University of Sydney

Thesis for the Degree of Master of Science in Botany

"ADAPTATION IN EUCALYPTUS TO THE WATERLOGGED ENVIRONMENT"

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[redacted]

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Preface: Throughout the text of this thesis Eucalyptus nomenclature has been taken according to Blakely, W.F. "A Key to the Eucalypts" 2nd edition, Forestry and Timber Bureau. Canberra. 1955. The generic name Eucalyptus has been abbreviated to E. and a small initial letter has been used in all specific names.

ABSTRACT

The distribution of Eucalyptus species in relation to waterlogged conditions is discussed and it is shown that only a small percentage of the total species number, occur naturally in areas subject to waterlogging for long periods.

These have been grouped as occurring

(a) in swampy habitats and largely confined to them e.g. E. robusta, E. camphora

(b) often in habitats which are periodically water-logged for a prolonged time e.g. E. rudis, ovata, aggregata, camaldulensis, stellulata

In addition, there are species which occur typically on well drained sites, but which are sometimes found in areas subject to occasional waterlogging for short periods e.g. E. rubida, blakelyi, viminalis, stuartiana

Species distribution

Field transects have shown that there are no species of Eucalyptus which grow in permanently waterlogged soil in the sense that Typha, Phragmites, Carex and Restio do.

Species which occur on swampy areas are largely confined to them as adult trees, although as seedlings they may be present on adjacent well drained sites. Species of sites adjacent to swamp areas do not occur as seedlings on waterlogged ground.

Adaptations

Several morphological features have been examined experimentally and the evidence suggests that they are of adaptive value. These include

(a) the habit of surface rooting systems under conditions of waterlogging

(b) development of aerenchyma on submerged stems

(c) formation of cladogenous roots

The presence and variation in degree of seed dormancy between E. pauciflora and E. stellulata are discussed and the effect this characteristic may have on field germination on wet and dry sites is considered.

Broadcast sowing and seedling transplant trials have been carried out with E. pauciflora, E. stellulata and E. camphora, E. dalrympleana in field situations where these species occur. The results from these trials indicated that the survival rate on subalpine swamp sites is low for all species despite high germination rates. The final pattern of distribution is the result of a number of interacting factors one of which is the ability to withstand waterlogging.

The results of pot trials in different soils and with different watertables indicate that Eucalyptus species which are largely confined to waterlogged sites are adapted to these conditions, although growth is better on well drained soil. This indicates a difference in the "ecological" and "physiological" tolerances of these species and suggests that interspecific competition may be an additional factor controlling species distribution.

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ADAPTATION IN EUCALYPTUS TO THE WATERLOGGED ENVIRONMENT

CHAPTER 1

INTRODUCTION

The genus Eucalyptus, comprising more than five hundred species, is the dominant feature in the Australian vegetation in all but the very dry inland and tropical rain forest areas.

Most species do not occupy large continuous areas, but occur in sharply defined habitats indicating a close site/species interaction in undisturbed natural communities. Because of this, together with the high degree of speciation in the genus, it is not surprising that there is usually a particular Eucalyptus species occupying each ecological situation.

Swampy sites, and areas subject to periodic or continuous waterlogging, represent one of the more difficult ecological situations for plant growth in general, and for tree growth in particular. Such areas support distinctive plant communities composed primarily of hydrophytes possessing adaptations which enable them to grow under conditions of poor substrate aeration, and in largely aquatic environments.

Eucalyptus as a genus reaches its best development in well watered but well drained areas, and the number of species found growing naturally on soils subject to waterlogging is small. Table 1.

The fact that a few species do occur in waterlogged situations, and in most cases, are restricted to such sites, suggested that they may possess adaptations which enable them to live under these exacting environmental conditions.

The purpose of this study was to examine some of the Eucalyptus species which occur under waterlogged conditions, and by observation and experiment, to determine to what extent adaptation to the waterlogged environment exists in Eucalyptus.

Scope of the study

The study has been divided into three major sections -

(a) an examination of species distribution, by belt transects to determine the relationship between areas of poor drainage and the occurrence of regeneration and adult trees. This involved a complete assessment of Eucalyptus species, both adult and regeneration, an inventory of the herbaceous layers and an examination of the soils at representative points;

(b) comparative growth studies, under experimental conditions of differing soil type and degree of waterlogging and inundation, to determine whether certain morphological features observed in the field were of adaptive value;

(c) field studies involving transplant experiments and direct seedings to study survival and growth rates under conditions approaching, as closely as possible, those of the natural situation.

Previous work

Adaptation to the waterlogged environment has been widely studied with numerous hydrophytes, particularly members of the *Juncaceae*, *Cyperaceae*, *Typhaceae* and *Gramineae*. Work relating to tree species is more limited.

Submerging trials with *Taxodium distichum* were carried out by Demaree (1932). Emerson (1921), Laing (1932) experimented with some coniferous species in relation to varying degrees of waterlogging. Cannon (1920), Leyton (1958) observed the root growth of a number of tree species at various oxygen tensions. Kramer (1950) examined tree growth in relation to soil aeration.

With regard to Eucalyptus, Arthur (1952) studied the growth rate of E. camaldulensis under different water table levels. There are no other records of investigations with Eucalyptus in relation to a high water table or to waterlogged conditions.

TABLE 1

EUCALYPTUS SPECIES OCCURRING NATURALLY ON POORLY DRAINED SITES SUBJECT TO WATERLOGGING

Subgenus	Species Occurrence	
	Swampy habitats and largely confined to them	Often in habitats which are periodically water-logged for a prolonged time
MACRANTHERAE	robusta camphora	occidentalis amplifolia seeana var. constricta camaldulensis rudis ovata aggregata parvifolia rubida
RENANTHERAE		umbra stellulata* megacarpa

*Pryor and Johnson (in press) consider that this species is wrongly placed by Blakely in the Macrantherae.

In addition to the above, a number of species which occur typically on well drained sites are sometimes found in areas subject to occasional waterlogging for short periods. It has not been possible to examine these species to determine whether ecotypes exist, which are adapted to waterlogged conditions.

CHAPTER 2

SPECIES DISTRIBUTION

Because the species listed as occurring naturally on poorly drained soil subject to water-logging are widely scattered throughout both eastern and western Australia, it was not possible to study all of them in detail.

It was decided therefore, to concentrate on three species which were accessible for field study of the genus: E. robusta Sm (Macrantherae, Section Transversae), E. camphora R.T. Baker (Macrantherae, Normales) and E. stellulata Sieb (Renantherae).

The characteristic of Eucalyptus distribution whereby species change with change in microhabitat, is particularly evident in areas where sites of poor drainage are surrounded by well drained sites. Here there is an abrupt species change, when passing from the swamp to the adjacent and relatively drier site. The sharp nature of these boundaries, suggested that comparative studies between the species on the wetter and drier sites might show whether any adaptations are present which enable each species to develop better on its own site.

It is generally accepted that the genus Eucalyptus consists of at least four subgenera which are, almost entirely, reproductively isolated from one another Pryor (1959). In large portions of the continent, separate species from two or three of these subgenera grow closely mixed without any sign of interbreeding, although species from the same subgenus will often interbreed where they come in contact at the boundaries of their separate populations.

It is rare also to find members of the same subgenus growing together in a truly mixed stand. In many situations where this appears to be the case it can be shown that relatively minor habitat variations are associated with the species changes, and the species are in fact occupying distinct ecological situations. Thus it was decided to compare species of the same systematic group. For example, E. camphora (Macrantherae) occurs on subalpine swamps with E. dalrympleana Maiden (Macrantherae) and E. robertsoni Blakely (Renantherae) mixed on the adjacent drier ground. The comparison was therefore made between E. camphora and E. dalrympleana, both of the Macrantherae.

The three species pairs on which detailed study has been made are:-

Wet Site	Dry Site	Subgenus
E. robusta Sm.	E. botryoides Sm.	Macrantherae Transversae
E. camphora R.T. Baker	E. dalrympleana Maiden	Macrantherae Normales
E. stellulata Sieb.	E. pauciflora Sieb.	Renantherae

Species occurrence

E. robusta "swamp mahogany"was described in 1793 by Smith. In 1811 it was named E. multiflora by Poir.

Mueller (1879 - 1884) records that the species appears to have adaptability to stagnant, swampy or marshy localities and quotes the observations of a Mr. Kirton of Bulli N.S.W. "In low, sour, swampy ground near the sea coast, where other Eucalyptus look sickly, E. robusta is the picture of perfect health." This species is described by Blakely (1955) as "a magnificent tree for rich subsaline areas near the coast".

It is confined to coastal areas of New South Wales and Queensland from Twofold Bay to Fraser Island and is found mainly on areas of poor drainage often subjected to waterlogging,but also grows satisfactorily on light sandy clays and is found on pure sands on Stradbroke, Morton and Fraser Islands off the Queensland coast. In the North Coast area of N.S.W. it sometimes occurs in subsaline areas with waterlogging resulting from tidal flooding.

In its principal range, the climate is subtropical, but in central and southern coastal N.S.W. the climate is warm temperate. Summer temperatures are warm, and winter frosts are rare or lacking. The humidity is generally high, and the annual rainfall is 40 - 60 inches. In the northern part of the range there is a summer maximum whilst in the southern parts the rainfall distribution is more nearly uniform. The species is sporadic in its distribution usually growing as scattered trees or small groups without associated species.

It has been planted widely overseas in many tropical and subtropical countries, and on the Hawaiian Islands it is used as one of the Major Plantation species for timber production.

Hybridisation

E. robusta commonly hybridises in the field with E. grandis Hill ex Maiden, E. saligna Sm., E. umbellata Gaertn Domin and E. botryoides. (The hybrid with E. umbellata was described as the species E. patentinervis R.T. Baker syn. E. kirtoniana F.v.M. and the combination with E. botryoides as E. grandis var grandiflora Maiden, Anderson (1956)

Manipulated hybrids have been produced using E. cinerea F.v.M., Pryor (1954) and E. pulverulenta Sims, Pryor and Boden (1962) as female parents. These two species are geographically separated from E. robusta by distances of at least forty miles, Previous ecological studies

Davis (1936) working on the south coast of N.S.W. describes the E. robusta associes as "a stage in the Subsaline Lagoon Succession with ground layers of members of the preceding seres, e.g. Cladium junceum, Juncus maritimus, Phragmites communis, Casuarina glauca and Gahnia psittacorum."

Pidgeon (1937) describes E. robusta as forming a typical hind swamp or lagoon forest on the coastline of N.S.W.

There are no records of any experimental studies with this species.

Comparative species

There is no one species of the Transversae which occurs on sites adjacent to those of E. robusta throughout the full length of its range.

E. botryoides which occurs from Southern Victoria to just north of Newcastle N.S.W. is often found growing on adjoining sandysites in the Central and South Coast of N.S.W. as also is E. saligna in some locations. On the North Coast of N.S.W. in the vicinity of Coff's Harbour, E. saligna is a ridge type species and grows on sites well removed from the swampy sites of E. robusta. Its place is taken here by E. grandis which occurs on flats and the lower slopes of deep fertile valleys often adjoining E. robusta. Hybrids between the latter two species are fairly common at the stand junctions.

E. propinqua Deane and Maiden occurs in coastal areas of eastern Australia from Sydney to Maryborough in Queensland, usually on lowlands, low hills and ridges within fifty miles of the sea. In certain situations, it may be found growing on sites adjacent to those carrying E. robusta. Comparative studies have therefore been made between E. robusta and some other members of the Transversae group in general, rather than any one particular species.

E. camphora R.T. Baker "broad leaved sally", was described in 1899. It was formerly recognised as a variety of E. ovata Labill with which it has close affinity, differing mainly in the length of the operculum, fruit size and broader typically blunt leaves with a small point. It is an umbrageous tree 30 - 60 ft. high usually of rather crooked growth, (Fig. 1 & 2). It is found almost entirely between 3,000 - 4,000 ft. on subalpine swampy areas which are very cold in winter. It occurs occasionally along the banks of creeks or rivers, as for instance on the Delegate River in southern N.S.W. It is often associated with E. stellulata in such situations.

The species is confined to Victoria and southern N.S.W. It is largely sporadic in its distribution and is considered as a restricted species. This is particularly so in contrast with E. ovata with which it has close affinity. This species is widespread occurring in N.S.W., Victoria, Tasmania and South Australia.

Both E. camphora and E. robusta occur in areas of comparable total annual rainfall; however, it is of quite different distribution. Whereas E. robusta receives the greater proportion of its rain in the summer months, E. camphora occurs in typically winter rainfall areas which also receive some snow. There is, therefore, a major difference in the time when waterlogging is most frequent such that E. robusta is mostly waterlogged during the summer months, which is the normal growing period,

Fig. 1

E. camphora MacPherson's Swamp. Note white stems of *E. pauciflora* in background; *E. camphora* regeneration on swamp edge extreme right.

Fig. 2

E. camphora MacPherson's Swamp; note dense growth of grass, sedge and reed.

whilst E. camphora is waterlogged in winter when little growth is taking place. It has been observed in the field however, that E. camphora commences growth soon after winter when in many cases, soils are still waterlogged. Observations in the Wee Jasper area of N.S.W. have shown E. camphora with new, green vigorous shoots during late September and October, when free water is above the soil surface.

Hybridisation

E. camphora flowers in March and April and hybridises commonly with E. dalrympleana and E. viminalis Labill, which flower at the same time.

R.R. Willing has produced manipulated hybrids with E. viminalis as the female parent.

Previous ecological studies

Pryor (1939), working in the Australian Capital Territory, considered E. camphora as a consocies of the E. viminalis-fastigata and E. gigantea-dalrympleana associations. It is distinguished by a shrub layer three feet high of Epacris breviflora and Leptospermum myrtifolium, and a continuous ground cover of Carex appressa, Echinopogon intermedius and Juncus sp.

Costin (1954) working in the Monaro Region of N.S.W. lists associations of the E. pauciflora/ stellulata alliance which develop on soils moister, and with deficient aeration, as compared with soils of other associations of the alliance. With decreasing temperature and soil aeration, the associations E. pauciflora/ E. stellulata, E. stellulata, E. stellulata/ E. camphora and finally E. camphora are developed whilst the associations on warmer, moister areas with slightly impaired aeration are E. pauciflora/ aggregata, E. aggregata and E. pauciflora/

ovata.

There are no references to ecophysiological studies with E. camphora.

Whereas E. robusta because of its extended range can be compared with a number of species of the same subgenus E. camphora is almost entirely associated with the E. dalrympleana/viminalis species complex as far as members of the same subgenus are concerned.

Comparative species

E. viminalis and E. dalrympleana are far more widespread than E. camphora and generally occur on moist but well drained sites with E. dalrympleana at a higher altitude than E. viminalis. These two species hybridise freely and it is often difficult to obtain uniform progeny even though the seed has been collected from a phenotypically pure species. This occurs particularly with seed lots collected from E. dalrympleana at its lower elevations in the A.C.T.

The species change from E. camphora on the swamps to either E. viminalis or E. dalrympleana on the adjacent and well drained site is extremely abrupt; therefore, these species were the most suitable for comparative studies with E. camphora.

E. stellulata Sieb, "black sally" was described in 1828. It is a species of the tablelands of Victoria and N.S.W. extending as far north as Glen Innes.

A small to medium sized tree, rarely up to fifty feet with a dense spreading crown of typical woodland form. Fig. 3 and 4. It is usually found on damp flats near watercourses, on basaltic and light granitic or gritty alluvials. It can withstand extremely cold and damp conditions and grows at elevations up to 5,500 ft.

Fig. 3

E. stellulata Cotter Hut A.C.T.

Fig. 4

E. stellulata mature trees and regeneration on flats and E. pauciflora confined to well drained slopes. Transect 4.

It is largely a species in pure stands, although sometimes occurs with E. camphora.

The species has been linked with E. pauciflora in most ecological studies, and, although the two species grow in close proximity over wide areas, they do not grow in a truly intermixed pattern; minor site changes give damper conditions which are linked with the occurrence of E. stellulata whilst E. pauciflora does not grow in, or extend away from, well drained sites.

Hybridisation

E. stellulata is a member of the Renantherae and hybridises freely with other members of the group with which it comes in contact and whose flowering times coincide. These include E. robertsoni Pryor (1953) and E. macrorryncha F v M. (The latter combination has been described as E. macrorryncha var minor, Blakely.)

The species E. laseroni R.T. Baker of the Northern Tablelands of N.S.W. is considered as a hybrid between E. stellulata and E. caliginosa Blakely and McKie. Anderson (1956)

Because of the close association in the field it might be expected that hybrids would occur between E. pauciflora and E. stellulata. This is not the case however, as hybrids have never been recorded in the southern tablelands area, although they have been looked for over a number of years. (Pryor personal communication). The occurrence of a single individual purported to be a hybrid was noted from the Tomalla tableland, Earp private communication; however viable seed to provide seedlings for a progeny test has not been found.

E. pauciflora flowers late spring to early summer, individuals from lower elevations flowering earlier in the season than those from higher altitude, whilst E. stellulata is a late autumn flowering species, often still in flower at the end of May.

It is probable therefore, that the separation in times of flowering is sufficient to reduce the possibility of hybridisation.

This idea has been confirmed by the production of manipulated hybrids between the two species - (R.R. Willing). Pollen of E. stellulata was taken in April and stored in the deep freeze at -16°C for a period of six months. In October, when E. pauciflora was in flower, the pollen of E. stellulata was put onto emasculated flowers. The seedlings resulting from this cross showed seedling characters intermediate between those of the parents. Thus there is no genetic barrier to hybridisation between E. stellulata and E. pauciflora. The rare occurrence of hybrids may result from occasional out of season flowering, e.g. one E. pauciflora individual was observed in flower in May, 1962 at Cooma, but the fact that only one or two hybrids have been found indicates that the separation in flowering time is an effective barrier to hybridisation.

Previous ecological studies

McLuckie and Petrie (1927) discuss the various associations occurring in the Kosciusko Plateau. A single association of Eucalyptus forest is named with three consociations. One of these is E. stellulata consociation occurring in small areas between 4,000 - 5,000 ft.

They state "we have not, up to the present been able to discover definitely the factors leading to the interruption of the ecotone, (E. coriacea - gunnii ecotone) by occasional consociations of of E. stellulata, but it is possible that a slightly greater degree of exposure may be the key to its presence. Nor did we observe any difference in the floristic composition of the two communities".

Pidgeon (1937) working in the Central coast of N.S.W. describes the E. pauciflora - stellulata association, which characterises the areas of the tablelands approaching subalpine conditions, and is represented in the locality west of Moss Vale, N.S.W. It was considered that the association was controlled by subclimatic rather than edaphic factors.

Fraser and Vickery (1939) in discussing the vegetation of the Barrington Tops district of N.S.W. state that E. stellulata is "most commonly found near water and forms a community along creek banks and swampy margins". Changes from swamp to grassland and grassland to forest occur as a result of swamp drainage by entrenchment of the main stream. E. stellulata becomes established along the banks of streams after the stream has become entrenched to a depth of 3 - 4 ft.

"The absence of E. pauciflora from the region immediately surrounding the swamps is probably due to the waterlogging of the soil. E. stellulata appears to be capable of growing under conditions of greater soil moisture than E. pauciflora as it is common along the margins of streams and parts of the swamps".

Pryor (1939) describes the development of the E. pauciflora/stellulata association in the Australian Capital Territory. The association is developed on high tablelands at an elevation of 3,000 ft. but the limits vary from 2,000 ft. to over 4,000 ft.

depending on microclimatic compensations. It is considered that the association is controlled by the interplay of temperature and rainfall from Gudgenby 3,200 ft. and 32" rainfall to Canberra 2,000 ft. and 23" rainfall. The short growing season either through temperature or lack of rainfall precludes other vegetation types.

The soils are mostly derived from granite, some from quartz porphyry and some from sedimentary rock.

Costin (1954) describes the E. pauciflora/ E. stellulata alliance of the Monaro Region and lists a number of associations including E. pauciflora/ E. stellulata, E. stellulata and E. stellulata/camphora. These associations are developed under moist conditions on cold and poorly aerated soils. The E. stellulata/ E. parvifolia association is restricted to poorly aerated soils of the eastern montane tract.

The soils carrying the E. pauciflora/ E. stellulata association in the subalpine areas at approximately 4,000 ft. have been classed as alpine humus, whilst at lower elevations the soils are brown soils of light texture, meadow soils or brown podsolics.

Comparative species

E. pauciflora occurs on a greater variety of sites than E. stellulata. It is found from near sea level to altitudes of 5,500 ft., in areas of from 20 - 60 inch rainfall, and on a variety of soil types. It is a species of well drained often quite dry sites.

E. pauciflora shows considerable variability and a number of cline forms have been described, Pryor (1956). The form generally associated with E. stellulata is a woodland type although in some areas, e.g. the headwaters of the Cotter River, A.C.T. the montane form is found bordering on subalpine flats carrying E. stellulata.

Comparisons between the two species have been made over a range of elevations from 2,000 - 4,500 ft.

Experimental studies

Moore (1962 unpublished) has carried out field and laboratory experiments to determine the limits of cold temperature tolerance of E. pauciflora and E. stellulata and found that one year old plants of the latter species were the more cold tolerant, but are killed by exposure to temperatures below 18°F for two hours.

Other species

The following species have been studied briefly under experimental conditions or observed in the field in relation to waterlogged conditions.

E. aggregata Deane and Maiden, "black gum" is an umbrageous tree up to 60 ft. high. It occurs in Tasmania and on the southern and central tablelands of N.S.W., always in damp situations, often marshy and with impeded drainage.

E. macarthuri Deane and Maiden, "Camden woolly butt" is a spreading tree with dense crown occurring in restricted areas of the southern and central tablelands of N.S.W. It grows mainly on flats subject to flooding, or adjacent to streams on heavy alluvial soils.

E. ovata Labill "swamp gum" is a widespread species occurring in Tasmania, Victoria, New South Wales, and South Australia. It grows mainly on damp poorly drained land from sea level to elevations of 4,000 ft. and survives on areas subject to inundation for part of each year.

Patton (1929) describes E. ovata in Victoria as an inhabitant of areas that have a constantly moist soil. Its distribution is controlled by soil water and it occurs on a wide range of soil types. Clifford (1952) discussing the distribution of E. ovata in the Dandenong Range, Victoria, states that "usually, E. ovata is restricted to sites that are badly drained, where the soil aeration is bad, as is evident from the gleying of the subsoil". It has been observed growing where the surface soil is waterlogged for several months of the year. It grows equally well on krasnozem, silty loam podsol, sandy loam podsol and alluvium.

E. parvifolia Cambage "small leaved gum". This species is endemic to a restricted area of the eastern montane tract of the Monaro Region of N.S.W. and occurs only on poorly aerated soils. It is a small tree, 20 - 30 ft. high of compact form.

E. rudis Endl "moitch" is a member of the Series Exsertae and apart from E. camaldulensis, is the sole species of this group found in Western Australia. It is a tree 30 - 50 ft. high, and is confined to streams, river banks and damp depressions subject to flooding, in the south west corner of Western Australia.

E. camaldulensis Dehn "Murray red gum". This is probably the most widespread species of Eucalyptus. The best known occurrence is along the Murray River and its tributaries, but it occurs also quite extensively in all other mainland states. It is typically a riveraine species, but also occurs extensively on flood plains. In some parts of South Australia it is found on higher hill slopes, but the areas where this occurs are small. In Central Australia it is found in water courses often dry for lengthy periods.

E. camaldulensis is an important timber species in Australia and has been planted widely overseas.

Jacobs (1955) discusses the distribution of this species in relation to soil water, and outlines characteristics which are considered of adaptive value in enabling E. camaldulensis to grow under waterlogged conditions. Patton (1929) considers that the distribution of E. camaldulensis, like that of E. ovata, is controlled by soil moisture.

Summary

The major feature in the distribution of species which occur naturally on soils subject to waterlogging for a large part of each year, is their general restriction to sites of poor drainage and absence from the drier adjoining areas where other species occur. Their distribution is sporadic and usually discontinuous. In most cases they occur in pure stands.

CHAPTER 3

FIELD TRANSECTS

In order to study species distribution in the field transects were put down in typical field situations where the species to be studied occurred. From observation the boundaries appeared to be sharp, the species of the swamp areas being confined to the flat, poorly drained sites, and the species of the drier area restricted to the slopes. This was apparent for the mature trees, and easily identified saplings, but without assessment it was not possible to determine the distribution pattern of the regeneration to know whether seed from the swamp species, which must fall on dry ground, fails to germinate or in fact germinates and produces seedlings which, for some reason are later eliminated and prevented from reaching maturity. Equally, the crowns of the species of the drier sites often overhang the swampy areas and seed must certainly be shed onto those soils. However no seedlings appear able to establish themselves.

Method of assessment

Sites representative of the distribution pattern, and amenable to accurate mapping were selected at each location. The aim was to commence the transect within the type of the drier slope, move downslope onto the low lying, swamp area and in some cases up the other side. Using the longer side of each transect as base line the co-ordinate of each tree was measured and recorded. The species was identified, and the diameter at breast height over bark and the crown spread were measured. The crown spread was taken as the mean of two measurements at right angles. The total height was estimated to the nearest three feet, occasional spot checks were carried out using topographic abney level to determine the accuracy of this estimation.

With seedlings up to two feet in height, all individuals were first located and marked with a cardboard marker using a different colour for each species. As the location of each plant was recorded, the marker was removed to ensure that none was missed. It was necessary to adopt this method of marking as in some cases there were more than 120 separate seedlings in an area of only half a square chain.

The transect lengths varied from 3 to 5 chains depending on the situation, and most were ½ chain wide, although two of 1 chain were laid out.

As there are very few records available in Australia for the establishment of permanent plots to assess Eucalyptus growth and regeneration patterns, it was decided to mark these transects permanently and to plot all trees, both adult and juvenile, so that future measurements can be made, to determine the fate of the present seedling population.

A collection of the plants in the subordinate layers of shrubs and grasses was made for each plot, separating them into two classes, those on the swamp and those removed from it. Generally speaking, the edges of the swamps were recognised as delineated by the presence of Carex appressa.

Soils were examined at representative points in each transect and profile descriptions taken. Particular note was made of the effective root depth in each profile, and the density of the grass cover.

The altitude, degree of slope and aspect, were recorded for each transect.

Descriptions and details of the transects are given in Appendix A.

The results have been prepared in the form of transect plans drawn to a scale of 1 inch = 1 foot and reduced photographically. The location and crown diameter were plotted for each tree, the dotted line of crown spread indicating that this portion of the crown was below that of another tree. The crown spread has been depicted as a circle for convenience in plotting although in fact the shape is usually somewhat irregular.

Where a complete assessment of regeneration was made the location of each plant has been plotted and designated by a symbol for each species. The size of the symbol does not bear any relation to seedling height or spread.

The transect elevations were drawn to the same scale and show diagramatically tree heights and crown diameter for each species. The lines beneath each profile denote the presence of regeneration either as continuous or scattered.

Soil constants of field capacity, waterholding capacity and wilting point were determined by methods of Piper (1942) for the top 4" in swamp and dry site soils at Cotter Hut A.C.T. and Coree A.C.T. E. camphora and E. dalrympleana occur in the latter area in a pattern of distribution similar to that at Wee Jasper and the soils have a similar morphology at both locations.

Soils profiles drawn to scale as indicated, depict soil types at points along the transect.

Results

The results are based on the detailed assessment of each transect and field observations made over a number of locations in areas within the A.C.T. and N.S.W.

E. pauciflora/stellulata: Transects 1 - 4

The transects carried out at Peppercorn N.S.W. altitude 4,450 ft. and Cotter Hut A.C.T. altitude 3,460 ft. show clearly the distribution of E. pauciflora and E. stellulata in rebtion to sub alpine swamps. Neither species occurs on permanently swampy ground and where E. stellulata occurs in low lying areas it is generally on slight rises which, although only inches above the surrounding area, are above the region of permanent waterlogging.

Temperature and rainfall figures representative of the two areas are given in Appendix B. Snow would commonly lie for some months each year at Peppercorn and for short periods on the flats in the Cotter Hut area.

E. stellulata is present as regeneration at and below the boundary line between forest and grassland at Peppercorn (Fig. 5) but there are clear indications of frost damage on most seedlings below this line. E. pauciflora does not extend into low lying ground either as mature trees or regeneration.

In the Peppercorn area it is clear that regeneration becomes established largely in the openings and not under the tree canopies.

Both species are represented in the tree and regeneration strata on the drier sites in the Peppercorn area approx. rainfall 60" per annum, but E. stellulata as trees are largely confined to the wetter sites in the Cotter Hut area approx. rainfall 40" per annum. Although regeneration of the latter occurs largely on the wetter sites, it is also present with E. pauciflora indicating that germination takes place on the drier sites but that the seedlings are usually eliminated in some way before reaching maturity.

Fig. 5

E. stellulata regeneration on stream bank Peppercorn N.S.W. Natural "tree line" with E. pauciflora and occasional E. dalrympleana in background.

The soils differ between the higher and lower altitude sites. At Peppercorn the soils are alpine humus derived from granite. Depth to parent material is approx. 24 - 28", root penetration to 18 - 20". Where E. stellulata occurs on the swamp edge the soils are much deeper and more highly organic. Fig. 10 shows the roots of one seedling penetrating through the black humus layer into a band of deposited gravel at a depth of 28".

In the Cotter Hut area the soils are red brown podsolics on the drier sites and alluvials on the swamps. The effective root depth varies from 12" to 26" respectively indicating that the aeration of the alluvial soils is good throughout probably due to the high content of sand and gravel. The permanent wilting point, field capacity and waterholding capacity percentages are higher for the swampy soils than the dry site soils.

TABLE 2

SOIL CONSTANTS COTTER HUT A.C.T.

Soil Constant as % of oven dry weight	Swamp Site Soil	Dry Site Soil
Permanent Wilting Point	17.1	10.5
Field Capacity	57.5	30.3
Water Holding Capacity	72.9	50.6

The evidence suggests therefore that

1. E. stellulata, whilst not occurring under permanently waterlogged conditions is more tolerant of wet conditions than is E. pauciflora.

2. Although _E. stellulata_ is present as regeneration with _E. pauciflora_ in drier sites in areas of 40" rainfall it is largely eliminated before reaching tree height, suggesting that it is less resistant to dry conditions than _E. pauciflora_.

