

ECO-PHYSIOLOGICAL STUDIES OF FACTORS DETERMINING THE  
DISTRIBUTION OF SUBALPINE EUCALYPTS AT SNUG PLAINS,  
SOUTHERN TASMANIA

by

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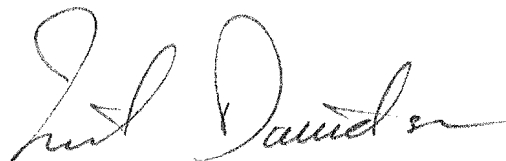


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### DECLARATION

Except as stated, herein, this thesis contains no material which has been accepted for the award of any degree or diploma in any university and to the best of my knowledge and belief, the thesis contains no copy or paraphrase of material previously published or written by another person, except where due reference is made in the text of the thesis.

A handwritten signature in cursive script, appearing to read 'N.J. Davidson', written in dark ink.

N.J. DAVIDSON

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## ABSTRACT

An examination was made of the ecological factors causing the changes in dominance between six eucalypt species; E. delegatensis, E. coccifera and E. pulchella (subgenus Monocalyptus); and E. gunnii, E. unigera and E. johnstonii (subgenus Symphyomyrtus) which formed a mosaic within and surrounding a shallow depression on a subalpine plateau (approximately 600 m in altitude) at Snug Plains, southern Tasmania. The populations of the six species at the 1 square kilometre study area were in most cases lower altitude ecotypes of subalpine species. However, morphometric studies of foliar samples from field trees and glasshouse grown seedlings of the one lowland species, E. pulchella, suggested that the Snug Plains E. pulchella population was of hybrid origin ("phantom hybrid") with E. coccifera and E. pulchella as the putative parents.

Reciprocal transplant trials established in six locations in the field at Snug Plains demonstrated that the key factors influencing seedling survival in the low lying sites were: severity of frost, waterlogging and phytophagous insect attack. Differences in soil nutrition and texture had little influence on seedling growth and seedlings in elevated, well drained sites grew rapidly. There was also a strong tendency in the field transplant trials for the species naturally dominant at the site to become dominant or show greatest growth on a relative basis at its site of origin.

A record frost, with an absolute minimum temperature of  $-22^{\circ}\text{C}$  at the radiating surface, was recorded at Snug Plains in June 1982. Temperature measurements made in a transect across the study area indicated a marked vertical stratification of the air body occurred (up to  $9^{\circ}\text{C}/\text{m}$ ) and a steep gradient in minimum temperature ( $7.3^{\circ}\text{C}$  over 200 m) was established between the base of the depression and the ridge top. The natural distributions of the six species studied were closely related to the minimum temperature recorded. Frost damage incurred by mixed pole stands on the margins of the depressions was, in places, severe. Interspecific differences in frost hardiness were in the order (from greatest to least): E. gunnii > E. coccifera > E. johnstonii > E. delegatensis > E. pulchella. The severe frosts caused marked changes in dominance in mixed stands, even though they resulted in few deaths. Exceptional frosts like those of June 1982 may have an important effect on the distributions of subalpine eucalypts. In the reciprocal transplant trials, growing season frosts of  $-5.5^{\circ}\text{C}$  inflicted severe damage on the unhardened seedlings of all species except E. gunnii, which exhibited outstanding frost resistance in the unhardened state. Winter frost of  $-10.5^{\circ}\text{C}$  caused markedly less damage which

suggests that growing season frosts may play an important role in determining the distribution of subalpine eucalypts. Frost chamber experiments confirmed the importance of hardening pretreatment on relative frost resistance of the species studied, and demonstrated a significant interactive effect of waterlogging on frost resistance. The Monocalyptus species were more susceptible to frost in waterlogged soils, whereas no such relationship existed for the Symphyomyrtus species.

Damage inflicted on seedlings in the transplant trials during a frost free period when waterlogged conditions prevailed, indicated that the Symphyomyrtus species E. gunnii, E. urnigera and E. johnstonii were more waterlogging tolerant than the Monocalyptus species E. pulchella, E. coccifera and E. delegatensis. This was confirmed by glasshouse based trials which showed marked differences existed between the subgenera in tolerance to waterlogging. After 30 days of waterlogging the Symphyomyrtus species had significantly higher midday stomatal conductances and water potentials than the Monocalyptus species. Further, Symphyomyrtus species exhibited stem hypertrophy and developed extensive, aerenchymatous, adventitious root systems. The Monocalyptus species demonstrated no such morphological adaptations. The results suggest that the Monocalyptus species will be absent from waterlogged sites, which agrees with the distributions of the species and measurements of soil moisture-status in the field.

Phytophagous insect attack which affected 3 transplant trials caused severe damage to E. gunnii, E. urnigera and E. johnstonii seedlings (up to 75% leaf loss) but only slight damage to E. delegatensis, E. coccifera and E. pulchella (up to 10% leaf loss). This suggests that selective insect grazing may have an important effect on the dominance patterns in regenerating mixed eucalypt stands at Snug Plains.

Glasshouse based drought trials suggested differences in drought resistance existed between the subgenera. The Monocalyptus species maintained higher relative water contents (R.W.C.) at low water potentials than the Symphyomyrtus species. Therefore, low tolerance to drought might be an important factor in explaining the absence of Symphyomyrtus species from the ridge tops at Snug Plains. During the 1982-83 summer season south-eastern Tasmania was exposed to a drought of near record severity. As the drought developed dawn to dusk measurements of stomatal conductance and water potentials made in a mixed stand of the three Monocalyptus species on a ridge top at Snug Plains showed these species differed only slightly in water potential

down to -4.3 MPa. The leaf water potentials of all species reflected the soil water potential. However, measurements of R.W.C. demonstrated that E. pulchella maintained a higher R.W.C. (61%) than either E. coccifera (55%) or E. delegatensis (48%) at these low water potentials. E. pulchella also exhibited less crown damage than the other two species during the drought and, after the first effective rains, demonstrated more rapid restoration of high R.W.C. and recommencement of shoot extension. Anatomical and morphological characters such as linear leaves and recovery from drought via epicormic buds near the branch tips also favoured E. pulchella in survival during and recovery after drought. An investigation of soil depths in the field, and glasshouse trials including drought treatments confirmed that differences in drought tolerance were not due to interspecific differences in root pattern or depth. It was concluded that superior drought resistance was the primary reason for the presence of E. pulchella on the ridgetop sites. The relative drought resistance of the other two Monocalyptus species may also have influenced the positions they occupy on the rocky ridges at Snug Plains.

The breadth of the ecological study conducted allowed the ecological niche occupied by each of the species studied to be defined in some detail, and the main factors involved in the changes in dominance between species to be outlined. Furthermore, the study provided strong evidence of morphological and physiological differences between the subgenera Monocalyptus and Symphyomyrtus which may help to explain differences in the ecological positions occupied by the subgenera in allopatry and the niche differences of the subgenera in sympatry.

## CHAPTER 1

### INTRODUCTION AND STUDY SITE

A large portion of Australia is vegetated by forests which are dominated by a single genus, Eucalyptus. The genus contains between 600 and 700 species (Pryor & Johnson 1971) some of which are widely distributed, but many have narrow geographic ranges within which the species are closely delimited by the distribution of particular microhabitats (Pryor 1953, 1959a, 1959b). Generalising from a study of eucalypt distributions in the Pierce's Creek area, A.C.T., Pryor (1959a, 1959b) proposed two rules which govern the pattern of eucalypt species distributions in south-eastern Australia and the south-west of Western Australia: (1) interbreeding eucalypt species (from the same subgenus) form separate circumscribed stands each occupying distinct ecological situations, and (2) mixed species stands of eucalypts are comprised of species which are genetically isolated (from different subgenera). However, subsequent research has not given these rules unqualified support (Austin et al. 1983; Kirkpatrick 1981; Florence 1981; Rogers & Westman 1979; Morrow 1977; Gill & Ashton 1971; Parsons & Rowan 1968; Ridley 1961). In the mountainous terrain in south-eastern Australia Pryor's rules are generally supported but with some modifications (Florence 1981; Austin et al. 1983). Ecological studies by Florence (1963, 1964) led him (Florence 1981) to propose some modifications to Pryor's rules based on the distribution and characteristics of the Monocalyptus species: (1) Monocalyptus species tend to replace one another in gradients of habitat quality (e.g. altitude); (2) Monocalyptus species tend to be more site sensitive than species from other subgenera; (3) a Monocalyptus species may occur in pure stands over part of its habitat range; and (4) Monocalyptus species may be substantially or totally replaced by Symphyomyrtus species in particular habitats (e.g. heavy textured or poorly aerated soils). In a study of a range of habitats from the Blue Mountains to the coast in southern New South Wales, Austin et al. (1983) showed subgeneric combinations in these eucalypt forests were not at random and certain combinations (e.g. Monocalyptus dominant and Symphyomyrtus subdominant) were more common than others, but that with the modifications suggested above (Florence 1981), Pryor's rules were generally upheld. However, the rules were most applicable to the mountainous region and many exceptions occurred where stands contained more than one representative from a single subgenus. Accounts of mixed eucalypt stands containing more than one species representative from a subgenus have also been reported from other parts of south-eastern Australia (e.g. Gill & Ashton 1971; Kirkpatrick 1981; Duff et al. 1983). In a phytogeographical study conducted in the Eastern

Tiers of Tasmania, Kirkpatrick (1981) reported that from a total of 13 randomly selected stands 9 comprised mixtures of two Monocalyptus species and only 3 stands were comprised of 1 Monocalyptus and 1 Symphyomyrtus species. Outside the mountainous areas of south-eastern Australia extensive con-subgeneric stands of eucalypt species have been described. Parsons and Rowan (1968) reported E. gracilis and E. calycogona (Symphyomyrtus) co-occur over wide areas of north-west Victoria and Rogers and Westman (1979) describe the co-occurrence of E. umbra and E. signata (Monocalyptus) on North Stradbroke Island (south-east Queensland) and over large areas of coastal New South Wales and southern Queensland. The exceptions to Pryor's rules, particularly outside the mountains of south-eastern Australia, raise doubts about their general applicability.

Whatever the origin of the genus Eucalyptus, whether monophyletic or polphyletic (Johnson 1972; Pryor 1976) the subgenera which comprise the genus have undoubtedly evolved under different selection pressures (Florence 1981). The current differences in geographic distribution (Johnson 1972) and differences in ecological position occupied by the subgenera (Austin et al. 1983; Florence 1981; Ridley 1962) attest to the basic differences between the subgenera, both ecological and physiological. These differences may allow members of different subgenera to cohabit in a stand without niche overlap thus resulting in the erection of Pryor's rules for the mountains of south-eastern Australia, but does not preclude the presence of two members of the same subgenus (interbreeding species) cohabiting if the niches occupied are distinct (Rogers & Westman 1979). Rogers and Westman (1979) and Westman and Rogers (1977a, 1977b) have outlined a number of features possessed by a cohabiting pair of Monocalyptus species (E. umbra and E. signata) which may reduce niche overlap and competition for resources and allow potentially interbreeding species to co-occur.

It is evident that the factors controlling the distribution of species within stands, and dominance changes between stands of Eucalyptus are poorly understood at the species and subgeneric level. This has been exacerbated by a tendency, in comparative ecological studies of eucalypt species, to concentrate on the relative tolerances (or success) of a pair or group of species to a single ecological factor such as drought (e.g. Sinclair 1980; Mayers & Neales 1984), waterlogging (e.g. Sena-Gomes & Kozslowski 1980; Blake & Reid 1981), frost (e.g. Sakai et al. 1981; Paton 1980) or phytophagous insects (e.g. Burdon & Chilvers 1974; Morrow 1977). Few studies involving Eucalyptus have attempted to elucidate the complex of factors causing the changes in species dominance.





Plate 1.1 Snug Plains.



Plate 1.2 The study area (in the background).

The most recent studies to approach the question were at Ocean Grove, Victoria (Withers & Ashton 1977; Withers 1978a, 1978b, 1979a, 1979b) where factors involved in the dominance change from E. ovata to Casuarina littoralis were being studied, and at Seventeen Flat in the Snowy Mountains, New South Wales where a series of researchers (Moore 1959a, 1959b, 1961; Moore & Williams 1976; Harwood 1976, 1980, 1981, 1983) studied the ecological factors involved in producing the woodland-grassland boundary and changes in eucalypt dominants in its vicinity.

Studies of this kind have not been attempted in Tasmania although descriptive accounts of eucalypt distributions (Martin 1940; Barber 1955, 1965; Barber & Jackson 1957; Jackson 1965, 1968a, 1968b, 1973) and phytosociological studies (Kirkpatrick 1981; Kirkpatrick & Nunez 1980) have been conducted. Through studying a group of species which include members from both the Tasmanian eucalypt subgenera, Monocalyptus and Symphyomyrtus (Pryor & Johnson 1971), the current investigation aims to elucidate the ecological relationships between the species and the subgenera.

### The Study Area

Snug Plains is an undulating subalpine plateau ranging in altitude from 580 m to 700 m which surmounts on isolated mountain block at the southern end of the Wellington Range (latitude 40°05' south and longitude 147°10' east) in southern Tasmania (Fig. 1.1, Plates 1.1 and 1.2). The plateau region is geologically complex, consisting of a mosaic of the two rock types Jurassic dolerite and Triassic sandstone (Roger 1957; Farmer 1975). Further, the soils generated from these two rock types differ greatly in structure and chemical composition (Loveday 1957). The undulating nature of the plateau and the presence of a mosaic of soil types has resulted in a very varied ecology. The hollows in the landscape are poorly drained and frost prone in winter. The ridge crests are rocky with shallow soils which tend to become droughted during extended rain-free periods in summer. The diverse array of habitats from warm dry ridge sites to cold waterlogged depressions which occur on both dolerite and sandstone derived soils support a similarly diverse array of eucalypt species.

The study area was an approximately 1 km square segment of Snug Plains encompassing a single depression and its surrounding ridge slopes (Fig. 1.2, Plate 1.2). The area was populated by six species of eucalypt, three species from subgenus Monocalyptus: Eucalyptus delegatensis R.T. Blake, E. coccifera Hook.f, and E. pulchella Desf.; and three species from subgenus

**FIGURE 1.1 : LOCATION OF SNUG PLAINS**

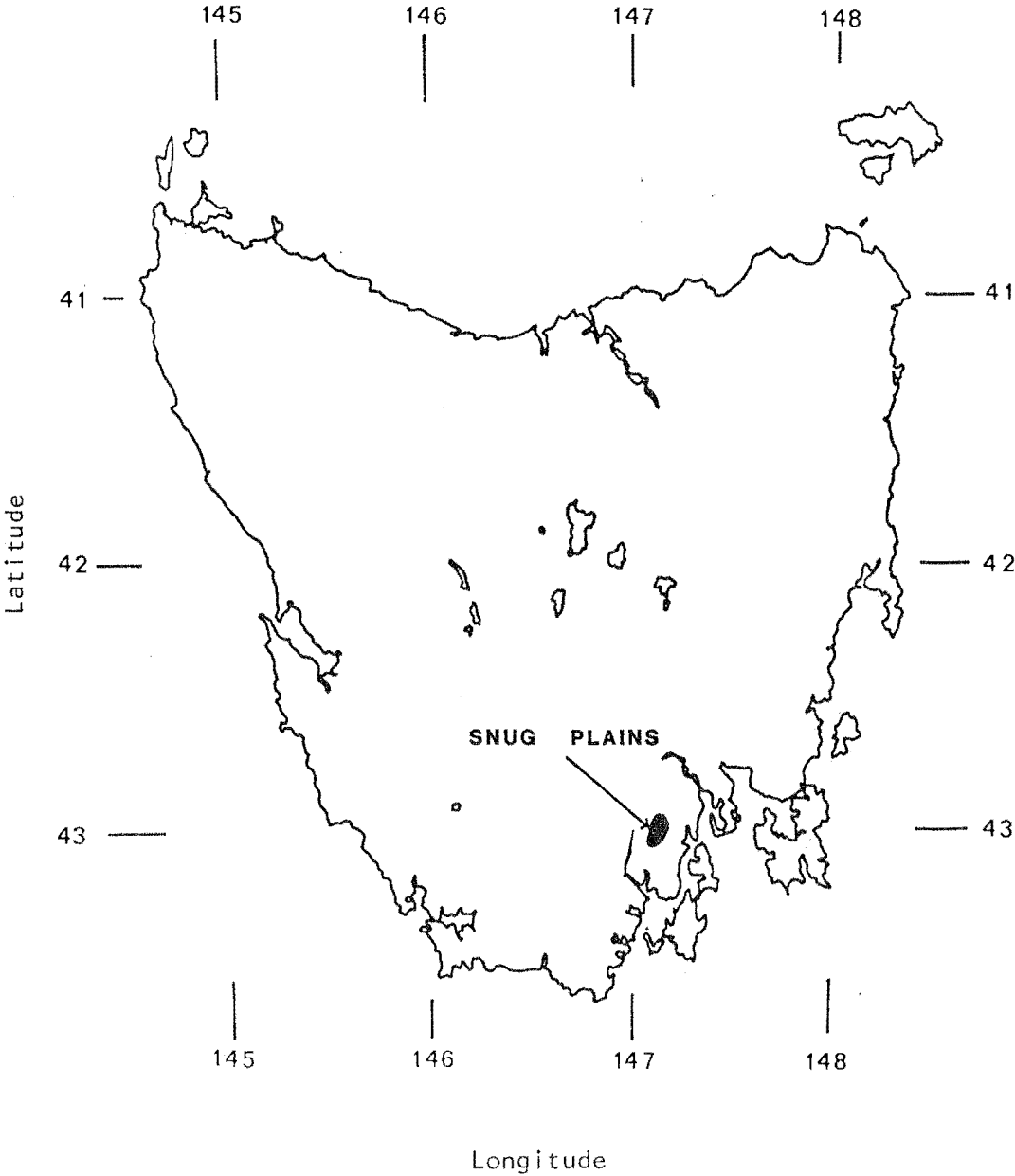
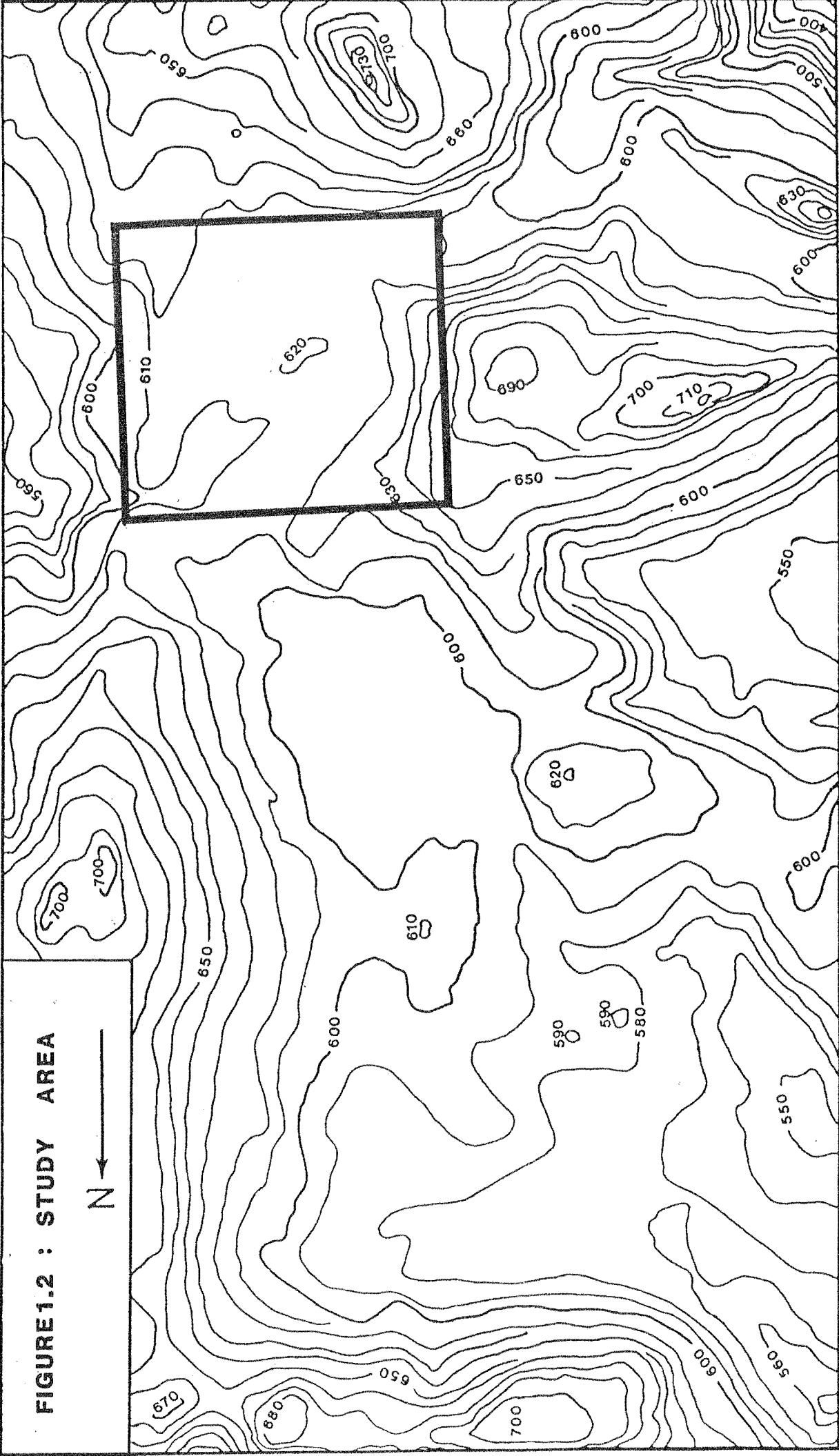


Figure 1.2

Topographic map of Snug Plains (scale: 64 mm represents 1 km) with major study area marked (black border).



Symphyomyrtus: E. gunnii Hook.f., E. urnigera Hook.f., and E. johnstonii Maiden; which formed a complex of mosaic of eucalypt distributions (Fig. 3.2). The advantage of addressing a small geographic area, that included a set of differentiated and coadapted ecotypes of the species studied (sensu Rogers & Westman 1979), was that it avoided complications of possible clinal and ecotypic variation which may occur over short distances (e.g. Pryor 1957a; Thomas & Barber 1974a, 1974b; Ladiges & Ashton 1974; Ladiges 1974, 1976).

The intention of the current study was to identify the major ecological factors which were instrumental in the changes in species dominance between eucalypt stands in the study area at Snug Plains and to determine at which stage during stand ontogeny (seedling, pole or tree stand) they might be operating. Further, these investigations may allow ecological and physiological comparisons to be made at the subgeneric as well as at the species level.

## CHAPTER 2

### THE SPECIES STUDIED AND HYBRIDISATION

#### INTRODUCTION

Studies in Eucalyptus have consistently shown that a high degree of ecotypic and clinal variation exists for many eucalypt species (Pryor 1976). Clines in morphological characters have been shown to occur over both geographic (e.g. Phillips & Reid 1980; Kirkpatrick 1975; Jackson 1960; Potts 1983) and altitudinal gradients (e.g. Pryor 1957a; Jackson 1960; Barber & Jackson 1967; Thomas & Barber 1974). Clinal variation in morphological characters may be matched by variation in the physiological characters of the species (Pryor 1957a; Phillips & Reid 1980; Slatyer 1978). Similar broad ecotypic variation in both morphological and physiological characters was found in eucalypt species which were not varying clinally (e.g. Ladiges & Ashton 1974, 1977; Clucas & Ladiges 1979; Ladiges 1974, 1975, 1976). In the current study the eucalypt populations at Snug Plains represented only a small part of the total geographic distribution of each of the six species studied and may well encompass only a portion of the total species variation. The following chapter describes the Snug Plains ecotypes of the species studied and investigates the possible hybrid origin of the Snug Plains E. pulchella population.

#### 1. THE SPECIES INVESTIGATED

Classification will follow Pryor and Johnson (1971) unless otherwise stated.

Eucalyptus gunnii Hook.f.

E. gunnii ssp. gunnii (Pryor & Johnson 1971)

Subgenus Symphyomyrtus, series Viminales.

E. gunnii is endemic to Tasmania and occurs principally on undulating plains in the Central Plateau of Tasmania at altitudes of 600 m to 1000 m above sea level where the rainfall is between 800 mm to 2800 mm per annum. However small isolated populations of E. gunnii also occur in mountains to the south and west of the Central Plateau, for example Mt. Field and Snug Plains (Davies 1977; Boland et al. 1984). E. gunnii forms an open woodland on poorly drained rocky ground subject to numerous and severe frosts (Boland et al. 1984;

Jackson 1973). The Snug Plains population represents the most southerly distribution of the species. This population differs from other E. gunnii populations in a number of adult and seedling characteristics, reflecting its isolation and unique position (Potts & Reid 1985a, 1985b). However, leaf, bud and fruit characteristics are well within the the normal range for the species (Curtis & Morris 1975). At Snug Plains E. gunnii is the sole dominant in the shallow dish shaped depressions in the landscape.

Eucalyptus urnigera Hook.f.

Subgenus Symphyomyrtus, series Viminalis.

E. urnigera is endemic to Tasmania occurring on mountain slopes at altitudes between 500 m and 1000 m above sea level in the south-east of the state. The principal locations are Mt. Field and Mt. Wellington. Stands of E. urnigera range from open mountain woodland on well drained tallus slopes to tall wet sclerophyll forest in deep moist soils, often associated with other species (e.g. E. delegatensis and E. coccifera, Martin 1940; Thomas & Barber 1974; Curtis & Morris 1975; Hall et al. 1980). Over its altitudinal range on Mt. Wellington E. urnigera shows clinal variation in a number of characters (Barber & Jackson 1957; Thomas & Barber 1974) including glaucousness of the juvenile leaves. Thomas and Barber (1974) showed progeny of trees from the low altitude end of the cline had bright green leaves whereas high altitude progeny were highly glaucous. At Snug Plains the juvenile leaves of E. urnigera were invariably green, suggesting the Snug Plains stands were the low altitude ecotypes of E. urnigera. However, in all leaf, bud and fruit characteristics the Snug Plains E. urnigera was within the normal range for the species (Curtis & Morris 1975). At Snug Plains E. urnigera occupied deep dolerite derived soils on shallow to steep tallus slopes.

Eucalyptus johnstonii Maiden

E. vernicosa ssp. johnstonii (Pryor & Johnson 1971).

Subgenus Symphyomyrtus, series Viminalis.

E. johnstonii is also endemic to Tasmania with a distinctly south-eastern distribution. It occurs in subalpine forests between 450 m to 900 m in altitude growing mainly in poorly drained and acid Triassic sandstone derived soils (Boland et al. 1984; Curtis & Morris 1975). E. johnstonii forms stands which vary from an open woodland on acid sandstone soils to closed wet sclerophyll forest in association with other species (e.g. E. coccifera and E. delegatensis) on more favourable soils. Jackson (1960) demonstrated that a morphological



series existed between the shrubby alpine species E. vernicosa and the tall forest tree E. johnstonii and suggested that E. johnstonii was a cline form of E. vernicosa. This conclusion was supported by Pryor and Johnson (1971). In the current study nomenclature for this species will follow Curtis and Morris (1975). E. johnstonii trees at Snug Plains exhibited fruit, bud and leaf characteristics which conform with the descriptions of the species given by Jackson (1960) and Curtis and Morris (1975). At Snug Plains E. johnstonii formed pure stands on the sandstone plateau area and on the margins of depressions in the landscape on both dolerite and sandstone derived soils.

Eucalyptus delegatensis R.T. Blake

Subgenus Monocalyptus, series Obliquae.

E. delegatensis is a tall forest tree found in the cooler parts of south-eastern Australia. It occurs in the southern extensions of the Australian Alps in Victoria and southern New South Wales at altitudes between 900 and 1500 m and in the Tasmanian forests at altitudes between 160 m and 1200 m (Boland et al. 1984; Curtis & Morris 1975). Generally E. delegatensis occupies deep well drained soils on the upper slopes in mountainous country, in areas receiving a rainfall between 700 mm and 1250mm per annum (Boland et al. 1984; Jackson 1965, 1973). At Snug Plains extensive stands of E. delegatensis occur on the ridge slopes of the plateau often forming pure stands, although E. delegatensis will also form mixed stands with E. urnigera and E. johnstonii. At Snug Plains E. delegatensis trees had leaf, bud and fruit characteristics consistent with the normal range for the species in Tasmania as described by Curtis and Morris (1975).

Eucalyptus coccifera Hook.f.

Subgenus Monocalyptus series Piperitae.

E. coccifera is endemic to Tasmania growing on shallow rocky soils on mountain tops and plateau (Hall et al. 1970), invariably present as the treeline species on dolerite mountains of central and south-eastern Tasmania. E. coccifera tends to occur on better drained sites at altitudes from 600 m to 1430 m above sea level which receive rainfall of between 900 mm to 2000 mm per annum (Hall et al. 1970; Jackson 1973). However, E. coccifera may be present in a variety of vegetation types from alpine woodland to sub-mountain forests (Hall et al. 1970; Jackson 1973) extending from the wet sclerophyll to the dry sclerophyll forests.

At Snug Plains E. coccifera grows on exposed ridge tops and at the margins of depressions in the plateau. The fruit, bud and leaf characteristics of E. coccifera trees at Snug Plains were not always within the normal range for the species (Curtis & Morris 1975). Some stands contained trees with smooth slightly glaucous buds and a near hemispherical operculum, which were distinct from the normal glaucous, clavate, angular buds with a depressed, rugose operculum (Curtis & Morris 1975). Fruit size was also at the lower end of the normal range, although leaf shape was normal. These features were particularly evident in places where E. coccifera abutted the distribution of another Monocalyptus species from series Piperitae, for example: E. pulchella (in the study area); E. tenuiramis (at the south-eastern margins of Snug Plains); and E. nitida (on the north-eastern margins of Snug Plains).

Eucalyptus pulchella Desf.

Subgenus Monocalyptus, series Piperitae

E. pulchella is endemic to Tasmania and restricted to dolerite derived soils in the south-east of the state. It is usually a lowland species normally occupying shallow soils in hilly to undulating terrain from sea level to an altitude of 450 m above sea level (Boland et al. 1984; Jackson 1965) where the mean annual rainfall is between 500 and 1000 mm. However occasional populations occur at altitudes up to 1000 m. Under these conditions E. pulchella may be sole dominant in open dry sclerophyll forests. At Snug Plains E. pulchella is at its upper altitudinal limit and is present in pockets in skeletal soils on the ridge tops. Leaf, bud and fruit characteristics for trees in these small populations of E. pulchella were outside the normal range for the species (Curtis & Morris 1975). Many individuals had larger fruit and buds, and shorter, broader leaves than is expected for E. pulchella. Also, great variability was evident in seedling leaf shape in naturally regenerating stands. The Snug Plains populations of E. pulchella invariably abutted the distributions of E. coccifera and E. delegatensis.

In general, at the study area on Snug Plains, E. gunnii, E. urnigera, E. johnstonii, E. coccifera and E. delegatensis displayed adult and juvenile characteristics consistent with descriptions of the species in Tasmania (Curtis & Morris 1975), although the Snug Plain populations were distinct ecotypes in some cases. In comparison, the population of E. pulchella demonstrated marked departures from the expected leaf, bud and fruit characteristics for the species. A possible cause of the departure in expected characteristics for E. pulchella (subgenus Monocalyptus series Piperitae) was hybridisation either with the

closely related species E. coccifera (subgenus Monocalyptus series Piperitae) or the more distantly related species E. delegatensis (subgenus Monocalyptus series Obliquae). The following section outlines an investigation into the possible hybrid origin of the Snug Plains E. pulchella population.

## 2. HYBRIDISATION STUDIES

Although in Eucalyptus genetic isolation is maintained at the subgeneric level (Pryor 1959a, 1976), there appear to be no absolute barriers to interbreeding between species within a subgenus. Natural hybridisation between sympatric or parapatric species from the same subgenus is a widespread phenomenon (e.g. Pryor 1951, 1955a, 1955b, 1959, 1976; Jackson 1968; Hopper et al. 1978; Drake 1980, 1981a, 1981b). Hybrid swarms have frequently been reported between members of the Tasmanian Piperitae (Potts & Reid 1983; Curtis & Morris 1975) although only a few records exist of inter-series hybrids between the Piperitae and Obliquae (e.g. Curtis & Morris 1975; Jackson 1958; Pryor 1957; Potts & Reid 1983). Previously reported hybrids involving E. pulchella include E. pulchella x E. amygdalina (Curtis & Morris 1975), E. pulchella x E. tenuiramis and E. pulchella x E. obliqua (Potts & Reid 1983). In the current study the possibility of E. pulchella hybridising with both E. coccifera and E. delegatensis is investigated.

## MATERIALS AND METHODS

The site of the investigation was a shallow rocky ridge on the eastern side of the study area, near garden 1 at Snug Plains (Figs 3.1 and 6.2) where a small population of E. pulchella abutted populations of both E. coccifera and E. delegatensis. At this site herbarium samples of adult foliage (Fig. 2.1) and fruit were collected from 6 trees of E. delegatensis, E. coccifera and E. pulchella, and from 6 trees which were identified as possessing features intermediate between those characteristic of the Snug Plains populations of E. pulchella and E. coccifera ("putative hybrid" trees). A separate collection of herbarium specimens and fruit was also made for 6 trees from a lowland population of E. pulchella at a site 5 km east of the study area, at an altitude of approximately 100 m. Six representative leaves and 20 capsules were selected from the material collected for each tree. A set of definitive morphological characters were measured for the adult leaves and air-dry weights were obtained for the capsules. The leaf characters measured were a subset of those used by Potts

Figure 2.1.

Representative adult leaves for: 1, lowland E. pulchella; 2, Snug Plains E. pulchella; 3, "putative hybrid" trees; 4, Snug Plains E. coccifera; and 5, Snug Plains E. delegatensis.

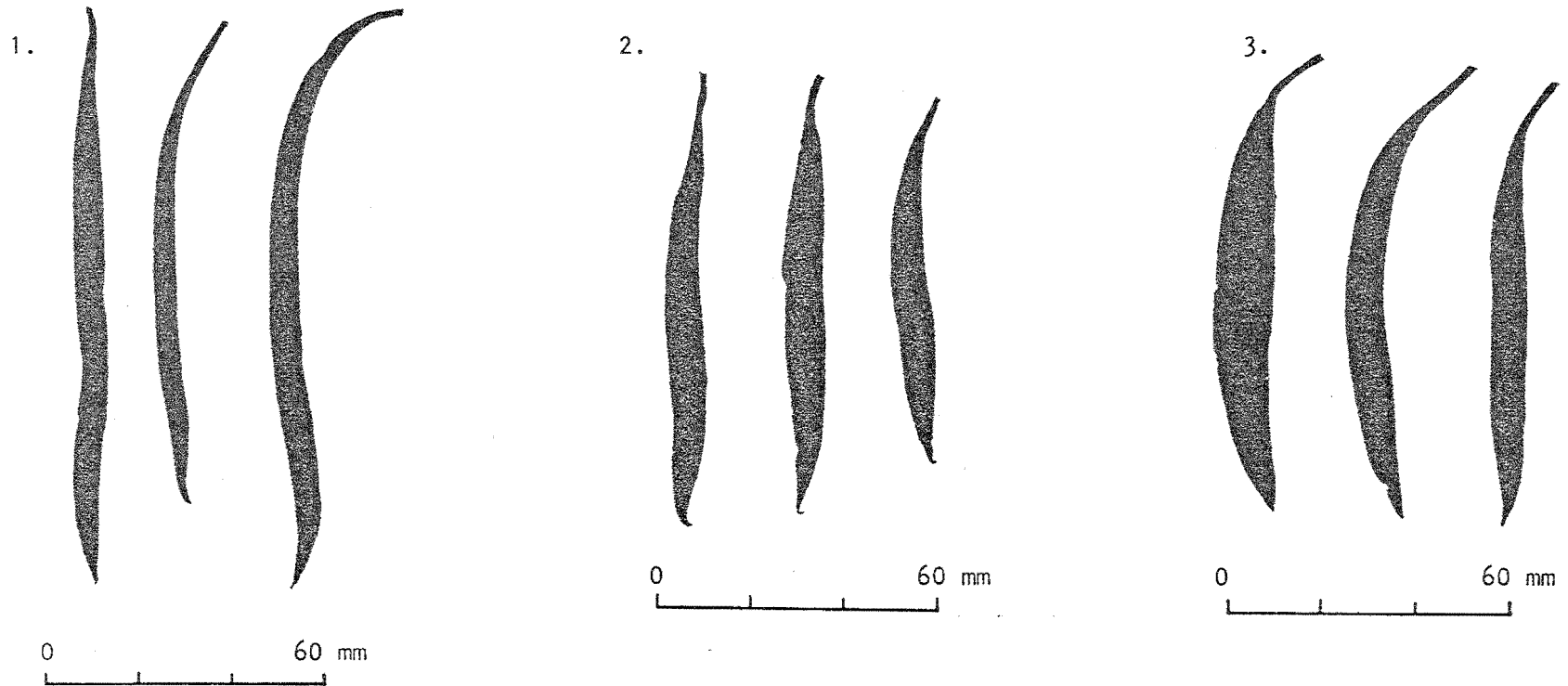


Figure 2.1 (cont'd)

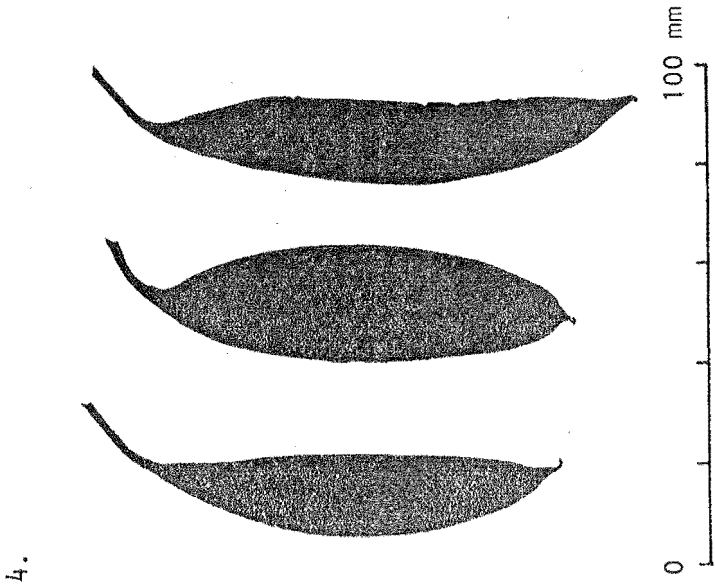
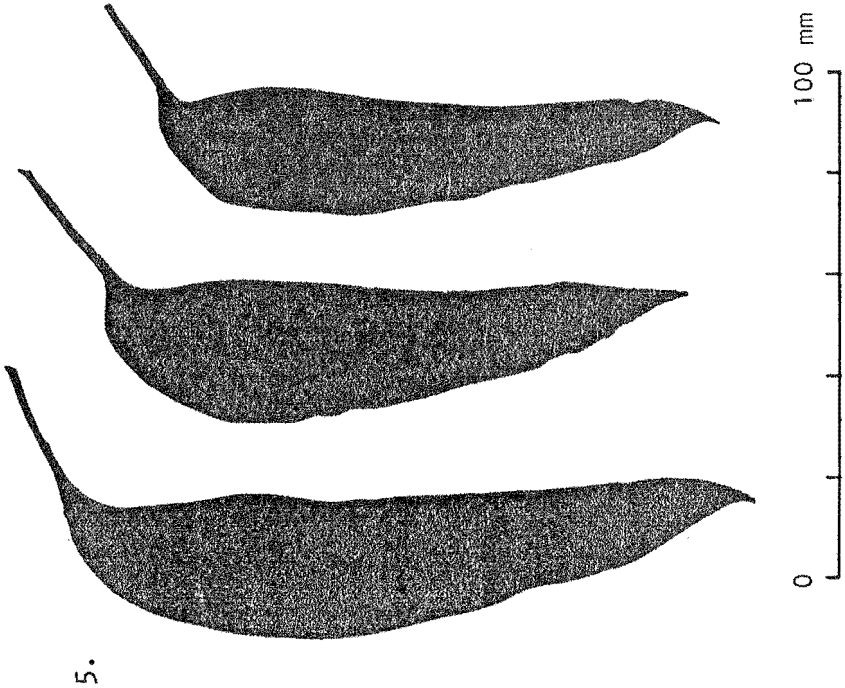
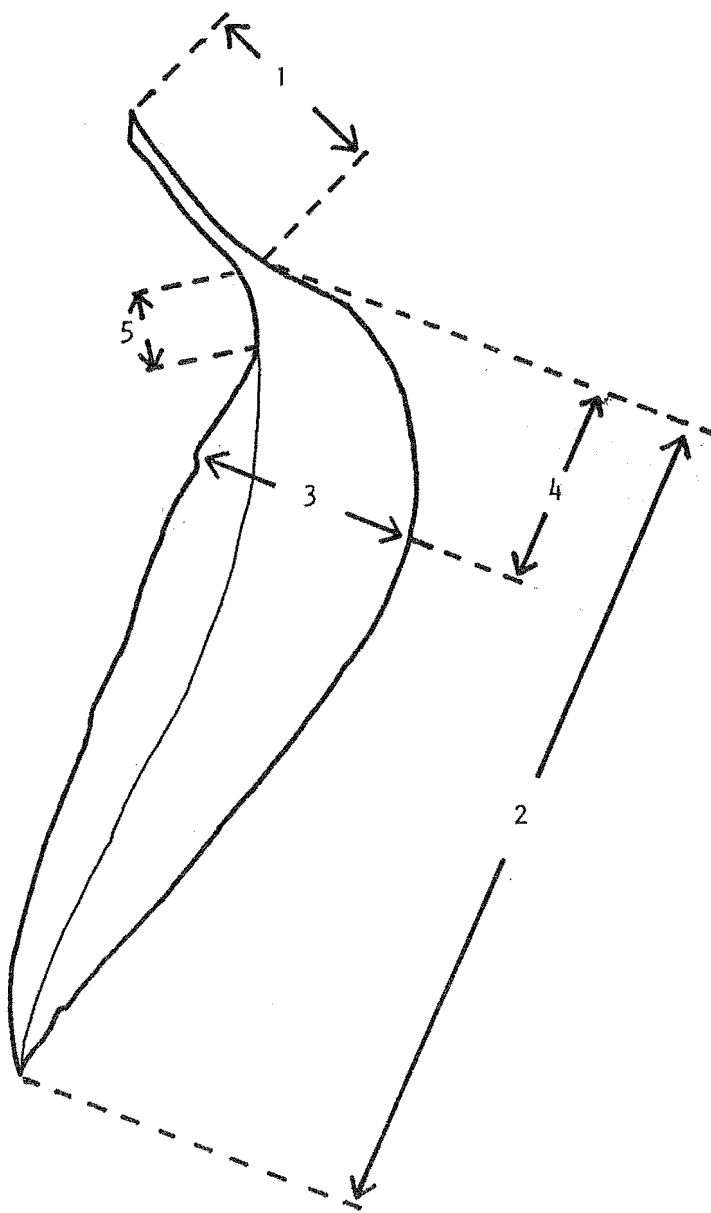


Figure 2.2

The morphological characters measured for adult leaves:  
1, petiole length; 2, lamina length; 3, lamina width; 4, length  
to widest point of the lamina; and 5, basal asymmetry of the leaf.



and Reid (1983) and included: petiole length, leaf lamina length, leaf lamina width, length to widest point of the leaf, and basal asymmetry of the leaf (Fig. 2.2). Statistical analysis of the adult leaf and fruit data set included analysis of variance and canonical variates analysis. Canonical variates analysis (discriminant functions, Fisher 1936) has been widely used in the study of hybridisation in *Eucalyptus* (e.g. Potts & Reid 1983; Hopper *et al.* 1978; Kirkpatrick 1977). It maximises the differences between populations sampled relative to the variation within populations sampled which makes the technique particularly suitable for hybrid studies (Hopper *et al.* 1978; Hopper 1977).

Progeny trials were conducted for the 5 groups identified in the field (lowland *E. pulchella*; Snug Plains *E. pulchella*; "putative hybrid" trees; Snug Plains *E. coccifera*; and Snug Plains *E. delegatensis*). The seed, which was collected concurrently with the herbarium samples from adult trees, was stratified for 4 weeks at 4°C in a cold room, then germinated on moist vermiculite and pricked out, at the cotyledonary stage, into plywood veneers tubes filled with potting soil. Ten replicate seedlings were planted for each tree (a total of 360 seedlings). The seedlings were arranged in a randomised block design, with an edge row in a glasshouse at the University of Tasmania, Hobart. The seedlings were watered three times weekly and nutrient was supplied via slow release fertilizers (osmocote, and blood and bone) present in the potting mix.

After 4 months growth a single leaf was removed from nodes 5, 7 and 10 of each seedling and a set of definitive morphological characters measured for each leaf. The set of measurements made for the seedling leaves were the same as those measured for adult leaves apart from addition of measures of leaf glaucousness (scored on a 1 to 5 scale), lamina thickness and rotation of the leaf to the vertical (scored on a 1 [horizontal] to 4 [vertical] scale) (Figs 2.3 and 2.4). For seedling leaves petiole length was recorded as a combination of two measures. Where leaves were petiolate the petiole length alone was measured (this was recorded as a positive distance). Where seedling leaves were sessile (e.g. *E. coccifera*) leaf width was measured at a tangent to the stem (a measure used by Pryor 1955; this was recorded as a negative distance) (Fig. 2.4). Two stem characters were also measured on the seedlings at nodes 5, 7 and 10. These were internode length and intranode length. Internode length was measured between the node at which the leaf characters were measured and the immediately preceding node. Analysis of variance and canonical variates analysis was performed on the above set of seedling morphological characters.

Figure 2.3

Representative 10th node seedling leaves from: 1, lowland E. pulchella; 2, Snug Plains E. pulchella; 3, "putative hybrid" trees from Snug Plains; 4, Snug Plains E. coccifera and 5, Snug Plains E. delegatensis collected from glasshouse grown seedlings.



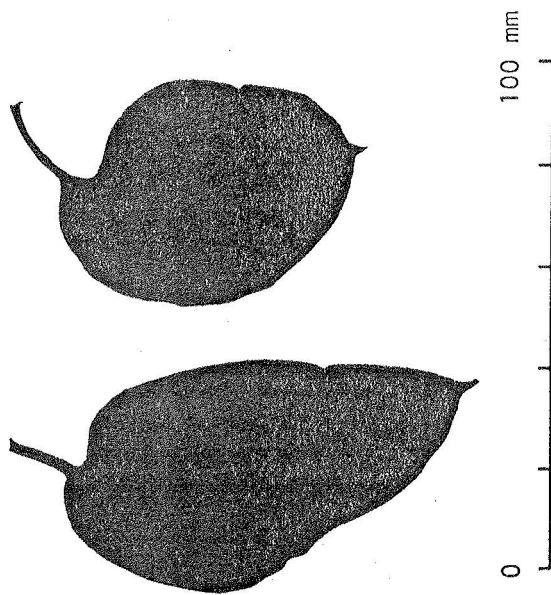
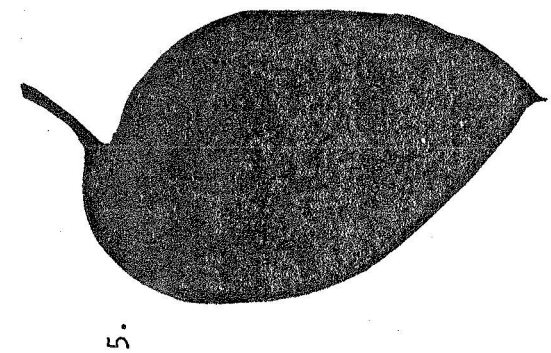
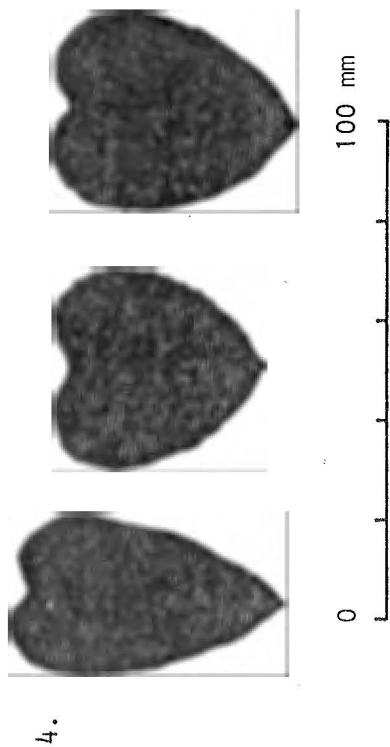
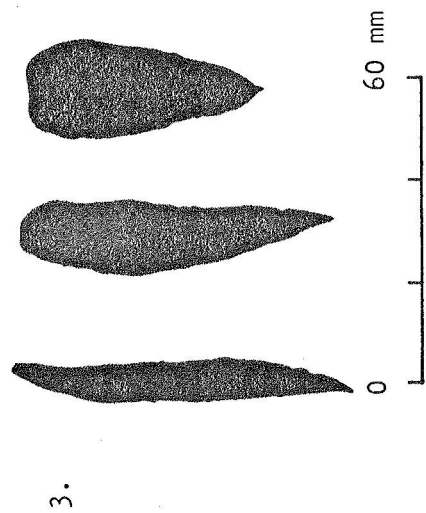
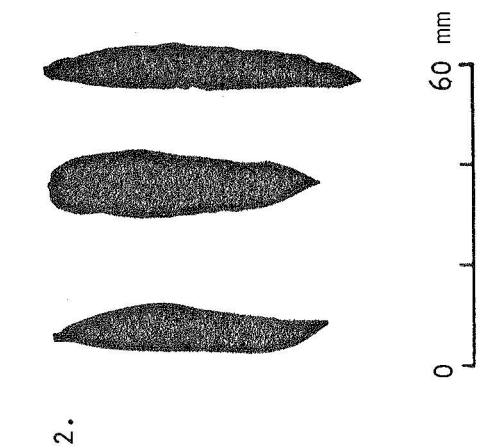
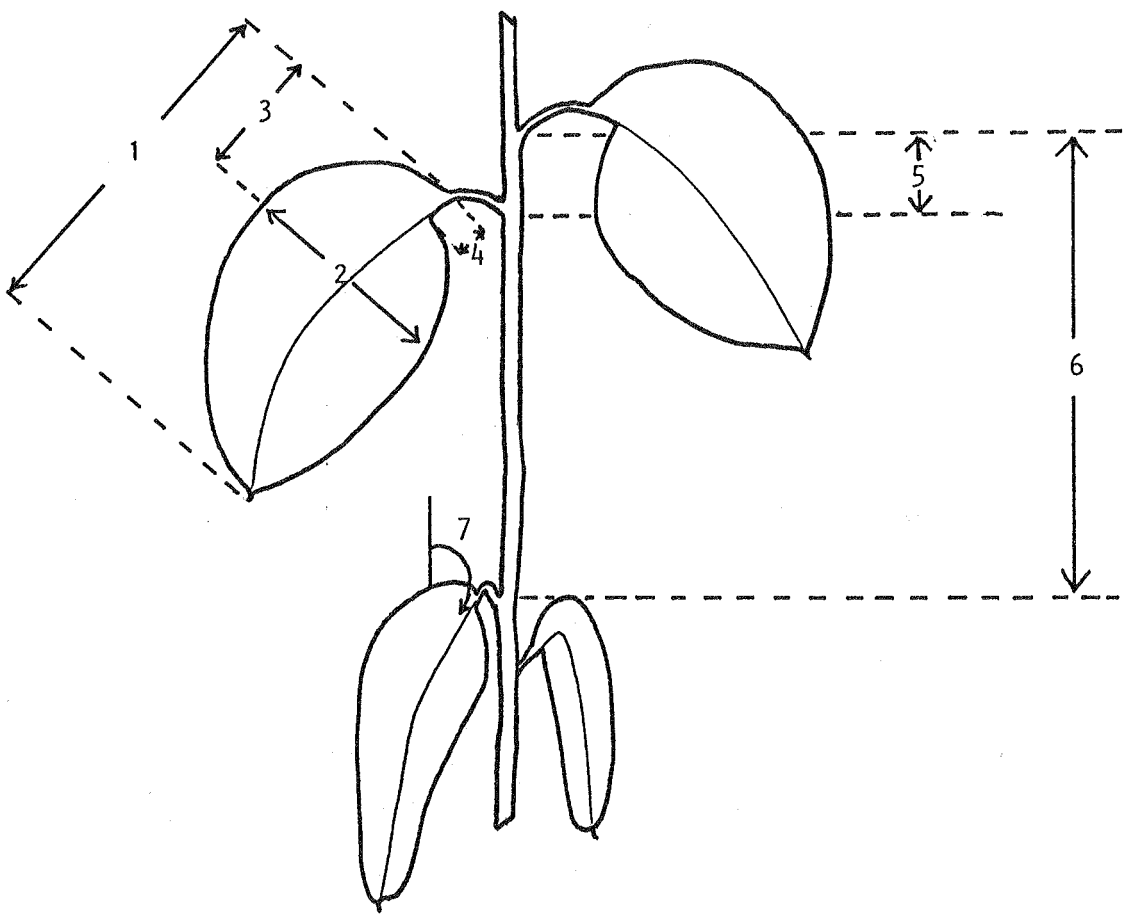


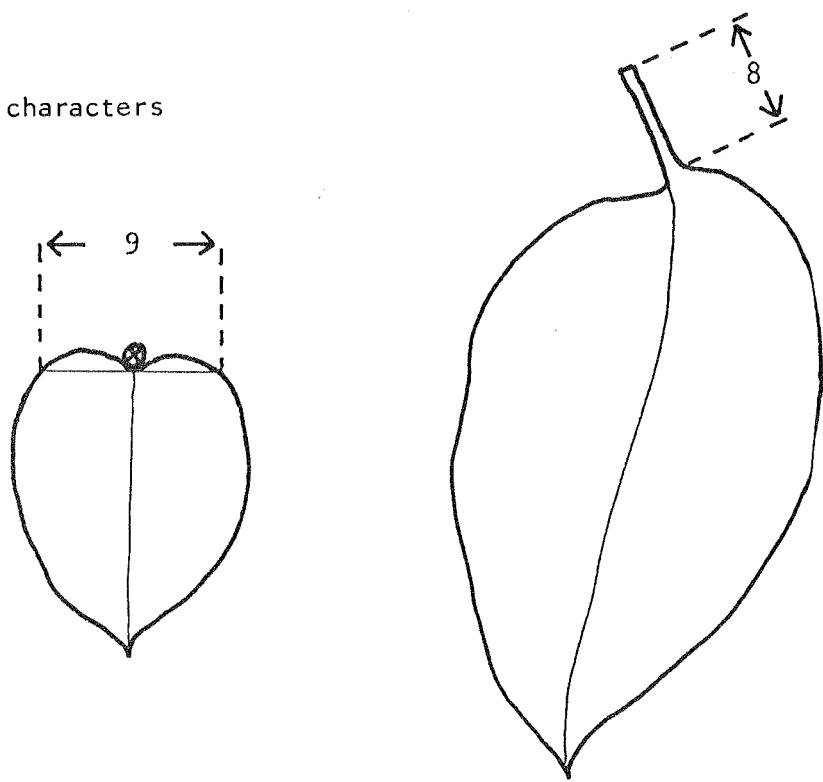
Figure 2.4

The morphological characters measured for seedling leaves:  
1, lamina length; 2, lamina width; 3, length to widest point of the lamina; 4, basal asymmetry of the leaf; 5, intranode length; 6, internode length; 7, leaf rotation (from the vertical); 8, petiole length (positive measure); 9, petiole length (negative measure); glaucousness and lamina thickness (not depicted).

(a) Leaf and node characters



(b) Petiolar characters



The field populations of E. pulchella, E. coccifera and E. delegatensis at the study site on Snug Plains and the lowland population of E. pulchella were also assessed for time and intensity of flowering. Thirty trees were visually assessed in each population. The sites were visited fortnightly between October 1981 and April 1982 and the intensity of flowering was scored on a 1 to 10 scale.

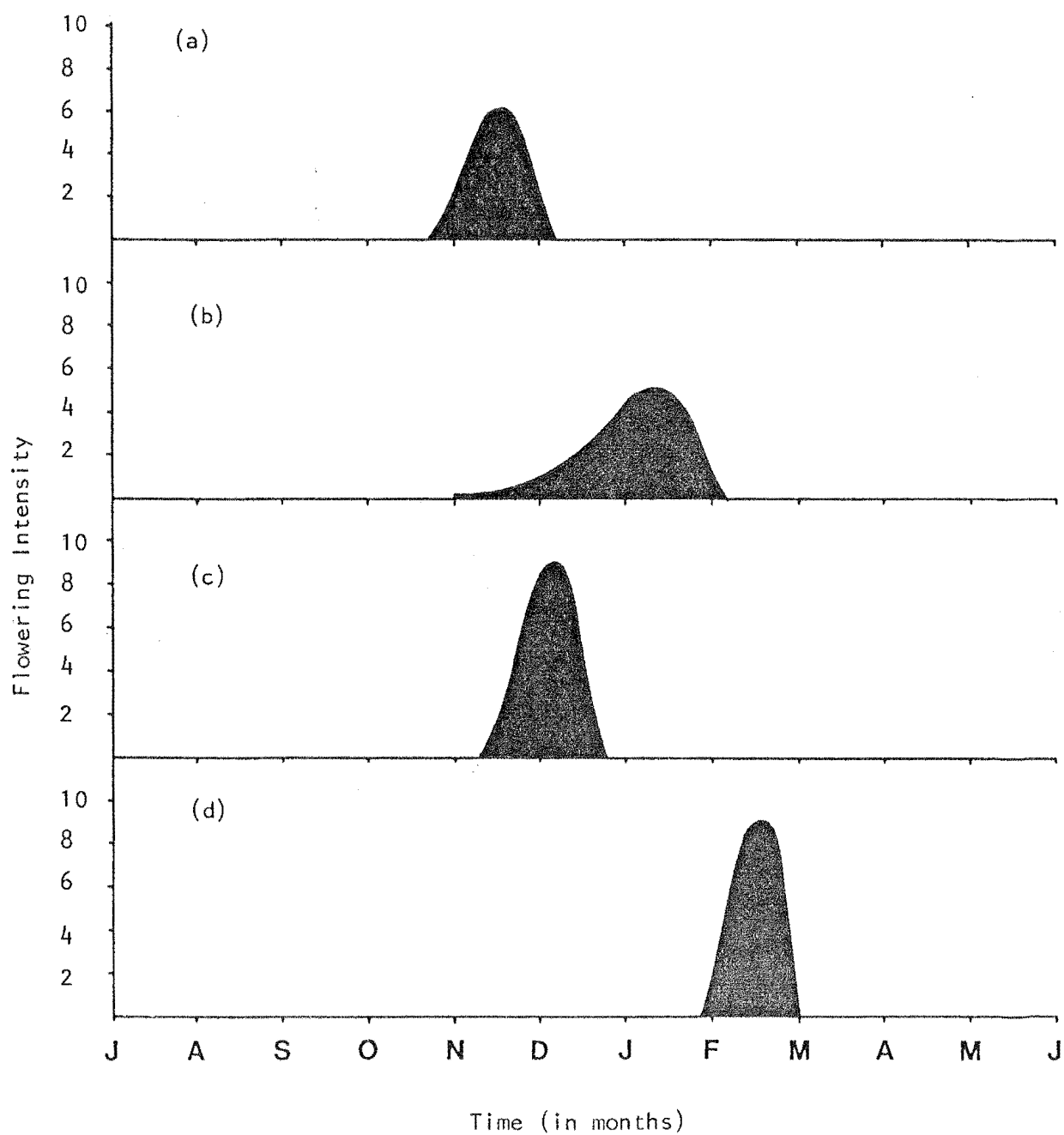
## RESULTS

The flowering time of the Snug Plains E. pulchella overlapped the flowering periods of the two other parapatric Monocalyptus species, E. coccifera and E. delegatensis at Snug Plains (Fig. 2.5). The peak flowering time for Snug Plains E. pulchella was midway between the peaks of E. coccifera and E. delegatensis but flowering started at low intensity before, and continued throughout, the flowering period of E. coccifera. The flowering time for the lowland E. pulchella and the Snug Plains E. delegatensis populations fell within the ascribed mean flowering periods for these species (Potts & Reid 1983), but at Snug Plains the E. coccifera population was flowering more than a month earlier than normal, and the peak flowering period for E. pulchella at Snug Plains was two months later than at the lowland E. pulchella stand. Observations of the movements of New Holland honeyeaters (Phylidonyris novaehollandiae), yellow wattle birds (Anthochaera paradoxa) and a variety of pollinating insects which fed from flowers in the crowns of each of the species at Snug Plains indicated that these pollinators move indiscriminately across species boundaries during occasions when the flowering periods of the eucalypt species overlapped.

The morphometric analysis of the adult characters (Fig. 2.6) indicated that the Snug Plains E. pulchella and "putative hybrid" trees were subsets of the same population. All except two of the "putative hybrid" trees fell within the range of the "Snug Plains E. pulchella" population. As a combined group the "Snug Plains E. pulchella" and "putative hybrid" trees were discrete and distinct from the other populations studied (lowland E. pulchella, Snug Plains E. coccifera and Snug Plains E. delegatensis). Apart from two of the "putative hybrid" trees the whole population showed no more variability in morphology than any of the three possible parental species. The 5 populations sampled differed significantly (at the 0.001 level) in the analysis of variance (Table 2.1). In all characters except leaf lamina length and basal asymmetry of the leaf the Snug Plains E. pulchella and "putative hybrid" trees were intermediate between

Figure 2.5

Flowering period and flowering intensities (on a 1 to 10 scale) for: (a) lowland *E. pulchella*; (b) Snug Plains *E. pulchella*; (c) Snug Plains *E. coccifera*; and (d) Snug Plains *E. delegatensis*, during 1981.



lowland E. pulchella and the two other possible parental species E. coccifera and E. delegatensis (Table 2.1a). The canonical variates analysis clearly separated the 5 populations sampled into four clusters using the CV1 and CV2 axes (Fig. 2.6). Canonical variate 1 (CV1) and canonical variate 2 (CV2) respectively contained 81.3% and 16.6% of the variation in the characters measured (Table 2.2). Separation of species along the CV1 axis was largely on the basis of a comparison between lamina length and length to the widest point of the leaf whereas on the CV2 axis species were discriminated by capsule weight, lamina length and basal asymmetry of the leaf (Table 2.2). The intermediacy of the morphological characters of the Snug Plains E. pulchella population suggests it has had a hybrid origin, with lowland E. pulchella and E. coccifera as the putative parents. However the leaf length of the Snug Plains E. pulchella and "putative hybrid" trees was less than other groups (Table 2.1a) suggesting this character may be under independent selective control; unless inherited as a ratio of leaf parameters. Short leaves may confer a selective advantage under conditions of high wind velocity and ice loading in a subalpine environment (Pryor 1957).

The absence of lowland E. pulchella phenotypes in the mature Snug Plains stand raises the possibility of the stand being a "phantom hybrid" swarm; that is a hybrid swarm which as a result of climatic or habitat changes no longer has representatives of one of the putative parental species (Pryor 1951, 1955b, Parsons & Kirkpatrick 1972; Kirkpatrick *et al.* 1973). Further, all the Snug Plains E. pulchella trees, except for two of the "putative hybrid" trees, were similar to the putative E. pulchella parent, which suggests these trees may be backcrosses to E. pulchella and/or intercrosses amongst themselves. The two outlying putative hybrid trees could conceivably be F<sub>1</sub> hybrids or backcrosses to the E. coccifera parent.

The morphometric analysis performed on the seedling progenies from the above five populations supports the contention that the Snug Plains E. pulchella population is of hybrid origin. Visual assessment of the canonical variates plot suggests that the progeny of Snug Plains E. pulchella trees showed much greater morphological variability than the allopatric lowland E. pulchella and considerably more variability than the parapatric E. coccifera and E. delegatensis populations (Fig. 2.7). Analysis of variance indicated significant differences (at the 0.001 level) existed between the five populations studied (Table 2.3). The canonical variates analyses which were performed on the 5th, 7th and 10th node characters all showed similar trends, therefore node 10 results only are presented. The tenth node canonical variates analysis clearly

Figure 2.6

Canonical variate 1 versus canonical variate 2 derived from an analysis of 6 morphometric characters measured on adult foliar and capsule material collected in the field for: lowland *E. pulchella* (●); Snug Plains *E. pulchella* (Δ); "putative hybrid" trees (□); Snug Plains *E. coccifera* (■); and Snug Plains *E. delegatensis* (▲). Means are shown for each population.

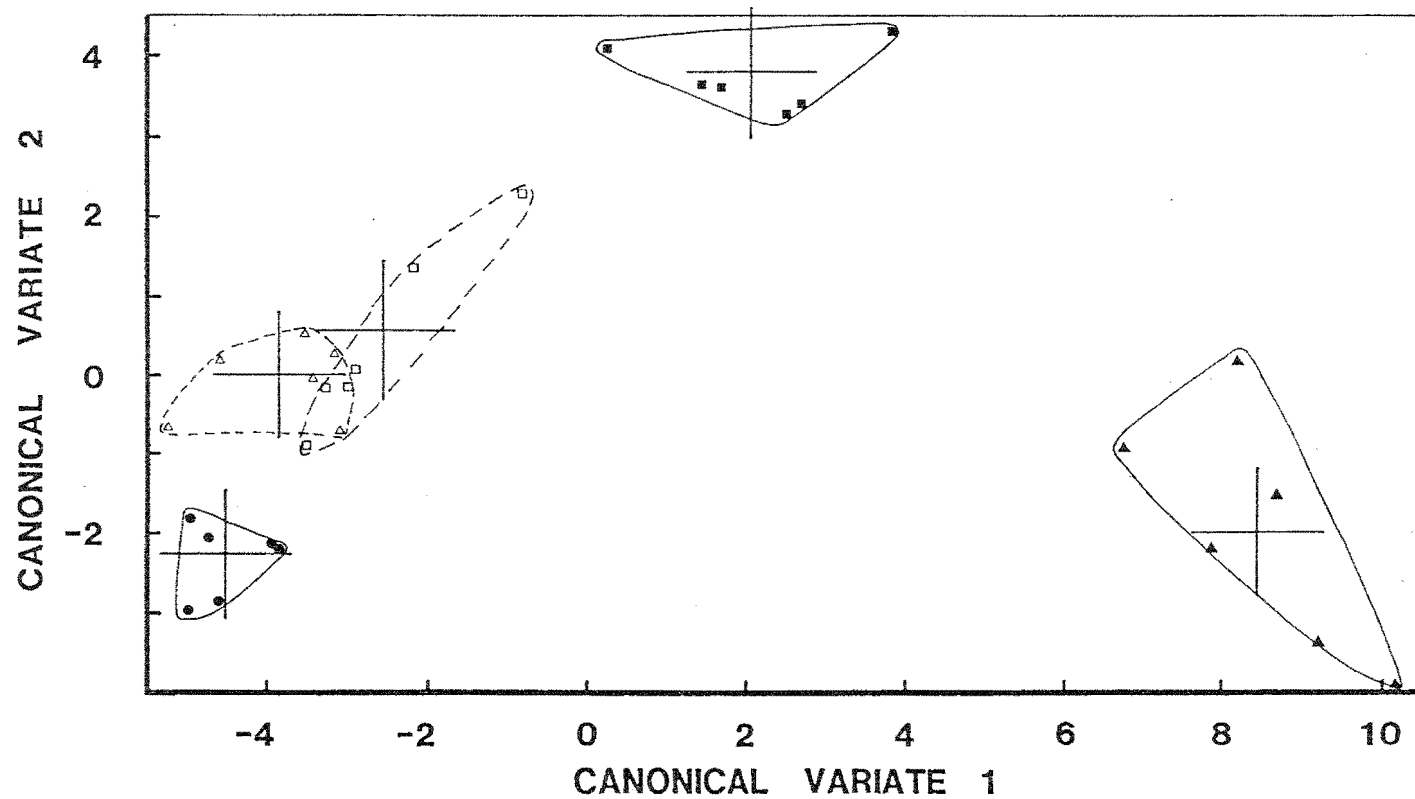


Table 2.1

(a) Means  $\pm$  SE and (b) analysis of variance performed on the morphological characters: leaf lamina length (LL), leaf lamina width (LW); length to the widest point of the leaf (LWP); petiole length (PL); basal asymmetry of the leaf (Basym); and capsule weight (cap. wt.), measured for adult foliar and capsule material (see Fig. 2.3) collected from 5 groups of trees: 1, lowland E. pulchella; 2, Snug Plains E. pulchella; 3, "putative hybrid" trees; 4, Snug Plains E. coccifera; and 5, Snug Plains E. delegatensis respectively.

Table 2.1(a)

| Species                       |           | LL<br>(mm)           | LW<br>(mm)          | LWP<br>(mm)         | PL<br>(mm)          | Basym<br>(mm)        | Cap. wt.<br>(g)      |
|-------------------------------|-----------|----------------------|---------------------|---------------------|---------------------|----------------------|----------------------|
| E. pul (low)<br>(Group 1)     | $\bar{x}$ | 105.36<br>$\pm 2.54$ | 6.36<br>$\pm 0.09$  | 54.62<br>$\pm 1.57$ | 6.59<br>$\pm 0.18$  | 0.156<br>$\pm 0.005$ | 0.053<br>$\pm 0.002$ |
| E. pul (SP)<br>(Group 2)      | $\bar{x}$ | 79.36<br>$\pm 1.31$  | 7.68<br>$\pm 0.13$  | 42.43<br>$\pm 0.53$ | 7.54<br>$\pm 0.20$  | 0.144<br>$\pm 0.010$ | 0.135<br>$\pm 0.006$ |
| Putative hybrids<br>(Group 3) | $\bar{x}$ | 79.62<br>$\pm 0.73$  | 9.15<br>$\pm 0.44$  | 39.73<br>$\pm 0.40$ | 10.17<br>$\pm 0.54$ | 0.213<br>$\pm 0.009$ | 0.170<br>$\pm 0.014$ |
| E. cocc (SP)<br>(Group 4)     | $\bar{x}$ | 84.07<br>$\pm 1.47$  | 19.44<br>$\pm 0.96$ | 35.31<br>$\pm 0.88$ | 16.21<br>$\pm 0.62$ | 0.383<br>$\pm 0.097$ | 0.346<br>$\pm 0.004$ |
| E. del (SP)<br>(Group 5)      | $\bar{x}$ | 111.94<br>$\pm 1.97$ | 26.27<br>$\pm 0.27$ | 29.79<br>$\pm 0.75$ | 21.59<br>$\pm 0.61$ | 6.839<br>$\pm 0.379$ | 0.266<br>$\pm 0.009$ |

Table 2.1(b)

| Morphometric character | Between groups variance | Within groups variance | F. Ratio | Probability |
|------------------------|-------------------------|------------------------|----------|-------------|
| LL                     | 1388.0                  | 108.49                 | 12.79    | < 0.001     |
| LW                     | 446.98                  | 8.469                  | 52.78    | < 0.001     |
| LWP                    | 518.02                  | 31.46                  | 16.46    | < 0.001     |
| PL                     | 240.67                  | 7.446                  | 32.32    | < 0.001     |
| Basym                  | 52.10                   | 1.148                  | 45.38    | < 0.001     |
| Cap. Wt.               | 0.0777                  | 0.00196                | 39.71    | < 0.001     |



Table 2.2

Canonical variate scores and the percentage of total variation for the canonical variates analysis of adult foliar and capsule material collected in the field.

| Character                     | CV1     | CV2     | CV3     | CV4     |
|-------------------------------|---------|---------|---------|---------|
| Leaf lamina length            | 0.6447  | -0.5289 | 0.8004  | 0.4023  |
| Leaf lamina width             | 0.2211  | 0.2498  | 0.2585  | -0.5767 |
| Length to widest point        | -0.6894 | 0.2950  | -0.0236 | -0.3760 |
| Petiole length                | 0.0852  | 0.0124  | -0.2701 | 0.5709  |
| Basal asymmetry of leaf       | 0.1308  | -0.4511 | -0.4385 | -0.1952 |
| Capsule weight                | 0.1391  | 0.6059  | 0.1636  | 0.0155  |
| Percentage of total variation | 81.29   | 16.62   | 1.97    | 0.12    |

separates the progenies of upland E. pulchella, Snug Plains E. coccifera and Snug Plains E. delegatensis populations on the CV1 and CV2 axes (Fig. 2.7). Canonical variate 1 (CV1) and canonical variate 2 (CV2) respectively contained 76.3% and 21.5% of the variation in the characters measured (Table 2.4). Species were separated along the CV1 axis primarily on the basis of petiole length and leaf lamina width (Table 2.4) whereas on the CV2 axis species were discriminated by leaf lamina width, petiole length and lamina length.

Interestingly, although the Snug Plains E. pulchella population as a whole had a broad range of morphological variability, the two sets of Snug Plains E. pulchella trees sampled; Snug Plains E. pulchella and "putative hybrid" trees, differed markedly. The Snug Plains E. pulchella trees produced segregates which varied from individuals indistinguishable from lowland E. pulchella seedlings, to individuals which approached E. coccifera seedlings in character, and a cluster of individuals intermediate between E. pulchella and E. delegatensis seedlings (Fig. 2.7). The discreteness and intermediacy of this cluster of individuals strongly suggests they are  $F_1$  hybrids between E. pulchella and E. delegatensis. The "putative hybrid" trees produced segregates which varied from individuals indistinguishable from lowland E. pulchella to individuals indistinguishable from E. coccifera. However, subsequent checks on the origin of these seedlings showed all E. coccifera-like segregates were progeny from the two outlying "putative hybrid" trees in the adult morphometric analysis. Further, the six "putative hybrid" trees were chosen because of their possible E. coccifera affinities and may well have been early flowering phenotypes (E. coccifera flowering before E. pulchella) thus preventing hybridisation with E. delegatensis. As was found for the E. pulchella trees in the adult morphometric analysis, the majority of segregates from the Snug Plains E. pulchella progeny were more similar to the putative lowland E. pulchella parent than to E. coccifera.

## DISCUSSION

Although there are several intrinsic mechanisms by which natural hybridisation between eucalypt species from the same subgenus may be reduced or prevented (Pryor 1959; Barber 1965; Hopper *et al.* 1978; Rodgers & Westman 1979; Drake 1980, 1981a, 1981b; Ashton 1981), the major isolation mechanisms which normally prevent hybridisation between E. pulchella and E. delegatensis or E. coccifera are spatial and ecological. Stands of E. pulchella are rarely found in contact with stands of either E. coccifera or E. delegatensis and the

Figure 2.7

Canonical variate 1 versus canonical variate 2 derived from an analysis of 10 morphometric characters measured at the tenth node of the glasshouse grown seedling progeny of: lowland *E. pulchella* (●); Snug Plains *E. pulchella* (Δ); "putative hybrid" trees (□); Snug Plains *E. coccifera* (■); and Snug Plains *E. delegatensis* (▲). Means are shown for each population.

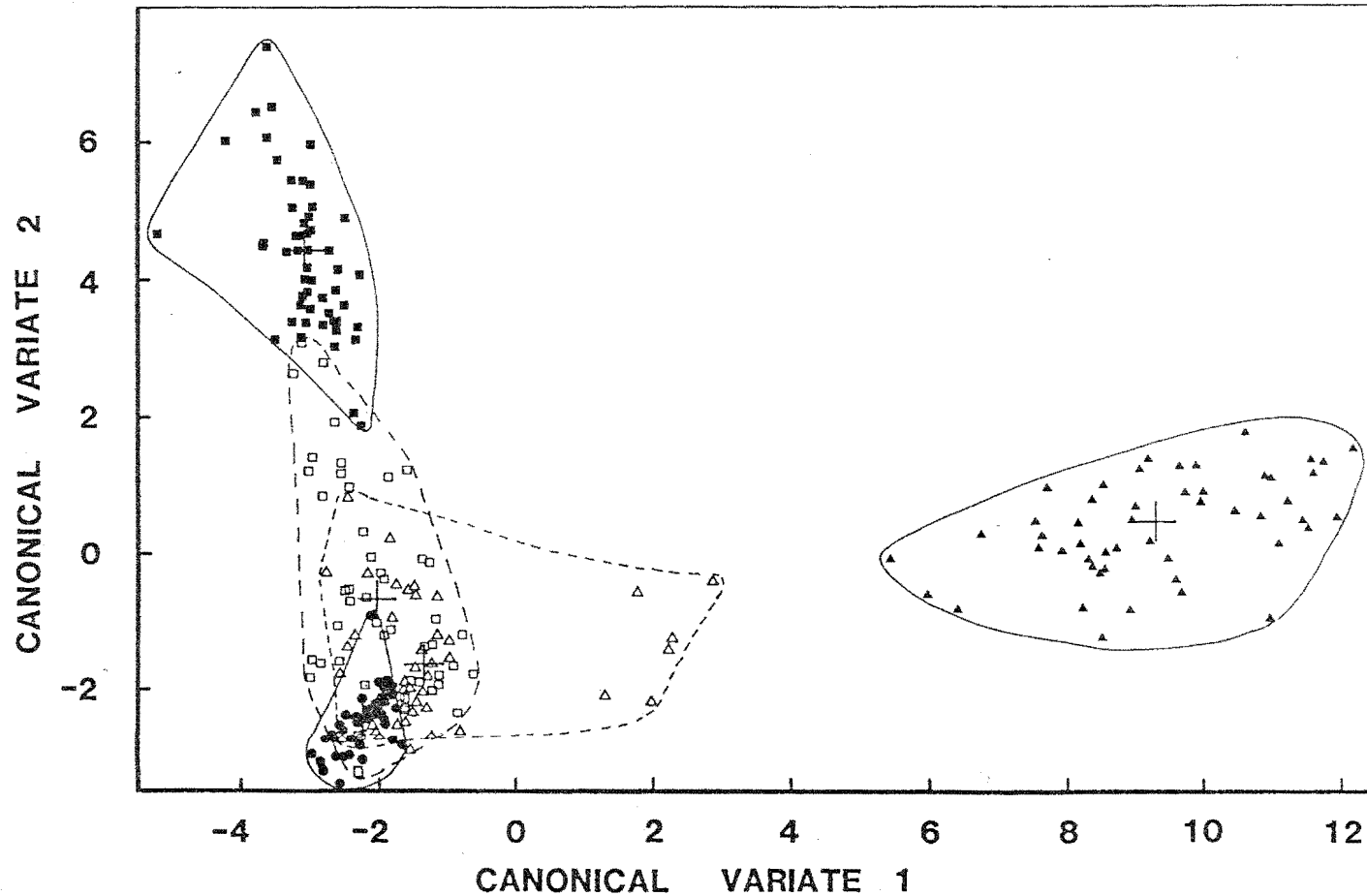


Table 2.3

Analysis of variance performed on the morphological characters (see Fig. 2.5) measured at the tenth node of glasshouse grown seedling progeny of 5 groups of trees: 1, lowland E. pulchella; 2, Snug Plains E. pulchella; 3, "putative hybrid" trees; 4, Snug Plains E. coccifera; and 5, Snug Plains E. delegatensis respectively.

| Character              | Between groups variance | Within groups variance | F. ratio | Probability |
|------------------------|-------------------------|------------------------|----------|-------------|
| Lamina length          | 8755.3                  | 83.35                  | 105.04   | < 0.001     |
| Lamina width           | 13354                   | 26.19                  | 509.93   | < 0.001     |
| Length to widest point | 3366.3                  | 29.18                  | 115.36   | < 0.001     |
| Glaucousness           | 13.63                   | 0.2447                 | 55.71    | < 0.001     |
| Lamina thickness       | 23.81                   | 3.944                  | 6.04     | < 0.001     |
| Basal asymmetry        | 161.49                  | 0.5935                 | 272.08   | < 0.001     |
| Leaf rotation          | 131.20                  | 0.4079                 | 321.64   | < 0.001     |
| Petiole length         | 11048                   | 18.53                  | 596.08   | < 0.001     |
| Internode length       | 10712                   | 115.37                 | 92.84    | < 0.001     |
| Intranode length       | 5221.4                  | 24.61                  | 212.15   | < 0.001     |

Table 2.4

Canonical variate scores and the percentage of total variation for the canonical variates analysis of morphological characters measured at the tenth node of glasshouse grown seedlings.

| Character                     | CV1     | CV2     | CV3     | CV4     |
|-------------------------------|---------|---------|---------|---------|
| Lamina length                 | -0.1907 | -0.4596 | -0.4885 | -0.8159 |
| Lamina width                  | 0.6492  | 0.5871  | 0.1373  | 0.1852  |
| Length to widest point        | -0.0299 | 0.1225  | 0.8264  | 0.2429  |
| Glaucousness                  | -0.0098 | 0.2187  | 0.0334  | -0.1938 |
| Lamina thickness              | -0.0563 | 0.0043  | 0.0337  | 0.3148  |
| Basal asymmetry               | 0.1340  | 0.0171  | -0.0535 | -0.1514 |
| Leaf rotation                 | 0.2151  | 0.0260  | -0.0838 | 0.1190  |
| Petiole length                | 0.6683  | -0.5967 | -0.1523 | 0.2377  |
| Internode length              | 0.0721  | -0.0201 | 0.0228  | -0.1000 |
| Intranode length              | 0.0778  | 0.1545  | 0.1541  | 0.0287  |
| Percentage of total variation | 76.31   | 21.60   | 1.69    | 0.40    |

flowering times are more or less distinct. In their normal ecological positions flowering in E. pulchella stands is almost complete at the time E. coccifera starts to flower, and is quite distinct from the later flowering E. delegatensis (Potts & Reid 1983). However the flowering period for the Snug Plains E. pulchella population fell between and partially overlapped with the flowering periods of both E. coccifera and E. delegatensis. Shifts in flowering time may be affected by altitudinal or seasonal differences within the geographic range of a species (Pryor 1956, 1976; Ashton 1975, 1981). At Snug Plains both E. pulchella and E. coccifera were near the limit of their altitudinal ranges (E. pulchella at the upper limit and E. coccifera at the lower limit). The respective shifts in flowering time in response to altitudinal influences appear to have resulted in a substantial overlap in flowering time and a reversal in the normal order of flowering for two species, with E. coccifera flowering before E. pulchella at Snug Plains. It is possible that secondary isolating mechanisms (for example flowering time shifts) have also been operating to reduce the selective load which would be imposed by hybridisation. If this was the case the low level flowering of E. pulchella which overlaps the peak flowering in E. coccifera may represent either early flowering hybrid segregates or residual early flowering E. pulchella phenotypes. For example, Potts and Reid (1983) reported E. obliqua x E. pulchella hybrids had a flowering time intermediate between those of the putative parents. The net result of the relative shifts in flowering time which put the flowering of E. pulchella ahead of that for E. coccifera is to place the E. pulchella flowering period where it also overlaps with the early flowering E. delegatensis trees facilitating hybridisation between the three parapatric Monocalyptus species.

Barber and Jackson (1957) citing evidence from steep clines in glaucousness in various Tasmanian eucalypt species suggested much of the variability in eucalypt populations could be under the control of selection along an ecological gradient. They maintained that selection itself may create genetic diversity in the localised populations in different habitats or microhabitats, and produce intermediates between two forms in the field which might be difficult to distinguish from the effects of introgression. However, from a range of studies into hybridisation and introgression (Anderson 1953; Pryor & Johnson 1962; Hopper 1977a, 1977b; Hopper et al. 1978) a set of criteria can be established which allow a convincing decision to be made on the possibility of hybrid origin. These were summarized by Hopper et al. (1978):-

1. Intermediate morphology of suspected hybrids.
2. Occurrence of hybrids in sympatric parental stands.
3. Phenotypic segregation in hybrid progeny.

4. Close agreement in morphology between expected and experimentally synthesised hybrids.
5. Occurrence of hybrids in disturbed or relatively youthful habitats.
6. Impaired reproductive capability of hybrids relative to parental individuals (i.e.  $F_2$  breakdown).
7. Occurrence of interspecific pollen exchange by indiscriminant vectors in sympatric parental stands.

At least four of these criteria are satisfied in the upland E. pulchella population at Snug Plains. The E. pulchella trees sampled at Snug Plains were intermediate between lowland E. pulchella and E. coccifera in adult morphology and exhibited marked phenotypic segregation in their progenies. The Snug Plains E. pulchella, E. coccifera and E. delegatensis occurred in sympatric or closely parapatric stands in the field (although no lowland E. pulchella phenotypes were present). The flowering periods of the three species overlapped and pollen vectors were observed moving indiscriminately between the species canopies. Although the habitat has been repeatedly disturbed by fire in the recent past the trees used in the current study were established mature trees which undoubtedly predated white man's disturbance of the area which started with logging operations in the 1920's. Therefore hybridisation at the study site at Snug Plains was not of recent origin.

Pryor (1951, 1955a) and Pryor and Johnson (1971) report several instances of "phantom hybrids" but these were not verified unequivocally by progeny trials. Similarly Parsons and Kirkpatrick (1972) and Kirkpatrick *et al.* (1973) studied eucalypt populations which were possible "phantom hybrids": E. cypellocarpa x E. goniocalyx and E. cypellocarpa x E. globulus respectively, but progeny trials were inconclusive. In the current study the hybrid origin of the Snug Plains E. pulchella population was confirmed and the clear absence of lowland E. pulchella phenotypes in the mature stand makes it unequivocally a "phantom hybrid" stand. The presence of lowland E. pulchella phenotypes in the progeny but their absence in the mature suggests strong selection is occurring against these phenotypes at Snug Plains. The low variability in the mature Snug Plains E. pulchella stand suggests strong selection is occurring for particular hybrid phenotypes unless convergence in morphology is occurring during ontogeny. In the frost prone environment at Snug Plains (see Chapter 4) the introgression of E. coccifera genes might confer a degree of frost resistance through morphological and/or physiological characters which would be a selective advantage for the Snug Plains E. pulchella segregates possessing these traits. Therefore hybrid individuals may well be at a selective advantage in comparison with the lowland E. pulchella parental genotypes on the rocky ridge at the study site on Snug Plains.

The absence of one of the parental species from a "phantom hybrid" stand has often been attributed to climatic changes which have resulted in elimination of the parental phenotypes (Pryor 1951, 1955a; Parsons & Kirkpatrick 1972; Kirkpatrick et al. 1973). At Snug Plains the E. pulchella population occupied a rocky ridge crest which amounted to a warmer drier microhabitat in an essentially cool to cold, moist subalpine environment. Since the Tertiary, which ended with the Pleistocene glaciations, the Australian climate has fluctuated considerably (Barlow 1981; Davies 1974). For E. pulchella, a lowland species which normally occupies dolerite derived soil on dry aspects, the upland habitats of Snug Plains would probably have been made available during periods of drier climate. Slight shifts in climate on these marginal sites may well have subsequently selected against E. pulchella in favour of the hybrids. However, there is also evidence of separate selective forces operating on particular morphological characters of the Snug Plains E. pulchella (e.g. leaf length).

The phantom hybrid population at Snug Plains has morphological characteristics skewed towards those of lowland E. pulchella. However, the progeny of hybrid plants generally do not show the morphological variability expected if random rearrangement of characters had occurred (Anderson 1953). In Eucalyptus a degree of recombination of morphological characters occurs in hybrid progenies (Pryor 1955, 1958; Ashton 1958), but there is a tendency for coherence of parental combinations (Pryor 1957b; Hartley 1965; Potts & Reid 1983) which may be caused by backcrossing linkage, pleiotropy or inviability of extreme recombinants (Anderson 1939; Dempster 1949; Clausen & Hiesey 1960; Goodman 1966). Although the current study does not allow separation of these effects, inference from other studies (e.g. Hopper et al. 1978, Potts & Reid 1983) suggest backcrossing is a major contributing factor to character cohesion in Eucalyptus. The similarity of the majority of adult trees and their progeny to the E. pulchella parent strongly suggests that the Snug Plains E. pulchella population has had its origin through hybridisation followed by backcrossing and interbreeding within the stand. Introgression of some E. coccifera characters has produced a distinct, but "E. pulchella like", population. Generations of backcrossing and interbreeding tends to lead to reduced variability within a population of hybrid origin (Anderson 1953; Hopper et al. 1978; Hopper 1977) and may lead to speciation (Anderson 1953; Hopper 1977). However in the Snug Plains E. pulchella population, gene flow is continuing, as evidenced by the two outlying "putative hybrid" trees and the progeny variability. Isolating mechanisms have not become established.



The presence of a discrete group of individuals in the Snug Plains E. pulchella progeny which were intermediate between E. delegatensis and E. pulchella was good evidence that  $F_1$  hybrids were occurring between these two species. Hybrids between E. delegatensis (series Obliquae, subgenus Monocalyptus) and E. pulchella (series Piperitae, subgenus Monocalyptus) have not been reported previously, although other interseries hybrids between Tasmanian members of the series Obliquae and Piperitae have been described (Curtis & Morris 1975; Pryor 1957; Jackson 1958; Potts & Reid 1983). Therefore the Snug Plains E. pulchella population is in the rare position of hybridising concurrently with two parapatric Monocalyptus species.

## CONCLUSION

In regional ecological studies conducted on eucalypt species attention is seldom drawn to the ecotypes of the species being studied despite the fact some eucalypt species have been shown to encompass a broad range of ecotypic variants and cline forms (e.g. Ladiges 1974, 1975; Anderson & Ladiges 1982; Ladiges & Ashton 1974, 1977; Jackson 1960; Pryor 1957). In general, the eucalypt populations at the intermediate altitudes of Snug Plains either represent lowland ecotypes of subalpine species (e.g. E. urnigera, E. coccifera, E. johnstonii, E. gunnii) or upland ecotypes and introgressed hybrids of lowland species (e.g. E. pulchella). Part of the complexity of the distributions of the species at Snug Plains is a function of this intermediacy in altitude and the possibility that two sets of species (lowland and highland species, Jackson 1965) may occupy each of the sets of soil type and water relations niches at Snug Plains depending on subtle differences in climatic regime.

The following chapters will address the ecological factors affecting the distribution and changes in dominance of the aforementioned species ecotypes in the knowledge that they may represent only a small portion of the ecological amplitude of the species studied.

## CHAPTER THREE

### SEEDLING TRANPLANT TRIALS

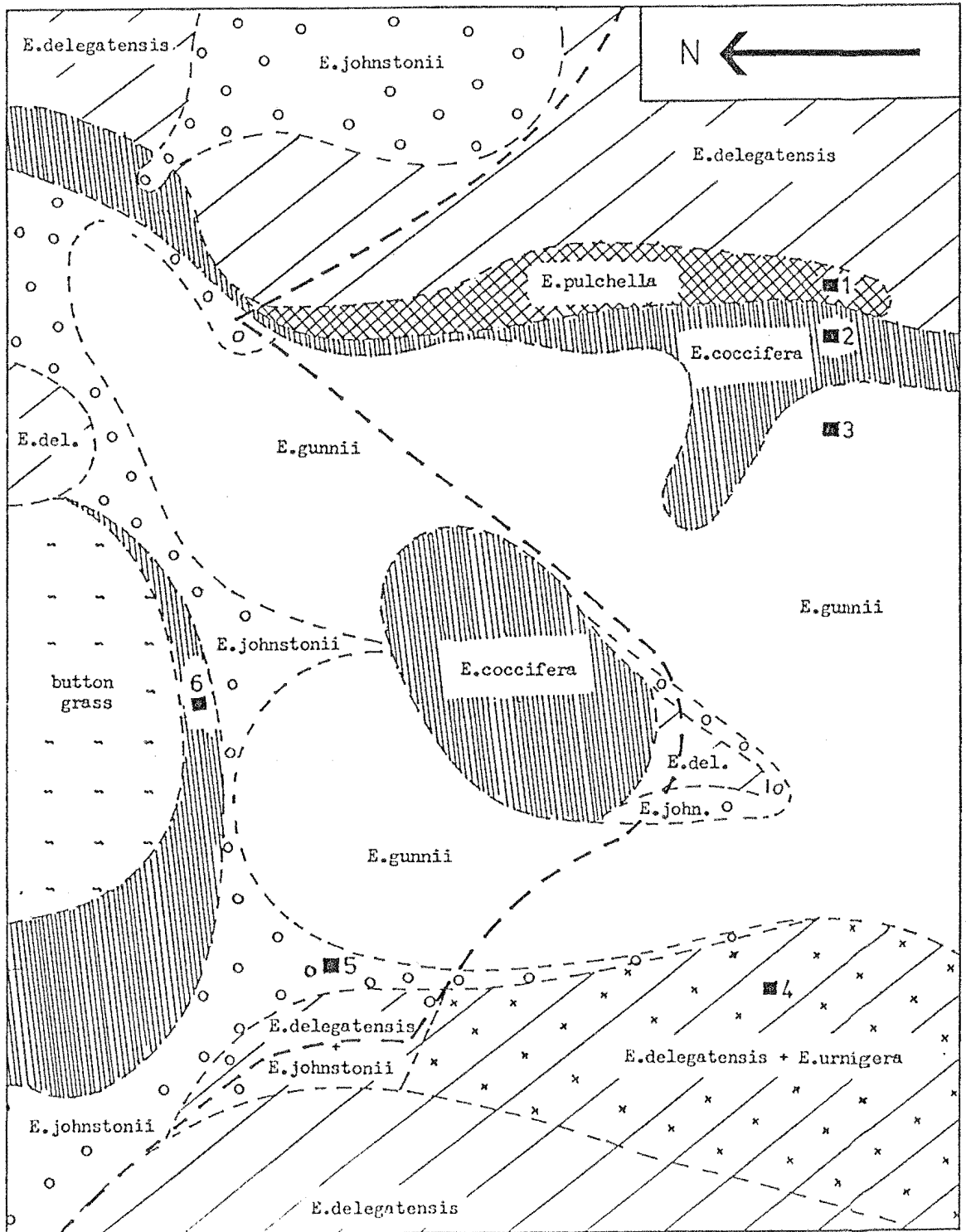
#### INTRODUCTION

The early stages of seed germination and seedling establishment may be critical in eucalypt forest regeneration, particularly if the eucalypt dominants are killed by an event which does not clear the understorey (Jackson 1973; Harwood 1983; Parsons 1968). Eucalypt regeneration is inhibited by competition with established grassland species (Harwood 1976, 1983; Moore & Williams 1976) or under a dense tree or shrub understorey (Gilbert 1959; Withers 1978a). Further, eucalypt seed seldom survives on the forest floor for more than a year (Ashton 1958). Seeds are either harvested by ants (Ashton 1979; Withers 1978a), or seed germination and seedling establishment is prevented by low light intensities, "damping off" by fungi (Ashton 1958; Ashton & Macaulay 1972; Ashton & Turner 1979, Withers 1979), and allelopathic and microbial activity at the soil surface (Ashton & Willis 1982; Florence & Crocker 1962). However, once the forest understorey has been cleared by a disturbance such as fire, eucalypt seedling regeneration proceeds rapidly with the first flush of plant growth in high light intensities, stimulated by abundant nutrients (Renbuss *et al.* 1972; Pryor 1976) and amelioration of the antagonistic conditions at the soil surface (Ashton & Willis 1982; Florence & Crocker 1962). On the other hand, the regenerating seedlings at the forest floor will often be exposed to environmental conditions more extreme than those at the forest canopy: temperature fluctuations, particularly frosts, are more severe near the ground surface (Geiger 1971; Harwood 1983); the surface soils dry out rapidly during rain free periods so seedlings are more at risk from drought, particularly during the summer period (Withers 1978b, 1979; Noble 1982); transpirational losses from the canopy are dramatically reduced because mature trees are often completely defoliated by fire and soils are more prone to saturation and waterlogging during periods of heavy rain, particularly if soils are poorly drained; and the new nutrient rich flush of seedling growth is more prone to browsing by marsupial and insect herbivores (Gilbert 1961; Burdon & Chilvers 1974). Eucalypt forest regeneration starts at the first flush of growth after disturbance and therefore by implication natural selection for the stand dominants also starts at this stage.

