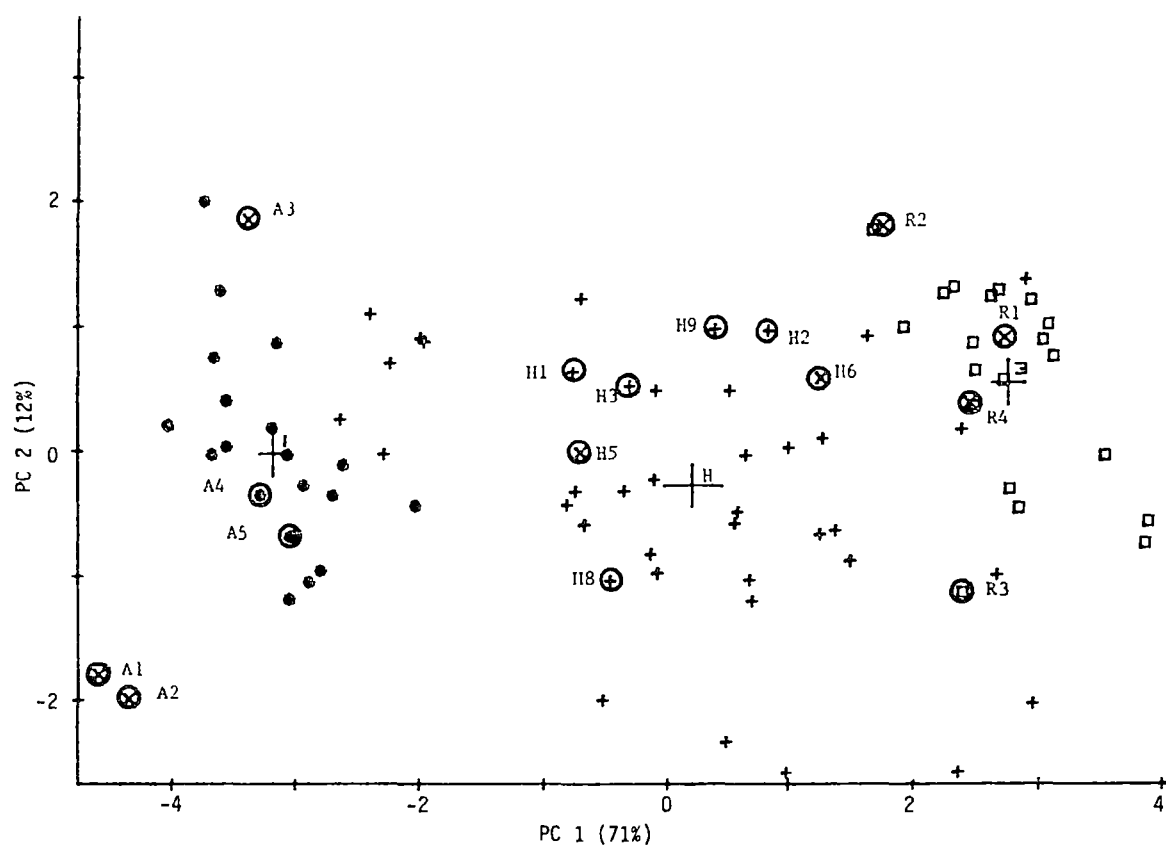


Fig. 6.9. PCA ordination (based on 8 characters) of *E. risdonii* (□), *E. amygdalina* (●) and hybrid phenotypes (+). Individuals used in the progeny trial are circled and codes correspond to Table 6.2. Those individuals which were not used in the initial analysis are indicated (X).

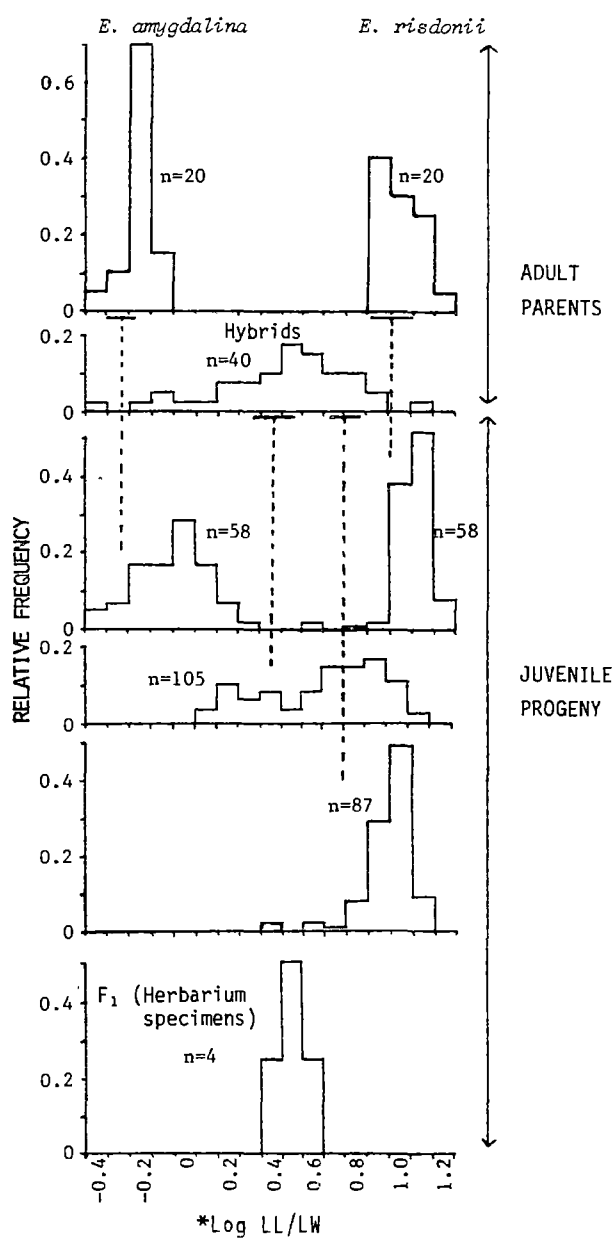


Fig. 6.10. Variation in leaf shape in adult samples and progenies. Leaf shape is measured on a log LL/LW scale and standardized so that *E. amygdalina* and *E. risdonii* have a grand mean of 0 and 1 respectively (see Table 6.3). Progenies are pooled from mothers of similar phenotype (i.e. R, A, H and RH morphological classes: Table 6.3).

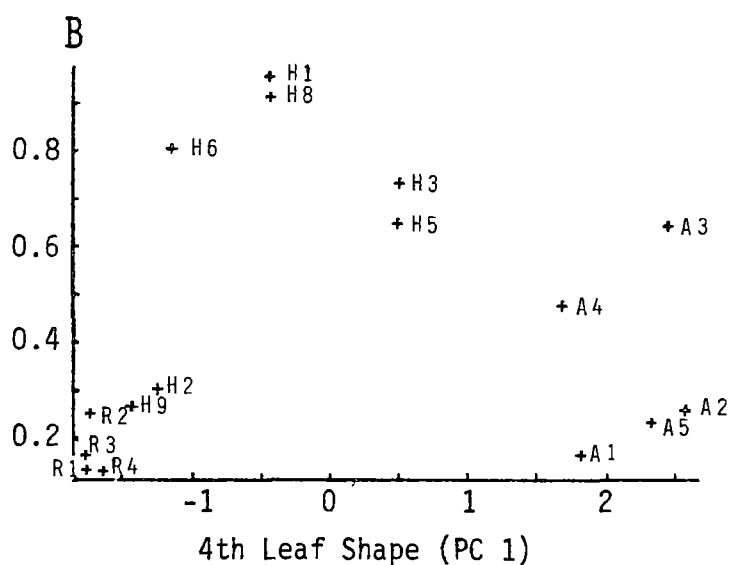
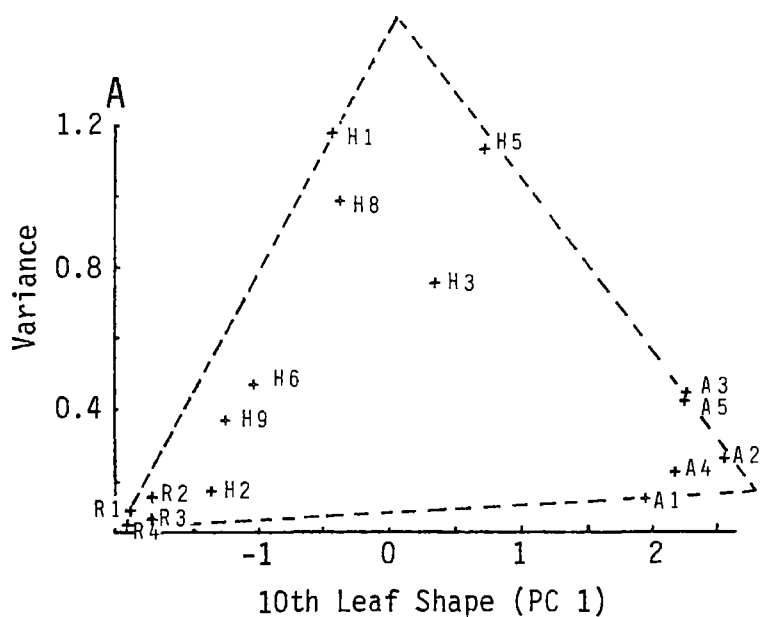


Fig. 6.11. Variation in leaf shape at the 10th (A) and 4th (B) nodes within progenies of *E. risdonii*, *E. amygdalina* and hybrids. Leaf shape is measured using the first principal component (TOT CORR; 11, lw, lwp, P/C) and the progeny variance is plotted against the mean value in the same manner as Clifford (1954).

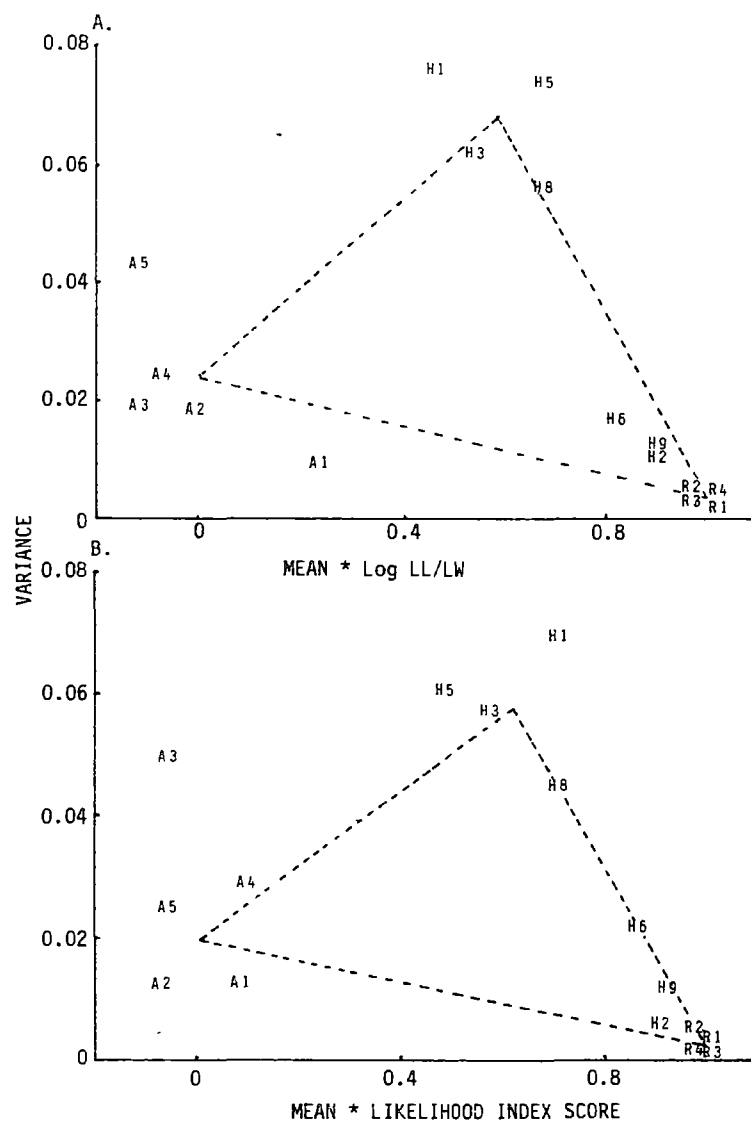


Fig. 6.12. Variance in (A) seedling leaf shape (i.e. standardized $\log LL/LW$ values) and (B) likelihood index scores plotted against the mean value (as in Fig. 6.11).

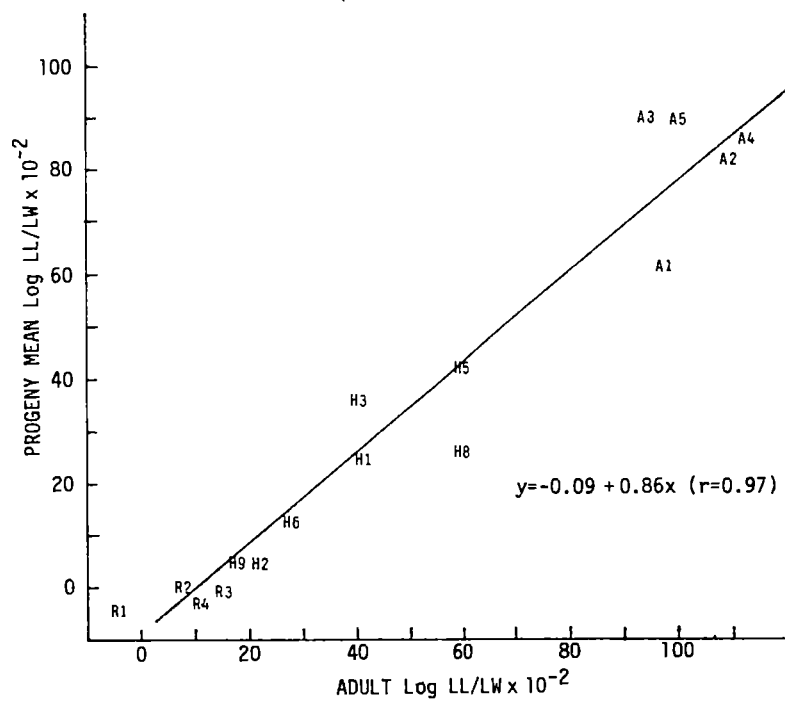


Fig. 6.13. The relationship between adult and seedling leaf shape as measured by log LL/LW.

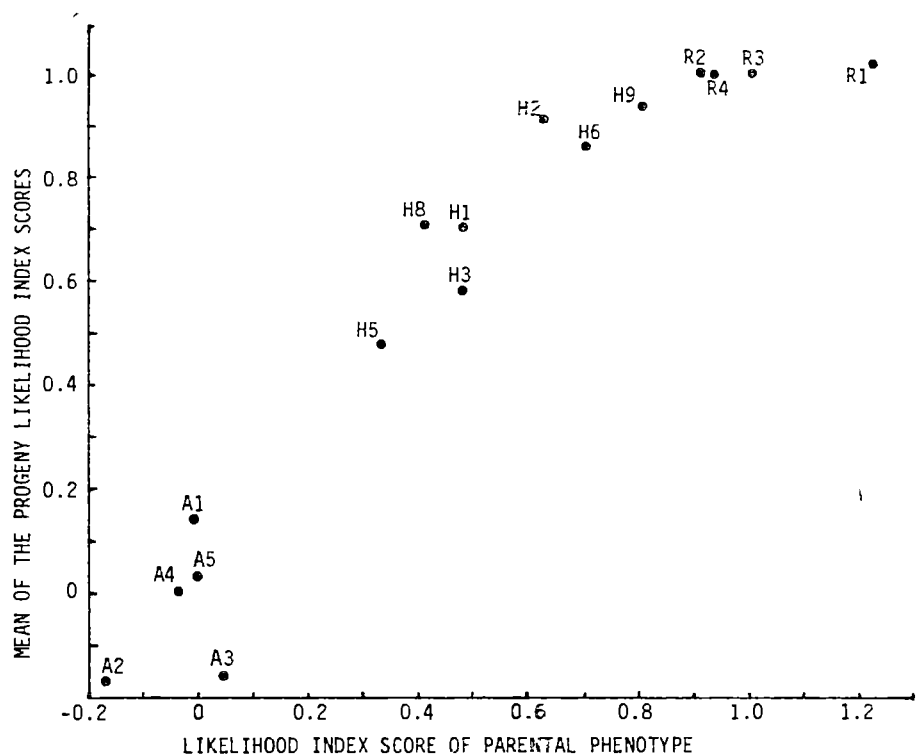


Fig. 6.14. Relationship between the adult and seedling phenotype. The mean value of the standardized likelihood index score for progenies plotted against that of the parents.

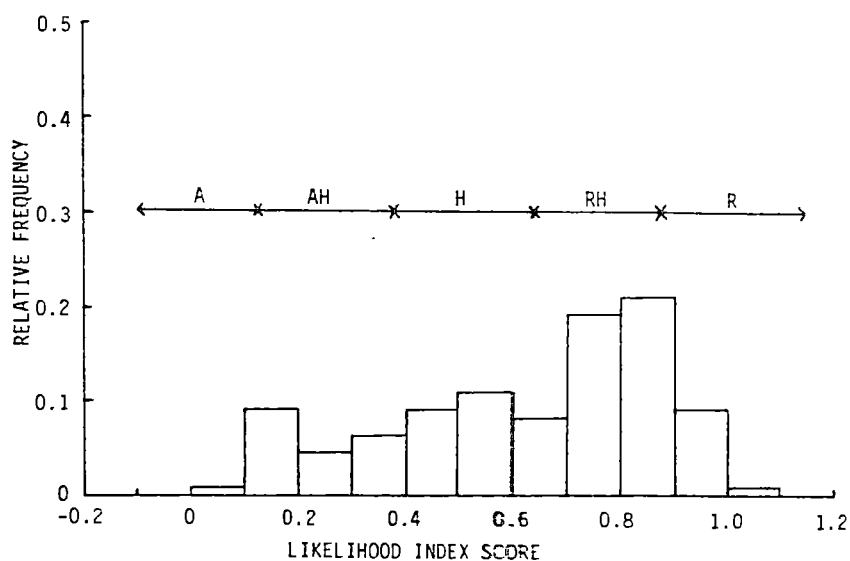


Fig. 6.15. Relative frequency histogram of standardized likelihood index scores from pooled progenies of intermediate (H_1 , H_3 , H_5 and H_8) mothers. The boundaries of phenotypic classes (A, AH, H, RH and R; see Table 6.3) are indicated.

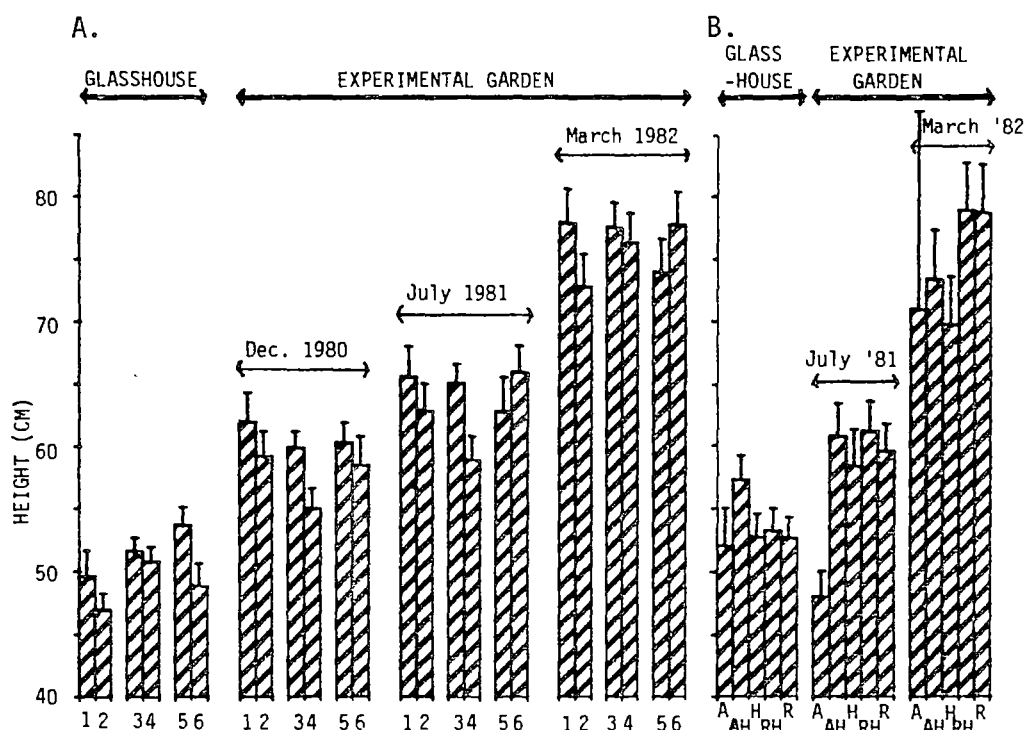


Fig. 6.16. (a) Mean seedling height (cm; \pm SE) in the glasshouse and experimental garden for pooled progenies of *E. risdonii* (centre $R_3, R_4 = \{n=33\} = 5$; margin $R_1, R_2 \{n=41\} = 6$), *E. amygdalina* (Risdon $A_3, A_4, A_5 \{n=59\} = 2$; Tinderbox $A_1, A_2 \{n=24\} = 1$) and hybrids (Intermediate (H) $H_1, H_3, H_5, H_8 \{n=81\} = 3$; RH types $H_2, H_6, H_9 \{n=54\} = 4$).

(b) Mean seedling height (cm; \pm SE) in the glasshouse and experimental garden of seedlings in each morphological class (see Fig. 6.15; Table 6.3) from the pooled progenies of intermediate (H) hybrid mothers (H_1, H_3, H_5, H_8).

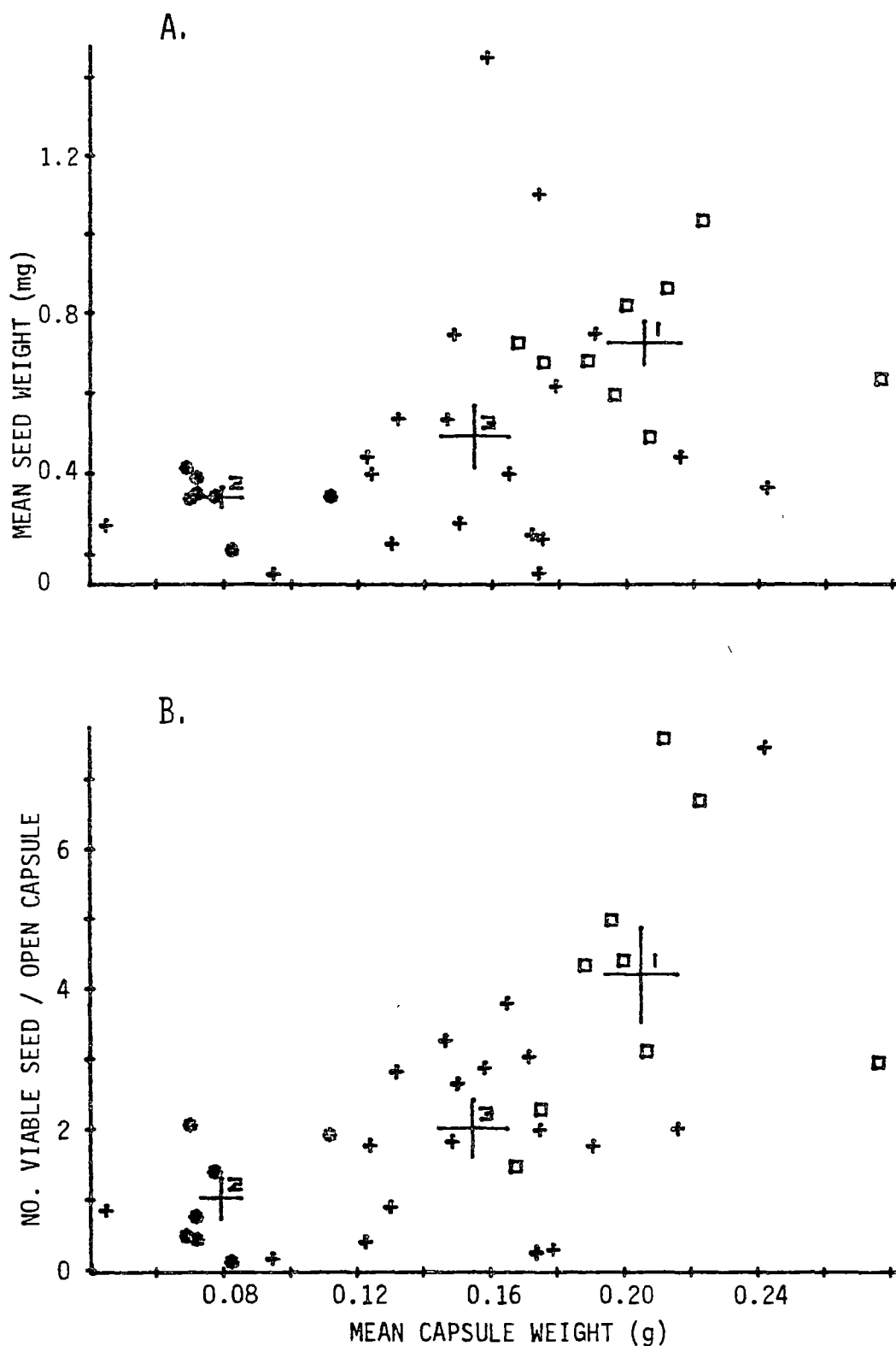


Fig. 6.17. Weight of seed (mg;A) and number of viable seed per open capsule (B) plotted against capsule weight (g) for *E. risdonii* (\square ,1), *E. amygdalina* (*,2) and hybrid swarm (+,3) samples. Sample means (\pm SE) are indicated.

