AN ECOLOGICAL ANALYSIS OF THE RESPONSE OF A *EUCALYPTUS MACULATA* FOREST TO CLEARFELLING

By

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Statement of Originality

With the exception of data in Chapter 3, which is based on sampling of soils carried out by J.J. Russell-Smith and S.M. Davey, and except where otherwise acknowledged, this thesis is my original work.

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Abstract

Between 1967 and 1973, about 1000 ha of mature, mixed species eucalypt forest containing *Eucalyptus maculata* Hook. was clearfelled on Kioloa State Forest. While most of the species responded well, the development of *E. maculata* has been highly variable. An investigation has been made of the ecology of the clearfelled stand in order to interpret its response to this silvicultural treatment.

Within the regrowth stands, *E. maculata* may have an inferior structural position relative to other eucalypt species on sites which formerly carried mature large-boled *E. maculata* dominants. This is often associated with a decline in both the stocking and vigour of *E. maculata* from upper to lower slopes, and a corresponding increase in the stocking of *Acacia*.

Regeneration of *E. maculata* on the upper slopes may have come from both lignotuberous advance growth and new seedlings, but on lower slopes, any regeneration present may have originated primarily from new seedlings. The greater accumulation with time of *E. maculata* lignotubers on upper slopes may be related in part to a preconditioning of seedlings associated with exposure to periodic environmental stress. The preconditioning effect may strengthen the lignotuberous seedling, and enhance its response to release.

An ordination technique has been used to better appreciate the location of the problem regrowth sites within the vegetation and environmental gradients which comprise the forest. This suggests the gradient in vegetation, rainforest → wet sclerophyll forest → dry sclerophyll forest → heath, may correspond to a gradient of decreasing soil fertility. Within this gradient, *E. maculata* has an extensive range, occurring on sites which have moderate to high levels of soil nutrients. Despite the large diameter and height of the original *E. maculata*, the clearfelling regimes seem to have been largely associated with sites towards the lower end of *E. maculata's* soil fertility range. Against this background, the investigation focused on the possible role of limited nutrient supply in explaining the regrowth phenomena.

Glasshouse studies have been used to compare the growth of a number of eucalypt species and an *Acacia* species, and their responses to nutrients. In a moderately fertile south coast soil where competition was excluded, *E. maculata* grew at a similar rate to three other eucalypt species from the same forest. The relative growth rate of height of *E. maculata* increased with increasing nutrient supply, while that of *E. pilularis* decreased. At low nutrient supply, the net assimilation rate of these two species was similar but as nutrient supply increased, *E. maculata* maintained a consistently greater net assimilation rate than *E. pilularis*. Finally, *Acacia mabellae* grew consistently and considerably better than *E. maculata* in a soil low in nitrogen, but where the supply of nitrogen was increased, *E. maculata* performed better than *A. mabellae*.

In a field experiment on a site which had carried *Acacia* regrowth for 13 years, both *E. maculata* and *E. pilularis* seedlings responded strongly to added phosphorus, but not to nitrogen or calcium. In relative terms, *E. maculata* responded better to phosphorus than *E. pilularis*. Alternatively, on a site formerly occupied by a mature *E. maculata* community, *E. maculata* seedlings responded strongly to nitrogen, suggesting that nitrogen supply might be critical for this species at the establishment phase on a previously undisturbed site. Where 13-year-old *E. maculata* was already present, but suppressed by *Acacia*, it was not able to respond to fertilizer alone but responded strongly to the removal of surrounding *Acacia* competition. Once this was done, *E. maculata* was also able to respond to fertilizer, suggesting that competition for soil nutrients was a critical factor in its suppressed condition.

The potential access of seedlings to soil nitrogen on a number of sites was next examined by comparing rates of nitrogen mineralization in soils collected from a range of sites on Kioloa State Forest carrying mature *E. maculata*. This showed the rate of nitrogen mineralization was lower in soils from the lower quality dry sclerophyll sites than on the higher quality wet sclerophyll site. Soil disturbance had little effect on the rate of nitrogen mineralization but soil heating stimulated it markedly. Limited nitrogen availability may have been one factor restricting the development of *E. maculata* following clearfelling.

A final study was based on the hypothesis that some south coast species may differ in the morphology of seedling roots and hence in their access to limited soil nutrients. Where grown in long tubes, *E. maculata* had less root biomass, and a less well developed fine root system in the upper soil horizons, than other eucalypt species and an *Acacia* species. A field investigation confirmed that *E. maculata* had fewer fine surface roots than *Acacia* species and *E. pilularis*.

It is concluded that in the absence of fire, and in the presence of a dense stratum of successional species, the poor performance of *E. maculata* may be due to limited advance growth on some lower slope sites, and to a weak competitive ability where nitrogen and other nutrients are in short supply or are in strong demand. The results of the investigation are discussed in relation to continuing forest management of these south coast forests.

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A *Eucalyptus maculata* stand on the south coast of N.S.W.

CHAPTER 1

INTRODUCTION TO THE STUDY

1.1 INTRODUCTION

Between 1967 and 1973, about 1000 ha of mature mixed species eucalypt forest containing *Eucalyptus maculata* Hook. was clearfelled on the south coast of New South Wales. The regeneration and subsequent development of *E. maculata* has been variable. There is excellent regrowth on some sites, but on others, both the stocking and vigour of *E. maculata* regrowth is poor. Although there was no post-logging fire, dense *Acacia* regrowth developed, and 12 to 18 years later, still overtops *E. maculata* regrowth on sites that had carried large old-growth trees of this species. Elsewhere, there may be a good stocking of *E. maculata* regrowth, but it remains overtopped by other eucalypts, notably *E. pilularis* and *E. globoidea*. The aim of this project is to provide an ecological interpretation of the highly variable performance of *E. maculata* following clearfelling, and to explore the consequences for continuing forest management.

As an introduction to the study, a brief historical account of silvicultural practices on south coast *E. maculata* forests is given, in order to place the clearfelling program in a management perspective. A summary is also given of the results of a study carried out by the author on the condition of the regrowth stands (Neave 1983).

An Historical Background to the Practice of Clearfelling

The management history of the forests in the Batemans Bay Management Area provides background for interpreting the present condition and status of the forest. Much of the information in the following description is derived from the Batemans Bay Management Plan (Forestry Commission of N.S.W. 1983), Furrer (1971) and Neave (1983).

Logging began in the forests of the Batemans Bay Management Area around 1870, and is known to have occurred on the Benandarah, North Brooman, South Brooman, Boyne and Kioloa State Forests in the 1880s. This early logging was selective by size, quality and species, and the openings created by such scattered removals were generally insufficient to encourage regeneration. The harvesting of favoured species, notably *E. pilularis* and *E. saligna*, sometimes resulted in their depletion and replacement by the then less favoured *E. maculata* and understorey regrowth.

Silvicultural treatment of the forests on the south coast commenced in 1911, and can be described in terms of four treatment periods: 'ringbarking', 'group selection', 'advance growth salvage' and 'clearfelling'. Such treatments have been confined to *E. maculata* and *E. pilularis* types which occur mainly in coastal forests, and to a lesser extent in the lower foothills forests.

The practice of ringbarking was introduced into the south coast forests in the 1920s. The treatment was used to remove the large over-mature useless trees from the growing forests, to raise the quality of the residual growing stock, and to release useful advance growth. It was, in general, restricted to more open forests, usually with a sclerophyll type understorey and containing a dynamic lignotuber pool. The treatment achieved variable success, often limited by its failure to create sufficiently large openings for natural regeneration, or to control understorey competition.

From about the 1940s, the practice of group selection was adopted in response to a need to create larger openings in the forests to ensure development of new seedling regeneration, or the release of advance growth. With subsequent follow-up treatment, group selection was consistently more successful in encouraging regeneration than individual tree selection without treatment - although success tended to be confined to the more open upper slope positions. The failure to obtain regeneration on wet sclerophyll lower slope sites was attributed to a lack of lignotuber stock and to the rapid proliferation of *Acacia* and more mesic understorey species. Consequently, it soon became the practice to exclude moist gullies from this type of treatment.

By the 1960s, there was general dissatisfaction in N.S.W. with the condition of the forests managed in this way, and a trend developed towards heavier logging or total clearfelling of forest, and establishment of even-aged stands. Silvicultural practices on the south coast forests reflected these trends from the mid 1960s. For example, Furrer (1971) used a combination of 'quality stem retention' (QSR) and clearfelling regimes to try to improve the forest condition. Quality stem retention is a term used by Furrer to refer to a silvicultural practice where only that part of the growing stock capable of maintaining a high increment is retained, while all commercial trees and any useless and sub-standard stems which would suppress regeneration are removed. Because of the widely varying condition of *E. maculata* throughout the forest, retention varied from near full stocking on some sites, to virtual clearfelling on others. Reliance for regeneration was placed on a number of sources, including new seedlings, lignotuberous seedlings, other advance growth and coppice. The forest was clearfelled where there was little productive growing stock meeting prescribed bole and crown quality standards. This characterised forest where there was still a large component of old-growth trees, and early highly selective logging had not created gaps in which regrowth could develop in an unimpeded way through sapling and pole stages to maturity. Clearfelling, or virtual clearfelling under QSR, of relatively large areas of *E. maculata* forest (up to 350 ha) was carried out between 1967 and 1973 - sometimes with retention of seed-trees and sometimes without.

By and large, it was expected that forests subjected to these regimes would regenerate naturally, and highly productive even-aged stands would develop. Logging was carried out with crawler tractors which partially disturbed the forest floor. On the basis of previous experience, regeneration was expected to come from lignotuberous advance growth and new seedling regeneration. It was recognised that there were some sites where some supplementary regeneration treatment was needed, for example, moister sites with a more mesophytic understorey. Here the tractor was sometimes used to extend the area of disturbed soil, and this was spot sown with *E. maculata* or *E. pilularis* seed. In a few cases, sites were planted with jiffy pot seedling stock. It is apparent that this was not always successful, and some 12-18 years later, the forest consists of developing regrowth from dense to sparse, and the residual old-growth varies from nil to six trees per ha.

Although the Forestry Commission considered that clearfelling methods were generally successful in achieving a regenerated forest, the use of these techniques has been limited since 1975. A short to medium term decline in potential sawlog availability indicated a need for greater emphasis on retaining trees which have some potential for volume and value increment, than on regeneration for the longer term. And more generally, there is now a greater sensitivity to the adverse short-term environmental effects of such treatments. While adequate regeneration will be obtained on most sites, it is appreciated that there will be some sites where regrowth will be deficient or will not be obtained at all. In this case, the policy is to retain sufficient overwood to avoid undue degredation of the forest site.

An Analysis of the Condition of Regrowth on Clearfelled Sites

The forest condition on parts of Kioloa State Forest subjected to heavy logging or clearfelling from 1967 to 1973 has been analysed by

Neave (1983). The salient features of that study provide a quantitative basis for an hypothesis which this thesis sets out to explore.

Neave used stratified random sampling to establish 120 sampling sites, each circular with a 10 m radius, within 1000 ha of clearfelled *E. maculata* forest. At each site, floristic and structural data were obtained relating to the frequency, cover and abundance of species, and the growth condition of the stand components.

A number of features of the data were examined to show relationships between (a) the vigour of *E. maculata* regeneration, and the presence and vigour of other eucalypt species and the non-eucalypt component, and (b) slope position and the stocking and vigour of *E. maculata*. A brief summary of the main conclusions follows.

The relative vigour of the eucalypt species. A 2 x 2 matrix of information on eucalypt species (Figure 1.1) from 120 sites showed that vigorous *E. maculata* and vigorous 'other eucalypt species' co-existed on 46% of sites. Conversely, *E. maculata* and 'other eucalypt species' were both non-vigorous on 18% of sites. Of more interest, though, were the situations where the species groups had different vigour status. Only 4% of sites had vigorous *E. maculata* in association with non-vigorous stems of 'other eucalypt species'; in contrast, 32% of sites had vigorous stems of 'other eucalypt species' in association with non-vigorous *E. maculata*. It is inferred that, within the confines of the study area, and despite the presence and general dominance of *E. maculata* throughout the original forest, the competitive ability of regrowth *E. maculata* is generally weaker than that of other eucalypt species. The extent to which this may be related to the practice of clearfelling is unclear at this stage.

The stocking and vigour of *E. maculata* in relation to slope. Upper slope positions were found to be more likely to support a reasonable stocking of *E. maculata* regeneration while most lower slope positions

		E. MACULATA	
		NON-VIGOROUS	VIGOROUS
OTHER EUCALYPT SPECIES	NON-VIGOROUS	18	4
	VIGOROUS	32	46

Figure 1.1 A 2 x 2 matrix showing the percentage of sites sampled (see Neave 1983) falling into each of four eucalypt vigour combinations.

had a relatively poor stocking of *E. maculata* regrowth. The mid slope positions were intermediate in this respect. For example, stocking rates in excess of 500 stems per ha occurred on only 23% of the lower slope sites, 37% of the mid slope sites, and 67% of the upper slope sites.

While analysis of data from 120 sampling sites showed little direct association between the vigour of *E. maculata* and slope position, it is noted that over the 1000 ha of clearfelled forest, the physiography is quite variable, and consistent relationships between the vigour of *E. maculata* and position within the topography were observed in the course of sampling. In particular, where there was a well defined localized topographic gradient from ridge to gully, the vigour of *E. maculata* tended to decline along the slope. A site representative of this type is examined in Chapter 2 (Section 2.3.2).

***Acacia* species and slope position.** Moderate to heavy *Acacia* development characterised a high proportion (71%) of the 120 sites, and implies an extensive localized amplitude for this genus following severe site disturbance, even where fire is excluded. Intense *Acacia* development was particularly a factor towards the bottom of slopes. For example, heavy *Acacia* development occurred on 39% of the lower slope sites, 21% of the mid slope sites, and 8% of upper slope sites. It appears therefore that eucalypts occurring on upper slope positions would in general, suffer less from *Acacia* competition than eucalypts found on lower slope positions.

Sites without *E. maculata*. In quantifying the occurrence of eucalypt species, it was found that 20 of the 120 sites did not carry any *E. maculata* regrowth, and that most of these (18) fell on the mid and lower slope positions. This seems to indicate that on these sites either (a) *E. maculata* regeneration in the form of lignotuberous seedlings and new seedling growth was present at, or established following, clearfelling but subsequently succumbed to competition or (b) a pool of lignotubers was not present at the time of clearfelling, and new seedlings did not establish, or at least did not survive following clearfelling.

1.2 A GENERAL HYPOTHESIS

The hypothesis forming the basis of this study suggests that environmental factors, especially soil nutrient supply, may be marginal for *E. maculata* at the establishment phase on some sites following clearfelling, particularly where there is a rapidly developing and co-competing non-eucalypt component. The marginal nature of many sites for *E. maculata* may be reflected in the constantly changing mosaic of *E. maculata* and '*E. piperita*' communities associated with only relatively minor variations in topographic and edaphic factors

(McCutchan 1978). Under these conditions, a fine community balance may be maintained in the undisturbed forest through a sensitive interaction of environmental factors and co-occurring species. Thus following extensive and severe disturbance, it is possible the balance between species in their competition for site is upset, and it is only where *E. maculata* retains a strong competitive ability will it persist as a component of the dominant stratum. This thesis explores some possible factors and mechanisms affecting the occurrence and competitive ability of *E. maculata* within the regrowth mosaic.

1.3 BASIS AND PRESENTATION OF THE STUDY

This study seeks to provide an ecological interpretation of the response of *E. maculata* to a clearfelling regime, particularly the low stocking and poor vigour of *E. maculata* regrowth on sites where it might be expected to perform well. In pursuing this objective, it has been necessary to explore the relationship between environmental factors and the distribution of *E. maculata* in south coast forests, the growth characteristics and competitive relations of forest species, including *Acacia*, the rate of mineralization of plant available nitrogen, and differences between species in the way they may gain access to resources in limited supply. The historical background to the silvicultural practice which highlighted the regrowth phenomenon has been presented in this chapter, and a broad ecological hypothesis presented to explain it.

Chapter 2 will focus on the stocking of regrowth in the clearfelled forest. Regrowth vegetation at two sites is analysed, and possible relationships between the regrowth condition and environmental factors explored. The possible contributions of new seedlings and lignotuberous seedlings to regrowth stocking is examined. Because the distribution of lignotuberous advance growth in uncut forest may have much to do with the stocking of *E. maculata* in regrowth stands, a series of studies has been carried out on the nature of the lignotuber in the *E. maculata* forest and its contribution to stand dynamics. These studies relate to the distribution of lignotuberous advance growth in the forest, and the way its response to release may be affected by environmental factors.

Chapter 3 is concerned with the relationship between patterns of species distribution and environmental factors. The existing forest pattern may reflect responses of vegetation to a number of environmental variables. Where environmental factors are marginal for a given species, pattern may also reflect a variety of processes at the establishment and early successional stages. It is possible therefore, that the factors influencing the response of *E. maculata* to clearfelling might be the same as those contributing to the delimitation of *E. maculata* within the vegetation mosaic, i.e. pattern, process and the environment are interrelated. A number of studies (McColl 1965, 1969; McColl and Humphreys 1967; McCutchan 1978) on south coast forests have inferred that species, and hence species associations, may be aligned along a soil fertility gradient, although the precise nature of the vegetation-soil relationship had not been confirmed. The most recent study (Russell-Smith 1979) used multivariate classification and ordination techniques to identify consistent plant communities and to suggest the relationships of the communities to each other. In Chapter 3, the relationships between the distribution of species and a number of environmental factors are examined further. Based on univariate (analysis of variance) and multivariate (principal coordinate analysis) techniques, a range of soil physical, soil chemical and site attributes are related to vegetation communities which had been previously classified by S.M. Davey and J.J. Russell-Smith (pers. comm.).

An experimental basis is developed in Chapters 4 and 5 for the hypothesis that the response of *E. maculata* to clearfelling may be related to nutritional factors. This means soil nutrition may govern not only the species distribution patterns, but will affect as well, the relative competitive ability of *E. maculata* and other successional species at the establishment phase. Under conditions of intensive disturbance, species respond to a complex and interacting set of environmental conditions. Where these responses differ markedly, and/or the conditions vary between sites, it is often possible to identify some of the factors involved. This may infer a causal relationship between species response and environment. Experiments where one or more of the environmental factors are varied while others are kept constant are often used in ecological studies. Some factors that have been examined are nutrition (Lacey *et al.* 1966; Christensen 1974; Dell *et al.* 1983b; Cromer *et al.* 1984), moisture (Quraishi and Kramer 1970; Ladiges and Kelso 1977; Bachelard 1986), light (Awang 1977; Doley 1978; Turnbull 1979) and temperature (Stirling 1973; Cremer 1975; Shepherd *et al.* 1976). Because previous studies had identified soil fertility as being important in the delimitation of species on the south coast (McColl 1965, 1969; McColl and Humphreys 1967; McCutchan 1978; Russell-Smith 1979), it was decided to focus on the role of nutritional factors in the relative competitive response of species.

Three glasshouse experiments are described in Chapter 4. The first establishes whether there are any basic growth differences between seedlings of a number of south coast eucalypt species. The second and third experiments compare the growth and competitive ability of *E. maculata*, *E. pilularis* and *Acacia mabellae* seedlings at a number of nutrient levels; these three species compete directly with one another on many sites within the regrowth forest. Two field nutrient experiments are described in Chapter 5. The first examines the response of *E. maculata* and *E. pilularis* seedlings to a range of nutrients on a site formerly carrying 13-year-old *Acacia* regrowth. The second examines the response of 13-year-old *E. maculata* regrowth to release from surrounding *Acacia* competition, to fertilization, and to a combination of these two treatments. Finally, these experiments are discussed in the light of a field fertilizer experiment by J.D. Williams and D.M. Halsall of the Division of Plant Industry CSIRO, on a south coast site formerly carrying mature *E. maculata* forest.

The nutrient and competition studies tend to confirm the hypothesis that nutrients may be limiting the competitive ability of *E. maculata* at the early establishment phase. Two questions must now be addressed: why are nutrients, and nitrogen in particular, in limited supply in the *E. maculata* forest soils following clearfelling; and why might species other than *E. maculata* be so competitive in gaining access to what nutrient is available? The first of these questions is addressed in Chapter 6, and the second in Chapter 7.

A study has been made of the condition of the dynamic nitrogen pool in soils on a number of sites in the undisturbed forest. The availability of soil nitrogen for plant growth can be estimated indirectly by adding nitrogen under field conditions and measuring the response. Nitrogen availability can also be estimated more directly, by measuring the rate at which organic nitrogen is mineralized. Since J.D. Williams and D.M. Halsall had already conducted a nitrogen fertilizer experiment on a site adjacent to the regrowth forest, the decision was made to undertake a nitrogen mineralization study. Its main purpose was to estimate the potential rates of nitrogen release in soils from a range of vegetation/site types, all with an *E. maculata* component, adjacent to the clearfelled area. Undisturbed, disturbed, and heated soil samples were measured for their rates of nitrogen mineralization, to assess whether limited availability of mineral nitrogen may have restricted the development of *E. maculata*, and whether a regeneration burn may have provided a flush of nitrogen which could have enhanced *E. maculata's* competitive response.

There are several mechanisms which may confer a competitive advantage on species in an environment modified by intensive disturbance. Species will differ with respect to basic plant physiological processes. For example, there will be some differences in the internal requirement for important nutrient elements. In this case, the composition of the chemical soil environment will partly govern which species are able to gain a competitive advantage. A number of species are able to fix and subsequently utilize atmospheric nitrogen as a result of symbiotic associations with certain types of soil organisms. This includes *Acacia* species, many of which form a dominant component within the regrowth stands. Species with a nitrogen fixing capability may have a competitive advantage in environments where the amount of mineral soil nitrogen is limited. Another mechanism, and one on which Chapter 7 focuses, is that there may be differential access to important resources as a result of differences between species in root system configuration and morphology. From geometrical considerations, absorption of nutrients is largely dependent on fine roots (Nambiar 1981), and fine root length (including mycorrhiza) is a very good parameter to estimate ion uptake (Bowen 1981).

In the ecosystem considered in this study, differential access to plant available nutrients and water may be particularly important in determining the competitive response of species. An attempt has been made to determine whether there are any differences in root system configuration and development which might significantly influence access to important resources and hence affect the regrowth process. Thus Chapter 7 presents the results of two glasshouse studies which examine patterns of root development of several south coast eucalypt species and an *Acacia* species. It also presents the results of a field study of fine root length development in soils supporting the regrowth forest.

A general discussion and conclusions based on information gathered in the study are presented in Chapter 8.

1.4 THE FOREST STUDY AREA

The study has been carried out primarily within the Kioloa and South Brooman State Forests, located 20-30 km north of Batemans Bay on the south coast of New South Wales (Figure 1.2). The location of the clearfelled areas is shown in Figure 1.3. The features of the area have been described in detail by Russell-Smith (1979) and Neave (1983), a summary of which is given here.

The lower south coast of N.S.W. has a climate which may be classified as mesothermal with a uniformly distributed rainfall and a long mild summer (Köpen classification) (Kalma and McAlpine 1978). Mean average rainfall within the region is approximately 1000 mm but can vary considerably over short distances. Commonwealth Bureau of Meteorology records from 1958 to 1985 (Figure 1.4) indicate that Kioloa Station has the highest mean annual rainfall (1277 mm) within the area of interest.

Extended periods of drought have been recorded over the past century. Those most serious have occurred between 1901-1909, 1935-1942, 1964-1968 and 1978-1983. During these periods of heat and water stress, available soil moisture may become critically low, resulting in cessation of plant growth (Pook 1985, 1986). Less severe droughts of four weeks or more occur frequently during the summer months of the year (Water Resources Survey of the Clyde River Catchment 1970).

The mean temperatures recorded at the Kioloa Station range from 17.1°C in July to 24.3°C in January and February. For the great majority of days in the year, temperature is not a factor limiting growth (Russell-Smith 1979).

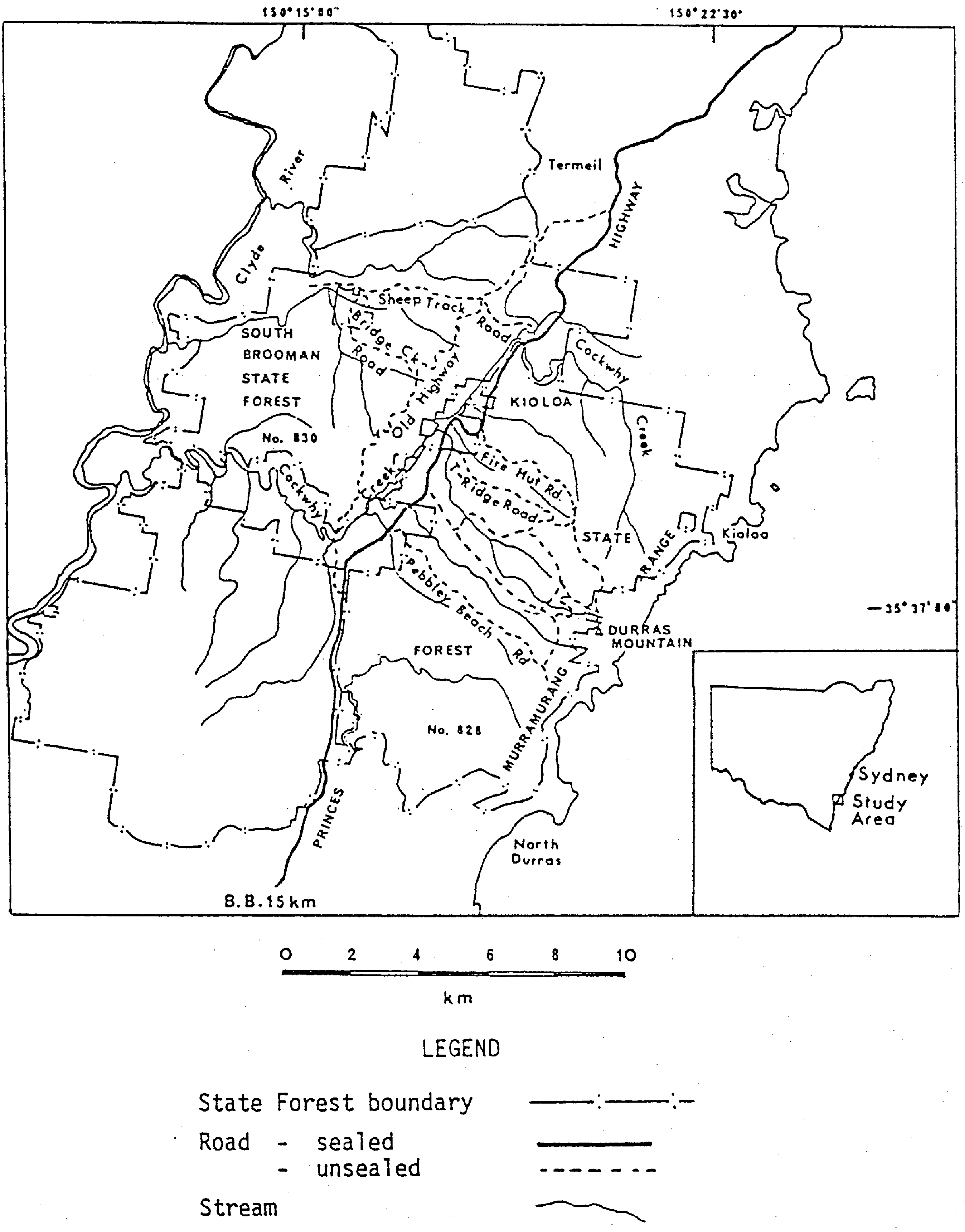
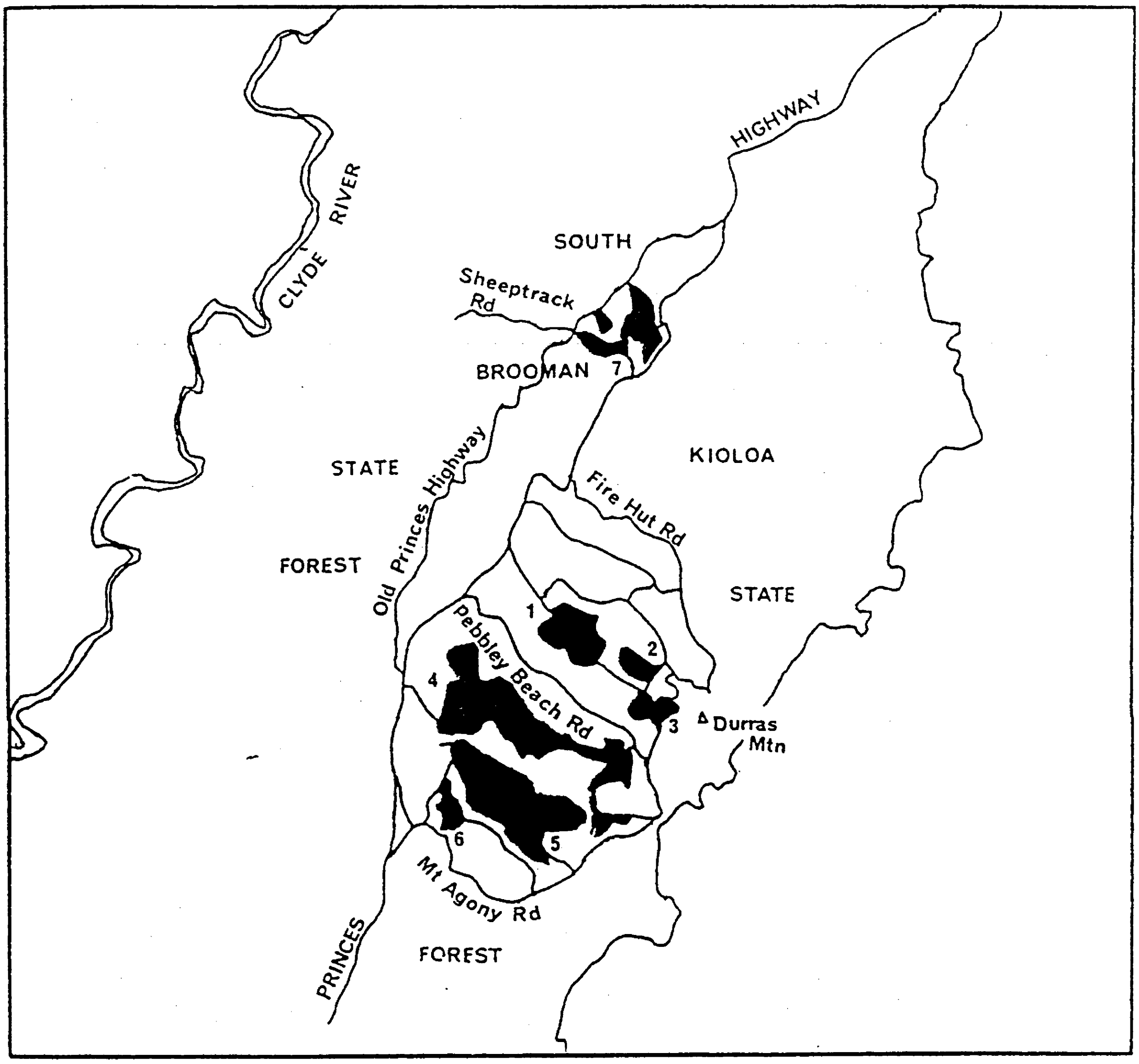


Figure 1.2 Location of the study area.



■ - CLEARCUT AREAS

1. Higgins Creek
2. Link Road
3. Cousins Gully
4. Livingstone Creek
5. Ryans Creek
6. Spotted Gum Road
7. Sheeptrack Road

Figure 1.3 Location of clearfelled areas.

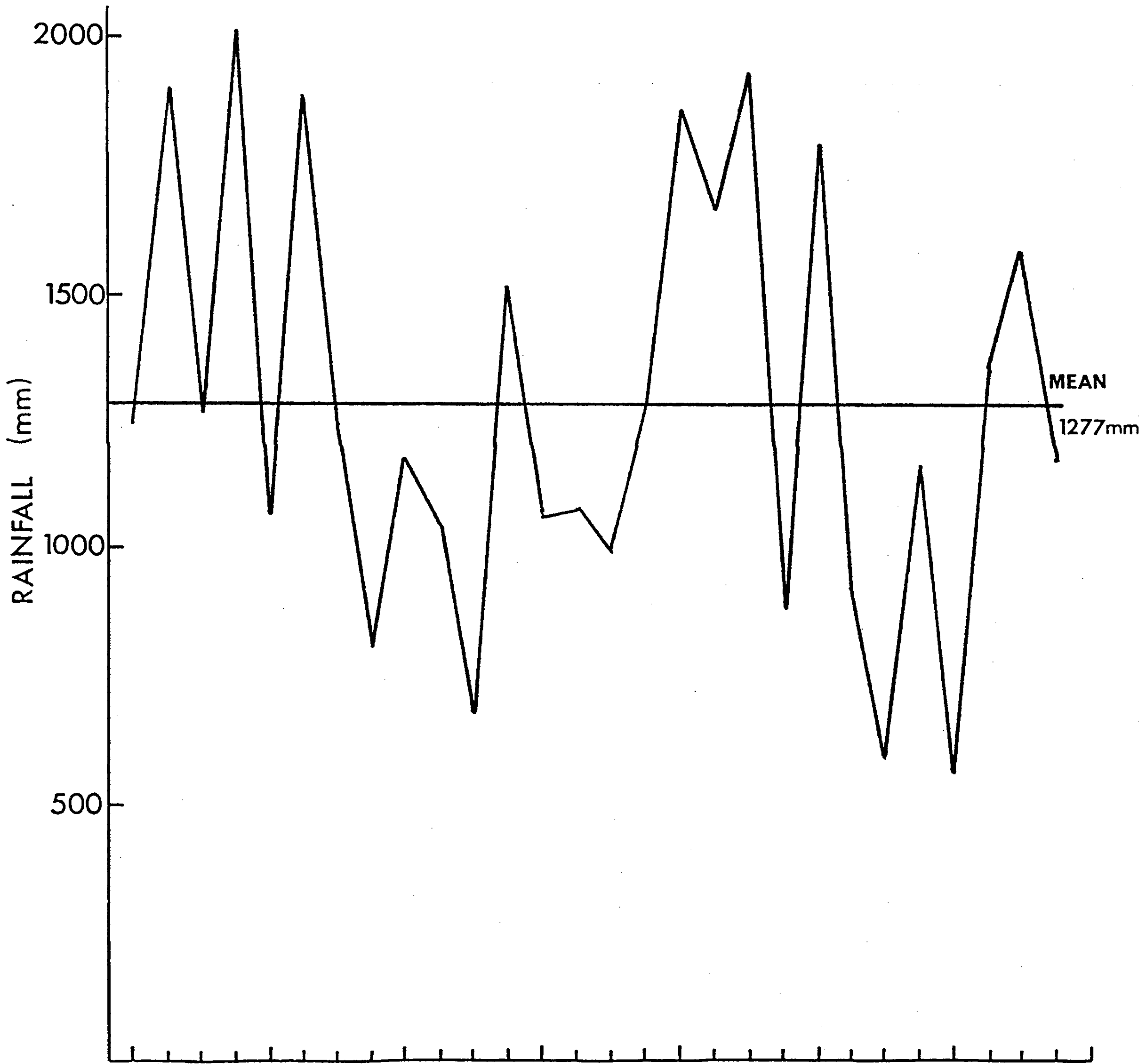


Figure 1.4 Yearly rainfall variation for Kioloa, N.S.W. (1958-1985) (Source: Commonwealth Bureau of Meteorology Records).

The Physical Environment

The studies are confined to the coastal lowland belt that extends the whole length of the N.S.W. south coast and westwards to the foothills of the Great Dividing Range (Galloway 1978b). Adjacent to the coast, the dominant feature of the area is the Murramurang Range which includes Durras Mountain (283 m above sea-level). From here, the range drops away and is generally only 120-150 m in elevation. To the west of this, the terrain falls gently away to the Cockwhy Creek. This area, which constitutes the greater part of Kioloa State Forest, consists of rolling and undulating terrain varying in elevation from 25-100 m above sea-level. Just west of Cockwhy Creek, the terrain again rises sharply to form Cockwhy Ridge (120-150 m elevation). West of this ridge, the terrain falls away to the Clyde River.

There are three geological formations within the forests of the study area (Figure 1.5). The oldest rocks are highly folded Early Ordovician sediments. These are associated with the steeper topography away from the coast and consist mainly of undifferentiated greywacke, shale, sandstone, argillite and phyllite with associated quartz veins (Gostin 1968; Galloway 1978a). Between the Ordovician sediments and the coast is a band of sediments of Permian age. These thicken eastwards in accord with the slope of the irregular, eroded surface of the older rocks on which they lie. Three formations have been recognised (Gostin and Herbert 1973). The Wasp Head Formation, about 100 m thick, is mainly felspatho-lithic sandstone but includes breccia lenses and clasts of volcanics and granite. The Pebbley Beach Formation is finer textured and consists of claystone, siltstone and fine sandstone. The Snapper Point Formation is predominantly sandstone with some conglomerate. Finally, there are a few localized areas of igneous intrusion within the study area, the most significant being at the peak of Durras Mountain. These consist of basic essexite of Mesozoic age.