E. dalrympleana/camphora: Transects 6 - 9

These transects were carried out in Wee Jasper State Forest N.S.W. at altitudes of 2,500 to 2,600 ft. _E. dalrympleana_ and _E. camphora_ are the main Macrantherous species present, with some _E. stuartiana_ F.v.M. The Renantherous species occurring are _E. pauciflora_, _E. dives_, _E. robertsoni_, _E. macrorrhyncha_ and occasional trees of _E. stellulata_.

Throughout the area the pattern of _E. camphora_ as the only Eucalyptus species on the swamps is clear and is shown by the transects. _E. camphora_ does not grow in running water but is common on flats which are almost continuously waterlogged (Fig. 1 & 2) _E. camphora_ regeneration is sparse on swampy sites and because of the dense growth of grass and sedges to a height of 12 - 18 inches seedlings are extremely difficult to locate until they appear above t this layer. The number of _E. camphora_ seedlings recorded off the swamp area with seedlings of the other tree species was greater than the number on the true swamp as shown in Transects 6 and 7. At the same time only a few of the mature trees of _E. camphora_ were located away from the swamp fringe and these were mainly in areas where no other Macrantherous species were present. _E. dalrympleana_ both as trees and regeneration does not occur on swampy sites although in many cases e.g. Transect 8 large trees carrying seed overhang these sites.

The swampy and dry site soils in this area differ markedly from one another. Those of the swamp being compacted clays, highly organic, with signs of gleying usually within a foot of the surface. The water table is high and at or above the surface for a large part of each year. Tree roots are abundant in the top 12 inches, although living roots, apparently of E. camphora, were found in the gley layers at depths up to 28". Off the swamp the soils are grey or brown podsolics derived from granite. The effective root depth is to the decomposing parent material in most cases but there is a congregation of roots in the upper 10".

The Permanent Wilting, and Water Holding Capacity percentages are higher for the swamp soil than the dry site soil.

TABLE 3

SOIL CONSTANTS COREE FLAT A.C.T.

Soil Constant as % of oven dry weight	Swamp Site Soil E. camphora	Dry Site Soil E. dalrympleana
Permanent Point	30.8	10.2
Field Capacity	not det.	43.2
Water Holding Capacity	85.7	48.0

The evidence from the transects suggests that:

1. E. camphora is clearly a species of the sub alpine swamps, occurring largely on heavy clay soils, poorly aerated and subject to inundation for lengthy periods.
2. E. camphora is well represented in the regeneration layers two to three chains away from the swamps but

poorly represented in the tree stratum at the same points.

3. E. dalrympleana is confined to well drained sites and does not occur as either seedlings or adult trees on low lying sites subject to waterlogging.

E. aggregata Transect 5

The transect is typical of the distribution of E. aggregata in areas of the southern tablelands of N.S.W. This species also occurs in the central tablelands of N.S.W. and in Tasmania but has not been studied in these areas.

The Macrantherous species present in Transect 5 are E. aggregata and E. viminalis, the Renantherous E. stellulata and E. pauciflora. E. aggregata and E. stellulata are more tolerant of poorly drained conditions than the other two species, neither of which are present on the swamp site.

The soils are loamy fine grained sands overlying coarser grained granitic parent material. The swampy soils contain more organic matter than those on the drier site and there are signs of orange mottling around the roots.

Figs. 6 and 7 show E. aggregata as trees and seedlings in relation to swamp conditions. Although it occurs on the swamp its growth appears to be much better on the swamp fringe where trees up to 60 ft. are common.

Fig. 6

E. aggregata Jerangle N.S.W. mature tree 60 ft. high on swamp edge.

Fig. 7

E. aggregata regeneration on swamp Jerangle N.S.W. Note dense grass and sedge growth.

PART II

ADAPTATIONS TO WATERLOGGED CONDITIONS

Daubenmire (1959) defines an adaptation as "any feature of an organism, or its parts, which is of definite value in allowing that organism to exist under the conditions of its habitat" and states that "a morphological feature is but an expression of physiologic processes otherwise unevident, and morphological characteristics should always be subjected to physiologic experimentation before they are classified as having survival value".

The structural characteristic common to most hydrophytes is the sponginess of their tissues, resulting from the development of enlarged cells or intercellular spaces which become, or remain, filled with gases. These cavities generally form a continuous system of air passageways by means of which submerged organs can exchange gases with the air by way of the stomata in the protruding organs. This gaseous exchange is necessary because of the decrease in oxygen resulting from the excess of water in the rooting medium. Evidence suggests Conway (1940), Russell (1958), that root development is affected if the oxygen content falls below 9 - 12% depending on the crop. The oxygen content in swamp soils is generally below this figure, although in free water above these soils it may be well above the critical concentration. It is stated by Went (1959) that the uptake of inorganic compounds necessary to enable growth is mainly in the form of ions. The accumulation of ions occurs against a concentration gradient and the energy required to enable this comes from respiration. Respiration is only possible with oxygen present therefore ion uptake is dependent upon an adequate supply of oxygen. Thus plants whose roots are under oxygen poor conditions usually require some means by which additional oxygen can be supplied to the roots.

Conway (1940) showed that the oxygen content of air from the internal spaces of roots of *Cladium mariscus* was 17% with tops attached and only 3% when tops above the waterlevel were removed; indicating that this species was adapted to waterlogged conditions not because of the ability to exist on lower oxygen concentrations but because of the internal structure which allowed rapid gas exchange from shoots to roots.

Alberda (1953) showed a similar effect with young plants of lowland rice. Older plants develop as well a superficial mat of fine roots that grow either horizontally in the irrigation water or vertically upward into the air and thereby absorb oxygen.

The development of pneumatophores in mangroves and knee roots in *Taxodium distichum*, *Pinus serotina* and *Nyssa aquatica* Wilson (1889) are considered as adaptations which assist in the absorption of oxygen.

Leyton (1958) found that *Salix atrocinerea* was able to continue growth in the complete absence of oxygen in the external medium but suggests that there may be an internal supply of oxygen reaching the roots by way of the shoots even though the obvious structural modifications of spongy tissues are not present in willow.

Emerson (1921), Weaver and Himmel (1930) describe the rooting systems of some hydrophytes and indicate that most show a strong development of horizontal roots above the water table. They consider that this assists in survival by bringing the root system into a relatively well aerated zone. The roots were generally of small diameter and possessed many fine laterals thus giving a large surface for the absorption of oxygen.

Bergmann (1921) and Laing (1932), discuss the development of adventitious roots in peat soils with high water tables and consider that the development of these roots in zones where oxygen content is normal enables the plants to survive. Laing lists *Picea excelsa*, *P. sitchensis*, *Pinus sylvestris*, *P. montana*, *Abies grandis* and *Larix leptolepis* as developing adventitious roots when planted in peat soils.

Musson and Carne (1910), described the development of adventitious roots on *Melaleuca linariifolia* and suggested that they are of assistance in upward sap movement during times of stress such as when soil roots are completely immersed in water and unable to function normally.

The major adaptations to waterlogged conditions are therefore considered to be (a) development of spongy aerenchymatous tissue (b) formation of adventitious roots (c) a shallow rooting system which brings the roots into a zone of normal oxygen concentration above the waterlogged soil. Each of these adaptations is found in some degree, in Eucalyptus species which occur naturally in areas subject to waterlogging for long periods.

CHAPTER 4

PRIMARY ROOT SYSTEMS

Toumey (1926) examined the progressive development of the root systems of nearly one hundred species of American trees from germination to the end of the first growing season. He found that the initial juvenile root system of all species, follows a definite pattern of development after germination, but that some species exhibit a much earlier tendency to change under change in external conditions. The degree of flexibility, and the inherent capacity for adjustment to variations in soil moisture conditions, appear to be one of the determining factors in survival following germination on any given site.

Acer rubrum occurs naturally both on swamps and dry upland sites. It was found that this species possessed a flexible root system, forming a short tap root and long laterals on swamps and a deeply penetrating tap root and short laterals when grown on dry sites. By comparison Taxodium distichum, a species found only in swampy sites, develops a short tap root and numerous laterals when grown under either swampy or dry conditions. It is argued that the formation of a shallow rooting system, and the inability to develop deep roots on dry sites, would prevent it from becoming established away from swampy regions.

The tap roots of most tree species will not penetrate waterlogged soil but die at the water aurface and horizontal laterals are formed above the waterlogged zone, e.g. Pinus strobus, Abies balsamea Emerson (1921), although it is claimed that the roots of Betula pumila Emerson (ibid) and some species of Salix are able to grow under water.

Jacobs (1955) states that E. camaldulensis develops a high root/shoot ratio which enables it to become established on flood plains. Seedling survival depends largely on its ability to drive its roots through gley layers to an aerated soil below, and if it is inundated for a long period before the roots are down to this level, it generally dies.

The gley layers vary in thickness from 6" to 5 ft. or more depending on the degree of flooding but below them the clay is reasonably well aerated and is moist but not sodden. In some cases sandy, well aerated, aquifers underly the gley layers.

Jacobs (ibid) considers that E. robusta has a root system similar to E. camaldulensis in its ability to penetrate below a flooded layer.

Zimmer and Grose (1958) studied the root systems of seedlings of fourteen Victorian Eucalypts and found that species native to dry areas develop a long tap root, with a few weak laterals, whilst those on more favourable sites usually form a shallow fibrous root system. All species were raised under similar conditions in grey, peaty sand and final assessment was carried out at 18 weeks of age.

Observations with E. camphora have indicated that, like E. camaldulensis, it develops a long initial tap root which will penetrate deeply into, and through, the gley layer. The areas where E. camphora occurs are generally alluvial fans formed by an obstruction, or deviation, in the original stream. Alluvial material has been transported and deposited over the original parent material followed by the formation of gleys. Waterworn floaters are common in the soil profile at depth and there are signs of an underlying gravel layer, which suggests that aeration may be better at depth than in the heavy aurface soils.

E. camphora seedlings dug up in the field, have had a long tap root with some horizontal laterals in the upper few inches, but with very few present over the rest of its length. In many cases this tap root was dead due possibly to long periods of inundation, although the plant was still growing, by virtue of horizontal roots in the upper well aerated layer.

One of the major functions of the rooting system is to provide structural support for the aerial parts. Ramification of roots throughout the soil provides resistance to overturning induced by wind pressure on the stem and leaves. In trees, the more deeply penetrating roots assist greatly in maintaining stability.

Overturning, due to wind, is fairly common with *E. stellulata* and *E. camphora* in waterlogged soils and almost invariably, when the roots of upturned trees have been examined, there was no sign of a broken tap root. The tap roots on these trees were probably killed in the seedling stage, as described above, and, although the tree has been able to grow due to a surface root system built up in the better aerated surface layers, it has not had normal resistance to wind.

When trees on dry sites are overthrown by wind they commonly die, in contrast to those on swamp sites, which mostly survive. On dry sites the roots are torn and broken and soon dry out, whereas on swamp sites the roots are not broken and remain alive due to the soft nature of the soil and the wet conditions. The normal inhibition of epicormic buds is removed when trees are blown over and numerous shoots develop from the stem. Fig. 8 shows this occurrence with a tree of E. stellulata which had been blown over approximately 3 months before the photograph was taken.

Layering, namely the formation of roots from stems which have been blown over and become partially embedded in the moist soil, sometimes occurs with E. camaldulensis, E. stellulata and E. robusta as a result of wind throw onto swampy ground.

It has been noted (Chapter 3), that the roots of E. stellulata were found at depth in the alluvial soils at Cotter Hut, and it appears that these roots penetrate through the surface layers to a well aerated, gravel layer beneath. The effective root depth of the soils of the wetter sites is greater than that of the soils from the drier sites, and although root systems of plants excavated in the field have shown marked differences in root lengths, these differences may be due largely to the soil type rather than the initial root habit of the species themselves.

The following experimental evidence supports this idea.

To compare the initial root habits of E. camphora and E. dalrympleana, a nursery cold frame was filled with a well drained sandy loam to a depth of 42 cm. and seed of both species collected at Coree, A.C.T. from adjacent sites, was broadcast onto the seed bed and covered lightly with sieved sphagnum moss. Germination occurred in both species within a fortnight (the trial was commenced in the open in August) and 15 seedlings for each species were sampled at intervals. The length of the root system was taken from the

Fig. 8

E. stellulata blown over. Roots alive in wet soil; epicormic shoots emerging from dormant buds on the stem.

Fig. 9

E. robusta grown for six months submerged to soil level. Dense growth of surface roots in the water.

hypocotyl to the end of the tap root, and the shoot length from the hypocotyl to the growing tip. At final assessment the division between root and shoot was taken at the base of the lowest lignotuber pair, i.e. the original level of the cotyledons.

The results are presented in Table 4. The root/shoot ratios for the two species are not significantly different although the rate of root and shoot growth was greater initially for E. dalrympleana.

TABLE 4

MEAN ROOT/SHOOT RATIOS FOR LENGTH

E. CAMPHORA AND E. DALRYMPLEANA

Age in weeks	length in mms.					
	E. camphora			E. dalrympleana		
	Root	Shoot	R/S	Root	Shoot	R/S
6	61.4	15.1	4.1	61.7	14.7	4.2
9	119.5	46.5	2.6	143.4	52.9	2.7
12	224.1	107.1	2.1	265.7	114.0	2.3
16	381.5	357.9	1.1	415.6	344.9	1.2

At age 16 weeks the roots of both species had penetrated almost the full depth of the soil in the cold frame.

It is clear therefore, that although these figures do not necessarily reflect the field situation they indicate that under uniform optimum consitions for growth there is no difference in the root/Shoot ratios for length of E. camphora and E. dalrympleana. It has not been possible to determine whether differences between the two species occur when both are grown in the field on dry and wet sites. Direct seedings in the field, followed by examination of root systems after seedlings have become established woul be necessary to elucidate this point. This has been commenced at Coree A.C.T., but to date, it has not been possible to get enough seedlings established to the stage where measurements can be taken.

Whilst there was no difference in the root/shoot ratios for length of both species, there was a difference in the number of laterals emerging and the position at which they emerged.

Measuring from the cotyledonary node, the number of lateral roots emerging was recorded for ten plants of each species at 43 weeks. These roots assumed an almost horizontal position. As seen from Table 5 a high percentage of lateral roots on E. camphora occurs in the first 2.5 cm., and 63% of all laterals to a depth of 50 cm. were found in the top 10 cm., whereas, those of E. dalrympleana are predominantly below 2.5 cm. The total number per plant for E. dalrympleana was higher than for E. camphora.

TABLE 5

MEAN NUMBER OF LATERAL ROOTS PER UNIT DEPTH FOR

E. CAMPHORA AND E. DALRYMPLEANA

Depth in cm.	*E. camphora* No.	*E. camphora* % of total	*E. dalrympleana* No.	*E. dalrympleana* % of total
0-2.5	4.9	31	0.9	4
2.5-5	2.6	16	4.6	22
5-10	2.5	16	5.3	26
10-15	1.2)		2.2)	
15-20	0.9)		2.3)	
20-25	1.2)	37	1.8)	48
25-30	0.4)		1.2)	
30-35	0.6)		0.6)	
35-40	0.5)		0.7)	
40-45	0.7)		0.3)	
45-50	0.3)		0.6)	
	15.8		20.5	

The difference in means of total number of lateral roots per species is significant $P<0.01$.

The presence of a large proportion of lateral roots in the top 5 cm. of the main root may indicate that drying of the surface soil layers could result in damage or death more quickly for *E. camphora* than for *E. dalrympleana*, where a high proportion of lateral roots are in the lower regions. The habit of forming surface roots whilst assisting the plant to survive on swamp soils with poor aeration, may be a disadvantage when seedlings of both species grow together under conditions of moisture stress in the surface soil layers.

Table 6 shows the results of a trial similar to that described above for root/shoot ratios which was carried out with E. pauciflora and E. stellulata using deep seed boxes. The mean of 20 plants for each species was taken. Medium sized plants were sampled.

TABLE 6

MEAN ROOT/SHOOT RATIOS FOR LENGTH E. PAUCIFLORA AND E. STELLULATA

Age in weeks	Length in mms.					
	E. pauciflora			E. stellulata		
	Root	Shoot	R/S	Root	Shoot	R/S
3	70.3	19.0	3.7	64.1	17.1	3.8
7	90.0	27.0	3.3	92.0	27.0	3.4
12	148.0	55.0	2.7	172.0	58.0	3.0

The root/shoot ratios for the two species are not significantly different although the primary root lengths at age 12 weeks are significantly different, at $P < 0.01$. This may suggest an initial rapid root extension for E. stellulata in comparison with E. pauciflora.

It is common for species of swampy sites, e.g. E. rudis, E. robusta, and E. camphora, to develop many roots right at, and above, the soil surface when subjected to waterlogging. With shallow submergence the roots leave the soil, grow up to the water level, bend and then grow down again so that part of the root lies on the water surface. This habit means that these roots are growing in a relatively well aerated zone.

The surface roots of young plants of these species when grown in the glasshouse, are vigorous with an extended root cap and zone of elongation, behind which many short laterals arise. In water the rapid development of these roots which are usually covered with heavy algal growth, forms a fibrous mass. Fig. 9 shows the dense growth of the surface roots from a plant of E. robusta which had been growing submerged to the soil surface for more than six months, some roots in this case were more than a metre long.

Fig. 11 shows the development of surface roots from E. robusta in comparison with E. propinqua where they are absent or occur to a much lesser degree. Both species had been grown in soil waterlogged to the surface of the containers. The tops were harvested at cotyledonary level before the photograph was taken. Oven dry weights of roots of both species grown under waterlogged and freely drained conditions are given in Table 7.

TABLE 7

OVEN DRY WEIGHT OF ROOTS GROWN UNDER WATERLOGGED AND FREELY DRAINED CONDITIONS

Water Table	Mean Oven Dry Weight in gms.	
	Treated 5 months	Age 7 months
	E. robusta	E. propinqua
Free drainage	3.7	3.8
Waterlogged free water on surface	3.8	0.8

There is no difference between the mean oven dry weight of roots of the two species, when grown in freely drained soil, but a highly significant difference when grown in waterlogged soil.

Fig. 11

Strong development of roots of E. robusta (left) on surface of waterlogged soil compared with E. propinqua grown under the same conditions. Tops removed at level of cotyledons.

Fig. 10

E. stellulata deeply penetrating tap root 75 cms. Strong lignotuber development.

Under freely drained conditions the roots of both species explored fully the soil content in the containers which were 30 cms. deep. However, under waterlogged conditions, the roots of E. robusta did not penetrate more than 7.5 cms., but instead, formed a dense matted growth on and near the surface. The primary roots of E. robusta developed aerenchymatous tissue similar to that described on the stems. (See Chapter 5)

From observation and experimental evidence it appears that the primary root systems of the Eucalyptus species studied are adaptable to changing conditions of soil permeability, depth and moisture content. At the same time the root systems of swamp species show adaptation to their environment in the formation of lateral roots at and close to the soil surface. This is often associated with an extended tap root which may assist in aeration at depth and stability in wet soils.

E. robusta has been planted widely and successfully overseas in well drained areas which indicates that its root system, whilst adaptable to swampy conditions, possesses a degree of flexibility and an inherent capacity for adjustment to variations in soil moisture conditions. This is in contrast to Taxodium distichum Toumey (1926) which possesses an inflexible root system.

CHAPTER 5

AERENCHYMA

Within one or two days of immersion in water the bark on seedlings of some species, e.g. *E. robusta*, *camphora*, *rudis* becomes spongy and thickened, the epidermis is ruptured, torn and often sloughed off. This development occurs first at the water level but soon extends over the full length of the submerged stem and to approximately a centimetre above the surface. Deep submergence results in slow formation of this tissue on the lower part of the stem but a rapid development still occurs near the water surface. Some species when grown in soil waterlogged to the surface develop this characteristic of spongy bark, both on the lower stem and main root. Fig. 12. After a longer period of immersion stem borne (cladogenous) roots develop on some species. The development of these roots will be discussed later.

Macroscopically the spongy bark resembles lacunose tissue formation found on *Lythrum salicaria* and defined as aerenchyma Shenck (1889) From a physio-ecological point of view Shenck considered that it might well assist in supplying air to the submerged parts.

Mylius (1913) examining aerenchyma from a purely histological point of view called it lacunose polyderm and defined it as a succession of endodermal layers, each separated from the next by one or more layers of non suberised cells with many intercellular spaces. The whole tissue may become twenty or more layers thick.

Küster (1925), a plant pathologist, proposed the term hyperhydric tissue, and considered that its

Fig. 12

E. robusta grown in waterlogged soil; Matted surface roots; aerenchyma formed on the stem.

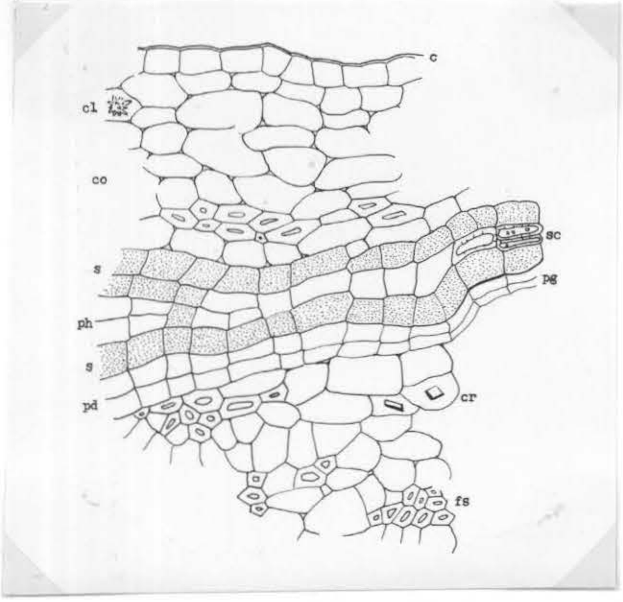
production is due to a surplus of water which causes radial lengthening of the cells and a reduction in the contact surface area of neighbouring cells which increases the intercellular spaces and leads to disintegration at its periphery. It is interesting to note that Küster rejects Schenck's assumption of improved air supply on the grounds that the tissue is also formed in humid air. He considers that the abnormal growth is useless and even disadvantageous as it exposes the torn and fissured surface to fungal invasion.

The only reference to aerenchymatous tissue on Eucalyptus is in the Report of Research and Investigation University of Melbourne 1952. In summarising work being carried out with E. camaldulensis. it is stated that a zone of proliferating tissue developed at and below water level on the stems of submerged seedlings. "No fungal association could be found in this tissue." There is no published record of this work and the manuscript has been lost Chinner (personal communication 1962)

Fig. 13 shows a cross section of the periderm of E. robusta age six months 2 cm. above the cotyledons. The plant had been grown under normal freely drained conditions. The cuticle is intact at this stage. The periderm is composed of layers of suberised and non-suberised cells.

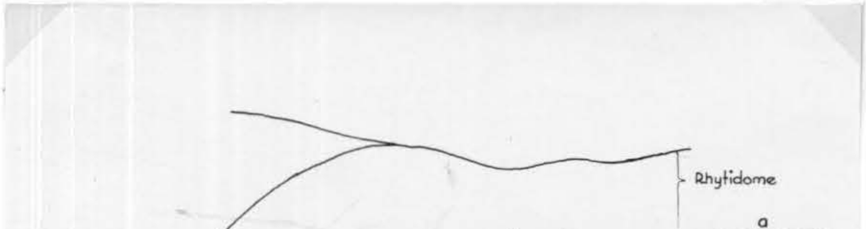
Fig, 14 shows diagramatically the development of the rhytidome in a seedling of E. robusta which had been submerged in water. The layers of suberised cells do not alternate regularly with non-suberised cells as in the formation of classical polyderm, but vary in thickness from one cell up to five cells deep in places without non-suberised cells between.

Fig. 13



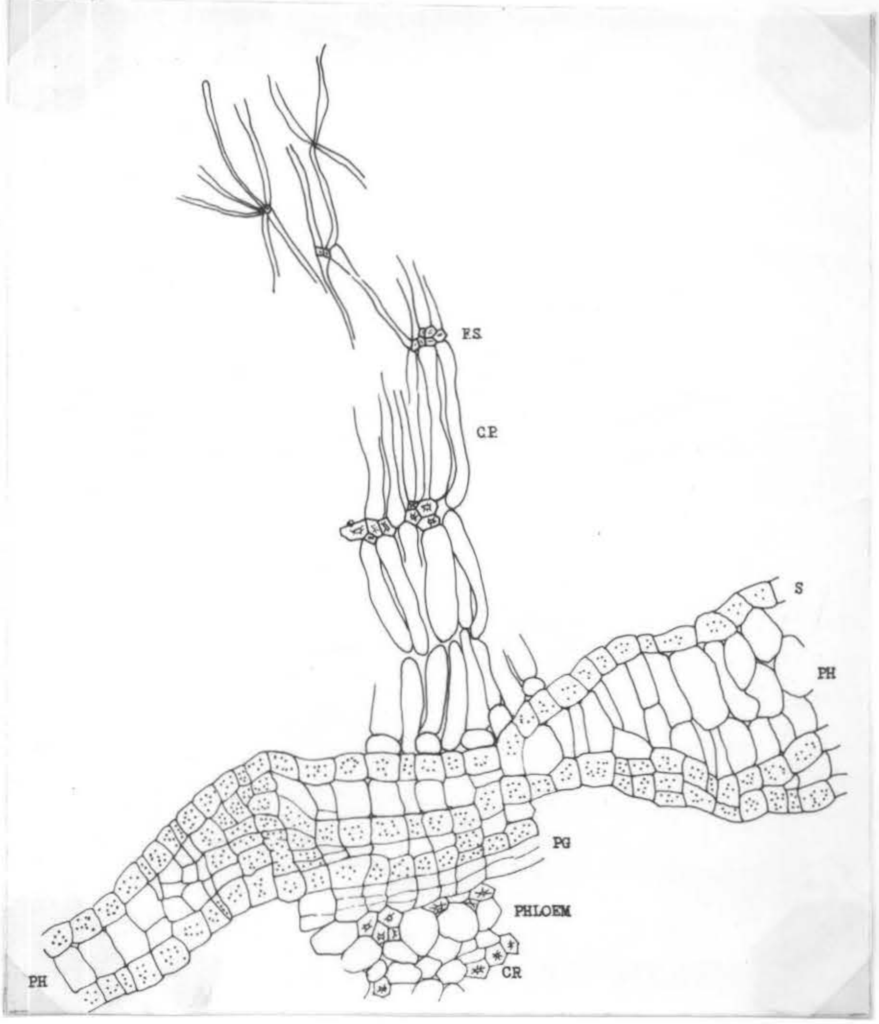
Cross section periderm of E. robusta age 6 months 2 cm. above cotyledons cuticle intact X 280
C cuticle, cl crystal cluster, cr single crystal, co cortex, s suberised cells of the periderm, ph non-suberised cells (phelloid), sc sclerified cells, ph phelloderm pg phellogen, fs fibre strands.

Fig. 14



Development of rhytidome in E. robusta seedling immersed in water a,b,c,d,e layers of suberised cells varying in thickness from one to five cells deep.

Fig. 15



Cross Section periderm of E. robusta seedling immersed in water for 3 months.
F.S. fibre strands, C.P. cortical parenchyma, torn and broken, large air passages present, S. suberised layer, P.H. phelloid cells, non-suberised, P.G. phellogen C.R. single oxalate crystals.

Fig. 15 shows in detail portion of the aerenchyma tissue on the stem of an E. robusta seedling which was immersed in water for three months. The outer layers are torn and broken and are merely a loose mass of parenchyma cells. Small bundles of fibre strands are present within the cortical parenchyma and act as "reinforcing rods" to hold this loosely packed tissue together. The layers of suberised cells are irregular in thickness and may be separated by non-suberised phelloid cells.

There was no sign of fungal invasion in the cells of the aerenchyma.

A number of experimental submergence trials were carried out to establish whether the formation of aerenchyma tissue on the stems was correlated with survival.

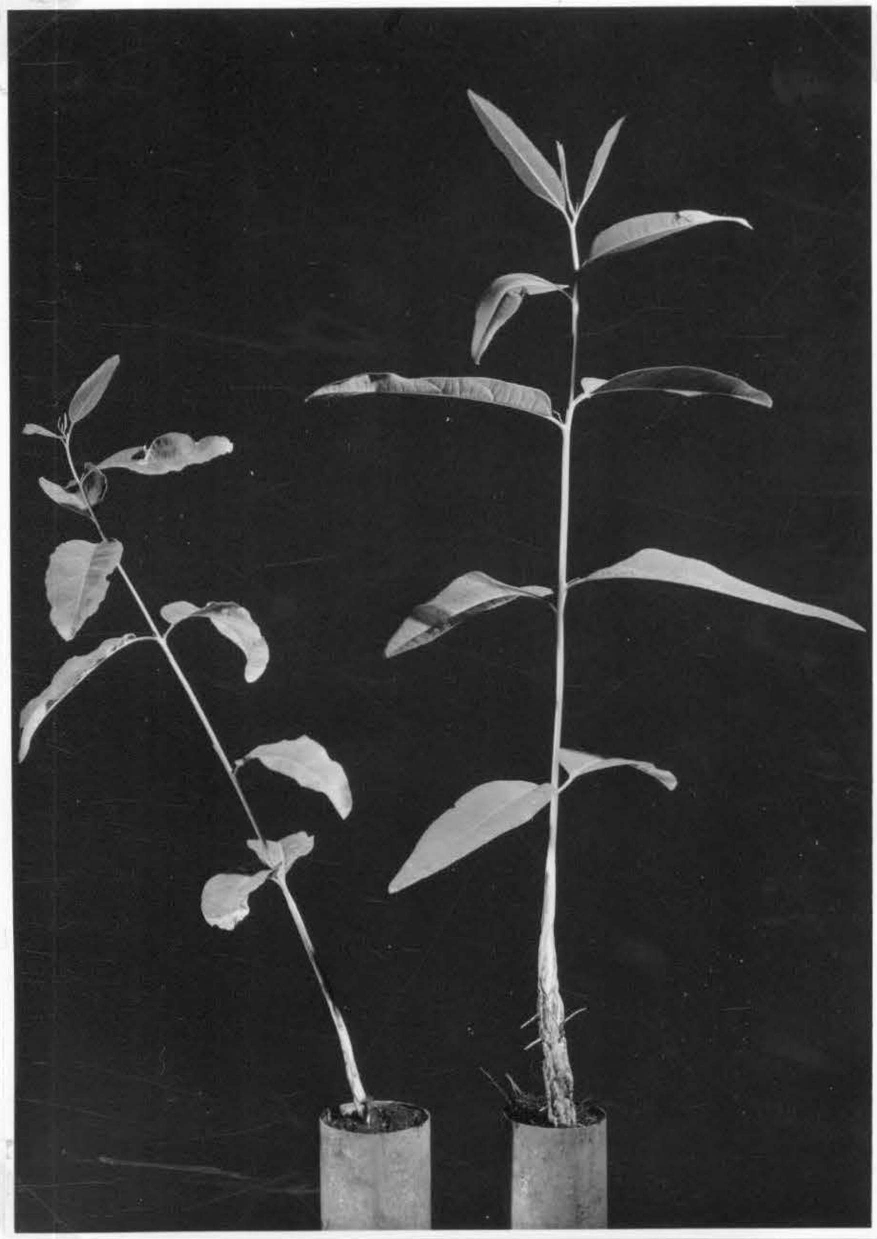
The results in Table 8 summarise observations made on three plants each of E. robusta and E. botryoides which were submerged to a depth of 27 cms. above soil level for a period of 46 weeks. All plants were the same age from seed and had been pricked off into galvanised planting tubes. When the plants were at least 50 cms. high they were placed together in a beaker and submerged to a depth of 27 cms.