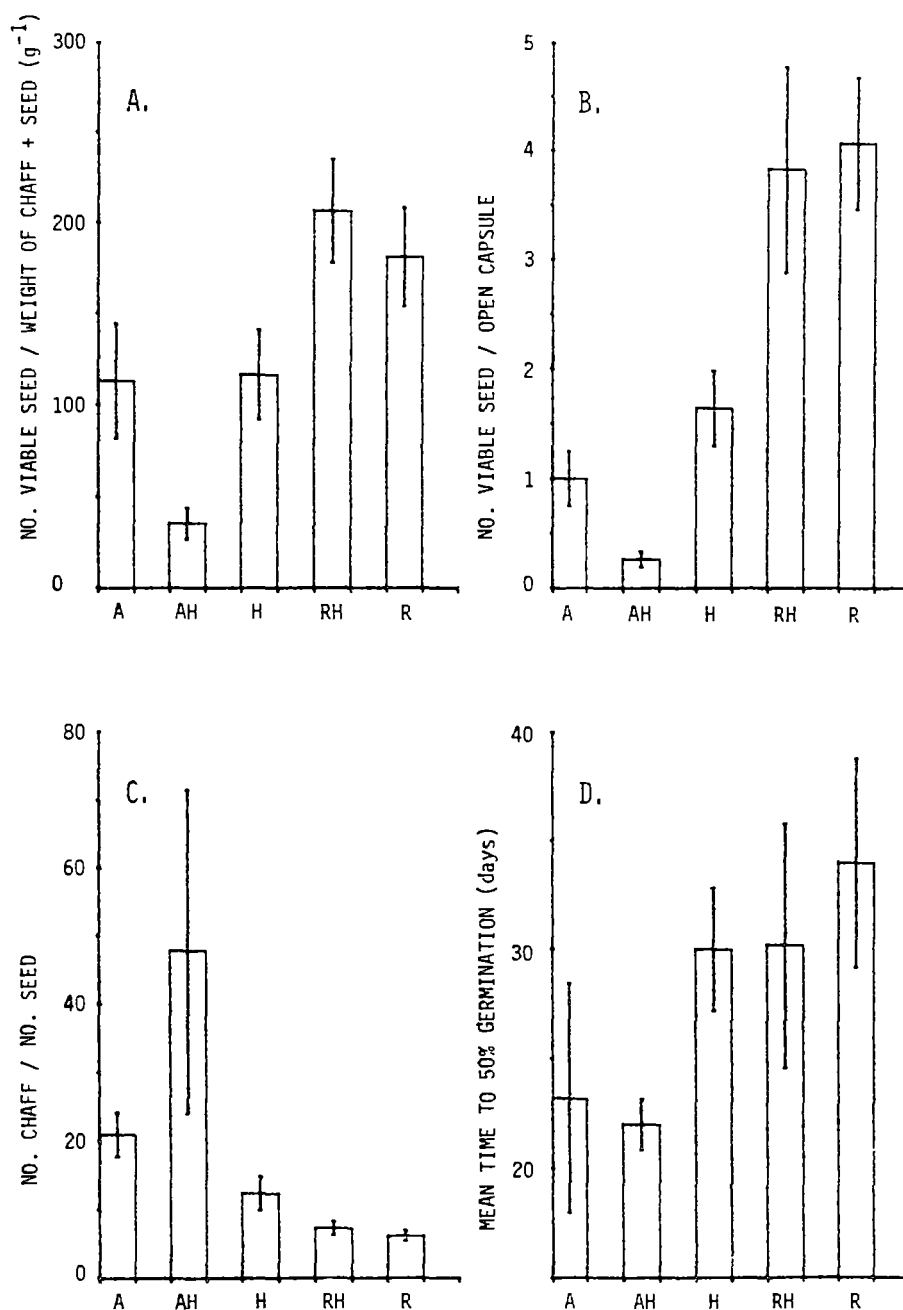


Fig. 6.18. Mean (\pm SE) seed output parameters for each morphological class. (a) The number of viable seeds per weight of chaff and seed. (b) The number of viable seed per open capsule. (c) The number of chaff per seed (viable & inviable). (d) Time (days) for 50% germination, calculated over the total number of seed germinated during the trial. Individuals were classified into morphological classes based on their adult likelihood index scores using the criteria given in Table 6.3.

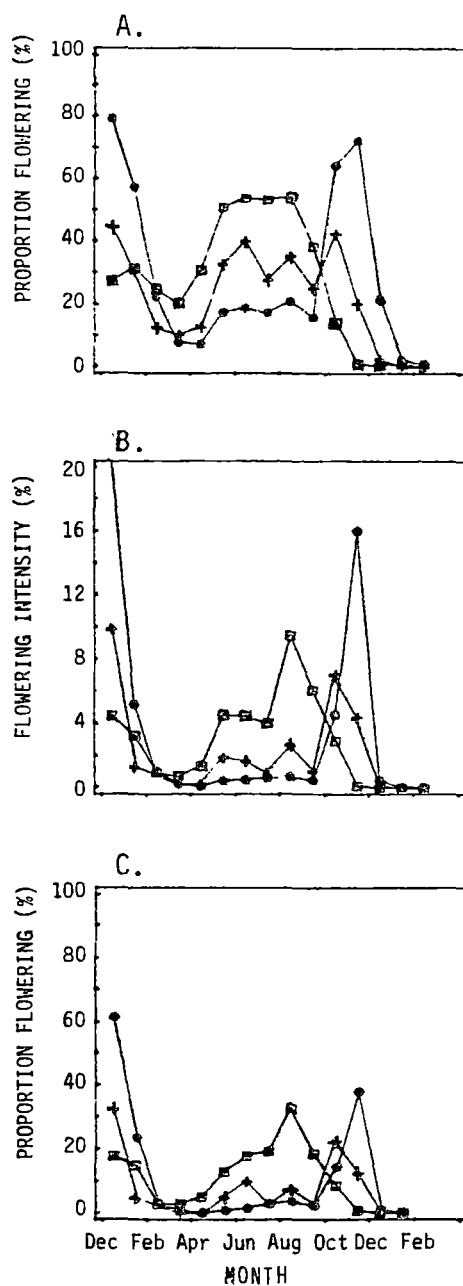


Fig. 6.19. The flowering behaviour of *E. amygdalina* (\square , $n=140$), *E. risdonii* (\bullet , $n=140$) and hybrid ($+$, $n=40$) trees over the period from December 1980 to February 1982. (a) The proportion of trees observed flowering. (b) The mean value of estimates of the relative proportion of buds in flower. (c) The proportion of trees observed flowering heavily (i.e. bud abundance scores greater than 1 and at least 10% of the buds in flower).

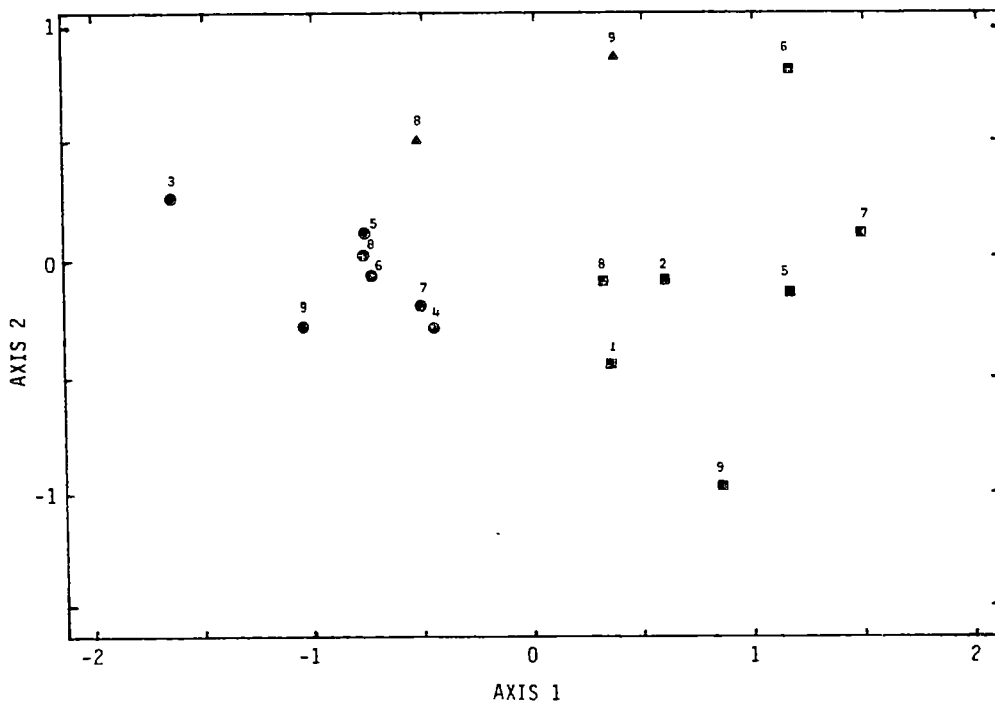


Fig. 6.20. Non-metric scaling ordination of *E. amygdalina* (■), *E. risdonii* (●) and hybrid (▲) stands based on flowering data (S_{ij}). Site numbers correspond to those in Table 6.10. The distances from one point to all others are in the same rank as the assortive mating index scores (S_{ij}) and thus are indicative of the inherent probability of populations acting as pollinators of the reference site when spatial considerations are ignored.

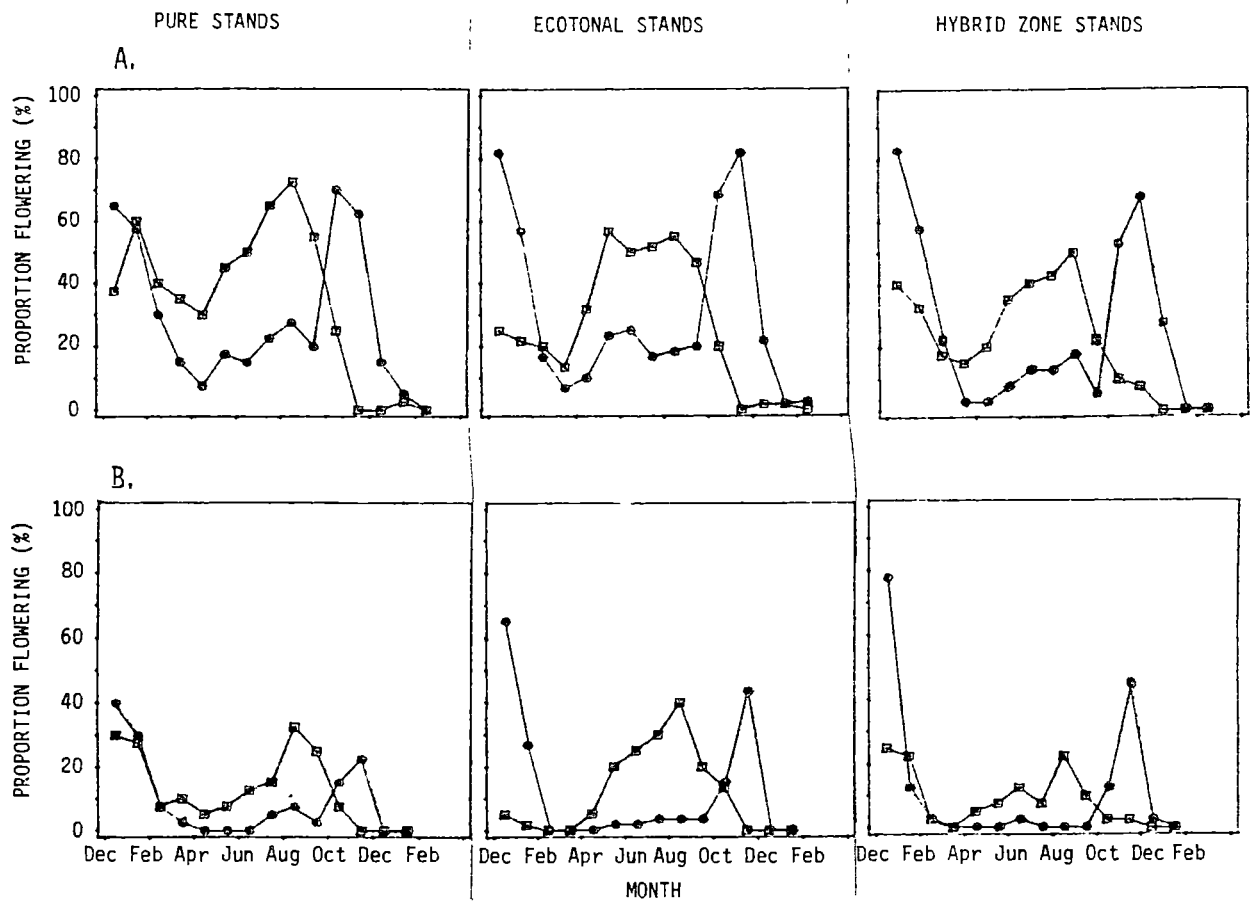


Fig. 6.21. The proportion of *E. amygdalina* (□) and *E. nrisdonii* (*) trees (a) flowering and (b) flowering heavily in stands from pure species (n=40), ecotonal (n=60) or hybrid zone (n=40) sites.

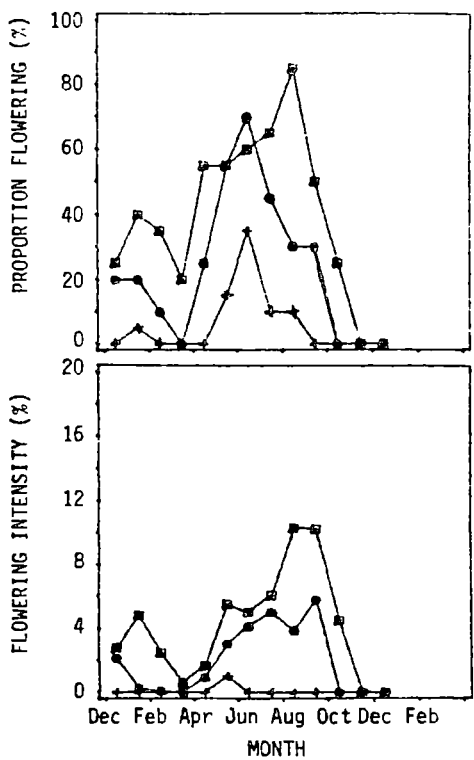


Fig. 6.22. Variation in flowering with aspect in *E. amygdalina*. Samples are from a south-east slope (□), ridge top (*) and north-west slope (+) stands (i.e. Fig. 6.3; sites 10, 11 and 12 respectively).

CHAPTER 7

The dynamics of hybridization between *E. risdonii* and *E. amygdalina* II. The competitive interaction of *E. risdonii*, *E. amygdalina* and their hybrids.

7.1 Introduction

The study area, including the hybrid swarm discussed in the previous chapter was burnt by a wildfire in February 1980. In the present chapter, the competitive interaction of *E. amygdalina*, *E. risdonii* and their hybrids is investigated by a comparative study of mortality, vegetative regeneration, reproductive output and seedling recruitment following this fire.

The significance of fire in the natural regeneration of *Eucalyptus* is well documented (e.g. Jacobs 1955; Gilbert 1958; Jackson 1968; Mount 1964, 1969, 1979; Gill 1975; Pryor 1976; Withers and Ashton 1977; Cremer *et al.* 1978; Ashton 1981b; Noble 1982) and in the study area Kirkpatrick and Nunez (1980) suggest^{that} there is little recruitment of eucalypt seedlings except after fire. In most eucalypts, seed is gradually shed over a 2-4 year period after ripening (e.g. Mount 1969; Cremer 1965a,b), although in the absence of fire seedling establishment is rare (e.g. Henry and Florence 1966; Onans and Parsons 1980; Duncan 1981). A pulse of seedling establishment often occurs after fire following the accelerated release of seed stored in the canopy coupled with temporary removal of competition from understorey species and pre-established eucalypts, release of nutrients and possible removal of pathogens and predators (see Mount 1964, 1969, 1979; Cremer *et al.* 1978; Ashton 1981b and references cited therein). Soil storage of seed is negligible (see Carr 1972; Drake 1981b) and the availability of seed following fire depends on the survival of the aerial 'seed bank' (e.g. Mount 1969; Ashton 1981b; Noble 1982). The extent of seedling establishment may vary considerably depending on numerous factors (see Mount 1969, 1979; Noble 1982) and where mixtures of species occur, their seedling proportions may depend on the relative seed supply in the crowns (e.g. White 1974). Drake (1981b) develops the argument that, where there is competition for a limited number of safe sites for seedling establishment, the taxon with the greatest probability of success is the one with the greatest number of seed available for dispersal to the soil surface.

The eucalypt vegetation of the Government Hills includes both open dry sclerophyll forest and low mallee. The latter vegetation type dominates the dry north-facing slope and in the specific areas studied (Fig. 6.3; sites

A,B,C,D and E), the majority of individuals were multistemmed 'whipstick' mallees 1-4 m high. However, neither *E. amygdalina* nor *E. risdonii* is genetically of the mallee habit and the extensive distribution of this form appears to be a result of the combined effects of a severe environment and a high fire frequency. Studies of the regeneration of mallee eucalypts clearly emphasize the significance of fire for seedling establishment (e.g. Zimmer 1940; Parsons 1968b; Holland 1969; Pryor 1976; Onans and Parson 1980; Noble 1982) and Noble (1982) notes that eucalypt seedlings are practically non-existent in most mallee communities except after fire. In mallee vegetation, fires generally result in the death of stems, and seedling establishment is possibly stimulated by a reduction in the community transpiration rate and competition with pre-established forms (e.g. Zimmer 1940; Parsons 1968b; Noble 1982). However, few individuals are actually killed by fire and the majority rapidly regenerate vegetatively from lignotubers (e.g. Zimmer 1940; Jacobs 1955; Holland 1969; Noble 1982). Noble (1982) suggests ^{that} "the regenerative strategy of burnt mallee depends on rapid refoliation to produce the pre-fire photosynthetic surface area as quickly as possible." Similarly, in most dry sclerophyll forests, the mature stand is seldom completely killed by wildfire and recovers vegetatively from lignotuber or epicormic shoots (Jacobs 1955; Pryor 1976). Accordingly, seedlings which become established following fire are usually rapidly suppressed by the more vigorous vegetative regrowth. Survivors are assimilated into a dynamic regeneration pool of suppressed lignotuberous seedlings (e.g. Jacobs 1955; Henry and Florence 1966). Stands are invariably multi-aged although for mallee, stems as opposed to individual genotypes may frequently be even aged, and successful recruitment appears to depend on adult mortality (Noble 1982).

The extent of damage by the 1980 fire in the study area is indicated in Fig. 7.1. The fire, fanned by gusty, NW winds, burnt rapidly up the north slope through the low mallee vegetation and dropped to a ground fire when burning more slowly down the south slope. The crowns generally remained undamaged in the open forest with only the understorey shrubs and saplings burnt. However, on the northern slope virtually all stems were killed, although the rapid passage and relatively low intensity of the fire resulted in very few crowns being totally consumed and a large portion of the foliage and capsule crop was unburnt and retained on the stems after the fire. The ridge area, including the site of the hybrid swarm (Fig. 6.3, sites A and B) represented a transitional area where all crowns were killed but subsequent regeneration varied coming from lignotubers or epicormic

buds, depending mainly on stem diameter. The area appeared to have been burnt in a similar manner in 1960/1961 and ring counts and the absence of fire scars suggested that most stems on the northern slope were lignotuberos regeneration from this fire. Based on the presence of fire scars on stems in the ridge area, it appears successive fires are gradually extending the area occupied by forms regenerating from lignotubers and thus gradually reducing the area supporting fire protected stems or canopy in the manner indicated by Lacey (1983).

7.2 Methods

Initial seedling establishment

A series of 3 x 50 m transects was established along the species' boundary and in pure species stands to monitor initial seedling establishment (Fig. 7.1; 1-11). All transects were scored in October and December, 1980, and transects 1, 3 and 4 (Fig. 7.1) were scored in July. At each site, the position and microhabitat preference of each cotyledonary seedling was scored.

The number of surviving seedlings from the previous scoring as well as the number of new recruits could be identified and mortality and recruitment rates calculated.

Demographic survey

A series of permanent quadrats was established to estimate the reproductive and vegetative vigour, the distribution of lignotuber size classes of the phenotypic classes indicated in Table 6.3 (i.e. R, RH, H, AH, A and V) as well as to monitor vegetative regeneration and seedling establishment. These quadrats were located on the ridge in the hybrid swarm (Fig. 6.3 - site A {40 x 60 m²}; site B {20 x 20 m²}, along the species boundary on the north slope (Fig. 6.5; site C {20 x 80 m²}). and in pure stands of either species (Fig. 7.1; sites D and E {10 x 50 m²}). The quadrat at the boundary on the north slope was subdivided into 20 x 20 m² subplots, each of which was centred on the boundary between *E. risdonii* and *E. amygdalina* and results were pooled. The main quadrat in the hybrid zone (site A; 40 x 60 m²) was centred on an area of high phenotypic diversity so as to include a wide array of phenotypes from a single localized area. Quadrats were scored in the autumn of 1981 and for each individual all characters listed in Table 7.1 were scored as well as its position in the coordinate system of each quadrat. In addition, the position, height and phenotype of each seedling established following the 1980 fire was

recorded although it was only possible to accurately classify seedlings into three phenotypic classes (i.e. *E. amygdalina* A and AH; hybrid H; *E. risdonii* (RH and R). At the time of scoring a large portion of the foliage and capsule crop was still retained on the dead stems and individuals established prior to the fire were subjectively classified into phenotypic classes following Table 6.3 on the basis of adult (dead leaves and capsules, etc.) and coppice morphology. In addition a single typical tenth node leaf was measured from the coppice of all abnormal (i.e. non-pure species) phenotypes (RH, H and AH; Table 6.3) and random samples of the pure species (i.e. A and R) were measured at each site. Coppicing involves a reversion to the juvenile leaf shape and thus leaf shapes were comparable to the glasshouse grown seedlings and genetic affinity was measured on the same scale as in Fig. 6.10 (i.e. $\log LL/LW$). To obtain a sufficient sample for estimating the demographic structure of the pure species stands (sites D and E) lignotuber diameter was also scored from an adjacent 10 x 50 m quadrat. Individuals in the largest lignotuber size class in this quadrat were also scored for the complete data set to increase replication. With the exception of the hybrid swarm site B (20 x 20 m) and the southern section of the main hybrid swarm quadrat (site A) all stems were killed in the 1980 fire with the vast majority also killed in the previous fire in 1960/1961. An estimate of productivity over a 20 year period was therefore obtained from individuals which had all above ground biomass killed in 1960/1961 by measuring the basal area of dead stems arising from each individual lignotuber. The demographic study involved nearly 2000 individuals and for comparisons between phenotypic classes, individuals were grouped into four lignotuber size classes (0-21 cm (saplings); 21-42 cm; 42-63 cm; greater than 63 cm). The number of replicates for each phenotype in each lignotuber size class is indicated in Table 7.2 and corresponds to the level of replication used for comparing phenotypes and represents the frequency of each class in the quadrats sampled.

Estimation of seed output

An indication of the fitness of the phenotypic classes was obtained from the estimates of the relative contribution to the seed rain following the 1980 fire. Comparisons are thus made at a time when, due to the episodic nature of the regeneration process, there is the maximum likelihood of contributing to a subsequent generation. Seed output was estimated from the number of capsules retained on the stems or branches after the fire and estimates of the mean number of viable seed per capsule for each phenotypic

class obtained from the germination trial discussed in Chapter 6 (see Table 7.3). For the calculations it is assumed that the latter does not vary with either lignotuber size or site, although the possibility of variation in fire intensity affecting seed viability, possibly differentially, in undamaged capsules requires investigation. A large portion of the capsule crop was retained on the stems after the fire due to the rapid death of the stems preventing abscission layers being formed (see Cremer 1965a). Seed enclosed in capsules shed during the fire or prior to the capsules opening is unlikely to be significant as Cremer (1965a) notes enclosed seed probably produces relatively few seedlings. Losses following the fire were generally associated with fallen branches or stems and in most cases their origin was readily apparent and attached capsules were included in the count. Examination of capsules on the ground in the boundary quadrats indicated no obvious differential loss of capsules by either *E. amygdalina* or *E. risdonii*.

Comparison of phenotypic frequencies

Comparisons of phenotypic frequencies in the seedling cohort with that in the adult population necessitated the pooling of parental and backcross mature phenotypes as these classes could not be accurately differentiated at the seedling stage. Expected phenotypic frequencies in the seedling cohort were calculated from the estimated proportion of seed released by each phenotypic class following the fire. For the hybrid zone sites (A,B) a crude adjustment was also made for segregation and backcrossing on the basis of the data presented in Fig. 6.15 and Table 6.7 (i.e. A+AH adult→13%H, 87%A+AH; H adult→23%A+AH, 25%H, 50%RH+R; R+RH adults→1.3%H, 98.7%R+RH). All frequency data were tested using the χ^2 test.

7.3 Results

Reproductive and vegetative fitness

Reproductive output

At both the ecotone (site C) and hybrid zone (site A) sites, the number of capsules on *E. risdonii* (R) individuals was in general significantly ($P<0.001$) greater than for either *E. amygdalina* (A) or the hybrids for virtually all lignotuber size classes (Figs. 7.2 and 7.3). Furthermore, the number of capsules on backcross phenotypes (RH and AH) was generally significantly ($P<0.05$) less than on the corresponding parental phenotype, although usually greater than on the intermediate phenotype (H) at the hybrid zone

site (Fig. 7.2). For the majority of comparisons at the hybrid zone (site A; Fig. 7.2), the number of capsules on parental types significantly ($P < 0.001$) exceeds the number on the intermediate phenotype. However, at the ecotone site this was only the case for *E. risdonii* and a significant difference between the intermediate and *E. amygdalina* phenotypes was only apparent for the 42-63 cm lignotuber size class. The number of capsules on *E. amygdalina* at both the ecotone and hybrid zone site was usually significantly less ($P < 0.001$) than the corresponding lignotuber size class from the pure species stand. In contrast there is no significant difference between *E. risdonii* from the pure species stand or ecotone site but at the hybrid zone site there is a significantly ($P < 0.001$) greater number of capsules on the older *E. risdonii* (42-63 and 63+) than in the pure stand (Fig. 7.2). These trends are not a result of differences in biomass and are still apparent for the number of capsules per unit basal area (e.g. Fig. 7.4) as well as when the few individuals in the hybrid zone which regenerated from epicormic shoots after the 1960/61 fire are excluded.