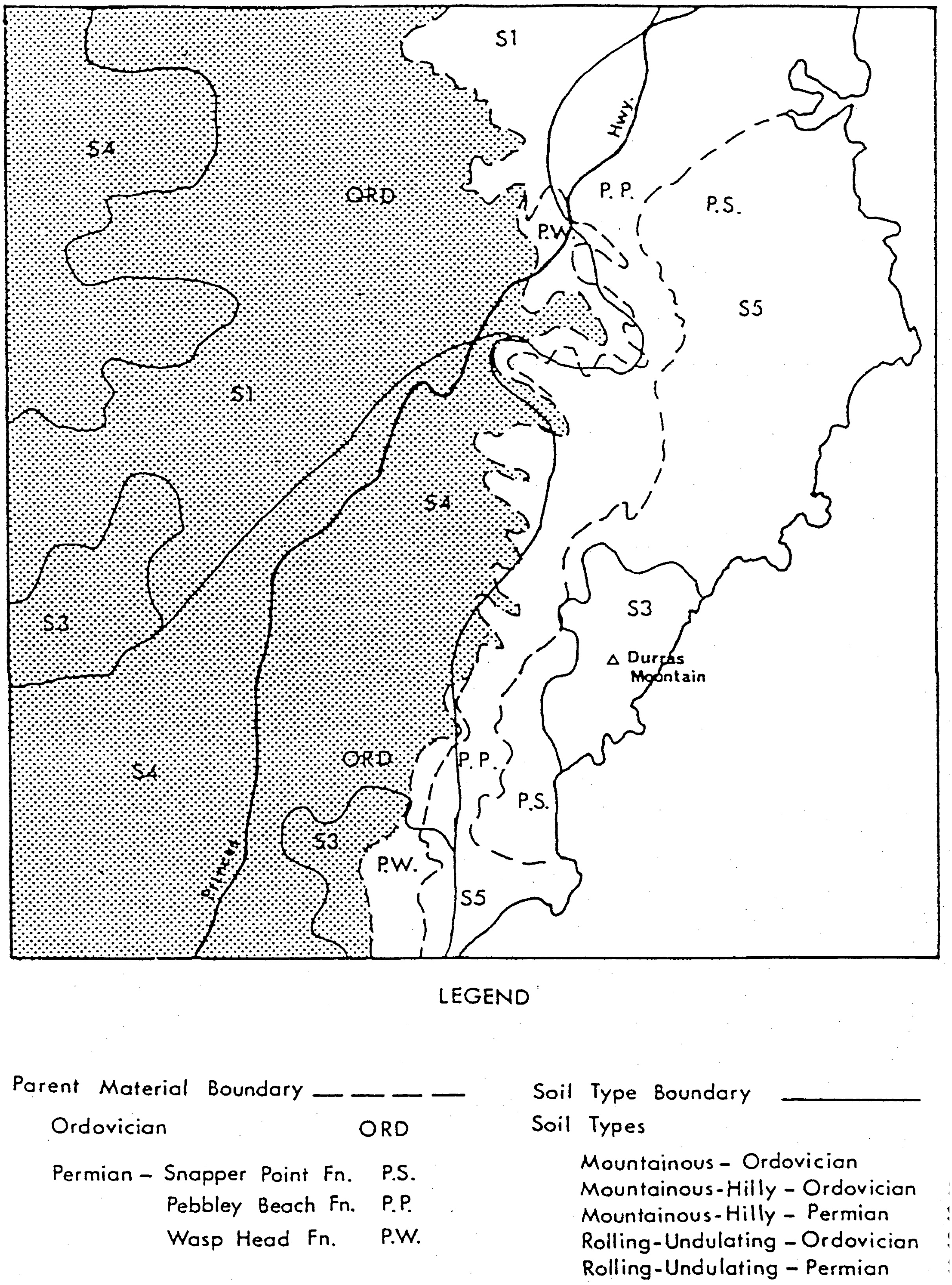


Figure 1.5 Geology and soil types of the study area (after Russell-Smith 1979).

Classifications of soils of the south coast are given by Walker (1960), Brown and Hogg (1973) and Gunn (1976, 1978). The last author provides more detailed descriptions, and is referred to here. The main soil types in the Kioloa region are brown and grey-brown soils, and closely related massive earths. Both types are characterised by gradational texture profiles in which the clay content gradually increases with depth, although on some of the Permian derived soils, there is a distinctive and sharply defined clay B horizon. The massive earths tend to possess a greater degree of structural aggregation. There is a trend for a decline in the soil gravel content to be associated with a decline in topographic relief.

The distribution of soils is controlled by the nature of the underlying rocks and by the spread of weathering and erosion products across slope profiles. The soils are moderately to strongly acid and kaolinite is the dominant clay mineral so that the nutrient status and available water storage capacities are generally poor. Available phosphorus* is generally low to very low (5-24 ppm) but rises (50 ppm) in some humic horizons of soils under virgin forest. Organic carbon (2-7%) and nitrogen (0.10-0.70%) are moderately high while potassium (0.2-3.2 m-equiv/100 g) is thought to be adequate for plant growth. The nature, size and shape of coarse fragments correlate well with underlying parent rocks. Most extensive are the soils derived from strongly folded Ordovician sediments which contain flattened fragments of slate, shale and sandstone. The sandstone basis of the Permian sequence produces more weathered coarse fragments, comprising mainly unconsolidated sandstone and siltstone. In contrast to the relatively infertile soils affiliated with the Permian and Ordovician sequences, the basaltic associations originating from Durras Mountain produce deeply weathered red kaolinitic clayey soils which are of higher fertility and superior physical structure (Brown and Hogg 1973).

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* as described by Gunn (1976, 1978)

Vegetation

The vegetation of the study area has been described most recently by Russell-Smith (1979) and may be placed into one of two broad categories; eucalypt dominated sclerophyll forest and depauperate warm temperate rainforest. The eucalypt forests comprise the predominant vegetation of the area and range in structure from tall open forest to low woodland (after Specht 1970). The associated understoreys range from mesic, or wet sclerophyll types, to heathy types. The rainforest is generally restricted to the sheltered gully situations. Structurally, it is of either closed-forest or low closed-forest form (after Specht 1970) and may be defined as simple evergreen notophyll fern forest following Webb's (1959, 1968) physiognomic-structural classification of Australian rainforests.

Austin (1978) and Austin and Sheaffe (1976) have described the vegetation of the Kioloa area as part of a broad-scale vegetation survey of the whole south coast. Four community types are identified which do not have an *E. maculata* component; these have varying frequencies of *E. piperita* Sm. *E. globoidea* Blakely and *E. pilularis* Sm. There are also four community types with an *E. maculata* component; these have *E. paniculata* Sm., *E. pilularis* or *E. saligna* Sm. as the major co-occurring species. *E. maculata* is also found in pure stands, or in association with minor species such as *E. piperita*, *E. globoidea*, *E. paniculata* and *E. pilularis*.

There is also a consistent relationship between tree overstorey species and understorey trees, shrubs and herbs. Understorey genera range from heath types (*Banksia*, *Hakea*, *Leptospermum*) on Permian sandstones, through characteristic xeromorphic types (*Acacia*, *Leucopogon*, *Hibbertia*) associated with open to tall open eucalypt forest, to the more mesic end of the forest spectrum (*Backhousia*, *Livistonia*, *Callicoma*) predominantly located on lower slope and gully positions.

Other studies of vegetation in the area are concerned more specifically with the relationship between environmental variables and vegetation pattern (e.g. McColl 1965, 1969, 1970; McColl and Humphreys 1967; McCutchan 1978; Russell-Smith 1979). These studies are discussed in more detail in Chapter 3.

1.5 GENERAL EXPERIMENTAL AND ANALYTICAL METHODS

An account is given here of experimental and analytical methods common to a number of studies described in the thesis. Experimental methods specific to each study are described in the introduction to that study.

Seed Source

In a comparative study of species performance, complications may arise from provenance variation within a species. For example, Awe *et al.* (1976) observed large differences in growth characteristics of several provenances of *E. camaldulensis*. Since the present study focuses on the ecological responses of species from the south coast, seed has been used, wherever possible, from the south coast region. This was facilitated by drawing on collections made by the CSIRO Division of Forest Research as part of its program for seed export and research. One species, *E. camaldulensis*, does not occur naturally on the south coast, and a seedlot from a similar latitude was selected.

Relatively large quantities of *E. maculata* seed were required because it was included in all growth studies conducted. A problem arose in that seed from the first seedlot was exhausted before all experiments had been completed. Consequently, *E. maculata* seed for some experiments has come from a different seedlot. *E. globoidea* also had seed from separate seedlots. In all cases, however, seedlots for a particular species were collected from geographically similar locations. In addition, within any experiment, the seed used was from a single seedlot. A description of seed sources is given in Table 1.1, along with the experiment for which it was used.

Description of Growth Analysis Parameters

This study uses the growth analysis formulae for mean relative growth rate (RGR), mean net assimilation rate (NAR), and mean leaf area ratio (LAR) to describe characteristics of plant growth. They are discussed by Wareing (1966), Radford (1967), Sestak *et al.* (1971), Evans (1972) and Ledig (1974).

Mean relative growth rate is the change in plant size (dry weight, leaf area, height etc.) per unit time per unit growing material and is given by

$$(\ln X_2 - \ln X_1) / (t_2 - t_1)$$

where t_1 and t_2 are times at first and second harvest respectively, and X_1 and X_2 are dry weight of total plant, shoot or root, or height, diameter or leaf area at t_1 and t_2 respectively.

Mean net assimilation rate is an index of physiological activity or a measure of photosynthetic efficiency and is defined as the rate of increase in total plant dry weight per unit of leaf per unit time. It is given by

$$(W_2 - W_1) (\ln A_2 - \ln A_1) / (A_2 - A_1) (t_2 - t_1)$$

where W_1 and W_2 are total plant dry weights at times t_1 and t_2 respectively, and A_1 and A_2 are total leaf areas at t_1 and t_2 respectively.

This formula is only applicable when the relationship between W and A is linear.

Mean leaf area ratio is an index of leafiness and is an important structural concept or morphological index because it expresses the proportion of assimilatory surface to respiratory mass. It is given by

$$\tfrac{1}{2}(A_1 / W_1 + A_2 / W_2)$$

The advantage of using RGR for comparisons is that it eliminates differences in growth rates due to differences in plant size (Wareing 1966). Hence, it is useful for comparing data from different experiments and for different treatments within an experiment (Radford 1967). In addition, the expression produces meaningful values even when only two harvests are taken. It is noted, however, that plants growing in identical environments with large differences in morphology and physiology can have identical RGR's. Such instances are produced by different mechanisms and involve quantitative compensations (Evans 1972).

NAR depends on the difference between net photosynthetic CO_2 uptake during the photoperiod, and respiratory CO_2 loss from the whole plant during the entire day, with the addition of any daily mineral uptake and overall metabolic balance (Evans 1972; Ledig 1974). The use of NAR is more restricted than that of RGR due to the requirement for an assumed linear relationship between W and A. Unfortunately, if only two harvests are taken, it is not possible to assess whether the relationship is linear or not. In this case, the simplest assumption (i.e. linearity) should be used (Radford 1967), and it is suggested that only where the relationship between W and A is vastly different from linear is it likely that large errors will be introduced. Sestak *et al.* (1971) suggests that if RGR_W/RGR_A ranges from 0.5 to 1.5, the formula assuming linearity should be used.

Table 1.1 Information on seed source.

Species	CSIRO Seedlot No.	Locality	ORIGIN Latitude		Longitude		Altitude	No Parent Trees	Viable Seed per 10 g	Chapter (C) and Experiment (E) No. for which seed was used
			Deg	Min	Deg	Min				
Eucalyptus maculata	13602	Batemans Bay, NSW	35	34	150	19	55	10	1000	C2 E1, C4 E1, C5 E1, C7 E1
E. maculata	11674	8.9 km W Wandandean, NSW	35	06	150	30	100	1	860	C4 E2, C4 E3, C7 E2
E. globoidea	10291	Nr Bens Creek, N Vic Border	37	19	149	44	50	1	660	C7 E1
E. globoidea	11202	4.8 km S Penrose, NSW	34	42	150	12	600	Unknown	560	C4 E1
E. gummifera	12285	Termeil, Nowra, NSW	35	28	150	23	30	Unknown	466	C4 E1, C7 E1
E. paniculata	13657	SW of Nowra, NSW	35	0	150	30	120	5	No test	C7 E1
E. pellita	11813	South coast, NSW	Unknown		Unknown		90	Unknown	860	C7 E1
E. pilularis	12136	Termeil S.F., Meroo Road, NSW	35	28	150	23	40	13	400	C4 E1, C4 E2, C5 E1, C7 E1, C7 E2
E. saligna	11675	North Durras, Kioloa S.F. NSW	35	35	150	15	30	3	2600	C7 E1
E. camaldulensis	10666	Lake Albacutya, Victoria	35	44	142	2	70	11	4400	C7 E1
Acacia mabellae	14400	Monga S.F., NSW	35	36	149	55	710	2	380	C4 E3, C7 E2

Statistical Analysis

Quantitative data from glasshouse and field studies have been analysed with appropriate statistical techniques using computer packages GENSTAT (General Statistical Program) (GENSTAT 1977; Alvey *et al.* 1982) and GLIM (General Linear Interactive Modelling) (Baker and Nelder 1978) on a UNIVAC 1100/82 computer. The statistical techniques used are analysis of variance (and covariance), regression analysis and principal coordinate analysis. A more detailed account of the range of analyses conducted, and the assumptions involved, is given in Appendix I.

Nutrient Determinations*

The following procedures have been used in determining nutrient concentrations in soil and leaf samples. Soil samples were air dried at room temperature and passed through a 2 mm sieve. Leaf material was ground in an electric coffee grinder to homogenise samples. Total nitrogen and phosphorus were determined using the Kjeldahl acid digestion technique on a Technicon Autoanalyser II continuous flow analytical instrument. Total and exchangeable cations potassium, calcium, magnesium and sodium were determined using the methods adopted by the Forestry Commission of N.S.W. (Lambert 1978). Organic carbon was determined using Walkley and Black (1934) wet digestion.

* Total cations were determined for plant material and exchangeable levels for soils.

* pH based on water extract

* Organic matter percentage was determined using loss on ignition

* soil bulk density was estimated by inserting steel rings (5cm dbh) of known volume; the soil samples were oven dried and bulk density expressed as gm per cubic cm

CHAPTER 2

STUDIES ON REGROWTH STOCKING

2.1 INTRODUCTION

A survey of vegetation on 120 randomly located sites within regrowth stands on Kioloa State Forest (Neave 1983) provided a broad appreciation of relationships between the development of *E. maculata* regeneration, that of other successional species, and topographic factors. It showed firstly that the stocking of *E. maculata* declined while the stocking of other regrowth species increased from upper to lower slopes, and secondly that where they occurred, other eucalypt species tended to be more vigorous than *E. maculata*.

In order to interpret these patterns, it was necessary to address two main questions: why does the stocking of *E. maculata* decline so markedly with slope, and why do the relative competitive abilities of *E. maculata* and other eucalypt species differ? Factors influencing the relative competitive ability of species are taken up in subsequent chapters. This chapter is concerned primarily with the question of stocking and its relationship to slope. There are a number of studies which relate to the condition of regrowth stands, and the distribution and characteristics of lignotuberous advance growth, as follows:

(i) Condition of regrowth. In order to establish more precisely the characteristics of regrowth stands, vegetation analyses have been made at two sites; both contained *E. maculata* as a stand dominant before harvesting. The first analysis, at the 'Link Road site', examines regeneration patterns where other eucalypt species tend to be more vigorous than that of *E. maculata*. An analysis of the adjacent mature forest at the Link Road site was also undertaken to characterise any changes in species frequency and dominance as a result of clearfelling. The second analysis, at the 'Livingstone Creek Road site', examines regeneration patterns along a slope; this represents the characteristic pattern of changing dominance of *Eucalyptus* and *Acacia* species from upper to lower slopes.

(ii) The stocking of *E. maculata* regrowth. The decline in regrowth stocking along a typical slope may have much to do with the presence of advance growth at the time the forest was clearfelled. It was necessary therefore to establish the effect of vegetation type and slope on the advance growth pool, and the contribution both advance growth and new seedling regeneration may have made to the regrowth stocking.

(iii) The effect of environmental factors on the vigour of lignotuberous seedlings. A factor which may influence the persistence and vigour of the lignotuber following release is the 'preconditioning' effect of environmental factors. Very little is known of this - at least in the forest situation. In order to establish some background to the *E. maculata* lignotuber, an experiment was conducted in which *E. maculata* seedlings were subjected to a number of treatments, and were harvested (following reshooting from the lignotubers) on a number of occasions.

2.2 BACKGROUND TO THE EUCALYPT LIGNOTUBER

In spite of the significance of the eucalypt lignotuber in the forest environment, there have been relatively few studies on this specialized organ. Morphological and anatomical studies have been undertaken by Kerr (1925), Chattaway (1958), Carr *et al.* (1982, 1983, 1984a, 1984b) and Lacey (1983). Jacobs (1955) related the eucalypt lignotuber to its role in the forest environment by describing its ability to produce shoots after destruction of the aerial portion, its persistence under continuous cycles of destruction and reshooting, and its role as a store of reserve food. More recent studies (Mullette and Bamber 1978; Jahnke *et al.* 1983; Lacey 1983) have examined some of the possible genetic and environmental factors responsible for the formation and subsequent development of the lignotuber. These have been useful for interpreting observed responses of the lignotuber in the field and have contributed to an understanding of its significance from both an evolutionary and silvicultural perspective.

Morphology and Anatomy of the Lignotuber

Chattaway (1958) first proposed that species which form lignotubers have two accessory buds, one above (adaxial) and one below (abaxial) the axillary bud - non lignotuberous species only had the lower accessory bud. The lignotubers are initiated as swellings in the axils of the cotyledons and in some species also at several succeeding nodes. Each lignotuber grows radially and may grow downwards to fuse with the swelling of a lower node or to envelop the hypocotyl and the upper part of the root (Lacey 1983). In a more recent morphological study, Carr *et al.* (1984a) supported Chattaways accessory bud theory, but with modification. They concluded that Chattaway probably only found the central adaxial bud from a suite of many, and that such a suite may also be present abaxially to the axillary bud.

The size of the lignotuber formed appears to bear a relationship to the initial complement of upper accessory buds (Carr *et al.* 1983). This number declines upward (acropetally) from the cotyledonary node. Nodes which have only a single upper accessory bud are in general, incapable of forming lignotubers since such nodes are sometimes located well above the last lignotuber-forming node on the seedling stem.

The capacity to form lignotubers is evidently inherited since some species are known not to have it (Jahnke *et al.* 1983). The genes for lignotuber formation appear to be dominant (Pryor 1957; Pryor and Byrne 1969; Barrett *et al.* 1975; Venkatesh and Sharma 1979; as seen in Jahnke *et al.* 1983). In many species, the penetrance of these genes is 100%

and lignotubers are thus formed irrespective of a wide variety of conditions. In others, penetrance is not complete or is absent; for example, formation or otherwise varies with provenance in *E. camaldulensis* (Jahnke *et al.* 1983).

Development of the Lignotuber

Lignotubers are most important for survival of young plants. In most species, they gradually merge at the young sapling stage (Carter 1929). In other species they persist and attain a large size, and give rise to a number of stems of distinctly separated bases (Lacey 1983).

Relatively little is known about the heritability of development and persistence of lignotubers. Apparently seedlings of lignotuberous species remain competent to form lignotubers over a long period of adversity during which lignotubers are not formed. This was demonstrated by Carr *et al.* (1982) who raised a population of lignotuberous seedlings in vermiculite, using only tap water. After one year, 8-10 leaf pairs had formed but there was no trace of cotyledonary accessory meristems. Where the seedlings were transplanted to good soil in the second year, all seedlings formed lignotubers. Thus, despite the nutritional adversity, the competence to form lignotubers was retained.

Some species exhibit dimorphism in relation to their growth habit (Lacey 1983). In the tree form of *E. gummifera*, lignotubers cease to be obvious after the plant reaches 2.5 to 4.0 m in height, but in the mallee form, one is always present and increases in size with age (Mullette and Bamber 1978). It was concluded that the proportion of plants with lignotubers and the proportion of the lignotuber in the biomass of the shoot system are inherited. However, because only two parent trees were used, Lacey (1983) considers that the results represent the difference between two individuals and not the difference between the tree and mallee populations.

Environmental Influences on Lignotuber Development

Several environmental factors are thought to influence the development of the eucalypt lignotuber. Lacey (1983) considers edaphic factors are probably the most important since they determine stem growth rates, potential size, and the capacity of the plant to recover from damage. The effects of soil nutrition have been studied by several workers. A pot experiment by Kerr (1925) found superphosphate and calcium more effective than nitrate in increasing the size of lignotubers in eucalypts that normally form them; potash had no effect. Beadle (1954, 1966, 1968), after stating that the lignotuber was an evolutionary response to low nutrient soils, presented evidence which showed that high phosphorus and nitrogen levels restricted lignotuber development in *E. oleosa*, *E. saligna* and *E. gummifera*. Weir (1969) found a decrease in the ratio of lignotuber size to seedling size in *E. radiata* following an increase in phosphorus from 1 to 50 ppm (i.e. more nutrient was directed to stem growth at higher phosphorus levels), unless a high nitrogen level (100 ppm) was also present. In contrast, Mullette and Bamber (1978) found that an increase in phosphorus levels stimulated lignotuber development in *E. gummifera*. Jahnke *et al.* (1983) re-interpreted these results and concluded that they support Beadle's original work, that is, there is a suppressing effect of high levels of phosphorus on lignotuber development at less than toxic levels.

Jahnke *et al.* (1983) have shown that when an effect of nitrogen on overall growth of *E. camaldulensis* is taken into account, there is no additional effect of phosphorus on lignotuber size or plant height. They also found lignotuber dry weight and diameter increased with increasing nitrogen supply at a constant high phosphorus level, although the increase just failed to reach statistical significance. In contrast, at a low level of phosphorus, Weir (1969) found a significant increase in lignotuber dry weight with increasing nitrogen levels in

E. radiata. However, Weir had not excised the lignotubers from the stem and the amount of stem tissue between the lignotubers influenced the result. Because nitrogen had a significant effect on stem diameter in Weir's experiments, the data could be misleading (Jahnke *et al*. 1983).

Jahnke *et al*. (1983) found that the percentage of lignotuber bearing seedlings of *E. camaldulensis* was highest at high levels of phosphorus, associated with low to intermediate levels of nitrogen. At the highest phosphorus and nitrogen levels, there was a significant reduction in the frequency of lignotubers while at high nitrogen levels, there was no statistical effect of a change in phosphorus levels on the percentage of lignotubers formed. These results suggest that high phosphorus levels are directly involved in increasing the frequency of lignotubers, only if the associated nitrogen levels are low. Jahnke *et al*. (1983) explained this by suggesting that high nitrogen levels may increase the rate of radial or secondary growth of the stem to such an extent that the lignotuber development is initiated, but the lignotuber remains morphologically inapparent.

Since repeated damage to the seedling shoot encourages further development of the lignotuber, Carr *et al*. (1982) proposed that the shoot may in some way suppress normal lignotuber development. Their experiment using reciprocal grafts of lignotuberous and non lignotuberous species indicated, however, that this was not the case.

Jacobs (1955) considered shading to be an important factor affecting the survival of the lignotuber. He cites the case of eucalypt lignotubers being rare where a dense understorey has grown up under a fairly complete canopy of eucalypts, and the light values on the forest floor have been kept to no more than 1% full sunlight for several years. Kerr (1925) found that shading retarded lignotuber growth in some eucalypt species; this differs from the findings of Weir (1969) who observed no such response.

Most of the studies on eucalypt lignotubers have considered the effect of environmental factors on lignotuber size. Presumably the larger the size, the greater is the storage capacity of the organ, and the greater are the number of adventitious buds. It is possible, however, that the vigour and persistence of the eucalypt lignotuber is not related solely to its size and that the 'preconditioning' effect of environmental factors may be important. Little work has been done on this, apart from some general observations. Jacobs (1955) suggested that lignotubers are of great significance in determining the persistence of eucalypts in a harsh environment, and describes the following possibility. Where a seedling of a lignotuberous species becomes established on a difficult site, the lignotuber may play a very important part in assisting the new individual to make a tree. The shoot may be destroyed by fire, drought or animals, but the buds and food reserves in the lignotuber permit it to shoot again when conditions are more favourable. The second shoot is usually stronger than the first, and in turn it strengthens the reserves in the lignotuber and roots. This process of production and destruction of new shoots may be repeated several times. Each new shoot is usually a little stronger than the previous one and when finally there is a gap in the overwood, the increasing strength of the 'seedling' permits it to develop into the opening. Thus environmental stress may be important in the development of a vigorous lignotuber. Lacey (1983) observed that *E. botryoides* produced large lignotubers in the mallee form where the water table was deep in the soil profile and total nitrogen and phosphorus were low. He concluded that on the excessively drained low fertility siliceous sands, the adverse effect of infertility on stem growth relative to that of the lignotuber may be enhanced by extremes in soil moisture. Kerr (1925) found that badly drained soil prevented the develpment of lignotubers and restricted growth in *E. coriacea**. In addition, she showed that

* *E. pauciflora*

checking growth by removal of the growing point caused a considerable increase in the size of lignotubers, provided there was a fair proportion of leaf area. Carter (1929) also expressed the view that the more adverse the climatic and soil conditions, the better developed are the lignotubers.

Finally, Henry and Florence (1966) examined some of the field responses of the eucalypt lignotuber in a dry sclerophyll *E. maculata*-*E. drepanophylla*-*E. siderophloia* forest. They observed a large positive response to complete removal of the canopy, but development of the lignotuberous seedlings was restricted for some distance from the edge of the surrounding canopy. The hypothesis was advanced that there may be a complex type of equilibrium in which the development of a given lignotuberous or advance growth stem is determined by the level of stocking in a wide arc of the surrounding stand, rather than by competitive pressure from the immediately adjacent or overtopping stems.

2.3 THE CONDITION OF REGROWTH STANDS

2.3.1 The Link Road Site

E. maculata clearly occupies a sub-dominant canopy position within some of the regrowth stands on Kioloa State Forest. However, observations on adjacent mature forest suggests that where *E. maculata* is a major stand component, it normally occupies a dominant/co-dominant position in the stand. Thus a comparative analysis of the composition and structure of adjacent uncut mature, and regrowth stands has been made to establish any changes in these stand parameters that may have occurred as a result of clearfelling. The study was carried out on Link Road.

Materials and Methods

An area either side of Link Road (Department of Lands Map 1970) was used to compare the structure of the mature forest and that of the developing regrowth forest. The sites were in close physical proximity, had similar soil type (loam, fine sandy), parent material, aspect and slope position. Both sites occupied a relatively flat mid slope position within a long slope gradient.

An area of 3.3 ha (300 x 110 m) was demarcated for assessment in the mature forest; the long axis was adjacent to the regrowth forest. In any sampling regime, the choice of plot shape is important in relation to the efficiency of sampling (Mueller-Dombois and Ellenberg 1974). Circular plots have the least perimeter for a given area and so reduce the likelihood of wrong inclusion of individuals on the boundary (Carron 1968). However, elongated rectangular plots may furnish a more accurate analysis of the composition of a stand than either circular or square plots having the same area when the long axis of the plot is orientated parallel to the axis of the environmental gradients (Mueller-Dombois and Ellenberg 1974). Because the site was flat, there was no obvious gradient in environmental factors. Consequently circular plots were used to record the vegetational data.

The sample size required to restrict the error to within a certain percentage of the mean was determined using the method of Snedecor and Cochran (1967), as follows:

$$n = (ct/e)^2$$

where

n = number of individual samples required

c = coefficient of variation

e = percentage error of the mean

t = students t value for small sample sizes ($n < 30$) at a given error level.

In order to obtain estimates within 5% of the true mean with 95% confidence, 239 plots would have to be sampled. An estimate within 20% of the true mean with 90% confidence is obtained by sampling 10 plots. With this in mind and taking account of time constraints, 12 randomly located plots were established, each with a 10 m radius (314 m^2). This provided a sample of about one third of a hectare or 8.8% of the assessment area.

The diameters of all overstorey stems by species were measured on each plot and basal area per ha calculated.

In sampling the regrowth forest, an area of about 1.76 ha (160 x 110 m) was demarcated for assessment, with the long axis adjacent to the area assessed in the mature forest. Twelve randomly located circular plots were used, each with a radius of 7.135 m (160 m^2). This provided a sample of about one fifth of a hectare or 9.2% of the assessment area.

The diameter at breast height over bark (dbhob) of all stems greater than 5 cm was recorded on each plot. The height of the two tallest of each eucalypt species, and the two tallest *Acacia* stems (regardless of species) were also measured. The N.S.W. Forestry Commission records (Batemans Bay region) were also consulted to determine the combined sawlog yield taken off the compartment containing the Link Road site. The combined yield was comprised of components from successive selection loggings and the final clearfelling operation. This information complements that gathered from the survey of adjacent uncut forest.

Results

The basal area of each species from the mature forest is given in Table 2.1, together with the percentage basal area of each eucalypt species as a proportion of all eucalypt species, and the percentage basal area of each tree species as a proportion of all tree species.

Table 2.1 Basal area estimates by species for Link Road mature forest site.

Species	Basal Area (m^2 ha^{-1})	Percentage Basal Area (all species)	Percentage Basal Area (eucalypt species)
Eucalyptus maculata	21.863	50.8	51.3
E. pilularis	8.626	20.0	20.2
E. globoidea	6.980	16.2	16.4
E. gummifera	3.869	9.0	9.1
E. pellita	1.303	3.0	3.1
Acacia spp.	0.340	0.8	-
Casuarina littoralis	0.067	0.2	-
Total	43.047	100.0	100.0

Where eucalypt species only are considered, *E. maculata* comprised more than 50% of the basal area on the site. *E. pilularis* made up 20.2%, *E. globoidea* 16.4%, *E. gummifera* 9.1% and *E. pellita* 3.1%. Where all tree species are considered, the percentage basal area of the eucalypts tended to be much the same as where eucalypts only were considered, that is, *Acacia* and *Casuarina* occupy a relatively small proportion of the total basal area in the uncut forest. These percentages are similar to the sawlog yield volume taken off the compartment. Since logging began, *E. maculata* has comprised 59% of the volume removed, *E. pilularis* 19% and other eucalypt species 22%.

The stocking of eucalypts within the mature forest is shown in Table 2.2, and the diameter distribution in Table 2.3. *E. maculata* had the greatest stocking (45.3%), followed by *E. globoidea* (28.3%), *E. pilularis* (14.5%), *E. gummifera* (8.6%) and *E. pellita* (3.4%). There were an equal number of *E. maculata* and *E. pilularis* stems greater than 80 cm in diameter, indicating that both species are dominants in the stand. In contrast, most of the *E. globoidea* and *E. gummifera* stems were in the smaller diameter classes. The species structure can also be illustrated by the fact that there were considerably fewer *E. pilularis* per hectare (45) than *E. globoidea* (88), yet the basal area of *E. pilularis* was greater.

The stand basal area and stocking on the regrowth forest are given in Table 2.4 and 2.5 respectively. Where eucalypts only are considered, *E. pilularis* had the greatest basal area (44.7% of total basal area), followed by *E. gummifera* (23.4%), *E. globoidea* (16.0%) and *E. maculata* (15.9%). In contrast, *E. maculata*, had the greatest stocking (35.0% of all eucalypts), followed by *E. pilularis* (29.2%), *E. gummifera* (27.5%)

Table 2.2 Stocking estimates by species for the Link Road mature forest site.

Species	Stocking (stems ha^{-1})	Percentage Stocking (all species)	Percentage Stocking (eucalypt species)
Eucalyptus maculata	141.7	41.7	45.3
E. globoidea	87.6	26.0	28.2
E. pilularis	45.1	13.4	14.5
E. gummifera	26.5	7.9	8.6
E. pellita	10.6	3.1	3.4
Acacia spp.	23.9	7.1	-
Casuarina littoralis	2.6	0.8	-
Total	337.0	100.0	100.0

and *E. globoidea* (8.3%). Thus, *E. maculata* had the greatest stocking, but the lowest basal area, indicating that its mean stem diameter is particularly small. In contrast, *E. pilularis* had a lower stocking than *E. maculata*, but a larger basal area - reflecting a much greater vigour and dominance over *E. maculata*. The other major eucalypt species on the site, *E. gummifera*, had a basal area which was similar to that of *E. maculata*, but this was distributed on considerably fewer stems.

Where eucalypt and *Acacia* species are considered together, *E. pilularis* continued to have the largest basal area (31.1% of total basal area), followed by *A. longifolia* (29.0%) (Table 2.4). *E. maculata* had a low basal area (11.1%). The stocking was dominated by *A. longifolia* with 58.3% of all woody stems (Table 2.5), however its percentage of the basal area (29%) was proportionally small, that is, the diameter of the mean *Acacia* stem is small. *E. maculata* and *E. pilularis* made up 14.2% and 11.9% of all stems, respectively.

The diameter distribution of eucalypt and *Acacia* species on all 12 plots in the regrowth forest is shown in Table 2.6. Most *E. maculata* were between 5.0-9.9 cm, and did not exceed 20 cm. The same was true of the *Acacia* species. On the other hand, most *E. pilularis* and *E. globoidea* stems were in the larger diameter classes, including some greater than 25 cm. *E. gummifera* was intermediate between these two species and *E. maculata*.

The mean heights of the two tallest trees of each eucalypt species and the two tallest *Acacia* stems, are shown in Table 2.7, together with the mean for all plots. Despite some lack of consistency in the height of species on individual plots, the two *Monocalyptus* species *E. pilularis* (13.69 m) and *E. globoidea* (14.56 m) had, overall, greater mean height than the two *Corymbia* species, *E. maculata* (11.04 m) and *E. gummifera* (12.10 m). The mean height of *Acacia* species (9.84 m) was markedly lower than any of the eucalypt species.

Table 2.3 Diameter distribution on the Link Road mature forest site - number of stems by species in 9.9 cm diameter classes from an area of 3768 m^2.

	Diameter Classes*											
Species	0-9.9	10-19.9	20-29.9	30-39.9	40-49.9	50-59.9	60-69.9	70-79.9	80-89.9	90-99.9	100-109.9	110-119.9
Eucalyptus maculata		2	14	9	16	4	4	1	1		2	
E. globoidea	4	8	7	8	5					1		
E. pilularis	2	5	3	2	1		1		1	1		1
E. gummifera			3	3	1	2		1				
E. pellita				3		1						
Acacia spp.	3	5	1									
Casuarina littoralis		1										
Total	9	21	28	25	23	7	5	2	2	2	2	1

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* The diameter class pattern suggests continuing regeneration from a good lignotuber pool on this site.

Table 2.4 Basal area estimates by species for Link Road cutover forest site. Stems less than 5 cm diameter not included.

Species	Basal Area ($m^2\ ha^{-1}$)	Percentage Basal Area (all species)	Percentage Basal Area (eucalypt species)
Eucalyptus pilularis	4.297	31.1	44.7
E. gummifera	2.247	16.3	23.4
E. globoidea	1.540	11.2	16.0
E. maculata	1.530	11.1	15.9
Acacia longifolia	4.000	29.0	-
A. mabellae	0.162	1.2	-
A. irrorata	0.019	0.1	-
Total	13.795	100.0	100.0

Table 2.5 Stocking estimates by species for Link Road cutover forest site. Stems less than 5 cm diameter not included.

Species	Stocking (Stems ha^{-1})	Percentage Stocking (all species)	Percentage Stocking (eucalypt species)
Eucalyptus maculata	218.8	14.2	35.0
E. pilularis	182.3	11.9	29.2
E. gummifera	171.9	11.2	27.5
E. globoidea	52.1	3.4	8.3
Acacia longifolia	895.8	58.3	-
A. mabellae	10.4	0.7	-
A. irrorata	5.2	0.3	-
Total	1536.5	100.0	100.0

Table 2.6 Diameter distribution on the Link Road cutover forest site - number of stems by species in 4.9 cm diameter classes from an area of 1920 m^2. Stems less than 5 cm in diameter not included.

	Diameter Classes (cm)				
Species	5-9.9	10-14.9	15-19.9	20-24.9	25-29.9
Eucalyptus maculata	31	9	2		
E. pilularis	5	10	12	5	2
E. gummifera	15	11	4	2	
E. globoidea	2		2	5	2
Acacia longifolia	148	24			
A. mabellae		1	1		
A. irrorata	1				
Total	202	55	21	12	4

A comparison of the regrowth and mature Link Road sites shows how the composition and dominance of species has altered as a result of clearfelling. Disregarding *Acacia*, *E. maculata* made up 51.3% of the eucalypt basal area in the mature forest, but only 15.9% in the regrowth forest. The diameter distributions show that *E. maculata* occupied a dominant/co-dominant position in the mature forest, but a sub-dominant position in the regrowth forest. *E. pilularis*, on the other hand, had doubled its representation as a result of clearfelling (20.2% of the eucalypt basal area in the mature forest and 44.7% in the regrowth forest). The diameter distributions show that *E. pilularis* occupied a dominant/co-dominant position in both the mature and regrowth forest. For *E. gummifera*, both the percentage basal area and stocking have increased in the regrowth forest relative to the mature forest.

Table 2.7 Tree heights on the Link Road cutover forest site - mean of two tallest stems of each eucalypt species and of *Acacia* on each of the 12 plots within the regrowth forest.

	Species				
Plot Number	*E. maculata*	*E. pilularis*	*E. gummifera*	*E. globoidea*	*Acacia* spp.
1	11.70	11.10	-	-	8.98
2	-	-	8.94	-	8.22
3	10.62	16.15	-	-	12.12
4	13.67	16.10	11.24	-	11.30
5	14.90	14.60	-	17.10	10.36
6	8.92	13.54	11.14	16.20	8.82
7	11.20	15.42	11.59	-	9.36
8	-	18.00	12.83	17.40	7.97
9	-	8.92	-	7.8	9.46
10	11.03	14.90	17.60	-	10.58
11	9.82	12.77	12.68	-	12.98
12	7.47	9.13	10.78	14.32	7.98
Mean	11.04	13.69	12.10	14.56	9.84

However, the diameter distribution of this species shows that on both sites, it was present mainly in the smaller diameter classes. *E. globoidea* had a similar percentage basal area in the regrowth and mature forests. However, the number of stems on which this was distributed differed; 28.2% of the stocking in the mature forest, and only 8.3% in the regrowth forest. The diameter distributions show that there were few *E. globoidea* stems in the regrowth forest but most had relatively large diameters. In contrast, in the mature forest *E. globiodea* had a relatively large number of stems in the smaller diameter classes.

Acacia species were poorly represented in the mature forest but were much more frequent in the regrowth forest. However, a large proportion was present in the small diameter classes and is unlikely to affect the continuous development of the dominant eucalypt species.