Rapid development of aerenchyma occurred on the stems of E. robusta but only slight development on E. botryoides. After ten weeks cladogenous roots had formed on the former species and were particularly well developed in the zone 3 - 4 cms. below water level.

By 46 weeks all plants of E. botryoides had died whilst the three E. robusta were still alive.

Fig. 16, 17 and 18 show comparative development of aerenchyma and cladogenous roots on E. robusta and E. botryoides. In this case cladogenous / roots

Fig. 16



E. botryoides (left) E. robusta (right)
immersed 24 days; seedlings 6 months old.

Photo N.I.B.

Fig. 17

E. robusta (right) E. botryoides (left)
Immersed 24 days. Strong development of aerenchyma, cladogenous roots and surface roots on E. robusta.

Photo N.I.B.

Fig. 18

E. robusta (left) E. botryoides (right) from Fig. 17 after immersion 5 months. Strong growth of cladogenous roots on E. robusta, absent on E. botryoides.

Photo N.I.B.

had formed within 24 days of submergence.

Tables 9 and 10 show the results of two submergence trials carried out with E. robusta, E. grandis, E. saligna and plants from field hybrids between E. robusta and the other two species.

Seedlings were raised under uniform conditions transplanted into boxes and allowed to grow for three months before submergence. The seedling heights varied from 13 - 33 cm.s thus some plants were completely immersed during treatment. Death occurred on all fully submerged plants within five weeks. The precise time when death occurred is not known as the plants remained beneath the water and showed no signs of deterioration until removed for assessment after 5 weeks.

Aerenchyma tissue was formed on all plants of E. robusta and those surviving after 42 weeks also possessed cladogenous roots. Only slight development of aerenchyma occurred on E. grandis and E. saligna and then only on some plants. After 42 weeks all plants of E. saligna had died and only one E. grandis remained alive; this plant showed some development of aerenchyma.

Both hybrid progenies showed variable development of aerenchyma both in degree and in numbers of plants on which it occurred. The general pattern was clear, namely that those individuals which developed aerenchyma survived submergence for longer periods than those which did not.

Since E. saligna lacks almost entirely the capacity to form aerenchyma there was a suggestion from the variation in the hybrid progeny that the ability to form this tissue is an inherited character.

During the period 9 - 42 weeks all plants were under treatment in the open in Canberra and were therefore subjected to cold as well as high water level and the temperatures experienced were lower than those to which the species would be subjected in their natural habitat.

E. robusta, saligna, grandis and botryoides are all members of the Transversae group of the genus and all are capable of withstanding periods of water-logging. By contrast the results in Table 11 show that E. pauciflora and E. stellulata, both members of the Renantherae, survive submergence for relatively shorter periods. There is no formation of aerenchyma on the stems of either of these species. There is some suggestion that E. stellulata has a slightly greater tolerance of submergence than E. pauciflora. Although the difference is only a matter of a few days it may be sufficient to favour the survival of E. stellulata over E. pauciflora under field conditions.

TABLE 8

OBSERVATIONS ON THE EFFECT OF SUBMERGENCE ON

E. ROBUSTA AND E. BOTRYOIDES

Depth of submergence 27 cms.

Three plants per species, age 6 months

Time of Submergence (weeks)	Species: E. robusta	Species: E. botryoides
3	Aerenchyma well developed on stems near ground level and at water level.	No development of aerenchyma.
7	Aerenchyma well developed on immersed stems. Plants growing well.	1 plant with slight development of aerenchyma.
10	Cladogenous roots appeared on all plants.	No development of cladogenous roots
11	Cladogenous roots up to 2 cm. in length; development in zone 3 - 4 cm. below water level. Aerenchyma best developed in this region.	2 plants with some aerenchyma. 3rd plant leaves wilting tip dying.
46	All plants alive. Cladogenous roots well developed.	All plants dead.

TABLE 9

EFFECT OF SUBMERGENCE ON SURVIVAL OF E. ROBUSTA, E. SALIGNA, AND E. ROBUSTA X SALIGNA FIELD HYBRID

Depth of submergence - 17 cm. Age 3 months.

	E. robusta	*E. robusta x saligna*	*E. saligna*
No. treated	8 (plus 6 fully immersed)	22 (plus 5 fully immersed)	9 (plus 9 fully immersed)
Time:weeks			
1	All apparently alive; healthy; bark splitting in initial stages of development of aerenchyma		
5	All fully immersed plants dead for all species.		
	1 dead 7 healthy aer. well dev.	2 dead 20 healthy variable dev. of aer.	3 dead 5 fair, leaves drying no dev. of aer.
9	6 healthy 1 " with clad.roots	13 healthy, aer. well dev. 7 poor, no dev. of aer.	3 poor, (one plant with aer.)
42	3 healthy All with clad. roots and aer.	All dead	All dead

aer. = aerenchyma   clad. = cladogenous

TABLE 10

EFFECT OF SUBMERGENCE ON SURVIVAL OF E. ROBUSTA, E. GRANDIS AND E. ROBUSTA X GRANDIS FIELD HYBRID

Depth of submergence - 20 cm. Age 3 months

	E. robusta	*E. robusta x grandis*	*E. grandis*
No. treated	10 (plus 6 fully immersed)	19 (plus 11 fully immersed)	10 (plus 5 fully immersed)
Time: Weeks 1	All alive, healthy, aerenchyma forming on the stems at the water surface and at ground level		
5	All fully immersed plants dead for all species		
	2 poor 7 healthy aer. well dev. 1 " " " " and clad. roots at ht.10-17cm.	5 dead 5 poor 9 healthy, dev. of aer.	2 dead 7 healthy, no aer. 1 " aer. developed
9	5 alive 4 healthy clad. roots dev. 1 poor, no clad. roots dev.	8 alive 5 aer. well dev. 1 aer. well dev. and clad roots 2 poor, no aer.	5 alive 2 healthy, aer. dev. 3 poor " " No dev. aer. on plants which have died.
42	4 alive, healthy	1 alive, clad. roots (e. grandis phenotype)	1 alive, aer. dev. no clad roots.

aer. = aerenchyma   clad. = cladogenous

TABLE 11

EFFECT OF SUBMERGENCE ON SURVIVAL OF E. PAUCIFLORA AND E. STELLULATA SEEDLINGS

Depth of submergence 9.5 cms.

	E. pauciflora	E. stellulata
No. treated	30	25
Av. height	12.8 cm.	15.9 cm.

Time in days	E. pauciflora	E. stellulata
3	tips dying	all healthy
6	all dead	tips dying
8		11 dead 3 poor 11 healthy
26		3 healthy Av. height 18.1 cm.
36		all dead

Fig. 19

L - R *E. camphora*; *E. camphora* and *E. dalrympleana* interplanted; *E. dalrympleana* waterlogged 23 weeks. Aerenchyma formed on stems of *E. camphora*. Poor survival of *E. dalrympleana*.

Photo N.I.B.

no formation of this tissue on E. dalrympleana.

It seems likely therefore that aerenchyma tissue formed on the stems of Eucalypts is of adaptive value in the survival and growth of species which occur naturally in areas subject to waterlogging.

CHAPTER 6

CLADOGENOUS ROOTS

The terms "cladogenous" and"phyllogenous" were propos ed by Strassburger (1954) to define roots borne on the aerial parts of plants. Such roots arise largely endogenously, occur in indefinite numbers and are borne close to or at the nodes; they are classified as either cladogenous or phyllogenous depending on their point of origin. The aerial roots forming on Ficus bengalensis and species of Rhizophora are described as typical examples of cladogenous roots.

"Adventitious" refers to structures arising as entirely new formations, although the term has been used in a much broader sense by some authors, Esau (1960). Carlson (1950) designates the roots formed at the nodes in willow as adventitious although they arise from dormant primordia.

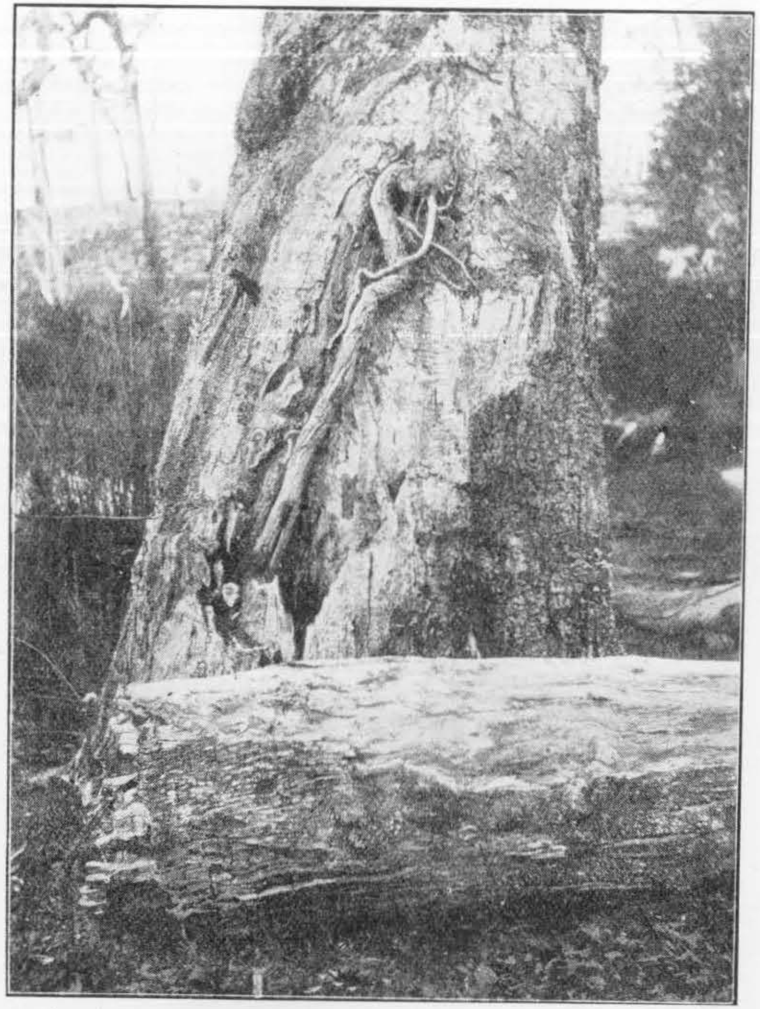
Whether stem borne roots in Eucalyptus are adventitious or arise from dormant primordia has not been determined, however it is clear that they arise endogenously, internodally (although may not be restricted to this region), and in no definite sequence up the stem, therefore, it is proposed to adopt the term cladogenous to describe stem borne roots formed in some members of the genus.

The earliest record of cladogenous roots in Eucalyptus is a photograph, Fig. 21 which appeared in the"Western Mail", Perth, in 1914. This shows the development of roots above a zone of ringbarking. The species referred to as"Flooded Gum" is almost certainly E. rudis.

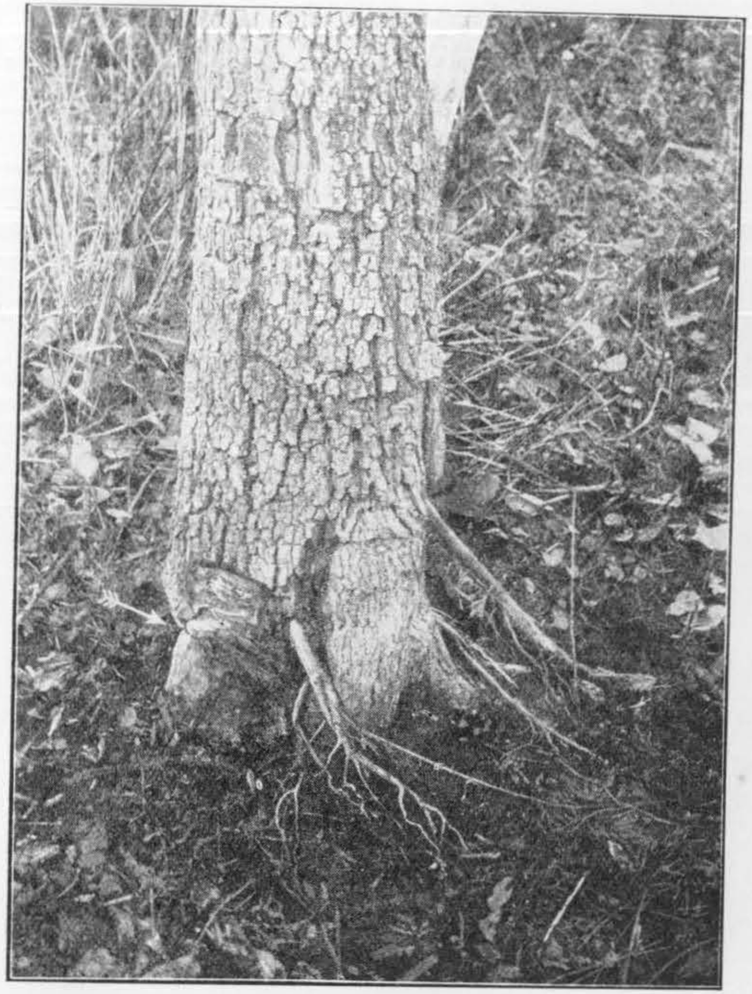
Auchterlonie (1953) described a large E. camaldulensis in Victoria which was blown over in

Eucalyptus rudis

FLOODED GUM KEPT ALIVE BY AERIAL ROOT, FERNDALE, BALINGUP.



AERIAL ROOT ON FLOODED GUM OF No. 1 WHICH HAS KEPT THE TREE ALIVE FOR YEARS AFTER RINGING.



RINGBARKED FLOODED GUM, FERNDALE, BALINGUP, WHICH HAS DEVELOPED AERIAL ROOTS ABOVE THE RINGING. (See Farm.)

18. 21

a storm but remained alive through some existing roots; eight years later, twelve feet of the lower trunk were removed. "Adventitious roots" had formed during the period the trunk and branches were resting on the soil and the tree remained alive supported by these roots.

Jacobs (1955) records the occurrence of aerial roots in E. camaldulensis and states that they are restricted to the parts of trunks that are submerged for several weeks each year. He also describes the phenomenon of layering in E. niphophila in peaty localities and in E. camaldulensis and E. robusta in wet soils. Layering is not common in dry country but has been observed with E. melliodora in sandy soils, and from a hillside occurrence of E. camaldulensis in the Mount Lofty Ranges in South Australia, Jacobs (ibid.)

Pryor and Clark (personal communication) report the common occurrence of stem borne roots on planted trees of E. robusta in Hawaii and Brazil respectively.

The author has observed, in the field, stem borne roots on E. stellulata and E. pauciflora in sphagnum beds, E. camphora in mud swamp and E. robusta in areas subject to flooding. Roots have been induced experimentally on E. robusta, rudis, camaldulensis, camphora and dalrympleana.

In all cases where the development of cladogenous roots has been induced experimentally their appearance was preceded by the development of aerenchyma. As the roots arise endogenously there may be no correlation between the two characteristics although the loosely packed nature of the cells of the rhytidome would allow an easy passage for the emerging roots. The lack of development of aerenchyma on stems of Renantherous species such as E. pauciflora and

E. stellulata has been discussed in Chapter 5, and where cladogenous roots have been found on these species there was no observable development of aerenchyma.

In the occurrence of cladogenous roots on E. robusta in a humid chamber Figs. 22, 23 there was only slight development of aerenchyma as observed macroscopically.

There is considerable variation in the number of plants forming cladogenous roots, the rate of development and the number and sequence of emergence on individual stems. Table 13 shows the number and length of roots formed on E. rudis. Nursery tubed stock approximately 8 months old and average height 30 cms. were transplanted into tins and submerged to a depth of 10 cms. The development of aerenchyma occurred within one week and formed along the length of the submerged stems and just above the water level. Some plants were not growing upright and therefore a length of stem greater than 10 cms. was under water; aerenchyma was developed over the entire submerged portion regardless of length. Numerous surface roots emerged from the top of the soil.

The first cladogenous roots appeared on one plant after 4 weeks. By five weeks, 3 plants, at 8 weeks, 7 plants, and at assessment after 10 weeks, 8 plants had formed cladogenous roots. All treated plants were alive and growing after 10 weeks submergence to 10 cms. and all showed strong development of aerenchyma. Eight of the fourteen had developed stem borne roots, the number per plant varying from 1 to 13 and root lengths from 2 to 690 mm.

This type of variation was shown by E. robusta also.

Figs. 22, 23 show the development of

Fig. 22

E. robusta seedling grown under bell jar. Cladogenous roots formed above zone of injury. Note abundance of root hairs. (Wilting due to heat of photographic lights.)

Photo N.I.B.

Fig. 23

E. robusta seedling as in Fig. 22. First formed cladogenous roots have entered soil. Dormant leaf buds have emerged; new stem borne roots further up the stem. Roots emerge at internodes.

Photo N.I.B.

cladogenous roots on a plant of <u>E. robusta</u> which had been grown under a bell jar. The lower part of the stem was damaged and partly ringbarked and roots appeared in the internodes above this zone. A second set of roots emerged at a later stage, by which time the first formed roots had reached, and become established in, the soil below.

TABLE 13

VARIATION IN CLADOGENOUS ROOT DEVELOPMENT ON E. RUDIS

No. of plants treated 14

No. of plants forming cladogenous roots 8

Plants 8 months old, average height 30 cms.

Depth of submergence 10 cms.

Time of submergence 10 weeks

Length of roots in mms.

Plant No.	1	2	3	4	5	6	7	8
No. of roots formed	5	7	5	7	4	6	1	13
	76	241	B	125	195	58	118	22
	49	200	35	179	36	185		115
	2	211	B	194	255	38		680
	111	62	B	189	B	72		113
	87	152	395	111		15		20
		130		177		39		159
		36		100				142
								260
								426
								267
								222
								565
								534

B = root broken

The lengths of roots were recorded in acropetal sequence. In general the length of the root indicates its age and it is clear that the roots are not formed in a definite sequence up the stem.

Table 14 shows the cladogenous root distribution on a plant of E. robusta which had been submerged to a depth of 95 mms. for a period of 29 days. The roots emerged largely at the internodes although as the internodal distance in the lower portion of the stem was small, and the roots emerged at an angle, it was not possible to state that no roots were formed at the nodes.

Throughout the period of study, a number of separate progenies of E. robusta of differing age and seed provenance were subjected to submergence to varying depths, and for varying periods. Approximately 50% of all plants treated produced cladogenous roots. Roots were not common on plants submerged to only 2 - 3 cms., although under these conditions, there was a strong development of surface roots which ramified in the water above the soil surface. Submergence to depths greater than 25 cms. usually resulted in a much slower development of aerenchyma, a lack of development of roots at the soil surface, and the formation of fewer cladogenous roots. Those forming were largely on the upper submerged portion of the stem. Differences in growth and development of roots occurred with differing sizes and growth stages of plants and with water temperature.

TABLE 14

CLADOGENOUS ROOT DISTRIBUTION ON E. ROBUSTA

Total plant height 45 cms.

Depth of submergence 95 mms.

Period of submergence 29 days

Cotyledons at soil surface

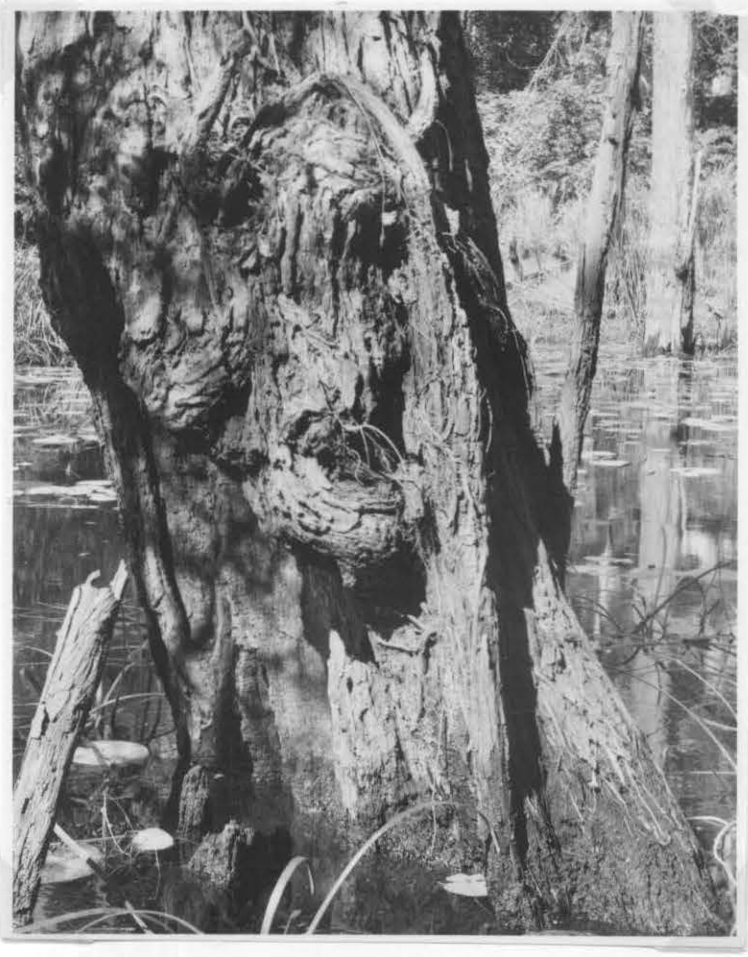
Nodes at mms.	Roots at mms.	Length of roots mms.
	8	2
	12	4
13	-	-
	23	5
25	25	6
38	-	-
	39	9
	44	17
	51	12
57	-	-
85	-	-

Field studies were made at Foreman's Creek near Coff's Harbour, N.S.W. following observations by R. Turnbull (private communication), who located a number of *E. robusta* trees with cladogenous roots. Evidence from local residents indicated that approximately twenty years previously the mouth of Foreman's Creek was blocked by sand drift. Subsequent flooding upstream resulted in the partial submergence of numbers of trees in a community of *E. robusta*, *Melaleuca quinquinerva*. The depth of flooding varied with the position of the trees on the gently sloping ground and the level of flooding could be recognised by the variation in height at which cladogenous roots were present, although the water level has since receded."

The period of initial flooding is not known, but the number and sizes of roots indicate that it occurred for a period of some months. At a later stage, the creek formed a new outlet to the sea, and the water receded, although not to the original level. This is indicated by trees such as shown in Fig. 24. This specimen must have become established before any flooding occurred, but is at present in approximately two feet of water, and has apparently been in this condition for upwards of twenty years. Although not vigorous, the crown is still alive, and the tree is about 45 feet tall and two feet in diameter at water level. Large cladogenous roots are present at a height of 8 - 10 ft. Other trees near the present water's edge have stem borne roots up to 1 inch in diameter emerging at heights of five feet whilst trees higher up the bank, Fig. 26 have aerial roots at 2 - 3 feet from the ground level. As shown in this figure, the roots have entered the soil and now resemble stilt roots.

Cladogenous roots are not present on all trees of E. robusta in the area, but are almost invariably found on Melaleuca quinquinerva. There were a number of dead standing Eucalyptus trees in the area, but it was not possible to identify these to determine whether they were E. robusta or possibly E. grandis, which borders the swamp area. Fig. 25 illustrates a cladogenous root from a standing tree of E. robusta which had emerged close to, and grown along the bark of, a fallen tree of the same species. The bark of E. robusta is spongy, fibrous and slightly

Fig. 24



E. robusta waterlogged approx. twenty years; old stem-borne roots formed at time of submergence.

Fig. 25

Cladogenous root of E. robusta, standing tree on the right, growing in the bark of fallen tree.

Fig. 26

E. robusta Foreman's Creek N.S.W.
Stilt-like cladogenous roots formed at level of previous submergence approx. 3 ft.

furrowed, and when moist, provides a suitable medium in which roots can grow.

Observations in the field support the experimental evidence from induced cladogenous roots on seedlings and indicate that the capacity to form roots in this species is not restricted to that part of the stem near ground level, or to the juvenile stage of the plant.

As discussed above, it has not been possible to assess the relative survival values of these three apparent adaptations to waterlogged conditions as shown in E. robusta, i.e. aerenchyma, cladogenous roots, and the formation of surface roots at soil level. It has been shown that about half of all seedlings which are immersed but not fully submerged form stem borne roots, although the number and position on the stem vary from plant to plant. The results in Tables 9 and 10 where with one exception, only those plants forming cladogenous roots in addition to aerenchyma, were alive at the end of the trial, suggest that these roots are associated with survival after prolonged immersion.

Stem borne roots observed in the field on other species, e.g. E. camphora, stellulata and pauciflora, were all found on seedlings growing in either sphagnum moss beds or mud swamp. These species all occur largely in tableland areas subject to winter flooding, with maximum humidity during the colder months. E. robusta on the other hand, occurs close to the sea in regions of high humidity and, whilst found both in winter and summer rainfall areas, shows the best development of stem borne roots in the latter situation. High temperatures and high humidity are associated with the growing season for this species.

The observations of Clark and Pryor cited above were made on planted trees of <u>E. robusta</u> growing in tropical areas of high humidity.

It appears therefore, that the formation of cladogenous roots is dependent upon conditions of high humidity, but it may be equally true that they arise only when the normal functioning of the root system is impeded by conditions of excessively high soil moisture.

Further work is necessary to determine the manner in which cladogenous roots assist in the survival of species subject to periods of waterlogging and to learn whether stem borne roots are capable of assuming the functions of the underground root system when it is inhibited by conditions such as reduced soil aeration.

CHAPTER 7

SEED GERMINATION AND SEEDLING GROWTH

(a) Seed dormancy

Evidence from a broadcast sowing trial at Cotter Hut A.C.T. suggested that there is a difference in the degree of dormancy between the seed lots of *E. pauciflora* and *E. stellulata*.

This was supported by observations in the glasshouse when raising seedlings of both species for pot trials. Almost invariably seed of *E. pauciflora* collected from a high altitude contained a high proportion of dormant seed and, although some seed from each collection germinated without pretreatment, it was generally necessary to stratify the seed in order to get uniform and reasonable percentage germination. *E. stellulata*, on the other hand, generally germinated quickly and uniformly without any pretreatment.

To determine the extent of this difference between the two species the effect of stratification on seed germination was studied.

Capsules were collected from five trees of each species growing in the vicinity of the broadcast sowing trial area and germination tests were carried out as soon as the seed was extracted. The germination medium was filter paper over vermiculite in petri dishes the temperature 20°C and time 14 days. Samples were taken by weight rather than by counting because of the difficulty of separating seed from chaff in Renantherous species. The number of seed per unit weight for *E. stellulata* is approximately 4 times that for *E. pauciflora* which mainly accounts for the large difference in number germinating per unit weight for the two species. The quantity of *E. pauciflora* seed collected did not allow a larger unit sample to be taken.

After fourteen days the dishes were placed in the refrigerator at 4°C for a period of 28 days and then removed to the incubator at 20°C for 21 days. In the case of E. pauciflora the dishes were returned to the refrigerator for a further 42 days and again placed in the incubator. The E. stellulata seed lots were not restratified as a previous trial had shown no response to pretreatment.

With E. pauciflora some seed germinated at the temperature of stratification. These were included in the germination counts for the following germination period.

The seed was tested regularly over a period of four months and the figures (Table 15) are the means of four germination tests of 0.3 gm. samples for each tree and each species calculated as percentages of the total germination. It is clear that E. pauciflora shows a marked response to stratification whereas the response shown by E. stellulata is small.

It is possible that the temperature of the germinating cabinet namely 20°C may have induced secondary dormancy (Grose 1957) in E. pauciflora, and further work would be necessary to establish this point. Temperatures of 20°C would be found in the field where seed is present on the forest floor and the comparison between the two species is valid whether or not secondary dormancy was induced by the germination conditions.

TABLE 15

RESPONSE TO STRATIFICATION IN SEED GERMINATION OF E. PAUCIFLORA AND E. STELLULATA

% of total germination for each treatment

E. pauciflora

	Untreated	4 wks.strat.	4 + 6 wks.strat.	Total as %	Actual Total
1	19.9	36.1	44.0	100	21.6
2	13.3	37.9	48.8	100	21.1
3	2.7	34.9	62.4	100	10.9
4	11.9	51.9	36.2	100	31.8
5	0.8	30.9	68.3	100	36.6

E. stellulata

	Untreated	4 wks.strat.	4 + 6 wks.strat.	Total as %	Actual Total
1	92.3	7.7		100	36.3
2	98.4	1.6		100	200.2
3	95.1	4.9		100	82.0
4	93.0	7.0		100	139.1
5	94.9	5.1		100	153.3

Total germination for each individual taken as 100%
Percentages given for mean number germinating for each treatment on the same seed sample.

It is interesting to note that considerable between tree variation particularly with <u>E. stellulata</u> where one tree gave a total germination of only 36 per unit sample whilst another gave 200 for the same weight. The germination figures were consistent for each tree for the four tests from which the mean was taken. e.g. <u>E. stellulata</u>

Tree no. 1	38	34	30	32	Mean	33.5
Tree no. 2	198	212	184	194	Mean	197.0

The difference in degree of seed dormancy between the two species may be related to successful establishment.