In terms of the estimated seed output following the 1980 fire, there is a marked fitness differential at the species boundary, with *E. risdonii* consistently superior to all other phenotypic classes (Table 7.4). The backcross class (RH) resembling *E. risdonii* surpasses *E. amygdalina* (A) in reproductive output but is consistently less fit than pure *E. risdonii* (R). The fitness of the intermediate hybrid (H) is comparable with *E. amygdalina*. The marked reduction in seed output by the larger *E. amygdalina* at the boundary is particularly significant in view of the fact that in pure stands, capsule production is dominated by individuals from the larger lignotuber size classes (Figs. 7.2 and 7.3). This is the case for virtually all comparisons and clearly indicates that the seed rain of a given taxon is generally monopolized by the relatively few dominant individuals in the stand (Figs. 7.2 and 7.3; Table 7.4b), due mainly to differences in biomass (e.g. Fig. 7.4). Nevertheless differences in biomass (e.g. basal area, number of stems - Table 7.5) does not account for the much greater seed output of phenotypes tending toward *E. risdonii* (R and RH) at the boundary between the two species. The mean number of seed per capsule is not available for *E. viminalis*, but even with a conservative estimate, the reproductive fitness of *E. viminalis* in the boundary quadrats can be considered as zero. This is due to virtually no capsules being retained on *E. viminalis* on the northern slope following the fire (Table 7.5). Differences in fire intensity and thus differential capsule destruction could possibly account for differences between phenotypes from different sites although this would not effectively account for the differential response nor the variation between phenotypes

at the boundary sites. The differences in estimated seed output between phenotypes and sites most likely reflect differences in reproductive effort (Drake 1981a) and observations when the morphometric collections were made from the hybrid swarm indicated *E. risdonii* had a greater capsule crop prior to the fire than *E. amygdalina*. Furthermore, similar trends are apparent in Table 6.10 from scoring the relative frequency of individuals without mature capsules at unburnt sites.

Vegetative vigour

An integrated measure of productivity over a 20 year period was obtained from a comparison of the total basal areas of stems representing lignotuber regeneration from the last fire (1960/1961) (Figs. 7.3 and 7.5).

E. risdonii was consistently ($P < 0.001$) more productive than *E. amygdalina* at the ecotone site (C) (Fig. 7.3), a trend which was also evident, but not significant in the hybrid zone (B) (Fig. 7.5). The larger lignotuber size classes of *E. risdonii* (i.e. 42-63; 63+) were significantly more productive at both boundary sites (A, $P < 0.05$; C, $P < 0.001$) than in the pure stand (D). In contrast, when the difference between *E. amygdalina* at the boundary and pure species stand (E) was significant ($P < 0.05$; i.e. Fig. 7.3), this involved a decrease in the productivity of *E. amygdalina* at the boundary. In most cases there was no consistent difference between the hybrids and parental classes from the same site, although at both sites there is a trend for the AH phenotype in the 21-42 cm lignotuber class to be the least productive.

There is no evidence for selection against *E. risdonii* saplings (e.g. Figs. 7.6, 7.7) or adults (e.g. Fig. 7.7) in the areas examined on the north slope and ridge dominated by *E. amygdalina*. In fact, isolated saplings of *E. risdonii* 20 meters from the boundary on the north slope (site C) appeared to be more vigorous than the surrounding *E. amygdalina* (Fig. 7.7), with no microhabitat difference obvious. In contrast, in *E. risdonii* dominated areas, *E. amygdalina* is subordinate with little reproductive potential (Fig. 7.7). Considerable areas of *E. amygdalina* on the ridge and west of the boundary across the north slope were noted to show a similar reduction in vigour to that demonstrated in Fig. 7.7. Such variation in vigour suggests that *E. risdonii* is currently favoured in some areas outside its present range and the population might be expected to be expanding.

Regeneration following the 1980 fire

Mortality

There was significantly greater ($P < 0.05$) mortality following the 1980 fire in the hybrid swarm site (B) than at the ecotone site (C) and there was no significant difference between pure species stands which were comparable with the hybrid zone site (Table 7.6). In the hybrid swarm, mortality was differentiated with a significantly greater ($P < 0.001$) proportion of *E. amygdalina* (A) and *E. viminalis* (V) individuals killed than *E. risdonii* or the backcross hybrid phenotypes (Table 7.7). This trend was evident but not significant at the ecotone site (C, Table 7.7). Pooled over all quadrats, there was no indication of age dependent mortality in *E. amygdalina* whereas a significantly greater ($P < 0.01$) proportion of *E. viminalis* individuals were killed with a lignotuber diameter greater than 21 cm.

Differential mortality of *E. amygdalina* and *E. viminalis* was not confined to the 1980 fire, but was evident in individuals scored as having been dead prior to the fire. In particular, the northern slope was scattered with large dead *E. viminalis* emergent above the low canopy and many of those killed in the fire were already dying. The existence of such large stems on the north facing slope attests to a previous fire-free interval of greater than 20 years. Survival of the stem and regeneration from epicormics was generally dependent on stem size. However, observations suggested a tendency for *E. viminalis* stems to be more fire resistant than comparable size stems of the *Piperitae* species and this appeared to be associated with *E. viminalis* having a thicker bark. Rarely did any 20 year old stems survive the 1980 fire suggesting a greater fire-free interval would be necessary for *E. viminalis* to achieve sufficient diameter to survive recurrent firing and achieve the diameter of these emergents.

Vegetative Recovery

The vast majority (97%) of individuals survived the death of all the above ground biomass by lignotuber regeneration. The 'average' height of the coppice regeneration from each lignotuber was used as a measure of the potential to vegetatively recover from fire and achieve height dominance (Fig. 7.8) and virtually identical results were obtained using the maximum coppice height. The coppice of *E. risdonii* was significantly ($P < 0.001$) higher than *E. amygdalina* in the boundary sites for most comparisons (Fig. 7.8). This trend was associated with a significant reduction

in the height of *E. amygdalina* coppice in boundary sites (particularly in the hybrid swarm) in comparison to the pure species stand. This reduction was not evident in *E. risdonii*, and is similar to the trend noted for capsule number. Coppice from the pure *E. amygdalina* stand was generally higher than the pure *E. risdonii* stand (Fig. 7.8). This was also reflected in the maximum stem height of the 20 year old regrowth (Table 7.8). Coppice height of the RH hybrid class did not differ significantly from the *E. risdonii* from the same site, but was generally greater than *E. amygdalina* (Fig. 7.8). The AH hybrid phenotype consistently had the lowest coppice, a trend also noted for basal area production. Within sites, the coppice height of the intermediate phenotype (H) was generally lower than *E. risdonii* and comparable with *E. amygdalina*. The trends exemplified in Fig. 7.8 were also apparent in a preliminary scoring of coppice height 9 months after the fire. The recovery of *E. viminalis* by lignotuber regeneration was exceptionally slow (Table 7.9) compared to the *Piperitae* phenotypes due partly to intense preferential grazing of the coppice by insects.

A comparison of the frequency of individuals which had initiated flower buds 15 months after the fire (Table 7.10) indicated a significant difference between *E. amygdalina* and *E. risdonii* from pure stands and the ecotone (site C) site with *E. amygdalina* recovering flowering ability more rapidly than *E. risdonii*. The vast majority of buds developed at this stage aborted, and capsules were rarely found 2½ years after the fire. Nevertheless, this precocious initiation is probably indicative of *E. amygdalina* reaching the reproductive phase earlier than *E. risdonii* or the other phenotypic classes following fire. However, this was not the case at the hybrid swarm site where vegetative recovery of *E. amygdalina* was slower. These results tentatively suggest that in the early stage of stand recovery there will be a phase in which *E. amygdalina* will dominate seed output on the northern slope. This would occur in any case due to all *E. risdonii* stems in the local area being killed or damaged whereas *E. amygdalina* and *E. viminalis* on the southern slopes were undamaged. Until the stand on the northern slope matures these trees will represent the only local seed source for the northern slope.

Seedling Establishment

Germination

The majority of seed had been shed from the capsules retained on the dead stems by 3 months after the fire. A thorough search of the north slope indicated no seed had germinated at this stage. Five months after the fire in July cotyledonary stage seedlings were first evident and seedling counts taken in October, 9 months after the fire, are given in Table 7.11. The density of cotyledonary stage seedlings was notably higher beneath the canopy of the mixed *E. viminalis*/*E. amygdalina* forest on the southern slope than in either the *E. risdonii* or *E. amygdalina* stands on the northern slope. The hybrid zone on the ridge appeared intermediate, although density estimates varied between the three transects, depending on their proximity to mature *E. risdonii*.

The mortality of germinants over the 3 months from July to October was in the order of 50% with seedling recruitment continuing (Table 7.12). Germination was still occurring up until December but at a relatively low rate in *E. amygdalina* dominated areas. This is consistent with the trend previously noted for the slower germination of *E. risdonii* seed (Fig. 6.18). It was not possible to distinguish the *E. amygdalina*/*E. risdonii* phenotypes at this early stage (July) although seedlings of *E. globulus* and *E. viminalis* could be distinguished from the *Piperitae*. Most of the *Piperitae* seedlings in *E. amygdalina* dominated stands on the north slope were more advanced than those on the southern slope by October. This could arise as a result of later seed release on the south slope due to stems not being killed or higher temperatures and greater incident radiation on the north facing slope. The light environment encountered by germinating seed or saplings regenerating from lignotubers would be far more differentiated than predicted by Nunez (1980; Fig. 6.4) due to the retention of the canopy on the south slope. Results indicated a reduction in radiation levels by up to 80% beneath the closed *E. amygdalina* canopy on the south slope as compared to full sunlight on the north slope (Table 7.13). The initial high density of cotyledonary-stage seedlings on the south slope (Table 7.11) may reflect greater moisture availability and better conditions for germination and could correspond to normal seasonal establishment of cotyledonary-stage seedlings observed in a wetter *E. amygdalina*/*E. viminalis* forest in the absence of fire (Duncan 1981). However transects in unburnt stands of both *E. amygdalina* and *E. risdonii* indicated no concurrent seedling germination or establishment although one 2 to 3 year old *E. risdonii* seedling was found which had obviously been recruited in the absence of fire. Duncan (1981) noted that very few

germinants survive due to competition, drought, fungal and insect attack and this was similarly the case beneath the forest canopy on the south slope following the relatively low intensity ground fire. The high mortality of germinants on the south slope (Table 7.12) was associated with a dense regeneration of grass and other ground-cover species which did not occur in the drier ridge and north slope sites.

Establishment niche

Establishment niches were observed to be of three types:-

- (1) open bare ground
- (2) physical microhabitats
- and (3) lignotuber microhabitats.

The physical microhabitat was a protected site created by, for example, a stone, hollow or fallen log. The lignotuber microhabitat involved burnt out lignotubers which formed hollows which had a high ash content and often collected litter. Both types of microhabitat offered protection from wind and dessication and were frequently observed to be moist when the surrounding soil surface was dry. In the initial stages of establishment the preference for the lignotuber microhabitat was marked and seedlings were more advanced than those growing on bare ground. By October the dense coppice regeneration had virtually eliminated this microhabitat due to the low light intensity. However, where coppicing was slow or the adult killed, this microhabitat appeared to afford an ideal growing site. Seedlings surviving in either type of microhabitat exhibited significantly greater height by December than those growing on bare soil regardless of phenotype (Table 7.14).

A greater proportion of seedlings of both *E. amygdalina* (A+AH) and *E. risdonii* (R+RH) were observed growing in microhabitats on the dry north facing slope than on the ridge or, in the case of *E. amygdalina*, the south slope (Table 7.15). This partly reflects a greater frequency of physical microhabitats on the north slope. However, there is a significantly ($P < 0.001$) greater proportion of *E. amygdalina* than *E. risdonii* types growing in microhabitats on the north slope. This possibly indicates a shift in the establishment niche of *E. amygdalina* from the open ground on the wetter sites to specific microhabitats on the drier slope. This is not as apparent in *E. risdonii* which is still capable of establishment on open exposed soil on the north slope, as well as in microhabitats. While *E. amygdalina* tends to be restricted to regenerating in less extreme microhabitats on the drier sites, it still appears capable of maintaining sufficient recruitment to match mortality in the absence of competition from *E. risdonii* (e.g. Table 7.6).

Phenotypic frequencies in established seedlings

Estimates of the relative contribution of each phenotype to the seed rain at the time of the fire are given in Table 7.5. As expected from the fitness data (Table 7.4), *E. risdonii* is dominating the seed rain in all boundary sites. Due to the low level (1.5%) of hybrid types detected in progenies of pure *E. risdonii* from the hybrid zone, virtually all of this seed can be expected to yield *E. risdonii* phenotypes. The other phenotypes would not be expected to breed true due to backcrossing and segregation (Table 6.7; Figs. 6.10 and 6.15). This is less of a problem at the ecotone site where the relative frequency of hybrids was lower (Table 7.5).

At the time of scoring it was only possible to accurately classify seedlings into three phenotypic classes (*E. amygdalina*, A+AH; hybrid, H and *E. risdonii*, R+RH). This required parental and backcross mature phenotypes to be pooled when comparing the relative frequency of phenotypes prior to the fire with that in the seedling sample. The sites sampled differed markedly in the density of seedlings established after the summer of 1981, approximately 15 months after the fire (Table 7.16). Seedling recruitment in both hybrid zone sites on the ridge (A,B) was much higher than any site on the northern slope (i.e. pure *E. amygdalina*, *E. risdonii* and ecotone). This did not appear to be a consequence of variation in the density or composition of the seed rain, but appeared to reflect a difference between sites in the probability of establishment (Table 7.16) which was consistent for each phenotypic class.

The proportion of phenotypes in the seedling cohort established following the fire differed significantly ($P < 0.001$) from the proportion in the adult population prior to the fire at all boundary sites (Table 7.17). The seedling cohort was dominated by *E. risdonii* type seedlings and at the boundary sites, these phenotypes even dominated seedling recruitment in areas dominated by hybrid (H) and *E. amygdalina* (A+AH) adults. *E. amygdalina* and hybrid seedlings were rare even in pure *E. amygdalina* stands on the north slope (e.g. site E), and no *E. amygdalina* seedlings were observed in *E. risdonii* dominated areas near the boundary. An expectation of the proportion of phenotypes in the seedling cohort was obtained from estimates of the proportion of seed released by each phenotypic class at the time of the fire (Table 7.5). At the ecotone site there was no significant difference between the expected proportions and that observed 15 months after the fire (Table 7.17). In contrast, at both hybrid zone sites (A,B), there was a significantly greater number of hybrid types than expected (Table 7.17). However, when the seed rain is adjusted for

segregation and backcrossing there is little difference between the proportion of each phenotypic class estimated in the seed rain and the proportion surviving before (site B, $P < 0.05$) and after the first summer (site A, NS; site B, NS). The marked fitness differential between *E. amygdalina* and *E. risdonii* at the boundary which was predicted from the reproductive vigour of individuals (Table 7.5) is thus directly reflected in the potential of either taxa to contribute to a subsequent generation (Table 7.19). The absence of *E. viminalis* seedlings was expected due to the very low capsule count. Even with an exaggerated estimate of 4 seeds per capsule, *E. viminalis* would only account for between 0 and 3% of the seed rain at the various sites. No *E. globulus* or *E. viminalis* seedlings were even observed to germinate on the north facing slope or ridge despite a wide search, although seedlings of both species were recorded on the southern slope. This suggests seed migration into these areas from sources on both south facing slopes or the gully at the base of the north slope is limited.

Seedling survival and vigour

The problem in observing selection in established phenotypes was the low density of both hybrid and *E. amygdalina* phenotypes. These were generally widely scattered and it was not possible to locate and monitor large numbers in a single area. The highest density of *E. amygdalina* seedlings observed in a localized area along the boundary was in the smallest quadrat in the hybrid zone (site B). A comparison of the proportion of seedling phenotypes in this quadrat before and after the first summer indicated no differential mortality (e.g. Table 7.17). A seedling mortality rate of 71% was recorded with no recruitment. Similarly, the proportion of phenotypes in a random sample of seedlings taken from the hybrid zone (site A) 2½ years after the fire (August, 1982) was not significantly different from the 15 month samples (Table 7.17). *E. risdonii* types still dominated the seedling recruitment, even on the *E. amygdalina* side of the boundary. While no difference in mortality was detected, *E. risdonii* seedlings on open ground were significantly taller than *E. amygdalina* types at the beginning of the first summer (Table 7.14). This difference was maintained after summer and in samples taken 2½ years after the fire (Table 7.18). This difference is interpreted as a true selective effect against *E. amygdalina* seedlings as no marked difference in the height growth of progenies was observed under glasshouse or plantation conditions (Fig. 6.18). Approximately half of the *E. amygdalina* seedlings scored in August 1982 showed

distinct signs of drought damage.

In the hybrid zone, seedlings of *E. risdonii* were effectively growing better in areas dominated by *E. amygdalina* or hybrid adults than in areas close to mature *E. risdonii* (Table 7.18). This is most likely a result of increased seedling density and hence density dependent selection closer to seed sources as well as competition with vigorous adults of *E. risdonii*. In contrast, the greater mortality during the fire (Table 7.7) and the less vigorous vegetative recovery (Fig. 7.8) of *E. amygdalina*, coupled with low seedling recruitment in *E. amygdalina* dominated areas, suggests established seedlings would be subject to a less intense competitive regime on the *E. amygdalina* side of the boundary. However at the ecotone site (C), a reduction in seedling height with proximity to *E. risdonii* was not evident (Table 7.18), probably as a result of higher seedling density (Table 7.16), and differential adult mortality (Table 7.7) and vegetative (Fig. 7.8; Table 7.9) recovery of either species in the hybrid zone (A) which was not as apparent at the ecotone site (C).

Evidence for range expansion by *E. risdonii*

There is no doubt that the current overall selective regime is favouring *E. risdonii* at the boundary and possibly in some areas currently dominated by *E. amygdalina*. This is evidenced by a general decrease in vigour of *E. amygdalina* with proximity to the boundary whereas *E. risdonii* tends to increase in vigour. The increase in the reproductive output is most marked in the hybrid zone (site A) and could be a result of less intense competition when growing with *E. amygdalina* and the hybrids than with individuals of the same species (e.g. site D). Phenotypes tending towards *E. risdonii* (R+RH) dominated the seed rain at all boundary sites (Table 7.17) and this was reflected in their proportion in the seedling cohort (Table 7.17). Furthermore, there was no evidence for selection against *E. risdonii* seedlings (Tables 7.14 and 7.17), saplings (Figs. 7.6 and 7.7) or adults (Figs. 7.7 and 7.8) which would restore the relative phenotypic frequencies at the boundary site to that prior to the fire. In fact, the contrary seems to be occurring with subsequent growth favouring *E. risdonii* over *E. amygdalina* and hybrid seedlings (Tables 7.14 and 7.18), even in *E. amygdalina* dominated areas.

The greater mortality of *E. amygdalina* and *E. viminalis* following the fire (Table 7.7), coupled with a predominance of *E. risdonii* (R+RH) recruitment constituted an effective shift in the species' boundary (as defined by equal relative frequency) and an expansion of the *E. risdonii* population.

Due to the low recruitment at the ecotone site (site C), the shift was about 0.5 m, whereas at the hybrid zone on the ridge, the boundary moved in the order of 7 m at both sites (sites A and B; see Fig. 7.9). These estimates were based on seedling frequencies 15 months after the fire and obviously with future seedling mortality this will diminish. However, the boundary at the hybrid zone (site A) could not return to the pre-fire position due to the number of *E. amygdalina* and *E. viminalis* killed following the fire surpassing the number of surviving seedlings.

The demographic structure of the boundary zone

The demographic structure of the boundary zone suggests that the current expansion of *E. risdonii* is not an isolated event and that selection has been favouring *E. risdonii* for several previous regeneration cycles at least.

Estimates of the demographic structure were based on the distribution of lignotuber size classes for each phenotype (Figs. 7.10 and 7.11). It is impossible to accurately age these lignotuberos individuals (e.g. Lacey 1983), although radiocarbon dates available for other species indicate central wood samples from large lignotubers (less than 2 m diameter) were younger than 200 years (see Wellington *et al.* 1979). Nevertheless the individuals are probably much older (see Lacey 1983; Noble 1982). Moran and Hopper (1983) suggest that the generation time for *E. caesia*, which appears to regenerate in a similar manner to the eucalypts in the study area, could be several hundred or even a thousand years. Lignotuber diameter is the only means by which to obtain estimates of the relative age of individuals in the study area and at the simplest level was used to classify individuals into sapling (<21 cm) and adult (≥ 21 cm) classes. Lignotuber diameter, as with stem diameter, may be influenced by numerous factors including phenotype, degree of suppression and productivity (see also Lacey 1983).

The lignotuber diameters of individuals which showed no signs of having been burnt in the 1960/1961 fire and which could be no more than 20 years old indicate a maximum lignotuber size of 13, 16 and 10 cm for *E. amygdalina*, *E. risdonii* and hybrids (H) respectively. These individuals probably represent a 20 year old cohort established following the 1960/61 fire. The relative frequency of phenotypes in this cohort (Table 7.5) clearly indicates that *E. risdonii* types also dominated seedling recruitment at the hybrid zone site (A) following the 1960/61 fire. In contrast, recruitment of *E. risdonii* and *E. amygdalina* at the other boundary

sites appears to have been comparable (Table 7.5).

The distribution of lignotuber diameters in the pure species stands (Fig. 7.10) tends toward an 'inverse J shaped' distribution which is often taken as indicative of a steady state population with a continuous regeneration strategy (e.g. Hett and Loucks 1976; Cawker 1980; Veblen *et al.* 1980). However where age classes are not utilized, it is difficult to distinguish between continuous establishment as opposed to relatively frequent episodic establishment coupled with varying degrees of suppression from pre-established individuals. Nevertheless the fact that there was no concurrent establishment of seedlings in unburnt areas as well as a relatively wide range of lignotuber size classes evident in the 1960/1961 cohort would favour the latter regeneration strategy. Furthermore, while seedling establishment may be episodic, the release of seedlings from suppression at these sites may be a more continuous process. In contrast to the pure species stands, the distribution of lignotuber sizes at the boundary sites is irregular and multi-modal (Fig. 7.10), and is indicative of episodes of seedling recruitment or adult mortality (e.g. Cawker 1980). A peak near the 30 cm lignotuber diameter class is evident at both boundary sites (sites A and C) and for all phenotypic classes, although it is less obvious in phenotypes tending toward *E. risdonii*. This peak suggests a major phase of recruitment of *E. amygdalina* phenotypes at these sites which appears to have been accompanied by recruitment of hybrid phenotypes (H+AH) in the hybrid zone (site A). This peak could arise with either a major episode of seedling establishment or release of suppressed saplings following high adult mortality. Hybridization between *E. risdonii* and *E. amygdalina* is not a recent phenomena at either of the boundary sites (e.g. Table 7.2; Figs. 7.10 and 7.11), and high phenotypic diversity is encountered in most cohorts (Fig. 7.11). While *E. amygdalina* appears to have at one time dominated recruitment at the hybrid zone site (A), *E. risdonii* types clearly dominate the younger cohorts (e.g. Table 7.17; Figs. 7.10 and 7.11). Furthermore, the prominent peak of smaller lignotuber diameter classes and which mainly comprise individuals classified as saplings (<21 cm) appears to be composed of several cohorts, with the saplings apparently established after the 1960/61 fire comprising only 10-20% of individuals with lignotuber diameters less than 21 cm. This suggests that *E. risdonii* types have dominated recruitment at the hybrid zone site (A) for at least several other regeneration cycles and that the fitness differential observed between morphs is not a short-term phenomenon.

A comparison of the relative frequency of sapling to adult individuals (Table 7.20) indicates no significant difference in the demographic structure of central pure species stands (i.e. sites D vs E) or between either species at the ecotone site (site C; Table 7.20; Fig. 7.10). However at the ecotone site, individuals of *E. risdonii* out from the boundary, scattered amongst the *E. amygdalina* are predominantly saplings whereas when *E. amygdalina* is encountered as scattered individuals in *E. risdonii* dominated areas there is usually a predominance ($P < 0.001$) of old adults and lack of saplings when compared to the surrounding *E. risdonii* or *E. amygdalina* from other areas (Table 7.20). While individuals of *E. risdonii* in *E. amygdalina* dominated areas near the boundary are relatively vigorous (Figs. 7.6 and 7.7), when *E. amygdalina* individuals are found in *E. risdonii* dominated areas, they are generally clumped in small, dense patches and subordinate to the surrounding *E. risdonii*, frequently not exceeding 1.5 m in height. These patches generally show little evidence of recent recruitment, although when saplings are encountered these are generally suppressed and usually within the patch, directly beneath the canopy of older individuals.

At the hybrid zone site (A) there is clearly a disproportionately high number of *E. risdonii* saplings compared to adults (Table 7.20). These *E. risdonii* saplings are not only established in areas dominated by *E. risdonii* adults but extend into areas dominated by older *E. amygdalina*. This is seen in Fig. 7.12 where the average lignotuber size of *E. risdonii* on the *E. amygdalina* side of the boundary is less than the surrounding *E. amygdalina* and the *E. risdonii* on the other side of the boundary. This is not a result of excessive suppression by *E. amygdalina* adults (e.g. Figs. 7.6 and 7.7) and appears to represent a spread of younger *E. risdonii* into the range of *E. amygdalina* and an invasion of areas dominated by *E. amygdalina* and hybrid phenotypes. Similar results were obtained from the smaller hybrid zone quadrat (site B). The boundary movement following the 1980 fire at both ridge sites appears to have been preceded by similar shifts in the recent past. The *E. risdonii* population appears to be expanding along the ridge and across the north slope. However, the expansion appears to be occurring at different rates along the boundary with some areas such as the northern boundary (site C) being relatively more stable.

7.4 Discussion (Chapters 6 and 7)

Hybridization

The evidence presented indicates that the morphological continuum between *E. risdonii* and *E. amygdalina* in the Government Hills is a result of interspecific hybridization which confirms previous observations (Brett 1938 and Barber 1955). Growth of open pollinated hybrid and parental progenies under glasshouse and plantation conditions indicates little difference in vigour or survival. In addition, the artificial production of the F_1 hybrid by Martin and Brett (see Barber 1955) and the subsequent growth of a viable F_2 (Barber and Jackson, unpubl.) indicates no major barriers to hybridization between *E. amygdalina* and *E. risdonii*. Nevertheless, specific identity is usually maintained in parapatry, often with no extensive hybridization evident. This is of particular significance in view of the close geographical association of these two closely related species. A range of isolating mechanisms appears to be operating to retard interspecific gene exchange, and in particular to maintain the genetic integrity of the smaller *E. risdonii* populations despite continuous proximity to *E. amygdalina*. In terms of the isolating mechanisms recognized by Levin (1978b), gene flow is restricted by pre- and post-mating reproductive barriers as well as spatial separation. The ecological preferences of both species (Hogg and Kirkpatrick 1974; Kirkpatrick and Nunez 1980) usually concentrates direct genetic interaction to a narrow boundary zone where reproductive isolation is reinforced by differences in flowering period and reduced hybrid fitness.