The vegetation analyses of the regrowth and mature Link Road sites have shown clearly that the composition and dominance (in terms of the number of trees in the larger diameter classes) of the forest has been altered markedly by clearfelling. On the regrowth site, *E. maculata* has been disadvantaged, whereas all of the other major eucalypt species have increased their representation. *Acacia* species occur in high numbers in the regrowth forest but these are almost exclusively in the smaller diameter classes and therefore are unlikely to develop at the same rate as the majority of eucalypt species. It is concluded that, on this site, intensive site disturbance may have swung the species balance away from *E. maculata* in favour of species which may be better adapted to cope with the conditions created by clearfelling.

2.3.2 The Livingstone Creek Road Site

Neave (1983) has shown there are a number of characteristic patterns in the way regrowth has developed on Kioloa State Forest - one being a changing pattern of species dominance along a slope. The aim of this vegetation analysis was to examine variations in the composition and structure of regrowth along a specific slope, and to determine whether these might be related to changes in one or more environmental factors.

Materials and Methods

The site was sampled by establishing eleven plots at 30 m intervals along the slope. Factors associated with slope may provide an environmental gradient, and it was therefore decided to use the elongated rectangular plot design. Each plot had an area of 160 m^2 (8 x 20 m).

The vegetation attributes measured were dbhob of all eucalypt and *Acacia* species greater than 5 cm diameter (enumerated by 5 cm diameter classes), and the height of the two tallest of each eucalypt species and the two tallest *Acacia* species. The basal area for each species was expressed on a per ha basis. The eucalypt species on this site were *E. maculata* and *E. pilularis*, and the *Acacia* species were *A. mabellae*, *A. irrorata* and *A. floribunda*.

A number of soil physical and soil chemical attributes were assessed to determine if there was a consistent relationship between vegetation and the measured edaphic factors. At the centre of each plot, two cores were extracted from the surface 5 cm of soil for determination of soil bulk density, and soils were sampled at depths of 5 and 30 cm for determination of gravimetric water content. Soils were also sampled by auger at 0-5, 7-12, 17-22 and 37-42 cm depths for determination of total nitrogen and phosphorus. There were three replications at each plot, and samples were analysed individually. A description of the physical soil profile was also made. One of the three auger holes was taken to a depth of 150 cm or to a depth where the auger was unable to penetrate further. The depth of the A horizon, the depth to C horizon and to parent material were measured, and the texture of the A, B and C horizons were assessed.

Results

The diameter distributions of all eucalypt and *Acacia* species greater than 5 cm diameter, from plot 1 (ridge position) to plot 11 (lower flat position), are given in Table 2.8 and summarized graphically in Figure 2.1. The number of stems of both *E. maculata* and *E. pilularis* declined from the upper to the lower slope. In contrast, the number of *Acacia* stems increased towards the lower slope. In fact, on plots 1 to 6, the eucalypt species occurred in greater numbers than the *Acacia* species; the reverse was true on plots 7 to 11. Where the eucalypts were most frequent (plots 1-6), *E. pilularis* occurred in consistently greater numbers than *E. maculata* and, except for plot 1, *E. pilularis* was the sole component of the largest diameter class. Within the lower slope plots (7-11), most of the stems, regardless of species, were in the smaller diameter classes (up to 15 cm). These were dominated variously by *A. mabellae* and *A. irrorata*. Regardless of slope position, *A. floribunda* was found almost exclusively as a small diameter tree (<10 cm).

The heights of the two tallest trees of *E. pilularis*, *E. maculata* and the *Acacia* species on each plot are given in Table 2.9. The relationship between tree height and slope is similar to that between tree diameter and slope. Within the five upper slope plots, the two eucalypt species were taller than any of the *Acacia* species although, on some plots, the differences were not large. Within the three lower slope plots (9-11), the *Acacia* species were taller than any eucalypts present. For the mid slope plots, *Acacia* species had top heights intermediate between the taller *E. pilularis* and the shorter *E. maculata*.

Table 2.8 Stocking (stems ha^{-1}) by diameter class of five major regrowth species over a slope on the Livingstone Creek Road site. Plot 1 is a ridge position and plot 11 is a lower fla position.

Plot No.	Diameter Class	*Eucalyptus maculata*	*E. pilularis*	*Acacia floribunda*	*A. mabellae*	*A. irrorat*
	5- 9.9 cm (i)	312	438	312	-	62
1	10-14.9 cm (ii)	62	250	-	-	-
	15-19.9 cm (iii)	-	62	-	-	-
	20-24.9 cm (iv)	125	62	-	-	-
	i	250	188	-	-	-
2	ii	62	125	-	62	-
	iii	125	188	-	-	-
	iv	-	62	-	-	-
	i	125	250	-	-	-
3	ii	312	312	-	62	-
	iii	62	125	-	-	-
	iv	-	62	-	-	-
	i	312	1062	188	250	-
4	ii	312	812	62	125	-
	iii	-	250	-	-	-
	i	562	875	312	-	-
5	ii	250	438	-	62	-
	iii	-	188	-	-	-
	i	250	312	125	-	500
6	ii	250	375	-	-	250
	iii	-	250	-	-	-
	i	188	-	1062	375	62
7	ii	250	62	125	188	62
	iii	62	-	-	62	188
	i	62	188	62	375	438
8	ii	-	188	-	62	438
	iii	-	62	-	-	62
	i	62	-	62	-	812
9	ii	-	-	-	-	1062
	iii	-	-	-	-	62
10	i	-	62	-	250	1250
	ii	-	62	-	-	562
11	i	-	125	-	1688	688
	ii	-	-	-	188	375

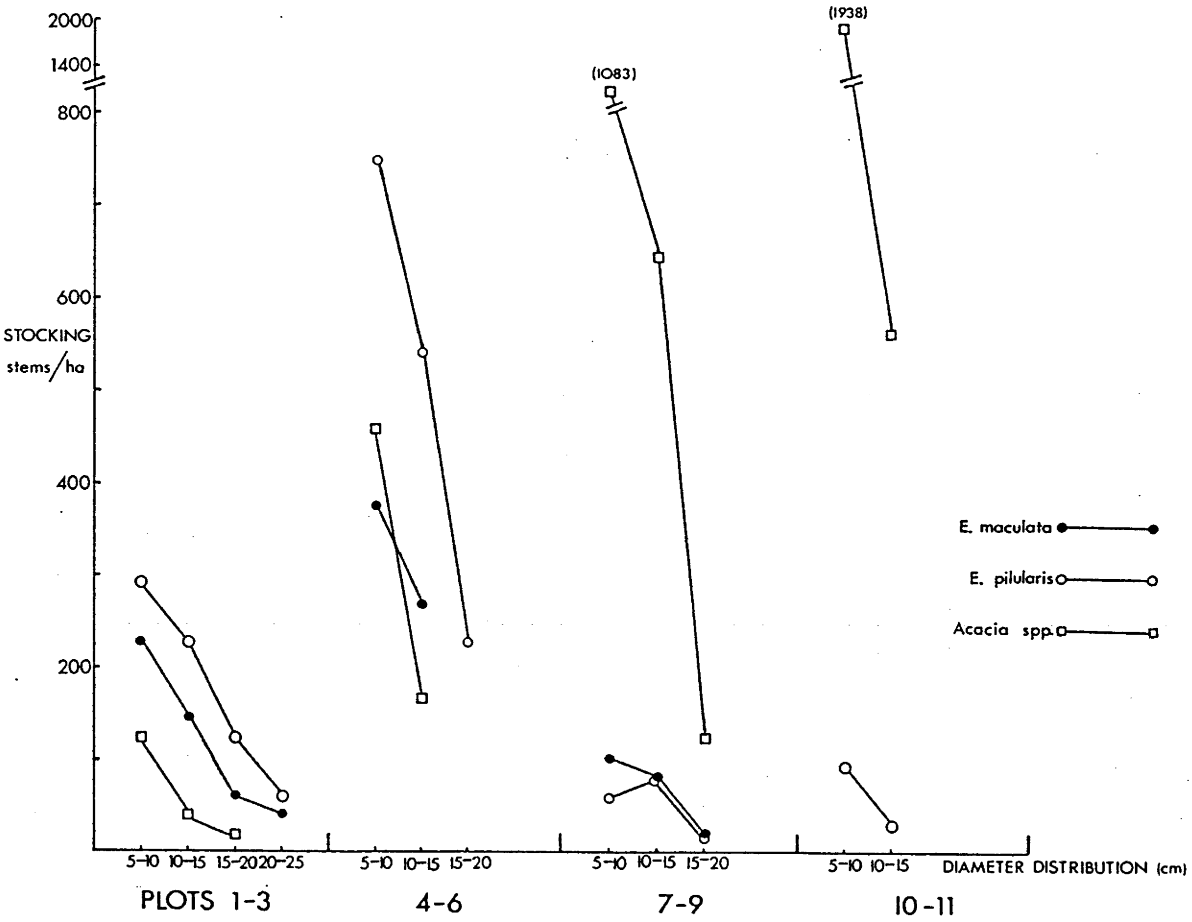

Figure 2.1 Stocking by diameter classes for two eucalypt species and an *Acacia* species. Plot 1 is a ridge position and plot 11 is a lower flat position.

The vegetation data illustrate that there are contrasting gradients in the vigour and particularly the stocking of the eucalypt and *Acacia* species along a single slope. Eucalypt species are dominant on the upper and *Acacia* on the lower slope positions, with intermediate positions being observed on the mid slopes. These patterns presumably reflect a marked change in the vigour and relative competitive ability of the eucalypts, and particularly *E. maculata*, and *Acacia* along the slope.

Table 2.9 Tree heights on the Livingstone Creek Road site - mean of two tallest stems of each eucalypt species and of *Acacia* over a slope. Plot 1 is a ridge position and plot 11 is a lower flat position.

Plot Number	Species *E. maculata*	 *E. pilularis*	 *Acacia* spp.
1	15.85	15.75	12.05
2	16.00	16.70	12.00
3	16.05	16.25	15.60
4	15.00	16.70	14.20
5	14.20	15.70	10.90
6	12.95	13.70	14.20
7	15.55	14.80	14.75
8	5.10	16.65	15.65
9	12.40	-	14.35
10	-	11.90	12.50
11	-	11.50	12.95
Mean	13.68	14.96	13.56

The physical soil attributes associated with the 11 plots are given in Table 2.10. There were few features which might help to explain the substantial changes in vegetation along the slope. The percentage moisture contents of the soil for each of the 11 plots did not change in any consistent way along the slope, at either the 5 or 30 cm soil depths. However, the depth of the A horizon, and the depth to the C horizon were somewhat less on the upper four plots (1-4) than for the

Table 2.10 Selected physical soil properties over a slope on the Livingstone Creek Road site. Plot 1 is a ridge position and Plot 11 is a lower flat position. Moisture content and bulk density measurements are means of two replications.

	Soil Physical Attributes								
Plot No	Moisture Content % 1-5 cm Depth	Moisture Content % 28-32 cm Depth	Bulk Density (g cm^{-3}) 1-5 cm Depth	Depth of A Horizon	Depth to C Horizon	Depth to Parent Material	Texture of A Horizon	Texture of B Horizon	Texture of C Horizon
1	10.39	14.02	1.24	10	-	65	Silty Loam	Silty Loam - Loam	-
2	11.30	10.25	1.00	10	60	125	Sandy Loam	Fine Sandy Clay Loam	Silty Clay
3	11.28	9.51	1.08	10	50	155	Loam, Fine Sandy	Sandy Clay Loam	Sandy Clay Loam
4	6.88	7.82	1.14	5	45	120	Sandy Loam	Sandy Clay Loam	Sandy Clay
5	9.70	8.32	0.80	30	80	95	Fine Sandy Loam	Fine Sandy Clay Loam	Light Sandy Clay Loam
6	11.44	9.60	0.90	25	65	145	Fine Sandy Loam	Loam, Fine Sandy	Sandy Loam
7	8.98	11.16	0.92	30	60	90	Fine Sandy Loam	Sandy Clay Loam	Sandy Loam
8	8.98	9.60	1.20	30	70	90	Fine Sandy Loam	Sandy Clay Loam	Sandy Loam
9	12.46	8.54	0.96	35	55	100	Loam, Fine Sandy	Clay Loam	Silty Clay Loam
10	8.58	9.57	1.12	40	85	-	Fine Sandy Loam	Clay Loam	Clay Loam
11	10.32	-	1.14	30	-	115	Sandy Loam	Clay Loam	-
Mean	10.37	9.84	1.05	23	63	110	-	-	-

majority of lower slope plots. This suggests that the volume of soil available for soil moisture storage may be less on the upper slope sites. The lack of differences in soil moisture in this study may be associated with seasonal climatic influences. Given that the south coast region experiences frequent short term moisture deficits of one month or more, and less frequent but longer term droughts on average once every 20 years (Kalma and McAlpine 1978), it is possible that differential access to soil moisture may affect the distribution of species. In relation to the Livingstone Creek Road site, the occurrence of *Acacia* primarily on the mid and lower slopes may reflect a preference for somewhat wetter sites. Russell-Smith (1979) suggested that *A. irrorata* and one form of *A. floribunda*, two of the three *Acacia* species found on this study site, are characteristically found where soil drainage is evidently poor. Cossalter (1986) considers that on the whole, *Acacia* species are sensitive to drought conditions.

There were few differences in soil texture and bulk density of the soil between the 11 plots. The A horizon soils all tended to be loams with a sand component, and the B horizon soils tended to be loams with a clay component. Some of the plots had a C horizon which was of the clay loam type, and for others, it was a sandy loam. These differences, however, were not consistent along the slope, and do not appear to be related directly to differences in the vegetation.

The concentrations of total soil nitrogen and phosphorus at three depths on the 11 plots are given in Table 2.11. These are perhaps the two most important elements affecting plant growth. Both nitrogen and phosphorus concentrations declined in a regular way down the soil profile on all plots. However, there was no consistent pattern in the way the concentrations of these two elements varied along the slope. For example, plot 1 (ridge position) had the second lowest, and plot 11 (lower flat position) the third lowest concentration of phosphorus at the 10 cm soil depth. A previous study (Neave 1983) showed that at 120 randomly located sampling sites within the regrowth stands, the concentrations of total nitrogen and phosphorus did not vary greatly from upper to lower slopes. This suggests there may not have been a great deal of colluvial enrichment of lower slope soils - that is, the movement of nutrients downslope, even over long periods of time, was probably quite small. Alternatively, nutrients may have been subjected to greater leaching in lower slope positions, and hence not incorporated and cycled within the plant-soil system.* Whatever the circumstances, the data suggest that the changes in the eucalypt-*Acacia* relationship along the slope are not influenced directly by the total concentrations of nitrogen and phosphorus. It is possible of course that the 'plant available' forms of these two elements may have a closer relationship with the vegetation response.

None of the environmental site factors assessed seem able to account adequately for differences in the condition of the regrowth at the Livingstone Creek Road site. It is possible that the changing eucalypt-*Acacia* pattern might be accounted for by stand factors at the establishment phase; for example, the decline in *E. maculata* stocking may reflect a decline in advance growth from upper to lower slope in the original forest. The lower slope stocking may come largely from new seedling regeneration and the upper slope stocking from advance growth and new seedlings; and, in the absence of site preparation, the seedling regeneration may have established slowly, and been subjected to unduly severe competition from concomitantly establishing species. Thus it is necessary to examine the likely distribution of advance growth in the stand before the harvest, and the contribution this and seedling regeneration may have made to the present regrowth stocking.

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* It is also possible that nutrients accumulating on lower slopes may have been incorporated into the biomass - so that there is still little change in the soil nutrient levels. Foliar analyses suggest that higher levels of soil nutrients may lead to greater growth rates and biomass, but foliar nutrient concentrations remain the same.

Table 2.11 Total soil nitrogen and phosphorus at three depths for 11 plots over a slope on the Livingstone Creek Road site. Plot 1 is a ridge postion and Plot 11 is a lower flat position. Each measurement is a mean of three replications. Least significant difference (LSD) at 95 percent level of probability.

Plot Number	Total Soil Nitrogen (ppm) Soil Depth 10 cm*	 20 cm	 40 cm	Total Soil Phosphorus (ppm) Soil Depth 10 cm	 20 cm	 40 cm
1	1114	856	629	95	83	69
2	2054	1369	887	122	102	72
3	2918	1757	866	156	115	76
4	1332	840	521	93	78	60
5	2747	1390	775	163	115	85
6	2795	1604	831	169	119	85
7	2315	1237	833	140	112	90
8	1923	1096	723	134	108	77
9	2439	1327	818	151	114	79
10	2478	1144	787	137	96	76
11	2259	1208	774	111	95	87
LSD	628	368	230	19	14	12

* sample depths 7-12 cm, 17-22 cm, 37-42 cm

2.4 THE POSSIBLE CONTRIBUTION OF SEEDLING REGENERATION OF *E. MACULATA* TO THE REGROWTH STAND

Within the regrowth stands on Kioloa State Forest, there is some uncertainty as to whether the non-vigorous *E. maculata* represents new seedling or lignotuberous material. If it is primarily from new seedlings, then the low vigour may reflect the need for *E. maculata* to persist for some time in the lignotuber form before it is able to respond effectively to overwood removal. Even then, there is no guarantee that the lignotuber would be able to beat competing vegetation. If however, the weakly vigorous *E. maculata* originates primarily from an established pool of lignotubers, then perhaps many of the sites are inherently marginal in terms of those factors necessary for rapid response of the lignotuberous seedlings to release. That is, despite an extended period of establishment involving extensive root development, *E. maculata* is still unable to compete effectively. In investigating the dynamics of *E. maculata* in the cutover stand, attention must be directed first of all to the origin of the regrowth.

The most obvious method of determining the origin of regrowth (i.e. new or lignotuberous seedling) is to determine the age of regrowth and compare this with the known date of clearfelling. A method of dating regrowth is to count growth rings. However, because of the largely non-seasonal coastal climate, eucalypt species either do not produce obvious growth rings, or do not produce them on a consistent annual basis (Mucha 1979; Dunwiddie and LaMarche 1980; Banks 1982; Turner 1984). An attempt was made to count growth rings from *E. maculata* regrowth of a known age, using stem cores and sanded cross-sections. These showed a variety of clear and not so clear rings, but whether these had formed in response to annual climatic influences was difficult to determine.

Another approach to determining whether stems within the regrowth stands are of new or lignotuberous seedling origin involves an examination of the external and internal features of the lignotuberous swelling that is invariably found at the base of the *E. maculata* stem. This swelling is present regardless of whether the seedling is 'old' and growth has been checked periodically (lignotuberous origin) or the seedling is 'young' and growth has been continuous (new seedling origin) (Carter 1929; Forestry Commission of N.S.W. 1985). Thus the presence of a swelling in itself, gives little indication of the plant's past status. However, there seem to be differences in the appearance of a swelling resulting from differences in seedling age, and from checked and continuous growth. It was determined that the following features may be useful in differentiating between *E. maculata* saplings of lignotuberous and seedling origin at the regeneration phase.

	Lignotuberous Seedling Origin	**New Seedling Origin**
i)	Absence of lateral roots on the upper part of the below ground swelling.	Presence of lateral roots on the upper part of the below ground swelling.
ii)	Presence of a lignified or woody outer shell.	Presence of softer live tissue including a papery appearance to the external surface.
iii)	The swelling less symmetrical in shape, indicating perhaps that the buds in the lignotuber have developed into shoots and died back on several occasions.	The swelling more symmetrical in shape, indicating perhaps that due to the vigour of the main stem, it has been unnecessary for buds in the swelling to shoot.
iv)	In cross-section, bud tissue extends to the outer edge of the swelling.	In cross-section, bud tissue confined to the inner part of the swelling.

Using this information, observations were made of the origin of *E. maculata* regrowth on the Livingstone Creek Road site. The swellings of three *E. maculata* stems were exposed at each of the 11 plots described in Section 2.3.2, where *E. maculata* regrowth was present. The swellings were visually examined, and using the first three criteria listed above, the stems were classified as being either of new seedling or lignotuberous origin. All regrowth stems examined in this way were considered to be of new seedling origin. There are other studies which suggest that regrowth development on wet sclerophyll sites would be of seedling origin, irrespective of the species. For example, although most species in the moist coastal hardwood types are lignotuberous, regeneration usually develops from newly germinated seedlings, not from a pool of lignotuberous advance growth (Van Loon 1966). As a result, it is common to find a large stocking of regeneration developing on upper slopes where a lignotuber pool may be present before harvesting, and a sparse stocking on lower slopes (Cremer *et al*. 1978).

The decline in the vigour of *E. maculata* over the Livingstone Creek Road slope (Section 2.3.2) may reflect the possibility that new seedlings which emerged soon after clearfelling were unable to compete effectively with a strongly developing *Acacia* component, particularly towards the lower slope. In addition, the decline in stocking of *E. maculata* over this slope may indicate many of the seedlings that did become established, soon succumbed to competition from other successional species, or alternatively that few seedlings became established. This concurs with Abbott and Loneragan (1984) who note the relatively low survival rate of new *E. marginata* seedlings compared to lignotuberous seedlings.

There is another approach to determining the origins of *E. maculata* regrowth which involves assessing the distribution of lignotuberous advance growth on adjacent mature forest. This may provide an indication of the likely contribution lignotuberous material may have made to the stocking of *E. maculata* in the regrowth stands.

2.5 THE DISTRIBUTION OF *E. MACULATA* LIGNOTUBERS IN MATURE FOREST

The contribution advance growth may have made to the mix of regenerating species on the study site will have depended on the size of the lignotuber pool prior to clearfelling. Thus it is necessary to assess the likely frequency and distribution of *E. maculata* lignotubers at the time of logging. A number of forest sites adjacent to, or in close proximity to the regrowth forest, were selected for this. These had not been logged in recent times or had been logged selectively and rather lightly. It is assumed that the stand conditions are similar to those of the regrowth forest before harvesting. Transect sampling has been used to cover the expected variation in the lignotuber pool along the slope.

Materials and Methods

There is a great deal of variation in the composition and structure of both overstorey and understorey components of the south coast forests. Within the forest occupied by *E. maculata*, Furrer (1971) recognises, quite simply, two broad silvicultural types - wet and dry sclerophyll. The former type is characterised by a closed overstorey and a mesic element understorey, and the latter by a more open overstorey and a sclerophyll shrub understorey. Both wet and dry sclerophyll types may occur within the vegetation mosaic, and at some sites, there is a characteristic transition from one to another along a slope. To determine the size of the lignotuber pool, sampling was restricted to sites which had an *E. maculata* component in the overstorey and which were in close proximity to the regrowth stands. The sampling was carried out along a number of slope transects. There were several reasons for this. The basic physiography of much of the study area is hilly to undulating, and the pattern of coupe cutting has relied heavily on ridges and gullies to form natural boundaries. And perhaps most significantly, previous reports (Furrer 1971; Forestry Commission Management Plan, Batemans Bay 1973) had indicated that the frequency of lignotubers varies with slope position.

Identification of potential sampling sites was done initially by locating 'typical' wet and dry sclerophyll types in mature forest around the perimeter of the regrowth areas. Following this, a topographic base map (Department of Lands 1970) was used to identify more specifically, sites which covered the entire slope gradient (i.e. from ridge to gully), and which had a moderate length and angle of slope. Four sites were selected in this way - two in wet and two in dry sclerophyll types.

At each site, the location of the first plot along the transect line was chosen randomly by step counting. The compass direction of the transect was determined at the first plot by taking a bearing at right angles to the contour of the slope. Subsequent plots were established systematically at pre-determined intervals, the distance depending on the length of slope as assessed from the base map. This varied for the four sites. The choice of plot shape has been discussed in Section 2.3.1. A rectangular plot with the long axis orientated across the slope was chosen because there may have been environmental gradients associated with the slope.

The distribution and frequency of *E. maculata* lignotubers were largely unknown, and a sampling design was required which was flexible in terms of sampling area. A nested plot design (Mueller-Dombois and Ellenberg 1974) was chosen. This method enabled the plot size to be increased progressively until a 'sufficient' number of lignotubers were sampled. Sampling was done in the following way. At each plot, two 30 m tapes were placed end to end, perpendicular to the direction of the main slope. This formed the long axis centre line of the rectangular plot. For three of the four forest sites, sampling was done two metres either side of the centreline. The first two metres along the centre line were marked off and an area of 8 m^2 (2 x 4 m) was sampled. By moving along the centre line the required distance, the sampling area was doubled progressively, and within each nested plot, the number of *E. maculata* lignotubers was recorded. On three of the four sites, the largest nested plot size was 256 m^2. On the fourth site, initial observations indicated there were very few lignotubers, and a distance of 4 m either side of the centreline was used. The largest nested plot size was 512 m^2 on this site.

Results

The results of *E. maculata* lignotuber sampling over the four forest sites are summarized in Table 2.12. The total number of lignotubers for each sample plot have been converted to a per ha basis. Sites 1 and 2 are made up largely of the dry sclerophyll forest type, and sites 3 and 4, the wet sclerophyll type.

Site 1 (Cold Chisel Road Transect). This site had a mixed overstorey of mature *E. maculata* and *E. pilularis*. The understorey was sclerophyllous on the upper slope but graded into a more mesic type on the lower slope. Plots 1 to 4 were upper to mid slope positions, and the stocking of *E. maculata* lignotubers ranged from 664 to 1445 ha^{-1} (Table 2.12). In the context of a clearcutting operation, this would make a reasonable contribution in terms of restocking the forest, assuming they were able to respond. Plot 5 had relatively few *E. maculata* lignotubers (156 ha^{-1}), but plots 6 and 7, which were further downslope, had more (664 and 1602 ha^{-1} respectively). Plot 8, which was a lower slope-gully position had again, relatively few lignotubers (156 ha^{-1}). While the distribution of *E. maculata* lignotubers was not consistent along the slope, there was a trend indicating lignotubers were more frequent on the upper than lower slope.

Site 2 (Dam Road Transect). This site had a mixed *E. maculata* - *E. globoidea* overstorey and a relatively open sclerophyllous understorey over the entire slope gradient. For comparable slope positions, this site had, overall, fewer lignotubers than Site 1. The three upper slope plots had stockings which ranged between 352 and 508 lignotubers ha^{-1}. Plots 4 and 5 had fewer lignotubers (117 and 273 ha^{-1} respectively), and on plot 6, there were no lignotubers. As with Site 1, there was a trend of declining numbers of lignotubers with movement downslope but on this site, it was more consistent.

Site 3 (Livingstone Creek Road - Transect No. 1). This site had a sclerophyllous understorey on the upper slope, but this graded quite rapidly into a more mesic element understorey on the mid slope. On the upper and mid slope positions, there was a mixture of species in the overstorey, including *E. maculata*, but further down the slope, *E. maculata* was absent. Consequently the lower slope was not sampled. On plots 1 and 2, there were 39 and 156 *E. maculata* lignotubers ha^{-1}

Table 2.12 The number of *E. maculata* lignotubers over four slopes. Each plot is 160 m^2 and numbers have been converted to a per ha basis. Plot 1 is a ridge position and each succeeding number represents a position further downslope. Sites 1 and 2 are largely dry sclerophyll forest and Sites 3 and 4 wet sclerophyll forest.

Plot No.	Site 1 - Cold Chisel Road	Site 2 - Dam Road	Site 3 - Livingstone Creek Road Transect No. 1	Site 4 - Livingstone Creek Road Transect No. 2.
1	1406	352	39	0
2	742	508	156	0
3	664	352	0	0
4	1445	117	0	
5	156	273	0	
6	664			
7	1602			
8	156			

respectively, but on plots 3, 4 and 5, no lignotubers were recorded. This change in lignotuber frequency corresponded with a change in the understorey vegetation, from species such as *Acacia longifolia*, *A. floribunda* and *Pultenaea blakelyi*, to typically more mesic species such as *Notolaea ovata*, *Tristaniopsis laurina* and *Cissus hypoglauca*.

Site 4 (Livingstone Creek Road - Transect No. 2). This site had a mesic element understorey over the entire slope gradient which became more dense further downslope. Because there appeared to be very few lignotubers on this site, each plot was 512 m^2 rather than 256 m^2. Plots 1, 2 and 3 had no lignotubers. After this point on the transect, the understorey of vines and dense mesic shrubs became virtually impenetrable and precluded the possibility of satisfactorily searching for *E. maculata* lignotubers. Because the other transects had fewer lignotubers on lower slopes, and no lignotubers were recorded on the first three plots at this site, it is likely there would be few if any *E. maculata* lignotubers on positions further downslope.

Discussion

Although the assessment of lignotuber populations was carried out on only a few sites, the observations are consistent with the pattern of lignotuber distribution recorded by others. Furrer (1971) recognised that the dry sclerophyll forest type has a lignotuber pool which is both larger and more dynamic than on the wet sclerophyll sites. The Forestry Commission Management Plan for Batemans Bay (1973) and the Forestry Commission of N.S.W. (1985) make several references to the paucity of lignotuberous material on the wet sclerophyll forest types in these south coast forests. Neave (1983) also suggested that *E. maculata* lignotubers are less frequent on lower slopes, usually in association with the wet sclerophyll forest type. Some general conclusions are:

1. Within the dry sclerophyll type, the number of *E. maculata* lignotubers tends to decline from upper to lower slopes, but within this pattern there is some variation. For example, there may be localized occurrences of relatively large numbers of lignotubers on some of the mid and lower slope positions.
2. Within the wet sclerophyll type, there may be very few, or a complete absence of *E. maculata* lignotubers, regardless of slope position.
3. Where the dry sclerophyll type grades into the wet sclerophyll type along the one slope, there is a corresponding reduction in the frequency of lignotubers.

The reasons for the pattern of lignotuber distribution are not entirely obvious although past silvicultural treatments may be partially responsible. It is possible that selection logging over several decades, without follow-up regeneration treatment, may have restricted the number of sites on which *E. maculata* seedlings could survive. This problem may have been exacerbated on the lower slope and wet sclerophyll sites where competition from a secondary stratum of mesic element species could have severely restricted seedling establishment. Jacobs (1955) suggested that the eucalypt lignotuber could not survive extended conditions of intense shading. Several workers have also reported that the development of the lignotuber is influenced by nutritional factors (Kerr 1925; Beadle 1954, 1966, 1968; Weir 1969; Mullette and Bamber 1978; Jahnke *et al.* 1983), although many of the results have been conflicting. Moisture effects have also been implicated (Kerr 1925; Lacey 1983). Thus the development of the seedling into the lignotuberous form may be influenced by a range of environmental factors.

The following section describes a glasshouse experiment in which the response of the *E. maculata* lignotuber to environmental stress is examined, and is designed to test the hypothesis that certain environmental factors may be important in influencing the development of the lignotuber.

2.6 RESPONSE OF *E. MACULATA* LIGNOTUBERS TO ENVIRONMENTAL STRESS

It has been shown that the pool of lignotuberous seedlings declines in general, from upper to lower slopes and that there are fewer lignotubers where a more mesic understorey element is present. It is possible therefore, that a gradient in some environmental factor which is related to slope position, or to the distribution of the wet and dry sclerophyll understorey types, may influence the vigour and persistence of the lignotuber. Traditionally, light has been implicated (Jacobs 1955), however, others have suggested that moisture and nutrients may also be involved. In order to test the hypothesis that moisture and nutrient levels could affect the vigour and persistence of the eucalypt lignotuber, a glasshouse experiment was conducted in which *E. maculata* lignotubers were subjected to several moisture and nutrient regimes. During the experiment, leafy shoots of the lignotuberous seedlings were cut back several times, and the response in terms of shoot dry weight production recorded. The dimensions of the lignotuberous swellings were measured to determine whether lignotuber size was related to the vigour of response.

2.6.1 Materials and Methods

Experimental Method

This experiment was arranged as a randomized complete block design in the glasshouse with three nutrient levels, three moisture levels and five replications.

Soil for the experiment was collected to a depth of 20 cm from the moderate quality mixed species Link Road site (Section 2.3.1) and was put through a 1 cm sieve before being adjusted for nutrient content. Three nutrient treatments were established - unamended (control), 'low' added nutrients and 'high' added nutrients. The two nutrient levels were based on those used by the National Botanic Gardens, their use reflecting differences in sensitivities of species to nutrient additions. The 'low' nutrient treatment contained 1.0 g of Osmocote, 0.8 g of Dolomite and 0.1 g of Micromax per litre of soil. The 'high' nutrient treatment was based on a potting mix for optimal growth of overseas species: 3.0 g of Osmocote, 2.4 g of Dolomite and 0.3 g of Micromax per litre of soil.

The Osmocote used in this experiment had an N:P:K ratio of 18.0:2.6:10.0 and a release period of eight to nine months. Once the release period had been exhausted, it is still likely that the fertility of these soils would remain higher for a period of time relative to the control treatment. The unamended soil had approximately 1223 and 108 ppm of total nitrogen and phosphorus respectively.

Three moisture levels were established, representing water deficit (drying), field capacity and waterlogging conditions. Field capacity was maintained by watering twice daily from above using an automatic dripper system. The application rate was adjusted seasonally to take account of differences in the rate of evapotranspiration. The dripper system failed during part of April 1985, and some of the 'field capacity' seedlings developed signs of temporary moisture stress before the fault was rectified.

The waterlogging treatment was established by placing the 20 cm pots* inside nine litre capacity buckets which were filled with water to a level equal to the level of soil in the 20 cm pots. Waterlogging was

* 5.1 litre capacity

maintained by refilling the buckets to the level of the soil every second or third day.*

The 'drying' treatment was established after a soil moisture curve was determined for the soil. The permanent wilting point (-15 bars) was extrapolated from points on the curve, and was considered to be at approximately 4% moisture content.

Soil moisture in the drying treatment was initially controlled by allowing the pots to dry out for periods of four to six days. After this, the soil was sampled for moisture content. The values ranged between 3.22% and 6.79%, depending on the period of time the pots had been left unwatered. The pots were then rewatered with 200 ml, and moisture contents determined 24 hours later. These values ranged between 9.13% and 13.83%. Following these initial determinations, 'drying' pots were subjected to cycles of drying and rewatering with 200 ml every four to six days.

The moisture content of the 'drying' treatments were not controlled precisely in that the moisture content of the pots may have been reduced, for example, to 5% over one cycle, and to 3% over the next cycle. Similarly, the moisture content following rewatering may have varied between cycles. Nevertheless, within the drying treatment, all pots recieved the same rate and quantity of water, and the same drying cycles. From this point of view, relative comparisons of growth rates between the drying, field capacity and waterlogging treatments, and between nutrient treatments within the the drying treatment are valid. There may, however, have been some variation in the rate of water usage and hence in soil moisture content within each of the moisture treatments, because of differences in growth rates.

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* The 20 cm pots inside 9 litre buckets created a closed system - there woul be no leaching of nutrients, only an exchange between water in the pots ar buckets. Thus differences in nutrient contents between the waterlogginc field capacity and drying treatments would be relatively small.

The following abbreviations for the treatments are used in the text; (W) waterlogging, (F) field capacity, (D) drying, (N_0) unamended nutrients, (N_1) low added nutrients, and (N_2) high added nutrients.

Growth

In October 1984, seed of *E. maculata* was sown in a medium consisting of equal parts perlite and vermiculite. At about three-leaf-pair stage (25 days after germination), four seedlings (later thinned to one) were transplanted into 20 cm (5.1 litre capacity) pots. All pots were watered daily to approximate field capacity for the following 41 days, whereupon the moisture treatments were started.

After 76 days (22.3.85), all plant dry matter above the forming lignotuber was detached. The nutrient and moisture treatments were continued, and all new plant dry matter was harvested 108 days (30.1.85) later and, again 206 days (14.10.85) later. After the third harvest, all pots were given the same moisture and nutrient treatments; the 'drying' and 'waterlogging' treatments were discontinued and all pots were given water to maintain approximate field capacity. All pots were also given 50 ml of half strength Hoaglands (No. 2) nutrient solution (see Appendix II for details of this solution) twice weekly for a period of 22 days, following which a full strength Hoaglands solution was used. The plants developed under this regime for 84 days when the shoots were cut back for a fourth time. In all, there were four separate harvest periods and the experiment ran for a total of 474 days.

At each harvest, plant matter above the lignotuberous swelling was detached, dried at 85°C until a constant dry weight was obtained, and weighed. At harvest 3, just prior to the standardization of treatments, the mean diameter of the lignotuber and stem combined was determined by measuring the maximum and minimum diameters. The mean diameter of the stem was subtracted from this to give the diameter of the lignotuber.

Because the lignotuberous swelling often did not develop in a regular way (i.e. shoots grew from different points of the lignotuber at different harvests), this measure is considered to be only a crude measure of lignotuber size. The occurrence of any plant deaths throughout the experiment were recorded.

The experiment was conducted in a naturally illuminated glasshouse with a temperature range of 18-37°C (8 h day) and 12-22°C (16 h night), and a relative humidity ranging from 20 to 100%. The natural light period was extended to 16 h with overhead fluorescent lighting. The glasshouse conditions described here also apply to the other glasshouse studies.

Shoot dry weight data from the first harvest was analysed factorially in 2^3 combination using analysis of variance. The two factors were nutrients and moisture. Assumptions regarding homogeneity of variance and normality (Neter and Wasserman 1974) were satisfied, if necessary by the transformation of the data. Before harvests 2, 3 and 4, all replications of one treatment (drying, high added nutrients) had died. The resulting unbalanced design meant that the main effects of nutrients and moisture could not be analysed - only individual treatment contrasts could be examined.

2.6.2 Results

Lignotuber Deaths

After the first harvest, all lignotubers from the drying, high nutrient (DN_2) treatment died. The combination of a high concentration of soil nutrients, a low level of available soil moisture and the associated cutting back of the leafy shoot may have produced excessive stress within the plant. In addition, two replications of the waterlogging, high nutrient treatment (WN_2) died. After harvest 2, one lignotuber from each of the WN_0 and FN_1 treatments died and after harvest 3, one lignotuber from the FN_0 treatment died.

Shoot Dry Weight Production

The results of analysis of variance and mutiple range comparisons of seedling means are presented in Tables 2.13a (Harvest 1) and 2.13b (all other harvests). Only untransformed means are referred to in the text.

Harvest 1. In this analysis, both the main and interaction terms were examined. The effects of moisture and nutrients on shoot dry weight production from harvest 1 were highly significant ($P<0.001$). The three moisture treatments differed significantly from one another in the order, drying < waterlogging < field capacity. Responses to the nutrient treatments were similarly divergent, in the order, unamended < low nutrient < high nutrient (Table 2.13a).

