

PROVENANCE VARIATION IN EUCALYPTUS

CAMALDULENSIS Dehn.

by

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STATEMENT OF ORIGINALITY

Except where specific acknowledgement is given,
this thesis is my own original work.

A handwritten signature in black ink, appearing to read 'J.O. Awe', written in a cursive style. The signature is positioned above a horizontal dotted line.

J.O. Awe

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SUMMARY

A study has been made of the influence of several environmental factors on seed germination and seedling growth of E. camaldulensis from a number of regions throughout its extensive range.

Seedlots from six provenances of E. camaldulensis were used to determine the effects of a range of temperature regimes on the germination behaviour of the species. There was no germination at the lowest temperature regime (15/10°C.) in any of the provenances at day 6 of seed germination. At the same period of seed germination, there was a marked north-south division at the temperature regime of 18/13°C. - the seeds of the southern provenances germinated rapidly but little or no germination was recorded for the seeds of the northern provenances. For all the provenances the optimum temperature for maximum seed germination was between 30/25°C and 33/28°C.

Some effects of light conditions on seed germination were examined in relation to provenances. There appears to be no distinct difference between provenances in light requirement for seed germination, but seeds may be positively photoblastic to red light region of the visible light spectrum.

Progenies of E. camaldulensis from several provenances were grown under a range of environmental conditions - three temperature and three photoperiod regimes. Temperature had significant effects on growth of E. camaldulensis, and the optimum temperature for many

of the seedling growth characteristics and dry weight productions was the medium temperature (27/22⁰C.). In these studies there were marked differences in seedling characteristics between provenances, suggesting a positive natural selection in northern regions of individuals with adaptation to harsher environmental conditions. There were some differences between provenances in their reaction to variation in photoperiod. The provenances differed in seedling height growth at 12- and 14-hour photoperiod, for example, at these photoperiods Todd River provenance had the greater height growth and Katherine provenance the least. However, it was demonstrated that in the case of Todd River provenance, seedlings responded in height, but not in dry matter production.

The effect of frost treatment on the provenances of the species was examined under a range of controlled conditions. Frost resistance in the species varies according to seed origin. For unhardened seedlings, the northern provenances were more frost resistant than the seedlings from the southern provenances. When seedlings were prehardened before frost treatment, there was a reversal of the results for unhardened plants, that is, the southern provenance seedlings were more resistant to frost than the seedlings of northern origin.

A study was made of the effect of provenances on early root development and results were compared with those obtained for 2 coastal eucalypts - E. saligna and E. pilularis. There were no marked differences between provenances of E. camaldulensis in their root production, but marked differences exist between E. camaldulensis

and the 2 coastal eucalypts in this respect. All the provenances of E. camaldulensis are capable of developing roots very rapidly to explore any drying soil, thereby helping ensure survival in harsh environmental conditions.

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The bulk of the experimental work was performed at CERES, the phytotron of CSIRO, Canberra. Space and equipment were made available by Mr R.L. Dunstone. I wish to thank Mr Dunstone and the staff of the Phytotron for their help.

All the frost treatments were carried out at Botany Department frost room. I wish to thank Dr D.M. Paton and Mrs P.G. Holden of Botany Department of their assistance and for the use of the frost room.

The whole project could not be carried out without the approval of Professor J.D. Ovington, Head of the Department of Forestry. I am therefore grateful to Professor Ovington for the assistance and the interest he showed in the study.

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CHAPTER 1

LITERATURE REVIEW

THE STUDY OF VARIATION AND IMPROVEMENT IN FOREST TREES

Foresters have recognised inherent differences between individuals within forest tree species as far back as the 16th century. Many techniques have been used to detect these differences and to describe them. Variation in tree species have been studied in taxonomic, genetic, and more recently in genecological terms. Genecological studies involve correlation between metric characteristics of the plants and their habitats. These can be carried out in field experiments to establish the genetic bases of variation, and in breeding experiments under controlled or natural conditions. Planting experiments have also been used to explain environmental selection and ecotypic differentiation in plants. Physiological and morphological characteristics of plants measured either in the natural habitat or in the controlled environment appear to be the essential tools of genecologists in studying variations and evolution in forest tree species.

1.1 Taxonomic Approach

Taxonomic investigations were the earliest applied to the study of variation in forest tree species. These were both inexpensive and rapid. A complete study may involve the use of herbarium material and collections made in local wild populations. Differences in

floral parts, buds, cones or seed capsules, leaves and tree barks are taken as indications of variation in the local population, but this does not permit separation of the environmental from the genetic effects. A number of examples of taxonomic study of variation follow. Forde (1964) made a thorough taxonomic investigation of Pinus radiata in its natural populations. She scored a number of morphological characters such as branches, cones, and needles collected from the wild tree population in California. She found that the species consists of three disjunct populations, and within the populations some variation was apparent.

Using the same type of approach, Daubenmire (1968) studied some geographic variations in Picea sitchensis and discussed their ecologic interpretations. His studies were concentrated in Northern California where he collected ovuliferous cones, twigs and needles of the wild trees and hybrids of the species to examine the morphological characteristics. Variability in the species was found to result from unrestricted gene flow in the population.

Another typical example of taxonomic approach to genealogical investigation is that of Critchfield (1957). Specimens of Pinus contorta were collected from wild and cultivated populations of the species and a study made of the way morphological characteristics vary with habitat. Analysis of numerous quantitative characters resulted in the division of the species into four taxonomic subspecies exhibiting geographic unity and heritable differences.

The taxonomic approach is a useful guide to variation in a forest tree species but in the past has sometimes been of limited

value because within-population variation has been based on limited field material. More recent studies however, include much more comprehensive collections and locality descriptions, permitting correlations to be made between the taxonomic characters and habitat.

1.2 Environmental and Genetic Variation

Two major categories of variation form the basis for all studies on variation and evolution in plants. The first kind of variation may be referred to as ENVIRONMENTAL VARIATION. Two plants having identical gene-makeup, will not necessarily receive exactly the same amounts of light, water, and nutrients - even where grown side by side in a field situation. Thus, when these two individuals develop some different morphological characteristics, we have environmental variation. The second type of variation in forest tree species occurs where there are differences in the genetic makeup of individuals. This may be caused by changes in the structure of genes, by mutation, and by recombination of genes associated with sexual reproduction. Sinnott, Dunn and Dobzhansky (1950) describe such variation as HEREDITARY OR GENOTYPIC VARIATION. According to Daubennuire (1967) genotypic variation within a species results from the cumulative effect of a long series of minute changes in the organism over a period of time. In nature, variation recorded in a species may be partly environmental and partly genetic in origin.

Adaptive selection. In any one environmental situation those plants survive that are in rhythm with diurnal and seasonal periodicities of the habitat, that can tolerate the moisture and wind conditions,

that can utilise the soil there, and that can compete with other plants and animals. The environment constantly eliminates unfit variants and in this manner acts as a sifting screen but the sifting of the various environments differs, and ecologically different races or "ecotypes" result. Turesson (1922a) first used the term ecotype and defined it as "the product arising as a result of the genotypical response of an ecospecies or species to a particular habitat". Ecotypic variation refers to differences in morphological and physiological characteristics of organisms which developed as adaptive features of the organisms to a particular environment.

This type of variation is recognised by the observation of habitat-correlated variation in morphological features. Many wide-ranging species are considered to possess a considerable amount of ecotypic variation. Where habitats differ in a number of ways, adaptation in several features will be essential for the survival of the organisms. Heslop-Harrison (1964) thought that, higher plants would need to adjust their "developmental cycle" for adaptation to a range of climatic changes. If a species is to survive adverse conditions a special mechanism for protection needs to be developed so that the species can make normal evolutionary progress only under suitable conditions.

Transplant experiments may be used to test this type of variation. Individuals or the offspring of many individuals from a range of ecological conditions are raised under controlled conditions, and differences between individuals which are observed when grown in similar environments are ascribed to differences in genotype.

Many attempts have been made by genecologists to demonstrate ecotypic variation in forest tree species. For example, Squillace and Silen (1962) established that the growth rate of ponderosa pine (Pinus ponderosa) from different habitats was strongly correlated with moisture distribution in the habitats. Ecotypic variation may also result where a species is subjected to variations in habitat temperature and daylength. Since seasonal variations in temperature and daylength serve as clocks in the plant habitat, thermal and photo-periodic responses become selective, and adaptation to the conditions can be achieved by the modification of thermo-photoperiodic reactions (Heslop-Harrison 1964).

Photoperiodic adaptation has been demonstrated in forest tree species which are distributed over a wide latitudinal range. Vaartaja (1954, 1959) found variation in the responses of northern and southern races in several tree species tested for growth rate and onset of dormancy under various photoperiods. Using controlled photoperiods in cabinets, he examined the growth rate of seedlings of many forest tree species grown from seeds derived from wild or natural populations. Due to the effect of long days, apical growth continued in northern races consisting of Pinus sylvestris, Larix ladicina and Picea abies, while some southern races required short photoperiod for apical growth.

Huxley (1938) used the term character gradient or cline to describe variation where a character gradient can be correlated with an ecological gradient. Most species that span a range of latitudinal and altitudinal climatic areas will possess clines for the physiological

and morphological characteristics adapting them to the ecological conditions present in different parts of their range.

There have been many investigations of clinal variation in forest tree species. For example, Langlet (1959), and Wright and Baldwin (1957) have shown intraspecific ecoclinal variation in scots pine (Pinus sylvestris). Ecoclines are clines related to ecological gradients within a restricted area. Clinal variation in scots pine, which spans over 25° of latitude, involved several morphological and physiological features such as leaf length, hardness, dormancy period and shoot extension rate. Both continuous (clinal) and discontinuous (ecotypic) variations were found in the species. In the 1938 international test involving fifty-two provenances, some northern provenances occupied latitudinal belts and had a clinal relationship to each other, while the southern provenances had no particular latitudinal or climatic limits.

Barber (1955), and Barber and Jackson (1957) have established the presence of clinal variation in several species of Eucalyptus in Tasmania. In field observations along a transect passing from altitudes of 2500 feet to 4000 feet in north central Tasmania, parallel clines were demonstrated in E. gigantea, E. gunnii and E. coccifera. For example, the authors suggest that changes in glaucousness of the leaves and stems represented changes in the gene complement controlling wax development; along the altitudinal transect there is a temperature gradient - there is a selective advantage in waxy surfaces and as the temperature decreases towards the high altitude, there is an increase in glaucousness.

In the like manner, Eldridge (1969) investigated clinal variation in E. regnans in Victoria (Australia). He used transplant experiments to examine the physiological characters of the seedlings raised from seeds of wild species collected along an altitudinal transect on Mount Erica, Victoria. He supplemented his field work with observations of the seedlings under controlled environments. Clinal variation was found between and within populations along the transect.

Similarly, Pryor (1956c) and Geen (1968) found that snow gum (E. pauciflora) populations vary clinally in several directions indicating correlation with habitat variations.

Use of planting experiments to investigate adaptive responses.

Planting experiments can be used to investigate adaptive responses of species to a range of diverse environmental conditions. Turesson (1922b), Gregor (1938a 1939) have shown by careful transplant experiments that species from different habitats retain their differences when planted in different conditions, and hence can be concluded as being genetically different. The species retained their genetical identity even when they were grown side by side in constant-environment gardens.

A refinement of the transplant techniques was developed with great success by Clausen, Keck, and Hiesey (1940) and Turrill (1940). These authors divided a single large perennial plant into several parts and grew the clonal divisions under different environmental conditions, thus retaining identical genetic complexity of the individual ramets. By this method important physiological differences in plants were discovered. Some genotypes have a

constitution which can be modified by the environment, and this in turn makes analysis of the results of transplant experiment hard to explain, but many species have a rigid genetical constitution that can be affected by environmental factors.

In Australia, Pryor (1956) and Green (1968) have used out-plantings to study clinal variation in snow gum (E. pauciflora). Seedlings raised from open pollinated seeds of the natural population at different elevations were transplanted. From the data obtained, it was evident that seedlings from high altitude were more resistant to frost than those from low altitude. The survival rate in winter was also higher in high altitude plants than in low altitude plants. Similarly, Pryor and Byrne (1969) used transplant techniques to study broad variation patterns and taxonomy of E. camaldulensis. They found both longitudinal and latitudinal variation within the species, and recognised two distinct ecotypes of northern and southern origin, based on variation on genetic properties such as glaucousness of leaves, and presence or absence of lignotubers. Their findings confirmed the results obtained by Karschon (1967) who grouped the species into two broad types, based on physiological characters of transplants. Burley, Wood and Hans (1971) used trees from 25 provenances of E. camaldulensis planted in 1967 at Chati Forest Reserve on the Zambian copper belt to investigate variation in physiological characters of the leaves. They found that provenances differed significantly in leaf length and width, base angle and oil gland density. Their results are in line with what other scientists have discovered about the same species.

Working on geographic variation in survival, growth and fusiform-rust infection of planted Loblolly pine, Wells and Wakely (1966) used the seedling outplanting technique and found that seedling survival, height growth and rust infection are genetically controlled within this species.

Very little attention has been given to provenance studies of tropical forest tree species. A few economic species such as teak (Tectona grandis), Acacia species and some tropical pines have received some attention over recent years. For example, in his studies on teak (Tectona grandis) in Thailand, Hedegart (1971) set up trial plots of teak at Huey Tak Teak plantation and Kiu Tup Yang plantation using seedlings from 63 natural populations. Seed size and weight varied considerably between the populations, as did the survival and height growth.

Biochemical studies. In recent years, the usefulness of biochemical criteria in evolutionary and systematic studies has been demonstrated. The chemical characters of forest tree species are examined and analysed to aid taxonomic classification and to explain the type of variation in plant kingdom.

Using paper chromatograms of needle extract substances, La Roi and Dugle (1967) carried out systematic and genealogical studies of two closely related spruce - Picea glauca and Picea engelmannii. Collections were made of branches, needles and cones of the species. Sampling was done in the wild populations throughout the range of the species. Arboretum, nursery and plantation specimens were also collected to supplement the studies on natural

population. Flavonoid and phenolic compounds from the various specimens were examined chromatographically, and morphological indices for a number of characteristics were also scored. The data were analysed to find out whether variation within the species could be correlated with habitat. The species exhibited distinct variation in their chemical composition, and the data were also found useful in distinguishing the species.

In the same manner, Banks and Hillis (1968) used a biochemical approach to demonstrate a northern and a southern ecotype in Eucalyptus camaldulensis. Chemical extracts from leaf and seed specimens of natural population of the species were chromatographically examined. These authors found they could divide the species into two distinctive groups based on the chemical data, and these groups were similar to those previously identified using morphological and physiological characteristics (Karschon 1967, Pryor and Byrne 1969).

The influence of environmental factors and the significance of physiological plasticity in the chemical characters can not be evaluated unless further studies are carried out in controlled environment and probably in provenance studies.

1.3 Genetic Studies on Forest Trees

Geneecological investigation of forest tree species need not be limited to the detection and description of variation in forest trees and the way variation correlates with environmental factors. It may also involve the study of those aspects of tree genetics which can have a direct bearing on tree breeding. Methods and techniques

for the study of the genetics based on theoretical principles, have been developed to help improve the genetic constitution of trees for man's benefit. These studies have concentrated on the study of adaptive properties of plants, heritability estimates, combination of genetic characteristics through hybridization, and tree breeding techniques generally.

(a) Adaptive properties of forest trees

Adaptive characters in plants are inherent characters which can not be affected by environment, but are genetically controlled. For example, Rudman and his associates have used X-ray densitometric techniques to study the wood density and the adaptive characteristics of three eucalypt species. The fibre length of the three species was also examined by measuring delignified fibres using a projection microscopy. They found both wood density and fibre length to be under strong genetic control. Therefore it would be possible to select for wood density and fibre length to develop genetically uniform stock for different products. Higgs (1969) investigated in more detail the factors affecting the wood density and fibre length of E. regnans by examining the wood properties of seedlings grown under controlled environment. He supplemented this work by examining the properties of wood from trees growing in wild populations of the species. He discovered that temperature affects both fibre length and wood density of seedlings growing under a range of temperatures. Fibre length was greater at higher temperatures in the range 15/10^o to 24/19^oC. (day/night) temperatures, but was smaller at 27/22^oC. than that at 24/19^oC. The variation in average wood density at different

temperatures differed from those for fibre length. Wood density tends to be smaller at higher temperatures. For adult plant in natural population, Higgs found that fibre length was greater at greater distance from the pith at all height levels of the tree.

(b) Heritability estimates

Heritability is the measure of strength of inheritance or transmissibility of a trait which might be selected for, or gained, in tree breeding. Heritability values can be estimated from information derived from a well-designed and replicated experiment which can indicate the variance of a particular characteristic, both between and within families of offspring.

Two types of heritability are commonly referred to are "narrow-sense" and "broad-sense" heritability. Broad-sense heritability of a trait can be measured by growing vegetatively reproduced clones in a uniform environment, and measuring the variation in that trait. In vegetative propagation of plants there is no change of gene constitution, and plants derived in this way are expected to have the same properties as their parents.

In any study of narrow-sense heritability, sexual reproduction is needed, and this involves the use of seedling stock derived from 'open' or controlled pollination experiments. The heritability values derived from the seedlings raised from seeds are expression of the genes transmitted during genetic recombination at meiosis. After sexual reproduction, narrow-sense heritability have been estimated for height, stem diameter, wood densities, and fibre length

in forest trees, and genetic control of their properties has been demonstrated. Higgs (1969) considered that the estimates of narrow-sense heritability in E. regnans are large enough to justify the implementation of tree improvement programmes for useful genetic gains.

(c) Hybridization

According to Wright (1962) hybridization in forest tree species is the crossing of distinct species, races or portions of clones for tree improvement purposes. The main goal of tree breeders is the combination of desirable characters from two or more parent trees. Wright has proposed a procedure for a hybridization programme: (i) The species 'crossability' should be determined, followed by repetition of successful crosses using several provenances of the parent species involved, (ii) nursery and field testing should be carried out to determine the hybrid vigour, and (iii) any promising hybrid of desired species should be mass produced.

Many investigations on hybridization have been carried out in both soft wood and hard wood species. One of the first recorded instances of hybridization was the cross between Larix leptolepis and L. europaea (Japanese and European larches) to produce the hybrid known as Larix eurolepis. The hybrid was of vigorous growth, but it was mainly its capacity for resistance to the dangerous "larch canker" which gave it popularity. Other examples of importance in plantation forestry in Australia relate to hybrids between Pinus radiata and Pinus attenuata, and between Pinus elliotii and Pinus caribaea. Hybrids of Pinus radiata and Pinus attenuata occur naturally in

Santa Cruz county, California and they have been produced artificially in California. These hybrids are found to be intermediate between the parents in growth rate, cold resistance, stemform and flowering time. The hybrids may not possess any advantage over the fast growing, high-quality Pinus radiata in warm areas of Australia, but they certainly offer a means of introducing valuable radiata pine genes into cool areas.

In Queensland, Slee (1968) found that the hybrid between Pinus elliottii var. elliottii and Pinus caribaea var. hondurensis has a seasonal growth pattern intermediate between that of the parents, and an adaptation to the soil conditions of the coastal lowlands of Queensland, that is more like that of the Pinus elliottii parent.

(d) Tree breeding

Many genealogical studies have been a basic part of tree breeding programmes. The main objective of tree breeders is to develop stands of individuals with the more desirable inherited characters. This may be achieved by increasing the plant growth rate, producing higher quality wood, and inducing resistance to biotic and non-biotic factors.

Many of the methods used in tree breeding are based on selection of the best populations or individuals within population, estimating of the heritability of desirable characters and the propagation in seed orchard of those individuals with desirable characters which are under a large degree of genetic control.

Methods of tree breeding have been classified into three major categories by Vidakovic (1969). These categories include -

- (a) Breeding by selection,
- (b) Breeding by hybridization, and
- (c) Breeding by mutation and polyploidy.

The description and applicability of each method have received attention by Duffield (1962), Wright (1962), Vidakovic (1969) and many other forest geneticists.

CHAPTER 2

INTRODUCTION TO STUDY OF EUCALYPTUS CAMALDULENSIS

2.1 Purpose of Study

Provenance differences can be expected to occur in E. camaldulensis because of its widespread distribution covering a wide range of environments. Provenance in this study will refer to seed of known origin, and origin the locality of collection. The distribution pattern of E. camaldulensis provides a logical basis for a division of the species according to major river systems in Australia (Larsen 1967), and almost limitless further sub-division is also possible into isolated populations in the tributaries of the major rivers. On account of the wide occurrence of E. camaldulensis the varieties listed by Blakely (1965 3rd Ed.) are now regarded as adaptations to particular habitats and are included with the species (Johnston, Marryatt 1965).

Provenance differences can be exhibited in many ways. Physical and physiological differences of possible ecological importance have been shown to occur in Eucalyptus, for example, occurrence of lignotubers (Karschon 1971), susceptibility to frost (Paton 1972), and glaucousness of the leaves (Barber 1955). Such reactions to changed environmental factors may be very pronounced and in some instances so pronounced as to render a provenance unsuited to a particular environment. Only recently has work on the eucalypts begun to document provenance differences but the importance

of these differences has long been recognised for many European species and provision made for these differences in forest practice [Langlet 1959, 1963].

The importance of understanding provenance variation in forest trees and in particular in E. camaldulensis can not be underestimated. The information provided by the studies on provenance assists the effective choice of provenance for the establishment of the species in plantations. A knowledge of the pattern of variation and adaptability of the species to certain environmental conditions may eventually help in directing a tree breeding programme for a particular locality.

The objective of this study, therefore, is to explore several of the ways in which provenance difference can be exhibited in E. camaldulensis under a range of controlled environmental conditions.

2.2 Distribution of E. camaldulensis, Dehn

Eucalyptus camaldulensis, Dehn, (Syn. E. rostrata, Schlechtend) is commonly known as river red gum. It is a medium to moderately tall tree, usually with a large diameter. In open forest formation, the bole is short and thick with a large crown. E. camaldulensis is the most widely distributed of all eucalypts in Australia. It is found throughout mainland Australia with the exception of the southern parts of Western Australia, the coastal fringes of Victoria, New South Wales and eastern Queensland (Figure 2.1). It is completely absent from Tasmania.

E. camaldulensis occurs along or near almost all the seasonal water courses in the arid and semi-arid areas of Australia and is found along many other streams and rivers in the south-east of the Great Divide (Hall, Johnston and Chippendale 1970). The principal location is along the Murray River and its tributaries and the lowlands of south-west Victoria (Hall, Johnston and Marryatt 1963). For the most part it forms open savannah woodlands and is limited to a narrow strip along the rivers which are regularly inundated by flood waters. The broader the river flood plain, the wider is the zone occupied by E. camaldulensis forest. Although mainly a tree of riverain and plain locations E. camaldulensis sometimes extends beyond this habitat. It can occur at quite high elevations as for example in the Mount Lofty and Flinders Ranges of South Australia and in the sub-tropics where the species extends to 600m at Alice Springs, Northern Territory. The altitude where satisfactory growth takes place is usually between 30 and 230m (Hall, Johnston and Marryatt 1963).

Latitudinally the principal occurrence is from 33° to 36.5° S but the range is very much wider, from 15.5° to 38° S.

E. camaldulensis grows under a wide range of climatic conditions, from tropical to temperate, but mainly in areas of low rainfall and high summer temperatures (Tables 2.1 and 2.2). The annual rainfall throughout its range of occurrence is mainly 200 to 600 mm, but limited areas receive up to 1000 mm. In areas of 200 to 350 mm rainfall the species relies on seasonal flooding or the presence of a high water table for establishment and survival. E. camaldulensis is resistant to drought as well as to winter frost.

Although E. camaldulensis thrives under seasonal inundation, it cannot tolerate submersion for a long time, especially during the summer when the soil temperature of the flooded areas is too high for the survival of the species. The highest quality of E. camaldulensis pure forest is generally found on the lower ground subject to regular flooding except in the case of permanent or quasi-permanent swamps which are only populated by reeds and swamp grasses (Jacobs 1955). With rising level and decreased frequency of flooding, the quality of E. camaldulensis forest tends to decrease. At levels where flooding is very infrequent, E. camaldulensis is of low quality and is mixed or replaced by box species such as yellow box (E. melliodora, A. Cunn. ex Schan.), grey box (E. microcarpa Maiden), and black box (E. largiflorens, F. Muell. Syn. E. bicolor A. Cunn.). In the Western forests of Victoria and New South Wales, black box (E. largiflorens) replaces E. camaldulensis on higher ground.

2.3 Economic Significance of E. camaldulensis

Eucalyptus camaldulensis serves a limited role in Australian forestry practice. However, it has some value for the production of hardwood along the Murray River. The areas has been cut over for logs, sleepers and piles for over 100 years. Past utilisation standards were high and selective logging has left some stands consisting almost entirely of over-mature trees. Early logging made use of the regular winter-spring floods which inundated the area and produce was removed by water traffic. Wheeled transport now operates in the dry summer-autumn months.

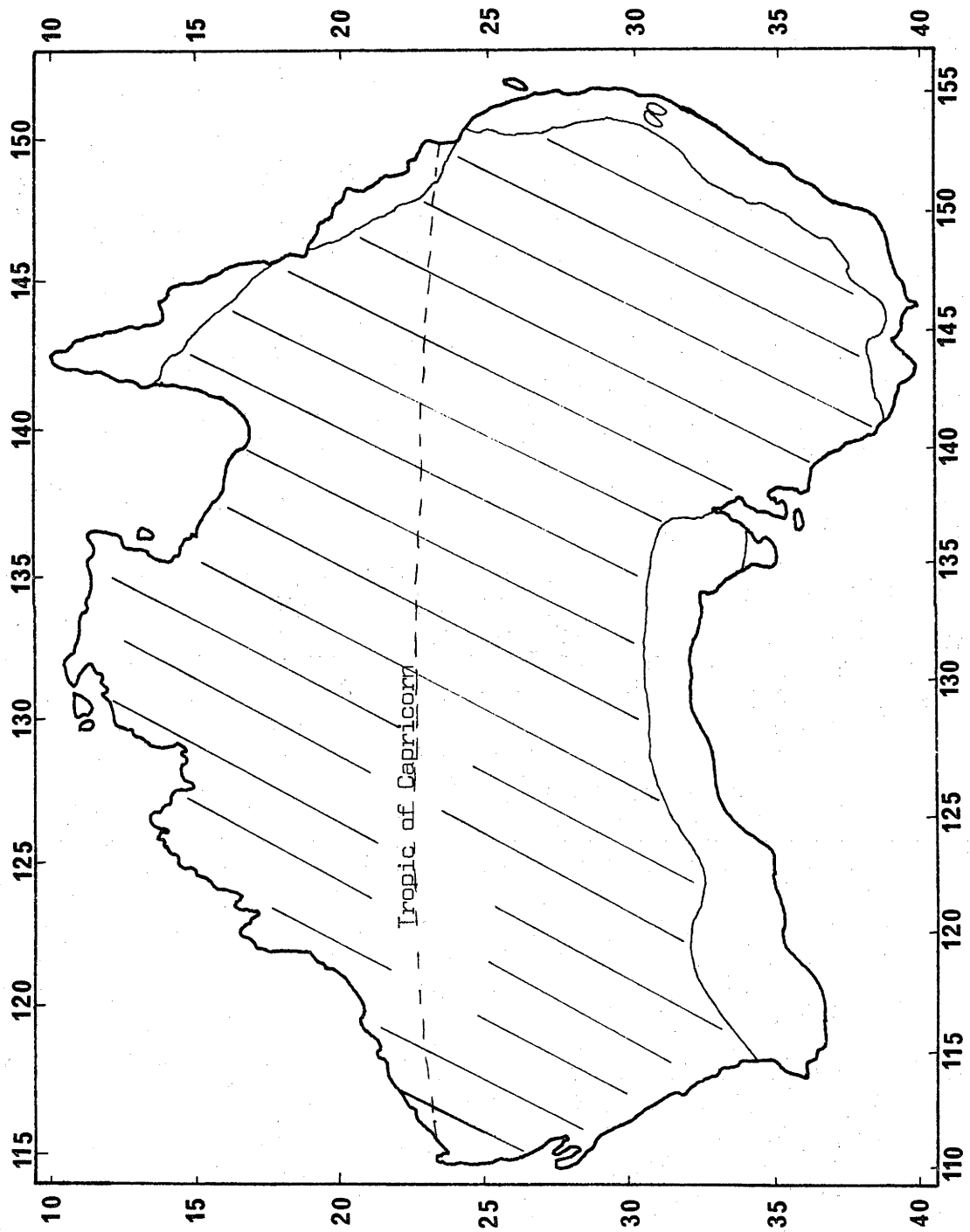


FIGURE 2.1 Distribution of E. camaldulensis in Australia
Source: Forest Trees of Australia (Hall, Johnston and Chippendale 1970).

TABLE 2.1 Average Monthly Precipitation (mm) of the Typical Location of E. camaldulensis.

Principal Locations	J	F	M	A	M	J	J	J	A	S	O	N	D	Total
Katherine	229.36	203.20	160.53	29.97	5.08	2.29	0.76	0.51	6.10	30.48	84.33	205.74	958.35	
Roy Hill	43.43	40.13	62.23	18.80	17.78	6.10	6.86	3.79	3.81	11.18	10.41	29.21	268.73	
Petford	228.85	237.49	119.39	77.47	48.26	32.00	26.16	14.22	13.72	20.57	69.09	140.21	1107.44	
Nathalia	30.73	35.05	31.75	39.37	44.20	56.13	51.56	52.07	48.26	49.02	32.51	35.81	506.48	
Gwydir R.	54.86	47.24	55.88	32.77	44.20	49.53	43.69	30.73	33.53	41.66	48.26	61.98	544.33	
Agnew	23.37	15.75	40.64	17.53	23.37	18.29	14.22	11.94	3.30	7.11	11.43	17.27	204.22	
Lake Albacutya	16.26	30.23	15.75	22.35	33.02	34.04	34.80	34.29	37.34	30.23	25.91	32.26	346.48	
Todd R.	44.20	33.53	27.69	9.91	15.24	13.21	7.37	7.87	7.11	18.03	29.21	38.86	242.22	
Mildura	18.29	20.32	15.75	13.21	25.40	28.18	25.15	21.84	18.54	23.88	19.30	16.26	234.12	

Source: Climatic Averages Australia. Bureau of Meteorology, Melbourne 1969.

TABLE 2.2 Average Daily Mean Temperatures (°C) of Typical Locations of E. camaldulensis.

Principal Locations	J	F	M	A	M	J	J	A	S	O	N	D	Yearly Average
Katherine	28.6	28.5	28.6	29.3	27.4	25.8	25.1	26.1	28.0	29.4	29.8	29.4	28.00
Roy Hill	30.64	29.86	27.52	23.07	18.07	13.84	13.18	15.46	19.63	23.35	27.52	29.47	22.63
Petford	23.13	22.68	21.91	20.07	18.01	16.46	15.29	16.01	18.40	20.68	22.07	23.13	19.79
Nathalia	22.57	22.41	19.68	15.51	11.95	9.23	8.62	9.95	12.18	15.18	18.24	20.91	15.51
Gwydir R.	27.6	26.9	24.5	19.7	15.3	11.8	11.0	12.7	16.6	20.5	24.2	26.3	19.79
Agnew	28.9	28.4	25.5	21.1	15.5	12.5	11.6	13.2	16.8	20.7	24.9	27.9	20.63
Lake Albacutya	22.1	22.4	19.23	14.4	10.7	7.8	7.3	8.4	11.0	14.1	17.3	20.7	15.79
Todd R.	28.13	27.52	24.69	19.79	15.35	12.34	11.62	14.34	18.18	22.85	25.52	27.47	20.63
Mildura	24.1	24.4	21.5	16.9	13.7	10.4	10.0	11.7	14.4	17.6	20.7	23.2	17.40

Source: Climatic Averages Australia. Bureau of Meteorology, Melbourne 1969.

The forest has been used for grazing of domestic animals for a long period of time. In the Victorian side of the Murray River, grazing in the E. camaldulensis forest commenced in the 1840's, when Edwin Curr ran 5 - 10,000 sheep on the Moira Lakes area, and has continued to the present day when cattle only are allowed to graze. There has been no evidence to suggest that domestic cattle kill young seedlings by grazing (Dexter 1967). The E. camaldulensis forest along the Murray River also provides a unique habitat for wild life, particularly water fowl (ibis, duck, egret, heron) and is recognised as out of the key breeding areas in Victoria.

The forest has considerable recreational value. It provides facilities for sightseers, campers, fishermen, bird watchers, bush walkers, scouting activities, shooters and picnic parties whilst the adjoining Murray River caters for water sports and boating as well. The area occupied by the E. camaldulensis forest along the Murray River plays a vital role in reducing flooding of valuable agricultural land in lower regions (Dexter 1966). During floods which may occur in winter and spring, the major part of the River Murray flow leaves the main stream below Tocumwal forming a temporary lake within the forest. As the level of the river may be too low in summer to permit irrigation in the agricultural areas, water flow regulators have been built on either side of the Murray River. These regulators have been placed across deep effluent creeks of the Murray River to control the flow of water into and out of the forest.

The wood of E. camaldulensis is red when cut and darkens on exposure to deep red. The sap wood is pinkish grey in colour. The grain of the wood is sometimes very attractive. It may be difficult to saw and plane on account of toughness but the wood gives a hard and glossy surface when scraped (Marsh and Poynton 1964).

As an exotic species, E. camaldulensis has become one of the main Eucalyptus species to be planted outside its native habitat. The most frequently planted eucalypts all over the world have been listed by Roberto de Mello Alvarenga (1964) as: E. saligna, E. citriodora, E. pilularis, E. robusta, E. grandis, E. viminalis, E. deglupta and E. rudis. From general accounts, a few other eucalypts have become popular in overseas tree planting. In addition to the Mello Alvarenga list the following eucalypts can be added: E. microtheca, E. dalrympleana, E. gomphocephala, E. occidentalis, E. sideroxylon, E. laevopinea, E. eugenioides and E. delegatensis. The initial interest in planting Eucalyptus species was probably simply that of a collector growing the exotic and unusual, especially in those countries where they survive out-of-doors (Pryor 1971). The greatest success with E. camaldulensis has been in semi-arid areas bordering the Mediterranean, notably in Israel and North Africa. The success of the species is due to the ease with which it can be grown, its rapid growth and its adaptability to a large range of environments (Penfold and Willis 1961). In Cyprus, E. camaldulensis is grown in low lands and foothills, between sea level and an altitude of 600 m, and it reaches its optimum development in river-beds and

fresh water marshes. On the siliceous soils of Libya and Portugal, the species grows very well. It also withstands low temperatures in Greece, France, Italy and many other Mediterranean countries.

Where E. camaldulensis has been well established it is used for many purposes as it furnishes a raw material suited to a wide range of uses. It supplies fuel, poles, posts, piles, sleepers, and sawn timber and industrial wood for board and pulp. For sometime in Brazil the bulk of the wood produced from E. camaldulensis was used for producing large quantities of charcoal for the steel industry (Metro 1955). The species is also grown in Laos to supply raw material to the local charcoal industry (Stevens 1972). In Morocco the species is grown on a coppice system for production of timber intended for the making of cellulose and white textile pulp (Metro 1955). Pryor (1971) pointed out that the current situation is that short-fibre material can be used not only for making a variety of papers but also various mixes involving some short-fibre Eucalyptus species such as E. camaldulensis and E. globulus are favoured and actively sought by the processors.

In addition, E. camaldulensis produces chemical by-products. In Spain, Portugal, Brazil and Belgium Congo, the leaves of E. camaldulensis and a few other eucalypts have been distilled for production of eucalyptus oils. Cultivation of the species on the Black sea coast of the Causasus for the production of the volatile or essential oils began about a century ago (Penfold and Willis 1961).

E. camaldulensis has also been planted for ornamental purposes, wind breaks, and on account of its reputed health giving

qualities. The planting of the famous Pontine Marshes of Italy and the planting of the Hadera in the coastal plain of Israel are classic examples of the use of the species for health giving purposes (Penfold and Willis 1961).

E. camaldulensis has been planted to serve other special purposes. It is planted to prevent wind erosion in some dry open spaces of the Negev in Israel (Karschon 1964). The species is used to restore long degraded soils and recently cleared land in Madagascar. It is also used to plant restored open-cast tin mines in the Jos Plateau of Nigeria (Wimbush 1963).

The establishment of plantations of E. camaldulensis and of forest trees in general accounts for the employment of thousands of people all over the world. In addition more people are employed in sawmill, charcoal industries, and paper manufacturing factories. It is difficult to assess the economic value of E. camaldulensis on a monetary basis alone, since not only does it provide fuel, building timber and industrial raw material which are of critical importance to living standards of the developing society, but it also provides shelter and aesthetic features, recreation, protection and reclamation of degraded land. Successful establishment of E. camaldulensis will surely provide ample opportunity for the economic development of some local industries which will alleviate the problems of unemployment in many countries of the world.

CHAPTER 3PROVENANCE VARIATION IN EUCALYPTUS CAMALDULENSISDEHN IN AUSTRALIA

As E. camaldulensis covers a wide range of habitats, some ecotypic variation would be expected to occur in the species. Most of the investigations into provenance variation of E. camaldulensis did not start until the mid 1960's. Prior to this time, some restricted studies were carried out on the seed germination of E. camaldulensis in Victorian forests. Grose and Zimmer (1958) examined some laboratory germination responses of the seeds of E. camaldulensis collected at different sites along the Murray River between Mildura and Tallangatta and from four non-riverine areas in Victoria. They found no relationship between environment of locality of seed collection and optimum conditions for germination of E. camaldulensis seeds. This was not unexpected because the geographic area of seed collection was still in the Murray River System, and represented a limited ecological situation among the multitude of natural habitats of E. camaldulensis. However, the work of Grose and Zimmer gave some useful indication of the germination responses of E. camaldulensis to temperature and light. E. camaldulensis seeds germinate best at a constant temperature of about 35°C. The species is positively photoblastic. The extent of germination at near optimum temperature is modified by the light requirements of the seeds and the amount and duration of illumination.

The results of their work led directly to a further study on seed germination (Chapter 4) and includes seedlots from a range of provenances covering the distribution of E. camaldulensis in Australia.

Because of the economic importance of E. camaldulensis as an exotic, many investigations of provenance variation have taken place outside. For example, notable work on variability in provenances has been carried out in the Mediterranean region particularly in Israel. In a number of small scale provenance trials in Israel, Karschon and Bolotin (1964) first recorded marked differences, according to seed source, in growth and lime tolerance of E. camaldulensis. This was followed by a series of investigations to examine ecological variation in E. camaldulensis, reported by Karschon in 1967. Variation within selected morphological features was investigated in 21 provenances representing most of the natural range of E. camaldulensis in Australia.

In all the attributes measured, Karschon (1967) found significant differences between provenances, and consequently he recognised two major ecotypes in E. camaldulensis:

1. A northern group with high lignotubers frequency, glaucous foliage, and high oil gland density. This group includes the Western Australia sub-group which has a low frequency or absence of lignotubers, and a low length-width ratio of the foliage.
2. A southern group with usually a low frequency or lack of lignotubers, green yellow to green-yellow-green foliage and low oil gland density.

On this basis, Karschon divided the natural distribution range of E. camaldulensis into two distinct geographical regions, that is, north and south.

Having divided E. camaldulensis into two major ecotypes, Karschon set out to investigate some specific problems associated with the growing of the species in the Mediterranean regions. In an attempt to do this he discovered morphological and physiological differences between the provenances of E. camaldulensis. In earlier studies of E. camaldulensis Pryor (1957) and Ashton (1958) showed that frost resistance in E. camaldulensis has some relationship to seed origin. Similarly, Karschon (1968), working on freezing trials of nursery stock in Israel under controlled conditions, confirmed that frost resistance varies according to seed origin. All the provenances used in his frost treatment came from the northern ecotype of E. camaldulensis including Katherine, Ashburton River and Alice Springs. The progeny from Alice Springs showed more resistance to frost than the two more northern provenances. The more northern provenances of E. camaldulensis have greater lignotuber frequency than Alice Springs provenance, but there appears to be no direct relationship between lignotuber frequency and frost resistance, as expressed by the capacity of the plant to replace frost-killed shoots after frost treatment. This opinion could be supported by the fact that the more northern region has fewer frosts than Alice Springs. This also suggests lignotuber frequency is not a selective adaptation to frost. This could have been suggested as lignotuberous seedlings would have greater survival capacity where frost damage is likely

to occur. The present study on frost treatment (Chapter 7) has also included some provenances from southern ecotype of E. camaldulensis to examine differences between the northern and the southern ecotypes of the species. Since E. camaldulensis is introduced as an exotic species into many parts of the world in areas of extreme climatic conditions, foresters are faced with the problem of finding the best provenance for particular environments. Karschon and Pinchas (1971) remarked that both low and high temperatures could inhibit the growth of or even be lethal to certain ecotypes of E. camaldulensis cultivated outside its natural habitats. This assumption led to their useful study of differences in heat resistance between provenances of E. camaldulensis. They concluded that the heat resistance of the species is not related to the climate at the seed source as sources from the cooler parts of Australia may adapt themselves readily to the Mediterranean environments. This opinion was supported by their finding that the heat resistance values of leaves of E. camaldulensis from the provenances under investigation varied within relatively narrow limits. Provenances from the southern ecotype of E. camaldulensis may possess some inbuilt resistance to heat damage, and glaucousness of juvenile leaves of the northern ecotype may provide an additional safety margin in preventing heat damage in seedling leaves. This finding contrasts somewhat with results of their earlier work in 1968, when Karschon and Pinchas discovered that there is latitudinal variation of leaf temperatures in provenances of E. camaldulensis. Over-temperature rate (the positive difference between leaf and air temperature) of progeny

from Katherine with bright foliage was found to be lower than that of progeny from Alice Springs with glaucous leaves. They also established that leaf surface temperatures of E. camaldulensis are not only related to the seed origin and the colour of the foliage but also to the soil moisture regime.

Apart from the work done in the Mediterranean regions, some morphological characters of E. camaldulensis grown elsewhere have been shown to vary in relation to the seed origin. Burley, Wood and Hans (1971), working on 2-year old trees of 25 provenances of E. camaldulensis grown in Zambia, established that provenances of E. camaldulensis differed significantly in certain morphological leaf characters. These included leaf length, width, base angle and oil gland density. A northern and a southern ecotype of E. camaldulensis were again recognised. Their findings were of taxonomic value as they found the southern provenances have shorter, and narrower leaves than those from the north. Further investigations of morphological features of leaves of certain provenances of E. camaldulensis are reported in the present work and confirm the findings of Karschon, and of Burley and his associates.

The work of Pryor and Byrne (1969) on variation and taxonomy in E. camaldulensis threw more light on the general pattern of provenance variation in the species. Experimental studies of variation based on selected characters among herbarium specimens and seedling progeny raised from 9 provenances indicated latitudinal variation in E. camaldulensis. In growth rate, there was some tendency for height to increase with decrease in latitude suggesting

a faster growth rate in the seedling stage for the northern populations. Frost damage and recovery of E. camaldulensis also indicated that northern provenances are more susceptible than southern populations. This was in agreement with the previous findings of Karschon (1968). Pryor and Byrne also recognised that the occurrence of lignotubers in E. camaldulensis varies with the seed origin. The occurrence of lignotuber decreases from the north to the south. The taxonomic and possible genetic inference from their work is that of dividing the total population of E. camaldulensis in Australia into two main taxa, one occupying a northern zone and the other a southern zone. The two taxa have in common a strong ecological preference for sites along or near stream banks.

Biochemical characters of E. camaldulensis have also been found to differ with seed origin. The pioneering work in this field of Hillis (1966) revealed variation in the nature of the flavonol glycosides in the leaves of E. camaldulensis indicating an association between composition and locality of seed origin. A further study by Banks and Hillis (1967, 1969) revealed that the populations of E. camaldulensis can be characterised by chemical features. By using a large number of provenances from more than 100 localities, Banks and Hillis (1969) distinguished between two distinct chemotypes of the species representing a northern and a southern division, and within each division, a further grouping into geographical regions was possible. There was similarity in the nature of polyphenols between all samples of the same type of tissue but there was variation in the number of compounds present in each type

of tissue. The mature leaves yielded more compounds for consideration compared with the seeds and seedling leaves.

In an effort to determine the origin of E. camaldulensis and possible classification of the total population of the species into two sub-species, Karschon (1971) carried out further studies on lignotuber occurrence and its phylogenetic significance. Working on 13 provenances from Australia, Karschon reaffirmed that lignotuber occurrence in E. camaldulensis is closely related to the seed origin and has a transient character. In all the progenies under investigation the frequency of lignotuber is not stable but increases or decreases with time. It was found that the lignotuber frequency is high in Northern Territory and northern Queensland progenies and low to nil in those from western Western Australia and the Murray River system. From the pattern of distribution of lignotuber and other primitive characters such as oil gland density, oil odour score and polyphenols in mature leaves, the origin of E. camaldulensis is thus suggested to be in the north or east of Australia. On account of high lignotuber frequency, Karschon (1971) postulated that the centre of origin of E. camaldulensis is in northern Queensland - the Pacific region of Banks and Hillis (1969) - rather than in the north of the continent. Pryor and Byrne (1969) have also pointed out that lignotubers are known to occur in most eucalypt species and are considered an ancient feature, their transient character or absence in populations of E. camaldulensis is considered to be a derived feature.

Where E. camaldulensis is planted either within or outside Australia it is almost always in situations where summer drought is a problem in successful establishment. Jacobs (1955) pointed out that E. camaldulensis has great ability to produce a prolific root system to meet the adverse conditions of the soil in the Murray River flood plains. This was supported by his finding of the high root shoot ratio for E. camaldulensis in the flood plains. Jacobs suggested that a very high root shoot ratio helps the species to penetrate the tight soils of the flood plains, and is a significant factor in the successful establishment of E. camaldulensis. In his investigation on flooding and regeneration of E. camaldulensis in Victorian forests, Dexter (1967) established that soil moisture, either alone or by interaction with other factors, was one of the important environmental factors affecting seedling establishment of E. camaldulensis. Where seedlings have to compete with ground vegetation and overstorey trees for the available soil moisture, they may die of soil drought in summer and autumn during their first year of growth. In the present study root development of several provenances of E. camaldulensis has been investigated in relation to soil moisture regime. The species has been grown in large pots and various droughting treatments applied. The pattern of root development of E. camaldulensis is compared with two other fast-growing eucalypts from the coastal environment - E. pilularis and E. saligna.

This literature review on E. camaldulensis shows clearly that there is very considerable variation in E. camaldulensis. The high level of provenance variation in the species strongly suggests

that very effective improvement could be made in the productivity of the species as an exotic by careful selection of seed source in tree introduction. This high level of variation makes the task of the forester difficult in choosing suitable provenances for afforestation. This review and the work reported both suggest that careful selection will achieve significant increase in production.

CHAPTER 4

SEED GERMINATION

4.1 Temperature Effects

4.1.1 Introduction

In many forest tree species, one of the effects of provenance is variation in germination behaviour. This study set out to investigate temperature effects on germination behaviour of seed from a number of provenances of E. camaldulensis.

Pioneering work in this field was done by Grose and Zimmer (1958) who found E. camaldulensis seeds germinate best at a constant temperature of 35°C - an unusually high optimal temperature for most Victorian Eucalyptus species (Grose 1962). However, this work was confined mostly to seed of Victorian origin. In the present study the work of Grose and Zimmer has been extended to include a broader spectrum of the distributional range of the species to cover provenances from very diverse ecological situations.

4.1.2 Materials and Methods

Seed of E. camaldulensis was collected by officers of the Forest Research Institute, Canberra, during 1964 to 1972 from sites throughout most of its natural range. The collection was made at the instigation of the FAO Forestry and Forest Products Division because of the widespread interest in this species in many parts of

the world. The distribution of the species within Australia is indicated on Figure 4.1, together with the sites for the F.R.I. collections.

From the seed available at the F.R.I., six sites were chosen for the present study. From these six localities seed had been collected from five trees and the seed from each tree had been kept separate. Details of the seed chosen for study are given in Table 4.1. These six provenances were selected so that three of them were located from the North while the remaining three were from the South. The boundary between the north and the south was arbitrarily chosen as the Tropic of Capricorn. The three northern provenances include Katherine, Roy Hill and Petford, while the southern ones were Mildura, Agnew and Gwydir River.

The seed samples consisted of a small number of viable seeds plus a large number of unfertilized ovules referred to as "chaff" (Larsen 1965). It was hard to distinguish some of the viable seeds from the chaff.

The germination dish

The preparation of this dish is very similar to the germination dish prepared by Crose and Zimmer (1958) except that a pad of filter paper was used instead of a gauze wick, and one disposable petri dish was used for each replicate as against one dish for five replicates (Figure 4.2).