Despite overlap in the flowering period of *E. amygdalina* and *E. risdonii*, a difference in the period of peak flowering has the potential to limit hybridization prior to fertilization. However, the flowering period within and between isolated populations of *E. risdonii* is relatively synchronous whereas there was considerable variation between sites in the continuous *E. amygdalina* population. The flowering period of *E. amygdalina* sampled from boundaries on the drier north facing slopes exhibited less overlap with *E. risdonii* than pure species' stands in the southern slopes, in a habitat from which *E. risdonii* is excluded. Ridge top, boundary stands of *E. amygdalina* are similar in flowering time, but not intensity to stands on the southern slopes. This may partly account for a greater frequency of hybrids at boundaries on ridge tops, although these boundaries are also more disturbed than those on the steeper north slopes. Superficially the variation in flowering behaviour within *E. amygdalina* could be explained

in terms of character displacement (Brown and Wilson 1956). However, as noted by Levin (1978b), such character displacement could arise from alternate mechanisms, the results of which are similar regardless of the cause {i.e. competitive or reproductive (Wallace Effect, Grant 1966, 1971) character displacement}. The latter process would involve selective displacement to avoid hybridization with *E. risdonii* and is contingent upon reduced hybrid fitness, sufficient variation in flowering period within a local population, and a bias in reproductive wastage toward *E. amygdalina*, all of which have been demonstrated. Nevertheless, an alternative explanation may be that variation in flowering time within *E. amygdalina* is related to a broader ecological range and involves an avoidance or inability to flower in the summer on drier sites. The shift away from *E. risdonii* may then be incidental and the by-product of a secondary factor. In either case, local variation in flowering behaviour of *E. amygdalina* may not only reduce the probability of hybridization with *E. risdonii* but may retard gene exchange within continuous stands of *E. amygdalina*. In contrast, the synchrony of flowering in *E. risdonii* would tend to promote gene exchange between the small isolated populations. However the weakness of flowering time as a barrier to hybridization is evidenced by the spatial and seasonal variation in the flowering period noted to occur in many *Eucalyptus* species (see Sections 1.6 and 5.4). In addition, flowering barriers may be rapidly degraded when hybrids exhibit an intermediate response and overlap with both parents as in the present example.

The other major barrier to hybridization is post-mating and ecological in nature. In natural stands, when the F_1 type is in competition with both species it is generally reproductively the least fit, although frequently vegetatively vigorous. Reduced fitness appears to extend to advanced generation hybrids as hybrid phenotypes resembling either parent (i.e. backcross and segregates) are on the average less fit than the corresponding parental type, although hybrids tending toward *E. risdonii* (RH) were more vigorous than *E. amygdalina* and the F_1 type at the boundary. Thus in direct competition with the parents, the backcross phenotype would tend to be outcompeted and replaced by the parental type. Similar post-mating barriers to gene exchange have been reported in *Eucalyptus* (Pryor 1956, 1976; Hopper *et al.* 1978) although studies attempting to quantify the selective difference between parents and hybrid phenotypes are rare (e.g. Drake 1981a, 1981b). Drake (1981a) presents a model of single plant seed output to estimate the fertility component of a scheme to estimate the evolutionary potential of taxa (Drake 1980) based on their reproductive and ecological status under existing conditions. In the present study, specific facets

of this seed output model are not examined, although the final and integrated result expressed as viable seed output per individual is presented as well as an examination of the post-dispersal phase. In *Eucalyptus*, which appear to depend on a high seed output, strategy for survival, Drake (1981b) argues that where safe sites are limiting, the relative probability of successful germination and seedling establishment is proportional to seed output. While Drake (1981a,b) only presents data for pre-dispersal parameters, seedling establishment at the *E. risdonii*/*E. amygdalina* boundary appears to confirm this argument, at least at the taxa level. The proportion of phenotypes established following wildfire more or less follows the estimated proportion in the seed rain up to 2½ years after seed release. Nevertheless, there is some indication that the two species may perceive 'safe sites' differently with a 'safe site' for *E. amygdalina* appearing to represent a more restricted portion of the habitat on the dry north facing slope than for *E. risdonii*.

Regeneration strategy

These results indicate a major burst of seedling establishment following wildfire, which was not apparent in unburnt stands. This is in accordance with the thesis for a general dependence of *Eucalyptus* on fire for seedling establishment in both wet (e.g. Gilbert 1958; Mount 1964, 1969, 1979; Jackson 1968; Cremer *et al.* 1978; Ashton 1981b) and dry (e.g. Zimmer 1940; Jacobs 1955; Withers and Ashton 1977; Noble 1982) sclerophyll communities. However the extent of seedling establishment varied markedly between sites, clearly indicating that even where sufficient seed is available, fire does not ensure seedling establishment. The extent of seedling establishment appears to be determined by an interaction between the intensity of the seed rain and 'safe site' availability, both of which are probably determined by the complex interaction between factors such as: (1) the demographic and genetic structure of the population; (2) fire intensity; (3) understory composition; (4) the vigour of vegetative recovery; (5) adult mortality; (6) the maximum carrying capacity of the environment; (7) the post-fire climatic regime, and many others (see Mount 1969, 1979; Noble 1982).

Seedling establishment in the central, pure species stands was low and in the *E. risdonii* stand this occurred in spite of the site receiving the heaviest seed rain. The low seedling establishment at this site could result from the stand being at the maximum stocking level, possibly as a result of relatively high recruitment following the 1960/61 fire.

Alternatively, the low probability of seedling establishment could reflect the severity of the habitat occupied by *E. risdonii* and it is possible the large seed size and high seed output of this species represents a specialized adaptive strategy for seedling establishment in an extremely dry habitat. The maximum density of seedlings occurred in the hybrid zone (sites A and B) and establishment was concentrated close to seed sources (i.e. *E. risdonii* types). This resulted in an increase in competition between seedlings of the same cohort, and thus density dependent selection, with proximity to the seed source. Furthermore, the vast majority of individuals recovered vegetatively following the fire, and fierce competition from individuals with pre-established root systems appears to be a major factor limiting seedling establishment. The high seedling establishment at the hybrid zone site (A) is probably related to a depletion of the mature stand, possibly due to the marked selective differential and the boundary being in a state of flux. Competition from pre-established individuals was clearly reduced following the 1980 fire due to the relatively high mortality of *E. amygdalina* and *E. viminalis* phenotypes coupled with slow vegetative recovery of survivors of either species which was not as marked at other sites.

There were several peaks in the distribution of lignotuber diameters in phenotypes from boundary stands which are absent from central pure species stands. These peaks suggest major episodes of seedling establishment or release of suppressed saplings at the boundary sites, whereas central stands appear to be more stable with recruitment appearing to be more continuous. These peaks could arise due to numerous factors affecting either seedling establishment or adult mortality (e.g. intense fire, natural senescence, change in the carrying capacity of the environment, unnatural disturbance, etc.), although it is significant that they are most pronounced at the boundary sites. This is consistent with the hypothesis that ecologically marginal sites are more vulnerable to fluctuations in the competitive regime and catastrophic selection (e.g. Lewis 1962) resulting in greater instability and fluctuation in population density compared with central stands. In the present case, there appears to be a major phase of recruitment of seedlings tending toward *E. risdonii* in the hybrid zone which appears to be associated with disequilibrium at the boundary and an invasion of *E. amygdalina* and hybrid dominated areas by *E. risdonii*.

Range expansion by *E. risdonii*

The marked fitness differential at the boundary suggests that *E. risdonii* might be expected to be invading the range of *E. amygdalina*, particularly where the latter species extends onto drier sites. Seedling regeneration following wildfire as well as the demographic structure of the hybrid zone indicate that this expansion is actually occurring. It could be argued that the boundary in mature individuals is stable and that selection would re-establish the original boundary position in later stages of regeneration. However, this is not supported by the data and there is no indication of selection against *E. risdonii* seedlings, saplings or adults in *E. amygdalina* dominated areas. Alternatively, this pattern of phenotypic fitness could represent equilibrium conditions under a balanced selection/migration model with asymmetrical gene flow shifting the species' boundary away from the null point (e.g. Endler 1977). However, in this case gene flow by both seed and pollen appears to be occurring in the reverse direction, from *E. risdonii* to *E. amygdalina*.

It is difficult to ascertain whether the disequilibrium in the study area is a short or long term phenomena. Evidence suggests *E. risdonii* has been favoured for at least 20 years, since the 1960/61 fire, over a period where drought-induced decline in other *Eucalyptus* forests in south-eastern Tasmania has been noted (West 1979). The period from 1960-1967 appears to be one of the longest periods of below average rainfall on record and was preceded by the longest period ever of above average rainfall from 1953-58 (West 1979). Water availability is almost certainly one of the main environmental factors controlling the competitive interaction of *E. risdonii* and *E. amygdalina* (Kirkpatrick and Nunez 1980) and results presented clearly indicate selection against the more mesic species, *E. amygdalina* and *E. viminalis*, in the study area. Low reproductive output is coincident with higher adult mortality and less vigorous vegetative recovery from fire for both species. Furthermore, there is strong evidence of selection against *E. amygdalina* and *E. viminalis* over the years immediately prior to the 1980 fire with both species in the vicinity of the study area suffering extensive insect defoliation. This followed an outbreak of *Stathorrhopa aphotista* (Lepidoptera: Geometridae) in 1974 which did not decline until 1977 (Elliot et al. 1980a,b). Defoliation was preferential with *E. amygdalina* the favoured host and *E. risdonii* least affected. Damage frequently involved complete defoliation with some mortality (11%) recorded. These authors note: "Recovery of defoliated trees was severely set back by the 1979-1980 drought and the general health of trees in the area is now (1980) worse than was the case immediately following the outbreak." This is particularly marked

in *E.amygdalina*/*E. viminalis* forests on the drier sites (Elliott, pers.com. 1982) and the drought referred to still persists (1982). It is most likely that large areas of the *E. amygdalina* population are presently under water stress or close to a threshold, perhaps resulting in trees being more susceptible to secondary selective agents such as insect predation and fire. As suggested by West (1979), physiological weakening of trees by drought may allow the effects of secondary agents to increase. Nevertheless, the distribution of hybrids as well as the demographic study suggests that *E. risdonii* may have dominated recruitment in a similar manner to that observed prior to insect defoliation and the 1960/1961 fire. With the large inertia in the response of these populations due to slow generation turnover and low migration rates (Chapter 8) it is possible the populations are still tracking a much earlier, perhaps even pre-historic change in the selective regime. While the activities of European man are unlikely to have initiated this disequilibrium, it may be accentuated by disturbance, particularly in the form of higher fire frequency increasing the rate of population response. However Pryor (1953) notes a comparable example where it is suggested that the increase in fire frequency since European settlement has contributed to the spread of hybrid swarms due to opening up of the forests as well as altering the competitive interaction between species. This may apply in the present case as both *E. amygdalina* and *E. viminalis* appear to be adversely affected by fire compared to *E. risdonii*. Nevertheless it is difficult to differentiate between a primary effect of fire and secondary interaction between fire and other factors (e.g. drought and insect predation).

Table 7.1 Characters scored from individuals in the demographic study.

<u>Character</u>	<u>Description</u>
1. Phenotype	A subjective classification into phenotypic classes based on adult and coppice morphology (R,RH,H,AH,A; Table 6.3).
2. Nos. Stems	Number of stems.
3. Lignotuber Diameter	Maximum diameter of the lignotuber (cm).
4. Av. Coppice Ht.	Estimated average coppice height (cm).
5. Max. Coppice Ht.	Maximum coppice height (cm).
6. Nos. Capsules	The total number of capsules retained on stems after the 1980 fire.
7. Basal Area	The total basal area of stems arising from each lignotuber, calculated from stem circumference at 0.5 m above ground level.

Table 7.2 The frequency of individuals in each phenotypic and lignotuber size class used in basal area, capsule, and capsules/basal area comparisons. The proportion of the *Piperitae* phenotypes in each lignotuber diameter class is indicated in brackets.

Phenotypic class	Lignotuber diameter class (cm)				Total
	0-21	21-42	42-63	63+	
<u>Hybrid Zone (A; 40x60 m²)</u>					
A	96 (0.28)	74 (0.48)	26 (0.41)	17 (0.35)	213 (0.35)
AH	25 (0.07)	12 (0.08)	5 (0.08)	0 (0.00)	42 (0.07)
H	37 (0.11)	16 (0.11)	7 (0.11)	10 (0.21)	70 (0.12)
RH	49 (0.15)	17 (0.11)	7 (0.11)	3 (0.06)	76 (0.13)
R	130 (0.39)	34 (0.22)	19 (0.30)	18 (0.38)	201 (0.33)
V	87	41	10	2	140
TOTAL PIPERITAE	337	153	64	48	602
<u>Ecotone (C; 20x80 m²)</u>					
A	153 (0.57)	91 (0.41)	30 (0.43)	14 (0.48)	288 (0.53)
AH	4 (0.01)	9 (0.05)	1 (0.01)	1 (0.03)	15 (0.03)
H	17 (0.06)	9 (0.05)	6 (0.09)	1 (0.03)	33 (0.06)
RH	7 (0.03)	3 (0.02)	3 (0.04)	3 (0.10)	16 (0.03)
R	89 (0.33)	66 (0.37)	30 (0.43)	10 (0.34)	195 (0.36)
V	20	6	4	2	32
TOTAL PIPERITAE	270	178	70	29	547
<u>Pure <i>E. amygdalina</i> (E)</u>					
A	54	35	19	21	114
<u>Pure <i>E. risdonii</i> (D)</u>					
R	52	54	25	21	140

Table 7.3 The mean number (\pm S.E.) of viable seed per capsule (see Chapter 6) used to estimate seed output from capsule counts.

Phenotypic class	\bar{x}	S.E.	n
A	0.88	0.233	8
AH	0.19	0.059	3
H	1.38	0.349	9
RH	3.55	0.990	5
R	3.93	0.622	10

Table 7.4 Estimates of the relative fitness of phenotypic and lignotuber size classes based on the estimated viable seed output and standardized (a) within lignotuber size classes, and (b) over-all lignotuber size classes. (- = insufficient replication, $n < 3$; + $n > 30$).

	Lignotuber diameter class (cm)				
Phenotypic class	0-21	21-42	42-63	63+	Pooled
(a)					
Hybrid zone (site A)					
A	0.03 +	0.06 +	0.03	0.02	0.04 +
AH	0.00	0.07	0.00	-	0.00 +
H	0.01 +	0.01	0.01	0.03	0.02 +
HR	0.21 +	0.43	0.21	0.58	0.28 +
R	1.00 +	1.00 +	1.00	1.00	1.00 +
Ecotone (site C)					
A	0.14 +	0.04 +	0.08 +	0.13	0.06 +
AH	0.00	0.00	-	-	0.00 +
H	0.09	0.07	0.02	-	0.08 +
HR	0.08	0.73	0.19	0.35	0.38
R	1.00 +	1.00 +	1.00 +	1.00	1.00
(b)					
Hybrid zone (site A)					
A	0.00	0.01	0.03	0.02	
AH	0.00	0.00	0.00	-	
H	0.00	0.00	0.01	0.03	
HR	0.01	0.09	0.16	0.58	
R	0.06	0.22	0.76	1.00	
Ecotone (site C)					
A	0.01	0.02	0.08	0.13	
AH	0.00	0.00	-	-	
H	0.01	0.03	0.02	-	
HR	0.01	0.31	0.17	0.35	
R	0.07	0.42	0.90	1.00	

Table 7.5 Total number of capsules, estimated total number of seed, total basal area (cm²), total number of stems, the estimated number of seed per unit basal area and per stem, the total number of individuals (N) and proportion in the 1960/61 cohort for each phenotypic class in each quadrat. The proportion of the *Piperitae* total is given in brackets and the area of each quadrat is indicated.

Phenotypic class	Total No. Capsules	Estimated number of seed	Total basal area (cm ²)	Total number stems	Nos. seed/ basal stem area		N	Proportion in the 1960/61 cohort
Hybrid zone (site A; 40x60 m ²)								
A	3768	3322 (0.04)	7002 (0.37)	466 (0.34)	0.5	7.1	213 (0.35)	0.05
AH	259	49 (0.00)	796 (0.04)	93 (0.07)	0.6	0.5	42 (0.07)	0.05
H	471	649 (0.01)	2736 (0.15)	182 (0.13)	0.2	3.6	70 (0.12)	0.12
RH	2399	8505 (0.10)	2222 (0.12)	162 (0.12)	3.8	52.5	76 (0.13)	0.12
R	20432	80359 (0.86)	6079 (0.32)	481 (0.35)	13.2	167.1	201 (0.33)	0.67
V	23		6054	176				
Ecotone (site C; 20x80 m ²)								
A	5504	4844 (0.09)	3153 (0.29)	593 (0.49)	1.5	8.2	288 (0.53)	0.49
AH	33	6 (0.00)	145 (0.01)	31 (0.03)	0.0	0.2	15 (0.03)	0.00
H	389	537 (0.01)	624 (0.06)	75 (0.06)	0.9	7.2	33 (0.06)	0.08
RH	484	1718 (0.03)	691 (0.06)	45 (0.04)	2.5	38.2	16 (0.03)	0.02
R	12348	48528 (0.87)	6096 (0.57)	477 (0.39)	8.0	101.7	195 (0.36)	0.41
V	37		3963	39			32	
Hybrid zone (site B; 20x20 m ²)								
A	603	532 (0.06)	3469 (0.58)	87 (0.41)	0.2	6.1	45 (0.47)	0.33
AH	515	97 (0.01)	741 (0.12)	10 (0.05)	0.1	9.7	6 (0.06)	0.00
H	772	1064 (0.13)	925 (0.15)	51 (0.24)	1.2	20.9	19 (0.20)	0.33
RH	0	0 (0.00)	10 (0.00)	5 (0.02)	0.0	0.0	3 (0.03)	0.00
R	1699	6682 (0.80)	850 (0.14)	57 (0.27)	7.9	117.2	23 (0.24)	0.33
V	35		1205	17			12	
Pure <i>E. amygdalina</i> (site E; 10x50 m ²)								
A	6797	5993 (1.00)	2983 (0.99)	239 (0.98)	2.0	25.1	114 (0.98)	1.00
H	11	15 (0.00)	28 (0.01)	4 (0.02)	0.5	3.8	2 (0.02)	0.00
V	0		843	6			5	
Pure <i>E. risdonii</i> (site D; 10x50 m ²)								
RH	0	0 (0.00)	6 (0.00)	2 (0.01)	0.0	0.0	2 (0.01)	0.00
R	10366	40769 (1.00)	4140 (1.00)	328 (0.99)	9.8	124.3	140 (0.99)	1.00
V	0	0 (0.00)	129	7			4	

Table 7.6 The number and proportion of individuals killed in the 1980 fire, the total number alive prior to the fire and the total number of seedling counted in April 1981.

Site	Number killed	Proportion killed	Total	Number of seedling in April 1981
pure <i>E. risdonii</i> (site D; 20x50 m ²)	11	0.036	309	8
pure <i>E.amygdalina</i> (site E; 20x50 m ²)	8	0.040	198	12
ecotone (site C; 20x80 m ²)	14	0.024	585	35
hybrid zone (site A; 40x60 m ²)	30	0.040	742	404

Table 7.7 The proportion of individuals in each phenotypic class killed in the 1980 fire at the hybrid zone (site A) and ecotone (site C) sites. Six individuals killed at the ecotone site could not be identified due to stems and foliage having been burnt. The significance of the χ^2 test for association between phenotypic class and mortality is indicated.

Phenotypic class	Hybrid zone (site A)		Ecotone (site C)		Pooled	
	Proportion killed	Total	Proportion killed	Total	Proportion killed	Total
A	0.052	213	0.017	288	0.032	501
AH	0.000	42	0.000	15	0.000	57
H	0.029	70	0.030	33	0.000	103
HR	0.000	76	0.000	16	0.000	92
R	0.000	201	0.005	195	0.003	396
V	0.121	140	0.031	32	0.098	172
Total N	30	742	8	579	38	1321
	***		NS		***	

Table 7.8 Mean maximum height (m) of 20 year old stems of
 individuals from pure *E. risdonii* (site D) and pure
 E. amygdalina (site E) stands.

	Total	Lignotuber diameter >42 cm
	<i>E. amygdalina</i>	
\bar{x}	3.2	4.2
SE	0.22	0.30
n	46	11
	(max. = 5.5 m)	
	<i>E. risdonii</i>	
\bar{x}	2.9	3.4
SE	0.14	0.16
n	45	10
	(max. = 4.5 m)	

Table 7.9 Mean coppice height (cm; S E) of *E. viminalis*
 15 months after the 1980 fire. Individuals regenerating
 from epicormic shoots have been excluded. The data are
 directly comparable with Fig. 7.8.

Lignotuber size class	Northern ecotone (site C)			Hybrid swarm (site A)		
	\bar{x}	SE	n	\bar{x}	SE	n
0-21	50.0	4.20	20	32.1	2.37	87
21-42	24.2	16.90	6	25.0	3.82	41
42-63	73.0	3.65	4	30.7	10.09	10

Table 7.10 The percentage of individuals of *E. amygdalina* (A) and *E. risdonii* (R) which had initiated buds 15 months after the 1980 fire.

Lignotuber size	Pure Stand		Ecotone (site C)		Hybrid Zone (site A)	
	R	A	R	A	R	A
	(site D)	(site E)				
0-21	0.0	18.7	3.3	10.5	0.8	1.0
21-42	0.9	38.7	6.0	19.8	0.0	2.7
42-63	0.3	29.2	0.0	10.0	0.0	3.8
63+	0.0	23.8	0.0	28.6	0.0	0.0

Table 7.11 Seedling density 5 and 9 months after the 1980 fire. The number of 3 x 50 m² transects scored is indicated in parenthesis and transect numbers correspond to Fig. 7.1.

	Seedlings/ 100 m ²	
	5 months (July)	9 months (October)
<i>E. risdonii</i> (centre; 1,2)	16 (1)	6.7 (2)
Hybrid Zone (ridge; 3,4,5)	7 (2)	19.5 (3)
Ecotone (north slope; 8,9)	-	9 (2)
<i>E. amygdalina</i> (north slope; 10,11)	-	3.3 (2)
<i>E. amygdalina</i> (south slope; 6,7)	-	41.8 (2)

Table 7.12 Seedling mortality and recruitment over the 3 months from (a) July to October, and (b) October to December.

(a)	Mortality	Recruitment
<i>E. risdonii</i> (centre; 1)	50%	14%
Hybrid Zone (ridge; 3,4)	47%	62%
(b) October to December		
<i>E. risdonii</i> (centre; 1,2)	23%	47%
<i>E. amygdalina</i> (south slope; 6,7)	78%	1%
(north slope; 10,11)	13%	0%

Table 7.13 Photosynthetically active radiation (PAR) levels (microeinsteins) directly beneath the canopy of *E. amygdalina* on the south slope and in full sunlight on the north slope. Readings were taken on a sunny day in late October, 1982.

	PAR (microeinsteins) (n=10)
Full sunlight (north slope)	1570±21.3
Beneath the <i>E. amygdalina</i> canopy (south slope)	338±27.2

Table 7.14 Mean seedling height (cm) of *E. risdonii* (R+RH), *E. amygdalina* (A+AH) and hybrid (H) phenotypes growing on open ground or in a specific microhabitat. The sample was taken at the hybrid zone (sites A,B) in December 1980 and within each phenotypic class sampling was random reflecting the relative frequency of seedlings in either type of habitat.

	A+AH		R+RH		H	
	Open ground	Micro-habitat	Open ground	Micro-habitat	Open ground	Micro-habitat
\bar{X}	2.7	5.8	4.0	9.8	2.7	7.4
SE	0.23	3.50	0.37	1.92	0.17	1.05
N	37	4	103	14	23	3

Table 7.15 The proportion of seedlings encountered growing on open ground or in specific microhabitats. The sample from the north slope represented a pooled sample from the ecotone (site C) and pure species' stands (1,2, 10,11; Fig. 7.1).

	Regeneration niche		N
	<u>open ground</u>	<u>microhabitat</u>	
<i>E. amygdalina</i> (A)			
south slope	0.93	0.07	75
hybrid zone	0.90	0.10	41
north slope	0.27	0.73	26
<i>E. risdonii</i>			
hybrid zone	0.88	0.12	117
north slope	0.68	0.32	63

Table 7.16

(a) Estimated intensity of the *Piperitae* seed rain following the 1980 fire (number of seed/m²), (b) the number of seedlings established in April 1981, (c) estimates of the probability of seedling establishment {(a)/(b)}, (d) the density of saplings considered to comprise the 1960/61 cohort and the density of (e) individuals, (f) stems and (g) basal area (cm²) prior to the 1980 fire.

	Hybrid zone		Ecotone	<i>E. risdonii</i>	<i>E. amygdalina</i>
	site A	site B	site C	site D	site E
Quadrat size	40x60 m ²	20x20 m ²	20x80 m ²	10x50 m ²	10x50 m ²
(a) estimated number of seed released/m ²	38.7	20.9	34.8	81.5	12.0
(b) number of seedlings/m ²	0.168	0.210	0.022	0.008	0.012
(c) probability of seedling establishment	1/230	1/100	1/1650	1/10200	1/1000
(d) number of saplings from the 1960/61 cohort/m ²	0.021	0.018	0.029	0.028	0.013
(e) number of individuals/m ²	0.31	0.32	0.36	0.29	0.24
(f) number of stems/m ²	0.65	0.57	0.79	0.67	0.50
(g) basal area (cm ²)/m ²					
(i) <i>Piperitae</i> only					
(A,AH,H,RH,R)	7.85	15.0	6.7	8.29	5.97
(ii) Total {(i)+V}	10.37	18.0	9.17	8.56	7.70

Table 7.17 The relative frequency of each phenotypic class (a) prior to the 1980 fire, (b) estimated in the seed rain and (c) in the seedling cohort established after the 1980 fire. The relative frequency of phenotypes established prior to the fire is indicated for the total, adult (lignotuber diameter >21 cm) and sapling population. The relative frequency in the seed rain is estimated from (i) the direct contribution of each phenotypic class to the seed rain or (ii) after an adjustment for segregation and outcrossing (see Section 7.2). (+ = random sample from within the area indicated).