The interaction between nutrients and moisture was also highly significant ($P<0.001$) (Table 2.13a). In the absence of added nutrients, the waterlogging (WN_0) treatment produced the least (1.09 g) and field capacity (FN_0) the greatest (1.98 g) shoot dry weight. The plants under the drying regime responded to both the low and high nutrient levels (4.48 and 6.23 g shoot dry weight respectively). The maximum response was recorded in the treatment maintained at field capacity, and with nutrients added (42.19 g at N_1 and 65.42 g at N_2). The waterlogged plants responded surprisingly well to nutrients (28.26 g and 37.28 g at N_1 and N_2 respectively). *E. maculata* seems well adapted to poor aeration.

As indicated, the death of all plants in the drying, high nutrient (DN_2) treatment soon after the first harvest has produced an unbalanced experimental design. For later harvests, the main effects of nutrients and moisture cannot be examined, and only the contrasts between individual treatments are considered.

Harvest 2. The effect of treatments on shoot dry weight production was highly significant ($P<0.001$) (Table 2.13b). The three unamended nutrient treatments produced the least shoot dry weight. Of these, waterlogging (WN_0) produced the least and field capacity (FN_0) the greatest dry weight. The three moisture regimes (D, F, W) associated with low added nutrients were next in the order of ranking; within this group the drying (DN_1) treatment produced significantly less shoot dry weight than the waterlogged (WN_1) and field capacity (FN_1) treatments. Under the high nutrient regime, seedlings subjected to waterlogging (WN_2) produced significantly more shoot matter than the lignotubers at field capacity (FN_2). The latter treatment had shoot weight which was not dissimilar to that of the field capacity, low added nutrient (FN_1) treatment.

Harvest 3. There was a highly significant ($P<0.001$) effect of treatments on shoot dry weight production for harvest 3. The ranked order of means was similar to that of harvest 2, but with fewer differences between treatments (Table 2.13b). In this case, however, the two waterlogged treatments with added nutrients (WN_1 and WN_2) produced the greatest shoot weights, although these were not significantly different from the two field capacity treatments where nutrients had been added (FN_1 and FN_2). A high level of adaptation to waterlogging where soil nutrient status is good, still showed after 390 days.

Harvest 4. This harvest measures shoot production 84 days after the nutrient and moisture treatments had been standardized. Any differences in shoot dry weight production probably reflect the effects on plant production of the differences in treatment histories. Lignotuberous seedlings from the former drying, low nutrient (DN_1) treatment produced significantly greater shoot dry weight (26.13 g) than all other treatments, and indeed was nearly double that of the next highest treatment (Table 2.13b). The lignotuberous seedlings that had been previously subjected to waterlogging (WN_1 and WN_2) produced consistently more shoot dry weight than those in which the soil had been

Table 2.13a Summary of the differences between attribute means associated with moisture, nutrients and the interaction between these for Harvest 1 as derived from two-way analysis of variance, and ranking of means for each treatment contrast. Values are shoot dry weight in grams.

Treatment effects	Significance	Ranked Order of Means								
Moisture	***		1.216 (4.09) D	2.307 (22.21) W	2.852 (36.53) F					
Nutrients	***		0.383 (1.54) N_0	2.820 (24.98) N_1	3.173 (36.31) N_2					
Interaction	***	0.036 (1.09) WN_0	0.441 (1.56) DN_0	0.670 (1.98) FN_0	1.433 (4.48) DN_1	1.775 (6.23) DN_2	3.317 (28.26) WN_1	3.568 (37.28) WN_2	3.711 (42.19) FN_1	4.177 (65.42) FN_2

Table 2.13b Summary of differences between attribute means associated with moisture and nutrient treatments for Harvest 2, 3 and 4 as derived from one-way analysis of variance, and ranking of means for each treatment contrast. Values are shoot dry weight in grams.

Harvest	Significance	Ranked Order of Means							
2	***	-1.031 (0.4) WN_0	0.858 (2.5) DN_0	1.274 (3.6) FN_0	2.292 (10.5) DN_1	3.260 (28.0) WN_1	3.465 (33.5) FN_1	3.513 (35.0) FN_2	4.026 (58.3) WN_2
3	***	-1.463 (0.55) WN_0	0.442 (1.69) DN_0	1.088 (2.99) FN_0	1.303 (3.76) DN_1	2.268 (9.74) FN_1	2.451 (11.79) FN_2	2.470 (12.23) WN_1	2.558 (13.99) WN_2
4	***	4.23 FN_0	5.31 WN_0	7.64 DN_0	11.46 FN_2	11.60 FN_1	14.96 WN_2	15.04 WN_1	26.13 DN_1
Cumulative total (Harvests 1,2,3)	***	-2.29 (0.8) WN_0	1.74 (5.8) DN_0	3.03 (8.6) FN_0	5.03 (18.8) DN_1	9.05 (68.5) WN_1	9.53 (86.7) FN_1	10.14 (112.3) FN_2	10.29 (114.0) WN_2

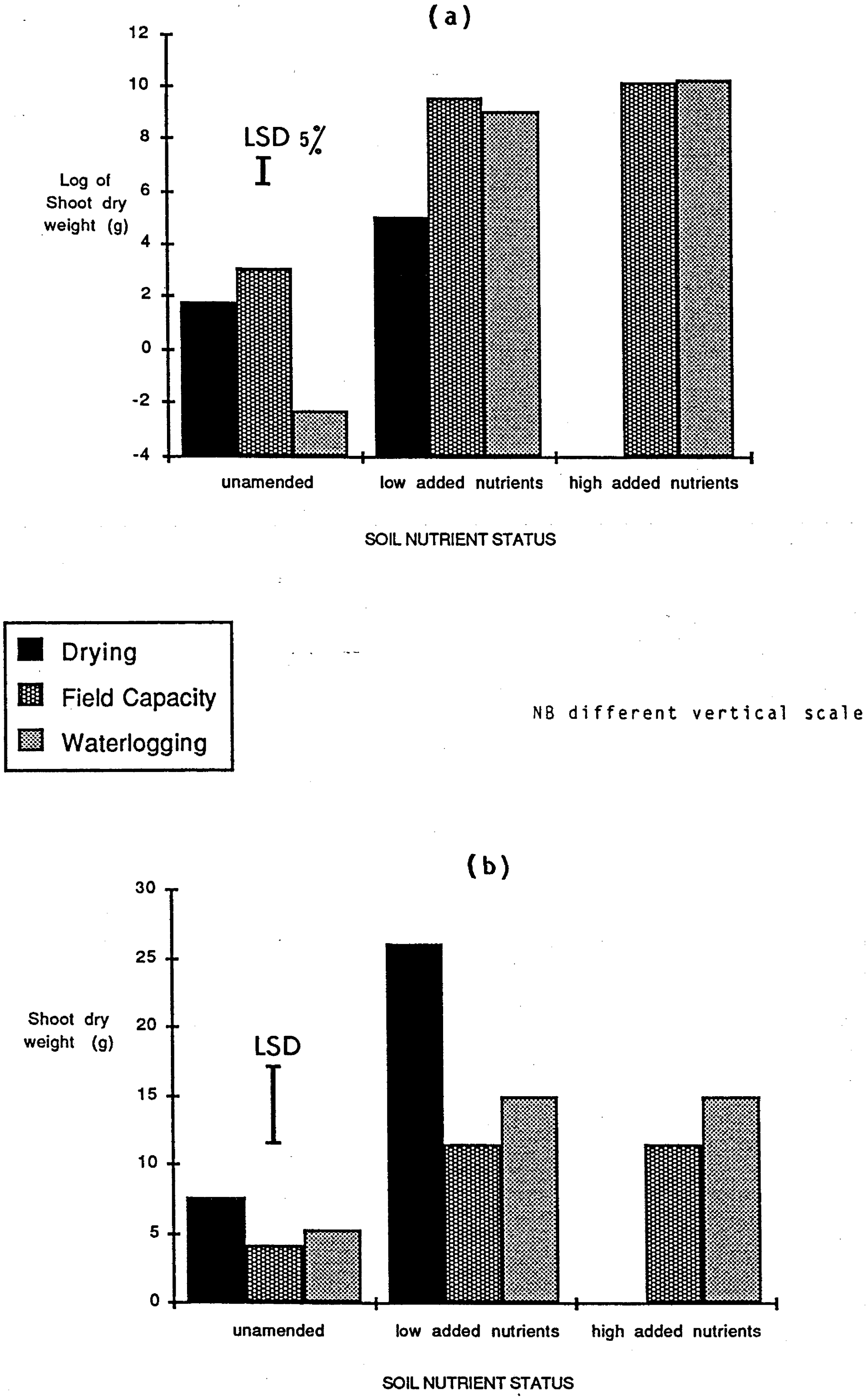
NOTE: i) * $P<0.05$; ** $P<0.01$; *** $P<0.001$; NS = not significant

ii) Treatments: D = Drying; F = Field Capacity; W = Waterlogging; N_0 = unamended nutrients; N_1 = low added nutrients; N_2 = high added nutrients.

iii) Treatments are ranked in increasing order of magnitude; horizontal bars span treatment means which do not differ significantly using LSD maintained at field capacity (FN_1 and FN_2). Where there had been no previously added nutrients, the drying (DN_0) treatment was most productive (7.64 g) and the field capacity (FN_0) treatment least productive (4.23 g). Thus within the two nutrient treatments where seedlings from all three moisture regimes survived (N_0 and N_1 treatments), seedlings which had been subjected to drying responded best, and those maintained at field capacity, least. This contrasts with the first three harvests where in general, seedlings from the drying treatments showed poorer growth than those maintained at field capacity.

Growth in this experiment can be divided into two distinct phases - the period when different nutrient and moisture treatments were applied (harvests 1 to 3) and the period when the nutrient and moisture treatments were standardized (harvest 3 to 4). The total shoot production for the first three harvests combined, and for harvest 4, are illustrated separately in Figure 2.2. The following comparisons are useful:

1. Seedlings from the DN_1 treatment grew relatively poorly over the first three harvests, but responded substantially better than seedlings from all other treatments when nutrients and moisture were standardized.
2. In the treatments without added nutrients, the seedlings at field capacity were most productive for the first three harvests but were least productive when treatments were standardized.
3. For the period of the first three harvests, seedlings from the FN_1, WN_1, FN_2 and WN_2 treatments produced similar total shoot dry weight. For harvest 4, seedlings from these two waterlogging treatments produced consistently more shoot dry weight than the seedlings from either of the field capacity treatments, although differences were not significant.



NB different vertical scale

Figure 2.2 Shoot dry weight production of lignotuberous *E. maculata* seedlings (a) before and (b) after standardization of nutrient and moisture treatments.

Lignotuber Size

The mean diameter of lignotubers at harvest 3 (i.e. just prior to standardization of nutrient and moisture treatments) is given in Table 2.14. This shows that the drying, low nutrient (DN_1) treatment had the second smallest lignotuber diameter. This was also the treatment which produced double the shoot dry weight of any other treatment at harvest 4. In this instance, lignotuber size and the vigour of the growth response do not appear to be positively related. There is however, a trend which suggests that the size of the lignotuber is stimulated by nutrients. Except for DN_1, treatments with added nutrients had larger lignotuber diameters than those without.

2.6.3 Discussion

It has been shown that initial shoot growth of *E. maculata*, and subsequent resprouting following the cutting back of shoots on several occasions, was significantly influenced by soil moisture and soil nutrient status. For the period of the experiment where treatments differed (harvests 1-3), the lignotubers at field capacity grew relatively well at each of the three nutrient regimes. In contrast, lignotubers subjected to soil moisture stress grew relatively poorly. This situation was reversed at harvest 4 when all lignotubers received equivalent quantities of nutrients and water for a period of time preceding the final harvest. In this case, seedlings previously subjected to the drying, low nutrient (DN_1) treatment produced substantially greater shoot dry weight than all other treatments. In addition, within the unamended nutrient treatments, the drying (DN_0) treatment also produced the best response.

Table 2.14 The mean diameter (cm) ± standard error of *E. maculata* lignotubers at Harvest 3 - based on the subtraction of stem diameter from the lignotuber plus stem diameter. See Table 2.13b for description of abbreviations.

Treatment	Mean ± S.E.
DN_0	0.72 ± 0.15
DN_1	0.66 ± 0.16
FN_0	0.91 ± 0.05
FN_1	1.28 ± 0.28
FN_2	1.10 ± 0.19
WN_0	0.45 ± 0.05
WN_1	1.17 ± 0.20
WN_2	1.04 ± 0.18

For the first three harvests, lignotubers exposed to waterloggng in the unamended soil consistently produced the least shoot growth. However, where nutrients were added to the waterlogged soil, shoot growth was consistently high. This suggests that *E. maculata* is able to efficiently convert added resources into increased growth in poorly aerated soils. At harvest 4, waterlogging produced shoot weights intermediate between the drying and field capacity treatments, within the two nutrient regimes where seedlings survived.

Differences in nutrient supply have also affected the response of the *E. maculata* lignotuber. Regardless of soil moisture status, lignotubers which did not receive added nutrients did not respond as well as those which did. In general, there was little difference in growth between lignotubers receiving low or high added nutrients. It would seem that following the cutting back of the shoot, the lignotuber is able to draw on the soil nutrient reserve to resume growth. Where the nutrient supply may be limited (i.e. unamended treatment), it is possible that the plant will also draw on the nutrient reserves, which it has been suggested (Jacobs 1955) are contained within the lignotuberous swelling.

Studies on the effect of environment on eucalypt lignotubers have considered the size of the lignotuber to be important (Kerr 1925; Weir 1969; Jahnke *et al.* 1983). Although based on only a relatively crude measure of lignotuber size, this experiment has provided evidence that the vigour of the lignotuberous seedling may not necessarily be related to the size of the lignotuberous swelling. For example, seedlings in the drying, low nutrient treatment had relatively small lignotubers compared to lignotubers from most other treatments, but responded very much better than the rest once the nutrient and moisture treatments were standardized. The 'preconditioning' effect of environmental factors therefore appears to be important.

The contrasts between growth responses prior to and following standardization of treatments suggest that the *E. maculata* lignotuber may benefit from exposure to environmental stress prior to conditions becoming more favourable for growth. In particular, exposure to a period of moisture stress may enhance the vigour of the lignotuber relative to those consistently maintained at field capacity. Lacey (1983) drew a similar conclusion concerning *E. boytryoides*. He suggested that on excessively drained low fertility siliceous sands, the adverse effect of infertility on stem growth relative to that of the lignotuber may be enhanced by extremes in soil moisture.

Waterlogging is also likely to provide stress for the plant. The results have shown that once treatments were standardized, lignotubers exposed to waterlogging also responded better than the 'field capacity' lignotubers, although the differences were not as marked as for the drying treatments. Kerr (1925) however, found that badly drained soil prevented the development of lignotubers and restricted growth in *E. coriacea*.

The concept that a degree of environmental stress may ultimately provide a more vigorous lignotuber shoot could be implicated in the distribution of lignotubers in the field. Jacobs (1955) originally proposed that shading influenced the success of the eucalypt lignotuber. Factors other than shading, and particularly soil moisture, may also vary with slope position. Over a topographic gradient, it is likely that soil moisture deficits are more common on upper than lower slopes. McColl (1969) found this to be the case in the south coast *E. maculata* forests. Given that the current experiment has shown a period of moisture stress may enhance the subsequent vigour of the lignotuber, it is possible that drier, upper slope sites could provide conditions for the development of more vigorous lignotubers than those occurring on moister, lower slope sites. It also follows that a more vigorous lignotuber will have a better chance of surviving the vagaries of nature and therefore will persist longer.

The study of the distribution of *E. maculata* lignotubers within forest adjacent to the clearfelled area (Section 2.5) had shown that in dry sclerophyll forest, lignotubers are more frequent on upper than lower slopes; where the wet sclerophyll forest type occupies the whole topographic gradient, lignotubers are infrequent regardless of slope position. Thus there is a limited lignotuber pool on sites that have more favourable moisture and perhaps nutrient regimes. In contrast, a greater frequency of lignotubers occurs on sites where moisture is likely to become at least temporarily limiting. This leads to the proposal that sites with greater fluctuation in moisture status may be, at least partially, involved in determining the vigour and hence the persistence of the *E. maculata* lignotuber.

The inherent vigour of the *E. maculata* lignotuber may have been particularly important in determining its success in the early establishment phase on the Kioloa forest. Where lignotubers were present, it is possible that those occurring on the drier, upper slope positions would have demonstrated a more rapid response than those on lower slopes. This may have provided the 'upper slope' lignotuber with the necessary stimulation to become an emergent species within the regrowth mix of components. In contrast, the 'lower slope' lignotuber (where present), may have succumbed more readily to competition from some of the faster growing successional species.

2.7 SUMMARY

The studies in this chapter have been concerned with the condition of regrowth stands and the possible contribution of lignotuberous advance growth and new seedlings to the regrowth stocking. These have shown a number of important features:

1. The stocking and vigour of eucalypt species declines and that of *Acacia* increases over some slopes.
2. Other regrowth eucalypt species may be more vigorous than *E. maculata* on some sites, even though *E. maculata* was a dominant tree in the mature forest.
3. Lignotuberous seedlings may have made a reasonable contribution to the stocking of *E. maculata* on upper slopes, but regrowth on the lower slopes may have originated primarily from new seedlings following clearcutting.
4. The greater stocking of lignotuberous advance growth on upper slope sites may be due in part to the 'preconditioning' effect of moisture stress, which appears to enhance the vigour of the lignotuber.

It is possible that factors determining the success of species in a successional environment may be the same as those determining species patterns in the mature forest. In the following chapter, the relationship between the distribution of vegetation and a range of environmental factors is examined.

CHAPTER 3

THE RELATIONSHIP BETWEEN SPECIES DISTRIBUTION PATTERNS AND ENVIRONMENT

3.1 INTRODUCTION

This and the following chapters explore the hypothesis that soil nutrient availability may be a factor limiting the competitive ability of *E. maculata* on certain sites following clearfelling, particularly where regeneration must come from new seedlings rather than established lignotuberous advance growth. In pursuing this objective, it is an appropriate starting point to examine the contribution of soil nutrients and other environmental factors to the highly variable nature of the '*E. maculata*' community, and to the mosaic pattern of *E. maculata* communities within Kioloa State Forest. If it is possible to establish that the distribution of *E. maculata* is sensitive to soil fertility, then there is a firm base for pursuing the concept that, under some stand and site conditions, the size of the available nutrient pool at a regeneration phase could be critical in determining the vigour, and hence the ultimate frequency of *E. maculata* in the community. This would imply that for some sites, 'pattern' and 'process' are closely interrelated.

There are three questions to be answered to resolve this.

(i) the role soil fertility and other environmental factors play in the distribution and composition of forest communities on Kioloa State Forest.

(ii) the part of the total fertility gradient which is occupied by *E. maculata*; the more extensive its occurrence, the more critical the available nutrient pool (and other environmental factors) may be for *E. maculata* towards the lower fertility end of the gradient.

(iii) the general location within the total fertility gradient of sites where *E. maculata's* competitive ability has been shown to be limiting under conditions of clearfelling and *Acacia* competition.

3.2 THE RELATIONSHIP BETWEEN SPECIES PATTERN AND ENVIRONMENT

General

Before examining possible species-environment relationships in the *E. maculata* forest, attention is focussed on the factors influencing the distribution of vegetation in the Australian environment generally. In the broadest terms, climatic factors define species distributions, but as the scale of definition is reduced, other factors and particularly edaphic factors become important in controlling vegetation pattern. Superimposed on these are the effects of fire and biotic factors (Beadle 1966; Gill 1975b; Florence 1969, 1981; Ashton 1976b). The extent to which each factor contributes to the observed pattern varies with species, community and site.

To interpret present day vegetation pattern, reference must be made to past geologic and climatic conditions. Three distinctive elements of the Australian flora have long been recognised: the Australian, Antarctic and Indo-Malayan (Hooker 1859; Crocker and Wood 1947; Burbidge 1960). Initially, it was held that theories of mass invasion from north and south of Australia could explain the origins of these elements (Beadle 1981). More recently, it has become widely accepted that the theory of continental drift (Keast 1971, 1981) better explains the origins and present day nature of the Australian flora (Specht 1972, 1981; Gill 1975a; Dettman 1981; Johnson and Briggs 1981; Martin 1981). The evolution of the vegetation has been basically influenced by climatic change; expressed in changes due to the northward drift of Australia, and in recurrent glacial and inter-glacial cycles.

There is a general view that Australia's flora evolved primarily in response to a drying climate. While there is little doubt climatic fluctuations have influenced the more general changes in vegetation, it is more likely the vegetation represents an evolutionary response to both a drying climate and declining nutrient status associated with erosion and laterization during continental drift, with fire being a secondary superimposed influence. The development of xeromorphy as a low fertility adaptation was postulated as early as 1916 (Andrews 1916), and more recently by others (Beadle 1954, 1966, 1968; Seddon 1974; Mak 1982). At the same time, the role of fire in developing the Australian flora has also been subject to wide speculation (Mount 1964, 1969; Gill 1975b; Johnson and Briggs 1981; Nix 1981; Recher and Christensen 1981; Specht 1981).

Eucalyptus is the principal genus dominating the Australian vegetation. In its natural environment, it is extremely sensitive ecologically, and in consequence the vegetation in many areas is characterised by a constantly changing mosaic of species associations. A given species, for example, may exhibit an apparent sensitivity to minor habitat variation within any one situation, but nevertheless it may occur over a wide geographic and habitat range (Florence 1964). In addition to the changing mosaic of eucalypt species associations, there is a complex relationship of eucalypt-sclerophyll and rainforest.

A number of studies have highlighted the importance of soil chemical properties in delimiting many vegetation communities in Australia. Most have relied on an autoecological approach, attempting to identify single controlling factors on what is usually a localized scale. Beadle (1953, 1954, 1962, 1966, 1968) first proposed the hypothesis that soil fertility, especially phosphorus, was the major factor delimiting vegetation at the formation level, that is, the vegetation gradient, rainforest ⟶ wet sclerophyll forest ⟶ dry sclerophyll forest → heath, is attributable mainly to a gradient of decreasing soil nutrient concentrations. While Beadle's contention has not been tested in a totally definitive way, it has been widely supported (Baur 1957; Florence 1964, 1981; Webb 1968, 1969; Cromer 1972; Ashton 1976a; Kelly and Turner 1978; Turner *et al.* 1978; Turner and Kelly 1981; Lambert *et al.* 1983).

It has also been recognised that soil attributes affecting the availability of phosphorus to plants may contribute to the delimitation of species. For example, aluminium may restrict the uptake of phosphorus and calcium by competing for absorption sites on plant roots, and through increasing acidity, reducing phosphate solubility (Wild 1961). McColl's (1969) generalized gradient of increasing soil phosphorus from ridge to gully sites (and its associated gradient from dry sclerophyll forest to rainforest) corresponds with a decrease in the concentration of aluminium ions over the same gradient. Low aluminium concentrations may have positive effects in stimulating the uptake of phosphorus while progressively higher concentrations begin to block the uptake of phosphorus and initiate phosphorus fixation (Mullette *et al.* 1974; Mullette 1975).

While soil phosphorus can usually be taken as a general index of soil fertility, a number of other nutrients have been implicated in the delimitation of forest communities; calcium (Moore 1959a, 1959b, 1961), manganese (Winterhalder 1963), iron and manganese (Andrew and David 1959), potassium and sodium (Ellis 1971b), and nitrogen (Groves 1967; McColl and Humphreys 1967; Moore and Keraitis 1971).

The soil physical condition, as determined by texture, structure, porosity, compaction, developmental stage and depth can affect plant growth by their influence on aeration, water movement, water retention and root ramification. Good soil physical properties and soil water status may also compensate for marginal nutrient availability (Florence

1981). Several studies have considered the nature of the physical soil environment to be the primary factor determining the distribution of species, and possibly their frequency within communities (Pidgeon 1940; Florence 1963, 1964, 1965, 1968; Lamb 1967; Parsons and Rowan 1968; Tracey 1969). The effect of physical soil properties on soil moisture availability may be particularly important (Patton 1930; Specht and Perry 1948; Litchfield 1956; Lange 1960; Martin 1961; Martin and Specht 1962; Florence 1964; Pook *et al.* 1966; Lamb and Florence 1973), although few of these studies have provided definitive relationships. It should be noted that soil properties considered here are often greatly influenced by local soil-forming factors including aspect and slope.

As with the delimitation of eucalypt species, the distribution, composition and physiognomy of rainforest are controlled by climatic, edaphic and topographic factors. Webb and Tracey (1981) point out that while in general there is a complex interaction between these factors, climate (temperature, light, water and wind) and topography (exposure and slope effects) are dominant at the limits of rainforest distribution. Within these limits, edaphic factors play a leading role in the differentiation of rainforest types and of rainforest from sclerophyll forest. The relationships between the rainforest-sclerophyll system and environmental factors are explored by Baur (1957), Wilde (1958), Beadle (1962, 1966), Florence (1964, 1968), Webb (1968, 1969), Tracey (1969), Ellis (1971a), Turner and Kelly (1981) and Webb and Tracey (1981).

Although vegetation pattern may be interpreted primarily as a sensitive expression of edaphic and topographic factors, and on a broader scale, of climate, other factors may modify these patterns. Of these, fire has been a significant factor influencing the composition of communities within forests, the extent being dependent on the resilience or susceptibility of communities and individuals to fire. There has been much discussion of the effect of fire on the distribution of rainforest in relation to sclerophyll forests. Authors differ in their views on the extent to which fire controls rainforest distribution. Some have concluded that mixtures of eucalypt forest and rainforest express the past impact of fire and are fire disclimaxes (Gilbert 1959; Cremer 1960; Mount 1964; Jackson 1968). Others have supported the contention that in the absence of fire, it is unlikely that factors of the environment would be adequate to enable a rapid and widespread development of a self-perpetuating rainforest following senescence of sclerophyllous species (Florence 1964, 1968; Webb 1968). In this respect, one may envisage, as Gill (1975b) has suggested, a gradient in habitat with permanent rainforest at one end and permanent eucalypt forest at the other, separated by a zone which has rainforest potential but is maintained at a wet sclerophyll eucalypt stage of succession by fire or allowed to develop into rainforest in the absence of fire.

Biotic factors are also thought to influence vegetation patterns. These include insect parasites (Chilvers and Brittain 1972; Burdon and Chilvers 1974; Morrow 1977a, 1977b; Springett 1978), soil micro-organisms (Florence and Crocker 1962; Florence 1981), and soil pathogens (Newhook and Podger 1972; Pratt and Heather 1973: Marks *et al.* 1975; Malajczuk and McComb 1977; Malajczuk *et al.* 1977; Halsall 1978).

The complexity associated with the distribution of eucalypt species and associations can be seen in a clearer perspective by referring to genetic groups. From an examination of the features of some eucalypt communities, Pryor (1953, 1959a) proposed that species within the same interbreeding group (subgenus) do not generally co-occur, and that species within the same interbreeding group occupy distinct ecological situations. These principals have been examined in subsequent studies (Davidson and Reid 1980; Florence 1981; Duff *et al.* 1983). For example, Florence (1981) sees pattern in terms of competition for site occupancy, firstly between subgenera having different ecological attributes, and secondly between species within subgenera. The subgenus *Monocalyptus*, which is restricted to the higher rainfall coastal zones of the south east and south west of the continent, tends to be excluded from soils of higher fertility, is site-sensitive, and is often replaced by *Symphyomyrtus* species at the base of a topographic sequence. On the other hand, species of the subgenus *Symphyomyrtus*, which are widely distributed, tend to possess broader ecological tolerances than *Monocalyptus* species and are found in diverse ecological situations (Florence 1981).

Much of the earlier ecological interpretation of pattern has been based largely on observation, supported by soil analyses and physiological experiments. More recent studies on vegetation-environment relationships have employed more sophisticated multivariate analytical techniques than those used in the traditional ecological studies, for example, gradient analysis, classification, ordination and discriminant analysis. These allow similtaneous comparisons of many variables to resolve an ecological problem. The conclusions drawn in such studies tend to be less definitive than those of single factor studies, but perhaps provide a better perspective of the ecological interrelationships involved. Examples of the use of multivariate techniques in the Australian context are those of Russell-Smith (1979, 1986), McCutcheon (1980), Gibson and Kirkpatrick (1985), Bowman (1986), Bowman and Dunlop (1986) and S.M. Davey (unpublished). Gillison and Anderson (1981) provide a review of some of these techniques, and numerical approaches are discussed by Austin (1981), and Dale (1981), Lance (1981), Williams (1981).

South Coast Forests

Within the south coast forests of New South Wales, the vegetation mosaic is best considered as an expression of complex environmental interactions (Russell-Smith 1979). Two distinctive eucalypt community types, dominated respectively by *Corymbia* species *E. maculata* and *E. gummifera* characterise this vegetation pattern. A limited number of studies in these forests support the hypothesis that edaphic factors are of primary importance in controlling the distribution of species and species associations.

In the first of two studies in the Benandarah State Forest on the south coast, McColl and Humphreys (1967) found that while the sharply delimited distributions of *E. maculata* and *E. gummifera* were not statistically correlated with differences in physical and chemical properties of the supporting soils, slight trends suggested that *E. gummifera* soils had different physical qualities and lower nutrient status than *E. maculata* soils. Moreover, from a series of pot trials, they proposed that the two species appeared to differ in their requirement for, and ability to take up, soil phosphorus, calcium, nitrogen and possibly manganese. Small differences between sites in both physical and chemical soil properties may have a relatively profound effect on the competitive ability of eucalypt species, and hence on community patterns within the forest.

In a second and complementary study in the same area, McColl (1969) examined some of the soil-plant relationships along a localized topographic gradient (Figure 3.1). There was a general gradient in soil physical and chemical properties from the ridge sites supporting the *E. gummifera* association, through those of the discontinuous *E. maculata-E. paniculata* and *E. maculata-E. pilularis* associations, to the lower slope *E. saligna* association. This species gradient corresponded with increasingly favourable concentrations of the major

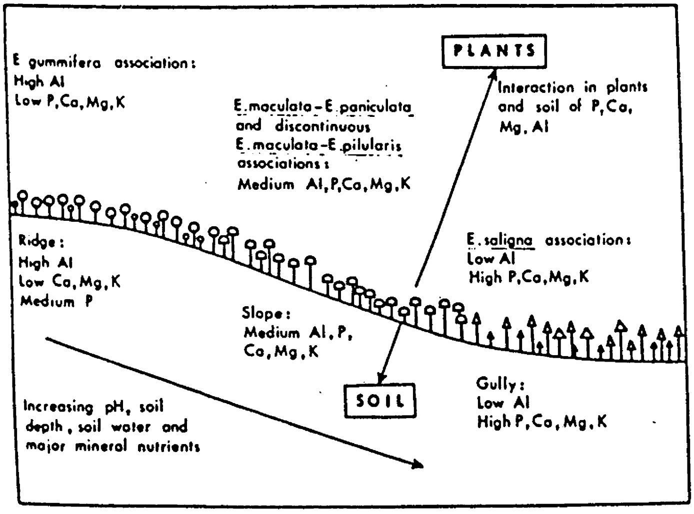


Figure 3.1 Idealized soil-plant relationships in *Eucalyptus* associations, Benandarah State Forest, N.S.W. (after McColl 1969).

soil nutrients, with the notable exception of aluminium, which was most abundant on the ridge site.

In a further study on Kioloa and South Brooman State Forests, McCutchan (1978) investigated the physical and chemical soil conditions associated with the mosaic distribution of *E. maculata*. As in McColl's (1969) study, McCutchan found the presence of *E. maculata* was correlated with somewhat greater levels of the major soil nutrients, but did not appear to be correlated with differences in physical soil parameters. However, on Permian parent materials, an interaction between moisture availability and storage, and conditions for root penetration was thought to be involved, at least in the delimitation of *E. maculata* and *E. pilularis*. In contrast, there was little measurable correlation between physical soil conditions and the occurrence of *E. maculata* on Ordovician parent materials.

The most recent study of pattern on the south coast has been that of Russell-Smith (1979) using data collected from 171 stratified random sample plots on Kioloa and South Brooman State Forests. Based on classification and ordination of a large number of vegetational and environmental attributes, it was possible to identify consistent plant communities and to suggest the relationships of the communities to each other. He concluded tentatively, that while the vegetation mosaic of the Kioloa area is best considered as an expression of complex environmental interactions, gradients relating to soil nutrient status are of primary importance in regulating the broad-scale distribution of vegetation. Although soil nutrient levels were not assessed, Russell-Smith suggested the analyses portrayed a gradient in vegetation from rainforest through to heath which can be explained satisfactorily only with reference to a corresponding gradient in soil fertility.* Physical soil attributes also appeared to contribute to species distribution patterns. For example, on upper slope, shallow gravelly Ordovician soils, the presence of good quality *E. maculata* and *E. paniculata*, and their replacement downslope by *E. pilularis*, suggests the former species are relatively more efficient in water usage, or may obtain adequate moisture by exploring fissures and cracks in underlying rocks to greater depth.**

Because it was possible to relocate the sample sites used by Russell-Smith (1979) to define community patterns on Kioloa and South Brooman State Forests, there was a base for examining more objectively, relationships between community patterns and environmental factors. It was important to do so in the context of the objectives of this study, that is, to establish the position of the clearfelled areas within the vegetational and environmental gradients which comprise these forests.

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* Russell Smith's assumption of a soil fertility gradient was based on an acceptance that the vegetational gradient, dry sclerophyll forest - wet sclerophyll forest - rainforest is associated with increasing soil nutrient status

** some water potentials of foliage were measured with a porometer, but the results were very variable

3.3 MATERIALS AND METHODS

Plot Selection

The study uses data collected from a sub-sample of plots established previously for the purpose of analysing vegetation patterns (Russell-Smith 1979). In that study, Russell-Smith used stratification based on physiography to collect data on a large number of vegetational and environmental attributes on the 171 sample plots.* Classification and ordination techniques were used to identify 14 consistent plant communities within this data set. (Recently, a more complex version of this community pattern has been derived by J.J. Russell-Smith and S.M. Davey (pers. comm.) using more sophisticated analytical techniques). The sampling plots for the present study were selected on a stratified random basis from those originally located by Russell-Smith. The stratification was based on his vegetation classification, with a total of 51 plots being sampled.

Sampling Procedure

Soils were sampled by auger for chemical analysis at 0-5, 7-12 and 17-22 cm depths. Thereafter the soil was sampled at 20 cm intervals to a maximum depth where possible of 165 cm. There were three replications at each plot with samples being analysed individually. Results of chemical analyses from the three depths in the 0-30 cm zone and the two depths in the 31-60 cm zone from each of the auger holes were meaned and regarded as representative of the A and B horizons respectively. These formed the chemical data sets. Soil preparation and nutrient analysis techniques are described in Chapter 1 (Section 1.5). The total anions nitrogen and phosphorus, and the exchangeable cations potassium, sodium, calcium, magnesium, aluminium and iron were determined. Organic matter was assessed using the technique of loss on ignition. Along with pH, these nine attributes made up separate nutrient data sets for the A and B horizons.

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* taking account of parent material, slope and aspect

The depth of A1 and A horizons, and the depth to the C horizon and to parent material were measured, and the texture of the A and B horizons, the gravel percentage and drainage class (based on soil profile and vegetation characteristics) were assessed. These formed the soil physical data set.

Slope, radiation index, position on slope, general topography, soil parent material, basal rock type, the major soil formation patterns (in-situ, colluvial, depositional, erosional) and proximity to permanent or intermittent surface water in creeks and major drainage lines were also recorded. These attributes formed the site factor data set.

Data Analysis

The data were analysed to determine possible relationships between the plant communities defined by Russell-Smith (1979) and a range of environmental factors using univariate and multivariate techniques. One-way analysis of variance was used to demonstrate the variation in the chemical properties of the soils which support the distinctive vegetation types. The analysis was performed on the soil nutrient data set derived from the A horizon, using the vegetation groups defined from numerical classification of the original 171 plots. The 3 and 7 group levels were selected for this analysis as these are readily identifiable in the field. The communities identified at these levels are shown in Table 3.1. A larger group level (i.e. more groups) could not be specified because only 51 plots had been sampled. The assumptions of analysis of variance were fulfilled, these being summarized in Appendix I. Heterogeneity of variance was corrected by the use of log or square root transformations. Only untransformed means are referred to in the text.

Table 3.1 Description of vegetation communities at the 3 and 7 group level of the vegetation classification (after S.M. Davey, in preparation).

3 Group Level

Vegetation Community	Abbreviation	Vegetation Description
E. piperita Group	Epip	Low quality dry sclerophyll and heath communities.
E. maculata Group	Emac	Moderate and high quality communities with an *E. maculata* component.
Rainforest Group	RF	Rainforest and rainforest ecotonal (wet sclerophyll) communities characterised by high species richness of mesic species in the understorey.

7 Group Level

Vegetation Community	Abbreviation	Vegetation Description
E. piperita-*E. globoidea*	P1	Low quality dry sclerophyll *E. piperita*-*E. globoidea* (peppermint-stringybark) communities.
E. piperita-Heath	P2	Low quality *E. piperita*-heath communities.
Ecotonal *E. piperita*-*E. maculata*	E1	Low to moderate quality ecotonal *E. piperita*-*E. maculata* communities characterised by xeric species in the understorey.
Moderate Quality *E. maculata*	S1	Moderate and high quality *E. maculata* communities with a range of understorey types.
High Quality Upper Slope	S2	High quality upper slope communities.
Temperate Rainforest	R1	Temperate Rainforest.
Ecotonal Wet Sclerophyll-Rainforest	R2	Ecotonal rainforest being dominated by *Eucalyptus*.

Principal coordinate analysis (ordination technique) was performed separately on the physical, site factor and A and B horizon chemical data sets. This technique differs from analysis of variance in that it enables variables to be considered simultaneously and allows the use of both quantitative and qualitative data. The relevant output includes an estimate of the percentage variance (or variation) explained by each vector (principal coordinate), a graphical representation of the relative spatial similarity of individuals (plots) by contrasting any two vectors, and an estimate (pseudo-F-statistic) of the contribution of each attribute to the definition of each vector. The operations and assumptions of principal coordinate analysis are described more fully in Appendix I. The 7 group level of the vegetation classification of plots was subsequently superimposed onto the arrangement of plots defined by vectors 1 and 2 from the ordination of the four separate environmental data sets. The separate contrasts of vectors 1 and 2 against vector 3 were also considered, but no useful patterns could be elucidated.