Figure 3.1

Map of the eucalypt distributions showing the location of the seedling transplant trials (Gardens 1-6) and approximate position of the geological boundary between the Jurassic dolerite (to the south) and Triassic sandstone (to the north) basement rocks (-----)

Figure 3.1



The current investigation of the factors influencing the distribution of eucalypts at Snug Plains included a study of the seedling stage of forest establishment. Reciprocal seedling transplant trials were conducted in the field at the study area on Snug Plains to assess the relative seedling tolerances to environmental conditions in stands of each of the major eucalypt assemblages. Seed germination and early seedling growth characteristics of the six species E. delegatensis, E. coccifera, E. pulchella, E. gunnii, E. urnigera and E. johnstonii used in the current study had already been investigated by Davidson and Reid (1980) and Davidson (1978) who studied the characteristics of 12 eucalypt species from Snug Plains grown in a variety of native forest soils and potting medium in glasshouse trials. However, comparisons of seedling growth under natural field conditions had not been studied. Previous studies have shown field transplant trials and provenance trials to be useful tools in assessing the suitability of sites for growing eucalypt species or ecotypes both in forestry (Ades & Burgess 1982; Granwald & Karschon 1982; Griffin et al. 1982; Griffin & Eldridge 1980; Rook et al. 1980; FAO 1981; Marion 1979) and ecological research (Ladiges & Ashton 1974; Anderson & Ladiges 1982; Potts 1983; Moore & Williams 1976; Harwood 1983; Ellis 1971).

## MATERIALS AND METHODS

### 1. Experimental Gardens

Six reciprocal transplant trials (experimental gardens; Plates 3.1-3.3) were established in homogenous stands of the six eucalypt species present in the study at Snug Plains. Gardens 1 to 3 were located on the eastern side of the study area (Fig. 3.1) and formed a transect down a west facing hillside from a shallow dolerite ridge to the base of a dish shaped depression. Garden 1 was situated on the well drained soils of a rocky ridge crest in an open dry sclerophyll woodland dominated by E. pulchella. Garden 2 was situated on the lower west facing slopes of the ridge, again on well drained soils in an open E. coccifera woodland. Garden 3 was at the base of the depression on boggy ground dominated by a sparse E. gunnii mallee woodland. Gardens 4 to 6 were arranged along the perimeter of the western side of the depression (Fig. 3.1). Garden 4 was situated on a shallow south-east facing slope in a densely regenerating wet sclerophyll forest dominated by E. delegatensis and E. urnigera. Garden 5 was on an east facing slope in an E. johnstonii stand with a dense understorey on poorly drained ground. Garden 6 was positioned at the top

Plate 3.1-3.3

Reciprocal seedling transplant trials (gardens) established in the field at Snug Plains, demonstrating seedling size 1 year after planting in November 1981.



Plate 3.1

Garden 1 established on a ridge top site naturally dominated by E. pulchella.





Plate 3.2

Garden 3 established in the base of a depression at a site naturally dominated by E. gunnii.



Plate 3.3

Garden 4 established on a ridge slope naturally dominated by a mixed stand of E. delegatensis and E. urnigera. The rain gauge, maximum-minimum thermometers attached to a wooden post and a Stevenson screen containing a thermohygrograph which were used to record weather data are depicted.

of a shallow sandstone rise on well drained soils in a sparse E. coccifera woodland. The gardens were established in approximately 15 m diameter natural clearings in each stand except for garden 4 which was located in an approximately 20 x 40 m man-made clearing. The sites were prepared by cutting and burning in situ all above ground plant material. Seed was collected from 5 trees of each of the six species E. delegatensis, E. coccifera, E. pulchella, E. gunnii, E. urnigera and E. johnstonii in stands adjacent to the experimental gardens (Fig. 3.1). The seed was stratified at 4°C on moist vermiculite for 4 weeks prior to germination. The seedlings were pricked out, at the cotyledonary stage, into 5 cm diameter wooden veneers tubes filled with potting soil. Seedlings were grown in the glasshouse for four months, then placed outside the glasshouse for four weeks before being transplanted into the 6 experimental garden sites. Each garden consisted of 144 seedlings (24 replicates of each species) planted in 4 abutting 6 x 6 latin squares to form a larger 12 x 12 latin square. An edge row was placed around each garden and the garden enclosed by a wire netting fence. Seedlings were spaced at 30 cm intervals and planting was completed by the 28th of October 1981. The garden at site 3 (garden 3a) was severely damaged by two frosts during November and so two additional 6 x 6 latin squares (12 replicates per species) were planted at this site (garden 3b) in late November 1981.

Measurements of stem height, stem diameter (just above the cotyledonary node), number of nodes expanded and number of expanded leaves were made at the time of transplanting (late November 1981) and at approximately six monthly intervals between November 1981 and December 1983 for each garden. In May 1982 a localised grass fire burnt garden 6 and measurements at this site were discontinued. For other gardens, stem diameter records were converted to stem basal area ( $\pi r^2$ ), and records of number of expanded leaves were converted to leaf area. Conversion to leaf area was performed by multiplying the leaf number by the mean area of a leaf for the respective species. The mean area of a leaf was calculated from the mean of 50 leaves, 10 leaves from each of five edge row plants at garden 4. Small intraspecific differences in leaf size did occur between gardens in response to the different environmental conditions. However, the changes in leaf size from garden to garden showed similar trends for all species and it was considered that interspecific comparisons would not be altered by using the same value of leaf mean area for a species in all gardens. Individual one-way analyses of variance were performed on height, stem basal area and leaf area data collected on each of 5 occasions (November 1981, April 1982, November 1982, April 1983 and



December 1983) for the six transplant trials (Gardens 1; 2; 3a [original transplant]; 3b [replant after frost damage]; 4 and 5). Significance levels and the species means  $\pm$  SE max. (maximum species standard error) for the analyses are given in Appendix 3.1. To provide a summary of Appendix 3.1 results for the last measurement (December 1983), means of seedling height, stem basal area (BA) and leaf area (LA) from each garden were expressed as a percentage of the largest seedling in all gardens for that trait (invariably a seedling from garden 4), and a mean growth score then calculated from the percentage scores for the three measures:

$$\text{mean growth score} = \frac{(\% \text{ max. height} + \% \text{ max. BA} + \% \text{ max LA})}{3}$$

for each species in each garden (Fig. 3.3).

Occasionally, environmental constraints such as frost, waterlogging or insect depredation inflicted severe damage on seedlings in one or more gardens. After these events seedling survival was assessed by scoring the remaining live leaf area on each seedling (after Ashton 1958). The amount of surviving leaf lamina was recorded to the nearest  $\frac{1}{4}$  leaf for each seedling and the seedling survival was then calculated as the mean leaf survival score expressed as a percentage:

$$\text{survival} = \frac{(a \times 0 + b \times \frac{1}{4} + c \times \frac{1}{2} + d \times \frac{3}{4} + e \times 1)}{a + b + c + d + e} \times 100\%,$$

where a, b, c, d and e are the number of leaves in each fractional damage class. Survival estimates were made after both spring and winter frosts in all gardens (see Chapter 4), after a period of waterlogging at garden 3b (see Chapter 5) and after insect depredation at gardens 1, 2 and 3.

## 2. Meteorological Records

Beside each experimental garden and within the enclosing fence were set a rain gauge, 3 maximum-minimum thermometers and a thermohygrograph inside a Stevenson screen (Plate 3.3). Details of the placement of the thermometers and thermohygrograph are given in Chapter 4. Regular records of rainfall and temperature were collected during the 2 year trials with intensive measurements made at times of environmental extremes, such as severe spring and water frosts (see Chapter 4) and summer drought (see Chapter 6).

Table 3.1:

The number of surviving seedlings for each eucalypt species at: (a) Garden 3a, a transplanted plot of 144 seedlings completed in October 1981 which was damaged by frosts in mid November 1981; and (b) Garden 3b, a replanted plot of 72 seedlings completed in late November 1981; recorded on five occasions (November 1981, April 1982, November 1982, April 1983 and December 1983).

(a) Garden 3a

| Species                | November 1981 | April 1982 | November 1982 | April 1983 | December 1983 |
|------------------------|---------------|------------|---------------|------------|---------------|
| <u>E. delegatensis</u> | 24            | 0          | 0             | 0          | 0             |
| <u>E. coccifera</u>    | 24            | 12         | 11            | 9          | 4             |
| <u>E. pulchella</u>    | 24            | 9          | 8             | 5          | 1             |
| <u>E. gunnii</u>       | 24            | 23         | 23            | 22         | 22            |
| <u>E. urnigera</u>     | 24            | 5          | 5             | 3          | 2             |
| <u>E. johnstonii</u>   | 24            | 8          | 6             | 6          | 2             |
| Total                  | 144           | 57         | 53            | 45         | 31            |

(b) Garden 3b

| Species                | November 1981 | April 1982 | November 1982 | April 1983 | December 1983 |
|------------------------|---------------|------------|---------------|------------|---------------|
| <u>E. delegatensis</u> | 12            | 8          | 2             | 0          | 0             |
| <u>E. coccifera</u>    | 12            | 12         | 10            | 8          | 5             |
| <u>E. pulchella</u>    | 12            | 11         | 10            | 9          | 5             |
| <u>E. gunnii</u>       | 12            | 11         | 11            | 11         | 11            |
| <u>E. urnigera</u>     | 12            | 9          | 8             | 5          | 5             |
| <u>E. johnstonii</u>   | 12            | 10         | 8             | 7          | 7             |
| Total                  | 72            | 64         | 49            | 40         | 33            |

### 3. Soils

At each experimental garden but outside the enclosing fence, soil pits were dug to bedrock (where possible). The depth of the soil and a description of each soil horizon was made. Soil samples were collected from each soil horizon for the determination of bulk density, pH (in soil paste and 1 M KCl solution, after Hesse 1971), nutrient status (carried out by the Government Analyst Laboratories, Hobart) and to generate pF curves (see Appendices 5.1 and 6.1). Periodically during the progress of the experimental gardens, soil pits were again dug at each garden and the percentage soil moisture obtained for each soil horizon. Using the pF curves an estimate of the soil water potential could be made (for details see Chapters 5 and 6).

## RESULTS

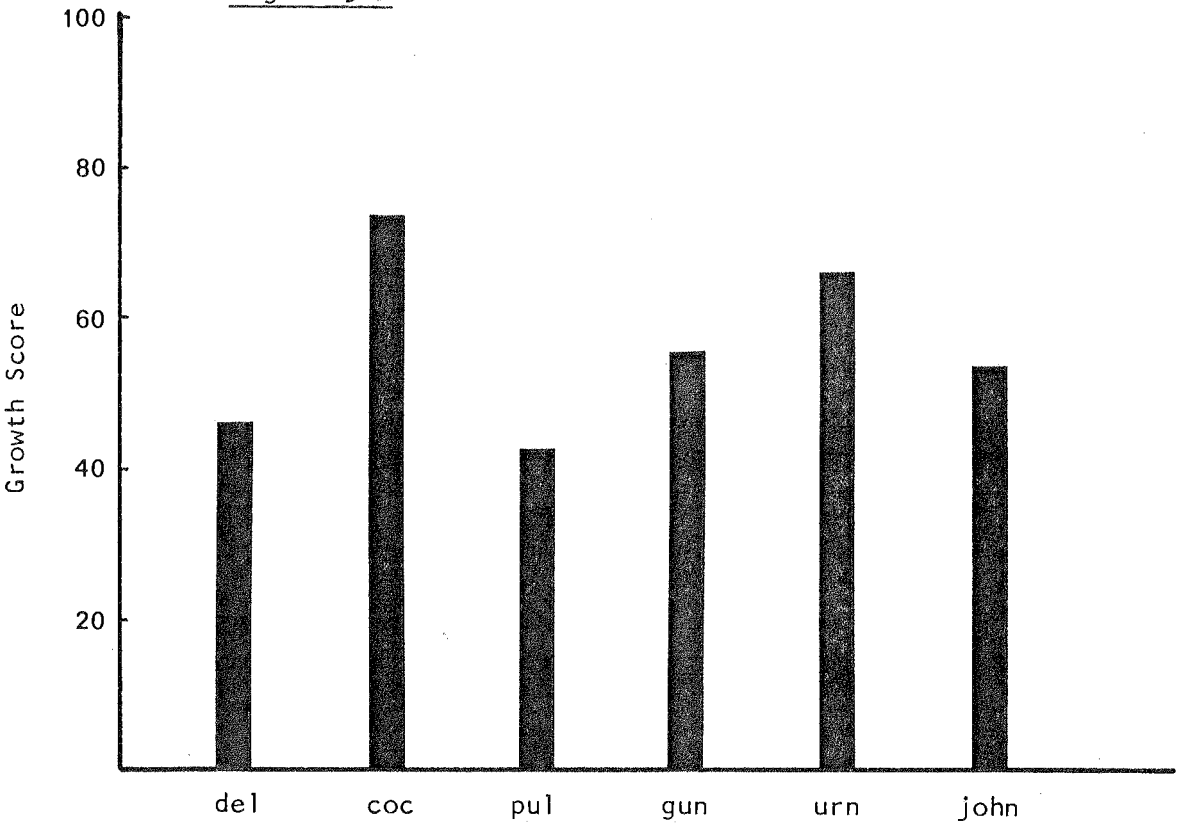
The three measures of seedling growth, stem height, stem basal area, and leaf area produced very similar trends in relative species success in the six gardens (Gardens 1, 2, 3(a), 3(b), 4 and 5; Appendix 3.1). Significant interspecific differences ( $P < 0.05$  to  $P < 0.001$ ) were found at every measurement time for each of the gardens 1, 2, 4 and 5 (except for the November 1982 records of basal area for gardens 1 and 2, and height records for garden 2) and for most measurements at gardens 3(a) and 3(b). The high attrition rate of seedlings at gardens 3(a) and 3(b) (Table 3.1), and the exclusion of dead plants from the analysis meant that some analyses failed to show significant differences (Appendix 3.1) despite species means differing greatly. Significant differences at the time of planting (in November 1981) were generally due to the Symphyomyrtus species E. gunnii, E. urnigera and E. johnstonii being larger than the Monocalyptus species E. delegatensis, E. coccifera and E. pulchella. Davidson and Reid (1980) found comparable early growth differences for members of these two subgenera. However, the November 1981 interspecific differences were not maintained, indicating that the early size advantage of the Symphyomyrtus species was not an important factor in the eventual dominance within the gardens. In later records significant interspecific differences were directly related to conditions at each of the gardens (Fig. 3.2).

Marked interspecific differences in seedling size were evident at all gardens by the end of records in December 1983. There was a strong tendency for seedlings of each species to become dominant, or at least show greatest

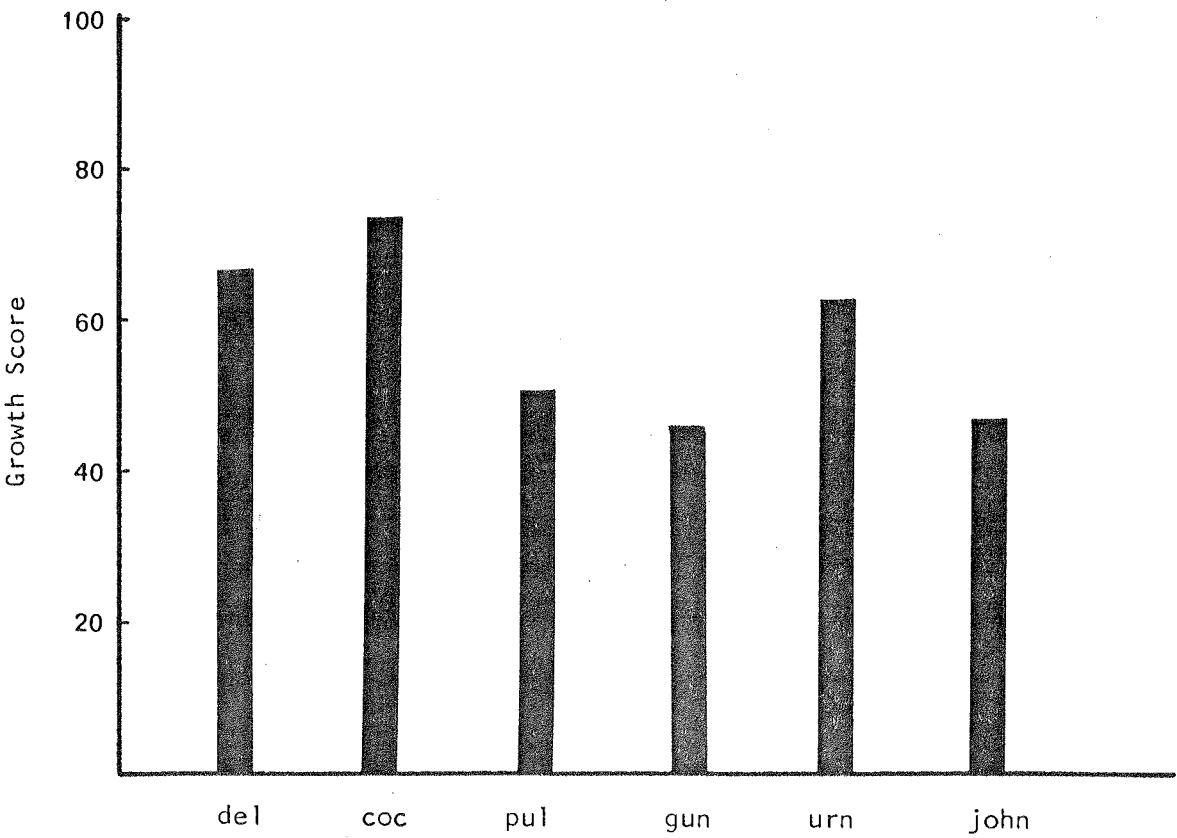
Figure 3.2

Mean seedling growth score [derived from the sum of percentage maximum growth in: height (H); basal area (BA); and leaf area (LA)  $(\frac{H + BA + LA}{3})$ ] from December 1983 records at gardens 1, 2, 3a, 3b, 4 and 5 for the six species: E. delegatensis (del), E. coccifera (coc), E. pulchella (pul), E. gunnii (gun), E. urnigera (urn) and E. johnstonii (john).

Figure 3.2



GARDEN 1



GARDEN 2

Figure 3.2 (cont'd)

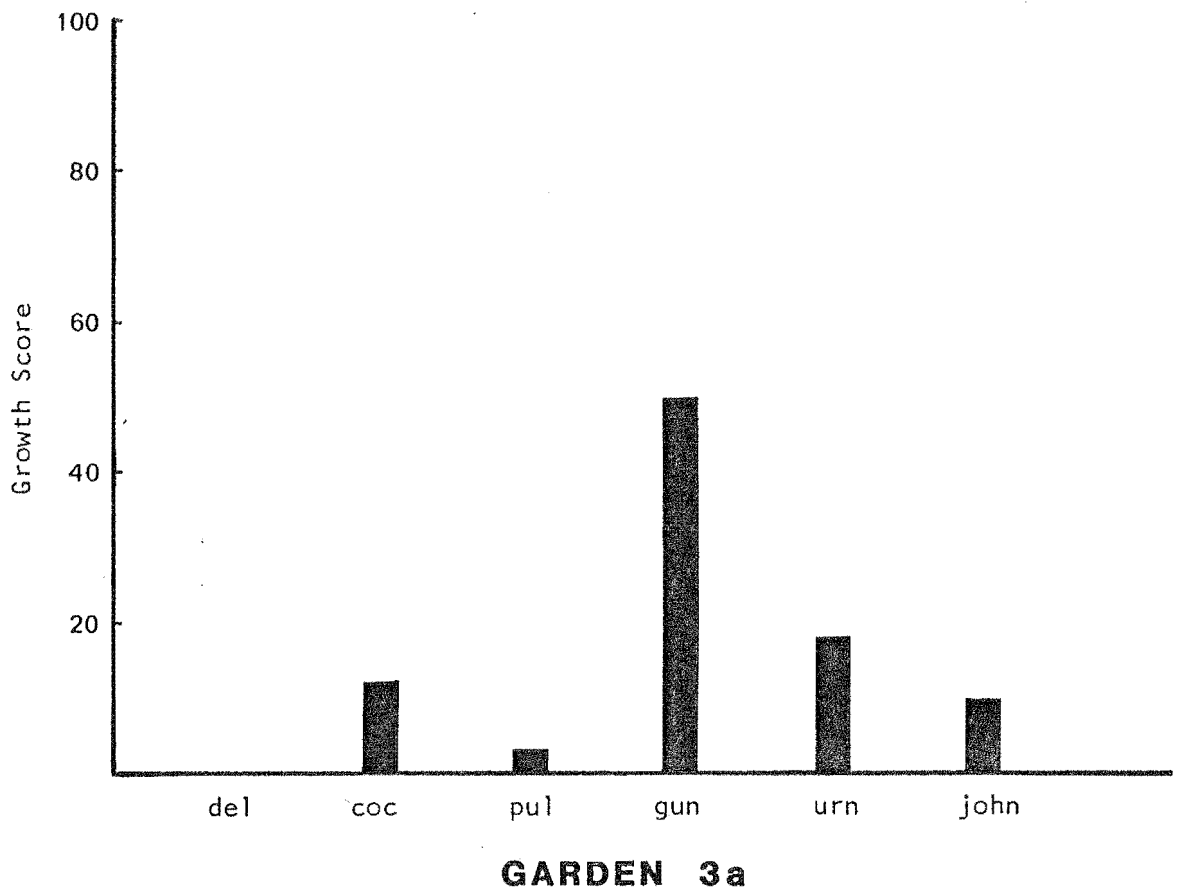
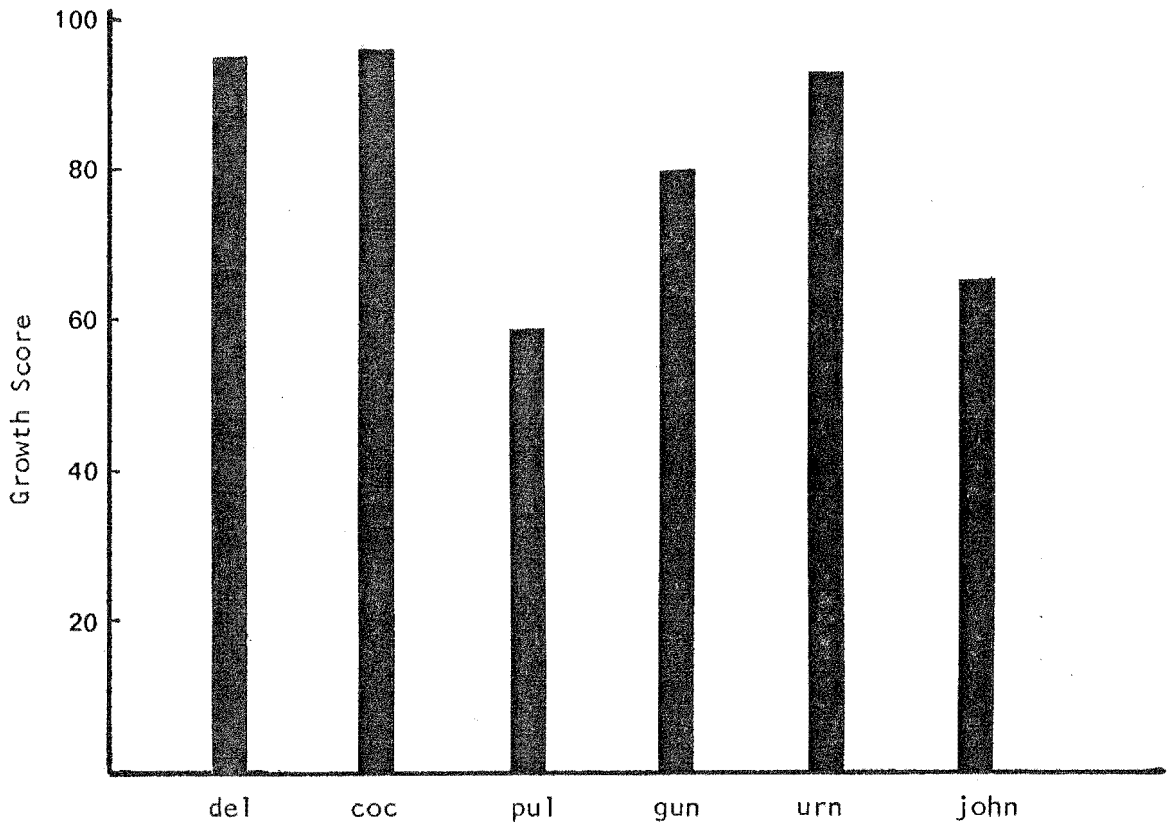
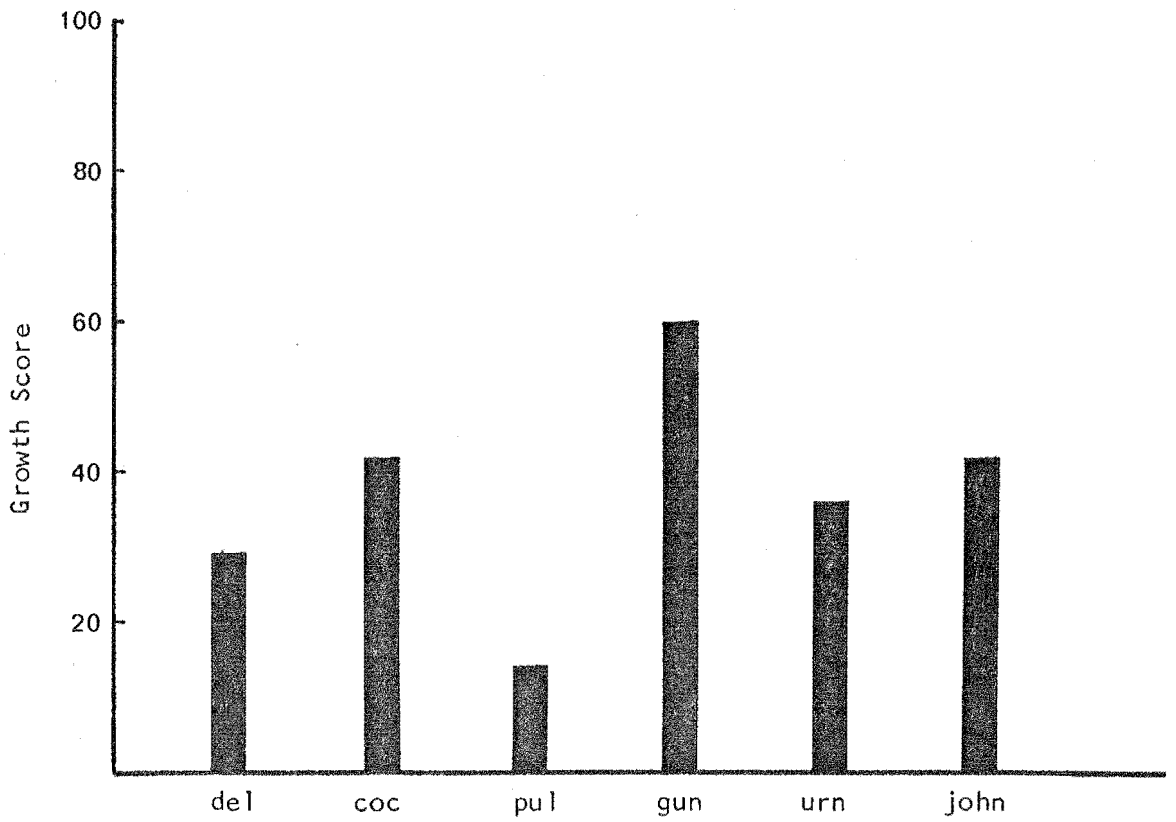


Figure 3.2 (cont'd)



**GARDEN 4**



**GARDEN 5**

growth on a relative basis in the garden of their site of origin (from separate height, stem basal area and leaf area records, Appendix 3.1, and from mean growth score, Fig. 3.2). The notable exception to this trend was E. pulchella at garden 1. At each of the gardens 1, 2 and 4 E. coccifera was dominant, but as site characteristics improved (in the order, garden 1, 2 and 4) E. delegatensis and E. urnigera came closer to arresting dominance from E. coccifera. E. coccifera was naturally dominant at garden 2 and showed dominance at garden 2. E. delegatensis and E. urnigera were dominant in the stand at garden 4 and showed relatively their greatest growth at garden 4. Factors other than those experienced during the growth span of the gardens (e.g. drought, Chapter 6) must be involved in the dominance of E. pulchella at the garden 1 site. At the last record (December 1983) the number of surviving seedlings at gardens 3a and 3b were 31 (22 of which were E. gunnii) and 33 (11 of which were E. gunnii) respectively in gardens which originally contained 144 and 72 seedlings respectively (Table 3.1). E. gunnii clearly showed superiority in stature and in number of surviving seedlings at its site of origin. In garden 5, although E. gunnii was again dominant, E. johnstonii exhibited its greatest growth, on a relative basis. Significantly, E. coccifera, which is naturally dominant on the neighbouring better drained sandstone derived soils at garden 6, showed seedling growths comparable with those of E. johnstonii at garden 5.

Measurements of soil nutrient status (Table 3.2), bulk density, pH, soil depth and development of the A soil horizon (Table 3.3) and studies of soil moisture status at gardens 1-6 carried out in the field during the 1982 and 1983 seasons (Chapters 5 and 6) showed marked differences existed between the soils at the various gardens. The nutrient status, pH and bulk density of the soils appeared not to be primary factors determining seedling growth at the 6 gardens (Fig. 3.3, Table 3.2, Appendix 3.1), whereas factors such as soil water status, soil depth and extent of development of the A horizon did broadly correspond with seedling growth at the gardens. The nutrient status, bulk density and pH of the dolerite derived soils at gardens 1 to 4 varied only subtly between gardens but differed markedly from the sandstone derived soils at gardens 5 and 6 (Tables 3.2 and 3.3). The nutrient status of the soils at Snug Plains were comparable with other eucalypt dominated east Australian soils (tabulated in Westman & Rogers 1977). The dolerite derived soils had substantially higher levels of "total phosphorus", magnesium, calcium and iron; approximately the same levels of "total nitrogen"; and less than half the amount of potassium found in the sandstone derived soils. Total phosphorus showed greatest variation between gardens, with levels at gardens 3 and 4 being almost



Table 3.2:

The nutrient status of the major soil horizons of soil profiles dug beside gardens 1-6 at Snug Plains. The elemental analyses were performed by the Government Analyst Laboratories, Hobart. (ND is not detectable).

| Garden | Dominant Eucalypt Species                      | Soil Horizon   | Total Nitrogen % | Available Phosphorus ppm | Total Phosphorus ppm | Potassium ppm | Magnesium ppm | Calcium ppm | Iron % | Sulphur % |
|--------|--|----------------|------------------|--------------------------|----------------------|---------------|---------------|-------------|--------|-----------|
| 1      | <u>E. pulchella</u>                            | B <sub>1</sub> | 0.15             | ND                       | 134                  | 63            | 212           | 825         | 3.26   | 0.46      |
| 2      | <u>E. coccifera</u>                            | B <sub>1</sub> | 0.09             | ND                       | 108                  | 63            | 500           | 725         | 2.96   | 0.86      |
| 3      | <u>E. gunnii</u>                               | A              | 0.98             | < 3                      | 227                  | 138           | 186           | 1925        | 5.87   | 1.00      |
|        |  | B <sub>1</sub> | 0.06             | ND                       | 90                   | 75            | 347           | 825         | 3.18   | 0.78      |
| 4      | <u>E. delegatensis</u><br>& <u>E. urnigera</u> | B <sub>1</sub> | 0.07             | ND                       | 212                  | 50            | 429           | 1025        | 5.25   | 1.30      |
| 5      | <u>E. johnstonii</u>                           | A              | 0.09             | ND                       | 19                   | 375           | 36            | 325         | 0.17   | 0.71      |
|        |  | B <sub>1</sub> | 0.03             | ND                       | 47                   | 275           | 31            | 400         | 0.47   | 0.07      |
| 6      | <u>E. coccifera</u>                            | A              | 0.05             | ND                       | 34                   | 350           | 61            | 325         | 0.22   | 0.04      |
|        |  | B <sub>1</sub> | 0.08             | ND                       | 28                   | 188           | 23            | 200         | 0.11   | 0.05      |

Available phosphorus was determined by acidified ammonium sulphate (Truvy) extract.

Table 3.3:

A description of the soil physical properties (soil colour and texture, soil depth and bulk density) and the pH (in soil paste and in 1 M KCl solution) of each soil horizon for soil profiles dug beside gardens 1-6 at Snug Plains.

| Garden | Dominant Species    | Basement Rock     | Soil Horizons  | Soil Colour and Texture               | Soil depth (cm) | Bulk density | pH         |         |
|--------|---------------------|-------------------|----------------|---------------------------------------|-----------------|--------------|------------|---------|
|        |                     |                   |                |                                       |                 |              | Soil Paste | 1 M KCl |
| 1      | <u>E. pulchella</u> | Jurassic Dolerite | A              | Dark brown humus                      | 0-0.5           | 0.87         | 5.5        | 4.9     |
|        |                     |                   | B <sub>1</sub> | Red-brown clay loam                   | 0.5-39          | 0.99         | 5.4        | 4.9     |
|        |                     |                   | C              | Massive unjointed bedrock             | 39              |              |            |         |
| 2      | <u>E. coccifera</u> | Jurassic Dolerite | A              | Dark brown-black humus                | 0-2             | 0.75         | 5.0        | 4.6     |
|        |                     |                   | B <sub>1</sub> | Red-brown clay loam                   | 2-38            | 1.10         | 5.4        | 4.8     |
|        |                     |                   | B <sub>2</sub> | Dense yellow-brown clay               | 38-58           | 1.47         | 5.3        | 4.7     |
|        |                     |                   | C              | Gravel over massive unjointed bedrock | 58              |              |            |         |
| 3      | <u>E. gunnii</u>    | Jurassic Dolerite | A              | Black peat                            | 0-30            | 0.31         | 4.5        | 3.8     |
|        |                     |                   | B <sub>1</sub> | Grey clay                             | 30-61           | 1.20         | 5.9        | 5.4     |
|        |                     |                   | B <sub>2</sub> | Dense brown clay                      | 61-190          | 1.41         | 5.8        | 5.4     |
|        |                     |                   | C              | Gravel and weathered bedrock          | 190+            |              |            |         |

Table 3.3 (cont'd)

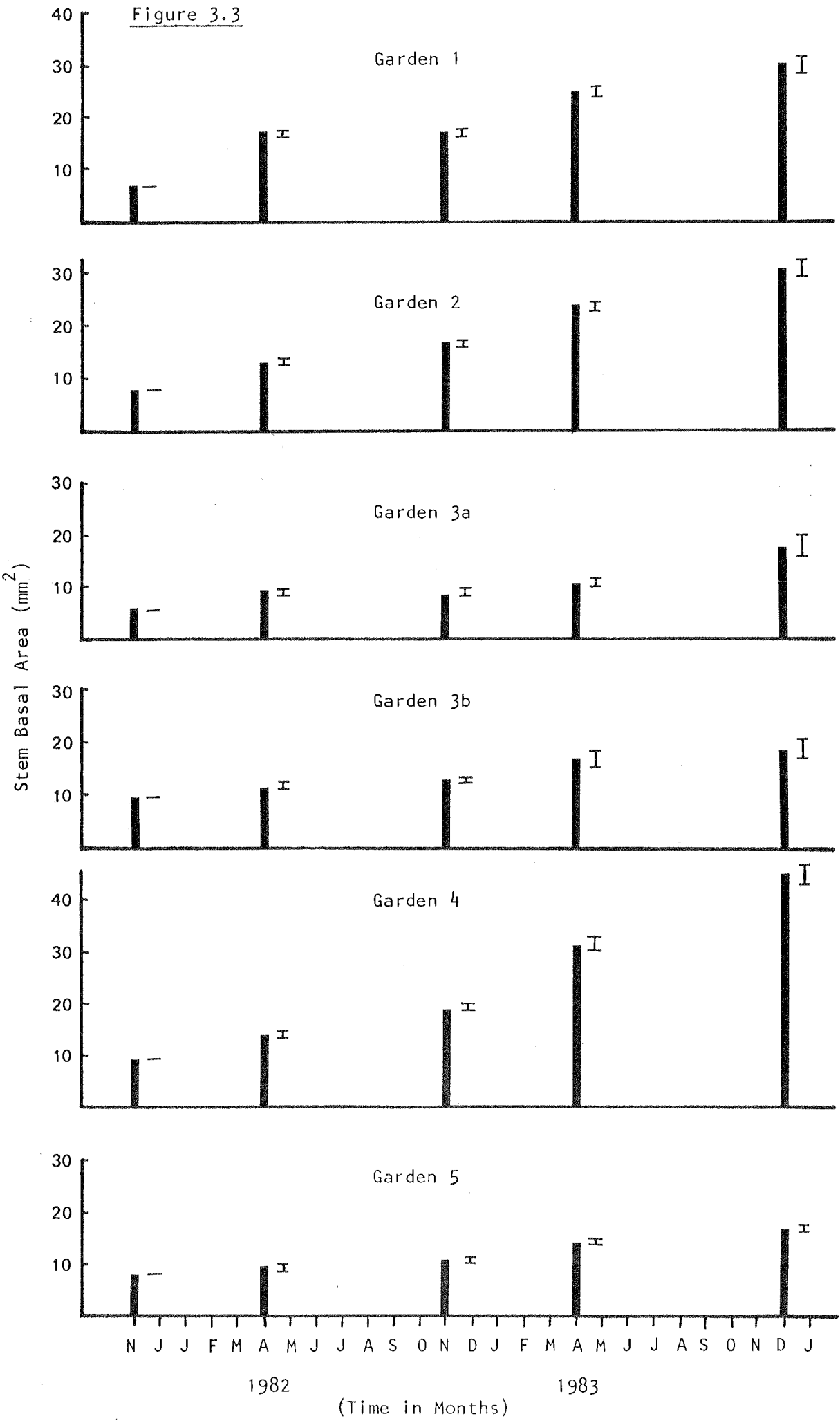
| Garden | Dominant Species                                    | Basement Rock      | Soil Horizons  | Soil Colour and Texture                               | Soil Depth (cm) | Bulk Density | pH         |         |
|--------|---|--------------------|----------------|---|-----------------|--------------|------------|---------|
|        |   |                    |                |   |                 |              | Soil Paste | 1 M KCl |
| 4      | <u>E. delegatensis</u><br>and<br><u>E. urnigera</u> | Jurassic Dolerite  | A              | Dark brown-black humus                                | 0-8             | 0.70         | 4.7        | 4.2     |
|        |   |                    | B <sub>1</sub> | Brown clay loam                                       | 8-80            | 1.15         | 4.9        | 4.4     |
|        |   |                    | B <sub>2</sub> | Dense yellow-brown clay                               | 80-120          | 1.33         | 5.0        | 4.5     |
|        |   |                    | C              | Large floating boulders, gravel and weathered bedrock | 120+            |              |            |         |
| 5      | <u>E. johnstonii</u>                                | Triassic Sandstone | A              | Black peat  | 0-20            | 0.24         | 3.6        | 3.2     |
|        |   |                    | B <sub>1</sub> | Grey sand   | 20-60           | 1.54         | 3.9        | 3.4     |
|        |   |                    | B <sub>2</sub> | Brown sandy clay                                      | 60-90           | 1.73         | 4.1        | 3.6     |
|        |   |                    | C              | Large floating boulders, gravel and weathered bedrock | 90+             |              |            |         |
| 6      | <u>E. coccifera</u>                                 | Triassic Sandstone | A              | Black humus rich sand                                 | 0-10            | 0.62         | 3.8        | 3.3     |
|        |   |                    | B <sub>1</sub> | Black sand  | 10-35           | 1.63         | 3.8        | 3.1     |
|        |   |                    | B <sub>2</sub> | Yellow sand   | 35-65           | 1.70         | 4.4        | 4.0     |
|        |   |                    | C              | Gravel, boulders and jointed weathered bedrock        | 65+             |              |            |         |

double those at gardens 1 and 2 but 4 to 8 times higher than at gardens 5 and 6. A shallow gradient of increasing soil bulk density (of the B horizon) and decreasing pH (of the upper horizons) also occurred on dolerite derived soils, in the order, gardens 1, 2, 4 and 3 respectively (Table 3.3). In comparison, the sandstone derived soils at gardens 5 and 6 exhibited substantially lower bulk densities and pH's than other gardens. However, seedling growth at gardens 3 and 5 showed considerable similarities (both gardens growing very slowly), both in mean seedling growth for the garden (Fig. 3.3) and in the relative species success at the garden (Fig. 3.2), but differ greatly in the aforementioned soil characteristics. Further, garden 4 which displayed great similarities to garden 3 in soil nutrient status, bulk density, and only slight differences in pH, proved very favourable for seedling growth (Figs 3.2 and 3.3). In comparison, studies of soil moisture status [at gardens 1, 2 and 3 (Chapter 6) and gardens 4, 5, and 6 (Chapter 5)], soil depth (Table 3.3) and extent of development of the A soil horizon (Table 3.3) show that gradients in these factors correspond well with seedling growth and success at the various experimental gardens (Figs 3.2 and 3.3). Soils at gardens 3 and 5 were deep and waterlogged for extended periods even in years of below average rainfall (years 1982 and 1983, Chapter 6) and much of the free water resided in the peat A horizon of the soil. Garden 4 soils were deep and moist, probably seldom prone to waterlogging, and very favourable for seedling growth (Figs 3.2 and 3.3). Soils at gardens 1 and 2 were shallow with little development of an A soil horizon. Garden 1 soils were extremely shallow, only about 30 cm deep with a low moisture holding capacity (Chapter 6). Evidence from observations of surrounding natural stands indicated that once a substantial plant biomass was drawing upon the water reserves of the soil, droughts occurred during rain free periods (Chapter 6). Apparently the biomass of garden 1 itself was not large enough to induce drought at the garden during these trials. Garden 2 soils were deeper but also prone to drying in the summer (Chapter 6).

During the growth of the gardens four ecological factors had a major and catastrophic influence on garden growth. These were fire, frost, waterlogging and insect depredation. A localised fire destroyed garden 6 (May 1982) and records were discontinued. Two frosting events had a major impact on the gardens. A spring frost in mid November 1981 inflicted severe damage on seedlings at garden 3a, considerable damage at gardens 2 and 5 and lesser damage at other gardens. A severe winter frost in June 1982 also caused substantial damage to the gardens (for details see Chapter 4). After the spring frosts in November 1981 the plot of replanted seedlings in garden 3b experienced an extended frost free period but displayed advanced symptoms of

Figure 3.3

Mean seedling stem basal area (in  $\text{mm}^2 \pm \text{SE}$ ) for gardens 1, 2, 3a (initial transplant trial), 3b (replant after frost damage), 4 and 5 at the five times of measurement (November 1981, April 1982, November 1983, April 1983 and December 1983).



waterlogging damage due to the continuously high water table at garden 3 (for details see Chapter 5). Frost and waterlogging had a major influence on seedling survival and dominance patterns within the gardens. Severe spring frosts at garden 3a and severe winter frosts combined with waterlogged conditions at gardens 3a and 3b caused widespread seedling deaths (Table 3.1) and complete elimination of *E. delegatensis*. Under these conditions the growth of *E. gunnii* was favoured over other species. Frost and waterlogging were also implicated in the slow growth rates of seedlings at garden 5. The improved relative performance of *E. johnstonii* at garden 5 may in part be attributable to low nutrient status and low pH at this site. However, evidence from comparisons between gardens 3b and 3a clearly showed that the absence of spring frosts improved the relative performance of *E. johnstonii* and *E. urnigera* (Fig. 3.2, Table 3.1). The fourth catastrophic event was localised to gardens 1, 2 and 3. An infestation of phytophagous insects, family Chrysomelidae (genus and species not identified), attacked the seedlings at gardens 1, 2 and 3, preferentially defoliating seedlings from subgenus *Symphyomyrtus* (Fig. 3.4). Significant differences in insect depredation ( $P < 0.001$ ) occurred in all three gardens. Grazing intensity was greatest in the lower ridge slopes and in the depression at gardens 2 and 3, and less intense at a distance from the depression at garden 1. There was no damage to *Monocalyptus* seedlings at garden 1 and slight damage to *E. pulchella* only at gardens 2 and 3. In comparison, the *Symphyomyrtus* species lost between 10 and 76% of their leaf area (Fig. 3.4). The worst affected species was *E. gunnii*. Insect depredation, although largely directed at the *Symphyomyrtus* species, did not prevent the *Symphyomyrtus* species from retaining dominance at garden 3 and did not greatly alter the relative success of species at other gardens, except in garden 2 where selective insect grazing may have been an important factor resulting in the eventual dominance of *E. coccifera*. *E. pulchella* exhibited the slowest growth rate of all species in gardens 1 and 4, and probably only shows improved performance in garden 2 because severe insect infestation in May 1982 drastically reduced the leaf area of the *Symphyomyrtus* species.

## DISCUSSION

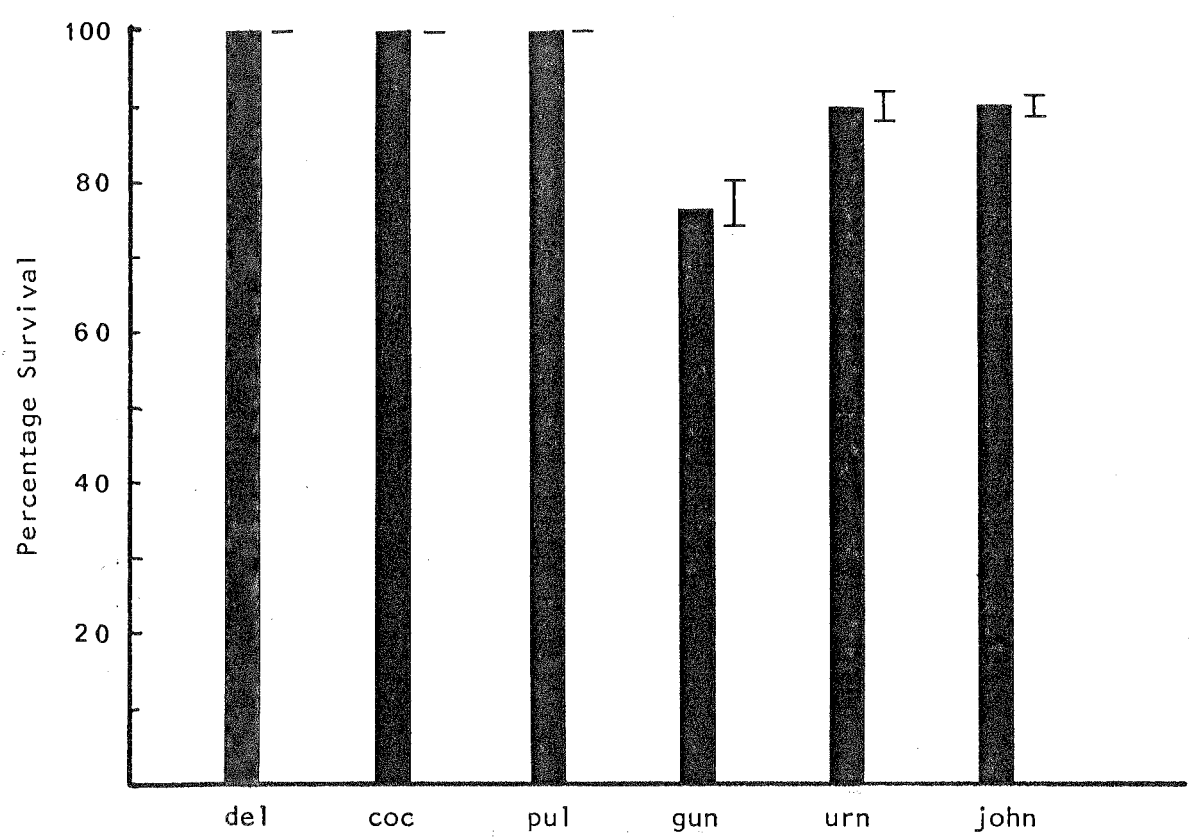
Studies of leaf damage inflicted on seedlings at gardens 1-6 (detailed in Chapters 4 and 5) demonstrated that significant interspecific differences in tolerance to frost and waterlogging existed. Further subgeneric trends were identified which suggested the *Symphyomyrtus* species were more tolerant of frosts in waterlogged soils than the *Monocalyptus* species. This was supported

Figure 3.4

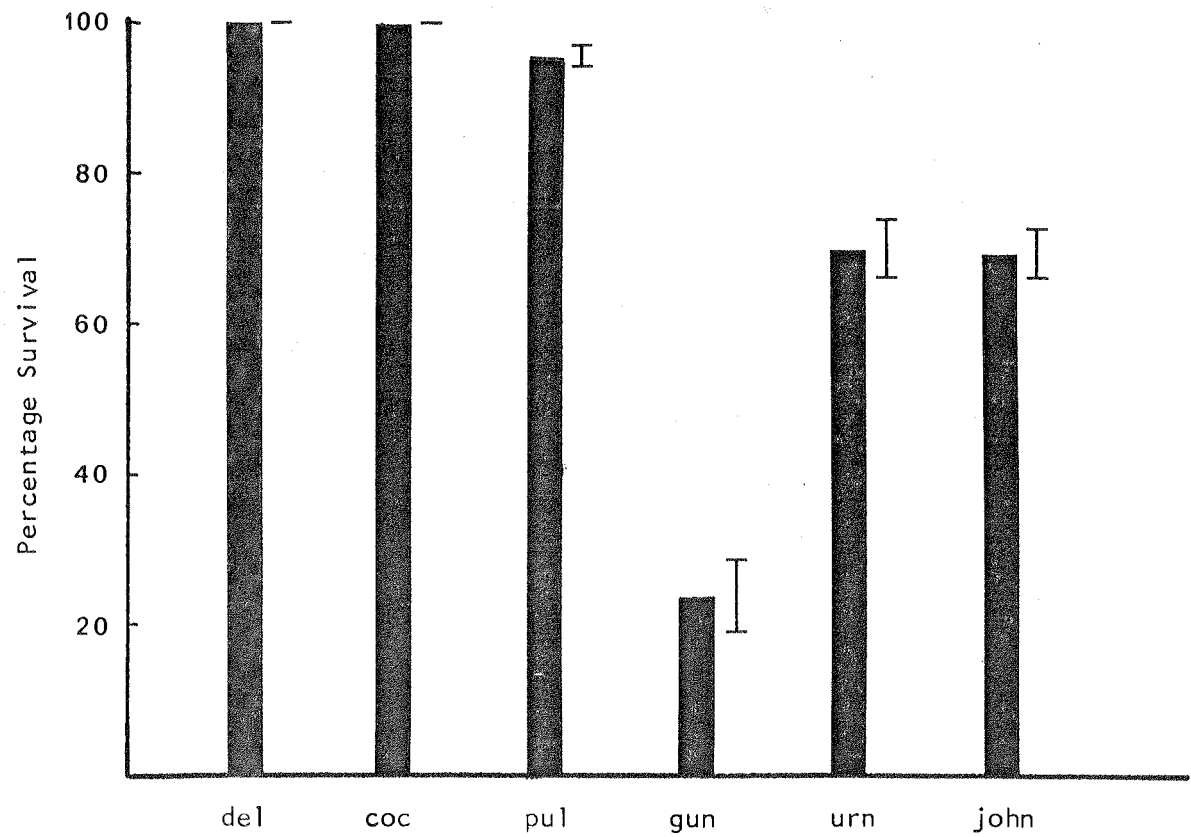
Mean percentage surviving leaf area ( $\pm$  SE) for seedlings of the six eucalypt species: E. delegatensis (del); E. coccifera (coc); E. pulchella (pul); E. gunnii (gun); E. urnigera (urn); and E. johnstonii (john) in each of the gardens 1-3 after grazing by phytophagous insects which occurred in the 2 weeks prior to the 22nd of April 1982.



Figure 3.4

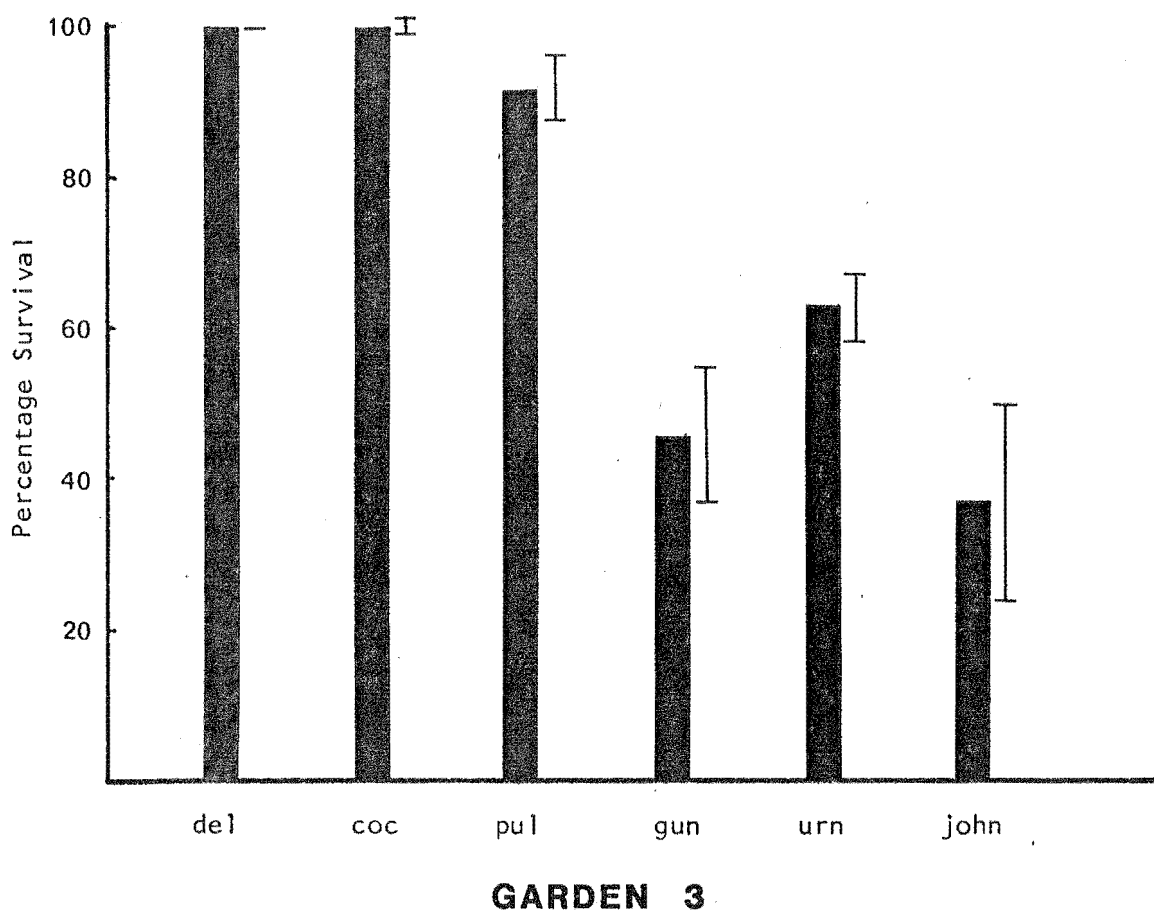


GARDEN 1



GARDEN 2

Figure 3.4 (cont'd)



by studies of seedling growth at the gardens. Generally, seedling growth and relative species success in each of the gardens was determined by site water relations and severity of frost while chemical properties of the soil and biotic influences played a minor role, despite the fact that major differences in soil nutrition occurred at geological boundaries. The dolerite derived soils exhibited much higher nutritional states (particularly phosphorus) than the sandstone derived soils. The importance of soil nutrition (particularly levels of phosphorus) in controlling forest patterns in eastern Australia have been emphasised by Australian ecologists (Beadle 1954, 1962; Webb 1968, 1969; Westman & Rogers 1977; Attiwill *et al.* 1978; Ashton 1978). Beadle (1954, 1962) proposed that within rainfall zones the major vegetational formations were delimited by soil fertility, although fire may have an important deflecting influence (Gilbert 1958; Jackson 1968a). However, many studies of Eucalyptus which have included investigation of soil nutrient status and its influence on eucalypt distributions (for example Parsons 1969; Florence 1964, 1968; Specht & Perry 1948; Martin & Specht 1962) show nutrition to be of minor importance in producing the abrupt changes to eucalypt dominance characteristic of south-eastern Australia (Pryor 1953). The tendency has been to emphasise the importance of physical properties of the soil as they relate to moisture holding capacity. A few studies have shown eucalypt distributions to be limited by high ionic concentrations of some soil elements. For example studies by Anderson and Ladiges (1982), Ladiges and Ashton (1977) showed that the distribution of eucalypt species ecotypes were limited to, or confined by, high levels of calcium (calcium carbonate) in the soil, and associated high pH. In other studies which suggested soil based properties were influencing eucalypt distributions (Ellis 1971; Jackson 1965; Ridley 1962; Florence 1982), or where deficiencies in phosphorus and calcium have been correlated with species dominance changes (McColl 1969; McColl & Humphries 1967; Moore 1959a, 1959b, 1961), it was not possible to determine the relative importance of soil nutrition and soil physical properties in delimiting the species addressed. In the current study the marked differences in nutrition and pH which existed between the dolerite derived soils (gardens 1-4) and sandstone derived soils (garden 5) were not matched by marked differences in seedling growth in the gardens. Poor soil nutrition and low pH may have influenced the patterns of seedling growth at garden 5 (with low pH and poor nutrition) which favoured E. johnstonii, but the effects of anoxia, low pH and low availability of chemical species caused by periods of waterlogging (Drew 1983) could not be separated from the inherent low nutrition at garden 5 as influences on seedling growth. However, similarities between the growth of gardens 3 and 5 would tend to suggest that waterlogging was the major influence. Also, glasshouse trials

conducted in low and high nutrient soils under waterlogged conditions (Chapter 5) showed no significant interspecific differences in growth for the three species E. gunnii, E. urnigera and E. johnstonii. However, these experiments do not rule out the possibility that ion antagonism and low pH may differentially effect the growth of these three species. For gardens other than garden 5 differences in soil nutrition were minor and appeared not to be involved in producing the major differences in seedling growth evident in these gardens.

In marked contrast to soil nutrition, soil water relations have been shown to directly effect eucalypt dominance on many occasions. Ecological surveys by Tracey (1969), Costin (1954), Lamb and Florence (1973), Specht and Perry (1948) and Jackson (1965, 1973) have highlighted the importance of soil water relations. These conclusions were supported both by comparative studies of waterlogging tolerance involving eucalypt seedlings (Sena-Gomes & Kozlowski 1980; Ladiges & Kelso 1977; Blake & Reid 1981; Clemens et al. 1978; Clemens & Pearson 1977) and field studies conducted during natural droughts (Sinclair 1980; Pook et al. 1966; Myers & Neales 1984) which indicated that site water relations had a major effect on eucalypt dominance patterns. In the present study gardens were situated in sites which spanned the full range of water relations characteristics: from garden 1, established within a stand which exhibited symptoms of drought stress during rain free periods in late summer (Chapter 6); to garden 3, which was subject to extended periods of waterlogging. Each garden site was naturally dominated by a different eucalypt species (or pair of species) and in each garden (except gardens 1 and 5) there was a strong tendency for the naturally dominant species to prevail, which suggests species may be occupying positions along a water relations gradient. Further, in garden 1, where the naturally dominant species E. pulchella showed slowest growth in the seedling trials, slow growth may well be an adaptive advantage in the shallow drought prone soils which were a characteristic of this site (see Chapter 6). In glasshouse pot trials involving the above species grown reciprocally in native soils collected from each stand in the field and exposed to waterlogged and dry treatments (Davidson 1978) seedlings also tended to show relatively greatest growth in the treatment most closely resembling the soil and water relations of their site of origin. The evidence from both gardens and glasshouse trials suggests that site water relations has a major influence on eucalypt seedling establishment at the Snug Plains study site.

The damage caused to seedlings in the low lying gardens (Gardens 2, 3 and 5) during spring and winter frosts clearly indicates frost is another major environmental constraint influencing seedling establishment at the study site on Snug Plains. In country of similar physiognomy, at Seventeen Flat in the Snowy Mountains of New South Wales, Moore and Williams (1976) and Harwood (1983) independently showed that eucalypt seedling establishment in the treeless plains at the valley bottoms was prevented by intense radiation frosts combined with competition from rapidly growing sedges and grasses.

Biotic factors such as phytophagous insect depredation may have a major impact on the productivity of eucalypt stands (Morrow 1977; Morrow & Fox 1980). Estimates made on 44 eucalypt species from a variety of habitats suggested that, on average, 15% of expanded leaf tissue was consumed by phytophagous insects (Fox & Morrow 1983). Further it has been suggested that selective insect grazing may contribute to niche differentiation in mixed eucalypt stands (Burdon & Chilvers 1974). In the current study selective insect grazing caused a major reduction in the leaf area of Symphyomyrtus species and particularly E. gunnii at gardens 2 and 3 on the single occasion when it occurred. Repeated and intense grazing could, therefore, dramatically alter the relative seedling growth rates. This could be particularly important in mixed stands as suggested by Burton and Chilvers (1974) and Morrow (1974). At Snug Plains selective grazing could be an important factor limiting the range of E. gunnii and selecting for E. urnigera or E. johnstonii in mixed stands of these species. Further the dynamic balance in the mixed stands containing Monocalyptus and Symphyomyrtus species might be determined by the relative frequencies of insect attack which would favour the Monocalyptus species and periods of waterlogging and frost which would favour the Symphyomyrtus species.

Aspect and exposure have been suggested as important ecological factors particularly in subalpine Tasmania and the Snowy Mountains of New South Wales (Jackson 1973; Costin 1954) and also in lowland habitats (Jackson 1965, 1968a; Pooke & Moore 1966). Subalpine and alpine Tasmania intercepts a strong predominantly westerly air stream which brings snow and glazing storms from the south-westerly quarter in winter (Jackson 1973) and hot dry winds from the north-westerly quarter in summer (Jackson 1968b) which will desiccate foliage and fan the flames of wildfires. The dense wet sclerophyll forest near garden 4 on the south eastern facing slopes of a high ridge would probably represents the most fire protected region of the study area. Microclimatic studies conducted during winter (see Chapter 4) also indicated that garden 4 was least subject to

extremes of temperature. The most exposed sites were those at garden 6 and garden 1 which were on ridge tops. However, fire frequency was probably greatest in the open woodlands which had sedge (mainly Gymnoschoenus sphaerocephalus) and heath understories and abutted gardens 6 and 3, as indicated by the fire that burnt garden 6 in May 1982 and also reached the boundaries of garden 3 but caused no damage to the seedlings.

In the early stages of forest establishment it appears catastrophic events such as frost, insect attack on waterlogging have a major influence on species dominance in seedling regrowth at sites prone to these "natural extremes in comparison with soil based characters (e.g. gardens 2, 3 and 5). However at gardens 1 and 4 where environmental conditions were more favourable interspecific differences in seedling growth were the prime determinant of species dominance.

Marked differences in seedling growth and relative success occurred within and between the gardens. In all but one of the seedling transplant trials the species naturally dominant at the site also became dominant or showed greatest growth on a relative basis in the garden of their site of origin. This strongly suggests that at least some of the selective forces naturally operating to produce the dominance patterns in the eucalypt stands at Snug Plains were also involved at the seedling stage in forest establishment. This conclusion is supported by results obtained from other field transplant trials (Ashton & Ladiges 1974; Anderson & Ladiges 1982; Potts 1983) which have been successfully used to identify the main ecological factors involved in the natural selection for a particular ecotype in a clinally varying or highly variable eucalypt species. The seedling transplant trials suggest the main ecological factors influencing seedling establishment were frost intensity and soil water relations and on this basis, and with support from observations of natural stands, subsequent studies were directed to these areas. The following chapters independently study the influence of frost, waterlogging and drought on the eucalypt stands at the study site on Snug Plains and assess the importance of these factors at the seedling, pole stand and mature forest stages of stand ontogeny.

## CHAPTER FOUR

### FROST

#### INTRODUCTION

Temperature minima recorded at the treeline in Australia are comparatively mild by Northern Hemisphere standards. Only in the Snowy Mountains of eastern Australia and the Central Highlands of Tasmania do temperatures below  $-12^{\circ}\text{C}$  occur with any degree of regularity (Hall 1972). The lowest temperature experienced in Australia was  $-22.2^{\circ}\text{C}$ , recorded at Charlotts Pass in the Snowy Mountains (Hall 1972). Therefore, much information on the interspecific differences in frost hardiness of eucalypt species in the field comes from records of the frost resistance of exotically planted trees in the British Isles and the USSR. Martin (1948) reported that during the severe frosts of the 1946-47 winter in the British Isles, Australian treeline species such as E. pauciflora spp niphophila, E. gunnii and E. vernicosa survived  $-18^{\circ}\text{C}$  whereas lowland species only survived temperatures of  $-7$  to  $-9^{\circ}\text{C}$ . Linnard (1969) described the catastrophic frosts of 1949-1950 in the USSR where vast areas of E. viminalis plantations near the Black Sea were killed by frosts of  $-11.5^{\circ}\text{C}$ . These observations are supported by field studies (Moore & Williams 1975; Harwood 1976, 1983) and frost chamber trials (Harwood 1980, 1981; Paton 1981; Sakai et al. 1981) which suggest that at temperatures between  $-16^{\circ}\text{C}$  and  $-18^{\circ}\text{C}$ , treeline eucalypt species approached the limit of their cold hardiness.

Although frost is recognised as an important factor limiting eucalypt distributions in the Australian subalpine environment (Costin 1954; Jackson 1973), few examples of interspecific differences in the frost resistance of eucalypts have been reported. Moore and Williams (1976) and Harwood (1980, 1981, 1983) reported that in a subalpine valley in the Snowy Mountains, Seventeen Flat, intense frost was an important factor in the absence of eucalypts from the valley floor and in some of the changes in eucalypt dominance on the surrounding valley slopes. Ashton (1958) also suggested that the absence of E. regnans from the depressions in the Victorian highlands was caused by frost. Apart from studies of the frost resistance of green and glaucous forms of E. urnigera along an altitudinal cline on Mt. Wellington (Thomas & Barber 1974; Paton 1981) and frost chamber trials by Sakai et al. (1981) which included Tasmanian species, no field ecological or laboratory studies or frost chamber trials have been conducted to determine the

interspecific differences in frost hardiness of Tasmanian eucalypt species. However, severe frosts may occur in the Tasmanian highlands. Calder (1850) and Hooker (1844) described exceptional frosts which killed large tracts of mature forests on the valley floors and drainage channels in the central highlands of Tasmania. Hooker (1844) also noted E. gunnii was the most resistant species to these frosts. Observations of the effects of natural frosts and survival of exotically planted eucalypts (Martin 1948; Marien 1979) suggest Tasmanian species may be amongst the most frost resistant in the genus. E. gunnii is perhaps the hardest species with E. coccifera and E. johnstonii in the upper range of frost hardiness.

Snug Plains, although distant from the coldest regions of Tasmania as described by Langford (1965), is similar in altitude and physiognomy to these regions. The rolling subalpine plateau of Snug Plains, with treeless sedgeland and low mallee shrublands in the depressions and subalpine woodlands on the rises is quite reminiscent of the Central Highlands of Tasmania and the treeless plains of the Snowy Mountains.

The current study investigates the variation in minimum temperatures at the study site on Snug Plains during the 1981 winter, and describes temperature profiles and the frost damage incurred by natural eucalypt stands during exceptionally severe frosts in June 1983. The study also reports differential frost damage which occurred to seedling transplant trials in the field and in frost chamber trials involving glasshouse grown seedlings.

A general review of frost acclimation and freezing injury is presented in Appendix 4.1.

## MATERIALS AND METHODS

### 1. Temperature Records

Weather recording stations were positioned at each of the 6 field gardens (see Chapter 3 for details) at the study site on Snug Plains (Figs 4.1 and 4.2). Three thermometers were mounted on a single wooden post (50 mm x 100 mm) at heights of 0.05 m, 0.6 m and 1.3 m above ground. They were positioned on the southern side of the posts and shaded by plywood hoods. The thermometers were read at weekly intervals for five months between May 1981 and September 1982, then monthly until December 1983. Thermohygrographs were installed at



FIGURE 4.1

TOPOGRAPHIC MAP OF SNUG PLAINS

Legend:

Scale: 63 mm represents 1 km.



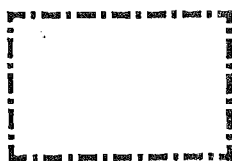
Sites of frost hollows and  
direction of cold air movement

Sites of Field transplant trials and associated  
weather recording stations.

- ① A ridge top site with open E.pulchella dry sclerophyll forest.
- ② A lower ridge slope with open E.coccifera sclerophyll forest.
- ③ A dish shaped depression with open E.gunnii mallee woodland.
- ④ A shallow slope with a dense E.delegatensis/E.urnigera wet sclerophyll forest.
- ⑤ A shallow slope with open E.johnstonii mallee woodland.
- ⑥ A shallow ridge top site with a tall open E.coccifera mallee woodland.

Regenerating eucalypt stands studied after severe frosts  
in June 1983

- (A) Pure pole stand of E.delegatensis.
- (B) Mixed pole stand of E.delegatensis, E.coccifera and E.gunnii.
- (C) Mixed pole stand of E.coccifera, E.johnstonii and E.gunnii.
- (D) Mixed pole stand of E.coccifera, E.johnstonii and E.pulchella.
- (E) Mixed pole stand of E.coccifera, E.gunnii and E.pulchella.
- (F) Mixed pole stand of E.delegatensis and E.pulchella.



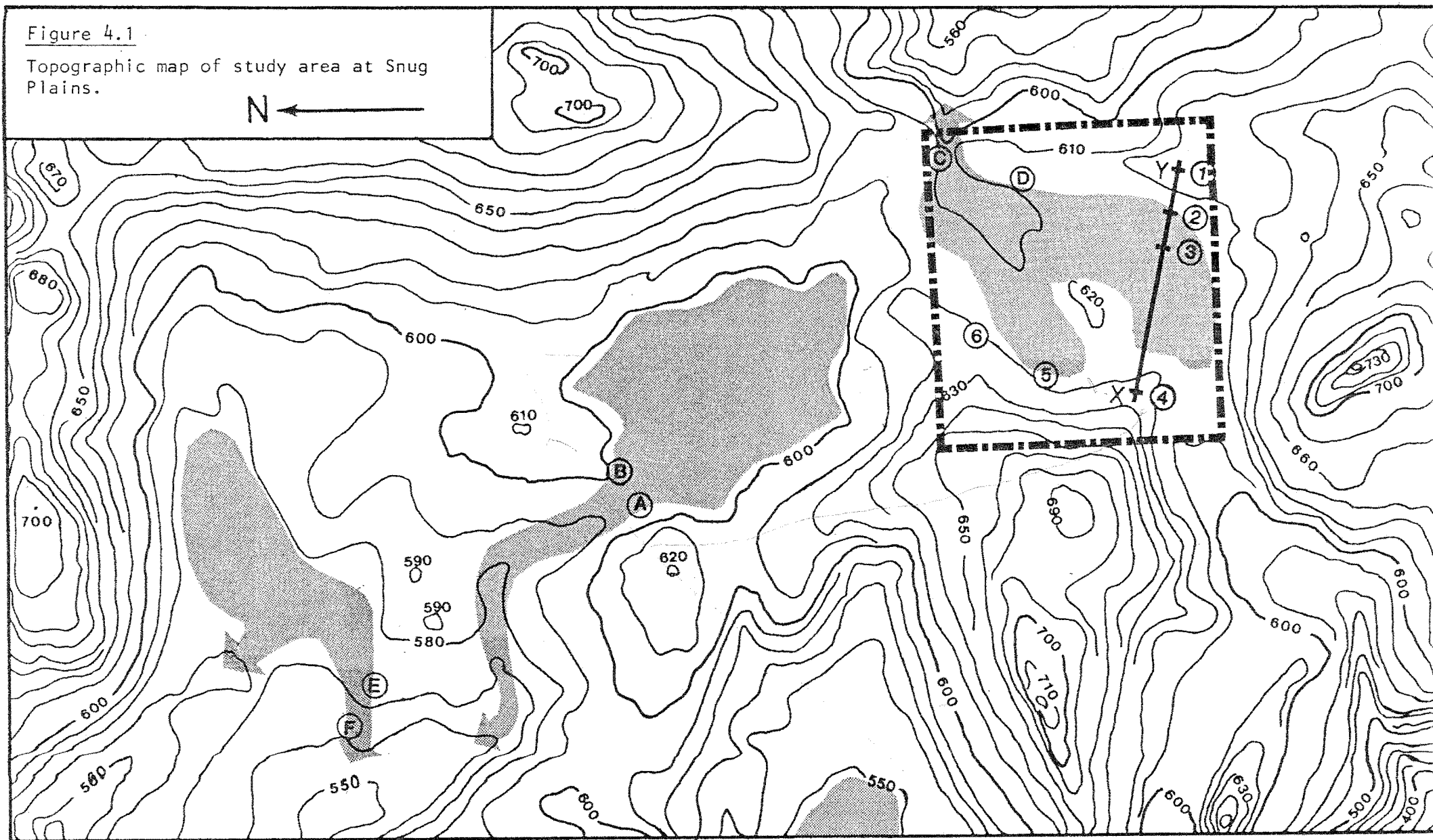
border defining major study area at  
Snug Plains and region for which  
species distributions are presented  
in Fig. 4.2

X-Y

Transect line for which data is presented  
in Figs 4.2 and 4.6

Figure 4.1

Topographic map of study area at Snug  
Plains.



three recording stations, sites 1, 3 and 4 (Figs 4.1 and 4.2). Each thermohygrograph was placed inside a screen box 0.05 m above ground level. Continuous temperature records were made from May to September 1981 from which daily maximum and minimum temperatures were obtained.

The maximum-minimum thermometers and thermohygrographs were calibrated at temperatures of  $-10^{\circ}\text{C}$ ,  $-2^{\circ}\text{C}$ ,  $5^{\circ}\text{C}$ , and  $21^{\circ}\text{C}$  before being placed in the field. The temperature characteristics of each unit was determined and any errors were adjusted for during field measurements. The calibration of the three thermometers at site 3 (where temperatures near  $-22^{\circ}\text{C}$  were recorded) were rechecked, against a gold line Corning thermometer at  $-21.5^{\circ}\text{C}$ , after field experiments were completed. All three thermometers were accurate to within  $1^{\circ}\text{C}$  of this temperature and minor corrections were made to field records where necessary. At temperatures between  $-10^{\circ}\text{C}$  and  $+21^{\circ}\text{C}$  the maximum-minimum thermometers proved to be accurate to 0.5 of a degree centigrade and the thermohygrographs to 0.2 of a degree centigrade. However, the maximum-minimum thermometers responded faster to temperature changes than the thermohygrographs which gave differences of up to  $2^{\circ}\text{C}$  in absolute minimum and maximum values obtained from the two recording instruments.

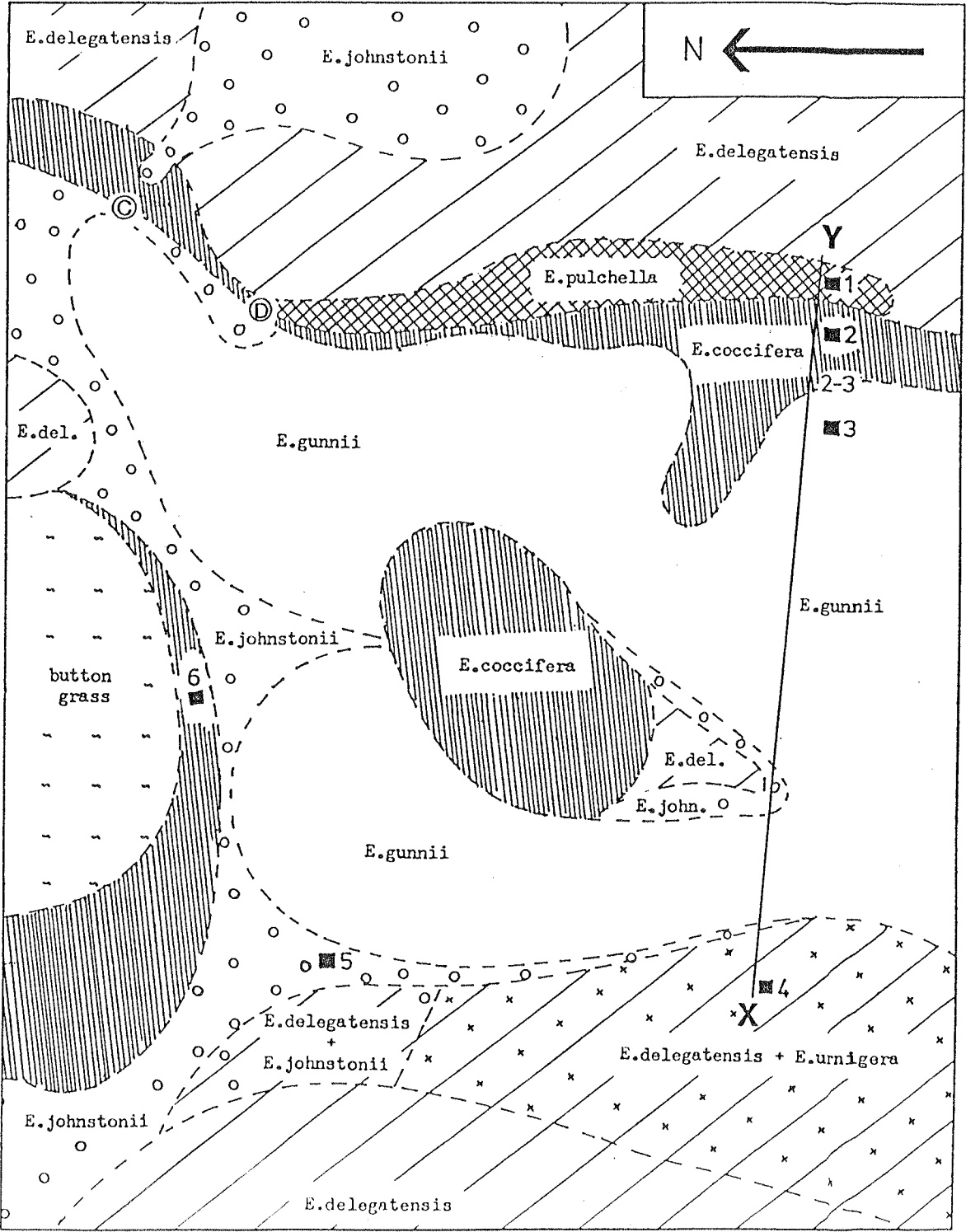
A Grant recorder was placed in the field on 15th June 1983 and retrieved on 10th July, after data from a severe frost had been recorded. The Grant recorder was positioned at site 2 and four long lead thermistors were placed to obtain a temperature profile spanning the 200 m distance down the shallow hillside from site 1 to site 3. A single thermistor was placed inside a short length of insulated conduit (oriented east-west), 2.0 m above the ground at each of the sites 1, 2, 3 and midway between sites 2 and 3 (Fig. 4.2). A single night's measurements from the Grant recorder and long lead thermistors, and records from maximum-minimum thermometers made on the 29-30th June 1983 are used to describe the temperature gradients which occurred in the study area during a severe radiation frost. The open understory of the eucalypt stands surrounding each garden would probably provide little impediment to cold air movement, so microclimate records were considered representative of the forest type in which they were situated.

## 2. Frost Damage to Natural Eucalypt Stands

After the severe frosts in June 1983, frost damage first became evident as blackening of the leaves. The killed leaves then became brown and crisp, but were retained within the crowns of the trees through the winter and into the

Figure 4.2

Map of the distribution of eucalypt species within the study area at Snug Plains (for legend see Fig. 4.1).



following spring. In August, when all frost damaged leaves had turned brown and were clearly visible the frost damage study was commenced (Plates 4.1 and 4.2).

One pure stand of E. delegatensis (stand A) and five mixed stands (stands B to F) of regenerating eucalypt species, growing on the margin of a frost hollow or in the path of cold air spilling from a frost hollow at Snug Plains, were chosen for the frost injury study.

The mixed stands studied were chosen on three criteria: (i) homogeneity of the mixed stand; (ii) presence of a broad range of ontogenetical stages and height classes for all species; and (iii) similarity of the level of frost injury throughout the stand. At each stand 3 to 6 contiguous quadrats (20 m x 30 m) were placed parallel to the margin of the frost hollow and the frost damage scored. Within each quadrat visual estimates of the percentage crown damage at each height interval (see below) were made to the nearest 10%, for every individual in the stand. For every stem, frost damage was estimated for the five height intervals: 0 to 0.5 m, 0.5 to 1.5 m, 1.5 m to 3 m, 3 m to 6 m and > 6 m above ground.

In stand A, three contiguous quadrats (20 m x 30 m) were placed transversing a shallow incline from the margin of a frost hollow into the forest and quadrats were scored in the same manner as those for the mixed stands.

Species comparisons (stands B to F) and quadrat comparisons (stand A) were made of data for each height interval using analysis of variance. The percentage frost damage scores were arc-sin transformed before analysis.

### 3. Seedling Transplant Trials (Gardens)

In 1981 field transplant trials involving glasshouse grown seedlings of the six species E. delegatensis, E. coccifera, E. pulchella, E. gunnii, E. urnigera and E. johnstonii were planted at each of the six field sites 1 to 6 (see Chapter 3 for details). Planting was completed on the 28th of October.

Before being transplanted into the field, the seedlings were placed outside the glasshouse at the University of Tasmania, Hobart, for four weeks to "harden". However, about 3 weeks after planting in the field two minor frosts occurred causing severe damage to seedlings at garden 3 and lesser damage to the other gardens. A replacement seedling plot was planted at garden 3 (garden

Plates 4.1 and 4.2

Frost damage incurred by regenerating eucalypt stands during a severe frost in June 1983 depicting severe frost damage at valley bottoms while shallow rises were relatively undamaged.



Plate 4.1



Plate 4.2



3b) beside the original in late November (see Chapter 3). No further frosts severe enough to damage the seedlings occurred before the winter of 1982. In July 1982 winter frosts again damaged gardens 1 to 6. After both the spring frosts (November 1981) and the winter frosts (July 1982) gardens 1 to 6 were scored for frost damage. The injury received by each leaf of each seedling was recorded to the nearest  $\frac{1}{4}$  of a leaf damaged. The percentage seedling survival was then calculated (after Ashton 1958; see Chapter 3). The percentage seedling survival values were arc-sin transformed and analysis of variance and Duncan's multiple range tests were performed on the data.

#### 4. Frost Chamber Trials

##### (a) Trials

Seed was collected from five trees of each of the six species E. delegatensis, E. coccifera, E. pulchella, E. gunnii, E. urnigera and E. johnstonii, from populations at the study site on Snug Plains. The seed was stratified on moist vermiculite for four weeks at 4°C prior to germination and the seedlings pricked out, at the cotyledonary stage, into plywood veneer tubes filled with potting soil. Seedlings were watered 3 times weekly and nutrients were provided via slow release fertilizer (blood and bone and osmocote) present in the potting soil. Seedlings were grown for two months inside the glasshouse at the University of Tasmania, Hobart, then placed outside for an initial hardening period of two months between September and October 1983, before imposing the experimental treatments.

At the end of October, 48 even-sized seedlings were selected from the progenies of each of the six species (a total of 288 seedlings). These seedlings were arranged in a latin square design in eight plastic trays with six replicates of each of the six species per tray. Four trays were then transferred to each of two large growth cabinets. Within each cabinet two trays (72 seedlings) were flooded to  $\frac{2}{3}$  of the height of the veneer ("wet") and two were left freely drained ("dry"). All seedling were watered three times weekly. The photoperiod for both cabinets was set at ten hours. Illumination was provided from a mixed bank of fluorescent and incandescent lights (approximately  $150 \mu\text{Em}^{-2}\text{sec}^{-1}$ ). The thermoperiod for both cabinets was set at ten hours with one cabinet receiving a 15°C day and 10°C night and the other a 9°C day and 4°C night. The choice of nocturnal and diurnal temperature for each cabinet was made to provide two hardening regimes; "hardened" (9°C day/4°C night) and "unhardened" (15°C day/10°C night). Harwood (1980) investigated the

importance of day and night temperature on hardening in *E. pauciflora* and determined that a night temperature of 4°C for three to four weeks would harden *E. pauciflora* to a -8.5°C frost (with 50% frost damage) whereas at nocturnal temperatures of above 9°C no hardening was developed in two species studied. Day temperatures varying between 9°C and 18°C had little influence on the development of hardening (Harwood 1980). However, a 5°C temperature difference between night and day was used in all the current trials. The seedlings were grown in the growth cabinets for eight weeks before frost chamber trials were begun. During this eight week period the cabinet set at 9°C day and 4°C night did not always hold the required nocturnal temperature due to icing of the cooling system. This occasionally reduced the thermoperiod from 12 hours to 6 or 7 hours.

After eight weeks of the prescribed hardening and water regimes the frost hardiness of seedlings of the six species in each treatment was investigated using a frost chamber (for details see Part(b) this section) at the four minimum temperatures of -4°C, -5°C, -6°C and -7°C. At this stage all seedlings were healthy and between 15 and 25 cm in height. Cooling and warming rates of 4°C per hour, similar to rates found in field radiation frosts by Harwood (1980, 1981) and at Snug Plains, were used in each trial and the minimum temperature was held for two hours. For each minimum temperature investigated three replicate individuals of each eucalypt species from each treatment were used. However, the frost chamber was limited in size, therefore at each minimum temperature three replicate trials were performed, each involving a single seedling from each species in each treatment.

In each trial one replicate seedling of each species was chosen at random and randomly placed in a plastic tray filled to a depth of 5 cm with dry vermiculite. Dry vermiculite was then poured between and around the 24 veneers containing the seedlings, and to a depth of 2 cm over the top of the veneers. Thus the soil and root systems of the seedlings were insulated from the minimum temperatures to which the stem and leaf tissues were exposed. Random checks of the veneers immediately after frosting indicated that no freezing of the soil or root systems of the plants had occurred during the experiment. Before a trial was commenced, seedlings were sprayed with water from a fine mist sprayer to simulate the effect of dew which usually proceeds frosts in the field (Thomas & Barber 1974). After a trial was completed, seedlings were removed from the insulating vermiculite medium and transferred to another plastic tray and placed in a large growth cabinet set at the same photoperiod, thermoperiod and temperature regime as the "unhardened" treatment (15°C day/10°C night). All seedlings were watered three times weekly and freely drained.



One week after the frost trials seedlings were scored for frost damage to the leaf tissue (after Ashton 1958, for details see Chapter 3). Two months after the frost experiment had been completed all plants were rescored for nodal damage (after Ashton 1958). Total percentage survival was then calculated from the mean of the two separate scores of leaf survival. The percentage survivals were arc-sin transformed and analysis of variance performed on the data. Analyses were performed on all species, and the separate subgenera, with and without *E. gunnii*, which, because of its extreme frost hardiness, may have exaggerated the effects and interactions of the analyses.

#### (b) The Frost Chamber

The frost chamber was constructed in the Botany Department of the University of Tasmania. It consisted of a simple steel framed box with thick insulated walls. The internal dimensions of the chamber were 0.5 m x 0.5 m x 0.75 m. A refrigeration coil was situated at the top of the chamber, reducing the effective height of the chamber to 0.6 m. The frost chamber operated on a proportional cooling system. The temperature was controlled by two solenoid valves which direct refrigerant either through a refrigeration coil inside the chamber (when cooling was required) or through an exterior evaporator (when cooling was not required). The temperature inside the frost chamber was measured by two temperature sensors; a solid state sensor with a slow response time, which gave a digital readout, and a bead thermistor with a rapid response time, which sensed the direction and magnitude of the temperature deviation about the required temperature. The output from these two temperature sensors then controlled the operation of the solenoid valves. The sensors were mounted on an adjustable stand towards the back of the chamber. The range of adjustments allowed the sensors to be placed in a suitable position amongst the foliage of the plants being tested.

Both the rate of temperature descent (or ascent) and the minimum temperature reached were programmed before the start of each trial. The rate of cooling or heating could be adjusted to between 3°C and 63°C per hour, and minimum temperatures down to -20°C were within the range of the cooling system. At the cooling and warming rates used in the current experiment (4°C per hour) temperature oscillations and the temperature lag of the sensors was of the order of 0.1°C. However, temperature gradients developed within the chamber were an order of magnitude larger than those perceived at the sensors, because of the stillness of the air within the chamber. The temperature characteristics of the frost chamber were obtained using an array of

thermocouples during several trials using both the empty chamber and the chamber containing a tray of plants (Hallum & Tibbets, unpublished). For the empty chamber stabilized at a set minimum temperature, the vertical temperature gradients were of the order of  $0.5^{\circ}\text{C}$  with an approximately linear decrease in temperature between the floor and the cooling coil. The horizontal temperature gradients were about  $0.2^{\circ}\text{C}$ . However, when the chamber first reached the set minimum temperature gradients could be as high as  $1.0$  to  $1.5^{\circ}\text{C}$ . There was some tendency for minimum temperature overshoot; about  $0.8^{\circ}\text{C}$  at fast rates of cooling, but substantially less at slow cooling rates. When a plastic tray filled with plants insulated with vermiculite was tested in the chamber, temperatures near the vermiculite surface (about 10 cm above) were  $2\text{--}3^{\circ}\text{C}$  higher than temperatures near the cooling coil, presumably because of the combined thermal inertia of the plants, plastic tray and vermiculite. Horizontal temperature gradients were only slight (approximately  $0.2^{\circ}\text{C}$ ).

For the current trials the temperature sensors were positioned about 15 cm above the vermiculite surface, amongst the foliage of one of the seedlings. Therefore the minimum temperatures reached during the frost trials were the temperatures near the plants not of air distant to the plants. At the time of the frost trials the plants tested were between 15 and 25 cm in height. If there was any marked temperature gradients over the height range of the seedlings, differences would have been observed in the frosted seedlings. This was not the case. Only at the vermiculite surface and to a distance of about 2 cm above it, did leaves appear to be protected by convected heat from the vermiculite.

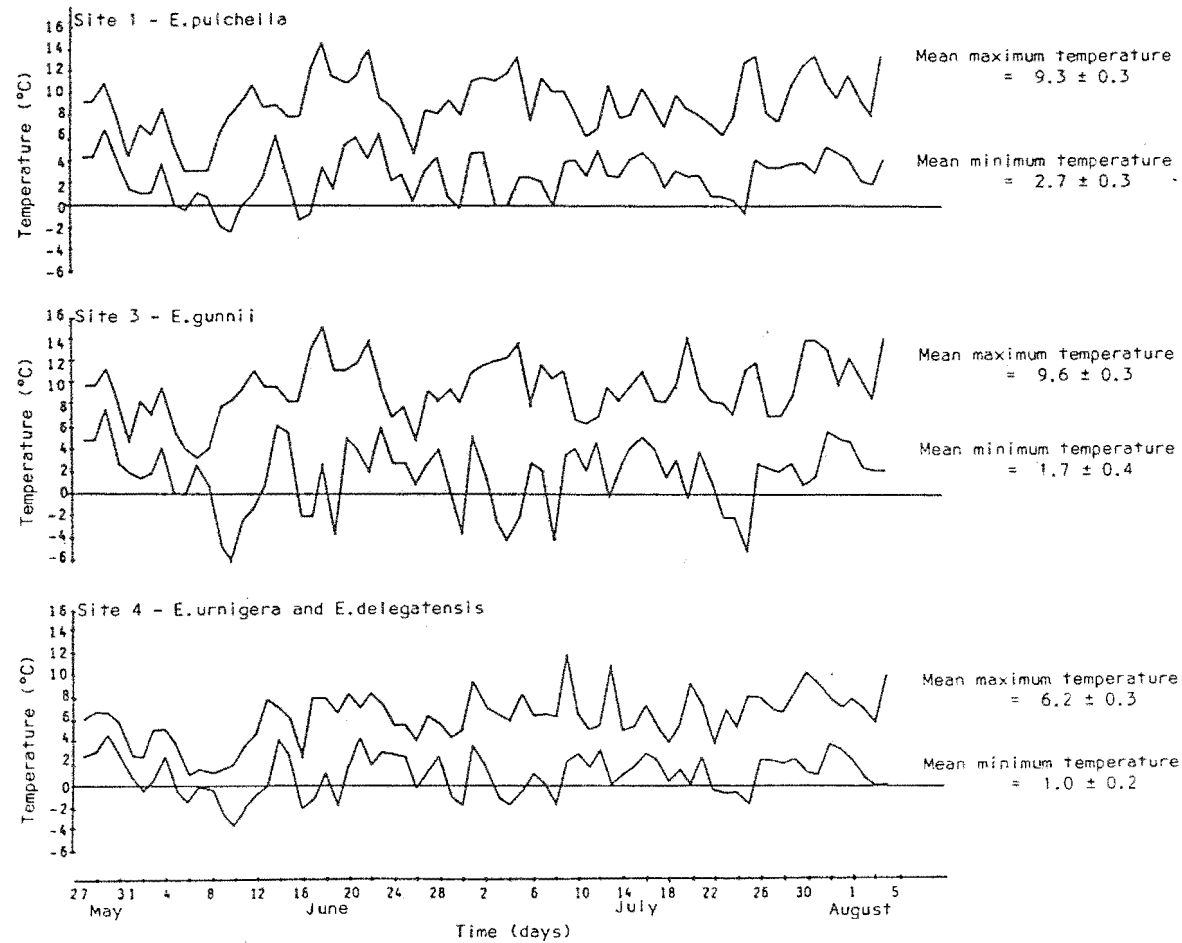
## RESULTS

### 1. Temperature Records

Daily maximum and minimum temperatures obtained from thermohygrograph records made between May and August 1981 indicate that marked differences in winter microclimate exist between sites 1, 3 and 4 which form a transect across the study site (Fig. 4.3). The mean minimum temperature on the ridgetop (site 1) was higher than other sites but temperatures fluctuated widely about the mean. Frosts were only occasional and mild. In the depression (site 3) the mean minimum temperature fell between those of site 1 and site 4. Temperature fluctuations about the mean were greater than in other sites and frosts were frequent and more severe

Figure 4.3

Daily maximum and minimum temperatures recorded on thermohygrographs installed in screens at ground level at sites 1, 3 and 4 between 27 May and 5 August 1981.