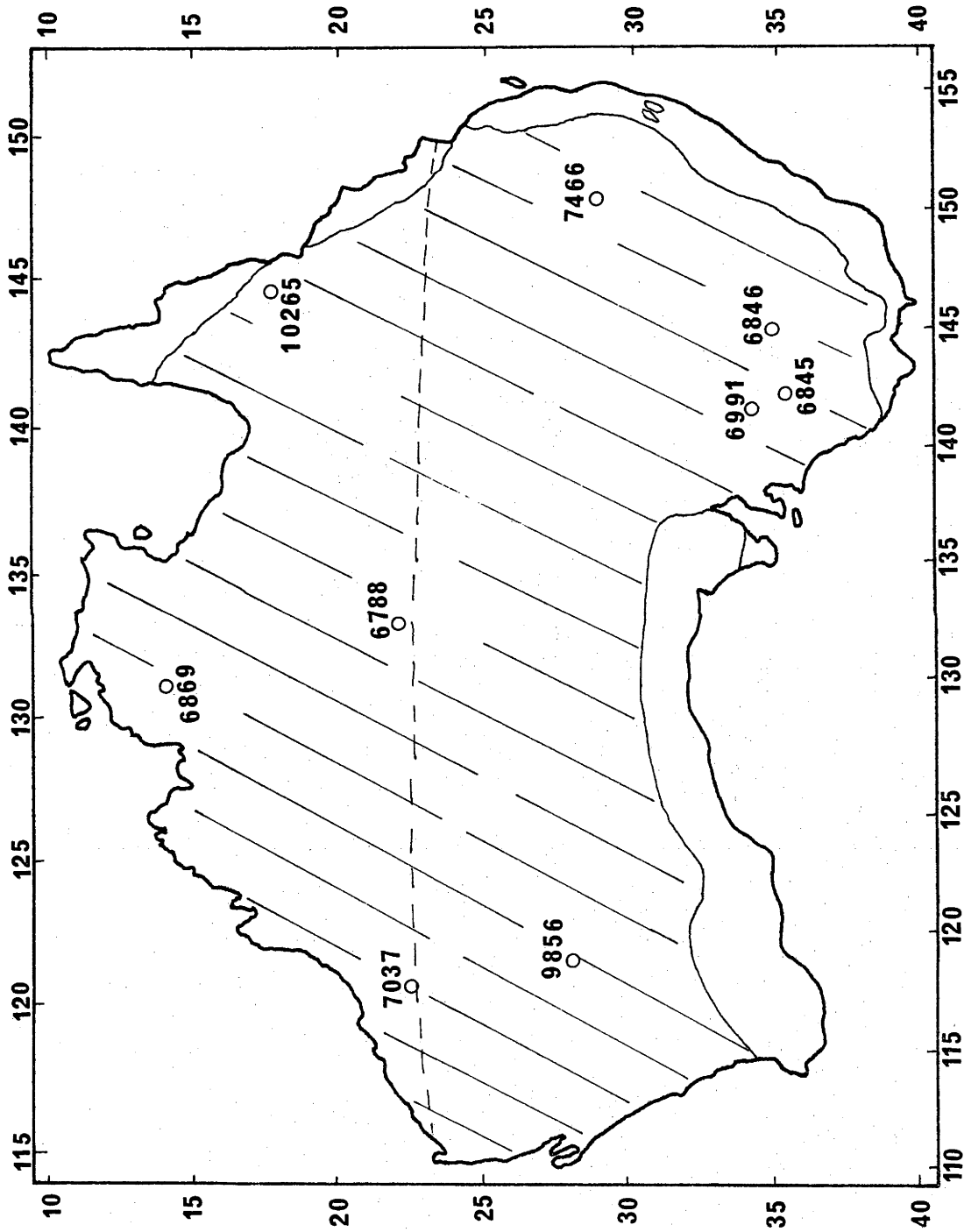


FIGURE 4.1 Distribution of *E. camaldulensis* in Australia Together with Sites of Seed Collection for this Study.

TABLE 4.1 Provenance Distribution of *E. camaldulensis* Dehn. and Other
eucalypts Included in the Study.

F.R.I. Seed No.	Provenance	Lat. ° S	Long. ° E	Altitude m	Nearest Meteorological Station	Average Daily Max. Temp. Warmest Month °C	Average Daily Min. Temp. Coldest Month °C	Absolute Min. Temp. °C	Soils
6869	Katherine, N.T.	14	132 15	110	Katherine, N.T.	38	13.2	2.2	Alluvial on levee bank of river
7037	Roy Hill, W.A.	23	06 120 08	305	Mundawindi, W.A.	38.1	5.2	-	Gravelly red sand pH 6.5
10265	Petford, Qld.	17	18 145 07	516	Herberton, Qld.	37.4	8.1	-	Sandy river gravels
6846	Nathalia, Vic.	36	00 145 10	150	Shepparton, Vic.	30.4	4.6	-4.4	Black clay
7466	Gwydir River, N.S.W.	29	35 149 38	183	Moree, N.S.W.	31.6	3.9	-5.5	Deep black soil pH7
9856	Agnew, W.A.	28	06 120 33	482	Lawlers, W.A.	35.6	5.6	-3.8	Red sandy loam
6845	Lake Albacutya, Vic.	35	50 142 00	183	Rainbow, Vic.	30.7	3.8	-	Sand deposits over grey clay
6788	Todd River, N.T.	23	38 133 35	580	Alice Springs, N.T.	35.2	3.8	-	Silty, sandy alluvial
6991	Mildura, Vic.	34	10 141 30	56	Mildura, Vic.	31.6	5.4	-	Heavy grey clay pH7
9458	<i>E. pilularis</i> (Coffs Harbour)	30	18 153 08	30	Clarence Heads, N.S.W.	26.6	6.5	-	Very light loam with shale
7821	<i>E. saligna</i> (Ulong)	30	9 152 49	6	Grafton, N.S.W.	30.5	5.9	-	Grey brown loam pH6

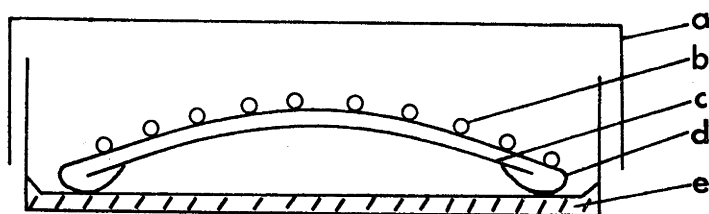


Figure 4.2 The germination dish. (a) plastic disposable petri dish; (b) seed; (c) watch glass; (d) filter papers; (e) water saturated filter papers.

Three 9 cm filter papers were placed at the bottom of the plastic petri dish to serve as a water reservoir. Two 11 cm filter papers were moistened with distilled water and then laid on the convex face of a watch glass of 7.6 cm diameter. The moistened filter papers were smoothed out and the overlapping portions of the filter papers were then folded under the edge of the watch glass.

The watch glass was then placed in the petri dish, convex side up, so that its perimeter rested on the water saturated filter papers at the bottom of the petri dish.

The weighed seed sample was coated with a pinch of fungicide (Zineb 65) to minimise fungal infection. The seeds were evenly spread on the prepared watch glass. A small water bottle was used to add water to the dishes as deemed necessary.

Selection of seed samples

From each provenance, seed was collected from 5 trees, and the seedlots for each tree were kept separate. Five sub-samples

were obtained for each tree to have a total of twenty-five sub-samples for each provenance. Using a "Gamet" seed divider the seedlots were randomly divided repeatedly into equal halves until a suitable sub-sample was obtained. The amount of seed used for the several provenances varied considerably because of the difference in seed size and the amount of chaff. The weights of sub-samples varied from 0.02 to 0.09 g for different provenances so that the number of fertile seeds per sub-sample could be maintained within the range of 80 to 100.

All the experiments were performed in CERES, the CSIRO phytotron in Canberra. The design and development of the CSIRO phytotron was described by Morse and Evans (1962).

The petri dishes were put on trays placed on trolleys in open glasshouses. Aluminium foil was used to cover the petri dishes to reduce radiation from the sun. Light could reach the seed from the sides and the seeds were exposed to light daily while counting the germinated seeds.

Eight temperatures regimes were used to determine temperature effects on seed germination of E. camaldulensis.

Regime	1	2	3	4	5	6	7	8
Day Temperature ($^{\circ}\text{C}$)	15	18	21	24	27	30	33	36
Night Temperature ($^{\circ}\text{C}$)	10	13	16	19	22	25	28	31

The glass houses were maintained at the day temperature for eight hours daily. Supplementary light in the open glass houses was used to provide a 16-hour photoperiod. Temperatures within the glasshouses may vary by $\pm 1.5^{\circ}\text{C}$.

Germination count expression and analysis of data

Germinated seeds were counted and removed daily. Seeds were regarded as germinated when the hypocotyl had emerged and grown to approximately 5mm in length. The end of the germination period for a given treatment was determined to be when the daily percentage germinations for each provenance fell below one percent.

In the treatments applied the germination period varied from 10 to 24 days depending on temperature. At high temperatures the seeds germinated very rapidly and completely. At the end of the germination period all the particles on the filter papers were squashed to determine the number of ungerminated fertile seeds regarded as 'viable' seeds.

The mean of the percentage germination of each of the twenty-five sub-samples was taken as the percentage germination for each provenance. The data so obtained were graphically represented in Figures 4.3(a) to 4.3(c) to give the pattern of provenance variation at any particular germination period for day 6, 10 and 14.

Progressive percentage germination was derived as a percentage of progressive total germination for each day to the total fertile seeds. Graphical representation of the progressive percentage germination was shown in Figures 4.5 and 4.6 for Katherine and Mildura representing a northern and southern ecotypes

of E. camaldulensis. The same pattern of figure was obtained for the other provenances under investigation. From the data obtained for the progressive percentage germination it was possible to estimate the days for a 50 percent germination at various temperatures and these were represented in Table 4.6.

Germination energy was expressed by an index (G.E.I.), derived from the modified Bartlett's index, by summing the progressive percentage germination period and dividing this total by the product of the number of days in the germination period and the final percentage germination (Grose, 1963). The germination period was taken to be 6 days. This was 2 days longer than the period used by Grose and Zimmer (1958) because the northern provenances were slow to germinate. The G.E.I. in effect gives an easily calculable numerical indication of the area under the curve of cumulative percentage germination plotted against time for a germination period of six days. A high value for G.E.I. denotes early and rapid germination, and a low value represents late and slow germination.

A period of 6 days was taken to provide numerical comparisons between energies of most seed lots in most treatments. The G.E.I. was calculated for a germination period of 10 and 14 days to see if there would be any change in the pattern of germination behaviour but this was not so.

For all analyses involving percentages, data were transformed to angular degrees (Snedecor, 1956). The means for the 5 transformed values for each provenance were used in analysis of variance.

4.1.3 Results and Discussion

There was no germination at the lowest experimental temperature regime of $15^{\circ}/10^{\circ}\text{C}$. in any of the provenances at day 6 of the germination period (Tables 4.2 and 4.3). At a similar low temperature Grose and Zimmer (1958) observed no germination of seed of E. camaldulensis from the Victorian forests. Maximum germination for 4 out of 6 provenances occurred at $30^{\circ}/25^{\circ}\text{C}$. and 2 out of 6 at $33^{\circ}/28^{\circ}\text{C}$. The percentage germination at day 6 for Katherine, Roy Hill and Petford in Table 4.3 is the result of a separate experiment. The Katherine provenance is common to both experiments and the results for this provenance agree well. The optimum temperature for maximum germination irrespective of provenance lies between the two regimes of $30^{\circ}/25^{\circ}\text{C}$ and $33^{\circ}/28^{\circ}\text{C}$. This temperature is slightly lower than the constant 35°C . found by Grose and Zimmer (1958) to produce optimum germination of E. camaldulensis. Under field conditions where there is marked variation in day and night temperatures it is expected that most seed of E. camaldulensis will germinate very rapidly and satisfactorily when daily maxima reach 30° to 33°C . and when moisture is not a limiting factor for germination.

Marked differences in germination behaviour between provenances occurred at the lower temperature regimes. There was a marked north-south division at the temperature regime of $18^{\circ}/13^{\circ}\text{C}$. at 6 days. Gwydir River provenance germinated rapidly but little or no germination was recorded for Katherine, Roy Hill and Petford (Tables 4.2 and 4.3).

The germination energy index (G.E.I.) at day 6 underlines germination behaviour of the provenances noted above. In the low temperature regimes the northern provenances from Katherine, Roy Hill and Petford have the lowest G.E.I. indicating slow and late seed germination in contrast to the southern provenances with high G.E.I.

For all the provenances, the days at which the progressive percentage germination at various temperatures would reach a 50 percent were calculated (Table 4.6). This is an alternative way of viewing speed of germination. In the three lower temperature regimes of $15^{\circ}/10^{\circ}$, $18^{\circ}/13^{\circ}$ and $21^{\circ}/16^{\circ}\text{C}$. the northern provenances took much longer to reach 50% germination but all of the provenances germinated completely and rapidly at the higher temperatures, when 50% germination is reached in 4 days.

The following hypothesis is suggested, as an explanation of the results to tie in with the ecological situation of each seed source. For the survival of E. camaldulensis, or for any eucalypt under conditions of natural regeneration, it needs to germinate very quickly and rapidly when moisture and temperature conditions are ideal and are likely to be maintained for an adequate period of time. A close look at the rainfall data of the provenances (Figure 2.1) indicates that the north (Katherine) has a summer rainfall pattern and flooding will most likely occur during the months of December to March. The average daily mean temperatures during the months of summer are high averaging about 29°C . (Figure 2.2). When flood waters recede in late summer and early autumn the temperature is

ideal for seed germination. In fact the temperature in the north is ideal throughout the year for the germination of E. camaldulensis seed, but moisture availability may result to the dormancy of the seed in winter. If northern provenance seed is brought to the south in winter between May and August when there is an adequate moisture, the temperature regime may become a limiting factor for its germination and successful establishment. Seed from southern provenances will have no problem of germinating in the north any time of the year provided there is enough moisture.

In the south, flooding of the E. camaldulensis forest will usually occur in winter and spring when temperatures are low. As the water recedes in late spring and summer, prolific natural regeneration of E. camaldulensis takes place. The temperature regime in late spring and summer is favourable to seed germination of these southern provenances of E. camaldulensis. The seed will germinate rapidly at temperatures in the region of 20°C. and the seedlings are able to become established before drought conditions set in later in the summer.

The evidence from these experiments indicates a genetic adaptation within the species to suit the germination conditions most likely to be encountered. The southern provenances have adapted to be able to germinate rapidly at low temperatures, an ability apparently not possessed by the northern provenances which occur in parts of Australia where autumn temperatures during the day rarely fall below 25°C.

Conclusions

Ecological variation exists in the seed germination behaviour of E. camaldulensis provenances. Marked differences occur between northern and southern provenances. At low temperatures seed from southern provenances germinates more rapidly and completely than seed from northern provenances. A marked N - S division is possible at temperatures of about 18°/13°C. at the 6th day of seed germination. For all the provenances the optimum temperature for germination is between 30° and 33°C. The northern provenances have a narrower range of optimum temperature for seed germination.

TABLE 4.2 Percentage Germination at Different Temperatures at Day 6 by Provenances.

Temp. (Day/ Night °C.)	Katherine		Mildura		Gwydir River		Agnew		L.S.D. (p=0.05)
	Per- cent	Angular Degrees ± S.E.	Per- cent	Angular Degrees ± S.E.	Per- cent	Angular Degrees ± S.E.	Per- cent	Angular Degrees ± S.E.	
15/10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18/13	1.11	3.16	23.51	26.91	52.69	50.19	27.07	34.81	5.58
21/16	1.73	5.01	28.61	31.69	62.00	56.34	38.11	42.78	6.49
24/19	3.43	10.31	65.94	54.32	77.48	66.03	75.53	63.56	4.34
27/22	47.43	47.13	86.98	67.76	87.58	74.87	96.55	81.11	2.55
30/25	88.78*	75.39	95.57*	79.86	96.49*	84.58	99.92*	89.04	0.68
33/28	74.46	66.03	92.82	75.53	92.20	78.54	98.30	81.93	1.22
36/31	76.44	64.96	92.67	74.50	93.38	77.60	99.37	83.91	0.51
L.S.D. (p=0.05)		10.91		9.80		13.17		8.02	

* Maximum Germination Percent.

TABLE 4.3 Percentage Germination at Different Temperatures at Day 6 for Only Northern Provenances.

Temp. (Day/ Night °C.)	Katherine		Roy Hill		Petford		L.S.D. (p=0.05)
	Per- cent	Angular Degrees ± S.E.	Per- cent	Angular Degrees ± S.E.	Per- cent	Angular Degrees ± S.E.	
15/10	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18/13	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21/16	0.0	0.0	7.81	16.54	11.11	20.18	14.06
24/19	0.12	0.78	94.09	74.63	73.33	61.29	11.84
27/22	2.75	8.44	96.46	78.18	84.71	75.93	9.78
30/25	16.89	24.57	99.16	83.24	92.41	74.19	9.72
33/28	60.57*	53.08	99.70*	85.82	94.73*	78.67	10.92
36/31	57.43	53.04	98.63	81.92	88.02	71.48	13.98
L.S.D. (p=0.05)		6.57		6.42		5.82	

* Maximum Germination Percent.

TABLE 4.4 Mean Germination Energy Index at Different Temperatures at Day 6 by Provenances.

Temperature (Day/Night °C.)	Katherine		Mildura		Gwydir River		Agnew	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
15/10	0.341	0.039	0.489	0.588	0.588	0.037	0.556	0.018
18/13	0.623	0.035	0.686	0.064	0.784	0.028	0.762	0.016
21/16	0.574	0.039	0.697	0.011	0.740	0.042	0.736	0.014
24/19	0.604	0.031	0.697	0.016	0.731	0.028	0.730	0.007
27/22	0.691	0.027	0.792	0.022	0.834	0.036	0.843	0.010
30/25	0.701	0.035	0.793	0.037	0.851	0.035	0.867	0.007
33/28	0.827	0.016	0.872	0.006	0.896	0.016	0.896	0.004
36/31	0.772	0.022	0.830	0.012	0.859	0.020	0.869	0.0

TABLE 4.5 Mean Germination Energy Index at Different Temperature at Day 6 by Provenance for Only the Northern Provenances.

Temperature (Day/Night °C.)	Roy Hill		Petford		Katherine	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
15/10	0.479	0.008	0.427	0.016	0.208	0.015
18/13	0.645	0.007	0.614	0.007	0.225	0.020
21/16	0.697	0.008	0.671	0.013	0.359	0.022
24/19	0.755	0.005	0.714	0.015	0.422	0.024
27/22	0.808	0.005	0.773	0.012	0.517	0.024
30/25	0.795	0.005	0.746	0.013	0.471	0.020
33/28	0.860	0.0	0.815	0.013	0.654	0.020
36/31	0.804	0.010	0.715	0.015	0.588	0.031

TABLE 4.6 Days at Which the Progressive Percentage Germination at Various Temperatures for Different Provenances Reached 50%.

	15/10	18/13	21/16	24/19	27/22	30/25	33/28	36/31°C
Katherine	16	11	10	8	6	4	4	4
Roy Hill	13	9	7	6	5	4	3	3
Petford	13	10	8	6	5	4	4	4
Mildura	12	8	7	6	4	3	4	4
Gwydir River	10	6	6	5	3	2	3	3
Agnew	11	7	7	6	4	2	4	3

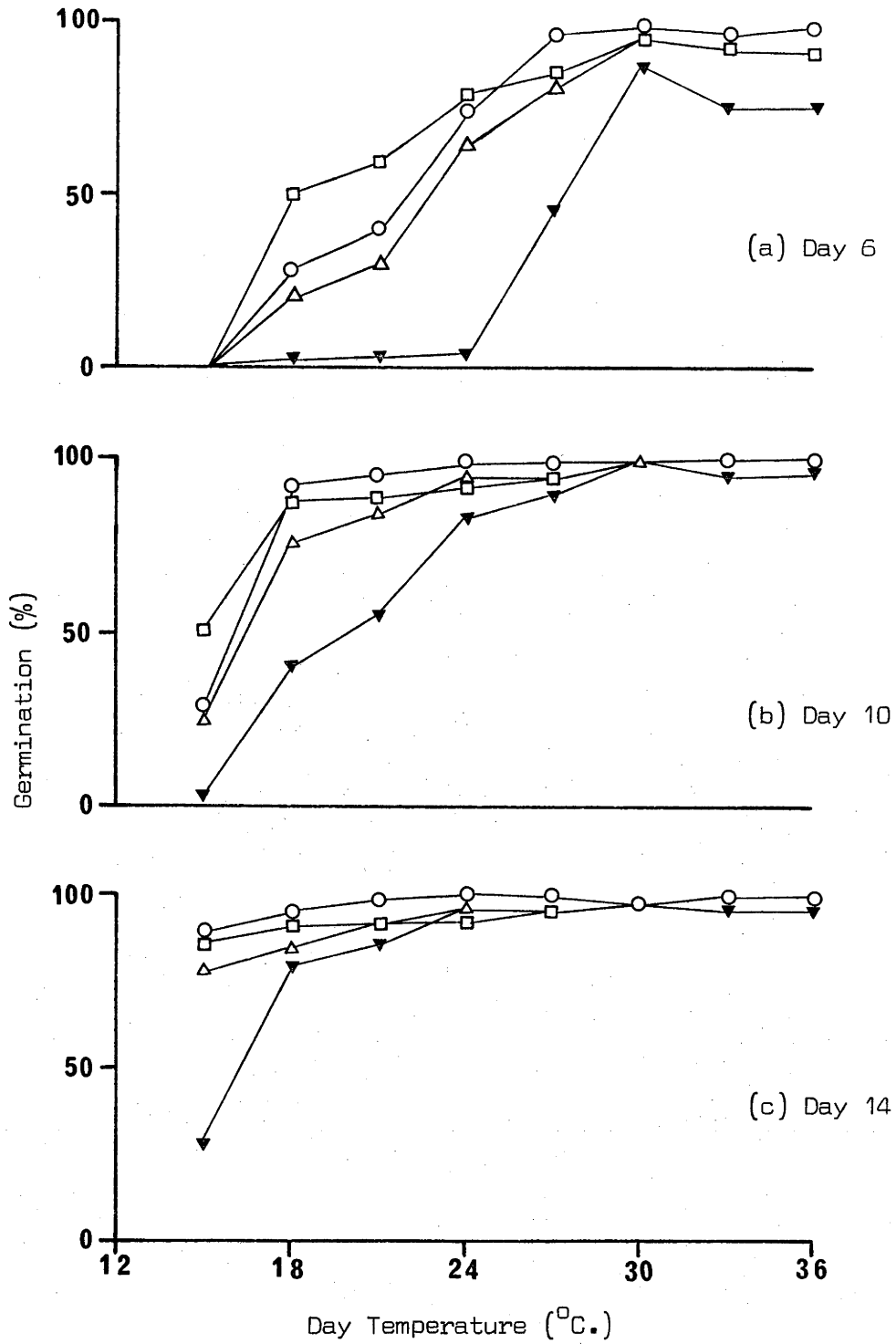


FIGURE 4.3 Percentage germination of *E. camaldulensis* seeds from 4 provenances of Katherine (▼), Mildura (▲), Agnew (○) and Gwydir River (□) at day 6 (a), day 10 (b), and day 14 (c). Night temperature is 5°C cooler than day temperature.

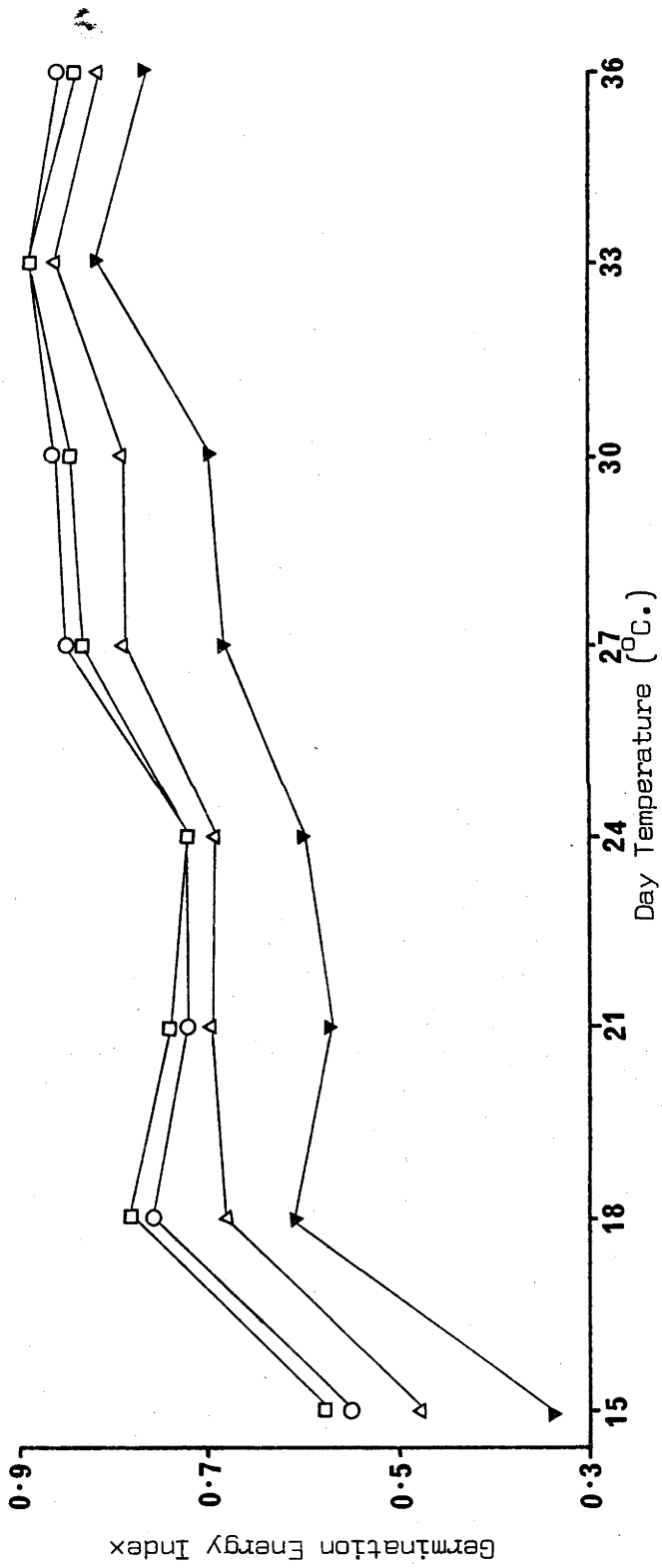


FIGURE 4.4 Germination Energy Index of *E. camaldulensis* from 4 Provenances of Katherine (▼), Mildura (Δ), Agnew (○) and Gwydir River (◻) at Different Temperatures. Night Temperature is 5°C. Cooler than Day Temperature.

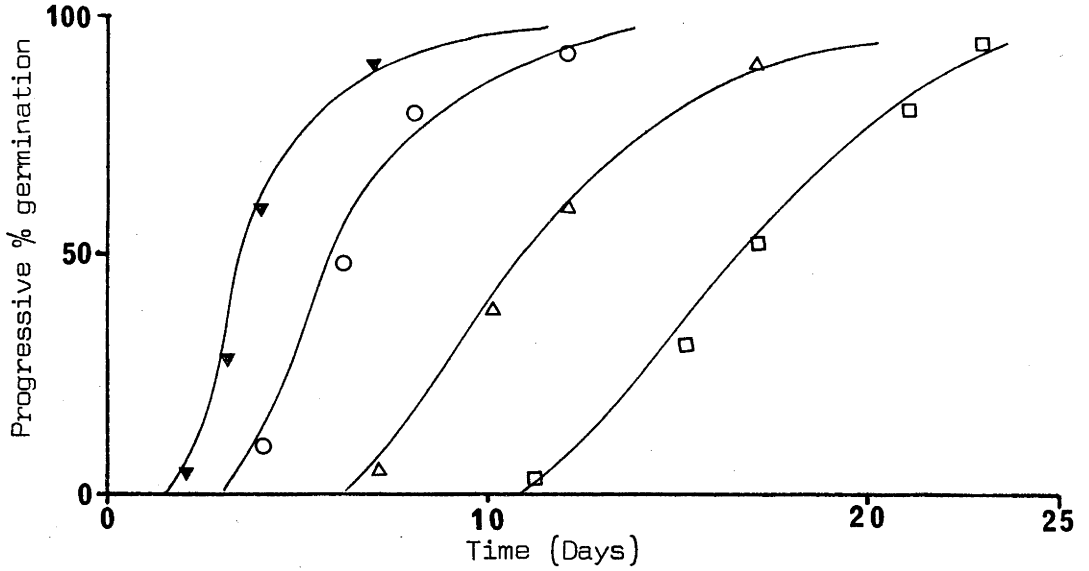


FIGURE 4.5 A typical graph of progressive percentage germination for the northern (Katherine) provenance of *E. camaldulensis* at different Day/Night temperature - 30/25°C. (▼), 27/22°C. (○), 18/13°C. (△) and 15/10°C. (□).

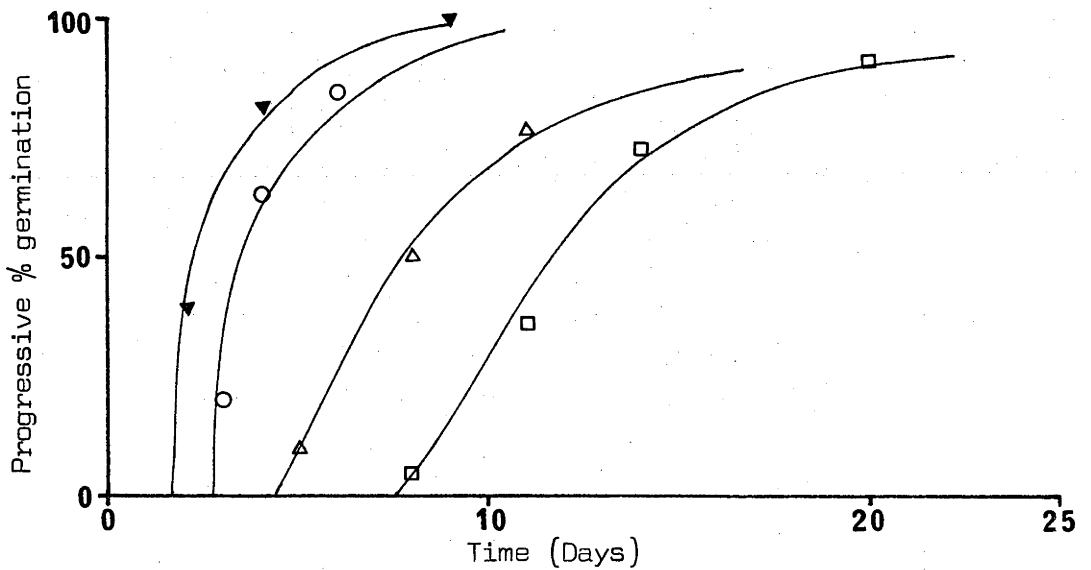


FIGURE 4.6 A typical graph of progressive percentage germination for the southern (Mildura) provenance of *E. camaldulensis* at different Day/Night temperature - 30/25°C. (▼), 27/22°C. (○), 18/13°C. (△) and 15/10°C. (□).

4.2 White Light Effects on Seed Germination of Eucalyptus camaldulensis.

4.2.1 Introduction

Clifford (1953), in his preliminary studies on light requirements for germination of seeds of some Eucalyptus species found that seeds of E. camaldulensis required light for satisfactory germination, particularly when the seed is not fully mature, but gave no detailed information on this or the light requirements of mature seeds.

Working on the effects of light on germination of E. camaldulensis seeds at constant temperature, Grose and Zimmer (1958) reported that certain amounts of light are required for satisfactory germination at all temperatures, but a daily dark period is also required for maximum germination at temperatures other than the optimum temperature of 35°C. They agreed with Clifford (1953) that light is essential for germination of E. camaldulensis and in further studies demonstrated there is variation in the light requirement for germination of E. camaldulensis. They reported that the variations in the light requirement does not depend on the maturity of the seed.

Both the studies on the effects of temperature on the seed germination of E. camaldulensis, and the studies of Grose and Zimmer (1958) on the effects of light on germination of red gum seeds were confined to seed collected in Victorian forests. In the present study some effects of light conditions on germination of E. camaldulensis seed have been examined in relation to provenances.

4.2.2 Materials and Methods

Seedlots of E. camaldulensis from 4 provenances of Katherine, Nathalia, Gwydir River and Agnew were used in this investigation. A full description of the seed sources is given in Table 4.1. For each provenance 25 samples were prepared using the same technique described in Chapter 4.1.2.

Three treatments were applied to determine the effects of light on the germination of E. camaldulensis seeds at a constant temperature of 27°C. The treatments were as follows:

1. Continuous light,
2. Continuous darkness,
3. Continuous darkness broken by short periods of light.

The periods of light consisted of 2, 10, 28 and 30 minutes of light given to the seeds at day 6, 11, 16 and 21 from the day they were placed in darkness.

In effect, the design of the treatments followed very closely the work of Grose and Zimmer to permit a reasonable comparison of the results. The experiments were set up in an environment growth cabinet maintained at a constant temperature of 27°C. and relative humidity of 70%. In the light treatments, the light intensity at the dishes was approximately 500 f.c. which was supplied by eight 40-watt white fluorescent tubes. The germination dishes were randomly arranged on a flat tray to expose the seeds to the light as uniformly as possible.

Germination Count

Germinated seeds were counted and removed daily in all the 3 light treatments. Treatments 2 and 3 which involved continuous darkness created some problems in counting germinated seeds. The problems were solved by using specially constructed green filtered light of extremely low light intensity. All counting was done at night. The end of the germination period for a given treatment was determined to be when the daily percentage germinations for each provenance fell below one percent.

4.2.3 Results and Discussion

The mean of the percentage germination of 25 samples for each day represents the daily percentage germination for each provenance. The daily percentage germination for all the four provenances is graphically represented in Figures 4.7 to 4.9, as follows:

Figures 4.7 Daily percentage germination in continuous light.

4.8 Daily percentage germination in continuous darkness.

4.9 Daily percentage germination in continuous darkness broken by short periods of light.

In continuous light, seed germination of all the provenances was rapid and almost completed within the first 10 days. For the three provenances of Nathalia, Gwydir River and Agnew the peak of maximum daily germination occurred between day 3 and 4. There was a delay of 2 days before Katherine provenance reached its peak of maximum daily germination. There were marked differences

between provenances in the maximum daily percent germination produced in the first 6 days. For example, Agnew produced the highest maximum daily percent germination of 58% while Katherine had the lowest maximum percent germination of 22%.

Nathalia and Gwydir River (both on the Murray River systems) had maximum daily percent germination of 38 and 33% respectively. The germination of northern (Katherine) provenance seed at continuous light was slower than the seed of the other three provenances. Agnew was obviously quite different in its germination at continuous light compared with Gwydir River and Nathalia. The inconsistency of pattern of differences between provenances beyond the first 6 days of germination made it difficult to give any meaningful interpretation to the results.

In continuous darkness, there was some germination, but the daily percentage germination recorded was much lower than that recorded for seed germination in continuous light. This suggested that light is essential for satisfactory germination of E. camaldulensis seeds. As in the continuous light treatment, seed of all provenances reached peak germination at 3 to 4 days. Under continuous light, Agnew provenance had greater peak germination rate, but under continuous darkness, Gwydir River seed had peak germination rate. For example, Gwydir River produced a maximum daily percent germination of 18% while the maximum for Agnew and Nathalia was about 8%. Katherine provenance still had the lowest maximum daily percent germination of 5% in the same period. There was no consistency in germination behaviour beyond day 6 of germination.

The seed germination behaviour in continuous darkness broken by short periods of light was quite interesting. Before the first period of light was introduced all the energy stored in the seed had been used as indicated by the drop in the daily percentage germination. At this stage, the rate and the pattern of germination for all the provenances were similar to those in the continuous dark treatment. When 2 minutes of 500 f.c. light was introduced at day 6, there was a large increase in germination. This was recorded on the second day after the exposure to light. For all the provenances the maximum daily percent germination produced from the reaction to 2 minutes of light was more than double that produced in continuous darkness. As the energy gained from the 2 minutes of light was utilised, there was a drop in daily percentage germination. A similar stimulus to germination followed by a decline in germination was recorded following exposure to light after most of 6-day germination periods at continuous darkness.

Germination responses to different light exposure periods at days 6, 11, 16 and 21 are shown in Figure 4.9. There was an increase in germination associated with each exposure of seeds to light, but greater exposure to light did not increase the germination rate.

There was no consistent pattern of variation between provenances in respect to germination response under the light treatment. The experiments were repeated for all the provenances at the lower temperature of 25°C. The results were similar to those reported in this investigation, - suggesting germination temperature may not affect the way seeds response to light.

A summary of the germination behaviour in the 3 treatments, at a constant temperature of 27°C., is presented as an histogram (Figure 4.10). This shows the total percentage germination for the 4 provenances, at continuous light and at the dark/light treatments. It also shows germination percent for the 4 provenances at day 6 for the continuous dark treatment. The percentage germination at day 6 for the dark/light treatment is also shown on the histogram for this treatment.

At continuous light there was no difference between provenances; more than 98% of viable seeds of all the 4 provenances germinated in continuous light. In continuous darkness, some differences between provenances occurred. Katherine produced the smallest percentage germination (4%) while Gwydir River produced the greatest percentage germination (43%). Agnew and Nathalia produced more or less the same percentage germination (around 20%). It is difficult to interpret this result. In the light/dark treatment peak percentage germinations at day 6 are very similar to those recorded under continuous darkness. The short period of light introduced to the seedlots at day 6 greatly increased the total percentage germination. More than 98% of seeds from 3 provenances of Nathalia, Gwydir River and Agnew germinated while 83% of Katherine seeds germinated.

Conclusion

Certain conclusions could be drawn from the main findings relevant to the present investigations, as follows:

1. Seed germination of E. camaldulensis is greatly stimulated

by light. For satisfactory germination, a short period of light is required in the early period of germination.

2. There appears to be no distinct variation between provenances in their light requirements for seed germination.
3. Under any light conditions, the northern (Katherine) provenance was slower to germinate than the southern provenances of Agnew, Gwydir River and Nathalia.

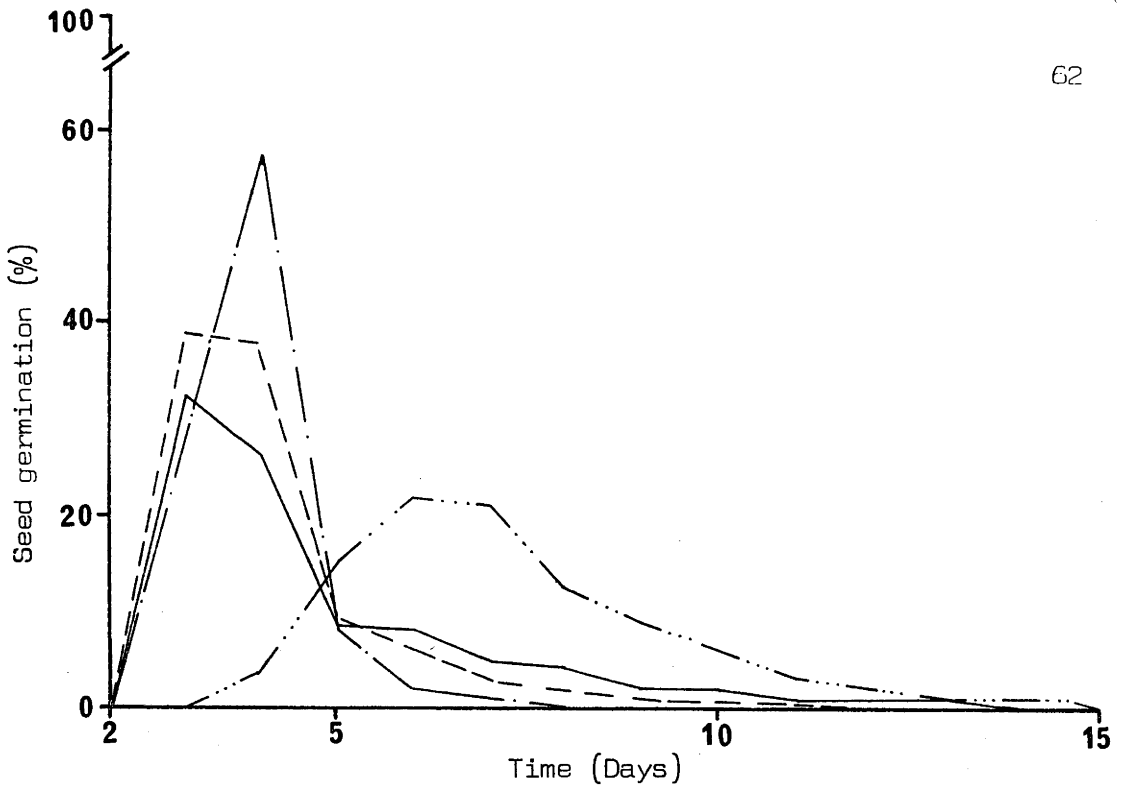


FIGURE 4.7 Seed germination of *E. camaldulensis* under continuous light at 27°C. from 4 provenances of Katherine (.....), Nathalia (---), Gwydir River (—) and Agnew (-.-).

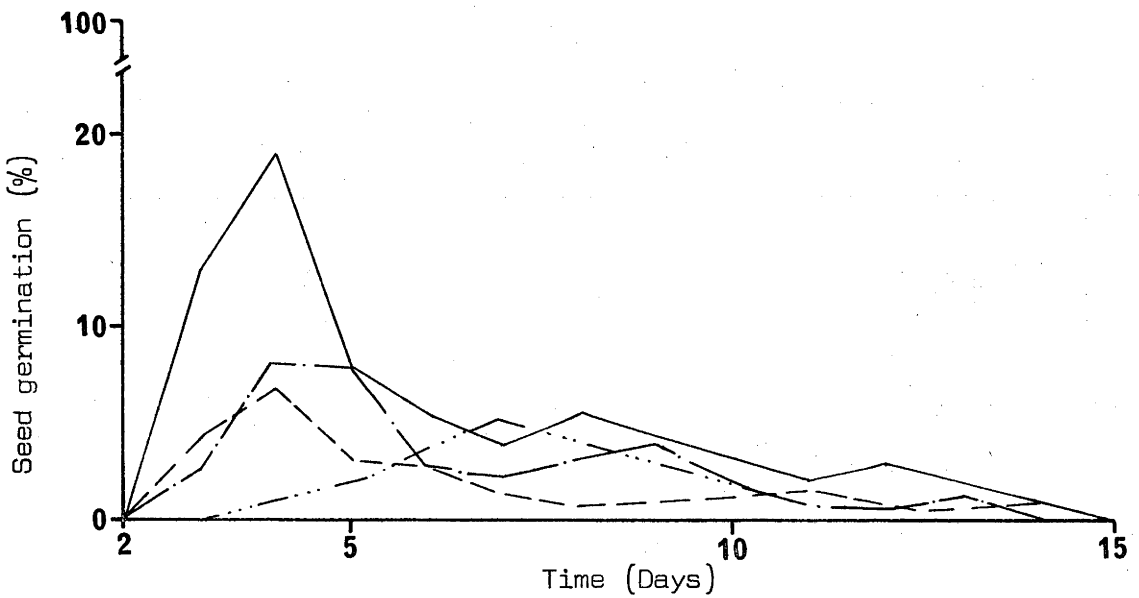


FIGURE 4.8 Seed germination of *E. camaldulensis* under continuous darkness at 27°C. from 4 provenances of Katherine (.....), Nathalia (---), Gwydir River (—) and Agnew (-.-).

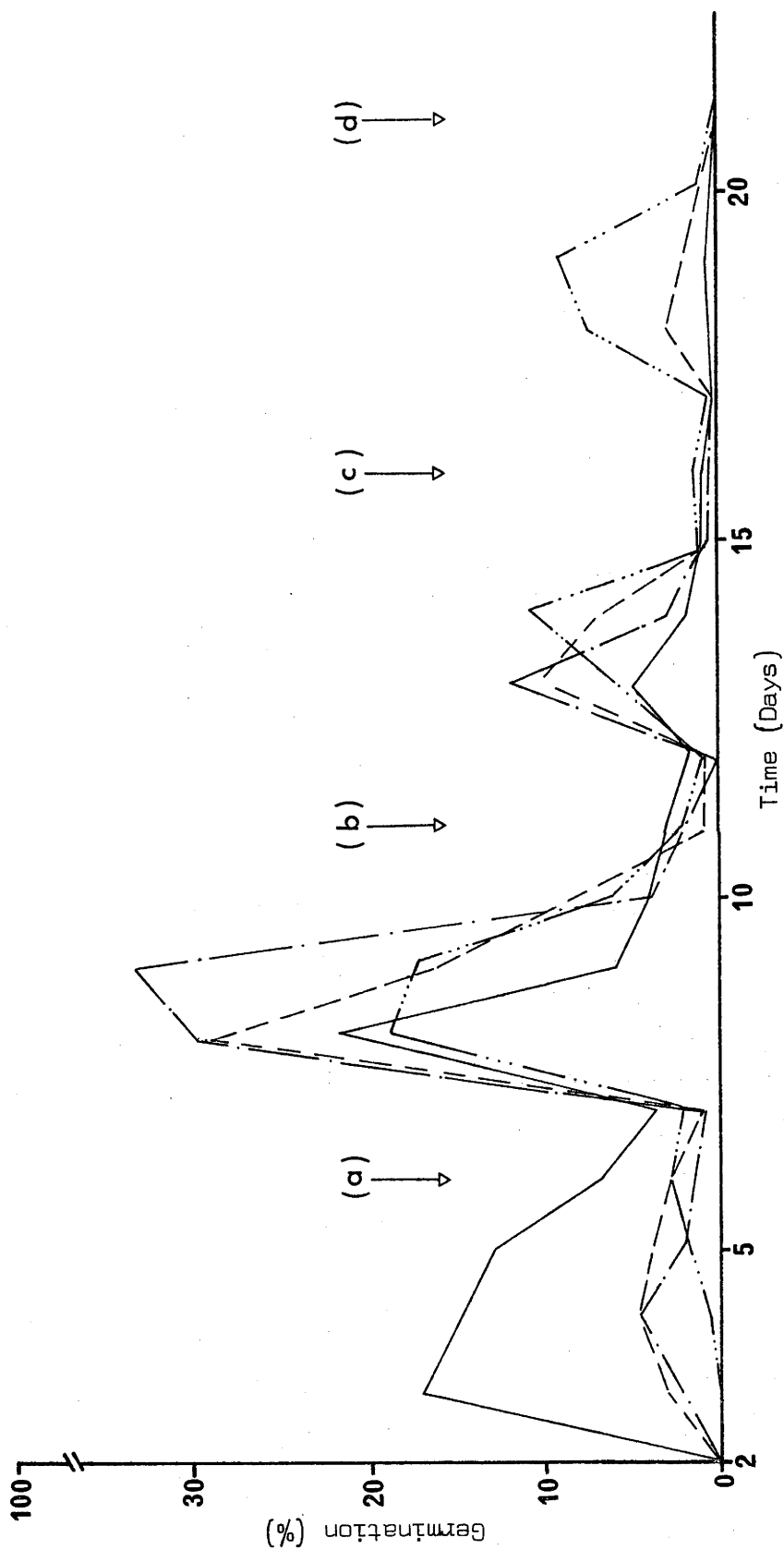


FIGURE 4.9 Light effects on seed of *E. camaldulensis* germinating under continuous darkness from 4 provenances of Katherine River (—), Nathalia (···), Gwydir River (---) and Agnew (-·-·). The arrows indicate the time of seed exposure to light.

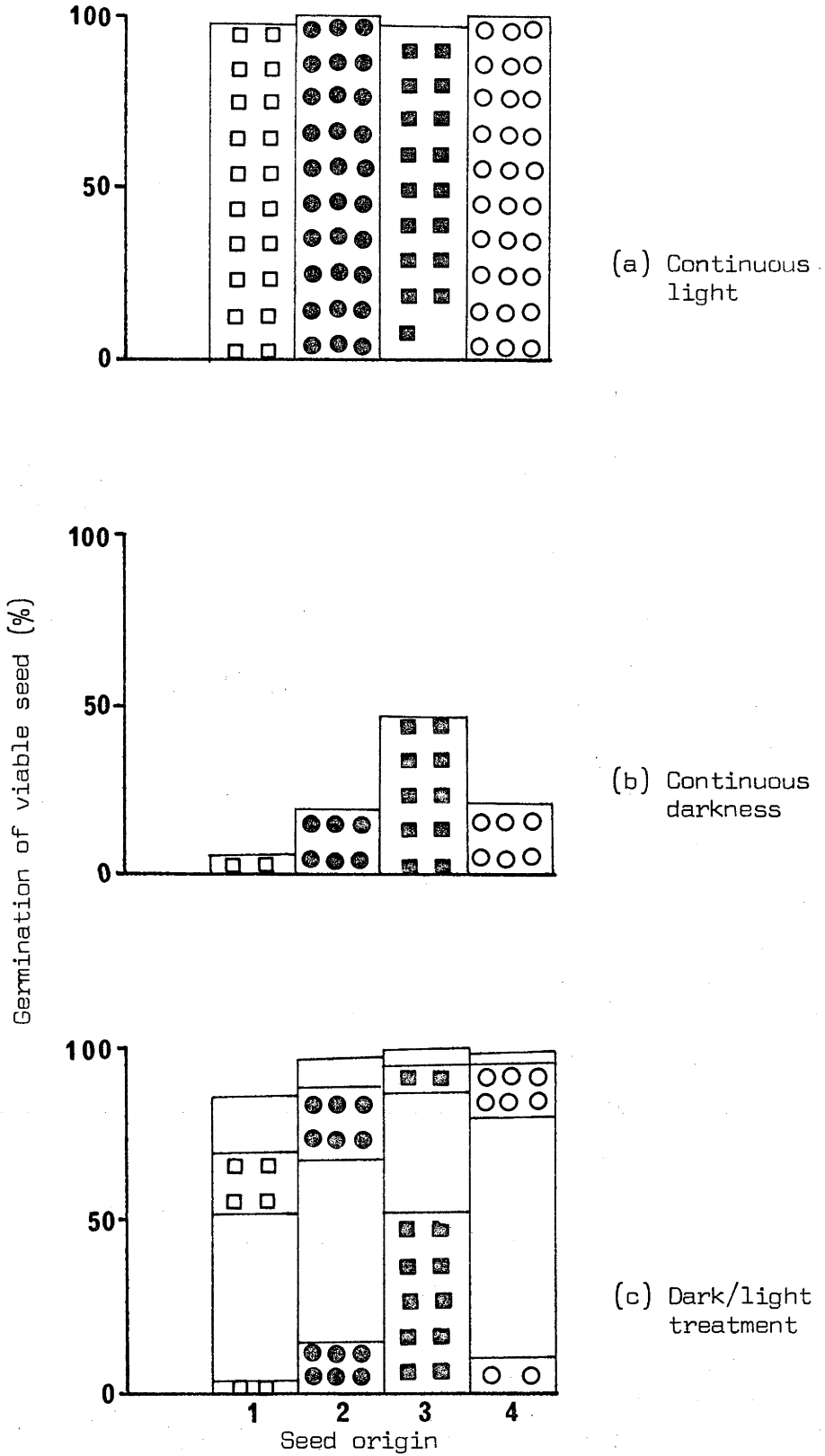


FIGURE 4.10 Summary of white light effects on seed germination of *E. camaldulensis* from 4 provenances of Katherine (1), Nathalia (2), Gwydir River (3) and Agnew (4) at 27°C.