Phenotypic Class	RELATIVE FREQUENCY							
	(a) Prior to the 1980 fire			(b) seed rain		(c) 1980 seedling cohort		
	TOTAL	ADULTS	SAPLINGS	(i)	(ii)	Prior to the first summer	After the first summer	2½ years after the fire
Hybrid zone (site A)								
A+AH	0.42	0.51	0.35	0.04	0.03	0.03	0.01	0.03
H	0.12	0.12	0.11	0.01	0.02	0.03	0.02	0.03
R+RH	0.46	0.37	0.54	0.95	0.95	0.94	0.97	0.94
(N)	(602)	(265)	(337)			(154)+	(404)	(68)+
Hybrid zone (site B)								
A+AH	0.53	0.62	0.36	0.07	0.10	0.06	0.05	
H	0.20	0.21	0.18	0.13	0.05	0.07	0.06	
R+RH	0.27	0.17	0.45	0.80	0.85	0.87	0.89	
(N)	(96)	(63)	(33)			(285)	(82)	
Ecotone (site C)								
A+AH	0.55	0.53	0.58	0.09	-	-	0.06	
H	0.06	0.06	0.06	0.01	-	-	0.03	
R+RH	0.39	0.42	0.36	0.90	-	-	0.91	
(N)	(547)	(277)	(270)				(35)	

Table 7.18 Mean seedling height (cm) 2½ years after the fire, for *E. risdonii* (R+RH) seedlings closer than 4 m from the nearest *E. risdonii* (R+RH) adult and pooled samples of *E. risdonii* and *E. amygdalina* seedlings. The significance of the 't' test is indicated.

	Hybrid zone (A,B)		Ecotone (C)		Pooled	
	<4 m	≥4 m	<4 m	≥4 m	<i>E. amygdalina</i>	<i>E. risdonii</i>
\bar{X}	25.1	39.2	38.3	39.9	19.3	30.4
SE	2.02	4.61	4.05	3.36	1.69	1.77
n	56	13	21	14	8	104
	P<0.01		NS		P<0.001	

Table 7.19 The relative fitness of *E. risdonii* (R+RH), *E. amygdalina* (A+AH) and hybrid (H) phenotypes calculated from the proportion of each phenotype in the 1980 seedling cohort (April 1981) relative to the proportion in (a) the total sample of established individuals and (b) the adult population (i.e. lignotuber diameter ≥21 cm). Values are indicative of the relative probability of either phenotypic class being represented in the seedling cohort.

	(a) total sample	(b) adults only
Hybrid zone (site A)		
<i>E. amygdalina</i> (A+AH)	0.01	0.01
hybrid (H)	0.08	0.06
<i>E. risdonii</i> (R+RH)	1.00	1.00
Hybrid zone (site B)		
<i>E. amygdalina</i> (A+AH)	0.03	0.02
hybrid (H)	0.09	0.06
<i>E. risdonii</i> (R+RH)	1.00	1.00
Ecotone (site C)		
<i>E. amygdalina</i> (A+AH)	0.05	0.05
hybrid (H)	0.21	0.23
<i>E. risdonii</i> (R+RH)	1.00	1.00

Table 7.20 The ratio of the relative frequency of saplings (lignotuber diameter <21 cm) to adults (lignotuber diameter ≥21 cm). The significance of the difference in the relative frequency of saplings between *E. risdonii* (R) and *E. amygdalina* (A) is shown and the number in each sample is indicated in parenthesis.

Sample site	pure species		hybrids			χ^2 test
	A	R	AH	H	RH	
Hybrid swarm (site A)	0.8 (213)	1.8 (201)	1.5 (42)	1.5 (70)	1.8 (76)	P<0.001
Hybrid swarm (site B)	0.3 (45)	1.3 (32)	2.00 (3)	0.20 (6)	0.5 (19)	P<0.01
Ecotone (site C)	1.1 (288)	0.8 (195)	0.4 (15)	1.1 (33)	0.8 (16)	NS
Scattered <i>E. risdonii</i> 20 m out from the boundary at site C in an <i>E. amygdalina</i> dominated area	2.6(243)	11.3 (49)	2.2(35)	5.2(57)	7.0 (8)	P<0.001
Scattered <i>E. amygdalina</i> toward the centre of the <i>E. risdonii</i> stand	0.2 (28)	1.4 (77)	-	-	-	P<0.001
Pure species stands (D,E)	0.9 (198)	0.8 (309)	-	-	-	NS

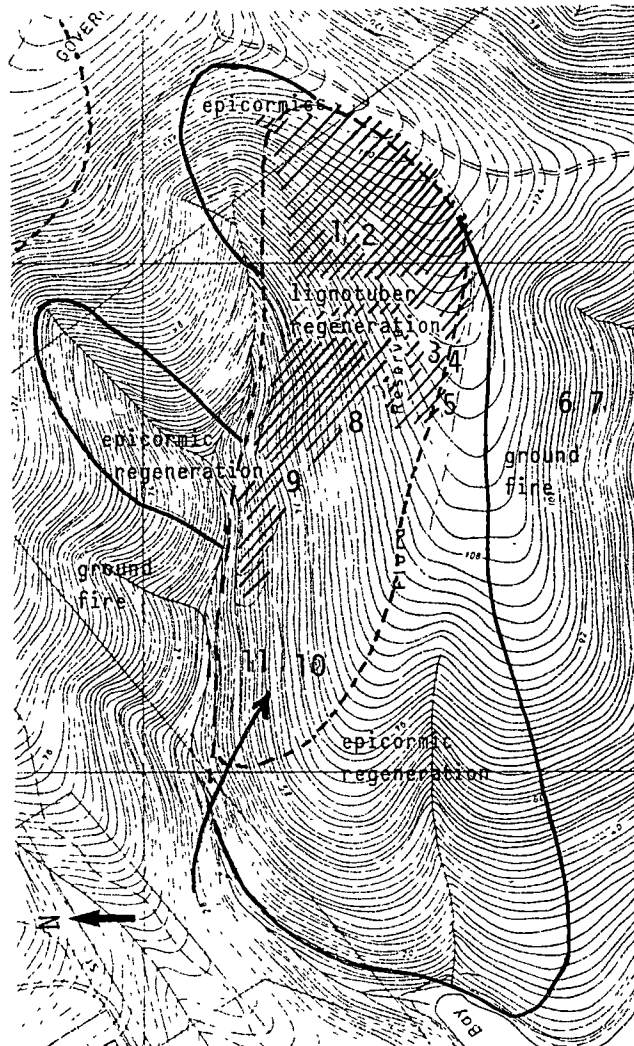


Figure 7.1 The study area in the Government Hills showing the location of transects (1-11) used to monitor seedling establishment after the 1980 fire. The extent of damage caused by the fire is indicated and areas in which regeneration was from lignotuberous shoots only, mainly from epicormic shoots or where the fire was confined to the ground and trees were virtually undamaged are shown. The direction of the main fire front is indicated by the arrow.

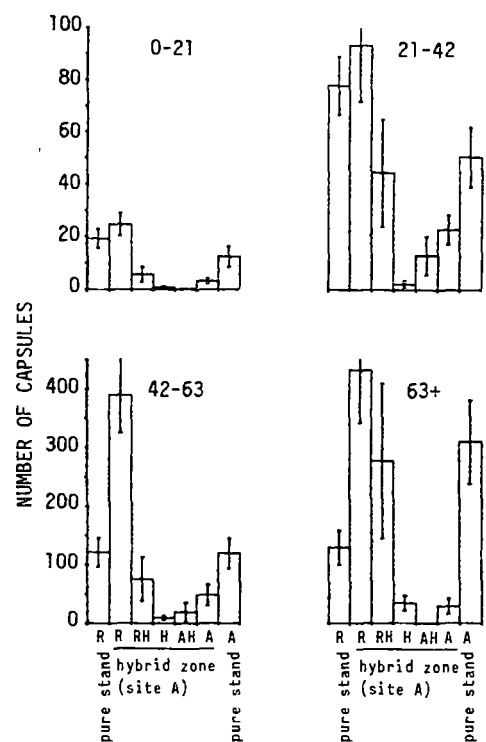


Figure 7.2 Mean (\pm S.E.) number of capsules for each phenotypic class (R, RH, H, AH, A; see Table 6.3) from the hybrid zone (site A) and samples from pure species stands of *E. risdonii* (R; site D) and *E. amygdalina* (A; site E). Individuals are partitioned into four lignotuber diameter classes (<21 cm saplings; <42 cm; <63 cm and \geq 63 cm).

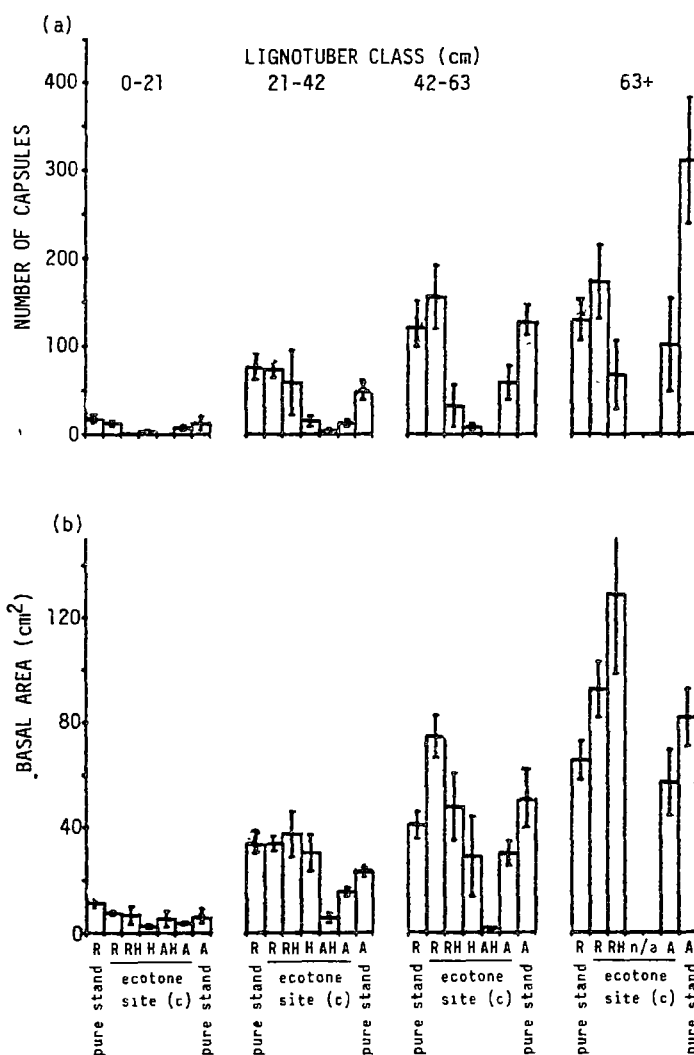


Figure 7.3 Mean (\pm S.E.) (a) number of capsules and (b) basal area (cm^2) for each phenotypic class from the ecotone (site C) and samples from pure species' stands (see Fig. 7.2). Mean basal area was calculated using only individuals on which all stems were lignotuberous regeneration from the 1960/61 fire and is thus indicative of the productivity over a 20 year period.

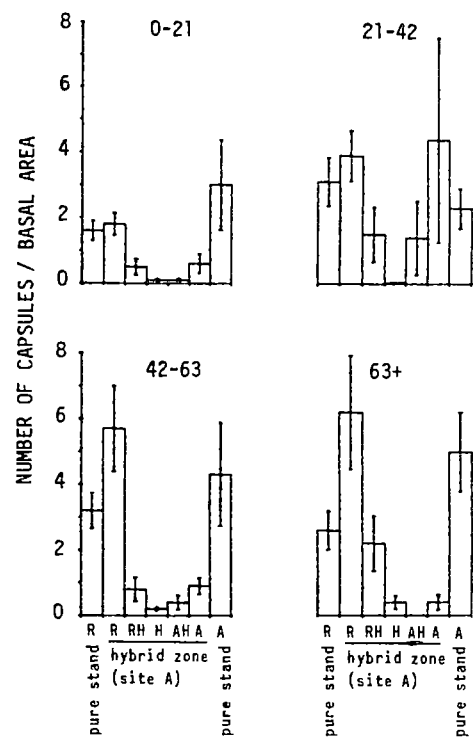


Figure 7.4 Mean (\pm S.E.) number of capsules/basal area for each phenotypic class (R,RH,H,AH,A; see Table 6.3) from the hybrid zone (site A) and samples from pure species' stands of *E. risdonii* (R; site D) and *E. amygdalina* (A; site E). Individuals are partitioned into four lignotuber diameter classes as in Fig. 7.2.

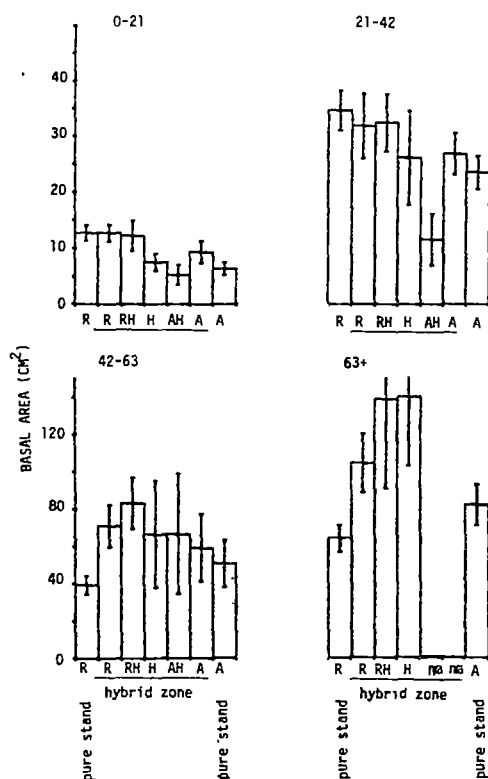


Figure 7.5 Mean (\pm S.E.) basal area (cm²) for each phenotypic class from the hybrid zone (site A) and samples from pure species' stands (see Fig. 7.2). Mean basal area was calculated using only individuals on which all stems were lignotuberous regeneration from the 1960/61 fire (see Fig. 7.3).

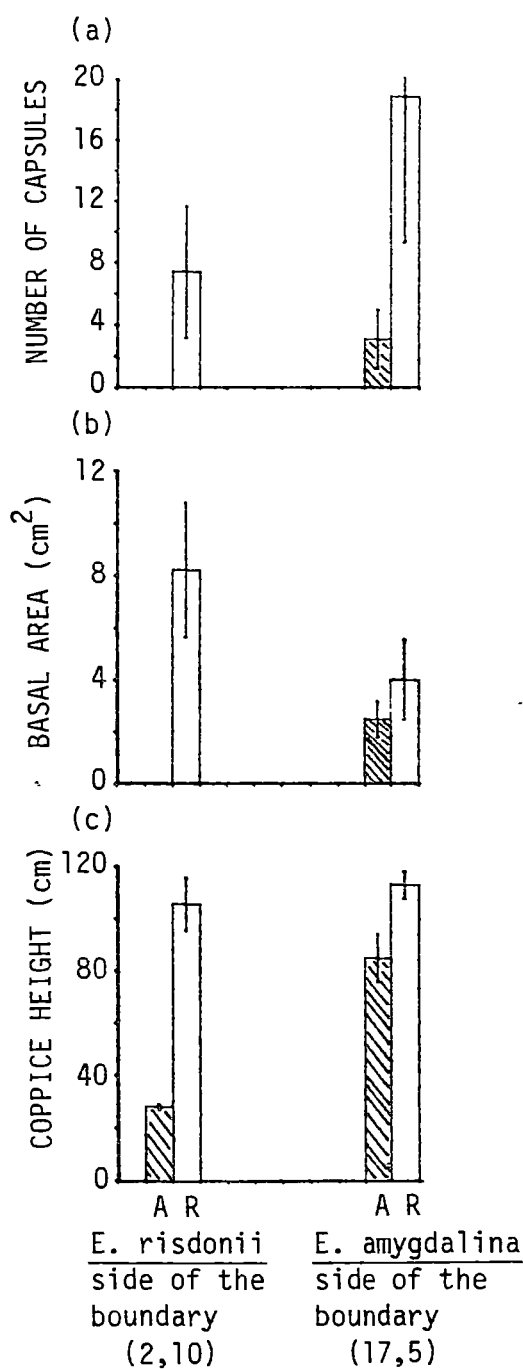


Figure 7.6 The mean (\pm S.E.) (a) number of capsules, (b) basal area (cm^2) and (c) coppice height (cm) of individuals which showed no signs of having been burnt in the 1960/1961 fire and which were assumed to represent a 20 year old cohort. Samples of both species were taken from the *E. amygdalina* and *E. risdonii* side of the northern boundary (site C). No capsules or stems greater than .5 m high were recorded on *E. amygdalina* individuals on the *E. risdonii* side of the boundary. The number of individuals scored is indicated in brackets.

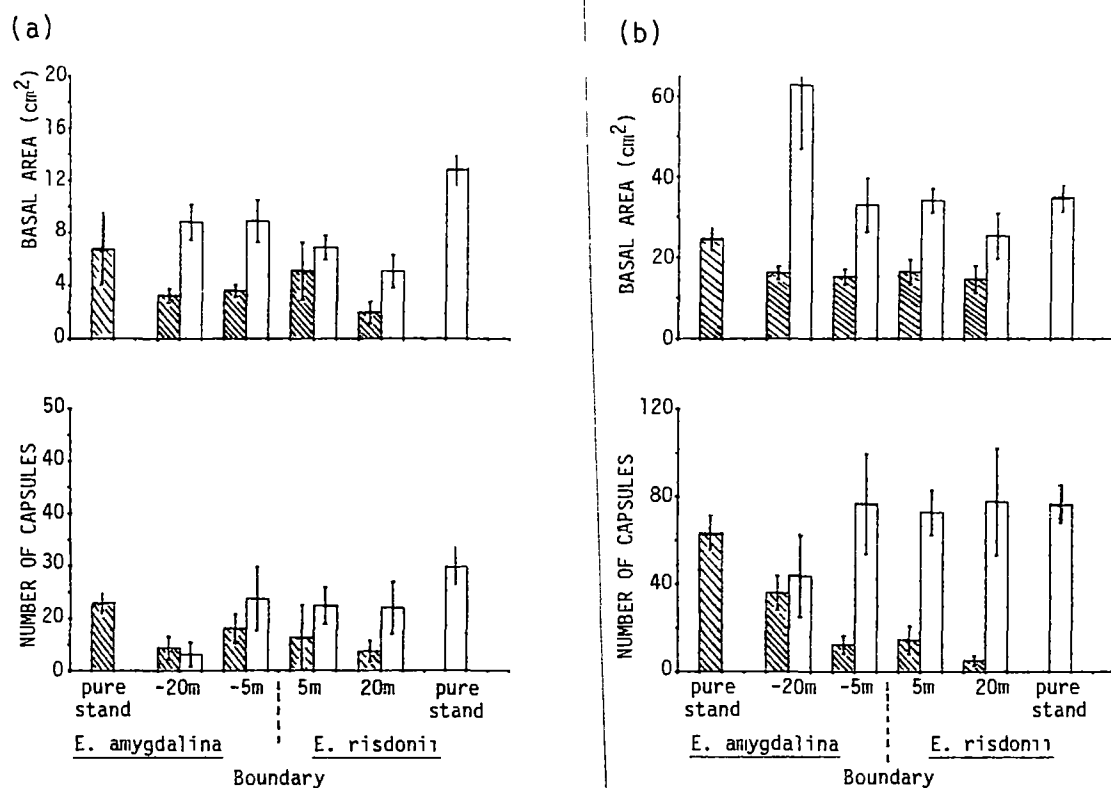


Figure 7.7 Mean number of capsules and basal area per individual (\pm S.E.) for samples of *E. amygdalina* (hatched) and *E. risdonii* (open) phenotypes with increasing distance from the boundary on the northern slope (site C) for lignotuber size classes (a) 0-21 cm and (b) 21-42 cm. The number of individuals scored are from left to right-(a) 54, (23,65), (132,26), (21,62), (20,16), 52 (b) 35, (26,3), (67,13), (23,52), (21,11), 54.

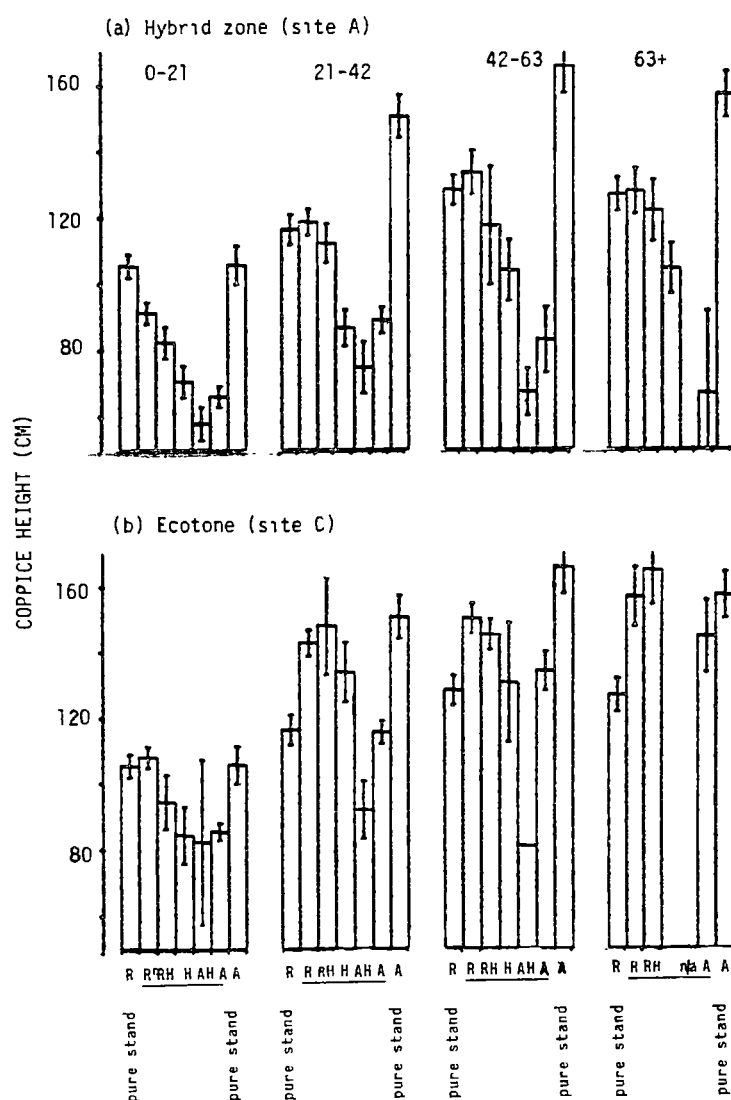


Figure 7.8 Mean (\pm S.E.) 'average' coppice height (cm) for phenotypic classes from (a) the hybrid zone (site A) and (b) the ecotone (site C) (presentation follows Fig. 7.2). Individuals regenerating from epicormic buds have been excluded and pure species' stand comparisons (i.e. sites D and E) are shown.

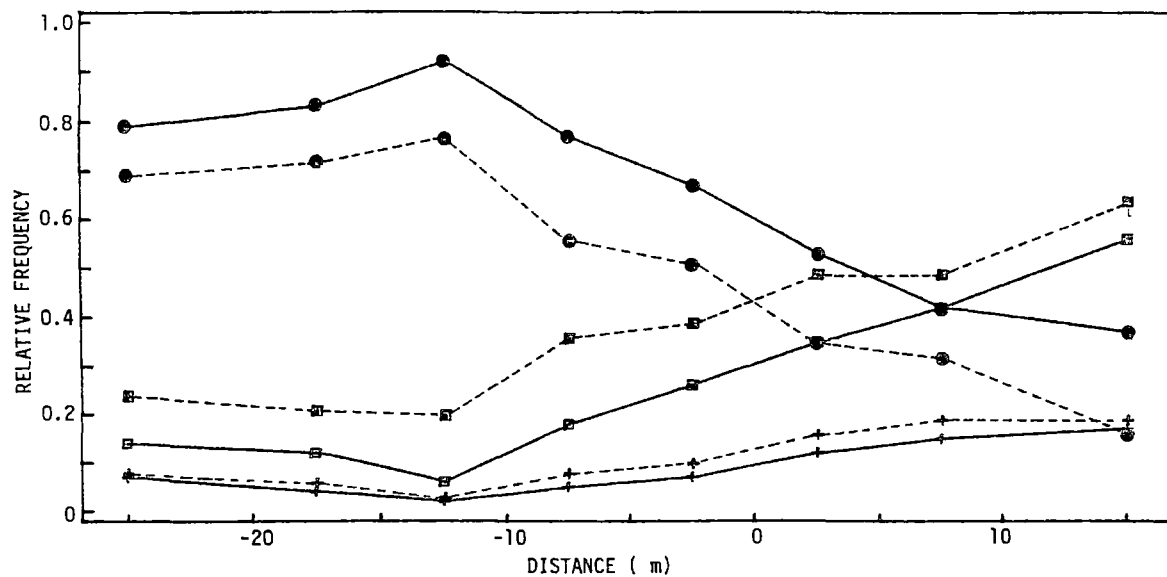


Figure 7.9 Relative frequency of *E. amygdalina* (A+AH, \square), *E. risdonii* (R+RH, \bullet) and hybrids (H, +) phenotypes across the boundary in the hybrid swarm (site A) prior to the 1980 fire (---) and 15 months after the fire (—). The latter calculations integrate adult mortality and seedling recruitment.