(Table 4.1). The east facing slope at site 4 exhibited the lowest mean minimum temperature but least fluctuation about the mean. Frosts were most frequent at this site, but usually minor. With low mean minimum and maximum temperatures site 4 would probably provide a most suitable climate for frost acclimation. At near zero temperatures subalpine eucalypts will rapidly harden to frosts (Paton 1981) and as long as minimum night temperatures are below  $+4^{\circ}\text{C}$  frost hardening will develop in eucalypts (Harwood 1980). During the 71 days of measurement, minima of  $+4^{\circ}\text{C}$  and below occurred on all but three days for site 4, more frequently than other sites (Table 4.1).

The records from maximum-minimum thermometers indicate that site 3 receives the lowest minima followed in order by sites 5, 6 or 4, 2 and 1, in agreement with thermohygrograph results (Table 4.2). The maximum-minimum thermometer records also show that at some sites weak vertical gradients in air temperature exist.

During the latter part of June 1983 Tasmania experienced a "cold snap" and severe frosts were recorded in many centres throughout the State (Bureau of Meteorology, Tasmania). On 30th June, at the height of the freeze, record minimum temperatures were reported for several weather stations in the central highlands of Tasmania, for example, Shannon, Butlers Gorge and Lake St. Claire (Appendix 4.2). A record minimum for Tasmania of  $-13^{\circ}\text{C}$  occurred during this period (recorded at Shannon and Butlers Gorge).

The nearest station to the study site at Snug Plains was at Grove, 12 km to the north-west, at an elevation of 60 m in the rolling farming country at the foothills of Snug Plains. At Grove the minimum of  $-6.5^{\circ}\text{C}$  recorded on 30th June 1983 was one of the two most extreme minima recorded in 25 years (Fig. 4.4 and Appendix 4.2). Further, only one day in the preceding 15 had a minimum temperature above zero.

At Snug Plains the "cold snap" began with a fall of 0.5 m of snow, followed by 14 days of subzero minimum temperatures. At dusk on 30th June temperatures dropped rapidly at sites 3 and 2-3 but more gradually at sites 1 and 2 (Fig. 4.5). In the 1 hr 40 min immediately after sunset temperatures at site 3 fell from  $+2.8^{\circ}\text{C}$  to  $-8^{\circ}\text{C}$ , a rate of  $6.5^{\circ}\text{C}$  per hour, although the average rate of cooling was  $3.9^{\circ}\text{C}$  per hour, which is comparable to cooling rates of  $2-4^{\circ}\text{C}$  per hour obtained by Harwood (1980). By 8 pm (20.00 hrs) the rate of temperature descent at all sites had become gradual. The gradual lowering of temperature continued until just before dawn when the most extreme minima

TABLE 4.1

Summary of minimum thermohygrograph temperatures recorded at sites 1, 3 and 4 in the field at Snug Plains during the period 27th May 1981 to 5th August 1981 (from Fig. 4.3).

(a) Number of days recording minimum temperatures below 4°C ('hardening' minima)

| Site                              | 1                   | 3                | 4   |
|-----------------------------------|---------------------|------------------|---|
| Eucalypt species present          | <u>E. pulchella</u> | <u>E. gunnii</u> | <u>E. delegatensis</u><br>&<br><u>E. urnigera</u> |
| No. of days with minima below 4°C | 49                  | 51               | 68  |
| Duration of records (in days)     | 71                  | 71               | 71  |

(b) Number of days of frost and its severity for each site.

|                          |            | Frequency of frosts |                  |   |
|--------------------------|------------|---------------------|------------------|---|
| Site                     |            | 1                   | 3                | 4   |
| Eucalypt species present |            | <u>E. pulchella</u> | <u>E. gunnii</u> | <u>E. delegatensis</u><br>&<br><u>E. urnigera</u> |
| Temperature Interval     | 0 to -0.9  | 4                   | 2                | 12  |
|                          | -1 to -1.9 | 2                   | 4                | 9   |
|                          | -2 to -2.9 | 1                   | 4                | 1   |
|                          | -3 to -3.9 |                     | 2                | 1   |
|                          | -4 to -4.9 |                     | 3                |   |
|                          | -5 to -5.9 |                     | 1                |   |
|                          | -6 to -6.9 |                     | 1                |   |
| Total number of frosts   |            | 7                   | 17               | 23  |

TABLE 4.2

Weekly maximum-minimum thermometer records from sites 1 to 6 in the field at Snug Plains for the period 28th June 1981 to 8th August 1981

| Site of Weather Station | Thermometer height <sup>1</sup> (in m) | 3.7.81 |      | 10.7.81 |      | 17.7.81 |      | 24.7.81 |      | 31.7.81 |      | 8.8.81 |      |
|-------------------------|--|--------|------|---------|------|---------|------|---------|------|---------|------|--------|------|
|                         |  | Max.   | Min. | Max.    | Min. | Max.    | Min. | Max.    | Min. | Max.    | Min. | Max.   | Min. |
|                         |  |        |      |         |      |         |      |         |      |         |      |        |      |
| 1                       | 1.3                                    | 10     | 0.5  | 9.5     | -2.5 | 11      | 0.5  | 11      | -1   | 14      | 0.5  | 14.5   | 2.5  |
|                         | 0.6                                    | 10     | 0    | 9       | -3   | 11      | 0    | 12.5    | -1   | 14      | -0.5 | 16     | 1    |
|                         | 0.05                                   | 8.5    | -0.5 | 8       | -3   | 9.5     | 0    | 10.5    | -1   | 13      | -1.5 | 14.5   | 1    |
| 2                       | 1.3                                    | 10.5   | -2.5 | 9.5     | -3   | 11.5    | 0    | 11.5    | -3   | 15.5    | -2.5 | 16.5   | -1   |
|                         | 0.6                                    | 10.5   | -4   | 9       | -4   | 11.5    | 0    | 11      | -2.5 | 16.5    | -2.5 | 17     | -1   |
|                         | 0.05                                   | 11     | -3.5 | 9       | -4   | 12.5    | -0.5 | 11.5    | -2   | 17      | -3   | 18     | -1   |
| 3                       | 1.3                                    | 10.5   | -5   | 11      | -7   | 11      | 0    | 10      | -3   | 14      | -4   | 14.5   | -3   |
|                         | 0.6                                    | 9.5    | -5   | 11      | -7   | 11.5    | -0.5 | 12      | -3.5 | 16      | -4.5 | 17.5   | -4   |
|                         | 0.05                                   | 7.5    | -4.5 | 11.5    | -8   | 12.5    | -0.5 | 13      | -4.5 | 16.5    | -5   | 19     | -4   |
| 4                       | 1.3                                    | 10.5   | -2.5 | 10      | -3   | 8       | -0.5 | 10      | -2.5 | 14.5    | -2   | 14     | -0.5 |
|                         | 0.6                                    | 10     | -2.5 | 9       | -3   | 8       | -0.2 | 9       | -3   | 14      | -2   | 12.5   | -1.5 |
|                         | 0.05                                   | 7      | -3   | 9       | -4   | 7.5     | -0.5 | 9       | -3   | 10      | -3   | 10     | -1.5 |
| 5                       | 1.3                                    | 10.5   | -3.5 | 10.5    | -4   | 12      | -1   | 13      | -3.5 | 14      | -2   | 15.5   | -1   |
|                         | 0.6                                    | 11     | -3   | 12.5    | -3.5 | 12      | -1   | 15      | -3   | 16.5    | -2.5 | 17.5   | -1.5 |
|                         | 0.05                                   | 11.5   | -4   | 11.5    | -4.5 | 9       | -2.5 | 14.5    | -4   | 17.5    | -3.5 | 17.5   | -2.5 |
| 6                       | 1.3                                    | 9.5    | -3.5 | 11.5    | -4   | 10.5    | 0    | 9       | -2.5 | 11.5    | -0.5 | 14     | 0    |
|                         | 0.6                                    | 11     | -2.5 | 12      | -3   | 12      | 0    | 12      | -2   | 14.5    | -1.5 | 16.5   | -0.5 |
|                         | 0.05                                   | 9.5    | -3.5 | 10      | -4.5 | 12      | -0.5 | 11      | -2.5 | 15      | -3   | 17     | -2   |

<sup>1</sup> height of the thermometer above ground

Figure 4.4

Daily maximum and minimum temperatures for Grove Weather Station from 1st June to 31st August in (a) 1981, (b) 1982 and (c) 1983.

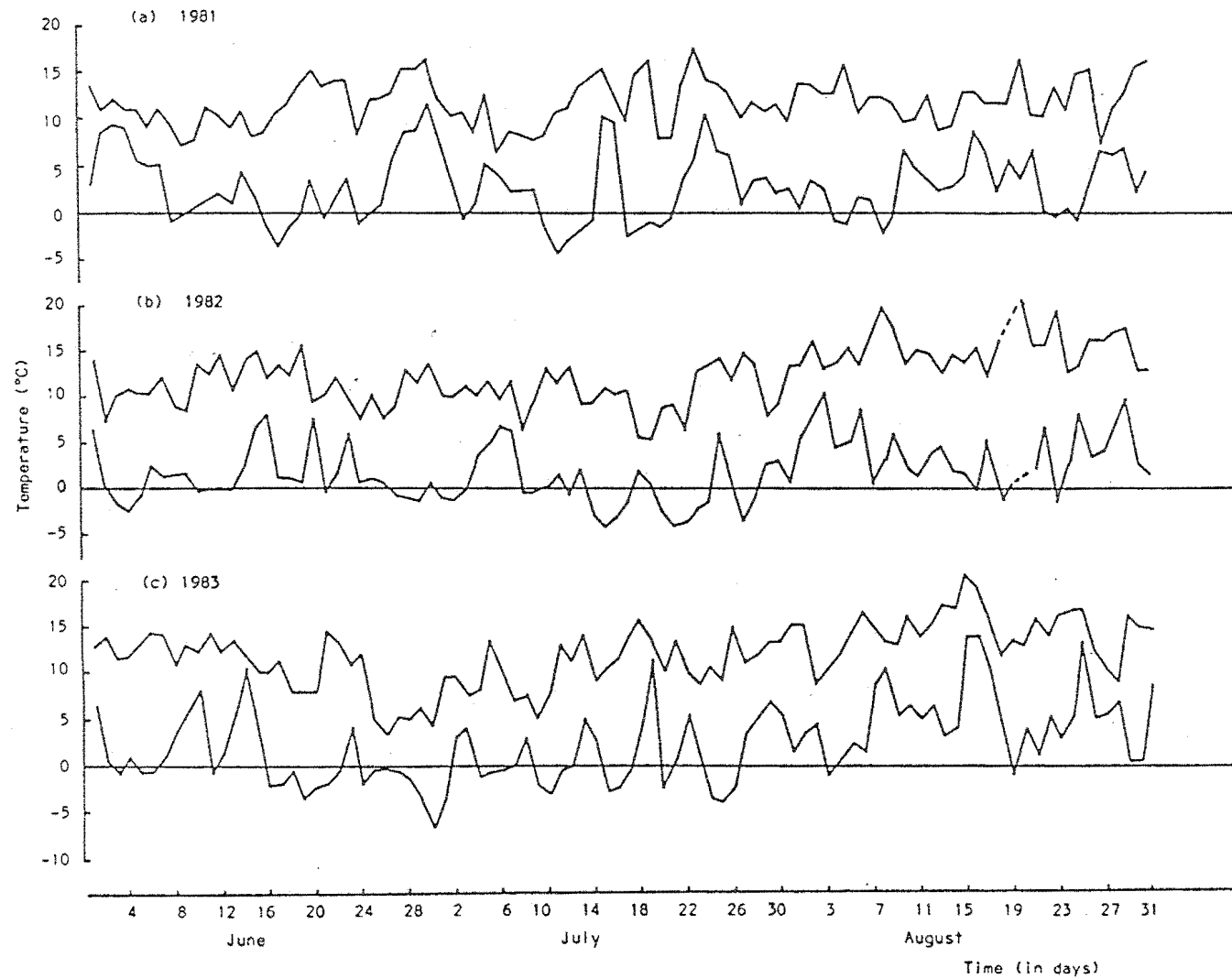
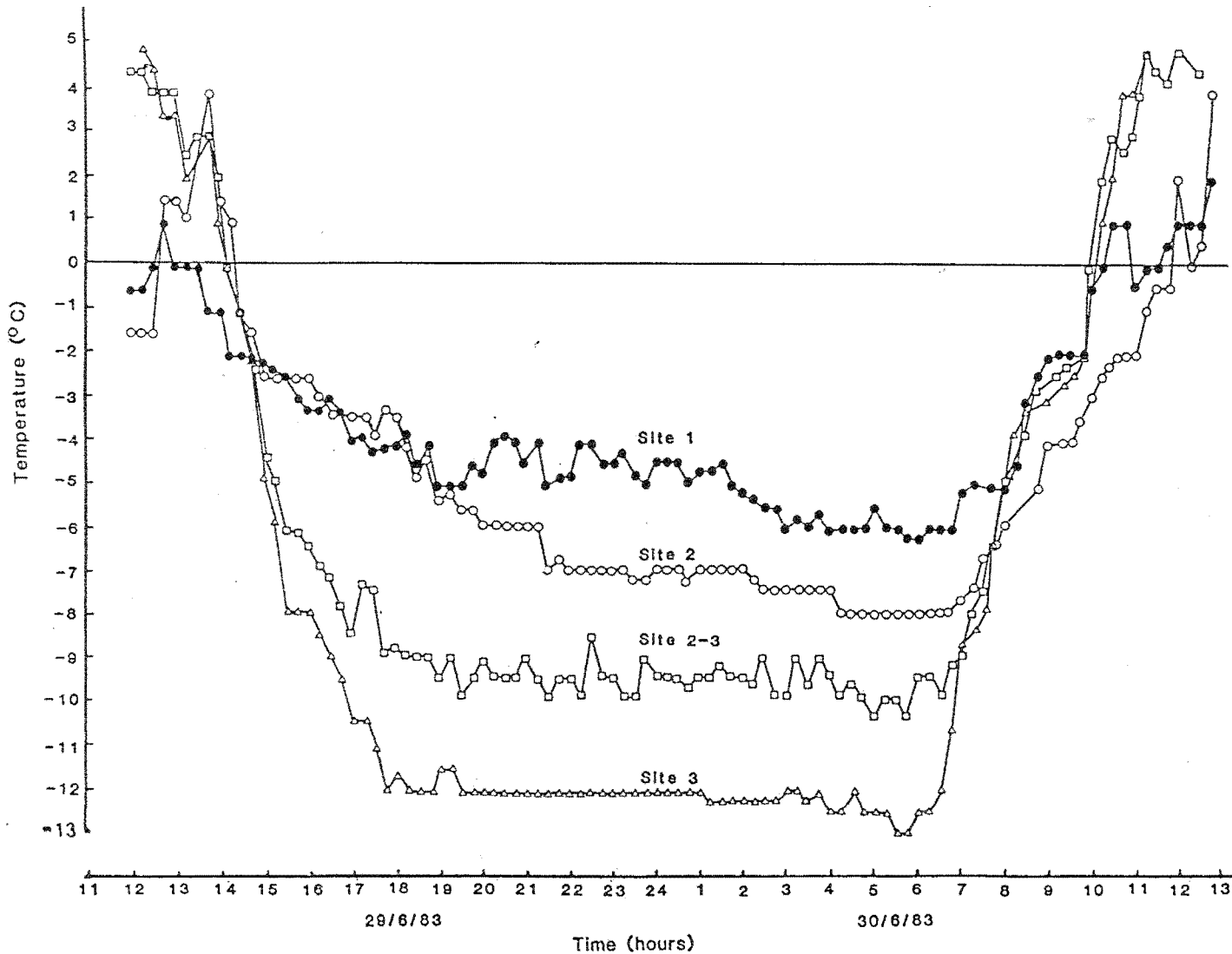


Figure 4.5

Quarter hourly temperature records made at 4 sites (sites 1, 2, 2-3 and 3) along a transect (Figs 4.1, 4.2 and 4.6) from a shallow ridge top to a dish-shaped depression. Measurements were made on one night (the 29-30/6/83) using a Grant recorder and long lead thermistors, installed 2 m above ground.





were recorded (Fig. 4.5). The lowest of the thermometers (at 0.05 m above ground) was protected by an insulative layer of snow. Therefore, it was at 0.60 m above the ground, just above the radiating surface, that the lowest minima were recorded (Fig. 4.6). An extreme minimum of  $-22.5^{\circ}\text{C}$  was recorded near the radiating surface at site 3 which is a record minimum temperature for Australia. A strong stratification of the air body, of up to  $5.7^{\circ}\text{C}$  per metre ( $8^{\circ}\text{C}$  in 1.4 m), existed at site 3. This was matched by steep gradients in temperature, of up to  $7.2^{\circ}\text{C}$ , between the ridgetop at site 1 and the base of the depression at site 3, a distance of 200 m. Similarly steep temperature gradients have been observed at Seventeen Flat in the Snowy Mountains by Moore and Williams (1976) and Harwood (1983) and in other shallow dish shaped depressions (Hocevar & Martsolf 1971; Jennings 1979; Geiger 1971; Laughlin 1982).

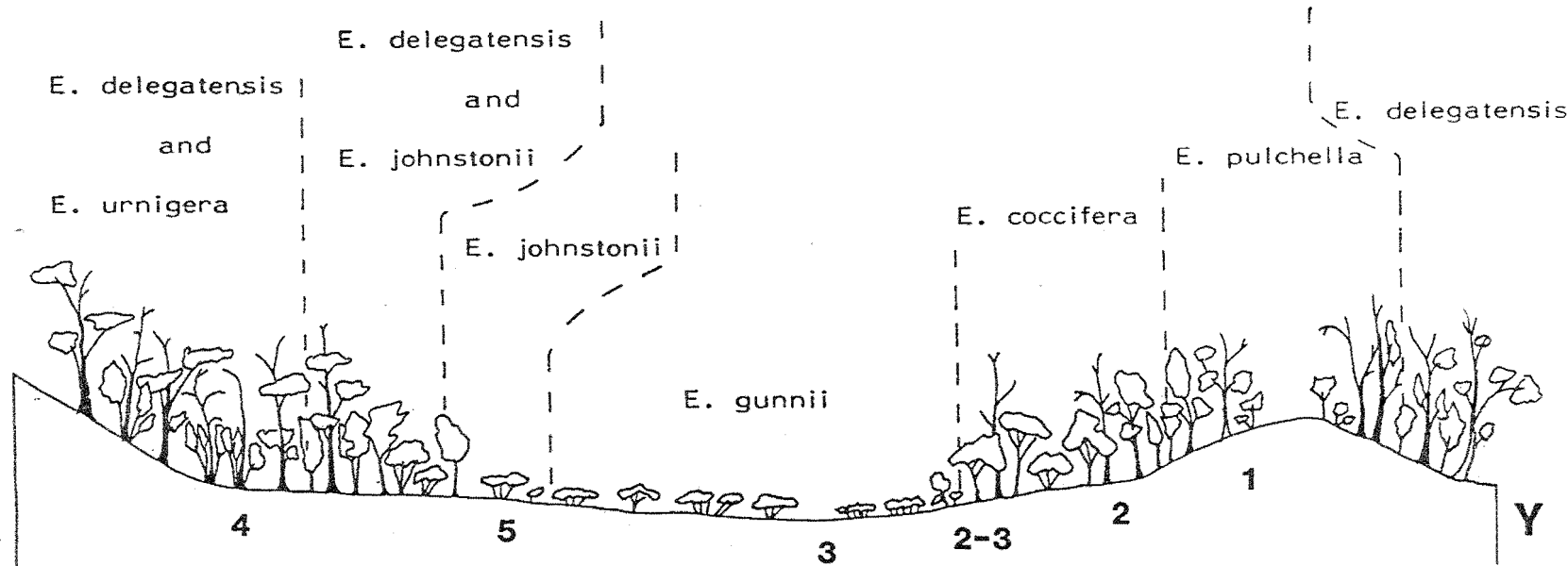
The warming rates at dawn were quite comparable with the cooling rates at dusk. The warming rate for the first 90 minutes after dawn (dawn at 6.30 am) was  $5.9^{\circ}\text{C}$  per hour with an average warming rate of  $3.9^{\circ}\text{C}$  per hour. The rates were lower than the  $5\text{--}7^{\circ}\text{C}$  per hour warming rates obtained by Harwood (1980) but were probably a function of the lower sun angle and therefore lower insolation rates experienced in the winter at latitude  $42^{\circ}$  south in comparison with those at the Snowy Mountains (at  $36^{\circ}$  south).

## 2. Frost Damage in Natural Eucalypt Stands

The cold air which collected in the depression at Snug Plains during the severe frost of 29-30th June made its way down-slope, following shallow valleys and creek lines in the plains until it reached the edge of the plateau (Plates 4.1 and 4.2). The passage of these intensely cold air masses could be mapped by the extensive frost damage they inflicted on the vegetation as they passed (Fig. 4.1). In all stands studied (stands A-F; Fig. 4.1) foliage less than 0.5 m in height above the ground was protected by an insulative layer of snow and received little frost damage. The greatest frost damage occurred to foliage just above the snow surface in the 0.5 m to 1.5 m height interval, which corresponded to the region of most extreme temperatures recorded during the frost. Harwood (1976, 1983) also suggested that the region, just above the radiating surface, provided the most precarious existence for establishing seedlings, although rapid warming or cooling at sunrise or sunset may contribute to the severity of frost damage (Harwood 1981; White & Weiser 1970; Horiuchi & Sakai 1978).

Figure 4.6

Eucalypt species distributions along a 1 km transect (X-Y) across the study area at Snug Plains and minimum temperatures recorded on a single night (29-30/6/84) at sites 1-5 obtained using a Grant recorder and long lead thermistors (installed 2.0 m above ground) and maximum-minimum thermometers (installed at 1.3, 0.6 and 0.05 m above ground).



| Instrument           |       | Minimum Temperature Recorded |       |       |       |       |      |
|----------------------|-------|------------------------------|-------|-------|-------|-------|------|
| Height of Instrument |       |                              |       |       |       |       |      |
| Grant Recorder       | 2.0m  |                              |       | -13.1 | -10.4 | - 8.0 | -6.3 |
| Max-Min thermometer  | 1.3m  | -8.5                         | - 9.5 | -16.0 |       | - 8.5 | -6.5 |
| " "                  | 0.6m  | -9.5                         | -10.0 | -22.5 |       | -12.0 | -9.0 |
| " "                  | 0.05m | -5.0                         | - 4.0 | -15.0 |       | - 5.0 | -4.5 |

In stands on the margins of frost hollows, for example stands D, E and F, frost damage decreased steeply at heights of greater than 1.5 m above ground. However, where a stand was located near the base of a frost hollow, or near the exit route for cold air spilling out of a frost hollow (stands A, B and C, Fig. 4.1) frost damage was inflicted for considerable heights up the tree (Figs 4.7 and 4.8). In stands A to C frost damage was still severe (80% to 100% leaf kill) at heights greater than 3.5 m above ground for many species. The extent of damage may be governed by the thickness of the lens of cold air which collect at the base of the depression. In some locations the height of the pool of cold air was marked in the crowns of the trees by a distinct disjunction between dead, frost-killed leaves and green, undamaged leaves. The stratification of the air may be very marked (Moore & Williams 1976; Geiger 1971) and the pool of air 5 m or more in depth (Moore & Williams 1976). Further, cold air is viscous and slow moving on shallow slopes (Geiger 1971), and its movement may be hampered or halted by obstacles or constrictions in the terrain (Geiger 1971). The constricted exits to the frost hollows at Snug Plains may have provided obstacles to the movement of cold air, restricting its progress and damming it to considerable heights before the resistance to flow was overcome.

In the pure E. delegatensis stand (stand A, Fig. 4.7) significant differences ( $P < 0.001$ ) in frost damage to the foliage were found for each height interval above 1.5 m for the 3 quadrats traversing a shallow incline from the margin of the frost hollow to a distance 30 m into the E. delegatensis forest (Figs 4.1 and 4.7). At the margin of the frost hollow foliage was completely killed by frost to a height of 4.5 m, whereas 30 m into the forest and away from the frost hollow defoliation only extended from 0.5 to 1.5 m up the stems. The main influence on frost damage was probably the increased height above the valley floor, although the resistance to cold air movement afforded by the dense E. delegatensis forest (Weiser 1971) and the insulation effect of the forest canopy (Nunez & Sander 1981; Horiuchi & Sakai 1978; Dale 1973) may have buffered temperatures in the forest.

In stands B to F, which were comprised of mixtures of 2 or 3 species of eucalypt, interspecific comparisons of frost injury could be made. Significant interspecific differences ( $P < 0.01$ ) occurred at height intervals between 0.5 and 6.0 m for all species, and for the two most severely frost damaged species in each stand (Table 4.3). E. gunni received least frost damage at each stand, and in each height interval in which it was represented, and was clearly the most frost hardy species (stands C, B and E). E. coccifera (stands B, C, D and E) was the next most hardy species followed by E. johnstonii and E. delegatensis. As

Figure 4.7

Stand A

Mean percentage crown damage caused by frosts in June 1983, against height above ground for *E. delegatensis* in 3 contiguous 10 x 30 m quadrats traversing a single incline (stand A; Fig. 4.1). Generally SE were too small to indicate but for individual points varied between 0.1% and 8.4% of the mean.

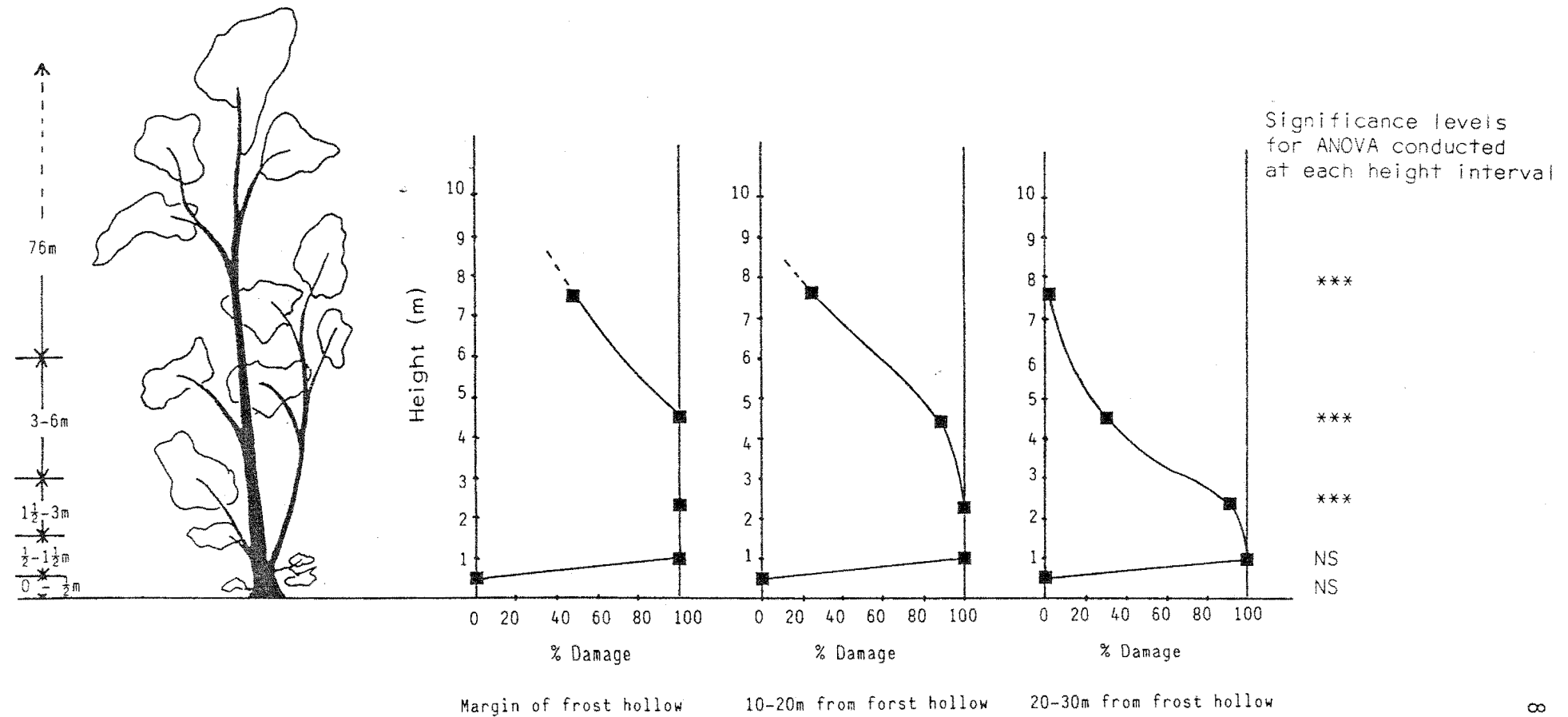
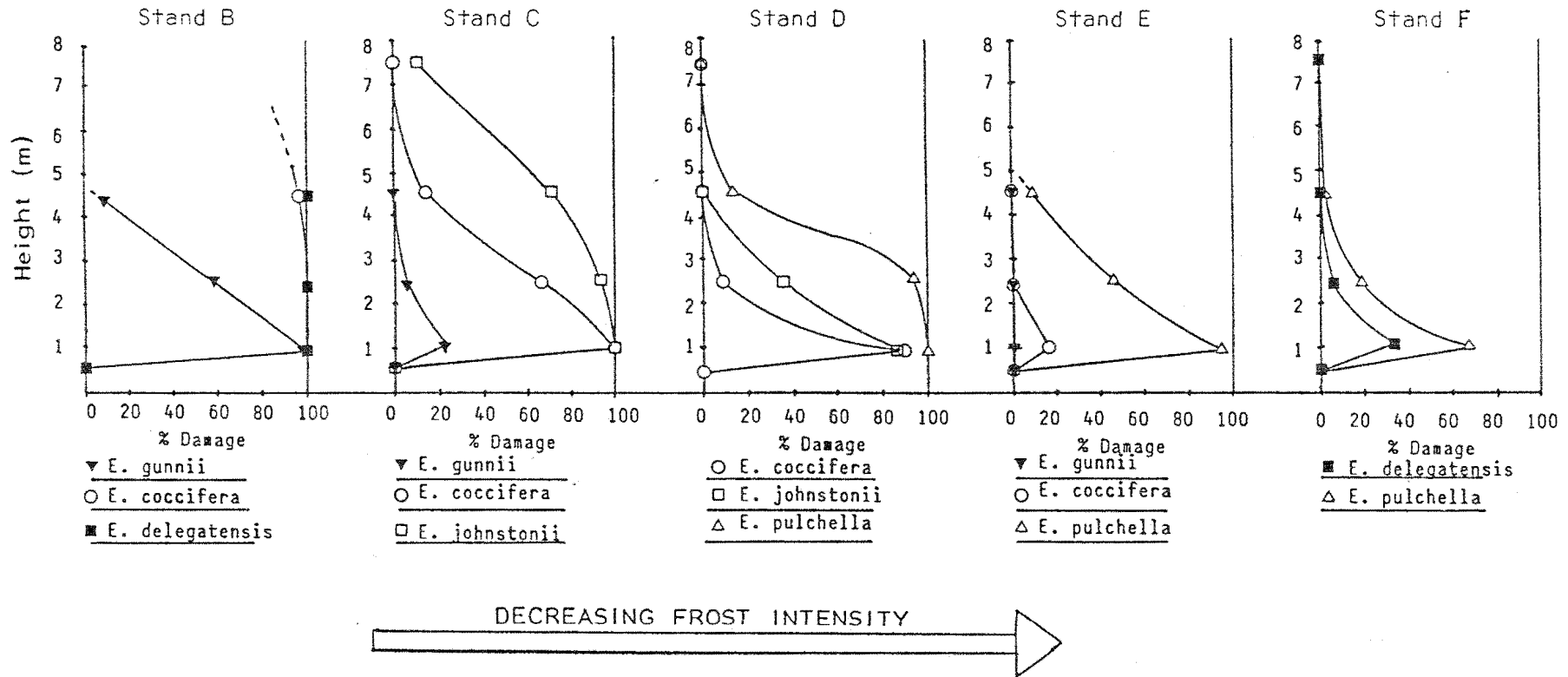


Figure 4.8

Mean percentage crown damage caused by frosts in June 1983, against height above ground for mixed regenerating eucalypt stands (between 454 and 983 stems per stand) at Snug Plains (stands B-F; Fig. 4.1). Generally the SE were too small to indicate but for individual points varied between 0.3% and 14.4% of the mean.



Species order of frost hardiness:-  $E.gunnii > E.coccoifera > E.johnstonii \geq E.delegatensis > E.pulchella$



there were no direct comparisons between E. johnstonii and E. delegatensis (i.e. with both species in the same stand) their relative position in the species order of frost hardiness was inferred by comparisons with other species. E. pulchella was clearly the least frost hardy of the species studied showing substantial defoliation even when other species were virtually undamaged. Comparisons involving E. urnigera were not possible due to lack of suitable stands.

The resulting species order of frost resistance for natural pole stands was (from greatest to least):

E. gunnii > E. coccifera > E. johnstonii > E. delegatensis > E. pulchella.

The order of frost resistance agrees with the natural distributions of the species relative to the depressions at Snug Plains and corresponds with the order of minimum temperature recorded in sites 1 to 6 in stands of each of the species during the severe frosts of 30th June 1983. This strongly suggests that occasional exceptional frosts may be an important factor in determining the distribution of these species in the study site at Snug Plains.

Observations made in the frost damaged stands in the following summer growing season indicated that although many stems were completely defoliated by frost, few individuals were killed outright by frost. The severely frost damaged trees regenerated via epicormic shoots on the stem or lower branches, and coppiced from the lignotuber, which at the time of frost was insulated under 0.5 m of snow. Only in E. delegatensis stands were individuals killed by frost. This was probably a result of the frost sensitivity of the species combined with its characteristically low ability to coppice from the lignotuber. The trees not completely defoliated by the frost regenerated from epicormics on the smaller branches and twigs and rapidly re-established a crown.

Although deaths were not frequent, the dominance patterns within some naturally regenerating stands at Snug Plains were altered substantially by the severe frosts of June 1983. For example, in stand B, a mixed stand of E. gunnii, E. coccifera, and E. delegatensis, most E. delegatensis stems were killed and the remainder severely damaged by frost. Most E. coccifera trees were also severely damaged but resprouted from epicormic shoots between ground level and 0.5 m up the stem (the region insulated by snow). E. delegatensis and E. coccifera were originally co-dominant in the stand with E. gunnii more numerous but subdominant. A single frost nearly eliminated E. delegatensis from the stand, relegated E. coccifera to an infrequent subdominant, and

resulted in dominance passing to E. gunnii. In a mixed stand of E. gunnii and E. johnstonii, near stand C, E. johnstonii received extensive frost damage in comparison with E. gunnii. In places all E. johnstonii individuals had been killed to the lignotuber leaving E. gunnii as dominant in an original codominant mixed stand. At one place in the depression, 50 m south of stand C, all the eucalypt stems including E. gunnii were killed to a height of 0.5 m (approximate snow height on 30th June 1983) by frost.

### 3. Frost Damage to Field Transplant Trials

During October 1981, while the seedlings to be transplanted into the field were "hardening" outside the glasshouse (at the University of Tasmania, Hobart), the temperatures were mild (Fig. 4.9a). The temperatures for Hobart fell below 5°C on only three nights during October and maximum temperatures did not fall below 12.5°C. After transplanting into the field at Snug Plains (on 28th October) the seedlings continued to be exposed to relatively mild conditions. Temperature records for Grove weather station (12 km from the study site) registered only five days with minima below +4°C within the first three weeks of planting (Fig. 4.9b), two days of which were recorded as minor frosts at Snug Plains (Table 4.4). Both the temperature conditions received outside the glasshouse in Hobart and in the field at Snug Plains did not fulfil the temperature pretreatments required for eucalypt seedlings to gain frost hardiness (Harwood 1980; Paton 1981). Either a period of four weeks with nocturnal minima below 4°C (Harwood 1980) or two days of consistent near zero temperatures (Paton 1981) are required for eucalypt seedlings to develop hardiness to frost. Therefore at the time of the frosts in November 1981, the field planted seedlings were in a "softened" state, and likely to be susceptible to frost damage. Two frosts occurred in November 1981, one on the 7th and the other on the 16th. The second of these two spring frosts was the more severe, with subzero minimum temperatures being recorded at all gardens. The frost caused major damage to the "softened" seedlings at two gardens (gardens 3 and 5) and lesser damage in gardens 2, 4 and 6 (Table 4.4, Fig. 4.10a). In all gardens damaged by frosts (gardens 2 to 6) significant interspecific differences existed ( $P < 0.001$ ; Fig. 4.10a). The most severely frost damaged garden was garden 3, where minimum temperatures 0.05 m above ground were -5.5°C (Table 4.4, Fig. 4.10a). All E. delegatensis seedlings were killed while E. pulchella, E. coccifera, E. johnstonii and E. urnigera were reduced to between 5 and 15% of their original leaf tissue. E. gunnii exhibited outstanding resistance to frost while in the "softened" state retaining 85% of its leaf tissue. Duncan's multiple range test for garden 3 indicated that the means for E. gunnii and E. delegatensis were significantly different from means of the other species ( $P < 0.05$ ).



Figure 4.9

Daily maximum and minimum temperatures for Hobart and Grove Weather Stations from 1st October to 30th November 1981.

(Courtesy of the Bureau of Meterology, Hobart)

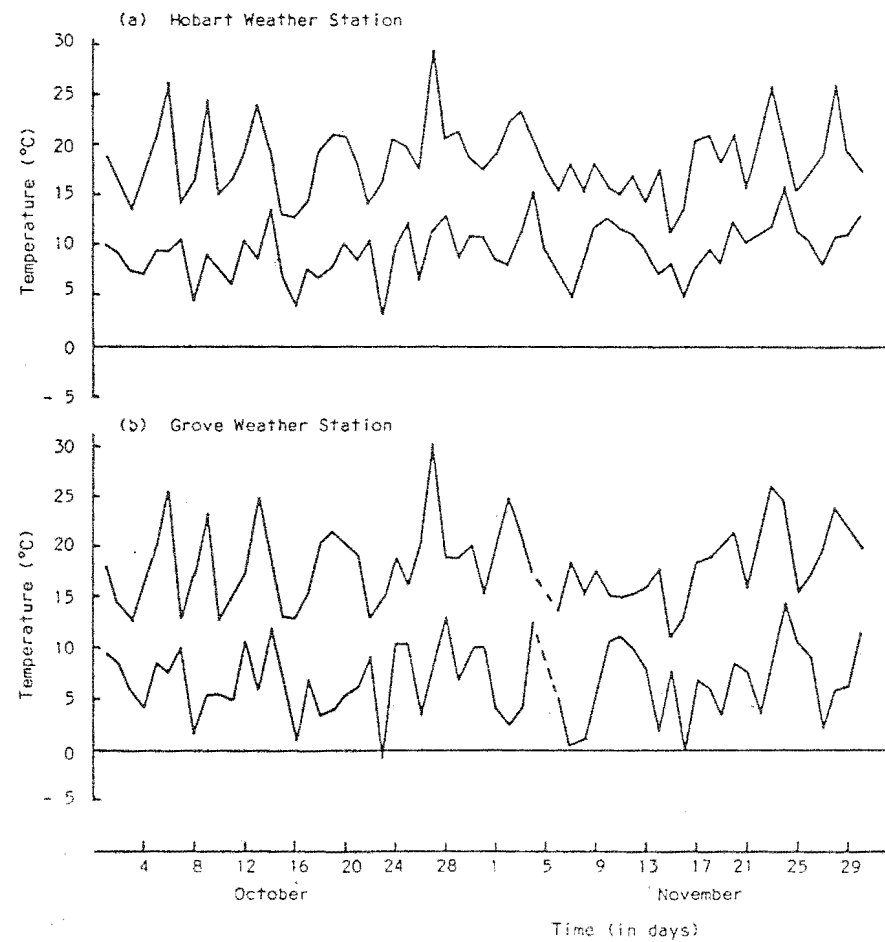


TABLE 4.4

Fortnightly<sup>1</sup> maximum-minimum thermometer records from sites 1 to 6 in the field at Snug Plains for the period 27th August 1981 to 4th December 1981.

| Site of Weather Station | Thermometer height <sup>2</sup><br>(in m) | 9.9.81  |      | 22.9.81 |      | 1.10.81 |      | 14.10.81 |      | 28.10.81 |      | 8.11.81 |      | 24.11.81 |      | 4.12.81 |      |
|-------------------------|---|---|------|---------|------|---------|------|----------|------|----------|------|---------|------|----------|------|---------|------|
|                         |   | Max.  | Min. | Max.    | Min. | Max.    | Min. | Max.     | Min. | Max.     | Min. | Max.    | Min. | Max.     | Min. | Max.    | Min. |
| 1                       | 1.3                                       | 10.5  | 3.5  | 12.5    | 3    | 13      | 3.5  | 13       | 0.5  | 19       | 2.5  | 14.5    | 4    | 12       | -1   | 15      | 3    |
|                         | 0.6                                       | 11.5  | 2    | 12.5    | 2.5  | 14      | 2    | 13       | 0.5  | 19       | 0    | 18      | 3.5  | 13       | -1   | 15.5    | 2.5  |
|                         | 0.05                                      | 11.5  | 1    | 14      | 1    | 15      | 0.5  | 15       | -1   | 20       | -1   | 19      | 3    | 14       | -1   | 16.5    | 2.5  |
| 2                       | 1.3                                       | 11.5  | 1.5  | 14      | 1.5  | 12.5    | 0    | 14       | 0.5  | 18.5     | -1   | 20      | 1    | 12       | -1.5 | 16      | 2.5  |
|                         | 0.6                                       | 12  | 1.5  | 12.5    | 1.5  | 13      | -0.5 | 15.5     | -0.5 | 19       | -1   | 21.5    | 0.5  | 14.5     | -1.5 | 17.5    | 1.5  |
|                         | 0.05                                      | 12  | 1    | 16      | 0.5  | 14      | -0.5 | 17       | -0.5 | 21       | -0.5 | 23.5    | -1.5 | 16       | -0.5 | 20.5    | 1.5  |
| 3                       | 1.3                                       | 11.5  | 3    | 11.5    | 1.5  | 12      | 1    | 11.5     | 0    | 15.5     | 0    | 18.5    | -2   | 10.5     | -3   | 13      | 0    |
|                         | 0.6                                       | 13  | -0.5 | 14      | 0    | 12.5    | -2.5 | 14       | -1.5 | 18.5     | -1.5 | 18.5    | -4   | 12.5     | -5   | 16      | 0    |
|                         | 0.05                                      | 14  | -0.5 | 17.5    | -1.5 | 15      | -3   | 15       | -2   | 20       | -2   | 20      | -4.5 | 14.5     | -5.5 | 17      | -1   |
| 4                       | 1.3                                       | 12  | 1    | 15      | 1.5  | 13.5    | 1    | 15.5     | -0.5 | 20       | -1   | 21      | 2    | 18       | -0.5 | 17      | 2    |
|                         | 0.6                                       | 11  | 1    | 14      | 0    | 14      | -0.5 | 14.5     | -1   | 19.5     | -1   | 22.5    | 1    | 15.5     | -1   | 17.5    | 2    |
|                         | 0.05                                      | 12  | -0.5 | 14.5    | -0.5 | 15.5    | -0.5 | 18.5     | -1   | 22.5     | -2   | 27      | 1    | 17.5     | -2   | 22.5    | 0.5  |
| 5                       | 1.3                                       | 14.5  | -0.5 | 15      | 0    | 15      | 0.5  | 16.5     | -1   | 19       | -2   | 12      | 1.5  | 11.5     | -2.5 | 13      | 1    |
|                         | 0.6                                       | 15.5  | -0.5 | 18      | -1   | 12.5    | 0    | 14       | -2   | 20.5     | -3   | 19.5    | 1.5  | 15       | -2.5 | 15      | 1.5  |
|                         | 0.05                                      | 16  | -2   | 20.5    | -2   | 18      | -1   | 16       | -3   | 22.5     | -4   | 21.5    | 0    | 17       | -3.5 | 17      | 1    |
| 6                       | 1.3                                       | 11  | 4.5  | 12.5    | 0.5  | 10      | 4.5  | 12.5     | 1.5  | 16.5     | 1.5  | 15      | 3    | 13       | -0.5 | 18.5    | 2.5  |
|                         | 0.6                                       | 11.5  | 2.5  | 15.5    | 2    | 13.5    | 2.5  | 12.5     | -0.5 | 19       | -1   | 19.5    | 2.5  | 16       | -1   | 19      | 2.5  |
|                         | 0.05                                      | 14  | 1    | 18.5    | -0.5 | 15      | -0.5 | 16       | -1.5 | 20.5     | -2   | 24.5    | 0.5  | 18       | -1.5 | 21.5    | 2.5  |
| Dates of major frosts   |   |   |      |         |      |         |      | 8.10     |      | 23.10    |      | 7.11    |      | 16.11    |      |         |      |
|                         |   | Planting of seedlings in the field was completed on the 28th October 1981 |      |         |      |         |      |          |      |          |      |         |      |          |      |         |      |

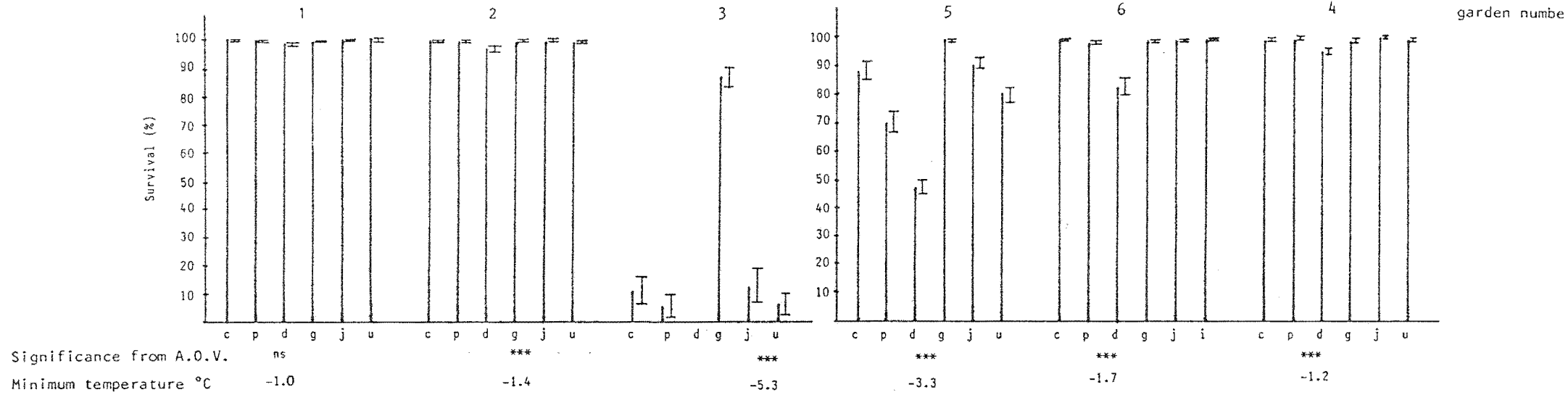
<sup>1</sup>Fortnightly maximum-minimum thermometer records are at approximately 14 day intervals. Each fortnight ends at the date which heads each column.

<sup>2</sup>Height of thermometer above ground.

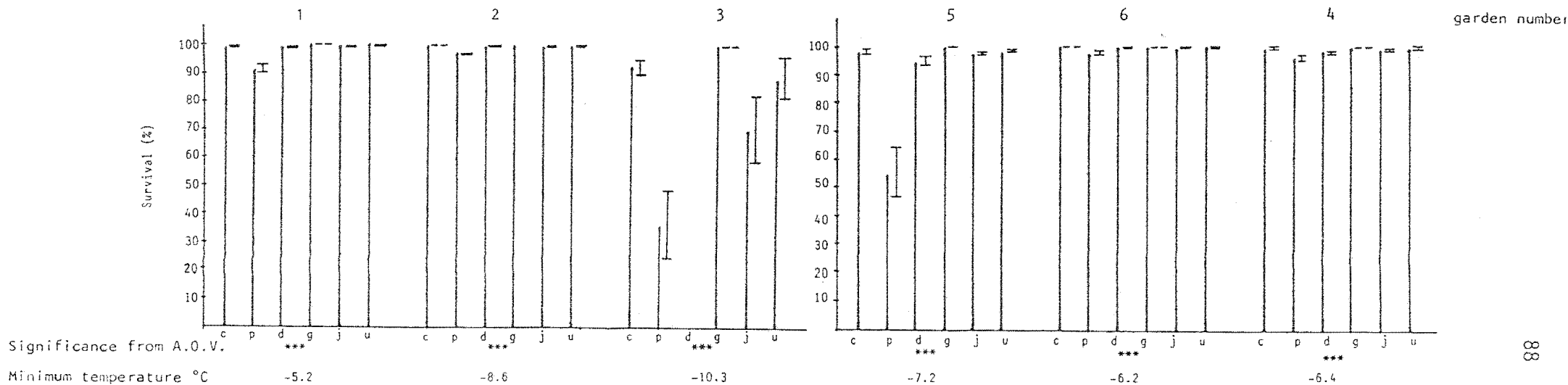
Figure 4.10

Mean percentage surviving leaf area for seedlings of *E. coccifera* (c), *E. pulchella* (p), *E. delegatensis* (d), *E. gunnii* (g), *E. johnstonii* (j) and *E. urnigera* (u) growing in six reciprocal transplant trials (gardens 1-6) at Snug Plains (see Fig. 4.1) and damaged by frosts (a) in the growing season on the 16/11/81 and (b) in winter on the 21/7/82.

(a) Growing season frost



(b) Winter frost



In garden 5 which received a minimum temperature of  $-3.5^{\circ}\text{C}$  frost damage was less catastrophic and interspecific differences in frost survival were clearly demonstrated. E. gunnii survived the frost, retaining nearly 100% of its foliage, followed by E. coccifera and E. johnstonii with about 90% survival. The sequence of species frost survival was then E. urnigera (80%), E. pulchella (70%) and E. delegatensis (approx. 45%). Duncan's multiple range test indicated that all means differed significantly at the 0.05 level, except for: E. coccifera and E. johnstonii; E. coccifera and E. urnigera; and E. urnigera and E. pulchella. In all the gardens damaged by frost E. delegatensis exhibited the lowest frost survival and E. gunnii the greatest. From these results, a species order of frost survival, for "softened" seedlings exposed to growing season frosts in the field could be proposed:

E. gunnii > E. johnstonii > E. coccifera > E. urnigera > E. pulchella >  
E. delegatensis;

In comparison the severe frosts which occurred in the following winter, on the 15th and 21st July 1982, represented two low minima in a period of sustained low temperatures. Temperature records from the Grove weather station indicate that in the 28 days preceding the 21st July only four daily minima were above  $2^{\circ}\text{C}$ , and for 15 days subzero minima were recorded (Fig. 4.4). As field planted seedlings had probably also received near zero nocturnal minima for about four weeks before the severe frosts in July (Table 4.5) it is likely that seedlings were well hardened (Harwood 1980; Paton 1981).

It is evident from comparisons of the frost damage incurred by seedlings exposed to spring and winter frosts that the winter temperature climate at Snug Plains induced the development of a high degree of frost hardiness in several of the species tested. An indication of the extent to which seedlings hardened is given by a comparison of the seedling frost damage which occurred at garden 3 during November with that which occurred at garden 1 in July (both gardens receiving minimum temperatures of about  $-5^{\circ}\text{C}$ ) (Fig. 4.10b). Further, despite the fact that, during the winter frost, temperatures fell to  $-10.5^{\circ}\text{C}$  at garden 3, five degrees lower than in the spring frost ( $-5.5^{\circ}\text{C}$ ), the mean seedling damage at garden 3 was markedly less than for the spring frost (Table 4.5, Fig. 4.10b). The relative severity of frost damage caused by winter and spring frosts at Snug Plains suggests that resistance to frosts during the growing season may be more important than hardiness to winter frosts in determining the survival of seedlings of the species studied.

TABLE 4.5

Monthly<sup>1</sup> maximum-minimum thermometer records from sites 1 to 6 in the field at Snug Plains for the period 8th April 1982 to 7th August 1982

| Site of Weather Station | Thermometer height <sup>2</sup> (in m) | 4.5.82 |      | 10.6.82 |      | 7.7.82      |      | 23.7.82      |       | 7.8.82 |      |
|-------------------------|--|--------|------|---------|------|-------------|------|--------------|-------|--------|------|
|                         |  | Max.   | Min. | Max.    | Min. | Max.        | Min. | Max.         | Min.  | Max.   | Min. |
|                         |  |        |      |         |      |             |      |              |       |        |      |
| 1                       | 1.3                                    | 18     | 0.5  | 12      | -1.5 | 12.5        | -0.5 | 12.5         | -4    | 14.5   | 3    |
|                         | 0.6                                    | 18     | 0.5  | 13      | -2   | 13          | -1   | 13           | -5    | 15     | 2    |
|                         | 0.05                                   | 16.5   | -0.5 | 12      | -2   | 12          | -1.5 | 11           | -5    | 14     | 1    |
| 2                       | 1.3                                    | 17.5   | 0.5  | 14      | -1   | 13.5        | 0    | 14           | -4    | 15.5   | 2    |
|                         | 0.6                                    | 17.5   | -1   | 13      | -2.5 | 11.5        | -1.5 | 13           | -6    | 14     | 0.5  |
|                         | 0.05                                   | 18.5   | -1.5 | 13      | -3.5 | 11.5        | -2.5 | 13           | -8.5  | 13.5   | -1   |
| 3                       | 1.3                                    | 16     | -3   | 12.5    | -6   | 12.5        | -2.5 | 11.5         | -8.5  | 14     | 0.5  |
|                         | 0.6                                    | 17.5   | -4   | 13.5    | -7   | 12.5        | -2.5 | 12.5         | -10   | 13.5   | -0.5 |
|                         | 0.05                                   | 18     | -3.5 | 13.5    | -6.5 | 13          | -2.5 | 12.5         | -10.5 | 14.5   | -1   |
| 4                       | 1.3                                    | 16.5   | -5   | 11      | -1.5 | 11.5        | -0.5 | 9.5          | -5    | 13.5   | 0.6  |
|                         | 0.6                                    | 16     | -1   | 10.5    | -2.5 | 11.5        | -1   | 8            | -6    | 13     | -0.5 |
|                         | 0.05                                   | 13.5   | -1.5 | 10      | -2.5 | 8.5         | -2   | 8            | -6.5  | 12.5   | -0.5 |
| 5                       | 1.3                                    | 16.5   | -1.5 | 12.5    | -2.5 | 13.5        | -2.5 | 13           | -5.5  | 17     | -0.5 |
|                         | 0.6                                    | 18.5   | -1.5 | 14.5    | -3   | 15          | -2.5 | 15           | -5.5  | 18.5   | -1   |
|                         | 0.05                                   | 19.5   | -2.5 | 14      | -4   | 15          | -3.5 | 13.5         | -7    | 19.5   | -2.5 |
| 6                       | 1.3                                    | 16.5   | -0.5 | 13      | -2.5 | 12.5        | 0    | 11           | -5    | 14     | 2    |
|                         | 0.6                                    | 18     | 0    | 14.5    | -1.5 | 13          | -0   | 11           | -5    | 14.5   | 2.5  |
|                         | 0.05                                   | 17.5   | -0.5 | 12.5    | -2.5 | 13          | -1.5 | 12.5         | -6    | 15     | 0.5  |
| Dates of major frosts   |  |        |      |         | 4.6  | 29.6<br>2.7 |      | 15.7<br>21.7 |       |        |      |

<sup>1</sup>Monthly maximum-minimum thermometer records are approximately one month's duration of records. Each recording month ends at the date which heads each column.

<sup>2</sup>Height of thermometer above ground.

The winter frosts produced significant interspecific differences ( $P < 0.001$ ) in seedling frost survival at all gardens (Fig. 4.10b). Seedlings at garden 3 sustained the most severe frost damage (as was the case for spring frosts) with less frost damage inflicted on other gardens experiencing higher minimum temperatures. The severe frost of  $-10.5^{\circ}\text{C}$  at garden 3 produced an order of interspecific differences in frost survival similar to those obtained in spring frosts. E. gunnii survived the frost retaining nearly 100% of its foliage, followed by E. coccifera (90%), E. urnigera (85%) and E. johnstonii (70%). E. pulchella and E. delegatensis with percentage frost survival of 35% and 5% respectively showed least resistance to winter frost. Duncan's multiple range test indicated that the means of all species differed significantly (at the 0.05 level) except for E. coccifera and E. urnigera; and E. johnstonii and E. urnigera. However in all other gardens (1, 2, 4, 5 and 6), receiving minima between  $-5.5$  and  $-7^{\circ}\text{C}$ , E. pulchella showed least frost resistance. Therefore there is evidence to suggest that once hardened, E. delegatensis may be more frost resistant than E. pulchella during winter frosts.

From the results of field planted seedlings exposed to natural frosts during winter a species order of frost resistance for hardened seedlings can be proposed (from greatest to least):

E. gunnii > E. coccifera > E. urnigera > E. johnstonii > E. delegatensis  
> E. pulchella

In spring and winter frosts the species order of frost resistance is quite similar. E. gunnii exhibited outstanding frost resistance in both seasons. E. coccifera, E. johnstonii and E. urnigera show considerable frost hardiness in winter and reduced frost hardiness to spring frosts but with only minor differences in the relative positions of the three species. Relatively speaking, of the three species, E. coccifera showed slightly greater frost resistance in winter, and E. johnstonii showed slightly greater frost resistance in spring frosts. However, the reversal in the order of frost resistance for E. johnstonii and E. urnigera in spring compared with winter frosts may have some ecological significance. E. johnstonii, which naturally occupies the margins of the frost hollows prone to frost at any time of year, showed greater frost resistance to growing season frosts than E. urnigera, which naturally forms stands some distance from the depressions. Further, in all gardens, except garden 3, E. delegatensis and E. pulchella also reversed their relative positions in the order of frost resistance in spring, as compared with winter frosts. In winter E. delegatensis appears to be able to frost harden to a greater extent than E. pulchella. This is not unreasonable when the natural distributions of these two

species are considered. E. delegatensis is a subalpine species normally found in more continental environments with a distinct cold winter season. In comparison, E. pulchella is a coastal species largely confined to dry dolerite ridges in the south-east of Tasmania and experiences a distinctly maritime climate. Selective pressures for the development of winter frost hardiness are unlikely to be very strong in most lowland environments occupied by E. pulchella. The low percentage survival of E. delegatensis at garden 3 in comparison with E. pulchella may not be purely a function of minimum temperature. Garden 3 is situated at the base of a depression at the study site (Fig. 4.1) and is predisposed to severe frosts because of the tendency of cold air to collect at the base of natural depression in the landscape. For the same reasons garden 3 is also predisposed to poor water drainage. High water tables and poor aeration of the soil (Kawase 1981; Bradford & Yang 1981) may well interact with low minimum temperature (Olien 1969; Burdasor in Holubowicz 1978; Regehr et al. 1975) to inflict a greater frost damage on E. delegatensis than other species at garden 3. The greater frost damage inflicted on the Monocalyptus species (E. delegatensis, E. pulchella and E. coccifera) in gardens 3 and 5 than in other gardens also suggests there may be a subgeneric component to the interaction between waterlogging and frost resistance in the eucalypt species tested. In gardens 1, 2, 4 and 6, all situated on well drained sites and receiving temperatures  $-5.0^{\circ}\text{C}$  and  $-8.5^{\circ}\text{C}$  (Fig. 4.10), similar levels of frost damage were recorded. However in garden 5, in a site prone to waterlogging which received a moderate minimum temperature of  $-7^{\circ}\text{C}$ , the Monocalyptus species exhibited relatively greater frost damage than the Symphyomyrtus species, a trend also evident in garden 3.

#### 4. Frost Chamber Trials

Significant interspecific differences in frost survival ( $P < 0.001$ ) were obtained in the frost chamber trials (Appendix 4.3). These interspecific differences in frost hardiness were similar to those obtained in field transplant trials and in the studies of frost injury incurred by naturally regenerating stands in the field. The species order of frost hardiness from frost chamber trials (Fig. 4.11a vi) was:

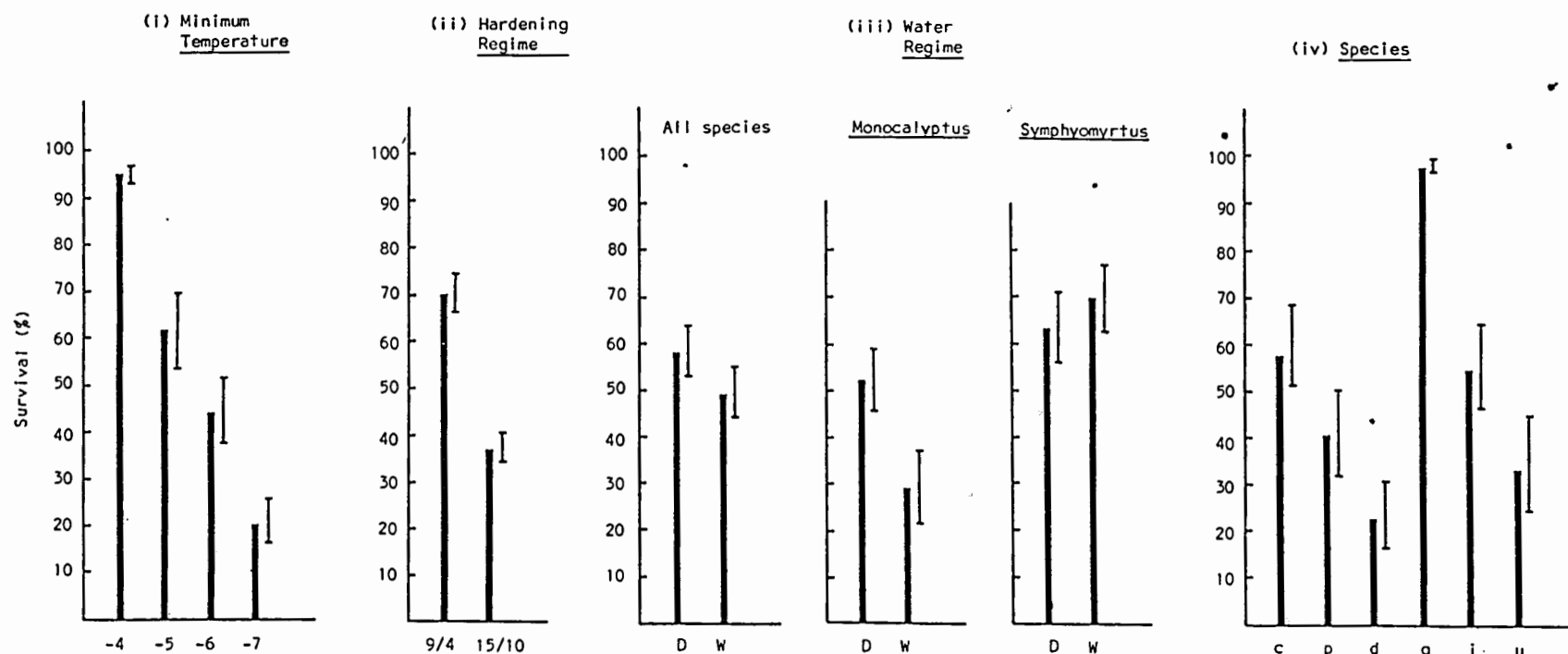
E. gunnii > E. coccifera > E. johnstonii > E. pulchella > E. urnigera >  
E. delegatensis

Duncan's multiple range test indicated the following means were significantly different at the 0.05 level:

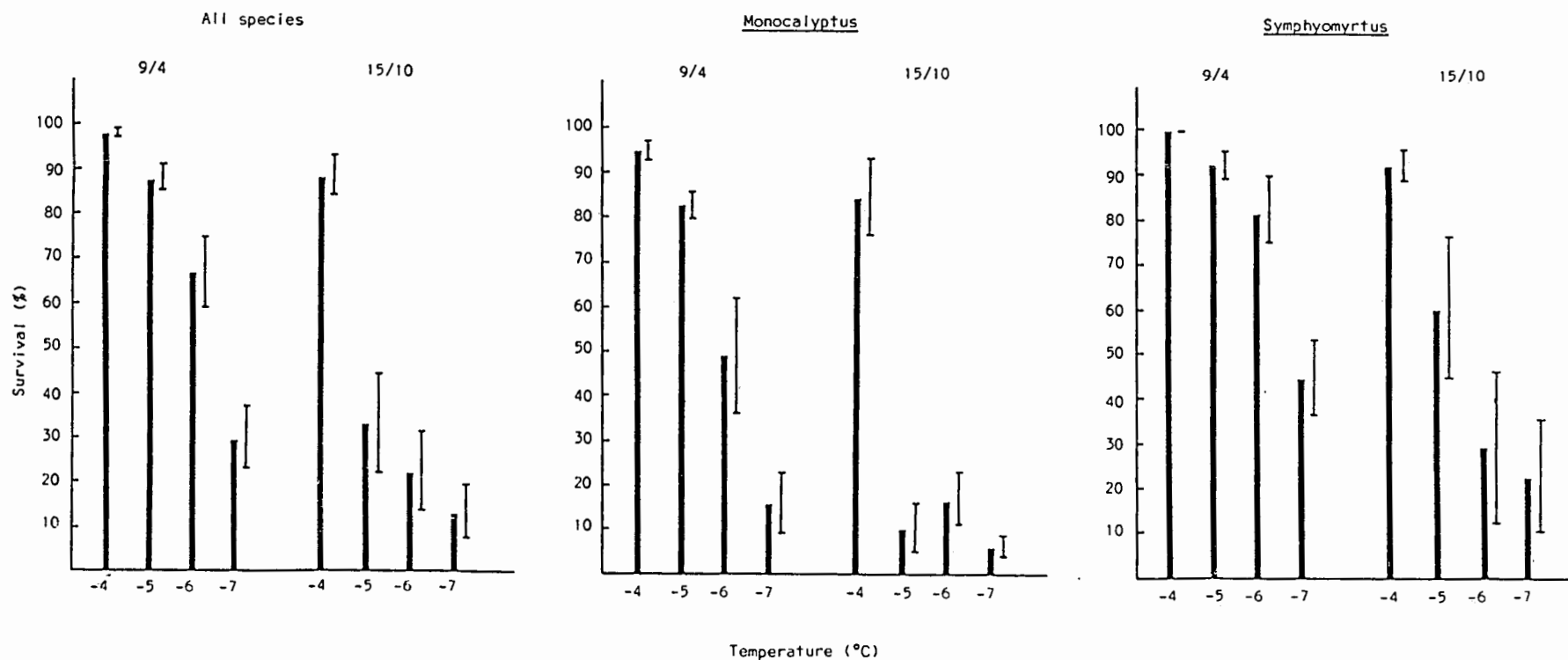
Figure 4.11

Mean percentage seedling survival (undamaged leaf lamina and leaf nodes) for seedlings of *E. coccifera* (c), *E. pulchella* (p), *E. delegatensis* (d), *E. gunnii* (g), *E. johnstonii* (j), *E. urnigera* after frost chamber trials. Presented below are (a) treatment means for (i) minimum temperature ( $-4^{\circ}\text{C}$ ,  $-5^{\circ}\text{C}$ ,  $-6^{\circ}\text{C}$  and  $-7^{\circ}\text{C}$ ), (ii) hardening regime (9°C days/4°C nights and 10°C days/10°C nights), (iii) water regime (fully drained veneers, dry treatment "D" and waterlogged to 2/3 veneer height "W") (for all species data, *Monocalyptus* species data and *Symphyomyrtus* species) and (iv) species; and (b) second order interactions between minimum temperature and hardening regime (for all species data, *Monocalyptus* species data and *Symphyomyrtus* species data), from 4 way analysis of variance performed on the data (Appendix 4.3 and Table 4.6).

(a) Treatment means



(b) Means for minimum temperature x hardening regime interaction





E. gunnii > all other species

E. coccifera > E. urnigera and E. delegatensis

E. johnstonii > E. urnigera and E. delegatensis

E. pulchella > E. delegatensis

Not unexpectedly, frost chamber trials showed that the minimum temperature and the hardening regime had a significant effect on seedling survival. The second order interaction between the above two factors was also significant ( $P < 0.001$ ). However this interaction was largely contributed to by Monocalyptus species. For the Symphyomyrtus species (Fig. 4.11b; and analyses 4 and 5, Table 4.6, Appendix 4.3), both "hardened" and "unhardened" plants showed the same relative responses to minimum temperature; but for the Monocalyptus species (Fig. 4.11b ii; analysis 3, Table 4.6) in the "unhardened" treatment, at temperatures below  $-4^{\circ}\text{C}$ , a dramatic drop in percentage survival occurred which was not evident for "hardened" plants. This suggests that "unhardened" Monocalyptus species are particularly sensitive to severe frosts, a trend which was not evident for the Symphyomyrtus species tested. This result may partly explain the absence of Monocalyptus species from the base of the frost prone depression at Snug Plains, which may receive frosts of  $-5^{\circ}\text{C}$  during the growing season.

Examination of the second order interactions (analysis 1; Appendix 4.3, Table 4.6) of species x hardening regime (Fig. 4.12b) and species x minimum temperature (Fig. 4.12a) indicates that although these interactions are significant ( $P < 0.001$ ) the effects are, to a large extent, conferred by the outstanding frost resistance of E. gunnii. The analysis of the data excluding E. gunnii (analyses 2 and 5; Appendix 4.3, Table 4.4) shows these interactions are not significant (NS) without E. gunnii. Although E. gunnii exhibits exceptional frost hardiness, it probably responds in the same manner as other species to minimum temperature and hardening regime, only the temperature threshold for these responses is substantially lower than the other species tested. These results support field evidence of the outstanding frost resistance of E. gunnii.

The extent of hardening developed by seedlings in the current experiment was not so great as obtained by Harwood (1980) for E. pauciflora. However, E. gunnii was not tested to minimum temperatures which caused any more than minor frost damage. Harwood (1980) showed that three to four weeks exposure to  $16^{\circ}\text{C}$  days and  $4^{\circ}\text{C}$  nights hardened E. pauciflora to frosts of  $-8.5^{\circ}\text{C}$  (with a mean leaf damage of 50%). For the current experiment, after exposure to eight weeks of  $10^{\circ}\text{C}$  days and  $4^{\circ}\text{C}$  nights, E. gunnii exhibited only 9% leaf damage

TABLE 4.6

Table of significance levels for four-way analyses of variance performed on the results of frost chamber trials. Five analyses were performed grouping species in different ways (analyses 1-5; Appendix 4.3).

|                           |      | Analysis       |   |   |  |  |
|---------------------------|------|----------------|---|---|--|--|
|                           |      | (1)<br>all sp. | (2)<br>all sp.<br>(w/o <i>E. gunnii</i> ) | (3)<br><i>Monocalyptus</i><br>(all sp.) | (4)<br><i>Symphyomyrtus</i><br>(all sp.) | (5)<br><i>Symphyomyrtus</i><br>(w/o <i>E. gunnii</i> ) |
| Main effects              | A    | ***            | ***                                       | ***                                     | ***                                      | ***  |
|                           | B    | ***            | ***                                       | ***                                     | ***                                      | ***  |
|                           | C    | **             | **  | ***                                     | NS                                       | NS   |
|                           | D    | ***            | ***                                       | ***                                     | ***                                      | **   |
| 2nd order<br>interactions | AB   | ***            | ***                                       | ***                                     | NS                                       | NS   |
|                           | AC   | NS             | NS  | NS                                      | NS                                       | NS   |
|                           | AD   | ***            | NS  | *                                       | ***                                      | NS   |
|                           | BC   | NS             | NS  | NS                                      | NS                                       | NS   |
|                           | BD   | ***            | NS  | NS                                      | ***                                      | NS   |
|                           | CD   | ***            | **  | NS                                      | NS                                       | NS   |
| 3rd order<br>interactions | ABC  | NS             | NS  | NS                                      | NS                                       | NS   |
|                           | ABD  | *              | NS  | NS                                      | NS                                       | NS   |
|                           | ACD  | NS             | NS  | NS                                      | NS                                       | NS   |
|                           | BCD  | NS             | NS  | NS                                      | NS                                       | NS   |
|                           | ABCD | NS             | NS  | NS                                      | NS                                       | NS   |

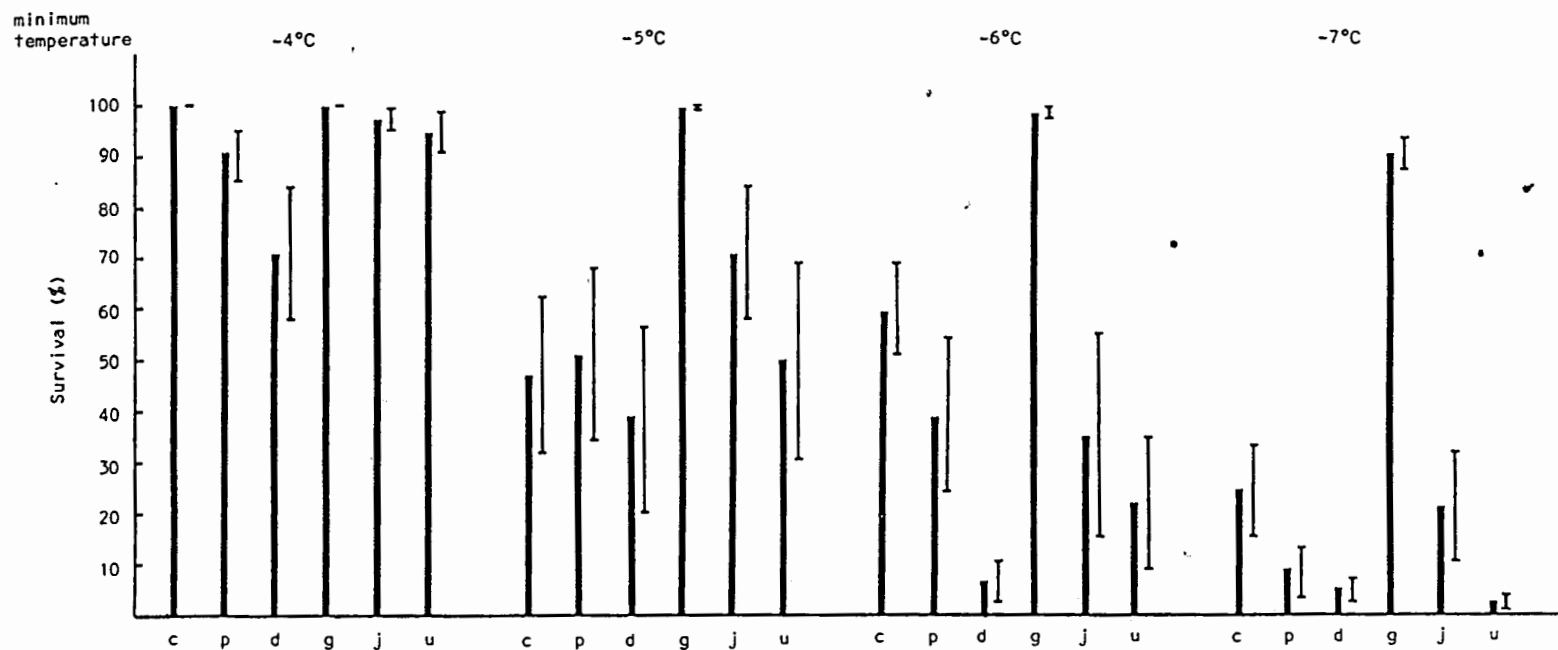
Factors: A - minimum temperature (-4, -5, -6 and -7°C); B - hardening regime (9/4°C or 15/10°C);  
 C - water regime (freely drained or flooded to 2/3 height of the veneer); D - species:-  
 (1) *E. coccifera*, *E. pulchella*, *E. delegatensis*, *E. gunnii*, *E. johnstonii*, *E. urnigera*;  
 (2) *E. coccifera*, *E. pulchella*, *E. delegatensis*, *E. johnstonii*, *E. urnigera*; (3) *Monocalyptus*,  
*E. coccifera*, *E. pulchella*, *E. delegatensis*; (4) *Symphyomyrtus*, *E. gunnii*, *E. johnstonii*,  
*E. urnigera*; (5) *Symphyomyrtus*, *E. johnstonii*, *E. urnigera*

Significance levels: 0.001 \*\*\*; 0.01 \*\*; 0.05 \*; not significant NS

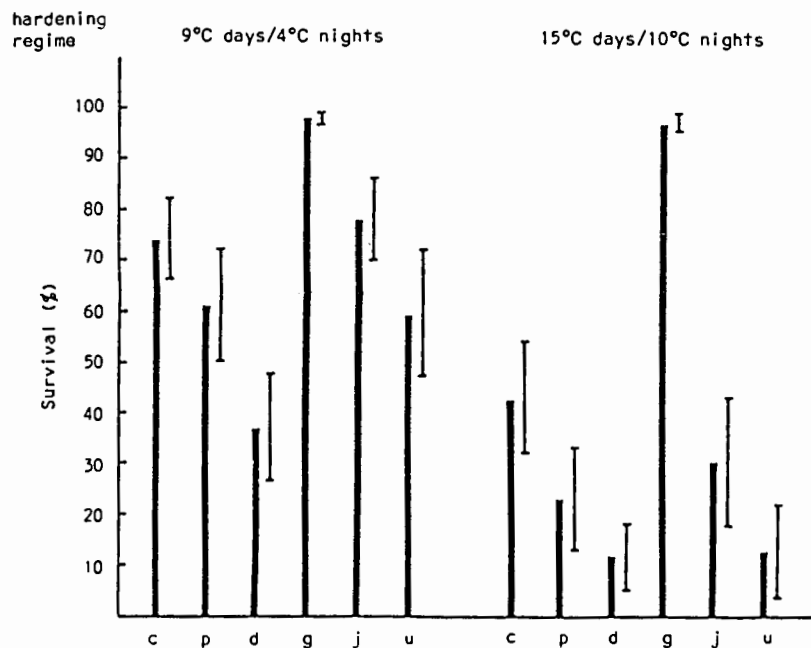
Figure 4.12

Mean percentage seedling survival (undamaged leaf lamina and leaf nodes) for seedlings of *E. coccifera* (c), *E. pulchella* (p), *E. delegatensis* (d), *E. gunnii* (g), *E. johnstonii* (j), *E. urnigera* (u) after frost chamber trials. Presented below are second order interactions between species and (a) minimum temperature, (b) hardening regime and (c) water regime, from 4 way analysis of variance performed on the data (Appendix 4.3, Table 4.6).

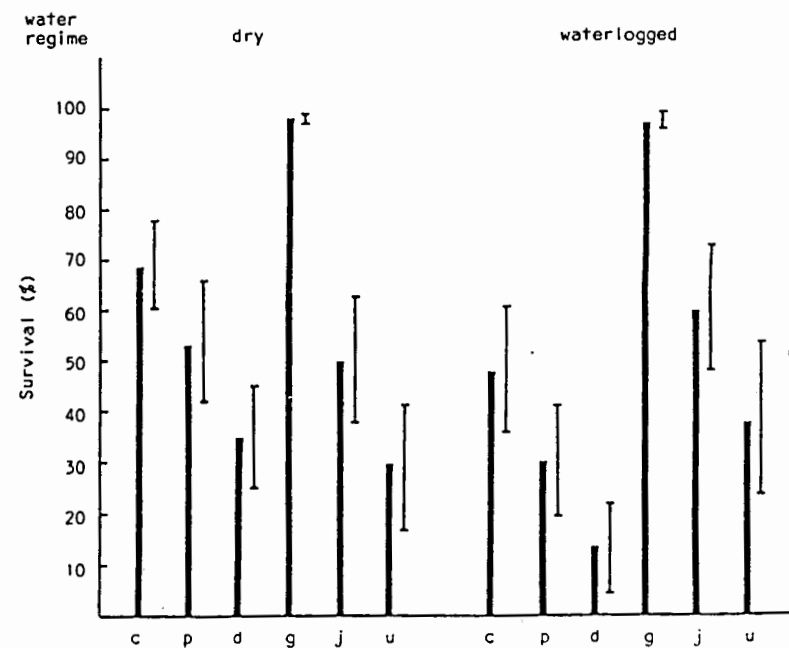
(a) Means for species x minimum temperature interaction



(b) Means for species x hardening regime interaction



(c) Means for species x water regime interaction



when exposed to  $-7^{\circ}\text{C}$ , although other species suffered between 60% and 90% leaf damage. It is possible hardening may have been delayed or reversed by occasional rises in temperature within the growth cabinet used for "hardened" treatment, caused by icing of the cooling system. Rapid dehardening may occur in eucalypts exposed to periods of warm conditions (Paton et al. 1979; Paton 1980, 1981). Alternatively, exposure to near zero temperatures for short periods (Paton et al. 1979; Paton 1980, 1981) may be necessary to develop frost hardening in seedlings which approaches that observed in the field.

The water regime also influenced the seedling survival in the frost chamber trials. After frost, the percentage survival of seedlings exposed to the "dry" treatment (freely drained veneers) was significantly greater ( $P < 0.01$ ) than the "wet" treatment (water table at  $2/3$  the height of the veneer) (Appendix 4.3, Table 4.6, analyses 1 and 2; Fig. 4.11a iii). However, this effect was largely contributed by seedlings from subgenus Monocalyptus (Table 4.6, analyses 3 and 4, Fig. 4.11b). Analyses performed on subgenus Monocalyptus and Symphyomyrtus separately indicated the effect of water regime was significant for Monocalyptus ( $P < 0.001$ ) but not for Symphyomyrtus. Further, the within subgenus interactions of water regime x species were not significant for either subgenus (Table 4.6, analyses 3, 4 and 5), yet the interaction for analysis including all species (Table 4.6, analysis 1) was significant ( $P < 0.001$ ). This suggests that the water regime x species interaction in analysis, performed on all species, was largely an inter-subgeneric effect. This agrees with the natural distribution of these species at the study site on Snug Plains. At Snug Plains species from subgenus Symphyomyrtus tended to inhabit the less well drained sites. The distribution of E. gunnii was largely restricted to the waterlogged and frost prone habitats. The distribution of E. johnstonii also included such sites, while the distribution of E. urnigera had less tendency to include frost prone and waterlogged sites at Snug Plains. On the other hand, species from subgenus Monocalyptus tended to inhabit drier or better drained sites, including shallow ridge slopes or better drained rises in the low lying areas (see Figs 4.1 and 4.2).

## DISCUSSION

An examination of the temperature microclimate within the study site on Snug Plains indicated that marked temperature gradients existed over short distances during radiation frosts. As much as  $7.3^{\circ}\text{C}$  difference in minimum temperature near the radiating surface may occur between the base of the

depression and the neighbouring ridge slopes, a distance of 200 m. Temperature gradients of this magnitude have not previously been recorded in Tasmania and are quite comparable with those recorded for Seventeen Flat (Harwood 1981, 1983; Moore & Williams 1976) and Cooleman Plain (Jennings 1979) in the Snowy Mountains. An absolute minimum temperature of  $-22.5^{\circ}\text{C}$  was recorded near the snow surface during a severe frost in June 1983, which is a record for Australia. Frosts of this severity have been reported in the past (Calder 1850; Hooker 1844) but probably only occur on average once every 25 to 100 years.

A severe frost may have a more pronounced effect on a eucalypt forest than a fire (Jackson 1973). When individuals killed by frost release seed from the crown, the seed falls, not into the open seed bed left by a fire but into the grass sward understory vegetation which survived the frost. Slow regeneration rates in frost killed stands in the depression in the landscape may also lead to more waterlogged soil conditions at these sites (Jackson 1973). The survival and establishment of eucalypt seedlings in waterlogged condition and in competition with the grass sward may be very low (Harwood 1976, 1983; Jackson 1973). After exceptional frosts like those described by Calder (1850) and Hooker (1844) where large tracks of mature eucalypt forest were killed by frost, there may be little or no regeneration from the original stand (Calder 1850), and reinvasion of these frost prone habitats may be dependent on marginal encroachment from stands on the surrounding hill slopes. The same rationale holds for mixed eucalypt stands in which one member of the stand is eliminated by frost, as occurred in stand B at Snug Plains.

Frost damage incurred by natural mixed stands in the field demonstrated that marked interspecific differences in frost resistance existed for the 5 species studied. The species order of frost hardiness obtained (*E. gunnii* > *E. coccifera* > *E. johnstonii* > *E. delegatensis* > *E. pulchella*) agreed with the order of minimum temperatures recorded within stands of each of the species during the June 1983 frost and with the natural distribution of the species with respect to the depressions in the landscape at Snug Plains and strongly suggests that occasional severe frosts are a major factor determining the distribution of eucalypts in the subalpine environment at Snug Plains. The order of frost resistance obtained for the above species also agrees with observations of frost damage on exotically planted trees (Martin 1948) and from frost chamber studies (Sakai *et al.* 1981). Further, these interspecific differences in frost resistance were demonstrated for species from the same small geographical area. Results were not complicated by the clinal (Pryor 1956; Green 1969) or

ecotypic (Pryor 1956; Ashton 1958; Green 1969; Boden 1958; Paton 1972; Eldridge 1968; Kirkpatrick 1975; Marien 1980; Potts 1983; Harwood 1981) variation in frost resistance common in the genus.

Generally the severe frosts killed few individuals in a stand, most resprouted from lignotubers or epicormic buds. However, the differential frost damage inflicted in mixed stands caused changes in species dominance which could have an important effect on the eventual dominance in the stands.

In the Snowy Mountains and the Highlands of Tasmania frosts may occur in any month of the year (Jackson 1973; Harwood 1980; Jennings 1979; Costin 1954; Paton 1981). Although winter frosts are more extreme and may inflict damage on hardened trees in the field during exceptional winters, frosts during the growing season may inflict more damage both on crop plants (Horuichi & Sakai 1978) and forest trees growing in frost prone sites (Burke et al. 1976; Harwood 1976, 1983). The development of hardening in plants and its importance in protecting living tissue against the extreme minimum temperatures experienced during winter has been studied and discussed in great detail, not only for the hardy deciduous and evergreen trees of the Northern Hemisphere (Weiser 1970; Burke et al. 1976; Li & Sakai 1978) but also in the subalpine and treeline species in Australia (Sakai et al. 1981; Paton 1980, 1981; Harwood 1980, 1981; Moore & Williams 1976) (See Appendix 4.1). However, apart from studies of seasonal changes in the frost hardiness of E. pauciflora and E. stellulata seedlings (Harwood 1976, 1983), little attention has been drawn to the importance of the relative frost resistance of eucalypts in the unhardened state in environments where unseasonal frosts are a common occurrence. At Snug Plains growing season frosts of  $-5.5^{\circ}\text{C}$  inflicted substantially more severe frost damage on seedling transplant trials than did winter frosts of  $-10.5^{\circ}\text{C}$ . E. gunnii was the only species to show substantial resistance to these growing season frosts. The exceptional frost resistance of E. gunnii while in the unhardened state may be as important in conferring a selective advantage in frost hollow sites as resistance to frost damage during severe winter frosts. Other species exhibited low levels of survival in growing season frosts.

Generally the order of frost resistance obtained from the seedling transplant trials and the frost chamber trials agreed with the species order obtained in the frost damaged mixed stands in the field. However in the field transplant trials, two of the species tested exhibited markedly different relative frost hardiness in growing season frosts in comparison with winter

frosts. During growing season frosts and in the unhardened state, E. pulchella was more frost resistant than E. delegatensis, but once hardened, the species positions were reversed. This probably reflects the difference in habitat normally occupied by the two species. E. delegatensis is a more continental species normally occupying upland and subalpine regions far from maritime influences, with a distinct cold winter season. In comparison E. pulchella is a coastal species, almost exclusively confined to dry dolerite hillsides, an environment in which strong selective forces for the development of winter frost hardiness are not present. The distributions of E. pulchella and E. delegatensis at Snug Plains supports this contention. E. pulchella is confined to the least frost prone sites on the ridge tops, and is probably limited in its distribution by occasional severe winter frosts. The stands of E. delegatensis are generally on ridge slopes or higher ground away from the frost hollow, but in stands near the frost hollow, E. delegatensis occupies sites which experience consistently low minimum temperatures in winter, suitable for rapid development of hardening and sites protected to some extent from growing season frosts. However, for E. pulchella hardiness to spring frosts may be, in part, a preadaptation, conferred by extreme drought hardiness (see Chapter 6). Studies of water stress and its influence on frost hardiness indicate that prior exposure to water stress increases frost hardiness in many species (Parsons 1978; Parsons & Li 1978; Chen & Li 1977; Chen et al. 1975, 1977; Cloutier & Simonovitch 1982), although Kirkpatrick (1975) concluded that frost and drought hardiness were not correlated for E. globulus. Further, the frost hardiness observed in the Snug Plains population of E. pulchella may be greater than is characteristic for the species as a result of hybridisation and introgression with E. coccifera (see Chapter 2) at their common boundaries. Some introgression of E. coccifera genes conferring an increased frost resistance in the Snug Plains population of E. pulchella cannot be ruled out.

The reversal of relative frost hardiness of eucalypt species exposed to winter frost (while plants are in a hardened state) and growing season frosts (while plants are in an unhardened state) have not previously been demonstrated, although the importance of growing season frost and their influence on the distribution of eucalypt species has been recognised (Costin 1954; Jackson 1973; Harwood 1983; Zohar et al. 1981). The relative frequency of severe winter frosts and growing season frosts may have an important bearing on the distribution of eucalypt species in regions with a complex array of lowland and upland eucalypt species such as Snug Plains.

To a large extent the importance of waterlogging of the soil and its influence on frost hardiness has been overlooked in ecological studies. High soil moisture levels influence frost hardiness by affecting tissue hydration (Olien 1969; Burke et al. 1976) and soil temperature, through the buffering effect of the latent heat of fusion of water (Burke et al. 1976). When the soil temperature and air temperature differ greatly, as occurs in waterlogged soils during frost, there is a tendency for more severe frost damage to be inflicted on the plants present (Holubowicz 1978; Zohar et al. 1981; Burke et al. 1976). Hardening in many woody plants involves reducing tissue water content either by increasing root resistance or by increased transpiration (Parsons 1978; McKenzie et al. 1974). This may be of particular importance for plants occupying waterlogged sites. For eucalypts it has been shown that seasonal factors such as high soil moisture may reduce resistance to frost (Zohar et al. 1981) and that waterlogging influences dehardening (Paton et al. 1979) by reducing metabolic activity of the root system. There is also evidence to suggest that the root system of species from subgenus Symphyomyrtus are more tolerant of waterlogged conditions than species from subgenus Monocalyptus by maintaining an active root system (see Chapter 5). The current results indicate that Symphyomyrtus species harden more effectively in waterlogged conditions than do Monocalyptus species. This may be facilitated by a more active root system (Paton et al. 1979) which either promotes increased root resistance (Paton 1978) or produces hardening promoting factors (Paton 1981). Alternatively increased transpiration may allow the necessary tissue hydration changes for hardening in subgenus Symphyomyrtus (McKenzie et al. 1974).

The current studies demonstrated marked changes in relative resistance to frost in waterlogged and dry soils for the species studied, both in field transplant trials and frost chamber studies. For example, in frost chamber trials the species order of frost hardiness in "wet" treatments was: E. gunnii, E. johnstonii, E. coccifera, E. urnigera, E. pulchella, E. delegatensis, but in "dry" treatments was: E. gunnii, E. coccifera, E. pulchella, E. johnstonii, E. delegatensis, E. urnigera. It is possible that the coldest sites on Snug Plains may be occupied by stands of E. gunnii, E. coccifera or E. johnstonii depending on the interactive effects of frost and waterlogging. The distribution of these species in the field support this being the case. E. gunnii occupies sites at the base of the frost hollows where minima are most extreme and soils consistently waterlogged. On slightly elevated areas, waterlogged but with some throughflow of water, E. johnstonii is present. On the better drained rises still within the frost hollow and exposed to intense minima E. coccifera is present.



In a similar manner, the relative species representation in mixed stands of E. delegatensis and E. urnigera may in part be determined by the interactive effects of frost and waterlogging.

As well as distinct interspecific differences in frost resistance, the current studies provide strong evidence that differences exist between the eucalypt subgenera in their responses to frost. Both the field transplant trials and frost chamber studies suggest that the Monocalyptus species incurred relatively greater frost damage in the unhardened state than the Symphyomyrtus species. Further, Monocalyptus species were less frost resistant in waterlogged soils than in dry soils, a characteristic not evident in the Symphyomyrtus species. The frost sensitivity of Monocalyptus species in waterlogged soils may preclude their presence in these sites at Snug Plains. The natural distribution of the Monocalyptus species at Snug Plains agrees with this being the case. The Monocalyptus species occupy the well drained ridge slopes surrounding the frost hollows and better drained rises within the frost hollows. The Symphyomyrtus species, particularly E. gunnii and E. johnstonii occupy the poorly drained and frost prone depressions, with E. gunnii sole dominant at the base of the frost hollow.