For diagram "c" - Germination percentage figure derived from four periods a b c and d from Figure 4.9

4.3 Spectrum Action and Seed Germination

4.3.1 Introduction

The effects of light spectrum on the germination of many agricultural plants such as tomato and lettuce have been well documented. Evenari (1965) reported that the influence of light on the germination of seeds could either be positive or negative. The germination of nearly all the positively photoblastic seeds of agricultural crops has been stimulated by red light of wavelength of about 630 to 680 mu (Evenari and Neumman 1953). The blue region between 400 to 500 mu has been shown to have no consistent effects, as it can either inhibit or promote seed germination.

A limited amount of work has been done on the effects of light spectrum on the seed germination of forest tree species. Black and Wareing (1959) reported that blue light alone had no effect on Betula pubescens, but it either promoted or inhibited germination depending upon whether it was applied before or after an irradiation with red light.

From the results of the direct effects of white light on seed germination of E. camaldulensis it was shown that the species is positively photoblastic. This is in agreement with the work of Grose and Zimmer (1958) on the white light effects on the seeds of E. camaldulensis from Victorian forests.

This study set out to determine which part of the visible light spectrum is critical for seed germination of E. camaldulensis. Seed from the southern population of Lake Albacutya has been used in this experiment.

4.3.2 Materials and Methods

Special germination dishes of rectangular shape made out of glass, measuring 11 x 5 x 2 cm and 0.6 cm thick, were painted black and used for the experiment. Cotton wool was placed in the dishes and saturated with distilled water which had already been coloured with dull black solution.

A layer of filter paper was placed on the saturated cotton wool. Weighed seedlot of 0.02 gm was thinly spread on the prepared germination dish and very quickly covered by a dull black cardboard protector that prevented any radiation reaching the seeds. The germination dishes were carefully arranged in small trays that held 4 germination dishes each. The dishes were immediately covered with two layers of black cloth before they were kept in a temperature controlled darkroom for the required period of imbibition which varied between 24 and 72 hours. The temperature of the darkroom was set at 27°C. and controlled to within $\pm 1^\circ\text{C}$. This temperature was found from the earlier experiments to be close to the optimum temperature for seed germination of E. camaldulensis.

The Light-spectrum Treatments

The light treatments involved exposure of the seedlots to a range of light spectrum regimes. At a CSIRO phytotron darkroom the white light is broken down into components and these are focused on a graduated dark board. The light spectrum is marked on this board into wavelengths ranging from 380 to 720 millimicrons. Between any two component wavelengths there is a difference of 20 millimicrons, which on the board spans a length of 4.00 cm. In

this experiment seeds were exposed at 10 millimicrons intervals. The time of exposure of light to each seedlot in different wavelengths was calculated to give equal energy to the seedlots at every wavelength. The time of exposure of the seedlots to different wavelengths varied from 10 to 142 secs. for an energy level of $7410 \text{ m watt cm}^{-2} \text{ sec}^{-1}$.

For each treatment 4 lots of 0.02 gm of seeds were exposed to a given wavelength. A dark laboratory coat was worn by the operator throughout the operation to minimise the amount of light reflection into the seeds. Each germination dish was also shaded by a dull black cardboard to 15 cm above the dish to allow the wavelength to fall directly on the seeds during the time of exposure. Each treated seedlot was quickly returned to the temperature controlled darkroom.

At the end of day 6 when most of the seeds under continuous light have germinated all the treated seeds were scored for germination.

Germinated seeds were counted and removed. All the particles on the filter papers were squashed to determine the number of viable seeds. The mean of the percentage germination of four seedlots was taken as the percentage germination for each wavelength. The data are graphically presented in Figure 4.11.

4.3.3 Results and Discussion

The response of E. camaldulensis to different light wavelength is presented in Table 4.7 and graphically illustrated in Figure 4.11, showing the seed germination expressed as a percentage after 24, 48 and 72 hours of imbibition of seedlots.

There is no consistent relationship between the imbibition period before exposure to the light spectrum, and the percentage of seeds germinated. Generally, the greater the period of seed imbibition before exposure to light, the greater the percentage germination, but this relationship appears to vary with the part of the light spectrum the seeds are exposed to.

In the blue light region of the spectrum (380 to 500 mu) there was little stimulus to germination. Some germination was recorded, but it was far less than that recorded at the red light region of the spectrum. This means that red light region of the spectrum (600 to 700 mu) promotes and stimulates seed germination of E. camaldulensis. There was a strong indication that the region of the red light critical to seed germination is between 620 and 640 mu wavelength. In the far red region (720 mu) there was a reduction in the percentage germination.

Conclusions

From the present investigation it could be concluded that E. camaldulensis seeds are positively photoblastic to red light (600 to 700 mu). Blue light and far red regions of the visible light spectrum seem to have very little influence on seed germination of E. camaldulensis. The period of imbibition of seed before exposure to light radiation has limited effects on seed germination.

The present results could only be regarded as introductory to the studies of spectrum action on species of eucalypts and other forest tree species.

TABLE 4.7 The Germination Expressed as a Percentage for *E. camaldulensis* at Different Wavelengths for Equal Energy Level of $7410 \text{ m watt cm}^{-2} \text{ sec}^{-1}$.

Wave-lengths (m μ)	Duration of irradiation after imbibition at 27°C (sec.)	Germination (%)		
		After 24 hours of imbibition	After 48 hours of imbibition	After 72 hours of imbibition
380	142	19.64	30.41	-
400	60	17.24	21.25	-
420	26	2.78	12.28	-
440	14	7.77	10.13	-
460	10	7.44	21.35	-
480	12	12.48	29.57	-
500	11	22.34	15.13	-
520	23	25.93	19.13	-
540	23	32.85	20.65	-
560	30	39.48	42.56	21.57
580	24	32.93	25.00	27.05
600	38	24.72	50.56	49.32
620	47	32.09	53.18	67.40
640	57	44.40	67.98	66.29
660	71	46.73	44.37	55.88
680	114	39.46	28.27	52.60
700	142	27.84	21.66	43.71
720	142	9.16	19.21	18.01

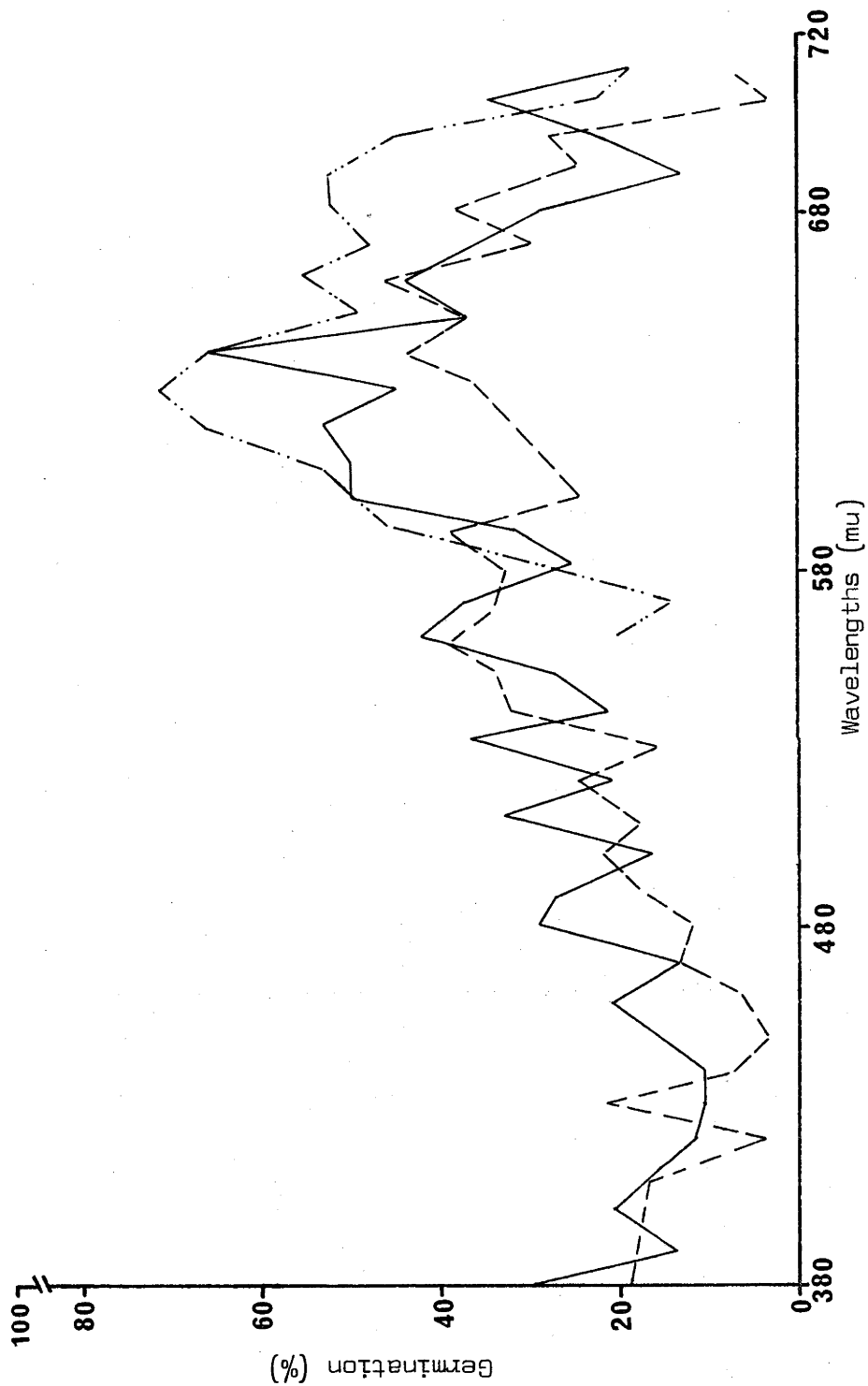


FIGURE 4.11 Germination percentages of the seeds of *E. camaldulensis* from Lake Albacutya, irradiated with light spectrum after different imbibition times. 24 hours imbibition time (---), 48 hours (—), and 72 hours (—·—).

CHAPTER 5

TEMPERATURE AND SEEDLING GROWTH

5.1 Introduction

The effects of specific environmental factors on plant growth can be investigated under controlled conditions (Green 1967), but in trees only the seedling stage of the life cycle can be studied in this way. For example, some effects of varying temperatures on growth of E. camaldulensis seedlings have been previously examined. Karschon and Pinchas (1968) showed that variation in leaf surface temperatures of E. camaldulensis was related to the seed origin, and in studies of the growth rate of progenies raised from 9 provenances, Pryor and Byrne (1969) established a strong indication of latitudinal variation in response to temperature. In the latter study, there was some tendency for height to increase with decrease in latitude suggesting a faster growth rate in the seedling stage for the northern populations of E. camaldulensis.

This study set out to further investigate seedling growth under a range of temperature regimes, as a means of understanding the possible nature of environmental influences on the provenances of E. camaldulensis.

5.2 Materials and Methods

Seedlots of Eucalyptus camaldulensis from four provenances - Katherine, Lake Albacutya, Gwydir River and Agnew - were used for

this investigation (Table 4.1). For each provenance seed had been collected from 5 trees, and each seedlot was kept separate. The study therefore involved progenies of 20 trees. The five best seedling progenies were selected for each tree - making a total of twenty-five seedlings for each provenance. The experiment was carried out at the CSIRO phytotron in Canberra. Seedlings were grown in the three temperature regimes as follows:

Series - Open Glasshouse	1	2	3
Day Temperature ($^{\circ}\text{C}.$)	21	27	33
Night Temperature ($^{\circ}\text{C}.$)	16	22	28

The glasshouses are maintained at the day temperature for eight hours daily. Supplementary light in the open glasshouses is used to provide a 16-hour photoperiod. Temperatures within the glasshouses may vary by $\pm 1.5^{\circ}\text{C}.$

Before sowing the seed was coated with fungicide (Zineb 65). Seed was sown in small, germination pots containing a mixture of equal parts of perlite and vermiculite, and the seed was thinly covered by perlite after sowing. The germination pots stood in a tray of water and shaded with nylon cloth to provide about 70 percent shade. The shade remained on the pots for 3 weeks. The seed was germinated at $27/22^{\circ}\text{C}.$ which is close to the optimum temperature for germination of Eucalyptus camaldulensis. At exactly 4 weeks after sowing, two seedling progenies from each parent tree were pricked out into each of twenty-five 13cm plastic pots containing a

mixture of equal parts of perlite and vermiculite. After pricking out the seedlings were left at 27/22⁰C. for one week to establish hair roots. Before transfer to the experimental treatments, the seedlings were reduced to the best seedling per pot and all pots for each temperature treatment were randomly arranged on trays. The seedlings were watered twice daily, - with a modified "Hoagland" nutrient solution in the morning and tap water in the afternoon. The composition of the Hoagland solution is in Appendix 1.

The following parameters were measured every ten days:

Seedling height

Basal stem diameter

Number of leaves on stem

Number of leaves on branches

Number of branches

Number of internodes

The seedling height was measured from the cotyledon to the estimated position of the apical meristem. The basal diameter was measured between the cotyledon and the first leaf pair. The relative positions of the plants were changed at random at every measurement day. Before the final harvest was carried out, the following additional data were obtained for each seedling:

Length of 6th leaf

Length of 7th leaf

Length of 8th leaf

Breadth of 6th leaf

Breadth of 7th leaf

Breadth of 8th leaf

Thickness of 8th leaf

Basal angle of 8th leaf

Lignotuber diameter

The leaf length was taken as the distance between the petiole and the apex of the leaf. The leaf breadth was the widest section of the leaf, this usually being at one third of the leaf length. The leaf thickness was the mean of four readings taken at different points - two on each side of the leaf; in this, care was taken to avoid any strong lateral vein on the leaf.

Final Harvest

After all these plant parameters were recorded, the shoot was cut off and placed in a paper bag. The roots were carefully washed clean of potting media, and placed in another paper bag. The plants were then dried in an oven at a temperature of 80°C. for seven days. The oven dry weight was determined by weighing the dried matter at a room temperature.

5.3 Results

I. Seedling Growth

A. Graphical Presentation of Growth Data.

The growth of Eucalyptus camaldulensis seedlings from 4 provenances at each of the three temperature regimes are shown graphically in Figures 5.1 to 5.7 for each of the 6 parameters measured, as follows:

- Figures 5.1 Height growth,
5.2 Basal diameter,
5.3 Number of leaves on stem,
5.4 Number of leaves on branches,
5.5 Number of branches,
5.6 Number of internodes,
5.7 Response of the provenances at day 50, to
the 3 temperature regimes.

In all six attributes measured, and for all temperature regimes there was a more or less progressive increase in seedling growth with time. For some of the parameters, for example height growth, leaves on branches and number of branches, rate of growth was somewhat slower during the 10-20 or 10-30 day period than in the 20-50 or 30-50 day period, but there after there was a straight line relationship between the parameter and time.

In all six attributes, there were marked differences between the provenances. Seedlings from the southern provenances, Lake Albacutya and Gwydir River, had generally greater growth rates than seedlings from the northern provenances of Katherine and Agnew. In most of the parameters, the northern and southern provenances are quite distinct, but in a few, the growth of Katherine provenance was equal or close to that of the growth of the southern provenances. The Agnew provenance was consistently below that of the other 3 provenances. One of the more extreme differences between provenances is in the number of leaves on seedling branches. The southern

provenances produce far more branches and leaves on branches than the northern provenances.

The effects of temperature on seedling growth are shown in Figure 5.7 for the four provenances at day 50 after transfer to the respective temperature treatments. The optimum temperature for growth was 27/22°C., for all provenances, and with one exception, for all attributes measured. The one exception was the "number of branches on seedlings" (Figure 5.7e) where the 27/22°C. temperature was distinctly superior for only one provenance (Gwydir River).

Seedling height growth was greater at 33/28°C. than 21/16°C. for the Lake Albacutya, Gwydir River and Katherine provenances, but not for the Agnew provenance. Perhaps on the hottest and driest environment such as Agnew, there has been natural selection against seedlings which grow most rapidly at high temperatures - thus increasing chances of seedling survival. It is significant that the Agnew provenance also has the slowest growth rate of the 4 provenances at any temperature.

For growth parameters other than seedling height, pattern of seedling response at 33/28°C. and 21/16°C. varied; for example the number of leaves on branches, and the number of internodes were greater at 33/28°C. than 21/16°C., while seedling basal diameter and number of leaves on branches tended to be greater at 21/16°C. than 33/28°C.

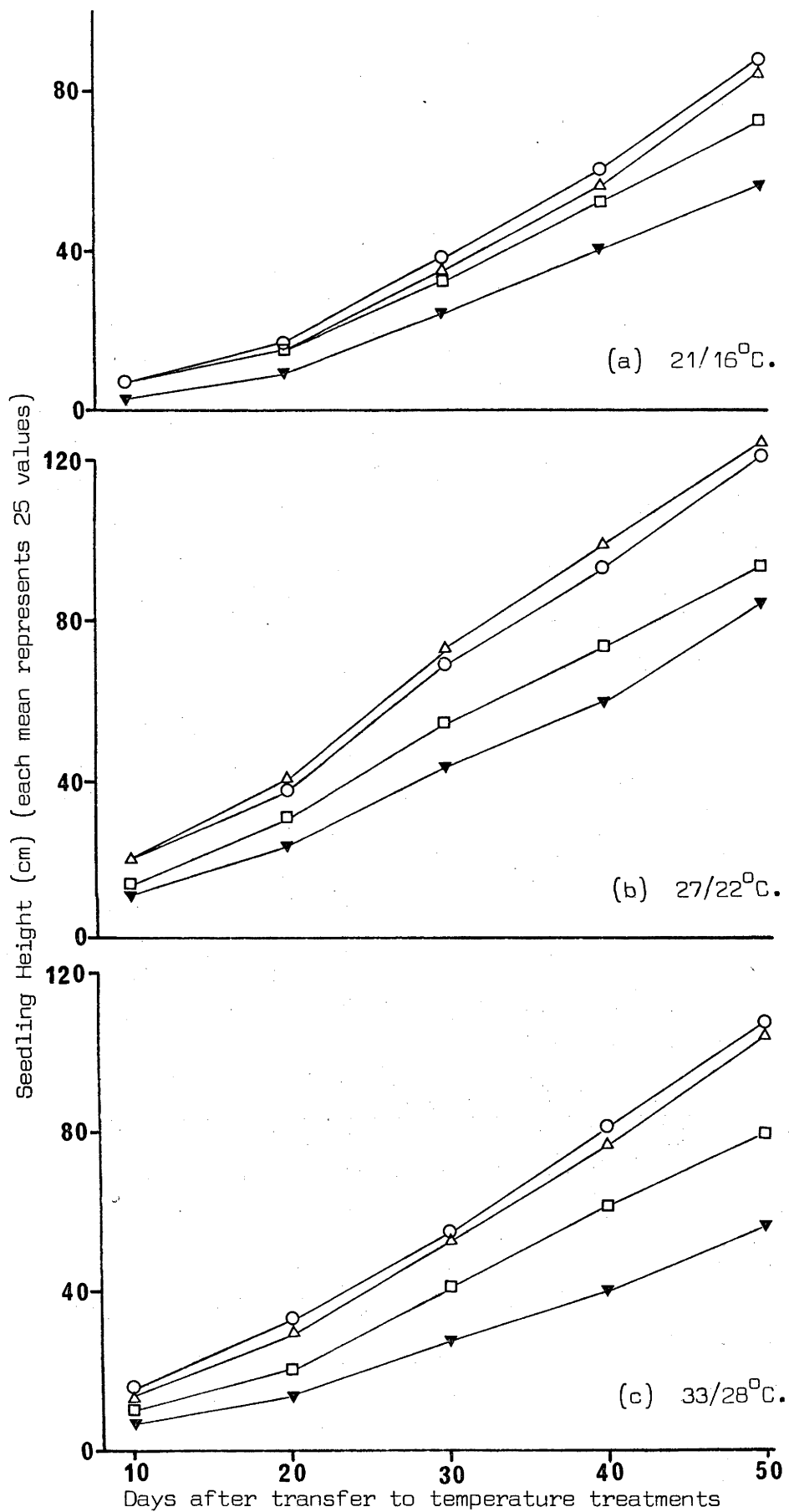


FIGURE 5.1 Variation in the response to temperature of seedling height of *E. camaldulensis* from 4 provenances of Katherine (□), Lake Albatutya (○), Gwydir River (△) and Agnew (▼).

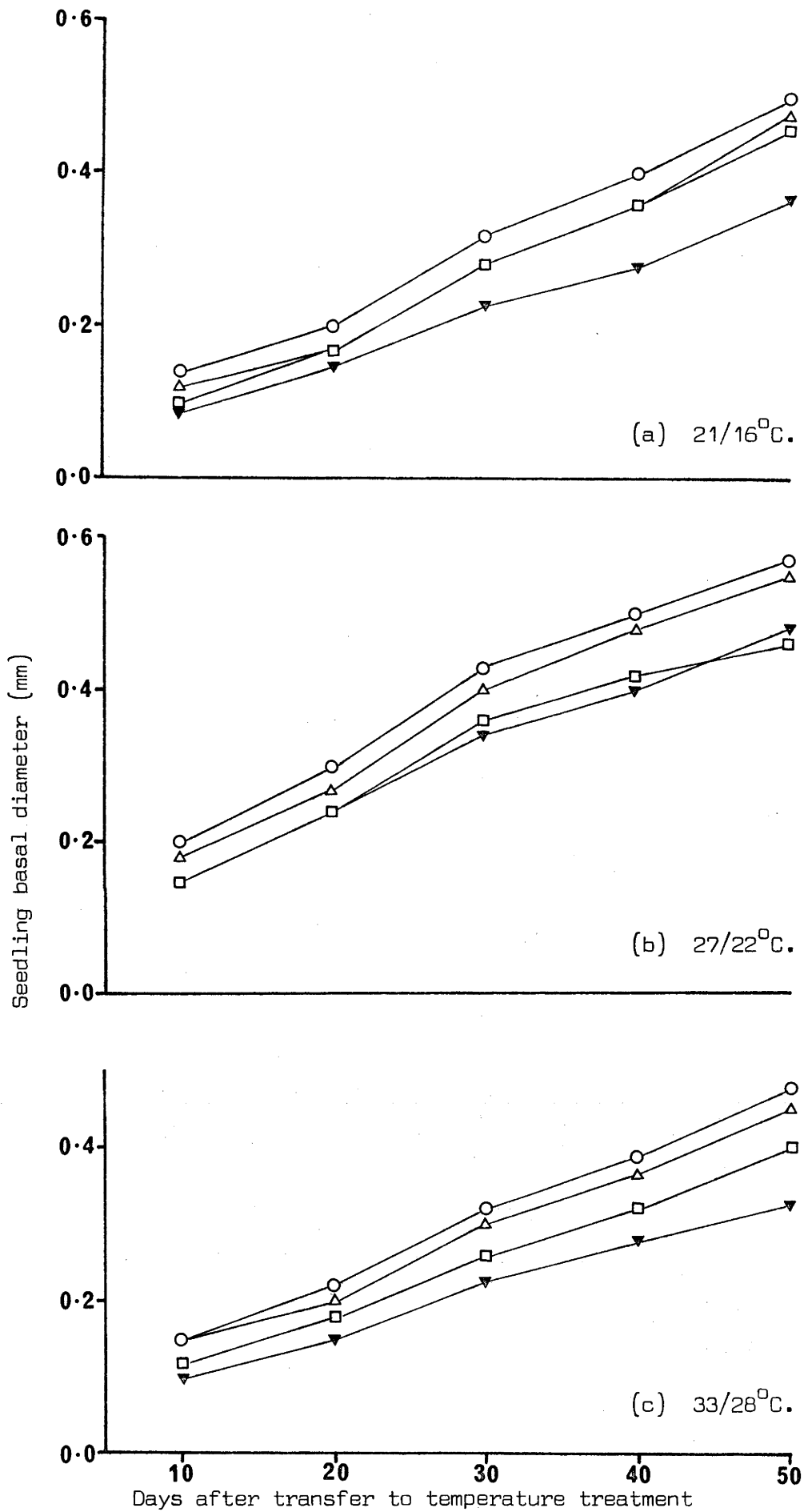


FIGURE 5.2 Variation in the response to temperature of seedling basal diameter of *E. camaldulensis*. Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

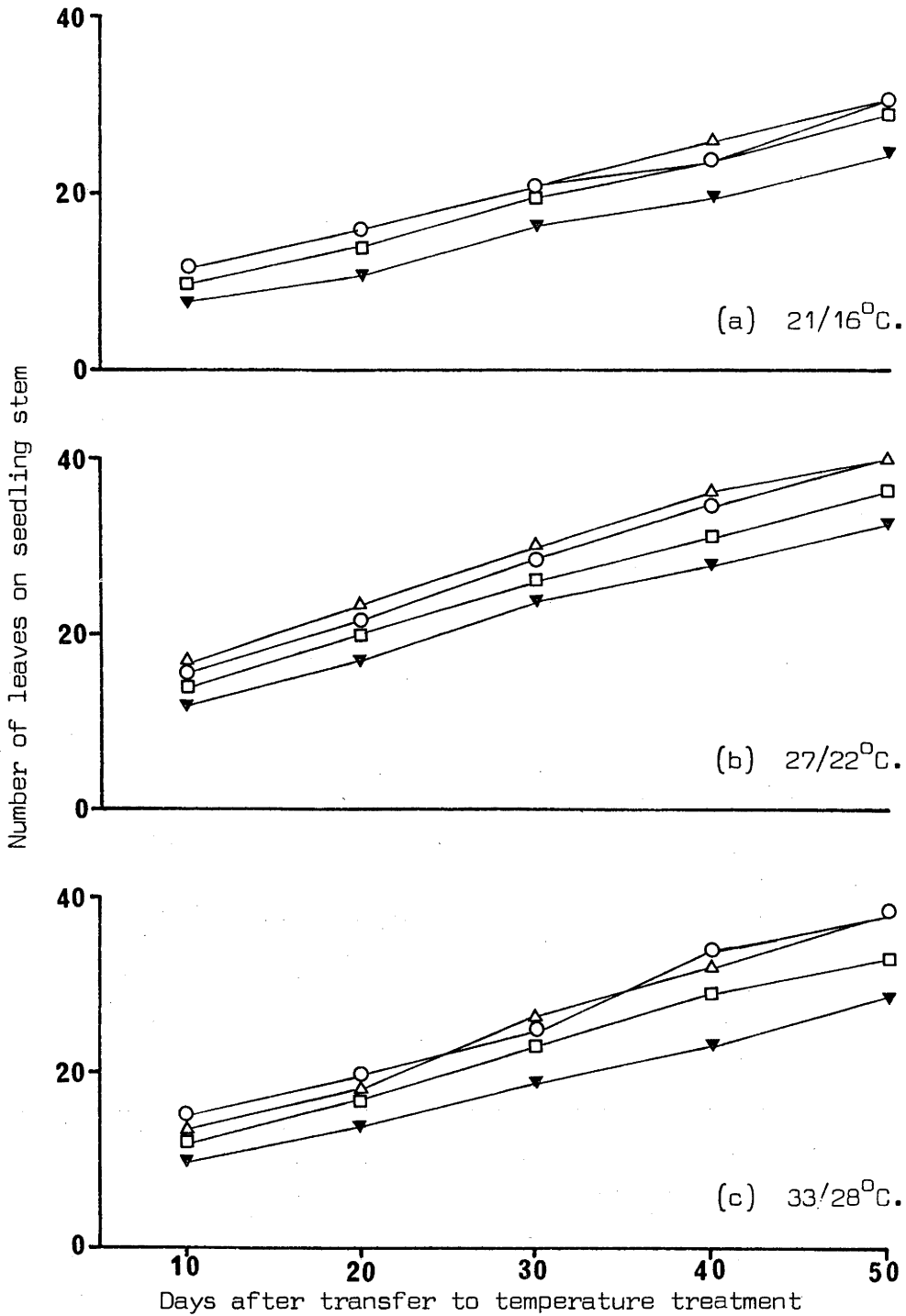


FIGURE 5.3 Variation in the response to temperature of the leaf production on the stem of seedlings of *E. camaldulensis* from 4 provenances of Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

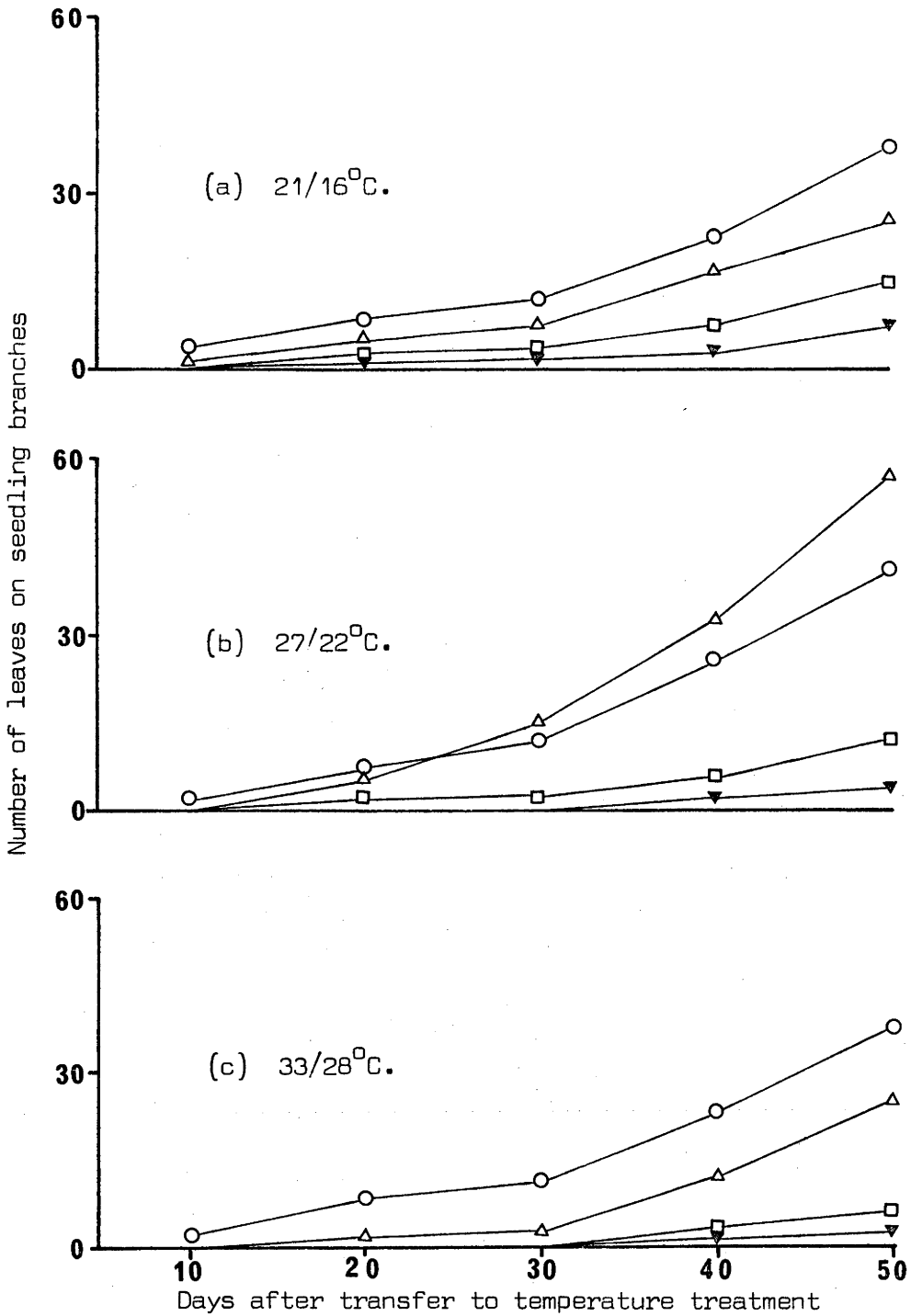


FIGURE 5.4 Variation in the response to temperature of the leaf production on the seedling branches of *E. camaldulensis* from 4 provenances of Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

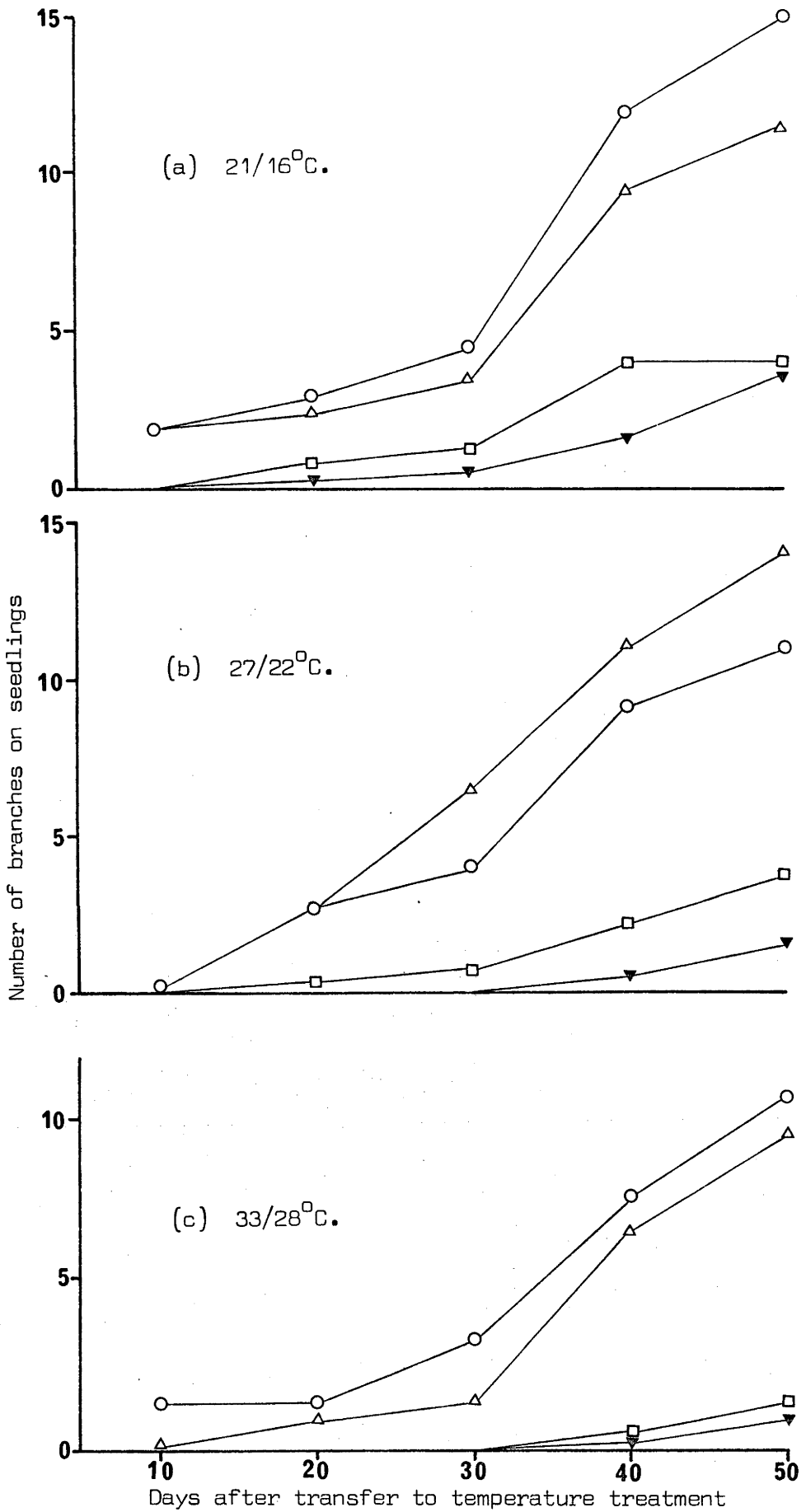


FIGURE 5.5 Variation in the response to temperature of the branch production of *E. camaldulensis* from 4 provenances of Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

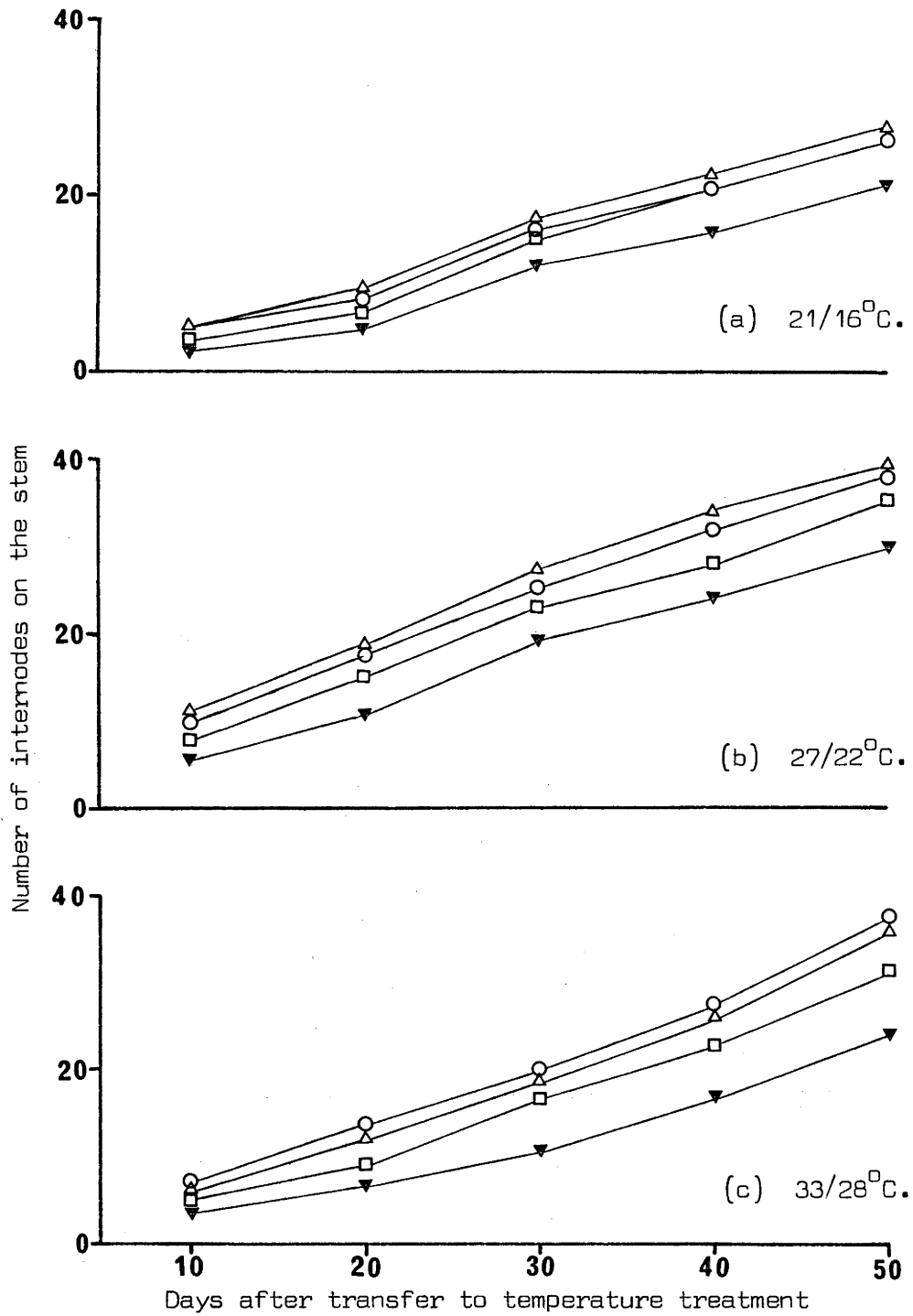


FIGURE 5.6 Variation in the response to temperature of the number of internodes on the seedling stem of *E. camaldulensis* from 4 provenances of Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

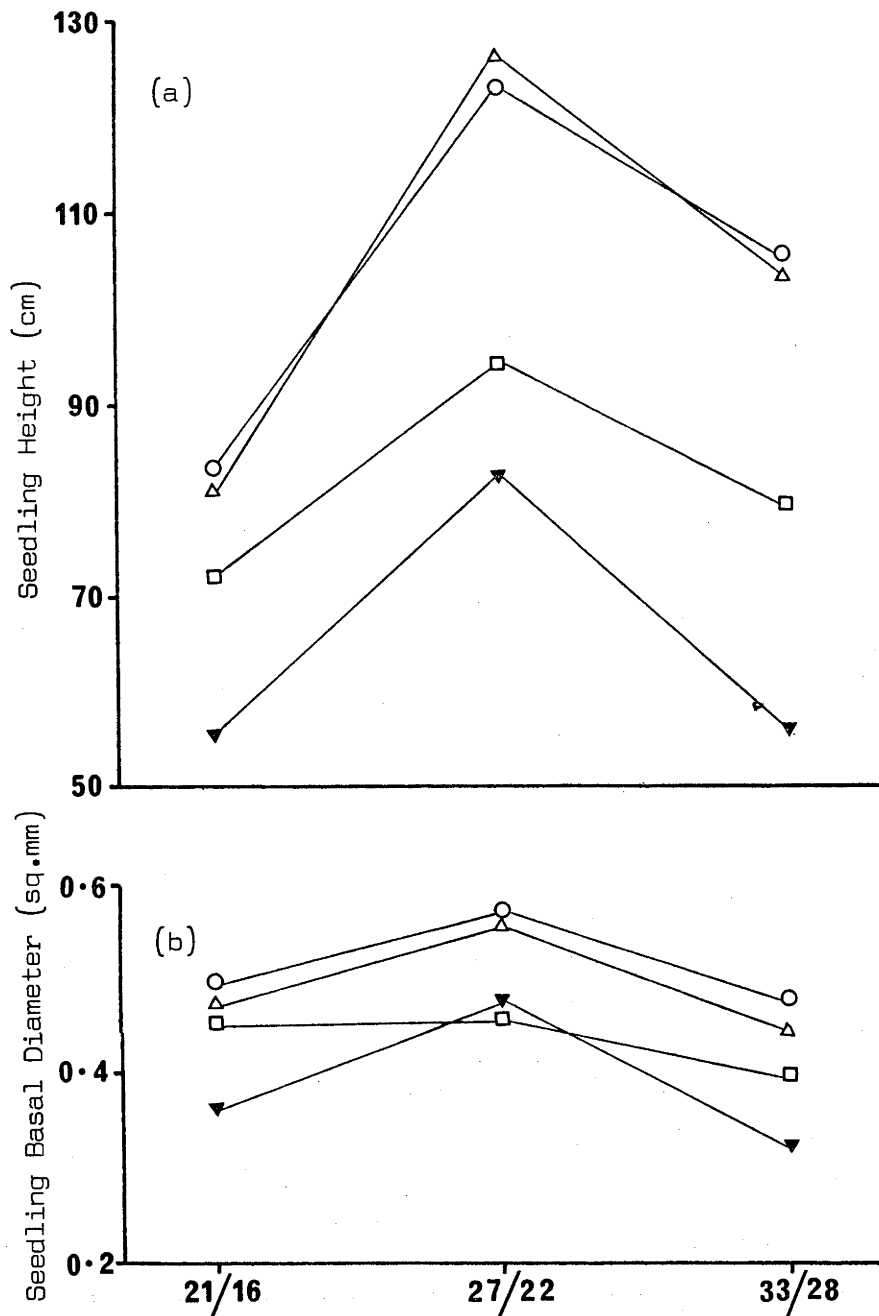


FIGURE 5.7 Provenance Variation in Response of Seedling Progenies of *E. camaldulensis* from 4 Provenances of Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼) to Variation in Temperature at Day 50 After Transfer to Temperature Treatment.

- (a) seedling height
 (b) seedling basal diameter

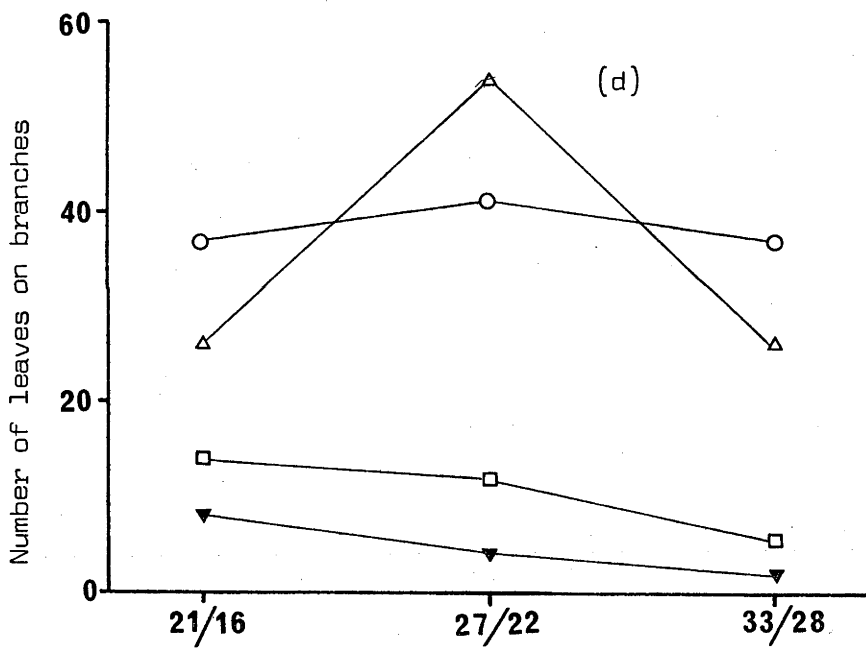
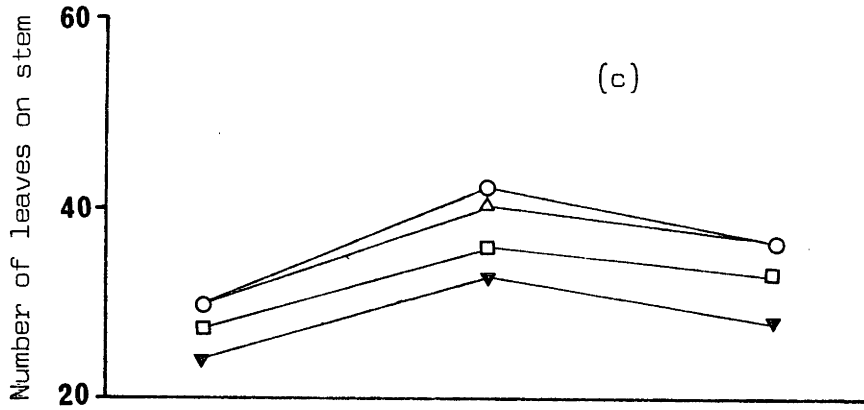


FIGURE 5.7 (Cont'd.)

- (c) number of leaves on stem
 (d) number of leaves on branches

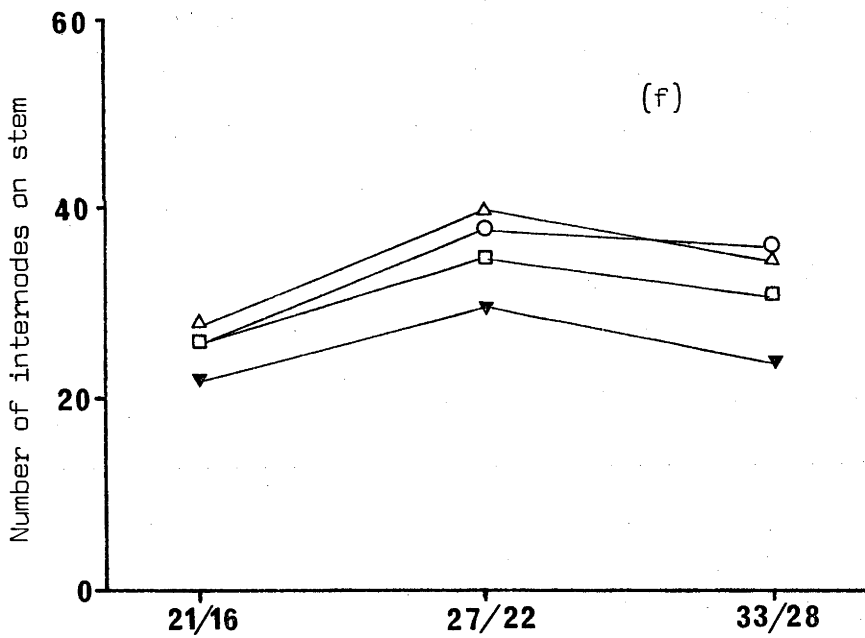
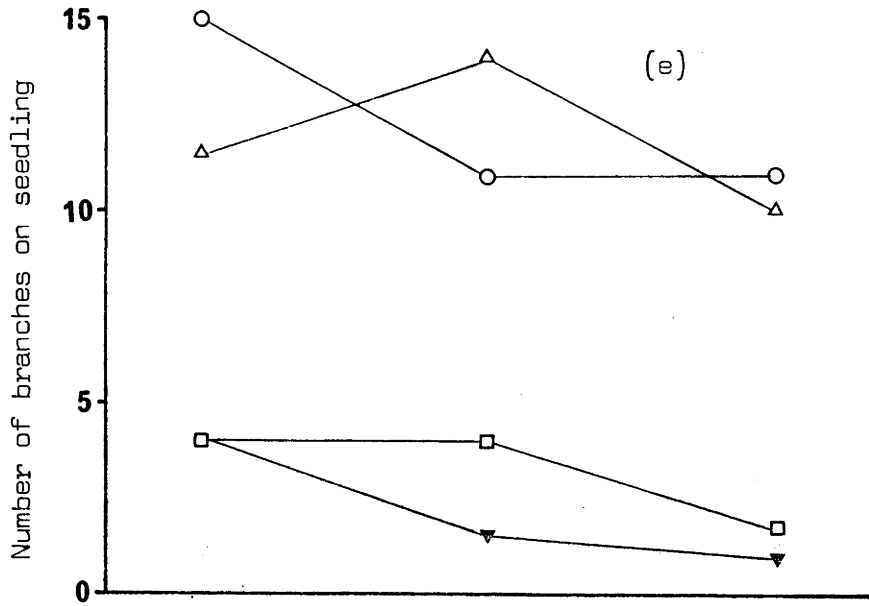


FIGURE 5.7 (Cont'd.)