Bioassay Experiment

In order to confirm that differences in soil fertility shown by chemical analysis are meaningful, a bioassay of soils from several horizons of sites supporting distinctive '*E. maculata*' and '*E. piperita*' communities was conducted. The term '*E. piperita* community' is used here to characterise the range of dry sclerophyll forest communities which do not contain *E. maculata*, or in which *E. maculata* is present at a very low frequency. *E. piperita* is common to most dry sclerophyll communities which do not contain *E. maculata*. Both of the soils sampled were on Permian parent material. *E. maculata* seedlings were grown singly in 15 cm pots containing soil from the A horizons, and the clay B horizons of the two sites. Seedlings were also grown in decomposing sandstone from the C horizon of the *E. maculata* site, but not in a similar substrate from the *E. piperita* site because the C horizon was inaccessible. In a second treatment, all nutrients except phosphorus were added to soil from each site and horizon - in order to assess differences in the level of phosphorus availability. There were four replications of each treatment and shoot dry weight was measured at the end of the experiment.

3.4 RESULTS

3.4.1 Analysis of Variance

Analysis of variance demonstrated consistent differences in the chemistry of the A horizon at both the 3 and 7 group classification levels (Table 3.2). At the 3 group level, A horizon soils supporting the *E. piperita* group of communities had significantly lower concentrations of organic matter than the rainforest group of communities, and significantly lower concentrations of all nutrient elements except aluminium and iron. The A horizon soils supporting various *E. maculata* and ecotonal communities had intermediate concentrations of all nutrient elements except aluminium. The ratio of exchangeable aluminium to total exchangeable bases (Al:TEB)* for the *E. piperita* group was significantly larger than for either the *E. maculata* or rainforest groups.

A finer distinction between communities can be made at the 7 group classification level (Table 3.2). This reveals certain differences in soil chemistry between site/vegetation units within the groups defined at the 3 group level. The lower quality dry sclerophyll P1 (*E. piperita*-*E. globoidea* forest) and P2 (*E. piperita*-heath forest) groups had the lowest mean concentrations of exchangeable sodium, potassium, and magnesium, and total nitrogen and phosphorus.

* The ratios are on a ppm basis.

Table 3.2 Ranking of means from analysis of variance of A horizon (0-30 cm) soil nutrient concentrations (ppm) for the 3 group and 7 group level of the vegetation classification.

NUTRIENT ELEMENT	3 GROUP LEVEL			7 GROUP LEVEL						
Nitrogen	613 Epip	1219 Emac	1963 RF	429 P2	716 P1	1122 S1	1170 E1	1657 S2	1895 R2	2046 R1
Phosphorus	67 Epip	130 Emac	207 RF	45 P2	80 P1	111 E1	125 S1	186 S2	204 R2	211 R1
Potassium	3.85 (51) Epip	4.60 (120) Emac	5.08 (210) RF	3.57 (37) P2	4.01 (59) P1	4.15 (74) E1	4.76 (133) S1	4.94 (149) R2	4.97 (170) S2	5.25 (282) R1
Calcium	4.64 (127) Epip	5.22 (280) Emac	5.43 (364) RF	4.38 (100) P2	4.77 (133) S1	4.79 (142) P1	5.07 (300) R2	5.44 (342) E1	5.85 (440) R1	6.34 (671) S2
Magnesium	4.68 (113) Epip	5.34 (234) Emac	5.59 (289) RF	4.45 (87) P2	4.80 (127) P1	5.26 (228) E1	5.27 (202) S1	5.56 (287) R2	5.63 (299) R1	5.77 (358) S2
Sodium	73.5 Epip	110.3 Emac	133.4 RF	67.1 P2	77.0 P1	101.1 E1	102.0 S2	110.3 R1	118.0 S1	152.6 R2
Aluminium	170 Emac	193 Epip	198 RF	103 R1	109 P2	117 S2	156 E1	194 S1	240 P1	277 R2
Iron	2.20 (27) RF	2.87 (32) Emac	3.30 (32) Epip	9.6 S2	19.2 P2	24.9 R1	28.0 R2	34.5 S1	37.9 E1	39.0 P1
Organic Matter *%	1.76 (6.11) Epip	2.02 (8.08) Emac	2.23 (9.71) RF	1.50 (4.52) P2	1.90 (7.28) E1	1.91 (6.99) P1	1.99 (7.62) S1	2.05 (8.00) R1	2.36 (11.32) S2	2.39 (11.13) R2
pH	6.000 RF	6.193 Epip	6.204 Emac	5.92 R2	6.04 E1	6.10 R1	6.12 P1	6.23 S1	6.32 P2	6.45 S2
Al:TEB ratio	0.48 (0.30) RF	0.52 (0.30) Emac	0.74 (0.58) Epip	0.30 (0.12) R1	0.34 (0.13) S2	0.52 (0.31) E1	0.58 (0.36) S1	0.62 (0.45) R2	0.66 (0.46) P2	0.78 (0.64) P1

* loss on ignition

NOTE:

i) Vegetation Communities (3 group level): Epip = lower quality *E. piperita* group; Emac = moderate and higher quality *E. maculata* group; RF = wet sclerophyll-rainforest group.

ii) Vegetation Communities (7 group level): P1 = *E. piperitia* - *E. globiodea* forest: P2 = *E. piperita* - heath forest; E1 = ecotonal *E. piperita* - *E. maculata* forest; S1 = moderate quality *E. maculata* forest; S2 = high quality upper slope forest; R1 = temperate rainforest; R2 = ecolonal wet sclerophyll-rainforest.

iii) Vegetation groups are ranked in increasing order of magnitude; horizontal bars span means which do not differ significantly using LSD

The P2 soils also had the lowest exchangeable calcium concentration of any group. At the other end of the spectrum, the rainforest groups R1 (temperate rainforest) and R2 (ecotonal wet sclerophyll-rainforest), and the S2 group (high quality upper slope forest) had the greatest levels of these nutrient elements. For example, the mean phosphorus concentrations for the P2 and P1 plots were 45 and 80 ppm respectively, and for R1, R2 and S2, 186, 204 and 211 ppm; the mean calcium concentrations for the P2 and P1 plots were 100 and 142 ppm respectively, and for R1 and S2, 440 and 671 ppm. The E1 (ecotonal *E. piperita-E. maculata* forest) and S1 (moderate quality *E. maculata* forest) groups were generally intermediate between these extremes. The mean organic matter percentages for these 7 community groups show a similar trend.

While there is a consistent relationship between characteristics of the vegetation groups and the major nutrient elements, this does not apply to aluminium and iron. Mean exchangeable aluminium values ranged from 103 to 277 ppm. Within this range, the rainforest group R1 had the lowest and R2 the highest aluminium concentrations. The P2 and P1 concentrations (109 and 240 ppm respectively) were similarly divergent. In this sense, the aluminium values might be used to differentiate between groups that have similar concentrations of other soil nutrient elements.

The relationship between the Al:TEB ratio and vegetation pattern is affected by the variable aluminium level. Nevertheless, the P2 and P1 groups had the highest Al:TEB ratios (0.46 and 0.64 respectively) and the R1 and S2 groups the lowest (0.12 and 0.13 respectively). The R2 ecotonal rainforest had a high Al:TEB ratio of 0.45.

3.4.2 Bioassay Experiment

The differences between the *E. maculata* and *E. piperita* soils in their chemical attributes are reflected in differences in productivity. The mean shoot dry weight of *E. maculata* seedlings grown in different horizons of a typical Permian '*E. maculata*' soil and a typical Permian '*E. piperita*' soil are shown in Table 3.3.

Table 3.3 The mean shoot dry weight (g) ± standard error of *E. maculata* seedlings grown in different soil horizons of a Permian '*E. maculata*' soil and a Permian '*E. piperita*' soil. Seedlings were grown without any added nutrients (Nil), and with all added nutrients except phosphorus (-P). Each mean is based on four replications.

Soil Type	Soil Horizon	Nutrient Treatment	Mean ± S.E.
'*E. maculata*'	A	Nil	4.64 ± 0.62
'*E. piperita*'	A	"	2.83 ± 0.29
'*E. maculata*'	B	"	1.05 ± 0.12
'*E. piperita*'	B	"	0.45 ± 0.08
'*E. maculata*'	C	"	0.32 ± 0.05
'*E. maculata*'	A	-P	8.76 ± 0.75
'*E. piperita*'	A	"	6.52 ± 0.62
'*E. maculata*'	B	"	2.58 ± 0.19
'*E. piperita*'	B	"	0.72 ± 0.08
'*E. maculata*'	C	"	All Dead

Seedlings in the untreated '*E. maculata*' A horizon soil grew better (4.64 g) than those in the '*E. piperita*' A horizon soil (2.83 g). In the second treatment (-P), in which all nutrients except phosphorus were added to the soils, growth in the '*E. maculata*' soil (8.76 g) and in the '*E. piperita*' soil (6.52 g) was enhanced. It might be inferred that a reasonable amount of phosphorus is available for seedling growth in the A horizons of both these soils.

Seedlings in the untreated '*E. maculata*' clay B horizon soil grew better (1.05 g) than those in the '*E. piperita*' clay B horizon soil (0.45 g). In the '-P' treatment, the shoot dry weight in the '*E. maculata*' soil was 2.58 g, and in the '*E. piperita*' soil, 0.72 g. In this case, it might be inferred that there is some plant available phosphorus in the clay B horizon of the '*E. maculata*' soil, but very little in the same horizon of the '*E. piperita*' soil.

In the decomposing C horizon substrate, the *E. maculata* seedlings grew very poorly (0.32 g). Where the '-P' treatment was applied, all seedlings died, suggesting a nutrient imbalance involving phosphorus. These responses indicate there is very little fertility in the C horizon substrate, and particularly, virtually no plant available phosphorus.

3.4.3 Principal Coordinate Analysis

So far, the analysis has shown the relationship between the community groups and individual nutrient element concentrations. However, vegetation may be an expression of a number of nutrients acting simultaneously, and this can be demonstrated using the technique of principal coordinate analysis. Moreover, vegetation is likely to be a function of factors other than nutrient concentrations. The role of many of these factors can often be expressed only in qualitative terms, e.g. 'slope position' and 'drainage class'. Principal coordinate analysis is an analytical program which is able to handle this type of data, enabling the contribution these factors make to vegetation pattern to be evaluated. The program also provides a visual representation of the relationships.

Initially, the four environmental ordinations (A and B horizon nutrient data sets, soil physical and site factor data sets) with the imposition of the 7 group level vegetation classification, are discussed separately.* Patterns resulting from the individual ordinations are then drawn together to form a general discussion of vegetation-environment relationships in south coast forests.

Ordination of the A Horizon Nutrient Data Set

This ordination demonstrates the degree of similarity of 51 plots with respect to eight nutrient elements, organic matter and pH within the 0-30 cm soil horizon. This shows a broad relationship between south coast vegetation and soil fertility status. The first three vectors (axes) explain separately 26.9%, 15.6% and 5.6%, and cumulatively 48.1% of the total variation in the data set. The relative positions of 51 plots with respect to A horizon nutrients is shown by contrasting the two most important vectors, 1 and 2 (Figure 3.2). Those attributes contributing to the definition of the first two vectors are listed in order of importance (pseudo-F-statistic), in Table 3.4. The nutrient elements magnesium, nitrogen, phosphorus, calcium, potassium and sodium, and organic matter percentage decline in value from the negative to positive end of vector 1. This first vector represents a broad gradient in vegetation from rainforest and wet sclerophyll forest at the negative, high nutrient end, through a range of dry sclerophyll communities dominated by *E. maculata*, ecotonal *E. maculata-E. piperita* communities, to *E. piperita-E. globoidea*-heath communities at the positive, low nutrient end.

The elements aluminium and iron, and soil pH, contribute to the definition of vector 2 (Table 3.4). Of the 7 groups defined by the

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* Analysis of the combined data sets had been tried, but the resultant patterns were less clear than when separate data sets were analysed.

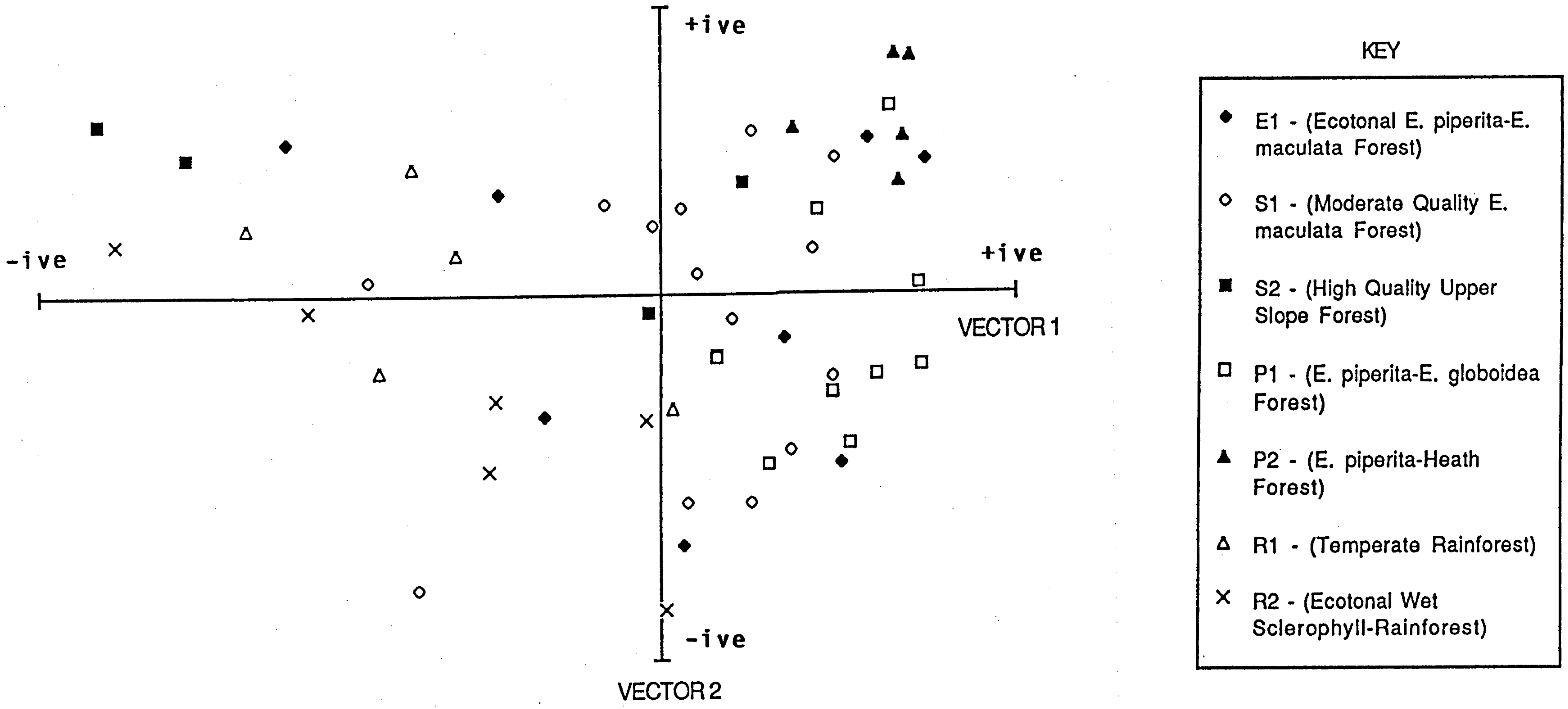


Figure 3.2 Ordination of the A horizon nutrient data and imposition of the 7 group level vegetation classification.

vegetation classification, only the P2 and S2 communities seem to be effectively discriminated with respect to this vector, i.e. the P2 (*E. piperita*-heath) and S2 (high quality upper slope) groups have consistently low concentrations of both aluminium and iron in the 0-30 cm soil zone. However, from the analysis of variance, it was apparent that aluminium was a discriminator of the R1 and R2 rainforest groups. This is reflected to a certain extent over vector 2 in that the majority of R1 plots are at the positive, lower aluminium end while the majority of R2 plots are at the negative, higher nutrient end. That the ordination has not succinctly separated the two rainforest groups is not unexpected since the other major attribute to contribute to the alignment of plots along vector 2 is iron. R1 and R2 plots have very similar concentrations of soil iron (24.9 and 28.0 ppm respectively).

Ordination of the B Horizon Nutrient Data Set

Only 47 of the total 51 plots were used in the ordination of the B horizon (31-60 cm) nutrient data set because soil profile characteristics at four plots (one S2 plot, one R1 plot and two R2 plots) prevented sampling beyond about 30 cm.

This ordination has been less successful than the previous ordination in defining vegetation-soil fertility gradients. The three most important vectors of this ordination explain separately 16.2%, 11.8% and 10.1%, and cumulatively 38.1% of the total variation in the data set. The analysis has not been as efficient as the ordination of A horizon nutrients in isolating variation to the two most important vectors.

The contrast of vector 1 and vector 2 is shown in Figure 3.3, and the attributes contributing to those vectors in Table 3.4. All attributes defining vector 1 decline in magnitude from the negative to positive end of the x-axis but there is no readily definable

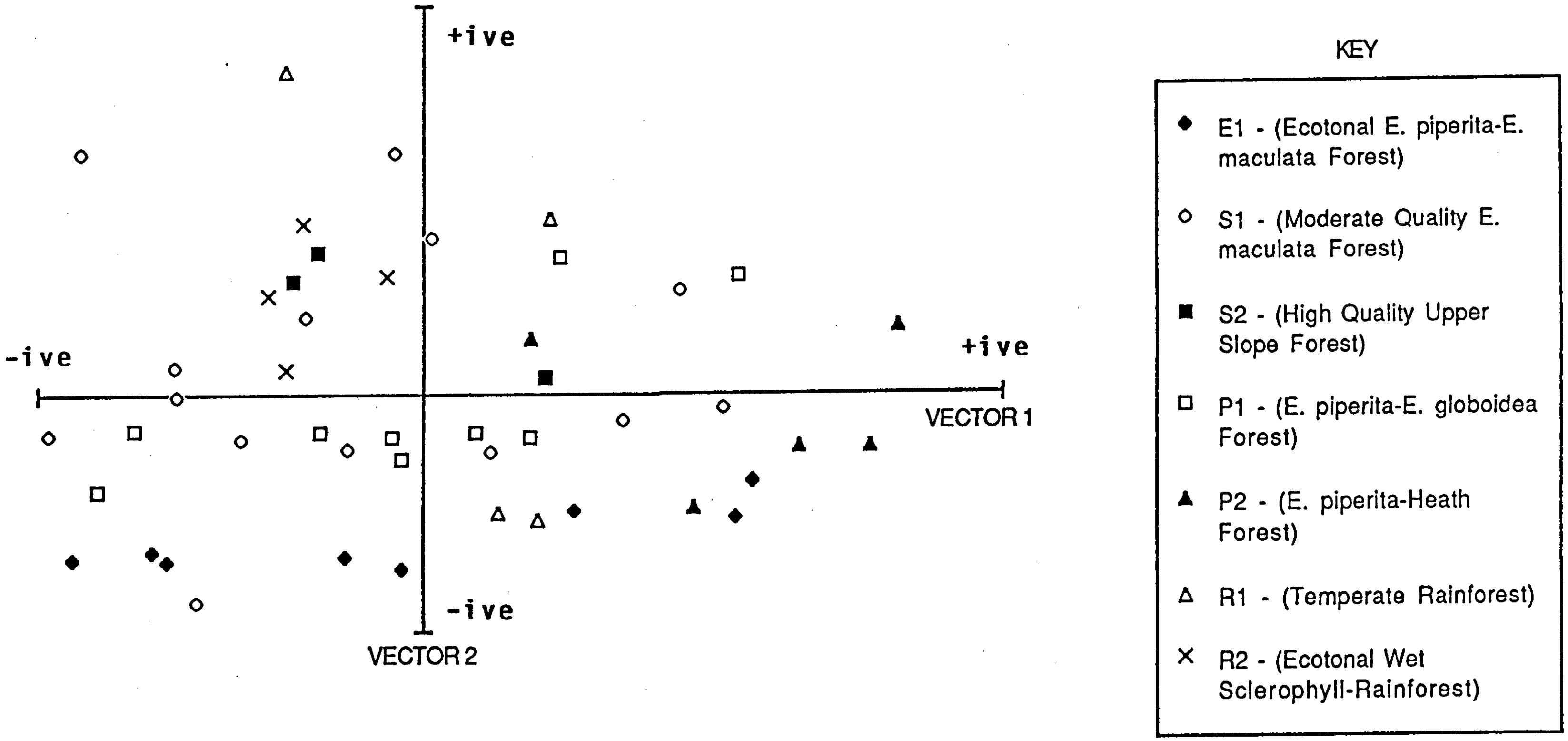


Figure 3.3 Ordination of the B horizon nutrient data and imposition of the 7 group level vegetation classification.

nutrient-vegetation pattern. In this analysis, aluminium and iron are included with the nutrient elements potassium, phosphorus and nitrogen, and organic matter percentage as the data set contributors to vector 1. Aluminium is the most important contributor to vector 1 by a factor of two, and is perhaps part of the reason why there is a far less defined gradient from rainforest to heath over this vector. It is possible the element aluminium overrides the effects of those elements which contributed strongly to the fertility-vegetation gradient associated with vector 1 of the A horizon nutrient ordination.

The attributes pH, potassium, iron, nitrogen and organic matter percentage define the arrangement of plots over vector 2. While there is again little definable soil nutrient-vegetation pattern, the eight E1 ecotonal plots are consistently found at the negative end of vector 2, that is on soils with a B horizon tending to contain some of the lowest values for pH, potassium, nitrogen and organic matter percentage, and higher concentrations of iron.

The fertility range within the B horizon does not seem to be as important in delimiting many vegetation groups. Since the majority of fine, translocating roots are likely to be concentrated in the first 30 cm of the soil profile (Carbon *et al.* 1980; Feller 1980), it is not surprising that a data set based on chemical soil attributes within the 31-60 cm zone is a weak indicator of soil fertility-vegetation relationships.

Ordination of the Soil Physical Data Set

This ordination arranges the 51 plots with respect to soil physical attributes. There are a number of these which seem to be contributing to the delimitation of communities. The first three vectors explain separately 17.0%, 13.2% and 12.0%, and cumulatively 42.2% of the total variation in the data set. This value is less than for the A horizon nutrient ordination, but more than for the B horizon nutrient ordination.

The contrast of vector 1 and vector 2 (Figure 3.4) shows the relative position of 51 plots with respect to this data set, and the attributes contributing to these vectors are listed in Table 3.4. The attribute 'drainage class' dominates the definition of the x-axis by a factor of two, and would appear to demonstrate a gradient in moisture relations. Plots at the negative end of vector 1 have a more freely draining soil profile, a shallower depth to the C horizon, and a higher gravel percentage than those at the positive end of the vector.

Of the three attributes defining the arrangement of plots over vector 2, two, 'depth of A1 horizon' and 'depth of A horizon' are strongly associated. Both may reflect differences in the ability of soils to provide available nutrients and surface soil moisture. Plots at the negative end of vector 2 have shallower A1 and A horizons, and a heavier textured A horizon than those at the positive end of the vector.

The relationship between community groups and physical soil attributes is demonstrated by imposing the 7 group level vegetation classification on the arrangement of plots produced by the ordination (Figure 3.4). The plots within three of the groups form tight clusters. Along vector 1, the S2 high quality forest group and the R2 rainforest group, with the exception of one plot, are found on soils with good drainage, a shallow depth to the C horizon and a high percentage of gravel. In contrast, the E1 ecotonal group, with the exception of one plot, and to a lesser extent the P1 (*E. piperita*-*E. globoidea*) group, are found on soils with more restricted drainage, greater depth to C horizon and a low gravel percentage.

From the arrangement of plots along vector 2, the R1 rainforest group is consistently found on soils with a lighter textured A horizon and deeper A1 and A horizons, the latter two attributes perhaps reflecting soils of superior fertility status.

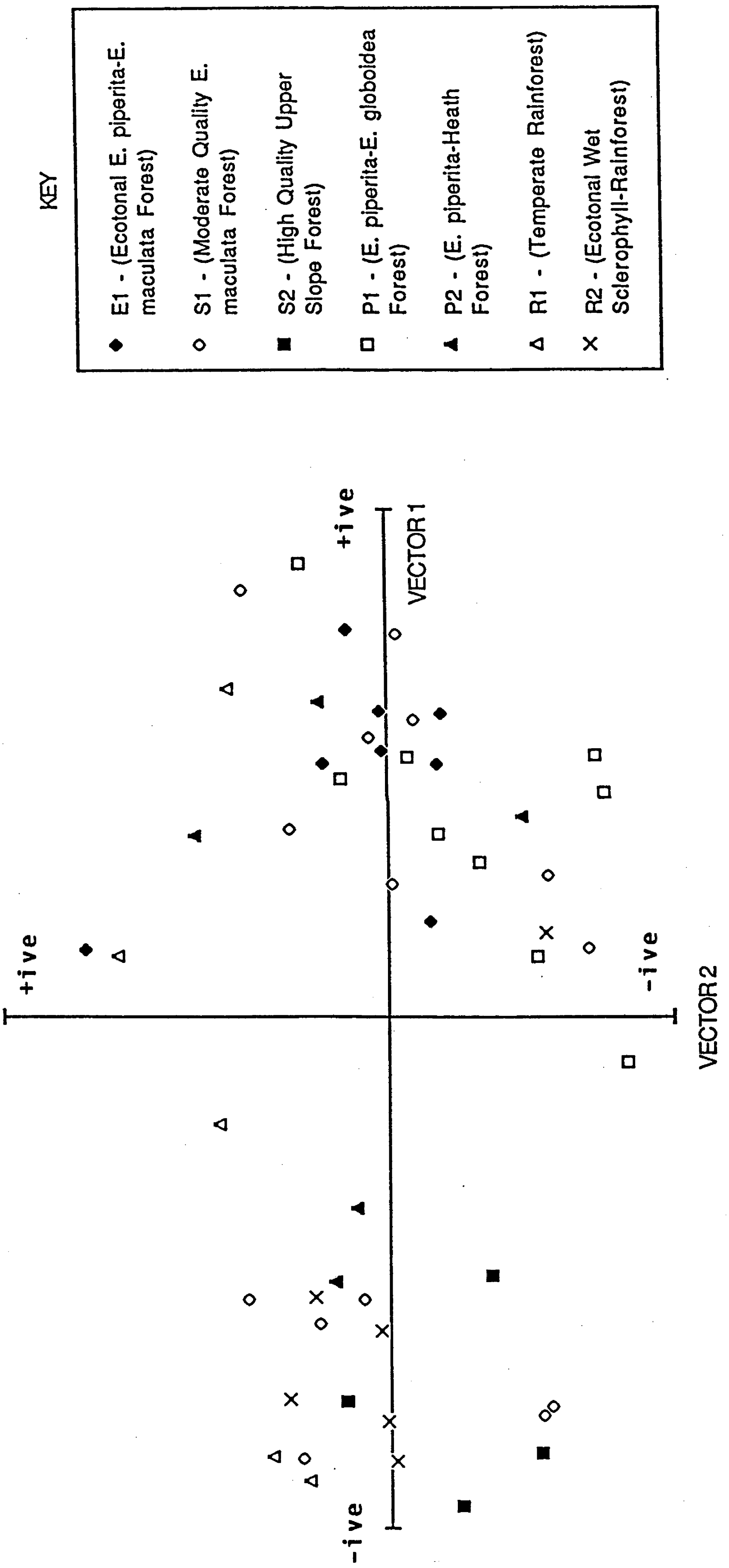


Figure 3.4 Ordination of the soil physical data and imposition of the 7 group level vegetation classification.

The S1 (*E. maculata*) and P2 (*E. piperita*-heath) groups separately occupy the whole range of positions in Figure 3.4, that is, there are few similarities in the physical soil attributes collected which allow either the S1 or P2 groups to be effectively discriminated.

Ordination of the Site Factor Data Set

This ordination arranges the 51 plots with respect to a number of physical site attributes. The three most important vectors explain separately 25.2%, 15.3% and 13.5%, and cumulatively 54.0% of the total variation in the data set. This is at least as successful as the first of the four ordinations in terms of variance explained and in the demonstration of relationships between vegetation and environmental site factors.

The contrast of vector 1 and vector 2 is shown in Figure 3.5 and the attributes contributing to vector definitions are listed in Table 3.4. The relationships between community groups, as defined by the 7 group level classificaton, and the site factor data set indicate further useful clusterings of plots with similar species compositions. Only the S2 and P2 groups tend to form tight clusters over vector 1 and vector 2; however, four of the remaining five vegetation groups are characterised by a specific set of site attributes over either vector 1 or vector 2.

The four S2 plots, are characterised by Ordovician parent materials, mudstone basal rock type, steep slopes within steep topography, soil formed in-situ and subject to erosional processes, upper positions on slope and relatively large distances to surface water. Plots supporting the P2 group of communities occur on flat to undulating terrain where slope is less than nine degrees, and mostly two to three degrees. The communities are not found near surface water, soil formation patterns are either in-situ or colluvial, and rock type, with the exception of one plot, is sandstone.

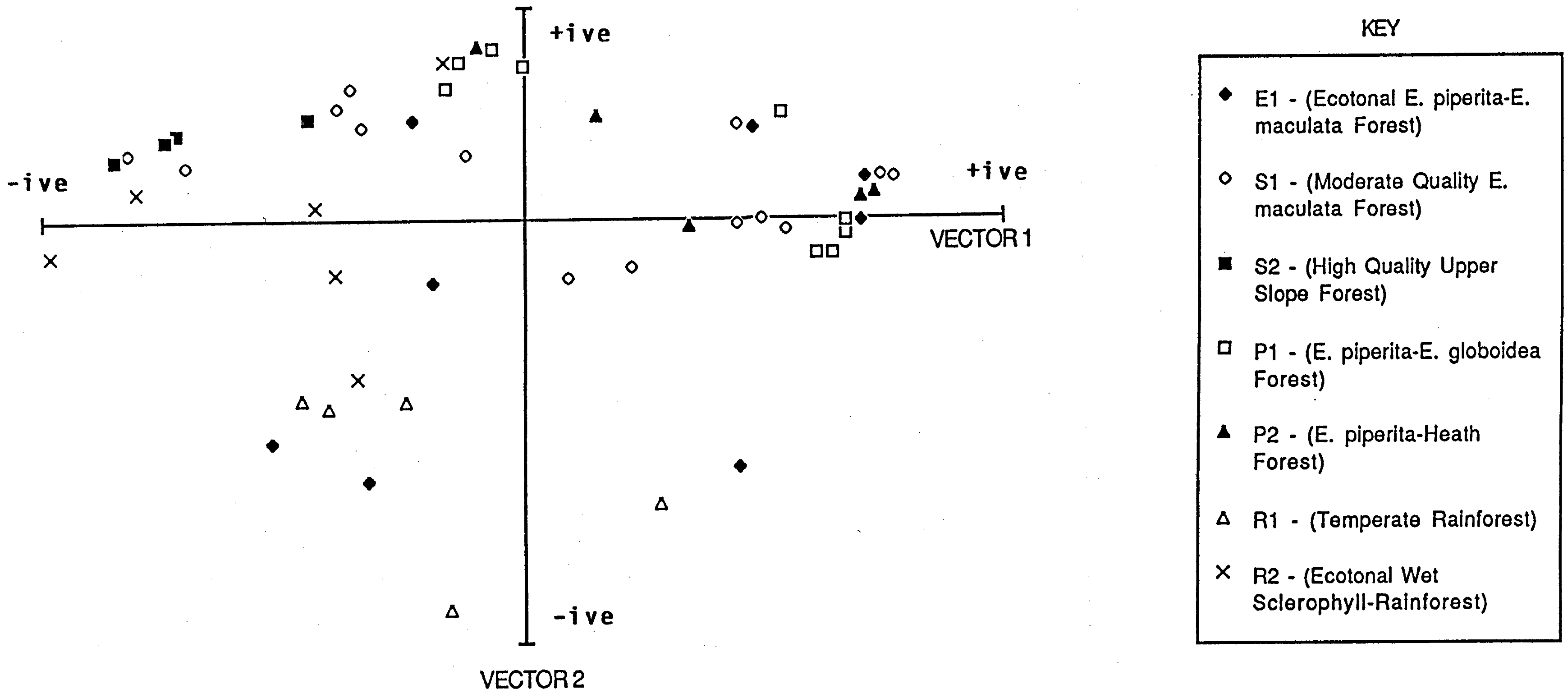


Figure 3.5 Ordination of the site factor data and imposition of the 7 group level vegetation classification.

Table 3.4 Attributes identified in principal coordinate analyses of the A horizon and B horizon nutrient data, and the soil physical and site factor data. Pseudo-F-statistic (in brackets) ranks the relative contribution of each attribute to the ordination.

A Horizon Nutrients		B Horizon Nutrients		Soil Physical Data		Site Factor Data	
Vector 1	Vector 2	Vector 1	Vector 2	Vector 1	Vector 2	Vector 1	Vector 2
Magnesium (222)	Aluminium (139)	Aluminium 75	pH (26)	Drainage (100)	Depth of A1 Horizon (27)	Permian - Pebbley Beach (109)	Alluvial (67)
Nitrogen (203)	Iron (57)	Organic Matter (39)	Potassium (25)	Depth to C Horizon (48)	Texture of A Horizon (22)	Ordovician (74)	In-situ (44)
Phosphorus (171)	pH (20)	Potassium (27)	Iron (18)	Gravel % (21)	Depth of A Horizon (21)	Erosional (34)	Permian - Snapper Point (18)
Organic Matter (82)		Phosphorus (16)	Nitrogen (15)			Slope (31)	Surface Water Availability (17)
Calcium (51)		Nitrogen (10)	Organic Matter (12)			Colluvial (19)	Position on Slope (15)
Potassium (46)		Iron (8)				Basal Rock Type (19)	
Sodium (27)					Topography (13)		
Iron (10)							

NOTE:

i) The 'Drainage' attribute is a qualitative assessment of the moisture holding characteristics of the soil, ranging from very well drained to permanently waterlogged.

ii) The site factor attributes associated with parent materials (Permian, Ordovician) and soil formation patterns (in-situ, colluvial, depositional, erosional) are based on their presence or absence.

Plots comprising the R2 rainforest group are at the negative end of vector 1 and are associated with Ordovician parent materials and steep slopes within steep topography. Plots supporting the R1 group of communities are found at the negative end of vector 2, and are characterised by Snapper Point derived soils (Permian) - with the exception of one plot, lower slopes, and close proximity to surface water in the form of seepage or intermittent creeks. The P1 (*E. piperita-E. globoidea*) group also tends to have a number of distinctive site attributes. As with the P2 plots, there are both in-situ and colluvial soil formation patterns, slopes are less than nine degrees, topography is flat to undulating and there is no associated surface water. Finally the majority of S1 communities occur on plots which have steep to undulating topography, moderate slopes, an absence of surface water and in-situ and colluvial formation patterns.

3.5 DISCUSSION

The Soil Fertility Ranges of Rainforest and the Eucalypt Communities

The distribution of 51 plots over the first vector of the A horizon nutrient ordination can be used to give an indication of the fertility range of the rainforest communities and the main eucalypt species on the forests (Figure 3.6). The species are listed in their subgeneric groups. Those nutrients contributing to the definition of vector 1 are listed in Table 3.4.

The range of a species along the total soil fertility gradient was defined in the following way. 'Information values' were assigned to all eucalypt species (greater than 10 cm dbh and 2 m in height) found within the confines of the plot, and were in the form of an importance value.

$Y_i = \frac{1}{2}$ (Basal Area X_i/Total Basal Area + Stocking X_i/Total Stems) x 100

where (1) Y is the importance value of a species,

(2) species $_i$ is a member of a number of species on a plot.

Any plot in which a given species had an importance value of 10 or greater, was used to illustrate the fertility range of that species. Hence the location of the two extreme plots (both containing a species with an importance value of 10 or greater) at the positive and negative ends of vector 1 of the A horizon nutrient ordination, were used to define the approximate soil fertility range of the species.

A number of species are restricted to the lower end of the soil fertility gradient on the forest (*E. globoidea*, *E. piperita*, *E. gummifera*, *E. pellita*) (Figure 3.6). Others have a wider fertility range; *E. pilularis* extends from the low to moderate fertility soils and *E. maculata* from the low to higher fertility soils. Species comprising the rainforest groups are found on the moderate to higher fertility sites only.

Florence (1981) has suggested the distribution of subgeneric groups is associated with soil fertility status. Generally, the *Symphyomyrtus* (S) species occupy sites of higher fertility, and *Monocalyptus* (M) species, sites of lower fertility. *Corymbia* (C) species occupy sites with a range in soil nutrient status. Within the limitations of the sample size, the concept is supported by this analysis. The *Monocalyptus* species *E. piperita* and *E. gummifera* are consistently found at the low nutrient of the spectrum. *E. pilularis* (M) is found on low nutrient soils, but is also capable of competing on higher fertility sites where the soil texture and structure is favourable. The two *Corymbia* species form a replacement series on the sites examined. *E. gummifera* (C) is restricted to soils of low nutrient status, while *E. maculata* (C) occupies sites from low to higher fertility. There is some overlap in the fertility range of *E. gummifera* and *E. maculata*, although sites on which the two species occur in mixture are infrequent and tend to be of low forest quality. Hybrids between these two species are found in these situations.