The current study indicates that frost may be an important selective agent in determining the composition of eucalypt stands in subalpine environments. However in the early stages of stand ontogeny (the seedling stages) the type of frosts which cause damage to a stand differ from those which cause damage to a sapling or mature stand. In the early seedling stages of a forest, frosts which occur in the growing season producing subzero temperatures in regions close to the ground surface may be very damaging, as observed in the field transplant trials at Snug Plains. Also during the early stages in forest ontogeny, the total transpiration levels are low and there is more tendency for soils to become waterlogged, thus species sensitive to frost in moist soils will be selected against in the seedling stage. However, seedlings have the advantage of being protected from intense winter frosts by an insulative layer of snow which invariably falls preceding a period of intensely cold conditions. Once a forest has reached the pole stand stage (for this discussion, a pole stand consists of trees between 2 and 6 m in height) mild growing season frosts do not pose so much of a threat to survival because the sensitive growing apices are above the zone where subzero temperatures occur. On the other hand pole stands are exposed to the rigours of intense winter frosts which may develop a lens of cold air 1 m to 10 m thick (Moore & Williams 1976). Therefore intense winter frosts as opposed to growing season frosts are

probably most damaging to forests in the pole stand stage. Once forest trees have gained crown heights exceeding that of the lens of cold air which collects during intense winter frosts the crowns are safe from frost damage. Temperatures below  $-16^{\circ}\text{C}$  are required before the stem tissue of eucalypts is killed (Sakai *et al.* 1981; Martin 1948). The presence of a dense forest stand may also halt or inhibit the movement of cold air within the stand (Geiger 1971) and reduce the radiant heat loss from the forest floor (Nunez & Sander 1982) thus ameliorating the microclimate within the stand.

Thomas and Barber (1974) suggested that the glaucous-leaved cline form of *E. urnigera* survived more extreme frosts than the green-leaved cline form by supercooling of the leaf tissue thus avoiding freezing, although (Paton 1981) reported little consistency in the relationship between glaucousness and frost resistance for *E. urnigera*. The current frost trials provided no evidence to suggest leaves were supercooling or that glaucousness was influencing frost survival. Observations of seedlings exposed to frosts during the frost chamber trials indicated that, at all trial temperatures ( $-4^{\circ}\text{C}$  to  $-7^{\circ}\text{C}$ ) the leaf tissue of the seedlings tested was frozen. Leaves were rigid as a result of intra- or extra-cellular freezing (Weiser 1970). Of the three most frost hardy species *E. gunnii*, *E. coccifera* and *E. johnstonii*, two were glaucous (*E. gunnii* and *E. coccifera*) and one was green (*E. johnstonii*). The least frost hardy species was *E. delegatensis*, which has glaucous juvenile leaves. However, the glaucousness of *E. delegatensis* was a "structural" glaucousness (Barber 1955) in comparison with the "waxy" glaucousness found in the other species tested. Seedlings that survived frosts of  $-4^{\circ}\text{C}$  to  $-7^{\circ}\text{C}$  in the current trials survived by tolerance of extracellular ice formation (Weiser 1970) rather than by avoidance through supercooling (Thomas & Barber 1974; Burke *et al.* 1976). This agrees with results obtained in frost chamber trials on other eucalypt species (Harwood 1980; Paton 1981).

## CHAPTER 5

### WATERLOGGING

#### INTRODUCTION

In the previous chapter it was demonstrated that subgeneric differences in tolerance to frost in waterlogged soils existed for the 6 eucalypt species tested. In particular the Symphyomyrtus species were more tolerant to frost in waterlogged soils than the Monocalyptus species. In this chapter interspecific differences in tolerance to waterlogging are investigated further. Although Eucalyptus is more characteristic of dry environments, its distribution encompasses periodically waterlogged sites (Boden 1963; Ladiges & Kelso 1977). Like many other woody species which occupy waterlogged habitats (Gill 1971), eucalypt species which naturally occur in waterlogged sites may exhibit morphological adaptations in response to waterlogged conditions (Clemens & Pearson 1977; Clemens et al. 1978; Pereira & Kozlowski 1977; Sena-Gomes & Kozlowski 1980; Ladiges & Kelso 1977; Boden 1963). Marked differences in tolerance of waterlogging and in morphological adaptations produced in response to waterlogging, have been demonstrated both intraspecifically (Ladiges & Kelso 1977; Ladiges & Ashton 1974; Clucas & Ladiges 1979) and interspecifically (Clemens & Pearson 1977; Clemens et al. 1978; Pereira & Kozlowski 1977; Sena-Gomes & Kozlowski 1980; Boden 1963; Davidson 1978) for eucalypts. However, few studies have investigated the importance of waterlogging as an ecological factor in delimiting the distributions of eucalypt species. From the results of glasshouse trials, Ladiges and Kelso (1977) suggested the respective ecological positions of E. ovata and E. viminalis might be determined by differences in growth in waterlogged conditions. Davidson (1978) also demonstrated that differences in waterlogging tolerance existed for glasshouse grown seedlings of 6 eucalypt species (E. gunnii, E. johnstonii, E. urnigera, E. delegatensis, E. coccifera and E. pulchella) grown in field soils and exposed to a range of water regimes from waterlogged to freely drained. Some preference for soil type was also observed with many species growing better, on a comparative basis, in the soil type and water regime most similar to those at the site of origin of the species in the field. Further, these differences in tolerance to waterlogging showed distinct subgeneric trends.

In order to determine whether waterlogging was an important factor in delimiting the eucalypt stands at Snug Plains, investigations were made of the water status of the soils in naturally occurring mixed and pure eucalypt stands at the study site and of the comparative growth of seedlings in a transplant trial established in a waterlogged site at Snug Plains. These investigations were supplemented by glasshouse trials in which the physiological and anatomical effects of extended periods of waterlogging were investigated using mixed pairs of eucalypt seedlings. Preliminary studies designed to investigate the influence of soil nutrient status on the competitive ability of three Symphyomyrtus species grown in waterlogged soils were also conducted.

A literature review outlining the biochemical effects of waterlogging, and the morphological and physiological adaptations of plants to waterlogging is presented in Appendix 5.1.

## MATERIALS AND METHODS

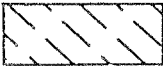




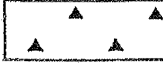

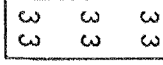
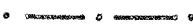
### Field Studies of Soil Moisture Status

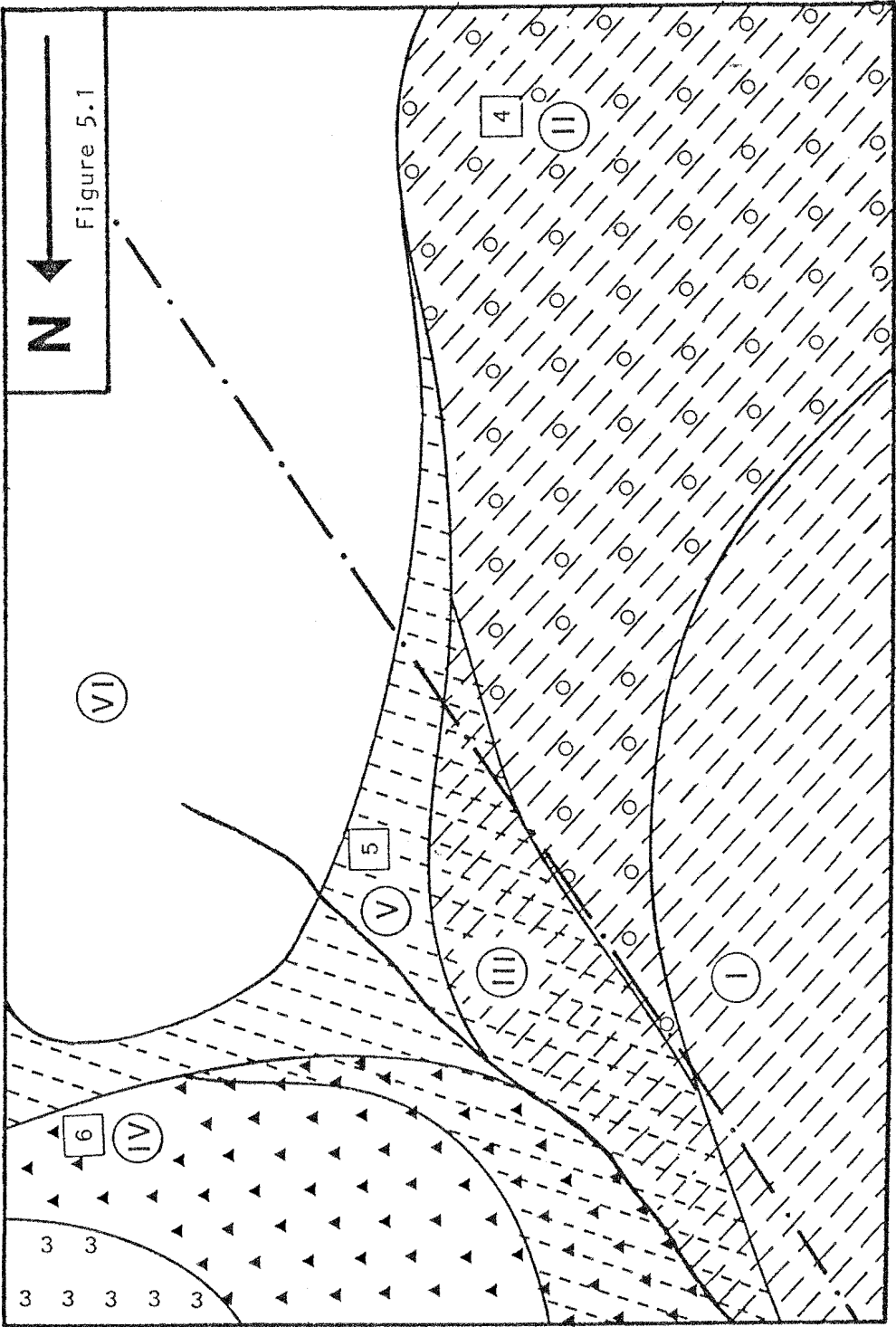
At the western side of the study area (Fig. 4.1, Chapter 4) a steep east facing ridge forms a boundary to the frost hollow and rises to a height of 100 m above the frost hollow. On the lower slopes of this ridge a complex mosaic of eucalypt distributions are present comprised of three species from subgenus Symphyomyrtus (E. gunnii, E. johnstonii and E. urnigera) and two species from subgenus Monocalyptus (E. coccifera and E. delegatensis). Abrupt boundaries occur between species from the same subgenus but species from different subgenera intergrade forming mixed stands (Fig. 5.1). The region is almost bisected by a major geological disconformity. The north-eastern part of the region has a bedrock of Triassic sandstone whereas the south-western portion has a bedrock of Jurassic dolerite (Fig. 5.1). After weathering the soils derived from these two rock types differ considerably in structure, pH and nutrient status (Tables 3.2 and 3.3, Chapter 3).

Six sites (I-VI, Fig. 5.1) representative of the various stands in the region were chosen for measurement of soil moisture status. Soil profiles were dug at sites I-VI on five occasions between December 1982 and April 1983. From the approximately 1.0 m deep profiles, dug on a single day, soil samples were collected from each of the major soil horizons and returned to the laboratory where the gravimetric water contents were measured and pF curves were

Figure 5.1

Map of the distribution of eucalypt species in the northwestern corner of the study area, and position of the stands (I-VI) in which soil studies were conducted.

| <u>Legend</u>   | <u>Stand Composition</u>  |
|---|---|
|    | <u>E. delegatensis</u>  |
|   | <u>E. delegatensis</u> and <u>E. urnigera</u>   |
|  | <u>E. delegatensis</u> and <u>E. johnstonii</u>   |
|  | <u>E. johnstonii</u>  |
|  | <u>E. johnstonii</u> and <u>E. coccifera</u>  |
|  | <u>E. coccifera</u>   |
|  | <u>E. gunnii</u>  |
|  | Hummock sedgeland (mainly <u>Gymnoschoenus sphaerocephalus</u> )  |
|  | Geological boundary between bedrock of Jurassic dolerite (to the southwest) and Triassic sandstone (to the north east). |
| 4, 5 & 6  | Sites of reciprocal transplant trials.  |



generated. The gravimetric water content was obtained for approximately 50 g of soil, oven dried at 105°C. The pF curves were generated using the filter paper method (after Hamblin 1981).

To obtain the pF curves the soil was air dried, ground and passed through a 2 mm sieve. Twelve replicate 30 g samples of soil from each horizon were placed in tared soil tins and 2 ml incremental aliquots of distilled water from 0 to 20 ml inclusive were added to the respective tins. The soil and water in each tin was then mixed thoroughly with a glass stirring rod and three "Whatman 42" filter papers placed on the soil surface before the lids were sealed. The tins were left at room temperature for five days before the gravimetric moisture content of the soil and the middle filter paper were obtained. The water potential of the soil for each tin was then obtained knowing the moisture retention characteristics of the filter paper (Hamblin 1981; Fawcett & Collis-George 1967), and the pF curves plotted (Appendix 5.2). The pF curves were then used to convert the gravimetric moisture contents of the field samples to water potentials (matrix potentials). Although pF curves produced by the filter paper method may be approximate, because of changes in pore size and bulk density caused by drying and grinding soil samples, they provide a quick and acceptably accurate method for ecological research (Hamblin 1981).

### Field Transplant Trials

Six reciprocal seedling transplant trials were established in the field at Snug Plains were completed in October 1981 (for details see Chapter 3). In the most waterlogged of the gardens (garden 3), situated at the base of the frost hollow, seedlings were extensively damaged by frost soon after planting and a replacement plot (garden 3b) was planted (for details see Chapter 4). Seedling height, stem diameter, number of nodes and number of expanded leaves of the garden 3b seedlings were measured on two occasions (29/11/81 and 2/1/82) during a frost free period. The morphological adaptations and the symptoms of injury in response to waterlogging were recorded for each seedling, and the percentage of live leaf area remaining was calculated. Analysis of variance and Duncan's multiple range test were performed on the angularly transformed data of percentage surviving leaf area for garden 3b.

### Glasshouse Waterlogging Trials

Seed was collected from six trees of each of the Monocalyptus species, E. coccifera and E. delegatensis, and the Symphyomyrtus species, E. urnigera and E. johnstonii growing in natural stands in the study area. Seeds were stratified, germinated on moist vermiculite and at the cotyledonary stage were pricked out into 5 cm diameter plywood veneer tubes filled with potting soil. The seedlings were grown in the glasshouse at the University of Tasmania for three months and transferred outside the glasshouse for a further three months to harden. From the large progenies grown vigorous seedlings were selected on the basis of similarity in size and planted in pairs into large, 4 litre plastic pots filled with potting soil. For each pot two seedlings of different species were planted together (stems 5 cm apart) at the centre of the pot. Two species combinations were grown: E. delegatensis plus E. urnigera and E. coccifera plus E. johnstonii. Sixteen replicate pots were planted for each species combination. The pots were placed in randomised block design, and grown for six months in the glasshouse. Seedlings were watered daily. Nutrient was provided as slow release fertilizer (osmocote and blood and bone) present in the potting soil.

By December 1982 (27/12/82) the mean height of seedlings was about 0.7 m. Inspection of selected pots indicated that the root systems of both species had ramified through each pot and were intimately intertwined. Eight replicate pots for each species combination were then randomly chosen and transferred to the waterlogging treatment. These pots were placed inside plastic 2 gallon buckets filled with water and the position of the pot adjusted so that the water table in the bucket was level with the soil surface of the pot (Plate 5.1). Both the waterlogged pots (16 pots for 2 species combinations) and the remaining freely drained (control) pots (16 pots for 2 species combinations) were placed in randomised blocks with an edge row on the apron of the glasshouse (Plate 5.1). During the experiment all seedlings were surface watered three times weekly. Seedling height, stem diameter, number of nodes, number of leaves and details of the plants' conditions were recorded for each seedling on one occasion prior to (18/11/82), and four occasions during the waterlogging trials (27/12/82, 21/1/83, 6/2/83, 3/8/83). Leaf number was converted to total leaf area (see Chapter 3). Analysis of variance was performed on the data.

In late January dawn to dusk measurements of water potential and stomatal conductance were made on the waterlogged and control seedlings. Diurnal fluctuation in stomatal conductance and water potential were measured





Plate 5.1

Glasshouse waterlogging trial involving two seedlings from different subgenera grown in the same pot.

on clear and cloudless days: on the 24/1/83 for the E. coccifera plus E. johnstonii mixed seedling pairs; and on the 29/1/83 for the E. delegatensis plus E. urnigera mixed seedling pairs; 27 and 32 days respectively, after the commencement of the waterlogging experiment. For logistical reasons measurements were made on the first 4 replicates of each treatment only. Stomatal conductances were measured using a Licor Li 700 diffusion porometer on the adaxial surface of upper seedling leaves (leaves were amphistomatous) and the water potentials were measured using a pressure chamber (Scholander et al. 1965) made in the Botany Department of the University of Tasmania. Single leaves or small shoots were used in the pressure chamber. The total of 7-9 leaves sampled for water potential measurements was considered to have a negligible effect on the leaf area of the 1.0-1.3 m high seedlings. The temperature and relative humidity in the glasshouse were monitored using a thermohygrograph placed in a Stevenson screen.

After the dawn to dusk measurements had been conducted selected pots were harvested and the root systems investigated. The distribution of roots within the pot was investigated for each species and transverse sections of primary and young secondary roots were cut.

### Glasshouse Nutrient-Waterlogging Trials

For the three Symphyomyrtus species E. gunnii, E. urnigera and E. johnstonii seed was germinated and seedlings were grown as described (previous section). From a large progeny of 2 month old seedlings growing in 5 cm diameter veneers, seedlings were chosen, on the basis of similarity in size, and transplanted into 72, 15 cm diameter pots containing potting soil. Two seedlings of differing species were planted in the same pot (as described above). All species combinations were represented giving the three mixed species pairs: E. gunnii plus E. urnigera; E. gunnii plus E. johnstonii and E. urnigera plus E. johnstonii; twenty-four replicate pots for each species pair. Twelve replicates of each species pair were planted in pots containing slow release fertilizer (osmocote and blood and bone) - the high nutrient treatment, and twelve replicates were planted in pots containing no added fertilizer - the low nutrient treatment. The sandy-loam and peat moss used as a basic mixture for the potting soil was nutritionally very poor, thus the two nutrient treatments, although arbitrary, differed greatly.

The seedlings were grown in the two nutrient treatments for 2 months before the waterlogging treatments were commenced. On 23/8/83 half the replicates (18 pots) in each nutrient treatment were flooded in large trays with the water table maintained at the soil surface. The remaining pots were freely drained. All pots were surface watered three times weekly. The resulting factorially designed experiment consisted of four treatments: waterlogged - high nutrient; waterlogged - low nutrient; freely drained - high nutrient; freely drained - low nutrient, with 18 pots in each treatment (6 replicate pots for each of the three species pairs). The pots were arranged in a randomised block with an edge row. Seedlings were grown in their treatments for five months during which time measurements of seedling height, stem diameter, number of nodes and number of leaves were made on three occasions (23/8/83, 19/10/83, 14/1/84). Analysis of variance was then performed on the data.

## RESULTS

### Field Studies of Soil Moisture Status

The period during which soil moisture measurements were made (the 1982-83 summer) coincided with a severe drought (discussed in detail in Chapter 6) and records should be considered in this context.

The gravimetric soil moisture content and the soil water potentials measured for field soils in the north-western region of the study site (Fig. 5.1) indicated that marked differences in soil moisture status existed between stands of the five species at sites I-VI (Fig. 5.2). The soils occupied by pure stands of the two Monocalyptus species at sites I and IV (E. delegatensis and E. coccifera respectively) exhibited the lowest water potentials in February 1983 and showed greatest fluctuation in water potential throughout the study period. Of the two species, E. coccifera occupied the driest site; that which experienced the lowest soil water potentials (down to -1.1 MPa in the B soil horizon). The deep, friable and well-drained soils occupied by the Monocalyptus species were clearly the driest sites in drought years and are probably also the driest sites in years of average rainfall. Waterlogging is unlikely to occur in any season.

In contrast, the pure stands of the Symphyomyrtus species, E. johnstonii and E. gunnii (stands V and VI), growing in soils with impeded drainage near the base of the depression (Fig. 5.1), experienced consistently high water potentials

Figure 5.2

The percentage soil moisture and the soil water potentials for the "A" (solid line) and the "B" (broken line) soil horizons of soils at stands I-VI (Fig. 5.1) recorded at approximately monthly intervals (1, 17/12/82; 2, 17/1/83; 3, 18/2/83; 4, 26/3/83; 5, 29/4/83) between December 1982 and April 1983.

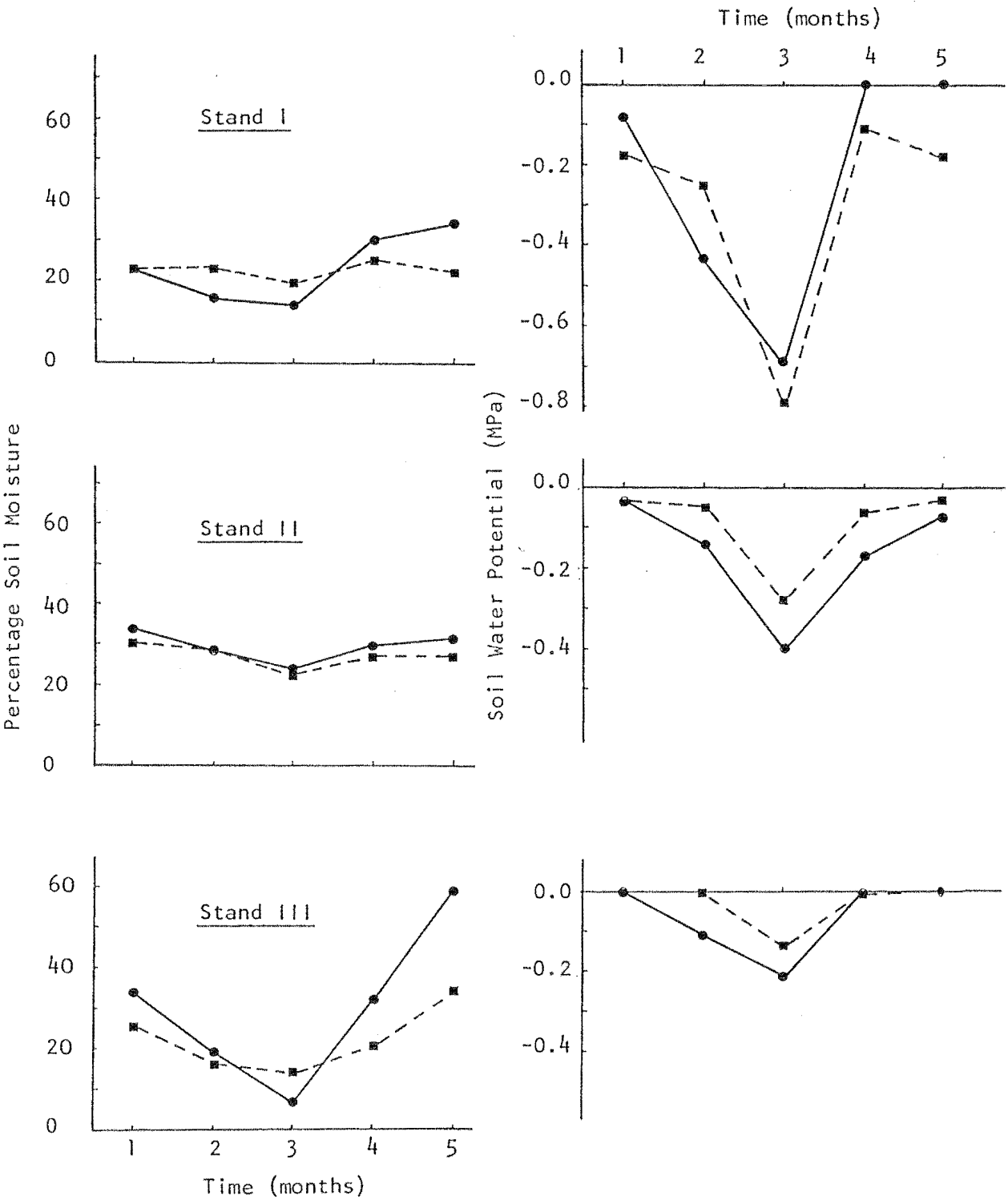
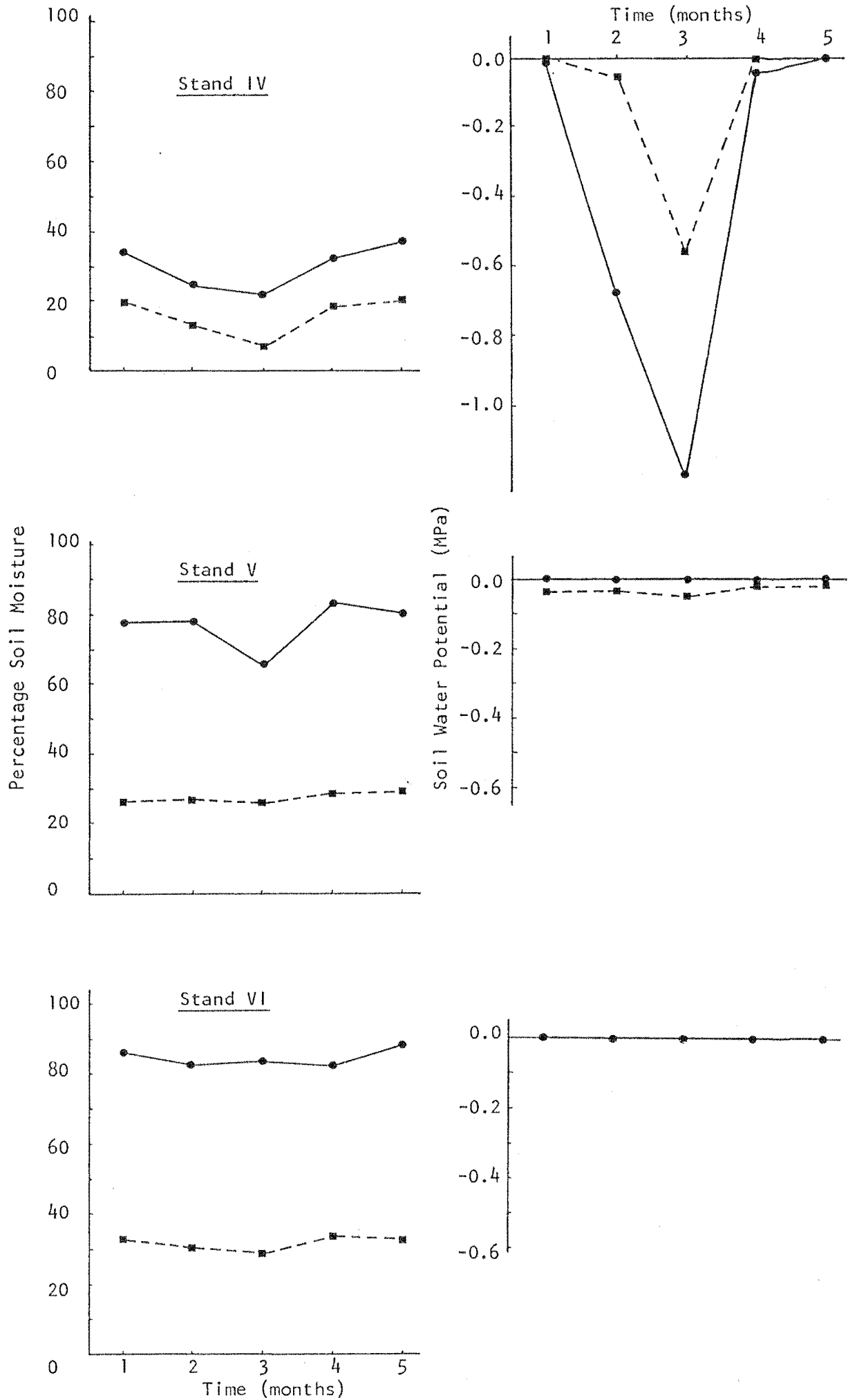


Figure 5.2 (cont'd)



(above -0.5 MPa) even during a period of severe drought. This suggests that these sites would be waterlogged for extended periods in years with average rainfall.

The soil moisture status at the mixed stands of E. delegatensis with E. urnigera, and with E. johnstonii (stands II and III) were intermediate between those of the pure Monocalyptus and Symphyomyrtus stands during the study, but with the E. delegatensis plus E. urnigera stand occupying slightly drier soils (Fig. 5.2). The mixed stands also tended to occupy the ecologically intermediate position growing on the inflection of the slope between the pure Monocalyptus and pure Symphyomyrtus stands. Here soils were less well drained and may tend to become waterlogged after heavy rains. Observations made after heavy winter rains support this suggestion.

### Field Transplant Trials

In the four weeks following planting in the field significant interspecific differences ( $P < 0.001$ ) in survival were recorded for the 6 species E. delegatensis, E. coccifera, E. pulchella, E. johnstonii, E. urnigera and E. gunnii grown in the replanted trial at garden 3 (Table 5.1). No frosts occurred during the four week period after planting and differences in seedling survival were attributed to effects of waterlogging. Throughout this period the soils at site 3 were saturated with the water table present 1 to 2 cm below the soil surface. The seedlings showed symptoms typical of waterlogging injury and adaptation (Boden 1963; Clemens & Pearson 1977; Clemens *et al.* 1978; Gill 1977; Ladiges & Kelso 1977; Pereira & Kozłowski 1977; Sena-Gomes & Kozłowski 1980). The lower seedling leaves turned a purply-red colour or became chlorotic and premature leaf abscission progressed from lower to upper leaves in badly affected plants. There was evidence of stem hypertrophy just above the soil surface, and epinasty for seedlings of the Symphyomyrtus species, but for Monocalyptus species the only visible symptoms were wilting, leaf chlorosis and abscission.

Generally the Monocalyptus species were more severely damaged by waterlogging than the Symphyomyrtus species (Fig. 5.3). E. delegatensis, E. coccifera and E. pulchella retained 30%, 68% and 78% of original leaf tissue respectively; whereas the Symphyomyrtus species retained between 79% and 96% of leaf tissue. However, significant differences between species were limited; with E. delegatensis differing from all other species and E. gunnii

Table 5.1

Tables of (a) analysis of variance and (b) Duncan's multiple range test performed on percentage survival data (percentage live leaf area, arc-sin transformed) for seedlings of six eucalypt species (E. delegatensis, E. coccifera, E. pulchella, E. gunnii, E. urnigera and E. johnstonii) transplanted into a waterlogged site in the field at Snug Plains. Twelve replicate seedlings for each species were measured at the time of transplanting and four weeks later, spanning a period free from frosts. Significance levels are: not significant (NS); significant at 0.05 level (\*); significant at 0.01 level (\*\*); and significant at 0.001 level (\*\*\*).

(a) Analysis of Variance

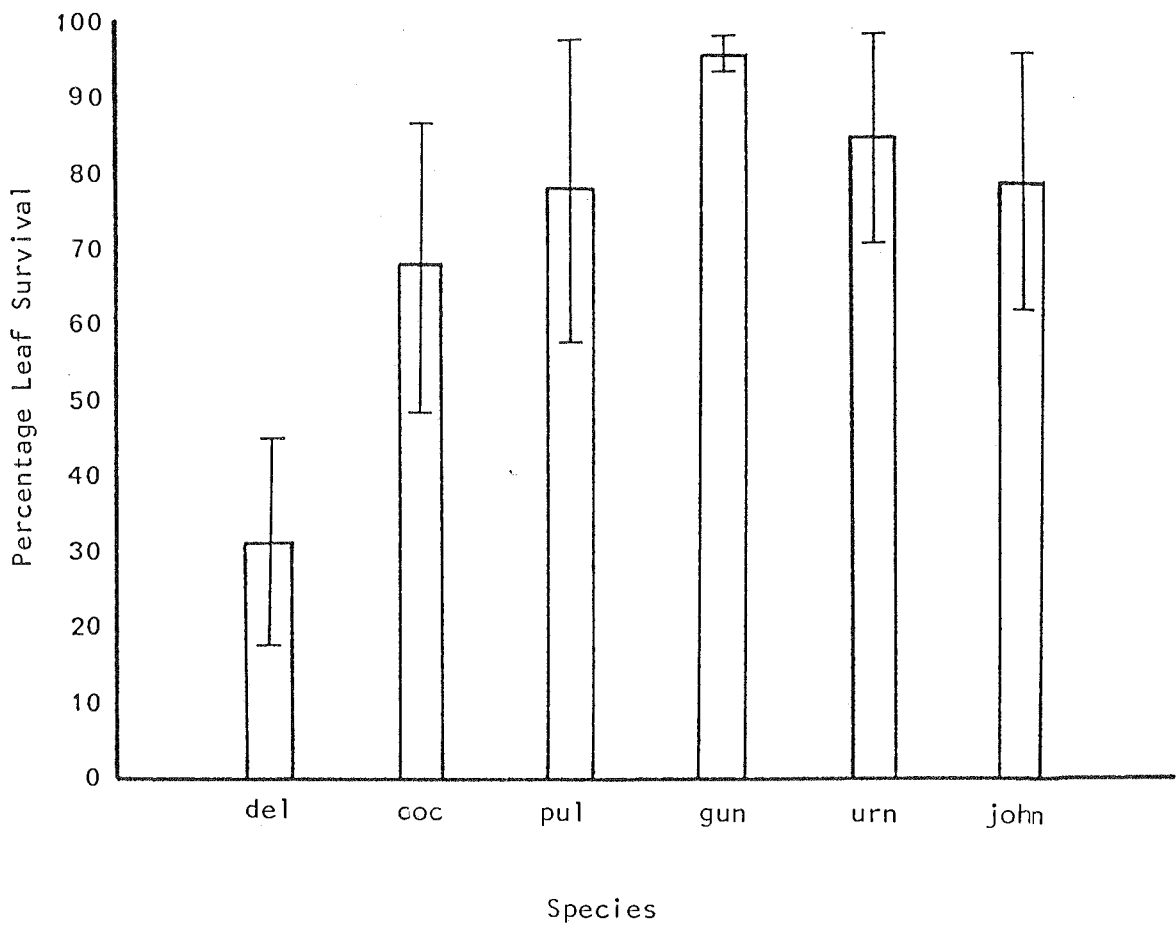
|         | Sum<br>of Squares | df | Mean<br>Square | F     | Probability |
|---------|-------------------|----|----------------|-------|-------------|
| Between | 13323.90          | 5  | 2665.0         | 7.570 | 0.000       |
| Within  | 23233.09          | 66 | 352.0          |       |             |
| Total   | 36556.99          | 71 |                |       |             |

(b) Duncan's Multiple Range Test

|   | 1   | 2 | 3  | 4 | 5 | 6 |
|---|-----|---|----|---|---|---|
| 1 | -   |   |    |   |   |   |
| 2 | *   | - |    |   |   |   |
| 3 | **  | - | -  |   |   |   |
| 4 | *** | * | ** | - |   |   |
| 5 | *** | - | -  | - | - |   |
| 6 | **  | - | -  | * | - | - |

Figure 5.3

The mean percentage survival (live leaf tissue)  $\pm$  S.E. for seedlings of the six eucalypt species E. delegatensis (del), E. coccifera (coc), E. pulchella (pul), E. gunnii (gun), E. urnigera (urn) and E. johnstonii (john) transplanted into a waterlogged site (Garden 3, Fig. 4.1) in the field at Snug Plains. The twelve replicate seedlings for each species were measured at the time of transplanting and four weeks later spanning a period free from frosts.





differing from all other species except E. urnigera. E. gunnii showed the greatest waterlogging tolerance followed by E. urnigera, E. johnstonii, E. pulchella, E. coccifera and E. delegatensis, which supports previous waterlogging studies conducted on these species (Davidson 1978), except for the relatively high resistance of E. pulchella to waterlogging found in the present study. However, this may be related to the species inherent drought resistance (discussed later).

### Glasshouse Waterlogging Trials

Marked interspecific differences in seedling tolerance to waterlogging were observed for two paired combinations of species from different subgenera: E. delegatensis plus E. urnigera and E. coccifera plus E. johnstonii. After 27 and 32 days respectively in the waterlogged conditions, the Monocalyptus species, E. delegatensis and E. coccifera, exhibited significantly lower stomatal conductances and water potentials than the Symphyomyrtus species, E. urnigera and E. johnstonii, growing in the same pot (Figs 5.4a and 5.5a). In comparison, the control exhibited no marked interspecific differences in stomatal conductances or water potential during the experiment except in the mornings when E. delegatensis and E. coccifera tended to open their stomata more fully than E. urnigera and E. johnstonii (Figs 5.4b and 5.5b).

The stomatal conductance and water potential curves for the waterlogged E. delegatensis and E. coccifera seedlings were very similar, and indicated both species were suffering from water deficits (Hinckley *et al.* 1978). Stomatal conductances were low (up to  $0.05 \text{ cm sec}^{-1}$ ) and the water potentials declined to a late afternoon minimum of approximately  $-2.2 \text{ MPa}$  restoring only slightly at dusk, in contrast with control plants. On the other hand, E. urnigera and E. johnstonii seedlings exhibited moderate conductances (up to  $0.2 \text{ cm sec}^{-1}$ ) and high dawn water potentials. Water potentials of waterlogged treatments were again lower than those of controls. The results for the above species differ markedly from results obtained by other workers (e.g. Pereira & Kozlowski 1977) in which eucalypt seedlings exhibited significantly lower stomatal conductances but higher water potentials in waterlogged soils.

As well as distinct subgeneric differences in water relations, interspecific differences within a subgenus were evident. Stomatal conductances for waterlogged E. johnstonii seedlings were near control levels whereas conductances for E. urnigera seedlings only reached about 30% of that recorded

Figure 5.4

Dawn to dusk measurements of the leaf water potential and the stomatal conductance (mean  $\pm$  S.E.) for paired seedlings of E. coccifera (squares) and E. johnstonii (triangles) grown in the same pot under (a) waterlogged conditions, with the water table at the soil surface (solid symbols) and (b) freely drained conditions (control plants, open symbols). Measurements were made in a glasshouse on a single summer's day (24/1/83) on the 27th day of a waterlogging trial.

Figure 5.4(a)

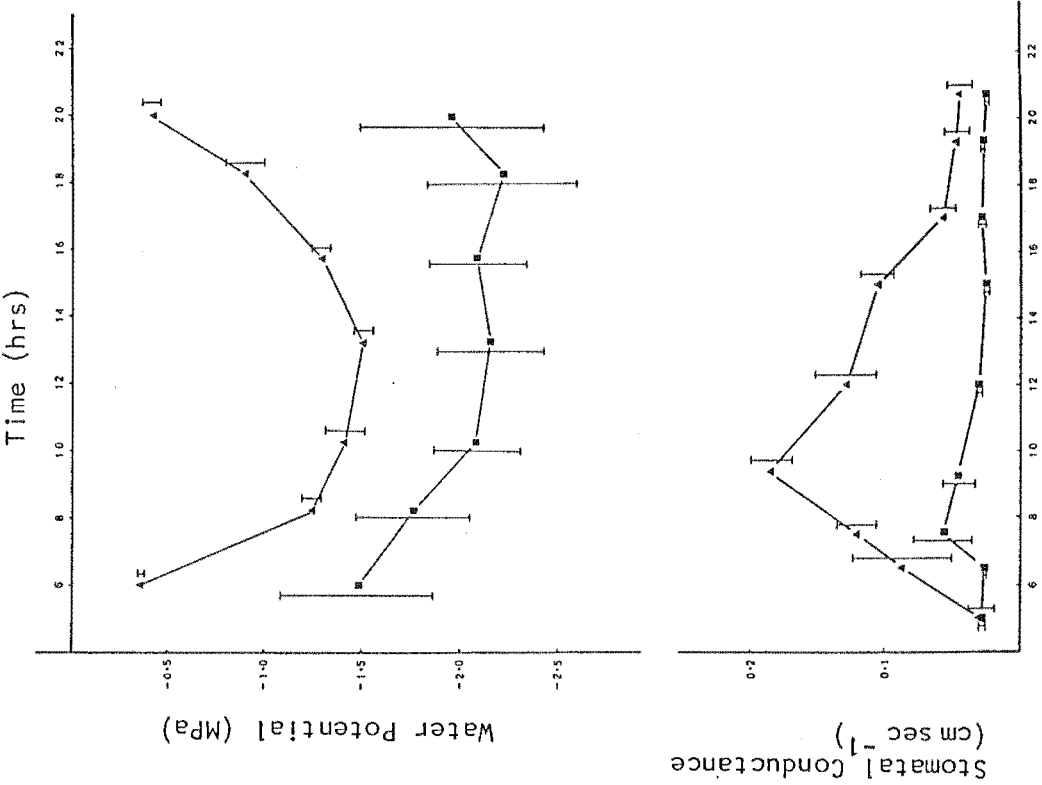


Figure 5.4(b)

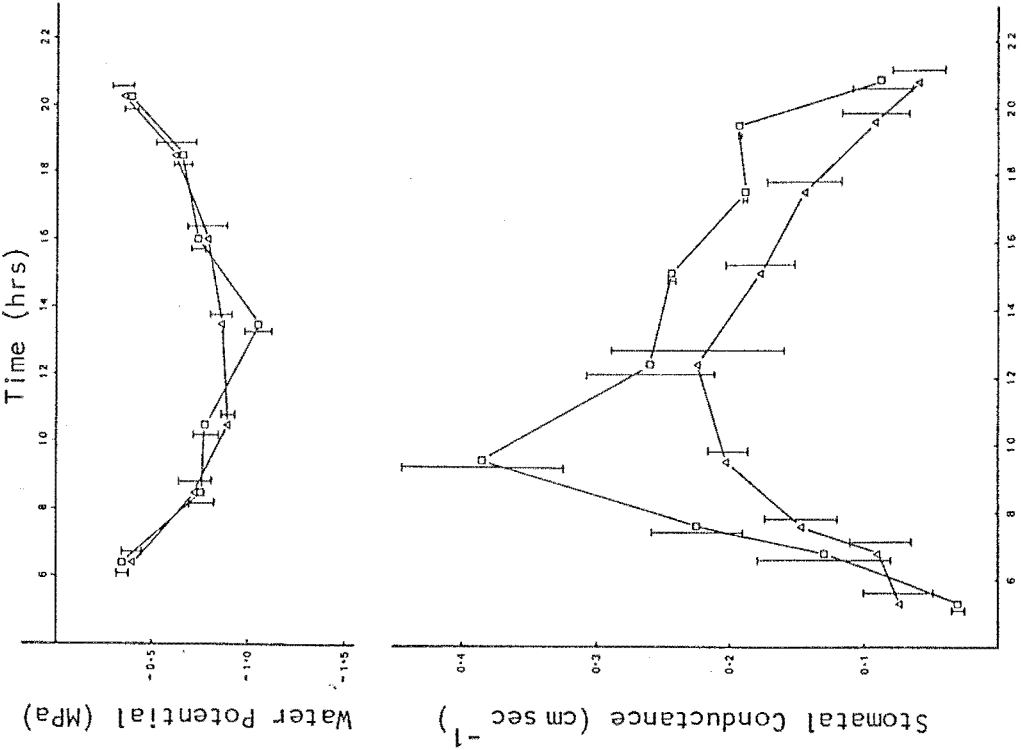


Figure 5.5

Dawn to dusk measurements of the leaf water potential and the stomatal conductance (mean  $\pm$  SE) for paired seedlings of E. delegatensis (triangles) and E. urnigera (circles) grown in the same pot under (a) waterlogged conditions, with the water table at the soil surface (solid symbols) and (b) freely drained conditions (control plants, open symbols). Measurements were made in a glasshouse on a single summer's day (29/1/83) on the 32nd day of a waterlogging trial.

Figure 5.5(b)

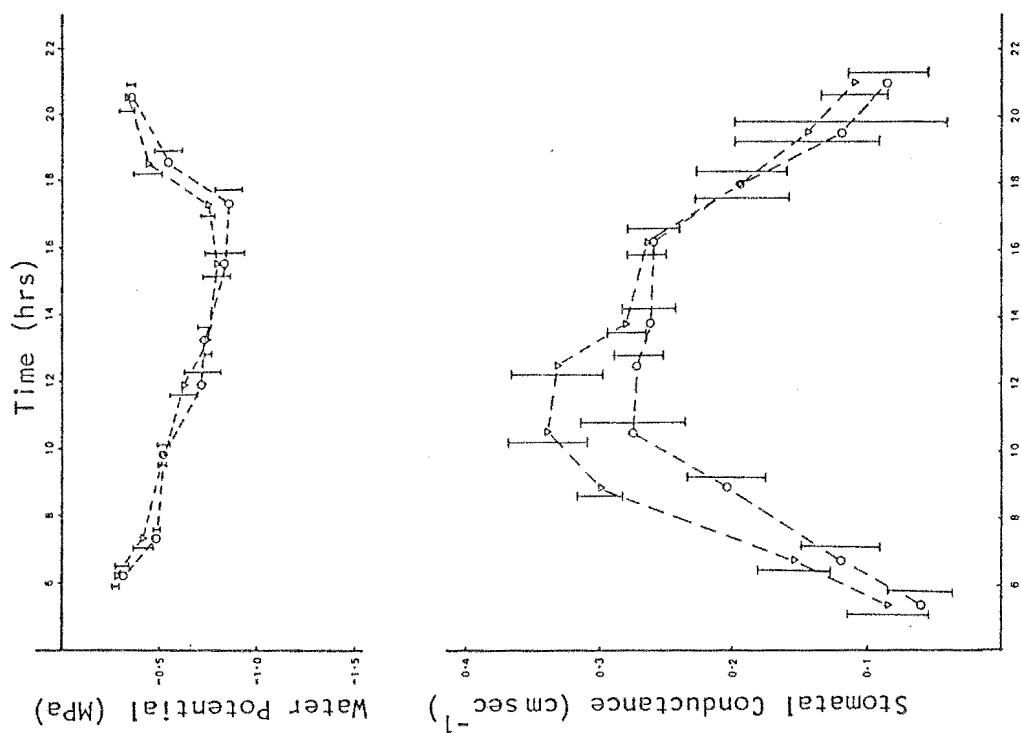
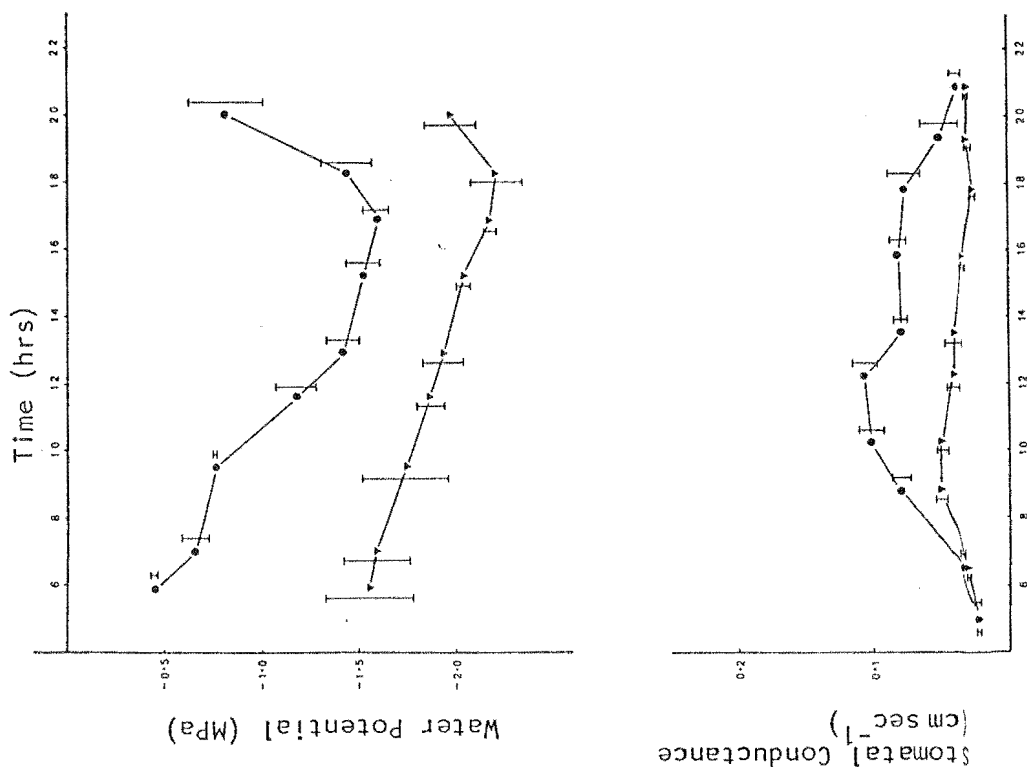


Figure 5.5(a)



for control plants. Further, the water potential curve for *E. urnigera* was distinctly skewed towards a late afternoon minimum, a feature not evident in the *E. johnstonii* records. These symptoms of water deficit (Hinckley *et al.* 1978) suggest *E. urnigera* is less tolerant to waterlogging than *E. johnstonii*.

Comparisons between the waterlogged and control treatments on the basis of growth in height and leaf area, indicated that, between day 24 and 40 of the waterlogged conditions, all species experienced restricted growth (Fig. 5.6) and a reduction in leaf area (Fig. 5.7). Continued waterlogging resulted in a halt in growth, complete defoliation and death for the *Monocalyptus* species, but for the *Symphyomyrtus* species only caused a temporary reduction in leaf area and restriction to height growth. After 8 months of the waterlogging treatment the *Symphyomyrtus* species were exhibiting moderate rates of growth in height and leaf area in comparison with control plants, although one of the eight *E. urnigera* replicates died in the latter stages of the experiment. In comparison, growth of the controls continued unchecked and after 8 months interspecific differences in height growth were minor, although leaf areas differed substantially (Figs 5.6 and 5.7).

Observations of root distribution and studies of root anatomy carried out on the above four species during waterlogging trials revealed further subgeneric differences in response to waterlogging. By day 40 of waterlogging all species were exhibiting recognisable symptoms of waterlogging injury or adaptations (Boden 1963; Clemens & Pearson 1977; Clemens *et al.* 1978; Gill 1977; Ladiges & Kelso 1977; Pereira & Kozlowski 1977; Sena-Gomes & Kozlowski 1980). These symptoms progressively became evident during the period from day 24 to day 40. The *Symphyomyrtus* species showed evidence of stem hypertrophy, adventitious roots, leaf epinasty, leaf chlorosis and premature leaf abscission. In comparison, the only symptoms exhibited by the *Monocalyptus* species were chlorosis, wilting and extensive leaf abscission. The *Symphyomyrtus* species *E. urnigera* and *E. johnstonii* developed a ramification of adventitious roots at the soil surface (Plates 5.2 and 5.3) and an extensive shallowly descending root system reaching to about one-third of the depth of the pot (Plate 5.4). An anatomical study of these roots showed the vast majority to be primary in structure. The open cortical parenchyma of these primary roots (Figs 5.8 and 5.9) contained numerous air spaces which could facilitate air conduction. Sectioning of the lower stem of the same plants showed evidence of aerenchyma development, similar to that described by Boden (1963), which extended from just above the soil surface into the major root branches. Further, individual primary roots of the waterlogged *Symphyomyrtus* seedlings did not differ in anatomy or size from the primary roots of the control plants of

Figure 5.6

Growth in (a) height and (b) leaf area (mean  $\pm$  SE) for paired seedlings of E. coccifera (squares) and E. johnstonii (triangles) grown in the same pot under (i) waterlogged conditions, with the water table at the soil surface (solid symbols) and (ii) freely drained conditions (control plants, open symbols). The waterlogging treatment was commenced on day 1 (28/12/82).

Figure 5.6(a)

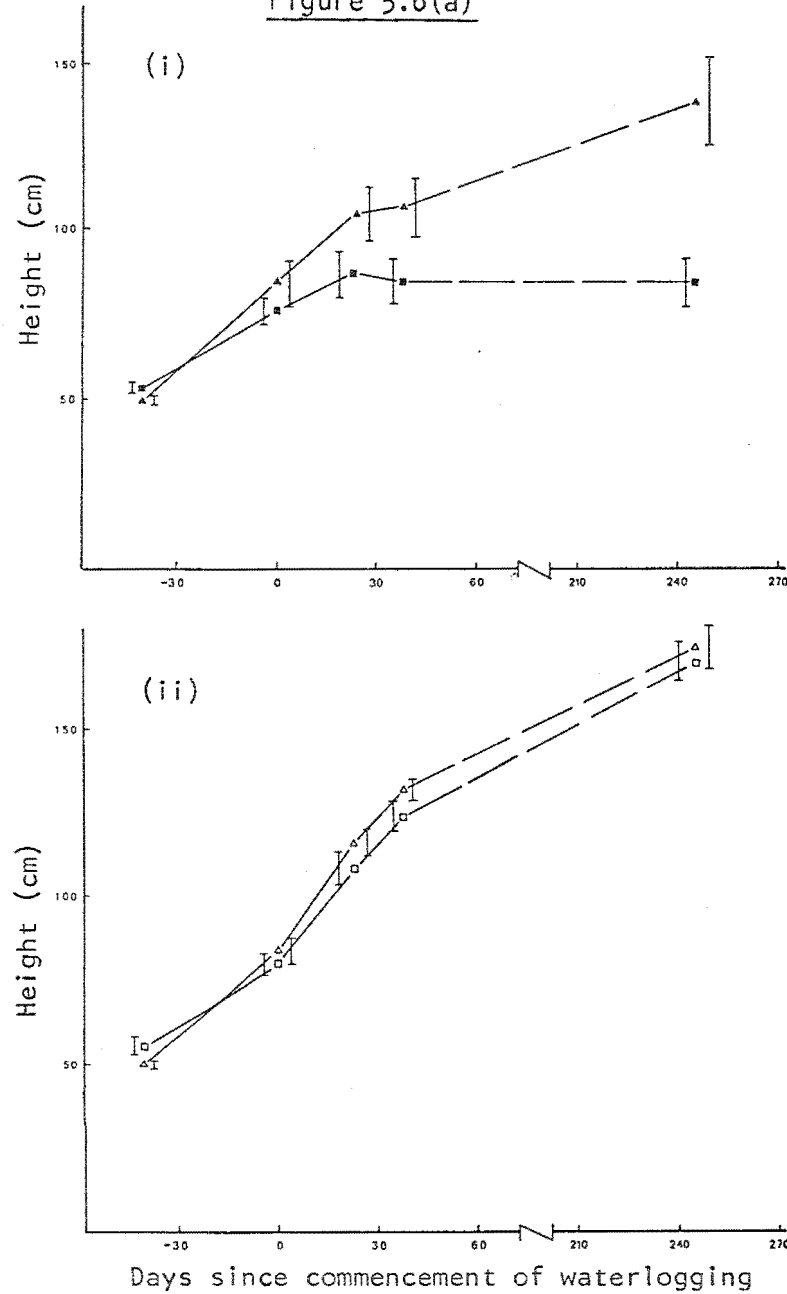


Figure 5.6(b)

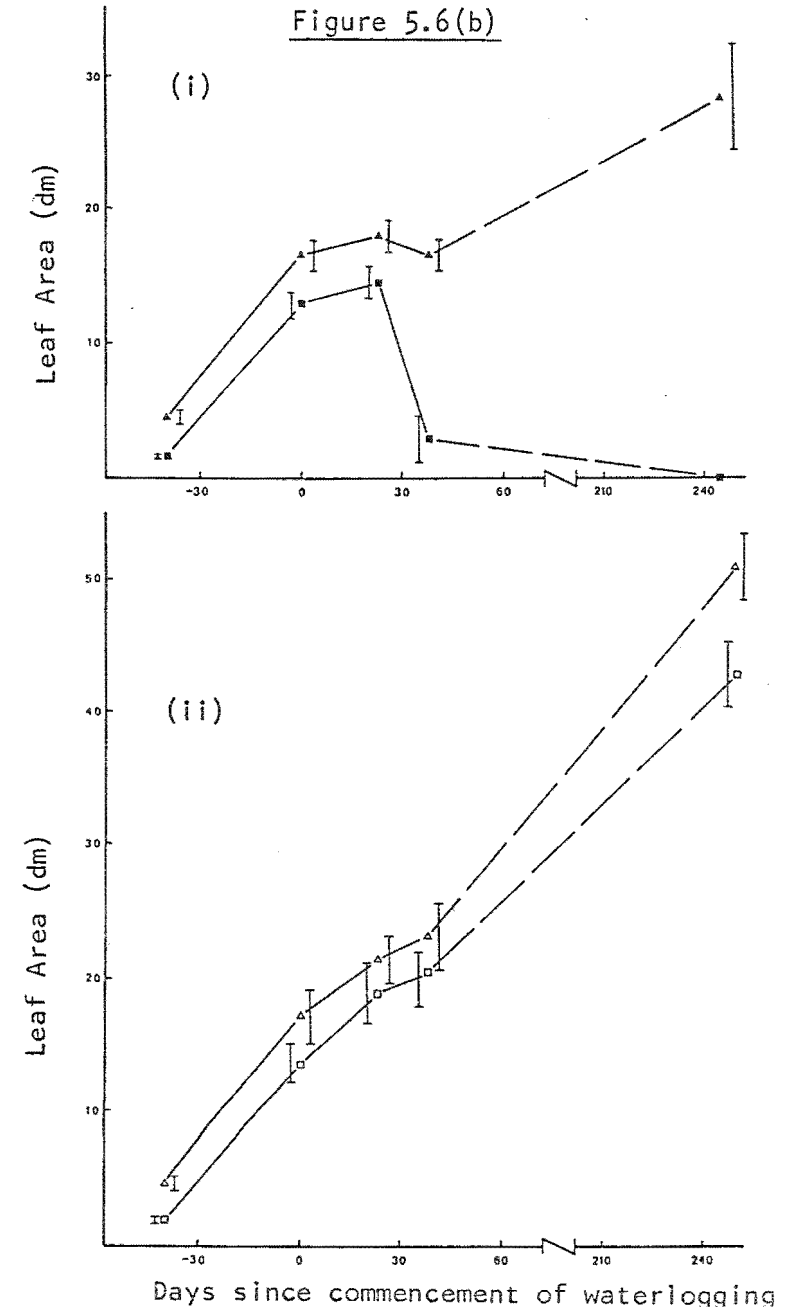
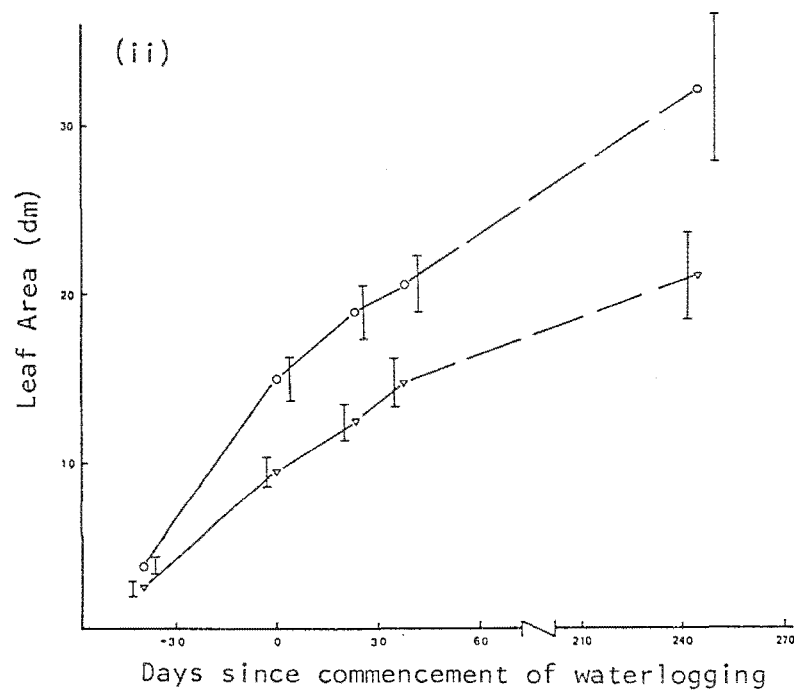
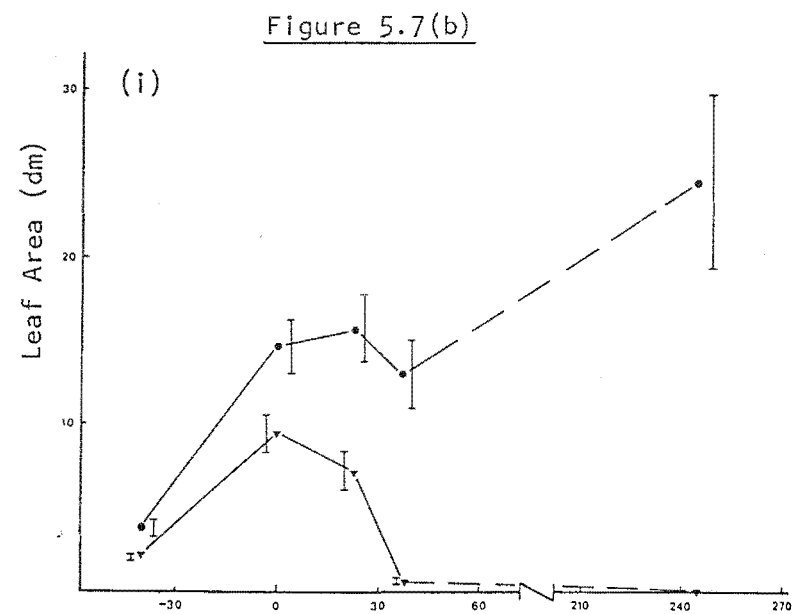
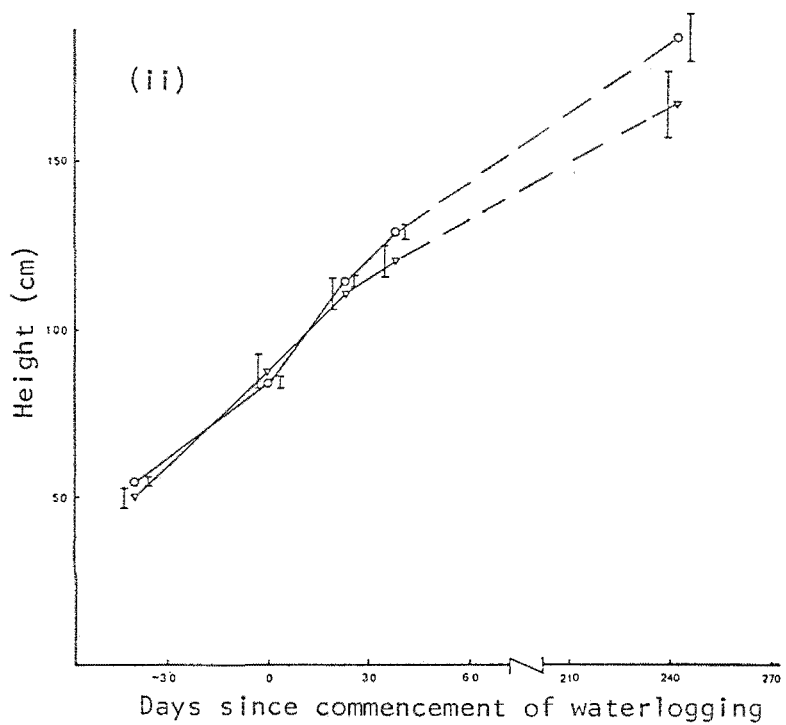
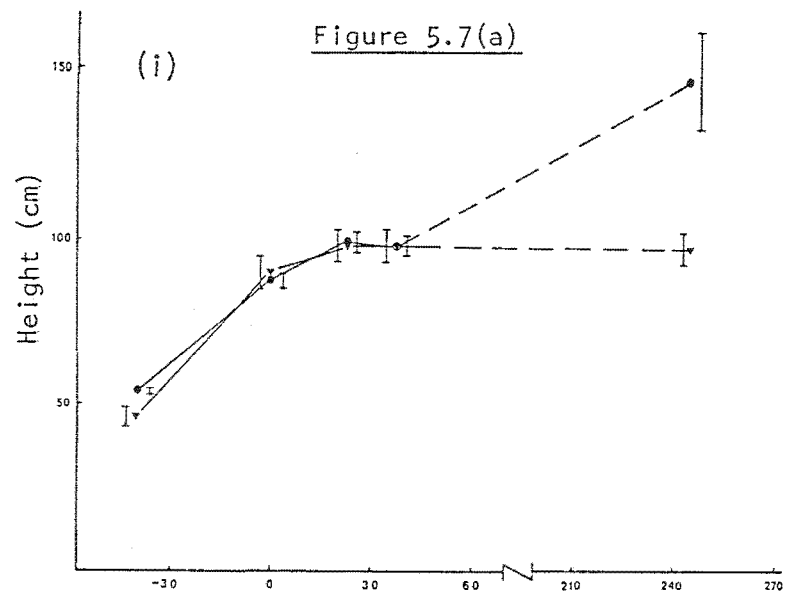




Figure 5.7

Growth in (a) height and (b) leaf area (mean  $\pm$  SE) for paired seedlings of E. delegatensis (triangles) and E. urnigera (circles) grown in the same pot under (i) waterlogged conditions, with the water table at the soil surface (solid symbols) and (ii) freely drained conditions (control plants, open symbols). The waterlogging treatment was commenced on day 1 (28/12/82).



Plates 5.2-5.4

The adventitious primary root systems of the living Symphyomyrtus species E. johnstonii and E. urnigera in comparison with killed Monocalyptus species E. delegatensis and E. coccifera which exhibited no morphological adaptations to waterlogged conditions.



Plate 5.2(a)



Plate 5.2(b)



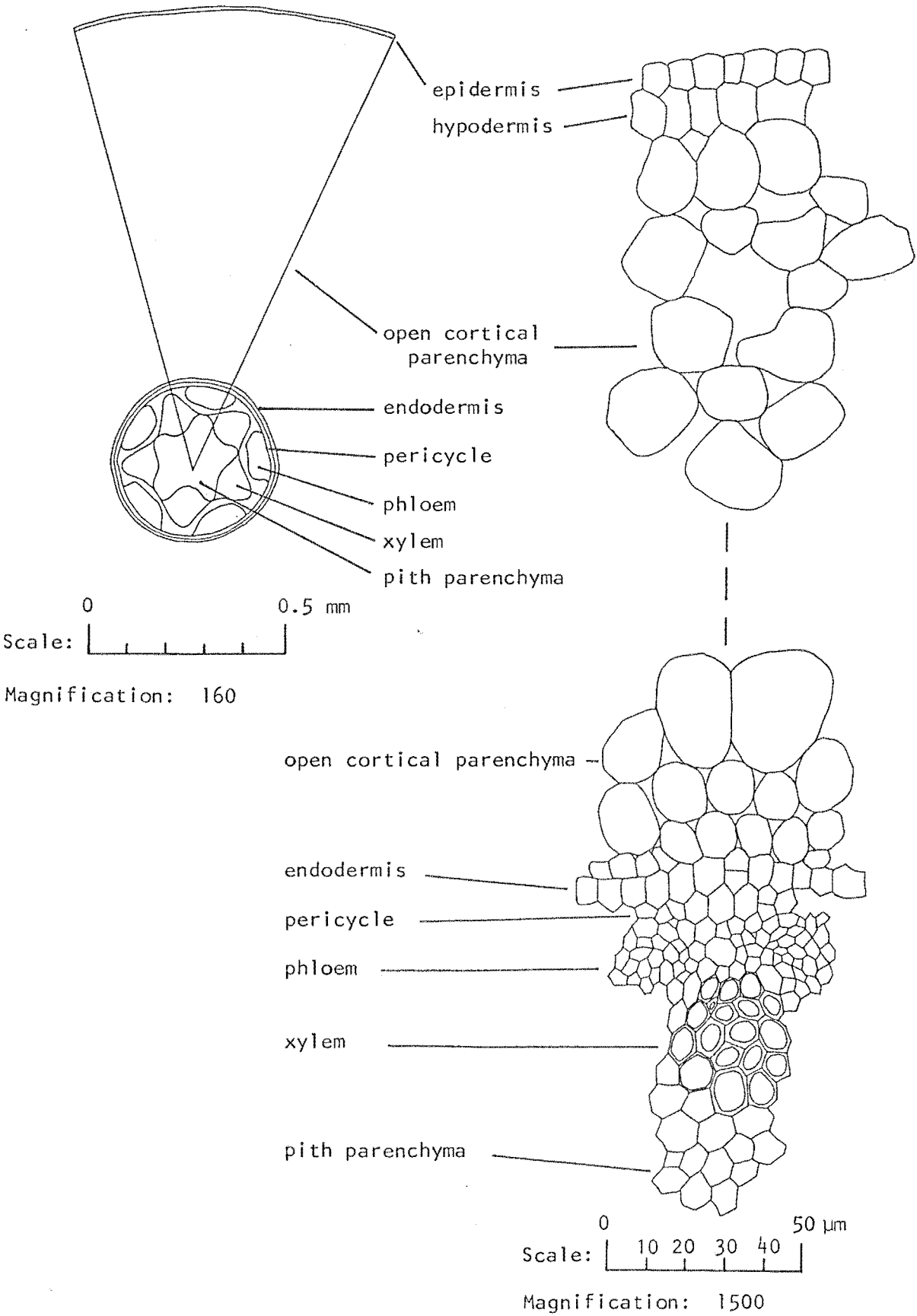
Plate 5.3



Plate 5.4

Figure 5.8

Tissue map and high power diagram of a typical primary adventitious root of an *E. urnigera* seedling exposed to waterlogged soil conditions for 30 days.





either subgenus (Figs 5.8 and 5.9). This may indicate that the root systems of the Symphyomyrtus species were rapidly regenerating, or alternatively, that development of secondary tissue was delayed thereby retaining the air conductive facilities of the primary root tissue. In comparison, the Monocalyptus species showed evidence of reduced root growth and root atrophy in the waterlogged treatment, but demonstrated no morphological adaptations of the root system. The inability of the Monocalyptus species to rapidly develop morphological adaptations to the waterlogged environment may be an important factor contributing to the absence of these species from waterlogged sites in the field.

### Glasshouse Nutrient-Waterlogging Experiments

Significant interspecific differences in seedling height, stem diameter, number of nodes, number of leaves, stem basal area and total leaf area were developed by the three Symphyomyrtus species, E. gunnii, E. urnigera and E. johnstonii grown reciprocally in pairs in the four waterlogging and nutrient treatments (Table 5.2). However, the trends did not clearly separate the three species on the basis of nutrient and waterlogging preferences (Fig. 5.10). E. gunnii grew more rapidly than other species in all treatments. E. johnstonii generally showed slowest growth, although a slight relative increase in growth was discernible in waterlogged soils compared with the freely drained treatment. E. johnstonii showed no relative increase in growth in low nutrient soils even though low nutrient status was a characteristic of soils naturally occupied by most of the E. johnstonii stands at Snug Plains (Table 3.2, Chapter 3). Similarly, E. gunnii which inhabits peat soils of high nutrient status in the field at Snug Plains (Table 3.2, Chapter 3), did not show a marked relative increase in growth in high nutrient treatments. Instead, all species showed a dramatic increase in growth in high nutrient as compared with low nutrient treatments.

All species except E. johnstonii showed a slight increase in growth in the freely drained treatment compared with waterlogged treatment. This was in contrast to other seedling experiments which indicated marked interspecific differences in waterlogging tolerance. However, on at least two occasions during this waterlogging experiment the water table was found to have dropped, greatly ameliorating the conditions in the waterlogged treatment. This suggests that prolonged periods of waterlogging (as occurred in other experiments) may be necessary before interspecific differences are developed.



Table 5.2. Nutrient-Waterlogging Trials.

Significance levels for analyses of variance performed on seedlings of 3 eucalypt species (E. urnigera, E. gunnii, E. johnstonii from subgenus Symphyomyrtus) grown in 2 waterlogging regimes (flooded and freely drained) and two nutrient treatments (high - with fertilizer, and low - without fertilizer). Records of height, stem diameter, number of nodes expanded, number of leaves and derived values of stem basal area and total leaf area were made on three occasions (23/8/83, 19/10/83, 14/1/84). The significance level for each of the main effects and interactions are; not significant (NS); significant at 0.05 level (\*), significant at 0.01 level (\*\*) and significant at 0.001 level (\*\*\*).

| Effects and Interactions          | Significance Levels for Characters Measured |               |                 |                  |                 |           |
|-----------------------------------|---|---------------|-----------------|------------------|-----------------|-----------|
|                                   | Seedling Height                             | Stem Diameter | Number of Nodes | Number of Leaves | Stem Basal Area | Leaf Area |
| Time                              | ***   | ***           | ***             | ***              | ***             | ***       |
| Nutrient                          | ***   | ***           | ***             | ***              | ***             | ***       |
| Waterlogging                      | *   | NS            | ***             | **               | NS              | ***       |
| Species                           | ***   | *             | ***             | ***              | *               | ***       |
| Time x nutrient                   | ***   | ***           | ***             | ***              | ***             | ***       |
| Time x waterlogging               | NS  | NS            | *               | NS               | NS              | NS        |
| Time x species                    | ***   | NS            | ***             | ***              | NS              | ***       |
| Nutrient x waterlogging           | NS  | NS            | *               | **               | NS              | *         |
| Nutrient x species                | ***   | NS            | ***             | ***              | NS              | ***       |
| Waterlogging x species            | NS  | NS            | NS              | NS               | NS              | NS        |
| Nutrient x waterlogging x species | NS  | NS            | NS              | NS               | NS              | NS        |

Figure 5.10

Means  $\pm$  SE's from an analysis of variance (Table 5.2) performed on measurements of height (solid symbols) and number of nodes expanded (open symbols) for seedlings of the three Symphyomyrtus species E. gunnii (g), E. urnigera (u) and E. johnstonii (j) grown in a glasshouse trial.

(a) The main effects: (i) time of measurement (1, 23/8/83; 2, 19/10/83; 3, 14/1/84); (ii) nutrient status (H; high; and L, low); (iii) waterlogging treatment (W, water table at the soil surface; and D, freely drained); and (iv) species.

(b) The first order interactions: (v) time x species; (vi) waterlogging x species; (vii) nutrient x species,

(c) The second order interactions: (viii) nutrient x waterlogging x species.

Figure 5.10(a)

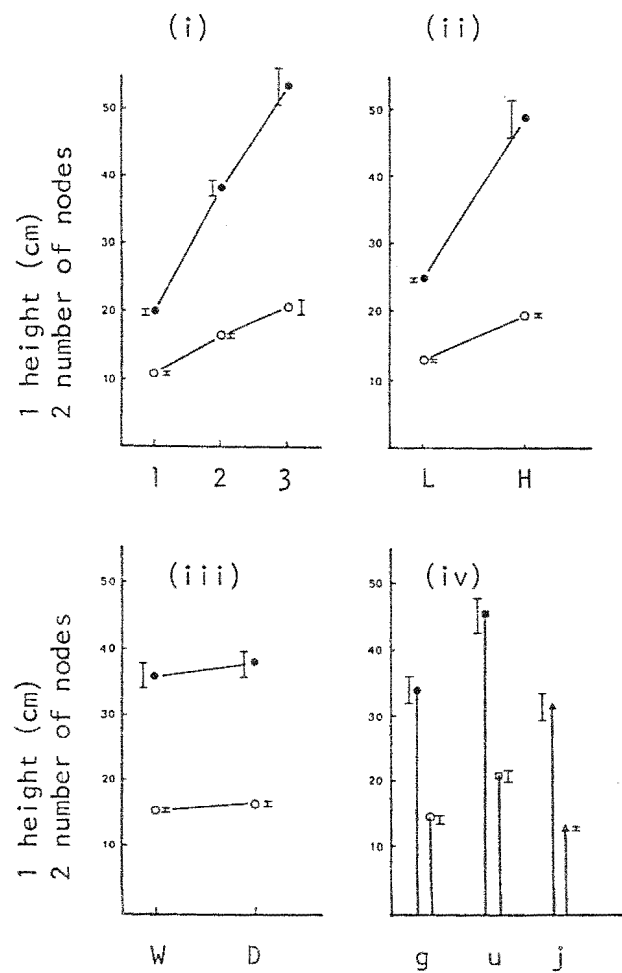


Figure 5.10(b)

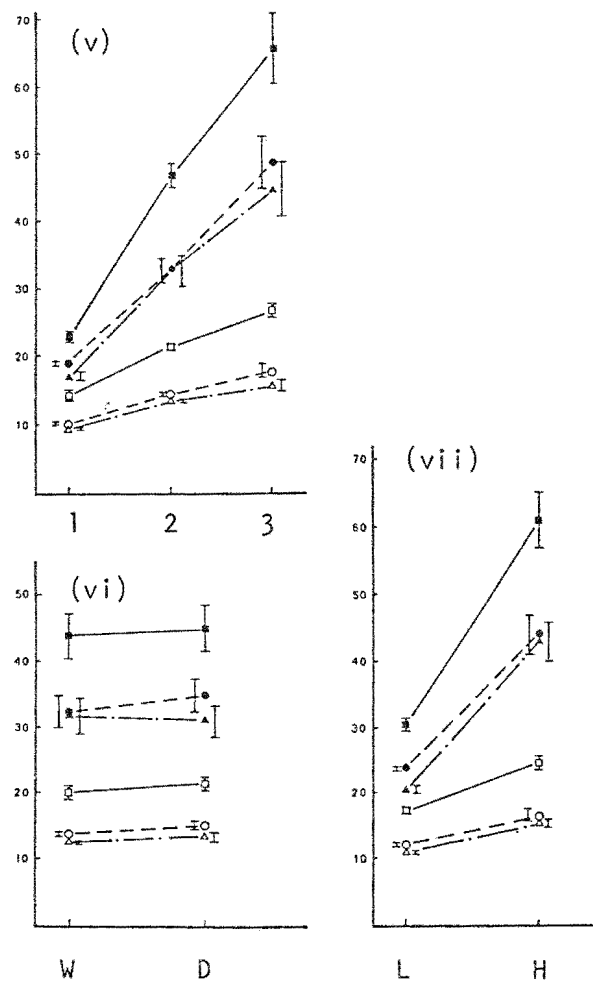
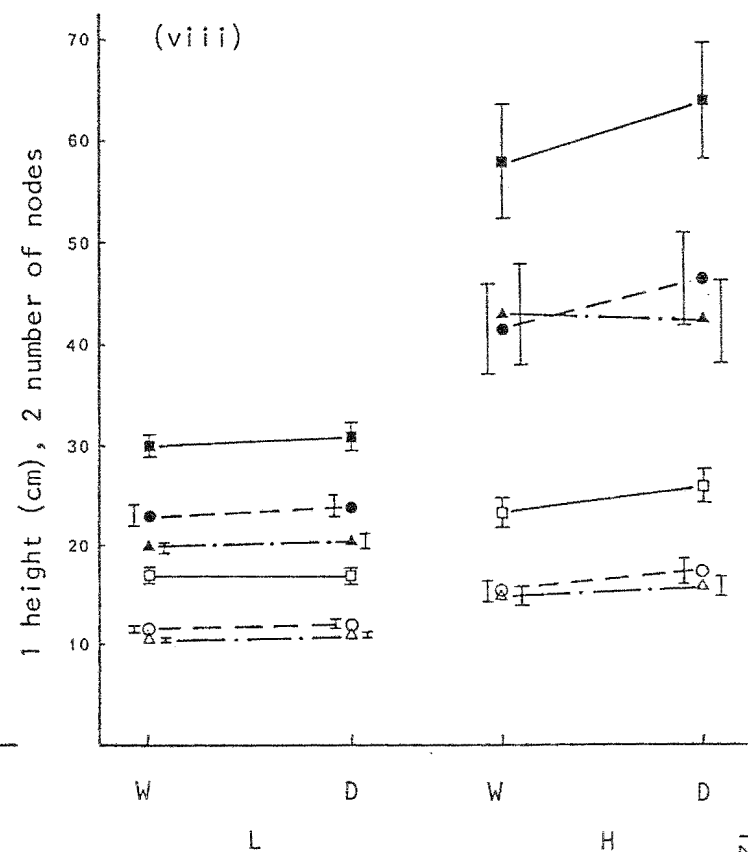


Figure 5.10(c)



Therefore it appears that the soil nutrient status-waterlogging interaction is not the key to determining the niches occupied by the three Symphyomyrtus species, E. urnigera, E. gunnii and E. johnstonii. Analysis of variance also indicated no significant biotic influence on growth was caused by the presence of a different paired species sharing the same pot in the nutrient-waterlogging experiment.

## DISCUSSION

Several studies of the relative waterlogging tolerance of pairs or suits of eucalypt species have been conducted in the last 10 years, but most of these have been concerned with species known to inhabit waterlogged environments and usually involved species from the subgenus Symphyomyrtus (e.g. Clemens & Pearson 1977; Clemens et al. 1978; Clucas & Ladiges 1979; Ladiges & Kelso 1977; Pereira & Kozlowski 1977; Sena-Gomes & Kozlowski 1980). Studies including members of other subgenera are few and far between. Parsons (1968) studied the effect of waterlogging and salinity on the three mallee species E. incrassata (Symphyomyrtus), E. oleosa (Symphyomyrtus) and E. diversifolia (Monocalyptus) but found no conclusive differences in waterlogging tolerance between the species. On the other hand, Boden (1963) concluded that E. robusta, E. saligna, E. grandis and E. botryoides (all members of subgenus Symphyomyrtus) were capable of withstanding periods of waterlogging whereas E. pauciflora and E. stellulata (both members of the subgenus Monocalyptus) survived submergence for relatively short periods. More recently Blake and Reid (1981) showed a marked difference in waterlogging tolerance of E. obliqua (Monocalyptus) in comparison with E. globulus and E. camaldulensis (Symphyomyrtus). Further, Davidson (1978) showed marked interspecific differences in tolerance to waterlogging were evident at the subgeneric level for the six species, E. pulchella, E. delegatensis, E. coccifera (Monocalyptus) and E. gunnii, E. johnstonii, E. urnigera (Symphyomyrtus) grown reciprocally in four field soils and exposed to three waterlogging treatments. The current experiments indicate that marked interspecific differences in the physiological responses and the morphological adaptations exist between the two subgenera Monocalyptus and Symphyomyrtus after exposure to waterlogging for extended periods.

In the glasshouse waterlogging trials Symphyomyrtus species developed morphological adaptations similar to those previously described for waterlogging tolerant species (Boden 1963; Clemens & Pearson 1977; Clemens et al. 1978; Gill 1977; Ladiges & Kelso 1977; Pereira & Kozlowski 1977; Sena-

Sena-Gomes & Kozlowski 1980). The seedlings exhibited leaf epinasty, stem hypertrophy, mats of adventitious roots on the soil surface and shallowly descending primary root systems. In comparison, the Monocalyptus species showed no tendency for morphological adaptation to the waterlogged treatment but exhibited symptoms of waterlogging injury which included severe wilting, leaf abscission and atrophy of the root system and ultimately died. Further, major differences in water relations also existed between seedlings of the Monocalyptus and Symphyomyrtus species tested during an extended period of waterlogging. The stomatal conductances and water potentials of the Monocalyptus species were very much lower than those recorded for the Symphyomyrtus species, which indicate physiological differences in waterlogging tolerance existed between the two subgenera.

There are two schools of thought in the interpretation of plant response to waterlogging. Firstly, if it is considered that anaerobic conditions in waterlogged soils reduce root permeability to water thereby increasing root resistance to water uptake then loss of water from the shoot may exceed water uptake. This will result in lower water potentials, reduced stomatal conductance, wilting and finally death if roots become severely damaged (Kramer 1951; Jackson 1979; Bradford & Yang 1981; Drew 1983). Secondly, for waterlogging tolerant species which have an innate ability to adapt morphologically to waterlogged conditions may result in low stomatal conductance and high water potentials. A reduction in stomatal conductance has been shown to occur in response to waterlogging alone, in the absence of low water potentials (Sojka & Stolzy 1980; Pereira & Kozlowski 1977; Blake & Reid 1981; Tang & Kozlowski 1984; Sena-Gomes & Kozlowski 1980; Bradford & Hsiao 1982), which has been correlated with increased ethylene concentrations in the shoot and the presence of abscissic acid and other growth hormones (Tang & Kozlowski 1984; Kawase 1981). Further, the reduction in stomatal conductance was associated with an increase, rather than a decrease in water potentials. In the present study, E. coccifera and E. delegatensis exhibited severe water deficits, a rapid onset of wilting and ultimately death, with no evidence of morphological adaptation to the waterlogged conditions. The morphological symptoms of waterlogging injury were characteristic of waterlogging intolerant species (Jackson 1979; Kramer 1951; Etherington 1984; Drew 1983). The physiological indicators (low water potentials and stomatal conductances) suggest shoot death occurred as a result of severe water deficits (Hinckley et al. 1978), possibly the result of deterioration and death of the root system. On the other hand E. urnigera exhibited moderate, and E. johnstonii slight, water deficits, while both species showed extensive morphological

adaptations to the waterlogged conditions. The morphological adaptations exhibited by the Symphyomyrtus species were characteristic of highly waterlogging tolerant species, but the physiological indicators suggest some mild water deficits were developed by both E. urnigera and E. johnstonii during waterlogging. However, there are two other factors which may be involved: the seedling size, and the timing of the water relations measurements.

Field observations of woody species inundated in natural floods suggests that mature vigorous individuals in a stand suffer less flooding damage, and that damage becomes progressively less severe with age of the tree (Gill 1970), but large plant size may not always be an advantage. Theoretically, as plant size increases, the rate of oxygen diffusion and the oxygen supply to the root via the stem becomes less (Gill 1970). Therefore, for a large plant, relatively more extensive morphological adaptations (in particular, aerenchyma and adventitious roots) are required to support the plant when the soil becomes waterlogged. Therefore, it is possible that during the period of morphological adaptation, there may be a critical stage where plant dependence is switching from the old root system to the new adventitious root system, which is as yet, not well developed. The 0.7 m high seedlings used in the current experiment were larger than those reported in other studies of waterlogging for Eucalyptus, and for the Symphyomyrtus species, mild water stress may have developed during establishment of the adventitious root systems of these large seedlings. The observed deficits may have been accentuated in the current experiment by the imposition of waterlogged conditions in mid-summer (27/12/82) during the growing season for these species, when transpiration rates were high (indicated by stomatal conductances of control plants) and water demand high (Gill 1970). This was supported by the fact that the measurement of water relations coincided with a period when restricted growth and a reduction in leaf area was occurring in waterlogged seedlings. Similar reductions in leaf area and restriction of height growth were observed for waterlogged seedlings of Symphyomyrtus species by Clemens and Pearson (1977) and Sena-Gomes and Kozlowski (1980). Therefore it appears the interspecific differences in water potential observed for the four species tested, may well reflect the state of physiological or morphological adaptation to waterlogging, and indicate their relative tolerance to waterlogging. The relative tolerance of the four species would then be, from most to least: E. johnstonii > E. urnigera >>> E. coccifera = E. delegatensis; the Symphyomyrtus species being much more tolerant of waterlogging than the Monocalyptus species.

The development of an extensive adventitious root system of primary structure by the Symphyomyrtus species in glasshouse waterlogging trials was of considerable interest. Even after 8 months of waterlogging the greater proportion of this root system was primary in anatomy. The maintenance of primary structure has the obvious advantage of facilitating oxygen translocation, and the retention of primary structures is reminiscent of the neoteny described for the foliage of some eucalypt species in extreme environments (Brooker & Hooper 1982; Pryor & Johnson 1981). However, a rapid turnover of root systems in waterlogged conditions may, in part, account for the high primary component observed.

The subgeneric character of waterlogging found in glasshouse trials was also reflected in the seedling transplant trials. E. gunnii exhibited greatest tolerance to waterlogging followed by E. urnigera, E. johnstonii, E. pulchella, E. coccifera and E. delegatensis. The anomalously high tolerance to short periods of waterlogging displayed by E. pulchella in comparison with previous studies (Davidson 1978) may reflect this species drought resistance (for details see Chapter 6). For the short duration of the field waterlogging trial (1 month), E. pulchella showed the same symptoms of waterlogging injury exhibited by the other Monocalyptus species, but to a lesser degree. The root damage caused by anaerobic conditions may have been the same for all the Monocalyptus species but E. pulchella's greater tolerance to tissue desiccation may have delayed leaf abscission, thereby conferring an artificially high resistance on E. pulchella seedlings in the present study. In waterlogging trials of longer duration E. pulchella exhibited low waterlogging tolerance (Davidson 1978). These two studies suggest that the probable relative order of waterlogging tolerance for the six species (from greatest to least) is: E. gunnii > E. johnstonii > E. urnigera >>> E. coccifera = E. delegatensis > E. pulchella. These conclusions agree with the natural distributions and records of soil water status obtained in natural stands for these species. At Snug Plains, pure stands of the Monocalyptus species, E. delegatensis and E. coccifera, were found in soils which were well drained and may develop low soil water potentials during dry summers. In comparison, the Symphyomyrtus species E. gunnii and E. johnstonii occurred in soils with impeded drainage, even during a period of drought were near field capacity.

Explanations for the occurrence of mixed eucalypt stands containing two or more species have included differences in modes of regeneration (Duff *et al.* 1982), differential insect depredation (Burdon & Chilvers 1974), temporal differences in resource utilisation (Rogers & Westman 1979) and differences in

early seedling growth (Davidson & Reid 1980). In the current studies, mixed stands of eucalypt with one representative from each of the subgenera Monocalyptus and Symphyomyrtus (e.g. E. delegatensis plus E. urnigera and E. delegatensis plus E. johnstonii) tended to occur in sites which were not well drained and cycled seasonally from dry in the summer to wet in winter. Therefore, because the subgenera differ in their tolerance to waterlogging, it is possible that the selective advantage enjoyed by each of the two species present in the mixed stand cycles in accordance with changes in soil moisture status. This may be an important mechanism by which mixed stands with one member from each subgenus are maintained. During early forest ontogeny soil water status may be of particular importance because the total transpiration is low and the stand is more susceptible to waterlogging. In the seedling stage of forest development heavy winter rains on poorly drained soils may waterlog the soils for extended periods strongly selecting against the Monocalyptus members of the regenerating stand.



## CHAPTER SIX

### DROUGHT

#### INTRODUCTION

In south-eastern Australia occasional severe droughts may occur causing acute drought stress and extensive crown damage in stands of eucalypt growing on shallow soils with low moisture storage capacity, particularly on sunny north and north-westerly aspects (Pook et al. 1966; Ashton et al. 1975; Sinclair 1980). In these exceptional droughts interspecific differences in drought resistance have been demonstrated in natural eucalypt stands highlighting the importance of drought as an ecological factor influencing the distribution of eucalypts in dry habitats.

At the study site on Snug Plains observations made in regenerating stands of ridge dwelling eucalypt species indicated that during the summer dry seasons of 1980/81 and 1981/82, selective drought-induced crown damage was occurring. These observations suggested drought tolerance might be a factor involved in delineating eucalypt species distributions in the ridge habitats. Accordingly, glasshouse trials and field studies were undertaken to establish whether interspecific differences in drought resistance existed for the six eucalypt species: E. delegatensis, E. coccifera, E. pulchella, E. gunnii, E. urnigera and E. johnstonii present at Snug Plains. Preliminary drought trials were conducted on seedlings of all six species, to identify the interspecific differences in water relations which develop during artificial drought under controlled conditions (in growth cabinets).

By 1982 Snug Plains and south-eastern Tasmania was experiencing a severe and extended drought. For six consecutive years Hobart had received an annual rainfall below average (631 mm) including a record minimum of 391 mm in 1979 and culminating in a near record minimum of 399 mm in 1982. During the 1982-83 summer, comparative studies were conducted in mixed stands of the three eucalypt species: E. delegatensis, E. coccifera and E. pulchella, which occupied ridge sites at Snug Plains to elucidate the interspecific differences in water relations during a natural drought.

Competition trials and studies of root growth involving seedlings of the three species: E. delegatensis, E. coccifera and E. pulchella were also undertaken to compare the water relations of seedlings with those obtained for mature trees studied in the field.

A literature review outlining the physical and biotic factors which influence plant water potential and stomatal conductance, with reference to the "Soil-Plant-Atmosphere-Continuum" model, is presented in Appendix 6.1.

## MATERIALS AND METHODS

### 1. Preliminary Drought Trials

Seed was collected from five trees of each of the six eucalypt species E. delegatensis, E. coccifera, E. pulchella, E. gunnii, E. urnigera, and E. johnstonii growing in natural stands in the study area at Snug Plains. The seed was stratified, germinated on moist vermiculite and at the cotyledonary stage seedlings were pricked out into 15 cm diameter plastic pots filled with potting soil. The potting soil had been passed through a 0.5 cm sieve and thoroughly mixed to ensure homogeneity of the soil. Nutrients were supplied in the form of slow release fertilizer (osmocote and blood and bone) and pots were watered daily while plants became established. Seedlings were grown inside the glasshouse at the University of Tasmania, Hobart, for three months then transferred to a site outside the glasshouse for a further three months to "harden" during the 1981/82 summer. Four replicate seedlings of each species were chosen on the basis of similarity in size, from the large progeny that was grown. Two replicate seedlings of each of the six species were placed in identical randomised blocks, with an edge row, in each of two growth cabinets and the seedlings left for another month to acclimatise to growth cabinet conditions.

The growth cabinets were both adjusted to a constant temperature of 28°C and a 12 hour photoperiod. Light was provided by a mixed bank of fluorescent and incandescent bulbs which delivered a photosynthetically active radiation (P.A.R.) of approximately  $150 \mu\text{E m}^{-2}\text{sec}^{-1}$  at the seedling canopy (Plate 6.1). The relative humidity was monitored using a thermohygrograph placed in each cabinet. When drought trials were commenced, in April 1982, all seedlings were healthy and about 75 cm in height. All the experimental pots in both cabinets were flooded, then allowed to drain for one hour. In one of the

Plate 6.1

The growth cabinet and eucalypt seedlings used in the preliminary drought trials.



cabinets, the "droughted" treatment, all pots were sealed by plugging the drain holes with plasticine, insulating the soil surface with polystyrene beads and covering the top of the pot with aluminium foil (Ashton et al. 1975; Withers 1978) (Plate 6.2). Water was withheld from these pots for the duration of the experiment (21 days). Empty pots containing no seedlings but sealed in the same manner as the "droughted" pots were also placed in the cabinet. In the second cabinet, the "control" treatment, the pots were sealed by plugging the drainholes only, and during the experiment pots were rewatered to the initial pot weight daily before dawn (i.e. prior to illumination).