- (e) number of branches on seedling
 (f) number of internodes on stem

B. Analyses of Seedling Growth Data

The experimental data have been analysed in a number of ways, - (i) to show the significance of differences between provenances at the 3 temperatures, and for the six growth parameters, (ii) to show inter-relationships between growth parameters, and (iii) to show which of the parameters were contributing most to variation within the species, and specifically, within each of the provenances.

(i) Comparison of provenance means for each growth parameter - at each temperature.

Means and standard errors for each of the growth parameters shown in Figures 5.1 to 5.7 are given in Tables of means in Appendix 2. These data were analysed and the least significant difference values at 5% level of probability are given to compare means of provenances at any one temperature and measurement period. In these Tables, each value represents the mean of 25 seedlings for each provenance.

A summary of the significance of differences between individual means, drawn from Appendix 2 is given in Table 5.1. This shows significance of difference between provenance means, for each of the 3 temperatures and 6 growth parameters. Most of the differences between provenance means were significant at the 5% level of probability. The consistent exception were as follows:

- (a) The Gwydir River and Lake Albacutya provenances (both southern provenances) did not differ significantly in height growth at any temperature. Otherwise, both northern provenances differed from both southern provenances, and the northern Agnew provenance differed from the northern Katherine provenance.

- (b) Gwydir River and Lake Albacutya provenances (southern provenances) did not differ significantly in the number of leaves on the stem - at any temperature.
- (c) Gwydir River and Lake Albacutya provenances again did not differ significantly in the number of stem internodes - at any temperature.

These results tend to express a general similarity in the two southern provenances. They show the southern provenances are closely similar in seedling height, leaves on stems, and number of branches; and that the southern provenances differed consistently in these respects from the northern provenances. The analysis also shows the northern provenances (Katherine and Agnew) differed, but not consistently in all attributes - for example, differences between the northern provenances did not differ significantly, either at 21^o or 33^oC., in "leaves on branches" and "number of branches".

- (ii) Differences between provenances, where responses at all 3 temperatures are taken into account.

For each of the six growth parameters, a univariate analysis of variance was carried out for data at day 50. A summary of the significance of differences between provenances is presented on Table 5.2. Where data for all 3 temperatures are taken into account, provenance differences were significant at the 5% level of probability, for all six growth parameters.

TABLE 5.2 Univariate Analysis of Variance for Seedling Growth
Characteristics at day 50 after Transfer to
Temperature Treatment.

Source	D.F.	Mean Square	Variance Ratio	Sig. 5%
Seedling Height (cm)				
Provenance	3	21650.90	88.98	*
Temperature	2	28097.06	95.60	
Prov. x Temp.	6	973.21	3.31	
Basal Diameter (mm)				
Provenance	3	0.24	44.86	*
Temperature	2	0.31	56.83	
Prov. x Temp.	6	0.01	2.65	
Leaves on Stem				
Provenance	3	943.07	33.02	*
Temperature	2	2164.69	75.80	
Prov. x Temp.	6	38.94	1.36	
Leaves on Branches				
Provenance	3	22088.34	43.66	*
Temperature	2	2788.76	5.51	
Prov. x Temp.	6	1704.33	3.37	
Number of Branches				
Provenance	3	2143.33	56.03	*
Temperature	2	235.99	6.17	
Prov. x Temp.	6	57.36	1.50	
Number of Internodes on Stem				
Provenance	3	1181.71	44.24	*
Temperature	2	2850.30	106.71	
Prov. x Temp.	6	78.35	2.93	

(iii) Inter-relationships Between Growth Parameters.

In plant development some growth parameters will always be highly correlated with others - for example, seedling height and seedling basal diameter. Alternatively, correlation between other growth characteristics need not be strong, for example that between height growth and the number of branches or height growth and the number of internodes on the stem.

For the data obtained in this study, a matrix of correlation coefficients for the six growth parameters has been prepared, for the species as a whole (Table 5.3) and for each of the provenances separately (Table 5.5). In preparation of this matrix, all data have been used, - that is, data for the three temperatures and the six occasions at which the measurements were taken.

For the species as a whole, seedling height was highly correlated with basal diameter, number of leaves on stems, and the number of internodes (correlation coefficient 0.9), and less highly correlated with the number of leaves on branches, and the number of branches (correlation coefficients 0.5 to 0.6). Where the correlation coefficients are examined separately for each provenance, there is some separation of the northern and southern provenances with respect to the correlations between seedling height, and the number of leaves on branches, and number of branches, respectively. For the southern provenances, these two correlation coefficients were 0.632 and 0.600 (Lake Albacutya), and 0.711 and 0.668 (Gwydir River), and for the two northern provenances, the correlation coefficients were 0.385 and 0.367 (Agnew), and 0.416 and 0.401

(Katherine). This means there could be some tendency for seedling branch characteristics to be more independent of height growth in the northern than in the southern provenances. Similarly, there is a better correlation in the southern provenances between number of leaves on stems and number of leaves on branches (0.643 for Lake Albacutya, 0.726 for Gwydir River) than in the northern provenances (0.397 for Katherine, 0.356 for Agnew). Northern provenance seedlings tend to be generally more variable in the way they develop than the southern provenance seedlings. That is, there could have been selection for branch, and leaf characters in the northern environment that have critical survival value.

(iv) Partitioning Contribution of the Six Growth Parameters to Total Variation Within the Species, and to the Variation Within each Provenance.

In the foregoing sections it has been shown that there are significant differences between provenances in respect to each of the six growth parameters measured, and that seedlings from northern provenances tend to be more variable with respect to particular characteristics than seedlings from the southern provenances. In this final analysis of the growth characters, variance components for each growth parameter are examined in a discriminant analysis to detect the proportion of total variance that is attributable to each parameter. This is done for all seedlings involved in the study (Table 5.4) and for each provenance separately (Table 5.6). Values reported in these tables are the percentage of total variation attributable to each parameter and their eigenvalues.

Where all seedling progenies are considered (Table 5.4), number of internodes accounts for 88 percent of the total observed variation, and number of internodes and height growth together account for about 93 percent of observed variation.

Where the provenances are considered individually, there is an interesting difference between the provenances. In three of the provenances, Lake Albacutya, Gwydir River and Agnew, the number of internodes on the stem is the main discriminator; in these provenances, the number of internodes on the stem accounted for around 90% of total variation. Alternatively, the main discriminator for the Katherine provenance was seedling height - constituting more than 90% of the total observed variation. Katherine is the most northern provenance examined - and has much greater variation in seedling height than the other 3 provenances.

TABLE 5.3 Correlation Coefficient Matrix for 6 Growth Parameters,
Based on Data at 3 Temperatures, 4 Provenances and
6 Measured Occasions.

	1	2	3	4	5	6
1. Seedling Height	1.000	0.937	0.971	0.571	0.544	0.978
2. Basal Diameter		1.000	0.927	0.660	0.636	0.939
3. Number of Leaves on Stem			1.000	0.566	0.543	0.984
4. Leaves on Branches				1.000	0.966	0.575
5. Number of Branches					1.000	0.549
6. Number of Internodes						1.000

TABLE 5.4 Absolute Eigenvalues and their Contributions to Total
Variation, Based on Data at 3 Temperatures, 4 Provenances,
and 6 Measured Occasions.

Order	% of Total Variation	Eigenvalues	t-test		Variates contributing at axis one only
			1%	5%	
1	88.093	19.243	**	*	Number of Internodes
2	5.186	1.133	**	*	Height
3	3.139	0.686	**	*	Number of Leaves on stem
4	1.444	0.315	**	*	Basal Diameter
5	1.287	0.281	**	*	Number of Branches
6	0.849	0.186	**	*	Number of Leaves on branch

TABLE 5.5 Matrix of Correlation Coefficients for 6 Growth Parameters, for Each of the 4 Provenance - Katherine, Lake Albacutya, Gwydir River and Agnew - Based on Data at 3 Temperatures and 6 Measured Occasions.

(A) Katherine	1	2	3	4	5	6
1 Seedling Height	1.000	0.946	0.977	0.416	0.401	0.983
2 Basal Diameter		1.000	0.927	0.547	0.530	0.943
3 Leaves on Stem			1.000	0.397	0.381	0.985
4 Leaves on Branches				1.000	0.988	0.415
5 Number of Branches					1.000	0.397
6 Number of Internodes						1.000

(B) Lake Albacutya	1	2	3	4	5	6
1 Seedling Height	1.000	0.929	0.969	0.632	0.600	0.975
2 Basal Diameter		1.000	0.922	0.710	0.685	0.932
3 Leaves on Stem			1.000	0.643	0.611	0.979
4 Leaves on Branches				1.000	0.946	0.654
5 Number of Branches					1.000	0.620
6 Number of Internodes						1.000

(C) Gwydir River	1	2	3	4	5	6
1 Seedling Height	1.000	0.930	0.966	0.711	0.668	0.976
2 Basal Diameter		1.000	0.926	0.797	0.756	0.937
3 Leaves on Stem			1.000	0.726	0.692	0.985
4 Leaves on Branches				1.000	0.957	0.741
5 Number of Branches					1.000	0.700
6 Number of Internodes						1.000

(D) Agnew	1	2	3	4	5	6
1 Seedling Height	1.000	0.948	0.972	0.385	0.367	0.978
2 Basal Diameter		1.000	0.941	0.443	0.430	0.952
3 Number of Leaves on Stem			1.000	0.356	0.339	0.984
4 Leaves on Branches				1.000	0.974	0.382
5 Number of Branches					1.000	0.364
6 Number of Internodes						1.000

TABLE 5.6 Absolute Eigenvalues and Their Contributions to Total Variation, for Each of the 4 Provenances - Katherine, Lake Albacutya, Gwydir River and Agnew - based on Data at 3 Temperatures and 6 Measured Occasions.

(A) Katherine

Order	% of total Variation	Eigenvalues	t-test		Variates Contributing at axis one only
			5%	1%	
1	92.224	19.928	*	**	Height
2	5.053	1.092	*	**	Number of Internodes
3	1.601	0.346	*	**	Number of Branches
4	0.587	0.127	*	**	Leaves on Stem
5	0.362	0.078	NS	NS	Leaves on Branches
6	0.173	0.038	NS	NS	Basal Diameter

(B) Lake Albacutya

Order	% of total Variation	Eigenvalues	t-test		Variates Contributing at axis one only
			5%	1%	
1	94.320	32.578	*	**	Number of Internodes
2	2.823	0.975	*	**	Seedling Height
3	1.438	0.497	*	**	Number of Branches
4	0.731	0.253	*	**	Basal Diameter
5	0.385	0.133	NS	NS	Leaves on Branches
6	0.301	0.104	NS	NS	Leaves on Stem

TABLE 5.6 (Cont'd.)

(C) Gwydir River

Order	% of total Variation	Eigenvalues	t-test		Variates Contributing at axis one of scaled vectors
			5%	1%	
1	90.607	24.480	*	**	Number of Internodes
2	4.422	1.195	*	**	Leaves on Stem
3	2.732	1.738	*	**	Basal Diameter
4	1.385	0.374	*	**	Number of Branches
5	0.510	0.138	NS	NS	Height
6	0.340	0.092	NS	NS	Leaves on Branches

(D) Agnew

Order	% of total Variation	Eigenvalues	t-test		Variates Contributing at axis one of scaled vectors
			5%	1%	
1	87.605	11.701	*	**	Number of Internodes
2	6.705	0.896	*	**	Height
3	3.607	0.482	*	**	Leaves on Branches
4	1.194	0.160	*	**	Leaves on Stem
5	0.624	0.083	NS	NS	Basal Diameter
6	0.263	0.035	NS	NS	Number of Branches

II. Effect of Temperature on Leaf Morphology

In the study of leaf morphology leaf characters were measured as follows: length and breadth of 6th, 7th and 8th leaves, mean leaf length, mean leaf breadth, the leaf length:leaf breadth ratio, leaf thickness, and leaf basal angle. All experimental data are summarised on Appendix 3. For each parameter - temperature combinations, the significance of the differences between provenances is given (LSD at 5% level of probability). Some of these data are illustrated graphically in Figures 5.8 to 5.12 as follows - using all seedling data:

- Figures 5.8 Influence of Temperature on mean leaf length
- 5.9 Influence of Temperature on mean leaf breadth
- 5.10 Influence of Temperature on leaf length:breadth ratio
- 5.11 Influence of Temperature on leaf basal angle
- 5.12 Influence of Temperature on leaf thickness.

A summary of the significance of provenance differences at each temperature is given for each of the 11 variables in Table 5.7, and the summary of the univariate analysis showing differences between temperature and between provenances is given in Table 5.8.

There was an increase in leaf length from 6th to 8th leaf at each temperature and for each provenance. There was a similar increase in leaf breadth. The 8th leaf represents an intermediate stage between the juvenile and the adult leaf. For comparative purposes the mean leaf length (6, 7, and 8th leaves) and the mean leaf breadth (6, 7, and 8th leaves) are taken as representing leaf size and shape for the whole seedling.

Seedling leaf size (mean leaf length, and mean leaf breadth) decreases with increasing growing temperature (Appendix 3(d), (h), Figures 5.8 to 5.9). For example, leaf length decreased from 10.47cm at 21/16°C. to 8.11 cm at 33/28°C. for the Lake Albacutya provenance, and leaf breadth decreased from 4.17 to 3.05 cm. Temperature has a significant ($p = 0.05$) influence on mean leaf length and breadth (Table 5.8).

There are some significant differences between individual provenance means in leaf length, leaf breadth, at each of the 3 growing temperatures, but it is difficult to interpret these in a meaningful way (Table 5.7). For example, at 27/22°C. the only significant difference in mean leaf length between provenances was that between Gwydir River and Lake Albacutya provenances - both southern provenances. The northern provenance (Katherine) did not consistently differ from southern provenances in leaf length, but it did differ significantly from most of the southern provenances in leaf breadth at all 3 temperatures. However, even here, the data are difficult to interpret - Katherine leaves were broader than Gwydir River and Agnew leaves at 21/16°C., and narrower than Gwydir River and Agnew leaves at 27/22°C and 33/28°C. Because of inconsistencies such as these, difference between provenances in leaf length and breadth when all temperatures are considered, are not significant (Table 5.8).

When leaf shape is expressed as the ratio of leaf length/leaf breadth, data show a significant difference between provenances (Table 5.8). The ratio for Agnew and Lake Albacutya is smaller than that for Katherine and Gwydir River at all temperatures, that is,

there is no obvious relationship between leaf shape and latitude of provenance. The ratio itself does not vary consistently with temperature (Appendix 3(i)).

Leaves grown at low temperature were generally thicker than those grown at high temperatures, and there was a significant difference between provenances in this attribute. At each of the 3 temperatures, leaf thickness was greater on Lake Albacutya and Agnew seedlings than on Katherine and Gwydir River seedlings. That is, the Lake Albacutya and Agnew seedlings had both a smaller length/breadth ratio and thicker leaves than the Katherine and Gwydir River seedlings. It is again, difficult to interpret this.

Finally, there was a significant difference between provenances in leaf basal angle (Table 5.8). The Katherine provenances had a smaller basal angle at each of the three temperatures. For example, at 27/22°C. it was 80.4° for the Katherine (northern most provenance), and 92.3° for Gwydir River, 93.1° for Agnew, and 108.5° for Lake Albacutya.

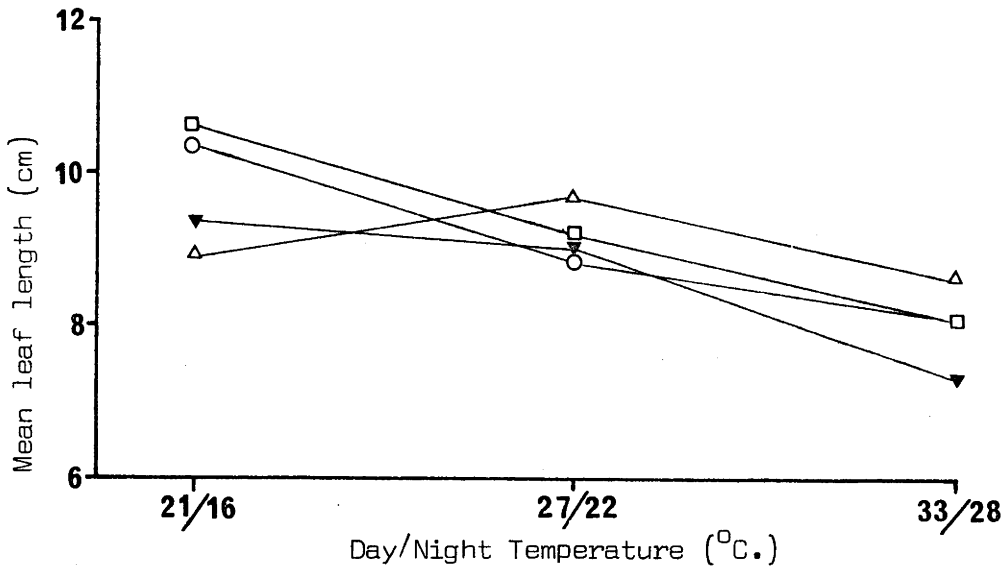


FIGURE 5.8 Provenance variation in response to temperature of mean leaf length of *E. camaldulensis* during period of 50 days. Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

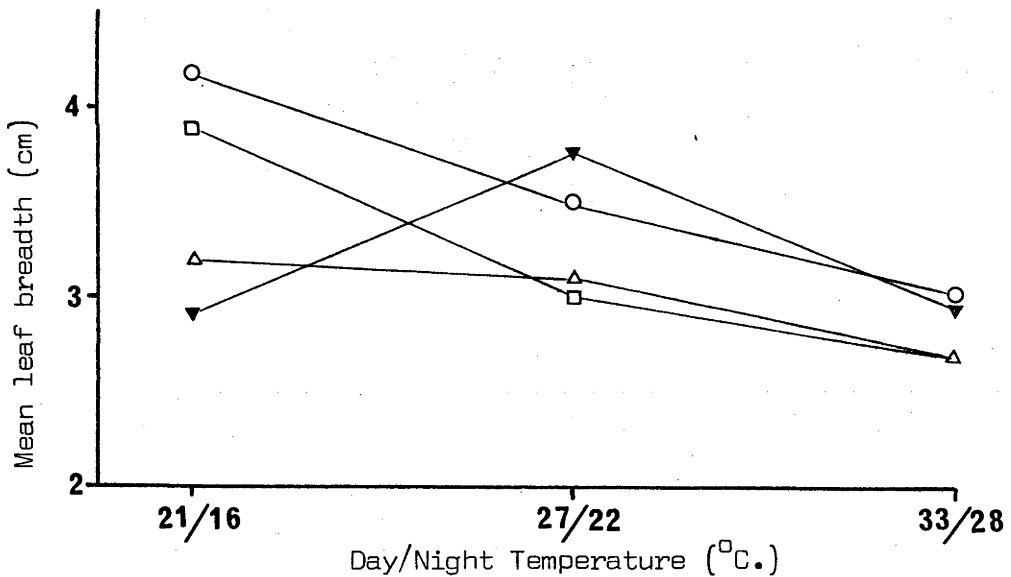


FIGURE 5.9 Provenance variation in response to temperature of mean leaf breadth of *E. camaldulensis* during period of 50 days. Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

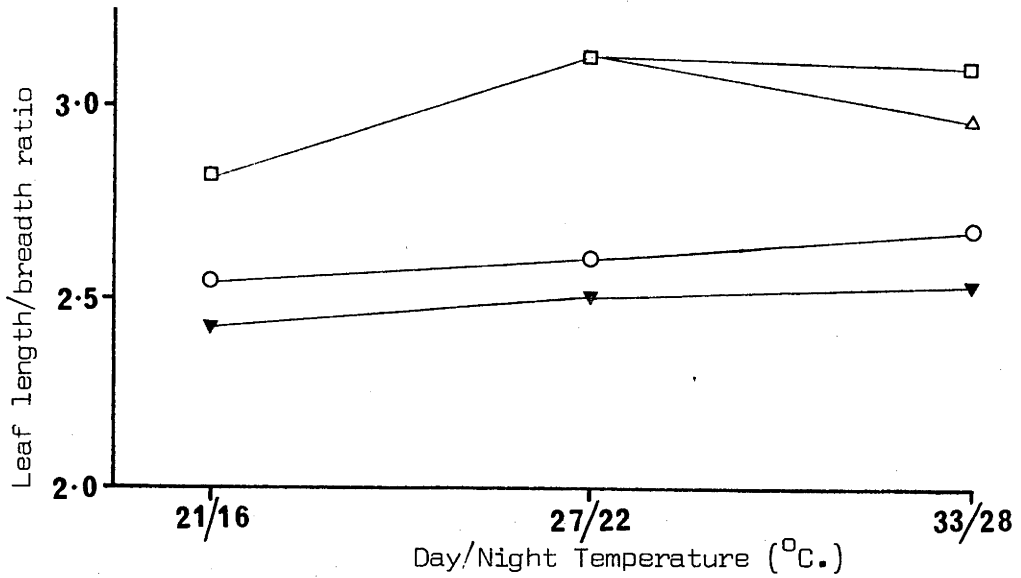


FIGURE 5.10 Temperature effect on leaf length/breadth ratio of *E. camaldulensis* during period of 50 days. Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

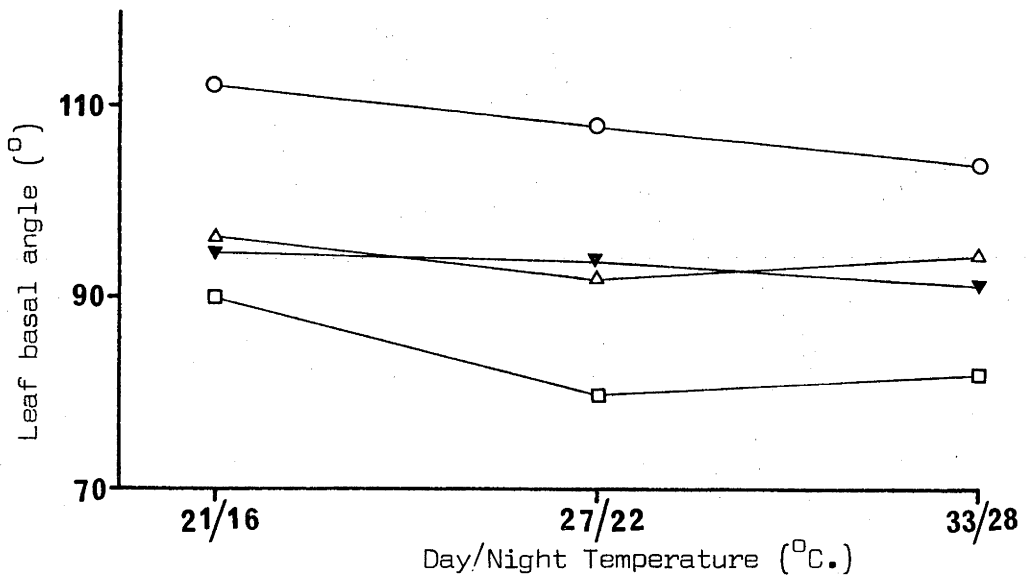


FIGURE 5.11 Temperature effect on leaf basal angle of *E. camaldulensis* during period of 50 days. Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

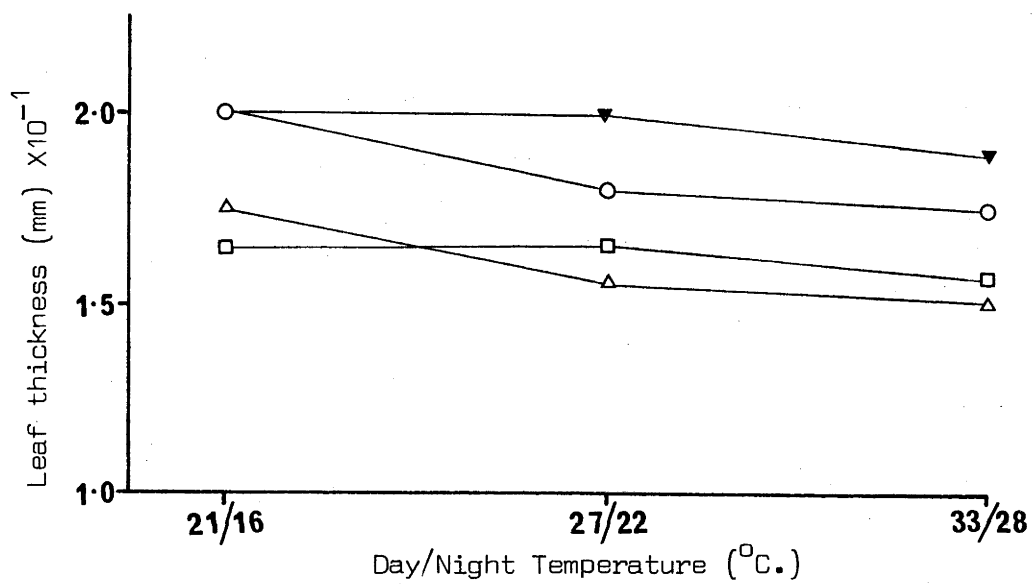


FIGURE 5.12 Temperature effect on leaf thickness of *E. camaldulensis* during period of 50 days. Katherine (\square), Lake Albacutya (O), Gwydir River (Δ) and Agnew (\blacktriangledown).

TABLE 5.8 Univariate Analysis of Variance for Leaf Characteristics
at Day 50 After Transfer to Temperature Treatment.

Source	DF	Mean Square	Variance Ratio	Sig.5%
6th Leaf Length				
Provenance	3	6.10	2.09	NS
Temperature	2	44.40	15.22	
Prov. x Temp.	6	8.97	3.08	
7th Leaf Length				
Provenance	3	7.95	2.46	NS
Temperature	2	106.68	33.00	*
Prov. x Temp.	6	12.53	3.88	
8th Leaf Length				
Provenance	3	8.61	2.42	NS
Temperature	2	135.14	37.97	*
Prov. x Temp.	6	10.23	2.88	
Mean Leaf Length				
Provenance	3	6.55	2.18	NS
Temperature	2	89.57	29.73	*
Prov. x Temp.	6	10.56	3.51	
6th Leaf Breadth				
Provenance	3	3.26	6.79	NS
Temperature	2	10.43	21.71	*
Prov. x Temp.	6	1.52	3.18	
7th Leaf Breadth				
Provenance	3	4.41	7.71	NS
Temperature	2	21.34	37.27	*
Prov. x Temp.	6	1.88	3.29	
8th Leaf Breadth				
Provenance	3	5.20	7.62	NS
Temperature	2	27.93	40.93	*
Prov. x Temp.	6	2.10	3.08	

TABLE 5.8 (Cont'd.)

Source	DF	Mean Square	Variance Ratio	Sig.5%
Mean Leaf Breadth (cm)				
Provenance	3	4.10	7.69	NS
Temperature	2	19.23	36.06	*
Prov. x Temp.	6	1.78	3.34	
Leaf Length/Breadth Ratio				
Provenance	3	5.33	20.22	*
Temperature	2	1.07	4.08	
Prov. x Temp.	6	0.17	0.67	
8th Leaf Thickness (mm)				
Provenance	3	0.02	77.18	*
Temperature	2	0.00	24.84	
Prov. x Temp.	6	0.00	2.80	
Leaf Basal Angle ($^{\circ}$)				
Provenance	3	7282.14	27.76	*
Temperature	2	886.08	3.38	
Prov. x Temp.	6	146.07	0.56	

III. Dry Weight Production and Lignotuber Diameter.

Graphical Presentation

At final harvest, components of dry weight production were measured as follows: leaf dry weight, stem dry weight, root dry weight and total dry weight. The leaf/stem weight ratio and the root/shoot weight ratio were calculated. Lignotuber diameter was also measured at harvest. The differences between provenances in the response to temperature of dry weight production, and lignotuber diameter, are illustrated in Figures 5.13 to 5.19 as follows:

- Figure 5.13 Leaf Dry Weight,
- 5.14 Stem Dry Weight,
- 5.15 Root Dry Weight,
- 5.16 Total Dry Weight,
- 5.17 Leaf/Stem Weight Ratio,
- 5.18 Root/Shoot Weight Ratio,
- 5.19 Lignotuber Diameter.

For all four provenances, greater dry weight productions of leaf, stem and total dry weight were recorded at the medium temperature (27/22°C.). There was some departure from this pattern for root dry weight. There were marked differences between the provenances in dry weight production. Agnew consistently produced the smallest amounts of dry matter (leaf, stem, root and total dry weight). In terms of dry weight production, Katherine is intermediate between the Agnew provenance and the two southern provenances of Lake Albacutya and Gwydir River.

The ratio of leaf weight : stem weight was largely unaffected by temperature for the Agnew and Gwydir River provenances, but there was a steep increase in the ratio for the Katherine and Lake Albacutya provenances at 33/28°C. It is difficult to place any meaningful interpretation on this.

The ratio of root weight : shoot weight is, with one exception, greater at the low (21/16°C.) than higher temperatures (27/22°C., 33/28°C.). If the behaviour of the Agnew provenance at 27/22°C. is excepted, there is little difference in root : shoot ratio at 27/22°C. and 33/28°C.

There was a notable difference between provenances in lignotuber production, for example, Katherine provenance had by far the greatest associate of lignotuber with seedlings at all the 3 temperatures. The frequency of lignotuber occurrence (%) in all the 4 provenances was summarised as follows:

Lignotuber Occurrence (%)

	21/16°C.	27/22°C.	33/28°C.
Katherine	10	72	72
Lake Albacutya	0	0	0
Gwydir River	4	4	20
Agnew	0	12	20

The most southern provenance (Lake Albacutya) produced no lignotubers at any temperature. Increase in temperature beyond 21/16^oC. induced lignotuber occurrence in the Agnew and Gwydir River. Lignotuber diameter on Katherine seedlings was far greater than on the Agnew and Gwydir River seedlings.

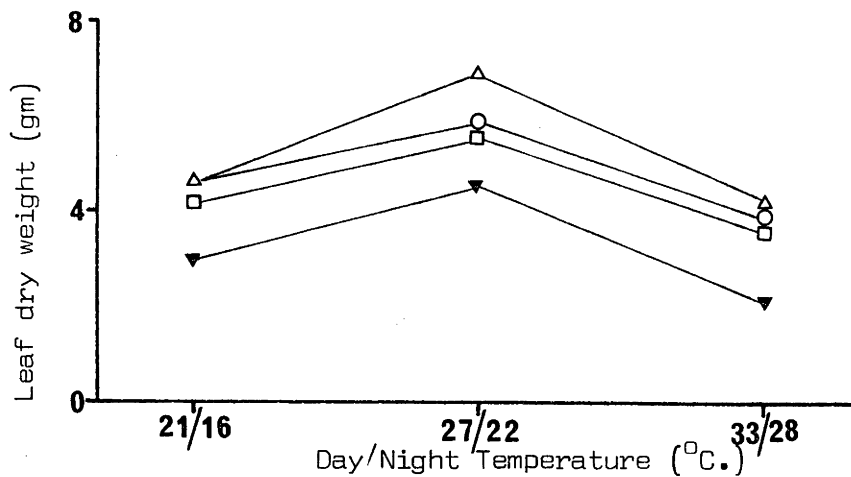


FIGURE 5.13 Temperature effect on leaf dry weight of *E. camaldulensis* during period of 50 days. Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

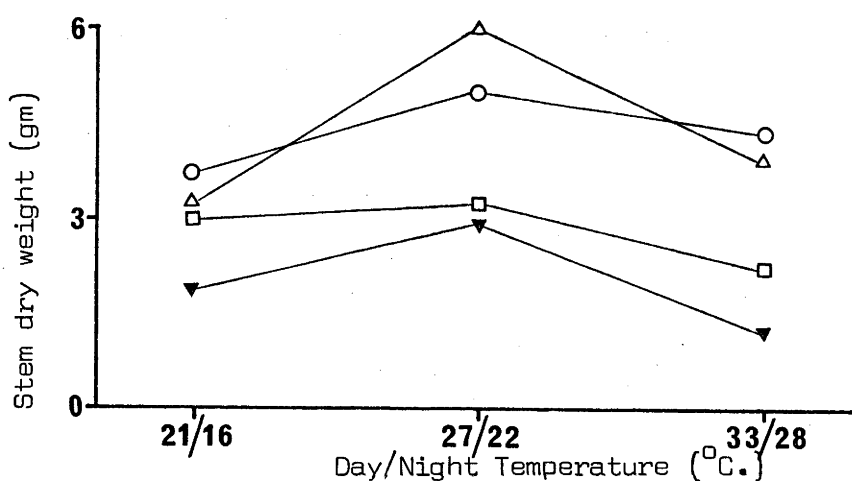


FIGURE 5.14 Temperature effect on stem dry weight of *E. camaldulensis* during period of 50 days. Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

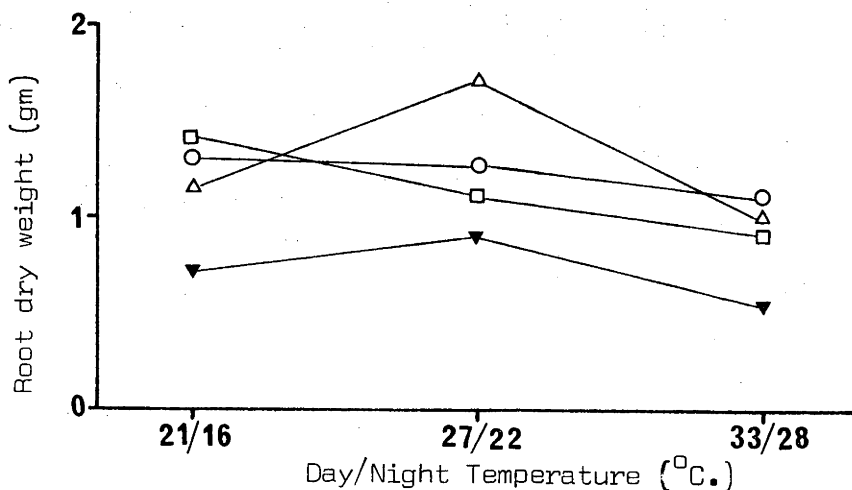


FIGURE 5.15 Temperature effect on root dry weight of *E. camaldulensis* during period of 50 days. Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

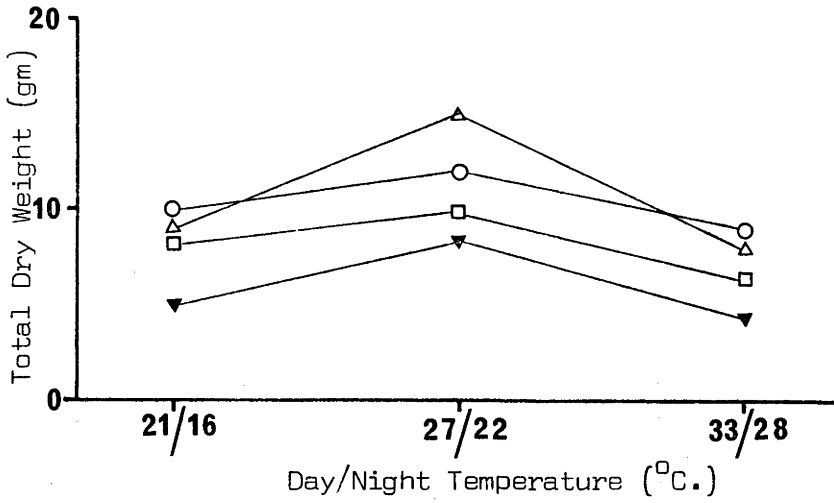


FIGURE 5.16 Temperature Effect on Total Dry Weight of *E. camaldulensis* During Period of 50 Days. Katherine (□), Lake Albacutya (O), Gwydir River (Δ) and Agnew (▼).

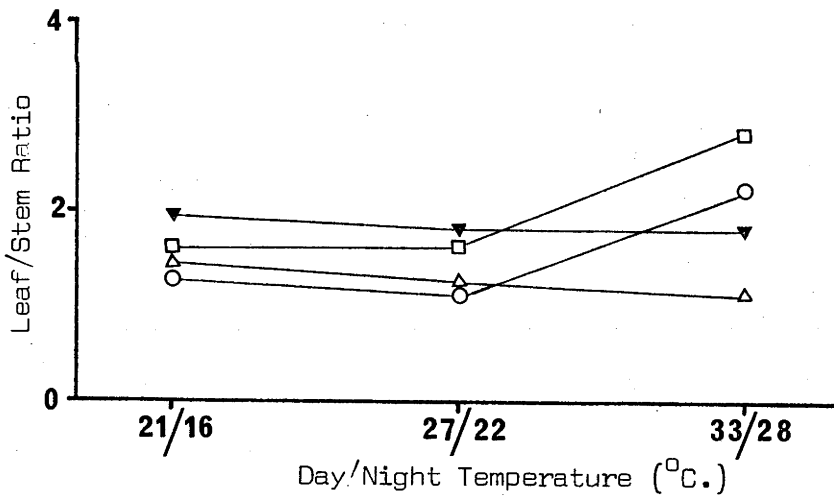


FIGURE 5.17 Temperature Effect on Leaf/Stem Ratio of *E. camaldulensis* During Period of 50 Days. Katherine (□), Lake Albacutya (O), Gwydir River (Δ) and Agnew (▼).

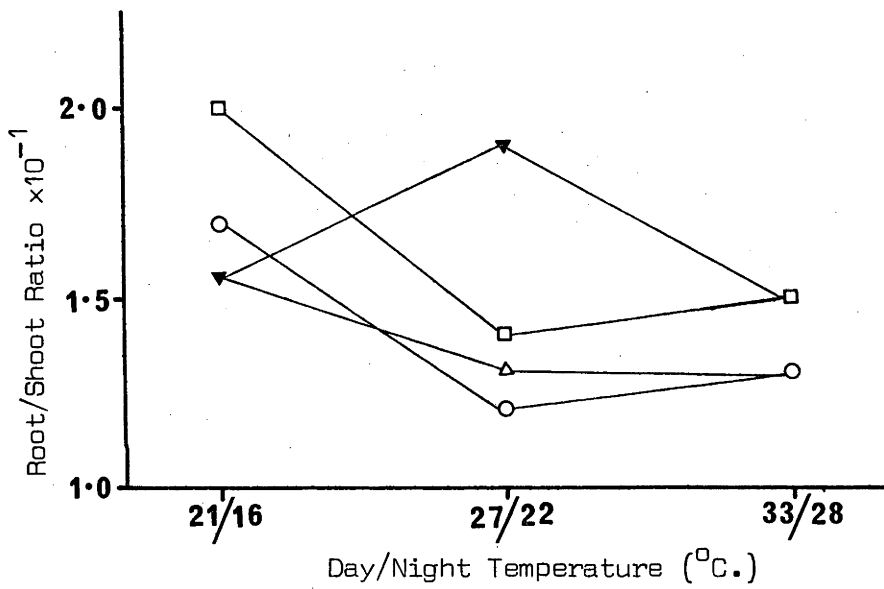


FIGURE 5.18 Temperature Effect on Root/Shoot Ratio of *E. camaldulensis* During Period of 50 Days. Katherine (□), Lake Albacutya (○), Gwydir River (△) and Agnew (▼).

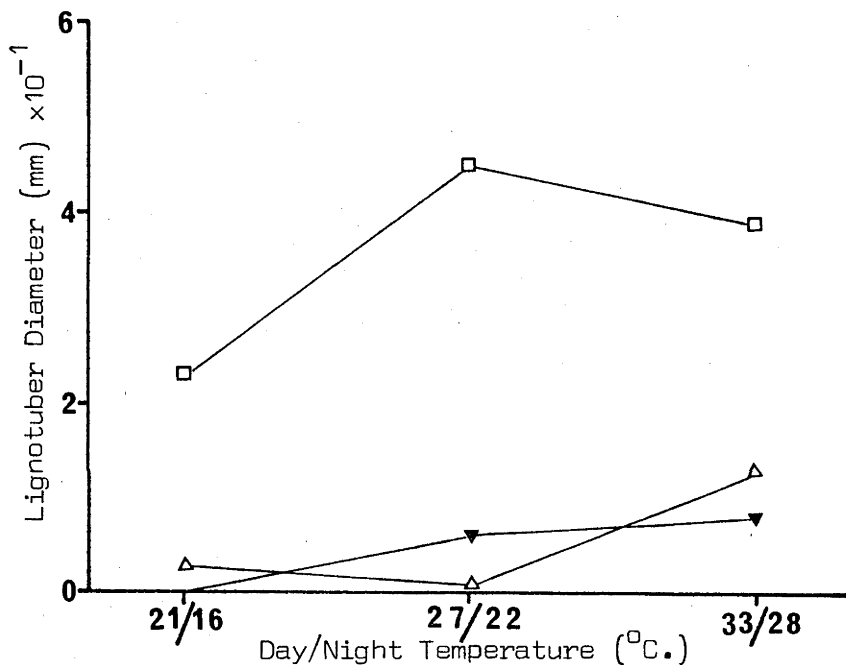


FIGURE 5.19 Temperature Effect on Lignotuber Diameter of *E. camaldulensis* During Period of 50 Days. Katherine (□), Lake Albacutya (○), Gwydir River (Δ) and Agnew (▼).

Analyses of Dry Weight Production and Lignotuber Diameter.

Means and standard errors for each of the separate dry weight measurements, the derived leaf/stem weight and root/shoot weight ratios, and lignotuber diameters, shown in Figures 5.13 to 5.19, are given in Appendix 4.

These data were analysed and the least significant difference values at 5 percent level of probability are also given in Appendix 4. A summary of the significance of differences between provenance means at each temperature is given in Table 5.9.

In almost all the dry weight parameters measured at the 3 temperatures, there were significant differences ($p = 0.05$) between Katherine and Agnew provenances, and these 2 provenances differed significantly from Lake Albacutya and Gwydir River provenances in most attribute/temperature combinations. There were significant differences between the southern Lake Albacutya and Gwydir River, and these were at the 27/22°C. growing temperature. These results were not unexpected as the two southern provenances are from the Murray River system while Katherine and Agnew are from different river systems and widely different environments. There was strong indication that the 4 provenances perform very well in the medium temperature of 27/22°C. For each of the seven variables, a univariate analysis of variance was also carried out, and the summary of significant results is presented in Table 5.10.

Where effects of temperatures are taken into account on the analysis, there were significant differences ($p = 0.05$) in all attributes except for the root : shoot weight ratio. This is despite

TABLE 5.10 Univariate Analysis of Variance for Dry Weight
Production and Lignotuber Diameter of E. camaldulensis
at 3 Temperature Regimes.

Source	DF	Mean Square	Variance Ratio	Sig.5%
Leaf Weight (gm)				
Provenance	3	42.74	14.61	*
Temperature	2	114.80	39.23	
Prov. x Temp.	6	3.95	1.35	
Stem Weight (gm)				
Provenance	3	104.20	64.48	*
Temperature	2	66.94	29.86	
Prov. x Temp.	6	7.15	3.19	
Root Weight (gm)				
Provenance	3	4.74	20.65	*
Temperature	2	3.41	14.85	
Prov. x Temp.	6	0.86	3.75	
Total Weight (gm)				
Provenance	3	335.70	26.87	*
Temperature	2	424.54	33.98	
Prov. x Temp.	6	27.89	2.23	
Leaf/Stem Ratio				
Provenance	3	7.91	20.14	*
Temperature	2	9.18	23.35	
Prov. x Temp.	6	4.34	11.04	
Root/Shoot Ratio				
Provenance	3	0.00	5.23	NS
Temperature	2	0.04	28.06	
Prov. x Temp.	6	0.00	1.53	
Lignotuber Diameter (mm)				
Provenance	3	2.01	60.71	*
Temperature	2	0.19	5.97	
Prov. x Temp.	6	0.09	2.95	

IV. Correlation of 14 Leaf and Dry Weight Characteristics.

In a final analysis of experimental data, a matrix of correlation coefficients was drawn up showing inter-relationships between 14 seedling characteristics including leaf size, and thickness, lignotuber diameter, leaf basal angle, and leaf, stem and root weights (Table 5.11). For the species as a whole, seedling stem weight was highly correlated with leaf weight and root weight (correlation coefficient 0.8), and weakly correlated with leaf basal angle, lignotuber diameter, leaf thickness and leaf size (correlation coefficients 0.1 to 0.3). Leaf weight was slightly more correlated with stem weight (correlation coefficient 0.905) than with root weight (correlation coefficient 0.809). There was also a strong correlation between mean leaf length and mean leaf breadth (correlation coefficient 0.6).

The contribution of all the characteristics to total variation within seedling progenies is shown, for all seedling involved in the investigation, in Table 5.12. Both stem weight and leaf weight are found to be the main discriminators. For the species as a whole, the stem weight and the leaf weight accounted for more than 70 percent of total observed variation - each contributing about 35 percent.

TABLE 5.11 Correlation Coefficients for 14 Attributes Based on Data at 3 Temperatures,

4 Provenances and One Measured Occasion.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1.000	0.893	0.869	0.657	0.585	0.540	0.941	0.613	0.046	-0.029	-0.010	0.365	0.257	0.320
2		1.000	0.914	0.597	0.663	0.584	0.963	0.637	0.037	-0.051	0.028	0.418	0.307	0.377
3			1.000	0.585	0.614	0.635	0.958	0.636	0.106	-0.039	-0.018	0.410	0.271	0.384
4				1.000	0.897	0.874	0.632	0.949	0.279	-0.193	0.517	0.258	0.151	0.241
5					1.000	0.917	0.646	0.970	0.285	-0.193	0.508	0.291	0.173	0.283
6						1.000	0.610	0.967	0.330	-0.167	0.519	0.318	0.182	0.319
7							1.000	0.652	0.077	-0.058	0.006	0.420	0.296	0.382
8								1.000	0.305	-0.185	0.530	0.303	0.176	0.292
9									1.000	-0.212	0.175	-0.084	-0.184	-0.111
10										1.000	-0.278	0.004	-0.082	-0.018
11											1.000	0.132	0.202	0.169
12												1.000	0.905	0.829
13													1.000	0.809
14														1.000

TABLE 5.12 Absolute Eigenvalues and Their Contributions to Total Variation for 14

Attributes, Based on Data for 3 Temperatures, 4 Provenances and One Measured Occasion.

Order	% of total Variation	Eigenvalues	t - test		Variates contributing at axis one of scaled vectors
			5%	1%	
1	38.584	2.027	*	**	Stem weight
2	34.179	1.795	*	**	Leaf weight
3	10.670	0.561	*	**	Mean leaf breadth
4	7.216	0.379	*	**	7th leaf length
5	3.256	0.171	*	**	Leaf basal angle
6	2.892	0.152	*	**	Mean leaf length
7	1.380	0.073	NS	NS	6th leaf length
8	1.095	0.068	NS	NS	8th leaf length
9	0.299	0.016	NS	NS	Lignotuber diameter
10	0.239	0.013	NS	NS	8th leaf breadth
11	0.185	0.010	NS	NS	Leaf thickness
12	0.0	0.0	NS	NS	7th leaf breadth
13	0.0	0.0	NS	NS	Root weight
14	0.0	0.0	NS	NS	6th leaf breadth

5.4 Discussion

Summary of Findings

The main findings relevant to the present objectives were:

1. For all temperature regimes and provenances, there was a more or less progressive increase in seedling growth with time.
2. There were marked differences between provenances in their growth response to variation in temperature regimes. Seedlings from the southern provenances of Lake Albacutya and Gwydir River had generally greater growth rates than seedlings from the northern provenances of Katherine and Agnew.
3. The main discriminators for Eucalyptus camaldulensis as a whole, are seedling height, leaf and stem dry weights, that is, these attributes contribute more to total variation in seedlings than other attributes. Where parameters are considered independently, the number of internodes on the stem contributed most to total seedling variation in southern provenances, while for the northern provenances, the seedling height contributed most to seedling variation. There is much greater variation in seedling height in northern provenance than in the southern provenance.
4. Leaf size (length and breadth) decreases with increasing temperature, but there are no consistent and significant differences between provenances on this attribute.
5. Leaf shape is not affected by temperature; the leaf length : leaf breadth ratio is significantly smaller for Lake Albacutya and Agnew provenances than Katherine and Gwydir River provenances.

5. Seedlings grown at lower temperatures have significantly thicker leaves. Lake Albacutya and Agnew seedlings have thicker leaves than Katherine and Gwydir River seedlings.
7. Katherine seedlings have the smallest leaf basal angle, and Lake Albacutya the greatest; Gwydir River and Agnew are intermediate.
8. In term of dry weight production, greater dry weight of leaf, stem and total dry weight were recorded at the medium temperature (27/22°C.) for all the 4 provenances. The northern (Katherine) provenance is intermediate between the Agnew provenance and the two southern provenances of Lake Albacutya and Gwydir River.
9. Leaf weight : stem weight and root weight : shoot weight ratios were largely unaffected by temperature.
10. There was a notable difference between provenance in lignotuber production, lignotuber occurrence decreases from north to south. Temperature also induces lignotuber production for the intermediate provenances of Agnew and Gwydir River.

Discussion of Findings

Considerable differences exist between forest trees in the way they react to a range of growing temperature regimes (Hellmers 1962, Scurfield 1961). For many eucalypts the optimum phytotron growing temperature seems to be in the range 24/19^o (day/night) to 30/25^oC. Eldridge (1968) for example found the optimum temperature for seedling height growth of E. regnans was close to 27/22^oC. at the five-seven leaf stage, and Green (1967) established that the

optimum temperature for seedling height growth of E. pauciflora was between 24/19^o and 30/25^oC. In this present study the optimum temperature for height growth was consistently 27/22^oC. - where 3 temperature regimes were examined (21/16^o, 27/22^o and 33/28^oC.). Similarly, optimum temperature for dry weight production was 27/22^oC. - again for all 4 provenances.

Within E. camaldulensis, some marked differences in seedling development have been shown to be associated with differences in provenance.