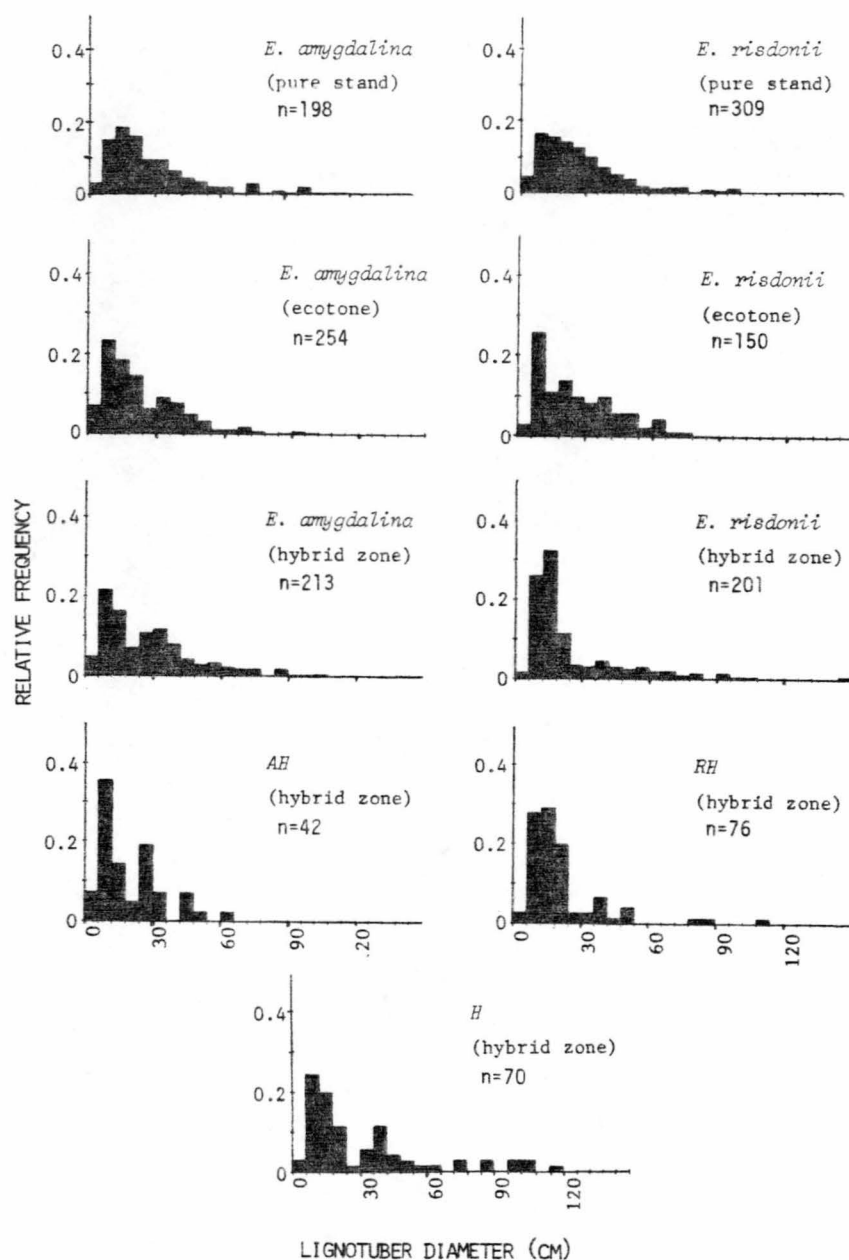


Figure 7.10 The distribution of lignotuber diameters (cm) for *E. amygdalina* and *E. risdonii* from pure stands (sites E and D), the ecotone on the northern slope (site C) and the hybrid swarm site (site A). The distribution for hybrid phenotypes is indicated for the hybrid swarm (site A).

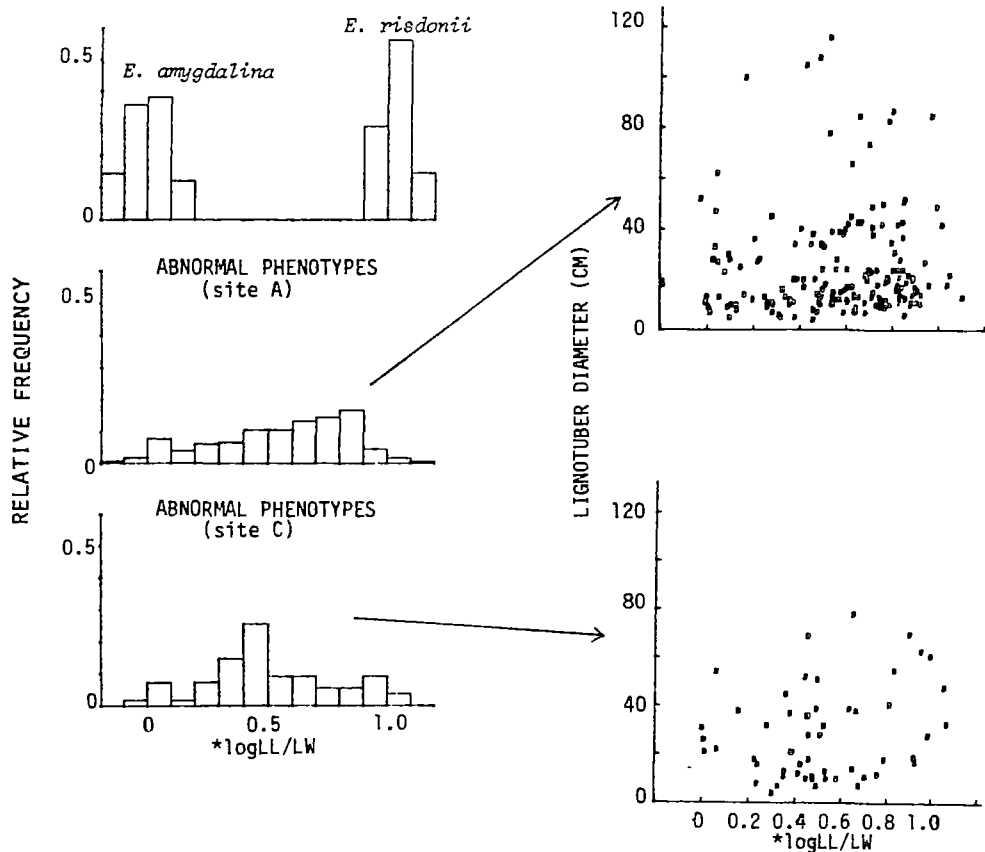


Figure 7.11 (a) The relative frequency distribution of coppice leaf shape (i.e. standardized values of $\log LL/LW$, see Fig. 6.10) for samples of *E. risdonii* (R) and *E. amygdalina* (A) from pure species' stands (sites D and E) and all abnormal phenotypes (i.e. non-pure species types - RH, H, AH) from the hybrid swarm (site A) and ecotone (site C) sites; (b) plot of the lignotuber diameter (cm) against coppice leaf shape (as in (a)) for abnormal phenotypes from the hybrid zone and ecotone sites.

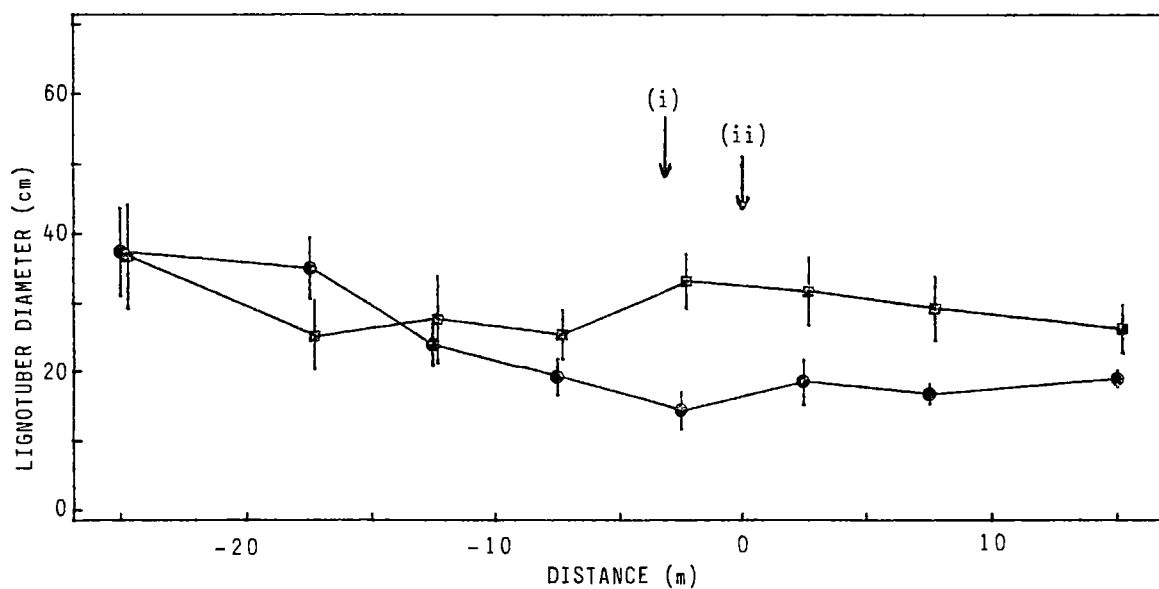


Figure 7.12 The mean (\pm S.E.) lignotuber diameter of *E. risdonii* (R, ●) and *E. amygdalina* (A, □) phenotypes across the boundary in the hybrid swarm (see Fig. 4.10). The position of the boundary (i.e. point of equal phenotypic frequency) as defined by (i) pure species' phenotypes (A/R) alone or (ii) incorporating backcrosses (A+AH/R+RH) is indicated.

The dynamics of hybridization between *E. risdonii* and *E. amygdalina*

III. Hybridization as a dispersal mechanism

8.1 Introduction

Biogeographical and palaeontological evidence leave no doubt that major geographical shifts in the distribution of *Eucalyptus* species has occurred in the past as a response to pre-historic climatic changes (e.g. Burbridge 1952, 1960; Pryor 1955b, 1976; Churchill 1968; Parsons 1968a, 1969b, 1973; Carr 1972; Kirkpatrick 1975b; Marginson and Ladiges 1982). In particular, the succession of Quaternary glacials has had a marked effect on species' distribution patterns (see Chapter 4) and in Tasmania, many of the extant forests and corresponding variation patterns are less than 11,000 years old (Macphail 1979, 1980). While species' replacement and population migration will frequently involve continuous migration routes (e.g. altitudinal shifts), the environment is frequently patchy (*sensu* Wiens 1976) with suitable habitats separated by expanses of unfavourable habitat which prevent or retard migration as a front. This is recognized in the broader ecological context of the early biogeographical theories of McArthur and Wilson (1967) where such patches are treated as 'Habitat islands'. The distinction between and correspondence of patchiness of habitat and patchiness in species' distribution is discussed by MacArthur (1972) and Vuilleumier and Simberloff (1980).

In general *Eucalyptus* populations appear to exhibit a coarse-grained response to variation in the environment and Pryor and Johnson (1971) consider that a precise ecological specificity (see Parsons and Rowan 1968 for exceptions) frequently results in many species being distributed as a mosaic of small isolated populations (see Moran and Hopper 1983). This distribution pattern is typical of many forest tree species (e.g. Fung and Wright 1972; Sterne and Roche 1974; Gordon 1976) and the problem of the origin of the mosaic and disjunct distribution pattern is well recognized particularly in the case of edaphic endemism (e.g. Stebbins 1942; Kruckeberg 1957).

In the present chapter, the dynamics of species' migration is discussed, particularly the process whereby a species (or pre-adapted genotype) may invade suitable habitats within the range of another potentially interbreeding species. The distribution and variation pattern in *E. risdonii* is typical of the mosaic distribution pattern frequently encountered in *Eucalyptus*. Furthermore, the genetic interaction of *E. amygdalina* and *E. risdonii* in parapatry appears to be comparable with that noted for numerous other taxa raised to specific rank in *Eucalyptus* (e.g. Brett 1938; Jackson 1958; Pryor 1951a,b, 1955a,b, 1976; Ashton 1958,

1981a; Pryor and Johnson 1971, 1981; Drake 1980, 1981a,b; Chapter 5). F_1 type hybrids are most common along boundaries and in terms of the complete geographical range of either species remain in low frequency. Nevertheless this does not imply their role in evolution is equally unimportant and in the present chapter it is argued these hybrids may be of major significance in the genetic and competitive interaction of the species' gene pools even though they may have no evolutionary potential as a unique taxon.

The evidence presented in Chapter 7 indicates a marked fitness differential between *E. amygdalina* and *E. risdonii* at their boundary and it is suggested that the current selective regime is not only favouring *E. risdonii* at the boundary, but in some areas currently dominated by *E. amygdalina*. A study of seedling establishment following wildfire and the demographic structure of boundary stands suggests that the boundary is moving and that in places *E. risdonii* is invading the range of *E. amygdalina*. The exact cause of this disequilibrium is unclear although it is suggested that some areas of the *E. amygdalina* population may be under drought stress, resulting in greater susceptibility to the effects of secondary selective agents such as insect predation and fire. Furthermore observations indicate many areas on drier aspects within the range of *E. amygdalina*, and well isolated from *E. risdonii*, in which the level of reproductive and vegetative vigour of *E. amygdalina* is comparable with that observed at the *E. amygdalina*/*E. risdonii* boundary. These areas are probably vulnerable to invasion by *E. risdonii* which seems to be the more drought tolerant species (Section 6.2) or, in the absence of invasion, local genetic restructuring. A simple model can be used to exemplify how such a disequilibrium could arise in a local area. This model is one of stable physical gradient interacting with a variable climatic factor to determine a primary selective gradient. In the case of a shallow physical gradient, as exemplified by the evaporative gradient along the north facing slope of the study area (Fig. 6.4), slight fluctuations in rainfall may cause a large geographical shift in the underlying primary selective gradient and hence the null point. A comparable situation could arise, for example, with altitudinal gradients (e.g. Chapter 1) where the interaction between topography and temperature may result in similar instability where the topographic gradient is shallow (e.g. plateaux). Slight climatic changes may result in a species or genotype being suddenly favoured well outside the range to which it can readily disperse by seed and this is accentuated in a patchy environment where migration as a front is prevented. In contrast, for a sharp physical

gradient, the population response is not limited by dispersal and the geographical position of the null point would be more stable. On a larger geographical scale, shallow gradients in the actual climatic factor may result in similar instability and Carr (1972) notes that small climatic changes could have very large effects on species' distributions. This is discussed by Davis (1981) who suggests that for much of the Holocene the geographic distribution of many north American forest species was in disequilibrium with the climate. The latter author suggests that the speed with which forests can adjust to climate may be far exceeded by the speed of climatic change and be limited by the availability of propagules and the ability of seedlings to survive in competition with plants already growing on a site.

The data presented in Chapter 7 suggest that the disequilibrium in the study area has probably persisted for at least several episodes of seedling establishment, although the extent of seedling recruitment following the 1980 fire indicates a basic inability of the *E. risdonii* population to track the prevailing selective regime. This appears to be due to both an extremely slow population turnover and limited dispersal potential. Successful seedling recruitment in these dry areas appears to occur at a very low rate and is probably dependent on adult mortality (e.g. Noble 1982). While the modes in the distribution of lignotuber size classes at the boundary (Fig. 7.10) may reflect periodic catastrophes befalling the dominants (e.g. fire, drought, insect predation), in most cases stands are buffered against catastrophic events by well developed mechanisms for vegetative recovery. Regardless of the relative fitness of phenotypes within a given cohort, younger cohorts will usually be at a disadvantage when competing with any adult with a well established root system. Furthermore, with the high seed output strategy of *Eucalyptus* (Drake 1981b) and recruitment dependent on adult mortality, in the absence of competition, viable populations may be still maintained on marginal sites, particularly where the seed rain is supplemented by dispersal from surrounding less marginal stands.

8.2 Seed dispersal

The extent of gene flow in plant populations is generally accepted to be limited and highly leptokurtic in form (e.g. Levin and Kerster 1968, 1974; Ehrlich and Raven 1969; Harper 1977; Levin 1981; Howe and Smallwood 1982; Hamrick 1982). In this respect *Eucalyptus* populations appear no different and Griffin (1980) suggests stands may be comprised of groups of individuals showing at least 1/2 sib relationships (see Linhart *et al.* 1981). Seed

dispersal in *Eucalyptus* is generally limited and is mainly by wind and gravity following release from capsules held in the canopy (e.g. Cremer 1965a,b, 1966, 1977). With the exception of the subgenus *Corymbia*, neither seeds nor fruits exhibit special adaptation to this mode of dispersal (Carr 1972; Parsons 1973; Kirkpatrick 1977b; Cremer 1977). Studies indicate that virtually all seed is deposited within a radius of twice the tree or canopy height (e.g. Gilbert 1958; Cunningham 1960; Floyd 1962; Cremer 1966) and Barber (1965) assumes the mean free path of seed to be about 50% of the tree height. The movement of seed once deposited on the ground is probably fairly limited (e.g. Floyd 1962) and the average distance travelled by a eucalypt seed is essentially proportional to canopy height, seed weight (i.e. terminal velocity) and windspeed (Cremer 1977). Furthermore, Cremer (1977) notes that the bigger seeds of a species tend to produce seedlings with faster initial growth and better survival and these will be deposited closer to seed sources.

Rare long distance dispersal events necessary for colonization and invasion may occur by several means. Under abnormal circumstances seed or capsules may be dispersed by birds, floods, storms, or in fire updrafts (e.g. Jacobs 1955; Carr 1972; Kirkpatrick 1977b). In the latter case, seed dispersal may be coincidental with conditions favouring Eucalypt regeneration and it is suggested that fire may facilitate the dispersal of seeds to distances greater than normal (Carr 1972). Kirkpatrick (1977b) suggests that small branches with capsules attached may be carried in fierce convectional updrafts during crown fires and deposited some distance from parent trees. However, this is more likely to be of significance in the wetter forests which support higher fuel loads, although Cremer (1965a) suggests that seed shed enclosed in capsules probably produce relatively few seedlings. While strong beaked birds such as cockatoos may break open the woody capsules to eat seed (Jacobs 1955; Cremer 1965a) their significance as a mode of dispersal has not been demonstrated (see Carr 1972) and no such predation or damage was observed in the study area. Water transport may be significant for species growing on river margins or floodplains (Carr 1972; Cremer 1977) and Carr (1972) suggests cataclysmic wind dispersal may explain the tropical, extra-Australian distribution of several species.

Migration of E. risdonii by seed

An estimate of the migration ability of *E. risdonii* by seed was obtained from variation in the relative density of seedlings established after the 1980 fire, with distance from a *E. risdonii* (R+RH) seed source (Fig. 8.1; Table 8.1). This makes the assumption discussed by Levin and

Kerster (1974) and Levin (1981) that the incidence of seedlings is generally distributed in a manner similar to the seed.

There is a rapid decline in the relative seedling density over 5 metres (1 to 2 canopy heights) from a seed source (Fig. 8.1; Table 8.1). Estimates of the mean free path of *E. risdonii* seed range from 2.5 m when dispersing upslope across the prevailing wind direction (Fig. 8.1b) to 4.3 m down wind of an isolated patch of *E. risdonii* (Fig. 8.1c). This is in vegetation with an average canopy height of about 4 m and contrasts with an estimate of 55 m by Barber (1965) for Gilbert's (1958) data for 100 m high *E. regnans*. There was no evidence for selection against seedlings established at a greater distance from a *E. risdonii* source and the opposite is probably the case due to greater intra-specific competition closer to seed sources (see Levin 1981). Estimates of the potential distance travelled by both *E. risdonii* and *E. amygdalina* seed were calculated at varying wind speeds by the relationship given by Cremer (1977). Even under gale conditions seed released from the low canopy is unlikely to travel beyond 50 m and this distance would be rarely realized with a closed canopy (e.g. Levin and Kerster 1974). The greatest distance a *E. risdonii* type seedling was observed from a source was 20 m (Fig. 8.1c). Nevertheless, in spite of limited seed dispersal, *E. risdonii* type seedlings still dominated establishment, up to 20 m from the boundary (i.e. position of equal frequency; e.g. Fig. 8.2) due to the low density of *E. amygdalina* seedlings. In relation to forest species (e.g. Gilbert 1958; Cunningham 1960; Floyd 1962; Cremer 1966) estimates of seed dispersal by *E. risdonii* in the low mallee vegetation on the northern slope of the study area are exceptionally limited. This is no doubt a result of the low canopy height (c. 4m), although this is typical for *E. risdonii*, which even in the tree form rarely exceeds 8 m in height. Similar low canopy heights are frequently encountered in *Eucalyptus* under extremes of altitude, fire or drought and is typical of the mallee communities in the drier areas of Australia (e.g. Jacobs 1955; Holland 1969; Noble 1982). In the latter case, Onans and Parsons (1980) note similar limited dispersal, and no eucalypt seedling was found more than 10 m from a seed source.

The limited dispersal potential of *E. risdonii* seed would severely retard the rate of invasion of suitable habitats within the range of *E. amygdalina*, particularly where, on both a local and broader geographical scale, suitable sites may be separated by expanses of less favourable habitat. Even within the confines of the study area, sites separated by only several hundred meters may be effectively isolated, particularly where dispersal must occur across gullies between north facing slopes or against

the prevailing wind direction, such as across the north slope of the study area. Seed dispersal into many sites would be hindered by the steep topography resulting in a general downslope migration due to gravity and water movement. There is circumstantial evidence that water movement has resulted in a few rare cases of long distance seed dispersal in the study area, but this is into unfavourable habitats (i.e. gullies). An assessment of the distribution of isolated adult and seedling *E. risdonii* within the range of *E. amygdalina* which could possibly represent founders, suggests that migration by seed is exceptionally limited and long distance (> 20 m) dispersal events are rare.

8.3 Pollen dispersal

In contrast to seed dispersal, the breeding system of *Eucalyptus* (Barber 1965; Pryor 1976), as well as many other woody plant genera (e.g. Stebbins 1950; Grant 1958) is adapted for gene flow within species by pollen dispersal. In *Eucalyptus*, flowers are generally protandrous (Pryor 1976; Griffin 1980) and outcrossing rates are high (40-82%; Brown *et al.* 1975; Phillips and Brown 1977; Moran and Brown 1980; Hopper and Moran 1981). Gene exchange is usually effected by active, generally non-specific, pollinating vectors such as birds and insects (e.g. Barber and Jackson 1957; Ashton 1958, 1975; Barber 1965; Pryor 1966; Hopper and Moran 1981). As with seed there is little doubt that the distribution of pollen is leptokurtic with the vast majority of pollen being distributed in the immediate neighbourhood of the parent (e.g. Barber 1965; Pryor 1957b, 1976; Hopper and Moran 1981). Nevertheless, as noted by Barber (1965) gene migration in *Eucalyptus* will be more a function of pollen than of seed, particularly where strong flying pollinating agents are involved. In effect, it is in the frequency of the rarer long distance events that pollen probably surpasses seed migration. This is exemplified by Levin and Kerster (1968), where the mean distance of dispersal of seed and estimated pollen dispersal were similar, but the variance associated with pollen dispersal was greater, particularly when pollinator escape and exploratory flights were considered (see also Beattie and Culver 1979).

This is simply extended to the case of genetic interaction between species as opposed to gene migration within species. In *Eucalyptus* strict genetic isolation appears to be only maintained at the subgeneric level (Pryor 1959a, 1976) and barriers to interspecific hybridization within subgenera are frequently weak (e.g. Brett 1938; Jackson 1958; Pryor 1955a, 1976; Pryor and Johnson 1971, 1981; Drake 1980, 1981a,b; Fig. 5.12). As

predicted by theories and models of reproductive character displacement (see Bigelow 1965; Crosby 1970; Endler 1977; Caisse and Antonovics 1978; Lande 1982) and appears to be the case in this study, such barriers may be developed strongest in the immediate vicinity of genetic interaction. Furthermore, while hybrids and hybrid swarms are often associated with unnatural site disturbance (e.g. Stebbins 1950; Anderson 1949; Pryor 1953, 1976), the significance of hybridization in response to natural changes in the environment is well recognized (e.g. Anderson 1949; Bigelow 1965; Remington 1968; Pryor and Johnson 1971, 1981).

The significance of hybridization to gene flow in the study area

The flow of *E. risdonii* genes into the range of *E. amygdalina* appears to be not only occurring by seed, but also by pollen migration. At all sites there is a significantly greater frequency of adult F_1 type (H) hybrids on the *E. amygdalina*, as opposed to the *E. risdonii*, side of the boundary (Table 8.2; Figs. 7.9, 8.2). The relative frequency of F_1 type hybrids drops dramatically on the *E. risdonii* side of the boundary and they are virtually absent from central *E. risdonii* stands (e.g. site D). A similar decline with distance from the boundary is also observed on the *E. amygdalina* side. However, hybrids are still found scattered in low frequency (1 to 2%) throughout the *E. amygdalina* forest 200 to 300 meters from the nearest *E. risdonii* and very occasionally occur up to 1 km from a source of *E. risdonii* pollen. The asymmetrical distribution of F_1 types across the boundary may reflect both differing probabilities of hybrid production and survival. Evidence from the progeny trial (Table 6.7; Fig. 6.10 indicates a greater proportion of hybrid seed is produced by *E. amygdalina* than *E. risdonii* mothers from relatively pure stands. This could reflect an inherent difference in the success rate for reciprocal crosses (e.g. Pryor 1956) or a greater relative abundance of *E. risdonii* pollen at the time *E. amygdalina* flowers are receptive. A reduction in the reproductive fitness of *E. amygdalina* could conceivably cause an increase in the relative proportion of hybrid phenotypes in outcrossed seed due to swamping by *E. risdonii* pollen. Furthermore, the fitness data presented in Chapter 7 suggests that the intermediate type (H) hybrid is also vegetatively and reproductively more competitive with *E. amygdalina* than with *E. risdonii* and under the current selective regime would have a much greater probability of survival in *E. amygdalina* dominated areas.

Several lines of evidence suggest that *E. risdonii* genes are swamping the hybrid swarm (site A) although intermediate hybrids (H) are predominantly

on the *E. amygdalina* side of the boundary (Figs. 7.9 and 8.2). The distribution of hybrid phenotypes in the hybrid zone is biased toward phenotypes tending toward *E. risdonii* (i.e. RH) which contrasts with the hybrid sample from the ecotone (site C) where hybrids are less frequent and predominantly F₁ types (H) (Fig. 7.11). Moreover, the demographic structure of the hybrid (RH, H and AH) samples from both sites indicates a relatively greater prevalence of phenotypes tending toward *E. risdonii* (RH) than toward *E. amygdalina* (AH) in the younger cohorts (e.g. sites A and C; Figs. 7.10 and 7.11; Table 7.20). However, the bias toward *E. risdonii* types in the hybrid swarm is not due to preferential hybrid pollination of *E. risdonii* mothers. On the contrary, this appears to result from both a greater fitness of the hybrid phenotype tending toward *E. risdonii* (RH) than either of the other hybrid phenotypic classes (H or AH) as well as swamping of the hybrid mothers by *E. risdonii* pollen. The latter is discussed in Chapter 6, where progeny trials suggest a predominantly uni-directional flow of genes by pollen migration from *E. risdonii* into the hybrid swarm and surrounding *E. amygdalina*. Moreover, the distribution of hybrids tending toward *E. risdonii* (RH) is similar to that noted for *E. risdonii* (Chapter 7, Fig. 7.12), with younger individuals tending to be found in areas dominated by hybrids (H) or *E. amygdalina* (A) with older individuals generally found in *E. risdonii* areas.