At the start of the experiment the leaf area for each seedling was estimated, by multiplying the number of leaves by the mean leaf area for the species (as described in Chapter 3) to allow estimates of seedling transpiration to be made from pot weights. During the experiment, predawn measurements (i.e. prior to illumination) of pot weights (recorded daily), relative water content (R.W.C., recorded daily), and xylem water potential (recorded every 4 days); and midday measurements of stomatal conductance (recorded daily) were made on all "droughted" plants. The same set of measurements was made on "control" plants on three occasions: days 4, 10 and 14 of the experiment. On these days "empty" pots were also weighed to detect any weight loss from the closed pot system.

Stomatal conductances were measured using a Licor Li 700 diffusion porometer. Records were made on a fully expanded leaf from the upper branches of each seedling. The temperature, light intensity were constant, and relative humidity (R.H.) was essentially constant, during each day's measurements and therefore calibration of the porometer was only required at the start of a set of readings.

Water potentials were measured using a pressure chamber made in the Botany Department, University of Tasmania. A single leaf from a lower branch of a seedling was rapidly transferred (within 60 secs) to the pressure chamber and the xylem balance pressure obtained. For a single seedling no more than six fascicles were taken for xylem balance pressure measurements, which, for seedlings with between 90 leaves (for E. delegatensis) and 654 leaves (E. pulchella), was considered to have a negligible effect on the other physiological factors measured. The R.W.C. was obtained for each seedling by punching 10 leaf discs from a single lamina (where possible). Fresh weight of the discs was obtained immediately. Discs were then incubated for 24 hours in distilled water at compensation point ( $35 \mu\text{E m}^{-2}\text{sec}^{-1}$ , Ranson 1979; Ashton & Turner 1979) to

Plate 6.2

Representative seedlings of *E. delegatensis*, *E. coccifera*, *E. pulchella*, *E. gunnii*, *E. urnigera* and *E. johnstonii* after the preliminary drought trials for (a) the droughted treatment and (b) the control (well watered) plants.



(a) Droughted plants



(b) Control plants

prevent weight loss by the discs through respiration, or gain through photosynthesis, before the imbibed weight was obtained. Finally discs were oven dried at 104°C, dry weights measured and R.W.C. calculated (Turner 1981).

At the end of the droughting experiment the percentage moisture in each of the "droughted" pots was obtained gravimetrically, and from the daily weight loss records, the percentage moisture content for each pot on each day of the experiment could be calculated. The mean (of two replicates) R.W.C., stomatal conductance, water potential and daily transpiration were then plotted against  $\log_{10}$  of the mean (of two replicates) gravimetric moisture content of the soil for each species. As care was taken to ensure the initial soil mix used to fill the pots was homogenous, a particular gravimetric moisture content should represent a comparable soil moisture status in all pots.

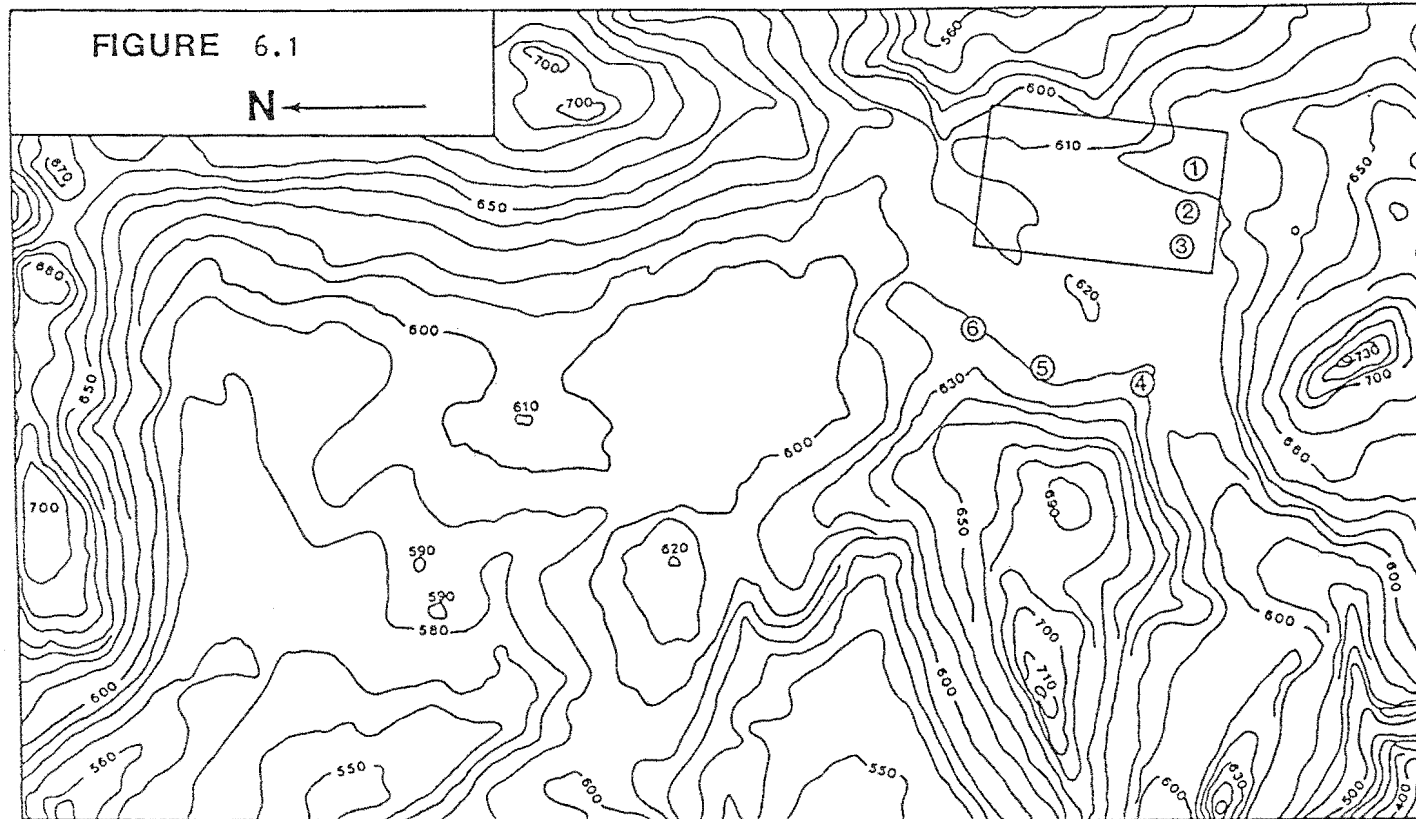
## 2. Field Studies

Field studies were conducted during the 1982/83 summer season on a low ridge oriented approximately north-south within the study area (Figs 6.1 and 6.2). Four eucalypt species were present in the vicinity of the ridge. E. gunnii (subgenus Symphyomyrtus) was sole dominant on the low lying, poorly drained and frost prone area on the western side of the ridge, while on the ridge top and slopes, three eucalypt species from the subgenus Monocalyptus formed a mosaic. E. pulchella was dominant on the ridge top and north-western slopes, E. coccifera dominated the lower western slopes of the ridge and E. delegatensis occupied the eastern slopes along most of the ridge crossing aspects at the southern end (Fig. 6.2). Repeated wild fires had killed many of the original stems on the ridge opening the canopy. Consequently, in the regenerating stands on the ridge, invasion of openings in the canopy by seedlings of neighbouring eucalypt species has produced stands which, in places, consists of a mixture of two or three species. This is particularly the case at the margins of the E. pulchella distribution (Fig. 6.2). However, judging by the distributions of the remaining old stems, the original stands may well have been monospecific with sharply defined boundaries.

### (a) Soils

A transect of soil pits was dug to bedrock at sites 0, 1, 2 and 3 across the ridge at the study site on Snug Plains. Soil pits 1 m<sup>2</sup> in cross sectional area were dug beside the reciprocal seedling transplant trials at sites 1, 2 and 3 (Fig.

Fig. 6.1: Topographic map of Snug Plains



① — ⑥ Sites of field transplant trials and weather recording stations

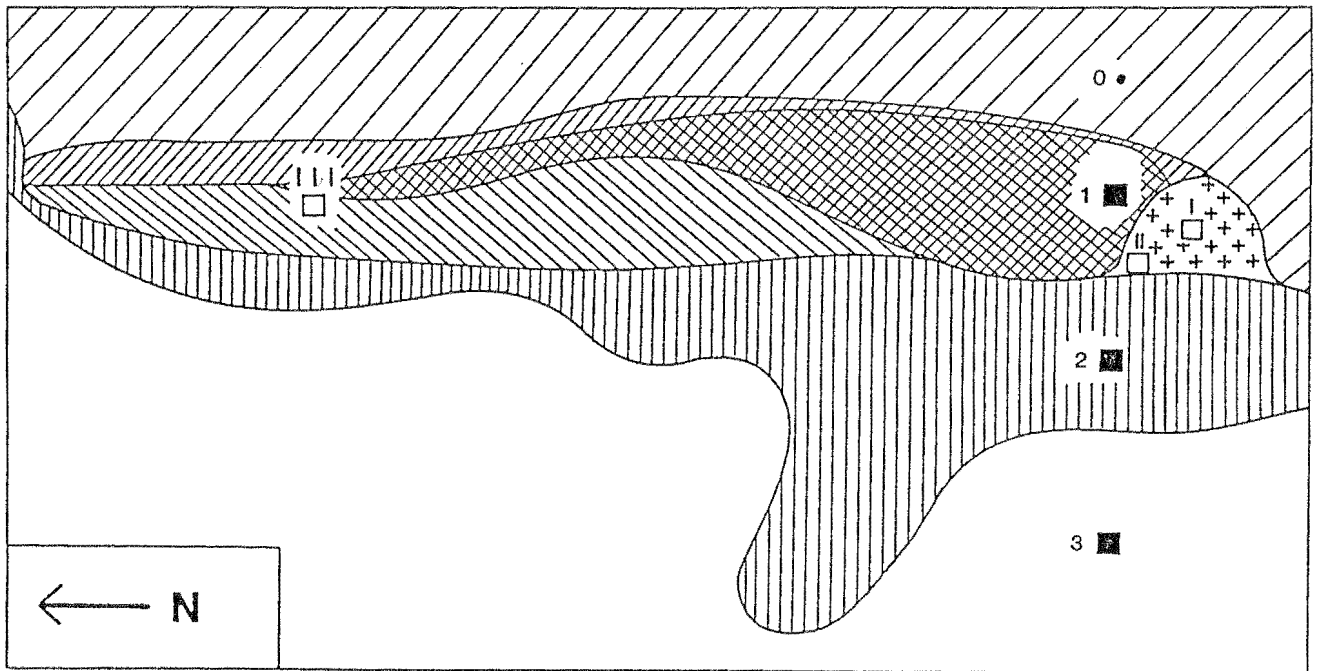
Scale 42 mm represents 1 km

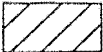


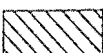





Region in which 1982/83 summer drought study was conducted



Fig 6.2: The distribution of eucalypts and the position of study sites on a low rocky ridge investigated during the 1982/83 summer drought (region marked in Fig. 6.1).



- |   |  |
|---|--|
|  | <u>E. delegatensis</u>   |
|  | <u>E. pulchella</u> and <u>E. delegatensis</u> mixed stand                       |
|  | <u>E. pulchella</u>  |
|  | <u>E. pulchella</u> and <u>E. coccifera</u> mixed stand                          |
|  | <u>E. coccifera</u>  |
|  | <u>E. pulchella</u> , <u>E. coccifera</u> and <u>E. delegatensis</u> mixed stand |
|  | <u>E. gunnii</u>   |

0,1,2&3 Sites where soil profiles were dug to bedrock

I-III Stands for which measurements of plant water relations were made during the 1982/83 summer drought



6.2). The soil pit at site 0 was dug within a pure stand of E. delegatensis on the eastern side of the ridge. In each pit the volume of rock was calculated by the water displacement (Pooke et al. 1966), and the volume of soil obtained by subtraction for each soil horizon. Representative soil samples were obtained from each horizon in the profile and, in the laboratory, measurements of gravimetric moisture content were made and pF curves were generated (described in Chapter 5; Appendix 6.2). The pF curves were then used to obtain the percentage moisture content of the soils at both field capacity (F.C.: -0.1 bar, -0.01 MPa) and permanent wilting point (P.W.P.: -15 bar, -1.5 MPa). From this an estimate of "extractable" moisture present in the soil profile could be made (after Specht 1972).

At approximately monthly intervals during the 1982/83 summer drought soil profiles were again dug at sites 0 to 3 and at stand I (see below) and soil samples taken from each of the soil horizons for measurement of gravimetric moisture content. From the percentage moisture content of the soils, and using the pF curves generated for each soil (Appendix 6.2), the soil water potentials could be obtained. Once the amount of moisture present in the soils at P.W.P. (above) was known, the moisture available to the plant community at various stages during the drought could also be obtained from the pF curves.

To obtain an indication of the topography of the underlying bedrock in the region between stand I and stand II (Fig. 6.3) a sharpened spike was driven into the soil to bedrock at the intersections of a 10 m grid laid across the region. At the intersection of the 10 m grid four spike depths were recorded and the mean depth calculated.

#### (b) Stands Studied

Four mixed regenerating pole stands of E. pulchella, E. coccifera and E. delegatensis and the seedling transplant trial at garden 1 were studied during summer droughts. However intensive studies were restricted to stand I.

Stand I: Stand I was situated in a dense mixed regenerating pole stand at an ecotone where E. delegatensis abutted the distribution of both E. pulchella and E. coccifera (Figs 6.2 and 6.3). A wooden platform was constructed amongst the crowns of nine eucalypt trees, comprising three replicate trees from each of the above species (Plate 6.3). The platform was 3.5 m in height and 4 m x 5 m in area and allowed ready access to the crowns of the trees

Fig. 6.3:

position of eucalypt stems

Stem identification:

|   |                        |
|---|------------------------|
| p | <i>E. pulchella</i>    |
| d | <i>E. delegatensis</i> |
| c | <i>E. coccifera</i>    |
| j | <i>E. johnstonii</i>   |
| u | <i>E. urnigera</i>     |

Suffixes A - J Denotes stems studied during general surveys of trees near Stand I.

Suffixes 1 - 6 Denotes stems for which measurements of water potential and stomatal conductance were made from dawn to dusk during the 1982/83 summer.

Stand I Near the ridge top a platform was constructed around the crowns of nine trees (p1-3, c1-3, and d1-3) at Stand I. These trees were monitored at regular intervals from November 1982 to March 1983.

Stand II On the lower slopes of the ridge of trees (p4-6, c4-6 and d4-6) were monitored on two occasions; 16.2.83 and 3.3.83 during the 1982/83 summer.

Stand III A seedling transplant trial where water potentials of the seedlings were measured at the height of the drought; 18.2.83.

X : 10 m grid intersection points at which four replicate soil depths were measured with a sharpened spike.

### STAND III

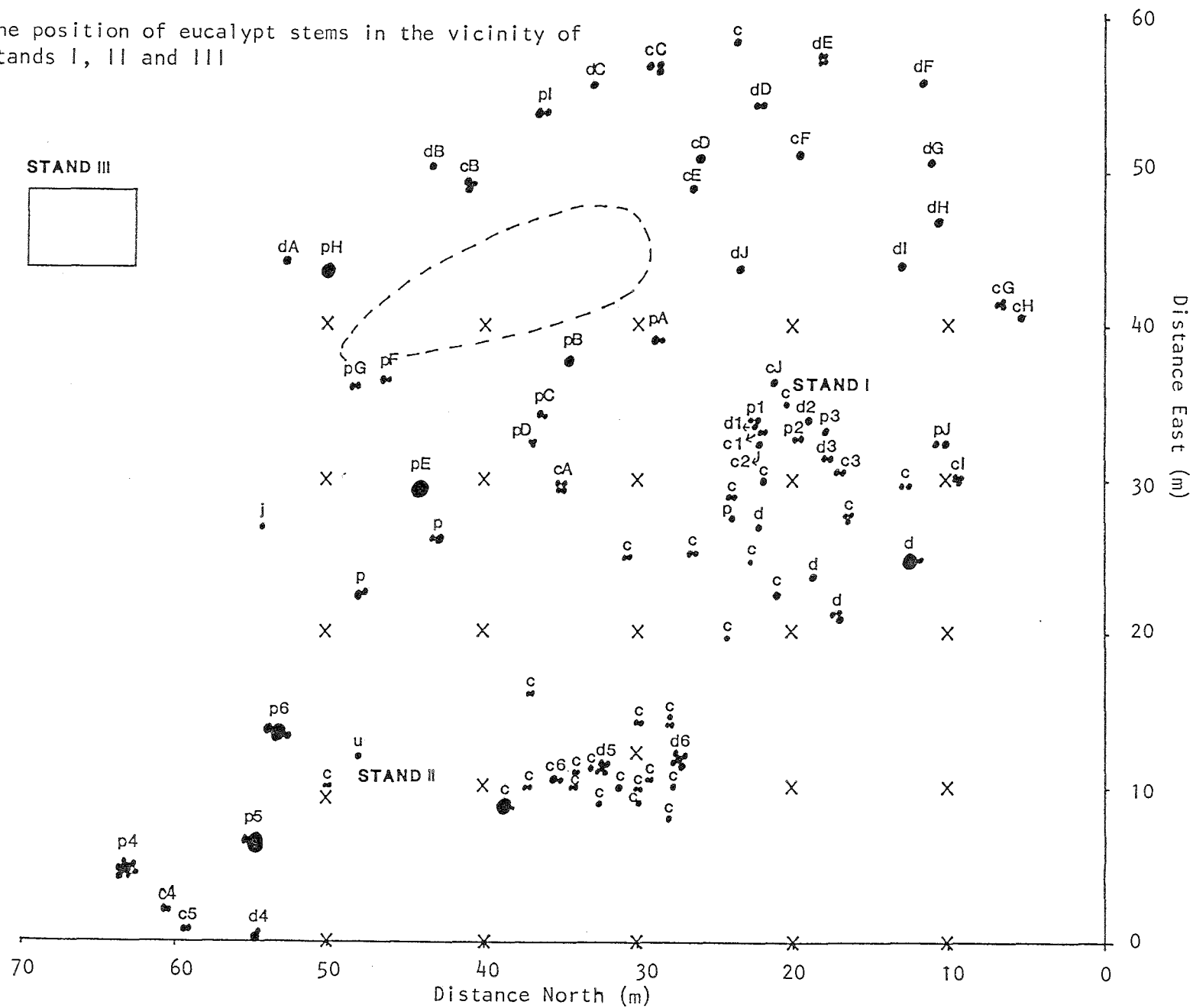


Plate 6.3

The platform, built at a height of 3.5 m amongst the crowns of nine trees (three trees of each of the three species - E. pulchella, E. coccifera and E. delegatensis), at stand I, from which physiological measurements were made on seven occasions during the 1982/83 summer. .



during water relations measurements. The nine trees studied had stems of similar height (7.1 m to 8.7 m), diameter (7.0-11.8 cm) and age (16 years) (Table 6.1). Ring counts of stems in a neighbouring stand indicated the stand was between 15 and 16 years old, regeneration from the intense bushfires in 1967. The nine individuals studied were, judging by the fire scars at ground level, all lignotuberous shoots from lignotubers which predate the 1967 fire. However, lignotuber sizes were very comparable (Table 6.1) suggesting they may all have originated as seedlings from a single previous disturbance. The nine trees at stand I; three E. pulchella trees (p1-3), three E. coccifera trees (c1-3) and three E. delegatensis trees (d1-3) were in close proximity to one another (Fig. 6.3) with crowns almost touching (Plate 6.3).

Stand II: Stand II was a mixed ecotonal stand of the above three species, near to stand I, but on the lower slopes of the ridge 35 m to the north-west. Like stand I, nine trees were studied, three E. pulchella trees (p4-6), the three E. coccifera trees (c4-6) and the three E. delegatensis trees (d4-6) (Fig. 6.3). Access was gained to the crowns of the trees via a ladder during water relations measurements.

Stand III: Stand III was situated 0.5 km north of stand I on the crest of the ridge (Fig. 6.2) and was comprised of a dense 2-5 m high pole stand of E. pulchella and E. coccifera with the occasional stems of E. delegatensis. Access to the crowns of the stems studied was gained from the ground or via a step-ladder.

Stand IV: Stand IV was a mixed regenerating pole stand of E. delegatensis and E. pulchella between 3.5 and 6.0 m in height situated 2 km north-west of stand I. An assessment of drought damage and stem growth was made in this stand on two occasions in 1981.

Garden 1: Described in Chapter 3.

### (c) Plant Water Relations and Drought Damage

Water potential, stomatal conductance and relative water content of the leaf tissue of the three eucalypt species E. pulchella, E. coccifera and E. delegatensis were recorded on various occasions during the 1982/83 summer at stands I to III and garden 1. Water potentials were measured using a pressure

TABLE 6.1:

Stem characteristics and crown damage for the trees at Stand 1. Mean  $\pm$  SE were calculated using primary stem (Stem 1) data only. The significance of interspecific differences was obtained from analysis of variance. (NS, not significant and \*,  $p < 0.05$ ).

| Species         | Tree No. | Stem No. | Stem height (m) | Stem diameter (cm) | Basal area at breast height (cm <sup>2</sup> ) |          | Lignotuber area (cm <sup>2</sup> ) | Crown Damage (%) |
|-----------------|----------|----------|-----------------|--------------------|--|----------|------------------------------------|------------------|
|                 |          |          |                 |                    | Each Stem                                      | Total    |                                    |                  |
| E. pulchella    | 1        | 1        | 7.8             | 9.5                | 71   | 120      | 581                                | 20               |
|                 |          | 2        | 6.0             | 7.9                | 49   |          |                                    |                  |
|                 | 2        | 1        | 7.8             | 11.8               | 109  | 148      | 694                                | 10               |
|                 |          | 2        | 5.2             | 7.0                | 39   |          |                                    |                  |
|                 | 3        | 1        | 7.1             | 8.9                | 62   | 62       | 173                                | 20               |
|                 |          | 2        | -               | -                  | -  |          |                                    |                  |
| Mean            |          |          | 7.6 ± 0.2       | 10.1 ± 0.9         | 80 ± 14  | 110 ± 25 | 481 ± 158                          | 17 ± 3           |
| E. coccifera    | 1        | 1        | 7.5             | 6.4                | 32   | 70.7     | 454                                | 35               |
|                 |          | 2        | 7.1             | 7.0                | 39   |          |                                    |                  |
|                 | 2        | 1        | 8.7             | 9.9                | 77.0   | 77.0     | 238                                | 20               |
|                 |          | 2        | -               | -                  | -  |          |                                    |                  |
|                 | 3        | 1        | 7.3             | 9.9                | 77   | 109.2    | 503                                | 20               |
|                 |          | 2        | 6.3             | 6.4                | 32   |          |                                    |                  |
| Mean            |          |          | 7.8 ± 0.4       | 8.7 ± 1.2          | 62 ± 15  | 86 ± 12  | 398 ± 81                           | 25 ± 5           |
| E. delegatensis | 1        | 1        | 8.1             | 8.9                | 62   | 62       | 302                                | 70               |
|                 |          | 2        | -               | -                  | -  |          |                                    |                  |
|                 | 2        | 1        | 8.2             | 11.5               | 104  | 149      | 442                                | 50               |
|                 |          | 2        | 6.2             | 7.6                | 45   |          |                                    |                  |
|                 | 3        | 1        | 7.6             | 8.9                | 62   | 80       | 622                                | 35               |
|                 |          | 2        | 6.1             | 4.8                | 18   |          |                                    |                  |
| Mean            |          |          | 8.0 ± 0.2       | 9.8 ± 0.9          | 76 ± 14  | 97 ± 27  | 455 ± 93                           | 52 ± 10          |
| Significance    |          |          | NS              | NS                 | NS   | NS       | NS                                 | *                |

chamber (described previously). Small shoots were cut with secateurs and transferred to the chamber (within 60 seconds) and the xylem balance pressure determined.

Stomatal conductance was measured with a diffusion porometer (described above). A single leaf was tagged and readings made on the same leaf for each tree throughout the summer. Occasionally mechanical damage was incurred by the leaf and in this case an adjacent leaf on the same shoot was used. Leaves chosen for measurement were average-sized 2 year old leaves on the shaded side of the crown. The porometer was periodically recalibrated throughout the day's readings, particularly during periods of rapid temperature change (Kanemasu *et al.* 1969; Morrow & Slatyer 1971).

Relative water content (R.W.C.) of the leaf tissue was obtained using two sets of leaf discs cut from a representative crown leaf using a 0.5 cm diameter cork borer. One set of 10 discs was placed in a sealed vial half-filled with distilled water and the other 10 discs were placed in a dry, tared vial and the lid tightly sealed. Samples were taken back to the laboratory (1 hour drive) and fresh weights obtained for discs in the dry vials. The leaf discs in distilled water were transferred to petri dishes containing distilled water and incubated for 24 hours at compensation point ( $35 \mu\text{E m}^{-2}\text{s}^{-1}$ , Ranson 1979; Ashton & Turner 1979) before the imbibed weights were obtained. Dry weights were obtained for both sets of discs. The above method was used because the discs cut in the field were unlikely to give a representative value for imbibed weight after extended travelling times, particularly in the case of droughted trees.

The standard formula for relative water content (Turner 1981) is:

$$\text{R.W.C.} = \frac{\text{FW} - \text{DW}}{\text{IW} - \text{DW}} \times 100\% \quad (3)$$

Adaptation of this formula for sets of discs gives:

$$\text{R.W.C.} = \frac{\frac{\text{FW} - \text{DW}_1}{\text{DW}_1}}{\frac{\text{IW} - \text{DW}_2}{\text{DW}_2}} \times 100\% \quad (4)$$

When dry weights of both sets of discs are identical (4) is equivalent to (3).

Continuous records of air temperature and humidity at crown height were obtained via a thermohygrograph placed in a Stevenson screen on the platform (3.5 m in height) at stand I (Plate 6.3). Humidities were converted to vapour pressure deficits (V.P.D.).

All water relations measurements (except those made on the 15/2/83 and 22/2/83) were made on clear and cloudless days so that stomatal conductance measurements and micro-environmental parameters were not influenced by large and sudden variations in light intensity (P.A.R.). On the 15/2/83 and the 22/2/83 atmospheric conditions were unsettled and the skies intermittently overcast. At this point in the drought the trees measured were severely stressed and variations in P.A.R. had little influence on stomatal conductance. Stomatal conductance and water potential were recorded from dawn till dusk (unless otherwise stated) for each day of measurement. The mean leaf area and mean stomatal counts were also obtained from leaves of each of the three species studied. The juvenile leaves measured were from seedlings at garden 1 and adult leaves were from trees at stand I.

The extent of drought damage was assessed immediately after the first rains. Drought damage to the crowns of the trees was visually estimated to the nearest 5%, and mean percentage crown damage calculated for each species in the stand (percentage values were angularly transformed before analysis). Qualitative assessments were also made of the form of leaf damage which occurred to each species and the rate of mode of recovery of the tree crowns after drought breaking rains. The stem growth (stem basal area increment) of trees damaged to varying extents during the 1980-81 drought was also assessed.

The water relations measurements and crown damage assessments made on each stand were as follows:-

Stand I: At stand I approximately hourly measurements of water potential and stomatal conductance were made from dawn to dusk on seven occasions during the 1982/83 summer (28/11/82, 29/12/82, 31/1/83, 15/2/83, 22/2/83, 25/2/83 and 2/3/83). Measurements were made on three replicate individuals for each of the species E. pulchella, E. coccifera and E. delegatensis. The relative water content of leaf tissue for the nine trees at stand I was obtained on three occasions during the summer: 16/2/83, 20/2/83 and 25/2/83. The crown damage sustained by the nine trees at stand I was assessed after the first rains.



On 16/2/83 a survey of the stomatal conductance and water potentials of 30 trees was conducted in the neighbourhood of stand I. Ten E. coccifera trees (cA-J), ten E. delegatensis trees (dA-J) and ten E. pulchella trees (pA-J) were measured during the two hour period from 12 noon to 2 pm (Fig. 6.3). These measurements were made to confirm that the nine trees at site 1 were representative of trees on the ridge. A second survey was conducted on the same 30 trees on 3/3/83 to confirm that all trees on the ridge were recovering from the drought. The crown damage inflicted by the drought on the survey trees was also assessed at the end of the drought, in March 1983, and mean percentage crown damage for each species calculated.

Stand II: At stand II approximately hourly measurements of stomatal conductance and water potential were made from dawn to dusk on two occasions during the 1982/83 summer drought. Measurements were made on 17/2/83 at the height of the drought, and after the drought had broken on 4/3/83. Three replicate trees of each of the three species E. coccifera, E. pulchella and E. delegatensis were measured.

Garden 1: Water potential measurements were made on five replicate seedlings of each of the three species E. coccifera, E. pulchella and E. delegatensis from edge row seedlings in the reciprocal transplant trial. Measurements were made on the 18/2/83, 12 hours after a light fall of drizzle at the study site on Snug Plains. Seedling water potentials were compared with those obtained simultaneously at the nine stand I trees.

Stand III: Stomatal conductance and water potentials were measured on nine E. coccifera and nine E. pulchella trees at stand III on the 17/2/84. Measurements were made on paired trees (one of each species) less than 2 m apart. All the stems measured were lignotuberous shoots from established lignotubers (judging by the fire scars at the base of the stem) and were between 2 m and 5 m in height. The height, diameter and percentage crown damage incurred during the drought were recorded for the E. pulchella and E. coccifera stems on which water relations measurements were made. A measurement of height and assessment of crown damage was also made for all E. delegatensis stems greater than 2.0 m in height in the vicinity. Drought damage was also recorded for 16, 5 x 5 m quadrats (subunits of a 20 x 20 m quadrat) which included trees used in the water relations studies at stand III. Crown damage was estimated for saplings in each of the height intervals: 0 to 1.0 m; 1.1 to 2.0 m; 2.1 to 4.0 m; and greater than 4.1 m, and the stem frequencies for each

height class were recorded. The mean percentage crown damage was calculated for each species present in the above height intervals. E. coccifera contributed by far the greatest proportion of stems to the quadrat, so, in order to determine whether stem density was influencing drought damage (Barber 1965), linear regressions of crown damage against stem frequency were performed for three height intervals (intervals up to 4.0 m high) in each of the 16, 5 x 5 m quadrats.

Stand IV: Crown damage (scored on a 1 to 5 scale) and stem diameters were recorded for 10 paired stems (stems less than 1 m apart) of E. pulchella and E. delegatensis on the 15/3/81, after the 1980-81 drought had broken. Six months later (on the 4/10/81) stem diameters were remeasured. The mean percentage basal area increment over the 6 month period for stems in each crown damage class was then calculated for both species.

### 3. Seedling Root Pattern

Seed was collected and germinated for each of the species E. pulchella, E. coccifera and E. delegatensis (as described previously). Seedlings were pricked out into tubular pots 800 mm long and 150 mm in diameter filled with potting soil (Plate 6.4). The tubular pots, made from lengths of plastic pipe with 2 mm flywire wired over one end, were stood in a shallow gravel-lined tray with the water table maintained at 3 cm from the bottom of the tubes (Plate 6.4). Seedlings received upwardly percolating water from the water table and were also watered daily throughout the experiment. Nutrients were provided in the form of slow release fertilizer only (osmocote and blood and bone) present in the potting soil. Four replicate pots containing two seedlings were planted for each species. The pots were thinned in favour of the most vigorous seedling after three weeks. Seedlings were grown for 14 weeks <sup>in a glasshouse</sup> by which time the first root was observed to reach the flywire base of the pot. All seedlings were then harvested. The flywire bottoms to the pots were removed, a plastic sleeve placed over the pot and the soil column allowed to slide out into the plastic sleeve. The soil column wrapped in plastic was then placed on a pin board, the sleeve slit and the soil carefully washed away from the roots using a hose. Finally the root system was photographed against a scale. From the photographs, drawings of a typical root system was made for each species and counts of the number of major roots and rootlets were made at 50 mm intervals between the soil surface and the bottom of the pot for each. The mean root frequency at each depth interval was calculated and a plot of root frequency against soil depth generated for each species.

Plate 6.4

Tubular pots containing seedlings of three species E. delegatensis, E. coccifera and E. pulchella involved in root pattern studies.



#### 4. Competition Trials

Seed was collected from five trees of each of the Monocalyptus species E. delegatensis, E. coccifera, and E. pulchella growing in natural stands in the study area at Snug Plains. Seeds were stratified, germinated on moist vermiculite and at the cotyledonary stage were pricked out into 5 cm diameter plywood veneer tubes filled with potting soil. Seedlings were grown in the glasshouse at the University of Tasmania for three months and transferred outside the glasshouse for a further three months to harden. From the large progenies grown in veneers vigorous seedlings were selected on the basis of similarity in size and planted in pairs into large 4 litre plastic pots filled with potting soil (as described in Chapter 5). For each pot, two seedlings of different species were planted together (stems 5 cm apart) at the centre of the pot. All three combinations of these species were planted as mixed species pairs. Sixteen replicate pots were planted for each of the three species combinations E. pulchella + E. coccifera, E. pulchella + E. delegatensis and E. delegatensis + E. coccifera. The pots were placed in a randomised block design with an edge row in the glasshouse and grown for six months. Seedlings were watered daily. Nutrient was provided as slow release fertilizer (osmocote and blood and bone) present in the potting soil and no extra nutrient was supplied. In early April 1983 the mean height of seedlings was about 1.3 m (Plate 6.5). Inspection of selected pots indicated that the root systems of the seedlings of both species had ramified through each pot and were intimately intertwined. Eight of the 16 replicate pots for each species combination were chosen on the basis of similarity in size and the drought trials begun. For logistical reasons the drought trials for each of the species combinations were performed separately and consecutively, each drought trial lasting about six days. The eight selected replicates pots for each trial were randomly placed into two treatments (four pots in each treatment). The remaining eight replicates were left in their positions in the randomised block design (controls). In treatment 1 (high V.P.D.), seedlings were placed in a rectangular plastic enclosure supported by a metal frame measuring 0.75 x 0.75 m in cross section and 2.0 m in height (Plate 6.6). A thermostatically controlled fan heater mounted at the top of the enclosure was adjusted to deliver a wind velocity of approximately  $4.2 \text{ m sec}^{-1}$  at a temperature of  $35^{\circ}\text{C}$  ( $\pm 2^{\circ}\text{C}$ ). The relative humidity of the air passing through treatment 1 was approximately 35% ( $\pm 4\%$ ) (V.P.D. = 3.58 KPa). For treatment 2 (low V.P.D.), seedlings were placed in a second identical enclosure with a fan mounted at the top. The fan was adjusted to deliver a wind of the same velocity as treatment 1 but the temperature and humidity were ambient for air in the glasshouse. During April 1983 the daytime glasshouse

Plate 6.5

Pairs of seedlings used in competition trials  
(a) before and (b) after droughting.

(a)



(b)





Plate 6.6

Plastic enclosures fitted with fan-heaters which house pots containing paired seedlings of different species, exposed to high V.P.D. (treatment 1), and low V.P.D. (treatment 2) during drought, used in the competition trials.



temperature was approximately  $19^{\circ}\text{C}$  ( $\pm 4^{\circ}\text{C}$ ) and humidity 61% ( $\pm 9\%$ ) (V.P.D. = 0.85 KPa). The fans were run from dawn to dusk (12 hours) on each day of the drought trials. Nocturnal temperatures and RHs for both treatments were ambient for the glasshouse (approximately  $15^{\circ}\text{C}$ ), and air was still. A continuous readout of temperature at various heights within the foliage of the experimental plants and the temperature of the soil in the pots was obtained via a Grant recorder and long lead thermistors, for the duration of the drought trials. Water potentials were measured using a pressure chamber (described previously). The seedlings studied were large having total leaf counts of 160 to 230 for E. delegatensis, 480 to 650 for E. coccifera and 1200 to 1800 for E. pulchella. Between 13 and 20 fascicles were cut from each seedlings (using secateurs) for water potential measurements. This amounted to a negligible proportion of the foliage for E. coccifera and E. pulchella but comprised 8 to 10% of E. delegatensis foliage. However, removal of E. delegatensis foliage would reduce the evapotranspirational area of the foliage and therefore enhance the performance of E. delegatensis in comparison with other species and reduce rather than increase interspecific differences. It was considered that the reduction in leaf area inflicted during water potential measurements would not alter the interpretation of results if interspecific differences were developed. Stomatal conductances were measured using a diffusion porometer (described previously). Single leaves in the upper seedling foliage were tagged and read throughout the trial. Occasionally, mechanical damage was incurred by the tagged leaf, and in this event, an adjacent leaf on the same branch was selected. The porometer was recalibrated for each set of measurements made in each of the treatments and time was allowed for the temperature of the sensor head to come into equilibrium with the air temperature of the enclosure. Water potential and stomatal conductance were recorded concurrently for the two treatments for each drought trial.

The drought trials were commenced on the 4/4/83. Watering was discontinued for experimental plants, fans were switched on and physiological measurements were begun. Xylem water potential and stomatal conductance were measured at approximately hourly intervals from dawn to dusk on day 1 for all trials. On subsequent days the measurements were made at between 2 hour and 4 hour intervals to provide an outline of the decline in plant water status without over sampling the seedlings. A preliminary experiment showed that seedlings did not deplete the water resources of the pot until day 3 and that water potential and stomatal conductance curves for day 1 and day 2 were very similar. Therefore readings were discontinued on day 2 of each drought trial. The drought trial was continued until all but the apical leaves of one of



the species had become wilted and dry. This stage in dehydration was quite readily identifiable (Plates 6.5b and 6.7). The pot was then removed from the trial and watered. By terminating the trial before the death of either species the recovery and growth of both species after the droughting event could be observed. In previous studies of drought resistance in eucalypt seedlings (Ashton *et al.* 1975), sunflowers (*Helianthus* sp) were planted in the same pots as the eucalypt seedlings to provide a bioassay of the water status of the soil. In general, the test plants wilted at the same time as the *Helianthus* sp. In the current experiment the bioassay for drought severity was the other member of the eucalypt species pair. When the drought trial was completed pots were watered and placed back in their original positions in the randomised block on the glasshouse apron. At the end of each trial representative leaves were sampled from seedlings in both treatments, the pattern of drought injury was visually assessed and the leaves were photographed.

Mean stomatal conductance and water potential were plotted for treatments 1 and 2 for each species pair. Occasionally pots with a pair of smaller seedlings took longer (up to a day) to wilt than larger plants. However, gravimetric soil moisture measurements obtained from a small core of soil taken from near the side of the pots each day allowed comparisons to be made between replicates.

At regular intervals during the growth of the seedlings, the height, diameter of stem (just above the cotyledonary node), and the number of leaves were obtained for each seedling in the experiment. For all seedlings, measurements were made on 18/11/82, 27/12/82, 21/1/83; at the start of the drought trial for each species pair (between 4 and 22/4/83, depending on the trial); at the end of the drought trial for each pair (between 10/4/83-5/5/83, depending on the trial); and approximately three months after drought trials. The mean leaf area for each seedling was obtained (as described previously). The mean seedling leaf area and the mean stem basal area were then plotted for treatment 1, treatment 2 and control plants for both species in each trial.

## RESULTS

### 1. Preliminary Drought Trials

Preliminary drought trials conducted on seedlings of all six eucalypt species studied demonstrated marked interspecific differences in drought tolerance.

Plate 6.7

An E. delegatensis seedling exhibiting severe drought damage, with all except apical leaves wilted and dried and a paired E. pulchella seedling (in the background), after drought treatment in the competition experiment.



All species showed a marked decline in xylem water potential with decreasing soil moisture content (Fig. 6.4) during the 21 day trial. However, marked interspecific differences in relative water content (R.W.C.) were developed as leaf water potentials fell (Fig. 6.5). For example, at  $-2.0$  MPa (a water potential which most mesophytes will tolerate; Hsiao 1973, interspecific differences were evident (Figs 6.4 and 6.5, Table 6.2). At this water potential, E. pulchella seedlings exhibited the highest R.W.C. (67%) followed by E. urnigera (51%), E. coccifera (49%), E. delegatensis (41%), E. johnstonii (41%) and E. gunnii (34%). The maintenance of high R.W.C. at low xylem water potentials has been described as a drought resistant trait in drought tolerant species such as eucalypts (Hinckley *et al.* 1978; Withers 1978; Ashton *et al.* 1975; Ladiges 1974, 1975; Levitt 1972). Therefore the order of R.W.Cs above provides a measure of the relative species order of drought resistance.

The soil moisture content at which each species wilted gave another measure of the relative drought resistance of the species tested (Table 6.3). The species order of wilting was: E. pulchella; E. coccifera; E. delegatensis and E. urnigera; E. johnstonii; and E. gunnii from lowest (9.3%) to highest (12.0%) moisture content of the soil.

The relative water content at which each species wilted (Table 6.3) gave a third estimate of drought resistance: that is, a measure of tissue tolerance of low relative water content (R.W.C.). E. pulchella and E. coccifera wilted at lowest R.W.C. (44%) followed by E. gunnii (67%), E. urnigera (68%), E. delegatensis (69%) and E. johnstonii (72%). Further, a measure of the rate of utilisation of the water resource in the pot is given by the time taken for the seedlings to wilt (Table 6.3) and gives a similar species order to those above.

All measures of drought resistance, for the species tested, generally agreed. E. pulchella was the most drought resistant species followed by E. coccifera. E. delegatensis and E. urnigera were similar in their drought resistance, and E. johnstonii and E. gunnii were the least resistance species in the preliminary drought trials. This agrees with the natural distribution of the species at Snug Plains. E. pulchella and E. coccifera occur naturally on the dry ridge tops and rocky rises, while E. delegatensis and E. urnigera dominate moister soils. E. gunnii and E. johnstonii occupy seasonally waterlogged sites.

Marked interspecific differences in stomatal conductances occurred during the preliminary drought trials (Fig. 6.6). The Monocalyptus species exhibited substantially higher stomatal conductances than the Symphyomyrtus

Figures 6.4-6.7

Plots of: mean leaf water potential (MPa) (Fig. 6.4); mean relative water content (%) (Fig. 6.5); mean stomatal conductance ( $\text{cm sec}^{-1}$ ) (Fig. 6.6); and mean temperature ( $^{\circ}\text{C}$ ) (Fig. 6.7), for two replicate seedlings of E. delegatensis ( $\Delta$ ), E. pulchella (o), E. coccifera ( $\square$ ), E. gunnii ( $\blacktriangle$ ), E. urnigera ( $\bullet$ ) and E. johnstonii ( $\blacksquare$ ), against  $\log_{10}$  percentage soil moisture during the preliminary drought trials.

Figure 6.4

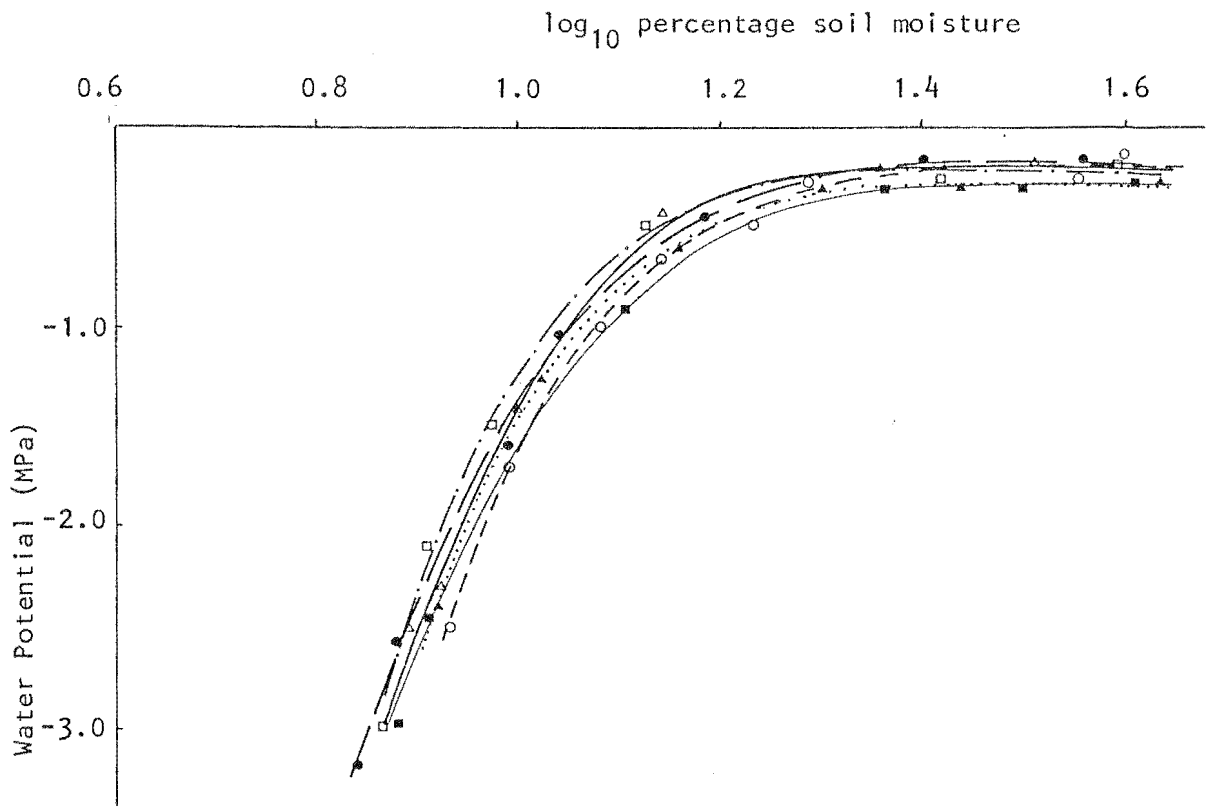


Figure 6.5

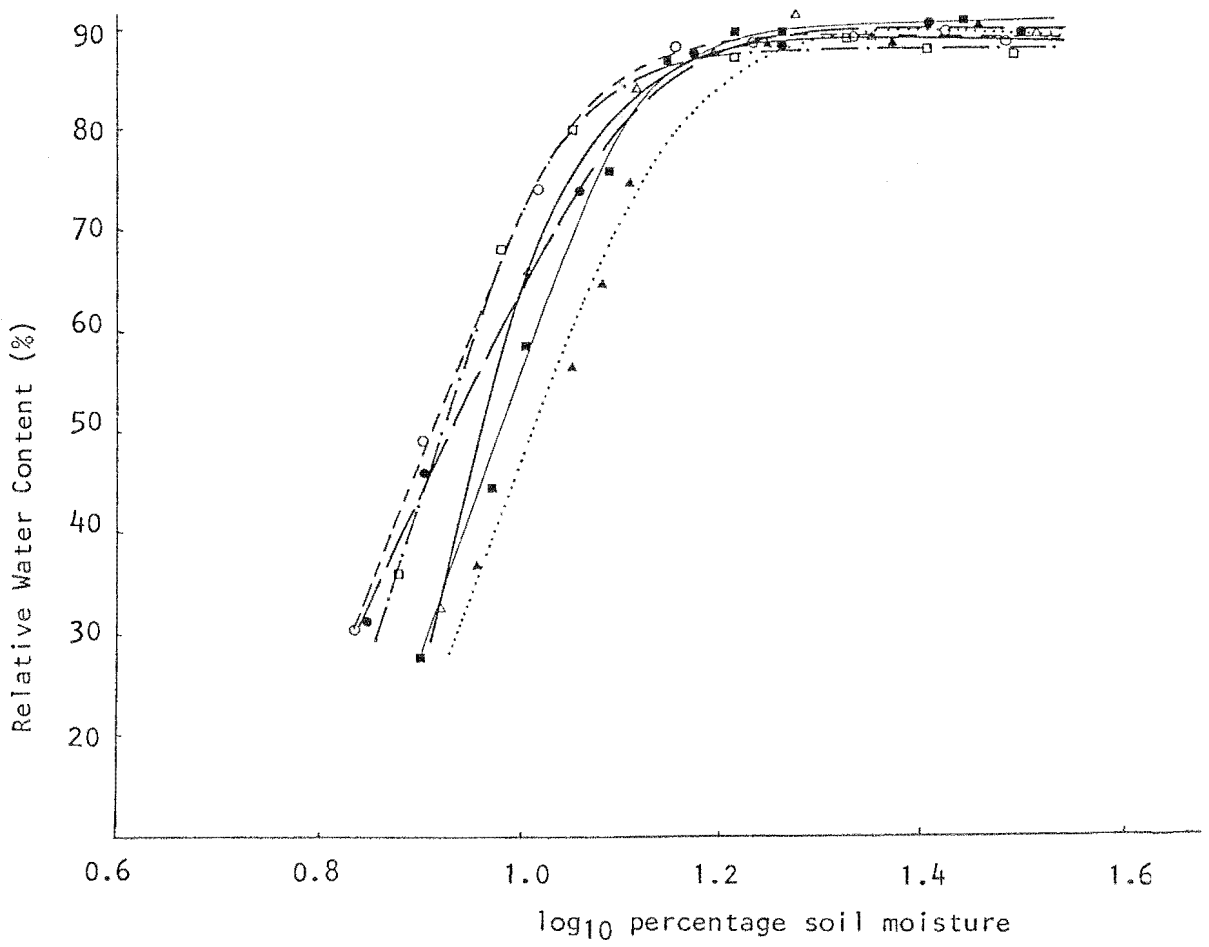


Figure 6.6

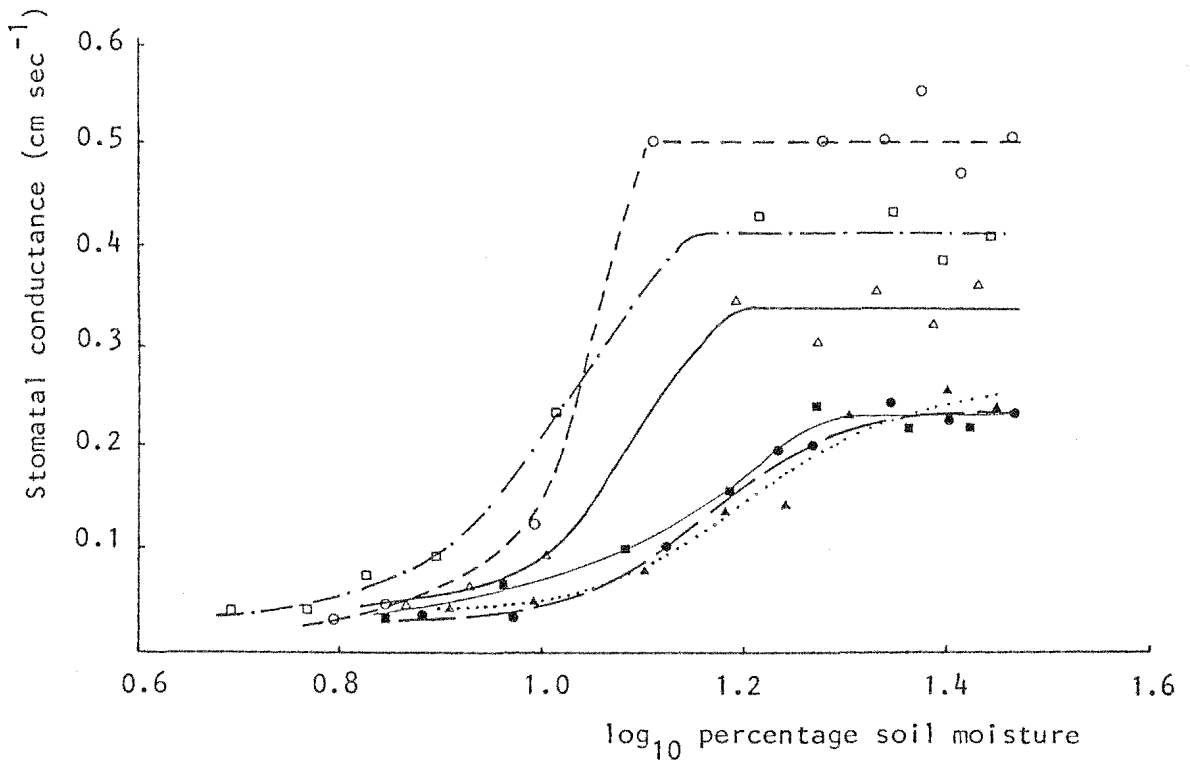


Figure 6.7

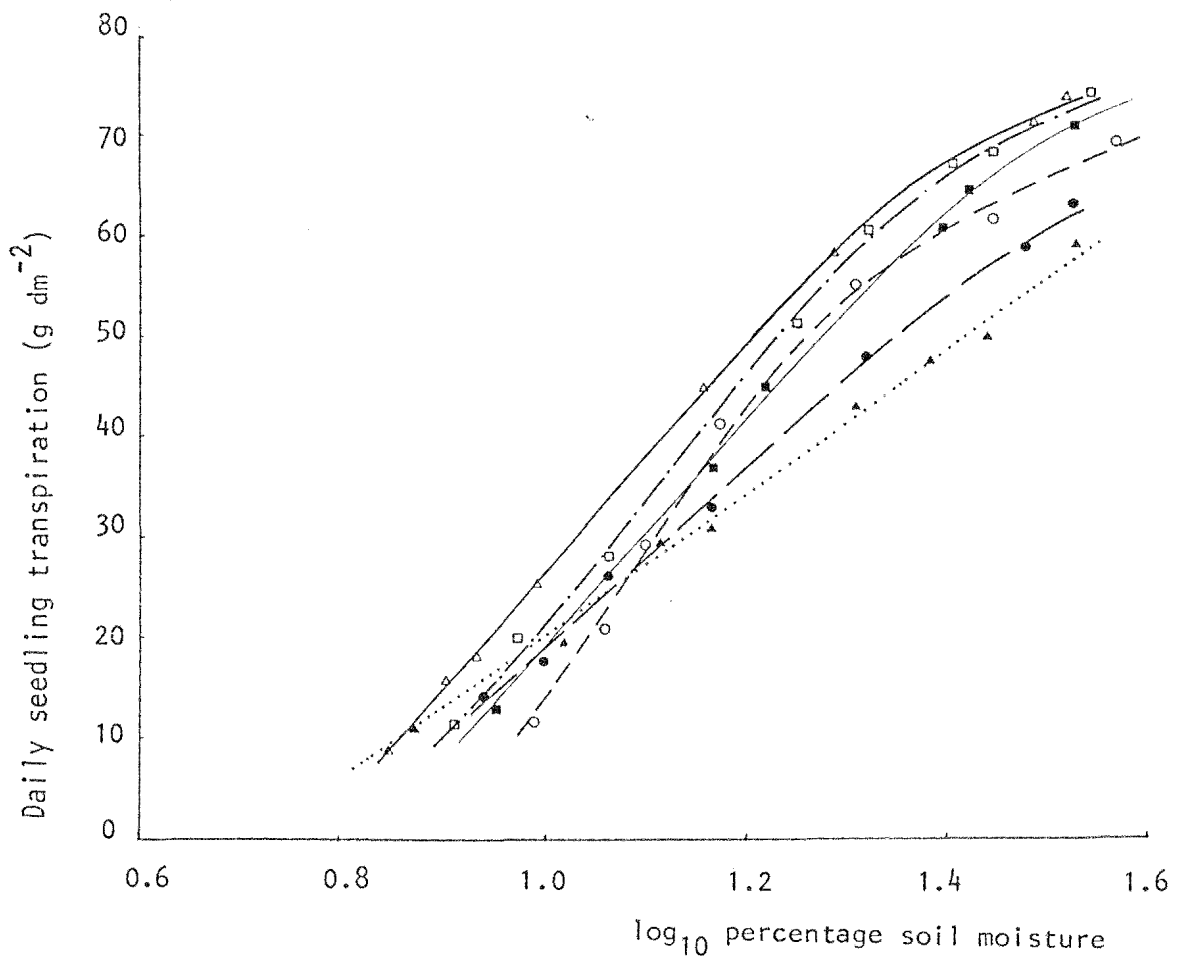


TABLE 6.2

The percentage soil moisture and relative water content of the leaf tissue for eucalypt seedlings at a water potential of -2.00 MPa (from Figs 6.4 and 6.5).

| Species                | Soil<br>moisture<br>SM (%) | $\log_{10}$ (SM) | Water<br>potential at<br>SM (MPa) | RWC<br>at SM<br>(in %) |
|------------------------|----------------------------|------------------|-----------------------------------|------------------------|
| <i>E. pulchella</i>    | 9.6                        | 0.98             | -2.0                              | 67                     |
| <i>E. coccifera</i>    | 8.3                        | 0.92             | -2.0                              | 49                     |
| <i>E. delegatensis</i> | 8.7                        | 0.94             | -2.0                              | 41                     |
| <i>E. urnigera</i>     | 8.5                        | 0.93             | -2.0                              | 51                     |
| <i>E. johnstonii</i>   | 8.9                        | 0.95             | -2.0                              | 41                     |
| <i>E. gunnii</i>       | 8.9                        | 0.95             | -2.0                              | 34                     |

TABLE 6.3

The percentage soil moisture (SW) and relative water content of the leaf tissue at the point of wilting (RWC at SW) for each eucalypt species during preliminary drought trials (from Fig. 6.6).

| Species                | Day of Wilting | Soil moisture at wilting SW (%) | $\log_{10}(\text{SW})$ | RWC at SW (%) |
|------------------------|----------------|---------------------------------|------------------------|---------------|
| <i>E. pulchella</i>    | 16             | 9.3                             | 0.89                   | 44            |
| <i>E. coccifera</i>    | 11             | 9.8                             | 0.91                   | 44            |
| <i>E. delegatensis</i> | 9              | 10.5                            | 1.02                   | 69            |
| <i>E. urnigera</i>     | 9              | 10.5                            | 1.02                   | 68            |
| <i>E. johnstonii</i>   | 7              | 11.5                            | 1.06                   | 72            |
| <i>E. gunnii</i>       | 8              | 12.0                            | 1.08                   | 67            |



species at high soil moisture levels and showed a more abrupt drop in stomatal conductance as soil moisture became limiting. In moist soils E. pulchella exhibited highest stomatal conductances, followed by E. coccifera and E. delegatensis while the Symphyomyrtus species all showed similarly low stomatal conductances.

The Symphyomyrtus species (except for E. urnigera) generally exhibited lower transpiration rates than the Monocalyptus species (Fig. 6.7). However the Symphyomyrtus species possessed a two to three times greater leaf area than the Monocalyptus species (Table 6.4). Therefore, even though stomatal conductances and transpiration rates for the Symphyomyrtus species were low, the large transpiration area possessed by these species may place them at a selective disadvantage in comparison with the Monocalyptus species in soils with limited water reserves.

## 2. Field Studies

The field studies conducted at Snug Plains during the 1982/83 summer coincided with a severe drought which was affecting the whole of south-eastern Tasmania. In the six previous years, the annual rainfall for Hobart had been below the 100 year mean (631 mm) and in two of these years, 1979 and 1982, extreme minimum rainfalls less than 400 mm had been recorded (Fig. 6.8, Table 6.5). During the 1982/83 summer season, the total rainfall for Hobart in the five month period from 1st October 1982 to 28th February 1983 was 76 mm (Table 6.5), a record low for this period. Daily rainfall records for Hobart from November 1982 to April 1983, and rainfall records obtained over this period at Snug Plains indicated that Snug Plains received slightly less rain than Hobart (Table 6.6). Droughts of the severity of those experienced in south-eastern Tasmania in 1982/83 are rare events, probably occurring on average only once every 100 years. Only on one previous occasion has Hobart recorded seven consecutive years with below average rainfall (1896-1902) but no rainfall totals below 400 mm were recorded during this period (Fig. 6.8).

### (a) Soils

The distribution of the four eucalypt species E. pulchella, E. coccifera, E. delegatensis and E. gunnii on a transect across the low ridge in the study area (Figs 6.2 and 6.3) were closely related to the soil characteristics, in particular

TABLE 6.4

The mean leaf area for eucalypt seedlings at the start of preliminary drought trials.

| Species                | Mean seedling leaf area<br>(cm <sup>2</sup> ) |
|------------------------|---|
| <i>E. pulchella</i>    | 546   |
| <i>E. coccifera</i>    | 733   |
| <i>E. delegatensis</i> | 588   |
| <i>E. urnigera</i>     | 1619  |
| <i>E. johnstonii</i>   | 1335  |
| <i>E. gunnii</i>       | 1831  |

Fig. 6.8: Annual rainfall figures for Hobart Weather Station between 1882 and 1983.

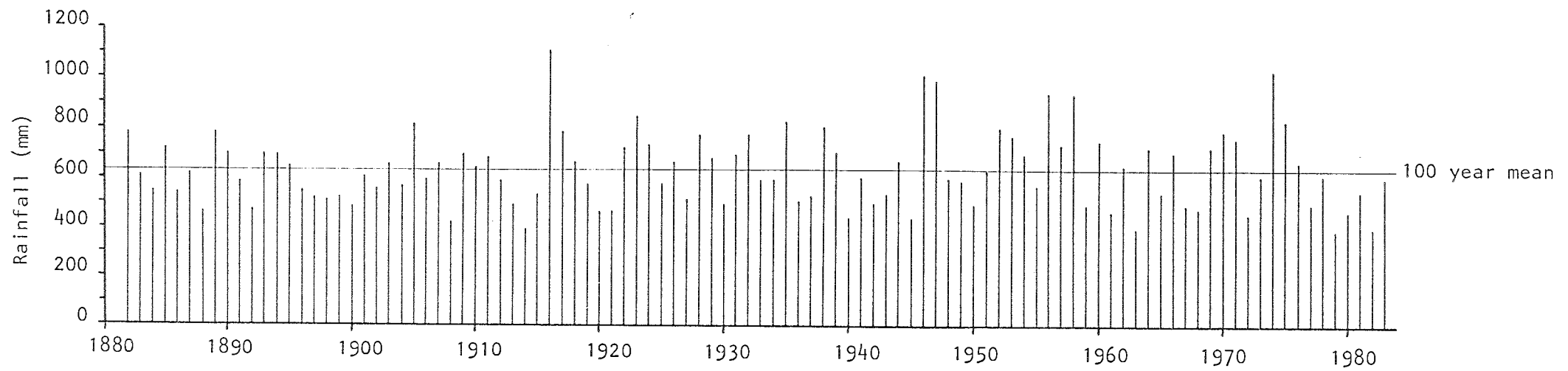


TABLE 6.5:

- (a) Monthly and annual total rainfall figures for the years 1973 to 1983, compared with the 100 year mean, and;  
 (b) years on which annual rainfalls of less than 400 mm were recorded, since records started in 1882, for the Hobart Weather Station.

| (a) | Year          | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Total |
|-----|---------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-------|
|     | 1973          | 35  | 53  | 29  | 63  | 99  | 55  | 12  | 19  | 36  | 95  | 62  | 47  | 605   |
|     | 1974          | 9   | 44  | 43  | 106 | 24  | 85  | 157 | 25  | 377 | 34  | 51  | 64  | 1019  |
|     | 1975          | 58  | 9   | 113 | 28  | 75  | 25  | 95  | 124 | 36  | 142 | 100 | 22  | 827   |
|     | 1976          | 75  | 6   | 47  | 18  | 28  | 41  | 30  | 148 | 46  | 71  | 85  | 70  | 665   |
|     | 1977          | 48  | 37  | 91  | 15  | 37  | 42  | 64  | 18  | 41  | 22  | 69  | 12  | 496   |
|     | 1978          | 37  | 87  | 15  | 32  | 49  | 51  | 44  | 109 | 14  | 26  | 94  | 52  | 609   |
|     | 1979          | 39  | 33  | 27  | 24  | 19  | 2   | 12  | 71  | 66  | 38  | 18  | 42  | 391   |
|     | 1980          | 8   | 28  | 58  | 27  | 22  | 45  | 29  | 37  | 67  | 73  | 43  | 27  | 464   |
|     | 1981          | 18  | 12  | 57  | 72  | 33  | 74  | 44  | 106 | 35  | 48  | 21  | 28  | 546   |
|     | 1982          | 36  | 25  | 77  | 12  | 58  | 35  | 35  | 9   | 64  | 9   | 25  | 14  | 399   |
|     | 1983          | 19  | 8   | 109 | 53  | 24  | 41  | 36  | 49  | 128 | 56  | 58  | 179 | 598   |
|     | 100 year mean | 48  | 41  | 42  | 57  | 49  | 58  | 53  | 52  | 55  | 63  | 56  | 56  | 631   |

| (b) | Year | Rainfall |
|-----|------|----------|
|     | 1914 | 395      |
|     | 1963 | 397      |
|     | 1979 | 391      |
|     | 1982 | 399      |

TABLE 6.6:

(a) Daily and monthly rainfall figures for Hobart Weather Station and (b) periodic rainfall records and approximate monthly totals for Snug Plains from November 1982 to April 1983.

| Day   | Nov   |   | Dec   |      | Jan   |     | Feb   |     | Mar   |      | Apr   |   |
|-------|-------|---|-------|------|-------|-----|-------|-----|-------|------|-------|---|
|       | a     | b | a     | b    | a     | b   | a     | b   | a     | b    | a     | b |
| 1     | 0.4   |   | 0.2   | ↑    | -     | ↓   | -     | ↑   | -     | ↑    | -     |   |
| 2     | -     |   | 0.2   | ↓    | 0.2   | ↓   | trace | ↓   | -     | ↓    | -     |   |
| 3     | -     |   | 1.6   | ↓    | 0.6   | ↓   | -     | ↓   | -     | 1.4  | -     |   |
| 4     | -     |   | -     | ↓    | 1.4   | ↑   | -     | ↓   | -     |      | 0.6   |   |
| 5     | 0.8   |   | 0.2   | ↓    | trace | ↓   | -     | ↓   | 2.4   | ↓    | 2.4   |   |
| 6     | -     |   | trace | ↓    | -     | ↓   | -     | 0   | trace | ↓    | 0.8   |   |
| 7     | 0.4   |   | trace | ↓    | -     | ↓   | -     | ↓   | trace | ↓    | 1.0   |   |
| 8     | trace |   | 8.6   | ↓    | 0.2   | 2.0 | -     | ↓   | 0.2   | ↓    | trace |   |
| 9     | 1.0   |   | trace | ↓    | -     | ↓   | -     | ↓   | 2.6   | ↑    | -     |   |
| 10    | 16.0  |   | trace | ↓    | trace | ↓   | 0.2   | ↓   | 16.4  | ↓    | -     |   |
| 11    | 0.2   |   | -     | 11.6 | trace | ↓   | 0.2   | ↓   | -     | ↓    | 9.6   |   |
| 12    | -     |   | -     | ↓    | 1.2   | ↓   | -     | ↓   | 7.8   | ↓    | 0.8   |   |
| 13    | -     |   | -     | ↓    | 0.8   | ↓   | -     | ↓   | -     | 22.3 | 0.6   |   |
| 14    | trace |   | trace | ↓    | -     | ↓   | -     | ↑   | -     | ↓    | 0.8   |   |
| 15    | -     |   | -     | ↓    | -     | ↑   | 0.6   | ↓   | trace | ↓    | 6.4   |   |
| 16    | 0.2   |   | -     | ↓    | -     | ↓   | trace | ↓   | -     | ↓    | 0.8   |   |
| 17    | 1.6   |   | -     | ↓    | 0.2   | ↓   | 1.2   | ↓   | -     | ↓    | -     |   |
| 18    | 1.2   |   | -     | ↓    | 0.4   | ↓   | -     | ↓   | -     | ↓    | -     |   |
| 19    | 0.2   |   | trace | ↓    | -     | 1.6 | -     | ↑   | -     | ↓    | -     |   |
| 20    | -     |   | 1.6   | ↓    | -     | ↓   | -     | ↓   | -     | ↓    | -     |   |
| 21    | -     |   | 0.8   | ↑    | -     | ↓   | 0.8   | ↓   | -     | ↓    | -     |   |
| 22    | -     |   | -     | ↓    | -     | ↓   | -     | ↑   | 3.2   | ↓    | -     |   |
| 23    | -     |   | -     | ↓    | trace | ↓   | 1.4   | ↑   | 74.0  | ↓    | -     |   |
| 24    | -     |   | 0.2   | ↓    | -     | ↑   | trace | ↓   | 2.6   | ↓    | -     |   |
| 25    | -     |   | trace | ↓    | -     | ↓   | -     | ↑   | 0.2   | ↓    | 21.8  |   |
| 26    | 3.2   |   | -     | ↓    | -     | ↓   | -     | ↑   | -     | ↓    | 7.8   |   |
| 27    | trace |   | -     | 2.5  | 14.0† | 0   | 3.2   | ↓   | -     | ↓    | -     |   |
| 28    | -     |   | -     | ↓    | -     | ↓   | -     | ↓   | -     | ↓    | trace |   |
| 29    | -     |   | -     | ↓    | -     | ↓   | -     | ↓   | -     | ↓    | -     |   |
| 30    | -     |   | 0.8   | ↓    | -     | ↓   | -     | ↓   | trace | ↓    | -     |   |
| 31    | -     |   | -     | ↓    | -     | ↓   | -     | ↓   | -     | ↓    | -     |   |
| Total | 25.2  | - | 14.2  | 13.4 | 19.0  | 4.4 | 7.6   | 5.7 | 109.4 |      | 53.4  |   |

† A thundershower which produced heavy rain in Hobart but did not cross Snug Plains.

soil depth and moisture holding capacity. Steep gradients in soil depth, texture and moisture holding capacity existed over short distances (50 to 200 m) between the ridge crest and the lower slopes which corresponded to sequence of dominance changes in the eucalypt species (Fig. 6.9, Table 6.7).

On the ridge top where E. pulchella was dominant the soil was shallow (0.1 to 0.3 m) light-textured and stoney (30% to 50% stones). The moisture storage capacity of these soils was very low. The total "extractable" moisture (that held between F.C. and P.W.P.) was between 29 mm and 36 mm for garden 1 and stand I respectively (Table 6.7). The upper ridge slopes and the ridge top was also characterised by regions of outcropping rock, in the form of massive exfoliating slabs of Jurassic dolerite bedrock which, from surface examination, showed no fissures or joints down which plant roots might penetrate. Soil pits dug to bedrock at several points on the ridge top, and soil depths measured at 10 m grid intersections over the ridge using a sharpened metal spike (Fig. 6.3, Table 6.8), confirmed that the soil was shallow and the underlying bedrock was massive and poorly jointed over most of the ridge. Therefore, it appears the root systems of all stand I trees are confined to the same shallow soils by the impervious unjointed bedrock beneath.

On the lower eastern slopes of the ridge, 50 m east of stand I, soils occupied by E. delegatensis were deep clay (1.0 to 1.5 m) with low stone content (20%) and moderately high levels of extractable moisture (132 mm; Table 6.7).

On the western side of the ridge the gradient in soil characteristics was less steep. E. coccifera was dominant in these soils of intermediate depth (0.6 to 0.7 m) and stone content (30%) with relatively low levels of extractable moisture (77 mm).

In comparison, at the base of the western slope E. gunnii occupied deep clay soils (1.9 m) with a thick peat A horizon, few stones (approximately 5%) and high levels of extractable moisture (344 mm; Table 6.7).

During the 1982/83 summer drought the extremes of soil water relations recorded at each of the sites (0 to 3 and stand I) were also closely related to the soil characteristics (Fig. 6.10). The shallow, light-textured and stoney soils of the ridge crest recorded the lowest soil moisture contents (13%), lowest soil water potentials (-4.5 MPa) and lowest levels of available soil moisture (-5 mm) (i.e. 5 mm less than the level of moisture held in the soil at P.W.P.) (Fig. 6.10),

Fig. 6.9: A relief diagram of the study ridge from sites 0 to 3 (Figs. 1 & 2) and the structure of the soil profile at each site, with massive dolerite bedrock beneath (+).

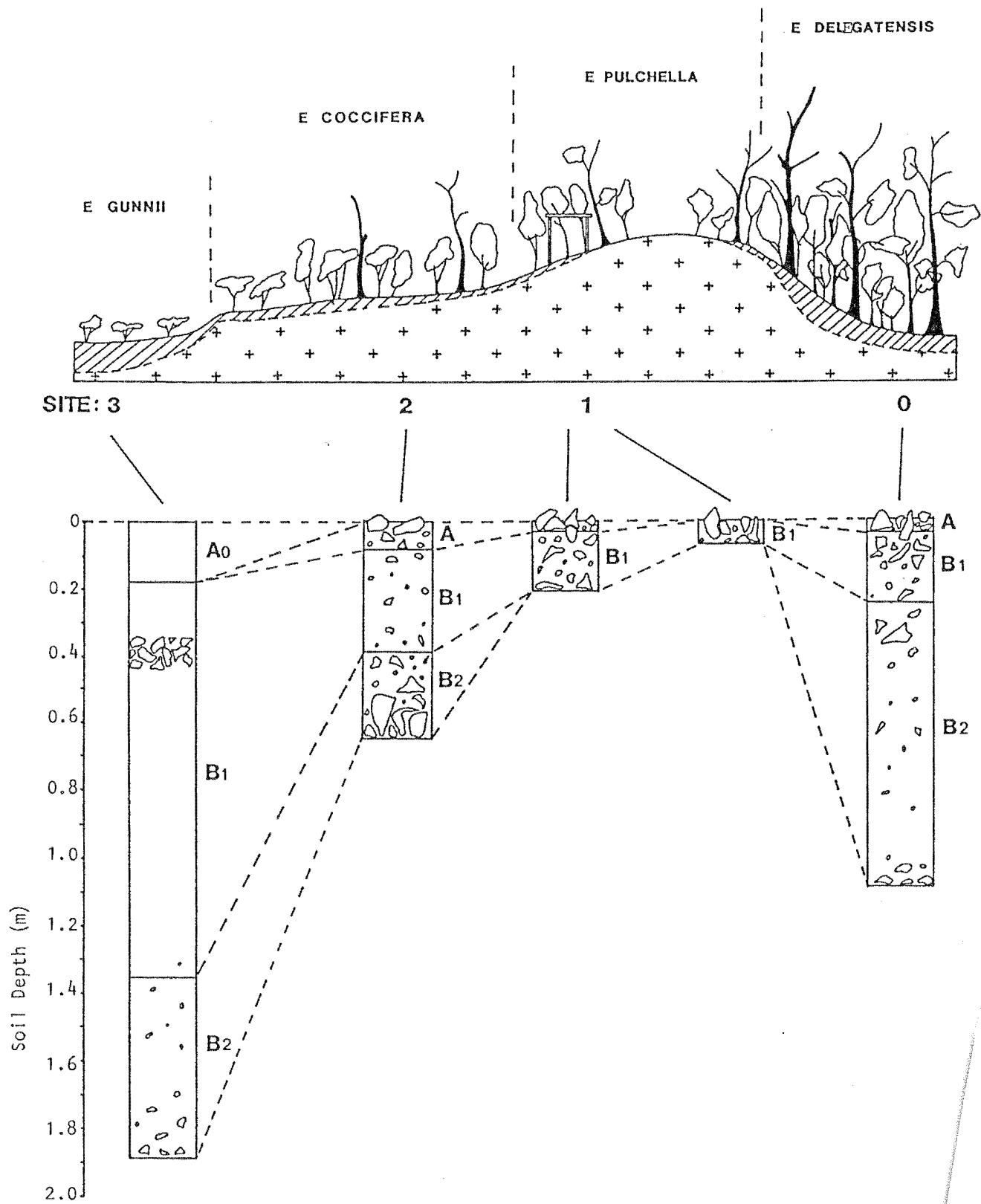


TABLE 6.7:

A summary of the properties measured for each horizon in soil profiles dug at intervals along a transect crossing a shallow ridge at Snug Plains (Fig. 6.9). The properties measured included; the volume (SV) and the percentage (SP) of soil and rock in a pit 1 m<sup>2</sup> in cross-sectional area dug to bedrock, the volume (MV) and percentage (MP) moisture held in the soil at field capacity (FC) and permanent wilting point (PWP) (obtained from pF curves, Appendix 6.2), and the volume of extractable moisture for each soil horizon ( $M_{extr} = MV_{FC} - MV_{PWP}$ ) and for the whole profile (after Specht 1972).

| Position along transect |       | E. delegatensis<br>Site 0 |                |                | E. pulchella<br>Site 1<br>Stand 1<br>(platform) |      |      |      | E. coccifera<br>Site 2 |                |                | E. gunnii<br>Site 3 |                |                    |
|-------------------------|-------|---------------------------|----------------|----------------|---|------|------|------|------------------------|----------------|----------------|---------------------|----------------|--------------------|
| Soil horizon            |       | A                         | B <sub>1</sub> | B <sub>2</sub> | A   | B    | A    | B    | A                      | B <sub>1</sub> | B <sub>2</sub> | A                   | B <sub>1</sub> | B <sub>2</sub>     |
| SV<br>(m <sup>3</sup> ) | Total | 0.04                      | 0.22           | 0.84           | 0.03  | 0.18 | 0.02 | 0.28 | 0.08                   | 0.31           | 0.26           | 0.18                | 0.17           | 0.53               |
|                         | Rock  | 0.02                      | 0.06           | 0.14           | 0.02  | 0.04 | 0.01 | 0.15 | 0.04                   | 0.13           | 0.03           | 0.00                | 0.06           | 0.03               |
|                         | Soil  | 0.02                      | 0.16           | 0.70           | 0.01  | 0.14 | 0.01 | 0.13 | 0.04                   | 0.18           | 0.23           | 0.18                | 1.11           | 0.50               |
| SP<br>(%)               | Rock  | 50                        | 28             | 17             | 67  | 23   | 50   | 54   | 50                     | 42             | 12             | 0                   | 5              | 6                  |
|                         | Soil  | 50                        | 72             | 83             | 33  | 77   | 50   | 46   | 50                     | 58             | 88             | 100                 | 95             | 94                 |
| MP                      | FC    | -                         | 32.0           | 32.5           | -   | 41.5 | -    | 39.5 | -                      | 39.5           | 39.5           | 64.5                | 36.8           |                    |
|                         | PWP   | -                         | 17.0           | 17.0           | -   | 15.6 | -    | 17.0 | -                      | 19.5           | 21.0           | 32.0                | 17.2           |                    |
| MV<br>(mm)              | FC    | -                         | 51.2           | 227.5          | -   | 58.1 | -    | 51.4 | -                      | 70.2           | 90.9           | 116.1               | 408.5          | 184.0 <sup>+</sup> |
|                         | PWP   | -                         | 27.2           | 119.0          | -   | 21.8 | -    | 22.1 | -                      | 35.1           | 48.3           | 57.6                | 190.9          | 86.0 <sup>+</sup>  |
| Mextr in horizon        |       | -                         | 24.0           | 108.5          | -   | 36.3 | -    | 29.3 | -                      | 35.1           | 42.6           | 58.5                | 217.6          | 98.0 <sup>+</sup>  |
| Mextr in profile        |       | 132.5                     |                |                | 36.3  |      | 29.3 |      | 77.7                   |                |                | 374.1               |                |                    |

<sup>+</sup> values estimated from moisture contents of the B<sub>1</sub> horizon, Site 3



TABLE 6.8:

Mean soil depths (m) measured with a sharpened spike at 10 m grid intersections (four replicate measures at each intersection) for the ridge slope between Stands I and II (see Fig. 6.3).

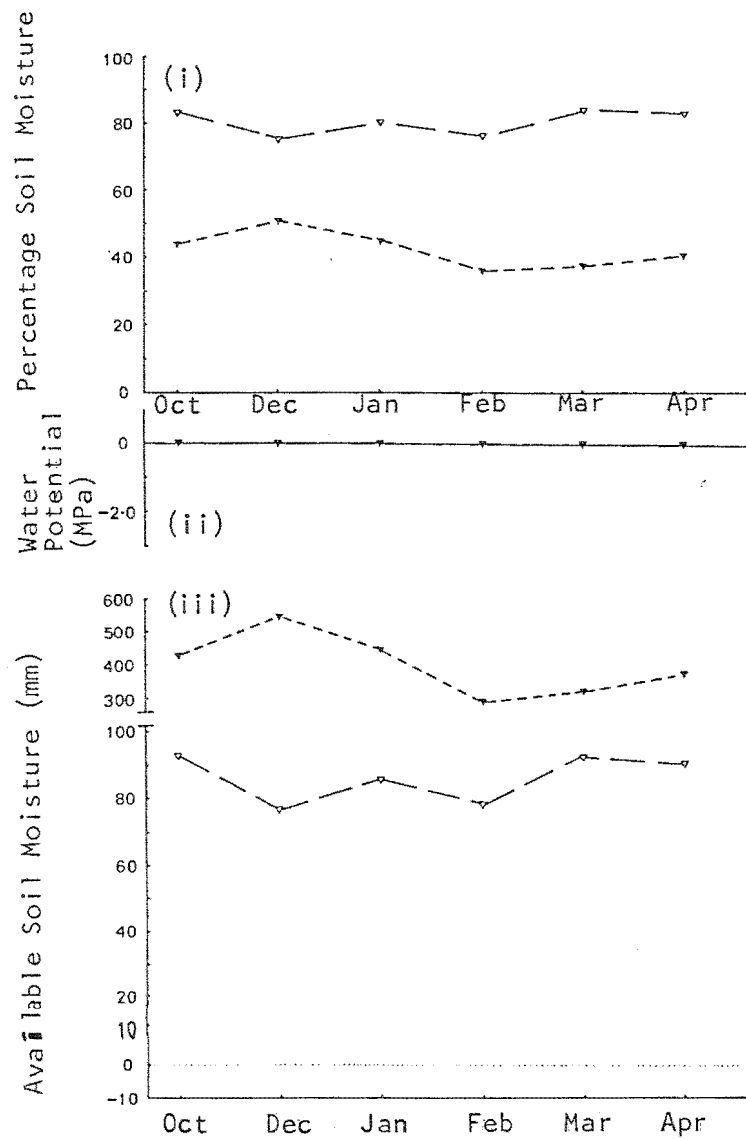
| Distance East<br>(see Fig. 6.3)  | Soil Depth (in m) |                 |                 |                 |                 |
|----------------------------------|-------------------|-----------------|-----------------|-----------------|-----------------|
| 40                               | $0.09 \pm 0.02$   | $0.0 \pm 0.0$   | $0.16 \pm 0.02$ | $0.36 \pm 0.04$ | $0.31 \pm 0.08$ |
| 30                               | $0.13 \pm 0.03$   | $0.10 \pm 0.03$ | $0.33 \pm 0.06$ | $0.31 \pm 0.08$ | $0.30 \pm 0.04$ |
| 20                               | $0.13 \pm 0.03$   | $0.18 \pm 0.03$ | $0.26 \pm 0.06$ | $0.24 \pm 0.07$ | $0.53 \pm 0.05$ |
| 10                               | $0.10 \pm 0.02$   | $0.09 \pm 0.02$ | $0.56 \pm 0.06$ | $0.60 \pm 0.08$ | $0.50 \pm 0.05$ |
| 0                                | $0.16 \pm 0.02$   | $0.59 \pm 0.03$ | $0.48 \pm 0.03$ | $0.58 \pm 0.06$ | $0.55 \pm 0.08$ |
| Distance North<br>(see Fig. 6.3) | 50                | 40              | 20              | 10              | 0               |

Fig. 6.10

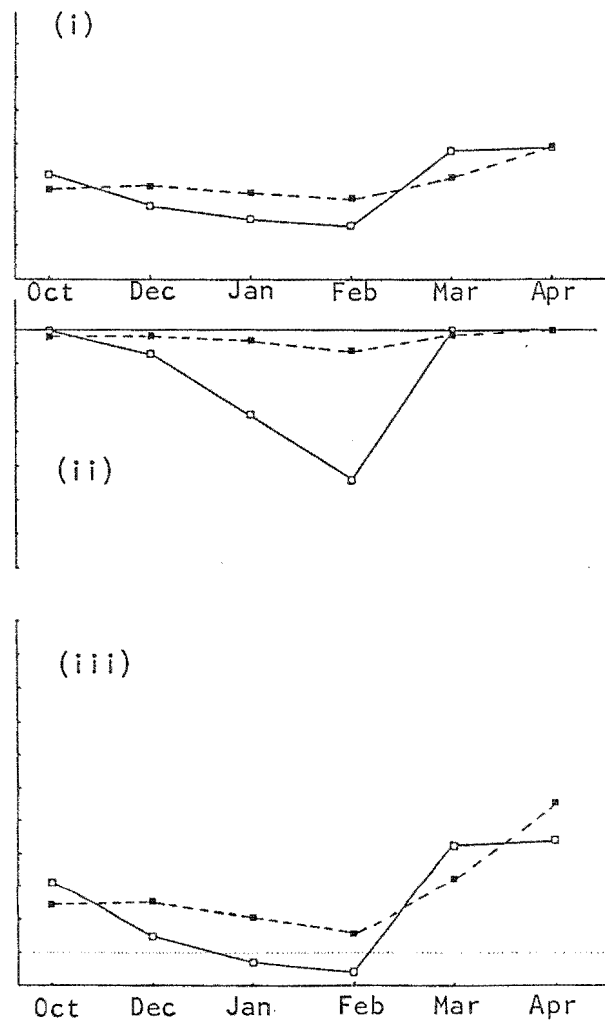
(i) percentage moisture (ii) water potential (MPa) and (iii) "available" moisture (mm) measured at monthly intervals between November 1982 and April 1983 for soil horizons at (a) Site 3 (b) Site 2 (c) Site 1 and (d) Site 0 where soil profiles were dug in stands of E. gunnii, E. coccifera, E. pulchella and E. delegatensis respectively (see Fig. 6.3). Soil horizons measured were; A (broken line) and B<sub>1</sub> (dashed line) for Site 3 and B<sub>1</sub> (dashed line) and B<sub>2</sub> (solid line) for Sites 2 and 0. For Site 1 the B<sub>1</sub> horizons of two, soil profiles Stand 1 (solid line) and Site 1 (dashed line), were measured.

Fig. 6.10

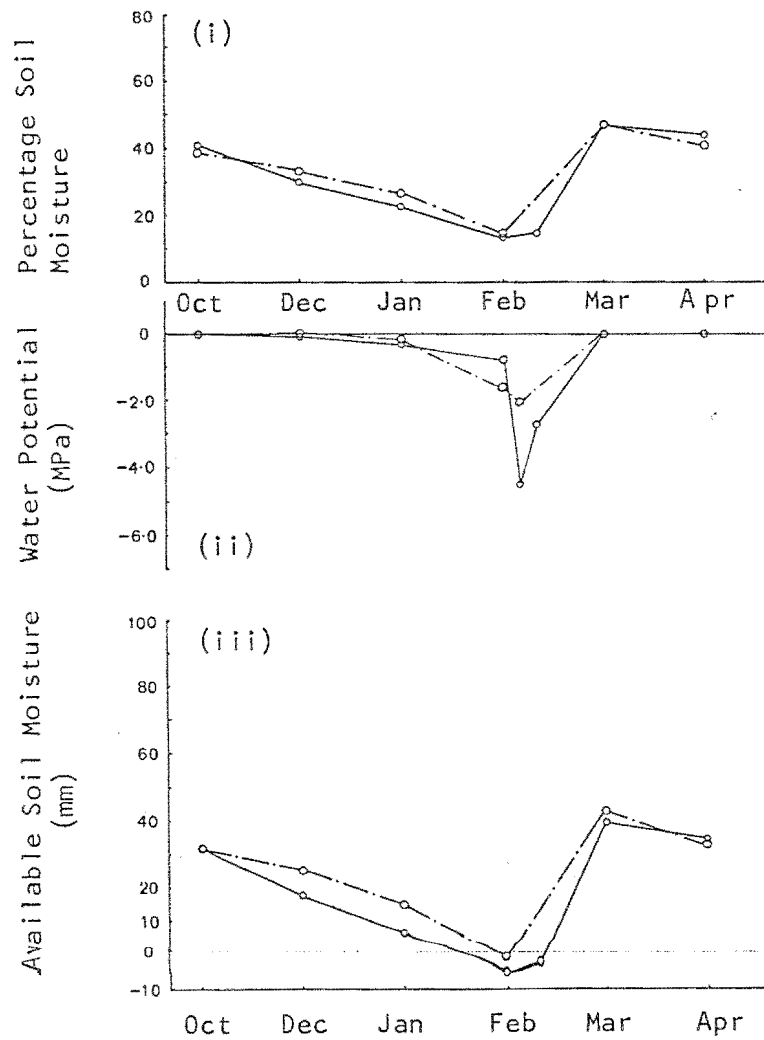
(a) Site 3: *E. gunnii*



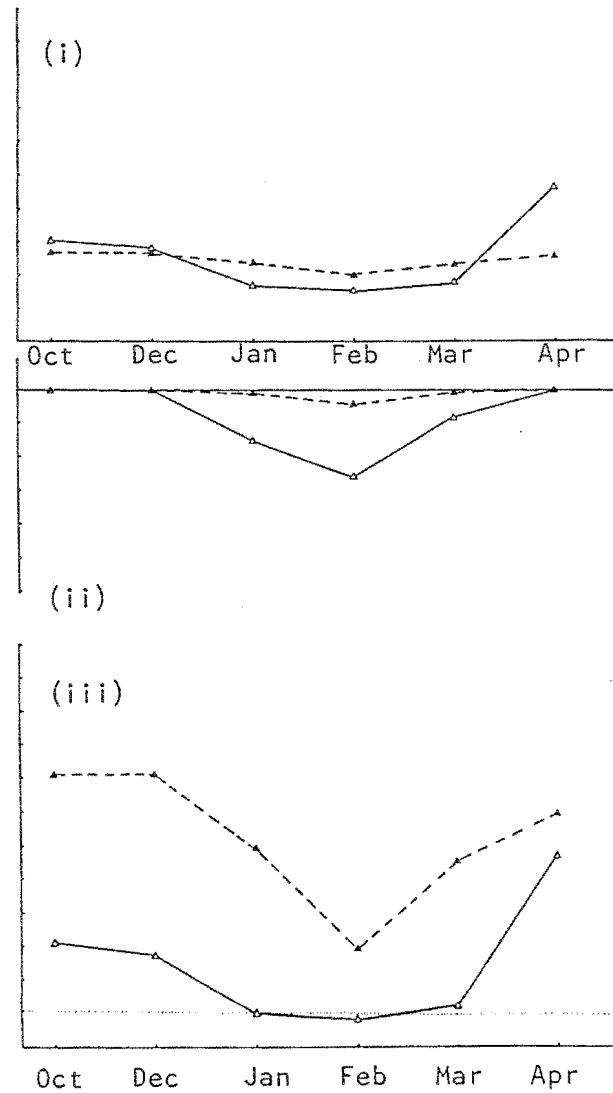
(b) Site 2: *E. coccifera*



(c) Site 1: *E. pulchella*



(d) Site 0: *E. delegatensis*



but for soils of the lower ridge slopes soil conditions were more moderate. In January and February 1983, the available soil moisture of the upper soil horizons was very low at most sites but on the deeper soils of the lower ridge slopes soil water relations were buffered by large moisture reserves in the lower soil horizons. Shallow soils exhibited short periods of extremely low water potentials and "available" soil moisture, whereas deep soils showed a more prolonged but less severe period of unfavourable soil water relations and a correspondingly longer rehydration curve after the first rains in late February.

## (b) Plant Water Relations

### (i) **During Drought**

Early in the 1982/83 summer interspecific differences in water relations between the three eucalypt species at stand I were minor. In November 1982 soil water potentials and "available" moisture in the soil was high (Fig. 6.10c). The 28/11/82 was a cool day (maximum of 13°C) and vapour pressure deficits (V.P.D.) were moderate (0.8 KPa maximum). The bell shaped stomatal conductance curves for each species were mirrored by the water potential curves (Fig. 6.11). Midday stomatal conductances for all species were high (between 0.3 and 0.4 cm sec<sup>-1</sup>) and water potentials reached a mild minimum (approximately -1.1 MPa).

In December (29/12/82) soil water potentials were again mild (-0.2 MPa; Fig. 6.10c) but temperatures and V.P.Ds were higher than in November (25°C and 2.4 KPa respectively; Fig. 6.12). Maximum stomatal conductance and minimum water potentials were lower than in November. Further, a marked reduction in stomatal conductance occurred in the afternoon which corresponded with high V.P.D. A hysteresis between water potentials and stomatal conductance was also evident, which provided an early indication of developing drought (Kaufmann & Levey 1976; Kaufmann 1977).

In mid summer, all three species were exhibiting drought symptoms, yet interspecific differences in water potentials and stomatal conductances were only detected on one occasion. By mid January soil water potentials had fallen to -0.8 MPa (Fig. 6.10c). On the 31/1/83 maximum temperatures and V.P.Ds were high (27°C and 2.3 KPa respectively, Fig. 6.13). The maximum stomatal conductances and minimum water potentials were lower than in December. Stomatal closure occurred at midday for all species, corresponding with the

Figures 6.11 and 6.12

Dawn to dusk (Eastern standard time, EST) records of (a) temperature ( $^{\circ}\text{C}$ , solid lines) and vapour pressure deficit (V.P.D.) (KPa, broken lines), (b) stomatal conductance ( $\text{cm sec}^{-1}$ ) and (c) leaf water potential (MPa) for trees on the ridge crest at stand I. Measurements were made on 28/11/82 (Fig. 6.11) and 29/12/82 (Fig. 6.12). Means  $\pm$  SEs are presented for three replicates of the three species E. pulchella (●, solid lines), E. coccifera (■, broken lines) and E. delegatensis (▲, dashed lines).