While some attempt will be made to interpret these differences in terms of environmental selection, this must be regarded as tentative only because so few provenances are involved, and there is no guarantee these responses reflect adaptation to specific environmental conditions. Moreover, the phytotron is an artificial environment, climate can vary in many ways, - and so can factors which may be critical in natural selection. Where one factor is varied, and others are held constant, it may be misleading to draw definitive conclusions from the results. Only where there is a consistent pattern in interpretation of data from experiment to experiment can a reasonable degree of confidence be placed in interpretation of environmental selection.

The growth of seedlings from the southern provenances of Lake Albacutya and Gwydir River was generally greater than that of seedlings from the northern provenances of Katherine and Agnew. The differences between Agnew seedlings and the southern provenance seedlings were particularly marked, and this applies both to height

growth and dry weight production. If the growth of these 4 lots of seedlings can be accepted as representative of the growth characteristics of seedlings from the more extreme parts of the species climatic range, then it might be inferred that progenies from hot dry regions of the range tend to be inherently slower growing than seedlings from that part of the range with a somewhat more moderate and uniform climate. It might further be inferred that inherent vigour has played a more important part in natural selection in the south than in the north. That is, many physiological factors other than inherent vigour are important in survival and competitive ability under conditions of more extreme environmental stress.

Such an hypothesis would receive additional support from a number of other growth characteristics. For example, the 2 southern provenances (Lake Albacutya and Gwydir River) tended to be similar in the number of leaves on stem, number of branches, and leaf production on seedling branches, while the northern provenance seedlings differed consistently from the southern provenance seedlings in these respects. The smaller number of branches on northern provenance seedlings and the smaller production of branch leaves, for example, were out of all proportion to the differences between the provenances in seedling height or dry weight production. It might be inferred from this that there has been selection of individuals in more extreme environments which have been able to grow effectively while producing less transpiring branch and leaf surface area. This concept might also be drawn from the correlation analysis. In the two southern provenances, seedling height

growth is better correlated with branch and branch-leaf production than in the northern provenances. That is, there is a tendency for seedling branch and leaf production to be more independent of height growth in the northern provenance seedlings, - suggesting a possible positive natural selection of individuals having fewer branches and leaves. Height growth was a particularly variable feature in the Katherine provenance. Here, variation in height growth accounted for 92% of total observed variation - while for the other provenances, the number of internodes accounted for a large part of the total observed variation.

While there were possibly meaningful difference between the northern and southern provenance seedlings in height, branch and branch leaf characteristics, there was surprisingly little consistent difference between the northern and southern provenances in leaf morphology. While there were significant differences between individual provenances in leaf size, length, breadth, shape and thickness, there was no apparent relationship between these characteristics and environmental conditions associated with the provenance.

The development of lignotubers may be another characteristic indicating selection of individuals with a greater survival potential under harsh environmental conditions. Katherine provenance produced by far the greatest number of lignotuberos seedlings. The result of lignotuber occurrence (in percentage of seedling progenies) indicated that 72% of Katherine seedlings produced lignotubers while no lignotuber was recorded on any seedling from the most southern provenance of Lake Albacutya. From Gwydir River and Agnew provenances only 20% of the seedlings developed lignotubers.

In conclusion temperature, as one of the environmental factors affecting tree growth, has significant effects on the survival values of E. camaldulensis and the optimum for many of seedling growth characteristics and dry weight productions was the medium temperatures of 27/22^oC. There were strong indications of provenance variation in E. camaldulensis. Two major provenances of northern and southern origins were recognised.

CHAPTER 6

PHOTOPERIOD

6.1 Introduction

The response in growth and development exhibited by plants in relation to the length of the daily light period has been described by Pauley and Perry (1954) as photoperiodism. Most earlier investigations of photoperiodism centered on the flowering response of various herbaceous plant species. The pioneering work on photoperiodism was carried out by Garner and Allard (1920). These workers observed that Mary Mammoth tobacco, which normally does not flower in the field during the summer season at latitude 39°N did flower profusely when grown in a greenhouse in Washington during the winter. It was thought that the short photoperiods of winter favoured flowering of the variety. Subsequent confirmation of this opinion was made through the use of carefully controlled experiments by Garner and Allard and numerous other workers.

Because of its ecological importance and especially in relation to forestry practice, the study of daylength effects on woody species began in the late 1920's. Photoperiodic studies of woody plants inevitably involve seedlings only, and consequently little is known of the influence of photoperiod on reproduction (Pauley and Perry 1954). This opinion was supported by Wareing (1956) when he noted that vegetative effects can be conveniently studied in seedling trees. Ecotypic differentiation in forest tree

species with respect to photoperiodic response is known to be correlated with differences in the day length conditions occurring over the natural geographic distribution of the species. Ecotypic variation in the growth response to photoperiod has been found in many northern hemisphere deciduous trees - north of 40° latitude, (Vaartaja 1959), and the main effect of photoperiod on growth is the control of leaf fall and terminal bud dormancy. Other vegetative processes in woody species which have been shown to be affected by daylength include the duration of extension growth, internode extension, leaf growth in conifers, duration of cambial activity, time of bud break and seed germination (Wareing 1956). Among species responding to photoperiodic treatments, there appears to be no exception to the rule that dormancy is hastened by shortdays and delayed by long days. Working in Boston U.S.A. on poplars seedlings, Pauley and Perry (1954) found that the more northern sources ceased growth before winter while those from warmer climates continued to grow until killed by the first frost. They also established that the colder the seed source region, the greater the provenance variation in response to photoperiods.

Within the tropical and subtropical regions of the world, there is little change in the length of the daylight period throughout the year, but outside these regions, marked seasonal differences occur (Pauley and Perry 1954). In low latitudes of Nigeria, Njoku (1963, 1964) observed that there was a marked annual periodicity in leaf production, leaf fall and vegetative bud dormancy in a number of rainforest tree species.

In Australia, photoperiodic behaviour of eucalypts has received little attention. Very recently, Green (1967) in his study of altitudinal variation in E. pauciflora found that there was no evidence of differential response to photoperiod among altitudinal progenies in terms of height growth, but there was an indication of photoperiodic influence on leaf shape of the species. When Eldridge (1969) grew E. regnans under long and short days at a series of day and night temperatures, he demonstrated large variation between treatments for height, height increment, and relative growth rate in height. He also established that seedlings of E. regnans from higher altitude had a greater response to photoperiod than the lower altitude seedlings in both growth rate and frost damage.

In this present study, photoperiod behaviour of Eucalyptus camaldulensis seedlings from three different latitudes in Australia (14° , 23° and 35° S) - Katherine, Todd River and Lake Albacutya, has been studied in the CSIRO phytotron.

6.2 Materials and Methods

Seedlots of E. camaldulensis from three provenances - Katherine, Todd River and Lake Albacutya - were used for this investigation (Table 4.1). For each provenance seed collected from five trees were thoroughly mixed and a sample of the mixed seedlots was used to raise seedlings in the CSIRO phytotron. Ten best seedlings were obtained from each provenance. The seedlings were raised in plastic pots containing a mixture of equal quantity of perlite and

vermiculite in a glasshouse at the phytotron regulated at a day and night temperature of 27/22°C. At 4-leaf pair stage, the seedlings were reduced to one best seedling per pot and transferred to 3 different photoperiod treatments. Treatments were applied to the seedlings in "C" growth cabinets (Morse and Evans 1962), under a temperature regime of 21/16°C. The three photoperiod regimes employed for this investigation were as follows:

Treatments	Daylight (hours)	Incandescent light (hours)	Darkness (hours)
1	8	2	14
2	8	4	12
3	8	6	16

The incandescent light was at least 50 fc at plant height. The mean air temperatures in the growth cabinets were controlled to within $\pm 0.5^\circ\text{C}$. Watering was done twice daily at 8.30 am and 4.00 pm. In the morning modified 'Hoagland' solution (Appendix 1) was used to water the plants while tap water was used in the afternoon.

The following growth characteristics were measured every ten days:

- Seedling height,
- Basal stem diameter,
- Number of leaves on stem,
- Number of leaves on branches,
- Number of branches,
- Number of internodes.

At the time of harvesting, the total leaf area for each seedling was determined by using an "Automatic Area Meter". The leaves, stem and roots were harvested and kept separate. The oven dry weight of each seedling was determined by weighing the dried matter at room temperature.

6.3 Results

Graphical Presentation of Growth Responses of the Three Provenances to Variation in Photoperiods.

The progressive growth responses with time, of the three provenances of E. camaldulensis growing under different photoperiod regimes are graphically represented in Figures 6.1 to 6.7 as follows:

Figures 6.1 Seedling Height

6.2 Basal Diameter

6.3 Leaves on Stem

6.4 Leaves on Branches

6.5 Number of Branches

6.6 Number of Internodes on Stem

6.7 Response of the Provenances at day 50, to the 3 Photoperiod Regimes.

After a slower 'establishment' period (10 - 20 days), there was a more or less straight line relationship between seedling height and time. The greatest seedling height growth was recorded at 14 hours for all provenances. The range of provenance means was 63 - 69 cm at 10 hours, 70 - 79 cm at 12 hours and 77 - 99 cm at 14 hours.

The mean seedling heights for each of the three provenances were closely similar at the 10-hour treatment, but were tending to separate with time. Alternatively, at 12 and 14 hours, the provenances were widely separated from about 30 days, and in the order:

Todd River (Central Australia) - greater height growth

Lake Albacutya (Southern Australia)

Katherine (Northern Australia) - least height growth.

At 14 hours and 50 days, Todd River mean height was 99.35 cm, and Katherine 77.35 cm, with Lake Albacutya intermediate of 88.75 cm.

The growth in basal diameter was similar to that of height growth in that the Todd River provenance had the greatest basal diameter, and Katherine the least, - at the 12- and 14-hour treatments. But unlike the height growth, there was no marked response in basal diameter to increasing photoperiod. Therefore, there is some change in seedling form with increasing photoperiod, that is in responding in height, the seedlings are becoming more spindly.

The mean number of leaves on the stem is generally similar for the 3 provenances - that is, there is no marked separation of the provenances graphically - at any photoperiod. Photoperiod has little effect on this growth parameter, although it may increase slightly with photoperiod. Seedling height is the only growth parameter for which there is a strong and direct relationship between photoperiod and growth.

There is a large difference between provenances in the number of leaves on branches at 10 and 12 hours, but not at 14 hours. The Todd River provenance had the greatest number of leaves on branches at all photoperiods, and the northernmost (Katherine) provenance the least. Number of leaves on branches of Todd River seedlings dropped sharply from 38 at 12 hours to 25 at 14 hours. Alternatively, number of leaves on branches were similar at 12- and 14-hour treatments for Lake Albacutya and Katherine, that is about 20.

The provenances differed in the way they responded to photoperiod in number of branches. Todd River seedlings produced relatively large numbers of branches at the 10- and 12-hour treatments (33 and 38 per seedling) respectively, but only 25 at 14 hours. Alternatively, Katherine and Lake Albacutya seedlings had fewer leaves on branches, but the number increased with photoperiod - with a maximum at 14 hours.

There was no consistent separation of provenances in number of internodes; the number of internodes was greater at 12 hours than at 10 hours, and the number at 14 hours could be slightly greater than at 12 hours.

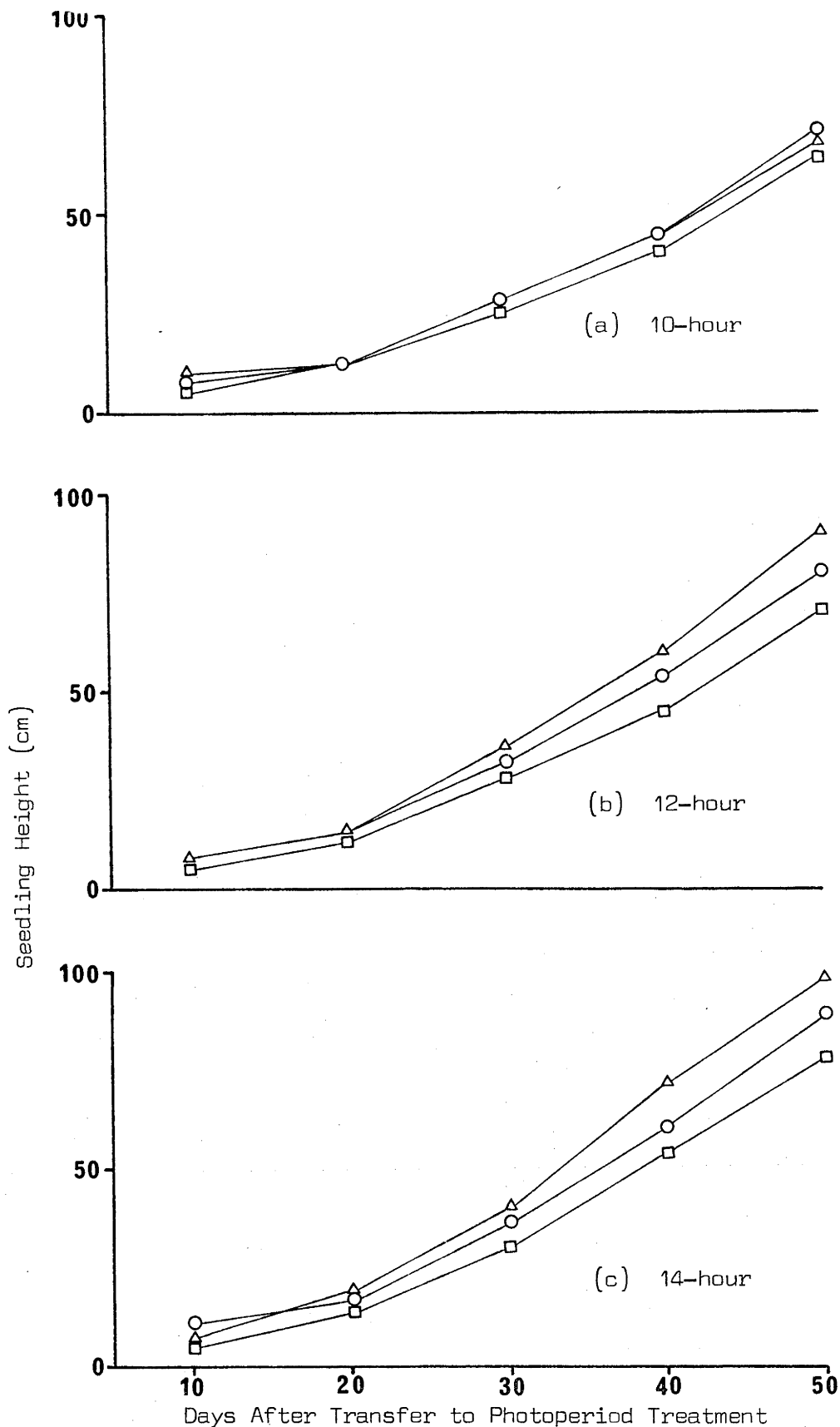


FIGURE 6.1 Provenance Variation in the Response to Photoperiod of Seedling Height of *E. camaldulensis*. Katherine (□), Todd River (Δ) and Lake Albacutya (○).

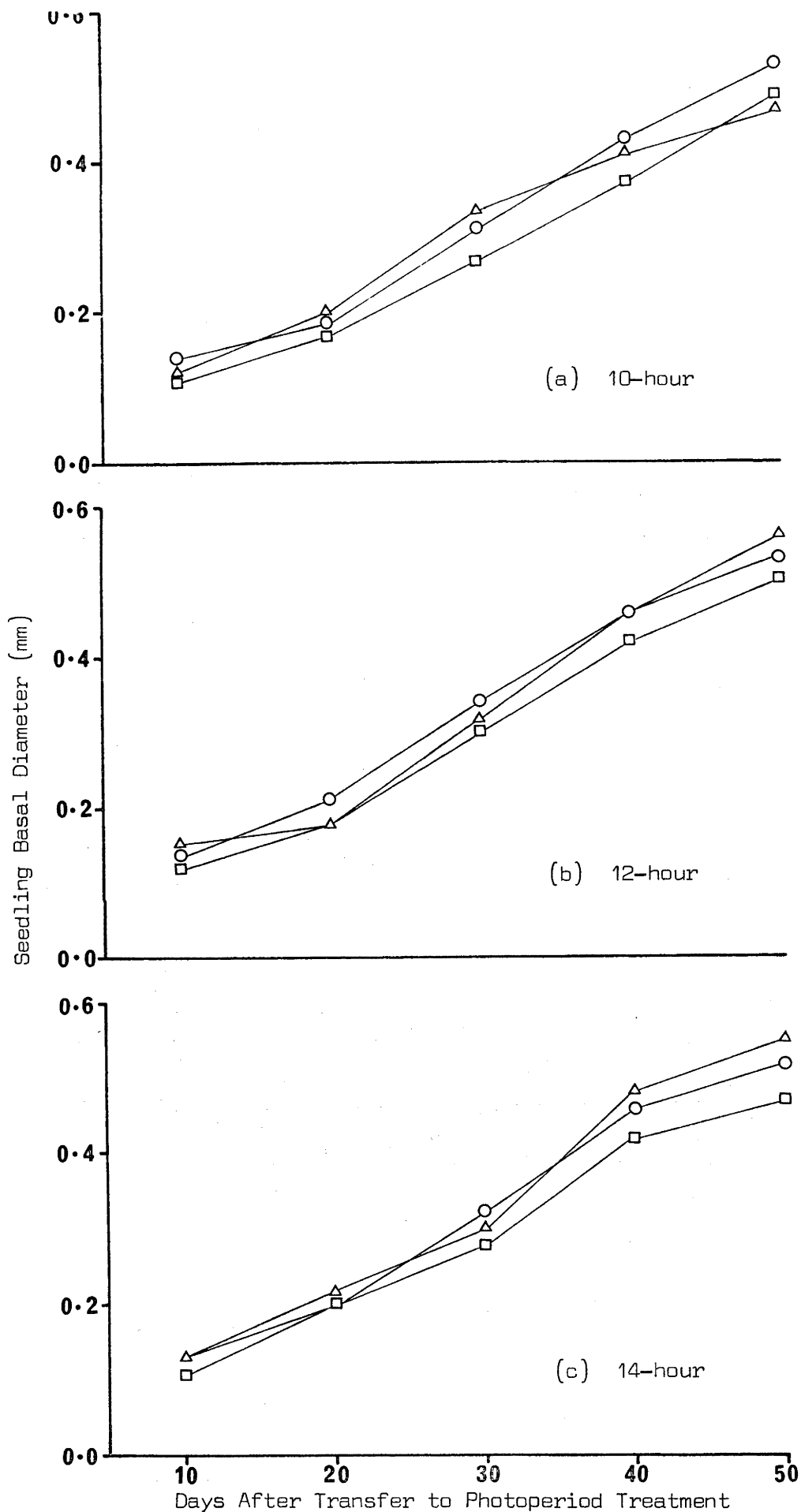


FIGURE 6.2 Provenance Variation in the Response to Photoperiod of Seedling Basal Diameter of *E. camaldulensis*. Katherine (□), Todd River (Δ) and Lake Albacutya (○).

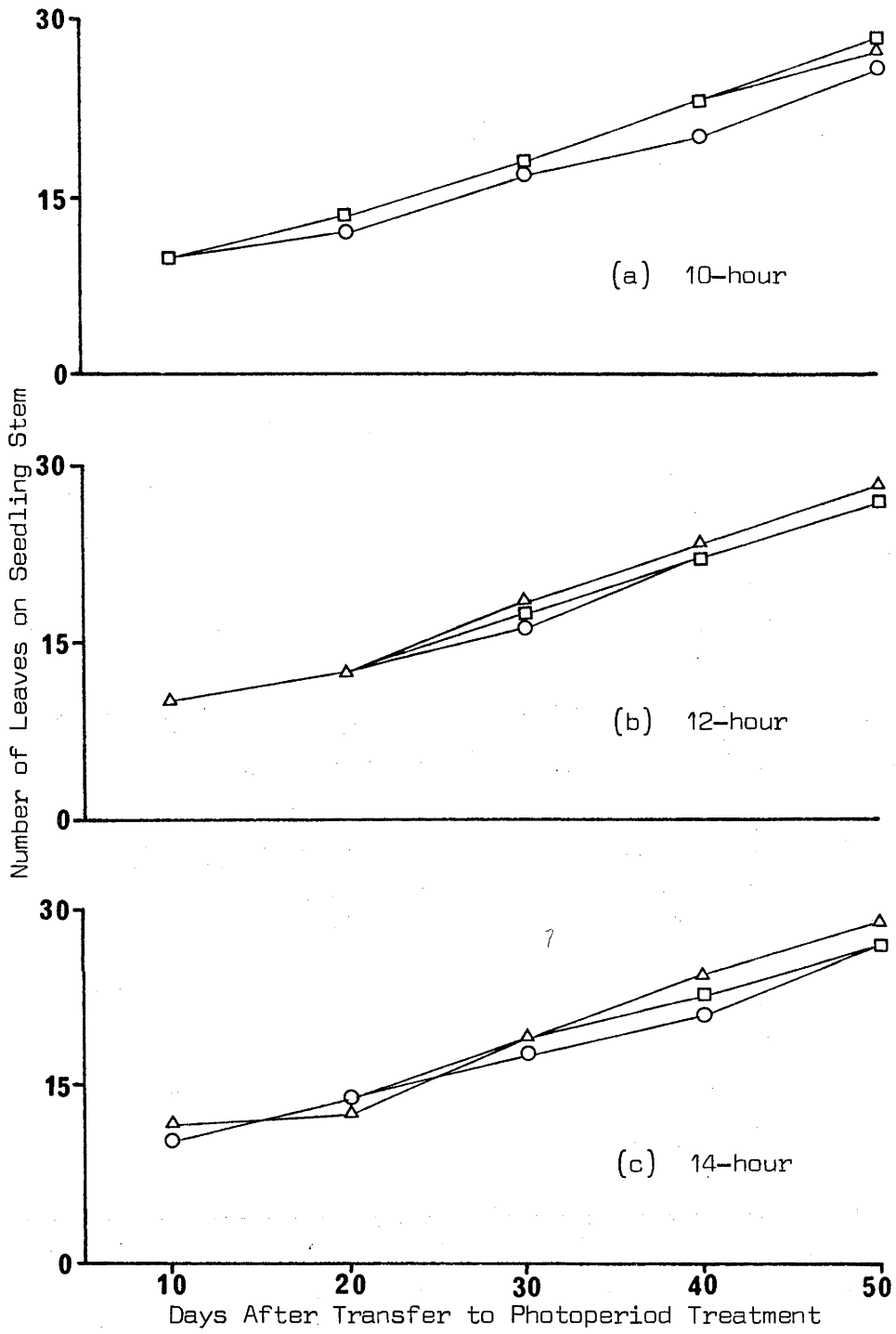


FIGURE 6.3 Provenance Variation in the Response to Photoperiod of Number of Leaves on Seedling Stem of *E. camaldulensis*. Katherine (□), Todd River (Δ) and Lake Albacutya (○).

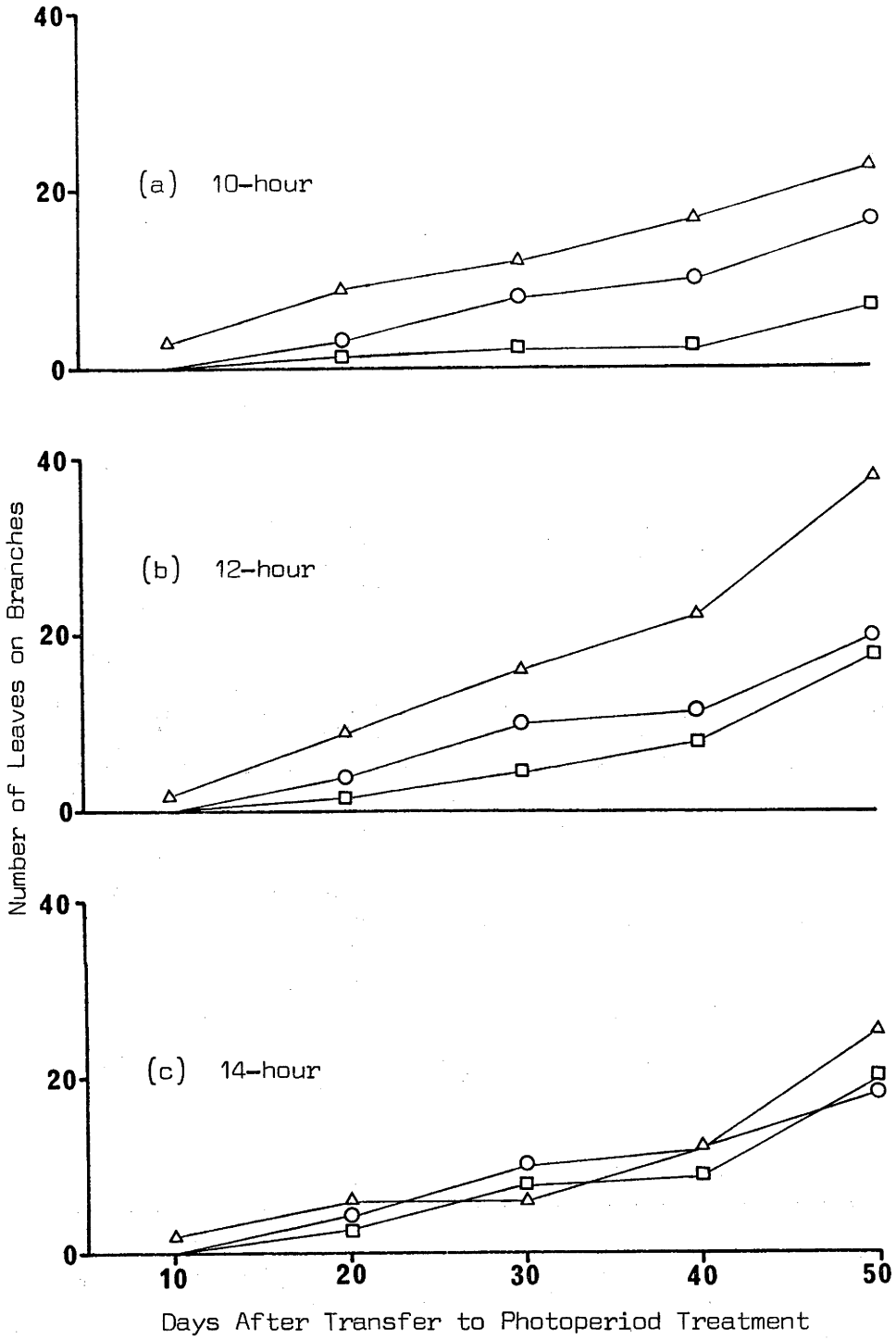


FIGURE 6.4 Provenance Variation in Response to Photoperiod of Number of Leaves on Branches of *E. camaldulensis* Seedlings. Katherine (□), Todd River (Δ) and Lake Albury (○).

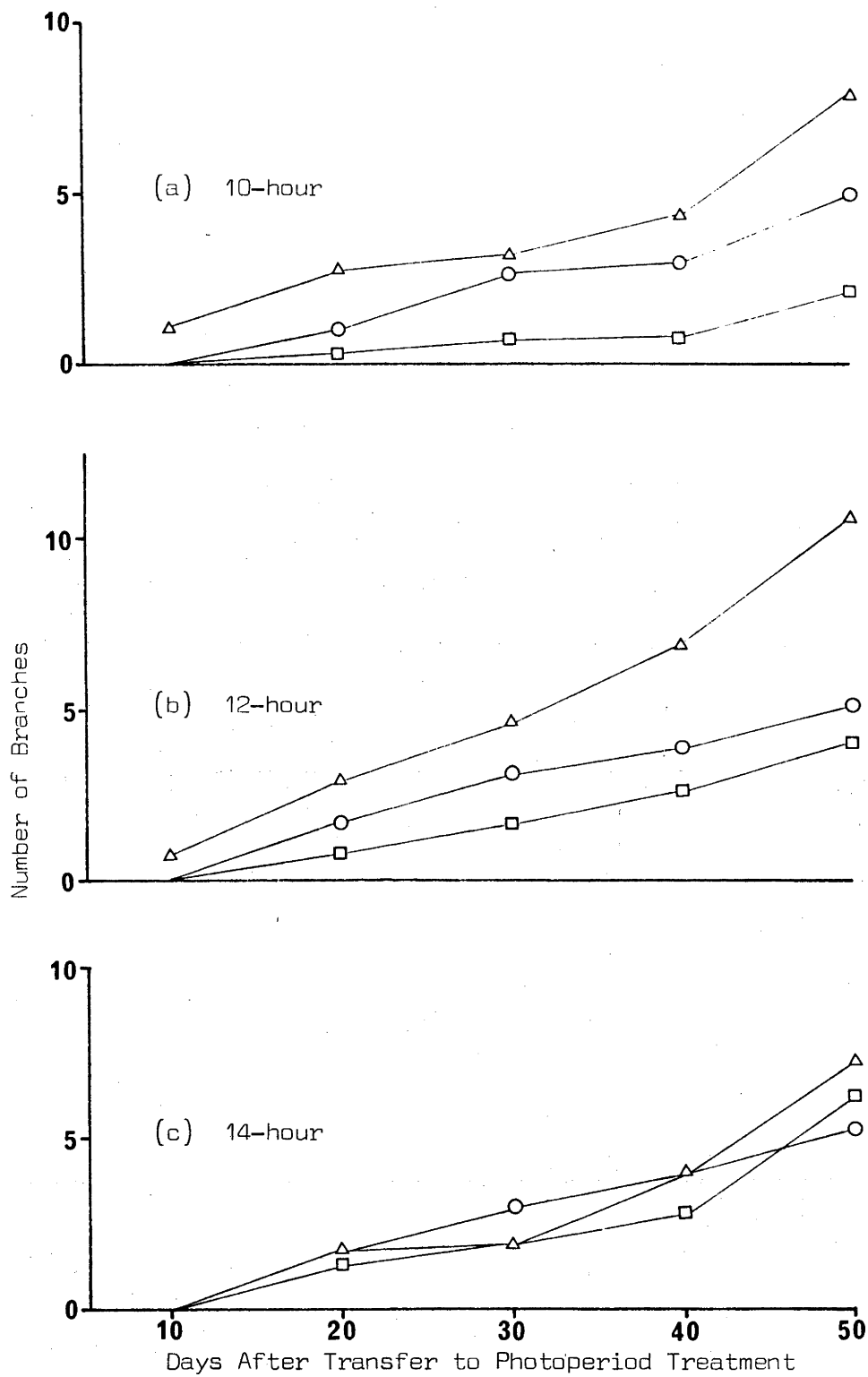


FIGURE 6.5 Provenance Variation in the Response to Photoperiod of Number of Branches of *E. camaldulensis*. Katherine (□), Todd River (Δ) and Lake Albacutya (○).

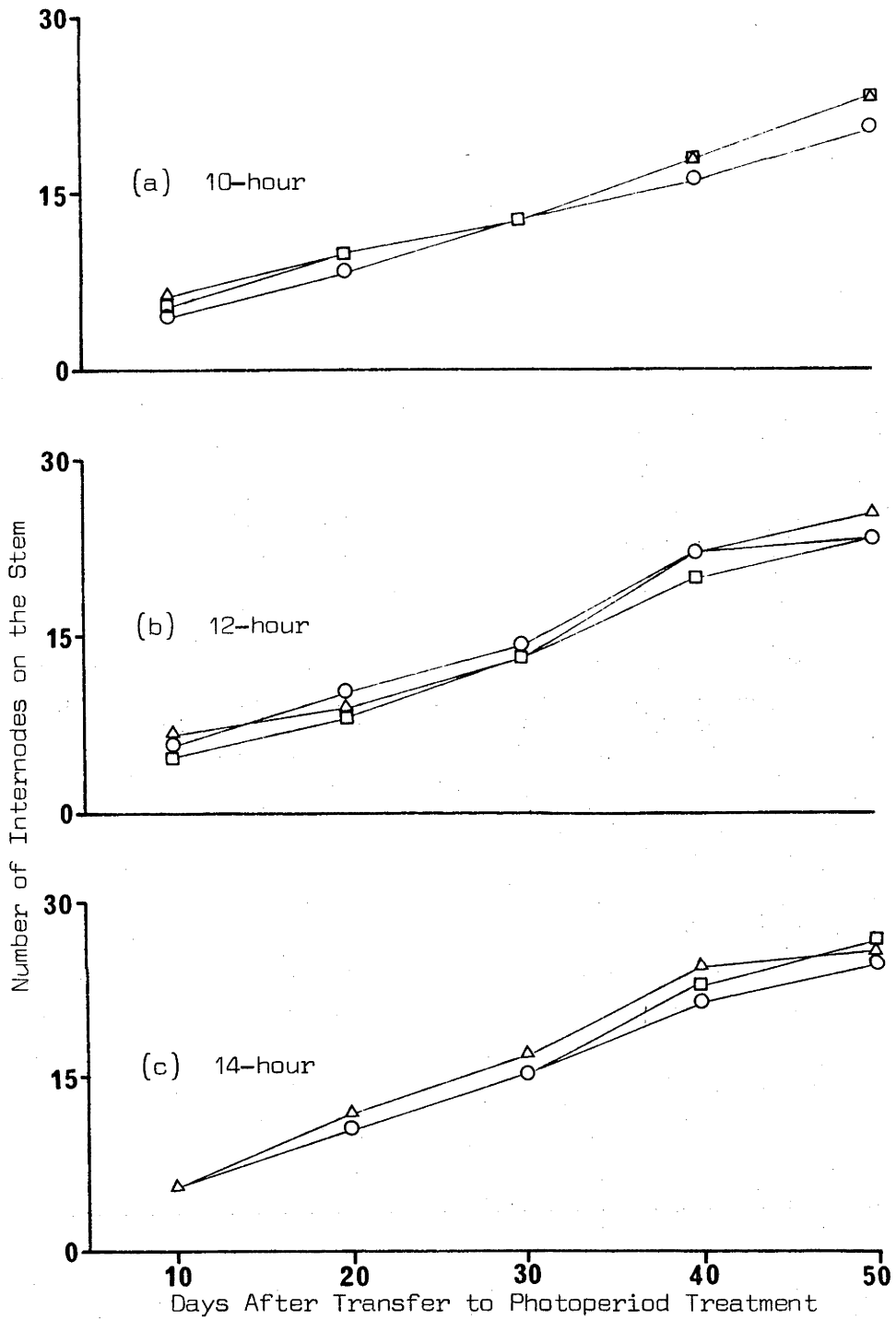


FIGURE 6.6 Provenance Variation in the Response to Photoperiod of Number of Internodes on Seedling Stem of *E. camaldulensis*. Katherine (□), Todd River (△) and Lake Albacutya (○).

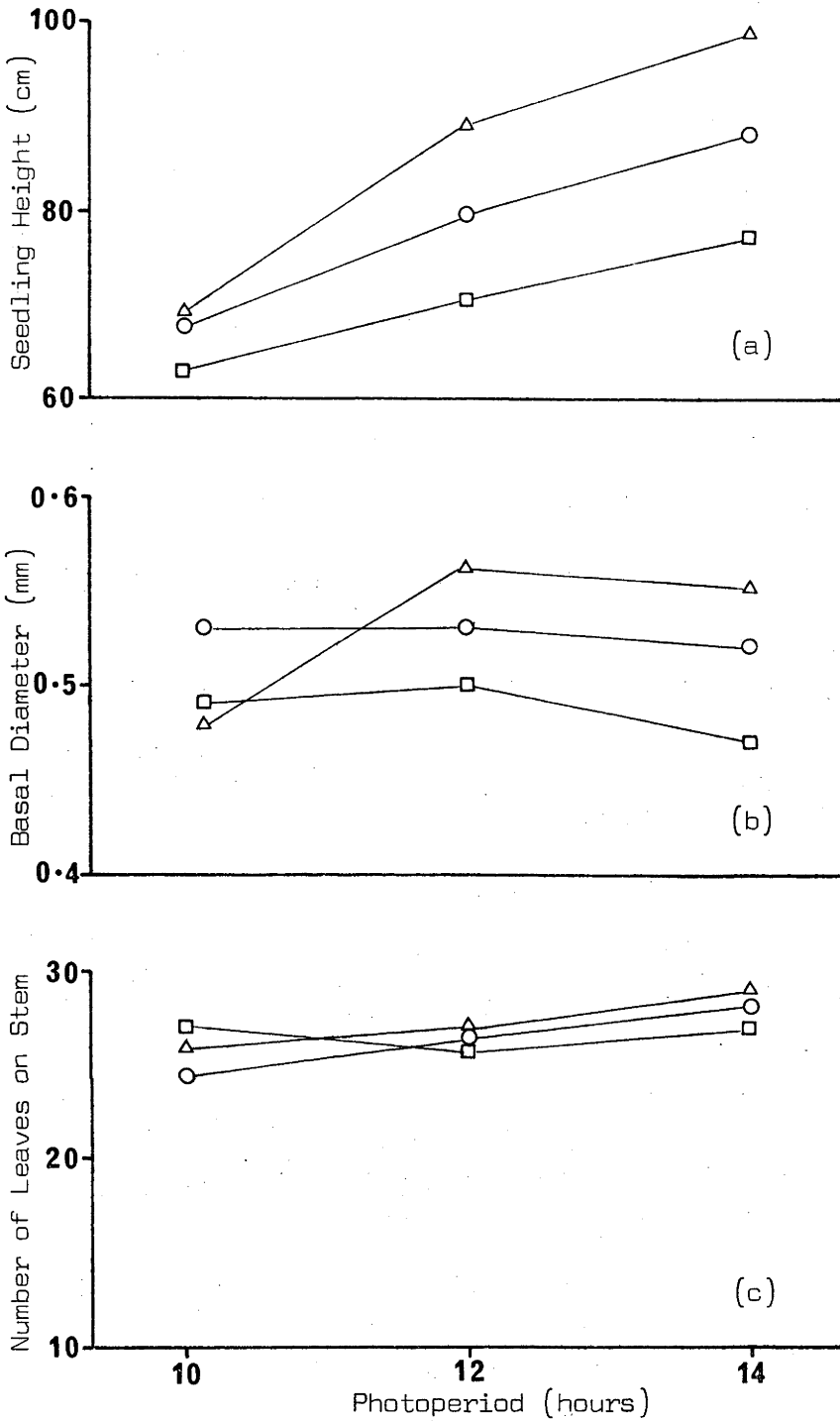


FIGURE 6.7 Provenance Variation in Response of Seedling Progenies of *E. camaldulensis* from 3 Provenances of Katherine (□), Todd River (Δ) and Lake Albacutya (○) to Variation of Photoperiod at Day 50 After Transfer to Photoperiod Treatment.

- (a) Seedling Height
- (b) Seedling Basal Diameter
- (c) Number of Leaves on Stem

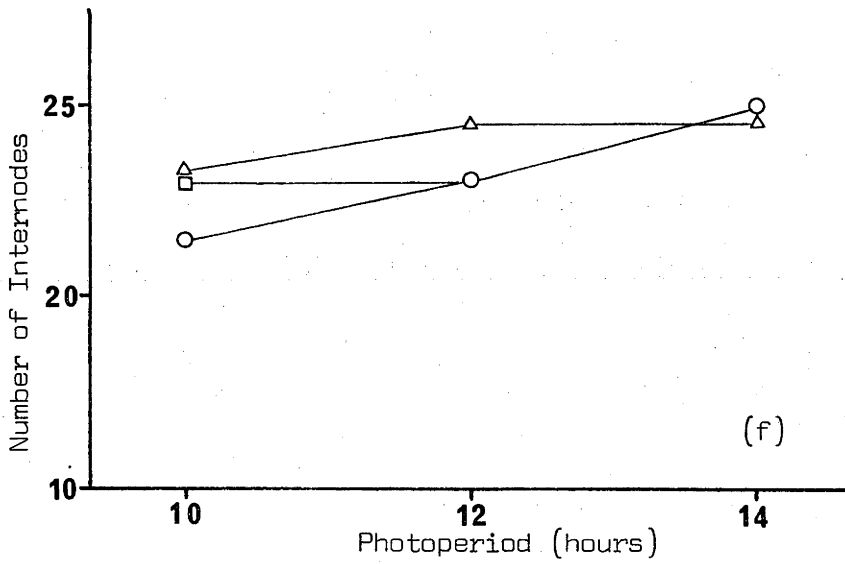
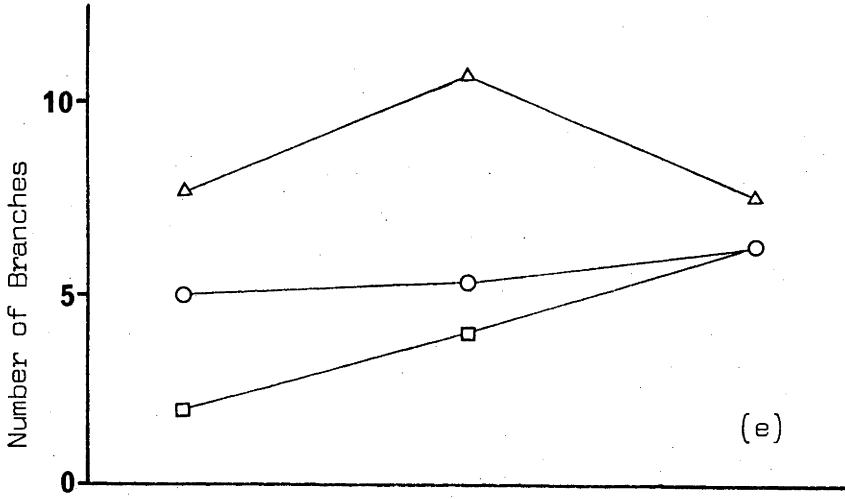
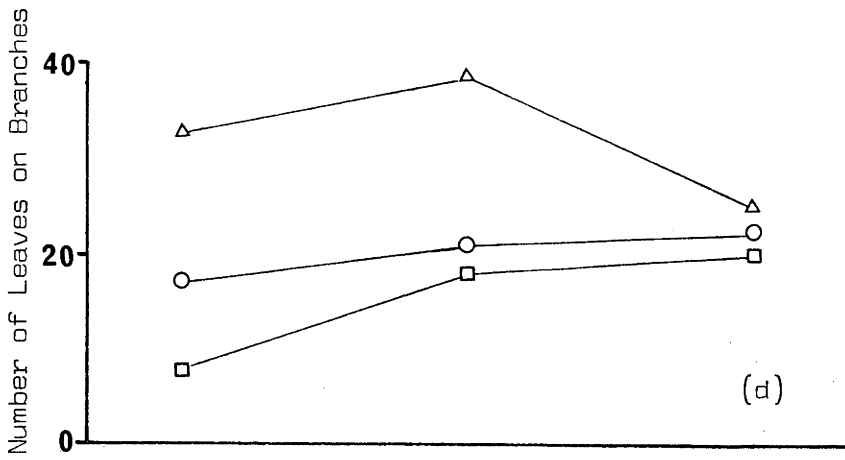


FIGURE 6.7 (Cont'd)

- (d) Number of Leaves on Branches
- (e) Number of Branches
- (f) Number of Internodes on the Stem of Seedlings

Analysis of Data for the Six Growth Characteristics.

Means and standard errors for each of the six measured parameters shown in Figures 6.1 to 6.7 are given in Tables of means in Appendix 5. These data were analysed and LSD values at 5% level of probability are given. In these Tables each value represents the mean of 10 seedlings for each provenance. A summary of significant results of analysis of the growth of the six attributes is presented in Table 6.1.

Main Points from Table 6.1 for

Characteristics Shown to Differ in Graphical Presentation.

Seedling Height. At 10 hours, differences between provenances were not significant, but most differences between individual provenances were significant at the 12- and 14-hour treatments. This reflects the greater separation of the provenances with greater photoperiod. Todd River seedlings responded most to greater photoperiod, and Katherine seedlings the least.

Number of Branches and Number of Leaves on Branches. For both these parameters, differences between provenances were not significant at 14 hours photoperiod, but there were significant differences at 10 and 12 hours photoperiod. This reflects the patterns illustrated in Figure 6.7 (d) and (e), - that is, there was a major response of Todd River seedlings under 10 and 12 hours photoperiod, but there was a sharp reduction in both parameters under 14 hours photoperiod. The Katherine and Lake Albacutya seedlings did not differ significantly at 10 and 12 hours, but both differed significantly from Todd River seedlings - that is, Todd River seedlings were particularly more vigorous in branch and branch leaf production.

Number of Internodes. There were no significant differences between provenances in number of internodes - at any of the 3 photoperiod regimes.

For each of the six growth characteristics a univariate analysis of variance was carried out. The summary is presented in Table 6.2. It is quite interesting to note that none of the attributes showed any significant difference for provenance and photoperiod interaction. Analysis takes into account response at all photoperiods collectively. Lack of significant differences between provenances means that while there are differences between provenances at individual photoperiods, the provenances are not responding in a consistent way at the different photoperiods. A good example of this is the number of branches - where there were marked differences at 10 and 12 hours, but not at 14 hours, because of the markedly different reaction of one provenance (Todd River) at 14 hours. This analysis contrasts with the similar analysis for temperature (Table 5.3). In the univariate analysis of differences between provenances in respect to temperature, differences between provenances were significant - that is, there was a more or less consistent difference between provenances at each of the temperature regimes.

TABLE 6.2 Univariate Analysis of Variance for Seedling Growth Characteristics at Day 50 After Transfer to Photoperiod Treatment.

Source	DF	Mean Square	Variance Ratio	Sig. 5%
Seedling Height (cm)				
Provenance	2	1803.61	8.24	NS
Photoperiod	2	3531.11	16.14	
Prov. x Photoperiod	4	195.61	0.89	
Basal Diameter (mm)				
Provenance	2	0.01	3.67	NS
Photoperiod	2	0.00	1.22	
Prov. x Photoperiod	4	0.00	1.32	
Leaves on Stem				
Provenance	2	12.13	1.14	NS
Photoperiod	2	40.13	3.76	
Prov. x Photoperiod	4	8.26	0.73	
Leaves on Branches				
Provenance	2	2315.91	5.64	NS
Photoperiod	2	276.04	0.67	
Prov. x Photoperiod	4	342.84	0.83	
Number of Branches				
Provenance	2	147.07	6.99	NS
Photoperiod	2	29.47	1.40	
Prov. x Photoperiod	4	24.89	1.18	
Number of Internodes on Stem				
Provenance	2	6.21	0.33	NS
Photoperiod	2	30.17	1.60	
Prov. x Photoperiod	4	6.07	0.32	

Dry Weight Production and Total Leaf Area.

The following parameters of dry weight production were recorded at harvest: leaf dry weight, stem dry weight, root dry weight, and root/shoot ratio. Total leaf area was also measured at harvest. The variation in these attributes with provenance and photoperiod at 21/16°C. are graphically represented in Figures 6.8 (a) to 6.8 (f) as follows:

- Figures 6.8 (a) Leaf Dry Weight,
- (b) Stem Dry Weight,
- (c) Root Dry Weight,
- (d) Total Dry Weight,
- (e) Root/Shoot Ratio,
- (f) Total Leaf Area.

The optimum photoperiod for dry weight production of E. camaldulensis grown at 21/16°C. was 12-hour photoperiod for all 3 provenances. This contrasts with growth in seedling height, where there was a progressive increase in height with increase in length of photoperiod, that is maximum height growth was recorded at the 14-hour treatment (Figure 6.7 (a)). This confirms the point made earlier in respect to growth in basal diameter, that the 14-hour photoperiod is producing spindly type seedlings.

At the 12-hour photoperiod, the southern provenance of Lake Albacutya produced greater dry weight than the others, but not markedly so in terms of total dry weight and leaf dry weight. It was close to the Todd River provenance in stem dry weight, and both Lake Albacutya and Todd River exceeded Katherine provenance

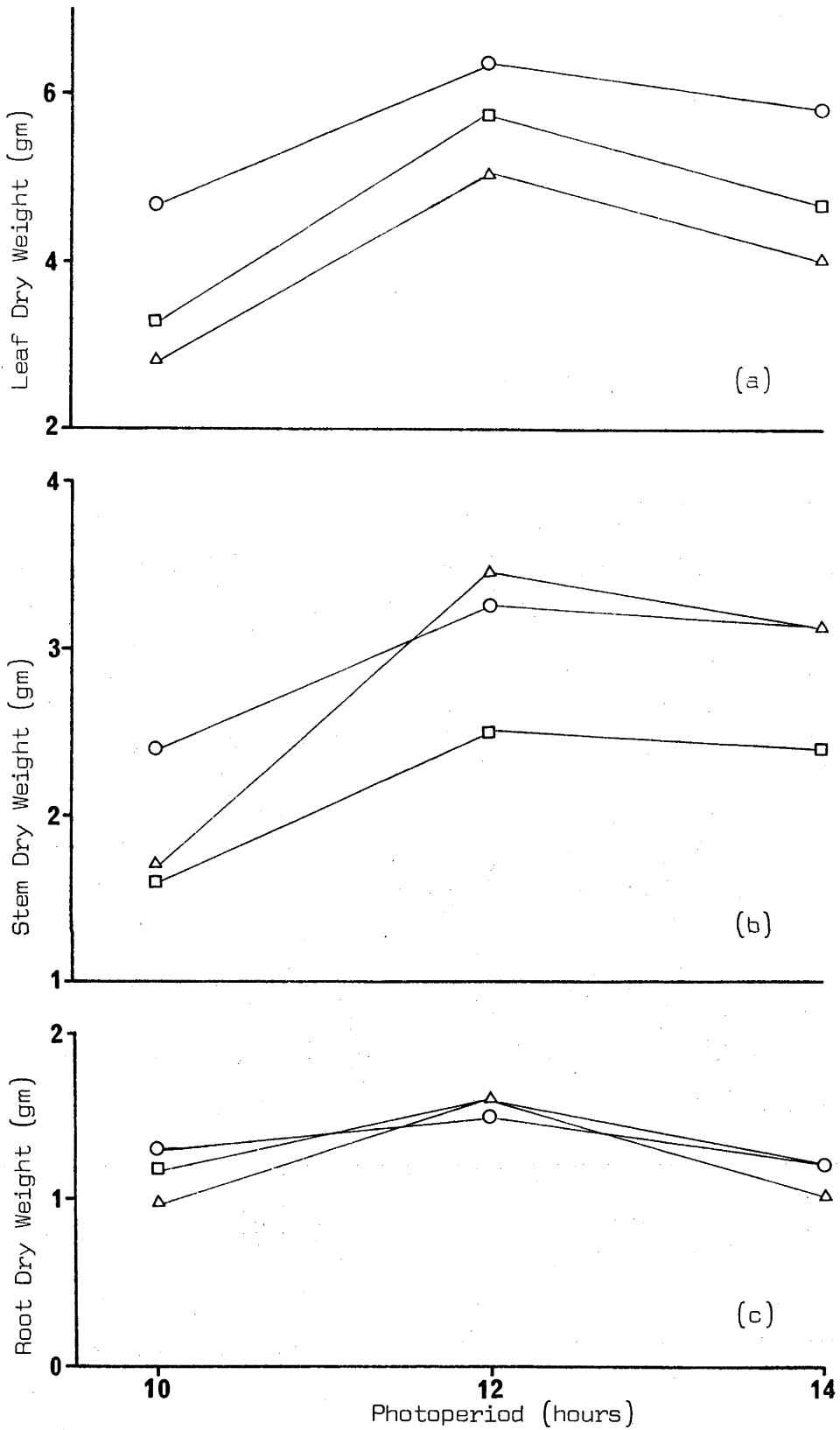


FIGURE 6.8 Provenance Variation in the Response of Dry Weight Production and Leaf Size of Seedling Progenies of *E. camaldulensis* to Variation of Photoperiod at Day 50. Katherine (□), Todd River (△) and Lake Albacutya (○).