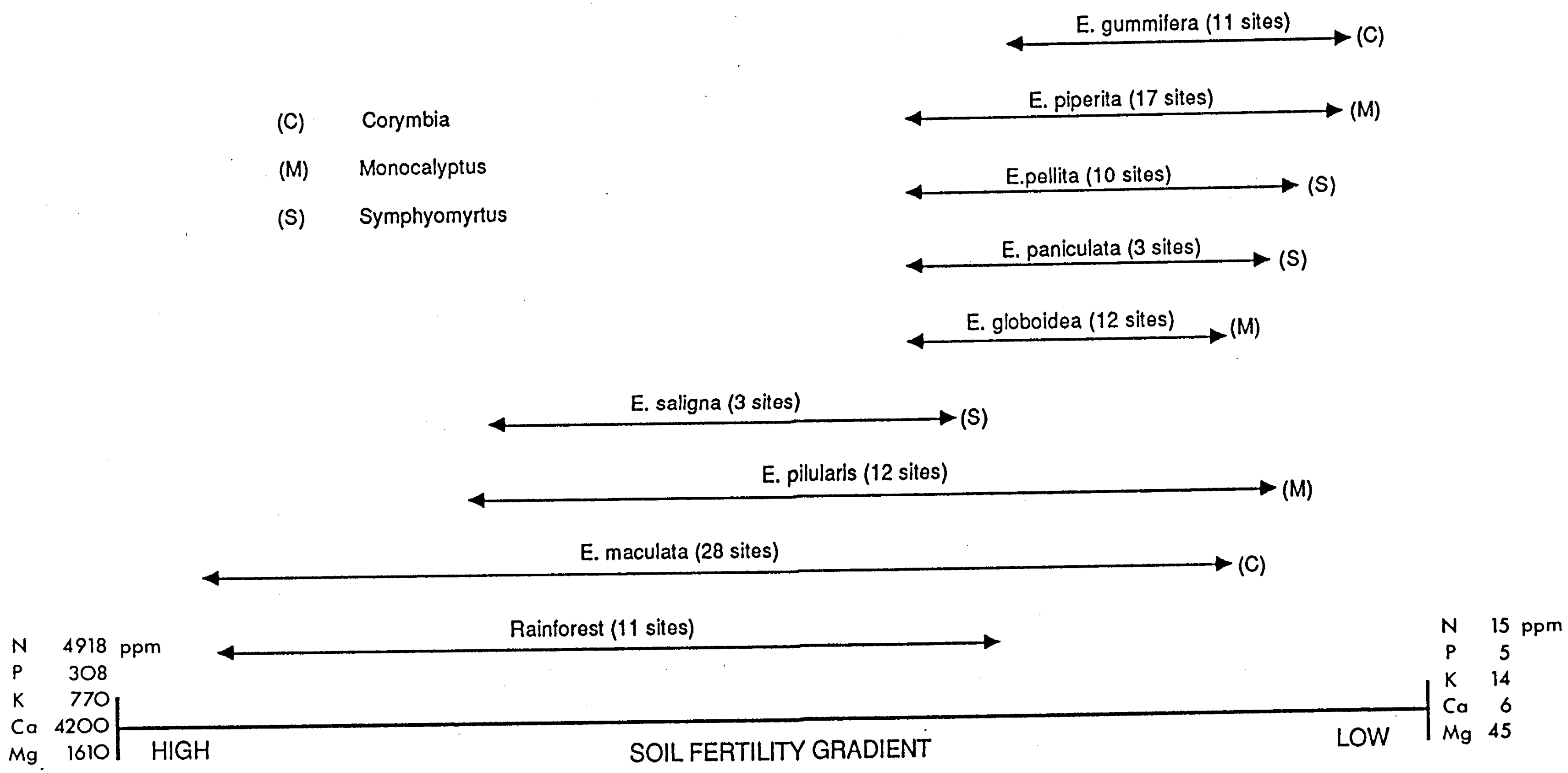


Figure 3.6 Fertility range of the rainforest communities and the major south coast eucalypt species as defined by Vector 1 of the A horizon nutrient ordination. The lowest and highest concentration for each soil nutrient element from the 51 sites, is listed. The number of sites on which a species occurred (with an importance value greater than 10) is given in brackets. See text for the derivation of this figure.

The fertility ranges of two *Symphyomyrtus* species *E. saligna* and *E. paniculata* are perhaps unrepresentative of their true extent because of the low sampling intensity (only three plots each with an importance value greater than or equal to 10). *E. saligna* (S) is commonly found as a dominant component of high quality ecotonal wet sclerophyll-rainforest associations. If a greater number of these sites had been sampled, it is expected that the range of *E. saligna* would extend further into the high quality end of the nutrient spectrum illustrated in Figure 3.6. *E. paniculata* (S) is often found in mixture with moderate to high quality *E. maculata*. Again, if a greater number of these sites had been sampled, it is likely that *E. paniculata* would extend at least to the mid range of the fertility gradient. *E. pellita* is a *Symphyomyrtus* species which is consistently found at the low nutrient end of the spectrum. However, it seems that the nature of the physical soil environment largely determines its occurrence. *E. pellita* is able to establish and compete effectively on sites of poor texture and structure where water and root movement is restricted, tending to form a replacement series with *E. pilularis*, the latter being limited to sites with a more favourable soil physical environment. The soil physical conditions which allow *E. pellita* to compete also tend to be associated with low fertility.

The soil fertility ranges of tree species making up the Kioloa forests suggests that *E. maculata* is more extensive than that of other species. However, at the lower end of the fertility range, its competitive ability is obviously weak, and communities consisting entirely of *E. gummifera* (bloodwood group of *Corymbia*) and a number of *Monocalyptus* species (mainly *E. piperita*, *E. globoidea* and *E. pilularis*) form a mosaic with *E. maculata* communities throughout the forest. It is likely that at the lower end of the soil fertility range, *E. maculata* has been able to maintain itself in the community only where other environmental factors are particularly favourable, or where its competitive edge is assisted by the accumulation of well established lignotuberous advance growth. Against this background, a profile of community-environment relationships can be built up.

Environmental Relationships of Plant Communities

Each of the four ordinations reveal important relationships between vegetation patterns and the environment. Where the community groups defined by the vegetation classification are imposed on the four separate environmental ordinations, six of the seven groups can be characterised by a number of attributes contained in one or more of the data sets. Only the S1 (*E. maculata*) group failed to form distinctive clusters of plots within any ordination, suggesting that this group occurs on environmentally diverse sites.

By combining results from the analyses of variance and ordinations, it is possible to establish a set of site attributes which are consistently related to a particular vegetation type, as defined by the vegetation classification.

The P1 (*E. piperita-E. globoidea*) and P2 (*E. piperita*-heath) groups have a number of site characteristics in common. Most important perhaps is that soils supporting both associations have relatively low concentrations of total nitrogen and phosphorus and exchangeable potassium, calcium, sodium and magnesium. In addition they occur on flat to undulating terrain (slopes <8 degrees) where soil development is influenced by in-situ and colluvial processes. These attributes indicate a particular adaption of the dry sclerophyll communities to low nutrient, highly weathered soils. There are a number of physical site attributes which may contribute to the differentiation of the P1 and P2 groups. The P1 plots are found on a range of rock types, the depth to the C horizon is relatively great and the percentage of gravel is small. In contrast, the P2 plots are found only on soils overlying a sandstone rock base, and the depth to the C horizon is variable. Another attribute which can be used to differentiate between the groups is soil aluminium. Communities comprising the P1 group occur on sites with significantly higher concentrations of soil aluminium than soils supporting the P2 group of communities.

The R1 (temperate rainforest) and R2 (ecotonal wet sclerophyll-rainforest) groups, and the S2 (high quality upper slope forest) group all have a set of characteristics in common, that is, they all occur on soils of relatively high fertility. Turner and Kelly (1981) observed a similar relationship for rainforest and wet sclerophyll forest on the north coast of N.S.W. Other attributes help to separate the community types. Pure rainforest communities (R1) are found on lower slopes in close proximity to some form of surface water. Soils are typically light textured in the A horizon while the A1 and A horizons are relatively deep. These characteristics suggest the true rainforest communities require sheltered sites where soil physical, chemical and moisture relations in the upper horizons are favourable. The R2 and S2 groups occur on sites characterised by Ordovician parent materials, good drainage, shallow depth to a C horizon, a high gravel percentage and steep slopes within steep topography. These groups are also known to occur on soils developed from Permian parent material where topography is relatively steep, but were not included in the sample. The characteristics common to the R2 and S2 groups suggest the occurrence of more active soil forming processes (particularly the steep slopes with shallow depth to parent material), and therefore more dynamic nutrient cycling in the biotic and abiotic components of the site. The concentrations of major nutrient elements in soils of R2 and S2 plots support this concept. The element aluminium is again useful in separating vegetation types which otherwise have similar site characteristics. Both R1 and S2 groups have significantly lower concentrations of soil exchangeable aluminium than the R2 group.

The basket of communities forming ecotones between *E. piperita* and *E. maculata* sites (E1) are generally found on sites of moderate fertility and are less well drained than sites supporting R2 and S2 communities. They also have a greater depth to a C horizon and low gravel percentage. The S1 association occurs on sites with few distinctive attributes which adequately define their occurrence. The sites tend to be of moderate fertility with steep to undulating terrain and moderate slopes; soils have either been formed in-situ or through colluvial processes, and the distribution of communities suggests they are not necessarily associated with surface water.

The capacity of soils to supply important nutrients may be reflected in Al:TEB ratios, given that aluminium is known to form insoluble complexes with nutrients essential for plant growth (Wild 1961; McColl 1969). Hence access to and uptake of potassium, calcium, sodium and magnesium and other nutrients as well, may be more active in the soils of the R1 and S2 group of communities than it is for the R2, P2 and P1 groups.

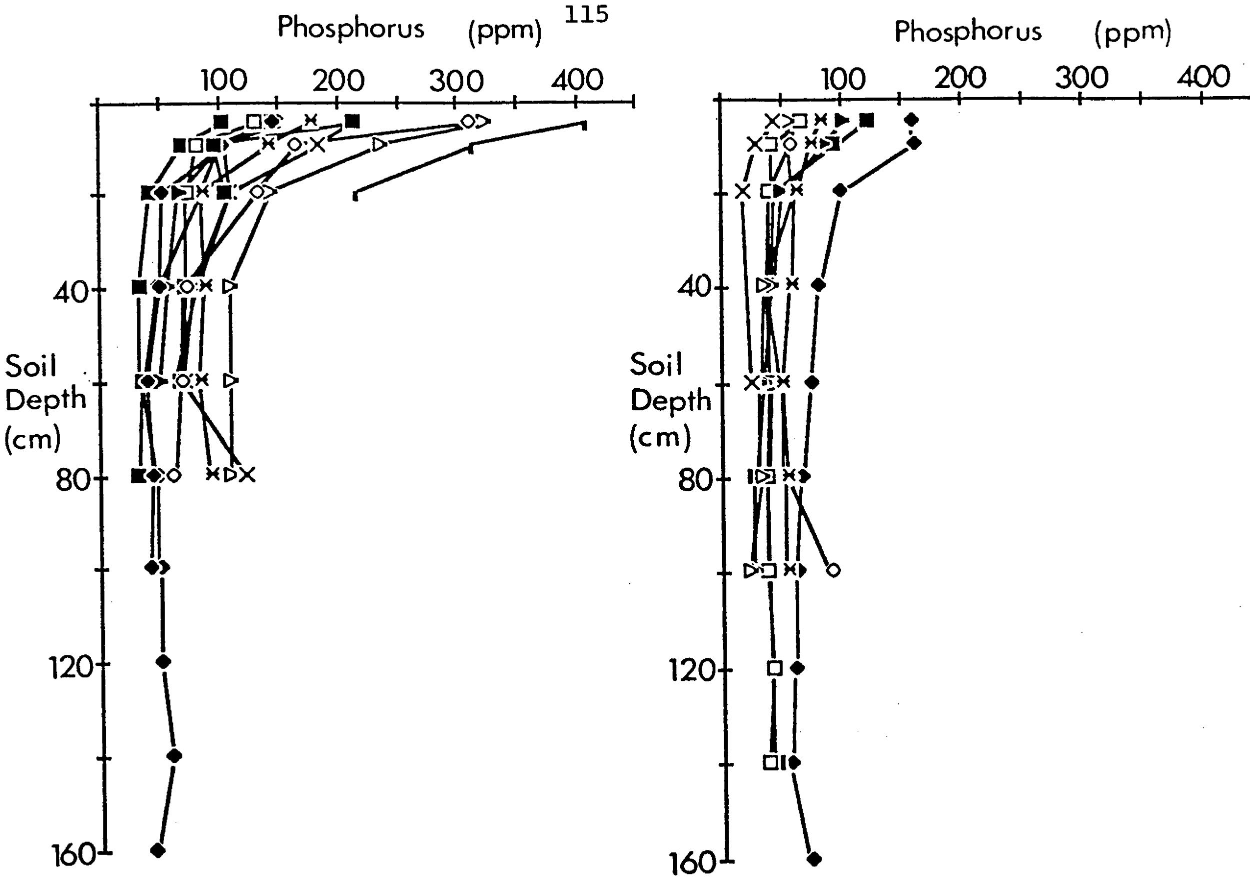
Some Soil Physical and Chemical Characteristics Influencing Nutrient Availability

It is now apparent there is a vegetational gradient from rainforest and wet sclerophyll communities, through a series of *E. maculata* and ecotonal communities, to dry sclerophyll (*E. piperita*) and heath communities; and this vegetation gradient is associated with a soil fertility gradient. The high quality *E. maculata* forests are at the upper, and the *E. piperita* communities at the lower end of the gradient. Poorer quality *E. maculata* with an *E. piperita* and *E. globoidea* component occur on soils that are intermediate between those giving rise to the more distinctive communities.

However, quite often a comparison of sites with appreciable differences in vegetation shows only relatively small differences in the fertility status of the soils supporting them. McColl and Humphreys (1967) and McCutchan (1978) found a similar pattern. In such cases, it is possible that the physical soil environment will be an important factor affecting access of fine roots to nutrients and water, and therefore the competitive ability of species.

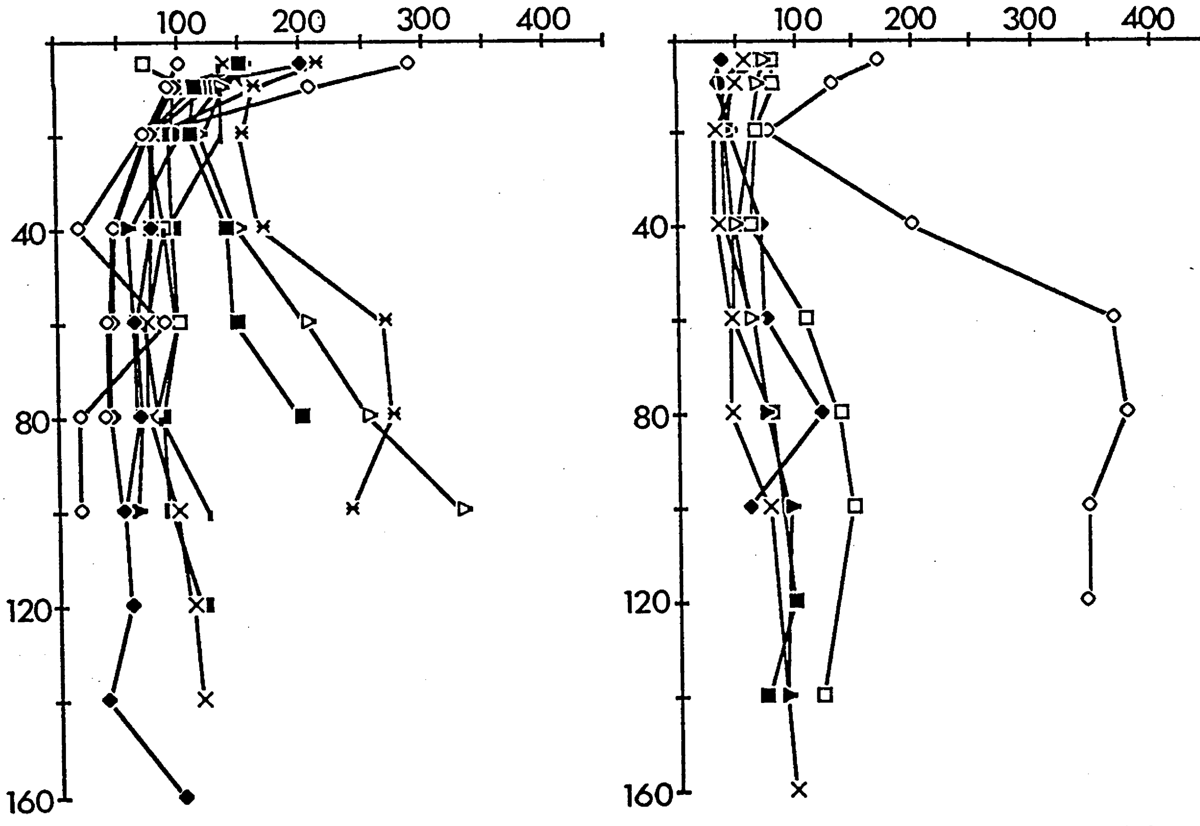
In exploring the role of the soil physical and chemical factors in the delimitation of species, it is necessary to illustrate some of the characteristics of soil profiles derived from the Permian and Ordovician parent materials.

The Permian derived soil invariably consists of a sandy A horizon with low to moderate phosphorus levels overlying a highly weathered, clay B horizon. However, there are some attributes of Permian derived soils which may affect vegetation. Physically, the clay B horizon of soils supporting *E. piperita* communities tends to be finer textured, less structured and more poorly drained than the B horizon of *E. maculata* soils. Chemically, the soil phosphorus profile on Permian derived soil can be unusual in that there may be an initial decrease in total phosphorus with depth, followed by a marked increase in the clay B horizon (Figure 3.7). It is inferred from this that much of the phosphorus in the B horizon of the Permian soils is immobilized in a form unavailable to plants, and hence not circulated through the tree-litter-soil system. The accumulation of phosphorus in the clay B horizon applies to soils supporting both *E. maculata* and *E. piperita* communities (Figure 3.7). Nevertheless, the results from the bioassay experiment suggest that the availability of phosphorus, and possibly other nutrients as well, differs between the clay B horizons of the *E. maculata* and *E. piperita* sites. *E. maculata* seedlings grew quite poorly in the clay B horizon soil from the '*E. piperita*' site, and



E. MACULATA ON ORDOVICIAN

E. PIPERITA ON ORDOVICIAN



E. MACULATA ON PERMIAN

E. PIPERITA ON PERMIAN

Figure 3.7 Individual soil phosphorus (total) profiles for four vegetation/soil types.

showed little further growth where all other nutrients except phosphorus were added. Growth of seedlings in the '*E. maculata*' B horizon soil was better, and this was enhanced markedly where the '-P' treatment was applied. This suggests firstly, that while there are sufficient nutrients in the '*E. maculata*' B horizon soil to support a reasonable level of seedling growth, this is not the case in the B horizon of the '*E. piperita*' soil. Secondly, the differences in seedling response to the '-P' treatment indicates that access to, or availability of phosphorus is appreciably better in the '*E. maculata*' soil. In addition to these differences, the bioassay experiment indicated that the A horizon soil from the *E. maculata* site was also more productive than A horizon soil from the *E. piperita* site.

In contrast to the Permian soils, communities based on Ordovician parent materials have more traditional phosphorus profiles (Figure 3.7), that is, the greatest concentrations are in the surface horizons and decline in a regular way down the profile. This suggests perhaps, that nutrient cycling and uptake processes within the soil profile are more active. Given this, and the fact that *E. maculata* soils have higher concentrations of all major nutrients than *E. piperita* soils, it is inferred that nutritional status is an important factor influencing the distribution of communities on the Ordovician parent material. This is consistent with McCutchan (1978) who stated that the soil chemical condition, or some aspect of nutrient status, is the major controlling influence of species distribution on these (Ordovician) sites. Moreover, the distribution of *E. maculata* may not be unduly restricted on soils with limited capacity for soil water storage. Most of the Ordovician *E. maculata* communities tend to occur on steeper upper slopes where the gravel content is relatively high and the depth to a C horizon or parent rock is relatively shallow. Since these features suggest that moisture on such sites may become temporarily limiting at certain times, it is possible that species which have a deeper penetrating root system will be able to obtain sufficient water in periods of stress by more efficient exploration of fissures and cracks in underlying rocks. J.R. Bartle (pers. comm.) has suggested that *E. maculata* has a reasonably well developed tap and deep root system compared to a number of other eucalypt species, and it will be shown later in the thesis that *E. maculata* seedlings devote more photosynthates to the development of a root system at depth than other major south coast eucalypts. It has also been noted that *E. maculata* appears to be able to extend its roots deeply into heavy soils (Forestry Commission of N.S.W. 1985). If this is the case, *E. maculata* may gain a competitive advantage over other species when soil moisture becomes limiting. Thus on Ordovician soils of moderate fertility, *E. maculata* may rely on differences in nutrient status and any preferential access to moisture in periodic drought to maintain dominance over species which make up the *E. piperita* communities.

The influence of soil and site factors on the delimitation of *E. maculata* and *E. piperita* communities on Permian parent materials is perhaps not so clear. McCutchan (1978) suggested that the delimitation of species on the Permian parent materials is less well defined but may be influenced by a combination of physical and chemical soil characteristics. From this study, it is nevertheless suggested that the greater fertility of the *E. maculata* sites is the single most important factor influencing the distribution of the two community types overlying the Permian substrate. This is reflected in the higher mean concentrations of all major nutrients and greater productivity in the '*E. maculata*' soils compared to the '*E. piperita*' soils, and in the greater nutrient availability, and particularly phosphorus availability, in the clay B horizon of the '*E. maculata*' soils. Differences in the physical soil environment could be important in marginal situations; the less favourable textural and structural characteristics of the

'*E. piperita*' soils may restrict the movement of deeper penetrating roots, thereby restricting access to nutrients and water in the lower horizons.

Location of Study Sites on the Environmental Gradient

In the context of the hypothesis underlying this thesis, it is important to locate the position of the clearfelled study sites within the site-community gradient. On the basis of the composition and structure of the eucalypt communities adjacent to the clearfelled areas, and from the character of the successional species within the regrowth stands, it appears that the greater part of the area subjected to clearfelling is located at the low to moderate fertility end of *E. maculata's* site range. For example, the Link Road clearfelled site (Section 2.3.1) has adjacent mature forest which is ecotonal between the more distinctive '*E. maculata*' and '*E. piperita*' community types. This would be at the lower end of the *E. maculata* fertility range. At the Livingstone Creek Road study site (Section 2.3.2), the upper slope of the clearfelled area carries a characteristic sclerophyll type understorey; and along this slope, there is little of the mesophytic understorey species normally associated with wet sclerophyll sites. This, and the total nitrogen and phosphorus concentrations along the slope (Section 2.3.2), would place the site at about the middle of *E. maculata's* fertility range. It is to be noted, however, that because of the likelihood of an effect of clearfelling on nutrient cycling processes, soil nutrient concentrations between logged and unlogged sites are not entirely comparable.

CHAPTER 4

GROWTH AND NUTRIENT STUDIES IN THE GLASSHOUSE

4.1 INTRODUCTION

The studies reported in this chapter seek to establish an experimental basis for the hypothesis that the variable response of *E. maculata* to clearfelling may be influenced by nutritional factors. In Chapter 3, it was shown that soil nutrients govern the broad vegetation patterns on the south coast forests, and that *E. maculata* occupies a broad range of sites along the total soil fertility gradient. In addition, some of the stands which were clearfelled appear to be at the low to moderate end of *E. maculata's* fertility range. It is possible that in such stands, nutritional factors govern also the relative competitive ability of *E. maculata* and other successional species at the establishment phase.

The response of species to nutrients is often examined in glasshouse pot studies. Usually this involves holding other factors constant while varying certain nutritional factors. Depending on the experimental objective, the approach may be to apply nutrients at a range of concentrations, or to add or withhold particular nutrient elements. Both of these techniques are used in this study.

The three experiments reported in this chapter compare the growth of seedling *E. maculata* and a number of other successional species, and are designed to help resolve a problem in stand dynamics. The first is preliminary, and assesses whether there are any basic differences in the seedling growth and form of four south coast eucalypt species. The second compares the response of seedling *E. maculata* and *E. pilularis* to a range of nutrient concentrations, in order to determine whether either species is able to gain a competitive advantage at particular fertility levels. The third compares the growth of *E. maculata* and *Acacia mabellae* in treatments where nitrogen and phosphorus are added and withheld in 2^2 factorial combination.

4.2 EXPERIMENT 1 : GROWTH CHARACTERISTICS OF FOUR SOUTH COAST EUCALYPT SPECIES

This glasshouse study examines the growth characteristics of four eucalypt species found on Kioloa State Forest. The experiment is designed to determine whether there are any morphological or physiological differences of seedlings which may help explain observed differences in the response of these species to clearfelling.

4.2.1 Materials and Methods

Experimental Design

The experiment was arranged as a randomized complete block design in the glasshouse with four species, five harvest periods and four replications. The four species came from two subgeneric groups - *E. maculata* and *E. gummifera* (*Corymbia*), and *E. pilularis* and *E. globoidea* (*Monocalyptus*). The seedlot and locality of seed of each species is listed in Table 1.1. All species occur either singly or in mixture in a mosaic pattern between Batemans Bay and Nowra on the south coast of N.S.W.

Experimental Method

Soil for the experiment was obtained from a site within Kioloa State Forest, and was collected by removing the top 20 cm layer of mineral soil. The site supported large-boled *E. maculata* dominants with an occasional mature *E. pilularis*. The soil was Permian in origin*, and consisted of dark grey loamy sand with a darker organic layer to about 4 cm depth. Bachelard (1986) has provided information on the characteristics of this soil.

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* the rock was Permian in origin; the soil is probably more recent

The soil was passed through a 1 cm sieve and placed in pots 20 cm in diameter. Seed of the four species was sown in equal parts of perlite and vermiculite. About 24 days after germination, seedlings were transplanted four to a pot. These were progressively thinned to one per pot, leaving the most uniformly sized seedling. The pots were free draining, and were automatically watered twice daily at a rate of two litres per hour for two minutes to maintain approximate field capacity. The glasshouse conditions are described in Section 2.6.1. The first harvest took place when the seedlings were about 70 days old. Four subsequent harvests were made at four-week intervals.

At each harvest, seedling height, shoot dry weight, root dry weight, basal stem diameter, number of axillary branches, leaf area and number of leaves were measured. Root:shoot ratio and specific leaf area were calculated. At three harvests (weeks 4, 12 and 20), the leaves of each seedling were sampled for determination of total nitrogen, phosphorus, potassium, calcium, magnesium and sodium.

The data were subjected to two-way analysis of variance, the factors being species and harvest. The procedures and assumptions for the analysis are described in Appendix I. Where heterogeneity of variance was indicated, an appropiate transformation of the data was made. Only untransformed means are referred to in the text.

4.2.2 Results

The results of the analyses of variance are summarized in Table 4.1. The overall ranked order of means, for harvests and species are given in Table 4.2. The responses of seedlings of each species at each harvest for the range of attributes are illustrated graphically in Figure 4.1a-j.

(i) Plant and Shoot Attributes

Shoot Height. Overall, shoot height increased significantly over the first four harvests, but remained constant between harvest 4 and harvest 5 (Table 4.2). Initially it was thought that the size of the pot may have become limiting for growth in the latter part of the experiment, but an examination of increases in plant dry weight over the same time period suggests this may not have been the case. Overall, species differences were highly significant (P<0.001). *E. pilularis* and *E. maculata* were significantly taller than *E. globoidea* and *E. gummifera*.

The species-harvest interaction was not significant. *E. globoidea* and *E. gummifera* continued to have smaller shoot heights than the other two species throughout virtually all harvests (Figure 4.1a).

Plant Dry Weight. There were significant increases in plant dry weight between each harvest. There was, however, no overall significant difference between species. Although the interaction term was also not significant, the response of each species over the five harvests (Figure 4.1b) reveals some changes in growth rates. *E. pilularis* grew fastest initially but then slowed relative to the other species so that it had the least dry weight at the final harvest. *E. maculata* also grew faster initially but was caught by *E. globoidea* and *E. gummifera* at harvest 4 (week 16). Similar growth rates were maintained by these three species to the final harvest (week 20).

Shoot Dry Weight. As with plant dry weight, overall shoot dry weight increased significantly with each successive harvest. The species effects were significant at the 5% level of probability. *E. globoidea* had significantly less shoot dry weight than *E. gummifera* and *E. maculata*.

The interaction between species and harvest was significant ($P<0.05$), and is illustrated in Figure 4.1c. *E. pilularis* had the greatest shoot dry weight at week 8, but at weeks 16 and 20, it was below all other species. *E. globoidea* was slowest initially but caught up to *E. maculata*, while *E. gummifera*, which grew at an equivalent rate to *E. maculata* for the first 16 weeks, increased its shoot dry weight most rapidly from week 16 to the final harvest.

Leaf Area. All five harvest periods were associated with significant increases in total leaf area. Both the species response and the interaction between species and harvests were highly significant ($P<0.001$). Overall, *E. pilularis* had significantly greater leaf area than the other three species.

The leaf area of seedlings for each species at each harvest is shown in Figure 4.1d. *E. globoidea* and *E. gummifera* initially produced less leaf area than *E. maculata* and *E. pilularis* over harvests 1 and 2. At harvest 3, all species were similar, indicating that *E. globoidea* and *E. gummifera* produced relatively more leaf area than the other two species between week 8 and week 12. The four species increased leaf area production at equivalent rates from week 12 to week 16, but after this, *E. globoidea* continued to produce leaf area whereas the other three species tended to decline in the rate of production.

Basal Stem Diameter. Both the main harvest and species effects were highly significant ($P<0.001$). Except for week 16 to week 20, each successive harvest was associated with a significant increase in basal stem diameter. As with some of the previous attributes, *E. globoidea* and *E. gummifera* were smaller than the other two species. *E. maculata* was also significantly smaller than *E. pilularis*.

The species-harvest interaction, which was significant at the 1% level of probability, is illustrated in Figure 4.1e. *E. globoidea* and *E. gummifera* had very small basal stem diameters relative to the other two species at week 4. Between week 4 and week 8, *E. maculata* was caught by *E. globoidea* and *E. gummifera*, and these three species grew at similar rates through to the final harvest. *E. pilularis* had the largest basal stem diameter from week 8 to week 20. For all species, there was a levelling out in diameter growth over the final two harvests.

(ii) Root Attributes

Root Dry Weight. The main effects of harvest and species, and the interaction between these were all highly significant ($P<0.001$). Overall, root dry weight increased significantly with each successive harvest (Table 4.2). Species differences show that *E. globoidea* and *E. gummifera* had smaller weights of roots than *E. pilularis* and *E. maculata*.

The mean root dry weight of seedlings for each species at each harvest is shown in Figure 4.1f. Ranked positions of species changed throughout the experiment. *E. globoidea* had the least early root development but grew more rapidly in the later weeks. *E. gummifera* grew relatively slowly throughout the experiment. *E. pilularis* had the largest weight of roots at all harvests except the first, although few of the differences were significant. *E. maculata* had the greatest early root growth (at week 4), and was intermediate between the other species at the final four harvests.

Root:Shoot Ratio. The effect of harvest period on the root:shoot ratio was highly significant ($P<0.001$). The root:shoot ratio at harvest 1 was double that at all other harvests. There were also significant ($P<0.05$) differences between species. The root:shoot ratio of *E. pilularis* was significantly greater than that of *E. gummifera* and *E. globoidea*.

The interaction between species and harvest was highly significant (P<0.001). The response of species over the five harvest periods is shown in Figure 4.1g. Each species showed a marked decline in root:shoot ratio from harvest 1 to harvest 2, and this was most pronounced in *E. gummifera*. This species and *E. maculata* also declined substantially between harvest 2 and harvest 3. *E. pilularis* increased its root:shoot ratio over this period. All species maintained relatively constant root:shoot ratios from week 12 to week 20 with *E. pilularis* having the largest and *E. gummifera* the smallest ratios at each of these.

(iii) Morphological Attributes

Number of Axillary Branches. The effects of harvest and species, and the interaction between these were all highly significant (P<0.001). Branch number increased with successive harvests except for the last harvest. Overall, *E. globoidea* had more axillary branches than all other species, while *E. pilularis* had significantly more than the two *Corymbia* species.

The number of branches for each species at each harvest (Figure 4.1h) shows that *E. globoidea* had the most branches at all harvests. *E. pilularis* had more branches than *E. maculata* and *E. gummifera* from harvest 2 onwards.

Number of Leaves. There were highly significant (P<0.001) differences in leaf number for each harvest and species, and in the interaction between these two factors. Except for weeks 16 to 20, all harvests showed significant increases in leaf number. All species responded differently, with leaf number increasing significantly in the order *E. gummifera* < *E. maculata* < *E. pilularis* < *E. globoidea*. While all species produced different numbers of leaves, three of the four species had similar leaf areas, indicating that the mean leaf size differed with species.

Species varied in their response at each harvest (Figure 4.1i). *E. maculata* had the greatest number of leaves at the first harvest. By week 8, *E. globoidea* and *E. pilularis* both had more, and the differences widened at week 12 and again at week 16. *E. globoidea* in particular was a prolific leaf producer. *E. gummifera* had a low number of leaves at all harvests, and was similar to *E. maculata* from week 8 onwards.

Table 4.1 Summary of the differences between attribute means associated with harvest period, species, and the interaction between these as derived from analyses of variance.

Attribute	Harvest	Species	Interaction
Shoot Height	***	***	NS
Plant Dry Weight	***	NS	NS
Shoot Dry Weight	***	*	*
Leaf Area	***	***	***
Basal Stem Diameter	***	***	**
Root Dry Weight	***	***	***
Root:Shoot Ratio	***	*	***
No. of Axillary Branches	***	***	***
No. of Leaves	***	***	***
Specific Leaf Area	***	***	**

* P<0.05; ** P<0.01; *** P<0.001; NS = not significant

Table 4.2 Ranking of seedling means for harvest period and species.

Attribute	Harvest					Species			
Shoot Height (cm)	2.57 (6.9) 1	4.75 (22.9) 2	5.79 (33.8) 3	6.42 (41.6) 4	6.43 (41.8) 5	4.73 (25.4) Eglo	5.04 (27.4) Egum	5.48 (32.1) Epil	5.52 (32.9) Emac
Plant Dry Weight (g)	0.50 1	2.97 2	8.12 3	13.73 4	17.68 5	8.09 Eglo	8.49 Epil	8.79 Egum	9.03 Emac
Shoot Dry Weight (g)	0.51 (0.29) 1	1.46 (2.19) 2	2.48 (6.24) 3	3.22 (10.46) 4	3.64 (13.39) 5	2.12 (6.05) Eglo	2.23 (5.99) Epil	2.32 (7.12) Egum	2.37 (6.88) Emac
Leaf Area (cm^2)	7.62 (62) 1	19.03 (373) 2	26.50 (708) 3	30.74 (953) 4	32.28 (1052) 5	22.08 (579) Egum	22.89 (646) Eglo	23.06 (593) Emac	24.91 (700) Epil
Basal Stem diameter (cm)	0.17 (1.20) 1	0.93 (2.58) 2	1.26 (3.56) 3	1.59 (4.94) 4	1.64 (5.22) 5	1.00 (3.10) Egum	1.04 (3.30) Eglo	1.14 (3.48) Emac	1.29 (4.12) Epil
Root Dry Weight (g)	-1.79 (0.20) 1	-0.32 (0.79) 2	0.56 (1.88) 3	1.16 (3.27) 4	1.42 (4.29) 5	-0.06 (2.02) Eglo	0.04 (1.67) Egum	0.42 (2.15) Emac	0.42 (2.50) Epil
Root:Shoot Ratio	-1.23 (0.30) 3	-1.17 (0.33) 4	-1.16 (0.33) 5	-1.04 (0.36) 2	-0.44 (0.71) 1	-1.14 (0.40) Egum	-1.06 (0.36) Eglo	-0.98 (0.42) Emac	-0.86 (0.45) Epil
No. of Axillary Branches	1.88 1	4.44 2	5.87 3	8.19 5	8.56 4	2.15 Egum	3.20 Emac	5.65 Epil	12.15 Eglo
No. of Leaves	2.72 (16) 1	3.58 (40) 2	3.93 (57) 3	4.22 (89) 5	4.26 (88) 4	3.27 (29) Egum	3.48 (34) Emac	3.82 (57) Epil	4.39 (111) Eglo
Specific Leaf Area	4.65 (107) 5	4.80 (123) 4	4.97 (147) 3	5.36 (214) 2	5.57 (268) 1	4.91 (152) Egum	5.00 (160) Emac	5.17 (182) Epil	5.20 (192) Eglo

NOTE:

i) Harvest period: 1 = 4 weeks; 2 = 8 weeks; 3 = 12 weeks; 4 = 16 weeks; 5 = 20 weeks.

ii) Species: Emac = *Eucalyptus maculata*; Egum = *E. gummifera*; Eglo = *E. globoidea*; Epil = *E. pilularis*

iii) Treatments are ranked in increasing order of magnitude; horizontal bars span treatments whose means do not differ significantly using LSD ($P<0.05$). Where transformations of the data have been made, the untransformed means are given in brackets.