Figure 6.11

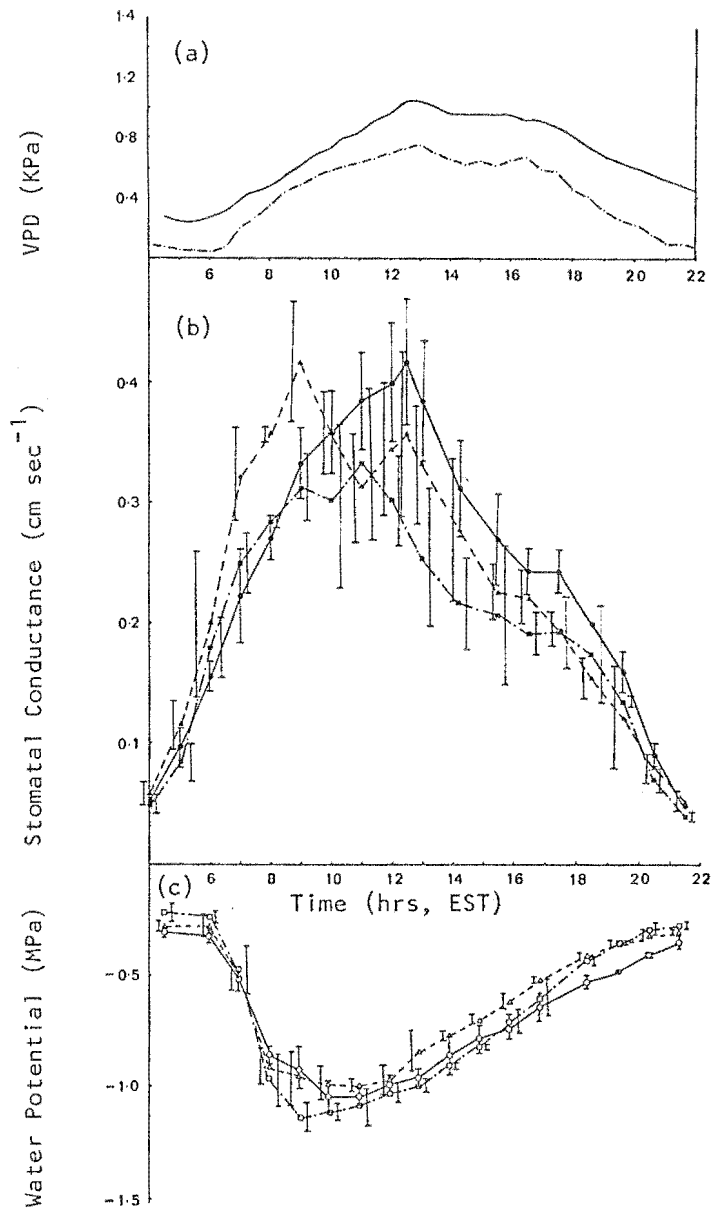
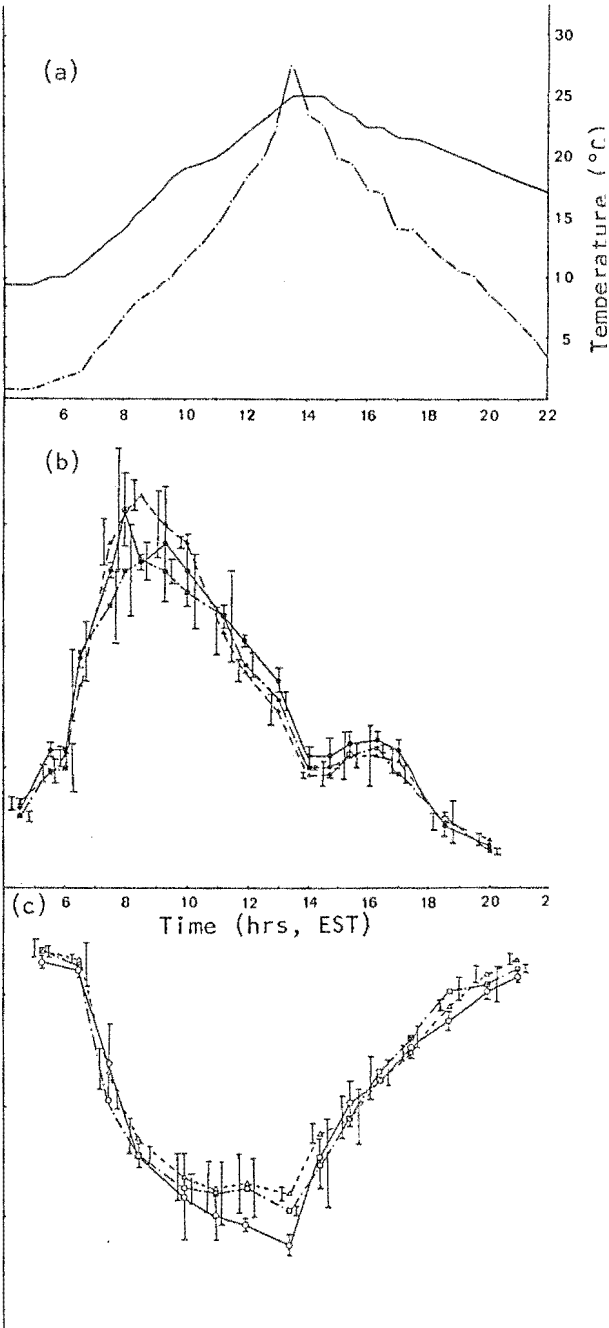


Figure 6.12



Figures 6.13, 6.14 and 6.16

Dawn to dusk (Eastern standard time, EST) records of (a) temperature ( $^{\circ}\text{C}$ , solid lines) and vapour pressure deficit (V.P.D.) (KPa, broken lines), (b) stomatal conductance ( $\text{cm sec}^{-1}$ ) and (c) leaf water potential (MPa) for trees on the ridge crest at stand I. Measurements were made on the 31/1/83 (Fig. 6.13), 15/2/83 (Fig. 6.14) and the 22/2/83 (Fig. 6.16). Symbols are the same as for Figs 6.11 and 6.12.



Figure 6.13

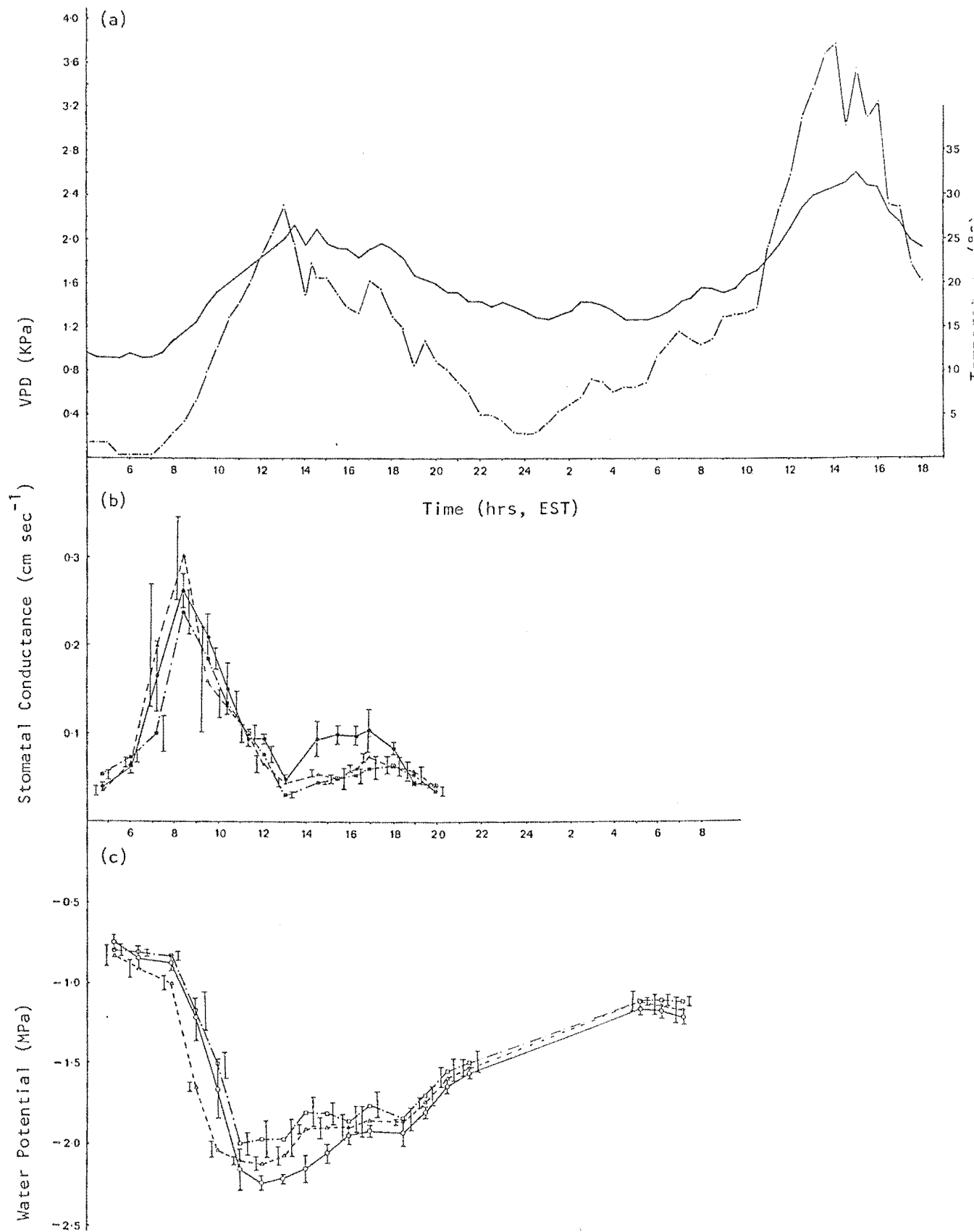


Figure 6.14

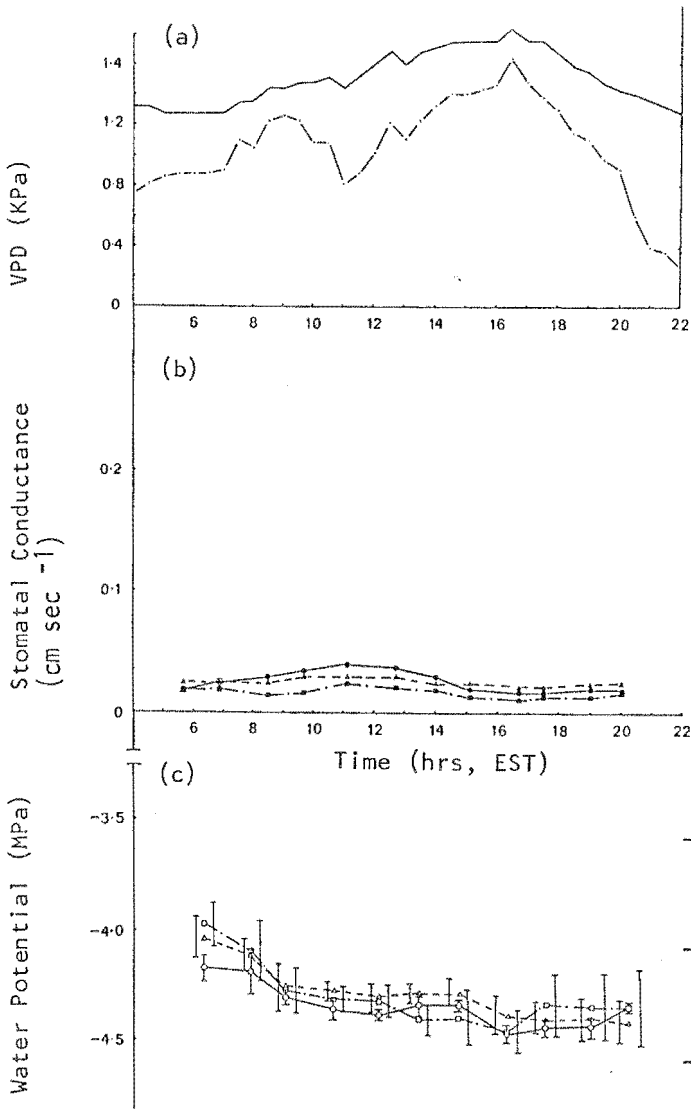
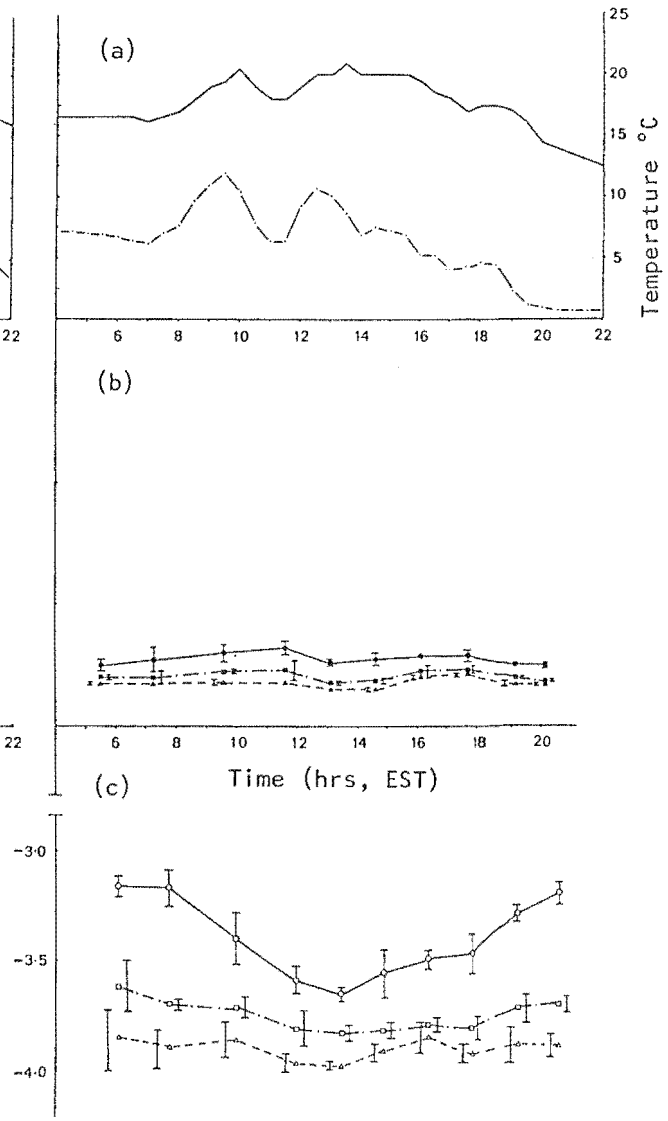


Figure 6.16



peak in V.P.D. Stomata of all species reopened to a small degree in the afternoon at lower V.P.Ds and significant interspecific differences ( $P < 0.01$ ) were developed. E. pulchella exhibited higher stomatal conductances than other species. The hysteresis between water potentials and stomatal conductances was more pronounced than in December, and significant interspecific differences in water potentials ( $P < 0.05$ ) occurred in the afternoon, with E. pulchella exhibiting lower water potentials than other species. At dusk the water potentials of all species were 0.8 MPa lower than at dawn and had not fully restored by the following dawn (Fig. 6.13); an indication of drought stress (Hinckley et al. 1978; Sinclair 1980).

The two weeks following the 31/1/83 included a number of hot windy days of exceptionally low humidity. For example, on the 1/2/83 the minimum and maximum temperatures were 16°C and 32°C respectively and a very high peak in V.P.D. of 3.8 KPa was recorded (Fig. 6.13), exposing the already droughted trees to high evapotranspirational stress. During this period soil water potentials fell steeply (Fig. 6.10). By mid February the drought at the study site on Snug Plains was severe. Only 6.2 mm of rain had fallen since early December and no measurable precipitation had been recorded since mid-January (Table 6.6). The soil water potential at stand I was -4.5 MPa and the available soil moisture was -5 mm (5 mm below P.W.P.) (Fig. 6.10b). The 15/2/83 was intermittently overcast with moderate temperatures and V.P.Ds recorded (Fig. 6.14). Interspecific differences in stomatal conductance and water potential were minor. The stomata of all species were closed for the whole day. Despite this water potentials fell gradually (by 0.4 MPa) during the day to a minimum near dusk of -4.4 MPa. These water potentials are comparable with the extreme values of -4.8 MPa obtained for E. obliqua during a drought in the Mount Lofty Ranges (Sinclair 1980). In two weeks the dawn water potentials of stand I trees had fallen from -1.2 MPa on the 1/1/83 to -4.0 MPa on the 15/1/83; a fall of approximately 0.2 MPa per day.

During early and mid summer as drought developed, dawn xylem water potentials for all stand I trees reflected the decline in soil water potentials. Further, maximum stomatal conductance declined as dawn water potentials fell. No threshold water potential was reached for the eucalypts tested, at which stomatal closure occurred. Similar conclusions were drawn by Connor et al. (1977) for E. regnans and by Pereira and Kozłowski (1976) for E. globulus and for E. camaldulensis seedlings. The minimum stomatal conductance recorded during daylight hours, on the other hand, corresponded with the peak in V.P.D.

This supports studies by Myers and Neales (1984) and Korner and Cochrane (1985) which show a relationship between stomatal conductance and V.P.D. for eucalypt species. However, significant interspecific differences in stomatal conductance and water potentials were only detected on one occasion at stand I during the developing drought. A general survey of water potentials and stomatal conductances made on thirty trees on the ridge crest near stand I (Fig. 6.3, Table 6.9a) confirmed that interspecific differences in water relations for ridge top trees were minor, although E. coccoifera showed significantly lower stomatal conductances than other species (Table 6.9a). However, generally, all the ridge top trees were suffering similarly severe drought stress.

Despite similarities in the stomatal conductances and water potential displayed by stand I trees, significant differences ( $P < 0.05$ ) in relative water content (R.W.C.) existed between the three species studied at stand I (Table 6.10). E. pulchella exhibited higher R.W.Cs (61.2%) than E. coccoifera (54.8%) which in turn was higher than E. delegatensis (47.8%) indicating that markedly different levels of tissue hydration existed between the three species at the height of the drought. The maintenance of high R.W.C. at low water potentials has been described as a drought resistance trait in drought tolerant species such as eucalypts (Hinckley et al. 1978; Withers 1978; Ashton et al. 1975; Ladiges 1974, 1975). Therefore, this suggests the species order of drought tolerance is: E. pulchella > E. coccoifera > E. delegatensis (from most to least tolerant). The records of R.W.C. above are similar to values of R.W.C. obtained by Pook et al. (1966) during the 1965 drought on the driest and most drought stricken sites on the hillsides near Canberra, A.C.T.

Half a kilometer north of stand I, at stand III, a mixed stand of the three above species growing on shallow soils, over massive bedrock, was suffering greater drought stress than stand I. Water potentials were extreme for E. pulchella (-5.4 MPa) and E. coccoifera (-5.1 MPa) but again did not differ significantly (Table 6.11). All E. delegatensis stems present in the stand had died during the drought, possibly indicating that water potentials had fallen below the level at which the critical minimum tissue hydration (R.W.C.) could be maintained. From figures of Pook et al. (1976), Withers (1978) and Ashton et al. (1975), this minimum probably lies between 38% and 54% (depending on the species). Small but significant differences in stomatal conductance were recorded for E. pulchella ( $0.025 \text{ cm sec}^{-1}$ ) and E. coccoifera ( $0.021 \text{ cm sec}^{-1}$ ) at stand III.

TABLE 6.9

Mean  $\pm$  SE xylem water potential, stomatal conductance and crown damage for 30 trees, 10 trees from each of the species E. pulchella, E. coccifera and E. delegatensis growing on the ridge top adjacent to Stand 1. Water potentials and stomatal conductances were measured on two occasions; (a) during a 2 hour period (10 am to 12 midday) on 16.2.83 at the height of the drought and (b) during 2 hour periods in the morning (10 am to 12 midday) and afternoon (3 pm to 5 pm) on the 3.3.83 after drought breaking rains, and (c) mean crown damage caused by the drought was assessed on 30.3.83. The significance of interspecific differences were obtained from analysis of variance (\*\* $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , NS, not significant).

(a)

|                 | Stomatal Conductance | Water Potential  |
|-----------------|----------------------|------------------|
| E. pulchella    | 0.031 $\pm$ 0.002    | -4.59 $\pm$ 0.09 |
| E. coccifera    | 0.024 $\pm$ 0.003    | -4.58 $\pm$ 0.08 |
| E. delegatensis | 0.029 $\pm$ 0.003    | -4.36 $\pm$ 0.09 |
| Significance    | **                   | NS               |

TABLE 6.9. (cont'd)

(b)

|                        | <u>Morning</u>       |   |       |                 | <u>Afternoon</u>     |   |       |                 |
|------------------------|----------------------|---|-------|-----------------|----------------------|---|-------|-----------------|
|                        | Stomatal Conductance |   |       | Water Potential | Stomatal Conductance |   |       | Water Potential |
| <i>E. pulchella</i>    | 0.16                 | ± | 0.019 | -1.39 ± 0.15    | 0.16                 | ± | 0.018 | -1.15 ± 0.16    |
| <i>E. coccifera</i>    | 0.14                 | ± | 0.014 | -1.48 ± 0.14    | 0.05                 | ± | 0.008 | -0.95 ± 0.16    |
| <i>E. delegatensis</i> | 0.13                 | ± | 0.017 | -1.24 ± 0.11    | 0.07                 | ± | 0.015 | -1.01 ± 0.14    |
| Significance           | NS                   |   |       | NS              | ***                  |   |       | NS              |

(c)

|                        | Number of Trees | Crown Damage |
|------------------------|-----------------|--------------|
| <i>E. pulchella</i>    | 10              | 13.5 ± 2.2   |
| <i>E. coccifera</i>    | 10              | 25.0 ± 4.3   |
| <i>E. delegatensis</i> | 10              | 54.0 ± 8.0   |
| Significance           |                 | ***          |

TABLE 6.10

- (a) The mean relative water content of the leaf tissue for Stand I trees measured; A on the 16.2.83 at the height of the drought, B on the 20.2.83 after the first light rains and C on the 25.2.83 after subsequent rains, and;
- (b) analysis of variance performed on the data (\*\*\*)  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , NS not significant).

(a) Relative Water Content

|                        | Relative Water Content (%) |                |                |
|------------------------|----------------------------|----------------|----------------|
|                        | A                          | B              | C              |
| <i>E. pulchella</i>    | $61.2 \pm 2.4$             | $78.4 \pm 7.2$ | $78.1 \pm 0.3$ |
| <i>E. coccifera</i>    | $54.8 \pm 3.1$             | $66.5 \pm 6.5$ | $77.7 \pm 1.3$ |
| <i>E. delegatensis</i> | $47.8 \pm 4.5$             | $57.3 \pm 1.8$ | $82.2 \pm 1.1$ |

(b) Analysis of Variance

| Source           | <u>DF</u> | <u>SS</u> | <u>MS</u> | <u>F</u> | <u>Prob</u> | <u>Signif</u> |
|------------------|-----------|-----------|-----------|----------|-------------|---------------|
| Species          | 2         | 179.02    | 89.51     | 4.38     | 0.028       | *             |
| Measurement time | 2         | 1062.03   | 531.01    | 25.98    | 0.000       | ***           |
| Species x time   | 4         | 222.21    | 55.55     | 2.72     | 0.063       | NS            |
| Cells            | 8         | 1463.26   |           |          |             |               |
| Within           | 18        | 367.96    | 20.44     |          |             |               |
| Total            | 26        |           |           |          |             |               |

TABLE 6.11

Mean tree height, stem diameter, water potential, stomatal conductance, crown damage and significance levels from analysis of variance for nine paired trees of E. pulchella and E. coccifera recorded at Stand III on 16.2.83, at the height of the drought (\*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , NS not significant). Mean tree height and crown damage was also recorded for four E. delegatensis at Stand III.

| Species                          | Tree height (m) | Stem diameter (cm) | Water potential (MPa) | Stomatal conductance (cm sec <sup>-1</sup> ) | Crown damage (%) |
|----------------------------------|-----------------|--------------------|-----------------------|--|------------------|
| 1. <u>E. pulchella</u>           | 4.0 ± 0.6       | 4.5 ± 1.0          | -5.41 ± 0.14          | 0.025 ± 0.001                                | 18 ± 9           |
| 2. <u>E. coccifera</u>           | 3.6 ± 0.5       | 3.5 ± 0.7          | -5.13 ± 0.23          | 0.021 ± 0.004                                | 40 ± 11          |
| 3. <u>E. delegatensis</u>        | 2.4 ± 0.2       | -                  | -                     | -  | 100 ± 0          |
| Significance (for species 1 & 2) | NS              | NS                 | NS                    | *  | **               |



Steep gradients in plant and soil water potentials existed between the ridge top and the lower ridge slopes. At stand II, 35 m to the north-west of stand I, soils were deeper than at stand I, and even in mid January the soil water potential of the B2 horizon was moderate ( $-0.5$  MPa), although A horizon potentials were low (Fig. 6.10b). The 17/2/83 was a warm day with moderate V.P.Ds during daylight hours (Fig. 6.15). The bell shaped stomatal conductance curve obtained at stand II were mirrored by the water potential curves, and were reminiscent of the November records at stand I. Interspecific differences were minor. Maximum stomatal conductances (between  $0.3$  and  $0.4$  cm sec $^{-1}$ ) were high and minimum water potentials were mild (approximately  $-1.2$  MPa). Dawn water potentials ( $-0.5$  MPa) were similar to water potentials of the B soil horizon. There was no evidence of drought stress in stand II trees. The short distance, over which this steep gradient occurred, encompassed the region of regenerating ecotonal mixed stands (Figs 6.2 and 6.3) between the pure *E. pulchella* and *E. coccifera* stands. This suggests that occasional severe droughts may be of considerable ecological importance in determining the position of species boundaries along this gradient.

## (ii) After Rains

On the evening of the 17/2/83 a light misty rain started to fall and continued through the night. A total of  $1.1$  mm was recorded (Table 6.6). The rain penetrated less than  $2$  cm into the soil yet combined with low V.P.D. it afforded some amelioration of the severe drought conditions at stand I. Immediately after these rains on 18/2/83 the water potential of seedlings at garden 1 were measured and compared with concurrent water potential measurements at stand I (Table 6.12). The soil water potentials at garden 1 were substantially higher than stand I ( $-2.0$  MPa and  $-4.5$  MPa respectively) during the drought (Fig. 6.10) and this was reflected in the xylem water potentials recorded. Seedling water potentials were mild (approximately  $-0.6$  MPa) in comparison with water potentials at stand I trees (approximately  $-4.0$  MPa) (Table 6.12).

On the 22/2/83 temperatures were moderate and V.P.Ds mild ( $20^{\circ}\text{C}$  and  $0.8$  KPa maximum respectively). The stomatal conductance of all species at stand I were low but significant interspecific differences existed ( $P < 0.01$ ); with *E. pulchella* exhibiting higher, and *E. delegatensis* lower stomatal conductances than other species (Fig. 6.16). A substantial recovery in water

Figures 6.15 and 6.19

Dawn to dusk (Eastern standard time, EST) records of (a) temperature ( $^{\circ}\text{C}$ , solid lines) and vapour pressure deficit (V.P.D.) (KPa, broken lines), (b) stomatal conductance ( $\text{cm sec}^{-1}$ ) and (c) leaf water potential (MPa) for trees on the lower ridge slopes at stand II. Measurements were made on 17/2/83 (Fig. 6.15) and 4/3/83 (Fig. 6.19). Symbols are the same as for Figs 6.11 and 6.12.

Figure 6.15

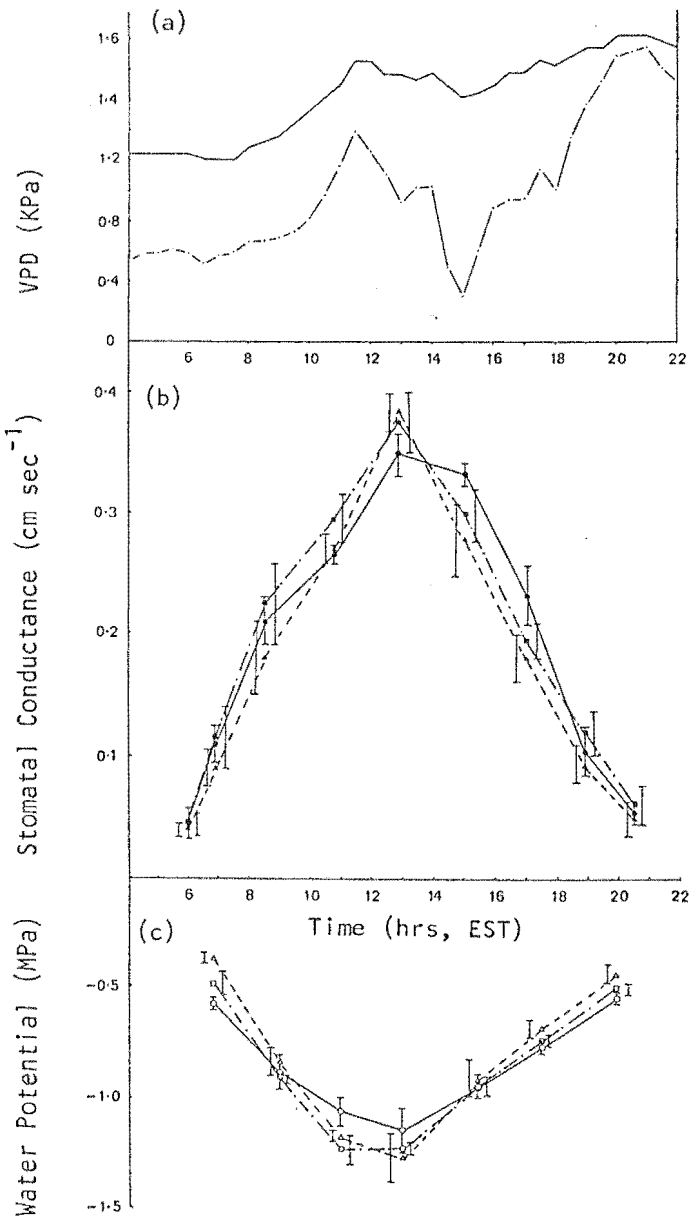


Figure 6.19

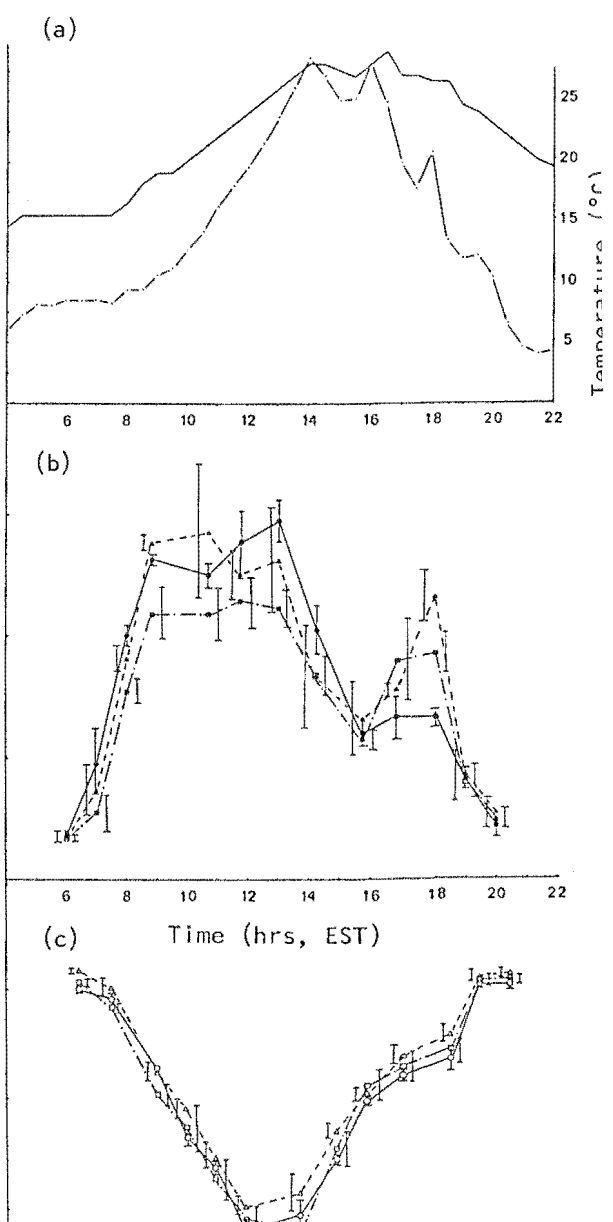


TABLE 6.12

Mean water potentials recorded for seedlings growing in a clearing at garden 1 and for trees growing in a dense stand at Stand I on 18.2.83, after the first light rains.

|                        | Water Potential (in MPA) |                          |
|------------------------|--------------------------|--------------------------|
|                        | Trees<br>(Stand I)       | Seedlings<br>(Stand III) |
| <i>E. pulchella</i>    | -3.8 ± 0.11              | -0.55 ± 0.07             |
| <i>E. coccifera</i>    | -3.7 ± 0.15              | -0.62 ± 0.14             |
| <i>E. delegatensis</i> | -4.0 ± 0.12              | -0.60 ± 0.06             |

potentials was shown by all species and significant interspecific differences ( $P < 0.001$ ) existed, with E. pulchella exhibiting higher, and E. delegatensis lower, water potentials than other species. The water potentials of all species restored fully at dusk which suggests the water stress had been alleviated.

Differences in the rates of recovery of the three species after rains in February appeared to be related to the R.W.Cs at the height of the drought (Table 6.10). E. pulchella exhibited highest R.W.C. at the height of the drought and showed greater recovery in stomatal conductance and water potential, followed by E. coccifera then E. delegatensis. The significant interspecific differences in R.W.C. observed at the height of the drought were not only maintained but increased (Table 6.10) after the first rains. E. pulchella attained near normal R.W.C. (78%) whereas the R.W.Cs of the other species were still low; E. coccifera (67%) and E. delegatensis (57%). This suggests that a competitive advantage may be afforded by high R.W.Cs which allows more rapid or more effective uptake of moisture after rains, thus favouring E. pulchella. However, interspecific differences in root distribution in the top 2 cm of soil (the depth to which rain penetrated) cannot be ruled out.

The second rains which fell between the 23rd and 24th of February (2.2 mm; Table 6.6) brought with them complete recovery from tissue water deficits (Table 6.10) and moderate water potentials for all species, yet the physiological effects of the preceding drought were still evident (Fig. 6.17). After these rains, which penetrated about 10 cm into the soil, all species had restored to near normal levels of R.W.C. (about 80% R.W.C.; Table 6.10). However, marked interspecific differences in stomatal conductances and water potentials still existed. On the 25/2/83 temperatures were moderate but V.P.Ds were high (24°C and 2.2 KPa maxima respectively). All stand I trees exhibited low stomatal conductances with a morning peak (Fig. 6.17). Afternoon reductions in stomatal conductance corresponded with a broad peak in V.P.D. Significant interspecific differences existed ( $P < 0.001$ ) for most of the day, with E. pulchella showing lower stomatal conductances than other species. All species exhibited similar and moderate dawn water potentials, but significant interspecific differences ( $P < 0.001$ ) existed during much of the day. E. pulchella showed lower, and E. delegatensis higher water potentials than other species. Water potentials for all species restored fully at dusk. The reversal of the species rank order in water potentials, in comparison with measurements made on the 22/2/83, probably reflects the relative states of stomatal activity (on 25/2/83) as distinct from the state of rehydration (on 22/2/83).

Figures 6.17 and 6.18

Dawn to dusk (Eastern standard time, EST) records of (a) temperature ( $^{\circ}\text{C}$ , solid lines) and vapour pressure deficit (V.P.D.) (KPa, broken lines), (b) stomatal conductance ( $\text{cm sec}^{-1}$ ) and (c) leaf water potential (MPa) for trees on the ridge crest of stand I. Measurements were made on the 25/2/83 (Fig. 6.17) and the 2/3/83 (Fig. 6.18). Symbols are the same as for Figs 6.11 and 6.12.

Figure 6.17

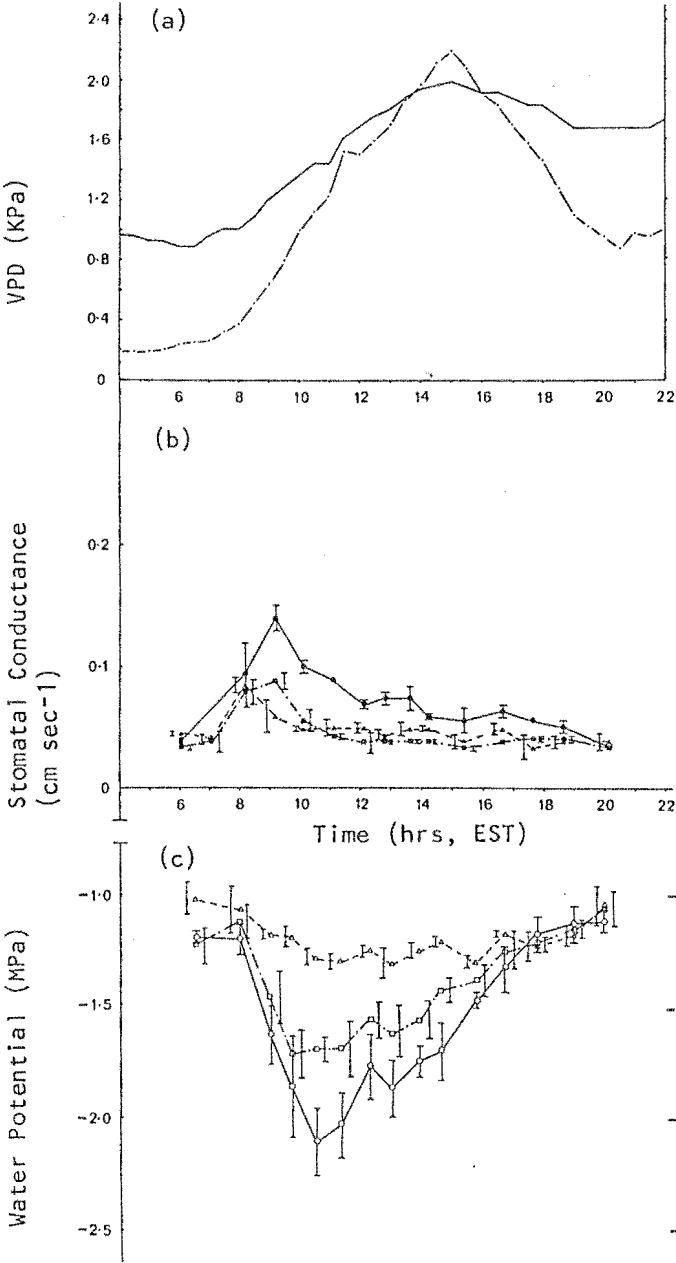
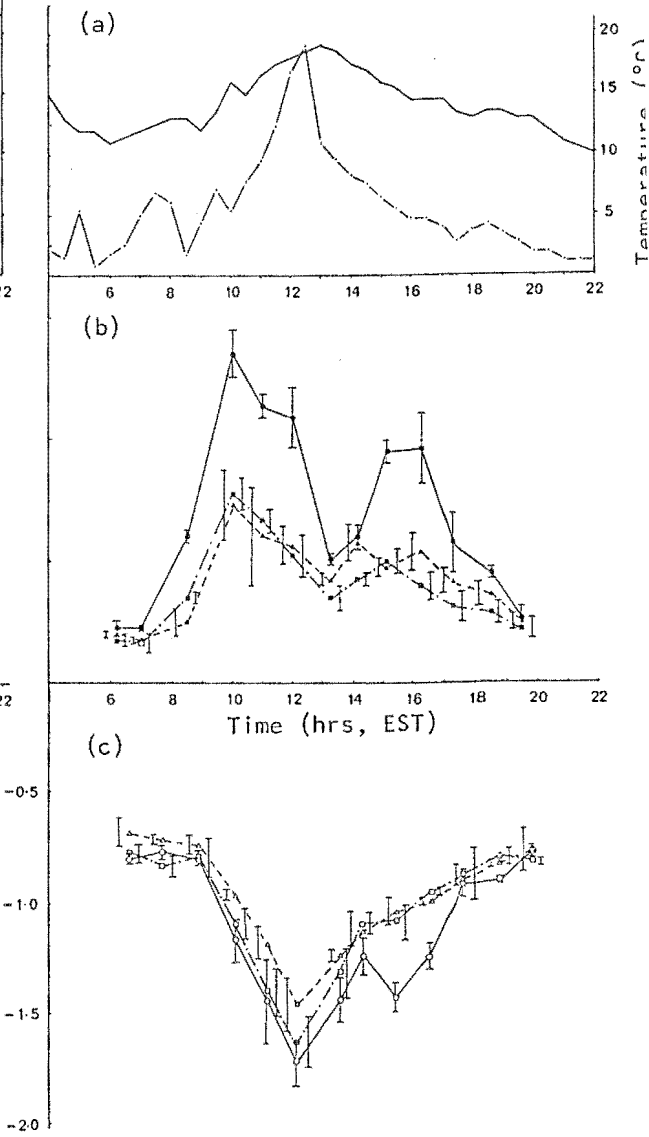


Figure 6.18



The physiological effects of the drought were still evident in stand I trees (Fig. 6.18) in early March (2/3/84) after a further 3.4 mm of rain had fallen (Table 6.6). Stomatal conductances of all species had increased substantially in comparison with records on the 25/2/83, but significant interspecific differences still existed ( $P < 0.001$ ) for much of the day. The relative species order was the same as for the 25/2/83. Again, a short midday period of reduced stomatal conductance corresponded to a narrow peak in V.P.D. Interspecific differences in water potential were evident for 2 hours only in the afternoon and corresponded to a greater increase in stomatal conductance by E. pulchella than by other species.

Remeasurement of the 30 trees adjacent to stand I (Fig. 6.3) on the 3/3/83 indicated less marked interspecific differences existed on the ridge top than at stand I (Table 6.9b), although E. pulchella exhibited significantly higher stomatal conductance ( $P < 0.001$ ) and slightly higher water potentials than other species in the afternoon.

Remeasurement of stand II trees after the February rains, on 4/3/83 (Fig. 6.19), indicated that trees on the lower slopes of the ridge were again unstressed. Water potential and stomatal conductance curves were essentially similar to those recorded at the height of the drought at stand II. However, temperatures and V.P.Ds were higher (28°C and 2.3 KPa maxima, respectively) than were recorded on 17/3/83, which resulted in lower midday water potentials and restricted stomatal conductance for a short period in the afternoon in response to high V.P.D. Again stand II trees exhibited no evidence of stress.

### (iii) Crown Damage and Recovery

During the 1982/83 summer drought, significant interspecific differences ( $P < 0.05$ ) in crown damage occurred at stand I (Table 6.1) and in the 30 trees surveyed in the adjacent stand ( $P < 0.001$ ; Table 6.9c). E. pulchella received least crown damage (13-17%) followed by E. coccifera (25-27%) and E. delegatensis (50-54%). The crown damage figures reflected the same species order of drought resistance indicated by R.W.C. (at -4.4 MPa) at the height of the drought (Table 6.10) and subsequent recovery in water potential and stomatal conductance after the first rains. Also, growth of tagged shoots in the crowns of each of the trees at stand I indicated E. pulchella recommenced active crown growth earlier than E. coccifera, which in turn commenced growth earlier than E. delegatensis, after the drought had broken.



At stand III where water potentials were more extreme (below -5.0 MPa) crown damage occurred in the same relative order but was more severe (Table 6.11). Significant interspecific differences occurred ( $P < 0.01$ ). E. pulchella incurred least crown damage (18%) followed by E. coccifera (40%), while all E. delegatensis stems were killed (100% crown damage) in the drought (Table 6.11). This supports results for stand I and suggests that selective elimination of E. delegatensis and ultimately E. coccifera would occur in mixed stands of the three species as droughts become more severe.

Studies of crown damage incurred by all stems in 16, 5 x 5 m quadrats placed at stand III indicated plant size was an important factor in drought damage (Table 6.13). Smaller (or younger) stems of E. pulchella and E. coccifera were more severely damaged than taller (or older) individuals. Significant interspecific differences in crown damage occurred in each height class ( $P < 0.001$ ) with E. pulchella showing very much lower levels of crown damage than E. coccifera. A regression analysis of crown damage against stem frequency for E. coccifera stems in each 5 x 5 m quadrat (Fig. 6.20) indicated that stand density had an effect on the crown damage. However, only stems in the 2.1 to 4.0 m height interval incurred significant density dependent crown damage ( $P < 0.05$ ). In comparison, the frequency of damaged stems in the quadrats tended to reflect microenvironmental characteristics in each quadrat. Soil pits dug in each of the 5 x 5 m quadrats indicated soil depth was of particular importance, with least crown damage and greatest stem frequencies occurring in the deepest soils.

Drought induced crown damage in all three species was manifest in two distinct ways. Firstly, as the drought increased in severity leaves from branches in the lower crown started to turn brown. The oldest leaves of the lowest crown branches were lost first with younger leaves at the branch apices retained until last. In many trees several of the lower crown branches were sacrificed in this way and was akin to a drought deciduousness (Kramer & Kozlowski 1960; Parker 1968). Crown damage of this type was most common in E. pulchella stems and least prevalent in E. delegatensis stems. The second form of drought damage occurred at the height of the drought and was characterised by leaves throughout the crown showing evidence of browning or "burning". "Burning" tended to occur inwards from the apex or margins of the leaf leaving patches or strips of green tissue near the midrib or on one side of the leaf. For E. delegatensis stems this type of crown damage formed a large component of the total crown damage (Plate 6.8) but was less important for E. coccifera. E. pulchella exhibited little crown damage by leaf "burning" but when it did occur, it always took the form of progressive death from the leaf apex down the lamina towards the petiole.

TABLE 6.13

Mean percentage crown damage  $\pm$  SE for all eucalypt stems in a 20 x 20 m quadrat at stand III divided into five height classes (0 to 1.0 m, 1.1 to 2.0 m, 2.1 to 4.0 m, greater than 4 m), recorded after the 1982/83 summer drought.

|                        | Height Class | Percentage Crown Damage | No. of Stems in Class |
|------------------------|--------------|-------------------------|-----------------------|
| <i>E. pulchella</i>    | 0 - 1.0      | 49 $\pm$ 5.4            | 15                    |
|                        | 1.1 - 2.0    | 39 $\pm$ 4.0            | 7                     |
|                        | 2.1 - 4.0    | 40 $\pm$ 6.6            | 8                     |
|                        | > 4.1        | 24 $\pm$ 4.0            | 6                     |
|                        |              |                         | 36                    |
| <i>E. coccifera</i>    | 0 - 1.0      | 81 $\pm$ 2.8            | 672                   |
|                        | 1.1 - 2.0    | 64 $\pm$ 3.8            | 515                   |
|                        | 2.1 - 4.0    | 52 $\pm$ 4.0            | 205                   |
|                        | > 4.1        | 44 $\pm$ 4.5            | 5                     |
|                        |              |                         | 1397                  |
| <i>E. delegatensis</i> | 0 - 1.0      | -                       | 0                     |
|                        | 1.1 - 2.0    | 100 $\pm$ 0             | 4                     |
|                        | 2.1 - 4.0    | 100 $\pm$ 0             | 4                     |
|                        | > 4.1        | -                       | 0                     |
|                        |              |                         | 8                     |

Fig. 6.20.

Linear regressions of severity of drought damage (using a 0-5 scale of crown damage) incurred by E. coccifera stems in the (a) 0-1.0 m (b) 1.1-2.0 m and (c) 2.1 to 4.0 m height classes in each 5 x 5 m subunit of a 20 x 20 m quadrat studied at Stand III against stem frequency of E. coccifera stems for that subunit.

Fig. 6.20

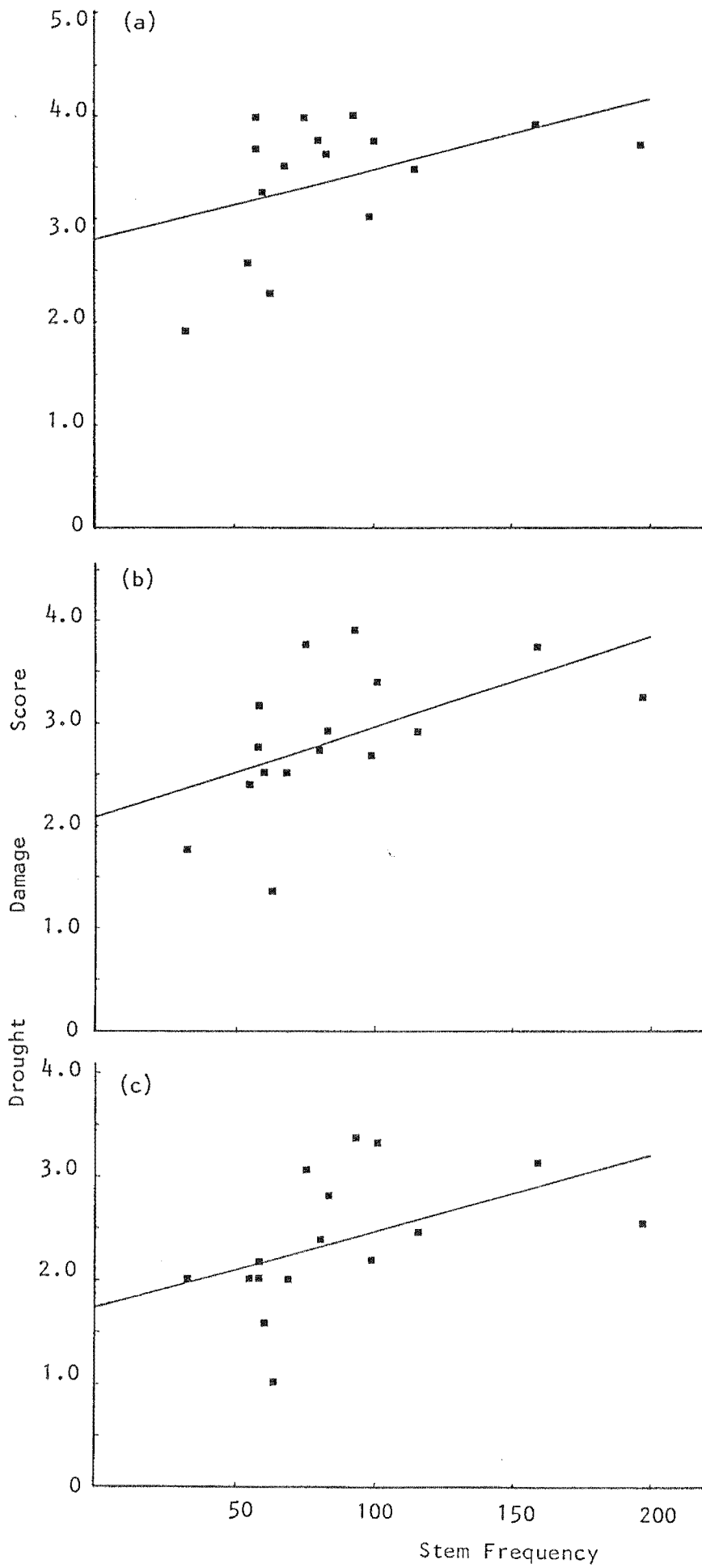


Plate 6.8

An E. delegatensis tree (tree dD, Fig. 6.3) near stand I exhibiting crown damage after the 1982/83 drought.



However, the character of the leaf damage may, at least in part be a function of the thermal properties conferred by leaf geometry (Cowan 1981). The leaf sizes of the three Monocalyptus species studied differed greatly. Adult E. delegatensis leaves were broad oblique and on average about twice the size of E. coccifera leaves which had an ovate lanceolate leaf (Table 6.14; and Fig. 2.1, Chapter 2). E. pulchella adult leaves were narrow linear and about half the size of E. coccifera leaves. Other interspecific differences in leaf morphology included significant differences in leaf thickness, stomatal frequency and guard cell length (Table 6.14). E. delegatensis tended to have thinner leaves, higher stomatal frequencies but smaller guard cells than other species (Table 6.14), but differences other than leaf area, were not large. All species had isobilateral and amphistomatous leaves with similar stomatal frequencies on adaxial and abaxial surfaces. However, size alone may confer differences in the thermal properties of a leaf. Large leaves are cooler and will transpire less rapidly than small leaves when leaf conductances are high and the atmosphere is dry. In comparison, if leaf conductances are small (as was the case for stand I at the height of the drought), and the leaf temperature is greater than the air temperature, the situation is reversed (Cowan 1981); that is, small leaves are cooler and transpire less rapidly. Therefore differences in leaf size may be an important factor influencing the levels of crown damage recorded for the various species at Snug Plains during the drought.

The form and rapidity of vegetative recovery by drought damaged trees was invariably dependent on the species and the extent of drought damage incurred. The most severe drought damage usually caused death to E. delegatensis stems, but only occasionally did so for E. coccifera and E. pulchella stems. The severely damaged stems of E. delegatensis, that survived the drought, recovered via epicormic shoots which emanated from the stem and lower branches (Plate 6.9) while those for E. coccifera usually recovered via epicormic shoots on the upper branches. However, in the very rare event that E. pulchella stems were completely defoliated (e.g. Plate 6.10a), recovery occurred via epicormic shoots at the branch tips (Plate 6.10b). Thus the E. pulchella stems maintain their original crown height even after severe drought, a characteristic not observed in the other species. The rate of growth of stems after a drought was very much dependent on the extent of drought damage (Table 6.15). For stems of E. pulchella and E. delegatensis suffering various degrees of drought damage, rates of growth in stem basal area in the six month period subsequent to drought varied from a 13% increase for lightly damaged trees to a 7% decrease for defoliated trees. However, interspecific differences were not evident, possibly due to the small number of stems measured and the non-orthogonality of the data.

TABLE 6.14.

Leaf and stomatal characteristics of adult and seedling leaves (10th node) for *E. delegatensis*, *E. coccifera* and *E. pulchella*. Mean  $\pm$  SE and significance levels from analysis of variance (\*\*\*)  $p < 0.001$  are presented.

|                  | Species                | Leaf Area<br>(one surface)<br>cm <sup>2</sup> | Leaf Thickness<br>$\mu$ m | Guard Cell<br>Length<br>$\mu$ m | Stomatal Frequency<br>Adaxial | Stomatal Frequency<br>Adaxial |
|------------------|------------------------|---|---------------------------|---------------------------------|-------------------------------|-------------------------------|
| Adult foliage    | <i>E. delegatensis</i> | 21.5 $\pm$ 3.5                                | 328.0 $\pm$ 8.5           | 20.5 $\pm$ 2.7                  | 133.9 $\pm$ 5.6               | 121.3 $\pm$ 4.2               |
|                  | <i>E. coccifera</i>    | 11.1 $\pm$ 3.7                                | 348.7 $\pm$ 6.8           | 32.2 $\pm$ 4.8                  | 112.4 $\pm$ 7.9               | 89.7 $\pm$ 4.8                |
|                  | <i>E. pulchella</i>    | 4.4 $\pm$ 0.7                                 | 374.7 $\pm$ 8.8           | 36.2 $\pm$ 8.5                  | 127.5 $\pm$ 7.5               | 109.9 $\pm$ 3.8               |
| Significance     |                        | ***   | ***                       | ***                             | ***                           | ***                           |
| Seedling foliage | <i>E. delegatensis</i> | 24.6 $\pm$ 5.7                                | -                         | -                               | 210.9 $\pm$ 7.4               | 132.6 $\pm$ 6.7               |
|                  | <i>E. coccifera</i>    | 10.1 $\pm$ 2.2                                | -                         | -                               | 163.8 $\pm$ 8.9               | 95.6 $\pm$ 2.7                |
|                  | <i>E. pulchella</i>    | 3.1 $\pm$ 1.1                                 | -                         | -                               | 157.8 $\pm$ 7.6               | 112.8 $\pm$ 4.9               |
| Significance     |                        | ***   |                           |                                 | ***                           | ***                           |

Plate 6.9

(a) A severely drought damaged mixed stand of E. pulchella, E. coccifera and E. delegatensis, (b) subsequent epicormic regeneration of a surviving E. delegatensis stem.



(a)



(b)



Plate 6.10

(a) A lone E. pulchella tree completely defoliated by the 1982/83 drought (RHS of Plate), (b) subsequent regeneration via epicormic buds at the branch tips.

(a)



(b)



TABLE 6:15.

Mean basal area increments in the six month period subsequent to the 1981/82 summer drought for stems of E. delegatensis and E. pulchella (at Stand IV) damaged to varying extents during the drought.

| Crown Damage Class | Species         | Diameter (cm) | % Increase in Basal Area | Mean % Increase in Basal Area |
|--------------------|-----------------|---------------|--------------------------|-------------------------------|
| 0<br>(0-5%)        | E. delegatensis | 6.28          | 13                       | 13                            |
|                    | E. delegatensis | 5.77          | 14                       |                               |
|                    | E. pulchella    | 3.28          | 13                       |                               |
| 1<br>(6-25%)       | E. delegatensis | 3.49          | 15                       | 14                            |
|                    | E. delegatensis | 5.45          | 15                       |                               |
|                    | E. pulchella    | 4.82          | 12                       |                               |
| 2<br>(26-50%)      | E. delegatensis | 3.07          | 6                        | 5                             |
|                    | E. pulchella    | 3.76          | 4                        |                               |
|                    | E. pulchella    | 4.04          | 8                        |                               |
|                    | E. pulchella    | 3.77          | 4                        |                               |
|                    | E. pulchella    | 4.13          | 2                        |                               |
|                    | E. pulchella    | 2.18          | 3                        |                               |
| 3<br>(51-75%)      | E. delegatensis | 3.41          | 1                        | 2                             |
|                    | E. pulchella    | 3.18          | 3                        |                               |
| 4<br>(76-95%)      | E. delegatensis | 3.07          | -7                       | -5                            |
|                    | E. delegatensis | 3.67          | -4                       |                               |
| 5<br>(96-100%)     | E. delegatensis | 3.51          | -4                       | -7                            |
|                    | E. delegatensis | 3.32          | -9                       |                               |
|                    | E. delegatensis | 1.81          | -3                       |                               |
|                    | E. delegatensis | 4.90          | -6                       |                               |
|                    | E. delegatensis | 2.81          | -6                       |                               |
|                    | E. delegatensis | 2.17          | -7                       |                               |
|                    | E. delegatensis | 3.67          | -16                      |                               |
|                    | E. delegatensis | 3.68          | -6                       |                               |
|                    | E. delegatensis | 4.08          | -8                       |                               |

### 3. Seedling Root Pattern

Substantial interspecific differences were evident in the rooting pattern of the three *Monocalyptus* species grown in large tubular pots in the glass house. *E. delegatensis* tended to have a main or tap root with few surface roots and extensive branching deeper in the soil profile (Figs 6.21 and 6.22). In contrast, *E. coccifera* had a more superficial root system. The tap root was less well developed with the major concentrations of roots and rootlets in the upper soil profile and few root branches at depth. For *E. pulchella* the tap root was even less pronounced and major lateral roots and rootlets extended through most of the soil profile. These differences in root pattern may be of some adaptive value in the respective soils naturally occupied by the three species.

### 4. Competition Trials

In both drought treatments 1 and 2 (high V.P.D. and low V.P.D. respectively) and all trials no symptoms of stress were evident on the first day (Figs 6.23, 6.24 and 6.25). Stomatal conductance and water potential curves were bell shaped. Water potentials were mild with maxima of between -0.7 and -1.0 MPa (depending on the trial). Stomatal conductances were high with maxima between 1.5 and 4.0 cm sec<sup>-1</sup> (depending on the trial). No marked reduction in stomatal conductance was elicited by high V.P.Ds on the first day of the seedling trials, which contrasts with results from field studies. This suggests seedlings responses to V.P.D. may differ from those of adult trees, although state of drought "hardening" may also be involved.

However, interspecific differences in stomatal conductance did exist. Under high V.P.Ds, *E. coccifera* exhibited significantly lower stomatal conductance ( $P < 0.001$ ) than other species (Figs 6.24 and 6.25), a characteristic also observed in field studies in the latter stages of the drought. In comparison interspecific differences in treatment 2 (low V.P.D.) were minor on the first day of drought trials.

After midday on day 3, all plants in the drought trials exhibited a steady decline in water potentials and stomatal conductance. The decline in stomatal conductance appeared to correspond with the falling water potentials until stomatal conductances were low (0.3 to 0.5 cm sec<sup>-1</sup>) at approximately -2.0 MPa. This compares with water potentials of approximately -4.0 Pa which corresponded with stomatal closure in trees at stand I on Snug Plains.

Figure 6.21

The root pattern for representative seedlings from the three species (a) E. delegatensis, (b) E. coccifera and (c) E. pulchella grown in tubular pots in the glasshouse.



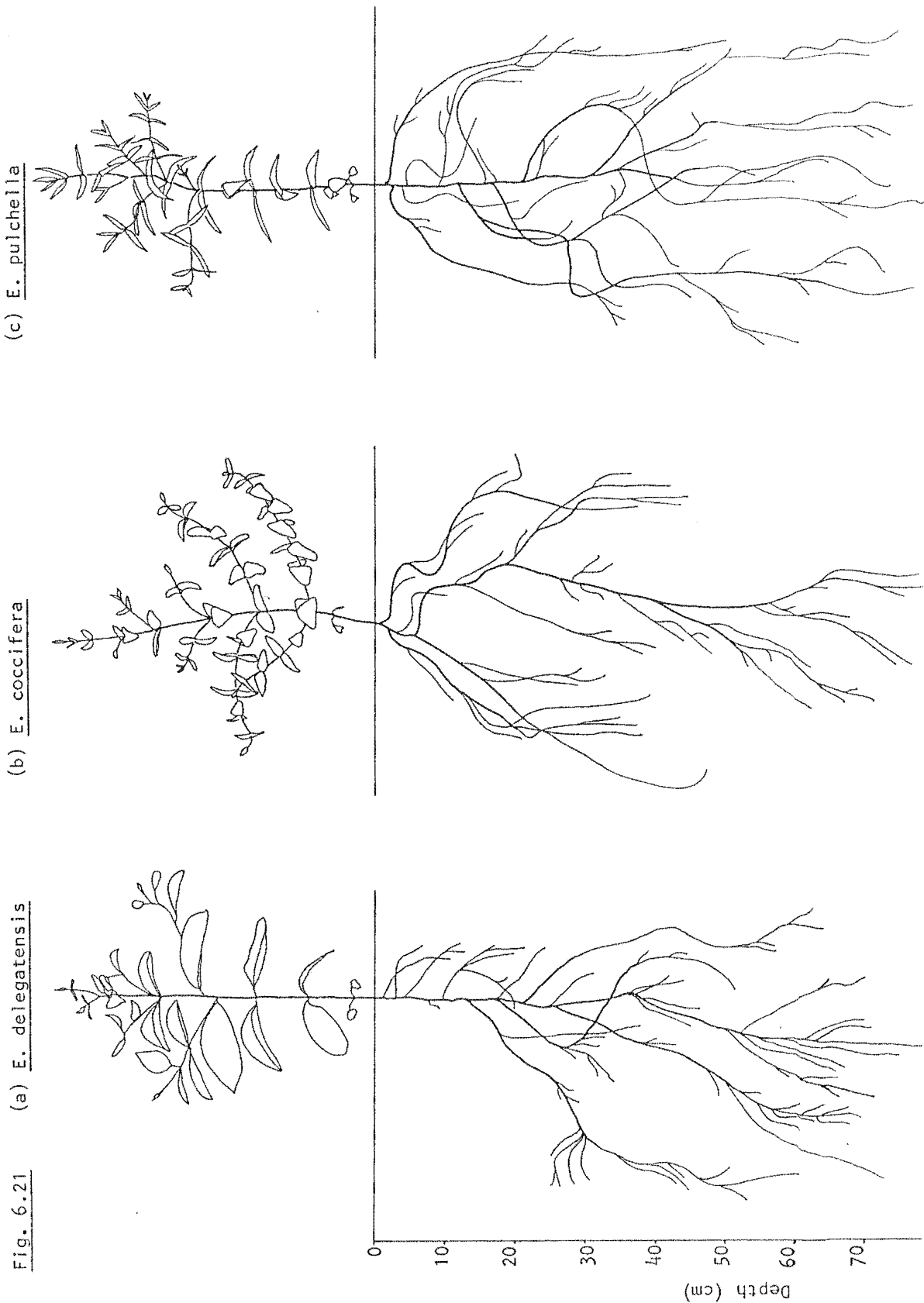
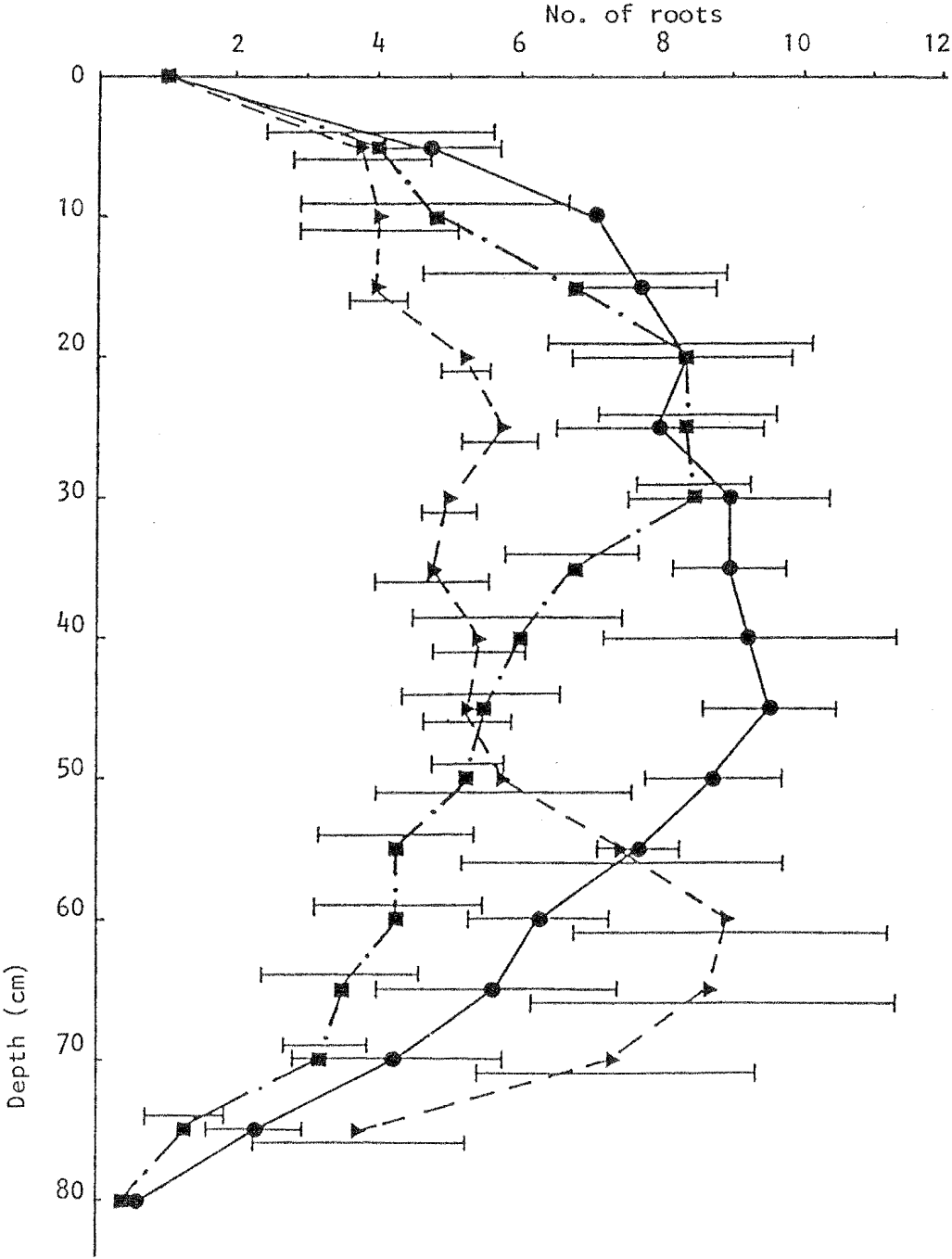


Fig. 6.22 The mean numbers of roots present at 5 cm intervals for seedlings of the three species of eucalypt *E. delegatensis* (▲), *E. coccifera* (■) and *E. pulchella* (●) grown in tubular pots in the glasshouse.





In each drought trial including E. delegatensis, this species incurred extensive drought damage (Figs 6.23 and 6.25) at water potentials above -3.0 MPa, causing the trial to be terminated. In comparison, the drought trial involving E. pulchella and E. coccifera continued to water potentials near -5.0 MPa before interspecific differences became evident, and even then significant interspecific differences in water potentials only occurred under high V.P.Ds (treatment 1).

At the end of each trial significant interspecific differences ( $P < 0.01$  to  $P < 0.001$ ) in stomatal conductance and water potentials had developed in both high and low V.P.D. treatments (except for water potential records in the E. pulchella and E. coccifera low V.P.D. treatment). E. pulchella exhibited lower stomatal conductance and lower water potentials than other species, while E. coccifera exhibited lower stomatal conductances and lower water potentials than E. delegatensis. Further, interspecific differences in water potential tended to be greater under conditions of high V.P.D., which suggests the occurrence of desiccating winds may be an important ecological factor during drought in the field.

The pattern of drought damage incurred by seedling leaves during the drought treatments differed markedly. As was found in the field studies, leaf "burning" in E. delegatensis and E. coccifera leaves occurred from the margins and apex of the leaf and resulted in losses of large areas of the lamina (Plate 6.11). However, for E. pulchella, leaf "burning" occurred progressively back from the leaf tip. Further, leaf damage to E. coccifera and E. delegatensis was relatively greater at high V.P.Ds (treatment 1) than at low V.P.Ds (treatment 2), a feature not evident for E. pulchella leaves. This is supported by evidence of the physical properties of leaves during drought. Small leaves tend to stay cooler and transpire less rapidly than large leaves when stomatal conductances are low and leaf temperature is higher than air temperature (Givinish 1978; Cowan 1981).

Marked interspecific differences in growth of the three species were evident after drought treatments were completed. E. pulchella, which was least damaged during the drought treatments, continued growth, after the drought, with the competitive advantage of a larger leaf area (Fig. 6.26). During subsequent growth E. pulchella maintained a larger leaf area and exhibited a greater growth in stem basal area than the other species in the same treatment. This contrasted with the control treatment where E. pulchella was the smaller species in each case. Similarly, E. coccifera maintained a

Figures 6.23, 6.24 and 6.25

Stomatal conductance ( $\text{cm sec}^{-1}$ ) and leaf water potentials (MPa) measured during competition trials under drought conditions in (a) treatment 2 (low vapour pressure deficit [0.8 KPa] and ambient temperature [about 19°C]) and (b) treatment 1 (high vapour pressure deficit [3.6 KPa] and high temperature [36°C]). Measurements were made on seedlings of the paired species combinations: E. pulchella (●, solid lines) + E. delegatensis (▲, dashed lines) (Fig. 6.23); E. pulchella (●, solid lines) + E. coccifera (■, broken lines) (Fig. 6.24); and E. coccifera (■, broken lines) + E. delegatensis (▲, dashed lines) (Fig. 6.25). Means  $\pm$  SE are presented for four replicates.

Fig. 6.23

Paired *E. pulchella* + *E. delegatensis* seedlings

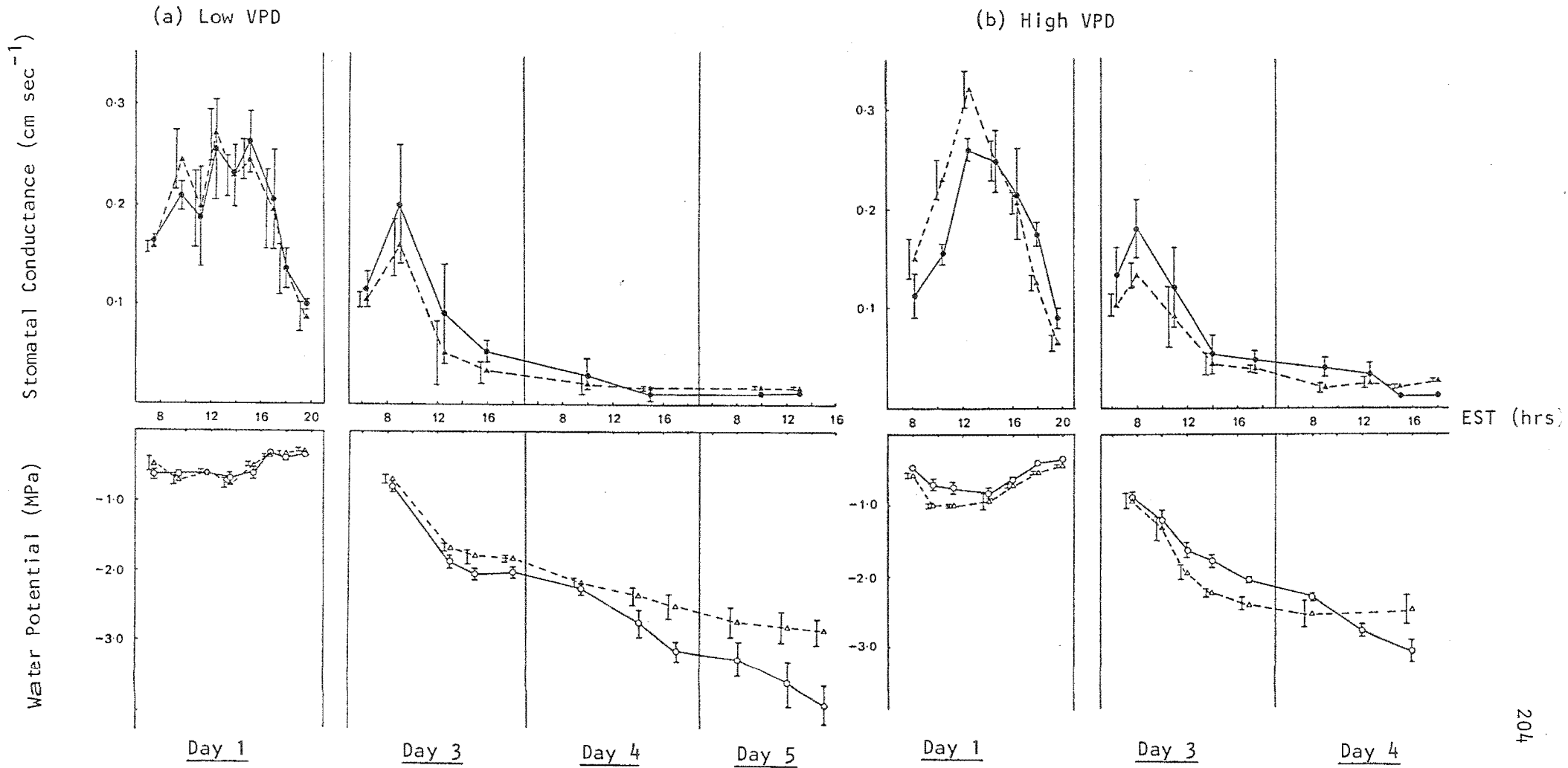


Fig. 6.24

Paired *E. pulchella* + *E. coccifera* seedlings

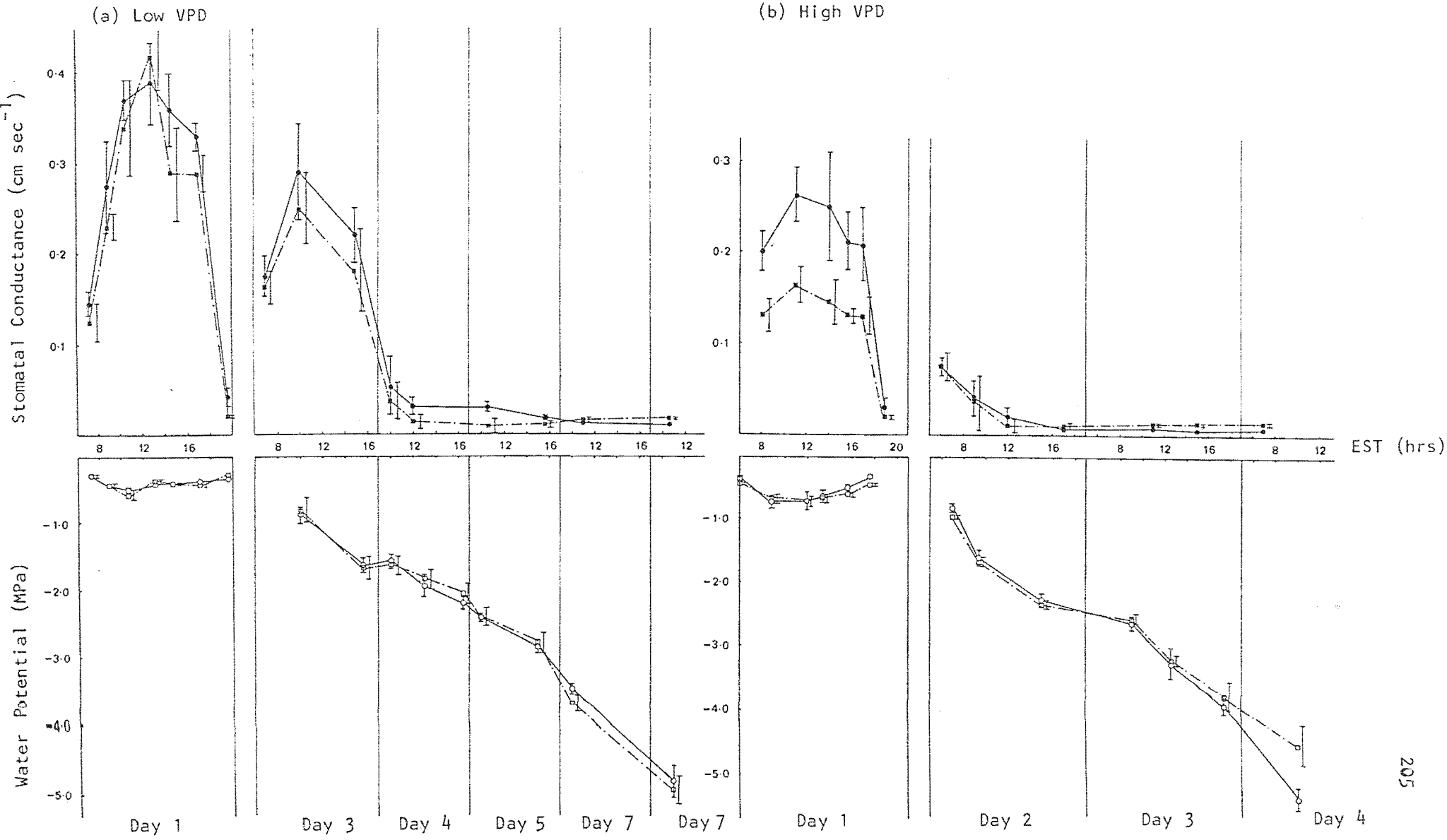


Fig. 6.25

Paired *E. coccifera* + *E. delegatensis* seedlings

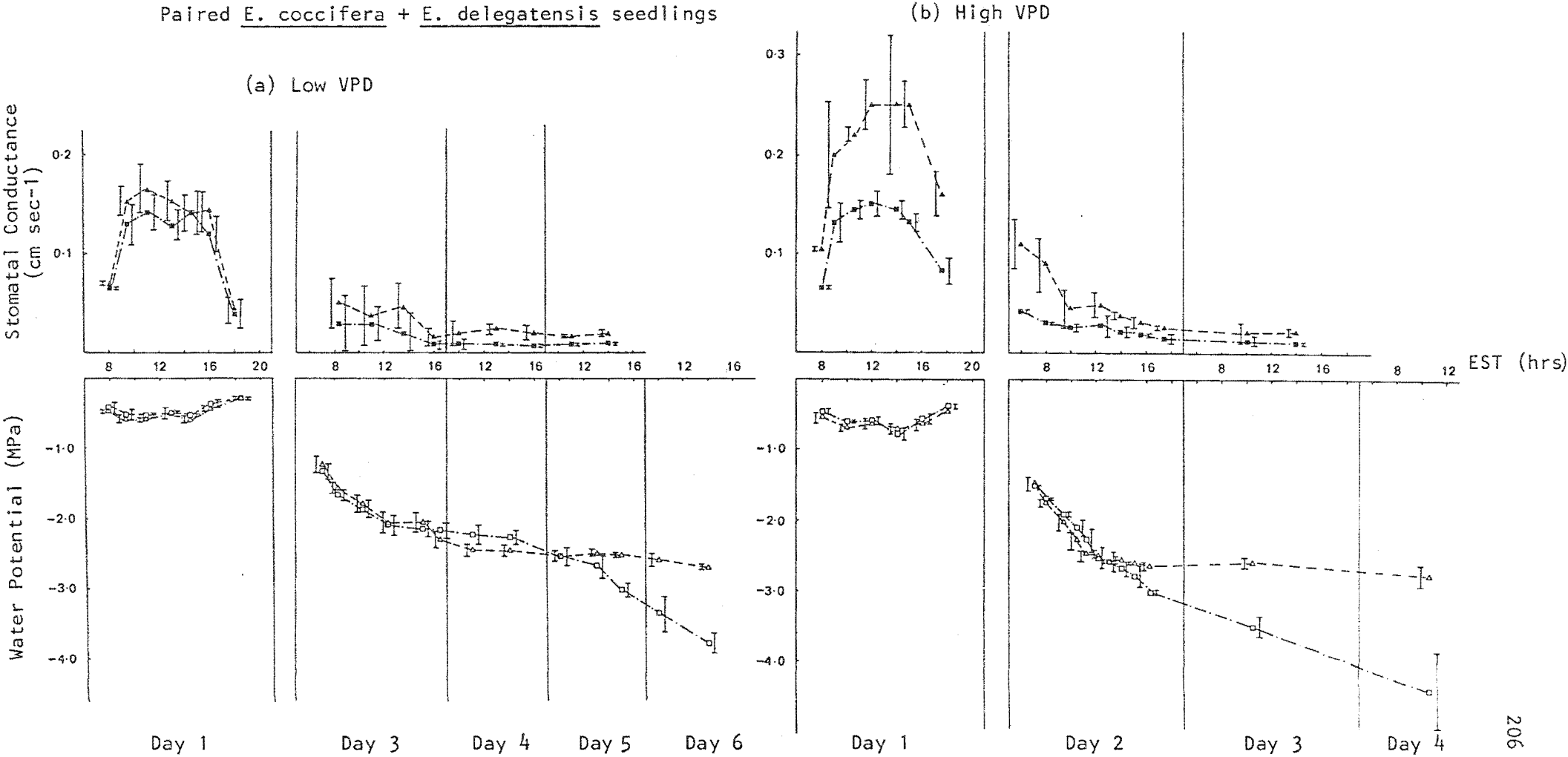
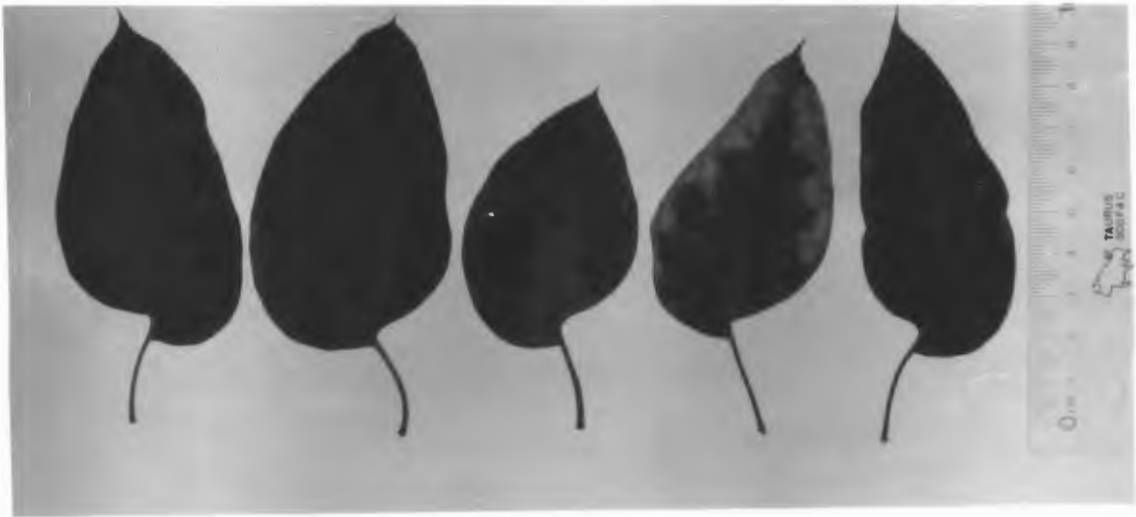


Plate 6.11

Pattern of leaf damage for representative leaves of (i) E. delegatensis, (ii) E. coccifera and (iii) E. pulchella seedlings after competition trials under drought conditions in (a) treatment 1 (high V.P.D. [3.6 KPa] and high temperature [36°C]) and (b) treatment 2 (low V.P.D. [0.8 KPa] and ambient temperature [approximately 19°C]), conducted in plastic enclosures in a glasshouse.

Plate 6.11(a)

(i)



(ii)



(iii)

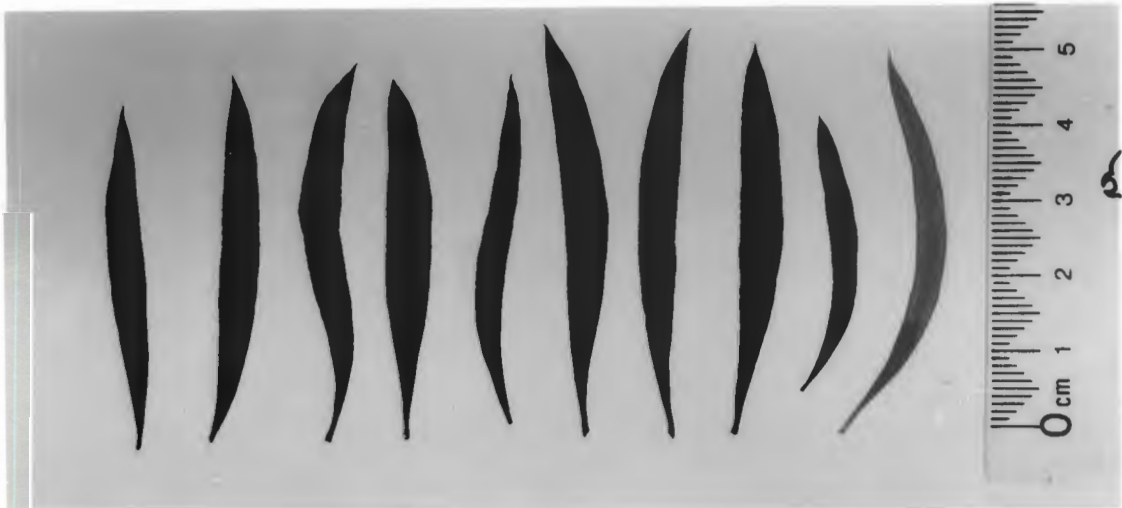


Plate 6.11(b)

(i)



(ii)



(iii)

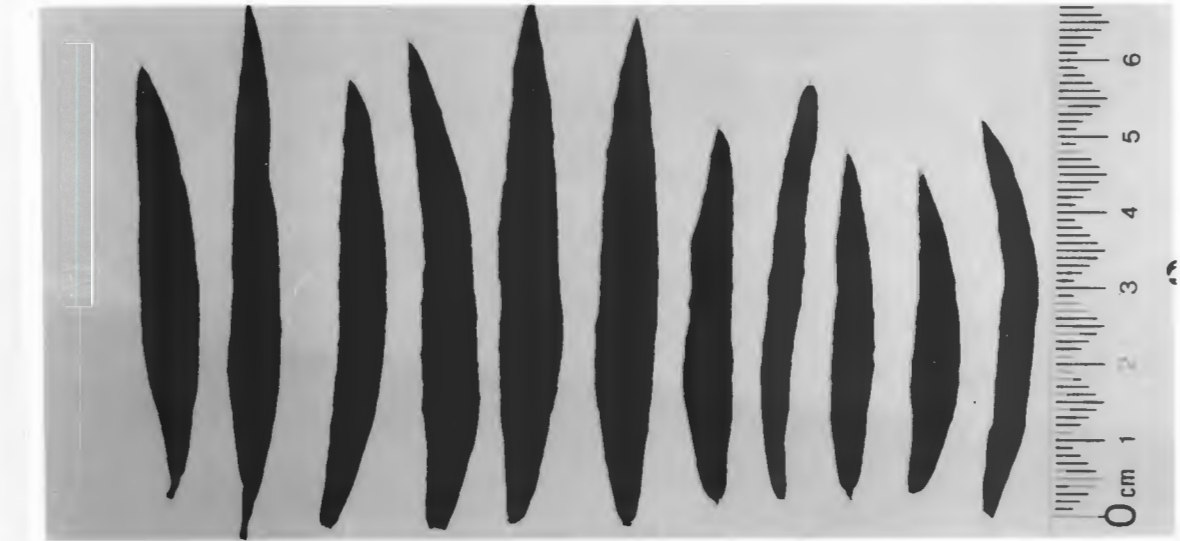




Fig. 6.26(a)

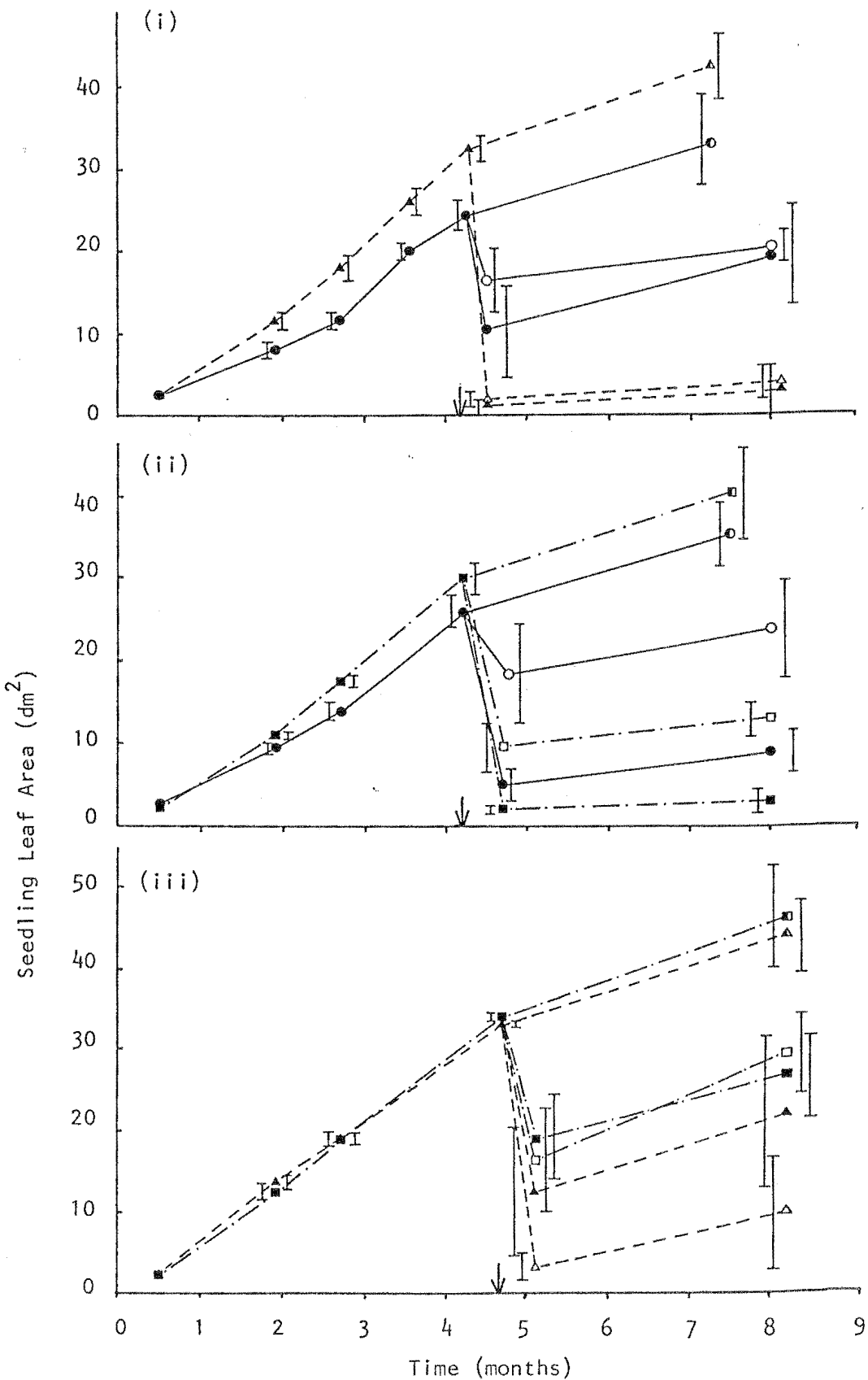
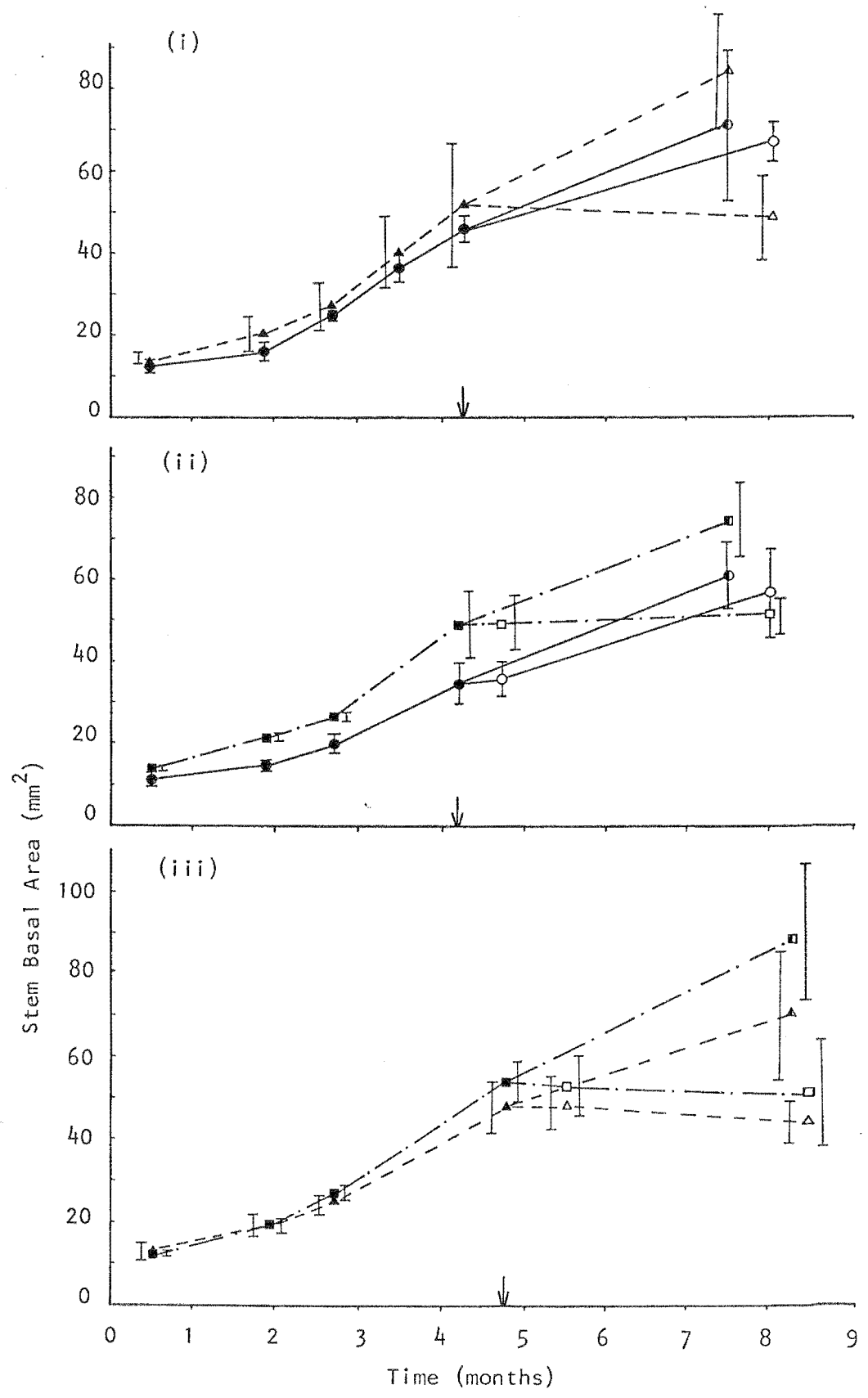


Fig. 6.26(b)



larger leaf area and greater growth in stem basal area than E. delegatensis in the same treatment after drought, although little differences in these measures existed for the control plants.