This study suggests that hybridization may occur as a result of natural disequilibrium and may be associated with species replacement. Where seed migration is limited, as in the present example, boundary movements may be preceded by a wave of hybridization due partly to swamping of the least fit species by pollen. It appears that in places *E. risdonii* is expanding as a slowly moving front which is heralded by a wave of F₁ hybrids. These hybrids may occasionally develop into hybrid swarms, which at the boundary are probably transitory and are in turn swamped by genes of the fitter species (i.e. *E. risdonii*). The asymmetry in hybrid distribution about such a moving boundary appears to contrast with that reported for animal based examples or models (see examples cited in Moran 1981) where introgressed derivatives trail the main front. Nevertheless, the full extent of introgression in the present case may not be revealed from morphological criteria alone (e.g. Alston and Turner 1962; Hopper 1978b).

Hybrid swarms are not only found at the immediate boundary between the two species, but patches containing a wide array of abnormal (i.e. non-*E. amygdalina*) phenotypes can be found well out from the boundary and up to 1 km within the range of *E. amygdalina*. These patches are localized and

are generally found on ridges or dry north to north-west facing sites. The phenotypic composition of a range of these patches on the north slope and ridge 200-300 meters from the main *E. risdonii* population is indicated in Figure 8.3 (see also Fig. 6.3). Many of these patches are dominated by *E. amygdalina* backcross (i.e. AH) or intermediate (H) phenotypes, yet there is a complete gradation to those dominated by *E. risdonii* phenotypes. At this distance from the main population *E. risdonii* types are not found as isolated individuals (Fig. 8.3). On the other hand the F₁ type hybrid is regularly encountered (1-2%) scattered throughout the forest. Whenever *E. risdonii* phenotypes are found in this area they are associated with patches of abnormal (i.e. non-*E. amygdalina*) phenotypes and the larger patches generally have a higher relative frequency of *E. risdonii* types (RH or R). These isolated patches could be interpreted as representing the genetic remnants of a wider distribution of *E. risdonii* in the past. However, in this case, the fitness differential at the boundary as well as the demographic structure of some of the patches suggest they may have arisen by active genetic invasion. Furthermore, there is good evidence that at least some of these patches have not been founded by seed migration, but are the result of long distance pollen dispersal since the demographic structure of several of the smaller patches in which all non-*E. amygdalina* individuals were scored (Fig. 8.4) suggests that in each case that the patch was founded by an F₁ type hybrid. The appearance of the *E. risdonii* type occurs well after the F₁ type and, in cases, at a stage where the patch has achieved considerable development. The absence of isolated or even small patches of pure *E. risdonii* phenotypes which could have arisen by seed dispersal in this area is strong evidence that phenotypes within these patches which tend toward *E. risdonii* have arisen from the hybrid swarm by segregation or even backcrossing to distant sources of *E. risdonii*. The patches with a greater proportion of *E. risdonii* phenotypes were at a similar distance from the main population to those in Fig. 8.4 but the exact origin of the latter patches cannot be inferred from their demographic structure. It is suggested that the patches in Figure 8.3 could represent a complete temporal sequence in the invasion by *E. risdonii* of suitable sites within the range of *E. amygdalina* by hybridization followed by back selection to the *E. risdonii* type from a segregating hybrid swarm.

8.4 Hybridization as a dispersal mechanism

Despite barriers to hybridization between *E. risdonii* and *E. amygdalina*, it is most likely that in terms of distance, the flow of *E. risdonii* genes into the range of *E. amygdalina* by pollen dispersal is more effective than by seed dispersal. F₁ type hybrids (H) are found scattered at low frequency throughout the *E. amygdalina* forest, often at some distance from a source of *E. risdonii* pollen. These hybrids serve as a basic source of genetic variation and a reservoir of *E. risdonii* genes. However many of these F₁ types are quite old and the absence of any detectable offspring in their vicinity suggests extinction. This will apply to most long distance dispersal events. Nevertheless, occasionally, particularly on the drier sites, hybrid swarms appear to have been initiated from a single F₁ founder at considerable distance from a *E. risdonii* seed source and in areas beyond the normal range for seed dispersal. Furthermore, in several cases it appears that within a single generation, the *E. risdonii* phenotype is recovered on sites independent of seed migration. This appears to have occurred in spite of barriers to hybridization as well as potential genetic swamping from the more frequent *E. amygdalina*.

It is proposed that such long distance pollen dispersal followed by interspecific hybridization may act as a potential mechanism for long distance species migration, particularly where movement as a front is retarded and seed dispersal is limited. This mode of invasion appears to be occurring in the study area and involves pollen dispersal and hybridization which in cases may be followed by reselection of the well adapted gene combinations of the pollen parent from a hybrid swarm (e.g. Benson *et al.* 1967). This mechanism of migration integrates several ideas which pervade the literature. For example, despite segregation of a wide array of phenotypes in the progeny of some interspecific F₁ hybrids, types close to the original parental species are often recovered (e.g. Pryor 1956; Stebbins 1950, 1959). In fact, there is frequently a tendency for parental characters to cohere in the F₂ (e.g. Anderson 1939, 1949; Ehrendorfer 1959; Clausen and Hiesey 1960; Hartley 1965; see Chapter 5). Moreover, recombinant or intermediate types are often less fit than individuals resembling either parent (e.g. Pryor 1956; Stebbins 1969) and this is commonly postulated to result from the disruption of the co-adapted genome of either species (e.g. Mayr 1963, Grant 1975; Solbrig 1980; Moran 1981). Furthermore, on suitable sites directional selection may shift the phenotypic composition of the hybrid swarm toward the pollen parent, independent of backcrossing (see Grant 1971; pp.175). On sites where the differences in fitness at the boundary are maintained, the appearance of the *E. risdonii*, or similar (RH), phenotype would be associated with

a marked increase in the reproductive output of the patch and a rapid shift toward the *E. risdonii* phenotype. Not only are these patches a source of *E. risdonii* genes by segregation, but they may act as a focal point within the *E. amygdalina* forest for future gene exchange, which in turn would speed the process of fixation. Once the patch achieves a threshold of both size and genetic structure, it may in itself become a significant source of *E. risdonii* seed and pollen. The patches of abnormal (non-*E. amygdalina*) phenotypes within the *E. amygdalina* forest form a complete transition from those dominated by intermediates to patches dominated by *E. risdonii* types. With no knowledge of this mechanism, patches dominated by, for example, the *E. risdonii* backcross phenotype (RH) would probably be interpreted as local variants of *E. risdonii* or possibly as *E. risdonii* exhibiting signs of introgression of perhaps a few genes from the local *E. amygdalina*. Alternatively, particularly where less differentiated species were involved, these patches may be erroneously interpreted as examples of sympatric speciation involving the gradual selection and recombination of genes inherent within a single species' gene pool (i.e. *E. amygdalina*). However, in the present study there is good evidence that the original intermediate phenotype is older and preceded phenotypes tending toward *E. amygdalina*. Furthermore, while seed migration cannot be excluded, it is possible that many of the larger patches may have arisen by virtually the complete introgressive replacement of the local *E. amygdalina* by *E. risdonii* genes. Bloom (1976) discusses a comparable example involving introgressive replacement and suggests that the apparent rarity of known cases of geographically extensive introgression may be due to introgression being so complete as to be normally undetectable.

The present study indicates that species migration by hybridization is a viable means of long distance genetic invasion. This will be particularly important where seed dispersal is limited compared to pollen dispersal and reproductive barriers between species are weak. Such is the case in many woody plant genera (e.g. Grant 1958; Stebbins 1950; Barber 1965; Mirov 1967; Tigerstedt 1967; Libby *et al.* 1969), particularly wind pollinated species (e.g. Endler 1977; Hamrick 1982; Millar 1983; cf. Linhart *et al.* 1981), and hybridization may represent a fairly general mechanism for species migration. It may be important in explaining the mosaic and disjunct distribution patterns of some species where neither range restriction nor parallel evolution suffice. Moreover, for species occupying specific localized habitats where an extreme environment necessitates large seed reserves (e.g. Baker 1972) there could be considerable advantage in maintaining an aggressive hybridization policy. In *Eucalyptus* there are sufficient reports of isolated

sporadic hybrids, hybrid swarms, phantom hybrid populations and convergence in the variation pattern (see Pryor and Johnson 1971; Chapter 5) to suggest this process should be given consideration in the interpretation of population variation and distribution patterns. Nevertheless, unless founder populations are observed and parental forms sufficiently distinct, detection of hybridization may be difficult. If this process is widespread, it would suggest that at the founder stage many 'species' populations have experienced a phase of hybridization. Even where *E. risdonii* seeds act as founders those were observed to be frequently involved in hybridization with the surrounding *E. amygdalina*. This would result from both the proximity of plants in the founder population to those of the other species as well as pollen swamping from the more common species. As expressed by Levin (1978a) "As the size of the unispecific aggregations expand, the probability of alien pollen receipt diminishes." At the founder stage a population less than several neighbourhood sizes in diameter will be continuously subject to genetic swamping from surrounding potentially interbreeding species, in a manner proportional to the population size (i.e. Levin 1978b). Populations initiated from founders (either seed or pollen) within the range of a potentially interbreeding species are most highly likely to have experienced a phase of hybridization which would allow the opportunity for either adaptative or non-adaptative gene exchange. This would be of less significance where the species was invading as a front, but may explain some of the variation between disjunct populations of a single species. In fact, Kirkpatrick (1976) suggests variation between populations of some *Eucalyptus* species may be as much related to gene exchange with associated species as divergence in response to differing environments.

The significance of hybridization in evolution is well recognized in terms of both speciation by allopolyploidy (see Grant 1971) and enhanced evolutionary flexibility associated with the release of variability (see Section 6.1). The present studies (e.g. Chapters 4, 7 and 8) suggest that hybridization may be an intimate part of the process of range restriction and expansion, and may be of greatest evolutionary significance in small relic or founder populations respectively. However, in addition to the role normally emphasized for hybridization, the present studies (Chapters 5 and 8) suggest that interspecific hybridization may also be of significance as a means of dispersing genes or co-adapted gene combinations where the adaptive response is limited by restricted seed dispersal. The probabilistic outcome of evolution in a changing environment may depend on a balance between the probability of migration of pre-adapted species or genotypes and *in situ* adaptation of the local population. The interplay between these two processes

may result in a feedback model whereby the greater time the local population has to adapt to a new environment, the lower probability of successful invasion. In this sense, hybridization may have a negative effect on evolution by enhancing the migration of pre-adapted, differentiated genotypes and as a consequence may reduce the opportunity for novel differentiation and even primary speciation in another species. The geographical range of one species may be increased at the expense of ecological range expansion by another. Nevertheless, in a changing environment there are clear evolutionary advantages for groups of species which remain interfertile with both the release of variability and increased dispersal potential enhancing the adaptive response.

Table 8.1 Variation in the relative density of *E. risdonii* seedlings (R+RH) across the *E. risdonii*/*E. amygdalina* boundary at site B (Fig. 6.3) prior to the 1981 summer. Data are derived from contiguous 5 x 20 m quadrats centred on the indicated distances from a source of *E. risdonii* (R+RH) seed and the density of seedlings relative to the total number counted is indicated in brackets. The reduction in seedling density in the first quadrat is probably due to competition with *E. risdonii* parents.

	Distance from source (m)	Estimated (R+RH) seed released/m ²	Seedling density
1.	0	46	60 (0.24)
2.	0	21	107 (0.43)
3.	2.5	0	64 (0.26)
4.	7.5	0	17 (0.07)

Table 8.2 The relative frequency (excluding *E. viminialis*) of intermediate type hybrids (H) on the *E. risdonii* and *E. amygdalina* dominated sides of the boundary in the hybrid swarm (site A) and at the northern boundary site (site C). Estimates are obtained from quadrat data and calculated over equal distances from the boundary. The significance of the Chi-squared test is indicated.

	<i>E. amygdalina</i> side	<i>E. risdonii</i> side	Significance
Hybrid Swarm (site A)	0.16	0.06	P<0.001
Northern Boundary (site C)	0.08	0.02	P<0.01

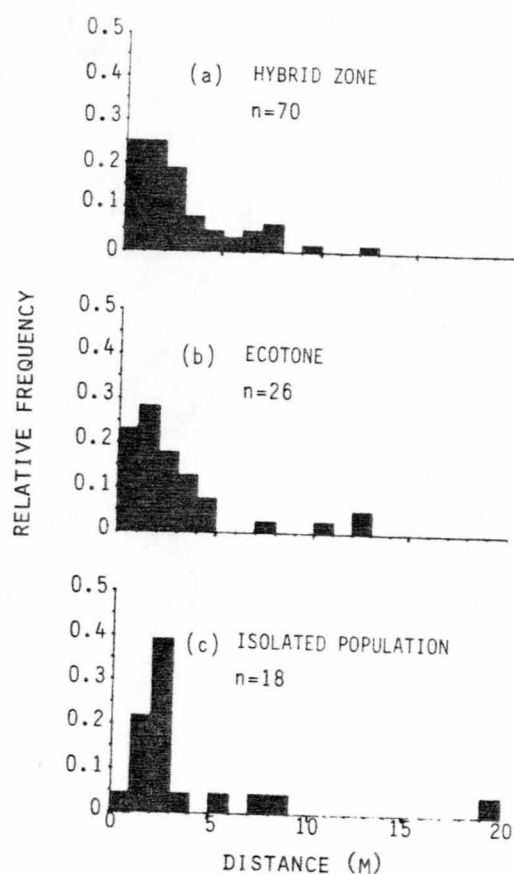


Figure 8.1 The relative frequency of 2½ year old *E. risdonii* (R+RH) type seedlings from the nearest *E. risdonii* (R+RH) adult. Samples were taken out from the boundary into *E. amygdalina* dominated areas in the vicinity of (a) hybrid swarm (site A), (b) the boundary on the northern slope (site C) and (c) an isolated patch of *E. risdonii*.

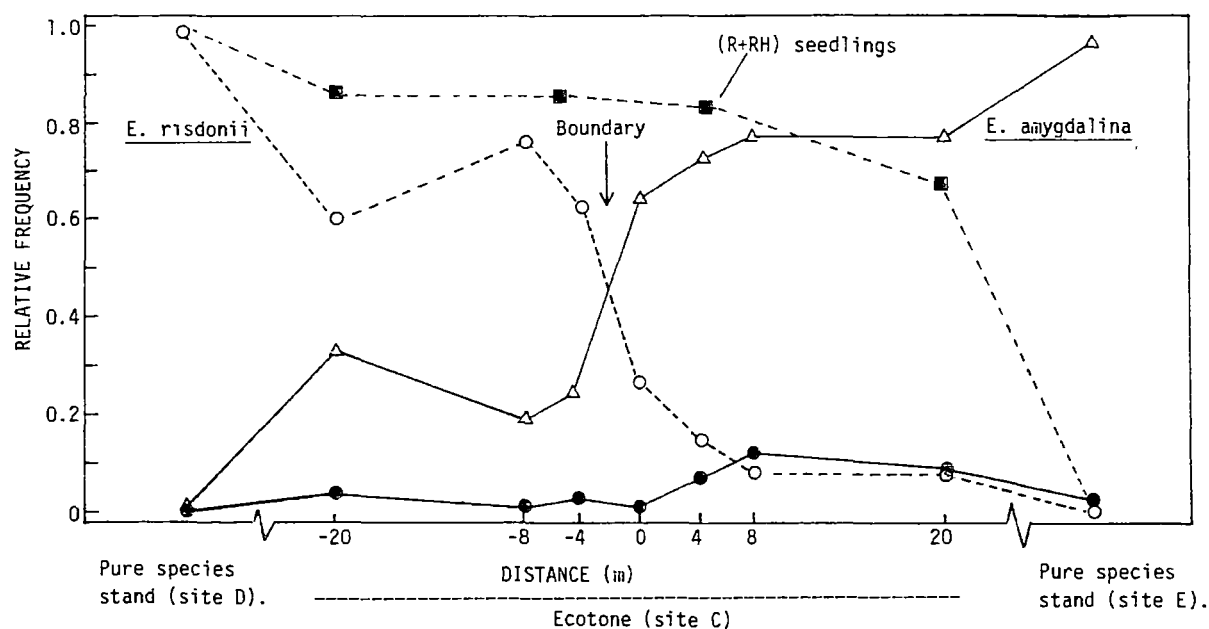


Figure 8.2 The relative frequency of *E. amygdalina* (A, Δ), *E. risdonii* (R, O) and F_1 type hybrid (H, ●) adult phenotypes and the frequency of *E. risdonii* (R+RH, ■) seedlings relative to the total number of seedlings across the boundary at the ecotone site (site C) and in pure species stands (sites D and E).

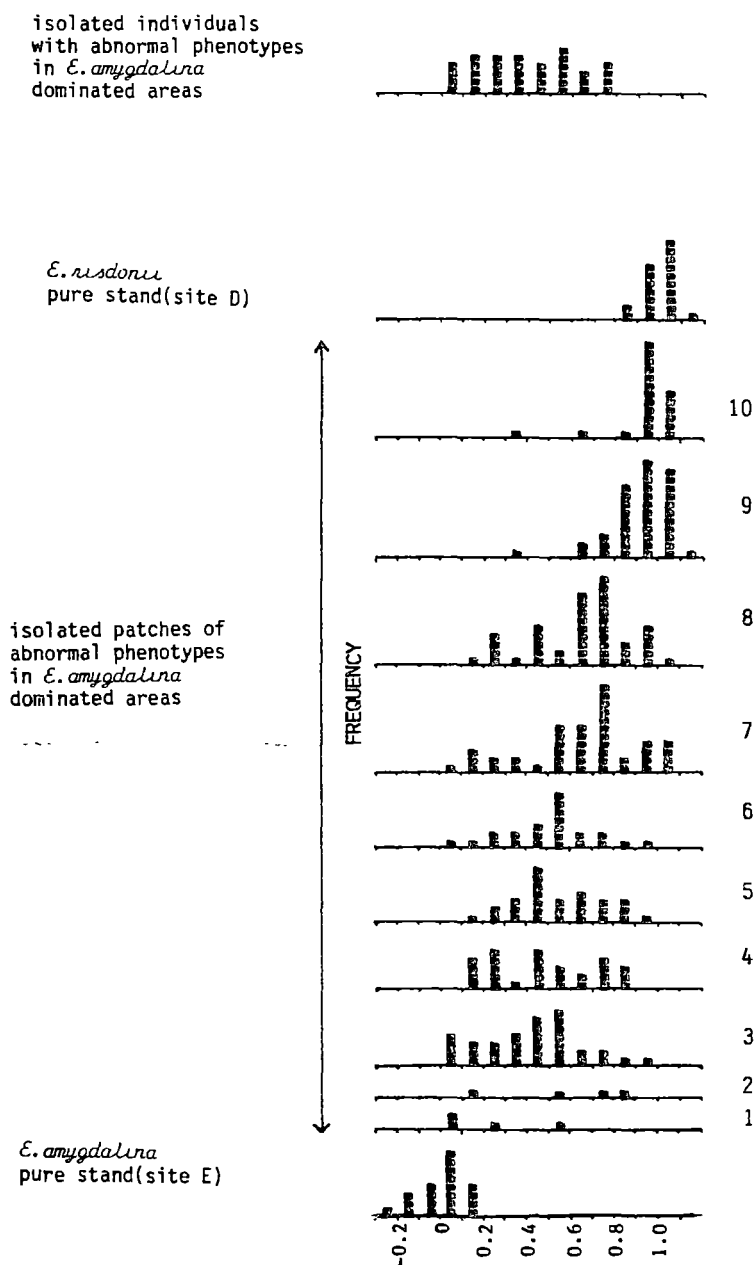


Figure 8.3 The relative frequency distribution of standardized $\log LL/LW$ values from coppice of abnormal (i.e. non-*E. amygdalina*) phenotypes in isolated patches within the range of *E. amygdalina* on the ridge and north slope of the study area. Random samples only were taken from patches 7 to 10 and the pure stand samples, whereas all abnormal individuals in patches 1 to 6 were measured (each square = 1 individual).