- (a) Leaf Dry Weight
- (b) Stem Dry Weight
- (c) Root Dry Weight

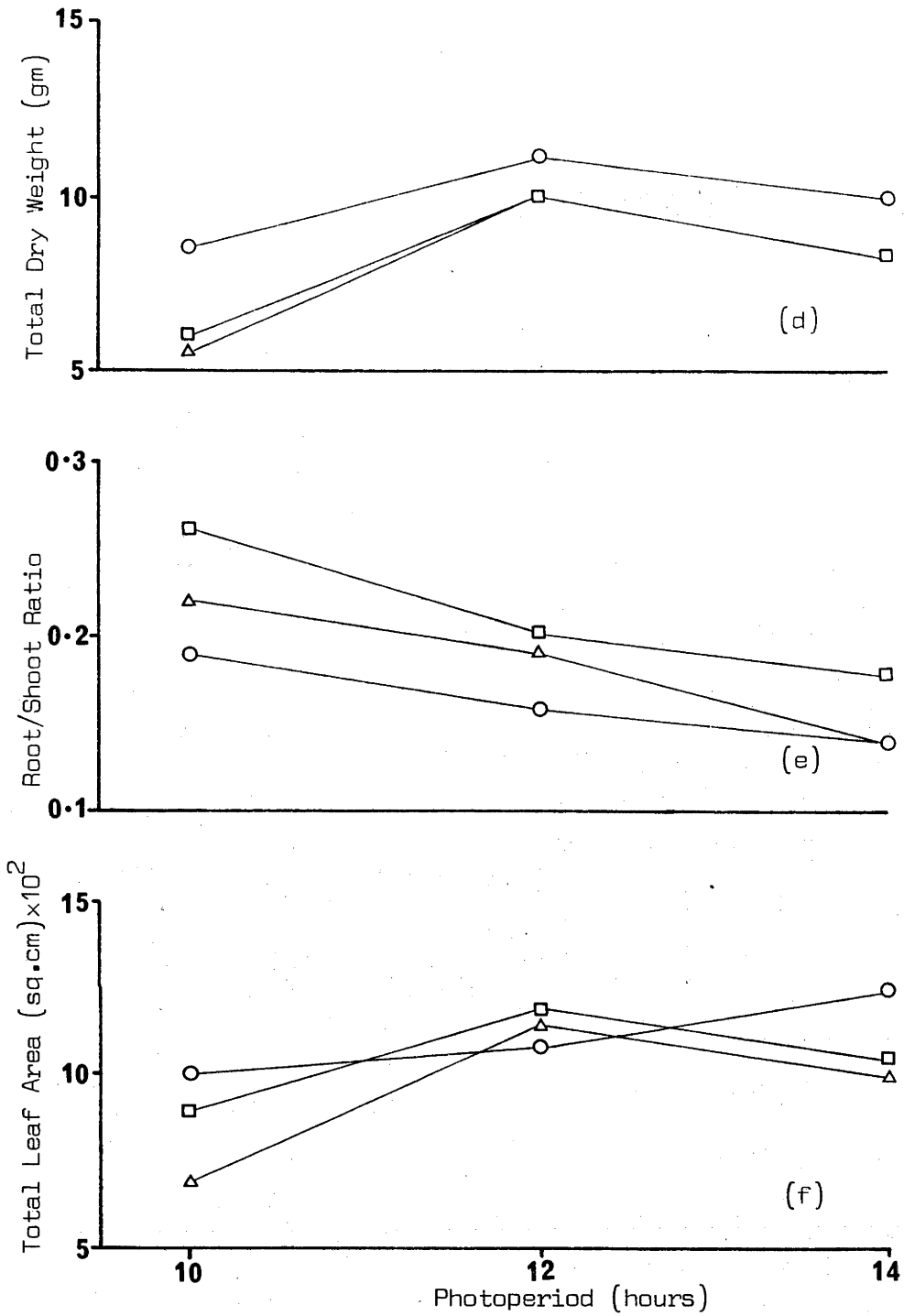


FIGURE 6.8 (Cont'd)
 Katherine (□), Todd River (Δ) and Lake Albacutya (○).
 (d) Total Dry Weight
 (e) Root/Shoot Ratio
 (f) Total Leaf Area

in this respect. These patterns differ from those for seedling height growth. At day 50, Todd River had the greatest height growth, followed by Lake Albacutya and Katherine in that order. This illustrates difference in form of seedlings - that is, Todd River seedlings had slightly less dry weight than Lake Albacutya - even though Todd River seedlings had greater height, greater number of branches and leaves on branches.

Despite differences in leaf dry weight, there was little, if any, difference between the provenance in leaf area at 12-hour photoperiod. There may be differentiation of provenances at 10- and 14-hour photoperiods. For example, leaf area for Katherine and Todd River are lower at 14 hours than at 12 hours, while Lake Albacutya leaf area is greater at 14 hours. This may again reflect selection against excessive leaf area in hotter environment and little selection against this at cooler environment.

At the shorter (10-hour) photoperiod, E. camaldulensis seedlings had greater root:shoot ratios than at larger photoperiod (12 and 14 hours). There was a progressive decline in the root : shoot ratio with photoperiod. The northernmost (Katherine) provenance seedlings had the greatest root:shoot ratio at all photoperiods, and the southernmost (Lake Albacutya) provenance the least. This again may represent selective adaptation to more extreme environmental conditions. The seedling producing more root growth in relation to shoot growth may be better able to withstand temperature extremes and more extended dry periods.

Analysis of Data for Dry Weight Production and Total Leaf Area.

Means and standard errors for each of the six parameters shown in Figures 6.8 (a) to 6.8 (f), are given in Tables of Means in Appendix 6. These data were analysed and LSD values ($P = 0.05$) are given. A summary of the significance of differences between individual means, drawn from Appendix 6 is given in Table 6.3. The main points from the analysis are now discussed.

Leaf Dry Weight. At 10 and 14 hours, there were significant differences between provenances but most differences between individual provenances were not significant at the 12-hour treatment. This may indicate little separation of the provenances with increase in photoperiod.

Root Dry Weight. Katherine and Lake Albacutya provenances did not differ significantly in this attribute at any photoperiod. Between the central (Todd River) and southern (Lake Albacutya) provenances, there were significant differences at 10 and 14 hours.

Leaf Area. In all photoperiods except at 14 hours there were no significant differences between the northern (Katherine) and the southern (Lake Albacutya) provenances. This may confirm a selection against excessive leaf size in hotter environment.

Root/Shoot Ratio. There were significant differences between provenances in all photoperiods. This reflects a strong separation of the provenances with photoperiod. The Katherine provenance responded most to all the photoperiods, and Lake Albacutya, the least.

A summary of the univariate analysis of variance, carried out for the dry weight production and leaf area, is presented in

Table 6.4. Like the results for the growth analysis in Table 6.2, there were no significant differences ($P = 0.05$) between provenances for any of the attributes.

Lack of significant differences between provenances may result from the fact that provenances are not responding in a consistent way at the different photoperiods even though significant differences between provenances may occur at individual photoperiods.

TABLE 6.4 Univariate Analysis of Variance for Dry Weight
Production and Total Leaf Area at Different
Photoperiods.

Source	DF	Mean Square	Variance Ratio	Sig.5%
Leaf Weight (g)				
Provenance	2	20.36	6.50	NS
Photoperiod	2	33.90	10.81	
Prov. x Photoperiod	4	0.48	0.61	
Stem Weight (g)				
Provenance	2	4.63	4.59	NS
Photoperiod	2	11.38	11.27	
Prov. x Photoperiod	4	9.71	9.71	
Root Weight (g)				
Provenance	2	9.18	1.12	NS
Photoperiod	2	1.61	9.55	
Prov. x Photoperiod	4	0.13	0.77	
Total Dry Weight (g)				
Provenance	2	48.37	4.91	NS
Photoperiod	2	123.50	12.54	
Prov. x Photoperiod	4	1.01	0.10	
Root/Shoot Ratio				
Provenance	2	0.01	7.35	NS
Photoperiod	2	0.03	15.42	
Prov. x Photoperiod	4	0.00	0.46	
Total Leaf Area (sq.cm)				
Provenance	2	358069.95	3.16	NS
Photoperiod	2	864884.00	7.63	
Prov. x Photoperiod	4	54119.23	0.48	

6.4 Discussion

Summary of Findings

The results show some clear differences between the three provenances, Katherine, Todd River and Lake Albacutya, in their reaction to variation in photoperiod.

There is a strong and direct relationship between photoperiod and seedling height growth for all 3 provenances, that is, there was a marked response in height growth to increasing photoperiod. Unlike the height growth however, there was no marked response in basal diameter and number of internodes on the stem to increasing photoperiod. Provenances differ in seedling height growth at both 12- and 14-hour photoperiod, the provenances were widely separated - Todd River had the greatest height growth and Katherine the least. From previous discussion, Todd River should have been slow-growing. This means there is some change in seedling form with increasing photoperiod, that is, in responding in height, the seedlings are becoming more spindly. This was confirmed in the dry weight production data where peak dry weight occurred at the 12-hour photoperiod.

There is a large difference between provenances in the number of leaves on branches and the number of branches at 10 and 12 hours. The Todd River provenance had the greatest number of leaves on branches at all photoperiods, and Katherine the least. Katherine and Lake Albacutya seedlings had fewer leaves on branches, but the number increased with photoperiod with a maximum at 14 hours. Todd River - a hot dry environment - might have been

expected to have fewer leaves on branches and number of branches than either Katherine or Lake Albacutya.

There was a progressive decline in the root:shoot ratio with increase in the length of photoperiod. The northernmost (Katherine) provenance seedlings had the greatest root:shoot ratio at all photoperiods, and the southernmost (Lake Albacutya) provenance the least.

Discussion on Findings

In this study the Todd River provenance had the greatest height growth. This provenance is associated with the harsher environmental conditions of central Australia, and its height growth pattern appears to negate conclusions drawn for the foregoing study, - that is that slower height production of northern (harsher environments) provenances may represent adaptation to these conditions. Moreover, the Todd River provenance had a greater number of branches and leaves on branches than the southern (Lake Albacutya) provenance - again appearing to negate the hypothesis that within harsher environments there has been selection favouring individual with smaller transpiring surfaces. Therefore it seems that either the Todd River provenance is atypical of northern provenances generally (for example, there may be some local environmental conditions which ameliorate the harsh environment), or the hypothesis developed in the foregone chapter is not tenable.

It is necessary therefore to look more closely at the Todd River seedling characteristics to see whether there are other growth characteristics which differ from the southern provenance

of Lake Albacutya, and which can be interpreted in terms of environmental selection for adaptation to harsh environment. A number of growth characteristics of the Todd River provenance are summarised.

1. Todd River seedling height growth did not differ significantly from Lake Albacutya and Katherine at the 10-hour photoperiod. The wide separation occurred only at photoperiods greater than 10 hours.
2. While the Todd River seedlings grew more height at 12 and 14 hours, they did not produce the greatest total dry weight at these photoperiods. In fact the Lake Albacutya seedlings produced more total dry matter at all photoperiods, and more leaf dry weight at all photoperiods. In leaf dry weight, Todd River produced less than both Lake Albacutya and Katherine at all photoperiods. The Todd River seedling under the growing conditions of the phytotron at least were producing larger spindly plants, and markedly lower leaf production in terms of leaf weight.
3. Despite the greater height growth at 12 and 14 hours, there was only a slight increase in number of leaves on stems. At the 12-hour photoperiod there were no significant differences between provenances in number of leaves on stem - but there were significant differences at 14 hours.
4. The Todd River seedling produced considerably more branches and leaves on branches than either Lake Albacutya or Katherine - particularly at 10- and 12-hour photoperiods.

There was little difference between provenance in leaves on stems. Yet despite this,

- (a) The Todd River seedling leaf dry weight production was less than that of Lake Albacutya and Katherine.
- (b) The Todd River seedling total leaf area was generally smaller than that of Lake Albacutya and Katherine.

This clearly indicates that Todd River seedlings not only produced spindly seedlings under conditions of the experiment, but leaf size (area) and probably thickness were considerably less than that of Lake Albacutya and Katherine. This may represent environmental selection of plants with smaller transpiring surface.

5. Finally, Todd River behaved differently from Lake Albacutya and Katherine in response of number of branches and leaves on branches at the largest photoperiod. At 14 hours, number of branches and number of leaves on branches dropped sharply; this did not happen with Lake Albacutya and Katherine. In Todd River environment - conditions at greatest photoperiod could be particularly severe. Reaction of Todd River seedlings could represent selection of individuals able to reduce leaf production (and transpiring surface) at longer days.

In conclusion, environmental selection of characteristics may be expressed in many ways. Todd River differed in growth characteristics than other northern provenance, yet its own growth

characteristics can in fact be also interpreted in terms of selection against harsh environmental condition - particularly lower total dry weight production, smaller leaf area, smaller leaf dry weight, and reaction in number of branches and leaves on branches at greatest photoperiod.

CHAPTER 7

FROST RESISTANCE IN EUCALYPTUS CAMALDULENSIS DEHN

7.1 Introduction

Frost resistance in eucalypts is one physiological attribute for which there may be considerable within-species variation. Differences in frost resistance between populations from a range of sites have been reported for a number of eucalypt species. Frost resistance has been found to increase with altitude in E. fastigata (Boden 1958, Sherry and Pryor 1967); in E. pauciflora (Pryor 1956, Green 1967); in E. regnans (Ashton 1956, 1958, Eldridge 1969); and E. viminalis (Paton 1972).

Frost resistance in E. camaldulensis was found to vary latitudinally according to seed source by Larsen (1967), Karschon (1968), and by Pryor and Byrne (1969). In all of these studies the northern ecotype was considered more susceptible to frost damage than the southern population. The work of Karschon on Frost resistance of E. camaldulensis was limited to 3 provenances from the northern ecotype of the species while that of Pryor and Byrne covered a wider latitudinal range but a narrow longitudinal range.

Frost injury can be assessed in a number of ways. Most authors have measured some frost injury parameter and used the coefficient of variation of the mean to indicate within provenance differences in frost resistance. This is only a qualitative

assessment of frost injury in plants in that it usually does not indicate extent of damage to individual seedlings. In an effort to describe quantitatively frost injury in Eucalyptus species, Paton (1972) developed a technique whereby direct quantitative assessment of frost injury for individual seedlings was possible. The frost injury was expressed as the percentage ratio of "dry weight" to "wet weight" for each seedling to indicate the relative amounts of dead leaf tissue - due to the loss of water and possibly other volatile substances - and the living leaf tissue after frost treatment. The "wet weight" is taken as the weight of all dead, injured, and unaffected leaves of each seedling - collected after frost treatment, and "dry weight" is the oven dry weight of the leaves. For example, for untreated seedlings the percentage ratio of dry weight to wet weight is normally around 30-40%. In frost treated seedlings, the greater the ratio of dry weight to wet weight, the greater the degree of frost injury. A completely killed seedling could have percentage ratio approaching 100%. The ratio is measured at a standard time after frost treatment, for example, 5 - 10 days. The ratio is assessed for each seedling and the extent of damage can be expressed by determining the proportion of seedling in different injury classes.

Paton's method was used in the present study for E. camaldulensis. The objective of the study is to test provenances of E. camaldulensis under a range of controlled conditions for differences in resistance to frost.

7.2 Materials and Methods

Preparation of seedlots

For Preliminary Experiments and Experiments 1 and 2, seedlots of E. camaldulensis from 4 provenances - Katherine, Nathalia, Gwydir River and Agnew - were germinated and grown in an open glasshouse. For a detailed description of the provenances, see Table 4.1. For each provenance, 4 seedlings were transplanted into each of twenty-six pots containing an equal mixture of perlite and vermiculite. The plants were maintained in the glasshouse for three months before being subjected to the frost treatment. Adequate nutrients were provided in twice weekly application of "Aquasol".

For Experiment 3, E. camaldulensis seedlings from 4 provenances - Katherine, Nathalia, Gwydir River and Agnew - were raised at the CSIRO phytotron. At two-leaf pair stage the seedlings were pricked and transplanted into 17 cm pots. Four seedlings were transplanted into each pot and there were 24 replicates for each provenance. The seedlings were arranged in a "C" cabinet set at 21/16°C and 8-hour photoperiod. When the plants had grown for 2 months, one half were gradually hardened in three stages by transferring them in "C" cabinets set at lower temperatures of 18/13°C, 15/10°C and 9/4°C respectively. At each temperature the seedlings were hardened for 5 days. The plants were taken directly from the phytotron to the frost room.

Preparation for frost treatments

The pots containing the seedlings were packed in wooden boxes and surrounded with dry perlite to protect the seedling roots from freezing during the frost treatment. The temperature of the frost room was gradually lowered to the required temperature before the cooling system was turned off and the room opened, and allowed to return to ambient temperature.

Frost treatment

All frost treatments were carried out at Botany Department frost room. The design of the frost room for radiation frost studies in Eucalyptus was described by Aston and Paton (1973). The frost room was initially at the day-room temperature of about 20°C. when the boxes containing the plants were brought in for the Preliminary Experiments and for Experiments 1 and 2. The initial temperature of the frost room was about 10°C. when the seedlings for Experiment 3 were brought in. To bring the temperature of the frost room to zero the temperature controller was set at -25°C. This allowed a gradual decrease in temperature of the frost room to reach zero and subsequently the leaf temperature to reach zero. Thermometer and thermocouple readings were used to check the frost room temperature. Measurements of leaf temperature were obtained from 12 thermocouples attached to the abaxial surface of the leaf. When the frost room reached a temperature of 0°C., the temperature was maintained until the leaf temperature dropped to 0°C. The temperature of the frost room varies by $\pm 0.13^{\circ}\text{C}$. The temperature

of the leaf was decreased in stages by 1°C . and maintained for 30 minutes at each temperature before being decreased further.

When the desired temperature was reached it was maintained for 30 minutes. The frost room was then opened to allow the plants to defrost. The treated plants were taken out of the frost room. The effects of frost on the plants were noted the following morning. The plants were watered and kept in a green house for 6 days to allow a full development of any frost injury.

Assessment of frost injury

For assessment of frost injury, all dead, injured, and unaffected leaves on each seedling were stripped at day 6 after frost treatment and wet weight determined. Any green leaves which were covered by perlite during treatment were excluded. Dry weight was determined when loss in weight in a drying oven at 80°C . had ceased.

7.3 Preliminary Frost Experiment Results

Three trial runs were made to determine the temperature at which 50% frost damage would occur in most of the provenances. In the first trial run, 20 seedlings of Katherine provenance were subjected to frost treatment. In the second trial run, seven seedlings from Nathalia, Gwydir River and Agnew provenances were subjected to frost treatment. Twelve seedlings from 3 provenances - Nathalia, Gwydir River and Agnew - were used for the third trial run. These seedlings represented regrowth of seedlings which had been cut back after having been exposed to frost treatment.

The mean heights of seedlings for each of the 4 provenances of E. camaldulensis before frost treatment was as follows:

	Height(cm)
Katherine	40.33
Nathalia	50.15
Gwydir River	52.20
Agnew	37.85

The mean ratio percentages of dry weight to wet weight for both treated and untreated seedlings are given in Table 7.1, for the 3 trial runs.

TABLE 7.1 Frost Injury (% Dry Weight/Wet Weight) for the Plants of E. camaldulensis for the 3 Trial Runs of Frost Treatments and the Ratio Percentages of Dry Weight to Wet Weight for Untreated Plants.

Frost Room Temperature (°C.)	Treated Seedlings			Untreated Seedlings
	-5.5	-4.5	-4.5	
Trial Run	1	2	3	
Katherine	96.01	-	-	37.50
Nathalia	-	68.19	65.82	40.75
Gwydir River	-	55.61	63.50	41.33
Agnew	-	64.28	70.27	34.53
L.S.D. (p = 0.05)	-		5.74	5.43

The data in Table 7.1 were analysed and the L.S.D. values at 5% level of probability are given. In untreated seedlings the ratio of dry weight to wet weight expressed as a percentage ranged from 34-41%.

Percentages greater than those for the untreated seedlings express the degree of frost damage. In the first trial run, all the seedlings of Katherine provenance were severely damaged by frost - all plants were totally killed - the percentage dry weight to wet weight at standard time of 6 days was 96.01%. Because of this a low temperature of -5.5°C . was considered unsuitable for running the major frost treatment. The results of the second and third trials at a treatment temperature of -4.5°C . were similar. For example, this temperature was found to produce frost damage symptoms on about half of the seedlings in three of the provenances. In the second trial run a frost damage index of 55.61% was recorded for Gwydir River provenance while Agnew and Nathalia scored 64.28 and 68.19% respectively. In the third trial run, Gwydir River scored 63.50% frost injury index while Agnew and Nathalia had 70.27 and 65.82% respectively. There was no significant difference between Nathalia and Gwydir River provenances but Agnew provenance was significantly different ($p = 0.05$) from the other two.

7.4 Experiment 1

In the first major experiment, seedlings from 3 provenances - Nathalia, Gwydir River and Agnew - were subjected to frost treatment. The number of seedling replicates for each of the three provenances was 43.

The total frost injury expressed as the percentage of dry weight to wet weight is set out in Table 7.2(a). Nathalia seedlings recorded the greatest frost injury index (89.91%), followed by Gwydir River seedlings with an index of 79.56%. Agnew provenance received the least frost damage (69.88%), that is, seedlings from Agnew provenance were the most resistant to frost. There was no significant difference between Nathalia and Gwydir River provenances, but these two provenances were significantly different from Agnew provenance.

The results of the frost injury are also presented in a series of histograms representing the percentage frequency within injury classes for each of the 3 provenances (Figure 7.1). Most of the seedlings from Nathalia and Gwydir River provenances were severely damaged by frost. For example, 70 to 80% of the plants were damaged to the extent that 90 - 100% of the plant matter was killed. Alternatively only 34% of the seedlings of Agnew provenance was severely damaged by frost. This suggests that under the experimental conditions, Agnew provenance was more tolerant to frost than the other two provenances.

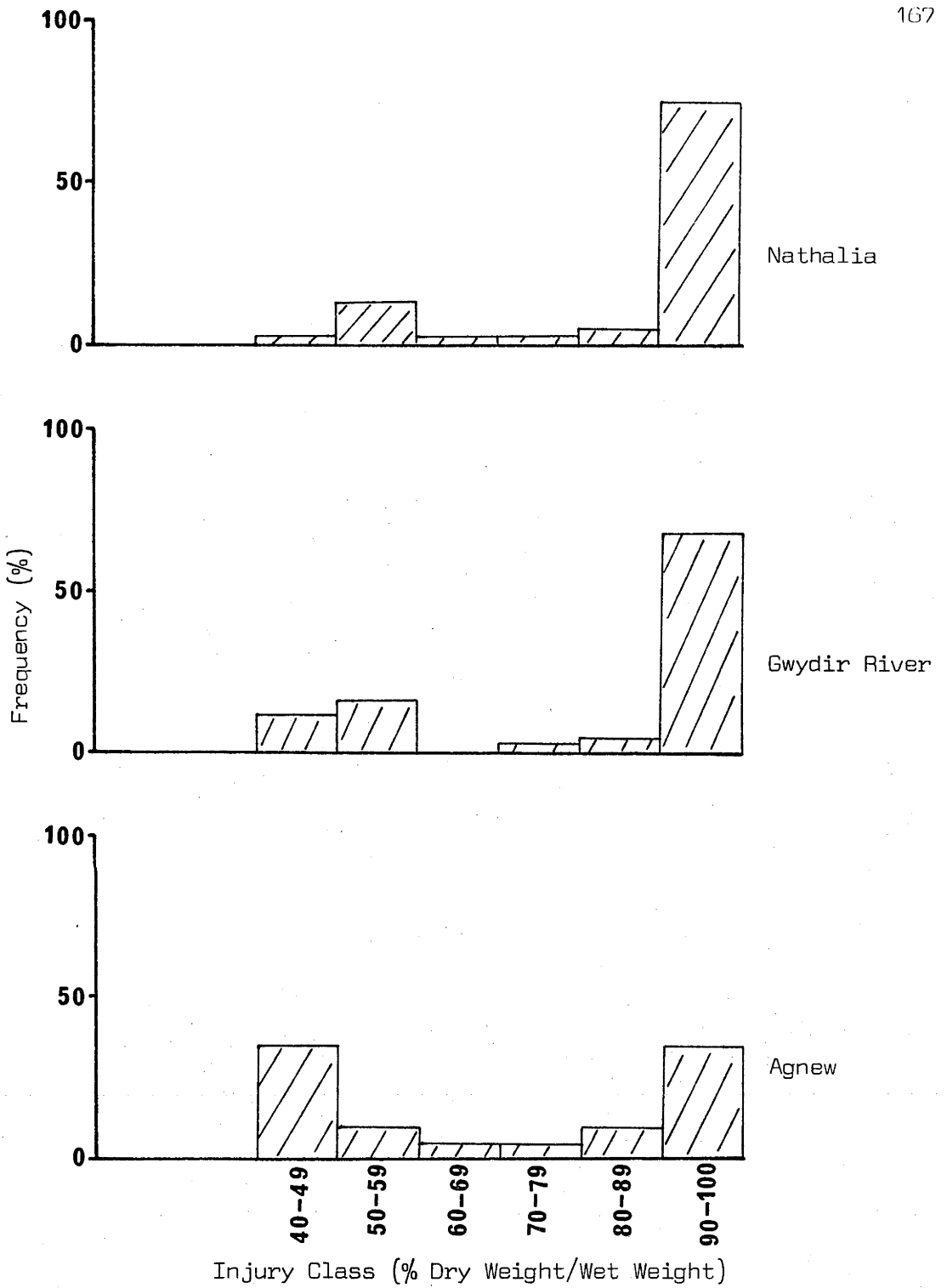


FIGURE 7.1 Histograms of Percentage Frequency Within Injury Classes for 3 Provenances of *E. camaldulensis* Grown in Open Glasshouse for Experiment 1 on Frost Resistance.

7.5 Experiment 2

At the harvest of seedlings of the preliminary experiment and of Experiment 1, the stem of each seedling for each of the 4 provenances - Katherine, Nathalia, Gwydir River and Agnew - was cut back to about 4 cm above the root collar to allow a few shoots to grow for a second run of the frost treatment. The plants were allowed to coppice to several shoots, then reduced to one shoot per plant. These coppiced plants were maintained in the glasshouse for 2 months until they were large enough to be subjected to a second frost treatment. The number of seedling replicates for each of the 4 provenances was 75.

The effects of frost treatment on the 4 provenances were not recognisable immediately the plants were taken out of the frost room. The day following frost treatment it was possible to score the number of seedlings affected by frost in each provenance. A rough estimate of the frost effects on each provenance was made by counting the number of injured seedlings. There was a strong indication of differences in provenance reaction to frost treatment. The greatest damage occurred in the Nathalia provenance with 96% of the seedlings being damaged by the frost treatment. This was followed by Gwydir River provenance with 84% damage. Agnew and Katherine received less damage with 73% and 69% of the plants being damaged respectively. These subjective results of frost damage of the seedlings compared very well with the subsequent objective scoring of frost injury. The total frost injury has been expressed as a percentage of dry weight to wet weight

(Table 7.2 (b)). Nathalia seedlings recorded the greatest damage index (94.80%), followed by Gwydir River with an index of 83.07%. Agnew had an injury index of 86.4% while Katherine received the least frost damage (72.21%). Under the experimental conditions, Nathalia, Gwydir River and Agnew seedlings were more susceptible to frost injury than seedlings from Katherine provenance.

The extent to which damage was done to the seedlings is presented in a series of histograms representing the percentage frequency within injury classes for each of the 4 provenances (Figure 7.2). Nathalia provenance was severely damaged by frost. All the seedlings from Nathalia received more than 50% injury, and a high proportion of the seedlings (95%) received more than 80% frost damage. This was followed by Gwydir River where 80% of the seedlings received over 80% frost damage. Agnew provenance had about 70% of the seedlings damaged to the extent that 80-100% of the plant matter was killed. Again, Katherine provenance was the least affected by frost - a smaller proportion of the seedlings (66%) received more than 80% frost injury, and about 30% of the seedlings had less than 50% frost damage.

In the present study the seedlings were not pre-hardened before being subjected to frost treatment, but under natural conditions where a period of cold weather precedes frosty winter conditions, plants may be hardened to withstand frost. The results indicate that the northernmost (Katherine) provenance where frosty conditions are less frequent than the southern provenances, was found to be more resistant to frost damage than the other 3 provenances.

There may be some physiological reactions in plants which permit prehardened plants in cold regions to withstand frost.

The third major experiment was designed to examine whether prehardening had any effect on subsequent frost injury, and whether there were significant differences between provenances in this respect.

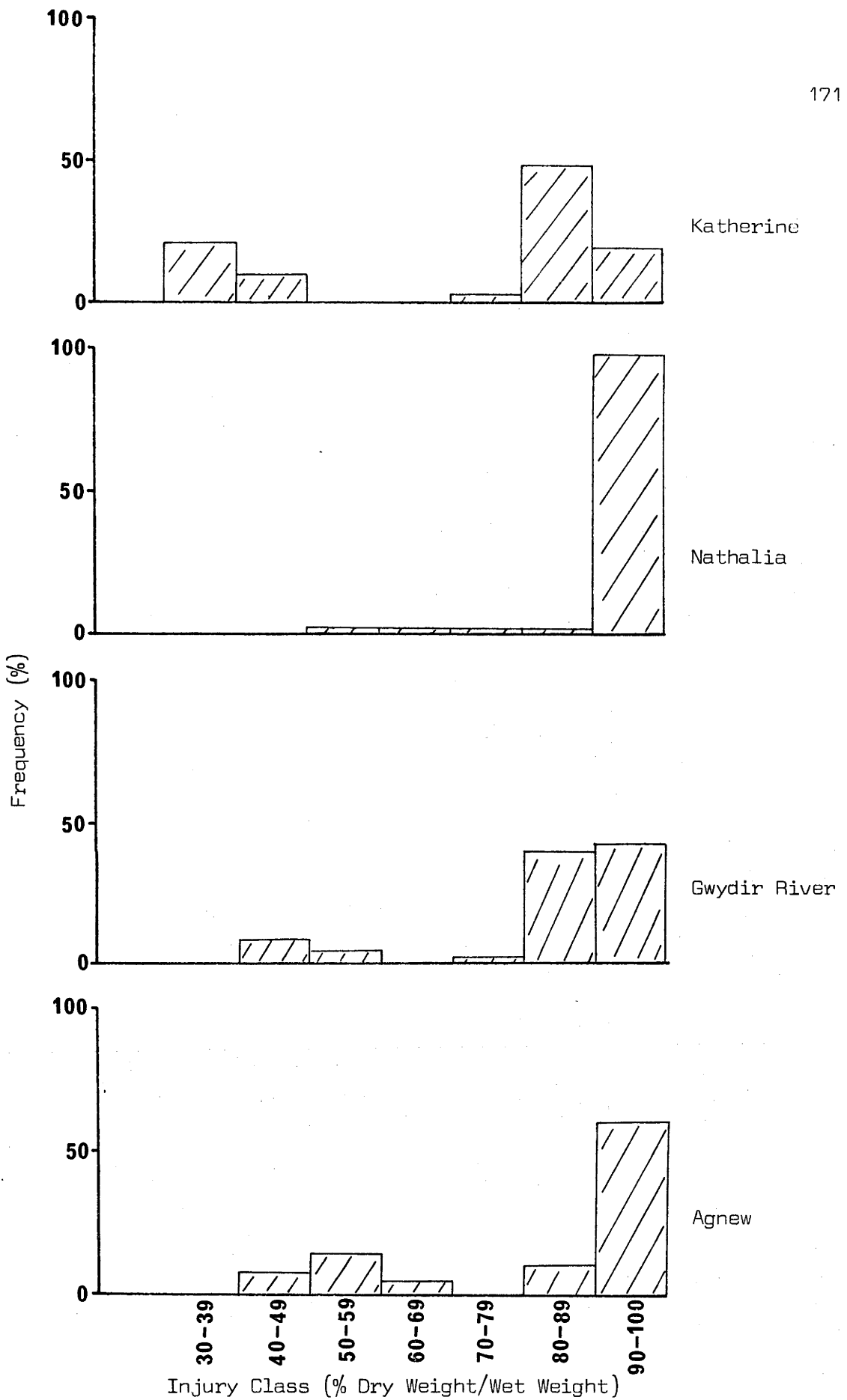


FIGURE 7.2 Histograms of Percentage Frequency Within Injury Classes for 4 Provenances of *E. camaldulensis* Grown in Open Glasshouse for Experiment 2 on Frost Resistance.

7.6 Experiment 3 - Effect of prehardening

In this experiment E. camaldulensis seedlings from 4 provenances - Katherine, Nathalia, Gwydir River and Agnew - were raised at the CSIRO phytotron and the frost treatment was carried out at Botany Department frost room.

The results of the frost injury to the seedlings are presented in a series of histograms representing the percentage frequency within injury classes for each of the 4 provenances and follows:

Figure 7.3 Percentage frequency within injury classes for unhardened seedlings grown at 21/16°C.

Figure 7.4 Percentage frequency within injury classes for seedlings hardened at 9/4°C.

When the plants grown at 21/16°C. were treated with frost (without intermediate hardening) the reactions were similar to those of Experiment 2, that is, the seedlings from the northern provenances of Katherine and Agnew were more resistant to frost than seedlings from southern provenances - Nathalia and Gwydir River. Most of the seedlings from southern provenances were severely injured. For Nathalia and Gwydir River, around 60-70% of plants were damaged to the extent that 50-70% of the plant matter was killed. About 50% of seedlings from Katherine had 20-60% leaf tissue damage. All the seedlings from Agnew received less than 60% damage to the leaves.

The total frost injury (expressed as the percentage of dry weight to wet weight) has been presented in Table 7.2(c).

Both Nathalia and Gwydir River seedlings recorded greatest frost damage index of 71.25 and 76.92% respectively. Katherine and Agnew had a low frost injury index of 48.83 and 47.75% respectively. There was no statistical difference between the 2 southern provenances - Nathalia and Gwydir River, and no significant difference ($p = 0.05$) was recorded between Agnew and Katherine provenances. However, there were significant differences between the northern and the southern provenances in their reaction to frost treatment.

Where the plants have been prehardened before the frost treatment, the reactions were quite different to those of unhardened plants. It was found that the northernmost (Katherine) provenance was severely damaged by frost. A very high proportion of the seedlings (80%) received more than 50% injury (Figure 7.4) - that is, only 20% received less than 50% injury. This contrasts greatly with effects of frost on Katherine provenance in Experiment 2. Alternatively 67% of the Gwydir River seedlings received less than 50% injury and 40% received less than 30% injury. For Nathalia, 48% of seedlings recorded less than 50% injury, but for Agnew, 64% of seedlings received less than 50% injury. Under prehardened conditions, the southern provenances and Agnew provenance are more resistant to frost than Katherine - that is, a reversal of results on unhardened plants. Gwydir River - which in unhardened treatment was the most damaged provenance - became the most resistant in prehardened treatment.

The total frost injury was also expressed as a percentage of dry weight to wet weight in Table 7.2(c). Katherine seedlings

recorded the greatest damage index (61%), followed by Nathalia (52.58%). Agnew had a 45.33% injury index while Gwydir River received the least frost damage index (41%). Under natural conditions where a period of cold weather precedes frosty winter conditions, plants may be hardened to withstand frost - as suggested earlier on. It could therefore be expected that the seedlings from the southern provenances of Gwydir River and Nathalia would be more resistant to frost than the northern (Katherine) provenance. Agnew is also found to be more frost tolerant than Katherine because Agnew is a much cooler area during winter (Table 4.1) than the northernmost (Katherine) area.

TABLE 7.2 Mean of Total Frost Injury (% Dry Weight/Wet Weight) to the Plants of *E. camaldulensis* for the Three Major Experiments. Frost Injury for (a) Seedlings Grown in an Open Glasshouse; (b) Coppiced Seedlings Grown in an Open Glasshouse; (c) Seedlings Raised in the Phytotron at 21/16°C. Temperature Regime and those Hardened at 9/4°C. Before Being Subjected to Frost Treatment.

Series	a		b		c	
	Experiment I		Experiment II		Experiment III	
	Open Glasshouse	Open Glasshouse	21/16°C.	9/4°C.		
Katherine	-	72.21	48.83	61.00		
Nathalia	86.91	94.80	71.25	52.58		
Gwydir River	79.56	83.07	76.92	41.00		
Agnew	69.88	82.64	47.75	45.33		
L.S.D. (p = 0.05)	8.24	5.57	11.74	13.48		

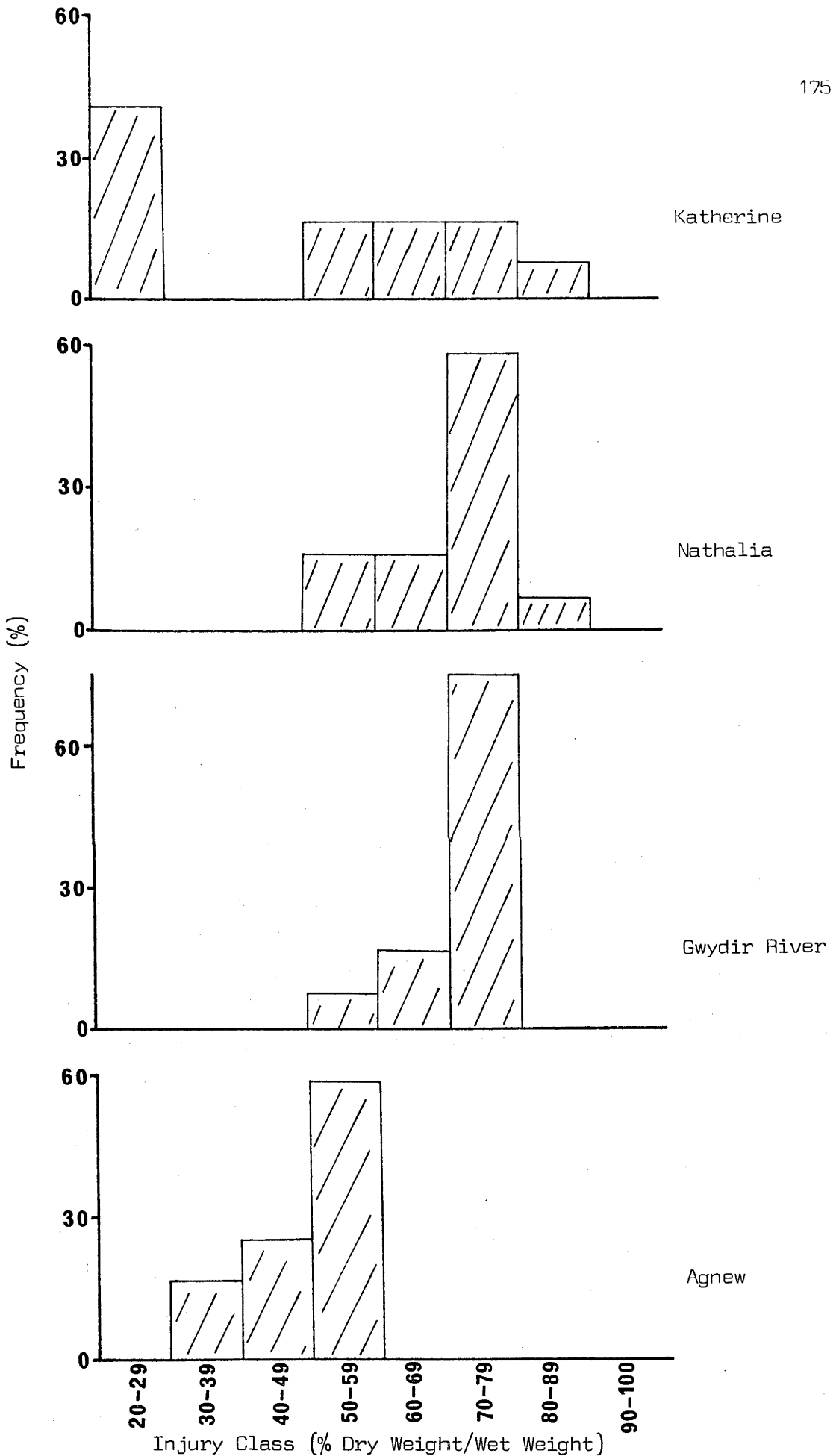


FIGURE 7.3 Histograms of Percentage Frequency Within Injury Classes for the Plants of *E. camaldulensis* of 4 Provenances Grown at 21/16°C. for Experiment 3 on Frost Resistance.

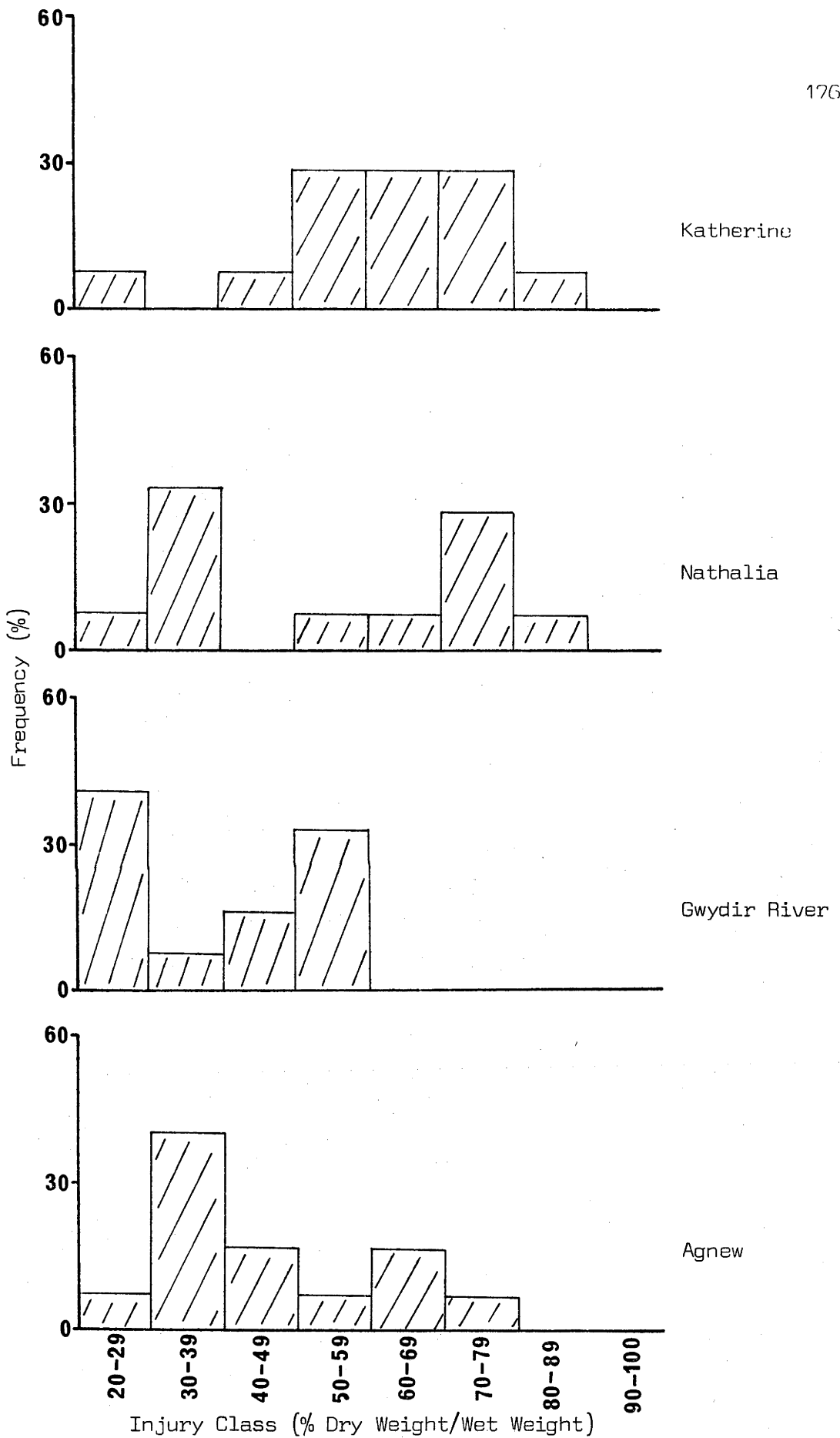


FIGURE 7.4 Histograms of Percentage Frequency Within Injury Classes for 4 Provenances of *E. camaldulensis* Grown at 9/4°C. for Experiment 3 on Frost Resistance.

7.7 Discussion

The results obtained in this study supports the findings of earlier work indicating that frost resistance in E. camaldulensis varies according to seed origin. However, the results are not altogether in agreement with some of this earlier work and suggest that some rather interesting variations in frost sensitivity in this species have developed in response to local selection.

It is evident that the unhardened seedlings of E. camaldulensis from Katherine and Agnew are more resistant to frost injury than seedlings from either Nathalia or Gwydir River provenances. This may suggest a selection for resistance to a sudden drop in temperature, whereby the northern provenances are more adaptable to a radical change in climatic conditions - ensuring their survival in any adverse environment. It is quite possible that provenances from continental areas - that is, where very marked daily temperature fluctuations may occur with severe night radiation frosts - may have greater capacity for frost resistance when no pre-hardening has been possible.

In continental areas, the most serious frost damage is probably caused either by sudden temperature falls which occur periodically throughout winter or by changes between day and night temperatures occurring in clear sunny weather. Solar radiation may raise the temperature of leaves and bark several degrees above the air temperature. At sunset the rate of temperature fall may be considerable. Injuries caused by such rapid temperature decreases are most probably due to intracellular ice formation (Aronsson and

Eliasson 1970). For the successful establishment of plants in some of the harsher environments such as Katherine and Agnew, the seedlings would have some ability to minimise dehydration of the plant tissue cells under the extreme weather conditions.

Resistance to intracellular freezing is an important component of forest hardiness in nature (Aronsson and Eliasson 1970). The seedlings of Nathalia and Gwydir River grown in the open glasshouse and at high temperature regime probably developed no physiological and biochemical mechanism to withstand sudden freezing test in the frost room; hence their low resistance to frost under the present experimental conditions. The results of the effects of frost on hardened seedlings of E. camaldulensis indicate that seedlings of Nathalia and Gwydir River provenances are more frost tolerant than those from Agnew and Katherine. In nature most of the plants from Nathalia and Gwydir River will possess the ability to harden to withstand the winter conditions. Tumavov and Krasavtsev (1959), Sakai (1960) and Parker (1962) showed that not even the temperatures of liquid nitrogen ($-196^{\circ}\text{C}.$) or helium ($-269^{\circ}\text{C}.$) will kill very hardy plant tissues. Eldridge (1969) also found that seedlings of Eucalyptus regnans hardened at a low temperature regime ($9/4^{\circ}\text{C}.$) are more frost resistant than seedlings grown at higher temperatures.

It is not unexpected to find that Karschon (1967), and Pryor and Byrne (1969) established that the northern ecotype of E. camaldulensis are more susceptible to frost injury than the southern ecotype when the seedlings of the species are grown in an

open area where hardening of plants is possible before harsher winter conditions set in. The results of the present investigation on the effects of frost on hardened seedlings of E. camaldulensis, more or less confirms that susceptibility of frost damage in the species is related to seed origin, and in particular decreases from north to south - Katherine (northernmost) provenance being the most susceptible and Gwydir River the least. Both Nathalia and Agnew provenances may be considered as intermediate in their reaction to frost.

CHAPTER 8

ROOT DEVELOPMENT OF E. CAMALDULENSIS DEHN

8.1 Introduction

As E. camaldulensis occurs in many hot dry areas of Australia it is quite possible that drought resistance in seedlings is a factor of importance in selecting the fittest individuals to survive in the population. E. camaldulensis occurs mainly on river banks or on flood plains of inland rivers. The seed germinates on moist soil after the flood waters recede (Jacobs 1955, Dexter 1967). Dexter noted that seed germinated under these conditions when seed bed temperatures were high, and postulated that the high optimum germination temperature of 35^oC. may be of adaptive significance for this reason. In the Murray valley, river flooding usually takes place in spring and the flood waters may not recede until well into the late spring and early summer. In northern Australia, in locations such as Katherine, summer flooding can be expected when average daily mean temperatures are almost 30^oC. (see Table 2.2).

Following the period of flooding, most of the sites occupied by E. camaldulensis are characterised by prolonged periods of dry weather, often with extremely high temperatures. To survive on these areas the newly germinated seedling must establish an adequate root system quickly. Among the eucalypts, red gum has a particularly high root:shoot ratio (Jacobs 1955). Possibly, the

ability to develop a strong root system rapidly is one reason for the success of the species in these flood bank and flood plain sites. Differences between provenances in their ability to withstand adverse establishment conditions would indicate variation in drought resistance of Eucalyptus camaldulensis .