There are no recorded observations of time of seed shed with these species although the time of flowering has been noted over a number of years. <u>E. pauciflora</u> in the region under study, flowers in December and January. <u>E. stellulata</u> does not flower until March or April. Development of the capsules is slow during winter and it is usually twelve months or more before seed of <u>E. pauciflora</u> is fully ripe. Seed falling on dry sites in autumn would largely lie dormant and be stratified under snow before germinating in the spring, whereas dormant seed falling onto the swamp would probably be lost or moved away during the cold period.

The mechanism of seed dormancy in <u>E. pauciflora</u> may reduce germination under unfavourable conditions, and allow it to occur over a longer period with the possibility of a greater number of seedlings surviving.

Germination of <u>E. stellulata</u> seed falling on drier sites may result in a large number of even aged seedlings which would be susceptible to unfavourable weather conditions such as dryness. Seedlings germinating on the flats in autumn would share the same fate as those of E. pauciflora and it seems likely that the conditions in early summer when free water has drained away but the soil is still moist, would be most suitable for germination.

The adaptive value of seed dormancy is not fully known. The characteristic is restricted largely to Renantherous species and then mainly to those from high altitudes. It is not apparent in seed of species such as E. dalrympleana and camphora which occur naturally too at relatively high altitudes indicating that it is not a characteristic essential for seedling establishment in cold locations.

(b) Direct seeding on to waterlogged and freely drained soils

To test the effect of waterlogged soil on germination and growth, seed of a number of Eucalyptus species were sown onto nursery flats in the glasshouse. The soil was a mixture of sand 40% and loam 60%. Boxes 4" deep were used, one set with normal free drainage, the other immersed so that a film of water was visible on the surface. Seed was sown directly onto the surface and covered with sphagnum moss.

The species were chosen to include members of the different systematic groups of the genus, and species from a variety of natural habitats.

In the first trial, all seedlings were thinned to twenty five, four weeks after sowing. At this stage, the water level was raised to approximately 0.5 cm. above soil level. The plants were assessed at age 27 weeks.

It was necessary to apply a 0.01% solution of potassium permanganate to reduce the heavy algal growth on the surface of the waterlogged soil. This solution was applied to the controls also.

At time of assessment, the height of each seedling from cotyledons to growing tip was measured and percentage survival recorded for each species. All plants survived under conditions of free drainage with the exception of E. maculosa and E. dives; in the former 10%, and the latter 5% failed. The survival under waterlogged conditions was variable as shown in Table 16, with some relationship between survival and natural habitat. Those of dry, well drained sites being generally more susceptible to conditions of poor drainage than those from wet, swampy or alluvial sites.

These results also suggested that species which occur in areas where waterlogging takes place during the growing season, showed greater adaptability to the warm wet conditions in the glasshouse, than species which are naturally subjected to waterlogging, mainly during the winter months, when temperatures are low and growth is not active. E. robusta, which occurs mainly in areas of summer rainfall, is subject to waterlogging during the summer, whilst by contrast, E. aggregata is a species of high elevations with winter rainfall and flooding occurs during the colder part of the year.

The vigorous growth of E. botryoides, robusta, saligna, punctata, camaldulensis, amplifolia, and camphora under waterlogged conditions was correlated with development of spongy aereachymatous tissue on stem at and below the waterlevel.

In the case of a few species, height growth under waterlogged conditions was greater than under conditions of free drainage. It is not possible, without more detailed experiment, to determine the reasons for this result. There was no apparent difference in the form of the seedlings grown under the different conditions, and no evidence that the waterlogged plants were etiolated.

As the seedlings were raised in boxes with seven species per box, it may be that interspecific competition was already taking place. The total height growth of all plants per box did not differ significantly between waterlogged and freely drained soils.

In the second trial, comparisons were made between species pairs which occur naturally on adjacent sites, one well drained, the other swampy. Seed was sown onto the soil surface, and covered with sphagnum moss. The plants were allowed to grow unthinned until assessment twenty three weeks later. Table 17.

As observed in previous experiments in raising Eucalypts, there was considerable variation in vigour in these seedling populations; this is partly genetic, and partly due to the differential rates of germination, namely those seedlings which germinate first have an immediate advantage over those germinating later.

The mean height of the best ten seedlings for each species was taken. It was considered that this figure reflected more closely field conditions where presumably only the most vigorous seedlings become established, the remainder being eliminated at an early age, although they may persist for some time under experimental conditions.

E. robusta and _camphora_ developed surface roots and, together with _E. propinqua_, formed aerenchyma on the stems. This did not occur with _E. stellulata_, _pauciflora_ or _dalrympleana_.

Assuming that the germinative and immediate post germination periods are the most critical stages in the life cycle, these two experiments were aimed at determining whether waterlogged soil would inhibit germination or cause early death.

The results show that germination will occur on waterlogged soil and that under experimental conditions, early growth of some species may even be better than on freely drained soil. These experiments did not take into account field conditions such as competition from existing vegetation, fluctuation in temperature and variation in soil type and therefore the results can only be taken as indicative of possible reactions in the field.

It seems clear that two members of the Renantherae used and ordinarily growing on well drained sites were more susceptible to waterlogged conditions both in growth and survival than members of the other systematic groups. These was no development of aerenchyma or surface roots with any of the Renantherous species and the height growth was much reduced in comparison with that on freely drained soil.

TABLE 16

HEIGHT GROWTH OF EUCALYPTUS SEEDLINGS SOWN ONTO FREELY DRAINED AND WATERLOGGED SOILS

Height in cms. cotyledons to growing tip

Age 27 weeks

Systematic Group		Species	Habitat	Freely Drained Ht.	Waterlogged Ht.	Waterlogged % survival
MACRANTHERAE	TRANSVERSAE	botryoides	Moist, warm	13.7	13.7	100
		robusta	Poorly drained wet, warm	21.3	28.2	100
		saligna	Wet, well drained	13.4	17.9	100
		punctata	Dry, warm	8.5	14.0	88
		aggregata	Marshy flats, cold	9.6	8.9	92
		amplifolia	Alluvial flats warm	7.2	10.9	100
		bicostata	Moist, cold well drained	12.3	7.8	100
		camaldulensis	Wet, poorly drained	15.8	21.0	96
		camphora	Cold wet flats poorly drained	8.3	8.5	92
		dalrympleana	Moist, well drained, cold	8.9	6.2	100
		rubida	Alluvial flats cold	9.6	8.6	84
		maculosa	Dry, cold	10.8	6.4	72
		bridgesiana	Alluvial flats cool	16.5	9.7	86
RENANTHERAE		dives	Dry cold	8.3	0.8	7
		lindleyana	Moist, well drained	12.5	1.2	30
		pauciflora	Well drained cold, moist	6.6	0.9	27
		pilularis	Well drained, warm	6.9	1.2	2
		stellulata	Wet, cold flats	No asses-ment	1.0	40
TERMINALES		melliodora	Alluvial flats cool	11.7	5.2	88
		polyanthemos	Moist to dry, well drained	6.4	4.8	84

TABLE 17

HEIGHT GROWTH OF EUCALYPTUS SEEDLINGS FROM SEED SOWN ONTO WELL DRAINED AND WATERLOGGED SOILS

Height in cms. cotyledons to tip

Age 23 weeks

Systematic Group		Species	Habitat	Freely Drained	Waterlogged
MACRANTHERAE	Transversae	propinqua	Well drained moist, warm	23.7	24.0
MACRANTHERAE	Transversae	robusta	Poorly drained warm, wet	32.0	33.6
MACRANTHERAE	Normales	dalrympleana	Moist, well drained, cold	22.3	13.6
MACRANTHERAE	Normales	camphora	Cold wet flats, poorly drained	13.7	22.5
RENANTHERAE		pauciflora	Cold, well drained, moist	10.6	1.6
RENANTHERAE		stellulata	Cold, wet flats	15.3	1.5

In the case of E. stellulata, the region of the hypocotyl was considerably extended, and in most cases more than 1 cm. in length.

PART III

FIELD TRIALS

CHAPTER 8

E. PAUCIFLORA: E. STELLULATA

(a) Broadcast Sowing

An area adjacent to transect No. 3 in the vicinity of Cotter Hut, A.C.T., altitude 3,490 ft., was chosen as a suitable site in which to carry out a direct seeding trial with E. pauciflora and E. stellulata. Fig. 27.

These two species are well represented in the area, and on the whole, occupy distinct sites. The former occurs on well drained locations which, although wet in winter, and at times snow covered, are never waterlogged, whereas E. stellulata occupies wetter sites of alluvial soil, which may be waterlogged for lengthy periods each year.

The aim of the broadcast sowing trial was to see whether the species separation evident in the adult trees had its basis in the failure of either species to germinate on sites other than its own. From the assessment of regeneration, this did not appear to be the case with E. stellulata which was present with E. pauciflora on the drier sites. However E. pauciflora regeneration was not found on wet sites, and it was thought that its absence may have been due to either failure to germinate or early post emergence death.

The plot was fenced to keep out horses and kangaroos; however, smaller animals such as wombats and rabbits, were not excluded.

To enable complete assessment of germination to be made, foot wide strips were chipped free of surface grass and sedges for the length of the transect, approximately 100 ft. Fig. 28. This meant that competition was temporarily removed but, as the maximum regeneration occurring naturally takes place after fire, when the competing grass cover has been temporarily removed the seed bed conditions were not far removed from normal.

The harvesting of Eucalyptus seed by ants has been observed and prevented by Jacobs (1955) using chlordane spray. The author has found 10% chlordane granules spread at the rate of ½ lb. per 500 sq. ft. effective in preventing harvesting by ants of newly sown grass seed. Therefore, these granules were used as a precautionary measure, and were scattered over the hoed lines at the above rate.

Three lines were chipped and seed broadcast as follows -

Line 1	<u>E. pauciflora</u>
Line 2	<u>E. stellulata</u>
Line 3	both species mixed together

The seed of each species was spread evenly along the lines and lightly covered with sieved sphagnum moss. Because of variations in seed size, purity and the presence of dormant seed, it was not possible to ensure that the same number of viable seed was sown per unit length for the two species. Grose and Zimmer (1958) give the following figures for viable seed per ounce for the two species -

	Viable seed per oz. of seed and chaff.	Range Minimum	Range Maximum
<u>E. pauciflora</u>	1,200	300	3,100
<u>E. stellulata</u>	4,700	1,200	9,800

Seed dormancy and response to cold moist stratification with some Eucalyptus species, has been discussed by Pryor (1954), Boden (1957) Grose (1957).

Fig. 27

Transplant and broadcast sowing plot Cotter Hut A.C.T. Abrupt boundary between Eucalypt forest and swamp. Epacris breviflora at boundary.

Fig. 28

Lines chipped for broadcast sowing. Dense snow grass and sedge growth on the flat. E. stellulata trunks background on left. Cotter River at end of plot.

The general conclusions are that seed dormancy is most common in alpine species of the Renantherae group, although it does occur in some Macrantherous species from high altitude. The most effective method of removing dormancy is cold moist stratification at a temperature of $4^{o}C$ for periods of from four to six weeks.

Assessment of germination on the seeded lines, both before and after winter, indicated that a large proportion of the seed of E. pauciflora had responded to cold stratification in the field over winter, whilst this had occurred only slightly with E. stellulata. Table 18. This was particularly so on the drier ends of each line, but not on the moister site adjacent to, but not on the swamp. It was possible to distinguish at assessment 29/11/61, those seedlings which had germinated before and after winter. Tables 19, 20, 21.

Grose (1957) has shown with E. delegatensis that conditions unfavourable for germination, e.g. high temperature, can induce secondary seed dormancy and it may be that the summer conditions after seed sowing in November induced this type of dormancy in seed of E. pauciflora sown on the drier site. With E. stellulata on the other hand, although it was not possible to detect dead seedlings on the dry site at assessment 18/5/61, the large difference in number found on the dry site 0 - 20 ft. 42 and on the moist site of different soil type, 20 - 35 ft. 314, suggests that the germination or immediately post germination conditions on the dry site may have resulted in failure to germinate or early death of E. stellulata.

The reduction in number of E. stellulata seedlings between the pre and post winter observations on the zone 20 - 35 ft. from 314 to 36, was presumably due to the severe winter conditions. The seedlings before winter were at the first leaf/pair stage only, and would be sensitive to prolonged cold periods.

At assessment 18/5/61 Line 1 in the zone 45 - 60 ft., which although on the flat swamp area was on a slight rise with moist, but not waterlogged soil, it was possible to count 27 seedlings of E. pauciflora which had only recently been killed, due presumably to cold or excessive moisture. There were 28 seedlings in the same zone which were still alive, all of these were lost by the next assessment after winter. Seed which had been sown on the swamp site, and which failed to germinate before winter, may have been destroyed or washed away during winter inundation.

TABLE 18

TIME OF GERMINATION FOR SURVIVING SEEDLINGS

OF E. PAUCIFLORA AND E. STELLULATA

Sown 20/12/60

Assessed 29/11/61

	E. pauciflora		E. stellulata	
	Before	After	Before	After
	Winter		Winter	
Zone in ft.				
0 - 5	3	13	1	1
5 -10	2	17	24	3
10 - 15	1	8	8	2
15 - 20	9	6	9	-
20 - 25	26	9	12	-
25 - 30	3	1	10	-
30 - 35	3	-	14	-
	47	54	78	6

The *E. stellulata* still surviving on the swamp site at 15/3/62 were all grouped on a slight rise of about an inch above the surrounding soil, indicating the importance of microhabitat to the survival of seedlings in difficult sites. Fig. 30 shows these seedlings growing amongst *Carex*, *Trifolium* and *Ranunculus* at 29/11/61. Age from seed 12 months.

The evidence from this trial shows that neither species is likely to become established on permanently swampy sites. Although germination occurs on areas on the flats which are well drained in summer, waterlogging and inundation associated with cold temperature during the following winter kill all but those seedlings which are in protected positions.

E. stellulata appears to be more tolerant of these conditions than is *E. pauciflora*, but the tree percent is extremely low compared with that on sites which are well drained.

(b) Transplant trial

In the area described for the broadcast sowing trial of *E. stellulata* and *E. pauciflora* a transplant trial was carried out.

Tubed nursery stock of both species, age from seed eighteen months were planted three feet apart on a transect from the well drained slope onto the swampy area. Thirty four plants of each species were used.

Planting was carried out in March 1960 and assessments have been made regularly since.

Number surviving for each species are listed in Table 22.

The surviving plant of *E. pauciflora* on the swamp site is poor with a coppice shoot from the lignotuber of only 6.0 cms. It is situated on a slight rise out of the swamp, on soil which is wet, but not waterlogged at the surface.

With E. stellulata on the swamp, one plant is growing well the other three have grown very little and the surviving shoots are coming from lignotubers. Fig. 29 shows one of these plants where the main stem has died and coppice shoots have appeared at the lower nodes. Growth of sedge and grass almost obscures the plants.

It is extremely rare to find a young plant of E. stellulata which has grown without tip damage having occurred at some stage. Generally there are several coppice shoots and a strong development of lignotubers. It is possible to estimate the age of some of these seedlings by the number of dead shoots, and the growth of the lignotubers, and many are five to ten years old before they finally become established or die. It appears that summer growth followed by winter damage proceeds to varying degrees depending on the severity of each season. Reserves are built up in the lignotubers and in the event of a mild winter the growth of the preceding summer may survive undamaged. The addition of the following season's growth may then be sufficient for the seedling to become established to a height where frost damage is not so severe. It is clear that survival and establishment are regulated to a large degree by seasonal variations in climate.

Chance location is also of importance, and individuals which germinate in protected positions or on slight rises in the swampy areas have a definite advantage. It appears that microclimate and chance distribution are of extreme importance in seedling germination and establishment, particularly on swampy areas.

TABLE 19

GERMINATION AND SURVIVAL OF E. PAUCIFLORA SOWN COTTER HUT A.C.T. 20.12.60

feet	0 - 5	5 - 10	10 - 15	15 - 20	20 - 25	25 - 30	30 - 35	35 - 40	40 - 45	45 - 50	50 - 55	55 - 60	60 - 65	65 - 70	70 - 75	75 - 80	80 - 85	85 - 90	90 - 95
18.5.61		Dry			Moist soil change			Free Water		Moist slight rise					Free Water				
5 Mth.																			
No.	3	2	1	14	44	43	41	3	0	8 6D	9 10D	11 11D	-	-	-	-	1	-	-
29.11.61		Dry			Moist			Free Water		Water logged					Free Water				
11 Mth.																			
No.	16	19	9	15 +5D	35	4	3	-	-	-	-	-	-	-	-	-	-	-	-
15.3.62		Dry			Moist					Free Water									
15 Mth.																			
No.	13	14	9	9	20	4	-	-	-	-	-	-	-	-	-	-	-	-	-

D = dead

TABLE 20

GERMINATION AND SURVIVAL OF E. STELLULATA SOWN COTTER HUT A.C.T. 20.12.62

0 - 5 - 10 - 15 - 20 - 25 - 30 - 35 - 40 - 45 - 50 - 55 - 60 - 65 - 70 - 75 - 80 - 85 - 90 - 95 feet	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-55	55-60	60-65	65-70	70-75	75-80	80-85	85-90	90-95
18.5.61		Dry			Soil Change Moist			Free Water		Moist Slight Rise							Free Water		
5 Mth.																			
No.	1	24	8	9	65	151	98	17	2	5	5	36	1	1	-	-	-	4	2
29.11.61		Dry			Moist			Free Water		Water Logged							Free Water		
11 Mth.										Slight Rise									
No.	2	27	10	9	12	10	14	-	-	-	+	49	-	-	-	-	-	-	-
15.3.62		Dry			Moist						Free Water on Surface								
15 Mth.																			
No.	4	29	15	8	8	3	10	-	-	-	-	9	-	-	-	-	-	-	-

TABLE 21

GERMINATION AND SURVIVAL OF E. PAUCIFLORA AND E. STELLULATA SOWN TOGETHER
COTTER HUT A.C.T. 20.12.60.

0 - 5 - 10 - 15 - 20 - 25 - 30 - 35 - 40 - 45 - 50 - 55 - 60 - 65 - 70 - 75 - 80 feet	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-55	55-60	60-65	65-70	70-75	75-80
18.5.61		Dry			Moist soil change			Water logged			Moist Slight rise				Free Water	
5 Mth.																
P	-	3	7	-	4	3	-	-	-	1	1	-	6	3	1	-
S	1	12	3	8	4	10	4	5	-	-	1	3	8	1	1	-
29.11.61		Dry			Moist			Free Water			Waterlogged				Free Water	
11 Mth.																
P	9	13	17	9	-	-	-	-	-	-	-	-	-	-	-	-
S	1	4	7	5	2	-	-	-	-	-	-	-	-	1 dead	-	-
15.3.62		Dry			Moist											
15 Mth.																
P	5	19	21	11	-											
S	2	5	6	7	1											

TABLE 22

SURVIVAL OF E. PAUCIFLORA AND E. STELLULATA TRANSPLANTED SEEDLINGS AT COTTER HUT A.C.T.

	E. pauciflora			E. stellulata		
	Zone			Zone		
	Dry*	Transition	Wet	Dry	Transition	Wet
No. planted	6	4	22	7	5	22
Time (mths)						
9	6	3	4	7	5	9
14	6	3	4	7	5	8
20	5	2	2	6	5	6
24	5	2	1	6	5	4

* 8 seedlings planted originally, two were destroyed by wombats

Fig. 29

E. stellulata planted March 1960 on swamp Cotter Hut A.C.T. Photographed Nov. 1961 Top dead, coppice shoots coming from lignotubers.

Fig. 30

E. stellulata seedlings from broadcast sowing Cotter Hut A.C.T. 11 months old. Dense growth of Carex and Trifolium.

CHAPTER 9

FIELD TRIALS E. CAMPHORA AND E. DALRYMPLEANA

(a) Broadcast sowing

An area at Coree Flat A.C.T. was selected on which to carry out direct seeding and transplant experiments with *E. camphora* and *E. dalrympleana*. Both species are present in the area, the former confined to swampy sites with heavy soils which are waterlogged for a large part of each year. There is a continuous ground layer in which *Juncus*, *Carex* and *Restio* are the main genera. An abrupt change in soil type, ground layer species and tree species occurs between the swamp and the adjacent well drained area where wet sclerophyll forest of *E. dalrympleana*, *E. robertsoni* and some *E. pauciflora* occurs on the easterly and south easterly aspects. *Acacia*, *Cassinia*, *Coprosma* and *Leptospermum* are present in the shrub layer and *Poa* occurs in the grass layer.

Both *E. camphora* and *E. dalrympleana* flower in autumn and hybrids between the two as well as either with a third species, *E. viminalis* can be found at the stand junctions, although they are not common. As the flowering times of these species overlap it is assumed that to maintain the identity of species populations the vigour of the hybrids produced must generally be less than either parent on its respective site.

Five plots were located in the area on an easterly aspect. The plots were 10' x 5' and approximately 45 ft. apart on a transect from the wet sclerophyll site to the swampy area.

Plot 1 wet sclerophyll freely drained

Plot 2 swamp edge but not waterlogged

Plot 3 swamp

Plot 4 swamp

Plot 5 swamp (beneath E. camphora trees)

The plots were chipped free of grass and herbs and chlordane granules were spread over the area to prevent removal of seed by ants.

(a) Broadcast sowing

In May 1961 seed of both species was broadcast on lines each 5' x ½' for each plot. The seed was lightly scratched into the surface soil. The results are given in Table 23.

No germination had occurred within six weeks. 24 weeks after sowing, germination of both species had occurred on all sites although few E. dalrympleana were found on the plots on the swampy area. The seedlings were at the first leaf pair stage on the dry site but at cotyledonary stage on the swamp. It was not possible to tell whether the difference in seedling heights was due to germination occurring on the drier sites before that on the wetter, or because growth rate was faster on the well drained plot.

By autumn, 41 weeks after sowing, few seedlings of either species remained, and all were on the well drained areas. Height at this stage was 2 - 3 cm. (plants of these species grown at near optimum conditions in the nursery were up to 30 cm. in the same period.)

By winter, 53 weeks after sowing, only six seedlings of E. camphora on plot 2 remained. These averaged 5 cm. in height.

The results from this trial do not give enough information to form any conclusions on differences in species behaviour although they suggest that either germination of E. dalrympleana is inhibited on wetter sites or seedlings are lost at a very early stage. Also, the wet wites are difficult for establishment even of the species (camphora) which occurs there naturally.

At the same time as the broadcast seeding was commenced, a trial using capsule bearing branches of both species was started. Branches were collected from trees in the area and pegged down on the plots aiming to have approximately the same number of capsules at each site. Chlordane granules were spread over the area. The aim was to simulate natural conditions where branches bearing capsules are blown to the ground before the seed is shed.

Observations after 24 weeks showed that many of the capsules were still holding seed, although some had shed and germination had commenced. Seedlings on the drier sites were up to the second leaf pair stage whilst those on the swamp were at cotyledon and first leaf pair stages. Germination was localised underneath the capsules. The branches were left in place and additional chlordane granules were spread over the area around them. The results are presented in Table 24. Germination was better for E. camphora on the wetter sites. The numbers of E. dalrympleana were not large enough to give a clear indication of the effect of site on germination. At the next observation the number of seedlings surviving had been reduced particularly for E. camphora.

By the beginning of winter, one year after seeding, there were only two E. camphora and eight E. dalrympleana surviving on the transition plot and two of the latter species on plot 3 on the swampy area.

These seedlings were only 1 cm. high indicating that growth rate is extremely slow.

TABLE 23

GERMINATION AND SURVIVAL OF <u>E. CAMPHORA</u> AND <u>E. DALRYMPLEANA</u> BROADCAST SOWING COREE FLAT A.C.T.

Sown 25/5/61

Plot no.	1	2	3	4	5
Site	dry	moist	wet	wet	wet
			E. camphora		
Time in weeks					
6	-	-	-	-	-
24	8	22	44	122 *	28
41	-	6	-	-	-
53	-	6	-	-	-
			E. dalrympleana		
6	-	-	-	-	-
24	16	22	1	1	-
41	1	5	-	-	-
53	-	-	-	-	-

* Seedlings at cotyledonary stage only; some doubt that all seedlings are <u>E. camphora</u>, Leptospermum, native to the area, also germinating.

TABLE 24

GERMINATION AND SURVIVAL OF E. CAMPHORA AND E. DALRYMPLEANA FROM SEED SHED FROM CAPSULE BEARING BRANCHES

COREE FLAT A.C.T.

Sown 25/5/61

Plot no.	1	2	3	4	5
Site	dry	moist	wet	wet	wet
			E. camphora		
Time in weeks					
24	-	55	80	59	47
41	-	9	-	10	2
53	-	2	-	-	-
			E. dalrympleana		
24	3	25	5	11	5
41	1	14	14	-	-
53	-	8	2	-	-

Transplant trial

Plants of both species were raised from seed collected in the area and planted out approximately 20 plants per species on each plot. 5 plants of each species per container. The seedlings were approx. 6 cm. high at the time of planting in late autumn. They had been grown in the nursery and were hardened off before planting.

Observations 6 weeks later, in mid winter indicated that survival of E. camphora on the swamp was greater than for E. dalrympleana although survival for both was better on the well drained site.

Frost heaving had taken place on the swampy areas some plants being lifted 3 cms. out of the soil.

Observations made 24 weeks after planting showed that only one E. camphora was surviving on the swamp site. Damage, presumably by wallabies, had reduced the number of plants considerably, many being eaten entirely or cut back to near ground level.

Further observations were made 41 and 53 weeks after planting. Table 25. At this stage the remaining E. camphora had died and plants of both species which remained were on the transition and dry site. Further animal damage had occurred and it was not possible to gain any information from height measurements.

In November 1961 a further transplant trial was commenced. Seedlings of both species were pricked off into 3" diameter peat pots containing a nursery soil mixture and 2 plants of each species were planted per pot. At time of planting the seedlings were well established approx. height 6 cm. and age from seed three months.

The pots were planted undisturbed, ten per plot on each of the five plots. Peat pots were used so that no root disturbance would occur at planting

TABLE 25

SURVIVAL OF E. CAMPHORA AND E. DALRYMPLEANA SEEDLINGS TRANSPLANTED AT COREE FLAT A.C.T.

Commenced 25/5/61

Age of seedlings 3 months

Average height 6 cm.

Plot no.	1	2	3	4	5
Site	dry	moist	wet	wet	wet
		E. camphora			
Time in weeks					
nil	19	19	21	21	19
6	19	11 (8 eaten)	18	- (7 eaten)	9 (4 eaten)
24	12	5	1	-	-
41	7	3	-	-	-
53	7	3	-	-	-
		E. dalrympleana			
nil	15	15	19	18	19
6	10	14	-	-	-
24	5	6 (5 eaten)	-	-	-
41	3	4	-	-	-
53	2	2	-	-	-

time. Height measurements were taken at planting.

At assessment four months later, survival of both species on all plots was high although damage from wallabies had occurred resulting in the loss of some plants. At this stage it was possible to detect a number of natural hybrids amonst the planted seedlings. These were not obvious at the time of planting. E. camphora juvenile leaves are ovate, non glaucous, petiolate and alternate at an early stage, whilst those of E. dalrympleana are glaucous, opposite, sessile and cordate to orbicular. A third species, E. viminalis has juvenile leaves which are opposite, pale green, sessile and lanceolate. The hybrids were probably between E. camphora and E. viminalis, and E. dalrympleana and E. viminalis as indicated by a tendency to opposite lanceolate leaves in E. camphora seedlings and non glaucous lanceolate leaves in E. dalrympleana plants. The heights of the hybrids were measured but not included in the mean.

A further assessment was made 7 months after planting before onset of winter.

Severe animal damage to plants on plots 2, 4 and 5 meant that no conclusive evidence could be gained from the measurements on these plots. Plants on plots 1 and 3, on dry and wet sites respectively, were untouched by animals and survival, height and increment for these are given in Table 26.

Survival at the onset of winter was 100% for each species on each site. At the end of winter 20% of E. dalrympleana plants on the swamp area had been killed. Increment figures show that there had been very little growth between the autumn and early winter measurements.

The initial heights of E. camphora were lower than E. dalrympleana on both plots but after one season's growth the heights of both species on both sites were similar. This meant that E. camphora had grown faster than E. dalrympleana under uniform growing conditions.

As mentioned above the juvenile leaves of E. dalrympleana are opposite whilst those of E. camphora are alternate and it may be that increase in height growth is not the most reliable measure of seedling growth, and the number of leaves produced may give a clearer indication of growth rates.

There are no records of studies on the adaptive role of opposite and alternate juvenile leaf patterns in Eucalyptus seedlings. In the case of swamp species which must grow through a dense layer of grass and sedge the capacity to extend rapidly in height may be of value in enabling seedlings to emerge and compete with the thick ground cover.

A study of the relative values of juvenile leaf arrangement in the survival of Eucalyptus seedlings may be rewarding.

The results of broadcast sowing and seedling transplant trials with E. camphora and E. dalrympleana were not conclusive, however a number of points emerged at least for the particular season of study.

Firstly, the survival rate on sub alpine swamps is presumably very low despite high germination rates.

Secondly, the germination rate on dry sites adjacent to the swampy areas is either very low or seed germinates but seedlings die within a short time. (This assumes that similar quantities of viable seed were sown on each site, and that chlordane granules were equally effective in preventing removal of seed by ants from both wet and dry sites.)

It is clear that there is a high rate of loss of Eucalypt seedlings to browsing animals such as wallabies and wombats, and that for adequate experiment fenced plots are necessary to ensure that a sufficient number of seedlings reach an age when climatic and edaphic effects of survival can be studied independently. of browsing animals. The latter however may be a relevant factor in natural conditions and it is possible that they may partly determine the outcome.

TABLE 26

SURVIVAL, MEAN HEIGHT, AND INCREMENT OF E. CAMPHORA AND E. DALRYMPLEANA PLANTED ON TWO SITES COREE A.C.T.