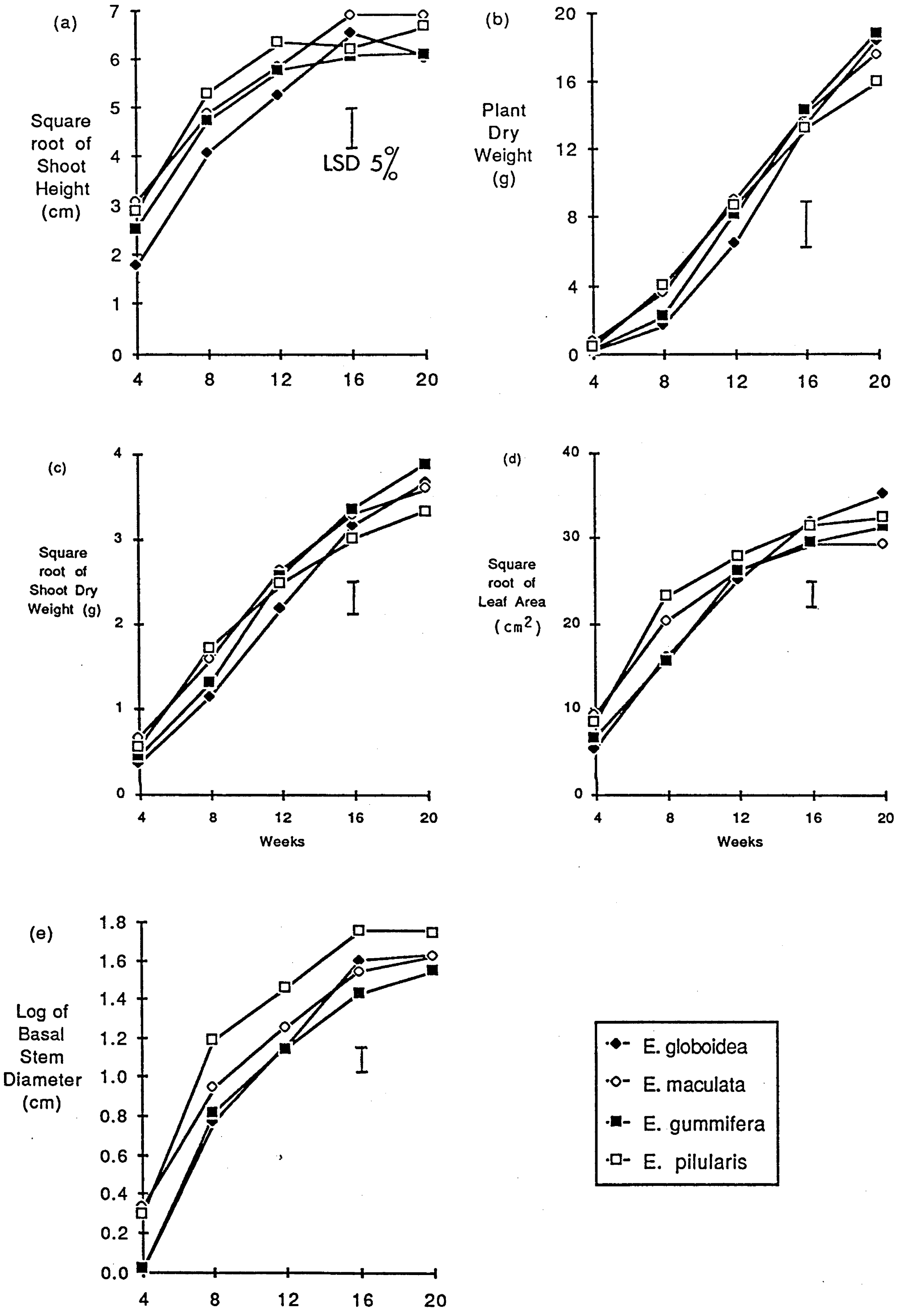

Figure 4.1 The response of (a) shoot height, (b) plant dry weight, (c) shoot dry weight, (d) leaf area and (e) stem diameter of seedlings of four eucalypt species.

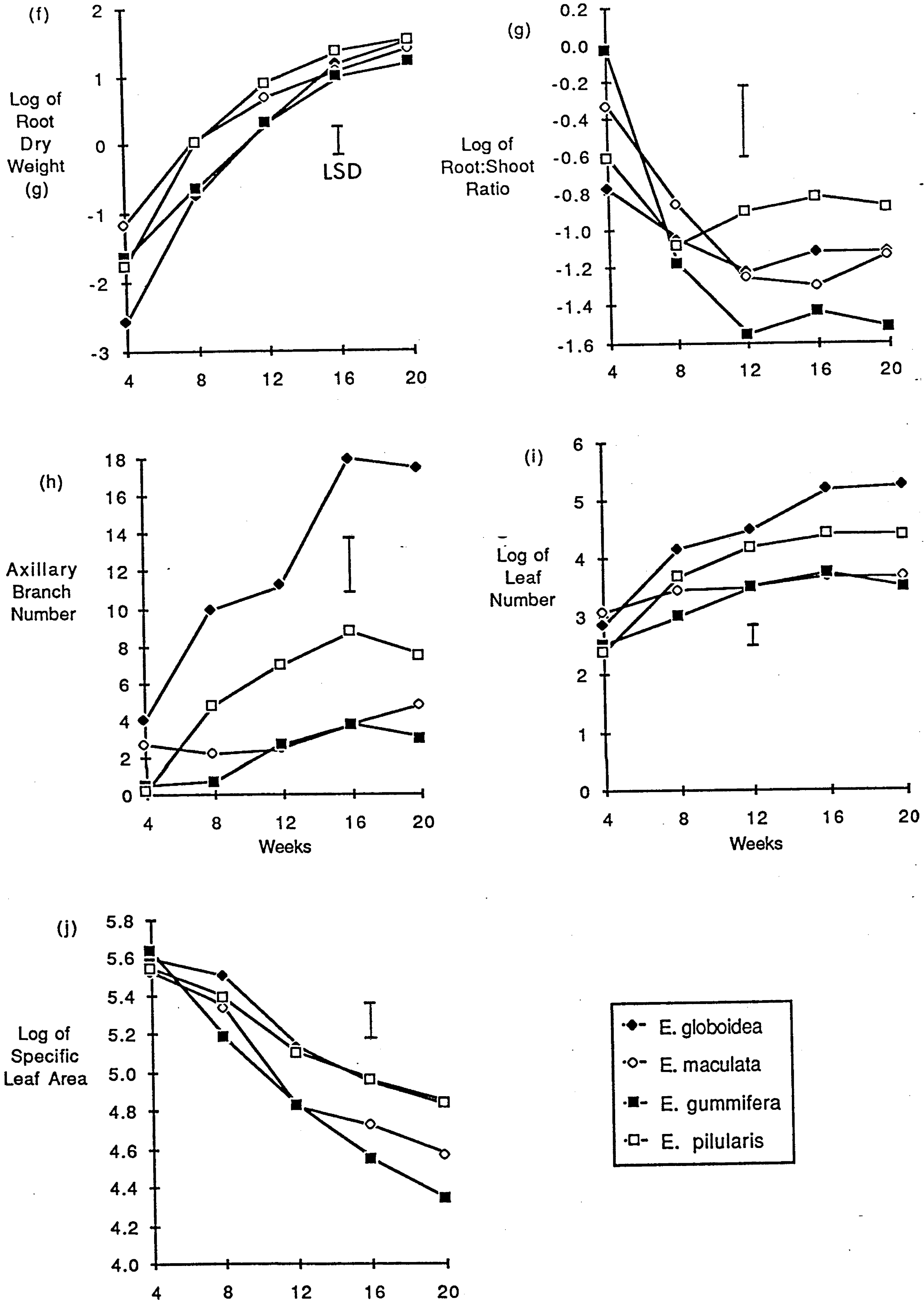

Figure 4.1 cont. The response of (f) root dry weight, (g) root:shoot ratio, (h) branch number, (i) leaf number and (j) specific leaf area of seedlings of four eucalypt species.

Specific Leaf Area. Specific leaf area is a ratio of leaf area to leaf dry weight. A lower value indicates that leaves are thicker (more sclerophyllous), and vice versa for a higher value.

The main effects of harvest and species were highly significant ($P<0.001$). Specific leaf area declined significantly with each successive harvest, that is, as seedlings age, their leaves become progressively thicker. Species variation has a possible subgeneric basis. *E. gummifera* (*Corymbia*) had the smallest specific leaf area. This was just significantly different from *E. maculata* (*Corymbia*), which in turn had a significantly smaller specific leaf area than the two *Monocalyptus* species, *E. pilularis* and *E. globoidea*.*

The interaction between species and harvest (Figure 4.1j) was significant ($P<0.01$). At harvest 1, all four species had similar specific leaf areas. Between weeks 4 and 12, *E. maculata* and particularly *E. gummifera* declined most rapidly so that for the final eight weeks, the two *Corymbia* species had appreciably smaller specific leaf areas than the two *Monocalyptus* species.

(iv) Foliar Nutrition

A summary of the analysis of variance of foliar nutrient concentrations is given in Table 4.3, and the ranked order of seedling means are given in Table 4.4. At successive harvests, the concentration of the elements nitrogen, phosphorus, potassium and sodium all decreased significantly, that is, as seedlings age, the foliar concentrations of these elements decline. For calcium and magnesium, there was no consistent way in which they varied over the three harvest periods. There were some pronounced differences between species. *E. maculata* had significantly higher concentrations of potassium and calcium, and a significantly lower concentration of magnesium than all other species. It also had the highest concentration of phosphorus, but this was not

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* it is not known how specific leaf areas obtained under glasshouse conditions relate to those in the field

significant. *E. maculata* had a significantly lower concentration of foliar nitrogen than *E. globoidea*, otherwise the four species were similar. *E. pilularis* had significantly greater sodium concentrations than all other species, while *E. gummifera* had a greater concentration of sodium than *E. maculata* and *E. globoidea*.

There were some interaction effects between species and harvest although none provided a consistent pattern of response.

Table 4.3 Summary of the differences between foliar nutrient element means associated with harvest period, species and the interaction between these as derived from analyses of variance.

Nutrient Element	Harvest	Species	Interaction
Nitrogen	***	*	NS
Phosphorus	***	**	NS
Potassium	***	***	**
Calcium	**	**	*
Magnesium	***	***	*
Sodium	***	***	*

* P<0.05; ** P<0.01; *** P<0.001; NS = not significant

Table 4.4 Ranking of foilar nutrient element means for harvest period and species.

Attribute	Harvest			Species			
Nitrogen	8.861 (7105) 5	9.267 (11411) 3	10.017 (22830) 1	9.314 (12328) Emac	9.363 (13103) Epil	9.372 (13585) Egum	9.477 (16112) Eglo
Phosphorus	6.106 (454) 5	6.502 (681) 3	7.229 (1405) 1	6.514 (746) Epil	6.561 (828) Eglo	6.634 (887) Egum	6.740 (937) Emac
Potassium	6364 5	9235 3	13342 1	8363 Eglo	8680 Epil	9400 Egum	12145 Emac
Calcium	2529 1	2951 5	3477 3	2428 Egum	2878 Epil	2927 Eglo	3712 Emac
Magnesium	7.573 (2022) 3	7.604 (2065) 5	7.908 (2802) 1	7.384 (1630) Emac	7.640 (2189) Egum	7.862 (2628) Epil	7.895 (2736) Eglo
Sodium	2071 5	2630 3	3708 1	1944 Emac	2345 Eglo	3074 Egum	3849 Epil

NOTE: i) Harvest period : 1 = 4 weeks; 3 = 12 weeks; 5 = 20 weeks.

ii) Species: Emac = Eucalyptus maculata; Egum = E. gummifera; Eglo = E. globoidea;
Epil = E. pilularis.

iii) Treatments are ranked in increasing order of magnitude; horizontal bars span treatments whose means do not differ signifcantly using LSD ($P<0.05$). Where transformations of the data have been made, the untransformed means are given in brackets.

4.2.3 Discussion

Where grown singly in pots on a 'moderately fertile' forest soil, there are only limited differences in seedling growth of four south coast eucalypt species, but more substantial differences in seedling form. Of the attributes measured, total plant dry weight production may arguably give the best indication of a seedling's growth capacity, and perhaps growth in height might infer differences in competitive ability at the early stage of the rotation. Under constant environmental conditions, there were no overall differences between species in plant dry weight production, although growth patterns differed somewhat over the 20 week period. *E. pilularis* and *E. maculata* grew fastest in the early stages but slowed relative to *E. globoidea* and *E. gummifera* later in the experiment - so that by the final harvest, *E. pilularis* had the least dry weight of any species. This pattern has been repeated to a certain extent for the attributes shoot dry weight and leaf area.

At each successive harvest, and over all harvests, *E. pilularis* and *E. maculata* had greater shoot height than *E. globiodea* and *E. gummifera*. Awang (1977) reported *E. pilularis* had stronger apical growth than the suite of eucalypt species he examined over many experiments. The enhanced early height growth of *E. pilularis* and *E. maculata* compared to *E. globoidea* and *E. gummifera* may be advantageous in situations where a large range of regrowth species are developing simultaneously.

E. pilularis and *E. maculata* also produced significantly greater root dry weight over the total growth period. However, root growth rates of the four species changed over time; the early growth of the *E. globoidea* root was slow, but was more rapid than that of *E. gummifera* and *E. maculata* over the latter part of the experiment. Over the whole experiment, the *E. gummifera* root grew relatively slowly and the *E. pilularis* root relatively faster.

There were some differences in root:shoot ratios. *E. pilularis* and *E. gummifera* had the highest and lowest values respectively over the last 4 harvests. All species however recorded a substantial decline in root:shoot ratios between weeks 4 and 8. *E. pilularis* also had a larger basal stem diameter at the final three harvests, and over all harvests, than the other three species. Both *E. globoidea* and *E. gummifera* had very small basal stem diameters early, but grew more rapidly than *E. maculata* later.

While there were relatively few growth differences between species, the form of that growth differed more markedly. This was reflected in the differences in the number of axillary branches and leaves, and in the specific leaf area. At any one harvest, the two *Corymbia* species, *E. maculata* and *E. gummifera* tended to be similar - with a substantially smaller number of branches and leaves than the *Monocalyptus* species, and more sclerophyllous leaves (i.e. a lower specific leaf area). *E. globoidea* had the largest number of axillary branches and leaves at all but the first harvest, and also the greatest specific leaf area at the early harvests. In addition, while there were marked differences in leaf number, three of the four species had similar leaf area, indicating that the mean leaf size differs with species. In particular, the mean leaf size for *E. globoidea* was much smaller than for the other species.

Basic differences in the form of seedlings suggest species may be adopting different strategies to cope with environmental limitations. The more sclerophyllous character of the leaves of *E. gummifera* and *E. maculata* suggest they may be better adapted to dry or low fertility environments (Beadle 1966, 1968). At the northern end of its range, *E. maculata* is a common dry country species; its leaf character may reflect greater evolutionary adaption to drought. *E. gummifera* is restricted to some of the less fertile, but not necessarily dry sites, on the south coast (Chapter 3); in this case, the more sclerophyllous leaf character may reflect adaption to low nutrient soils. Small leaf size, as is the case for *E. globoidea*, could be an adaption to maximization of water-use efficiency in a high radiation environment (Parkhurst and Loucks 1971) or to low nutrient soils (Beadle 1968, 1981). *E. globoidea* is commonly found on some of the lower fertility sites on the south coast (Chapter 3), and it may be that this factor is the major influence on leaf size for this species.

This experiment was designed to determine whether there were any basic physiological differences in the seedling growth and form of some south coast eucalypts, and in particular whether such differences might help to explain *E. maculata's* lack of regrowth vigour compared to other successional eucalypts on many sites within the regrowth stands. The results have shown that in an environment excluding competition, and where nutrients, water and the physical soil environment are not unduly limiting, the four species are physiologically similar in their ability to direct assimilates to growth. If this is largely true, the observed differences in the field distribution and vigour of the four species are due to differences in relative competitive ability of the species on particular sites. The following experiment examines the competitive abilities of two of these species, *E. maculata* and *E. pilularis*, where grown under a range of nutrient regimes.

4.3 EXPERIMENT 2 : COMPETITIVE RESPONSE OF *E. MACULATA* AND *E. PILULARIS* SEEDLINGS TO NUTRIENTS

Experiment 1 showed that there were few differences in the growth of *E. maculata* and *E. pilularis* when competition was excluded and soil resources were not unduly limiting. While their ranges broadly overlap, *E. pilularis* is a common component of communities at the low fertility end of the soil fertility gradient - communities from which *E. maculata* is excluded (Chapter 3). It is possible that the two species have different nutrient requirements which would provide them with a competitive advantage in the seedling stage of development. This experiment compares the response of *E. maculata* and *E. pilularis* at five nutrient levels. The species were grown in monoculture and in mixture to assess the effects of nutrient supply on inter- and intra-specific competition.

4.3.1 Materials and Methods

Experimental Design

The experiment was set out as a randomized complete block design with five nutrient levels, four species treatments, two harvest periods and five replications. Pots receiving the same treatment were paired at the first harvest to provide measures of relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR). The four 'species treatments' were:

1. *E. maculata* in monoculture.
2. *E. pilularis* in monoculture.
3. *E. maculata* in mixture with *E. pilularis*.
4. *E. pilularis* in mixture with *E. maculata*.

Treatments 3 and 4 were obtained by planting the two species in a single pot.*

Experimental Method

Seed of *E. maculata* and *E. pilularis* were sown in equal parts of perlite and vermiculite. At about 3-leaf-pair stage, eight seedlings were transplanted into 20 cm pots containing a 70:30 mixture of sand and vermiculite. This provided a medium for root growth which facilitated regular additions of nutrient solutions. For the following 25 days, all pots were watered weekly with 100 ml of 0.1 strength Hoaglands No. 1 nutrient solution (see Appendix II for details of this solution).

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* Treatments 3 and 4 are actually contained in the same pot, that is, two species planted in the same pot provide two treatments to measure. These are the growth of 'species 1' when planted with 'species 2' and the growth of 'species 2' when planted with 'species 1'.

Seedlings were then thinned to four per pot and the five nutrient treatments were started. Hoaglands No. 2 nutrient solution (Appendix II) was applied from above at a rate of 100 ml per week in concentrations of 0.10, 0.25, 0.50, 1 and 2 strength Hoaglands. Pots were watered twice daily, except for the days before and after the application of nutrients.* After 63 days, a pot from each paired set was randomly chosen for the first harvest.

At the first harvest two-way analyses of variance for height, dry weight and leaf area attributes indicated that for all four species treatments, the increase in growth in response to increasing nutrient concentration was largely linear. That is, luxury levels of nutrients for growth had not been reached. Since part of the experiment was designed to examine the response of the two species at higher nutrient levels, it was decided to double the concentrations by applying 100 ml of nutrient solution at the same concentrations, but twice weekly. This regime was maintained for 42 days, whereupon the second harvest was carried out.

At the first and second harvests, the primary attributes of shoot height, shoot dry weight, and leaf area were measured. Relative growth rates (RGR) for each attribute, net assimilation rate (NAR), leaf area ratio (LAR) and root:shoot ratio were derived from these measurements. Specific leaf area (SLA) was calculated from leaf area and leaf dry weight data from the second harvest. In addition, the leaves of *E. maculata* and *E. pilularis* were sampled at this harvest for determination of total nitrogen, phosphorus, potassium, calcium, magnesium and sodium concentrations.

Data were analysed using two-way analyses of variance, the factors being nutrient concentration and species treatment. Where there was heterogeneity of variance, a log or square root transformation was made. Only untransformed means are referred to in the text.

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* Watering via an automatic dripper system led to water passing through the pots; any leaching is presumed to be constant for all pots.

4.3.2 Results

The results of analyses of variance are summarized in Table 4.5, and mutiple range comparisons of attribute means in Table 4.6. The response of each species treatment, at each nutrient level, for the range of attributes assessed are illustrated in Figure 4.2a-h.

For most of the attributes, there were highly significant (P<0.001) differences between nutrient regimes. For many attributes, there were also significant differences between species treatments. Apart from total and relative shoot height, no attributes showed a significant species-nutrient interaction.

(i) Shoot Attributes

Total Shoot Height. The effects of nutrients, the response of the species treatments and the interaction between nutrients and species were all highly significant (P<0.001) (Table 4.5). Shoot height increased significantly with each successive increase in nutrient strength (Table 4.6). Overall, *E. pilularis* in monoculture grew significantly faster than the other three species treatments.

The height growth patterns are broadly similar for all species treatments (Figure 4.2a), even though the interaction effect was highly significant (P<0.001). Only at the lowest nutrient level (0.10 Hoaglands) did the species treatments vary markedly in their ranked order of means. The significance of differences at this nutrient concentration may be questioned because of the very poor growth of these seedlings over the life of the experiment. Fxcept for 0.10 Hoaglands, *E. pilularis* in monoculture consistently had the largest shoot height, although few of the differences were significant. The species treatments were more widely separated at the intermediate nutrient concentrations.

Relative Growth Rate of Shoot Height (RGR_h). The relative growth rate of shoot height of *E. maculata* tended to increase with increasing nutrient supply (Figure 4.2b) and that of *E. pilularis* tended to decline.

Overall, there was a significant ($P<0.01$) response of species treatments to nutrient supply; treatments with *E. pilularis* put on more height increment than treatments with *E. maculata*. The difference between *E. maculata* in mixture and *E. pilularis* in mixture was not significant (Table 4.6). The main effect of nutrients was not significant.

The interaction between species treatments and nutrients was highly significant ($P<0.001$) and is illustrated in Figure 4.2b. *E. maculata* in monoculture increased in RGR_h from 0.0066 cm cm^{-1} day^{-1} at the lowest nutrient regime to 0.0102 cm cm^{-1} day^{-1} at the highest. Relative height growth of *E. maculata* in mixture also increased from the lowest to the highest nutrient regime, but in more distinct stages. At 0.10, 0.25 and 0.50 strength Hoaglands, it had depressed relative height growth of around 0.0070 cm cm^{-1} day^{-1}. This increased to 0.0111 cm cm^{-1} day^{-1} at 1 strength Hoaglands and increased again to 0.0144 cm cm^{-1} day^{-1} at 2 strength Hoaglands.

In contrast to *E. maculata*, the relative height growth of *E. pilularis* declined with increasing nutrient supply. In monoculture, *E. pilularis* had relative height growth rates in the range 0.0126-0.0138 cm cm^{-1} day^{-1} at the lowest three nutrient regimes (0.10, 0.25 and 0.50 strength Hoaglands). This declined to 0.0091 and 0.0082 cm cm^{-1} day^{-1} at 1 and 2 strength Hoaglands respectively. The pattern of decline was similar for *E. pilularis* in mixture, although the significant fall occurred between 0.25 and 0.50 strength Hoaglands. At 0.10 and 0.25 strength Hoaglands, *E. pilularis* in mixture had relative height growth rates of 0.0153 and 0.0132 cm cm^{-1} day^{-1} respectively. At the three higher nutrient regimes, the rates were in the range 0.0080-0.0087 cm cm^{-1} day^{-1}. It highlights the fact that *E. maculata* and *E. pilularis* responded differently to increasing nutrient to say that the highest relative height growth rates for the two species were recorded at opposite ends of the nutrient spectrum.

Total Shoot Dry Weight. There was a highly significant ($P<0.001$) effect of nutrients - all five nutrient levels are associated with significant increases in shoot dry weight. Species and interaction terms were not significant. The similarity in response of the four species treatments at the five nutrient levels is illustrated in Figure 4.2c.

Relative Growth Rate of Shoot Dry Weight (RGR_s). Overall, the effect of nutrients was highly significant ($P<0.001$). Apart from the 0.25 and 0.50 strength treatments, each successive increase in nutrient concentration corresponded with a significant increase in RGR_s. Neither the effect of species nor the species-nutrient interaction term was significant. Figure 4.2d shows that there was some variation in species treatments at lower nutrient concentrations but the pattern is neither consistent nor pronounced.

(ii) Leaf Attributes

Total Leaf Area. Nutrient supply significantly ($P<0.001$) affected total leaf area. Increasing leaf area was associated with increasing nutrient concentration. There was also a highly significant ($P<0.001$) difference for the main effect of species treatments. *E. pilularis* in monoculture had significantly more leaf area than the other three species treatments, while *E. pilularis* in mixture had significantly more than the treatments with *E. maculata*.

The interaction between species treatment and nutrients was not significant. The patterns were similar for the four species treatments (Figure 4.2e) with the *Monocalyptus* species having slightly greater leaf area than the *Corymbia* species.

Relative Growth Rate of Leaf Area (RGR_a). The effects of nutrients and species treatment on relative growth rate of leaf area were highly significant ($P<0.001$). The 2 strength Hoaglands provided growth that was significantly greater than all other nutrient concentrations. *E. pilularis* growing in either monoculture or in mixture with *E. maculata*, had a greater RGR_a than *E. maculata* in monoculture or mixture.

The interaction term was not significant and while there was some variation in the response of each species treatment at the different nutrient levels (Figure 4.2f), the treatments with *E. pilularis* had consistently higher RGR_a than the treatments with *E. maculata*.

Leaf Area Ratio (LAR). Overall, there was only a slight significant ($P<0.05$) effect of nutrient supply on the size of the photosynthetic system, though the pattern was not consistent. Alternatively, the response of the species treatments was highly significant ($P<0.001$). *E. pilularis*, whether in monoculture or in mixture with *E. maculata*, had significantly greater LAR than *E. maculata*. The interaction between species treatments and nutrients was not significant, that is, the differences between species treatments at each of the five nutrient levels (Figure 4.2g) tend to be the same as those in the overall species response, with *E. pilularis* having greater LARs than *E. maculata*.

(iii) Net Assimilation Rate (NAR)

The derivation of NAR in this analysis is based on shoot dry weight only. The NAR of *E. maculata* had an increasing advantage over *E. pilularis* with increasing nutrient supply (Figure 4.2h).

The main effect of nutrient concentration on NAR was highly significant ($P<0.001$), increasing approximately linearly from 0.00842 g dm^{-2} day^{-1} at 0.10 strength Hoaglands to 0.02036 g dm^{-2} day^{-1} at 2 strength Hoaglands. There was also a significant ($P<0.05$) effect of nutrient supply on species treatments. *E. maculata* had a greater NAR than *E. pilularis*, whether in monoculture or in mixture with *E. pilularis*, though the difference between *E. maculata* in monoculture and *E. pilularis* in monoculture was not significant.

Table 4.5. Summary of differences between attribute means associated with nutrients, species treatments and the interaction between these as derived from analyses of variance.

Attribute	Nutrient	Species Treatment	Interaction
Total Shoot Height	***	***	***
Relative Growth Rate of Height	NS	**	***
Total Shoot Dry Weight	***	NS	NS
Relative Growth Rate of Shoot Dry Weight	***	NS	NS
Total Leaf Area	***	***	NS
Relative Growth Rate of Leaf Area	***	***	NS
Leaf Area Ratio	*	***	NS
Net Assimilation Rate (Shoot)	***	*	NS

* $P<0.05$; ** $P<0.01$; *** $P<0.001$; NS = not significant

Table 4.6. Ranking of seedling means for nutrients and species treatments.

Attribute	Nutrient					Species Treatment			
Total Shoot Height	1.90 (6.7) 0.1	2.35 (10.7) 0.25	2.79 (16.5) 0.5	3.21 (25.1) 1	3.72 (41.5) 2	2.73 (18.6) EmMon	2.75 (19.1) EmMix	2.77 (19.7) EpMix	2.92 (23.1) EpMon
Relative Growth Rate of Height	0.00953 1	0.00963 0.5	0.01007 0.25	0.01037 2	0.01039 0.1	0.00863 EmMon	0.00925 EmMix	0.01070 EpMix	0.01141 EpMo
Total Shoot Dry Weight	-1.38 (0.26) 0.1	-0.56 (0.58) 0.25	0.18 (1.21) 0.5	1.02 (2.88) 1	1.98 (7.44) 2	0.20 (2.48) EpMix	0.23 (2.42) EmMon	0.26 (2.49) EmMix	0.30 (2.51) EpMon
Relative Growth Rate of Shoot Dry Weight	0.01257 0.1	0.01624 0.25	0.01870 0.5	0.02217 1	0.02714 2	0.01836 EmMon	0.01935 EpMix	0.01984 EmMix	0.01991 EpMon
Total Leaf Area	3.56 (36) 0.1	4.37 (80) 0.25	5.09 (166) 0.5	5.85 (360) 1	6.74 (870) 2	4.98 (254) EmMon	5.04 (272) EmMix	5.18 (336) EpMix	5.29 (347) EpMon
Relative Growth Rate of Leaf Area	0.01375 0.25	0.01388 0.1	0.01496 0.5	0.01525 1	0.01924 2	0.01302 EmMon	0.01336 EmMix	0.01754 EpMon	0.01774 EpMix
Leaf Area Ratio	139.4 0.1	140.7 2	144.9 1	145.3 0.25	147.7 0.5	132.0 EmMon	133.7 EmMix	152.9 EpMix	155.8 EpMon
Net Assimilation Rate (Shoot)	0.00842 0.1	0.01120 0.25	0.01287 0.5	0.01594 1	0.02036 2	0.01244 EpMix	0.01295 EpMon	0.01439 EmMon	0.01525 EmMix

NOTE: i) Nutrient treatments: 0.1 = $^1/10$ strength Hoaglands; 0.25 = $^1/4$ strength Hoaglands; 0.5 = $^1/2$ strength Hoaglands; 1 = single strength Hoaglands; 2 = double strength Hoaglands.

ii) Species Treatments: EmMon = *Eucalyptus maculata* in Monoculture; EmMix = *E. maculata* in Mixture; EpMon = *E. pilularis* in Monoculture; EpMix = *E pilularis* in Mixture.

iii) Treatments are ranked in increasing order of magnitude; horizontal bars span treatments whose means do not differ signifcantly using LSD ($P<0.05$). Where transformations of the data have been made, the untransformed means are given in brackets.

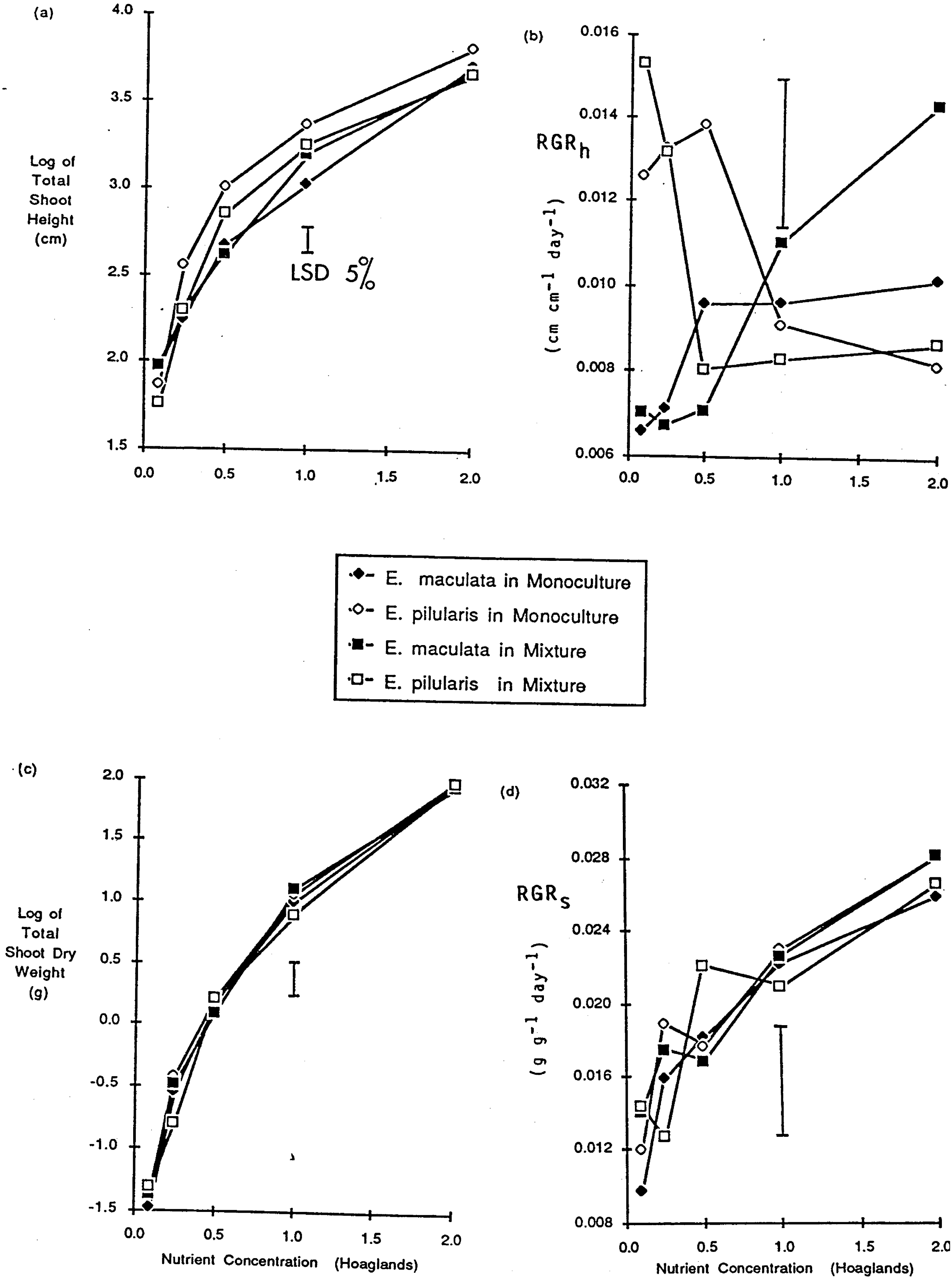

Figure 4.2 The response to five nutrient concentrations of (a) total shoot height, (b) relative growth rate of shoot height (c) total shoot dry weight and (d) relative growth rate of shoot dry weight of *E. maculata* and *E. pilularis* in monoculture and in mixture.

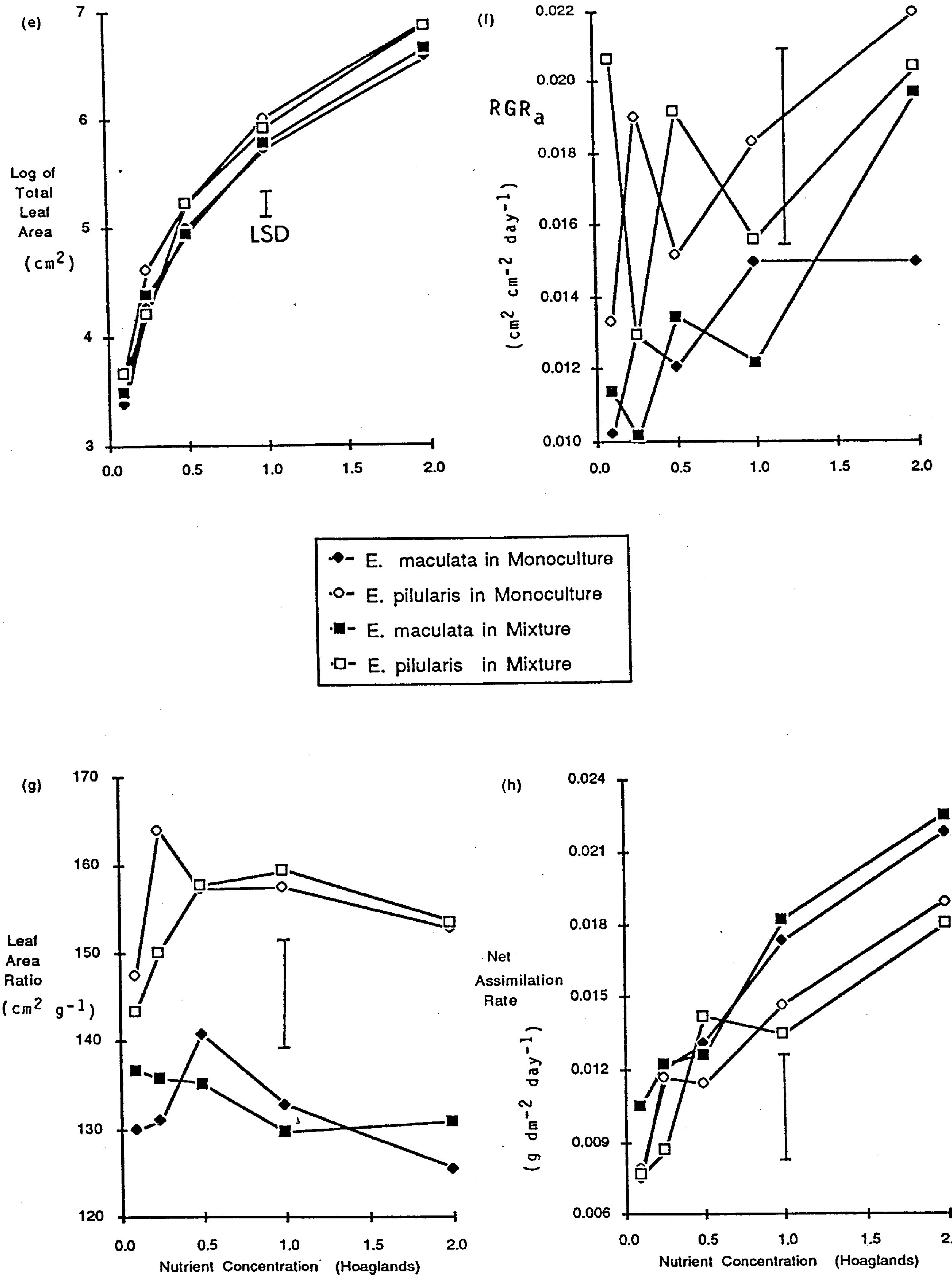

Figure 4.2 cont. The response to five nutrient concentrations of (e) total leaf area, (f) relative growth rate of leaf area, (g) leaf area ratio and (h) net assimilation rate of *E. maculata* and *E. pilularis* in monoculture and in mixture.

The interaction term was not significant. The response of species treatments to increasing nutrient supply is shown in Figure 4.2h. At the three lower levels, there was no consistent pattern in NAR for the species treatments. However, at the two higher nutrient levels, the differences between species treatments were more distinct. The two treatments with *E. maculata* had consistently higher NARs than the two *E. pilularis* mixes at 1 and 2 strength Hoaglands, though the differences between *E. maculata* in monoculture and *E. pilularis* in monoculture were not significant.

(iv) Foliar Nutrition

A summary of analysis of variance results are given in Table 4.7. In general, there were few striking differences in foliar nutrient concentrations between different Hoaglands nutrient treatments. The elements phosphorus, calcium and magnesium showed a consistent decrease in leaf concentrations with increasing Hoaglands concentration, for example, at 0.1 Hoaglands, the foliar concentration of phosphorus was 2077 ppm, and at 2 Hoaglands, 1403 ppm (Table 4.8). However, only some of the differences were significant. For the element nitrogen, the trend was reversed, although the differences between treatments were not particularly marked. At 0.1 Hoaglands, the concentration of foliar nitrogen was 12365 ppm and at 2 Hoaglands, 14382 ppm. There were no differences in foliar concentrations for the elements potassium and sodium.

The species contrasts show that *E. maculata* had significantly higher concentrations of nitrogen, phosphorus and potassium than *E. pilularis*, but significantly lower concentrations of magnesium and sodium. There were some interactions but the patterns were not consistent.

Table 4.7 Summary of differences between foliar nutrient element means associated with nutrients, species and the interaction between these as derived from analyses of variance.