A root study was undertaken to examine the pattern of establishment ability among six selected provenances of E. camaldulensis. For comparison, one provenance of each of two other eucalypts (E. saligna and E. pilularis) was included in the investigation. Both of these species occur in moist coastal regions of northern New South Wales where establishment conditions are usually not severe in terms of soil moisture availability.

8.2 Preliminary Experiments

White plastic pipe of 12 cm diameter was cut into 1-metre lengths to form open ended pots. These pots were halved by sawing through them length wise and reconstituted with insulating tape and copper wire. The pots were filled with a soil mixture of equal parts of top soil and river sand.

In preliminary experiments, three treatments were set up in the open glasshouse:

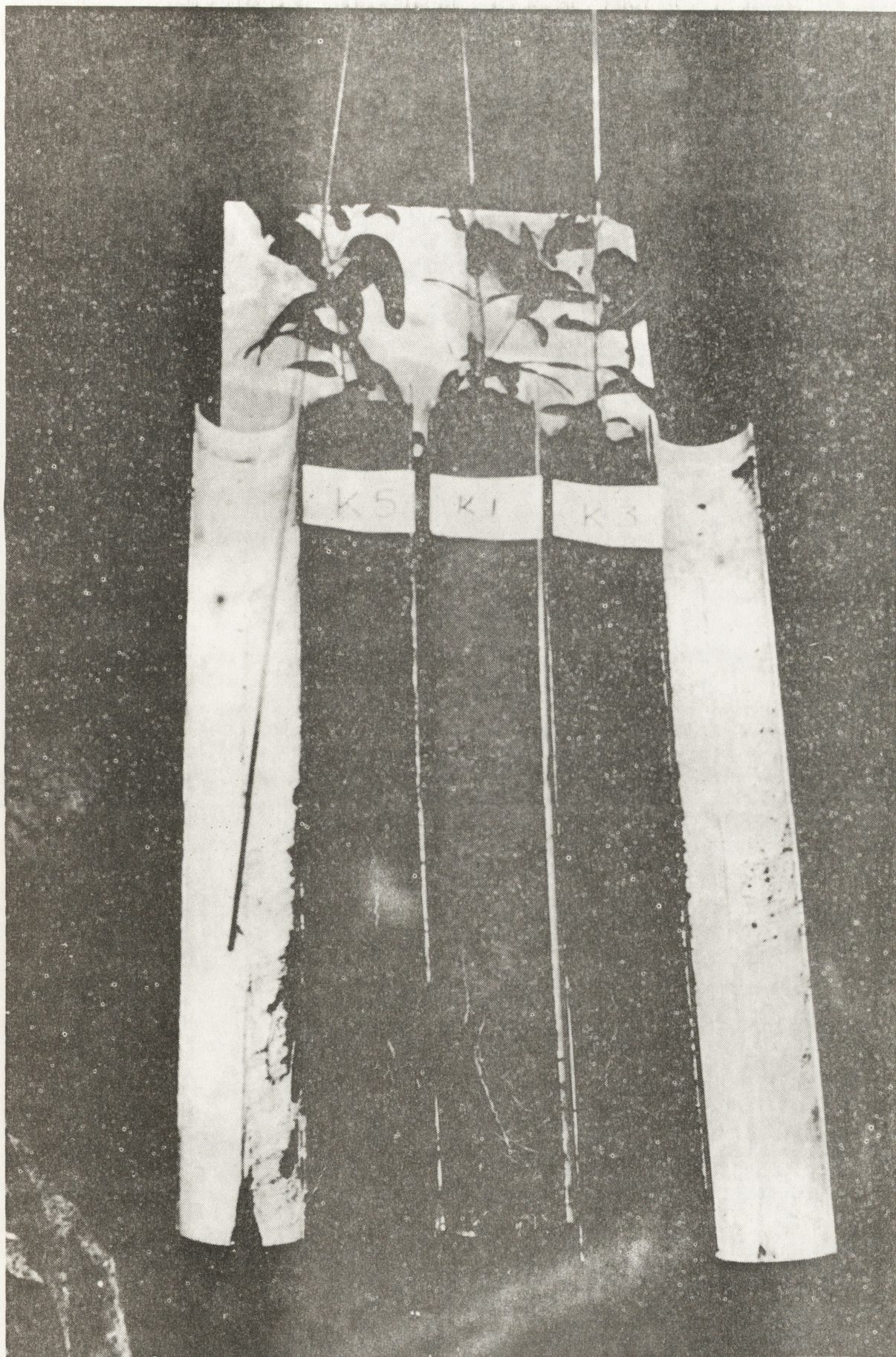
1. Normal watering of the plants was done until the fifth leaf pair appeared. Water was then withheld. As the soil column dried out at the top, the roots were expected to utilise the water remaining in the moist part of the soil at lower levels.

2. Normal watering was carried out twice daily throughout the duration of the experiment. Satisfactory growth of the plants was expected, and the results obtained in the treatment was to serve as a basis for comparison with the other experiments.
3. Watering continued until the fifth leaf pair appeared, and the pots were stood in a pool of water held by a 3-gallon kerosine tin. The idea was to keep the whole soil column moist by capillary movement of water from the 'water table' at the base of the pot.

A single provenance of E. camaldulensis from Katherine, N.T. was used for the experiment. Duplicate pots were used for each treatment. The seeds were germinated initially in small pots containing equal parts of perlite and vermiculite, and the seedlings were transplanted into the long pots one month from germination.

Parameters Measured

1. Every 10 days, the seedling height, basal diameter, number of leaves on stem, number of leaves on branches, number of branches, and number of internodes were measured.
2. At final harvest the pots were opened (photo plate 1), the metre long column of soil was cut into 20 cm sections and the amount of seedling roots in each segment measured. The oven dry weight of shoot and root were obtained.



PHOTOPLATE 1 Root Development of *E. camaldulensis* Seedlings Under 3 Moisture Regimes in the Preliminary Experiment on Root Development.

- K1 - drying soil
- K3 - moist soil
- K5 - water saturated soil

8.3 Results of Preliminary Experiments

In treatment 1 the roots were poorly developed but the plants survived the partial drought treatment. A large quantity of roots developed at the upper part of the pot. The tap root grown unrestricted until it reached the bottom of the pot.

In treatment 2 the total oven dry weight of the plants was much greater than that of treatment 1 and close to treatment 3. The roots developed evenly in the soil column and a large quantity of them concentrated at the bottom of the pot, indicating that there was no restriction on root development.

The third treatment was quite interesting. The bulk of the roots concentrated above the 'water table' in the kerosine tin (Table 8.2). The waterlogged area of the soil column in the container was poorly aerated and retarded the full development of the root system. The tap root was weakly formed but nevertheless passed through the damp soil. This is characteristic of root development of savannah woodland trees. According to Jacobs (1955) the various layers of roots appear to make use of different levels of soil water as the 'water table' changes. The deep-going roots support the existence of the plants in dry seasons while the shallow root system takes advantage of light rains which moisten the surface layers. It has also been noted by Jacobs (1955) that the two types of roots are very noticeable in trees of the drier areas including E. camaldulensis.

There was not much difference in the total dry weight between treatments 2 and 3, but the oven dry weight of treatment 3

was greater than the other two treatments. The greatest root:shoot ratio was recorded for treatment 1 (Table 8.1), - indicating an ability of E. camaldulensis to produce roots very rapidly to penetrate a poorly structured soil under sub-optimal moisture conditions, and this could be a significant factor in the successful establishment of E. camaldulensis.

From the preliminary investigations it became clear that E. camaldulensis has the ability to develop an extensive root system under sub-optimal moisture conditions. To study the degree of variation in this property among the provenances a major experiment on root development under sub-drought conditions was set up.

TABLE 8.1 The Oven Dry Weight (gm) of Root and Shoot of E. camaldulensis and the Root/Shoot Ratio for the Preliminary Studies

	Root Weight	Shoot Weight	Total Plant Weight	Root/Shoot Ratio
Treatment 1	2.01	1.66	3.67	1.21
Treatment 2	3.90	7.32	11.23	0.53
Treatment 3	4.90	7.12	11.93	0.63

TABLE 8.2 Oven Dry Weight (gm) of Roots of *E. camaldulensis* in Equal Sections of Soil in the Pot Starting from the Root Collar to the Bottom of the Pot for the Preliminary Studies

	0-20 cm.	21-40 cm.	41-60 cm.	61-80 cm.	81-100 cm.
Treatment 1	0.78	0.34	0.37	0.27	0.25
Treatment 2	1.96	0.49	0.39	0.38	0.67
Treatment 3	2.35	1.01	0.63	0.54	0.21

8.4 Experiment I

Materials and Methods

Seedlots were obtained from six provenances of E. camaldulensis, one provenance each of E. saligna and E. pilularis (Table 4.1). After treatment with the fungicide (Zineb 65), seeds were sown in pots containing a mixture of equal parts of perlite and vermiculite. A thin layer of perlite was used to cover the seeds. The pots were then stood in a pool of water to prevent excessive drying of the seeds. Watering was done twice daily. When all the seeds germinated, a nutrient solution of "Aquasol" was added once a week until the seedlings developed the third leaf pair. Most of the seedlings developed the third leaf pair about a month after germination. At this stage, the seedlings were transplanted into the prepared pots.

Preparation of the Pots

Pots 12 cm in diameter and 1 metre long were prepared as before. The soil mixture consisted of three parts of black top soil and one part of river sand thoroughly mixed in a cement mixer. Each standard pot was set in another 16 cm diameter pot containing a quantity of river gravel to facilitate drainage. The soil mix described differs from that of the preliminary experiment. In that experiment the soil appeared to be too friable when the pots were opened, and too reachly penetrated by roots.

Experimental Design

The six provenances of E. camaldulensis investigated were from Katherine, Agnew, Gwydir River, Lake Albacutya, Nathalia, and Todd River. The single provenance of E. saligna was from Ulong while that of E. pilularis came from Coffs Harbour in northern New South Wales (Table 4.1). From each provenance sufficient good seedlings were transplanted to obtain eight replications of each, with a seedling per pot. The pots were arranged as a randomised block experiment of eight provenances (treatments) with eight replications (photo plate 2). 8 spare pots of Katherine provenance were set aside to check progress of roots weekly. After transplanting, the seedlings were watered twice daily for 3 weeks until all the seedlings appeared vigorous and healthy. The seedlings were then left in the open glasshouse without watering.

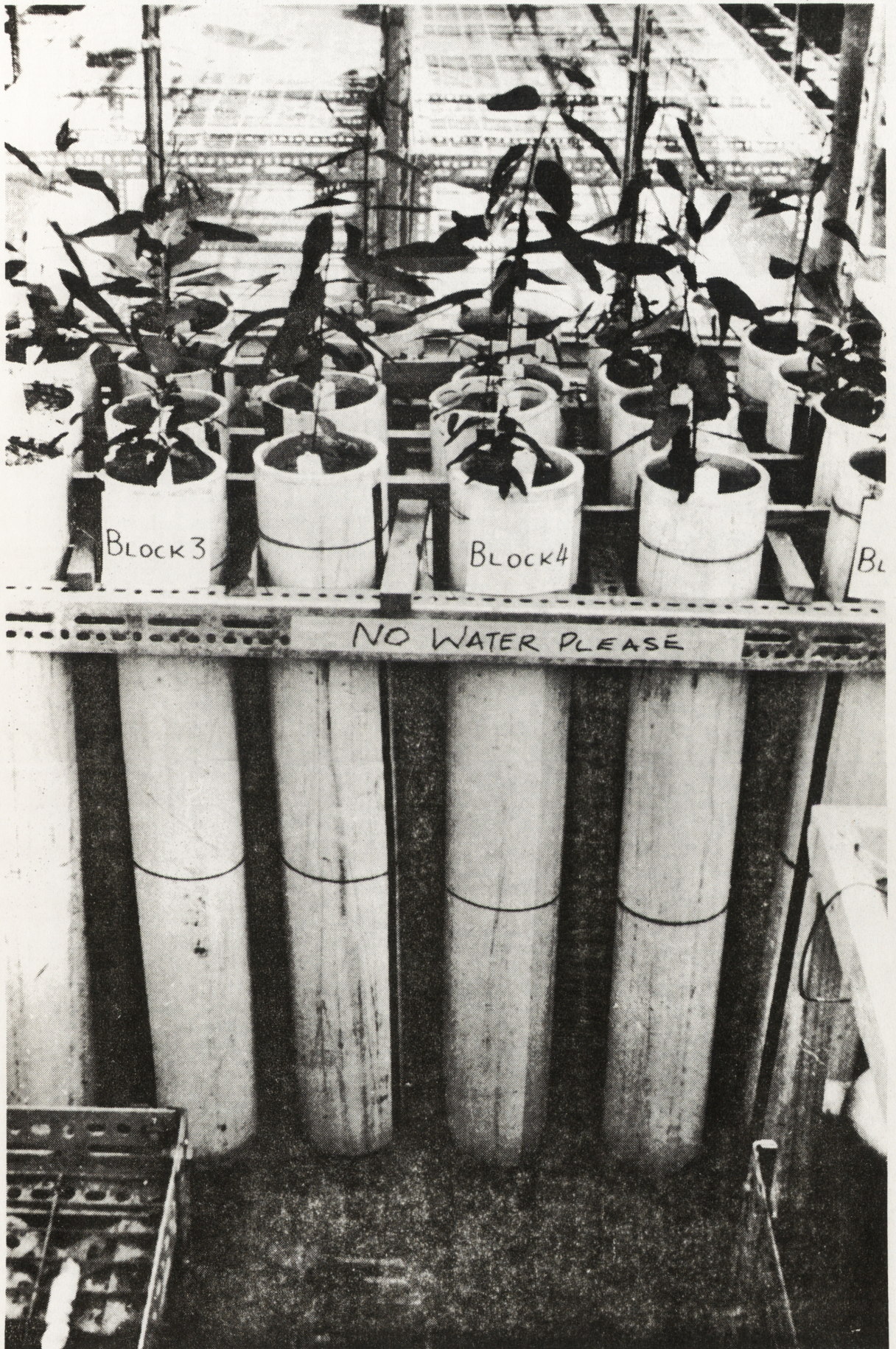
Parameters Measured

The following parameters were taken every 10 days:

- (a) seedling height
- (b) seedling basal diameter
- (c) number of leaves on stem
- (d) number of leaves on branches
- (e) number of branches
- (f) number of internodes

Final Harvesting

The leaves and stems were harvested and oven dried. The pots were opened and each soil column was cut into 5 equal parts



PHOTOPLATE 2 Randomised Blocks of the Specially Prepared Pots Used in Studies of Root Development.

of 20 cm long. The roots carefully washed and oven dried. Oven dry weights of the leaves, stems and roots were recorded.

8.5 Results of Experiment I

Visual observation indicated that all provenances of E. camaldulensis utilised the available water in the soil by developing an extensive root system and in most instances reached the bottom of the pots. In contrast E. pilularis was slow in extending a root system into the moist soil. E. saligna developed a poor root system but the roots reached the bottom of the pots.

The bulk of the root development for all the species was concentrated in the top 40 cm section of the pots (Table'8.3). In the case of E. camaldulensis, the tap root quickly penetrated the moist soil and formed a massive root carpet at the bottom of the pots. The roots of Lake Albacutya, Gwydir River and Todd River provenances were strongly developed at the bottom of the pots. The range in root weights in top 20 cm - were, with exception of Agnew provenance, 0.345 to 0.516 gm; the weights decreased down the pots and between 61 and 80 cm range was 0.076 - 0.250 gm. The build up at bottom of pots is shown by weights up to 0.468 grams at the 81 - 100 cm level. Alternatively, Agnew seedlings had 0.180 gm roots at 0 - 20 cm, 0.059 gm at 61 - 80 cm and 0.063 gm at 81 - 100 cm level. The roots of E. saligna and E. pilularis barely reached the bottom of the pots, and did not form a mat at the bottom of the pots. The two coastal eucalypts differed considerably in their root development - E. saligna had better and more extensive root systems than E. pilularis in the moist soil.

It is difficult to give any meaningful interpretation to the pattern of root development due to the fact that the conditions under which the seedlings were grown were too favourable for growing E. camaldulensis. It therefore became necessary to look more closely at the seedling growth characteristics to see whether there are any growth characteristics which can be interpreted in terms of environmental selection for adaptation to drought conditions.

Seedling Growth Characteristics

The growth characteristics of the seedlings were measured as seedling height, basal diameter, number of leaves on stem, number of leaves on branches, number of branches and number of internodes on the stem. Means for each of the growth parameters are given in Table 8.4. In this Table, each value represents the means of 8 seedlings for each provenance of E. camaldulensis as well as for the two coastal eucalypts (E. saligna and E. pilularis). These data were analysed and the least significant difference (LSD) values at 5% level of probability are given to compare means of provenances at any measurement period.

For each of the growth attributes there was a more or less progressive increase in growth with time. In height growth, basal diameter, leaves on stems, and number of internodes, there was no distinct difference between the provenances of E. camaldulensis, but E. camaldulensis seedlings had generally greater growth rate than seedlings of both E. saligna and E. pilularis. In most instances the growth rate of E. saligna was nearly double that of

E. pilularis. In all the growth parameters, the Agnew provenance was consistently below the other provenances of E. camaldulensis, but greater than that of E. pilularis.

Some of the more extreme differences between provenances were recorded in respect to the number of leaves on branches and number of branches.

Number of Leaves on Branches

There were marked differences between provenances of E. camaldulensis in the number of leaves on branches. At day 80 after seed germination, the southern provenances - Nathalia, Gwydir River and Lake Albacutya - had much greater number of leaves on branches than the northern provenances of Katherine, Todd River and Agnew (Table 8.4d). The number of leaves on branches produced by the southern provenances ranged between 8 and 15 with Nathalia producing the greatest, and Lake Albacutya, the least. From the northern provenances, Agnew produced the greatest number of leaves on branches (4.5) and Todd River had the least number (0.7). As suggested in previous chapters this may suggest a selection for reduced leaf surface under drier environmental conditions.

In contrast, E. saligna produced more leaves on branches than both E. camaldulensis and E. pilularis, but leaf size of E. saligna was very much less than that of either E. camaldulensis or E. pilularis. The total leaf area and leaf weight of E. camaldulensis was generally greater than that of E. saligna (Table 8.7).

Number of Branches

There were significant differences between provenances of E. camaldulensis in the number of branches produced in this experiment. The southern provenances produced more than twice the number of branches produced by the northern provenances. For example, at day 80 after seed germination, Gwydir River, Lake Albacutya, and Nathalia had produced 3.25, 2.25 and 4.25 branches per seedling, while Katherine, Agnew and Todd River had 0.62, 1.20 and 0.37. This again may reflect selection against excessive branching in hotter and drier environment where availability of moisture is important for successful establishment of E. camaldulensis seedlings.

In contrast again, E. saligna had the greatest number of branches (9.12) while E. pilularis produced only 2.50. However, the stem dry weight of the two coastal eucalypts was much lower than that of E. camaldulensis - suggesting that E. saligna may be more bushy than the other eucalypts, that is only fine branches were produced.

TABLE 8.3 Oven Dry Weight (gm) of Roots of *E. camaldulensis* and Two Coastal Eucalypts in Equal Sections of Soil from the Top to the Bottom of the Pot.

<u><i>E. camaldulensis</i></u>	Root Weight (gm) in Equal Soil Column				
	0-20	21-40	41-60	61-80	81-100 (cm)
1 Katherine	0.516	0.268	0.230	0.250	0.275
2 Lake Albacutya	0.430	0.200	0.210	0.183	0.468
3 Gwydir River	0.368	0.151	0.121	0.158	0.408
4 Todd River	0.345	0.165	0.141	0.141	0.215
5 Nathalia	0.389	0.126	0.087	0.076	0.120
6 Agnew	0.180	0.100	0.066	0.059	0.063
7 <u><i>E. saligna</i></u>	0.253	0.164	0.091	0.047	0.044
8 <u><i>E. pilularis</i></u>	0.139	0.100	0.040	0.016	0.015
L.S.D. (p = 0.05)	0.116	0.075	0.061	0.077	0.177

TABLE 8.4 Variation in Growth Characteristics (Height, Basal Diameter, Leaves on Stem, Leaves on Branches, Number of Branches and Internodes) of the Seedlings of *E. camaldulensis* from 6 Provenances, and *E. saligna* and *E. pilularis*.

(a)

Height (cm)	Days from the Start of Treatment		
	60	70	80
<u><i>E. camaldulensis</i></u>			
1 Katherine	8.98	15.76	23.81
2 Agnew	4.67	6.96	9.68
3 Gwydir River	7.23	12.43	20.75
4 Lake Albacutya	8.56	16.12	26.81
5 Nathalia	7.63	13.21	20.50
6 Todd River	9.01	12.93	17.50
7 <u><i>E. saligna</i></u>	5.63	7.77	10.08
8 <u><i>E. pilularis</i></u>	2.96	4.33	6.06
L.S.D. ($p = 0.05$)	1.51	3.11	4.95

TABLE 8.4 (Cont'd)

(b)

Seedling Basal Diameter (mm)	Days from Sowing		
	60	70	80
<u>E. camaldulensis</u>			
1 Katherine	0.147	0.210	0.272
2 Agnew	0.126	0.154	0.194
3 Gwydir River	0.146	0.219	0.310
4 Lake Albacutya	0.169	0.220	0.315
5 Nathalia	0.144	0.193	0.256
6 Todd River	0.146	0.196	0.250
7 <u>E. saligna</u>	0.120	0.169	0.214
8 <u>E. pilularis</u>	0.150	0.157	0.161
L.S.D. ($p = 0.05$)	0.019	0.034	0.048

(c)

Number of Leaves on Stem	Days from Sowing		
	60	70	80
<u>E. camaldulensis</u>			
1 Katherine	10.875	14.375	17.750
2 Agnew	8.250	10.125	12.500
3 Gwydir River	11.250	14.000	17.000
4 Lake Albacutya	11.000	13.500	17.500
5 Nathalia	10.750	13.000	16.250
6 Todd River	9.750	12.500	15.500
7 <u>E. saligna</u>	11.250	13.000	14.500
8 <u>E. pilularis</u>	5.500	7.000	8.000
L.S.D. ($p = 0.05$)	1.090	1.610	2.170

TABLE 8.4 (Cont'd)

(d)

Number of Leaves on Branches	Days from Sowing		
	60	70	80
<u>E. camaldulensis</u>			
1 Katherine	0.500	0.750	1.750
2 Agnew	1.500	3.250	4.500
3 Gwydir River	3.500	9.250	12.000
4 Lake Albacutya	2.750	6.000	8.750
5 Nathalia	4.250	9.000	15.250
6 Todd River	0.250	0.250	0.750
7 <u>E. saligna</u>	13.000	24.250	43.250
8 <u>E. pilularis</u>	1.875	3.000	5.500
L.S.D. (p = 0.05)	3.982	6.251	8.972

(e)

Number of Branches	Days from Sowing		
	60	70	80
<u>E. camaldulensis</u>			
1 Katherine	0.250	0.375	0.625
2 Agnew	0.625	1.125	1.200
3 Gwydir River	1.500	3.125	3.250
4 Lake Albacutya	0.875	1.875	2.250
5 Nathalia	1.500	3.000	4.250
6 Todd River	0.125	0.125	0.375
7 <u>E. saligna</u>	4.625	7.250	9.125
8 <u>E. pilularis</u>	1.125	1.500	2.500
L.S.D. (p = 0.05)	1.351	1.852	2.093

TABLE 8.4 (Cont'd)

(f)

Number of Internodes on Stem	Days from Sowing		
	60	70	80
<u>E. camaldulensis</u>			
1 Katherine	6.875	10.875	14.000
2 Agnew	4.375	6.250	7.875
3 Gwydir River	6.625	11.625	15.000
4 Lake Albacutya	6.125	9.750	14.375
5 Nathalia	6.500	9.250	13.125
6 Todd River	5.750	8.500	11.750
7 <u>E. saligna</u>	6.250	8.125	10.500
8 <u>E. pilularis</u>	2.625	3.750	4.625
L.S.D. (p = 0.05)	0.785	1.535	1.916

Analysis of Seedling Growth Characteristics

A summary of the significance of differences between individual means drawn from Table 8.4 at day 80 is given in Table 8.5. This shows significance of differences between provenance means for 6 growth characteristics.

Some of the differences between provenance means were significant at the 5% level of probability. Except in seedling height growth, E. saligna is consistently different from E. pilularis. The two coastal eucalypts were significantly different from E. camaldulensis in all attributes other than number of leaves on branches and number of branches. In these respects E. pilularis did not differ significantly from most of the provenances of E. camaldulensis.

In all the attributes except "number of leaves on branches" and "number of branches", there was no consistent difference between the provenances of E. camaldulensis. The northern provenances - Katherine, Todd River and Agnew are very similar in number of leaves on branches and number of branches, that is, they did not differ significantly in these attributes; and the southern provenances differed consistently in these respects from the northern provenances. The analysis also shows the southern provenances - Gwydir River, Nathalia and Lake Albacutya - did not differ significantly in number of leaves on branches and the number of branches.

For each of the six growth characteristics, a univariate analysis of variance was carried out for data at day 80. A summary of the significance of differences between provenances is presented in Table 8.6. Where data for all the eucalypts are taken into

account, provenance differences were significant ($p = 0.05$) for all the six growth parameters – suggesting great differences between E. camaldulensis and the other coastal eucalypts.

TABLE 8.5 Summary of Significant Results of Analysis of the Growth Characteristics at Day 80

	Seedling Height								Seedling Basal Diameter						
	8	7	6	5	4	3	2		1	8	7	6	5	4	3
1	*	*	*	NS	NS	NS	*	1	*	*	NS	NS	NS	*	*
2	NS	NS	*	*	*	*		2	NS	NS	*	*	*	*	
3	*	*	NS	NS	*			3	*	*	*	*	NS		
4	*	*	*	*				4	*	*	*	*			
5	*	*	NS					5	*	*	NS				
6	*	*						6	*	*					
7	NS							7	*						
8								8							

1 Katherine

4 Lake Albacutya

7 E. saligna

2 Agnew

5 Nathalia

8 E. pilularis

3 Gwydir River

6 Todd River

TABLE 8.5 (Cont'd)

	Number of Leaves on Stem							
	8	7	6	5	4	3	2	1
1	*	*	*	NS	NS	NS	*	
2	*	NS	*	*	*	*		
3	*	*	NS	NS	NS			
4	*	*	NS	NS				
5	*	NS	NS					
6	*	NS						
7	*							
8								

	Number of Leaves on Branches							
	8	7	6	5	4	3	2	1
1	NS	*	NS	*	NS	*	NS	
2	NS	*	NS	*	NS	*		
3	NS	*	*	NS	NS			
4	NS	*	*	NS				
5	*	*	*					
6	NS	*						
7	*							
8								

	Number of Branches							
	8	7	6	5	4	3	2	1
1	*	*	NS	*	NS	*	NS	
2	NS	*	NS	*	NS	*		
3	NS	*	*	NS	NS			
4	NS	*	*	*				
5	*	*	*					
6	*	*						
7	*							
8								

	Number of Internodes							
	8	7	6	5	4	3	2	1
1	*	*	*	NS	NS	NS	*	
2	*	*	*	*	*	*		
3	*	*	*	*	NS			
4	*	*	*	NS				
5	*	*	*					
6	*	NS						
7	*							
8								

1 Katherine

4 Lake Albacutya

7 E. saligna

2 Agnew

5 Nathalia

8 E. pilularis

3 Gwydir River

6 Todd River

TABLE 8.6 Univariate Analysis of Variance for Seedling Growth
Characteristics at Day 80 After Seed Germination

Source	D.E.	Mean Square	Variance Ratio	Sig. 5%
Seedling Height (cm)				
Treatment	7	445.7880	18.24	*
Error	56	24.434		
Basal Diameter				
Treatment	7	0.0235	10.41	*
Error	56	0.0022		
Leaves on Stem				
Treatment	7	85.7142	18.25	*
Error	56	4.6964		
Leaves on Branches				
Treatment	7	1514.9196	18.88	*
Error	56	80.2410		
Number of Branches				
Treatment	7	64.4196	14.75	*
Error	56	4.3660		
Number of Internodes				
Treatment	7	103.7767	28.35	*
Error	56	3.6607		

Analysis of Data for Dry Weight Production and Total Leaf Area

At final harvest, components of dry weight production were measured as follows: leaf dry weight, stem dry weight, shoot dry weight, root dry weight, and total dry weight. The root:shoot ratio was calculated. The total leaf area was also measured at harvest - using an automatic area meter.

Means for each of the seven parameters are given in Table 8.7. These data were analysed and the L.S.D. values at 5% level of probability are presented with the seedling means. A summary of the significance of differences between provenance means is given in Table 8.8.

With some limited exceptions, E. camaldulensis produced more dry weight and total leaf area than the two coastal eucalypts - E. saligna and E. pilularis. This contrasts with the situation in the seedling growth characteristics where in at least two instances E. saligna produced more leaves on the branches and a greater number of branches. In both dry weight production and leaf area there were significant differences between E. saligna and E. pilularis. E. saligna produced nearly twice as much dry weight and leaf area as E. pilularis. The only exception to this occurred in root: shoot ratio where the two coastal eucalypts did not differ significantly.

In dry weight production, there was a general tendency for two of the southern provenances - Gwydir River and Lake Albacutya - to produce more than the northern provenances of Agnew and Todd River. However, Nathalia and Katherine did not conform with the general trend of dry weight production. While the northern

Katherine provenance had one of the greatest total dry weight productions (3.72 gm) the southern Nathalia provenance had one of the lower total dry weight productions (2.01 gm). Katherine would not differ significantly from Gwydir River or Lake Albacutya - in fact all 3 are very close. The leaf area for Katherine is slightly greater than that for most of the northern provenances. As a whole, the southern provenances - Lake Albacutya and Gwydir River produced more leaf area than the northern provenances - Agnew and Todd River. Among the six provenances of E. camaldulensis, Agnew produced the least dry matter and leaf area. However, the Agnew root:shoot ratio was similar to that of Gwydir River and Todd River (0.48).

The most northern provenance (Katherine) and some of the southern provenances - Lake Albacutya and Nathalia - had very high root:shoot ratio ranging between 0.66 to 0.71. The inconsistency in the pattern of root:shoot ratio makes it difficult to give any meaningful interpretation to the pattern of root development. In support of this is the fact that the soil medium used in the root study was probably too rich for growing E. camaldulensis. Because of the rapid root production in all provenances and inconsistency in patterns, the second experiment was carried out, and in this experiment an attempt was made to simulate more closely field conditions.

A summary of univariate analysis of variance is presented in Table 8.9. For all the attributes except in root:shoot ratio, provenance differences were significant ($p = 0.05$) - indicating a marked variation between E. camaldulensis and the two coastal eucalypts.

TABLE 8.7 Variation in Dry Weight Production, Root:Shoot Ratio and Total Leaf Area of *E. camaldulensis* and Two Coastal Eucalypts - *E. saligna* and *E. pilularis* at Day 80 After Seed Germination

	Leaf Weight (gm)	Stem Weight (gm)	Shoot Weight (gm)	Root Weight (gm)	Total Dry Weight (gm)	Root/Shoot Ratio	Total Leaf Area (sq.cm)
<u><i>E. camaldulensis</i></u>							
1 Katherine	1.743	0.435	2.177	1.539	3.716	0.707	237.55
2 Agnew	0.826	0.157	0.977	0.465	1.442	0.476	95.51
3 Gwydir River	2.019	0.458	2.476	1.202	3.678	0.486	218.57
4 Lake Albacutya	1.622	0.584	2.206	1.490	3.696	0.675	224.57
5 Nathalia	0.856	0.352	1.209	0.799	2.008	0.661	122.30
6 Todd River	1.710	0.372	2.083	1.008	2.091	0.484	189.23
7 <u><i>E. saligna</i></u>	1.015	0.279	1.294	0.599	1.893	0.463	185.20
8 <u><i>E. pilularis</i></u>	0.550	0.105	0.655	0.310	0.965	0.433	83.63
L.S.D. (p = 0.05)	0.503	0.154	0.639	0.374	0.995	0.260	23.05

TABLE 8.8 Summary of Significant Results of Analysis of the Dry Weight Production and Total Leaf Area at Day 80.

	Leaf Weight							
	8	7	6	5	4	3	2	1
1	*	*	NS	NS	NS	*	NS	
2	NS	NS	*	NS	*	*		
3	*	*	NS	*	NS			
4	*	*	NS	*				
5	NS	NS	*					
6	*	*						
7	*							
8								

	Stem Weight							
	8	7	6	5	4	3	2	1
1	*	*	NS	NS	*	NS	*	
2	NS	NS	*	*	*	*		
3	*	*	NS	NS	NS			
4	*	*	*	*				
5	*	NS	NS					
6	*	NS						
7	*							
8								

	Shoot Weight							
	8	7	6	5	4	3	2	1
1	*	*	NS	*	NS	NS	*	
2	NS	NS	*	*	*	*		
3	*	*	NS	*	NS			
4	*	*	NS	*				
5	*	NS	*					
6	*	*						
7	*							
8								

	Root Weight							
	8	7	6	5	4	3	2	1
1	*	*	*	*	NS	*	*	
2	NS	NS	*	*	*	NS		
3	*	*	NS	*	NS			
4	*	*	*	*				
5	*	NS	*					
6	*	*						
7	NS							
8								

1 Katherine

2 Agnew

3 Gwydir River

4 Lake Albacutya

5 Nathalia

6 Todd River

7 E. saligna8 E. pilularis

TABLE 8.8 (Cont'd)

		Total Dry Weight							
		8	7	6	5	4	3	2	1
1	*	*	*	*	*	NS	NS	*	
2	NS	NS	NS	NS	*	*			
3	*	*	*	*	NS				
4	*	*	*	*					
5	*	NS	NS						
6	*	NS							
7	*								
8									

		Root:Shoot Ratio							
		8	7	6	5	4	3	2	1
1	*	*	*	*	*	*	*	*	*
2	NS	NS	NS	*	*	NS			
3	NS	NS	NS	*	*				
4	*	*	*	NS					
5	*	*	*						
6	NS	NS							
7	NS								
8									

		Total Leaf Area							
		8	7	6	5	4	3	2	1
1	*	*	*	*	*	NS	NS	*	
2	NS	*	*	*	*	*	*		
3	*	*	*	*	NS				
4	*	*	*	*					
5	*	*	*						
6	*	NS							
7	*								
8									

1 Katherine

2 Agnew

3 Gwydir River

4 Lake Albacutya

5 Nathalia

6 Todd River

7 E. saligna

8 E. pilularis

TABLE 8.9 Univariate Analysis of Variance for Seedling Dry Weight Production and Root:Shoot Ratio at Day 80 After Seed Germination.

Source	D.F.	Mean Square	Variance Ratio	Sig. 5%
Leaf Weight (gm)				
Treatment	7	2.3419	9.27	*
Error	56	0.2525		
Stem Weight (gm)				
Treatment	7	0.2034	8.63	*
Error	56	0.0235		
Shoot Weight (gm)				
Treatment	7	3.6793	9.05	*
Error	56	0.4065		
Root Weight (gm)				
Treatment	7	1.7541	12.59	*
Error	56	0.1393		
Root/Shoot Ratio				
Treatment	7	0.1868	2.78	*
Error	56	0.0671		

8.6 Experiment II

Purpose of the Experiment

In Experiment I the standard pots were planted with 1-month old seedlings which had been raised in pots containing a mixture of perlite and vermiculite, and were watered for 3 weeks after transplanting. Water was withheld and the pots were opened after a further 3 weeks. All species had reached the bottom of the pots, some provenances more vigorously than others, Blackbutt and Flooded gum weakly.

The second experiment aimed to simulate field conditions more closely where seed germinate on the moist soil surface as flood waters recede.

Materials and Methods

The pots were filled with the same soil mixture as used in Experiment I and watered well until the soil was at field capacity.

Seeds were sown directly on the moist soil surface. No further watering was carried out after sowing. It took 5 to 8 days for the seeds to germinate. Seedlings were then reduced to 3 per pot. When the roots in the Katherine provenance used as control plants had reached the bottom of pots, all the pots were opened.

The experimental design was the same as for Experiment I and occupied the same space in the open glasshouse.

Experimental Measurements

At day 75, the following measurements were made on the dominant seedling in each pot: seedling height, basal diameter,

number of leaves on stem, number of leaves on branches, number of branches and the number of internodes. At the final harvest, the roots were carefully extracted as a single piece - representing the total root growth for 3 seedlings in each pot. The total root length in each pot was measured and oven dry weights of the root and shoot were determined.

8.7 Results and Analysis of Data for Experiment II

A. Seedling Growth Characteristics

The means of the measurements made at day 75 after seed germination are presented in Table 8.10. In this Table, each value represents the means of seedlings growing in 8 pots for each provenance including E. saligna and E. pilularis.

It is quite evident that the plants in Experiment II were subject to a much greater environmental stress than in Experiment I in terms of moisture availability. Before the pots were opened nearly a third of E. pilularis seedlings had died. At this stage the surface soil was much harder and drier than the surface soil at the similar stage of the first experiment. The results corresponded to the observation made at day 80 for the first experiment.

In all growth characteristics the southern provenances of Nathalia and Lake Albacutya had greater values than the northern provenances (Agnew, Todd River and Katherine). For example, Nathalia and Lake Albacutya seedlings grew nearly twice as much on height (24.2 and 26.1 cm respectively) as the northern provenance seedlings (range 10.37 to 14.12 cm); they also had markedly greater

basal diameters, more leaves on stems than northern provenance seedlings. Alternatively the Gwydir River provenance in this experiment was more similar to the 3 northern provenances - in all attributes. The two coastal eucalypts E. saligna and E. pilularis - had much reduced growth rate under the dry experimental condition than E. camaldulensis. Similar to the results obtained in Experiment I, E. saligna grew better than E. pilularis.

Under more extreme environmental conditions than the plants have been previously subjected to, only the most southern provenance (Lake Albacutya) seedlings of E. camaldulensis produced any branches and leaves on the branches at all. Once again, this may point to a broadly based tendency within the species to reduce leaf surface area under harsher environmental conditions. E. saligna also had some branches and a few leaves on the branches. Although the amount of branches with leaves produced by E. saligna was greater than that of E. camaldulensis, the shoot weight of E. camaldulensis was far greater than that of E. saligna.

Analysis of Seedling Growth Data

The data for the seedling growth characteristics were analysed as a randomised block and the LSD values at 5% level of probability are given in the same table of means. A summary of the significance of differences between provenance means is given in Table 8.11 for the seedling height, basal diameter, number of leaves on stem and number of leaves on branches.

For all growth attributes, the 2 coastal eucalypts - E. saligna and E. pilularis - were consistently different from E. camaldulensis. There were also consistent differences between E. saligna and E. pilularis - the latter species doing very poorly under the particular conditions of this experiment.

There were no significant differences between Nathalia and Lake Albacutya provenances. These two provenances are from the southern ecotype of E. camaldulensis. There were no significant differences between any of the other four provenances - Katherine, Agnew, Gwydir River and Todd River. All four provenances may represent a drier environment than the other two provenances. The 3 northern provenances are certainly from environments with marked differences in climate from that of southern provenances. Lake Albacutya and Nathalia seedlings were consistently different in all attributes from the seedlings of the other 4 provenances.

A summary of significance of variance for seedling growth characteristics is presented in Table 8.12. This also indicates that for each parameter the seed lots differed significantly at 5% level of probability when all the eucalypts were taken into account. It confirms that E. camaldulensis is completely different from the two coastal eucalypts in physiological characteristics.

B. Dry Weight Production and Total Root Length

The following parameters of dry weight and root length were recorded at harvest: shoot dry weight, root dry weight, total dry weight, and total root length. The root:shoot ratio was

calculated. The differences between provenances in response to dry environmental conditions are illustrated in form of histograms in Figures 8.1 to 8.5, as follows:

- Figures 8.1 shoot dry weight
- 8.2 root dry weight
- 8.3 total dry weight
- 8.4 total root length
- 8.5 root:shoot ratio

For all parameters, E. saligna and E. pilularis seedlings produced less dry weight and total root length than E. camaldulensis seedlings. The southern provenances - Lake Albacutya and Nathalia - had much greater root weight, and total dry weight production than the northern provenances of Katherine, Agnew and Todd River. The seedlings of Gwydir River provenance produced the least root weight and total dry weight. In shoot weight production, Todd River provenance had a slightly greater figure of 0.86 gm than the other northern provenances of Katherine (0.65 gm) and Agnew (0.68 gm). Lake Albacutya provenance produced the greatest amount of shoot weight (0.97 gm) while Gwydir River provenance had the least (0.64 gm).

In root:shoot ratio, the figure for E. saligna compared very well with some of the provenances of E. camaldulensis. For example, Agnew, Gwydir River and Todd River provenances had root:shoot ratios of 0.41, 0.44 and 0.35 respectively, while the figure of root:shoot ratio for E. saligna was 0.39. Katherine, Lake Albacutya, and Nathalia provenances had a slightly higher root:shoot ratio of 0.55, 0.51 and 0.58 respectively. The total root length for

each of the 6 provenances of E. camaldulensis was nearly the same - ranging from 98 to 107 cm, but the two coastal eucalypts (E. saligna and E. pilularis) produced fairly short roots (41 and 17 cm respectively).

The data for dry weight production and total root length were analysed. The means and LSD values at 5% level of probability are given in Table 8.13. A summary of the significance of differences between provenance means is presented in Table 8.14.

In only the root:shoot ratio and total root length were there significant differences between E. saligna and E. pilularis. These coastal eucalypts consistently differed from E. camaldulensis in all attributes except in root:shoot ratio - where no difference was recorded between E. saligna and some of the provenances of E. camaldulensis. In total root length there was no significant difference between any provenance of E. camaldulensis - all had the capacity to rapidly explore a drying soil and in this respect differed markedly from the coastal eucalypts. In root weight, shoot weight, and total dry weight, there were consistent differences between the southernmost provenance (Lake Albacutya) and other provenances of E. camaldulensis.

The results of a univariate analysis of variance for the dry weight production and total root length were summarised in Table 8.15. For all the attributes, provenance differences were significant at 5% level of probability when all the eucalypts were taken into account. This also reflects marked differences between E. camaldulensis and the other coastal eucalypts.

TABLE 8.10 Variation in Seedling Growth Characteristics (Height, Basal Diameter, Leaves on Stem etc.) of E. camaldulensis and Two Coastal Eucalypts - E. saligna and E. pilularis at Day 75 After Seed Germination.

	Height (cm)	Basal Diameter (mm)	Leaves on Stem	Number of Internodes	Number of Leaves on Branches	Number of Branches
<u>E. camaldulensis</u>						
1 Katherine	14.125	0.122	12.00	7.500		
2 Agnew	10.375	0.126	11.25	6.750		
3 Gwydir River	12.500	0.131	12.50	7.125		
4 Lake Albacutya	26.125	0.182	14.50	11.000	0.50	0.25
5 Nathalia	24.250	0.189	14.50	11.250		
6 Todd River	14.125	0.123	11.00	6.500		
7 <u>E. saligna</u>	6.250	0.066	10.50	5.500	1.25	0.38
8 <u>E. pilularis</u>	3.375	0.031	4.50	2.375		
L.S.D. (p = 0.05)	4.261	0.031	2.097	2.011		

TABLE 8.11 Summary of Significant Results of Analysis of Growth Characteristics at Day 75 After Seed Germination.

	Seedling Height							
	8	7	6	5	4	3	2	1
1	*	*	NS	*	*	NS	NS	
2	*	NS	NS	*	*	NS		
3	*	*	NS	*	*			
4	*	*	*	NS				
5	*	*	*					
6	*	*						
7	NS							
8								

	Basal Diameter							
	8	7	6	5	4	3	2	1
1	*	*	NS	*	*	NS	NS	
2	*	*	NS	*	*	NS		
3	*	*	NS	*	*			
4	*	*	*	NS				
5	*	*	*					
6	*	*						
7	*							
8								

	Number of Leaves on Stem							
	8	7	6	5	4	3	2	1
1	*	NS	*	*	*	NS	NS	
2	*	NS	NS	*	*	NS		
3	*	*	NS	*	*			
4	*	*	*	NS				
5	*	*	*					
6	*	NS						
7	*							
8								

	Number of Internodes							
	8	7	6	5	4	3	2	1
1	*	*	NS	*	*	NS	NS	
2	*	NS	NS	*	*	NS		
3	*	*	NS	*	*			
4	*	*	*	NS				
5	*	*	*					
6	*	NS						
7	*							
8								

1 Katherine

4 Lake Albacutya

7 E. saligna

2 Agnew

5 Nathalia

8 E. pilularis

3 Gwydir River

6 Todd River

TABLE 8.12 Summary of Significance of Variance for Seedling
Growth Characteristics at Day 75 After Seed
Germination.

Source	D.F.	Mean Square	Variance Ratio	Sig. 5%
Height (cm)				
Treatment	7	503.26	27.81	*
Error	56	18.09		
Basal Diameter (mm)				
Treatment	7	0.02	23.06	*
Error	56	0.00		
Leaves on Stem				
Treatment	7	79.27	18.08	*
Error	56	4.38		
Number of Internodes				
Treatment	7	66.03	16.38	*
Error	56	4.03		

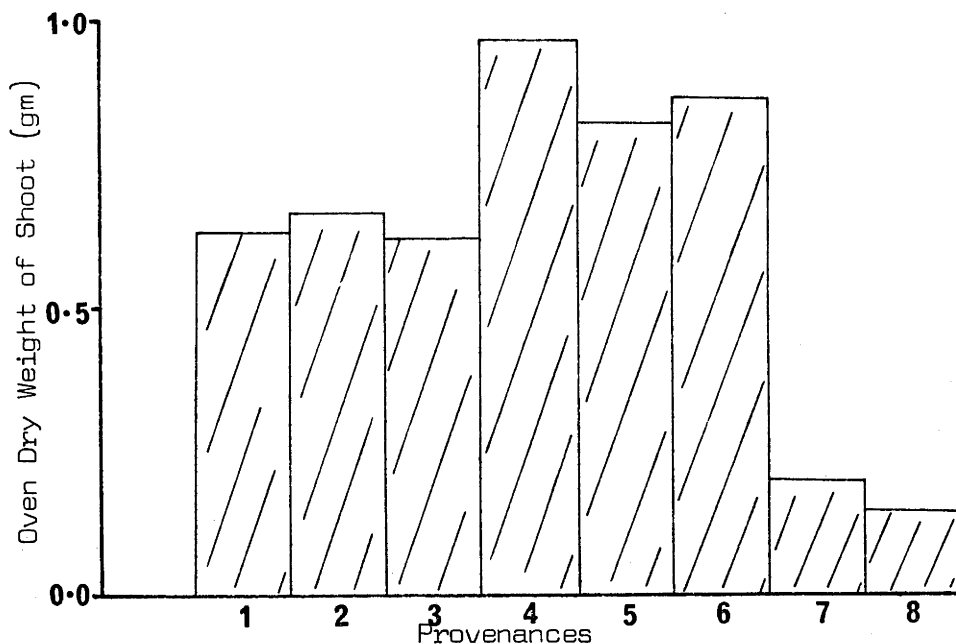


FIGURE 8.1 Variation Between Provenances in Over Dry Weight of Shoot in Response to Drying Soil. (1) Katherine; (2) Agnew; (3) Gwydir River; (4) Lake Albacutya; (5) Nathalia; (6) Todd River; (7) E. saligna; (8) E. pilularis.

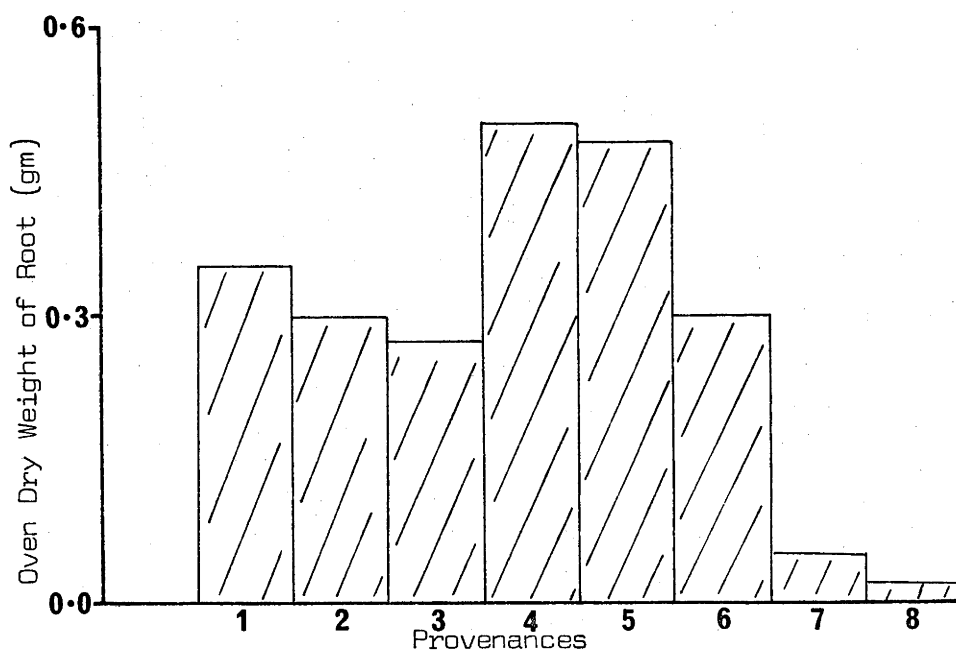


FIGURE 8.2 Variation Between Provenances in Over Dry Weight of Root in Response to Drying Soil. (1) Katherine; (2) Agnew; (3) Gwydir River; (4) Lake Albacutya; (5) Nathalia; (6) Todd River; (7) E. saligna; (8) E. pilularis.