Commenced 10/11/61

Age from seed 3 months

SITE	DRY		WET		SEASON
	C	D	C	D	
Time in weeks					
nil	20	20	20	20	Summer
17	20	20	20	20	Autumn
29	20	20	20	19	Winter
50	20	20	20	16	Spring
Mean Height cm.					
nil	4.7	7.9	4.3	7.0	Summer
17	14.0	18.7	16.5	14.8	Autumn
29	14.7	19.0	16.9	14.8	Winter
50	No growth during winter				
Mean Increment cm.					
nil					
17	9.3	10.8	12.2	7.8	
29	0.7	0.3	0.3	0.0	
Ratio Final to Initial Height					
	3.0	2.5	3.8	2.0	

CHAPTER 10

ADAPTATIONS AND SPECIES DISTRIBUTION

Field transects have shown that there is an abrupt change in species distribution between swamp and adjacent well drained sites. This is particularly so for adult trees although seedlings of species from the poorly drained areas are found on well drained sites. By comparison the species of well drained sites do not regenerate on the waterlogged areas and presumably the factors operating to prevent this do so at an early stage in the life of the plant.

Ellenberg (1952) distinguishes between physiological tolerance (plants growing in monoculture) and ecological tolerance (plants competing with each other) and concludes that the relative competitive ability of a species varies with the environment including competing species. Moore (1957) has studied a pair of Eucalyptus species from this point of view and considers that "the tolerance ranges for some edaphic factors overlap, and under these conditions the presence or absence of interspecific competition will determine the community which develops on a particular site."

These results were based on pot trials using soils taken from the sites of each species and the competitive factor was between two Eucalyptus species. Beadle (1962) warns that such comparisons may not be valid when extrapolated to field conditions where the competition may not be between related species of the same genus but between species of different genera. The factor controlling the distribution of one tree species may not be interspecific competition with a tree species of the same genus but competition with members of the grass or herbaceous layer.

Beadle (ibid) suggests that pot trials may give misleading results if the controlling factor in species distribution is an edaphic one as the physical structure of the profile is destroyed, and it is not possible to take into account the effects of the subsurface layers.

Whilst these facts are valid the pot trial remains a useful tool in a study such as the present one, particularly if it can be paralleled with field trials.

A number of pot trials were carried out during the course of this work the aim being to gain some idea of the role of adaptations to waterlogged conditions in the control of distribution patterns with different species.

Table 27 presents the results of a pot trial with E. camphora and E. dalrympleana grown in soils taken from beneath stands of each species in the same locality in the Australian Capital Territory.

Soil samples were taken from the top 6" of the profile after removal of the grass and litter layers. The soils were sieved to remove gravel and large roots and placed in 5" diameter unglazed earthenware pots an equal volume of soil per pot. There were three treatments with five replications at two water regimes for each soil. The treatments were E. camphora and E. dalrympleana grown both singly and interplanted. Waterlogging was achieved by blocking the drainage hole and flooding with water to the soil surface.

Seed from single trees of each species growing in the locality from which the soils were taken, was sown directly onto the soil surface and the pot covered with paper until germination had occurred.

Plants were thinned to 10 per pot for single species and in the case of mixed planting to 5 of each species per pot.

The pots were rotated at weekly intervals to reduce any effect due to position in the glasshouse.

Fig. 31 and 32 show the plants at time of assessment, age 20 weeks and the results in Table 27 indicate a number of points.

1. For both soils and both species the height growth under freely drained conditions was significantly greater than growth under waterlogged conditions.

2. Height growth of both species in the E. camphora swamp soil was significantly greater than that in the E. dalrympleana site soil.

3. At the time of assessment there was no significant difference between height growth of the two species when grown in mixture.

One point observed was the germination and growth of Juncus sp. in the waterlogged E. camphora site soil. This sedge is common in the area from which the soil was taken and presumably seeds were present in the sample. These germinated and grew well under waterlogged conditions, but were only sparsely represented in the same soil when freely drained. Collis George and Sands (1959) found that seed of Juncus sp. required low suction pressures i.e. high watertable, for successful germination and suggested that an effective control measure for Juncus may be found by draining soils to prevent waterlogging.

Beadle (1962) has shown that "the surface soils of swamps in the Hawkesbury sandstone area have about twice the phosphate content of upland soils, however the controlling factor for species distribution

Fig. 31

L - R E. dalrympleana, E. dalrympleana and E. camphora interplanted, E. camphora. Rear freely drained, front waterlogged. E. dalrympleana site soil.

Photo N.I.B.

Fig. 32

As above E. camphora site soil. Competition from sedge in waterlogged soil.

Photo N.I.B.

in these areas is the degree of waterlogging and the differences in soil phosphate are incidental."

TABLE 27

MEAN HEIGHT OF E. CAMPHORA AND E. DALRYMPLEANA GROWN SINGLY AND INTERPLANTED IN TWO SOILS AT TWO MOISTURE LEVELS

Age 20 wk. Ht. cm.

Freely Drained

	E. camphora Site Soil	E. dalrympleana Site Soil
E. camphora	19.7	13.9
E. camphora }	21.7	13.3
E. dalrympleana }	21.0	13.1
E. dalrympleana	22.0	14.2

Difference of means of species N.S. in both soils

Difference of means of sites $P < 0.01$

Waterlogged

	E. camphora Site Soil	E. dalrympleana Site Soil
E. camphora	9.4	10.4
E. camphora }	11.5	11.5
E. dalrympleana }	9.1	10.4
E. dalrympleana	6.9	10.6

Difference of means of species N.S.

Difference of means of sites N.S.

The results of this pot trial suggest that a similar case may exist in sub alpine swamp soils carrying E. camphora, although the soil phosphate determinations necessary to confirm this have not been carried out.

Fig. 33 and 34 show the root growth of both species in the E. dalrympleana soil waterlogged and freely drained. Under waterlogging the roots are largely confined to the upper soil layers whilst under freely drained conditions the roots occupy the soil completely.

Two points relating to the field distribution of these two species are suggested by the results. Firstly, as E. camphora grows better under freely drained conditions than when waterlogged it presumably does not require the latter condition for optimum growth and other things being equal would grow better away from the swamp. This is in contrast to genera such as Typha and Juncus for which it can be shown that a watertable at or above the surface is necessary for optimum growth. Secondly, as E. dalrympleana grew better in well drained swamp soil than in well drained soil from its own site, it suggests that soil fertility levels are not the factor precluding this species from becoming established on the swampy, poorly drained site.

Within the period of the experiment there was no evidence of interspecific competition between the species. At all times the watering was adequate by normal nursery standards, the humidity was high within the glasshouse. It may be that under conditions of water stress the effects of competition would become more evident.

At the time of assessment there was no

Fig. 33

Roots of E. camphora and E. dalrympleana inter-planted in freely drained E. dalrympleana soil.

Photo N.I.B.

Fig. 34

Roots of E. camphora and E. dalrympleana interplanted in E. dalrympleana soil waterlogged Roots mainly on the surface.

Photo N.I.B.

significant difference between the survival of each species under waterlogged conditions. This is in contrast to the survival of planted seedlings of both species grown waterlogged in metal containers. Chapter 5 As described above, the plants in this experiment were grown in clay pots waterlogged by sealing the drainage hole and flooding with water. Whilst this was a satisfactory method of maintaining a waterlogged condition there was some water loss and therefore some gas exchange through the walls of the pots. With plants grown waterlogged in metal containers this was not the case and the waterlogging conditions were probably of a more severe nature than those imposed on plants growing in clay pots.

In Chapter 5 the results are given of an experiment designed to determine whether aerenchyma was of adaptive value in the survival of <u>E. camphora</u> grown under waterlogged conditions. At the same time a comparison was made with plants grown under freely drained conditions to determine whether a high water-table was necessary for the optimum growth of <u>E. camphora</u> and by growing <u>E. dalrympleana</u> under comparable conditions to determine any relative growth rate difference between the two species when grown under uniform conditions.

Seedlings of both species were raised in boxes and pricked off at age 7 weeks into one gallon aluminium containers filled with nursery loam. There were two moisture treatments, waterlogged and freely drained, and the species were grown both singly at 10 plants and interplanted at 5 plants each per container. There were five replicates of each combination. The tins were placed in the open and were grown in Canberra for a period of 23 weeks from December to May.

The survival percentages have been discussed in Chapter 5 and it is clear that E. camphora, the species of the swamp site is better adapted to growth under waterlogged conditions than is E. dalrympleana a species of the relatively drier site. As these results were obtained during the late summer and autumn there was no effect of frost and low temperature and it appears that the controlling factor in survival was high watertable.

Mean height in cms. from the lignotuber to the growing tip are given in Table 28. The differences in mean of height growth at the two water regimes for both species were highly significant indicating again that the height growth of E. camphora is better under freely drained than under waterlogged conditions.

TABLE 28

MEAN HEIGHT OF E. CAMPHORA AND E. DALRYMPLEANA GROWN SINGLY AND INTERPLANTED AT TWO SOIL MOISTURE LEVELS

Age 30 wk. Period of treatment 23 wk.

Mean Ht. in cm.

	Freely Drained	Waterlogged
E. camphora	50.4	16.6
E. camphora }	50.2	14.9
E. dalrympleana }	36.8	7.5
E. dalrympleana	45.1	7.2

Difference of means of moisture levels significant $P < 0.01$ for both species.

Difference of means of E. camphora and E. dalrympleana freely drained N.S. at 1% level.

Difference of means of E. camphora and E. dalrympleana waterlogged significant $P < 0.1$

The results of a trial growing E. robusta at two soil moisture levels indicated that it grew better in height and dry weight under freely drained than under waterlogged conditions.

Seed of E. robusta was germinated in a nursery flat and pricked off at age two months at 6 plants to each of 10 one gallon aluminium containers filled with sandy loam. Five tins were flooded to the soil surfacce the remainder were allowed to drain freely. The plants were assessed at age seven months and height growth and oven dry weight of shoots and roots were determined. The division between roots and shoots was made immediately below the first lignotuber pair formed in the axils of the cotyledons.

The difference of means for height and oven dry weight of shoots were significant at $P < 0.001$ for the two moisture levels, but there was no significant difference in oven dry weight of roots, due to the development of a thick mat of surface roots under waterlogged conditions.

These results show that E. robusta, whilst adapted to growth under conditions of waterlogging, grew better under the freely drained conditions of this experiment.

The results from pot trialswith E. camphora and E. robusta suggest that these two species occur on swampy sites not because of a high watertable but in spite of it. Whether competition from other species of the tree and herbaceous layers is a factor which prevents invasion of these swamp Eucalypts onto drier and well drained sites has not been established.

TABLE 29

MEAN HEIGHT OF SHOOTS AND MEAN OVEN DRY WEIGHT OF SHOOTS AND ROOTS OF E. ROBUSTA AT TWO SOIL MOISTURE LEVELS

Ht. cm. Wt. gm. Age 30 weeks Period of treatment 23 weeks

	Freely Drained	Waterlogged
Ht. of shoots	70.9	38.1
Wt. of shoots	10.6	4.5
Wt. of roots	3.7	3.8

DISCUSSION AND CONCLUSIONS

The waterlogged environment provides one of the more specialised situations for plant growth and species occurring on such sites usually possess distinctive morphological or physiological adaptations which enable them to survive under conditions of poor substrate aeration.

These adaptations vary with the degree and intensity of waterlogging and include such characteristics as possession of stomata only on the upper leaf surface as in Nymphaea, formation of aerenchyma in stems of Typha, and the development in mangroves of a specialised root system with pneumatophores.

Some plants have become adapted to conditions of waterlogging to such a degree that a high watertable, and even free water, are necessary for continued survival. Floating hydrophytes such as Lemna and Eichornia are extreme examples of this. It can be shown with Typha that growth under conditions of free drainage is inferior to that under conditions of waterlogging with some free water on the surface even though excessive depth of water inhibits growth. Some species of Juncus, Phragmites and Restio behave in a similar way. Woody plants, and particularly those which propagate by sexual rather than vegetative means, are largely excluded from conditions of continuous waterlogging with free water on the surface.

Mangroves, occurring in the littoral zone, are a specialised group which occupy distinctive habitats subjected to regular periods of alternating submergence and exposure. Members of this group, which occur in a number of distinct families, are adapted to their environment in a number of ways, two of which are the formation of pneumatophores and vivipary.

Apart from this group, the number of arborescent species which occupy waterlogged sites is small. Salix species are considered as the trees most commonly found growing under conditions of waterlogging. Taxodium distichum native to the swamps of Florida, and largely though not entirely restricted to this area develops "knee roots" under waterlogged conditions. These have been considered as of survival value.

Alder, willow, and to a lesser degree poplar, are the common Northern Hemisphere examples of trees typical of poorly drained sites which are regularly flooded. These trees are deciduous and are usually subjected to the more severe conditions of waterlogging during the dormant period in winter.

Species of Melaleuca and Casuarina in Australia are amongst the few evergreen tree species which can be clearly grouped as occurring naturally on sites of extensive waterlogging.

It is necessary therefore in any discussion relating to adaptation to waterlogged conditions, to distinguish between plants which grow in, and require, a high watertable for optimum growth and those which may be classed as enduring waterlogged conditions. With tree species which occur on waterlogged sites it is also necessary to distinguish between those which are waterlogged during the dormant period when root activity is much reduced, although this in itself may be an adaptation, and those which are waterlogged during the active growth period.

As a genus, Eucalyptus reaches its best development in well watered but well drained areas, and the number of species found growing naturally on soils subject to waterlogging for long periods is small.

There are no species of Eucalyptus which grow on permanently waterlogged soil in the sense that Typha, Phragmites, Carex and Restio do, although species such as E. robusta and E. camphora are largely restricted to sites waterlogged for lengthy periods each year. Some species e.g. E. stellulata which are generally considered as species of swampy poorly drained flats, are found, on close field examination to occupy slight rises within swampy areas. This places these species slightly above the surrounding wetter areas and amounts to avoidance of the more extreme conditions. Their position in the field may be determined more by a high water requirement in summer than an ability to withstand waterlogging in winter.

There are other species which occur typically on well drained sites, but are sometimes found in areas subject to occasional waterlogging for short periods. E. stuartiana and E. rubida are typical of this group. Individuals of these two species may be found both on hard dry sites and on alluvial flats subject to seasonal waterlogging within the one general locality.

It would be of interest to determine whether the members of these species which occur in swampy sites, represent ecotypes which are adapted to growth in those situations. Pryor (unpublished) has shown that E. viminalis has several different ecotypes one of which is adapted to growth in moist gullies of wet sclerophyll forest, another to cold, dry sites in woodland communities. Seedlings from open pollinated seed from trees in both locations, maintain the characteristics of the parents when grown under uniform conditions in a neutral environment. Various workers have shown that clinal patterns exist for characteristics of frost resistance, glaucousness and seed dormancy, and it may be that variation in adaptation to conditions of waterlogging occurs at the intra as well as the interspecific level.

The features which characterise the genus Eucalyptus are a high level of speciation and a precise site/species correlation in undisturbed natural communities. The existence of these characteristics supports the view that Eucalyptus as a genus has evolved over a long period of time and that a precise degree of adaptation is present. Characteristics such as lignotubers, mallee habit, leaf and stem glaucousness, frost resistance and seasonal deciduous habit have been thought of as variable features which, when present, assist the survival of some species or some populations of species under the more specialised environmental conditions of a particular habitat.

This, together with the fact that swampy areas usually support distinctive plant communities possessing adaptations which presumably enable them to grow under conditions of poor substrate aeration, suggests that adaptations to waterlogged conditions may be expected to occur in Eucalyptus even if confined to but a few species.

The common morphological features possessed by hydrophytes, and considered of adaptive value, are the development of aerenchyma which allows effective gas exchange between roots and shoots, a specialised root system formed largely at or near the soil surface and the ability to form cladogenous roots under conditions of submergence and reduced aeration around the primary root system.

These features are found more or less in Eucalyptus species which grow naturally in swampy sites and the results presented above suggest that these characteristics are of adaptive value.

These morphological features may not be the only adaptations and evidence presented by Leyton (1958) indicates that some Salix species have a root system physiologically capable of growth at oxygen concentrations lower than that at which roots of other tree species, e.g. Picea, can grow, suggests that a study of the root growth of some Eucalyptus species at different oxygen levels may be of value.

The development of aerenchyma on the stems of some species when immersed in water has been described. This tissue which is formed by the phellogen is composed of alternating layers of suberised and non-suberised cells. The non-suberised cells are elongated radially and there are many intercellular spaces, giving the whole outer bark a spongy character.

The formation of this tissue occurs rapidly following immersion of some species and extends to just above the water level.

Whether the physiological capacity of this tissue aids gas exchange between the root system and the air above, or as has been suggested by Laing(1932) assists in the removal of excess water which the plant cannot remove in the normal way through the roots and shoots, has not been determined.

The evidence obtained indicates a close correlation between the development of aerenchyma on stems and continued survival under waterlogged conditions, and the development of this tissue occurs most strongly on those species which are naturally subjected to the more severe conditions of waterlogging.

Aerenchyma is formed on the stems of some members of the Transversae group of Eucalypts which occur in well drained habitats, although not to the same degree as on E. robusta. Daubenmire (1959) points out that "if adaptation by mutation is a random phenomenon unrelated to an organism's needs, warm climate vegetation should possess some individuals with cold tolerance, for in warm regions, a change in this direction would be neutral from a natural selection point of view". It may be analogous that the capacity to form aerenchyma under waterlogged conditions is a neutral character common to some members of the Transversae group but confers a benefit only on those species which grow often on waterlogged sites, e.g. E. robusta.

The capacity to develp cladogenous roots is present in a number of species representative of most of the major subgeneric groups within the genus. Stem borne roots have been recorded in the field on E. robusta, rudis, camaldulensis, camphora, stellulata, niphophila, nitens, melliodora, polyanthemos, and paniculata. In some cases roots have been found on only individuals within quite large populations. Generally those individuals forming cladogenous roots have been subjected to flooding at some previous time or have grown in sphagnum beds or as in the only recorded case of E. polyanthemos have been blown over onto swampy ground where layering has occurred. Whether the capacity to form cladogenous roots is inherent in a larger number of species and individuals but would only be revealed when plants are subjected to specialised environmental conditions has not been determined. Certainly some species e.g. E. botryoides for which numbers of seedlings have been subjected to experimental submergence, show no capacity to form cladogenous roots even under conditions favourable for their development in other species.

With E. robusta and E. rudis, the two species which readily form cladogenous roots, only about half the individuals in any population do so although all plants are subjected to uniform conditions. The number of roots per plant and the point of origin on the stem are also quite variable.

Within the limitations imposed by this variability however there are strong indications that the ability to form cladogenous roots is of adaptive value but probably only to those species which are normally exposed to the conditions favouring the development of these roots.

Within the genus there are some general variations within the major sub groups in the capacity to withstand waterlogged conditions. In particular members of the Renantherae tested have shown a fairly high degree of sensitivity to conditions of poor drainage. Of the large number of species comprising this group few can be regarded as occurring naturally in areas subject to waterlogging and although many occur in high rainfall areas, they are restricted to well drained sites. None of the morphological features considered as adaptations have developed, or been seen in the field on either E. stellulata or E. umbra, two of the Renantherous species recorded as occurring on poorly drained areas. There was some suggestion from experimental trials, that E. stellulata is more tolerant of waterlogging than E. pauciflora, although it is clearly far less tolerant of such conditions than Macrantherous species such as E. robusta and E. camphora.

Although many Eucalyptus species show a close relationship to particular sites in the field, they are generally capable of growing well when planted in habitats removed from their natural situation.

E. ficifolia, Red Flowering Gum, occurs naturally in restricted areas of Western Australia, but has been widely used and successfully planted in areas of south eastern Australia where the winter though colder than that of its natural habitat is not excessively so. E. maculosa has been used extensively as a street tree in Canberra. This species grows naturally in the dry sclerophyll forest on the hills surrounding the city, but does not occur naturally on the plain nor are there any indications that it has occurred there in the past.

E. camaldulensis, which occupies mainly a distinctive habitat bordering the inland river systems all over Australia has been planted widely overseas, as for example in the Middle East and India, where it thrives often in low rainfall areas not associated with river systems. This species, which appears to be closely associated with specialised field situations in Australia, has therefore shown remarkable flexibility when grown overseas. A similar case exists with E. robusta which in its natural habitat is usually restricted to swampy poorly drained areas and yet grows well under plantation conditions both in Australia and overseas.

These factors suggest that not only climate, physiography and edaphic factors control species distribution in Eucalyptus but that interspecific competition may play an important role in the delineation of species boundaries or perhaps even some other as yet undisclosed factor as Martin (1961) has suggested.

It would be interesting to determine whether interspecific competition is a factor preventing E. robusta from invading the E. botryoides site or E. stellulata the adjacent areas occupied by E. pauciflora. Extensive trials using broadcast sowing and field transplanting techniques, coupled with controlled pot experiments may help to provide such information.

It is indicated from this study that Eucalyptus as a genus does not thrive on poorly drained sites although a very few species have, by morphological adaptations, become better fitted than most species to grow on such sites and perhaps a few have developed a more specific physiological capacity to do so without a corresponding anatomical change.

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APPENDIX A

Transect No. 1 Date 17.1.61

Location: Peppercorn N.S.W.

Altitude: 4,450 ft.

Latitude: 35°40'S. Longitude: 148° 40'E.

Area: 4 ch. x ½ch.

Plot bearing: 180°

Eucalyptus species:

Adult:	E. pauciflora	Regeneration:	E. pauciflora
	E. stellulata		E. stellulata

Shrub and grass layer:

Dry:	Wet:
Poa caespitosa	Stylidium graminifolium
Brachycome sp.	Ranunculus pimpinelifolius
Helichrysum sp.	Juncus sp.
Euphrasia sp.	Restio australis
Bossiaea foliosa	Stellaria pungens
Wahlenbergia sp.	
Hypochaeris radicata	
Leptorrhynchus squamatus	

Description: This and Transect No. 2 were located in E. pauciflora - E. stellulata Association alpine woodland type. Throughout this area E. pauciflora and E. stellulata occur with some E. dalrympleana present. The tree line appears to be controlled by frost hollow effect combined with poor drainage occurring in areas adjacent to streams. Wherever a slight rise occurs throughout the area, E. pauciflora and E. stellulata occur with the latter species growing on the moister and possibly colder aspects, whilst E. pauciflora is on the rocky knobs away from areas of poor drainage.

The area has been grazed regularly during the summer period.

<u>Soil: Hole 1</u> Adult trees of <u>E. pauciflora</u> and <u>E. stellulata</u> present regeneration of both species. Continuous grass cover giving Ao of ½". Horizon boundaries diffuse throughout and changes in colour and clay content gradual. Some granitic floaters up to 4" diameter throughout the profile.

Many grass roots present in the upper 6" with large tree roots up to 1" diameter to depth of 10", smaller tree roots to 20" +.

Gradual change in colour from 0 - 26" nut brown to orange brown. Clay loam crumb structure changing gradually to gravelly clay loam; gravel content increasing to depth of 26" where decomposing granite parent material appeared.

<u>Hole 2</u>: End of plot, below present tree line, although some scattered regeneration of <u>E. stellulata</u> present. Continuous grass cover giving an Ao ½". Deep, brown, loamy soil with little differentiation to 26". Gravel content increasing below 18" depth. Some granite floaters up to 4" diameter present. Grass roots present to 18" abundant in the top 6". Colour change is from dark brown to light nut brown. Clay content increasing with depth. pH 4.5 throughout.

Soils in both profiles are very similar, that of Hole 2 being slightly darker in colour and of greater depth.

<u>Transect No. 2</u> Date 17.1.61

Location: Peppercorn N.S.W.

Altitude: 4,450 ft.

Latitude: 35° 40'S. Longitude: 148° 40'E

Area: 4 ch. x 1 ch.

Plot bearing 90°

Eucalyptus species:	Adult	Regeneration
	E. pauciflora	E. pauciflora
	E. stellulata	E. stellulata

Shrub and grass layer:

Dry	Wet
Poa caespitosa	Stylidium graminifolium
Brachycome sp.	Ranunculus sp.
Helichrysum sp.	Stellaria pungens
Hakea microcarpa	Juncus sp.
Epacris microphylla	Poa sp.
Hypochaeris radicata	Restio australis

Description:

This transect was located at right angles to Transect 1 to show the difference between the southerly and easterly aspects as regards E. stellulata and E. pauciflora distribution in this area.

It also shows clearly the abrupt tree line conditioned primarily by frost hollow effect and poor drainage.

There is some regeneration of E. stellulata on wetter and more low lying areas than where the last adult tree occurs. Most of these individuals show signs of past frost damage in dead shoots, and the resultant development of a very large lignotuber. Some of this damage may well result from summer grazing which is of such extent that it is rare to find a snow grass tussock uneaten. Cattle are unselective and any Eucalypt seedlings growing amongst the snow grass would be cropped also.

Soil:

Hole 1: as for Hole 1 in Transect 1.

Hole 2: Situated at the end of the transect. No adult trees present or signs of trees having been present in the past. Some regeneration of E. stellulata most showing the effects of frost damage. Lignotubers well developed. Continuous ground cover of Poa sp. Stellaria pungens, Stylidium graminifolium, Restio sp.

Juncus sp. and Epacris microphylla.

Ao well developed ¾". Many grass roots in the top 9". E. stellulata roots to 27". A 0 - 19" black humus clay, crumb structure, friable. 19 - 28" band of deposited gravel, 3 - 10 mms. diameter with an abrupt change at 28" to a yellow orange mottled clay containing some quartz grains up to 1 mm. in diameter. Moderate compaction, E. stellulata roots penetrate this layer.

Soil pH at 2" 4.6, 15" 4.5 and 29" 5.0.

Transect No. 3 Date 8.2.61

Location: Cotter House A.C.T.

Altitude: 3,490 ft.

Latitude: 35° 40'S. Longitude 148° 50'E.

Area: 3 ch. x ½ ch.

Plot bearing 71°

Eucalyptus species present:

Adult: E. pauciflora	Regeneration: E. pauciflora
E. stellulata	E. stellulata
	E. rubida

Shrub and grass layer:

Dry	Swamp
Themeda australis	Epacris breviflora
Poa sp.	Carex appressa
Tetratheca sp.	Juncus sp.
Discaria australis	
Eritrea centaurea	

Description: This plot was located adjacent to the area used for seeding and transplanting trials with E. pauciflora and E. stellulata. It extends from a typical E. pauciflora site onto a flat site carrying E. stellulata. The lower areas are water-logged throughout winter, the boundary of waterlogging indicated by a band of Epacris breviflora about half way down the transect. Snow would lie on the flats for some days each winter.

Soils: Hole 1.

At the beginning of 1st chain. Grass cover mainly Poa sp. not continuous. No occurrence of Juncus or Carex species.

A_0 ½" leaf litter and branchlets. A is light brown clay loam, nutty to crumby, containing some gravel ¼ - ½" in size. Roots present throughout this horizon which extends from 0 - 8" pH 4.5. B is a red brown to orange clay compacted shiny on cut faces pH 4.5. Occasional shale appearing at 15".

Hole 2.

Situated at the end of the first chain. Both E. pauciflora and E. stellulata are present in both the tree stratum and regeneration layer. Almost continuous grass cover giving a 1" A_0 layer. A horizon extends from 0 - 7", fine brown to black friable silty clay loam pH 5. Many roots in the 5 - 7" zone. Boundary to B horizon is sharp. B from 7 - 16"+ composed of yellow brown clay loam. Clay content and red colour increasing with depth. Blocky structure. Quartz crystals numerous pH at 14" is 5.0.

Hole 3.

E. stellulata only tree species present. Complete grass cover with some sedges. Thick A_0 1 - 1½" A 0 - 5" black heavy clay loam crumby containing many fine roots, pH 4.5 There is a sharp boundary to the B horizon which is orange grey mottled sandy clay containing water worn gravel. Signs of gley development at 15" due to waterlogging. Roots present to this depth pH at 14" 4.5 This site would be waterlogged for a large part of each winter. There is a rapid change in soil type over the length of the transect.

from a red brown podsolic derived from shale, to an alluvial soil highly organic. Subject to waterlogging although well aerated to about 15" due to high sand content.

Transect No. 4 Date 8.2.61

Location: Cotter Flats A.C.T.

Altitude: 3,460 ft.

Latitude: 35° 40'S. Longitude: 148° 50'E.

Area: 4 ch. x ½ ch.

Eucalyptus species present:

Adult:		Regeneration:	
	E. pauciflora		E. pauciflora
	E. stellulata		E. stellulata
	E. rubida		E. rubida

Shrub and grass layer:

Dry	Swamp
Themeda australis	Leptospermum myrtifolium
Poa sp.	Epacris breviflora
Wahlenbergia sp.	Stylidium graminifolium
Eritrea centaurea	Carex appressa
Discaria australis	Juncus sp.

Description:

This plot located ¾ mile on the Canberra side of Cotter Hut and extends from a dry E. pauciflora site down a steep slope to swampy flats sparsely treed but well grassed. The flats are more or less permanently wet throughout winter and because of cold air drainage are undoubtedly colder than the adjacent slopes.

E. stellulata occurs off the swampy area but is largely restricted to the sides of small creeks which run onto the flats. On the other hand, there are no E. pauciflora present either as trees or seedlings. on the wet flats.

It is clear that the E. stellulata

regeneration on the flats suffers from snow and cold during winter and most plants show signs of a number of annual shoots which have been frost damaged. This is shown by a mass of coppice shoots and strong lignotuber development.

On the drier sites, E. stellulata shows considerable fire damage and there are indications that it is less tolerant of fire than E. pauciflora.

Soils: Hole 1. Beginning of transect.

Predominantly E. pauciflora with some E. rubida, no adult E. stellulata present. 60% cover of grass and shrubs. Large quantity of Eucalypt leaf and twig litter. Ao thin $\frac{1}{8}$ - $\frac{1}{4}$". A horizon from 0 - 9" light brown clay loam smooth, crumb structure, numerous roots throughout with tree roots up to $\frac{3}{4}$" diameter. to 6" depth pH 4.5 Clear transition to B horizon, 9 - 23" red brown clay with yellow mottling shiny on cut faces, blocky. Silica crystals present throughout $\frac{1}{8}$" diameter pH 5.0 Effective root depth 12 - 14"

Hole 2:

E. stellulata only tree species present. Soil profile studied on a slight rise carrying thick grass cover, but no sedges. Soil profile wet throughout. An alluvial soil with high sand content, aeration good throughout as indicated by presence of roots to 26", abundant in top 3", tree roots to $\frac{1}{2}$" diameter present to 14". 0 - 3" fine sandy loam light brown, pH 4.5

Gradual transition to B. 3 - 23".Increasing proportion of sand with scattered water worn pebbles up to 1" diam. Light brown in colour changing at 26" to yellow grey brown sandy clay ph 4.5

This site would be waterlogged throughout /

winter

High sand content may ensure good aeration throughout the growing season.