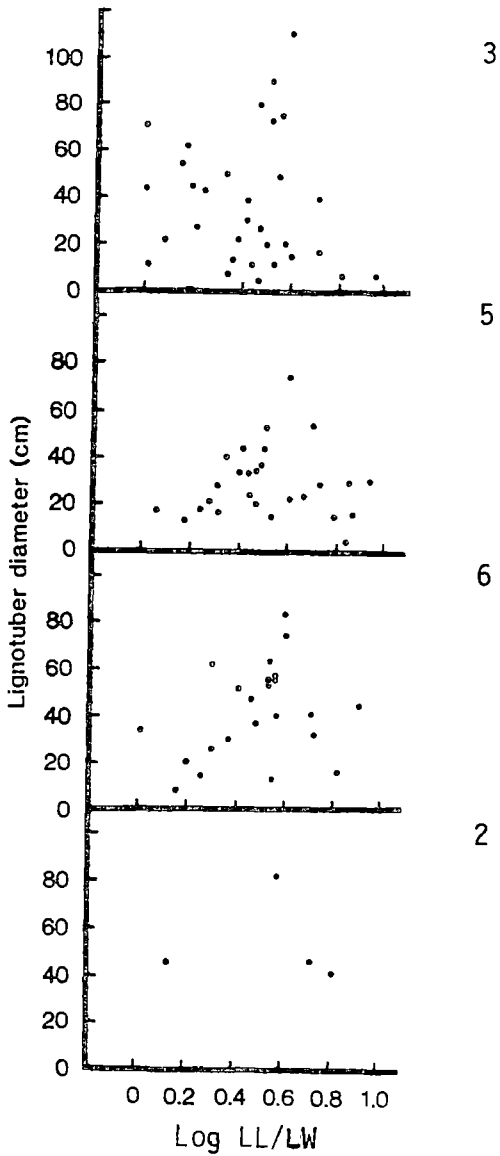
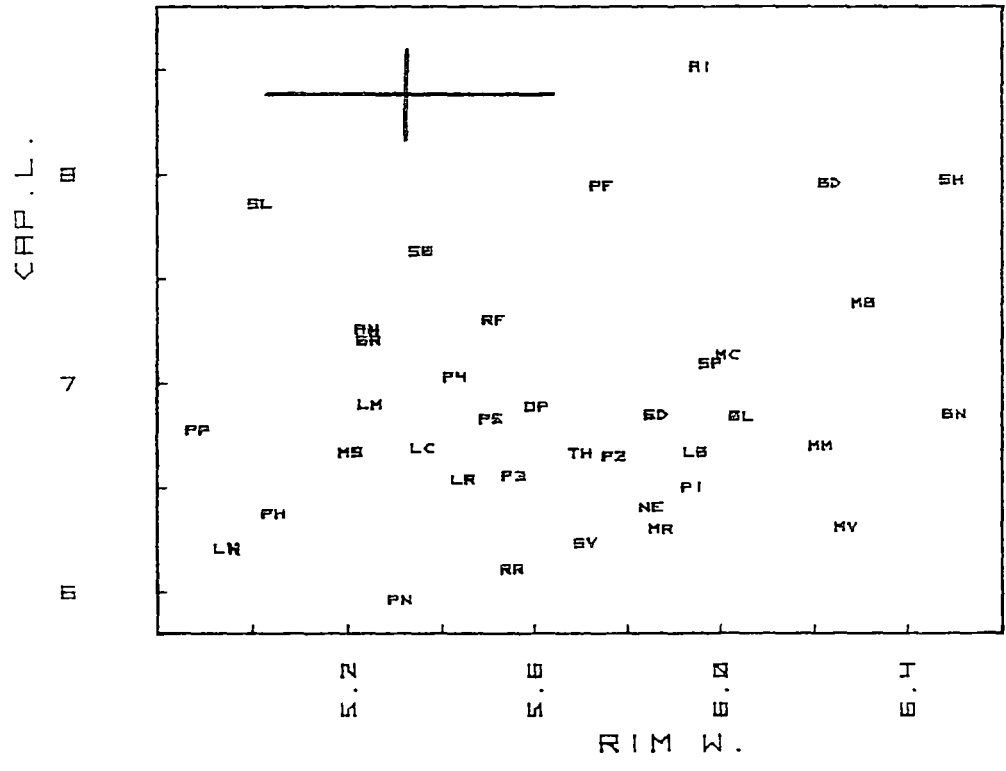
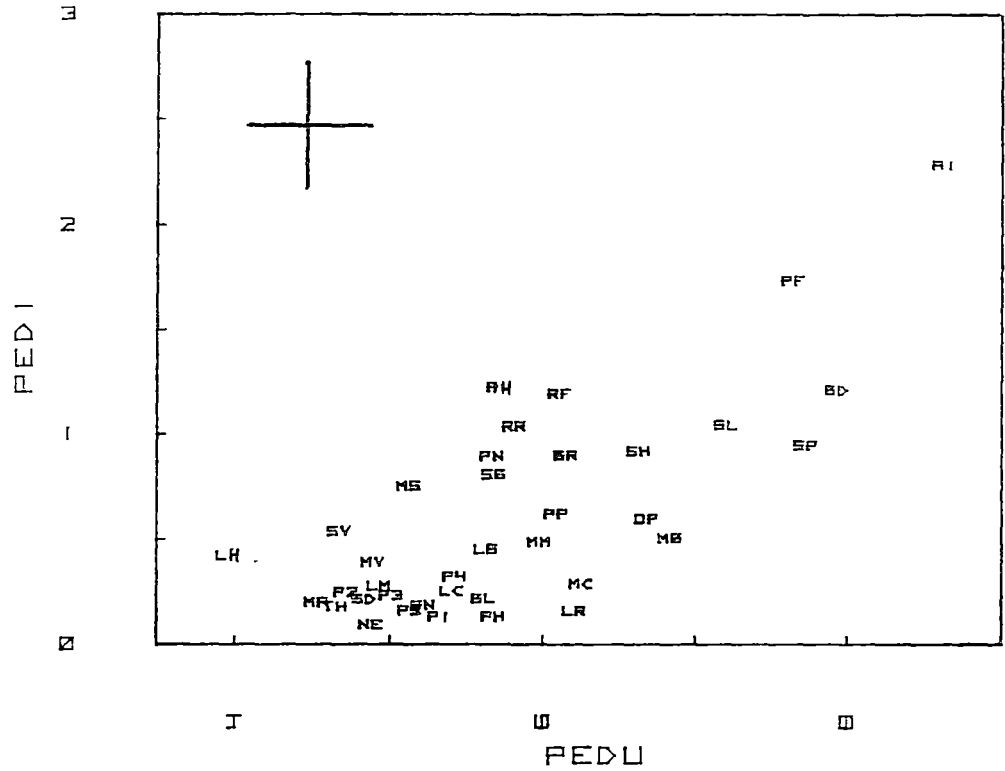
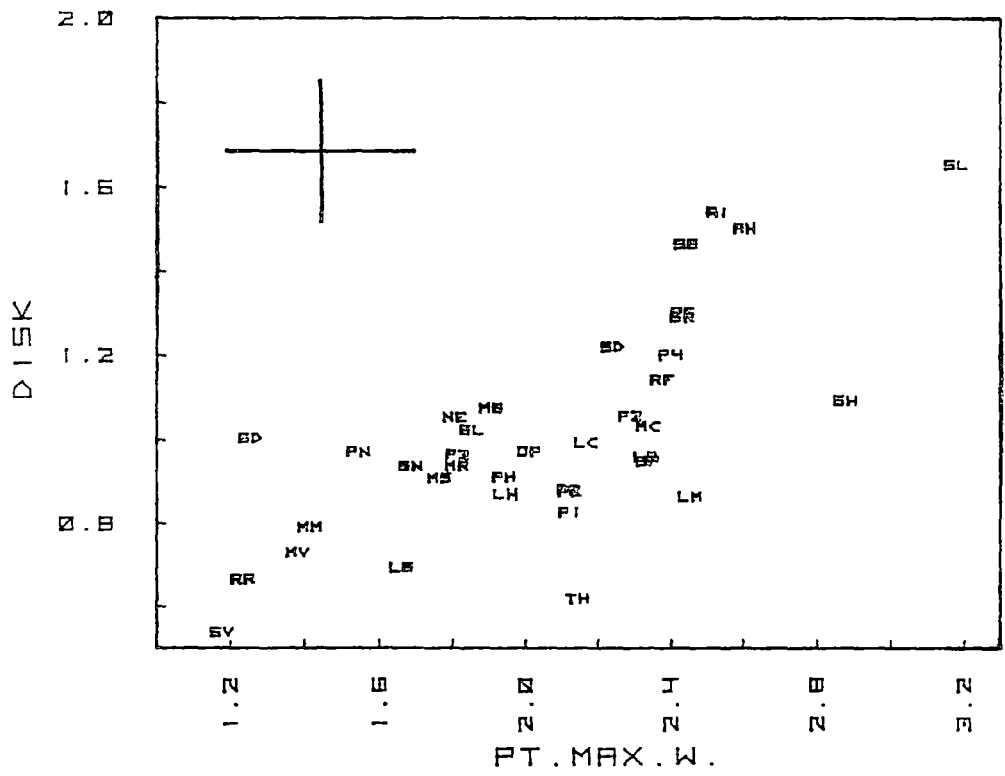
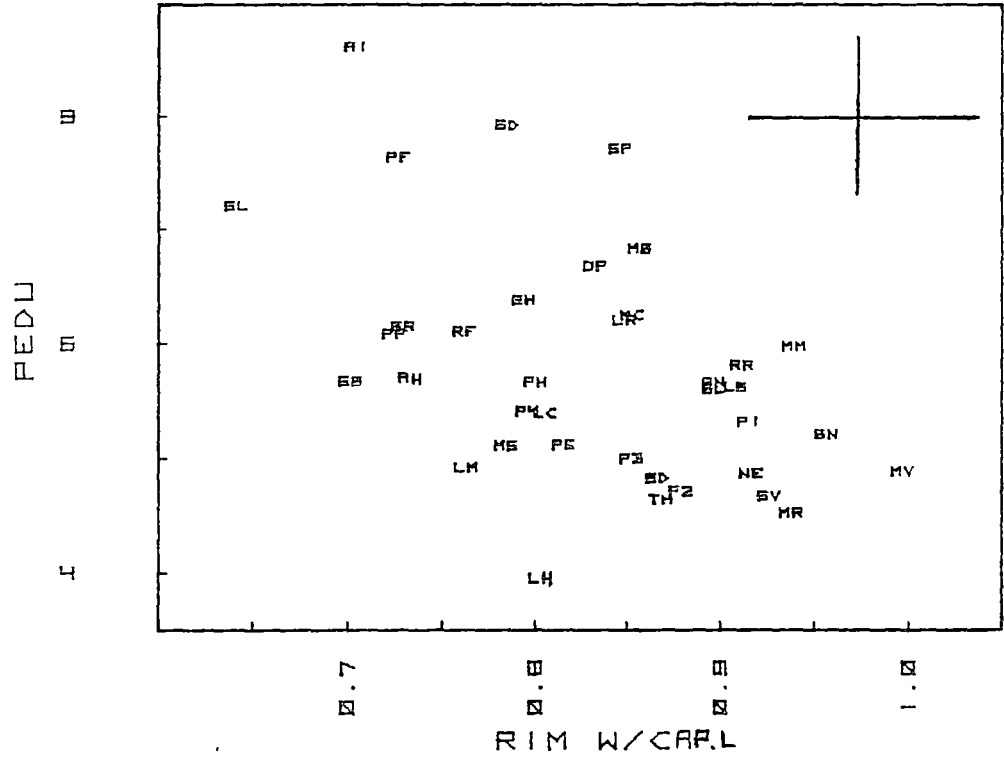
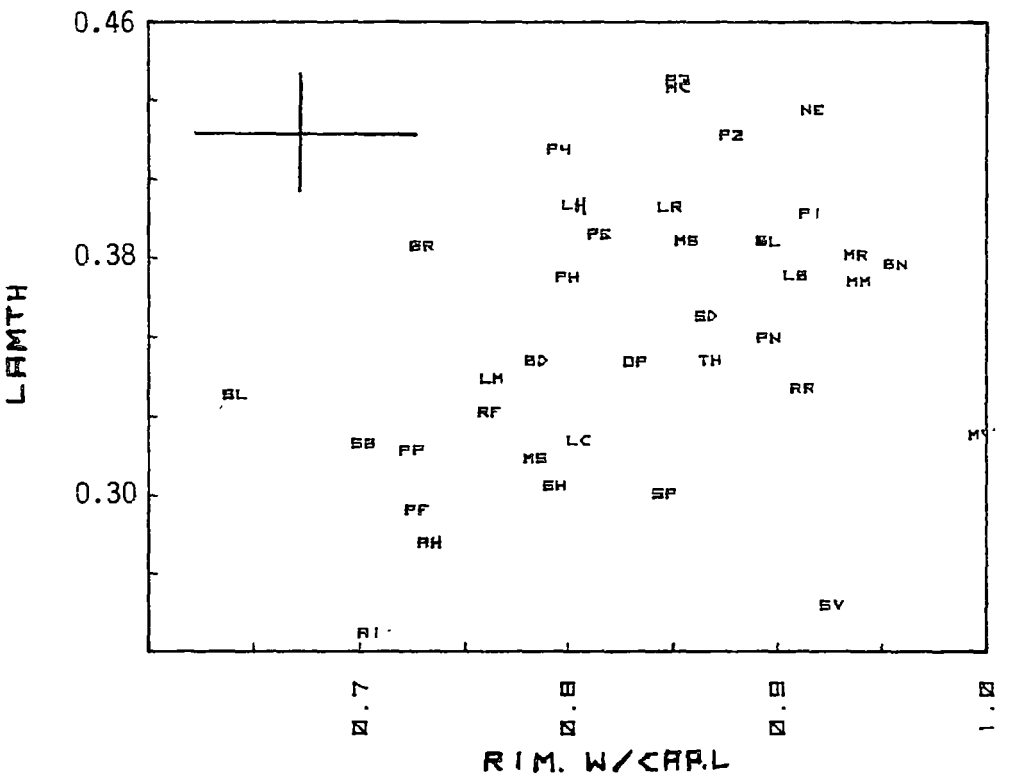
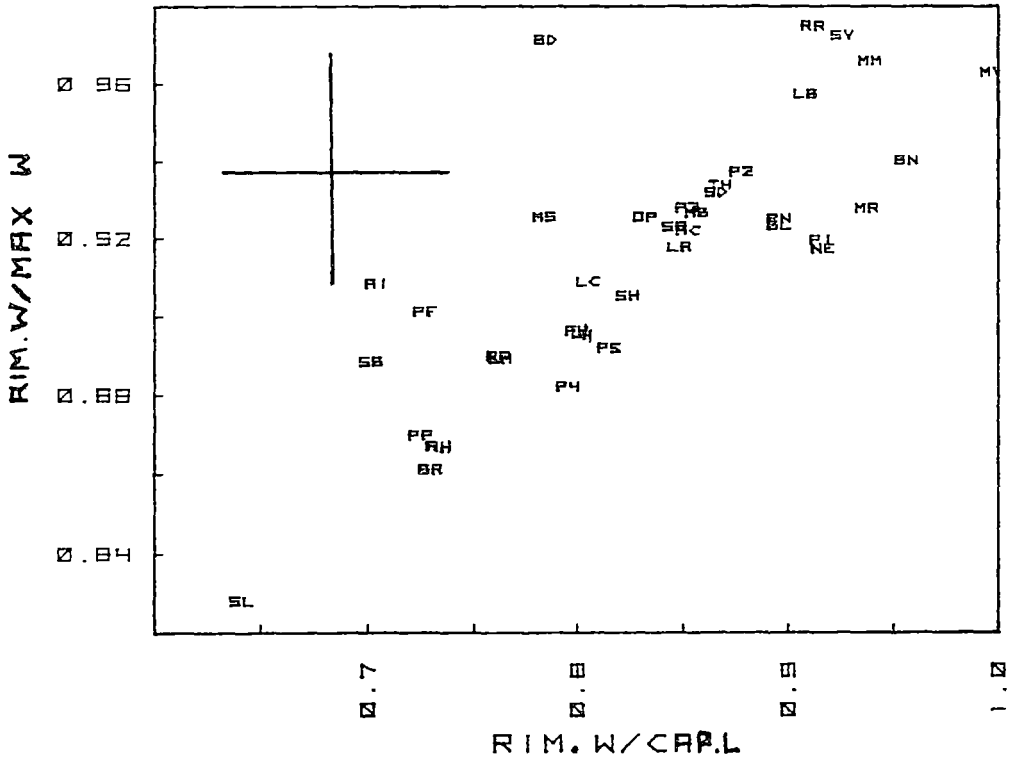


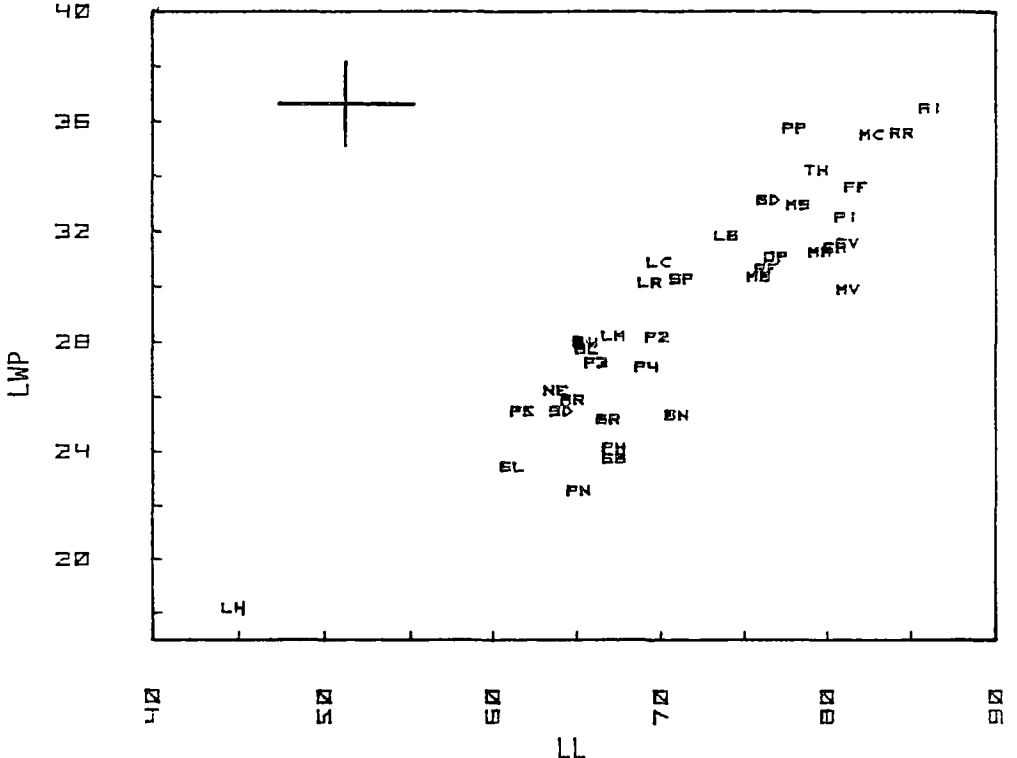
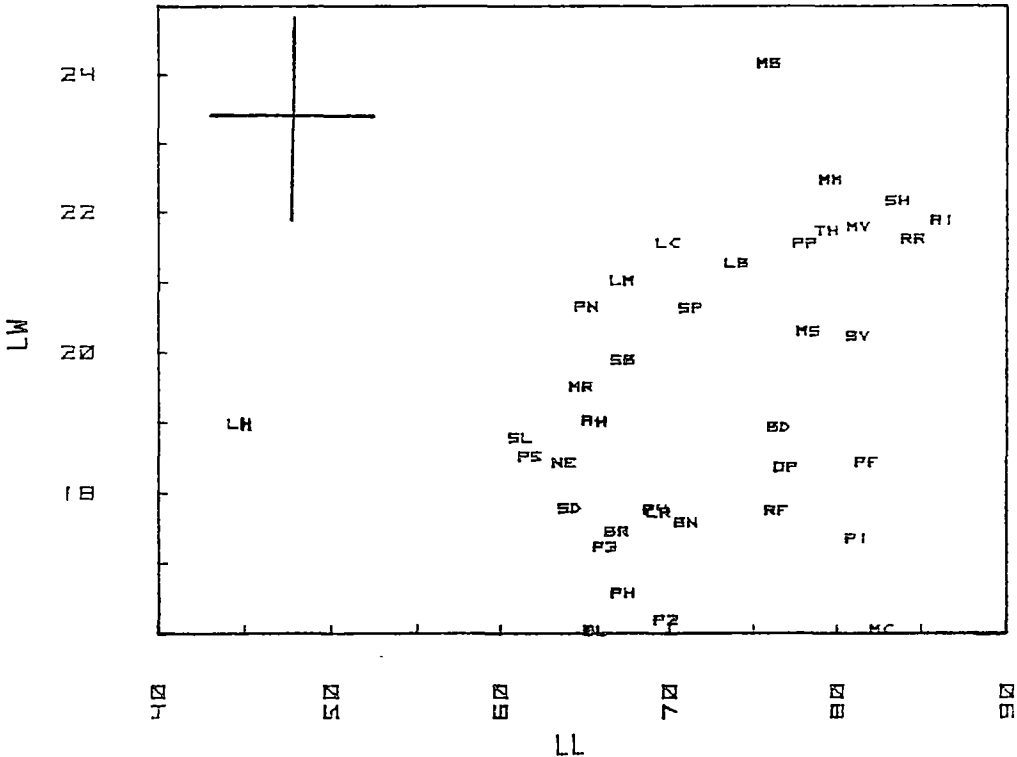
Figure 8.4 Lignotuber diameter versus standardized log LL/LW scores for coppice leaves from abnormal phenotypes in patches within the range of *E. amygdalina*. Patch numbers correspond to those in Fig. 8.3. All abnormal phenotypes within each localized patch have been scored.

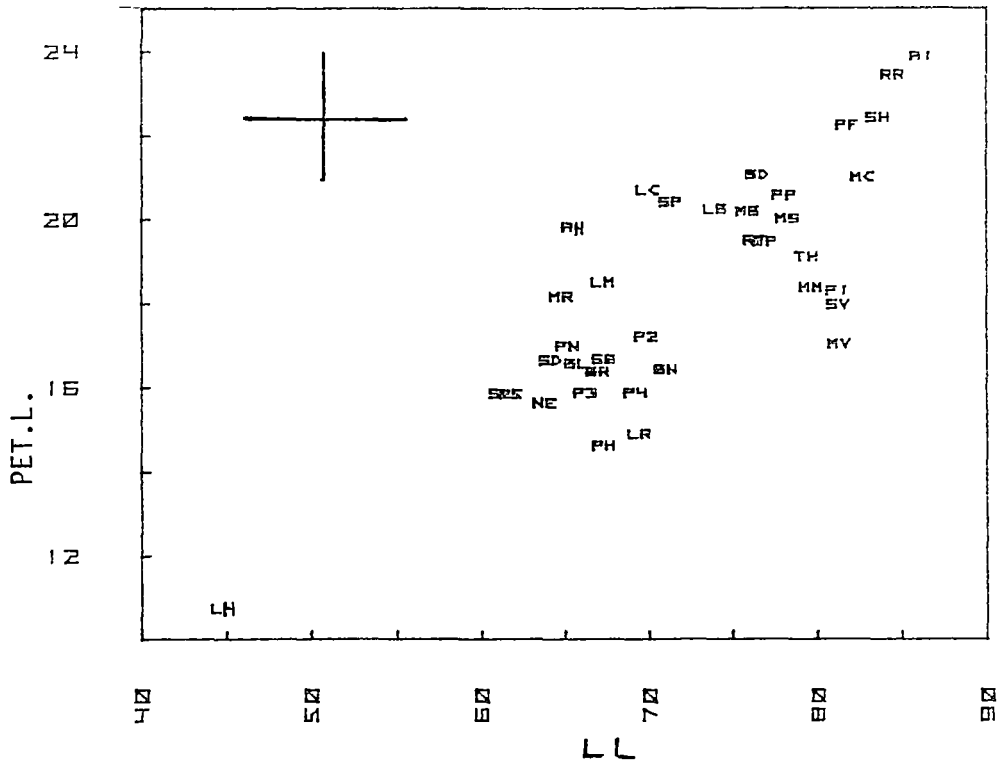
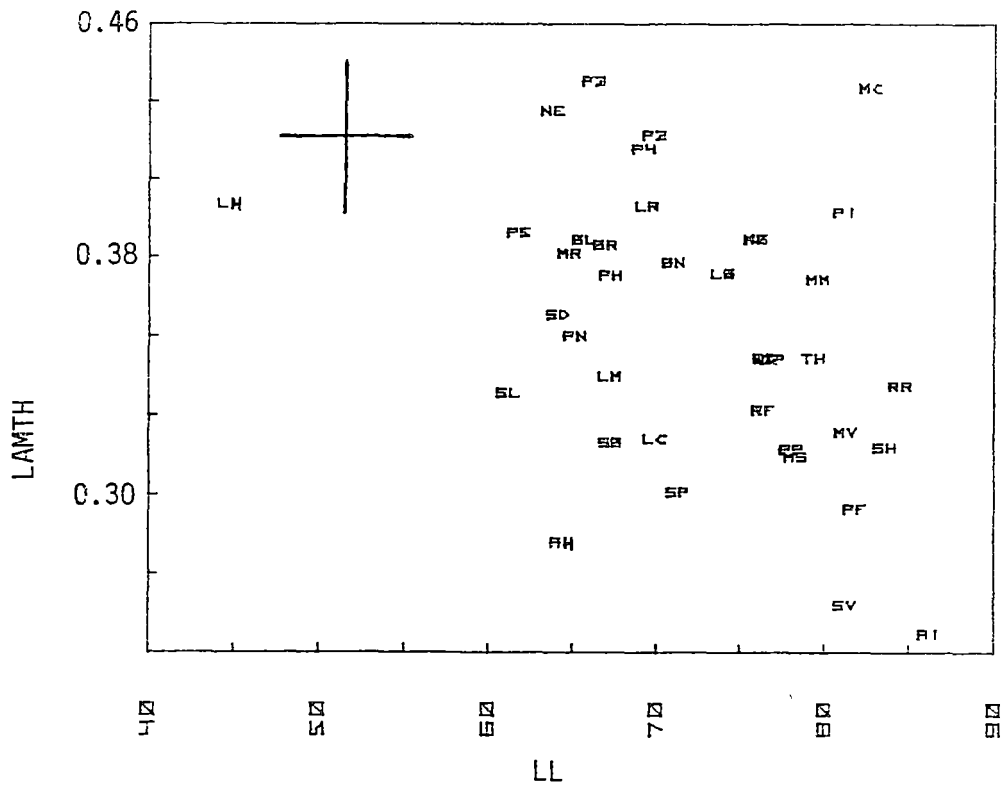
APPENDIX 1 Scatter plots of population means for a range of characters and ratios. Population and character codes are given in Tables 1.1 and 1.3 respectively. The 95% confidence limits based on n=20 are indicated.











Appendix 2

Models used to quantify the interbreeding potential of taxa stands based on flowering time data.

Two indices of interbreeding potential were used to assess and quantify the degree of reproductive isolation between populations and taxa which could potentially result from differences in flowering phenology. The first was used to quantify the potential for two populations to interbreed. In particular, this index (assortive mating index) describes the potential proportion of outcrossed seed from an individual i from material stand sample j which could be expected to result from outcrossing to trees from the local sample as opposed to trees from an alien stand sample k . This is estimated from

$$S(i,j,k) = 1/n \sum_{l=1}^n \frac{N_{(k,l)}}{N_{(k,l)} + N_{(j,l)}}$$

where n equals the number of times individual i,j was observed flowering with at least one other tree of population j and k , $N_{(j,l)}$ and $N_{(k,l)}$ equal the number of trees in populations j and k respectively which were flowering coincidental with individual i,j at time l . Values range from 0 to 1, with both 0 and 1 indicating assortive mating, with an absolute bias toward the local or alien population respectively, and .5 indicating random mating. The second index is indicative of the relative probability of an individual to be pollinated by either *E. amygdalina* or *E. risdonii* and in a similar manner as given by

$$P(i,j) = 1/n \sum_{l=1}^n Q(l), \text{ where}$$

$Q(l)$ is equal to the proportion of *E. amygdalina* trees out of the total number of trees of either species observed flowering at time l . In this case, the proportion $P(l)$ is estimated from equal size samples of either species (140/species) from pooled ecotonal, pure species and hybrid zone sites. Population statistics are derived from these indices after angular transformation and back transformed to proportions ($S_{j,k}; P_j$). The use of these indices is subject to the obvious assumptions including, firstly, that spatial relationships are ignored and that the potential for individuals to interbreed depends solely on coincidence of flowering. In respect of spatial arrangement, the model approximates the condition expected at the immediate boundary between two taxa. Secondly, if an individual is flowering at time l , it is equally likely to outcross to all other individuals observed flowering at time l . Thirdly, it is assumed

that the proportion of outcrossed seed set by an individual from each flowering observation is equal and independent of the absolute number of other trees observed flowering (except when no other trees flower, in which case, no outcrossed seed is set). And fourthly, each individual observed flowering throughout this period contributes equally to the pool of outcrossed seed in the population.

Table 1 Matrix of stand values for the assortive mating index ($S_{j,k}$). Location numbers correspond to Fig. 6.3 and Table 6.10.

		Alien Stand Type															
		<i>E. amygdalina</i>							<i>E. risdonii</i>							hybrid	
		pure species stands		ecotonal stands			hybrid zone		pure species stands		ecotonal stands			hybrid zone stands		hybrid zone	
Local Stand Type		1	2	5	6	7	8	9	3	4	5	6	7	8	9	8	9
<i>E. amygdalina</i>																	
pure species stands	1	-	0.47	0.42	0.25	0.30	0.45	0.36	0.09	0.40	0.19	0.23	0.36	0.18	0.12	0.21	0.20
	2	0.52	-	0.58	0.39	0.41	0.47	0.31	0.10	0.45	0.18	0.27	0.35	0.18	0.10	0.15	0.34
	5	0.40	0.44	-	0.31	0.44	0.40	0.26	0.03	0.25	0.11	0.14	0.20	0.07	0.13	0.11	0.26
ecotonal stands	6	0.24	0.50	0.51	-	0.45	0.38	0.15	0.14	0.27	0.25	0.21	0.31	0.14	0.12	0.36	0.33
	7	0.51	0.58	0.75	0.54	-	0.54	0.40	0.08	0.37	0.20	0.22	0.33	0.15	0.08	0.24	0.48
	8	0.66	0.53	0.50	0.26	0.36	-	0.46	0.20	0.51	0.36	0.35	0.48	0.30	0.24	0.27	0.36
hybrid zone stands	9	0.70	0.64	0.66	0.43	0.57	0.63	-	0.08	0.45	0.19	0.27	0.38	0.24	0.10	0.35	0.42
<i>E. risdonii</i>																	
pure species stands	3	0.34	0.35	0.16	0.17	0.10	0.47	0.24	-	0.65	0.68	0.68	0.69	0.68	0.66	0.61	0.37
	4	0.39	0.31	0.15	0.10	0.10	0.37	0.24	0.32	-	0.45	0.47	0.55	0.47	0.42	0.34	0.24
	5	0.28	0.22	0.11	0.12	0.08	0.34	0.17	0.39	0.53	-	0.59	0.58	0.61	0.53	0.46	0.27
ecotonal stands	6	0.24	0.17	0.08	0.08	0.06	0.27	0.15	0.32	0.45	0.47	-	0.51	0.56	0.46	0.39	0.21
	7	0.37	0.27	0.14	0.10	0.09	0.37	0.20	0.32	0.53	0.45	0.47	-	0.49	0.43	0.35	0.22
	8	0.24	0.15	0.06	0.07	0.06	0.23	0.15	0.28	0.41	0.43	0.50	0.45	-	0.42	0.37	0.17
hybrid zone stands	9	0.30	0.22	0.10	0.09	0.06	0.34	0.19	0.40	0.51	0.54	0.57	0.57	0.59	-	0.47	0.23
hybrid																	
hybrid zone stands	8	0.36	0.32	0.20	0.25	0.17	0.38	0.26	0.34	0.41	0.50	0.47	0.49	0.54	0.45	-	0.27
	9	0.54	0.69	0.68	0.69	0.68	0.71	0.46	0.38	0.60	0.58	0.58	0.56	0.56	0.40	0.63	-

Table 2 ANOVA for the difference in Pj values (e.g. Table 6.12) between trees from different species (*E. risdonii* or *E. amygdalina*) localities (pure species, ecotone, hybrid zone) and stands. (Error = between trees within stands; d.f. = 218).

Source of Variation	d.f.	F value
Between trees from different stands	15	19.3 ***
Between trees from different species	1	260.6 ***
Between trees from different stands		
within <i>E. amygdalina</i>	7	2.4 *
within <i>E. risdonii</i>	7	1.2
Between trees from different localities		
within <i>E. amygdalina</i>	2	3.5 *
within <i>E. risdonii</i>	2	1.6
Between trees from different stands		
within localities within <i>E. amygdalina</i>	4	1.8
<i>E. risdonii</i>	4	< 1

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