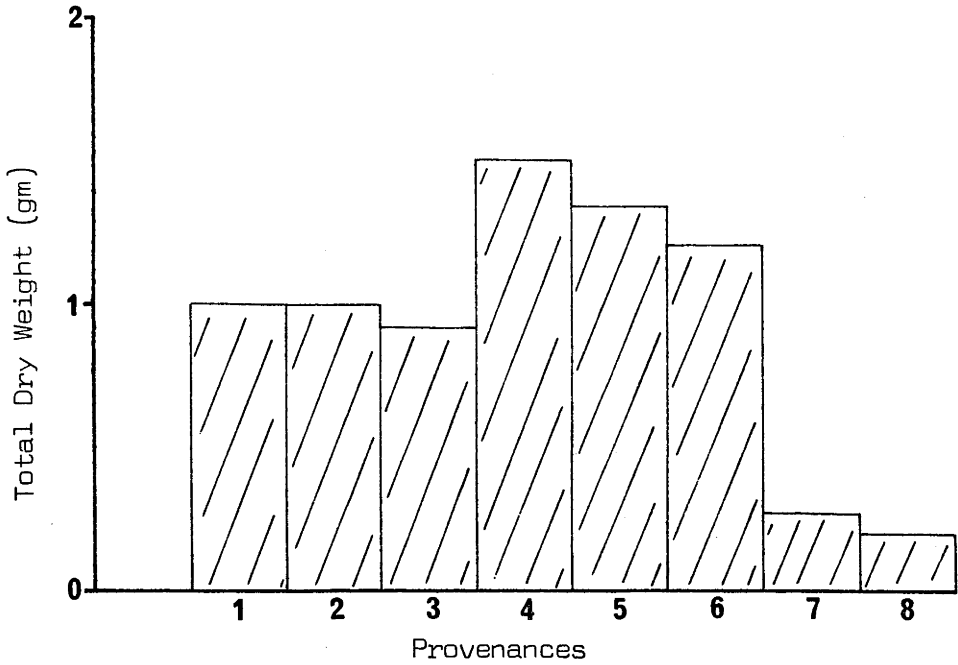


FIGURE 8.3 Provenance Variation in Total Dry Weight Production in Response to Drying Soil. (1) Katherine; (2) Agnew; (3) Gwydir River; (4) Lake Albacutya; (5) Nathalia; (6) Todd River; (7) E. saligna; (8) E. pilularis.

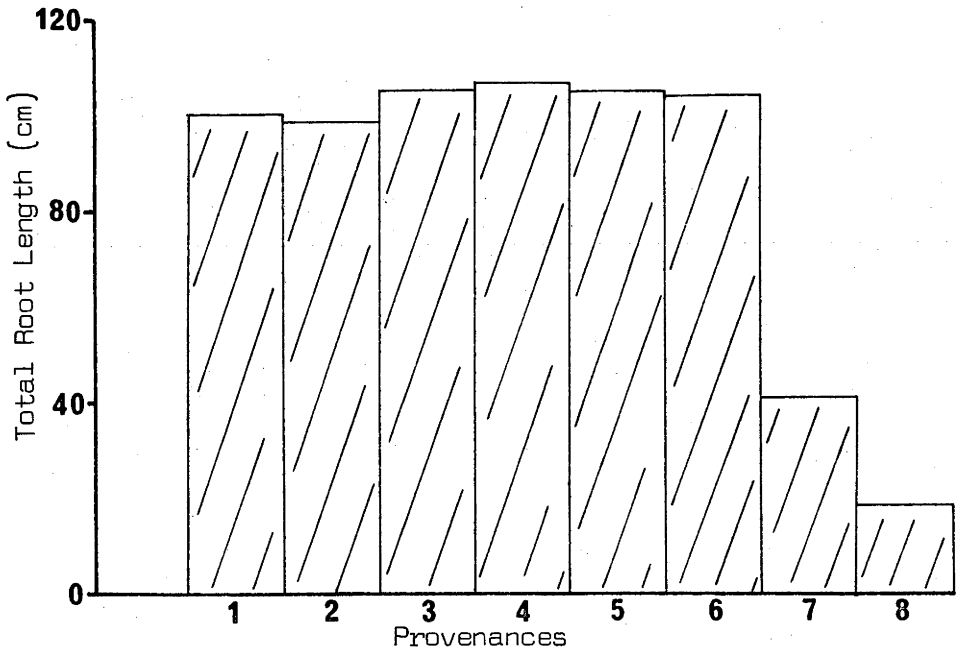


FIGURE 8.4 Provenance Variation in Total Root Length in Response to Drying Soil. (1) Katherine; (2) Agnew; (3) Gwydir River; (4) Lake Albacutya; (5) Nathalia; (6) Todd River; (7) E. saligna; (8) E. pilularis.

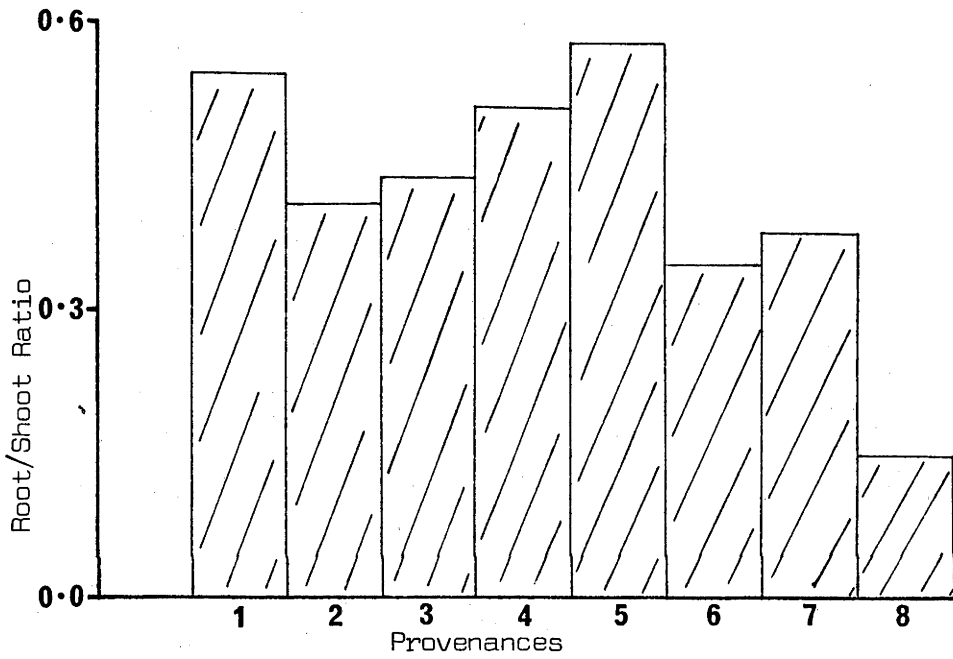


FIGURE 8.5 Provenance Variation in Root:Shoot Ratio in Response to Drying Soil. (1) Katherine; (2) Agnew; (3) Gwydir River; (4) Lake Albacutya; (5) Nathalia; (6) Todd River; (7) E. saligna; (8) E. pilularis.

TABLE 8.13 Variation in Dry Weight Production, Total Root Length, and Root:Shoot Ratio of *E. camaldulensis*, *E. saligna* and *E. pilularis* at Day 75 After Seed Germination.

	Total Root Length (cm)	Root Weight (gm)	Shoot Weight (gm)	Root/ Shoot Ratio	Total Dry Weight (gm)
<u><i>E. camaldulensis</i></u>					
1 Katherine	100.75	0.350	0.651	0.554	1.001
2 Agnew	98.87	0.304	0.684	0.413	0.987
3 Gwydir River	106.50	0.279	0.636	0.441	0.916
4 Lake Albacutya	107.62	0.507	0.974	0.512	1.481
5 Nathalia	106.25	0.483	0.819	0.586	1.301
6 Todd River	105.12	0.300	0.860	0.353	1.160
7 <u><i>E. saligna</i></u>	41.00	0.052	0.180	0.386	0.233
8 <u><i>E. pilularis</i></u>	16.87	0.020	0.140	0.153	0.160
L.S.D. (p = 0.05)	13.85	0.144	0.220	0.163	0.345

TABLE 8.14 Summary of Significant Results of Analysis of Dry Weight Production and Total Root Length at Day 75 After Seed Germination.

(a)		Root Weight							
		8	7	6	5	4	3	2	1
1	*	*	NS	NS	*	NS	NS		
2	*	*	NS	*	*	NS			
3	*	*	NS	*	*				
4	*	*	*	NS					
5	*	*	*						
6	*	*							
7	NS								
8									

(b)		Shoot Weight							
		8	7	6	5	4	3	2	1
1	*	*	NS	NS	*	NS	NS		
2	*	*	NS	NS	*	NS			
3	*	*	*	NS	*				
4	*	*	NS	NS					
5	*	*	NS						
6	*	*							
7	NS								
8									

(c)		Total Dry Weight							
		8	7	6	5	4	3	2	1
1	*	*	NS	NS	*	NS	NS		
2	*	*	NS	NS	*	NS			
3	*	*	NS	*	*				
4	*	*	NS	NS					
5	*	*	NS						
6	*	*							
7	NS								
8									

(d)		Root/Shoot Ratio							
		8	7	6	5	4	3	2	1
1	*	*	*	NS	NS	NS	NS		
2	*	NS	NS	*	NS	NS			
3	*	NS	NS	NS	NS				
4	*	NS	*	NS					
5	*	*	*						
6	*	NS							
7	*								
8									

1 Katherine

4 Lake Albacutya

7 E. saligna

2 Agnew

5 Nathalia

8 E. pilularis

3 Gwydir River

6 Todd River

TABLE 8.14 (Cont'd)

(e)

	Total Root Length							
	8	7	6	5	4	3	2	1
1	*	*	NS	NS	NS	NS	NS	
2	*	*	NS	NS	NS	NS		
3	*	*	NS	NS	NS			
4	*	*	NS	NS				
5	*	*	NS					
5	*	*						
7	*							
8								

1 Katherine

4 Lake Albacutya

7 E. saligna

2 Agnew

5 Nathalia

8 E. pilularis

3 Gwydir River

6 Todd River

TABLE 8.15 Summary of Significance of Variance of Total Root Length, Dry Weight Production and Root:Shoot Ratio at Day 75 After Seed Germination.

Source	D.F.	Mean Square	Variance Ratio	Sig. 5%
Total Root Length (cm)				
Treatment	7	10111.0714	52.80	*
Error	56	191.4910		
Root Weight (gm)				
Treatment	7	0.2486	12.08	*
Error	56	0.0205		
Shoot Weight (gm)				
Treatment	7	0.74459	15.44	*
Error	56	0.0482		
Root/Shoot Ratio				
Treatment	7	0.1504	5.72	*
Error	56	0.0263		
Total Dry Weight (gm)				
Treatment	7	1.8029	15.20	*
Error	56	0.1186		

8.8 Discussion

In this study there is a much evidence that all the six provenances of E. camaldulensis have a capacity to rapidly develop roots to explore any drying soil, thereby helping ensure survival in harsh environments. In total root length production there were no marked differences between any of the six provenances. In comparing E. camaldulensis with the 2 coastal eucalypts (E. saligna and E. pilularis), the results indicate that marked differences exist between the species. In most of the growth characteristics, dry weight production, total leaf area, and total root length, E. camaldulensis differed significantly from the two coastal eucalypts.

The results also show that marked differences exist between provenances of E. camaldulensis in some of the growth characteristics - notably in number of leaves on branches and number of branches. In the first experiment, where controlled environmental conditions were less extreme, the southern provenances - Nathalia, Gwydir River and Lake Albacutya - had greater numbers of leaves on branches than the northern provenances of Katherine, Todd River and Agnew.

The southern provenances also produced more than twice the number of branches produced by the northern provenances under these partially dry conditions. However, under the more extreme environmental condition of the second experiment only the most southern provenance (Lake Albacutya) seedlings produced any branches and leaves on the branches. The reaction of the Lake Albacutya seedlings tend to support the hypothesis that within the species

there has been selection for individuals growing under harsher environmental conditions, which have reduced leaf surface and other transpiring area. The results also show that the same seedlings which would produce branches and leaves on branches under good growing conditions, may not produce these when exposed to somewhat harsher environmental conditions.

CHAPTER 9GENERAL DISCUSSION AND CONCLUSIONS

A study has been made of ways in which provenance differences are expressed in seedling of E. camaldulensis grown under a range of controlled environmental conditions. Some marked differences between provenances of the species were found. The results of these investigations confirm the existence of two broader ecotypes of the species, that is, the northern and the southern ecotypes respectively. However, the differences between the northern and the southern ecotypes are not invariably well defined under all environmental conditions, and it is difficult to give meaningful interpretations to some of the results.

Marked differences in germination behaviour occurred at the low temperature regime (18/13°C.) where there was a distinct north-south division at day 6 of seed germination. At this temperature, the seed of Gwydir River provenance germinated rapidly, but little or no germination was recorded for the northern provenances of Katherine, Roy Hill and Petford. At higher temperatures, all the provenances germinated completely and rapidly; the optimum temperature for germination was between 30°C and 33°C. This optimum temperature is slightly lower than the 35°C. consistently found by Grose and Zimmer (1958) to produce optimum germination of E. camaldulensis. In a study of the light requirement for germination, the species was found to be positively photoblastic, that is, light

stimulated seed germination. The red light region of the visible light spectrum promoted seed germination of the only seedlot examined, that is, a southern ecotype of E. camaldulensis from Lake Albacutya. Alternatively, blue light and far red regions of the light spectrum had very little influence on seed germination. As a whole, there appeared to be no distinct difference between provenances in light requirements for seed germination under favourable temperature and moisture conditions.

The studies on seedling growth under a range of temperature regimes helped provide some understanding of the nature of environmental influences on the provenances of E. camaldulensis. The medium temperature (27/22°C.) was optimum for many seedling growth characteristics and dry weight production. There were marked differences between provenances in the way they responded to different temperature regimes. For some growth characteristics, there was a more or less consistent pattern of differences between provenances. For example, the growth of seedlings from the southern provenances of Lake Albacutya and Gwydir River was generally greater than that of seedlings from the northern provenances of Katherine and Agnew; the performance of Agnew provenance under the 3 temperature regimes was consistently poorer than that of Katherine, Gwydir River and Lake Albacutya provenances.

It is possible to offer only a tentative interpretation of these results for a number of reasons. A few provenances only were used, the phytotron environment is too artificial, it varies only one environmental factor at a time, and this may not represent

field environments or interaction of environmental factors in the several regions.

However, if the growth of seedlings from the 4 provenances - Katherine, Agnew, Lake Albacutya and Gwydir River - can be accepted as representative of the growth characteristics of seedlings from the more extreme parts of the species climatic range, then it might be inferred that progenies from hotter and drier regions of the range tend to be inherently slower growing than seedlings from that part of the range with somewhat more moderate and uniform climate. It might further be inferred that inherent vigour has played a more important part in natural selection in the south than in the north. A number of seedling growth characteristics supports such an hypothesis. For example, the two southern provenances - Lake Albacutya, and Gwydir River, tended to be similar in the number of leaves on stem, in the number of branches, and in leaf production on seedling branches, while the northern provenance seedlings differed consistently from the southern provenance seedlings in these respects. The northern provenance seedlings had fewer branches, and leaves on branches. Seedling height growth in the two southern provenances was better correlated with branch and branch-leaf production than in the northern provenances, that is, seedling branch and leaf production tended to be more independent of height growth in the northern provenances. This all suggests a positive natural selection in hotter and drier regions of individuals having fewer branches and leaves.

The development of lignotubers may be another characteristic indicating selection of individuals with a greater survival potential

under harsh environmental conditions. Katherine provenance produced by far the greatest number of lignotuberous seedlings, while at the other extreme in environmental range no lignotuber was recorded on any seedling from the most southern provenance of Lake Albacutya. While there were some meaningful differences between the northern and southern provenance progenies in height, branch, and branch-leaf characteristics, and lignotuber production there was surprisingly little consistent difference between the northern and southern provenances in leaf morphology. There were significant differences between individual provenances in leaf size, length, breadth, shape and thickness, but there was no clear relationship between these characteristics and environmental conditions associated with the provenance.

In the study of the effects of photoperiod on the growth of E. camaldulensis seedlings, there was increased growth with photoperiod in 2 provenances - Katherine and Lake Albacutya. The third provenance (Todd River) had a peak at 12-hour photoperiod. The differences between provenances were significant at 10 and 12 hours, but not at 14 hours. The Todd River results appeared to negate the hypothesis, that is, within harsher environments there has been selection favouring individuals with smaller transpiring surfaces, and slower height growth. The Todd River had the greatest height growth at all photoperiods and produced more branches and branch leaves at 12- and 14-hour photoperiod, than the southern (Lake Albacutya) provenance. However the Todd River seedlings were responding on height to increasing photoperiod by becoming more

spindly. This was confirmed in the dry weight production data where peak dry weight occurred at the 12-hour photoperiod. Moreover, the Todd River seedlings, despite advantages in height growth, number of branches, and leaves on branches, had lower total dry weight production, smaller leaf area and smaller leaf dry weight. At the greatest photoperiod of 14 hours, the number of branches, and number of leaves on branches of Todd River seedlings dropped sharply; this did not happen with Lake Albacutya and Katherine provenance seedlings. The Todd River seedling characteristics are in fact consistent with the hypothesis that there has been selection of individuals with the species giving adaptation to harsher environmental conditions.

The study of the frost resistance in E. camaldulensis supported the findings of Larsen (1967), Karschon (1968) and Pryor and Byrne (1969) - in that frost resistance in E. camaldulensis varies according to seed origin. However, the results for unhardened seedlings are not altogether in agreement with some of the earlier findings, and suggested that some rather interesting variations in frost sensitivity in E. camaldulensis had developed in response to local selection. It was evident that the unhardened seedlings of the species from northern provenance of Katherine and Agnew were more resistant to frost injury than seedlings from the southern provenances of Nathalia and Gwydir River. This may suggest a selection for resistance to a sudden drop in temperature so that the northern provenances are better adapted to a radical change in climatic conditions - ensuring their survival in any harsh environmental

conditions. It is quite possible that provenances from continental areas may have greater capacity for frost resistance when no prehardening has been possible. Where the plants had been pre-hardened before the frost treatment the responses were quite different. The seedlings of Nathalia and Gwydir River provenances were then more frost resistant than those of the Katherine and Agnew provenances. Seedlings from Agnew provenance were also found to be more frost resistant than those from Katherine provenance. In nature, most of the plants from the southern and cooler areas of Nathalia and Gwydir River will possess the ability to harden to withstand wintery weather. Under this environmental condition, the results of the present investigation on the effects of frost on hardened seedlings of E. camaldulensis indicated a decrease in susceptibility of frost damage in the species from north to south - the northern provenance of Katherine being the most susceptible and Gwydir River the least.

The results of the root studies of E. camaldulensis showed that all the six provenances of the species had a capacity to rapidly develop roots to explore any drying soil, thereby helping ensure survival in harsh environmental conditions. There were no marked differences between any of the six provenances in their root production. In a comparison of E. camaldulensis and two coastal eucalypts (E. saligna and E. pilularis), E. camaldulensis was shown to be able to develop roots through drying soil far better than the coastal species.

In conclusion it can be said that the results of the present study demonstrates provenance variation in E. camaldulensis seedlings and a north-south ecological division of the species is possible. To improve the interpretation of the results obtained for the present investigation further studies of the species involving many provenances will be desirable. An understanding of the growth rate of the adult trees of E. camaldulensis in its natural habitat may also elucidate some of the reactions of juvenile plants grown under controlled environmental conditions. A knowledge of the pattern of variation, and adaptability of E. camaldulensis and like species to certain environments will help in directing tree breeding programmes for a particular locality. The high level of provenance variation in the species strongly suggests that very effective improvement could be made in the productivity of E. camaldulensis as an exotic by careful selection of seed source in tree introduction.

APPENDIX 1 Composition of Nutrient Solution

Nutrient solution, is a modified Hoagland solution in which the iron is present as chelate (sequestrene).

Reference: Went, F.H. - The experimental control of plant growth.

Chronica Botanica Co., 1957, pp. 78-79.

The composition is as follows:

Ca (NO ₃) ₂ · 4H ₂ O	95g/100L
(NH ₄) H ₂ PO ₄	6 "
KNO ₃	61 "
MgSO ₄ · 7H ₂ O	49 "
H ₃ BO ₃	0.06"
MnCl ₂ · 4H ₂ O	0.04"
ZnSO ₄ · 7H ₂ O	0.009"
CuSO ₄ · 5H ₂ O	0.005"
H ₂ MoO ₄ · 4H ₂ O	0.002"
Co(NO ₃) ₂ · 6H ₂ O	0.0025g/100L
FeSO ₄ · 7H ₂ O	2.49 g/100L
EDTA	3.32 "
NaOH	0.50 "

APPENDIX 2

Provenance Variation in the Response of Seedling Progenies of *E. camaldulensis* to Variation of Temperature During Period of 50 Days. (a) Seedling Height; (b) Basal Diameter; (c) Number of Leaves on Stem; (d) Number of Leaves on Branches; (e) Number of Branches, and (f) Number of Internodes on Stem.

(a) Height (cm)

Temperature (Day/Night °C.)	Provenances	Days from Transfer from 27/22°C.											
		0		10		20		30		40		50	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
21/16°C.	Katherine	3.62	0.18	6.82	0.39	15.14	0.58	33.53	1.09	51.90	1.28	71.71	1.66
	Lake Albacutya	3.35	0.16	6.65	0.30	16.00	0.79	38.11	1.77	60.07	2.42	83.38	4.17
	Gwydir River	3.39	0.17	6.53	0.34	15.88	0.86	36.11	1.82	55.64	2.60	81.94	3.82
	Agnew	2.67	0.15	4.82	0.32	10.32	0.71	25.13	1.37	40.28	2.07	56.02	2.99
27/22°C.	Katherine	7.81	0.48	15.27	0.80	29.74	1.25	53.83	2.18	73.12	2.99	94.49	3.70
	Lake Albacutya	10.18	0.35	19.84	0.55	38.29	1.00	68.07	2.24	94.47	2.83	122.50	2.89
	Gwydir River	10.70	0.58	21.35	0.91	40.45	1.54	73.85	2.59	98.16	3.04	125.77	3.06
	Agnew	6.39	0.34	12.41	0.64	24.16	1.23	44.51	2.33	61.50	3.64	83.00	4.93
33/28°C.	Katherine	5.48	0.34	11.49	0.64	22.26	1.09	42.77	1.75	61.60	2.43	79.27	2.94
	Lake Albacutya	7.04	0.34	16.18	0.60	31.73	1.31	55.41	1.85	80.18	3.16	104.22	3.83
	Gwydir River	6.52	0.54	14.92	1.03	29.82	1.87	54.33	2.52	77.46	3.15	103.16	3.62
	Agnew	4.20	0.32	8.20	0.57	15.06	0.95	28.78	1.88	41.26	2.49	56.02	3.36
	LS.D. (p = 0.05)	0.581		1.017		1.855		3.210		4.404		5.510	

APPENDIX 2 (Cont'd)

(b) Basal Diameter (mm)

Temperature (Day/Night °C.)	Provenances	Days from Transfer from 27/22°C.											
		0		10		20		30		40		50	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
21/16°C.	Katherine	0.06	0.003	0.10	0.003	0.17	0.01	0.28	0.01	0.36	0.01	0.46	0.01
	Lake Albacutya	0.08	0.003	0.14	0.005	0.20	0.01	0.32	0.01	0.40	0.01	0.50	0.01
	Gwydir River	0.08	0.002	0.12	0.006	0.17	0.01	0.28	0.01	0.36	0.01	0.47	0.01
	Agnew	0.05	0.005	0.09	0.003	0.15	0.01	0.23	0.01	0.28	0.01	0.37	0.02
27/22°C.	Katherine	0.09	0.004	0.15	0.005	0.24	0.01	0.36	0.01	0.41	0.01	0.47	0.02
	Lake Albacutya	0.12	0.003	0.20	0.005	0.30	0.01	0.43	0.01	0.50	0.01	0.57	0.02
	Gwydir River	0.11	0.001	0.18	0.003	0.27	0.01	0.40	0.01	0.48	0.01	0.56	0.01
	Agnew	0.09	0.002	0.16	0.006	0.24	0.01	0.34	0.01	0.40	0.02	0.48	0.02
33/28°C.	Katherine	0.07	0.003	0.12	0.004	0.18	0.01	0.26	0.01	0.32	0.01	0.40	0.01
	Lake Albacutya	0.10	0.003	0.15	0.01	0.22	0.01	0.32	0.01	0.39	0.01	0.48	0.02
	Gwydir River	0.09	0.003	0.15	0.01	0.20	0.01	0.30	0.01	0.37	0.01	0.45	0.01
	Agnew	0.05	0.003	0.10	0.01	0.15	0.01	0.23	0.01	0.28	0.01	0.33	0.02
	L.S.D. (p = 0.05)		0.006		0.008		0.011		0.017		0.019		0.024

APPENDIX 2 (Cont'd)

(c) Number of Leaves on Stem

Temperature (Day/Night °C.)	Provenances	Days from Transfer from 27/22°C.											
		0		10		20		30		40		50	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
21/16°C.	Katherine	6.96	0.20	9.60	0.23	13.84	0.34	19.84	0.48	24.24	0.50	29.24	0.70
	Lake Albacutya	8.36	0.22	10.64	0.25	14.76	0.44	20.12	0.56	24.49	0.45	29.80	0.71
	Gwydir River	8.32	0.25	11.12	0.28	15.04	0.37	20.84	0.56	25.80	0.58	30.40	1.08
	Agnew	6.32	0.19	8.40	0.20	11.76	0.28	16.68	0.38	20.44	0.56	24.52	0.76
27/22°C.	Katherine	10.48	0.40	14.04	0.50	20.28	0.67	26.96	0.90	31.80	1.01	36.00	1.37
	Lake Albacutya	12.00	0.23	15.36	0.34	21.86	0.40	29.20	0.68	35.32	0.77	40.76	0.87
	Gwydir River	12.16	0.23	16.24	0.25	22.88	0.47	30.60	0.53	36.56	0.54	40.48	0.76
	Agnew	8.88	0.23	12.24	0.37	17.68	0.58	24.00	0.90	28.24	1.12	33.20	1.33
33/28°C.	Katherine	8.08	0.27	11.76	0.45	16.84	0.55	23.40	0.61	28.92	0.93	33.36	1.07
	Lake Albacutya	9.92	0.27	14.32	0.58	19.28	0.56	25.72	0.61	33.04	0.86	38.24	0.95
	Gwydir River	9.52	0.37	13.12	0.50	18.76	0.74	26.12	1.14	32.88	1.19	38.16	1.50
	Agnew	7.12	0.23	10.00	0.35	13.76	0.47	19.28	0.86	23.12	0.96	28.84	1.29
	L.S.D. (p = 0.05)		0.428		0.609		0.815		1.151		1.342		1.717

APPENDIX 2 (Cont'd)

(d) Number of Leaves on Branches

Temperature (Day/Night °C.)	Provenances	Days from Transfer from 27/22°C.											
		0		10		20		30		40		50	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
21/16°C.	Katherine	-	-	-	-	1.64	0.60	3.04	1.01	7.68	2.23	14.08	3.83
	Lake Albacutya	-	-	2.48	0.74	8.12	1.36	11.08	1.78	22.88	3.23	36.96	4.81
	Gwydir River	-	-	0.92	0.45	5.12	1.14	7.24	1.36	16.32	2.71	25.84	4.71
	Agnew	-	-	-	-	0.72	0.30	1.36	0.41	3.12	0.68	7.60	2.12
27/22°C.	Katherine	-	-	-	-	0.80	0.72	1.20	0.61	5.28	1.76	11.84	3.16
	Lake Albacutya	-	-	0.84	0.51	6.00	2.00	12.40	3.51	26.88	4.40	41.20	6.27
	Gwydir River	-	-	0.16	0.16	5.04	1.38	15.84	2.28	32.92	3.43	54.88	5.54
	Agnew	-	-	-	-	-	-	-	-	1.76	1.01	4.24	1.52
33/28°C.	Katherine	-	-	-	-	-	-	-	-	1.36	0.95	5.48	3.31
	Lake Albacutya	-	-	2.20	1.70	8.60	3.49	10.24	4.27	22.00	5.69	37.28	7.31
	Gwydir River	-	-	0.24	0.17	1.12	0.52	3.44	1.57	12.72	3.43	25.60	5.51
	Agnew	-	-	-	-	-	-	-	-	0.80	0.58	2.32	1.08
	L.S.D. (p = 0.05)	---		0.931		2.203		3.107		4.732		7.229	

APPENDIX 2 (Cont'd)

(e) Number of Branches

Temperature (Day/Night °C.)	Provenances	Days from Transfer from 27/22°C.											
		0		10		20		30		40		50	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
21/16°C.	Katherine	-	-	-	-	0.88	0.31	1.44	0.42	4.08	1.08	4.04	1.23
	Lake Albacutya	-	-	2.28	0.47	3.48	0.53	4.56	0.63	12.16	1.43	15.00	1.65
	Gwydir River	-	-	2.12	0.42	2.52	0.56	3.52	0.66	9.60	1.66	11.56	1.92
	Agnew	-	-	-	-	0.36	0.15	0.64	0.18	1.64	0.41	3.80	1.10
27/22°C.	Katherine	-	-	-	-	0.44	0.40	0.64	0.33	2.44	0.82	3.88	0.92
	Lake Albacutya	-	-	0.28	0.14	2.92	0.75	4.20	0.93	9.36	1.10	11.04	1.27
	Gwydir River	-	-	0.04	0.04	2.60	0.58	6.60	0.83	11.24	1.01	14.20	1.05
	Agnew	-	-	-	-	-	-	-	-	0.68	0.27	1.56	0.54
33/28°C.	Katherine	-	-	-	-	-	-	-	-	0.52	0.36	1.64	0.86
	Lake Albacutya	-	-	1.50	0.65	1.56	0.66	3.52	1.20	7.96	1.54	11.40	1.61
	Gwydir River	-	-	0.28	0.12	0.80	0.39	1.48	0.61	6.80	1.16	9.92	1.32
	Agnew	-	-	-	-	-	-	-	-	0.28	0.20	1.16	0.51
L.S.D. (p = 0.05)		--		0.438		0.718		0.990		1.682		1.988	

APPENDIX 2 (Cont'd)

(f) Number of Internodes on Stem

Temperature (Day/Night °C.)	Provenances	Days from Transfer from 27/22°C.											
		0		10		20		30		40		50	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
21/16°C.	Katherine	2.48	0.10	3.80	0.11	7.32	0.31	14.64	0.39	20.64	0.67	25.76	0.48
	Lake Albacutya	3.12	0.12	4.40	0.14	8.00	0.35	14.96	0.55	20.04	0.53	26.08	0.66
	Gwydir River	3.16	0.12	4.64	0.16	8.84	0.37	15.60	0.53	20.76	0.68	27.20	0.81
	Agnew	2.20	0.08	3.20	0.10	5.64	0.24	11.76	0.52	16.04	0.61	21.76	0.86
27/22°C.	Katherine	4.28	0.20	7.80	0.46	14.80	0.72	22.80	0.85	28.24	1.08	34.68	1.27
	Lake Albacutya	5.20	0.15	10.04	0.46	16.64	0.42	25.48	0.65	32.12	0.72	38.52	0.82
	Gwydir River	5.32	0.22	11.16	0.33	17.68	0.34	27.44	0.53	33.12	0.59	39.36	0.75
	Agnew	3.52	0.14	5.80	0.30	11.88	0.62	19.20	0.95	24.28	1.07	30.40	1.38
33/28°C.	Katherine	3.00	0.15	4.92	0.22	8.88	0.47	16.52	0.80	23.36	0.42	31.72	1.19
	Lake Albacutya	4.04	0.13	6.36	0.19	12.72	0.43	20.36	0.63	28.08	0.72	36.36	0.85
	Gwydir River	3.76	0.18	5.72	0.29	11.76	0.73	19.84	1.00	26.84	1.22	35.56	1.33
	Agnew	2.52	0.12	4.00	0.17	6.64	0.37	11.60	0.82	16.80	1.02	24.16	1.42
	L.S.D. (p=0.05)	0.242		0.440		0.766		1.143		1.367		1.661	

APPENDIX 3

Variation in Leaf Morphology of the Seedlings of *E. camaldulensis* from 4 Provenances at Three Temperature Regimes. (a) - (d) Leaf Length (cm); (e) - (h) Leaf Breadth (cm); (i) Leaf Length/Breadth Ratio; (j) Leaf Thickness of 8th Leaf ($\text{mm} \times 10^{-1}$); (k) Leaf Basal Angle of 8th Leaf ($^{\circ}$).

Temperature (Day/Night C.)	Provenance	(a)		(b)		(c)		(d)		(e)		(f)	
		6th Leaf Length (cm)		7th Leaf Length (cm)		8th Leaf Length (cm)		Mean of 6-8th Leaf Length (cm)		6th Leaf Breadth (cm)		7th Leaf Breadth (cm)	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
21/16°C.	Katherine	9.55	0.35	10.84	0.39	11.85	0.41	10.74	0.37	3.40	0.15	3.85	0.18
	Lake Albecutya	9.24	0.45	10.44	0.48	11.74	0.51	10.47	0.47	3.75	0.17	4.19	0.21
	Gwydir River	7.82	0.38	8.94	0.41	10.38	0.42	9.05	0.38	2.85	0.14	3.22	0.13
	Agnew	8.39	0.37	9.37	0.35	10.53	0.39	9.42	0.35	2.46	0.13	3.92	0.12
27/22°C.	Katherine	8.42	0.26	9.36	0.25	10.54	0.32	9.26	0.30	2.65	0.11	2.99	0.14
	Lake Albecutya	8.06	0.25	8.84	0.27	9.58	0.27	8.83	0.25	3.19	0.15	3.54	0.16
	Gwydir River	8.93	0.29	9.71	0.31	10.50	0.34	9.74	0.30	2.87	0.12	3.09	0.11
	Agnew	8.23	0.29	9.33	0.36	10.30	0.31	9.28	0.29	3.33	0.10	3.72	0.112
33/28°C.	Katherine	7.63	0.34	7.90	0.36	8.90	0.36	8.14	0.34	2.53	0.12	2.60	0.12
	Lake Albecutya	7.40	0.30	7.99	0.29	8.92	0.31	8.11	0.28	2.78	0.12	3.02	0.13
	Gwydir River	7.93	0.43	8.60	0.43	9.45	0.47	8.66	0.44	2.81	0.15	3.00	0.17
	Agnew	6.89	0.26	7.06	0.28	8.00	0.28	7.32	0.27	2.75	0.12	2.84	0.13
L.S.D. (p=0.05)		0.54		0.57		0.60		0.55		0.22		0.24	

APPENDIX 3 (Cont'd)

Temperature (Day/Night °C.)	Provenance	(g) 8th Leaf Breadth (cm)		(h) Mean of 6-8th Breadth (cm)		(i) Leaf Length/ Leaf Breadth Ratio		(j) Leaf Thickness of 8th Leaf (mm x10 ⁻¹)		(k) Leaf Basal Angle of 8th Leaf (Degrees)	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
21/16°C.	Katherine Lake Albacutya Gwydir River Agnew	4.37	0.21	3.87	0.18	2.83	0.10	1.65	0.03	90.4	2.3
		4.60	0.21	4.17	0.19	2.55	0.09	2.04	0.03	112.3	3.7
		3.61	0.17	3.22	0.14	2.84	0.09	1.75	0.02	95.8	2.2
		4.33	0.15	2.89	0.12	2.44	0.08	2.06	0.04	95.1	3.5
27/22°C.	Katherine Lake Albacutya Gwydir River Agnew	3.43	0.15	3.02	0.13	3.14	0.11	1.66	0.03	80.4	2.1
		3.79	0.18	3.50	0.16	2.64	0.14	1.82	0.03	108.5	4.6
		3.42	0.14	3.13	0.12	3.16	0.09	1.57	0.03	92.3	2.4
		4.21	0.12	3.75	0.10	2.50	0.09	2.05	0.03	93.1	2.7
33/28°C.	Katherine Lake Albacutya Gwydir River Agnew	2.86	0.13	2.66	0.12	3.12	0.12	1.57	0.03	82.4	2.5
		3.42	0.13	3.05	0.14	2.69	0.09	1.75	0.04	103.8	3.9
		3.20	0.16	3.00	0.16	2.95	0.14	1.52	0.030	94.5	4.1
		3.21	0.13	2.94	0.12	2.54	0.09	1.90	0.04	91.0	3.1
	L.S.D. (p=0.05)	0.26		0.23		0.16		0.06		5.20	

APPENDIX 4

Provenance Variation in the Response of Dry Weight Production and Lignotuber Diameter of Seedlings of *E. camaldulensis* to Variation of Temperature at Day 50. (a) Leaf Dry Weight; (b) Stem Dry Weight; (c) Root Dry Weight; (d) Total Dry Weight; (e) Leaf Weight/Stem Weight Ratio; (f) Root/Shoot Weight Ratio and (g) Lignotuber Diameter.

Temperature (Day/Night °C.)	Provenance	(a)		(b)		(c)		(d)		(e)		(f)		(g)	
		Leaf Dry Weight (gm)	S.E.	Stem Dry Weight (gm)	S.E.	Root Dry Weight (gm)	S.E.	Total Dry Weight (gm)	S.E.	Leaf/Stem Ratio	S.E.	Root/Shoot Ratio	S.E.	Lignotuber Diameter (mm)	S.E.
21/16°C.	Katherine	4.29	0.33	2.89	0.20	1.39	0.08	8.59	0.60	1.49	0.04	0.20	0.01	0.23	0.05
	Lake Albacutya	4.63	0.30	3.75	0.28	1.30	0.07	9.69	0.63	1.30	0.06	0.17	0.01	-	-
	Gwydir River	4.62	0.39	3.33	0.31	1.17	0.11	9.13	0.78	1.42	0.05	0.16	0.01	0.03	0.03
	Agnew	2.98	0.26	1.69	0.17	0.70	0.07	5.38	0.48	1.86	0.08	0.16	0.01	-	-
27/22°C.	Katherine	5.28	0.48	3.29	0.32	1.10	0.09	9.72	0.89	1.64	0.05	0.14	0.01	0.45	0.06
	Lake Albacutya	5.36	0.35	5.12	0.38	1.25	0.10	11.75	0.81	1.08	0.03	0.12	0.01	-	-
	Gwydir River	6.91	0.39	6.14	0.46	1.70	0.15	14.85	0.97	1.18	0.04	0.13	0.01	-	-
	Agnew	4.84	0.42	2.91	0.29	0.91	0.07	8.62	0.77	1.80	0.08	0.19	0.04	0.06	0.03
33/28°C.	Katherine	3.57	0.23	2.46	0.18	0.87	0.06	6.68	0.52	2.80	0.17	0.15	0.01	0.39	0.05
	Lake Albacutya	3.95	0.24	4.22	0.32	1.07	0.07	9.29	0.63	2.20	0.36	0.13	0.01	-	-
	Gwydir River	4.12	0.25	3.80	0.29	1.02	0.09	8.65	0.62	1.14	0.04	0.13	0.01	0.13	0.05
	Agnew	2.41	0.31	1.43	0.20	0.57	0.08	4.43	0.59	1.82	0.08	0.15	0.01	0.08	0.03
	L.S.D. (p=0.05)	0.55		0.48		0.15		1.136		0.202		0.013		0.05	

APPENDIX 5 Provenance Variation in the Response of Seedlings of *Eucalyptus camaldulensis* from Three Provenances to Variation of Photoperiod During Period of 50 Days. (a) Seedling Height; (b) Seedling Basal Diameter; (c) Leaves on Stem; (d) Leaves on Branches; (e) Number of Branches; (f) Number of Internodes.

(a) Height (cm)

Temperature (Day/Night °C.)	Provenances	Photo- period (hours)	Days from Transfer from 27/22°C.														
			10			20			30			40			50		
			Mean	S.E.		Mean	S.E.		Mean	S.E.		Mean	S.E.		Mean	S.E.	
21/16°C.	Katherine	10	5.63	0.64		10.70	1.32		24.65	2.71		40.15	3.75		63.45	4.65	
		12	6.55	0.78		11.90	1.63		28.70	2.82		46.15	3.16		70.70	3.63	
		14	6.47	0.50		14.05	1.19		30.55	2.22		54.30	3.27		77.35	4.29	
	Todd River	10	5.90	0.42		11.07	0.92		26.45	2.41		44.50	3.83		69.10	5.54	
		12	7.72	0.47		13.95	0.99		37.00	2.49		60.05	3.42		89.55	4.55	
		14	7.56	0.62		18.10	1.46		40.90	2.05		73.85	3.24		99.35	4.66	
	Lake Albacutya	10	7.11	0.35		11.65	0.81		27.45	1.90		45.05	3.09		68.20	5.05	
		12	7.92	0.52		14.45	1.13		32.95	2.74		54.15	3.51		79.05	4.68	
		14	8.82	0.42		17.19	0.82		34.45	1.76		60.50	4.94		88.75	4.71	
	L.S.D. (p=0.05)		0.885		1.915		3.861		5.888		7.599						

APPENDIX 5 (Cont'd)

(b) Basal Diameter (cm)

Temperature (Day/Night °C.)	Provenances	Photo- period (hours)	Days from Transfer from 27/22°C.											
			10		20		30		40		50			
			Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.		
21/16°C.	Katherine	10	0.11	0.01	0.18	0.01	0.27	0.01	0.37	0.02	0.49	0.01		
		12	0.12	0.01	0.18	0.01	0.30	0.01	0.42	0.02	0.50	0.02		
		14	0.11	0.01	0.20	0.01	0.28	0.15	0.42	0.02	0.47	0.02		
	Todd River	10	0.12	0.01	0.20	0.01	0.33	0.01	0.41	0.02	0.48	0.02		
		12	0.14	0.01	0.20	0.01	0.31	0.02	0.46	0.01	0.56	0.01		
		14	0.13	0.01	0.21	0.01	0.30	0.01	0.48	0.01	0.55	0.02		
	Lake Albatutya	10	0.13	0.01	0.19	0.01	0.31	0.01	0.42	0.02	0.53	0.02		
		12	0.13	0.01	0.21	0.01	0.34	0.01	0.46	0.02	0.53	0.02		
		14	0.13	0.01	0.20	0.01	0.31	0.01	0.45	0.02	0.52	0.01		
L.S.D. (p=0.05)			0.012	0.020	0.026	0.036	0.035							

APPENDIX 5 (Cont'd)

(c) Number of Leaves on Stem

Temperature (Day/Night °C.)	Provenances	Photo- period (hours)	Days from Transfer from 27/22°C.											
			10		20		30		40		50			
			Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
21/16°C.	Katherine	10	9.60	0.40	13.20	0.67	17.20	0.74	22.60	1.19	27.00	1.34		
		12	10.20	0.62	13.40	0.60	18.00	1.03	23.20	1.27	26.20	1.05		
		14	10.40	0.49	13.80	0.55	19.20	0.80	24.20	0.96	27.40	0.94		
	Todd River	10	9.80	0.46	13.00	0.53	17.00	0.68	23.10	1.64	26.20	1.28		
		12	10.40	0.40	14.00	0.42	19.00	0.80	24.40	0.58	27.20	0.95		
		14	11.00	0.44	13.40	0.94	19.30	0.91	26.00	0.66	29.40	0.94		
	Lake Albacutya	10	5.00	0.33	12.20	0.35	16.00	0.51	20.80	0.90	24.60	0.99		
		12	10.10	0.10	12.80	0.32	17.60	0.49	23.20	0.74	26.60	0.94		
		14	10.10	0.10	13.80	0.46	18.00	0.42	22.40	1.06	27.80	0.69		
	L.S.D. (p=0.05)		0.666		0.929		1.200		1.711		1.678			

APPENDIX 5 (Cont'd)

(d) Number of Leaves on Branches

Temperature (Day/Night °C.)	Provenances	Photo- period (hours)	Days from Transfer from 27/22°C.											
			10		20		30		40		50			
			Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
21/16°C.	Katherine	10	0.01	0.01	0.60	0.60	2.00	2.00	2.20	2.20	7.60	2.60	7.60	2.60
		12	0.01	0.01	1.02	1.02	4.40	3.55	8.40	5.72	17.80	7.80	17.80	7.80
		14	0.20	0.20	1.52	1.52	5.80	2.97	8.00	2.89	20.20	4.47	20.20	4.47
	Todd River	10	3.20	1.69	9.00	3.11	12.00	4.06	17.40	5.51	32.80	8.69	32.80	8.69
		12	2.20	1.41	8.80	2.75	15.80	4.07	22.20	5.51	38.60	7.76	38.60	7.76
		14	1.80	0.96	4.80	2.15	4.80	2.76	11.60	3.70	25.00	4.68	25.00	4.68
	Lake Albacutya	10	0.01	0.01	2.60	1.49	7.80	3.78	9.60	5.93	17.40	7.89	17.40	7.89
		12	0.01	0.01	3.80	1.13	10.40	2.66	11.20	2.75	19.60	4.44	19.60	4.44
		14	0.01	0.01	4.20	1.44	8.00	2.90	15.80	5.51	21.80	6.34	21.80	6.34
	L.S.D. (p=0.05)		1.307	3.027	5.308	7.459	10.409							

APPENDIX 5 (Cont'd)

(e) Number of Branches

Temperature (Day/Night °C.)	Provenances	Photo- period (hours)	Days from Transfer from 27/22°C.											
			10		20		30		40		50			
			Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
21/16°C.	Katherine	10	0.10	0.10	0.30	0.30	0.60	0.60	0.70	0.70	2.20	0.70	2.20	0.66
		12	0.10	0.10	0.80	0.51	1.60	1.18	2.60	1.39	4.20	1.39	4.20	1.10
		14	0.10	0.10	1.40	0.61	1.90	0.92	2.60	0.97	6.40	0.97	6.40	1.25
	Todd River	10	1.40	0.68	2.60	0.76	3.20	0.98	4.30	1.43	7.70	1.43	7.70	1.64
		12	0.70	0.36	3.10	0.80	4.60	0.85	6.90	1.39	10.60	1.39	10.60	2.46
		14	0.90	0.48	1.60	0.66	1.40	0.77	3.80	1.13	7.40	1.13	7.40	0.76
Lake Albatutya	10	0.01	0.01	1.10	0.69	2.80	1.22	2.90	1.08	5.00	1.08	5.00	1.82	
	12	0.01	0.01	1.70	0.49	3.20	0.64	3.70	0.73	5.30	0.73	5.30	0.98	
	14	0.01	0.01	1.90	0.58	3.00	0.97	4.70	1.40	6.20	1.40	6.20	1.42	
L.S.D. (p=0.05)			0.499	1.011	1.514	1.917	2.356							

APPENDIX 5 (Cont'd)

(f) Number of Internodes on Stem

Temperature (Day/Night °C.)	Provenances	Photo- period (hours)	Days from Transfer from 27/22°C.														
			10			20			30			40			50		
			Mean	S.E.		Mean	S.E.		Mean	S.E.		Mean	S.E.		Mean	S.E.	
21/16°C.	Katherine	10	5.30	0.30		9.70	0.93		13.40	0.95		19.60	1.54		23.30	1.62	
		12	5.30	0.39		9.30	0.74		14.40	0.74		20.20	1.15		23.10	1.23	
		14	5.70	0.26		10.40	0.66		15.30	0.66		21.90	0.95		24.90	1.15	
	Todd River	10	5.60	0.33		9.70	0.55		13.40	0.56		20.20	0.87		23.40	1.06	
		12	5.90	0.23		9.50	0.50		14.20	0.48		21.90	0.86		24.50	1.24	
		14	5.90	0.17		10.60	0.61		16.30	0.70		23.90	1.00		24.40	2.25	
	Lake Albacutya	10	4.90	0.17		8.60	0.49		13.00	0.76		18.70	1.19		21.50	1.23	
		12	5.60	0.30		10.10	0.50		14.40	0.68		22.00	1.22		23.20	1.19	
		14	5.90	0.10		10.00	0.44		15.10	0.43		20.90	0.88		24.90	0.88	
	L.S.D. (p=0.05)		0.437		1.016		1.110		1.844		2.233						

APPENDIX 6 Provenance Variation in the Response of Dry Weight Production and Leaf Total Area of Seedling Progenies of *Eucalyptus camaldulensis* to Variation of Photoperiod at Day 50. (a) Leaf Dry Weight; (b) Stem Dry Weight; (c) Root Dry Weight; (d) Total Dry Weight; (e) Root/Shoot Ratio; (f) Total Leaf Area.

Temperature (Day/Night °C.)	Provenances	Photo- period (hours)	(a)		(b)		(c)		(d)		(e)		(f)	
			Leaf Dry Weight (gm)		Stem Dry Weight (gm)		Root Dry Weight (gm)		Total Dry Weight of Plants (gm)		Root/Shoot Ratio		Total Leaf Area (sq.cm) x 10 ²	
			Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
21/16°C.	Katherine	10	3.34	0.42	1.61	0.25	1.17	0.11	6.13	0.76	0.26	0.02	8.80	1.11
		12	5.76	0.88	2.47	0.41	1.59	0.18	9.93	1.46	0.20	0.01	11.70	1.41
		14	4.68	0.67	2.42	0.36	1.18	0.11	8.39	1.12	0.18	0.02	10.48	1.45
	Todd River	10	2.82	0.32	1.73	0.20	1.00	0.12	5.51	0.62	0.22	0.01	6.79	0.76
		12	5.12	0.48	3.46	0.21	1.59	0.08	10.17	0.62	0.19	0.01	11.47	0.44
		14	4.18	0.27	3.15	0.25	1.02	0.08	8.35	0.62	0.14	0.01	9.84	0.47
	Lake Albacutya	10	4.75	0.55	2.39	0.27	1.34	0.05	8.46	0.93	0.19	0.01	9.94	1.21
		12	6.37	0.72	3.26	0.47	1.49	0.17	11.13	1.27	0.16	0.01	11.27	1.09
		14	5.86	0.37	3.12	0.27	1.24	0.09	10.24	0.68	0.14	0.01	12.55	0.78
L.S.D. (p = 0.05)			0.910		0.516	0.211		1.612		0.026		1.729		

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