Transect No. 5

Location: Jerangle Rd. N.S.W.

Altitude: 3,120 ft.

Latitude: 35^{o} 40'S. Longitude: 149^{o} 30'E.

Area: 4 ch. x $\frac{1}{2}$ ch.

Plot bearing: 43^{o}

Eucalyptus species:

Adult	E. aggregata	Regeneration:	E. pauciflora
	E. pauciflora		E. stellulata
	E. stellulata		E. aggregata
	E. viminalis		E. viminalis

Shrub and grass layer:

Dry	Moist
Themeda australis	Epacris paludosa
Poa sp.	Leptospermum sp.
Melichrus	Juncus sp.
	Utricularia dichotoma

Description:

Plot located in depauperate dry sclerophyll forest with some swamp areas with impeded drainage. Area has been grazed. E. aggregata occurs as single trees on sites of poor drainage seldom, if ever, on rocky sites.

Soils: Hole 1 Examined 22.8.61

Beginning of plot E. stellulata and E. pauciflora present. Thin grass cover. Ao very thin 1/10". A 0 - 5" loamy sand light brown in colour, no structure. Numerous fine roots. pH 4.5
B horizon 5 - 24"+ yellow brown sand with occasional large tree roots. pH 5.0 Water table at 24". No sign of parent material at this depth.

Hole 2: On the edge of swamp area E. aggregata regeneration present. Dense sedge growth giving an Ao of ½" A 0 - 11" black silty loam little sand. Roots numerous. Orange mottling around roots. pH 4 - 5. B 11 - 18"+ becoming lighter in colour to almost pure white fine grained sand, gradually becoming coarser at depth. pH 5. Soil waterlogged throughout.

Hole 3: End of transect. Adult trees of E. pauciflora and E. stellulata present. Regeneration of E. pauciflora, E. viminalis, E. aggregata. This grass cover, sparse litter.

A 0 - 3" light brown loamy sand with numerous roots, changing to yellow brown coarse loamy sand. Grain size increasing with depth. Compacted coarse grained granitic parent material. pH 1" 5.0, 10" 4.5, 19" 4.5 Soil on swamp area, carrying E. aggregata was more organic than soils on the drier sites but otherwise rather similar. Soil waterlogged throughout winter.

Transect No. 6 Date 15.11.60.

Location: Wee Jasper - Tumut Road N.S.W.

Altitude: 2,660 ft.

Latitude: 35° 10'S Longtitude: 148° 40'E.

Area: 3 ch. x 1 ch.

Plot bearing: 65°

Eucalyptus species present:

Adult:	Regeneration:
E. macrorrhyncha	E. macrorrhyncha
E. robertsoni	E. robertsoni
E. dives	E. dives
E. camphora	E. camphora
E. dalrympleana	E. dalrympleana
E. bridgesiana	E. bridgesiana

Shrub and Grass Layer:

Dry	Swamp
Poa sp.	Carex appressa
Hardenbergia violacea	Hydrocotyle sp.
Leptospermum juniperinum	Juncus sp.
Eritrea centaurea	Epacris palludosa
Exocarpus cupressiformis	

Description:

Transect proceeds from a point about 1½ chains up the western slope, down the slope, across the swamp area, and up the eastern slope for a distance of approximately 1 chain. The western slope falls at the rate of 20' per chain, whilst the eastern slope rises more gradually at about 13' per chain. Peppermints, particularly E. dives, predominate on the eastern slope which is clearly drier than the western. No Eucalyptus regeneration occurs in the swamp itself and although E. camphora occurs mainly on the swamp fringe, some individuals were found more than a chain up the slope. E. dalrympleana regeneration does not penetrate the swamp fringe and although E. dives and E. macrorrhyncha regeneration occur close to the swamp edge, they are in areas drier than those where E. camphora occurs. Overnight minimum temperatures taken at this site in November showed a difference of 3°F. between points at the beginning of the transect, and within the swamp area. It would be expected that winter temperatures on the swamp sites would be lower due to cold air drainage than those on the adjacent slopes.

Soils: Hole 1: Beginning of transect. Tree species E. macrorrhyncha, E. robertsoni. Profile is marked by lack of definite horizon development and the high content of quartz crystals giving a very rough texture

Although there is a moderate grass cover there is little Ao.

There is no differentiation of A_1 or A_2 horizons. The A horizon occurs from 0 - 3½" and transition to B horizon occurs over about 2".

The A is grey brown rough clay sand. Grains up to ⅜" diam. There are numerous roots up to ½" diam. in the A layer.

The B horizon is yellow grey in colour becoming greyer with depth with some blue grey tinges. Roots up to ¼" diam. occur in the B horizon to 1 ft. depth. There is little structure throughout the profile. The clay content increases with depth but at 26" still contains high proportion of quartz crystals. No sign of parent material at 26".

Shiny flecks of possibly mica or gold throughout the profile.

A 2" pH 6

B 12" pH 6

B 26" pH 6 - 6.5 (in grey soil)

Hole 2: Approximately 80 ft. down the slope from the beginning of transect. *E. camphora* prominent. Heavy grass mat A_o ¼ - ½". As in Hole 1, the changes are gradual and without marked development of horizons.

The A layer is from 0 - 6" with transition to B over 6 - 10". The B occurs from 10 - 29"+ the A is dark grey brown 0 - 3" becoming orange grey into the B and greyer with depth. There are many fine roots in 0 - 3" layer and larger tree roots up to ½" diam. in 3 - 7" layer. Live roots up to ¼" diam. were found as deep as 27". Water entered the profile at 29".

Texture as in Hole 1 gravelly loam with

increasing clay content with depth. Very high proportion of quartz crystals.

A $2\frac{1}{2}$" pH 6

transition 8" pH 5.5 - 6

B 24" pH 6 - 6.5

Hole 3:

At the end of 2nd chain on the edge of swamp *E. camphora* present.

Heavy grass growth with resulting marked black A layer approximately 5" with sharp boundary to grey sandy clay. B similar to B of Hole 2. The grey layer is mottled orange.

A 3" pH 6.5

B 12" pH 6.5

Hole 4: At the end of transect. *E. robertsoni*, *E. dalrympleana* and *E macrorrhyncha* present. Thinner grass cover A_0 $\frac{1}{4}$" A 0 - 3", transition 3 - 4" to B_1 4 - 12", transition 12 - 16", B_2 12 - 25"+. Boundaries of horizons muted. A is grey brown sandy loam with little clay. B_1 yellow brown sandy clay loam. B_2 red brown sandy clay (Shiny on cut faces) Many fine grass roots in top 2". Tree roots up to $\frac{1}{2}$" down to 10". Few roots only in B_2.

A $1\frac{1}{2}$" pH 6.5 - 7

B_1 9" pH 6.5

B_2 20" pH 6.5 - 7

Transect No. 7 Date 22.11.60

Location: MacPherson's Swamp Wee Jasper S.F., N.S.W.

Altitude: 2,550 ft.

Latitude: 25° 10'S. Longitude: 148° 40'E.

Area: 5 ch. x 1 ch.

Plot bearing: 130°

Eucalyptus species:

Adult:		Regeneration:
	E. bridgesiana	E. bridgesiana
	E. camphora	E. camphora
	E. dalrympleana	E. dalrympleana
	E. pauciflora	E. pauciflora
	E. robertsoni	E. robertsoni
	E. stellulata	

Shrub and Grass layer:

Dry	Swamp
Acacia siculiformis	Pimelea ligustrina var. glabra
Pultenaea polifolia	Epacris paludosa
	Isotoma fluviabilis
	Diuris pedunculata
	Restio australis
	Poa caespitosa
	Carex appressa

Description:

This plot was located on an area of sub-alpine swamp the past history of which includes restricted grazing and alluvial gold washing.

The transect proceeds from an easterly facing slope carrying mainly E. pauciflora across an open sparsely treed swamp area, and onto rising ground on a westerly aspect. The mature trees of E. camphora occurring on the swamp are of twisted growth and although some regeneration is present there is a complete absence of young saplings.

Where E. camphora occurs well off the swamp site, it is often distinguished as old coppice shoots which have grown up as a result of burning of the original tree.

Soils: Hole 1

E. pauciflora, robertsoni, dalrympleana present, moderate grass cover with some Pteridium A_0 $\frac{1}{4}$ - $\frac{1}{2}$"

A 0 - 7" brown clay loam with some granitic fragments up to ¾" diameter. Numerous fine roots pH 5. Boundaries are gradual. B 7 - 24" red brown loamy clay pH 5. Roots to 24". Parent material granite appearing at 24".

Hole 2:

On swamp at the end of 3rd chain. Continuous heavy grass and sedge growth. E. camphora present. A_0 thick, 2". A black heavy clay, blocky. pH 6.5 Tree roots present to 1 ft. depth. Water table at 1 ft.

Hole 3:

4½ chains from beginning, western aspect. E. camphora, pauciflora, bridgesiana present in open forest, almost continuous grass cover. Thin A_0 ⅛" A 0 - 5" dark grey brown sandy loam crumb structure, many silica grains more than 2 mms. diam. pH 5. Diffuse boundary to B which is yellow grey gravelly clay, high proportion of silica grains ⅛ - ¼" more or less granular. Some iron streaking. Profile becomes greyer and more gravelly with depth to 27". pH of B at 12" 4.5 Granite parent material. Roots numerous in A, generally lacking in B.

Transect No. 8 19.1.61

Location: Wee Jasper - Tumut Road, N.S.W.

Altitude: 2,660 ft.

Latitude: 35° 10'S. Longitude: 148° 40'E.

Area: 4 ch. x 1 ch.

Plot bearing: 60°

Eucalyptus species:

Adult	Regeneration
E. camphora	E. camphora
E. dalrympleana	E. dives
E. dives	E. macrorrhyncha
E. macrorrhyncha	
E. robertsoni	

Shrub and grass layers:

Dry	Swamp
Exocarpus cupressiformis	Carex appressa
Leptospermum juniperinum	Carex gaudichaudiana
Platolobium sp.	Juncus sp.
Brachycome sp.	Geranium pillosum
Hardenbergia sp.	Mentha sp.
Eritrea centaurea	Stellaria sp.
Stylidium graminifolium	Ranunculus sp.
Poa caespitosa	Epacris paludosa

Description:

Plot located in an area close to Transect 6. Proceeding from dry easterly aspect down and across swampy area to westerly aspect. Swamp here is caused by fanning out of small stream which has resulted in deposition of transported material. Heavy grass and sedge growth coupled with slow rate of decomposition has resulted in a highly organic profile developing. As the slopes are fairly steep, the boundaries between swamp and dry sites are sharp.

Soils: Hole 1

Beginning of transect E. dives, macrorrhyncha present. Moderate grass cover giving an A_0 $\frac{1}{4}$". A horizon 0 - 5" grey brown clay loam, gritty content increasing with depth. Roots numerous throughout up to $\frac{1}{4}$" diam. pH 5. B yellow brown gritty loam passing to decomposing granite parent material at 23". Scattered roots in B. pH 4.5

Hole 2:

Swamp edge. Dense ground cover of grass and sedge giving an A_0 layer of $\frac{1}{4}$".

A 0 - 6" black gritty numerous angular quartz crystals throughout. Roots numerous, some large tree roots in top 3" pH 5. Gradual transition to B which is blue grey gravelly clay with orange mottling. Roots present to 24". pH 5 at 14".

Hole 3:

End of plot. E. macrorrhyncha, dives present. Thin grass cover giving A_0 of $\frac{1}{8}$".

A_1 0 - 2" grey brown fine loam numerous quartz crystals, pH 4. Roots throughout.

A_2 2 - 12" orange yellow with blocky to gritty clay compacted. Numerous quartz crystals. Obvious effects of fire, with charcoal in upper A_1 pH 4.5

B horizon 12 - 18" red brown blocky clay shiny on cut faces, numerous quartz grains and decomposing granite pieces to 1" diam. in lower part of the horizon. pH 4

Transect No. 9 19.1.61

Location: MacPherson's Swamp, Wee Jasper S.F., N.S.W.

Altitude: 2,550 ft.

Latitude: 35° 10'S. Longitude: 148° 40'E.

Area: 4 ch. x $\frac{1}{2}$ ch.

Bearing: 5°

Eucalyptus species:

Adult	E. camphora	Regeneration	E. camphora
	E. dalrympleana		E. dalrympleana
	E. pauciflora		E. pauciflora
	E. robertsoni		E. robertsoni

Shrub and grass layer:

Dry	Swamp
Hibbertia obtusifolia	Carex appressa
Acacia juniperina	Juncus sp.

Dry	Swamp
Poa caespitosa	Ranunculus sp.
	Hydrocotyle sp.
	Stellaria sp.
	Epacris paludosa

Description:

Location similar to Transect 7. Open forest giving continuous grass layer with very few shrubs. Area has been lightly grazed in the past. This transect is on gently falling slope to a narrow swamp area, joining into the large swamp area known as MacPherson's Swamp. The transect crosses a small creek and rises sharply onto a drier site carrying less grass and more shrubs.

Soils: Hole 1

Beginning of transect. Some E. camphora and pauciflora present.

Almost continuous grass cover of Poa and Themeda

A_0 $\frac{1}{8}$ - $\frac{1}{4}$"

A_1 0 - 3" grey brown fine clay loam powdery, numerous roots throughout. Darker colour and presence of charcoal indicating past burning.

A_2 3 - 9" orange slightly coarser with occasional quartz grains. pH 4.5 few roots only.

B 9 - 25" orange red, clay content increasing with depth, blocky with moderate compaction; many fine quartz grains. pH 4.5 Roots rare or missing

Hole 2:

180' down transect. Carex appressa, Poa and Juncus present to give continuous cover.

A_0 1" of matted litter

A 0 - 3" black, clay crumb structure roots numerous pH 5, muted boundary to B horizon.

Grey clay crumby to blocky with fine quartz crystals.

Orange mottling increasing with depth to 28" pH 5.5 Roots present to 12". Profile wet throughout but no free water.

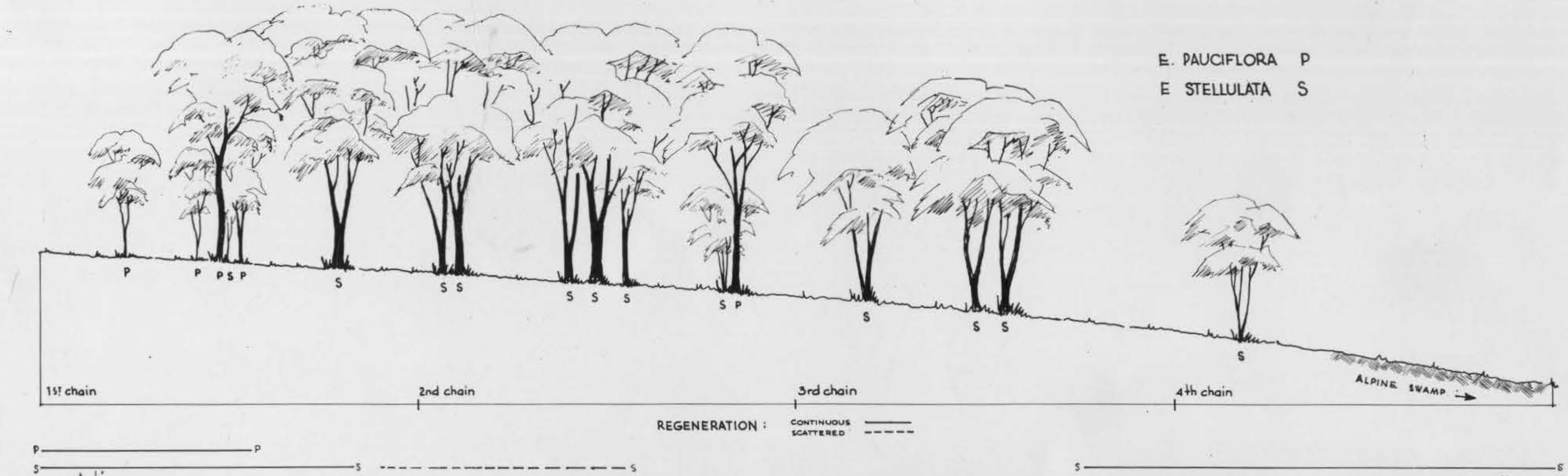
Hole 3:

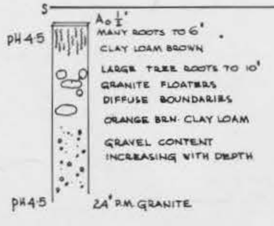
End of transect. E. robertsoni, pauciflora present, plus shrubs of Hibbertia and Acacia, snow grass tussocks not continuous, some Pteridium present.

A_0 thin $\frac{1}{8}$ - $\frac{1}{4}$"

A 0 - 7" clay loam nut brown crumb structure. Signs of burning in upper layer. Roots abundant to 3" pH 4.5

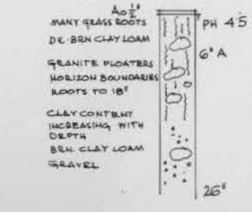
B red brown clay loam, clay content increasing with depth quartz crystals $\frac{1}{8}$" numerous, increasing in number with depth to 24" pH 5. Roots lacking in B.





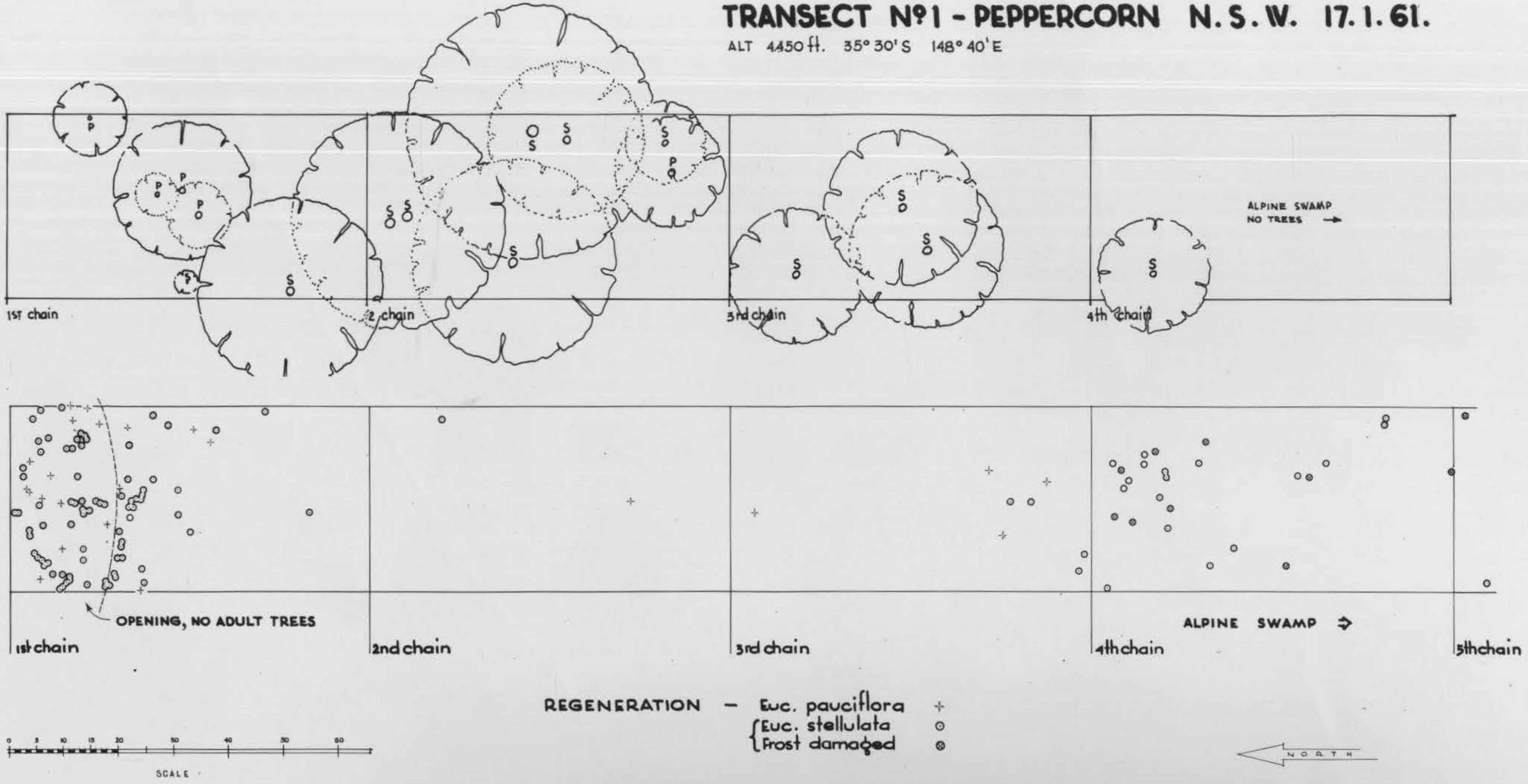
TRANSECT Nº 1 - PEPPERCORN N.S.W. ALT. 4.450 ft - 35° 30'S - 148° 40'E

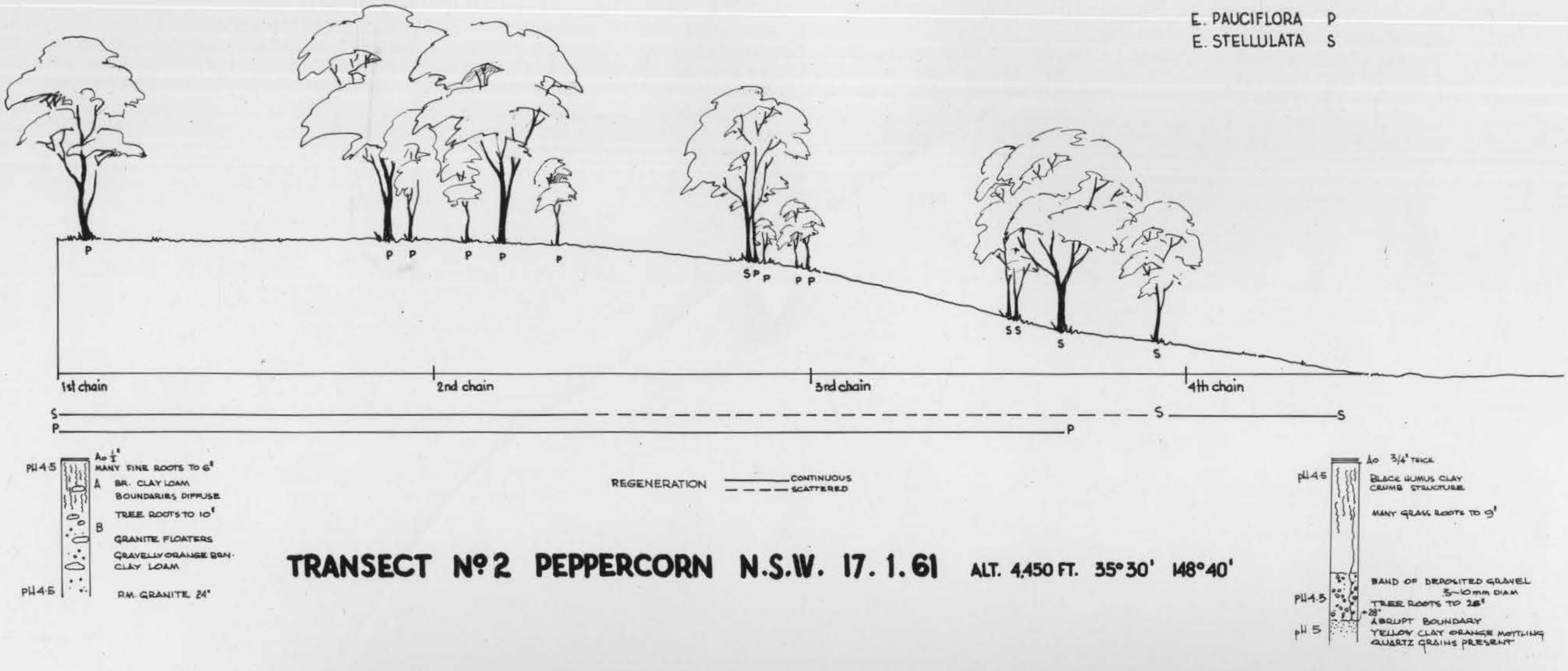
17. 1. 61.



TRANSECT Nº1 - PEPPERCORN N.S.W. 17.1.61.

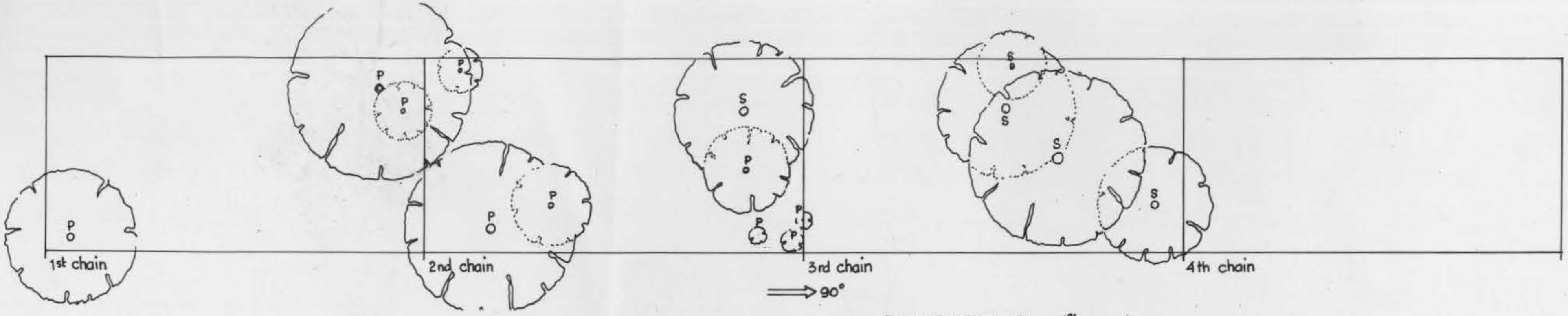
ALT 4450 ft. 35° 30' S 148° 40' E



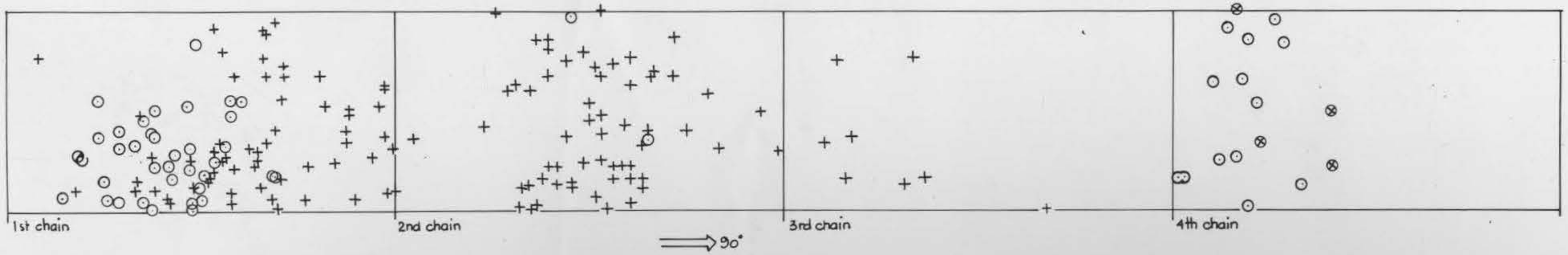


TRANSECT No 2 PEPPERCORN N.S.W. 17.1.61 ALT. 4,450 FT. 35°30' 148°40'

TRANSECT No. 2 PEPPERCORN N.S.W. 17. 1. 61 ALT. 4,450 FT. 35° 30' 148° 40'

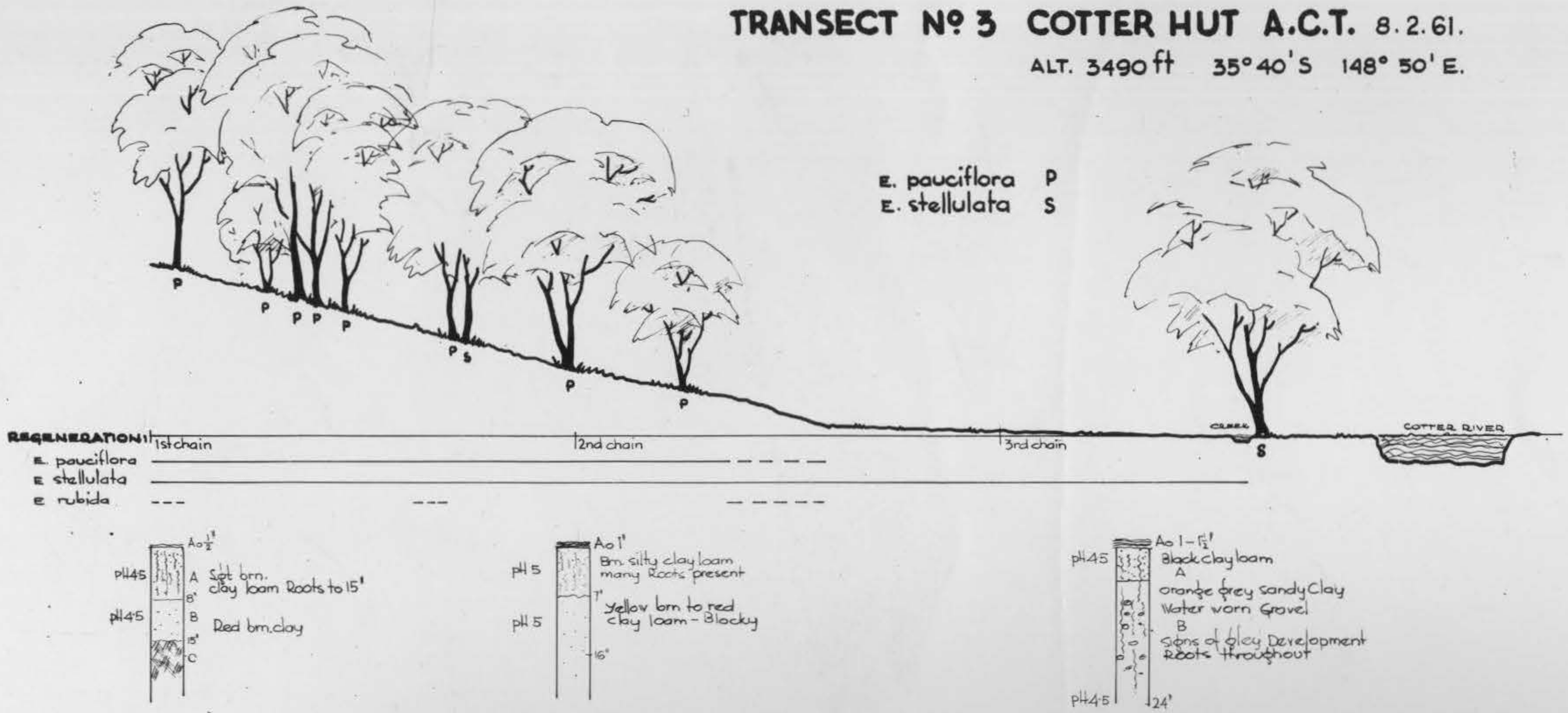


REGENERATION E pauciflora +
E. stellulata ⊙
E. stellulata frost damaged ⊗



TRANSECT Nº 3 COTTER HUT A.C.T. 8.2.61.