Interspecific differences in leaf area and stem basal area were enhanced by high V.P.Ds (treatment 1) in comparison to low V.P.Ds (treatment 2), which again suggests desiccating winds may be an important factor influencing drought damage in the field.

## DISCUSSION

Eucalypts appear to be drought tolerators rather than drought avoiders. Eucalypts do not close their stomata at high water potentials (Sinclair 1980; Connor et al. 1977) during drought but tend to maintain high levels of transpiration and photosynthesis even under moderate stress (Florence 1981) and rely more on access to a water supply than restriction of water loss (Sinclair 1980; Grieve 1956; Doley 1967). Interspecific differences in drought tolerance tend to be determined by the depth and effectiveness of the root system (Grieve 1956; Sinclair 1980) or by tolerance to cytoplasmic desiccation (Ladiges 1974, 1975, 1976; Ashton et al. 1975; Withers 1978). The more drought resistant eucalypt species and ecotypes have been shown to maintain high R.W.Cs at low water potentials (Ladiges 1974, 1975; Ashton et al. 1975; Withers 1978; Pereira & Kozłowski 1976) and have high tissue tolerance to low R.W.C. (Ladiges 1974, 1975; Ashton et al. 1975, Quraishi & Kramer 1970; Heth & Kramer 1975; Pook et al. 1966).

In preliminary drought trials conducted on seedlings of the six eucalypt species studied marked interspecific differences in drought resistance were evident. E. pulchella was clearly the most drought resistant species. It maintained higher leaf R.W.Cs at low xylem water potentials (-2.0 MPa) than other species, showed the first signs of wilting at lower R.W.C. and lower soil moisture contents than other species, and took longer to wilt than other species. Using these criteria, E. coccifera was less resistant to drought than E. pulchella, followed by E. urnigera and E. delegatensis with similar drought resistance and E. johnstonii and E. gunnii with low drought resistance. This species order of drought resistance agrees with the natural distributions of these species in the field at Snug Plains. E. pulchella occupies the dry rocky ridge tops; E. coccifera is present on well drained rises in the Plain, E.

delegatensis and E. urnigera naturally inhabit deep moist soils, whereas E. johnstonii and E. gunnii dominate seasonally waterlogged soils. Therefore, low drought resistance may be an important factor involved in the absence of the Symphyomyrtus species from the ridge tops and slopes at Snug Plains. Furthermore, the Monocalyptus species tended to exhibit higher stomatal conductance and higher transpiration than Symphyomyrtus species, as the soil moisture decreased, and exhibited a more rapid decline in stomatal conductance and transpiration when soil moisture levels became low. Higher initial levels of transpiration and a more rapid reduction in transpiration during drought have been shown characteristic of more drought resistant eucalypt species and ecotypes (Pereira & Kozlowski 1976; Ladiges 1974), affecting a more rapid control of water loss. These characteristics may also place <sup>these</sup> Monocalyptus species at an adaptive advantage in the shallow soils of the ridge top sites where water supplies are limited and dwindle rapidly.

During periods of natural drought, injury incurred by eucalypt stands has been reported to be more severe on shallow stoney and light textured soils (Pook et al. 1966; Ashton et al. 1975; Sinclair 1980). This suggests the moisture holding capacity of the soil (Specht 1972) may be an important influence on drought severity. At Snug Plains field water relations studies coincided with a drought, the severity of which probably only occurs once every 50 to 100 years. In a transect across a low ridge the soil depth and moisture holding capacity differed greatly and related directly to extremes of soil moisture status recorded during the drought. Shallow ridge top soils desiccated more rapidly during the drought, and rehydrated more rapidly after rains than lower ridge soils and steep gradients in soil water potentials developed during the drought. The shallow, stoney soils on the ridge top exhibited water potentials of -4.5 MPa and calculated total "available" moisture levels were very low. In comparison, the water relations of the soils on the lower ridge slopes were buffered by the moderate water potentials of the deeper soil horizons, even though surface soil horizons had water potentials comparable with ridge top sites. At the base of the ridge, soils were deep, soil water potentials were mild, and levels of available soil moisture were high. Changes in eucalypt dominance in response to soil water relations on potentially dry aspects have been suggested in several ecological surveys (e.g. Specht & Perry 1948; Pook et al. 1966; Florence 1963, 1964; Ashton et al. 1975; Kirkpatrick & Nunez 1980) but collaborative studies of plant water relations have been conducted on few occasions.

Physiological measurements made on ecotonal trees at the boundary between E. fasciculosa and E. obliqua populations (Sinclair 1980) showed that interspecific differences in drought resistance did develop during periods of stress and confirmed that water relations was an important factor in the distribution of eucalypt species on the dry and sunny ridge slopes of the Mt. Lofty Ranges. Interspecific differences in the R.W.C. of the sapwood and drought damage occurring in stands of eucalypts growing on soils of different depth and texture in the foothills around Canberra in the A.C.T. were reported by Pook et al. (1966). Further, on the slopes of Mt. Towrong in Victoria, Ashton et al. (1975) observed interspecific differences in drought damage in eucalypt stands which corresponded to differences in drought tolerance obtained in laboratory experiments. At Snug Plains, the steep gradients in soil water potential measured over a low ridge at the height of the 1982/83 drought were reflected in marked differences in xylem water potentials measured between the ridge top and the lower ridge slopes. On the ridge top sites (stands I and III), minimum xylem water potentials of between -4.4 MPa and -5.3 MPa were recorded, which were comparable with minimum potentials measured during severe droughts in the Mt. Lofty Ranges (Sinclair (1980). In comparison, 35 m away on the lower slopes of the ridge (at stand II) interspecific differences in water relations were minor throughout the year and late summer minimum xylem water potentials were mild (-1.2 MPa).

The marked interspecific differences in drought resistance demonstrated for the Monocalyptus species in field and glasshouse studies and the marked zonation of these species on the ridge together with the low water potentials measured in ridge top stands in the field, strongly suggest that site water relations is a major factor influencing the distribution of the Monocalyptus species on the ridges at Snug Plains. The superior drought resistance of E. pulchella and its presence only in skeletal ridge top habitats suggests water relations is a primary factor in this species' distribution.

Stand biomass and transpiration capacity may also influence the depletion of moisture reserves. Martin and Specht (1962) demonstrated that dense stands with large biomass in "mesic" sites have larger transpiration capacities and may become droughted before more open forest in "xeric" sites with lower transpiration capacity (Martin & Specht 1962). Further, dense stands on gully sides at Mt. Towrong in Victoria received severe drought damage during the 1967 drought (Ashton et al. 1975), whereas less dense stands some distance from the gully were relatively unaffected.

At Snug Plains the ridge top site recording the highest leaf water potentials during the drought (garden 1) was also the site with least biomass. In comparison, dense mixed stands at stand I and III with high biomass exhibited lowest leaf water potentials and incurred greatest crown damage. It was only in the stands of substantial biomass on the shallower ridge top soils that severe drought symptoms were evident during the 1982/83 drought, resulting in a patchwork of drought damage along the ridge crest. However, during the ontogeny of these stands future droughts which occur will probably continue to select for the drought resistant species in other parts of the stand when biomass becomes large enough to deplete soil moisture reserves.

Previous field studies comparing the water relations of pairs of eucalypt species have demonstrated that marked interspecific differences in water potential and stomatal conductance occur during dry periods. Sinclair (1980) demonstrated that adjacent E. fasciculosa and E. obliqua trees exhibited very different water potentials and stomatal conductance during drought and suggested these differences might relate to differences in extent and effectiveness of the root system. Grieve (1956) working on E. marginata and E. calophylla noted that in summer E. calophylla tended to close its stomata in the hottest part of the day, but this was not observed for E. marginata trees. Again differences in root distributions may account for these responses (Carbon et al. 1980, 1981). Myers and Neales (1984) found E. microcarpa had higher maximum stomatal conductances than E. behriana when water potentials were moderate (above -2.5 MPa) but the reverse was the case at low water potentials. However, for the duration of the drought at Snug Plains (except for a short period in the afternoon during December readings) interspecific differences in stomatal conductance and water potentials were minor. All species showed similar diurnal patterns of water potential and stomatal conductance during early and mid summer, to the point of stomatal closure for the whole day when water potentials were below -4.0 MPa.

The decline in the dawn water potentials of all trees at stand I corresponded with the decline in water potentials of the soil. The correspondence between leaf water potential and soil water potential are predicted by the "Soil-Plant-Atmosphere-Continuum" model of plant water relations (Huber 1924; van den Honert 1948; Elfving et al. 1972; Kauffmann & Hall 1974; Jarvis 1976):

$$\Psi_{\text{leaf}} = \Psi_{\text{soil}} + \Psi_{\text{gravity}} - \text{flux} (r_{\text{soil to leaf}}) \quad (1)$$

where the leaf water potential is dependent on the supply potential ( $\Psi_{\text{soil}} + \Psi_{\text{gravity}}$ ), the rate of water transport (flux) and the liquid phase resistance from soil to leaf ( $r_{\text{soil to leaf}}$ ). When the stomata are closed (e.g. at dawn) the flux is low and the last term in equation (1) contributes little to leaf water potential ( $\Psi_{\text{leaf}}$ ) (Hellkvest et al. 1974). The leaf water potential will then largely depend on the supply potential ( $\Psi_{\text{soil}} + \Psi_{\text{gravity}}$ ). Also, under static conditions a change in water potential of about 0.01 MPa per metre is expected from the soil to leaves (Hellkvest et al. 1974; Connor et al. 1977). Therefore, for the approximately 8 m high trees at stand I the gravitational component of water potential ( $\Psi_{\text{gravity}}$ ) would also contribute little to leaf water potential ( $\Psi_{\text{gravity}} \approx 0.08$  MPa) and leaf water potential would depend on soil water potential. However, differences in the horizon of the soil profile occupied by plant root systems or differences in tolerance or avoidance mechanisms (Levitt 1972) possessed by plants confound interpretation of natural systems. Despite this Sucoff (1972) found that after nocturnal equilibrium leaf water potentials and soil water potentials for red pine were in agreement.

Investigation of the topography of the bedrock underlying stand I indicated that the rock was massive and unjointed. Further, although rooting pattern studies conducted on seedlings of the three Monocalyptus species, E. pulchella, E. coccifera and E. delegatensis, indicated natural differences in morphology and branching pattern existed, the root systems of these species at stand I would probably be closely intertwined and entirely confined to the shallow surface soils. Under these conditions the three species might be expected to exhibit similar dawn water potentials. Further, the similarity in diurnal fluctuations in water potential attests to the similarity in stomatal control and internal resistance to water movement for the three species tested (see equation 1).

A correlation between maximum stomatal conductance and dawn water potentials has been described for several eucalypt species (Wellington 1981; Myers & Neales 1984; Korner & Cochrane 1985) and for other evergreen plants (Running et al. 1975; Running 1976; Hinckley et al. 1978, 1981; Poole et al. 1981; Schulze & Kupperts 1979). Field studies of Eucalyptus indicate that no threshold water potential is reached at which stomatal closure occurs (Connor et al. 1977; Sinclair 1980; Myers & Neales 1984; Korner & Cochrane 1985). Field studies at Snug Plains support these results. Maximum stomatal conductance of all trees at stand I declined progressively with declining dawn water potentials to the point of stomatal closure at water potentials near -4.0 MPa.

Recent studies by Myers and Neales (1984) and Korner and Cochrane (1985) also indicate that stomatal conductance in eucalypts is directly affected by high vapour pressure deficits (V.P.D.). A reduction in stomatal conductance in response to high V.P.D., regardless of the bulk water status of the plant, have been described for a variety of genera (Schulze et al. 1974; 1972; Comacho-B et al. 1974; Sherrif & Kay 1977; Turner et al. 1978) but only recently for Eucalyptus (Myers and Neales 1984; Korner and Cochrane 1985). The current study supports these results. All trees at site I exhibited marked reductions in stomatal conductance during daylight hours which corresponded directly to peaks in V.P.D. The response to high V.P.D. was also evident in unstressed stand II trees.

Drought tolerance, as distinct from drought avoidance (Levitt 1980), is conferred by a suit of characters including maintenance of R.W.C. at low water potentials (Parker et al. 1982). The maintenance of high R.W.C. has been shown to be an important factor in the drought resistance of eucalypts (Ashton et al. 1975; Withers 1978). Further, Ladiges (1974, 1975, 1976) demonstrated that drought resistant populations of E. viminalis could desiccate to lower R.W.C. without damage and had higher R.W.C. at a given water potential than seedlings from mesic habitats. Interspecific comparisons of drought tolerance in Eucalyptus have also emphasized the importance of maintaining high R.W.C. during a drought (Ashton et al. 1975; Kaplan 1974; Pallardy 1981). At Snug Plains, although marked interspecific differences in water potential and stomatal conductance did not develop for E. pulchella, E. delegatensis and E. coccoifera trees at stand I during the drought, significant interspecific differences in relative water content (R.W.C.) did occur. The leaf R.W.C. of E. pulchella trees at 61% were higher than E. coccoifera trees (55%) and E. delegatensis trees (48%). These results support conclusions from the preliminary drought trials which suggested E. pulchella was the most drought resistant species studied on the basis of several water relations characteristics including maintenance of high R.W.C. at low water potentials. The species order above also agrees with that found in the preliminary drought trials.

It appears that some eucalypt species are not able to tightly close stomata and effectively prevent water loss (Ashton et al. 1975; Withers 1978; Ladiges 1974; Sinclair 1980). Even at water potentials of -4.8 MPa, E. obliqua was exhibiting conductances of  $0.08 \text{ cm sec}^{-1}$  and ineffective control of water loss (Sinclair 1980). Similarly, Ashton et al. (1975) demonstrated poor control of water loss for adult and juvenile leaves of E. obliqua, although leaves of E. gonicalyx and E. radiata showed more control of transpirational water loss.



For the three Monocalyptus species at Snug Plains, even though stomata were closed, water loss was not prevented and all species exhibited similar water potentials; water potentials which reflected the supply potential (largely the soil water potential). Therefore, during the long rain free periods water potentials continued to fall in response to falling soil water potentials until tolerance limits were exceeded. At stand I water potentials of approximately -4.4 MPa were associated with crown damage of 14%, 25% and 54%; and R.W.Cs of 61%, 55% and 48%; for E. pulchella, E. coccifera and E. delegatensis respectively. These are comparable with values obtained by Ashton et al. (1975) where at -3.0 MPa seedlings of E. obliqua, E. radiata and E. gonicalyx suffered 100%, 40% and 1 to 50% leaf damage respectively. Critically low R.W.C. which are fatal for eucalypt species vary from 54% to 38% for individual species (Pook et al. 1966; Ashton et al. 1975; Ladiges 1974). At stand III, xylem water potentials fell to below -5.0 MPa and all E. delegatensis stems were killed, suggesting that the tolerance limits of E. delegatensis to low water potentials and/or low R.W.C. had been exceeded and the species eliminated from the stand.

Rapidity of recovery after drought has been associated with drought resistance (Hsiao 1973; Hand et al. 1982; Ladiges 1974; Quraishi & Kramer 1970). Seedlings from drought resistant population of E. viminalis showed a more rapid resumption of transpiration than plants from mesic environments after plants were watered (Ladiges 1974). Similarly, droughted seedlings of the more drought resistant E. polyanthemos showed a rapid recovery of high transpiration rates after watering in comparison with E. rostrata (Quraishi & Kramer 1970). After the rains at Snug Plains, significant interspecific differences in stomatal conductance, water potentials and R.W.C. were evident at stand I. E. pulchella exhibited more rapid restoration of high R.W.C. and more rapid return to moderate water potentials than other species in the few days after the first light rain. This possibly relates to the physiological state of each species at the end of the drought. The higher R.W.C. exhibited by E. pulchella may allow it to more effectively utilise the limited water resource provided by light rains in soil also occupied by roots of the other two species. After extensive rains E. pulchella exhibited a more rapid return to normal diurnal fluctuation in stomatal conductance and water potential and earlier commencement of shoot extension than other species. Further, E. pulchella incurred least crown damage in drought affected stands and displayed most effective crown regeneration after severe drought damage. Crown damage in E. pulchella was lower than for other species and was largely manifest as shedding of older leaves from the lower crown, a characteristic not as well

developed in other species. The reduction of transpiration area by leaf shedding is one of the most important drought resistance mechanisms (Kozlowski 1974). Regeneration of defoliated E. pulchella trees occurred via epicormic buds at the branch tips whereas, for other species, individuals not killed by drought regenerated via epicormic buds on the main trunk and larger branches. Thus, in mixed regenerating stands dominance changes as a result of drought heavily favoured E. pulchella; a characteristic also observed in glasshouse competition trials.

Slow plant growth and small biomass have also been associated with drought resistance in eucalypts (Ladiges 1974; Ashton et al. 1975; Parsons 1968; Martin & Specht 1962; Levitt 1972). E. pulchella exhibited slower growth rate than other species in field gardens (Chapter 3) and in competition trials in the glasshouse. Also E. pulchella trees were generally the smaller individuals in mixed stands in the field, prior to drought. E. pulchella also possesses smaller, narrower leaves than other species. Small leaves tend to remain cooler and transpire less rapidly than larger leaves at low stomatal conductances when the leaf temperature is greater than air temperature (Cowan 1981; Pallardy 1981; Givinish 1978). These attributes also place E. pulchella at a selective advantage in drought prone sites. Therefore, the superior drought resistance of E. pulchella is probably the primary reason for its dominance on the ridge crests characterised by shallow soils at Snug Plains. The relative positions of E. coccifera and E. delegatensis on the ridge slopes may also be influenced by differences in drought resistance. E. coccifera, which naturally occupies the lower ridge slopes, exhibited considerable drought resistance during the 1982/83 summer and appeared able to maintain lower stomatal conductances than other species during the later stages of the drought, thus reducing water loss. E. delegatensis was clearly the least drought resistant species, and this may be an important factor in confining E. delegatensis to sites with deep moist soils at Snug Plains.

Glasshouse competition trials support the results obtained in the preliminary drought trials and the field studies. Paired seedlings of E. pulchella, E. coccifera and E. delegatensis grown in restricted soil conditions (in the same pot) produced the same relative species order of drought tolerance as observed in the restricted soils at Snug Plains. Generally marked interspecific differences in water relations did not develop until an advanced stage in the competition trials which supported results from field studies. Further, the species order of wilting in response to falling leaf water potentials; the extent of crown damage incurred by seedlings and subsequent growth once rewatered, was the same as that found in the other studies.

However, the responses of seedlings in the competition trials differed from the field trees in two important ways. Firstly, the stomata of all seedlings closed at comparatively high water potentials ( $-2.0$  MPa). Stomatal closure at threshold levels of water potential have been described previously for eucalypt seedlings (Connor *et al.* 1977; Pereira & Kozlowski 1976) and for a large number of other woody plants (e.g. Federer 1976; Federer & Gee 1976; Hsiao 1973). This contrasts with results from mature trees (see earlier discussion). Secondly, the seedlings exhibited no reduction in stomatal conductance in response to high V.P.D. as observed in field studies (see earlier discussion). This suggests that seedling stomatal response to environmental factors may differ from that of mature trees, but the extent of "hardening" of the seedlings used may also be involved. Although the seedlings used were "hardened" outside the glasshouse during summer before experiments were conducted, several drying cycles may be required to induce the physiological changes for complete hardening (Stern *et al.* 1977; Kaufmann & Levy 1976; Jordon *et al.* 1975; Thomas *et al.* 1976; Tenhunen *et al.* 1981, 1982).

High V.P.D.s had a marked effect on interspecific differences observed during the competition trials. Interspecific differences in stomatal conductance, water potentials and crown damage which occurred near the end of drought trials, were accentuated by conditions of high V.P.D. This suggests that hot dry winds which often occur in late summer in Tasmania may be important in desiccating already droughted trees, particularly eucalypts, which appear to incompletely close their stomata (Sinclair 1980; Ashton *et al.* 1975; Quraishi & Kramer 1970).

Previous studies of interspecific differences in the physiology of eucalypt species during dry periods have largely concentrated on inter-subgeneric comparisons. During a Western Australian summer Grieve (1956) reported that *E. marginata* (*Monocalyptus*) maintained higher transpiration rates than *E. calophylla* (*Corymbia*) in an adjacent stand. Pook *et al.* (1966) observed that during the 1965 drought in A.C.T. *E. rossii* (*Monocalyptus*) was less drought resistant than *E. polyanthemos* (*Symphyomyrtus*) in mixed stands on shallow soils. Further, interspecific differences in drought damage which occurred in mixed stands of *E. rubida* (*Symphyomyrtus*), *E. viminalis* (*Symphyomyrtus*), *E. pauciflora* (*Monocalyptus*) and *E. stellulata* (*Monocalyptus*), indicated that the latter two species were more severely affected (Pook *et al.* 1966). Sinclair (1980) showed *E. obliqua* (*Monocalyptus*) was less resistant to drought than adjacent *E. fasciculosa* (*Symphyomyrtus*) and *E. leucoxylon* (*Symphyomyrtus*).

trees. In each of the above cases, the Monocalyptus species were more drought sensitive than Symphyomyrtus species, following the general categorization of preferred habitats as defined by Florence (1981). However the reverse was suggested by the current drought studies.

On the other hand, interspecific comparisons of drought resistance for the three species from a single subgenus studied at Snug Plains indicated that differences were more subtle than those established for inter-subgeneric comparisons. The interspecific differences in drought resistance obtained for Monocalyptus species were manifest as differences in tissue hydration and rates of recovery after drought and were more akin to those obtained for intraspecific comparisons (Ladiges 1974, 1975, 1976). Studies by Myers and Neales (1984) on two Symphyomyrtus species demonstrated similarly subtle interspecific differences. This might suggest there are marked differences in the sort of adaptations possessed by different subgenera to cope with desiccation and drought.

## CHAPTER 7

### CONCLUSION

It has been proposed that generally, eucalypts respond to subtle changes in site characteristics which produce a complex mosaic of species distributions within a single climatic region (Pryor 1953, 1959a, 1959b, 1976; Florence 1963, 1964, 1981, 1982). However, a number of investigations conducted on pairs or suits of eucalypt species have demonstrated that catastrophic events such as frost (Moore and Williams 1976; Harwood 1983), drought (Sinclair 1981, Pook *et al.* 1966) and insect attack (Burdon and Chilvers 1974; Morrow 1977) may be important in dominance changes between eucalypt species at particular locations prone to one or more of these environmental constraints. The current study indicates that the importance of catastrophic events in determining the distribution of eucalypts may have been underestimated.

In a single small geographic region (1 km square) at Snug Plains it has been possible to make direct comparisons between the coadapted ecotypes of 6 species without the complication of clinal or ecotypic variation, common in the genus (Pryor 1957; Barber 1955; Barber & Jackson 1957; Thomas & Barber 1974a, 1974b; Phillips & Reid 1980; Potts & Reid 1985a, 1985c) and which tends to confound interpretation in studies encompassing broader geographic regions. Investigations of the nutritional status and physical properties of field soils, together with evidence from seedling growth in reciprocal field transplant trials and glasshouse experiments, suggest that subtle site differences under equable climatic conditions have a minor effect on species dominance. These effects, however, may require longer term studies to elucidate. In contrast, it was the catastrophic events of frost, waterlogging, drought and insect depredation which had most influence on dominance changes in reciprocal seedling transplant trials and in natural stands in the study area.

#### Frost

A winter frost of record severity occurred at Snug Plains in June 1983, during which an absolute minimum temperature of  $-22^{\circ}\text{C}$  was recorded near the radiating surface, in a depression on the plateau. Temperature measurements made during the frost, along a transect crossing the study area, also demonstrated that a marked stratification of the air body occurred (up to  $9^{\circ}\text{C}/\text{m}$ ) and steep gradients in minimum temperature (up to  $7.3^{\circ}\text{C}$  over a

distance of 200 m) existed between the depression and an adjacent ridge top. Further, the natural distributions of the six species studied corresponded with the minimum temperatures recorded in stands of each species during the frost. In places, severe frost damage was inflicted on mixed pole eucalypt stands situated on the margins of the depression. Direct interspecific comparisons of frost damage within these mixed stands (except for E. delegatensis and E. johnstonii which was inferred from comparisons with other species) gave the species order of frost resistance (from greatest to least): E. gunnii > E. coccifera > E. johnstonii > E. delegatensis > E. pulchella. Interspecific comparisons involving E. urnigera were not possible because of a lack of suitable mixed stands. Although the severe frosts caused deaths to only a few individuals, marked changes in dominance occurred within some mixed stands. A mixed stand in which E. delegatensis and E. coccifera were codominant and E. gunnii was a more numerous subdominant was altered by the severe frost of June 1983 to be dominated by E. gunnii with E. coccifera an infrequent subdominant, while E. delegatensis was virtually eliminated from the stand. In another mixed stand, the severe frost killed the E. johnstonii stems to the height of the snow surface at the time of the frost, resulting in E. gunnii gaining dominance in an originally codominant stand. At one site near the base of the depression, all stems, including E. gunnii, were killed from the apex down to the height of the snow surface during the frost. Therefore, exceptional frosts like those in June 1982 may have an important effect on the distribution of subalpine eucalypts.

In reciprocal field transplant trials established at six sites in the study area a mild growing season frost (minimum of  $-5.5^{\circ}\text{C}$ ) occurred which inflicted severe damage on seedlings while they were in an unhardened state. The species order of frost resistance to this frost (from greatest to least) was: E. gunnii > E. johnstonii > E. coccifera > E. urnigera > E. pulchella > E. delegatensis; with E. gunnii exhibiting outstanding frost resistance. In comparison, a winter frost of  $-10.5^{\circ}\text{C}$  inflicted markedly less damage on seedlings which had been exposed to an adequate period of hardening. The resulting species order of frost resistance to winter frosts was (from greatest to least): E. gunnii > E. coccifera > E. urnigera > E. johnstonii > E. delegatensis > E. pulchella; which was similar to that obtained for natural stands. The more extensive damage inflicted on seedlings by mild growing season frosts suggests that the prevalence of growing season frosts may play an important role in determining the distribution of subalpine eucalypts.

Further, evidence from both field transplant trials and frost chamber trials indicated that the changes in relative species order of frost resistance for spring and winter frost were related to differences in the species requirement for hardening. Generally the Monocalyptus species E. delegatensis, E. coccifera and E. pulchella had a greater requirement for hardening than the Symphyomyrtus species E. gunnii, E. urnigera and E. johnstonii and this may be one factor involved in the absence of Monocalyptus species from the base of the depression at Snug Plains. However, differences also existed within each subgenus. In the field transplant trials E. johnstonii was more resistant to spring frosts than E. urnigera, which agrees with the natural distribution of these species, although the reverse occurred for winter frosts. This suggests that the prevalence of spring frosts may be an important factor in the relative positions of these two species. E. johnstonii naturally occupies the margins of the depression where growing season frosts are common, while E. urnigera forms stands on the ridge slopes. Also, in subgenus Monocalyptus, E. delegatensis showed greater resistance to winter frosts than E. pulchella, yet the reverse was the case for spring frosts. This also agrees with the natural distribution of these species. E. pulchella is predominantly a lowland, coastal species and is unlikely to be exposed to the selective pressures which may induce the development of frost hardening. However, the inherent drought resistance of E. pulchella may preadapt the species to resist spring frosts. Alternatively, introgression of E. coccifera genes may account for the higher than expected frost resistance exhibited by E. pulchella in spring frosts. On the other hand, E. delegatensis which naturally inhabits a more continental and subalpine environment, was shown to occupy sites at Snug Plains where long hardening periods prevail in winter.

Field transplant trials and frost chamber trials also demonstrated that the Monocalyptus species were more prone to frost in waterlogged soils, a characteristic not observed for the Symphyomyrtus. The low tolerance of the Monocalyptus species to frost in waterlogged soils may be an important factor in the absence of Monocalyptus species from the depressions at Snug Plains. Even the most frost resistant Monocalyptus species tested, E. coccifera, generally occupies well drained rises within, or on the margins of the depression, while the other species from this subgenus were dominant on well drained to dry soils away from the depression. In comparison, Symphyomyrtus species were invariably dominant in the periodically waterlogged and frost prone sites in the study area.

### Waterlogging

Investigations of the moisture status of field soils at the study area demonstrated that the natural distribution of the Monocalyptus species coincided with well drained and dry soils whereas the Symphyomyrtus species and mixed stands of the two subgenera were present on soils which may be prone to waterlogging. Further, seedlings grown in waterlogged conditions, both in the field transplant trials and in glasshouse trials, demonstrated marked interspecific differences in waterlogging tolerance. The Symphyomyrtus species rapidly developed morphological adaptations to the waterlogged environment which included aerenchymatous, adventitious root systems, stem hypertrophy and leaf epinasty. In comparison, the Monocalyptus species exhibited leaf abscission and root atrophy but no morphological adaptations to the waterlogged conditions. A study of the water relations of seedlings in glasshouse trials one month after waterlogging was commenced, indicated marked differences in stomatal conductance and water potential existed between pairs of seedlings from different subgenera. The Monocalyptus species, E. delegatensis and E. coccifera, showed signs of severe water stress exhibiting lower stomatal conductances and water potentials than the Symphyomyrtus species, E. johnstonii and E. urnigera, throughout the day. However, differences also existed between the two Symphyomyrtus species which suggested E. johnstonii was more waterlogging tolerant than E. urnigera. After 8 months in the waterlogged treatment all Monocalyptus seedlings had died while Symphyomyrtus seedlings were exhibiting moderate growth. Therefore, tolerance to waterlogging may be a major influence on the distributions of subalpine eucalypts.

Field studies conducted at Snug Plains indicated that the soil moisture status of mixed stands (containing one species from each subgenus) tended to be intermediate between those of the pure Monocalyptus and pure Symphyomyrtus stands. Seasonal fluctuations in soil moisture status, from waterlogged in winter to dry in summer, may be an important factor in the maintenance of mixed stands containing species from different subgenera, particularly considering the subgenera differ in their tolerance of, and morphological adaptations to waterlogging and drought.

### Drought

During the 1982-83 summer the study area at Snug Plains and the whole of south-eastern Tasmania was experiencing an exceptional drought, the severity



of which probably only occurs once every 50 to 100 years. A transect of soil pits dug across a low ridge indicated that steep gradients in soil characteristics existed between the ridge top and lower ridge slopes. Ridge top soils were shallow, stony and had a very low moisture holding capacity, while the lower ridge slopes soils were deep and had large moisture reserves. During the drought the water potentials of ridge top soils fell to  $-4.5$  MPa whereas soils on the lower ridge slopes were buffered by the moderate water potentials of lower soil horizons. The natural distribution of eucalypts on the ridge were related to these changes in soil properties, which suggested occasional drought might be an important factor involved in the changes in eucalypt dominance.

Dawn to dusk measurements of stomatal conductance and water potential made in a mixed ridge top stand comprised of the three Monocalyptus species, showed only minor interspecific differences occurred before the drought broke, even though water potentials fell to  $-4.3$  MPa. During this period it was demonstrated that leaf water potentials reflected soil water potentials; maximum stomatal conductance declined in response to falling dawn water potentials; and restrictions in stomatal conductance during the day corresponded to peaks in vapour pressure deficit (V.P.D.). However, at the height of the drought marked interspecific differences in R.W.C. existed, which indicated that E. pulchella maintained higher R.W.C. (61%) than either E. coccifera (55%) or E. delegatensis (48%) at the low water potentials recorded. E. pulchella also exhibited less crown damage than the other two species during drought and, after the first effective rains, demonstrated: more rapid restoration of high water potentials and high R.W.Cs; more rapid return to normal diurnal fluctuations in stomatal conductance and water potential; and an earlier recommencement of shoot extension than other species. E. pulchella also exhibited anatomical and morphological features which were an adaptive advantage during drought. E. pulchella had small linear leaves which would remain cooler and transpire less rapidly than large leaves during drought. Further, on the occasions that E. pulchella trees were defoliated by drought, regeneration of the crown occurred via epicormic buds at the branch tips; whereas stems of the other species, which were not killed by defoliation, regenerated via epicormic buds on the stem and larger branches. This resulted in marked dominance changes within severely drought affected stands. It was concluded that the superior drought resistance of E. pulchella was probably the primary reason for its presence on the ridge top sites at Snug Plains. In comparison E. coccifera was less drought resistant, and E. delegatensis exhibited low resistance to drought. Therefore, occasional severe droughts may

have a major influence on the eventual dominance patterns in the regenerating mixed stands on the ridge crest, and may be an important factor in determining the positions of boundaries between stands of the three Monocalyptus species on the ridge slopes at Snug Plains.

Studies of the root pattern of seedlings of the three Monocalyptus species grown in large tubular pots indicated that marked interspecific differences existed. E. delegatensis tended to develop a main tap root with few lateral branches, while E. pulchella produced a finely branched root system. The root system of E. coccifera was intermediate between the above two forms. However, field investigations of the topography of the bedrock beneath a ridge top stand of these three species (stand I) indicated that the roots of all species were probably confined to the same shallow soils. This suggested that interspecific differences in drought resistance demonstrated for the three Monocalyptus species at stand I were probably not a function of differences in the root distribution.

Competition trials conducted in restricted soils and involving seedlings of the three Monocalyptus species (two species per pot) produced the same species order of drought resistance as was found in field trials, supporting the contention that differences in root distribution was not a major cause of interspecific differences in drought resistance. The competition trials also demonstrated that greater interspecific differences in drought resistance were elicited under conditions of strong winds of high vapour pressure deficit (3.6 KPa) than winds of moderate V.P.D. (0.8 KPa), which suggests desiccating winds may be an important synergistic factor during droughts.

Preliminary drought trials conducted on potted seedlings indicated marked interspecific differences in drought resistance existed between the six species present at Snug Plains. Comparisons of water relations characteristics which included; maintenance of high relative water content (R.W.C.) at low water potential (-2.0 MPa), R.W.C. at time of wilting and soil moisture status at the time of wilting, provided a species order of drought resistance which was (from greatest to least) E. pulchella > E. coccifera > E. urnigera > E. delegatensis > E. johnstonii > E. gunnii. The generally low drought resistance of the Symphyomyrtus species in these experiments may explain their absence from the ridge top sites at Snug Plains, and agrees with their natural distribution in the field.

### Insect Attack

On the margins of the depression at Snug Plains insect depredation caused severe damage to seedlings in two field transplant trials. The phytophagous insect attack was selective, causing severe damage to E. gunnii, less damage to the other Symphyomyrtus species, but only minor damage to the Monocalyptus species. Therefore, selective insect grazing may have an important effect on dominance patterns in regenerating mixed stands at Snug Plains, selecting against the Symphyomyrtus species and in particular E. gunnii.

### Subgeneric Differences

Pryor (1953, 1959a, 1959b) suggested that the pattern of eucalypt distributions in the forests of south-eastern Australia were governed by two rules: (1) interbreeding eucalypt species (from the same subgenus) form separate circumscribed stands each occupying distinct ecological situations; and (2) mixed species stands of eucalypts are comprised of species which are genetically isolated (from different subgenera). However, subsequent research has raised some doubts about the general applicability of these rules in eastern Australian forests (Austin et al. 1983; Kirkpatrick 1981; Florence 1981; Rogers & Westman 1979; Morrow 1977; Gill & Ashton 1971; Parsons & Rowan 1968; Ridley 1961).

At Snug Plains the distributions of the six eucalypt species studied generally agreed with Pryor's rules, particularly when the modifications suggested by Florence (1981) are also considered.

Evidence from the fruit and floral anatomy of eucalypts, and their present geographic distributions, suggests that the major eucalypt alliances have followed separate evolutionary paths since the Tertiary (Pryor & Johnson 1981; Johnson & Briggs 1981). Further it has been proposed that the different ecological positions occupied by Symphyomyrtus and Monocalyptus and their co-occurrence in mixed stands may relate to the different ecological tolerances of the subgenera (Pryor & Johnson 1981; Florence 1981, 1982), but differences at the subgeneric level have not been demonstrated experimentally.

The current study demonstrates marked interspecific differences in ecological tolerance of the subgenera Symphyomyrtus and Monocalyptus:

1. Symphyomyrtus species exhibited the ability to rapidly develop morphological adaptations to waterlogged conditions, which included aerenchymatous, adventitious root systems; stem hypertrophy; and leaf epinasty, while the Monocalyptus species showed no such adaptations and rapidly succumbed to waterlogged treatments. These were matched by marked physiological differences between the subgenera during waterlogging trials. The Monocalyptus species showed signs of severe water stress and exhibited lower stomatal conductances and water potentials than Symphyomyrtus species.
2. In frost trials Monocalyptus species exhibited a greater requirement for "hardening" than Symphyomyrtus species.
3. Monocalyptus species exhibited reduced frost resistance in waterlogged soils, a characteristic not evident for the Symphyomyrtus species.
4. In preliminary drought trials Monocalyptus species were more drought resistant, maintaining higher R.W.C. at low water potentials than Symphyomyrtus species.

These differences in the ecological and physiological characteristics exhibited by the subgenera help to explain some of the trends in eastern Australian eucalypt forests outlined by Florence (1981) which include; topographic replacement of Monocalyptus species by Symphyomyrtus species; and complete replacement of Monocalyptus species by Symphyomyrtus species in specialised sites, such as poorly aerated soils. Further, differences in the ecological niche occupied by the Monocalyptus and Symphyomyrtus species, conferred by differences in ecological tolerance, may allow co-occurrence of two eucalypt species from different subgenera without direct competition for a resource.

Apparent contradictions between the statements by Florence (1981) and the studies at Snug Plains with respect to the relative drought resistance of Monocalyptus and Symphyomyrtus species may be associated with the restricted range of species present in Tasmania. The Tasmanian Symphyomyrtus species all belong to section Maidenaria; the distribution of which is restricted to cool moist regions of south-eastern Australia and only extends to low elevations in Tasmania (Pryor & Johnson 1981; Florence 1981). Other sections within Symphyomyrtus have a much greater ecological amplitude (Pryor & Johnson 1981; Florence 1981) and include species more drought resistant than the Monocalyptus species (e.g. Sinclair 1980).

## Hybrids

Another characteristic of eastern Australian eucalypt forest is the presence of hybrid individuals at the boundaries between potentially interbreeding species (Pryor 1953, 1959a, 1959b; Potts & Reid 1983, 1985c). Investigations of species boundaries at Snug Plains indicated that hybrids were rare at most stand boundaries. However, at the boundary between the E. pulchella and E. coccifera stands at the study area individuals of intermediate morphology were located. Morphometric studies of the Snug Plains populations of E. pulchella, E. coccifera and E. delegatensis and a lowland population of E. pulchella demonstrated that the Snug Plains E. pulchella population was a "phantom" hybrid population with E. coccifera and E. pulchella as the putative parents. This suggests that introgression of E. coccifera genes may have placed hybrid individuals at an adaptive advantage in comparison with the lowland E. pulchella phenotypes in the frost prone environment of Snug Plains.

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APPENDIX 3.1

HEIGHT, LEAF AREA AND STEM BASAL AREA RECORDS

### APPENDIX 3.1. HEIGHT, LEAF AREA AND STEM BASAL AREA RECORDS

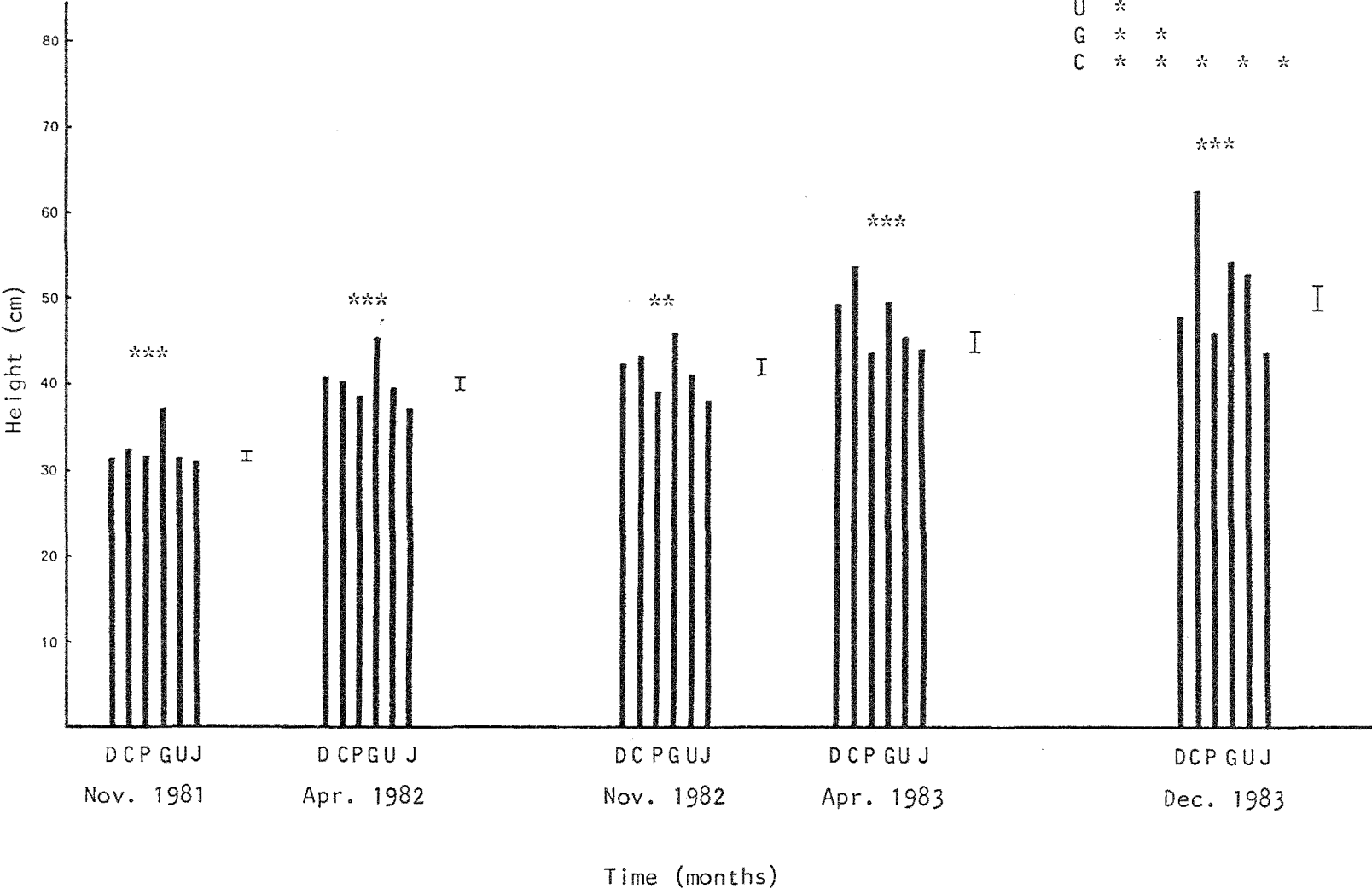
Mean height, leaf area, and stem basal area for seedlings at the six field transplant trials; gardens 1, 2, 3a, 3b, 4 and 5, planted at Snug Plains in October 1981 (3b was a replanted plot completed in November 1981). The six species planted: E. delegatensis (d), E. coccifera (c), E. pulchella (d), E. gunnii (g), E. urnigera (u) and E. johnstonii (j) were measured on five occasions: November 1981, April 1982, November 1982, April 1983 and December 1983. The maximum species standard error and significance level from the analyses of variance (not significant [NS];  $P < 0.05$  [\*];  $P < 0.01$  [\*\*] and  $P < 0.001$  [\*\*\*]) are shown for each measurement time. Bartlett's multiple range test shows groups which differ significantly ( $P < 0.05$ ) for the December 1983 measurements.

Appendix 3.1

Garden 1: Seedling height

Bartlett's Test

|   |   |   |   |   |   |   |
|---|---|---|---|---|---|---|
|   | J | P | D | U | G | C |
| J |   |   |   |   |   |   |
| P |   |   |   |   |   |   |
| D |   |   |   |   |   |   |
| U | * |   |   |   |   |   |
| G | * | * |   |   |   |   |
| C | * | * | * | * | * |   |

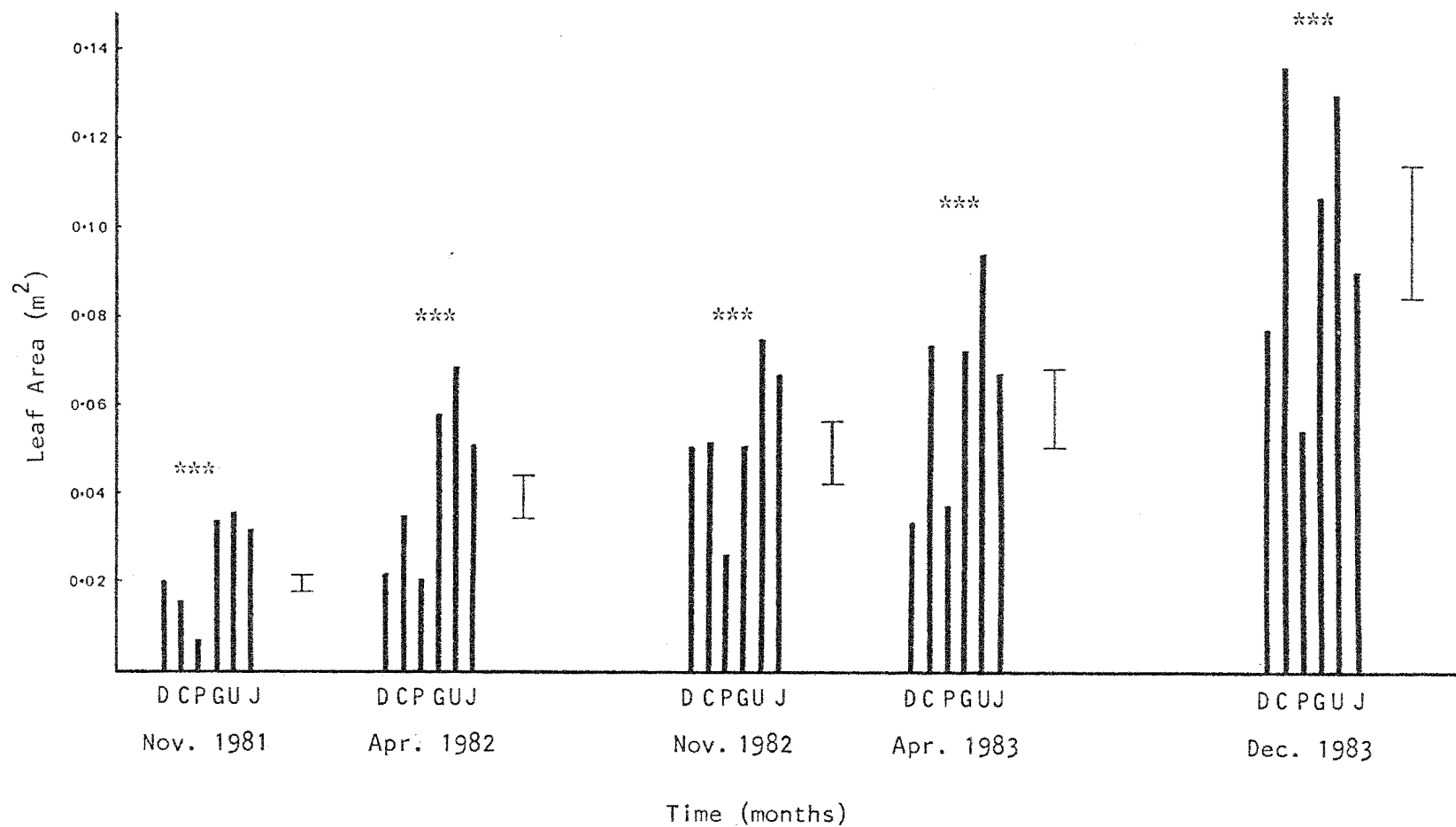


# Appendix 3.1 (cont'd)

Garden 1: Leaf Area

Bartlett's Test

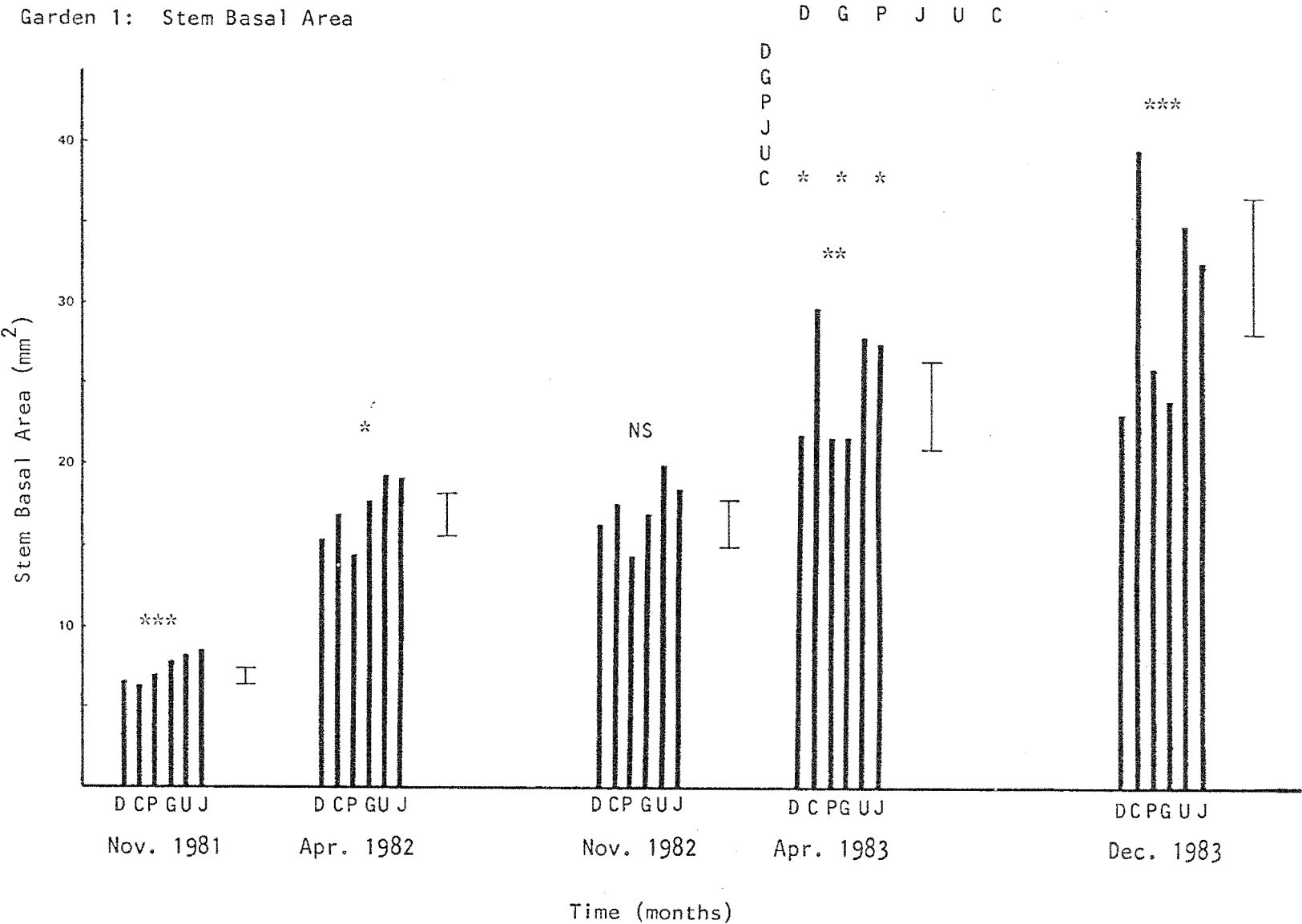
|   | P | D | J | G | U | C |
|---|---|---|---|---|---|---|
| P |   |   |   |   |   |   |
| D |   |   |   |   |   |   |
| J | * |   |   |   |   |   |
| G | * |   |   |   |   |   |
| U | * | * | * |   |   |   |
| C | * | * | * |   |   |   |



Appendix 3.1 (cont'd)

Garden 1: Stem Basal Area

Bartlett's Test

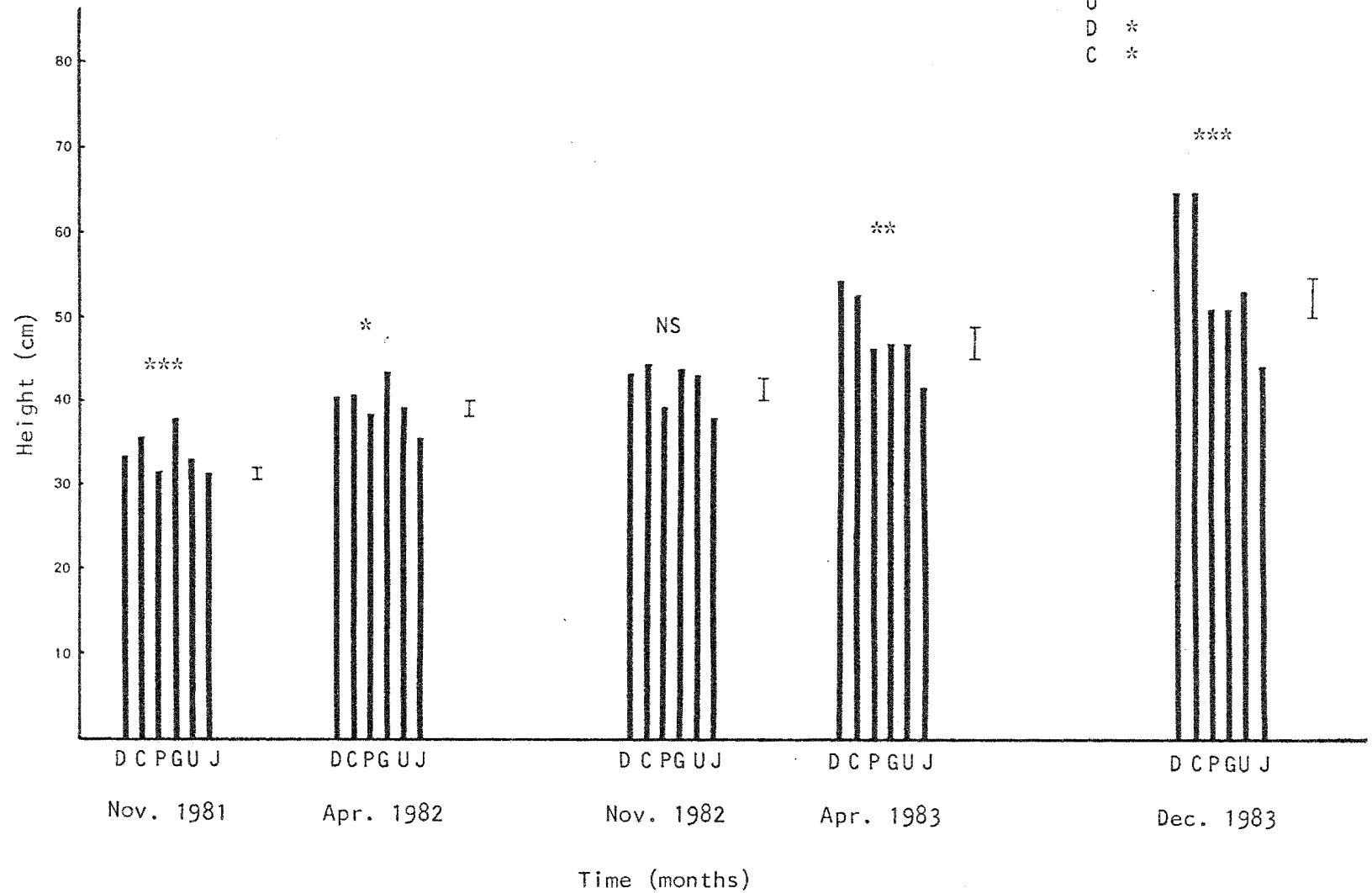


Appendix 3.1 (cont'd)

Garden 2: Seedling Height

Bartlett's Test

|   | J | P | G | U | D | C |
|---|---|---|---|---|---|---|
| J |   |   |   |   |   |   |
| P |   |   |   |   |   |   |
| G |   |   |   |   |   |   |
| U |   |   |   |   |   |   |
| D | * |   |   |   |   |   |
| C | * |   |   |   |   |   |

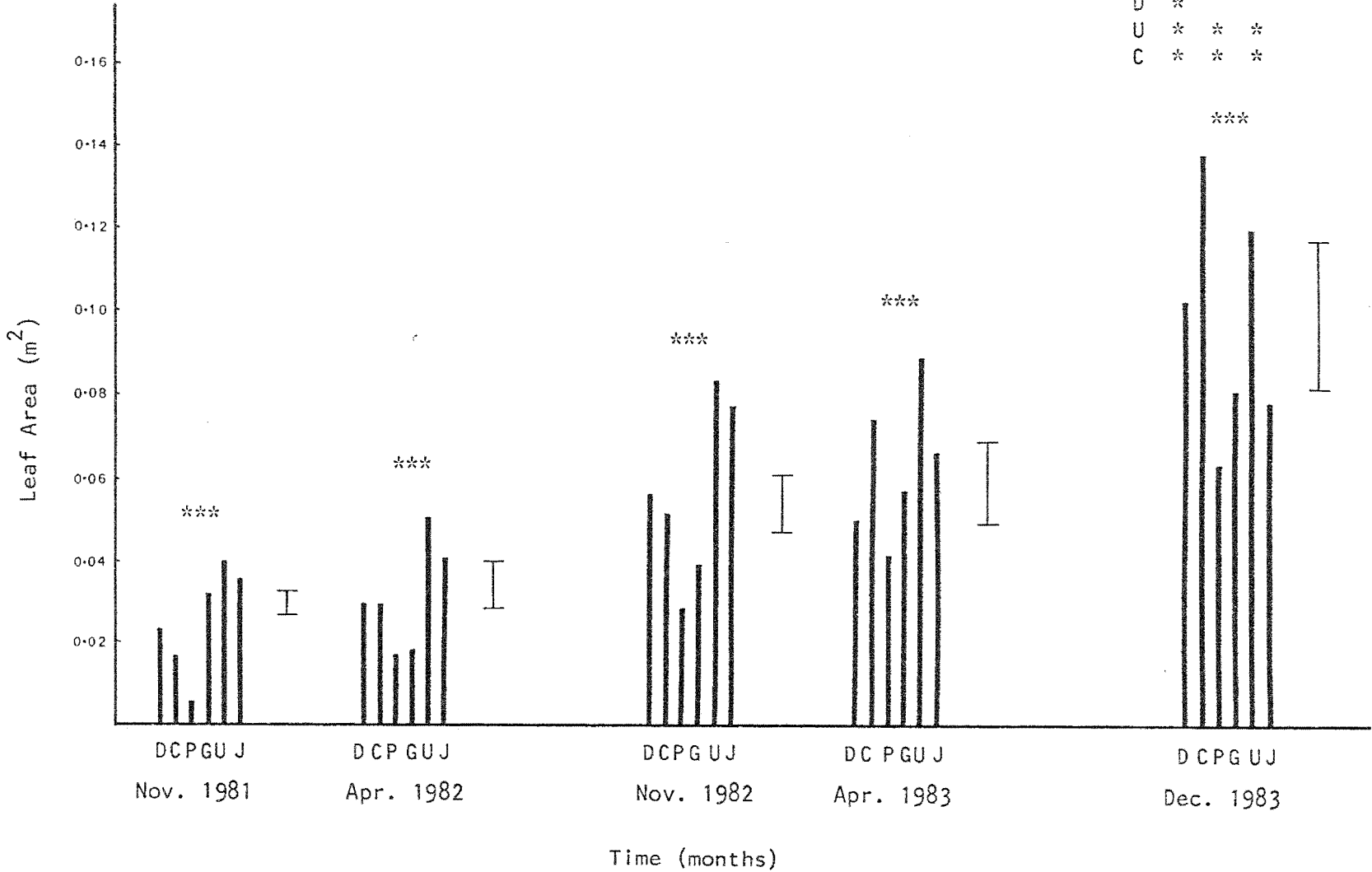


Appendix 3.1 (cont'd)

Garden 2: Leaf Area

Bartlett's Test

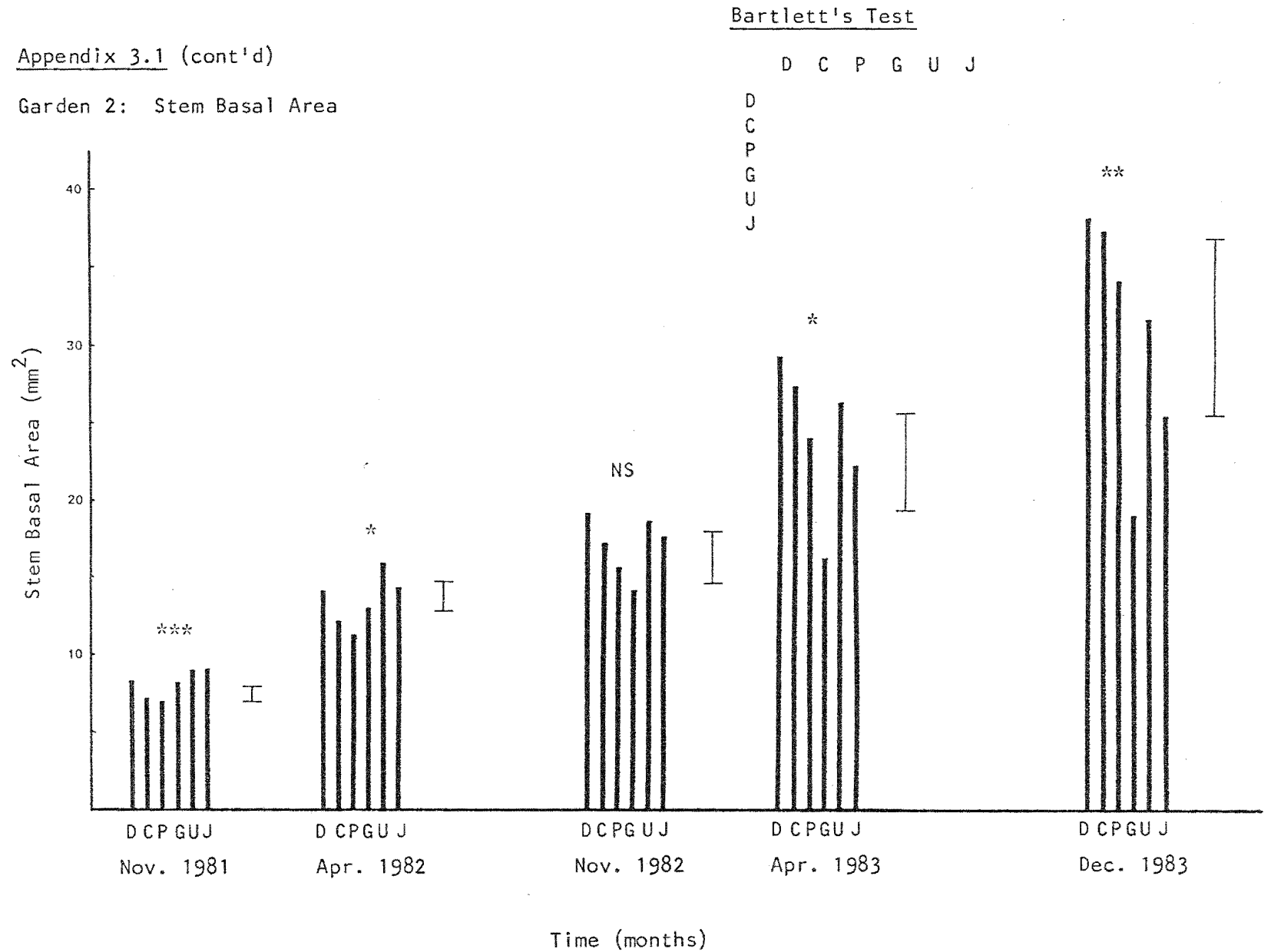
|   | P | J | G | D | U | C |
|---|---|---|---|---|---|---|
| P |   |   |   |   |   |   |
| J |   |   |   |   |   |   |
| G |   |   |   |   |   |   |
| D | * |   |   |   |   |   |
| U | * | * | * |   |   |   |
| C | * | * | * |   |   |   |





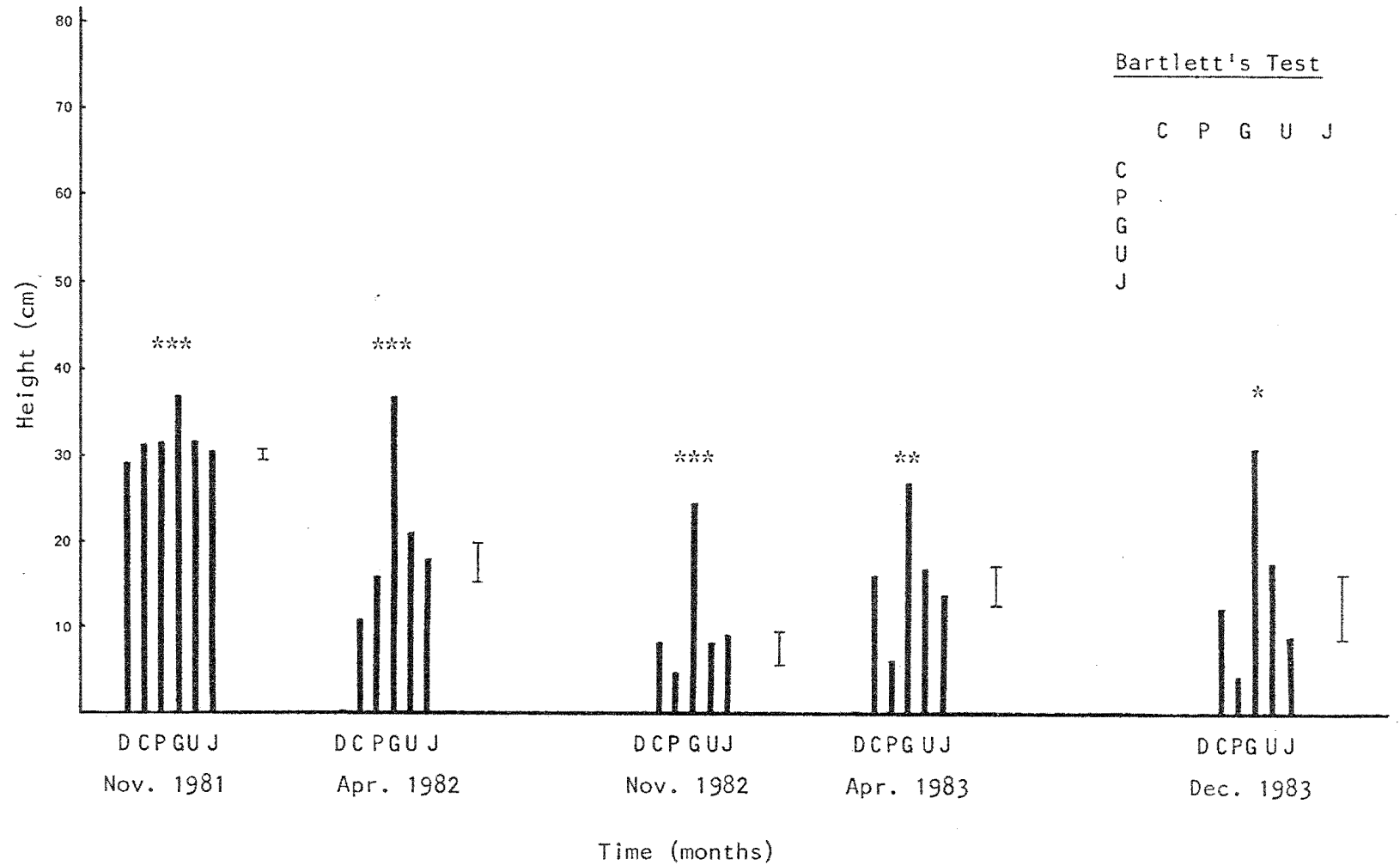
Appendix 3.1 (cont'd)

Garden 2: Stem Basal Area



Appendix 3.1 (cont'd)

Garden 3a: Seedling Height



Appendix 3.1 (cont'd)

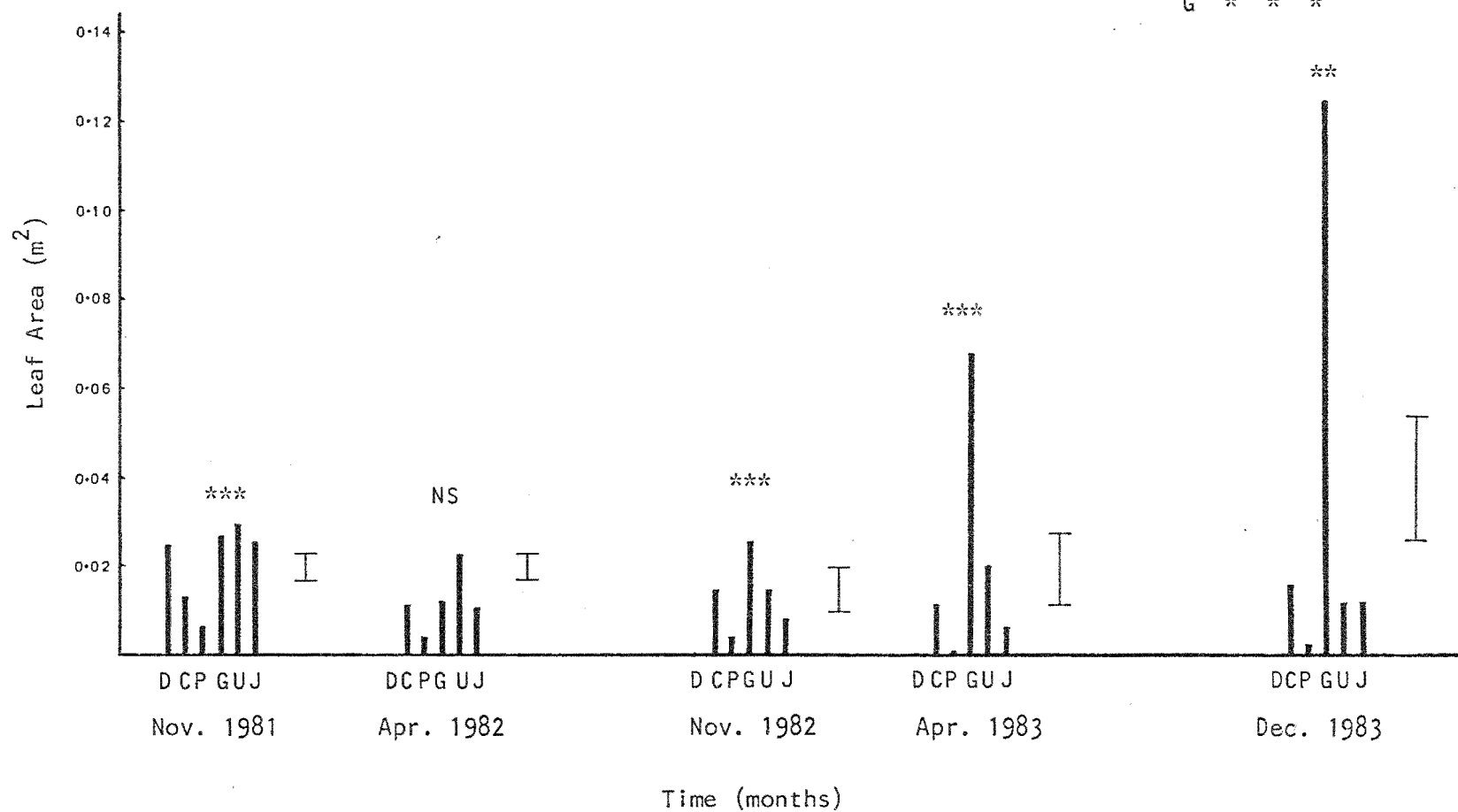
Garden 3a: Leaf Area

Bartlett's Test

P U J C G

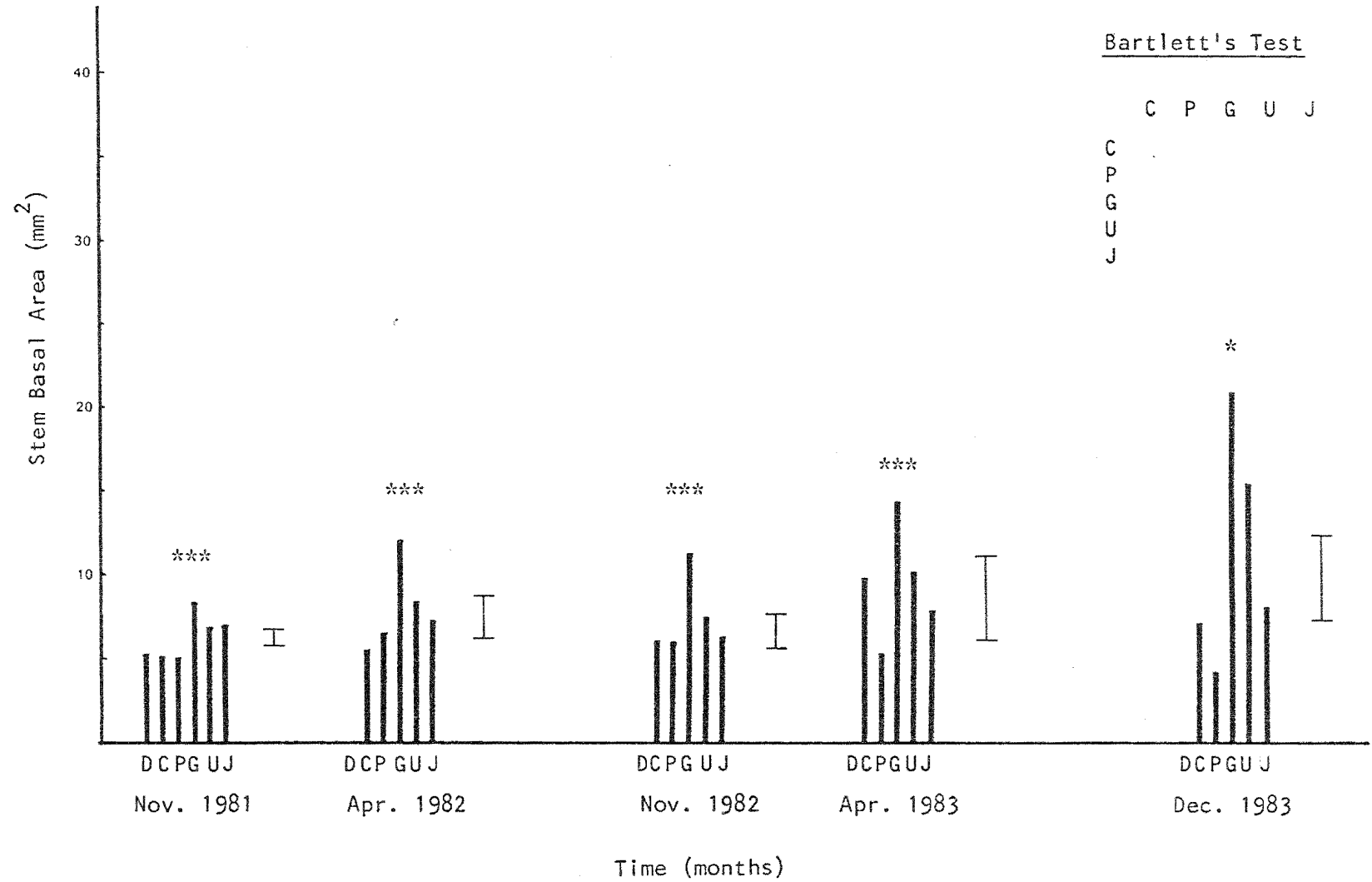
P  
U  
J  
C  
G

\* \* \*



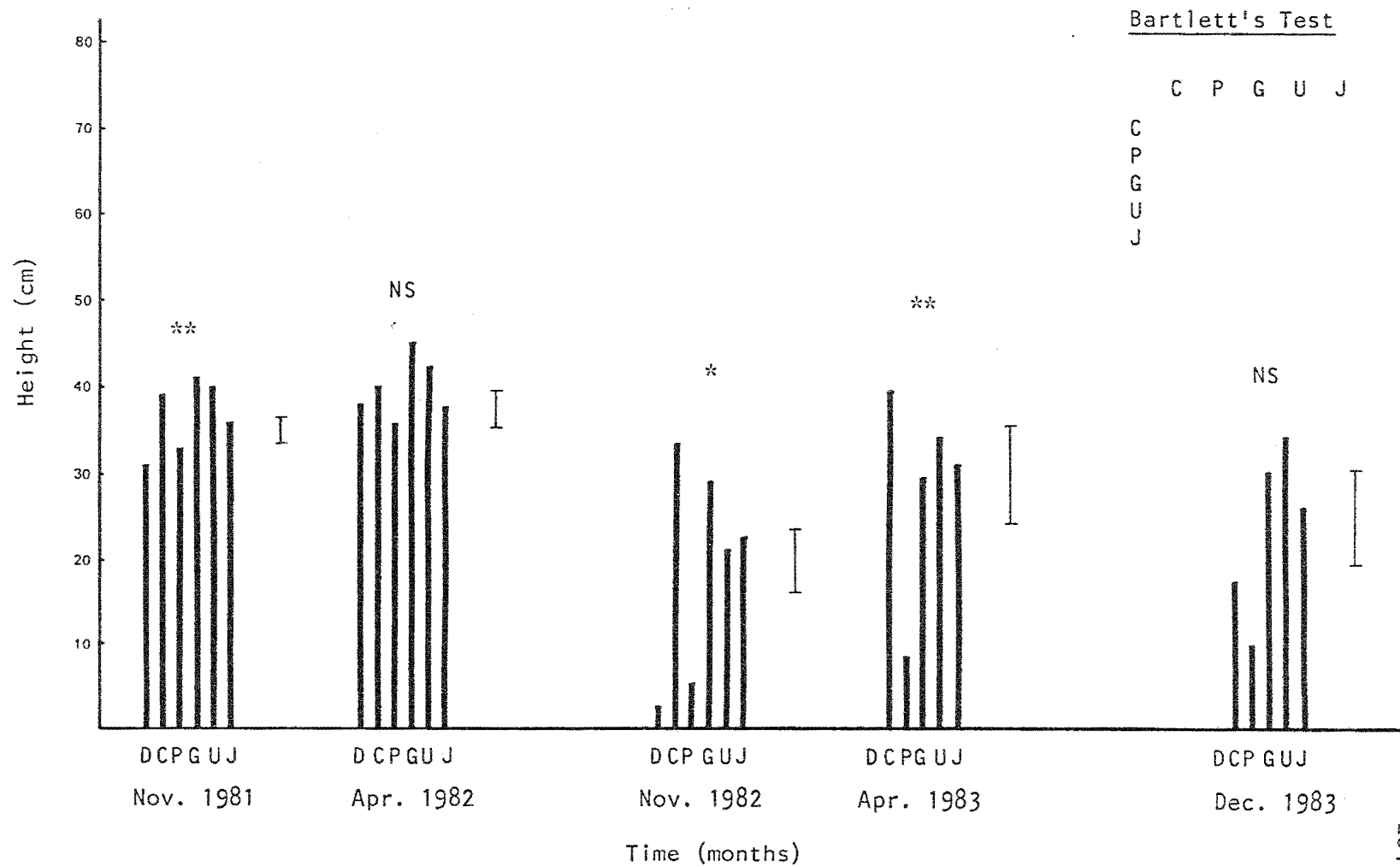
Appendix 3.1 (cont'd)

Garden 3a: Stem Basal Area



# Appendix 3.1 (cont'd)

## Garden 3b: Seedling Height

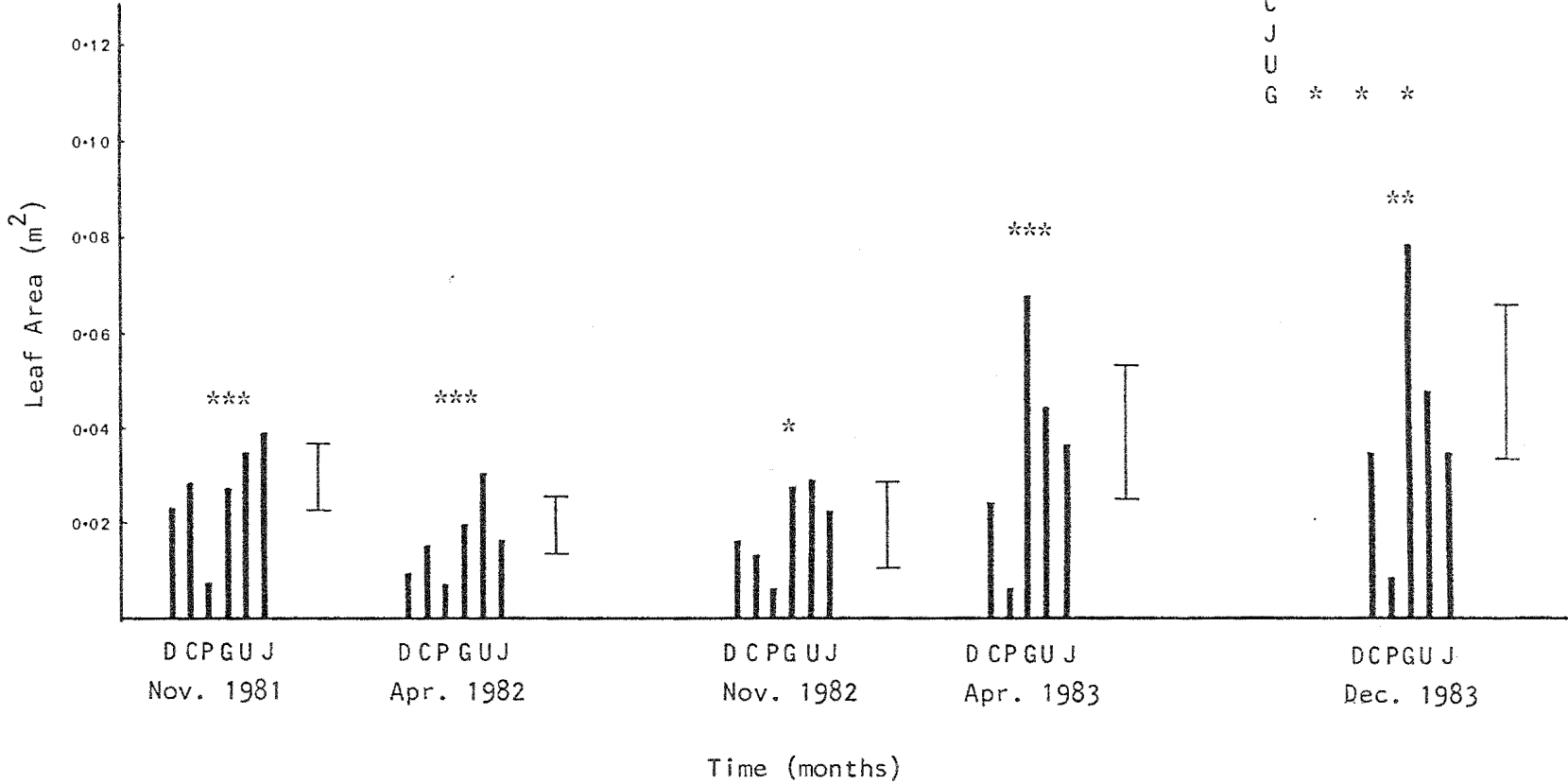


Appendix 3.1 (cont'd)

Garden 3b: Leaf Area

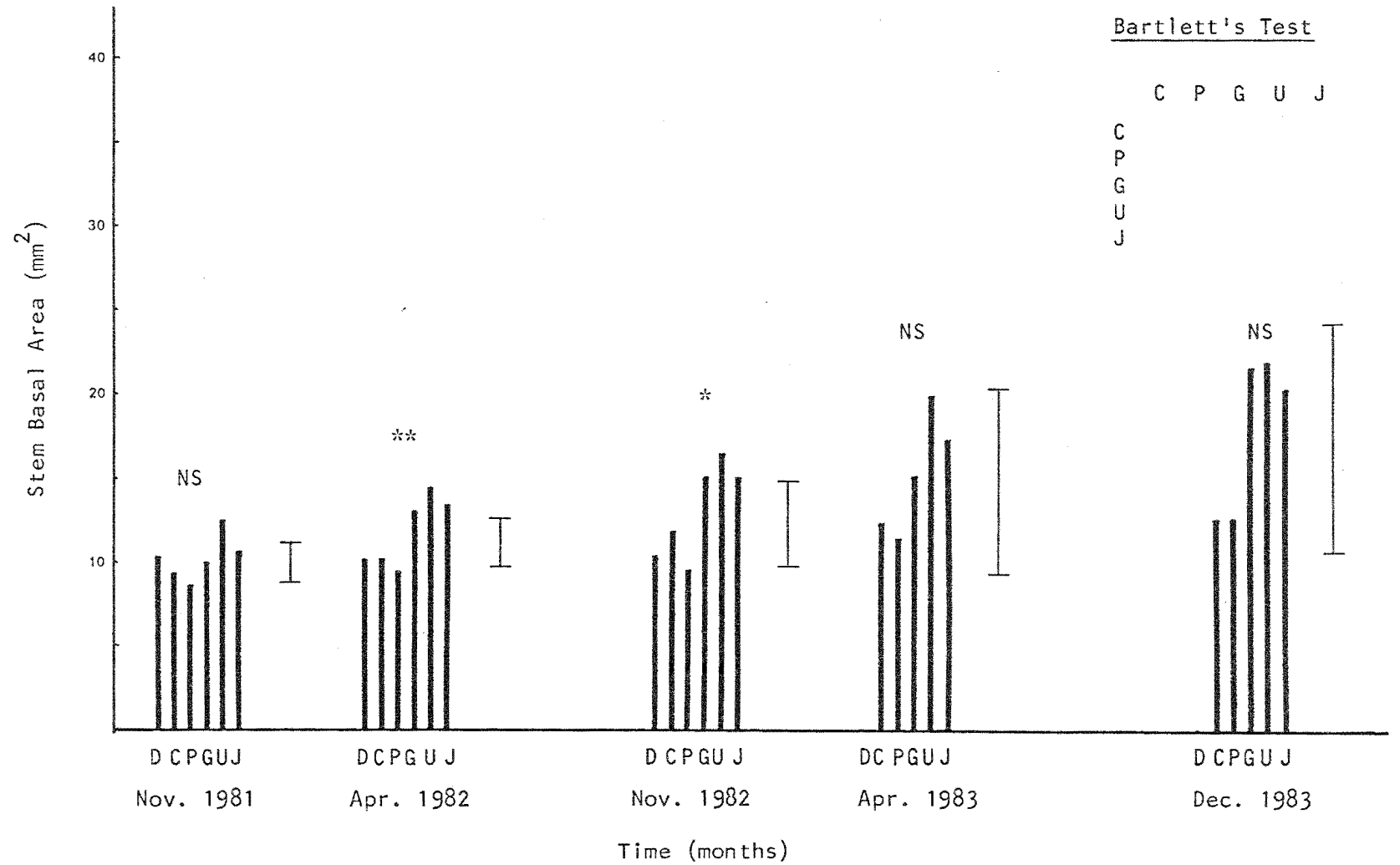
Bartlett's Test

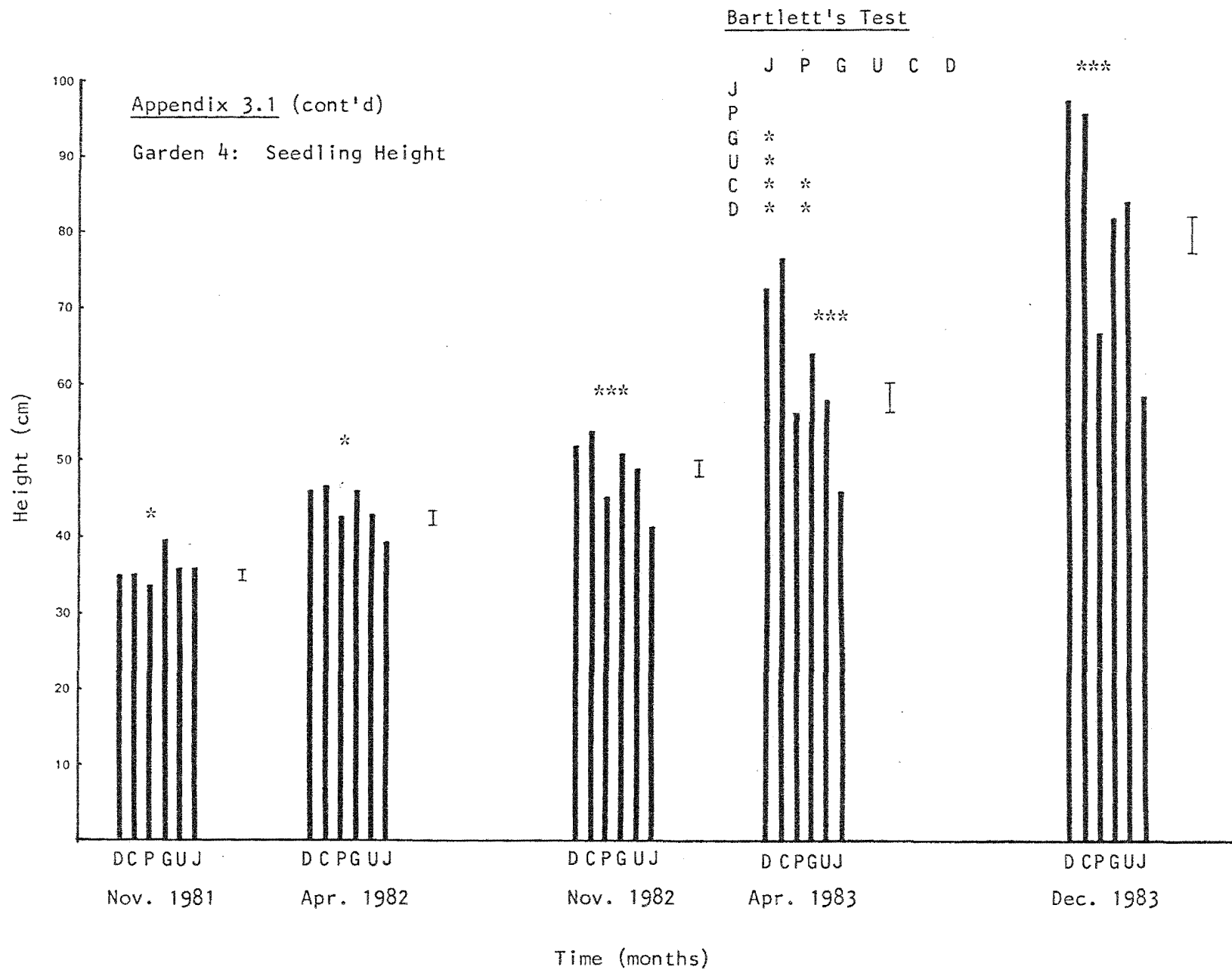
|   |   |   |   |   |   |
|---|---|---|---|---|---|
|   | P | C | J | U | G |
| P |   |   |   |   |   |
| C |   |   |   |   |   |
| J |   |   |   |   |   |
| U |   |   |   |   |   |
| G | * | * | * |   |   |



Appendix 3.1 (cont'd)

Garden 3b: Stem Basal Area





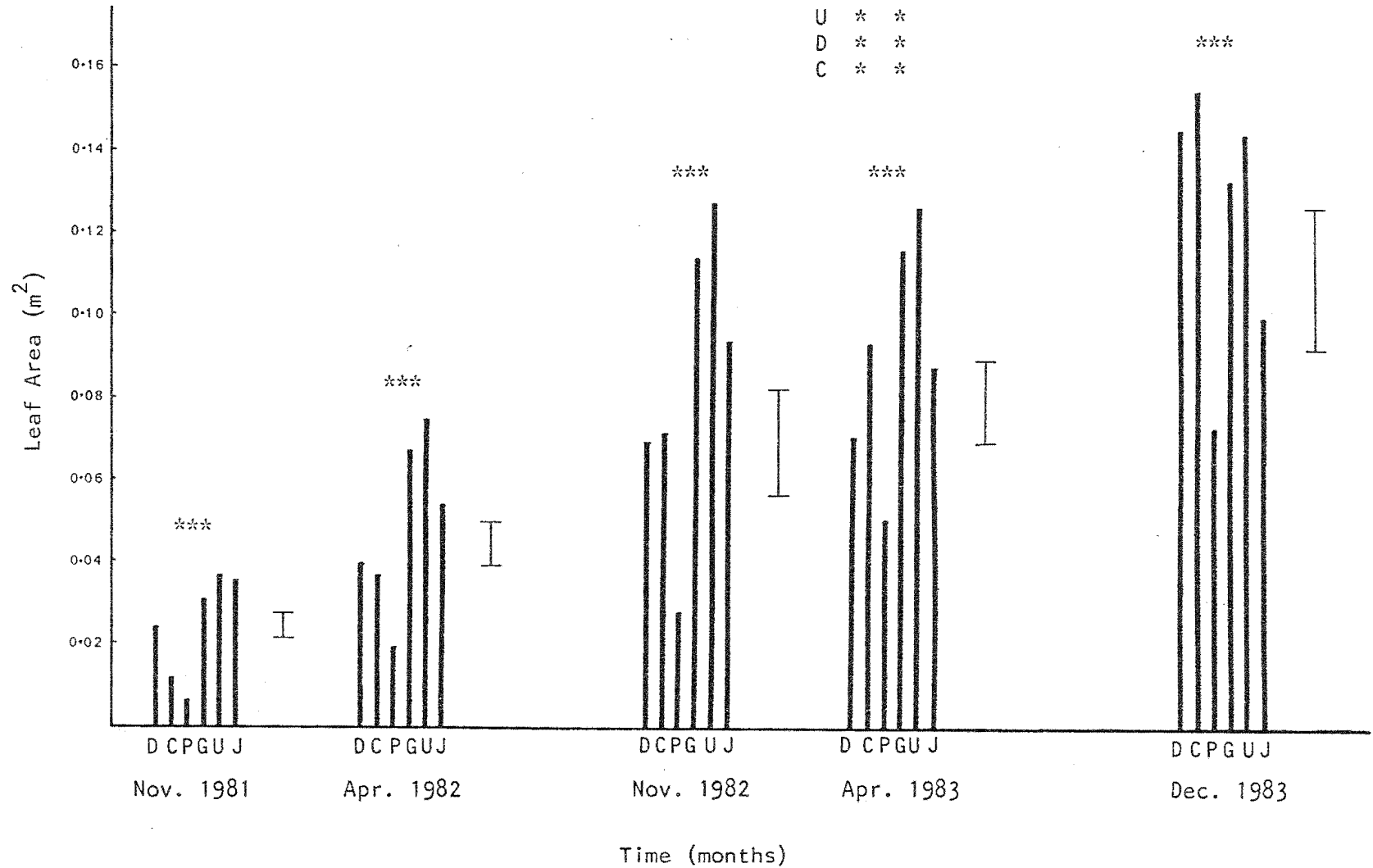


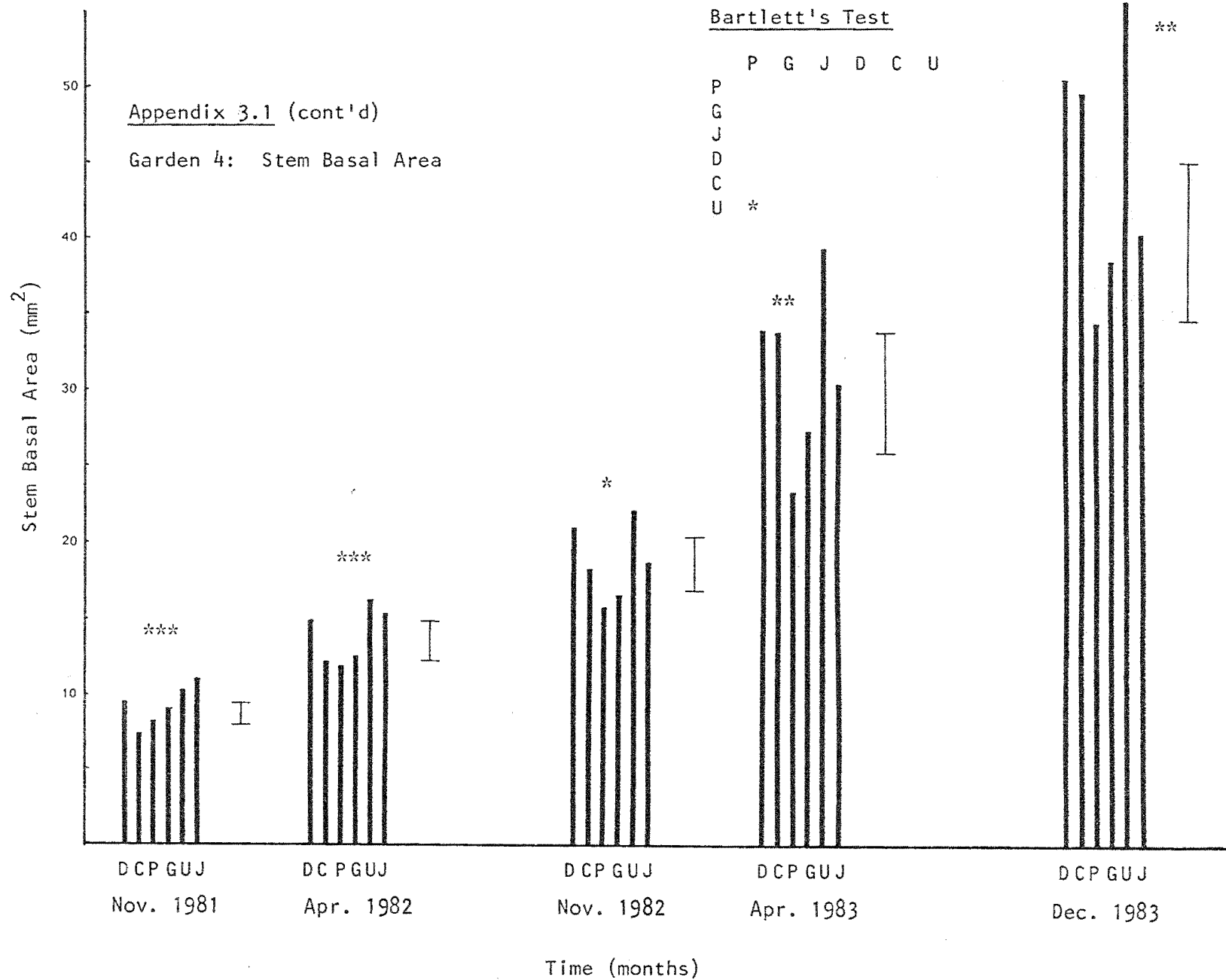
# Appendix 3.1 (cont'd)

Garden 4: Leaf Area

Bartlett's Test

|   | P | J | G | U | D | C |
|---|---|---|---|---|---|---|
| P |   |   |   |   |   |   |
| J |   |   |   |   |   |   |
| G | * |   |   |   |   |   |
| U | * | * |   |   |   |   |
| D | * | * |   |   |   |   |
| C | * | * |   |   |   |   |



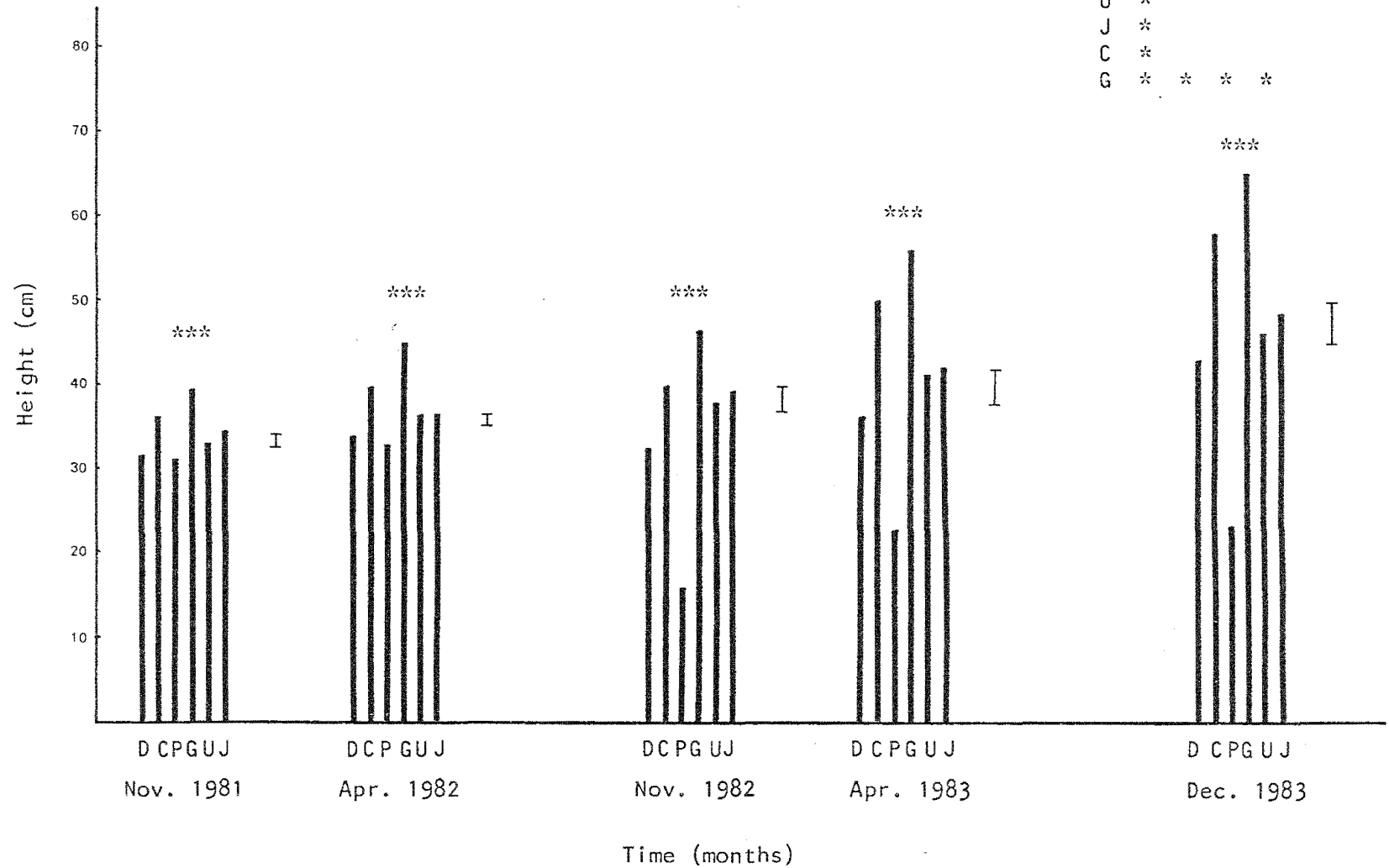


Appendix 3.1 (cont'd)

Garden 5: Seedling Height

Bartlett's Test

|   | P | D | U | J | C | G |
|---|---|---|---|---|---|---|
| P |   |   |   |   |   |   |
| D | * |   |   |   |   |   |
| U | * |   |   |   |   |   |
| J | * |   |   |   |   |   |
| C | * |   |   |   |   |   |
| G | * | * | * | * |   |   |

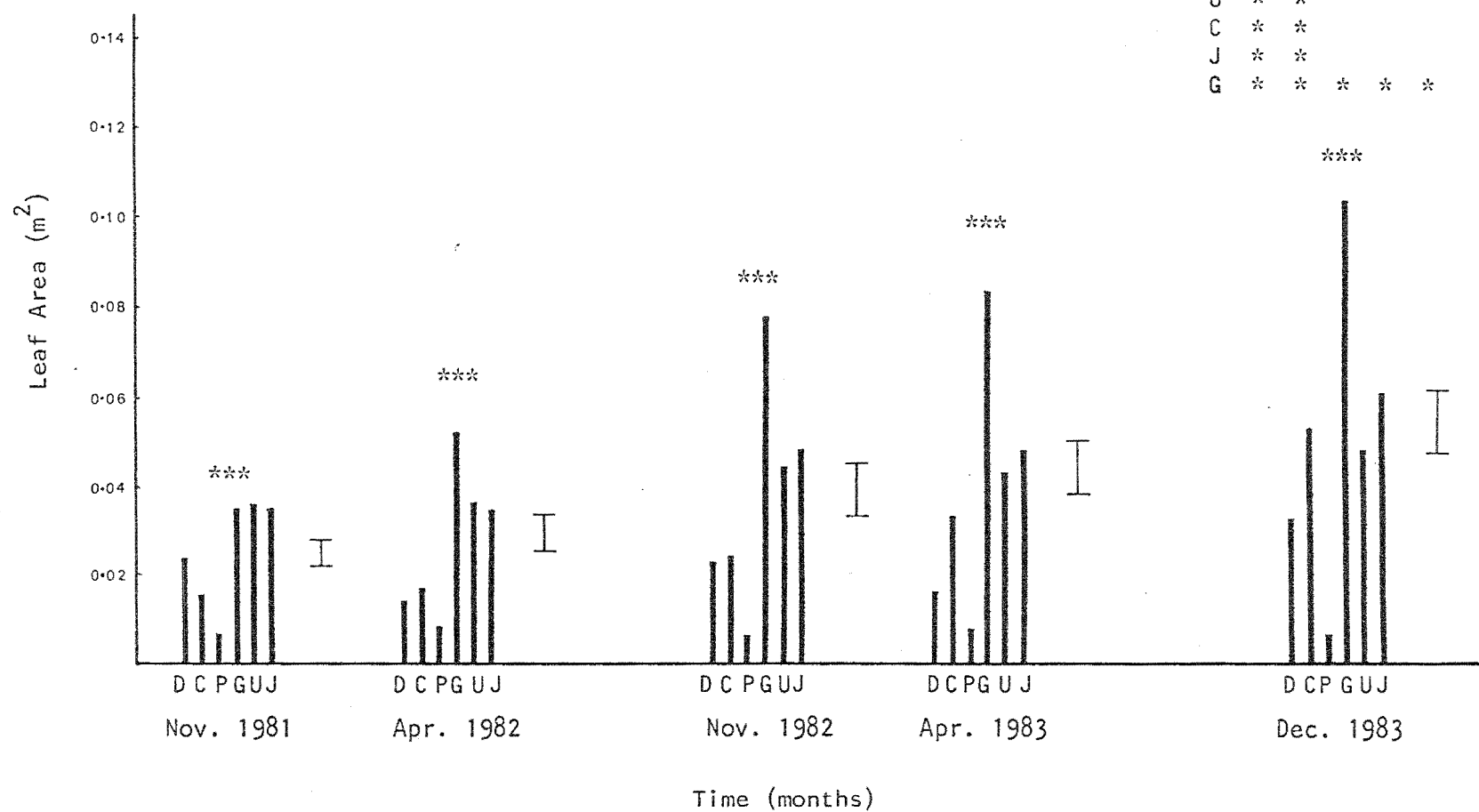


Appendix 3.1 (cont'd)

Garden 5: Leaf Area

Bartlett's Test

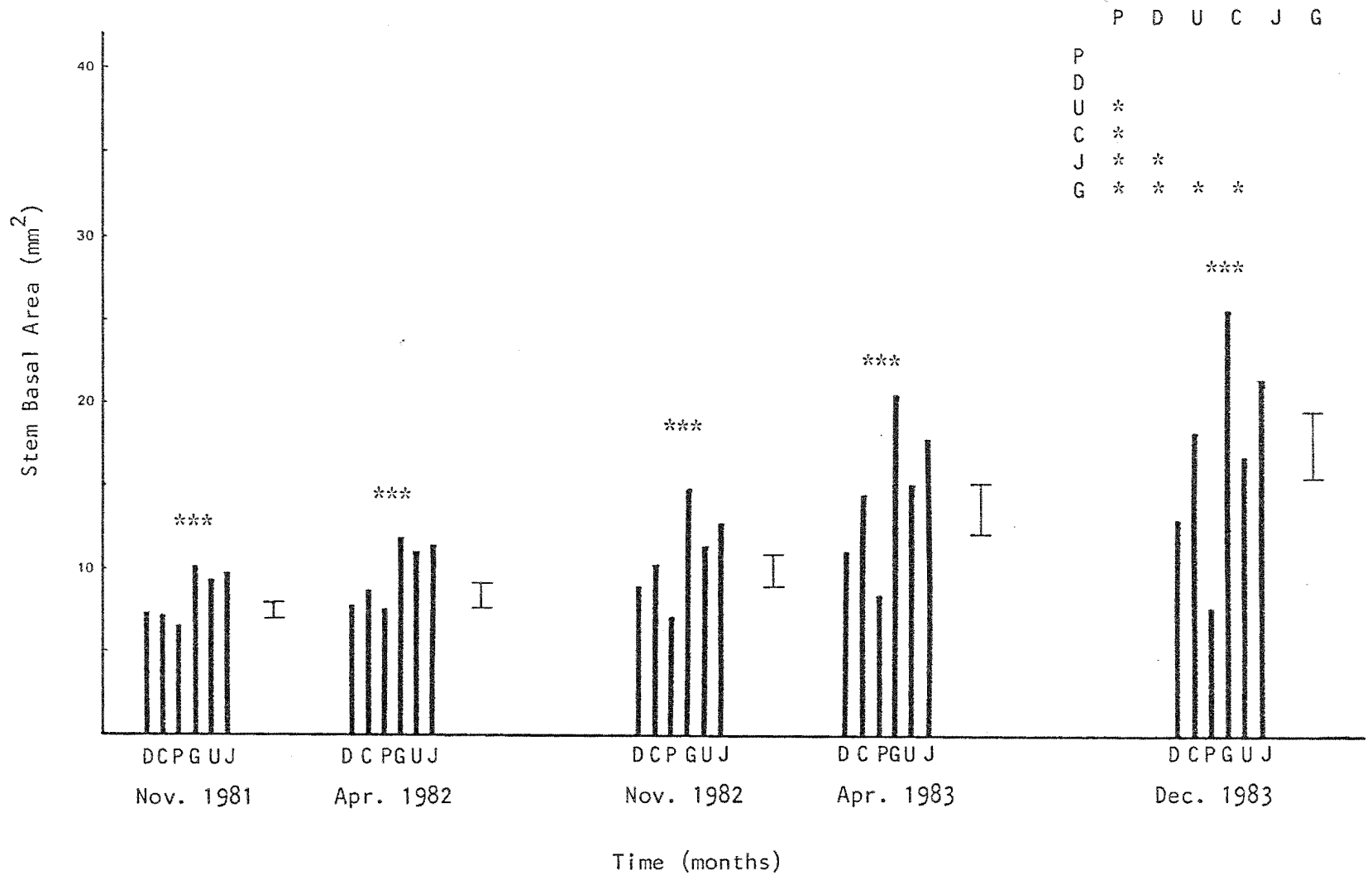
|   | P | D | U | C | J | G |
|---|---|---|---|---|---|---|
| P |   |   |   |   |   |   |
| D | * |   |   |   |   |   |
| U | * | * |   |   |   |   |
| C | * | * |   |   |   |   |
| J | * | * |   |   |   |   |
| G | * | * | * | * | * |   |



# Appendix 3.1 (cont'd)

Garden 5: Stem Basal Area

Bartlett's Test



## APPENDIX 4.1

LITERATURE REVIEW: FROST ACCLIMATION AND FREEZING INJURYINTRODUCTION

Some northern deciduous species, once fully acclimated by short days and light frosts, can survive temperatures below  $-100^{\circ}\text{C}$  (e.g. Populus deloides, Parsons 1978; Thuja occidentalis, White & Weiser 1964). In mid-winter the living bark of hardy species has been found to withstand cooling to  $-196^{\circ}\text{C}$  if the initial freezing rate to  $-30^{\circ}\text{C}$  is relatively slow (Sakai 1960; Weiser 1970). Minimum temperatures experienced in northern latitudes of North America are often below  $-40^{\circ}\text{C}$  (Burke et al. 1976) and may be as low as  $-87^{\circ}\text{C}$  (White & Weiser 1964). In Europe, winter minimum temperatures of  $-30^{\circ}\text{C}$  may occur (Linnard 1969), with an absolute minimum of  $-56^{\circ}\text{C}$  recorded (Geiger 1971). However, in the Southern Hemisphere very hardy tree species which will survive temperatures below  $-30^{\circ}\text{C}$  have not evolved (Sakai et al. 1981). This is probably a function of the mild oceanic winters characteristic of the Southern Hemisphere, and the barrier presented by the tropics preventing southward migration of hardy Northern genera (Sakai et al. 1981). The hardiest eucalypt species are reported to survive temperatures of  $-18^{\circ}\text{C}$  (Martin 1948; Sakai et al. 1981; Harwood 1980).

Although resistance to frost in Eucalyptus is poorly developed in comparison with Northern Hemisphere species, frost has been reported as a major factor determining the distributions of subalpine species of the genus (e.g. Costin 1954; Jackson 1973; Harwood 1983). Therefore an outline of the present knowledge of acclimation ("hardening") and freezing injury as it relates to Eucalyptus is pertinent to the current study.

(a) Acclimation

The development of frost hardiness (acclimation) in plants is partly a seasonal phenomenon. Even without a temperature pretreatment, some degree of frost hardiness can be conferred by cessation of growth (Fuchigami et al. 1971), differences in physiological age of plant tissue, and environmental stimuli other than temperature and photoperiod (Weiser 1970; Howell & Weiser 1970, Li & Palta 1978). However a period of short days and warm temperatures, followed by a period of low temperatures (near freezing) gives maximal acclimation to woody deciduous species (Weiser 1970).

For the hardy Northern Hemisphere deciduous trees and shrubs the process of acclimation can be divided into three stages (Weiser 1970). The first stage of acclimation involves cessation of growth (Irving & Lanphear 1967a) and production of a translocatable substance, produced in plant leaves, which promotes acclimation (Howell & Weiser 1970). This substance may be a hormone, possibly a growth inhibitor (Howell & Weiser 1970) or a sugar (Steponikus 1971). Acclimation will not occur if plants are severely depleted in photosynthate (Fuchigami *et al.* 1971; Irving & Lanphear 1967a, 1967b). In general, the first stage of acclimation is induced by short days and warm temperatures (Howell & Weiser 1970), although plants exposed to long days and frosts (or low temperatures) will develop some hardening but not beyond the first stage of acclimation (Fuchigami *et al.* 1971).

The second stage of acclimation is promoted by frosts or low temperatures (Weiser 1970). It is a metabolically active phase of physiological and biochemical adjustment. The cellular adjustments that have been shown to occur during the second stage of acclimation include a reduced hydration of the protoplast (Chen *et al.* 1977; Burke *et al.* 1976; Siminovitch & Cloutier 1982) produced by increasing root resistance or increased transpiration (Parsons 1978; McKenzie *et al.* 1974). Temperature sensitive cellular components assume more stable configurations (Olien 1969; Weiser 1970). The inhibition of intermolecular disulphide linkages between protein sulphydryl groups as the cell dehydrates, has been proposed (Levitt 1962). Sugars replace water in the protein hydration shells (Steponikus 1971). New peroxidase isoenzymes synthesised in autumn alter the protoplasm and unsaturated fatty acid components of the membrane (Weiser 1970). Quantitative changes in the synthesis of RNA (Oslund & Li 1972; Gusta & Weiser 1972) and many other components of the cell (Chen & Li 1977) have been shown to occur during the second stage of acclimation.

There also appears to be a third stage of acclimation in hardy woody species which is induced by very low temperatures, from  $-30^{\circ}\text{C}$  to  $-50^{\circ}\text{C}$  (Weiser 1970; Sakai 1960). It is suggested that this phase is a physical process associated either with the thermal motion of the macromolecules in the frozen cells or greater order in the quasi-crystalline structure in the cells (Weiser 1970).

The idealised model above, presented by Weiser (1970) for the hardy deciduous species of the Northern Hemisphere, is by no means generally applicable. Herbaceous plants, in general, cannot survive temperatures below  $-20^{\circ}\text{C}$  and do not require cessation of growth or short days to acclimate (Li & Pelta 1978). Hardiness in herbaceous plants is produced primarily by exposure to low temperatures. Hardiness in many plants may be increased by dehydration through water stress (Chen *et al.* 1977; Burke *et al.* 1976) or by near zero temperatures, without prior exposure to short days (Fuchigami *et al.* 1971). The ability of plants to acclimate in response to several environmental or endogenous stimuli may improve adaptability and enhance survival potential (Howell & Weiser 1970).

Acclimation for many hardy deciduous species requires four to six weeks of short days and low temperatures (Irving & Lanphear 1967a), and unseasonably warm temperatures are required for at least three days before dehardening starts (Horiuchi & Sakai 1978). However, limited dehardening due to warm conditions may occur over very short periods (Proebsting 1963). On clear winter days high levels of insolation may raise the unshaded portions of stem and branches above the minimum dehardening temperature (of  $15^{\circ}\text{C}$  for *Cryptomeria* spp, Horiuchi & Sakai 1978), despite low air temperatures, causing dehardening. In spring, dehardening is induced by long days and warm temperatures (Howell & Weiser 1970; Irving & Lanphear 1967a)

Soil moisture may also influence plant hardiness. Reduced water supply which causes dehydration or desiccation of tissue also confers a degree of frost hardiness (Chen *et al.* 1977; Siminovitch & Cloutier 1982; Burke *et al.* 1976). However, severe water stress may lead to less frost hardiness (Parsons & Li 1978). High soil moisture levels influence hardiness by affecting tissue hydration (Olien 1969; Burke *et al.* 1976) and soil temperature (Burke *et al.* 1976). The freezing of moist soil is buffered by the latent heat of fusion of large volumes of soil water (Burke *et al.* 1976) and by the high thermal conductivity of water in comparison to soil. When soil temperatures and air temperatures differ greatly during frosts, particularly if soil temperature is near zero (water unfrozen) both direct (Burdasor 1977 in Holubowicz 1978) and indirect (Salmon 1933 in Burke *et al.* 1976) injury to plants may be severe.

Acclimation in the genus *Eucalyptus* has more in common with the herbaceous plants of the Northern Hemisphere (Li & Pelta 1978) than with the hardy deciduous species described by Weiser (1970). Eucalypt species do show



photoperiodic responses (Eldridge 1968; Scurfield 1961; Paton 1978) but the temperature dependent photoperiodic responses observed in some species of Eucalyptus are very small in comparison with the sensitive photoperiodic responses observed in the hardy Northern Hemisphere species (Paton 1978). Eucalypts acclimate primarily in response to low temperature. The low temperature conditions required for acclimation appear to vary considerably. Harwood (1981) suggested that at temperatures below 9°C, slow plant growth rate and a genetic capacity to harden were the main criteria required for hardening. However, absence of active growth alone did not produce significant hardening (Harwood 1981). E. pauciflora leaves exposed to 9°C nights and day temperatures of 9°C to 18°C never harden below -5°C, whereas exposure to +4°C nights allows hardening to frosts of -14°C. Hardening could readily be reversed by high night temperatures (Harwood 1980, 1981, 1983).

In comparison, Paton (1980) showed that after two days pretreatment at 2°C, E. viminalis seedlings had hardened to -6.5°C frosts and, if successively exposed to -2.5°C then -6.5°C, would survive (with 50% frost damage) a frost of -14°C (on day 15). If hardening and dehardening of eucalypt seedlings can be accomplished within a few days, this could be as important to potential survival as frost resistance itself (Paton et al. 1979; Aston & Paton 1973).

Root temperature and water stress also influence acclimation in eucalypt species (Paton et al. 1979; Paton 1981). Low root temperatures (0.5°C to 1.0°C), flooding of the root system and desiccation of the plant retarded the dehardening of four eucalypt species when stems were subjected to warm temperatures (Paton et al. 1979). Delayed dehardening appeared to be related to the metabolic activity of the root system (Paton et al. 1979) although hardening appeared to be independent of these factors.

It has been suggested that hardening in Eucalyptus also involves a growth factor "G" (Paton et al. 1981) which may be analogous to the acclimation promotion factors involved in the first stage of acclimation in the hardy deciduous species of the Northern Hemisphere (Howell & Weiser 1970; Steponikus 1971). The extremes of temperature experienced at the treeline in Australia apparently do not require eucalypt species that occupy these sites to harden beyond the first stage of acclimation as described by Weiser (1970) and Howell and Weiser (1970).

Sakai *et al.* (1981) summarised the freezing resistance characteristics of the subalpine eucalypts as follows: "In the most cold resistant *Eucalyptus* species at least, the ability to respond rapidly to hardening and dehardening temperatures (Paton *et al.* 1979) appear partially to compensate for the absence of short day-low temperature induced winter dormancy that is so common in cold-resistant plants of the Northern Hemisphere."

#### (b) Freezing and Freezing Injury

During active summer growth plant tissue is particularly sensitive to frost injury. Hardy deciduous species which are resistant to  $-60^{\circ}\text{C}$  in winter frosts may be damaged by  $-2^{\circ}\text{C}$  to  $-3^{\circ}\text{C}$  as a result of intracellular freezing during the growing season (Burke *et al.* 1976). In autumn and winter once acclimation has been induced, freezing becomes extracellular minimising injury to the protoplast (Weiser 1970; Asahina 1978), although in some species freezing is avoided by "deep undercooling" (Burke *et al.* 1976; George *et al.* 1974).

According to Wieser (1970), once acclimated, the sequence of events as plant tissue is exposed to successively lower temperatures is as follows. At first, as the temperature is depressed below zero, there is a period of super cooling of from  $-2^{\circ}\text{C}$  to  $-8^{\circ}\text{C}$ , then extracellular freezing occurs in the non-xylem elements. The purer water in the intracellular spaces freezes with a rapid propagation of ice through the stem (Weiser 1970; Asahina 1978). The latent heat of fusion released during extracellular freezing raises the temperature by  $-0.3^{\circ}\text{C}$  to  $-1.0^{\circ}\text{C}$  (Weiser 1970). This is referred to as the first exotherm (Weiser 1970; Burke *et al.* 1974, 1976; Asahina 1978). Once all readily available water has frozen further cooling leads to exosmosis of protoplasmic water to extracellular ice nuclei in response to a vapour pressure deficit (Asahina 1978; Weiser 1970). There is then a second exotherm (near the first) when this water freezes. A further decrease in the temperature produces slow exosmosis of water from the protoplast to external ice nuclei with a corresponding shrinkage of the protoplast, plasmolysis and concentration of the solutes within the cell (Weiser 1970). Near the intracellular freezing point there is a lag in the calorimetric curve produced by freezing or cessation of water movement out of the protoplast (Weiser 1970). When intracellular freezing occurs it is invariably fatal (Asahina 1978; Burke *et al.* 1976), and is marked by a third exotherm. For the hardiest of plants experiencing the third acclimation phase the final exotherm is avoided and plants may be cooled to extremely low temperatures ( $-196^{\circ}\text{C}$ , Sakai 1960) without damage. Death occurs either, when all the remaining water in the protoplasm is "vital", that is,

in intimate association with the protoplasmic constituents, or when the intercellular ice crystallisation mechanically damages the cell membranes and constituents. The first hypothesis implies that the desiccation tolerance of the cell is reached before freezing, and the second, that freezing kills the cell (Weiser 1970).

Some of the less hardy of the Northern Hemisphere deciduous species exhibit a "deep undercooling". In these species some stem tissues, notably the xylem ray parenchyma, do not undergo the processes described above but super cool to temperatures as low as  $-40^{\circ}\text{C}$  (George *et al.* 1974; Burke *et al.* 1974, 1976), effectively avoiding the desiccation stress imposed by low temperatures (Levitt 1980). However when the temperature of homogeneous nucleation of water is reached (at about  $-40^{\circ}\text{C}$ ) intracellular freezing occurs which is invariably fatal to the tree (Burke *et al.* 1976).

The rate of cooling during frosts also influences the severity of freezing injury, even in hardened plants (Weiser 1970; White & Weiser 1964). Evergreen foliage which survived slow cooling to  $-87^{\circ}\text{C}$  was killed by rapid cooling (at  $8^{\circ}$  to  $10^{\circ}\text{C}$  per minute) to  $-10^{\circ}\text{C}$  (White & Weiser 1964). At the slow rates of cooling ice forms extracellularly and continual exosmosis of protoplasmic water prevents freezing of the protoplasm. Under rapid cooling regimes ( $10^{\circ}\text{C}$  to  $100^{\circ}\text{C}$  per minute) ice crystals form within the protoplast which invariably causes death.

In the genus Eucalyptus unhardened leaf and stem tissue may be damaged by intracellular freezing at  $-2.5^{\circ}$  to  $-4^{\circ}\text{C}$  (Ashton 1958; Paton 1972) but once hardened, eucalypt leaves freeze extracellularly (first exotherm, Weiser 1970) at between  $-2$  and  $-7^{\circ}\text{C}$  (Harwood 1980) without damage to leaf tissue. Subalpine species will survive further cooling to  $-16^{\circ}\text{C}$  to  $-18^{\circ}\text{C}$  (Harwood 1980; Sakai *et al.* 1981). Death at temperatures below these probably occur due to fatal intracellular freezing. Some species of eucalypt (for example E. urnigera) may avoid freezing (Levitt 1980) by super cooling to temperatures of  $-8$  to  $-10^{\circ}\text{C}$  (Thomas & Barber 1974) although subsequent experiments on E. urnigera cast doubt on these results (Harwood 1981; Paton 1981). It appears the majority of subalpine eucalypts tolerate extracellular freezing to near  $-16^{\circ}\text{C}$  (Sakai *et al.* 1981).

While the evidence presented in this review indicates eucalypts do not exhibit the same low temperature responses as Northern Hemisphere genera, it suggests that the ability of subalpine species to tolerate periods of intense cold would be an important factor in determining their distributions.

APPENDIX 4.2

TEMPERATURE RECORDS FROM FOUR TASMANIAN WEATHER STATIONS

APPENDIX 4.2. TEMPERATURE RECORDS FROM FOUR TASMANIAN WEATHER STATIONS

Frequency tables for monthly minimum temperatures (in °C)  
during the period from January 1957 to January 1983 for  
Meteorological Stations at Grove, Shannon, Butlers Gorge and  
Lake St Clair (courtesy of Bureau of Meteorology, Hobart).

GROVE RESEARCH

LATITUDE: 42 59S

LONGITUDE: 147 5E

ELEVATION: 60.0 M

## Temperature Range

## Frequency Analysis Table

|                  | JAN | FEB | MAR | APR | MAY | JUN | JUL | AUG | SEP | OCT | NOV | DEC | TOTAL |
|------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-------|
| -8.00 to < -7.00 |     |     |     |     |     | 1   |     |     |     |     |     |     | 1     |
| -7.00 to < -6.00 |     |     |     |     |     | 1   |     |     |     |     |     |     | 1     |
| -6.00 to < -5.00 |     |     |     |     |     |     | 1   |     |     |     |     |     | 1     |
| -5.00 to < -4.00 |     |     |     |     | 2   | 6   | 11  | 3   |     |     |     |     | 22    |
| -4.00 to < -3.00 |     |     |     | 1   | 12  | 15  | 27  | 20  | 4   | 1   |     |     | 80    |
| -3.00 to < -2.00 |     |     |     | 3   | 25  | 42  | 59  | 38  | 10  | 4   |     |     | 181   |
| -2.00 to < -1.00 |     |     | 1   | 8   | 28  | 71  | 93  | 68  | 31  | 10  | 2   |     | 312   |
| -1.00 to < 0.0   |     | 3   | 4   | 15  | 51  | 89  | 82  | 68  | 41  | 20  | 6   | 3   | 382   |
| 0.0 to < 1.00    | 1   | 1   | 12  | 33  | 56  | 84  | 94  | 92  | 67  | 37  | 15  | 5   | 497   |
| 1.00 to < 2.00   | 7   | 7   | 24  | 52  | 75  | 84  | 81  | 87  | 81  | 60  | 25  | 7   | 590   |
| 2.00 to < 3.00   | 12  | 16  | 37  | 54  | 75  | 71  | 73  | 78  | 87  | 61  | 34  | 19  | 617   |
| 3.00 to < 4.00   | 26  | 34  | 56  | 73  | 78  | 63  | 57  | 82  | 69  | 66  | 56  | 33  | 693   |
| 4.00 to < 5.00   | 28  | 29  | 40  | 64  | 78  | 57  | 57  | 70  | 70  | 74  | 58  | 41  | 666   |
| 5.00 to < 6.00   | 69  | 51  | 54  | 69  | 72  | 55  | 52  | 65  | 83  | 77  | 64  | 64  | 775   |
| 6.00 to < 7.00   | 68  | 53  | 79  | 71  | 72  | 36  | 39  | 50  | 66  | 78  | 89  | 64  | 765   |
| 7.00 to < 8.00   | 69  | 68  | 80  | 89  | 75  | 31  | 35  | 42  | 51  | 78  | 86  | 75  | 779   |
| 8.00 to < 9.00   | 80  | 62  | 80  | 55  | 60  | 27  | 14  | 16  | 26  | 60  | 89  | 91  | 660   |
| 9.00 to < 10.00  | 82  | 71  | 73  | 62  | 29  | 16  | 12  | 14  | 22  | 54  | 53  | 109 | 597   |
| 10.00 to < 11.00 | 99  | 91  | 96  | 58  | 13  | 12  | 10  | 8   | 18  | 46  | 42  | 75  | 568   |
| 11.00 to < 12.00 | 87  | 71  | 65  | 37  | 10  | 7   | 2   | 1   | 12  | 17  | 46  | 71  | 426   |
| 12.00 to < 13.00 | 61  | 79  | 54  | 21  | 10  | 5   | 4   | 1   | 7   | 10  | 23  | 50  | 325   |
| 13.00 to < 14.00 | 44  | 53  | 31  | 16  | 6   | 3   | 1   |     | 2   | 7   | 16  | 21  | 200   |
| 14.00 to < 15.00 | 29  | 24  | 26  | 12  | 3   |     |     |     | 1   | 6   | 4   | 21  | 126   |
| 15.00 to < 16.00 | 13  | 16  | 9   | 7   | 3   |     |     |     | 1   | 3   | 3   | 16  | 71    |
| 16.00 to < 17.00 | 10  | 7   | 3   | 2   |     |     |     |     | 1   | 1   | 4   | 4   | 32    |
| 17.00 to < 18.00 | 5   | 3   | 1   | 3   |     |     |     |     |     |     |     | 1   | 15    |
| 18.00 to < 19.00 | 8   | 12  | 1   | 1   |     |     |     |     |     |     |     | 2   | 24    |
| 19.00 to < 20.00 | 2   | 1   |     |     |     |     |     |     |     |     |     |     | 3     |
| 20.00 to < 21.00 |     | 4   |     |     |     |     |     |     |     |     |     |     | 4     |
| 21.00 to < 22.00 | 3   | 2   | 1   | 1   |     |     |     |     |     |     |     |     | 7     |
| 23.00 to < 24.00 | 1   |     |     |     |     |     |     |     |     |     |     |     | 1     |
| 24.00 to < 25.00 |     | 1   |     |     |     |     |     |     |     |     |     |     | 1     |
| TOTALS           | 804 | 759 | 827 | 807 | 833 | 776 | 804 | 803 | 750 | 770 | 716 | 773 | 9422  |

## Most extreme frosts

23rd June 1972 -6.2  
 24th June 1972 -7.5  
 7th July 1973 -5.6  
 30th June 1983 -6.5

SHANNON

96021 LATITUDE: 42 3S

LONGITUDE: 146 45E

ELEVATION: 940.0 M

## Temperature Range

## Frequency Analysis Table

|                    | JAN | FEB | MAR | APR | MAY | JUN | JUL | AUG | SEP | OCT | NOV | DEC | TOTAL |
|--------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-------|
| -11.00 to < -10.00 |     |     |     |     |     |     | 1   | 1   |     |     |     |     | 2     |
| -10.00 to < -9.00  |     |     |     |     |     | 2   | 3   | 1   |     |     |     |     | 6     |
| -9.00 to < -8.00   |     |     |     |     | 1   | 4   | 9   | 3   |     |     |     |     | 17    |
| -8.00 to < -7.00   |     |     |     |     | 1   | 8   | 9   | 5   |     |     |     |     | 23    |
| -7.00 to < -6.00   |     |     |     | 1   | 4   | 8   | 18  | 16  | 4   | 4   |     |     | 55    |
| -6.00 to < -5.00   |     |     |     | 2   | 6   | 18  | 24  | 15  | 9   | 4   | 1   |     | 79    |
| -5.00 to < -4.00   |     |     |     | 3   | 17  | 33  | 47  | 45  | 21  | 8   |     |     | 174   |
| -4.00 to < -3.00   |     | 1   | 1   | 18  | 29  | 58  | 75  | 72  | 49  | 29  | 5   | 1   | 338   |
| -3.00 to < -2.00   | 2   | 4   | 3   | 23  | 47  | 82  | 94  | 94  | 72  | 39  | 26  | 5   | 491   |
| -2.00 to < -1.00   | 6   | 8   | 25  | 41  | 69  | 91  | 104 | 103 | 111 | 74  | 44  | 9   | 685   |
| -1.00 to < 0.0     | 9   | 11  | 18  | 38  | 79  | 66  | 67  | 73  | 75  | 52  | 38  | 23  | 549   |
| 0.0 to < 1.00      | 37  | 30  | 48  | 98  | 101 | 83  | 119 | 117 | 93  | 114 | 85  | 59  | 984   |
| 1.00 to < 2.00     | 52  | 43  | 70  | 84  | 89  | 89  | 80  | 85  | 96  | 90  | 85  | 76  | 939   |
| 2.00 to < 3.00     | 69  | 45  | 93  | 90  | 78  | 73  | 42  | 61  | 71  | 74  | 92  | 84  | 872   |
| 3.00 to < 4.00     | 64  | 58  | 81  | 88  | 62  | 41  | 26  | 32  | 67  | 75  | 80  | 84  | 758   |
| 4.00 to < 5.00     | 62  | 43  | 55  | 43  | 43  | 21  | 15  | 15  | 21  | 44  | 53  | 46  | 461   |
| 5.00 to < 6.00     | 88  | 77  | 77  | 51  | 42  | 27  | 6   | 10  | 12  | 42  | 69  | 79  | 580   |
| 6.00 to < 7.00     | 73  | 64  | 62  | 31  | 35  | 5   | 2   | 1   | 3   | 31  | 42  | 71  | 420   |
| 7.00 to < 8.00     | 63  | 73  | 45  | 34  | 13  | 2   | 1   | 1   | 7   | 22  | 29  | 47  | 337   |
| 8.00 to < 9.00     | 59  | 51  | 51  | 26  | 5   | 3   | 1   |     | 4   | 13  | 19  | 39  | 271   |
| 9.00 to < 10.00    | 35  | 30  | 25  | 19  | 2   |     |     |     |     | 8   | 15  | 22  | 156   |
| 10.00 to < 11.00   | 32  | 39  | 33  | 21  |     |     |     |     |     | 11  | 17  | 24  | 177   |
| 11.00 to < 12.00   | 28  | 26  | 19  | 4   |     |     |     |     |     |     | 7   | 15  | 99    |
| 12.00 to < 13.00   | 14  | 20  | 14  | 3   |     |     |     |     | 1   | 1   | 1   | 8   | 62    |
| 13.00 to < 14.00   | 13  | 13  | 12  |     |     |     |     |     |     |     | 2   | 9   | 49    |
| 14.00 to < 15.00   | 5   | 10  | 2   |     |     |     |     |     |     |     | 1   | 3   | 21    |
| 15.00 to < 16.00   | 9   | 8   | 1   | 1   |     |     |     |     |     | 1   | 1   | 6   | 27    |
| 16.00 to < 17.00   | 7   | 6   |     |     |     |     |     |     |     |     |     | 1   | 14    |
| 17.00 to < 18.00   | 1   | 1   |     |     |     |     |     |     |     |     |     | 2   | 4     |
| 19.00 to < 20.00   | 3   | 1   |     |     |     |     |     |     |     |     |     |     | 4     |
| 20.00 to < 21.00   | 1   |     |     |     |     |     |     |     |     |     |     |     | 1     |
| TOTALS             | 732 | 662 | 735 | 719 | 723 | 714 | 743 | 750 | 716 | 736 | 712 | 713 | 8655  |

## Most extreme frosts

9th August 1960 -9.4  
 30th July 1971 -9.0  
 24th June 1972 -10.0  
 6th August 1974 -11.0  
 28th July 1976 -10.0

28th June 1978 -10.0  
 2nd July 1978 -9.2  
 20th July 1982 -10.2  
 30th June 1983 -13.0\*  
 \*record minimum for station and Tasmania

BUTLERS GORGE

LATITUDE: 42 17S

LONGITUDE: 146 16E

ELEVATION: 666.0 M

## Temperature Range

## Frequency Analysis Table

|                   | JAN | FEB | MAR | APR | MAY | JUN | JUL | AUG | SEP | OCT | NOV | DEC | TOTAL |
|-------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-------|
| -10.00 to < -9.00 |     |     |     |     |     |     |     | 1   |     |     |     |     | 1     |
| -9.00 to < -8.00  |     |     |     |     |     |     | 1   |     |     |     |     |     | 1     |
| -8.00 to < -7.00  |     |     |     |     |     | 2   | 7   | 1   |     |     |     |     | 10    |
| -7.00 to < -6.00  |     |     |     |     | 1   | 5   | 16  | 8   |     |     |     |     | 30    |
| -6.00 to < -5.00  |     |     |     | 1   | 4   | 18  | 34  | 15  | 6   | 3   |     |     | 81    |
| -5.00 to < -4.00  |     |     |     |     | 15  | 38  | 48  | 38  | 11  | 7   | 1   |     | 158   |
| -4.00 to < -3.00  |     |     | 1   | 11  | 24  | 61  | 54  | 51  | 40  | 8   | 5   |     | 255   |
| -3.00 to < -2.00  | 1   | 3   | 1   | 15  | 43  | 63  | 68  | 68  | 50  | 29  | 7   | 2   | 350   |
| -2.00 to < -1.00  | 5   | 8   | 20  | 31  | 72  | 71  | 90  | 105 | 81  | 57  | 22  | 11  | 573   |
| -1.00 to < 0.0    | 8   | 12  | 21  | 43  | 67  | 82  | 89  | 93  | 68  | 48  | 20  | 20  | 571   |
| 0.0 to < 1.00     | 18  | 16  | 37  | 86  | 111 | 109 | 138 | 131 | 131 | 103 | 68  | 24  | 972   |
| 1.00 to < 2.00    | 28  | 30  | 55  | 80  | 99  | 97  | 87  | 99  | 113 | 107 | 68  | 45  | 914   |
| 2.00 to < 3.00    | 53  | 48  | 76  | 80  | 73  | 72  | 72  | 64  | 93  | 100 | 83  | 59  | 873   |
| 3.00 to < 4.00    | 69  | 62  | 92  | 88  | 96  | 51  | 51  | 66  | 77  | 86  | 105 | 85  | 928   |
| 4.00 to < 5.00    | 79  | 57  | 60  | 72  | 49  | 46  | 26  | 38  | 47  | 84  | 94  | 85  | 737   |
| 5.00 to < 6.00    | 94  | 77  | 93  | 85  | 70  | 39  | 17  | 22  | 32  | 71  | 74  | 111 | 785   |
| 6.00 to < 7.00    | 137 | 93  | 99  | 67  | 41  | 12  | 5   | 4   | 16  | 45  | 68  | 113 | 700   |
| 7.00 to < 8.00    | 89  | 84  | 99  | 42  | 21  | 7   | 2   | 1   | 6   | 20  | 56  | 79  | 506   |
| 8.00 to < 9.00    | 75  | 93  | 55  | 25  | 10  | 6   |     |     | 2   | 10  | 31  | 66  | 373   |
| 9.00 to < 10.00   | 49  | 50  | 39  | 23  | 7   |     |     |     | 2   | 12  | 13  | 27  | 222   |
| 10.00 to < 11.00  | 48  | 42  | 36  | 11  | 1   |     |     | 1   |     | 8   | 14  | 37  | 198   |
| 11.00 to < 12.00  | 27  | 32  | 21  | 9   | 2   | 1   |     |     |     | 4   | 10  | 14  | 120   |
| 12.00 to < 13.00  | 9   | 18  | 13  | 1   |     |     |     |     | 1   | 2   | 6   | 11  | 61    |
| 13.00 to < 14.00  | 12  | 17  | 2   | 2   |     |     |     |     |     |     | 3   | 6   | 42    |
| 14.00 to < 15.00  | 10  | 4   | 2   | 1   |     |     |     |     |     |     |     | 2   | 19    |
| 15.00 to < 16.00  | 3   | 2   | 2   |     |     |     |     |     |     |     | 1   | 4   | 12    |
| 16.00 to < 17.00  | 3   | 4   |     |     |     |     |     |     |     |     |     | 1   | 8     |
| 17.00 to < 18.00  | 1   |     |     |     |     |     |     |     |     |     |     | 1   | 2     |
| 18.00 to < 19.00  | 2   |     |     |     |     |     |     |     |     |     |     |     | 2     |
| TOTALS            | 820 | 758 | 824 | 773 | 806 | 780 | 805 | 806 | 776 | 804 | 749 | 803 | 9504  |

## Most extreme frosts

11th July 1958 -8.9

6th August 1974 -10.0

30th June 1983 -13.0\*

\*record minimum for station and for Tasmania



LAKE ST CLAIR

LATITUDE: 42 6S LONGITUDE: 146 13E ELEVATION: 735.2 M

## Temperature Range

## Frequency Analysis Table

|                  | JAN | FEB | MAR | APR | MAY | JUN | JUL | AUG | SEP | OCT | NOV | DEC | TOTAL |
|------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-------|
| -9.00 to < -8.00 |     |     |     |     |     |     |     | 1   |     |     |     |     | 1     |
| -8.00 to < -7.00 |     |     |     |     |     |     | 2   |     |     |     |     |     | 2     |
| -7.00 to < -6.00 |     |     |     |     |     | 6   | 5   | 1   |     |     |     |     | 12    |
| -6.00 to < -5.00 |     |     |     |     | 1   | 5   | 4   | 7   |     |     |     |     | 17    |
| -5.00 to < -4.00 |     |     |     | 1   | 3   | 14  | 26  | 11  | 1   | 1   |     |     | 57    |
| -4.00 to < -3.00 |     |     | 1   | 1   | 13  | 37  | 38  | 24  | 8   | 5   | 3   |     | 130   |
| -3.00 to < -2.00 |     |     | 1   | 6   | 25  | 51  | 56  | 67  | 35  | 15  | 5   | 1   | 262   |
| -2.00 to < -1.00 | 2   | 1   | 4   | 22  | 44  | 81  | 103 | 95  | 60  | 30  | 10  | 2   | 454   |
| -1.00 to < 0.0   | 4   | 5   | 7   | 18  | 39  | 57  | 53  | 80  | 71  | 33  | 12  | 4   | 383   |
| 0.0 to < 1.00    | 12  | 11  | 26  | 48  | 111 | 110 | 153 | 114 | 107 | 102 | 58  | 21  | 873   |
| 1.00 to < 2.00   | 18  | 17  | 46  | 67  | 107 | 88  | 109 | 115 | 117 | 109 | 63  | 37  | 893   |
| 2.00 to < 3.00   | 42  | 33  | 47  | 88  | 96  | 90  | 83  | 75  | 105 | 99  | 82  | 49  | 889   |
| 3.00 to < 4.00   | 65  | 45  | 76  | 98  | 105 | 78  | 70  | 97  | 78  | 100 | 112 | 78  | 1002  |
| 4.00 to < 5.00   | 56  | 42  | 52  | 80  | 51  | 60  | 33  | 32  | 45  | 75  | 80  | 72  | 678   |
| 5.00 to < 6.00   | 98  | 74  | 100 | 86  | 96  | 55  | 29  | 41  | 50  | 69  | 80  | 90  | 868   |
| 6.00 to < 7.00   | 109 | 90  | 104 | 74  | 52  | 27  | 5   | 8   | 19  | 42  | 66  | 96  | 692   |
| 7.00 to < 8.00   | 77  | 98  | 86  | 51  | 40  | 12  | 2   | 1   | 7   | 29  | 66  | 83  | 552   |
| 8.00 to < 9.00   | 68  | 78  | 63  | 43  | 25  | 5   |     |     | 7   | 23  | 38  | 45  | 395   |
| 9.00 to < 10.00  | 49  | 49  | 45  | 25  | 11  | 1   |     |     | 3   | 15  | 19  | 31  | 248   |
| 10.00 to < 11.00 | 57  | 54  | 41  | 15  | 2   | 1   |     | 1   | 1   | 10  | 20  | 33  | 235   |
| 11.00 to < 12.00 | 28  | 38  | 24  | 12  | 2   |     |     |     |     | 10  | 12  | 23  | 149   |
| 12.00 to < 13.00 | 30  | 31  | 19  | 5   |     |     |     |     | 2   | 2   | 8   | 18  | 115   |
| 13.00 to < 14.00 | 19  | 16  | 11  |     |     |     |     |     |     |     | 6   | 10  | 62    |
| 14.00 to < 15.00 | 9   | 14  | 4   | 2   |     |     |     |     |     |     | 2   | 2   | 33    |
| 15.00 to < 16.00 | 10  | 8   | 2   | 1   |     |     |     |     |     | 1   | 1   | 3   | 26    |
| 16.00 to < 17.00 | 4   | 8   | 1   |     |     |     |     |     |     |     |     | 3   | 16    |
| 17.00 to < 18.00 | 4   | 7   |     |     |     |     |     |     |     |     |     | 3   | 14    |
| 18.00 to < 19.00 | 2   | 4   |     |     |     |     |     |     |     |     |     | 1   | 7     |
| 19.00 to < 20.00 | 1   | 2   | 1   |     |     |     |     |     |     |     |     |     | 4     |
| 20.00 to < 21.00 | 1   |     |     |     |     |     |     |     |     |     |     |     | 1     |
| TOTALS           | 765 | 725 | 761 | 743 | 823 | 778 | 771 | 770 | 716 | 770 | 743 | 705 | 9070  |

## Most extreme frosts

23rd July 1964 -7.8  
 6th August 1974 -8.5  
 2nd July 1978 -7.5  
 30th June 1983 -11.0\*  
 \*record for station

### APPENDIX 4.3

#### ANALYSES OF VARIANCE

#### APPENDIX 4.3. ANALYSES OF VARIANCE

Table of four-way analyses of variance performed on the results of frost chamber trials. Frost chamber trials involved six eucalypt species exposed to four minimum temperatures, two hardening regimes and two water regimes in a factorial design with three replicates per cell. Analyses were performed on five different species groupings (analyses 1-5).

A - minimum temperature (-4°C, -5°C, -6°C and -7°C)

B - hardening regime (9°C day/4°C night, 15°C day/10°C night)

C - water regime (freely drained veneers, flooded to 2/3 of the height of veneers)

D - Species : -

(1) E. coccifera; E. pulchella; E. delegatensis; E. gunnii;  
E. johnstonii; E. urnigera

(2) E. coccifera; E. pulchella; E. delegatensis; E. johnstonii;  
E. urnigera

(3) Monocalyptus; E. coccifera; E. pulchella; E. delegatensis

(4) Symphyomyrtus; E. gunnii; E. johnstonii; E. urnigera

(5) Symphyomyrtus; E. johnstonii; E. urnigera

#### Significance Levels

0.001            \*\*\*

0.01            \*\*

0.05            \*

Not significant NS

## Analysis (1) including all species

| Factor | S.S.       | d.f. | M.S.       | F-Stat | Prob.      |
|--------|------------|------|------------|--------|------------|
| A      | 7.2953E 04 | 3    | 2.4318E 04 | 114.24 | 0.0000 *** |
| B      | 2.1123E 04 | 1    | 2.1123E 04 | 99.23  | 0.0000 *** |
| C      | 1.3701E 03 | 1    | 1.3701E 03 | 6.44   | 0.0125 **  |
| D      | 6.0422E 04 | 5    | 1.2084E 04 | 56.77  | 0.0000 *** |
| AB     | 5.1419E 03 | 3    | 1.7140E 03 | 8.05   | 0.0001 *** |
| AC     | 4.0996E 02 | 3    | 1.3665E 02 | 0.64   | 0.5895 NS  |
| AD     | 1.1509E 04 | 15   | 7.6729E 02 | 3.60   | 0.0000 *** |
| BC     | 1.5000E 00 | 1    | 1.5000E 00 | 0.01   | 0.9332 NS  |
| BD     | 4.7853E 03 | 5    | 9.5706E 02 | 4.50   | 0.0009 *** |
| CD     | 4.4249E 03 | 5    | 8.8497E 02 | 4.16   | 0.0016 *** |
| ABC    | 3.3956E 02 | 3    | 1.1319E 02 | 0.53   | 0.6614     |
| ABD    | 5.7833E 03 | 15   | 3.8555E 02 | 1.81   | 0.0404     |
| ACD    | 2.8632E 03 | 15   | 1.9088E 02 | 0.90   | 0.5694     |
| BCD    | 5.4522E 02 | 5    | 1.0904E 02 | 0.51   | 0.7665     |
| ABCD   | 3.6278E 03 | 15   | 2.4186E 02 | 1.14   | 0.3321     |
| Error  | 2.5543E 04 | 120  | 2.1286E 02 |        |            |
| Total  | 2.2084E 05 | 215  |            |        |            |

Analysis (2) all species excluding E. gunnii

| Factor | S.S.       | d.f. | M.S.       | F-Stat | Prob.      |
|--------|------------|------|------------|--------|------------|
| A      | 7.8365E 04 | 3    | 2.6122E 04 | 109.56 | 0.0000 *** |
| B      | 2.4851E 04 | 1    | 2.4851E 04 | 104.23 | 0.0000 *** |
| C      | 1.5196E 03 | 1    | 1.5196E 03 | 6.37   | 0.0132 **  |
| D      | 1.1025E 04 | 4    | 2.7564E 03 | 11.56  | 0.0000 *** |
| AB     | 6.3998E 03 | 3    | 2.1333E 03 | 8.95   | 0.0000 *** |
| AC     | 4.1914E 02 | 3    | 1.3971E 02 | 0.59   | 0.6256 NS  |
| AD     | 4.4880E 03 | 12   | 3.7400E 02 | 1.57   | 0.1131 NS  |
| BC     | 1.2272E 01 | 1    | 1.2272E 01 | 0.05   | 0.8210 NS  |
| BD     | 1.0444E 03 | 4    | 2.6111E 02 | 1.10   | 0.3632 NS  |
| CD     | 4.2631E 03 | 4    | 1.0658E 03 | 4.47   | 0.0023 **  |
| ABC    | 6.1928E 02 | 3    | 2.0643E 02 | 0.87   | 0.4615     |
| ABD    | 4.3837E 03 | 12   | 3.6531E 02 | 1.53   | 0.1251     |
| ACD    | 2.6823E 03 | 12   | 2.2353E 02 | 0.94   | 0.5133     |
| BCD    | 5.1109E 02 | 4    | 1.2777E 02 | 0.54   | 0.7097     |
| ABCD   | 3.0099E 03 | 12   | 2.5082E 02 | 1.05   | 0.4087     |
| Error  | 2.3842E 04 | 100  | 2.3842E 02 |        |            |
| Total  | 1.6744E 05 | 179  |            |        |            |

Analysis (3) Monocalyptus species

| Factor | S.S.       | d.f. | M.S.       | F-Stat | Prob.      |
|--------|------------|------|------------|--------|------------|
| A      | 4.1113E 04 | 3    | 1.3704E 04 | 76.28  | 0.0000 *** |
| B      | 1.0621E 04 | 1    | 1.0621E 04 | 59.12  | 0.0000 *** |
| C      | 5.0841E 03 | 1    | 5.0841E 03 | 28.30  | 0.0000 *** |
| D      | 8.2236E 03 | 2    | 4.1118E 03 | 22.89  | 0.0000 *** |
| AB     | 5.7592E 03 | 3    | 1.9197E 03 | 10.69  | 0.0000 *** |
| AC     | 4.3579E 02 | 3    | 1.4526E 02 | 0.81   | 0.4941 NS  |
| AD     | 2.8092E 03 | 6    | 4.6821E 02 | 2.61   | 0.0260 *   |
| BC     | 2.8009E 01 | 1    | 2.8009E 01 | 0.16   | 0.6943 NS  |
| BD     | 1.3339E 02 | 2    | 6.6694E 01 | 0.37   | 0.6914 NS  |
| CD     | 3.7167E 01 | 2    | 1.8583E 01 | 0.10   | 0.9019 NS  |
| ABC    | 1.0086E 03 | 3    | 3.3621E 02 | 1.87   | 0.1440     |
| ABD    | 2.3496E 03 | 6    | 3.9160E 02 | 2.18   | 0.0573     |
| ACD    | 9.0908E 02 | 6    | 1.5151E 02 | 0.84   | 0.5416     |
| BCD    | 3.9646E 02 | 2    | 1.9823E 02 | 1.10   | 0.3384     |
| ABCD   | 5.3018E 02 | 6    | 8.8363E 01 | 0.49   | 0.8119     |
| Error  | 1.0779E 04 | 60   | 1.7965E 02 |        |            |
| Total  | 9.0217E 04 | 107  |            |        |            |

Analysis (4) Symphyomyrtus species

| Factor | S.S.       | d.f. | M.S.       | F-Stat | Prob.      |
|--------|------------|------|------------|--------|------------|
| A      | 3.2601E 04 | 3    | 1.0867E 04 | 44.16  | 0.0000 *** |
| B      | 1.0502E 04 | 1    | 1.0502E 04 | 42.68  | 0.0000 *** |
| C      | 3.5934E 02 | 1    | 3.5934E 02 | 1.46   | 0.2316 NS  |
| D      | 3.9747E 04 | 2    | 1.9873E 04 | 80.76  | 0.0000 *** |
| AB     | 1.5872E 03 | 3    | 5.2906E 02 | 2.15   | 0.1033 NS  |
| AC     | 3.5044E 02 | 3    | 1.1681E 02 | 0.47   | 0.7011 NS  |
| AD     | 7.9392E 03 | 6    | 1.3232E 03 | 5.38   | 0.0002 *** |
| BC     | 1.2676E 01 | 1    | 1.2676E 01 | 0.05   | 0.8212 NS  |
| BD     | 4.6517E 03 | 2    | 2.3259E 03 | 9.45   | 0.0003 *** |
| CD     | 3.1435E 02 | 2    | 1.5718E 02 | 0.64   | 0.5315 NS  |
| ABC    | 7.1827E 02 | 3    | 2.3942E 02 | 0.97   | 0.4115     |
| ABD    | 1.2292E 03 | 6    | 2.0486E 02 | 0.83   | 0.5496     |
| ACD    | 1.5779E 03 | 6    | 2.6298E 02 | 1.07   | 0.3913     |
| BCD    | 1.0957E 02 | 2    | 5.4787E 01 | 0.22   | 0.8011     |
| ABCD   | 1.7103E 03 | 6    | 2.8505E 02 | 1.16   | 0.3406     |
| Error  | 1.4764E 04 | 60   | 2.4607E 02 |        |            |
| Total  | 1.1317E 05 | 107  |            |        |            |

Analysis (5) Symphyomyrtus species excluding E. gunnii

| Factor | S.S.       | d.f. | M.S.       | F-Stat | Prob.  |     |
|--------|------------|------|------------|--------|--------|-----|
| A      | 3.8245E 04 | 3    | 1.2748E 04 | 39.03  | 0.0000 | *** |
| B      | 1.5138E 04 | 1    | 1.5138E 04 | 46.35  | 0.0000 | *** |
| C      | 6.6006E 02 | 1    | 6.6006E 02 | 2.02   | 0.1629 | NS  |
| D      | 2.6161E 03 | 1    | 2.6161E 03 | 8.01   | 0.0072 | **  |
| AB     | 2.0824E 03 | 3    | 6.9412E 02 | 2.13   | 0.1122 | NS  |
| AC     | 4.8763E 02 | 3    | 1.6254E 02 | 0.50   | 0.6860 | NS  |
| AD     | 6.8705E 02 | 3    | 2.2902E 02 | 0.70   | 0.5569 | NS  |
| BC     | 8.8889E-01 | 1    | 8.8889E-01 | 0.00   | 0.9587 | NS  |
| BD     | 3.5556E 00 | 1    | 3.5556E 00 | 0.01   | 0.9174 | NS  |
| CD     | 1.3889E 00 | 1    | 1.3889E 00 | 0.00   | 0.9483 | NS  |
| ABC    | 1.1232E 03 | 3    | 3.7441E 02 | 1.15   | 0.3421 |     |
| ABD    | 5.9230E 02 | 3    | 1.9743E 02 | 0.60   | 0.6159 |     |
| ACD    | 1.2690E 03 | 3    | 4.2299E 02 | 1.30   | 0.2893 |     |
| BCD    | 9.8000E 01 | 1    | 9.8000E 01 | 0.30   | 0.5869 |     |
| ABCD   | 9.6710E 02 | 3    | 3.2237E 02 | 0.99   | 0.4086 |     |
| Error  | 1.3064E 04 | 40   | 3.2659E 02 |        |        |     |
| Total  | 7.7035E 04 | 71   |            |        |        |     |

## APPENDIX 5.1

### LITERATURE REVIEW: THE EFFECTS OF WATERLOGGING

Generally for high productivity, woody species require an environment in which soils are neither too wet nor too dry. When soil becomes saturated the air in the interstitial spaces in the soil is replaced by water. Oxygen supply is then restricted by the very slow diffusion rates of oxygen in water (Drew 1983) and the root systems of plants in waterlogged soils are suddenly subjected to an anaerobic environment (Kawase 1981).

#### Biochemical Effects of Waterlogging

An oxygen deficit in the soil causes roots to switch to anaerobic respiration with a consequent reduction in ATP yield and depletion of organic reserves. This in turn reduces absorption of water and mineral ions (Kawase 1981; Bradford & Yang 1981; Drew 1983). Sustained anaerobic conditions causes root injury and suppression of synthesis and translocation of gibberellins and cytokinins in the root (Kawase 1981; Bradford & Yang 1981). Low oxygen concentration at the root also promotes the synthesis of an ethylene precursor ACC (1-aminocyclopropane-1-carboxylic acid) which passes in the transpiration stream to the aerial portions of the plant (Yang 1980; Bradford & Yang 1981). Once ACC passes into the aerobic environment of the shoot it is converted to ethylene (Yang 1981; Drew 1983) and it is ethylene acting as a chemical trigger which is implicated in many of the morphological adaptations characteristic of plants in waterlogged environments (Kawase 1979; 1981; Yang 1980; Bradford & Yang 1981). High ethylene concentrations have been associated with the processes of leaf epinasty (e.g. Jackson & Campbell 1976), stem hypertrophy (e.g. Wample & Reid 1978), aerenchyma production and the production of adventitious root (e.g. Wample & Reid 1978, 1979). On the other hand, stomatal closure under waterlogged conditions has been shown to be triggered at the leaf by ABA (abscissic acid) (Hiron & Wright 1973) but the messenger compound, which is synthesised at the root (Sojka & Stolzy 1980), is not known (Bradford & Yang 1981; Drew 1983). Nutrition of the shoot is also profoundly modified by flooding of the root system and has been shown to influence leaf chlorosis, leaf abscission, recycling of nutrients within the plant and expansion and growth of newly formed leaves (Drew 1983).

### Changes in Water Relations

At the time waterlogging occurs the anaerobic conditions at the root result in reduced rates of respiration (anaerobic) and correspondingly lower root permeability (Kramer 1951; Drew 1983). Lower root permeability and increased resistance to water uptake may cause a drop in leaf water potential, wilting, and stomatal closure in response to low water potential, particularly if transpirational demand is high (Kramer 1940, 1951, 1979; Hiron & Wright 1973; Drew 1983; Bradford & Yang 1981). Hence, historically there was a tendency to consider waterlogging stress as a subset of drought stress. However, more recent work has shown that, for waterlogging tolerant species, partial stomatal closure may occur in the absence of low water potentials (Pereira & Kozlowski 1977; Regehr *et al.* 1975, Kozlowski & Pallardy 1979) in direct response to root anaerobiosis (Sojka & Stolzy 1980). The stomatal closure then causes a rise, rather than a fall in water potentials so that the water potentials of waterlogged plants are higher, not lower than corresponding control plants in freely drained treatments (Pereira & Kozlowski 1977; Blake & Reid 1981; Tang & Kozlowski 1984). This is consistent with the requirement of high cell turgidity for the processes of leaf epinasty and adventitious root development (Bradford & Yang 1981; Regehr *et al.* 1975).

### Morphological Changes

The documented adaptations to the waterlogged environment are predominantly morphological; specific modifications of biochemical pathways to cope with anaerobic conditions at the root appear not to have developed (Bradford & Yang 1981; Drew 1983). On the other hand, morphological changes undergone by waterlogging tolerant species when exposed to waterlogged conditions are extensive. These include leaf epinasty, leaf abscission, stem hypertrophy, aerenchyma production and development of adventitious roots. The major thrust of morphological adaptation has occurred in the direction of providing an efficient air translocation system to the root, thus relieving the anaerobic conditions. Increased oxygen conduction to the root alleviates oxygen deficiency within the roots. Further, oxygen diffusion out of the root system into the rhizosphere alleviates reducing conditions in the soil in the immediate vicinity of the root (Philipson & Coutts 1978; Coutts & Philipson 1978). Prior exposure to waterlogged conditions may result in increased diffusion of oxygen from the roots into the rhizosphere (Philipson & Coutts 1978). However, it appears some waterlogging intolerant species may not



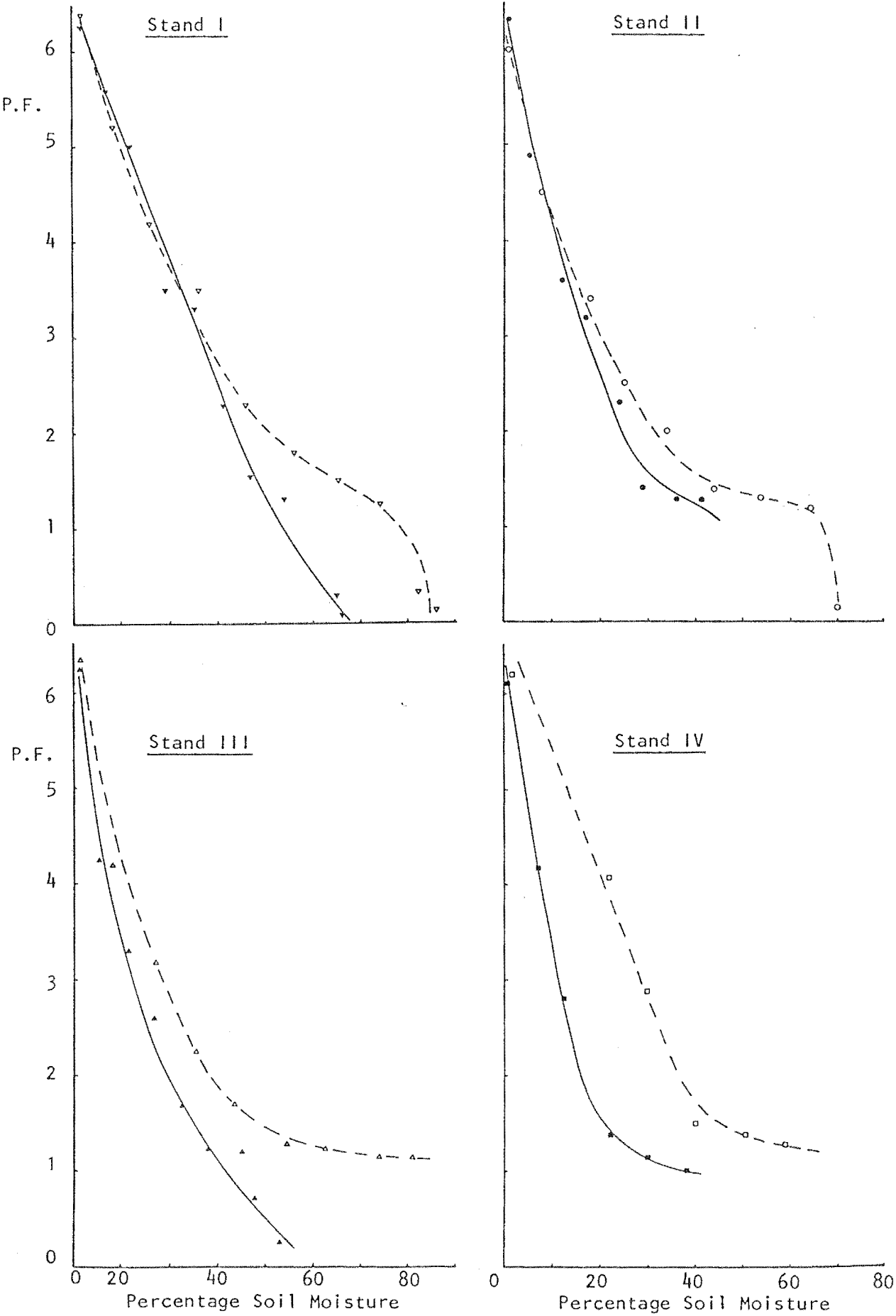
possess the inherent ability to undergo radical morphological adaptations in response to waterlogging (Hook & Brown 1973; Jackson 1979; Etherington 1984; Drew 1983). Instead, these species rapidly exhibit symptoms of waterlogging injury (wilting and leaf abscission) and little or no morphological adaptations to the waterlogged conditions (Jackson 1979; Etherington 1984).

## APPENDIX 5.2

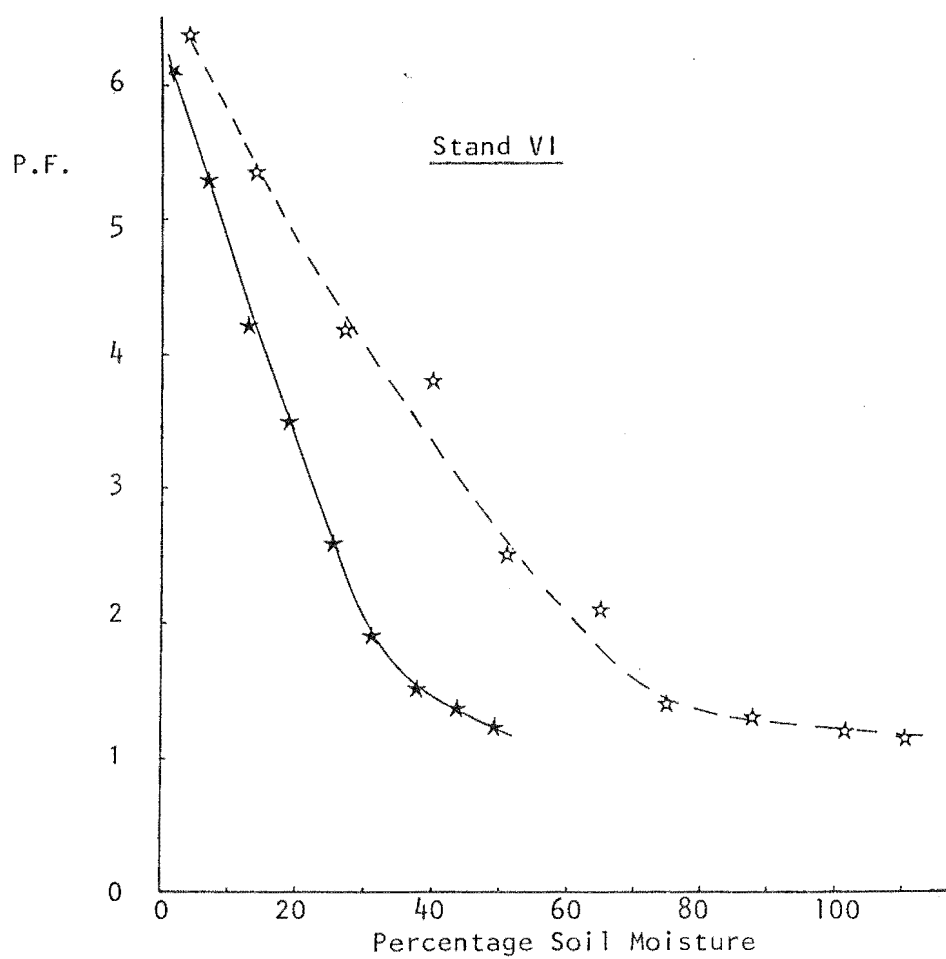
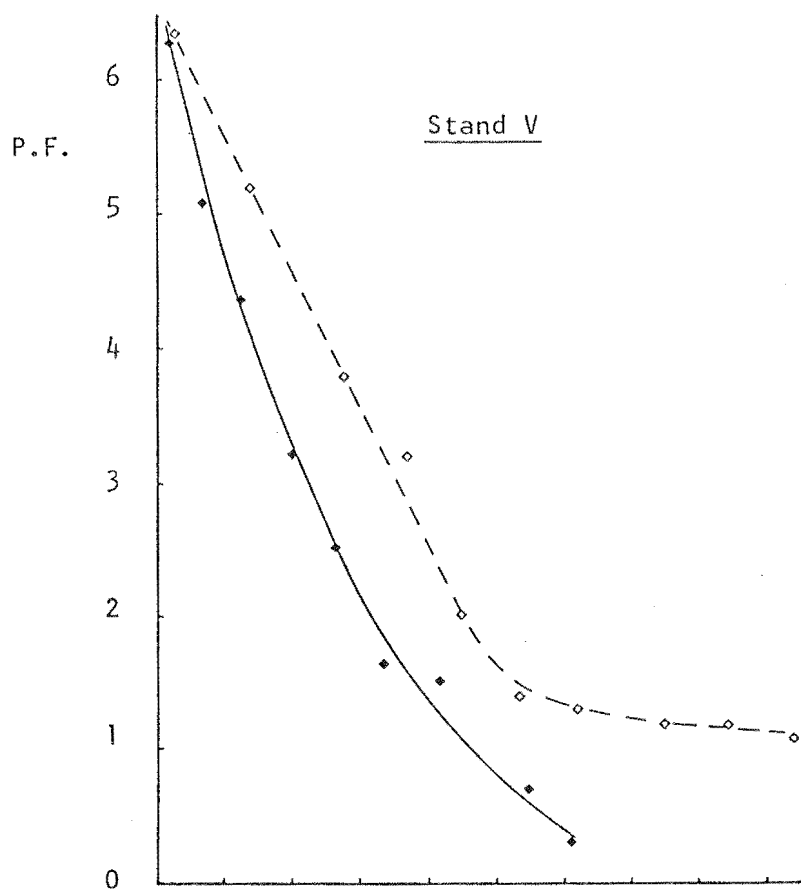
### P.F. CURVES

APPENDIX 5.2. P.F. CURVES

P.F. curves for the "A" (broken line) and the "B" (solid line) soil horizons of stands I-VI (Fig. 5.1) generated using the filter paper method (after Hamblin 1981).



## APPENDIX 5.2 (cont'd)



## APPENDIX 6.1

LITERATURE REVIEW: PLANT WATER RELATIONSINTRODUCTION

With the advent of practical field equipment has come an increased interest in detailed evaluation of water relations in natural communities. Simultaneous measurements of photosynthetically active radiation (P.A.R.), humidity (or vapour pressure deficit, V.P.D.), temperature (of leaf and atmosphere) as they relate to stomatal conductance, xylem water potential and photosynthesis are now possible (Landsburg *et al.* 1975; Reich & Hinckley 1980; Turner *et al.* 1978). However the subtleties of the interactions of all these factors are not well understood (Kaufmann 1982a). Species responses, particularly under drought conditions, have to be interpreted in the light of the salient climate of the site of origin of the plant (Kaufmann 1982a), and in the light of the immediate past climatic history (Sterne *et al.* 1977).

Despite these problems of interpretation attempts have been made to determine the importance of water relations in defining the niches occupied by forest trees (Reich & Hinckley 1980; Kaufmann 1979; Sinclair 1980; Parker *et al.* 1982; Ladiges 1974, 1975, 1976; Withers 1978).

Water Potential

A great deal of research time and effort has been spent on the topic of plant water relations but there still is not complete agreement on which technique; pressure chamber, or thermocouple psychrometer best estimates the water potential. The psychrometer more accurately measures water potential but the pressure chamber is a more practical instrument for use in field studies (Miller 1982). There is also uncertainty about whether total water potential ( $\Psi$  total) or some fraction of total water potential (matrix, pressure or osmotic potential) best represents the water status of a plant (Richter 1976; Oertli 1976).

$$\Psi \text{ total} = \Psi \text{ matrix} + \Psi \text{ pressure} + \Psi \text{ osmotic}$$

Further, in drought prone environments the physiological and morphological features represented in the species assemblage may vary very greatly (Openheimer 1960; Grieve 1956; Grieve & Helmuth 1970; Givinish 1978). Each species has its own combination of "tolerance" and "avoidance" strategies (Levitt 1972; Sheriff & Kay 1977; Grieve & Hellmuth 1970), or method of maximising water use efficiency in conversion of CO<sub>2</sub> to dry matter (Hsiao & Acevedo 1974; Cowan 1977; Cowan & Farquhar 1977; Farquhar *et al.* 1980; Farquhar 1978; Rawson *et al.* 1978). The past history of exposure to drying cycles and droughts also affects the physiological responses of a plant to subsequent droughts (Jordon *et al.* 1975; Thomas *et al.* 1976). Interpretation and comparison of results, therefore, has to be approached with caution. Generally, in drought prone environments, most plants will survive soil water potentials of -2 MPa and some as low as -10 MPa, although little water is held in the soil between -2 MPa and -10 MPa (Passioura 1981) unless the soil has a high clay content.

The last decade of study into water transport through plants has led to renewed interest in the steady state model originally proposed by Huber (1924) and von den Honert (1948). The "Soil-Plant-Atmosphere Continuum" model considers the leaf water potential of a plant can be described in terms of the supply potential ( $\Psi_{\text{soil}} + \Psi_{\text{gravity}}$ ), the rate of water transport (flux) and the liquid phase resistance ( $r_{\text{soil to leaf}}$ ) (Elfving *et al.* 1972; Kaufmann & Hall 1974; Jarvis 1976).

$$\Psi_{\text{leaf}} = \Psi_{\text{soil}} + \Psi_{\text{gravity}} - (\text{flux})(r_{\text{soil to leaf}}) \quad (1)$$

In this equation the flux of water through the plant (or transpiration) is largely dependent on the absolute humidity difference between leaf and air ( $\Delta W$ ) and the stomatal conductance. A good estimate of flux is obtained by:

$$\text{flux (transpiration)} = \Delta W \times \text{stomatal conductance}$$

(Kaufmann 1981; Comacho-B *et al.* 1974).

The resistance to water flow ( $r_{\text{soil to leaf}}$ ) in the path from the soil to the leaf has numerous components whose contributions vary with values of  $\Psi_{\text{soil}}$  and  $\Psi_{\text{leaf}}$ . Firstly, the movement of water from distant soil to soil close to the root system is only important in wet soils whose hydraulic resistance is low (Passioura 1981). It is unlikely to be important during drought and need not be considered further. For movement of water within 1 cm distance from the root, the most influential parameters are root lengths (lengths of absorptive

surface) and the diffusivity of water (Passioura 1981). Diffusivity typically has a range of  $10^{-5}\text{cm}^2\text{sec}^{-1}$  in fairly dry soil ( $\Psi = -1.5$  MPa) to greater than  $10^{-3}\text{cm}^2\text{sec}^{-1}$  in moist soils ( $\Psi = -0.01$  MPa). However, resistances within the soil may be minor in comparison with the resistances at the interface between root and soil, and between the cortex and the stele of the root. Once inside the cortex of the root (at approximately the same potential as the soil) water diffuses in towards the stele. The largest drop in water potential in the plant usually occurs somewhere between the surface of the root and the xylem (Kramer 1969; Ramos & Kaufmann 1979); due in part to the tortuous path of water through the cortex and endodermis into the stele (Passioura 1981).

Once in the xylem of the root axial transport carries water to the leaf. In large plants and trees under static conditions a gravitational potential of  $-0.01\text{MPa m}^{-1}$  ( $-0.1\text{ bar m}^{-1}$ ) is present over the distance between the soil and the canopy. Also, during periods of high transpirational demand significant resistance to flow may occur in the trunks of trees. Up to  $-0.2\text{MPa m}^{-2}$  have been recorded in Sitka Spruce (Hellkvest *et al.* 1974). Radial movement of water in the crown presents still higher resistance, with resistances in secondary branches being twice that in primary branches which in turn are twice that in the trunk (Hellkvest *et al.* 1974; Hinckley *et al.* 1978). However when path lengths are considered the major resistance is in the trunk.

When leaf water potentials are measured throughout the height and breadth of the crown of a tree it becomes evident that differences in leaf potentials are very much a function of the vertical and lateral resistances within the trunk and branches. Hellkvest *et al.* (1974) found that leaf water potential generally increased with height through the crown but the apex of the crown exhibited lower water potential than the branches immediately below. This was apparently the result of a larger cross sectional area of xylem (hence lower resistance to flow) supplying the actively growing crown apex than supplying the branches below.

When moisture stress develops, the zones within the crown exhibiting symptoms of water stress are not always exposed to the microenvironmental extremes (Hinckley & Ritchie 1970). Water potential and stomatal conductance appear to be influenced independently by the microenvironment at each leaf and by the activity in other sections of the crown. There also seems to be substantial redistribution of water throughout the crown (Hinckley & Ritchie 1970).

Extremes of temperature also affect the resistance to water flow from soil to leaf. Low soil temperatures (below 7°C for temperate species) both increase the viscosity of water and lower the permeability of the root system to water (Kaufmann 1979; Kaufmann 1977). The high root resistances produced at low temperatures can depress leaf water potential even under moderate transpiration fluxes (Kaufmann 1977).

While soil moisture is not limiting and under moderate atmospheric conditions, the leaf water potentials of most plants will exhibit a rapid decline at dawn when stomata open; remaining at depressed levels during the day and restoring fully at dusk when stomata close (Hinckley *et al.* 1978). The extent of depression of leaf water potential will depend on the transpirational flux and the resistance to water flow from the soil to the leaf (equation 1). As the reserve of soil moisture is depleted the midday leaf water potentials become further depressed, and the facility to restore water potential at dusk to the levels of those at dawn is lost (Cowan 1965). For most plants suffering periods of low soil moisture or drought, some regulation of moisture loss is afforded by a rise in stomatal resistance or stomatal closure (Hinckley *et al.* 1981). The extent of stomatal closure and the threshold levels of water potential at which they close varies greatly from species to species (Sherrif & Kay 1977; Levitt 1972). Early in a drought, during periods of high evaporative demand, there is a hysteresis developed between water potential and stomatal resistance (Kaufmann & Levey 1976; Kaufmann 1977). Later, during severe droughts, stomata are closed all day and water potentials remain at low levels throughout the day (Sinclair 1980; Reich & Hinckley 1980; Hinckley *et al.* 1978).

Repeated exposure to drought or drying cycles induces physiological changes or "hardening", both by increasing stomatal resistance during periods of high evapotranspirational demand (Kaufmann & Levey 1976) and by reducing the depression in water potential necessary to induce stomatal closure (Thomas *et al.* 1976; Jordan *et al.* 1975).

### Stomatal Conductance

During the process of photosynthesis there is an unavoidable loss of water vapour through the leaves associated with the opening of stomata to obtain CO<sub>2</sub>, and with the elevation of leaf and air temperature in sunlight. Where supply of soil water is limited sensitive control of stomata is paramount in the conservation of dwindling water resources, particularly for woody perennial



plants. The threshold levels of stomatal response to the key environmental factors (light, temperature,  $\text{CO}_2$  concentration, absolute humidity difference between leaf and air, and water status) which affect stomatal conductance vary greatly from species to species (Sherrif & Kay 1977; Hinckley *et al.* 1981) giving rise to the classical divisions of "drought avoiders" and "drought tolerators" (Levitt 1972).

Stomatal conductance is governed independently by the five environmental factors: photosynthetically action radiation flux (P.A.R.); the absolute humidity difference between leaf and air ( $\Delta W$ ); carbon dioxide concentration ( $[\text{CO}_2]$ ); temperature; and water stress (usually measured as water potential,  $\Psi$ ) (Kaufmann 1981a, 1981b). However, the primary factors influencing leaf conductance are P.A.R. and  $\Delta W$  (Kaufmann 1982a, 1982b; Schulze *et al.* 1972, 1973, 1974). Temperature and water stress do not influence leaf conductance until they become extreme. The inhibitory effect of  $\text{CO}_2$  on stomatal conductance is in inverse proportion to its concentration over a broad range of concentrations (West & Gaff 1976; Hall & Kaufmann 1976). As the concentration of  $\text{CO}_2$  is relatively stable in the field it is not considered a major influence on stomatal conductance.

In the absence of light, stomata are closed or have a low conductance. An increase in P.A.R. elicits a proportional increase in stomatal conductance until a threshold conductance is reached above which increased P.A.R. has no effect. The value of P.A.R. at which no further increase in stomatal conductance occurs is very variable, depending on the species and the past history of the light climate (Kaufmann 1982a; Jordan *et al.* 1975; Thomas *et al.* 1976). The threshold P.A.R. may be anywhere between 10 and 90% of sunlight.

The absolute humidity difference between the leaf and air ( $\Delta W$ ) has an inhibitory effect on stomatal conductance. The stomatal conductance is inversely proportional to  $\Delta W$  to the point of stomatal closure at extremes (Schulze *et al.* 1972; Camacho-B *et al.* 1974; Sherrif & Kay 1977) regardless of the bulk water status of the leaf. The effect of  $\Delta W$  can be accentuated by strong winds which break down the diffusion barriers around the stomatal pores, effectively increasing the steepness of the diffusion gradient (Heath 1975; Mansfield & Davies 1981).

A rise in stomatal conductance with increased temperature reported by some investigators can largely be accounted for in terms of changes in  $\Delta W$  with temperature (Kaufmann 1981b). In fact the effects of temperature on leaf conductance are minor except when rapid changes occur or when temperature is extreme (West & Gaff 1976; Kaufmann 1981a, 1981b).

Water stress is a dependent rather than independent variable in its effect on stomatal conductance. When water stress becomes severe, that is, for many plants when leaf water potential approaches  $-2$  MPa, a large number of physiological and biochemical factors within the plant become affected (Hsiao 1973). Water stress has been shown to effect the response of stomatal conductance to absolute humidity difference from the leaf to air ( $\Delta W$ ) (Jordan *et al.* 1975; Thomas *et al.* 1976) and to  $\text{CO}_2$  concentration (Gaff & West 1976) by increasing stomatal sensitivity to changes in these two factors and, by lowering the threshold level at which a response is first elicited. Many plants, if exposed to repeated drying cycles of the same intensity, will exhibit earlier and more complete stomatal closure in response to lowering  $\Delta W$  and rising  $\text{CO}_2$  concentration (Hall & Kaufmann 1976; West & Gaff 1976; Mansfield & Davies 1981). Stomatal closure at low leaf water potentials has also been linked with the release of the plant hormone abscisic acid (ABA). ABA may directly induce stomatal closure or may act to increase the sensitivity of stomata to such factors as  $\Delta W$  and  $\text{CO}_2$  concentration (Raschke 1975a, 1975b; Mansfield & Davies 1981).

It is not yet possible to predict the effects of P.A.R.,  $\Delta W$ , temperature and  $\text{CO}_2$  concentration on leaf conductance when all factors vary (Kaufmann 1981a) particularly when these are complicated by interactions with water stress and ABA release.

### Biochemical Influences on Stomatal Action

There is good evidence to suggest that the guard cells of the stomata are not interconnected to the other epidermal cells, or to the mesophyll through plasmodesmata (Allaway & Milthorp 1976; Mansfield & Davies 1981). The transport of ions and metabolites both into and out of the guard cells is therefore subject to the constraints of transport across membranes. Without cytoplasmic continuity with the surrounding cells steep ionic and osmotic gradients can be developed between the guard cells and their neighbours.

Studies by Wilson *et al.* (1978) and Penny & Bowling (1974) indicate that coincident with the opening of stomata is an influx of  $K^+$  ions into the guard cells and a reduction in the number of starch granules present in the guard cells. It has been suggested that the  $K^+$  ion enters the guard cell and is instrumental in developing the osmotic gradient required for the inward diffusion of water (Meidner & Mansfield 1968; Itai *et al.* 1978). The starch content of the guard cell is lowered by its conversion to the malate ion (Willmer & Rutter 1977), a negative ion produced in the amounts necessary (in concert with  $Cl^-$  ions) to balance the charge ratio within the guard cell. The combined effect of the two osmotica ( $K^+$  and malate $^-$  ions) is to set up an osmotic gradient sufficient for the guard cells to become turgid (Mansfield & Jones 1971; Humble & Raschke 1971).

In many plants when leaf water potential is reduced below a threshold level (about -2 MPa, but this depends greatly on the species and the previous climatic history of the individuals tested) hormonal inhibition of stomatal action may occur via release of large amount of abscisic acid (ABA) (Wright 1969; Wright & Hiron 1969). Studies of detached epidermal strips indicate that the site of ABA production is not within the epidermis of the leaf. However, external application of ABA to epidermal strips causes stomatal closure, apparently by altering the permeability of the guard cells to  $K^+$  ions and mediating in the loss of malate from the guard cell. The result is a substantial loss of turgidity of the guard cell (Mansfield & Jones 1971; Mansfield & Davies 1981).

The site of production and storage of ABA appears to be in the chloroplasts of the mesophyll (Loveys 1977; Itai *et al.* 1978). The release of ABA is triggered by the blocking of one step in the biosynthesis of geranyl-geranyl pyrophosphate from farnesyl pyrophosphate. The biosynthetic block results in the production of large amounts of all-trans-farnesol (Mansfield *et al.* 1978). All-trans-farnesol has the effect of dramatically increasing the permeability of the chloroplast membranes to ABA and stimulates the rapid synthesis of more ABA (Fenton *et al.* 1977). The result is a massive efflux of ABA from the mesophyll. ABA acts as a messenger from the mesophyll passing through the plasmodesmata to the epidermal cells (cells other than the guard cells of the stomata, which have no plasmodesmata). Once it has reached the guard cells ABA appears to interfere with the ion exchange of the guard cells, inhibiting the uptake of the  $K^+$  ion and triggering the loss of starch through the efflux of the malate ion to neighbouring cells (Mansfield & Jones 1971; Mansfield & Davies 1981; Dittrich & Raschke 1977). The loss of osmotica causes a corresponding loss of guard cell turgor. Recovery is slow and is further retarded by the lack of plasmodesmata to the guard cells.

## APPENDIX 6.2

### P.F. CURVES

#### APPENDIX 6.2. P.F. CURVES

PF curves obtained in the laboratory using the filter paper method (after Hamlin 1981) for soils at (a) Site 0, (b) Site 1, (c) Site 2 and (d) Site 3 where soil profiles were dug in stands of E. delegatensis, E. pulchella, E. coccifera and E. gunnii respectively (see Fig. 6.9).

PF curves were obtained for soil horizons B<sub>1</sub> (dashed line) and B<sub>2</sub> (solid line) at sites 0 and 2, and for horizons A (broken line) and B<sub>1</sub> (solid line) at site 3. At site 1 PF curves were generated for the B<sub>1</sub> horizons of two soil profiles; stand 1 (solid line) and garden 1 (broken line). Curves were used to calculate moisture reserves between F.C. and P.W.P. for soils at each site (Table 6.7).

APPENDIX 6.2.