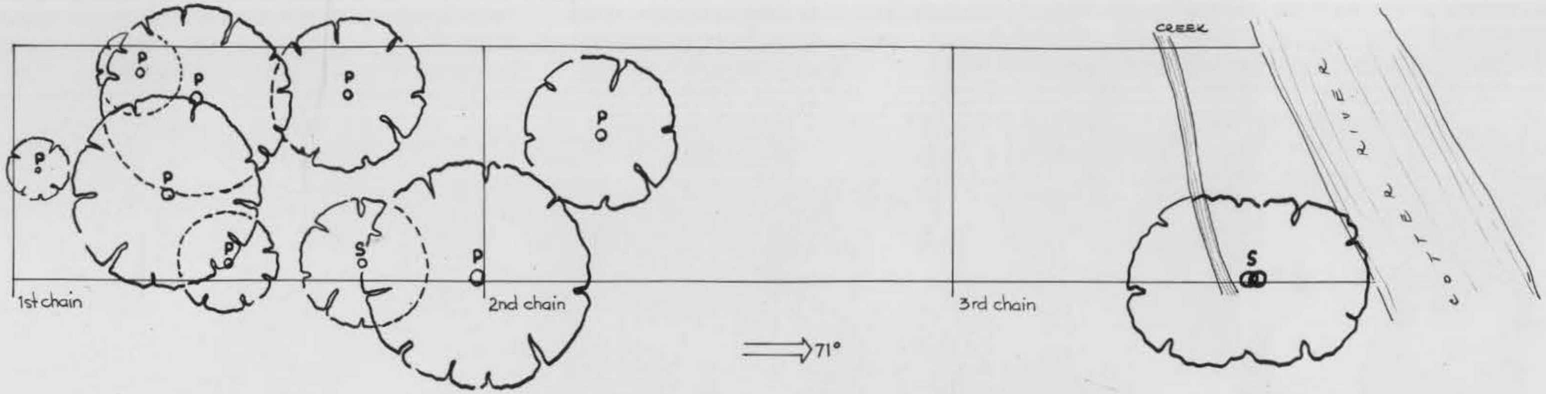
ALT. 3490 ft 35° 40' S 148° 50' E.



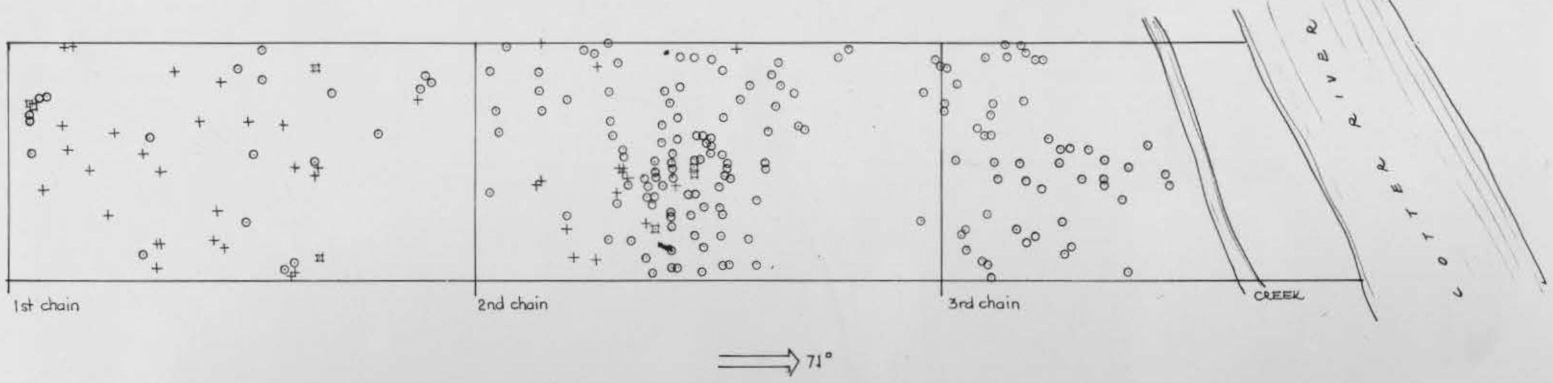
TRANSECT Nº 3 COTTER HUT A.C.T. 8.2.61.

ALT. 3490 ft. 35° 40' S 148° 50' E

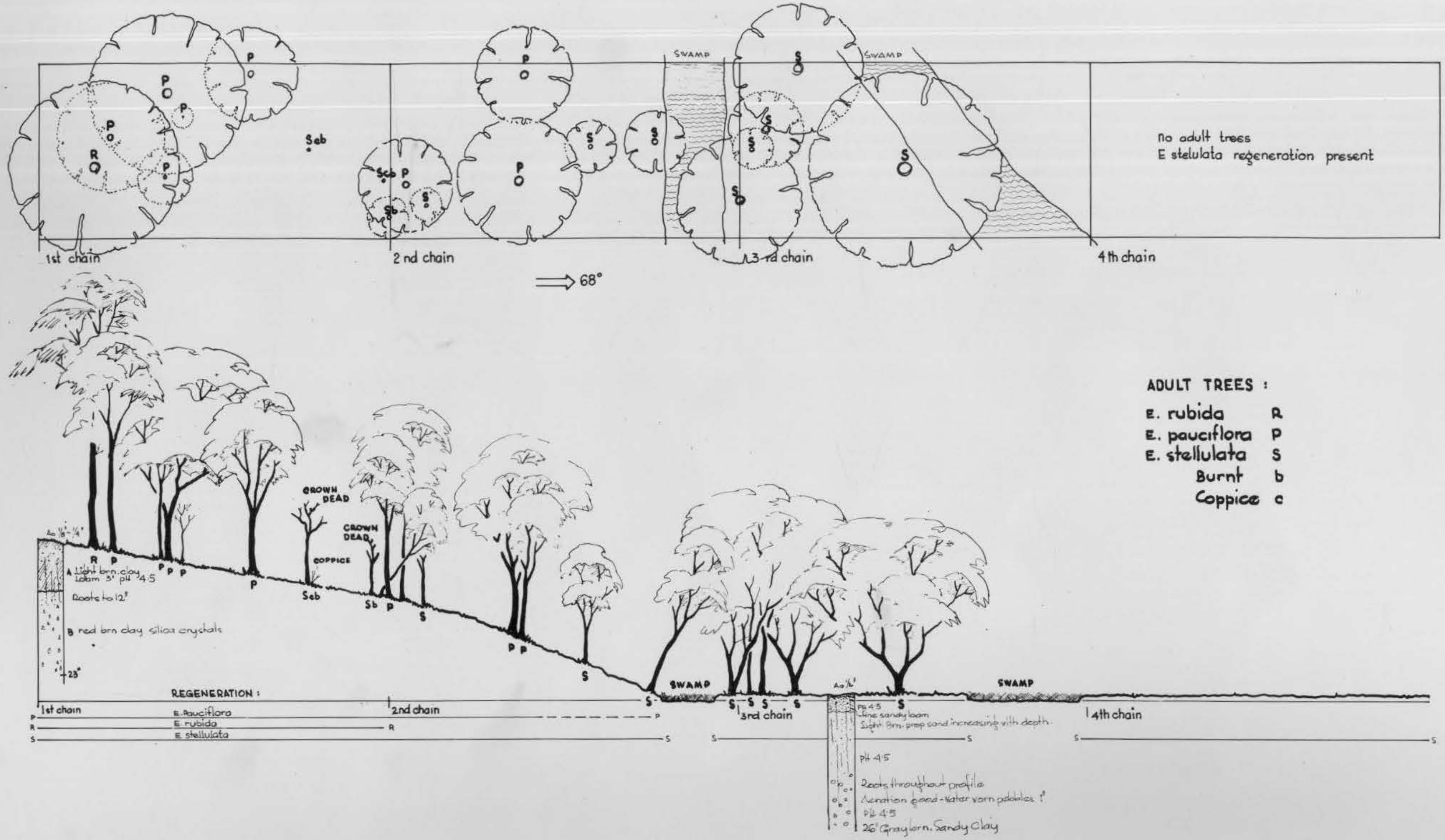
ADULT TREES: E. pauciflora P
E. stellulata S



REGENERATION: E. pauciflora +
E. stellulata ⊙
E. rubida ⊡

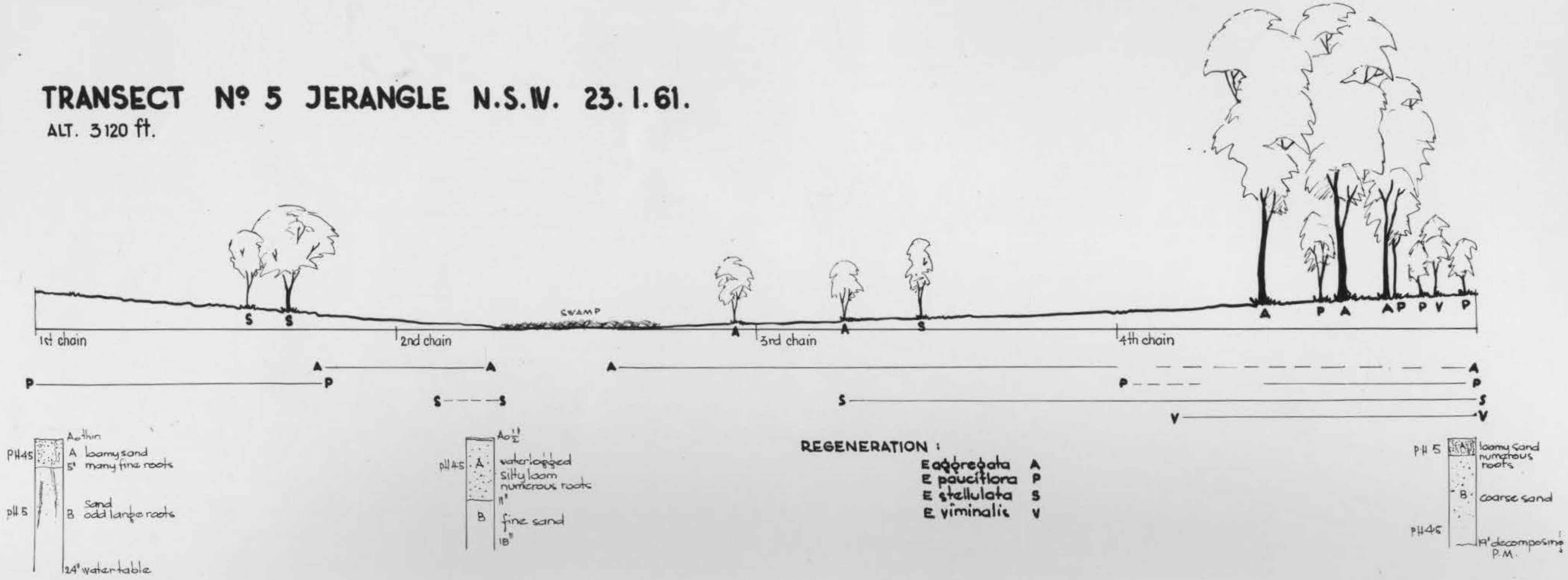


TRANSECT Nº 4 COTTER FLATS A.C.T. 8.2.61 ALT. 3460 ft. 35° 40' S 148° 50' E



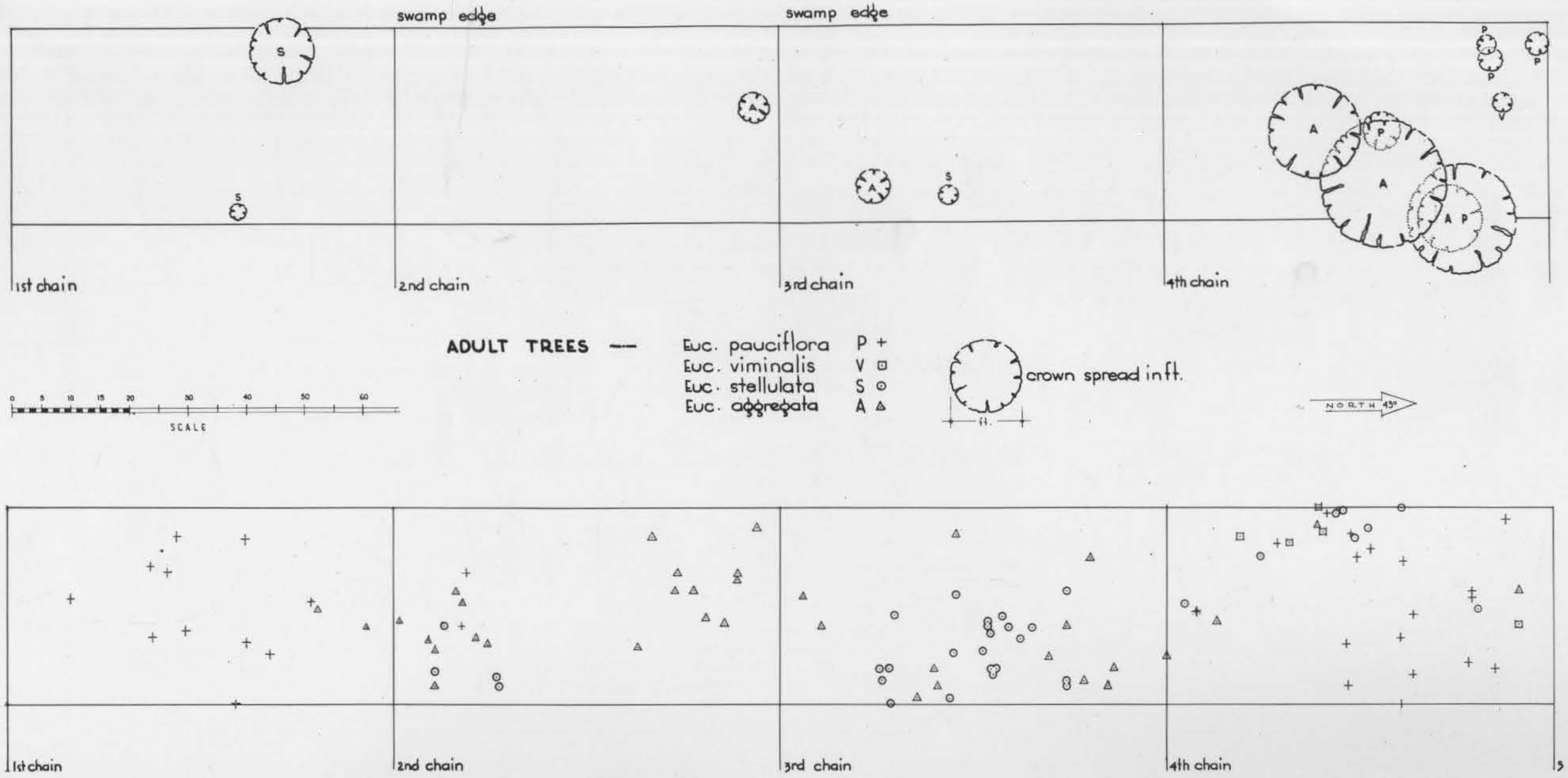
TRANSECT Nº 5 JERANGLE N.S.W. 23.1.61.

ALT. 3120 ft.

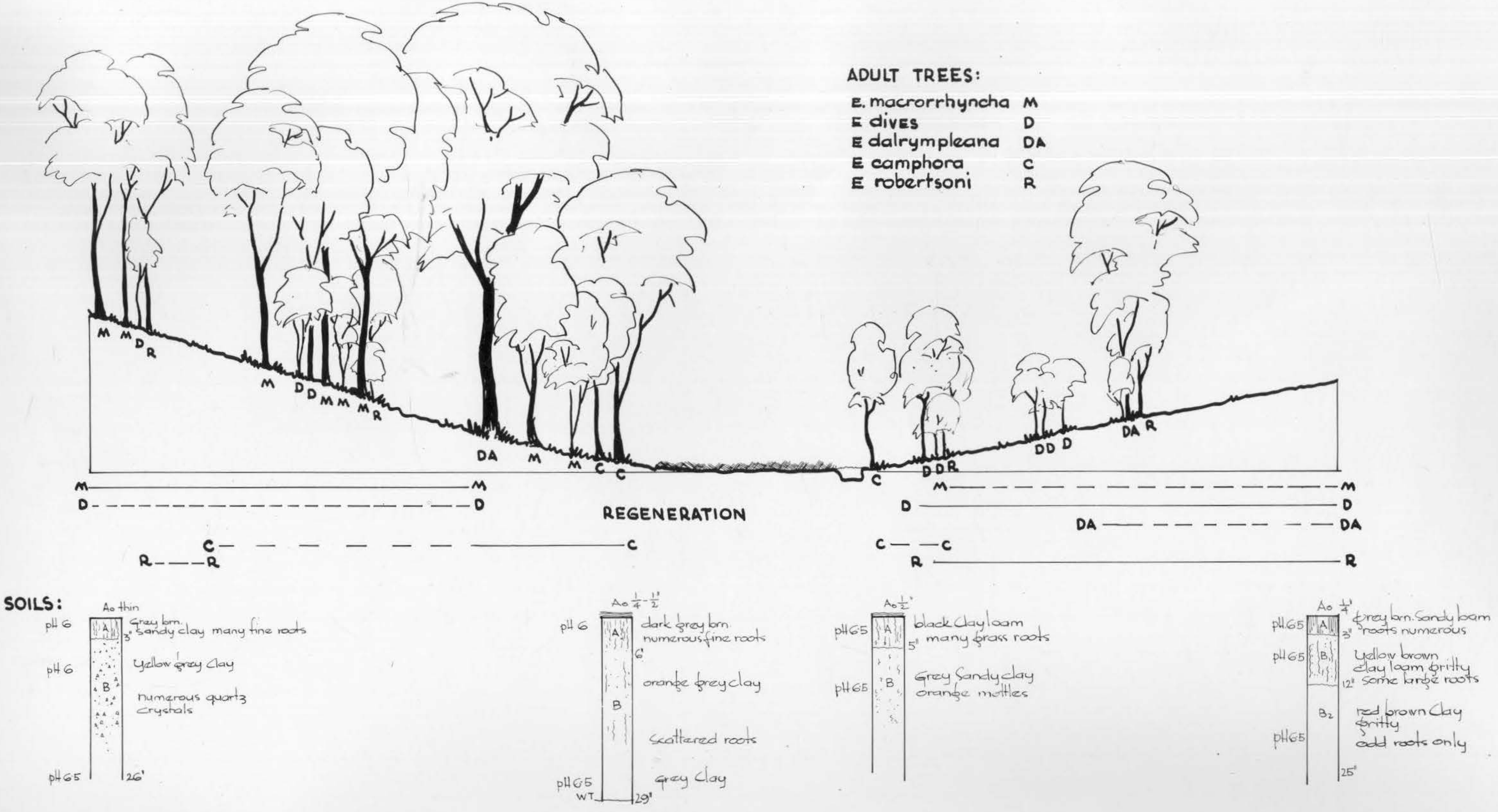


TRANSECT Nº 5 – JERANGLE N.S.W 23.1.61.

ALT. 3120 ft

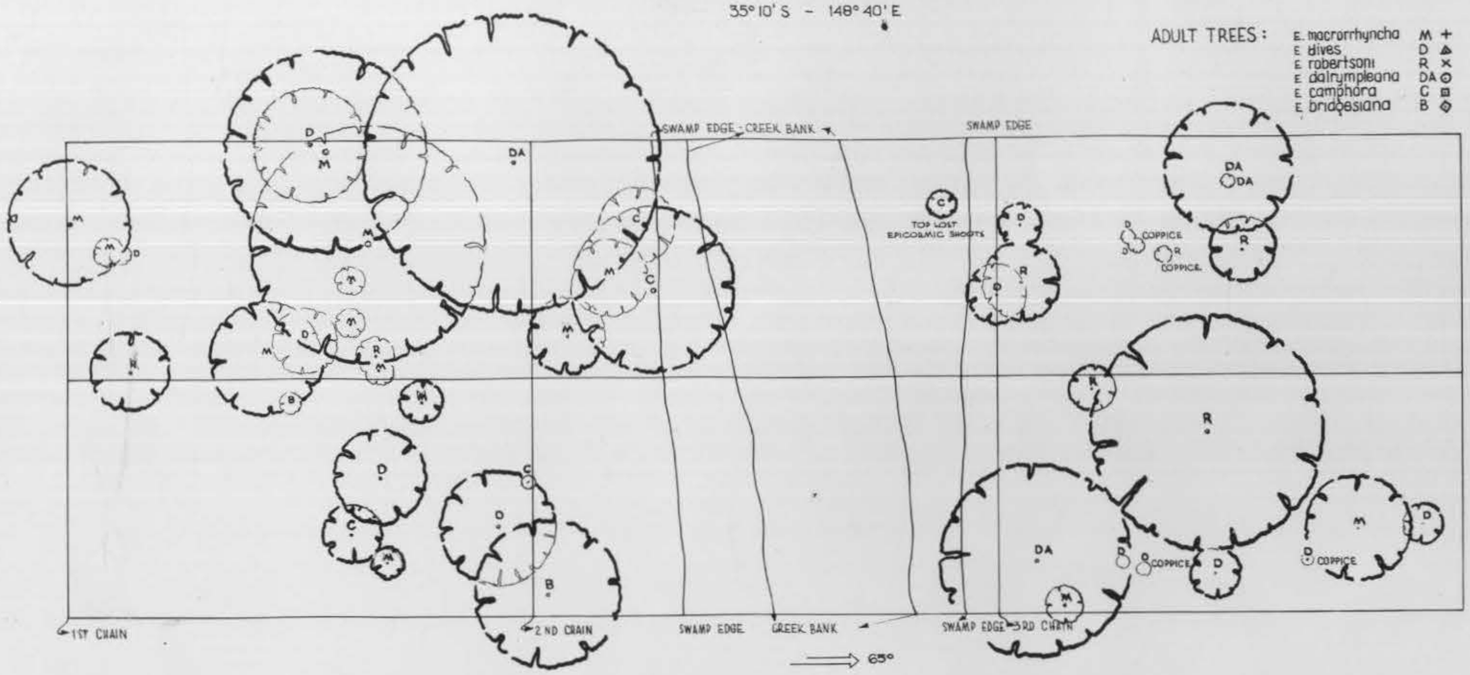


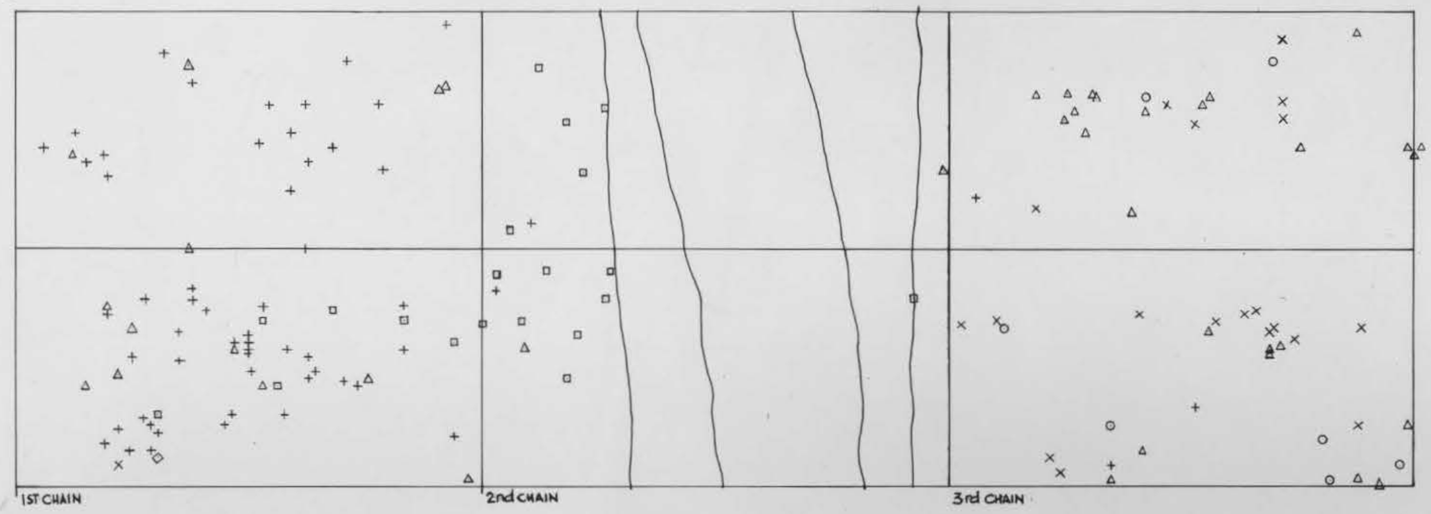
TRANSECT No. 6 WEE JASPER S.F. N.S.W 15.11.60. ALT. 2660 ft. 35° 10' S 148° 40' E



TRANSECT Nº 6
WEE JASPER S.F. N.S.W. ALT. 2660 FT.

35° 10' S - 148° 40' E

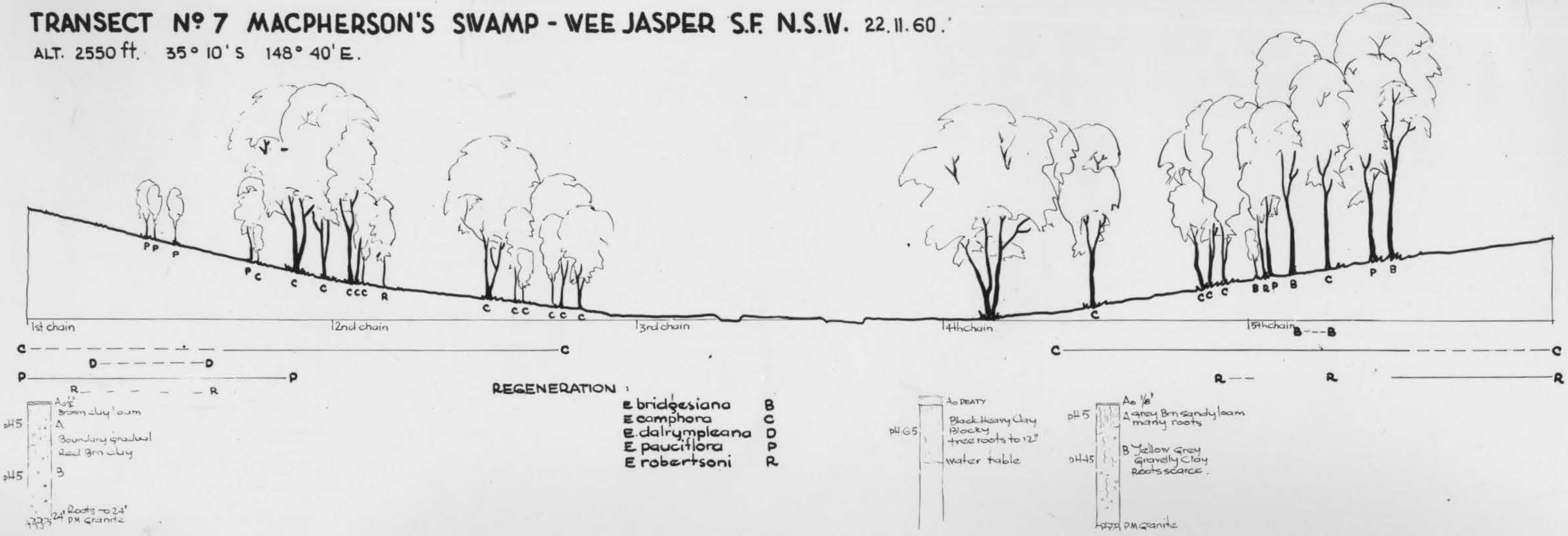




REGENERATION

TRANSECT Nº 7 MACPHERSON'S SWAMP - WEE JASPER S.F. N.S.W. 22.11.60.

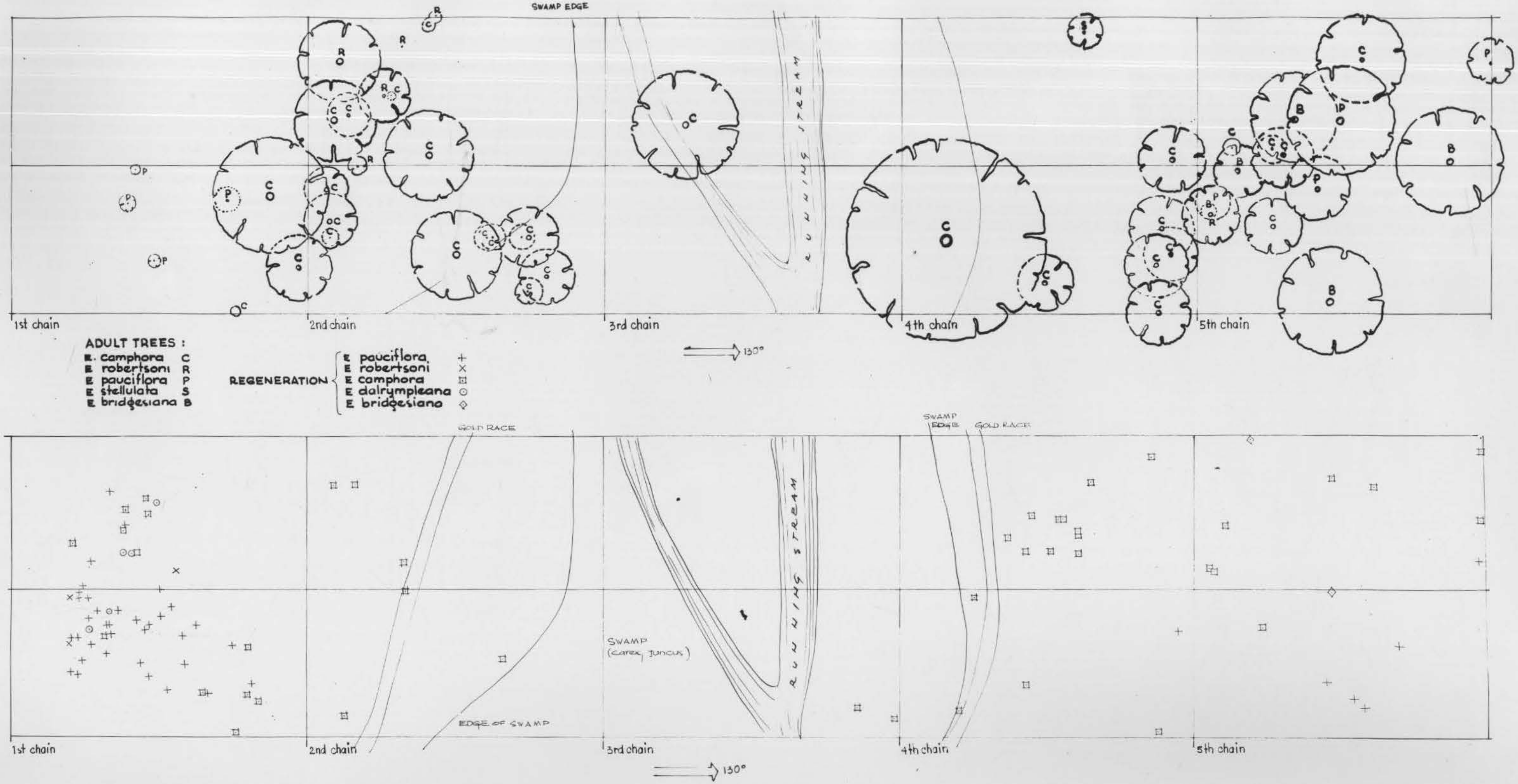
ALT. 2550 ft. 35° 10' S 148° 40' E.



REGENERATION :

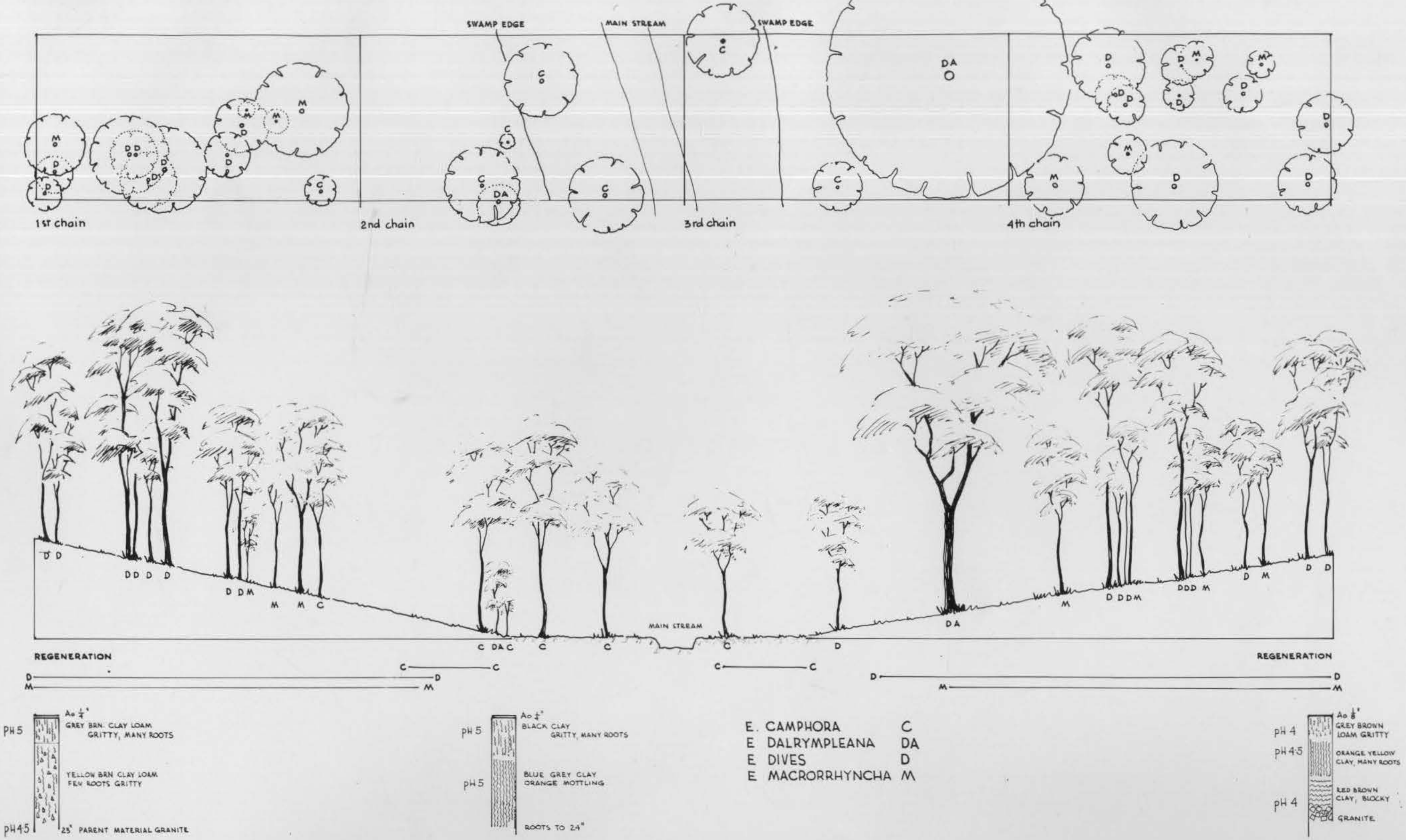
E bridgesiana	B
E camphora	C
E dalrympleana	D
E pauciflora	P
E robertsoni	R

TRANSECT Nº 7 WEE JASPER S.F. N.S.W. ALT. 2550 ft 35° 10' S 148° 40' E



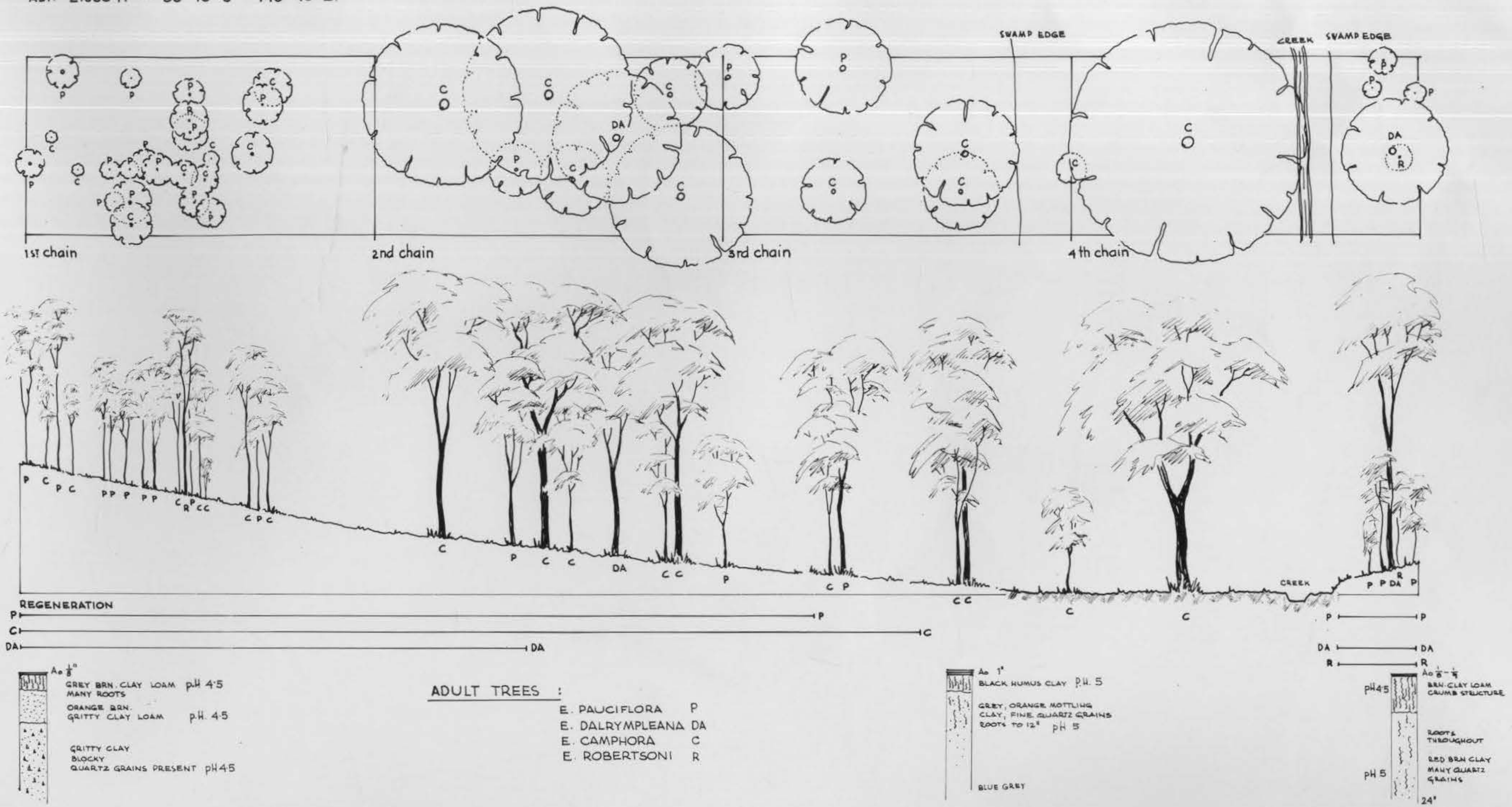
TRANSECT Nº8 – WEE JASPER N.S.W. 19. 1. 61.

ALT. 2660 ft. 35° 10' S 148° 40' E



TRANSECT Nº 9 - WEE JASPER S.F. N.S.W. 19. 1. 61.

ALT. 2.550 ft - 35° 10' S 148° 40' E.



APPENDIX B.

Fig 1

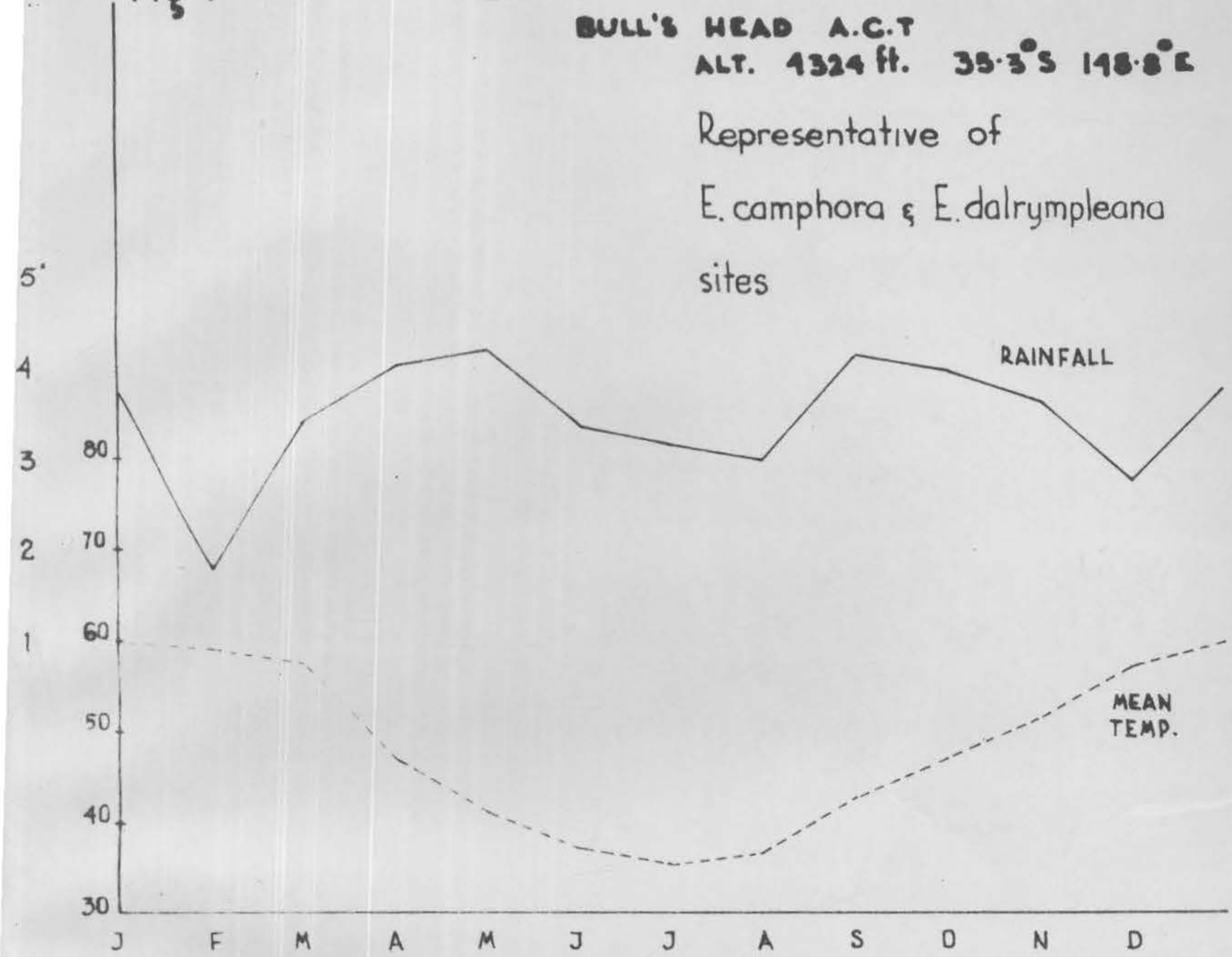


Fig 2

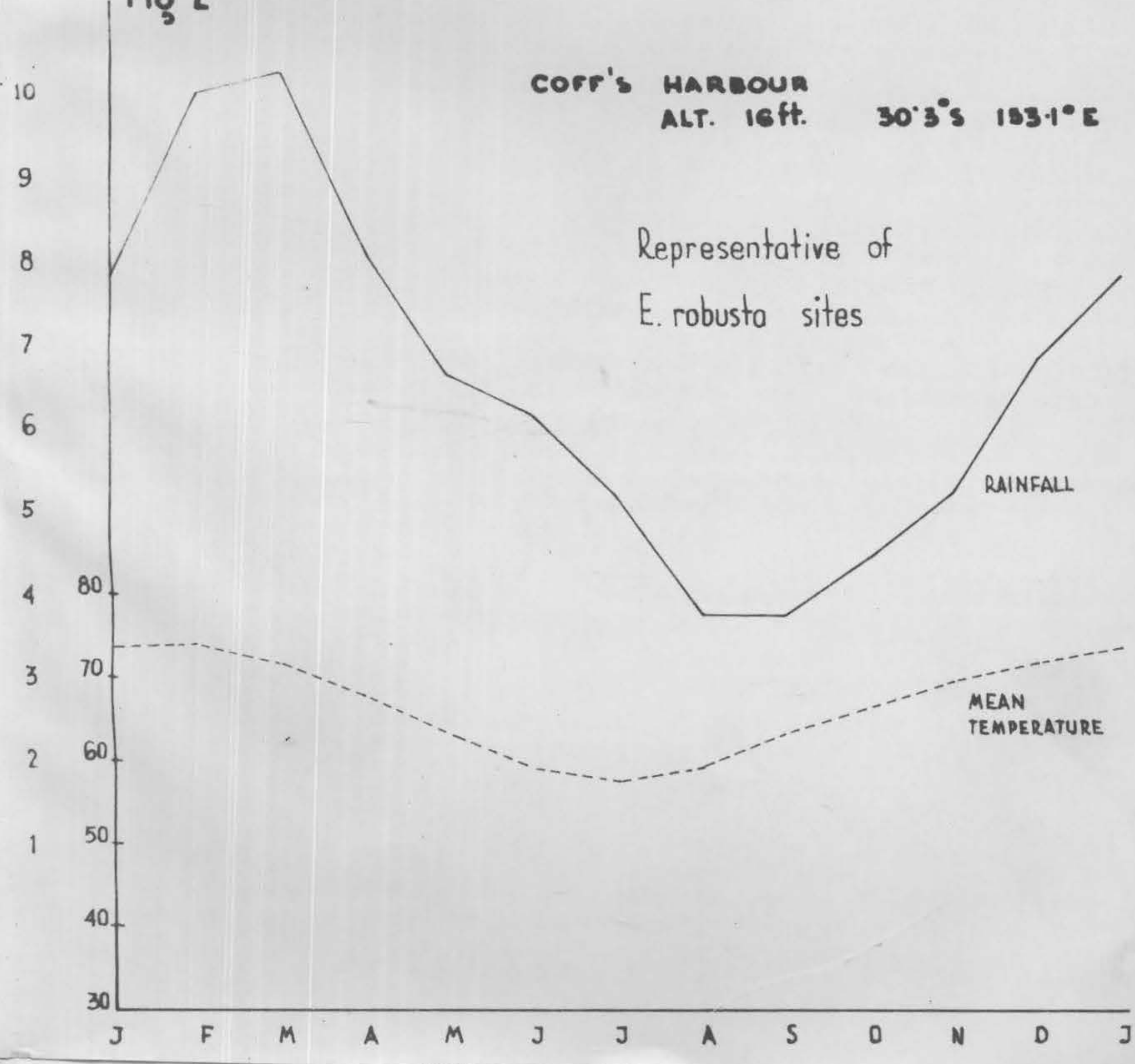
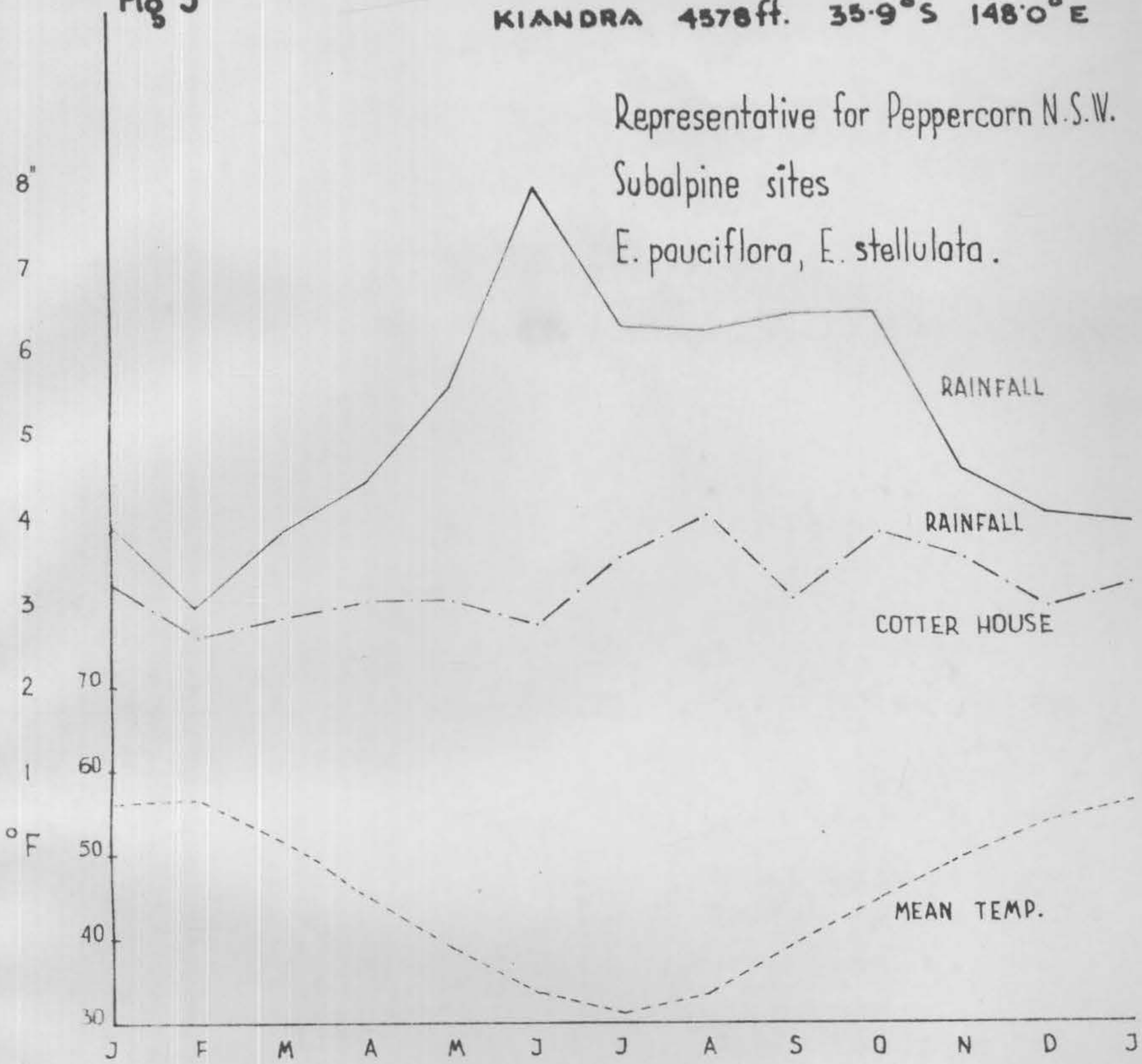


Fig 3



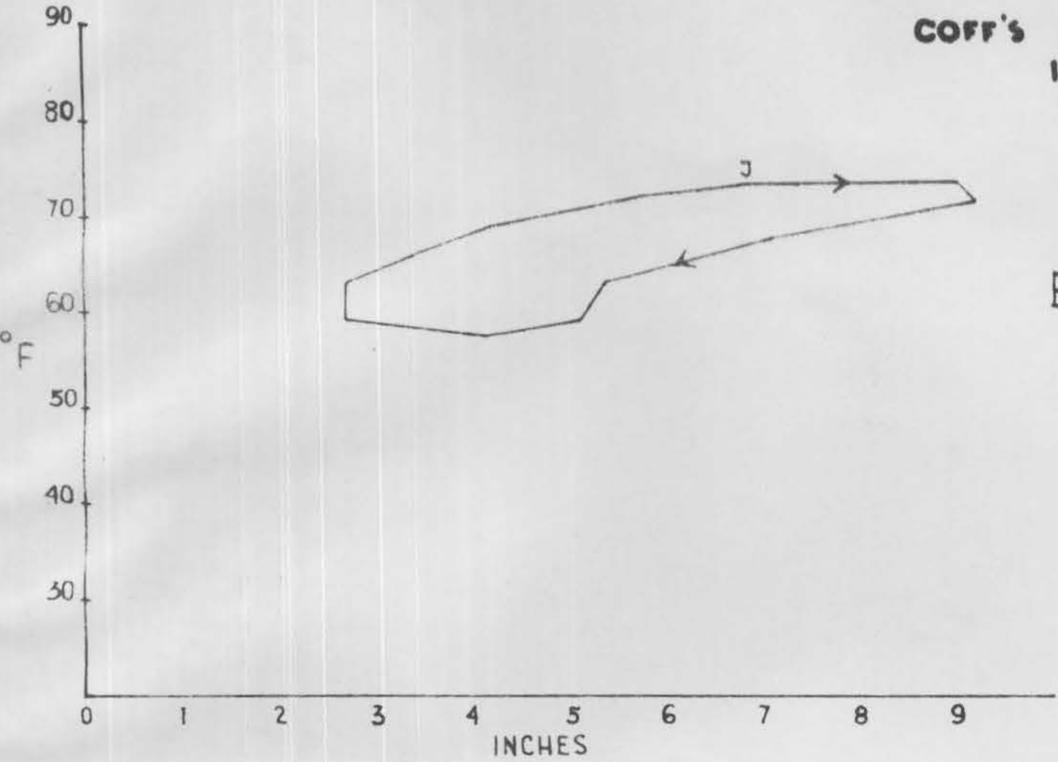
Notes:

Fig. 1 Rainfall comparable but temperatures probably slightly colder than those normally occurring on E. camphora sites. Wetter months largely during periods of low temperature.

Fig. 2 Typical summer rainfall area: maximum rainfall associated with high temperatures. Contrasted with Fig. 1.

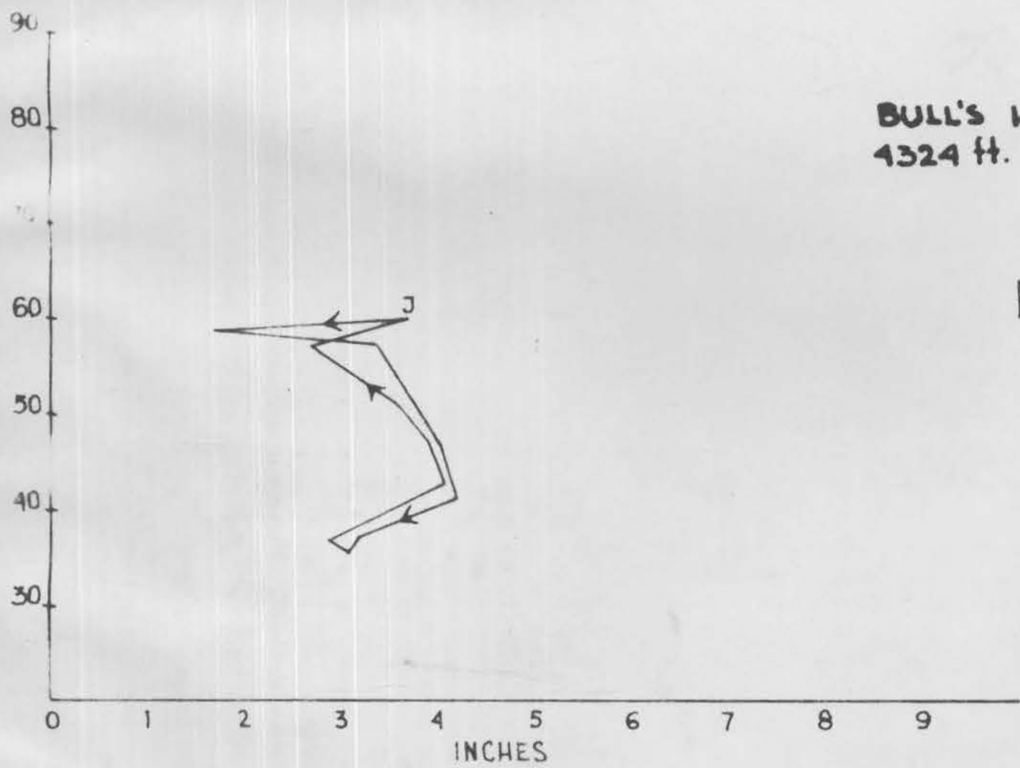
Fig. 3 No temperature figures available for Cotter House. Higher rainfall at Peppercorn than at Cotter House. Largely winter rainfall area.

CLIMATOGRAMS



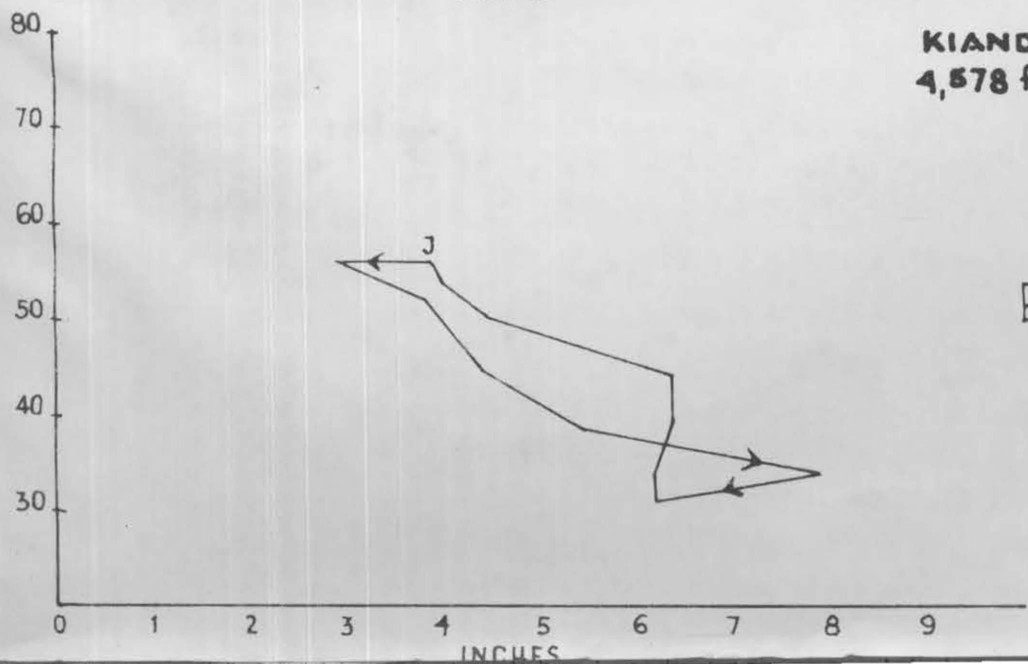
COFF'S HARBOUR
16 ft 30·3°S 153·1°E

E. robusta



BULL'S HEAD
4324 ft. 35·3°S 148·8°E

E. camphora



KIANDRA
4,578 ft. 35·9°S 148·0°E

E. stellulata
sub alpine