Attribute	Nutrient	Species	Interaction
Nitrogen	***	***	***
Phosphorus	***	***	***
Potassium	NS	***	NS
Calcium	***	NS	***
Magnesium	***	***	NS
Sodium	NS	***	NS

* $P<0.05$; ** $P<0.01$; *** $P<0.001$; NS = not significant

4.3.3 Discussion

There are a some differences in the way seedlings of *E. maculata* and *E. pilularis* respond to nutrient availability, and such responses are to a certain extent determined by the type of competition present (i.e. intra- or inter-specific competition).

For all primary growth attributes (shoot height, shoot dry weight and leaf area), and for two derived growth attributes (relative growth rate of shoot dry weight and net assimilation rate), there was largely a positive linear response to increasing nutrient concentration. While the way tree seedlings respond to increasing nutrient supply varies with species, similar responses for some plant attributes have been reported elsewhere for *E. maculata* and *E. pilularis* (Halsall *et al.* 1983), and

Table 4.8 Ranking of foliar nutrient element means for nutrient treatments and species.

Attribute	Nutrient					Species	
Nitrogen	9.408 (12365) 0.1	9.465 (13025) 0.25	9.525 (13838) 0.5	9.554 (14128) 2	9.573 (14382) 1	9.422 (12468) Epil	9.588 (14627) Emac
Phosphorus	7.244 (1403) 2	7.336 (1545) 1	7.388 (1663) 0.5	7.400 (1678) 0.25	7.601 (2077) 0.1	7.243 (1405) Epil	7.545 (1941) Emac
Potassium	11638 0.1	11955 1	12103 0.5	12434 0.25	12551 2	10423 Epil	13849 Emac
Calcium	8.259 (3904) 2	8.320 (4172) 1	8.348 (4283) 0.5	8.380 (4417) 0.25	8.735 (6506) 0.1	8.386 (4442) Epil	8.430 (4870) Emac
Magnesium	8.229 (3819) 2	8.333 (4238) 1	8.507 (5044) 0.5	8.709 (6159) 0.25	8.777 (6636) 0.1	8.346 (4324) Emac	8.676 (6034) Epil
Sodium	1877 2	1999 0.25	2078 0.5	3111 1	2118 0.1	1384 Emac	2690 Epil

NOTE: (i) Nutrient treatments: 0.1 = ^{1}/10 Hoaglands; 0.25 = ^{1}/4 Hoaglands; 0.5 = ^{1}/2 Hoaglands; 1 = single Hoaglands; 2 = double Hoaglands.

(ii) Species: Emac = *Eucalyptus maculata*; Epil = *E. pilularis*.

(iii) Treatments are ranked in increasing order of magnitude; horizontal bars span treatments where means do not differ significantly using LSD ($P<0.05$). Where tranformations of the data have been made, the untransformed means are given in brackets.

also for *E. saligna* and *E. microcorys* (Awang 1977), and scribbly gums and *Angophoras* (Mowatt 1981). The linearity of response suggests that up to the highest nutrient levels, the seedlings of *E. maculata* and *E. pilularis* have been able to convert additional nutrients directly into increased growth and this indicates that luxury levels of nutrients were not reached. This experiment may therefore reflect the responses of seedlings at the low to medium end of the nutrient spectrum. For some derived attributes (relative growth rates of shoot height and leaf area) the response to nutrients has been more variable with no consistent pattern emerging.

The way *E. maculata* and *E. pilularis* have responded to increasing nutrient supply is perhaps the most important result in the context of the general hypothesis (Chapter 1). This proposes that *E. maculata* may be more competitive on higher fertility sites but as fertility declines, *E. maculata* would lose its competitive advantage to other, better adapted species (e.g. *E. pilularis*).

There was a significant interaction between species treatment and nutrients for relative growth rate of shoot height. This attribute compares growth without the often variable effect associated with the initial establishment phase. There is a difference between species responses as nutrient concentration changes. The relative growth rate of shoot height of *E. maculata* increases, and that of *E. pilularis* decreases as nutrient supply increases. This implies that under field conditions, the relative competitive ability of these two species in terms of height growth may change with changes in site fertility. On higher nutrient sites, *E. maculata* may be able to emerge from the regrowth species more rapidly than *E. pilularis* of similar size, but as sites become marginal for *E. maculata*, *E. pilularis* may develop a competitive advantage whereby it is able to achieve a dominant position more rapidly.

The response of the species also varied with nutrient supply, in terms of net assimilation rate. At lower nutrient levels, the NAR of species was similar, but at the higher concentrations, *E. maculata* was superior to *E. pilularis*. The largest differences occurred between *E. maculata* in mixture and *E. pilularis* in mixture, suggesting that the enhanced response of *E. maculata* at the higher nutrient concentrations may have had the effect of reducing the NAR of *E. pilularis*. As with relative growth rate of shoot height, the differences between species in NAR suggest *E. maculata* may be more competitive on sites of higher fertility. Such responses may be implicated in the variable development of these two species in the regrowth stands on Kioloa State Forest, as described in Chapter 2.

E. pilularis had greater total and relative leaf area growth than *E. maculata*. A similar pattern was shown in Experiment 1, suggesting that *E. pilularis* may be an inherently leafier species. *E. pilularis* also had consistently higher LARs than *E. maculata* at each nutrient level. A larger LAR may be due to a larger leaf surface area per unit leaf weight (specific leaf area), or to a larger proportion of the plant's total assimilate being used in leaf production (Turnbull 1979). Experiment 1 has shown that *E. pilularis* has a larger specific leaf area than *E. maculata*, and therefore this component may be at least partly responsible for the differences in LAR in the present experiment. The consistently superior performance of *E. pilularis* over *E. maculata* in terms of leaf growth attributes may indicate a competitive advantage in situations where it becomes important to harvest adequate light for photosynthesis. Such situations are likely to occur in rapidly developing regrowth stands.

The species treatments produced similar total and relative shoot dry weight at each nutrient concentration. The point is made that while seedling attributes associated with photosynthetic efficiency (NAR) and shoot elongation (shoot height), varied between species with changes in nutrient supply, the attributes which measure the capacity of seedlings to produce assimilate for growth (total and relative shoot dry weight) did not. Thus where other factors are controlled, seedling *E. maculata* and *E. pilularis* could have equal competitive abilities over a range in nutrient supply, in terms of above-ground assimilate production. The mechanisms by which this is achieved, however, may differ. Compared to *E. pilularis*, *E. maculata* at the higher nutrient concentrations showed greater efficiency of its assimilatory surface to capture, convert and conserve energy (i.e. higher NAR), while maintaining a smaller area of transpiring leaf surface (i.e. lower LAR) (Awang 1977).

The differences in foliar nutrient concentrations between the five Hoaglands nutrient treatments were not exceptional. In contrast, the growth rates were markedly different. As was suggested previously, the plant may be able to convert the additional nutrients into increased growth. In fact, for phosphorus, calcium and magnesium, there has been a dilution effect in that higher soil nutrient concentrations are associated with lower foliar nutrient concentrations. Other workers (Cromer and Williams 1982; Crane 1984) have reported similar responses.

E. maculata had significantly higher concentrations of nitrogen, phosphorus and potassium than *E. pilularis*. These three elements are particularly important for plant growth generally (Russell 1973), including the eucalypts (Schönau 1984). Given that shoot dry weight production for *E. maculata* and *E. pilularis* was similar at each of the five soil nutrient concentrations (Figure 4.2c), the differences may indicate that *E. maculata* has a greater requirement for nitrogen, phosphorus and potassium for equivalent growth rates.

Foliar nutrient concentrations were also examined in a 13-year-old *E. maculata* and *E. pilularis* regrowth stand, covering a range of vigour classes (Table 4.9). Young fully expanded leaves were sampled from the region of apical extension at the highest point on the plant. Within each species, there was generally little consistency in foliar nutrient

Table 4.9 Foliar nutrient concentrations of 13-year-old *E. maculata* and *E. pilularis* regrowth for three vigour classes.

Attribute	Treatment					
Nitrogen	13482 EpMv	15048 EmLv	15710 EmMv	15778 EpHv	15785 EmHv	16034 EpLv
Phosphorus	665 EpMv	762 EpLv	810 EpHv	943 EmMv	987 EmLv	1049 EmHv
Potassium	3756 EpHv	4640 EpMv	6166 EpLv	9747 EmHv	11724 EmLv	11788 EmMv
Calcium	1530 EpHv	1790 EpMv	3208 EmHv	3477 EmLv	3450 EmLv	4374 EmMv
Magnesium	1694 EmLv	1795 EmHv	1911 EmMv	1915 EpLv	2273 EpHv	2401 EpMv
Sodium	1359 EmHv	1624 EmMv	1919 EpMv	2230 EmLv	2205 EpHv	2938 EpLv

NOTE: (i) Em = *Eucalyptus maculata*; Ep = *E. pilularis*.

(ii) Lv = Low vigour stem; Mv = Medium vigour stem;

Hv = High vigour stem.

(iii) Values are ppm.

(iv) Treatments from the Low and Medium vigour classes represent the mean of 10 replications; treatments for the High vigour classes represent the mean of 5 replications.

(v) Treatments are ranked in increasing order of magnitude; horizontal bars span treatments whose means do not differ significantly using LSD ($P<0.05$).

concentrations between the vigour classes, i.e. growth response and concentrations of leaf elements are not directly related. This is consistent with the findings of the glasshouse experiment. The between species contrasts show that *E. maculata* had consistently higher concentrations of phosphorus and potassium, and lower concentrations of magnesium than *E. pilularis*, differences again reported in the glasshouse experiment.

An interesting aspect of these studies relates to a comparison of foliar nutrient concentrations for *E. maculata* and *E. pilularis* in Experiments 1 and 2. The age of seedlings when foliar nutrients were determined was fairly similar - for Experiments 1 and 2, 196 and 180 days respectively. The concentrations of the six foliar elements for Experiments 1 and 2 are shown in Table 4.10. This shows that comparably aged seedlings from the two experiments had foliar nutrient concentrations which were substantially different. For example, *E. maculata* had foliar nitrogen levels of around 14500 ppm at all levels of nutrient supply in Experiment 2, but a foliar nitrogen concentration of only 7326 ppm in Experiment 1. Seedlings were vigorous and healthy in both cases. This pattern was repeated for most other nutrients, and related to the foliar concentrations in *E. pilularis* as well. Because large differences in nutrient supply had little effect on foliar nutrient concentrations (Experiment 2), differences in nutrient supply between experiments are unlikely to have caused the large differences in foliar nutrients. It is suggested, therefore, that the differences between experiments are due to factors associated with the physical soil environment. In Experiment 1, the soil was from a moderately fertile forest site on the south coast. In Experiment 2, the growth medium was a mixture of sand and vermiculite. The mechanism by which foliar nutrient concentrations vary with growing medium is unknown but, it is possible that physical conditions associated with root growth influence the distribution of nutrient elements within the plant.

Table 4.10 A comparison of foliar nutrient concentrations between Experiment 1 and Experiment 2.

Experiment 1(a)

Species	Nutrient Element (ppm)					
	N	P	K	Ca	Mg	Na
E. maculata	7326	535	7686	4052	1532	1724
E. pilularis	7120	444	5744	2843	2589	2935

Experiment 2$^{(b)}$

Species	Hoaglands Nutrient Concentration	N	P	K	Ca	Mg	Na
E. maculata	0.1	14282	2614	13546	8185	5468	1509
	0.25	14628	2003	14433	4309	5268	1431
	0.5	14468	1987	13538	4565	4113	1325
	1	14927	1674	13599	3775	3613	1522
	2	14093	1429	14131	3518	3159	1130
E. pilularis	0.1	10448	1540	9731	4826	7804	2726
	0.25	11421	1353	10435	4525	7049	2567
	0.5	12470	1339	10669	4002	5974	2830
	1	13838	1417	10310	4568	4862	2700
	2	14163	1377	10972	4289	4479	2624

NOTE:

(i) Seedlings from Experiment 1, 196 days old; seedlings from Experiment 2, 180 days old.

(ii) Experiment 2 lists foliar nutrient concentrations for seedlings grown at five Hoaglands soil nutrient concentrations.

(a) Each nutrient concentration represents the mean of 4 replications.

(b) Each nutrient concentration represents the mean of 5 replications.

To summarize, this experiment has shown that for some attributes, *E. pilularis* grew consistently better than *E. maculata*, regardless of nutrient concentration, and for others, there was no difference. However, for the attributes relative growth rate of shoot height and net assimilation rate, the response varied as soil nutrient concentration changed. *E. maculata* was more efficient in producing dry matter and directing it to height growth as nutrient supply increased.

4.4 EXPERIMENT 3 : COMPETITIVE RESPONSE OF *E. MACULATA* AND *ACACIA MABELLAE* SEEDLINGS TO NUTRIENTS

It seems likely from the foregoing experiment that differences in the way species respond to nutrients could play some role in the delimitation of *E. maculata* and *E. pilularis* along a soil nutrient gradient, and in the earlier emergence of *E. pilularis* from shrub successional species developing after clearfelling of mixed species forest. We might now turn to the question - to what extent might the continuing dominance of *Acacia* species reflect the greater competitive ability of these species on sites with a limited soil nutrient pool? It is possible *Acacia* may be able to respond better than *E. maculata* at low nutrient regimes, and thereafter maintain dominance over *E. maculata*. In this section, the responses of *E. maculata* and the wattle, *Acacia mabellae*, in monoculture and in mixture, to four nutrient regimes are compared.

4.4.1 Materials and Methods

Experimental Design

The experiment was laid out as a randomized design with four nutrient regimes, four species treatments, two harvest periods and five replications. Pots receiving the same treatment were paired at the first harvest to provide measures of relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR). The four species treatments were:

1. *E. maculata* in monoculture
2. *A. mabellae* in monoculture
3. *E. maculata* in mixture with *A. mabellae*
4. *A. mabellae* in mixture with *E. maculata*.

Treatments 3 and 4 were obtained by planting the two species in a single pot.

Experimental Method

Seed of *E. maculata* and *A. mabellae* were sown in equal parts of perlite and vermiculite. The *Acacia* seed was pretreated in boiling water for three one minute intervals, taking out each time those seed which had imbibed water. About 30 days after germination, four seedlings (later thinned to two) were transplanted into 15 cm pots containing a sandy loam soil taken from a commercial soil yard. This growth medium unlike a forest soil, allowed regular addition of nutrients in solution and was selected in preference to a pure sand to provide more realistic structure for root penetration. The soil contained 205 and 162 ppm of total nitrogen and phosphorus respectively. The basal level of phosphorus in this soil is not particularly low and being a sandy loam, a substantial part of this could be 'available' phosphorus.

At 21 days after transplanting the seedlings, the soil was inoculated with an appropriate rhizobium inoculum (obtained from J. Brockwell, CSIRO Division of Plant Industry) and nutrients treatments were started. Four nutrient regimes were based on modifying a complete nutrient solution used by Halsall *et al.* (1983). Nitrogen and phosphorus were added and withheld in 2^2 factorial combination, with a basal level of all other nutrients added to all pots. Details of the nutrient solutions are given in Appendix III. The nutrients were applied from above at a rate of 50 ml twice weekly. For the first and second applications, solutions were applied at $^1/_4$ and $^1/_2$ strengths respectively. Pots were watered daily, except for the days before and after the application of nutrients. After 51 days, a pot from each pair was randomly chosen for the first harvest. The same nutrient regime was maintained for another 52 days, whereupon the second harvest was done.

At the first and second harvests, the primary attributes of shoot height, shoot and root dry weight (which included nodule weight), and leaf area were measured. Relative growth rates (RGR) for each attribute, net assimilation rate (NAR), leaf area ratio (LAR) and root:shoot ratio were derived from these measurements. Data were analysed using two-way analyses of variance, the factors being nutrient regime and species treatment.

4.4.2 Results

The results of analyses of variance are summarized in Table 4.11, and mutiple range comparisons of attribute means in Table 4.12. The response of each species treatment to each nutrient regime, for the range of attributes assessed, are illustrated in Figure 4.3a-m. There were considerable differences in the way the species treatments responded to nutrients and some differences between responses of species where grown under intra- and inter-specific competition. In the text, treatments without added nitrogen or phosphorus are referred to by the subscripts N_0 and P_0 respectively. Those with added nitrogen or phosphorus are N_1 and P_1.

In this study, the interaction effects (i.e. how each species treatment responds to the different nutrient regimes) are considered to be most important. However, to maintain a logical sequence within the text, these are not discussed until the main treatment effects have been examined, although this may only be done briefly.

(i) Plant and Shoot Attributes

Total Shoot Height. The effect of nutrients on total shoot height was highly significant ($P<0.001$) (Table 4.11). The two treatments with added nitrogen (N_1P_0 and N_1P_1) produced significantly greater shoot height than the two low nitrogen (N_0P_0 and N_0P_1) treatments (Table 4.12). The responses of the species treatments also differed significantly ($P<0.01$) - *E. maculata* in monoculture grew significantly less in height than *A. mabellae* in monoculture, *E. maculata* in mixture, and *A. mabellae* in mixture.

The interaction between nutrient and species treatment was highly significant ($P<0.001$). The response of each species treatment at the four nutrient regimes is shown in Figure 4.3a. Several points can be noted.

1. For each species treatment, there was a significant increase in height between treatments without (N_0), and treatments with (N_1) added nitrogen.
2. In the two low nitrogen treatments, shoot height of *A. mabellae*, and particularly *A. mabellae* in mixture, was greater than *E. maculata*, whether grown in monoculture or mixture with *A. mabellae*.
3. For both *E. maculata* in monoculture, and *A. mabellae* in monoculture, the difference in shoot height between the N_1P_0 and N_1P_1 treatments was not significant, that is, neither species treatment responded appreciably to added phosphorus. However, where *E. maculata* was grown in mixture with *A. mabellae*, there was a significant increase in shoot height in the N_1P_1 treatment when compared with the N_1P_0 treatment, that is, there was an additional response of *E. maculata* to phosphorus. In contrast, where *A. mabellae* was grown in mixture with *E. maculata*, there was a significant decrease in

shoot height when phosphorus was added to an already high nitrogen environment, suggesting that *E. maculata* may be suppressing *A. mabellae* in the presence of a large nutrient supply.

4. There were no differences in shoot height between species treatments in the N_1P_0 treatment, but at N_1P_1, shoot height of *E. maculata* in mixture was significantly greater than that in any other treatment.

These growth patterns show that although the major response in shoot height for both species was to nitrogen, *E. maculata* responded more to nitrogen than *A. mabellae*. In the low nitrogen environment, *A. mabellae* had a clear advantage over *E. maculata*, but lost that advantage where nitrogen was added (N_1P_0). However, where phosphorus was added in combination with nitrogen (N_1P_1), the vigorous *E. maculata* in mixture appeared to depress the shoot growth of *A. mabellae*.

Relative Growth Rate of Shoot Height (RGR_h). Overall, the effects of nutrients and species treatments, and the interaction between these two factors were all highly significant ($P<0.001$); the two treatments without added nitrogen had greater relative growth rate of shoot height than the two treatments with added nitrogen (Table 4.12). This was due to the appreciable relative height response of *A. mabellae* in the low nitrogen treatments. Over all nutrient regimes, the two treatments with *A. mabellae* had greater RGR_h than either of the treatments with *E. maculata*.

The response of each species treatment at the four nutrient regimes is shown in Figure 4.3b. The important points are:

1. For the two treatments with *E. maculata* (in monoculture, and in mixture with *A. mabellae*), RGR_h was significantly greater where nitrogen was added.

2. For the two treatments with *A. mabellae*, RGR_h was high in the low nitrogen (N_0P_0, N_0P_1) treatments, and was significantly depressed where nitrogen was added.
3. In the low nitrogen treatments, *A. mabellae*, and particularly *A. mabellae* in mixture with *E. maculata*, had significantly greater RGR_h than *E. maculata*, whether grown in monoculture or in mixture with *A. mabellae*.
4. There were no marked differences in RGR_h between any of the four species treatments in the two high nitrogen treatments.

Total Plant Dry Weight. The main effects of nutrients and species treatments, and the interaction between these were all highly significant ($P<0.001$). The two treatments with added nitrogen produced significantly more plant photosynthate than the two treatments without added nitrogen. For the species treatments, there was a significant increase in plant dry weight in the following order; *A. mabellae* grown in mixture with *E. maculata* < *A. mabellae* in monoculture < *E. maculata* in monoculture < *E. maculata* grown in mixture with *A. mabellae*.

The response of each species treatment at each nutrient regime is shown in Figure 4.3c. For all four species treatments, plant dry weight was greater where nitrogen was added (N_1P_0 and N_1P_1), the response to added nitrogen being more substantial for *E. maculata* than for *A. mabellae*. In the low nitrogen environments, *A. mabellae* consistently produced more dry matter than *E. maculata*, but the reverse was true in the high nitrogen treatments. Where phosphorus was added in the presence of high nitrogen (N_1P_1), growth of *A. mabellae* was depressed while growth of *E. maculata* in mixture was enhanced. For *E. maculata* in mixture, the improved growth was significant and in fact this treatment produced more photosynthate than all others.

Relative Growth Rate of Plant Dry Weight (RGR_p). The main effect of nutrients on relative growth rate of plant dry weight was significant

($P<0.01$). Seedlings receiving nitrogen had higher RGR_p than those without (Table 4.12). There was a highly significant ($P<0.001$) species treatment response, with the two *E. maculata* treatments having significantly lower RGR_p than the two *A. mabellae* treatments.

The interaction term was highly significant ($P<0.001$) and is illustrated in Figure 4.3d. For both *E. maculata* treatments, RGR_p was particularly low under the low nitrogen regimes (N_0P_0, N_0P_1), but was substantially greater where nitrogen was added. In contrast, the RGR_p for *A. mabellae* was greater in the low than in the high nitrogen treatments. There was no substantial response of either *E. maculata* or *A. mabellae* to phosphorus in the presence of added nitrogen, although *A. mabellae* in mixture with *E. maculata* recorded a non-significant increase. The greatest contrast between *E. maculata* and *A. mabellae* occurred at the low nitrogen levels. Both *E. maculata* treatments had particularly low RGR_p, while both *A. mabellae* treatments produced their highest relative growth rates. In the two high nitrogen treatments, the two treatments with *E. maculata*, and *A. mabellae* in monoculture, produced similar RGR_ps. Where *A. mabellae* was grown in mixture with *E. maculata*, however, its growth was depressed at the two high nitrogen treatments, perhaps again, as a result of competition from vigorous *E. maculata*.

Total Shoot Dry Weight. The differences in growth response of total shoot dry weight were similar to those for total plant dry weight, and therefore are not discussed. The individual responses of species to nutrients are shown in Figure 4.3e.

Relative Growth Rate of Shoot Dry Weight (RGR_s). The response of RGR_s was similar to that of RGR_p. Individual species responses are shown in Figure 4.3f.

(ii) Leaf Attributes

Total Leaf Area. The effect of nutrients on total leaf area was highly significant ($P<0.001$). The two low nitrogen treatments produced about one fifth of the leaf area of the high nitrogen treatments (Table 4.12). The response of species treatments was also highly significant ($P<0.001$). *E. maculata* in mixture with *A. mabellae* produced substantially more leaf area than any other species treatment; *A. mabellae* in mixture with *E. maculata* had the least leaf area.

The interaction between nutrients and species treatments was also highly significant ($P<0.001$) and is illustrated in Figure 4.3g. For each of the four species treatments, leaf area is larger where the level of nitrogen is increased. However, for the two treatments with *E. maculata*, there was about a 15 fold increase in leaf area while there was only a 2 to 3 fold increase associated with the two *A. mabellae* treatments. Of the species treatments, only *E. maculata* had responded to phosphorus, and only where growing in mixture with *A. mabellae* where the nitrogen level was increased.

At low nitrogen levels, *A. mabellae* did consistently better than *E. maculata*. At high nitrogen levels, the reverse was true. *E. maculata*, and particularly *E. maculata* in mixture with *A. mabellae*, produced more leaf area than either of the *A. mabellae* treatments. As with other attributes, *A. mabellae* in mixture with *E. maculata* was depressed in the presence of vigorous *E. maculata* under conditions of high nitrogen.

Relative Growth Rate of Leaf Area (RGR_a). Overall, the effect of nutrients on relative leaf area production was not significant. The species response, however, was highly significant ($P<0.001$). The two *E. maculata* treatments had lower RGR_a than the two *A. mabellae* treatments.

The interaction term was also highly significant ($P<0.001$). The pattern of response was similar to other relative growth rate parameters (Figure 4.3h). The two treatments with *E. maculata* had appreciably higher RGR_a in the high, as opposed to the low nitrogen treatments. In contrast, the two treatments with *A. mabellae* had their greatest RGR_a in the low nitrogen treatments, these being the highest values for any nutrient-species treatment combination. The comparison between species shows that at low nitrogen levels, *A. mabellae* had a RGR_a about five to six times greater than those of *E. maculata*. At high nitrogen levels, three of the four species treatments had very similar RGR_a values. Only *A. mabellae* in mixture with *E. maculata* was depressed in these nutrient regimes.

Leaf Area Ratio (LAR). The main effects of nutrients and species treatments, and the interaction between these two factors were all highly significant ($P<0.001$). The two treatments with added phosphorus had larger LARs than the treatments without added phosphorus (Table 4.12). The two *E. maculata* treatments had lower LARs than the two *Acacia* treatments.

The response of each species treatment to each nutrient regime is shown in Figure 4.3i. For the two *E. maculata* treatments, LAR was smaller in the low nitrogen treatments. For the two *A. mabellae* treatments, there was some variation in LAR over the four nutrient regimes, but for virtually all treatments, *A. mabellae* had larger LARs than *E. maculata*.

(iii) Root Attributes

Total Root Dry Weight. The effect of nutrients and species treatments, and the nutrient-species treatment interaction were all highly significant ($P<0.001$).

The individual responses of species treatments to the four nutrient regimes are shown in Figure 4.3j. There was an appreciable positive response to added nitrogen in each of the four species treatments, and as with the previous total growth attributes, this response was greatest in *E. maculata*. Of the species treatments, only *E. maculata* in mixture with *A. mabellae* responded positively to the addition of phosphorus, and only where nitrogen was present. The previous primary growth attributes have shown a similar growth response.

At the high nitrogen level, *A. mabellae* grown in mixture with *E. maculata* produced about half the root dry weight of *A. mabellae* in monoculture, suggesting that where it is responding vigorously to added nutrients, *E. maculata* can restrict the root growth of *A. mabellae*.

Relative Growth Rate of Root Dry Weight (RGR_r). The relative growth rate of root dry weight was significantly ($P<0.001$) influenced by nutrients and species treatments, and there was also a significant ($P<0.001$) interaction.

The responses of individual species treatments are shown in Figure 4.3k. At low nitrogen, the RGR_r of *A. mabellae* was greater than that of *E. maculata*. The RGR_r of *E. maculata* (in monoculture and mixture) responded to nitrogen, but that of *A. mabellae* was variable. This is difficult to interpret, although a nutrient imbalance may be involved.

Root:Shoot Ratio. The effect of nutrients on the root:shoot ratio was highly significant ($P<0.001$). There was a greater root:shoot ratio in the unamended soil; addition of phosphorus (N_0P_1) depressed the ratio. The addition of nitrogen (N_1P_0) had a variable but even more depressive effect. The main effect of species treatment was not significant.

The interaction term was highly significant ($P<0.001$). The response of species treatments to the nutrient regimes (Figure 4.3l) showed no consistent pattern in the way species allocated photosynthates to roots and shoots, although *E. maculata* may devote relatively more photosynthate to shoot production in response to nitrogen, that is, it had a lower root:shoot ratio. *E. maculata* had a more variable root:shoot ratio over the four nutrient treatments than *A. mabellae*. For example, the root:shoot ratio for *A. mabellae* in monoculture was in the range 0.32 to 0.50 while the range for *E. maculata* in mixture was 0.19 to 0.57.

(iv) Net Assimilation Rate (NAR)

NAR was significantly ($P<0.001$) affected by nutrients and species treatments. NAR was significantly lower at low nitrogen levels, and *A. mabellae* grown in monoculture had a significantly higher NAR than the other species treatments (Table 4.12).

The interaction effects (Figure 4.3m), which were highly significant ($P<0.001$), showed NAR at low nitrogen was substantially greater for *A. mabellae* (0.028-0.038 g dm^{-2} day^{-1}) than for *E. maculata* (<0.020 g dm^{-2} day^{-1}). However, the NAR of *E. maculata* was strongly affected by nutrient addition; at the high nitrogen level, it was double that at the low nitrogen level. The NAR of *A. mabellae*, in monoculture at least, was not strongly affected by nutrient addition in such a consistent way. Where *A. mabellae* was grown in mixture with *E. maculata*, its NAR was substantially lower under the high nitrogen regimes (<0.020 g dm^{-2} day^{-1}). Again it was possible that vigorous *E. maculata* in these treatments depressed the response of *A. mabellae*.

Phosphorus addition also had some affect on NAR. For example, in the high nitrogen low phosphorus treatment (N_1P_0), *E. maculata* in both monoculture and mixture, and *A. mabellae* in monoculture, had similar NARs, while *A. mabellae* in mixture with *E. maculata* had a considerably lower NAR. However, where phosphorus was added as well (N_1P_1), the two *E. maculata* treatments had substantially larger NAR's than either of the

A. mabellae treatments and especially *A. mabellae* in mixture with *E. maculata*. This may be because the NAR of *A. mabellae* is depressed, rather than the NAR of *E. maculata* being enhanced at high nitrogen and phosphorus.

Table 4.11 Summary of the differences between attribute means associated with nutrients, species treatments and the interaction between these as derived from analyses of variance.

Attribute	Nutrient	Species Treatment	Interaction
Total Shoot Height	***	**	***
Relative Growth Rate of Shoot Height	***	***	***
Total Plant Dry Weight	***	***	***
Relative Growth Rate of Plant Dry Weight	**	***	***
Total Shoot Dry Weight	***	***	***
Relative Growth Rate of Shoot Dry Weight	*	***	***
Total Leaf Area	***	***	***
Relative Growth Rate of Leaf Area	NS	***	***
Leaf Area Ratio	***	***	***
Total Root Dry Weight	***	***	***
Relative Growth Rate of Root Dry Weight	***	***	***
Root:Shoot Ratio	***	NS	***
Net Assimilation Rate	***	***	***

* $P<0.05$; ** $P<0.01$; *** $P<0.001$; NS = not significant

Table 4.12 Ranking of seedling means for nutrients and species treatments.

Attribute	Nutrient				Species Treatment			
Total Shoot Height	14.04 N_0P_1	14.84 N_0P_0	38.26 N_1P_1	38.36 N_1P_0	22.62 EmMon	26.69 AmMon	27.48 EmMix	28.71 AmMix
Relative Growth Rate of Shoot Height	0.0113 N_1P_0	0.01195 N_1P_1	0.01448 N_0P_1	0.01755 N_0P_0	0.00737 EmMon	0.00850 EmMix	0.01776 AmMon	0.02148 AmMix
Total Plant Dry Weight	1.247 N_0P_0	1.279 N_0P_1	7.650 N_1P_0	8.010 N_1P_1	2.819 AmMix	3.728 AmMon	4.801 EmMon	6.837 EmMix
Relative Growth Rate of Plant Dry Weight	0.02124 N_0P_0	0.02284 N_0P_1	0.02591 N_1P_0	0.02643 N_1P_1	0.01766 EmMon	0.01893 EmMix	0.02824 AmMix	0.03159 AmMon
Total Shoot Dry Weight	0.84 N_0P_0	0.98 N_0P_1	6.02 N_1P_0	6.31 N_1P_1	2.13 AmMix	2.56 AmMon	3.86 EmMon	5.60 EmMix
Relative Growth Rate of Shoot Dry Weight	0.02074 N_0P_0	0.02345 N_0P_1	0.02502 N_1P_1	0.02590 N_1P_0	0.01723 EmMon	0.01889 EmMix	0.02869 AmMix	0.03031 AmMon
Total Leaf Area	101 N_0P_0	106 N_0P_1	515 N_1P_0	540 N_1P_1	243 AmMix	289 AmMon	299 EmMon	431 EmMix
Relative Growth Rate of Leaf Area	0.01669 N_0P_0	0.01693 N_1P_1	0.01794 N_1P_0	0.02038 N_0P_1	0.01135 EmMon	0.01336 EmMix	0.02205 AmMix	0.02518 AmMon
Leaf Area Ratio	87.6 N_1P_0	87.7 N_0P_0	94.8 N_1P_1	97.0 N_0P_1	77.9 EmMix	78.1 EmMon	102.0 AmMon	109.0 AmMix
Total Root Dry Weight	0.29 N_0P_1	0.41 N_0P_0	1.63 N_1P_0	1.70 N_1P_1	0.68 AmMix	0.94 EmMon	1.17 AmMon	1.23 EmMix
Relative Growth Rate of Root Dry Weight	0.01788 N_0P_1	0.02418 N_0P_0	0.02709 N_1P_0	0.03139 N_1P_1	0.01942 EmMon	0.02014 EmMix	0.02798 AcMix	0.03300 AcMon
Root:Shoot Ratio	0.312 N_1P_0	0.361 N_1P_1	0.398 N_0P_1	0.518 N_0P_0	0.374 EmMon	0.395 AmMix	0.396 EmMix	0.424 AmMon
Net Assimilation Rate	0.02577 N_0P_1	0.02611 N_0P_0	0.03115 N_1P_1	0.03266 N_1P_0	0.02594 AmMix	0.02753 EmMix	0.02818 EmMon	0.03404 AmMon

NOTE: i) Nutrient treatments: N_0P_0 = no added nitrogen, no added phosphorus; N_0P_1 = no added nitrogen, added phosphorus; N_1P_0 = added nitrogen, no added phosphorus; N_1P_1 = added nitrogen, added phosphorus.

ii) Species Treatments: EmMon = Eucalyptus maculata in Monoculture; EmMix = E. maculata in Mixture; AmMon = Acacia mabellae in Monoculture; AmMix = A. mabellae in Mixture.

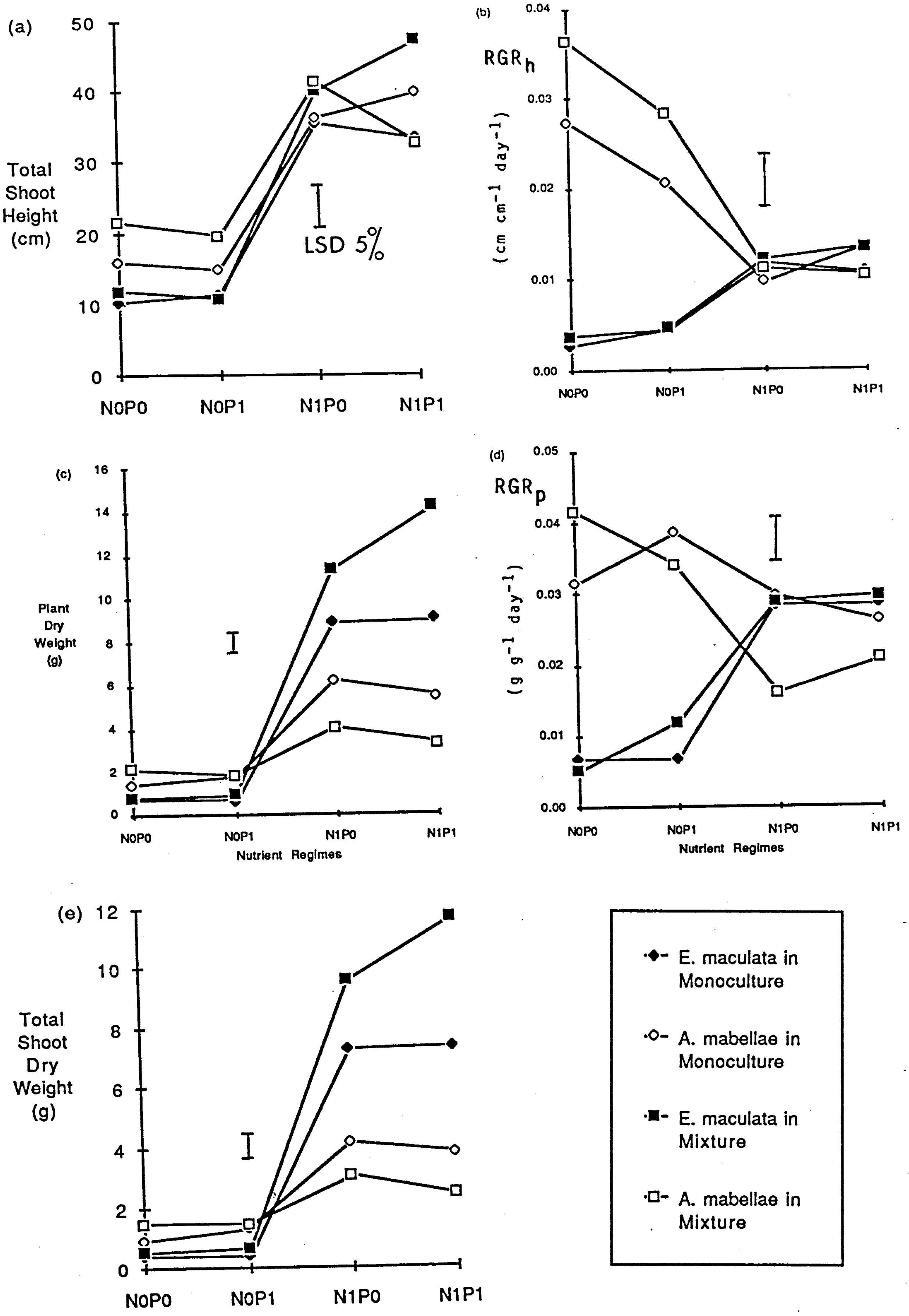

Figure 4.3 The response to four nutrient regimes of (a) total shoot height, (b) relative growth rate of shoot height, (c) total plant dry weight, (d) relative growth rate of plant dry weight and (e) total shoot dry weight of *E. maculata* and *A. mabellae* in monoculture and in mixture. N_0 and P_0 indicate no added nitrogen and no added phospuorus respectively; N_1 and P_1 indicate added nitrogen and phosphorus.

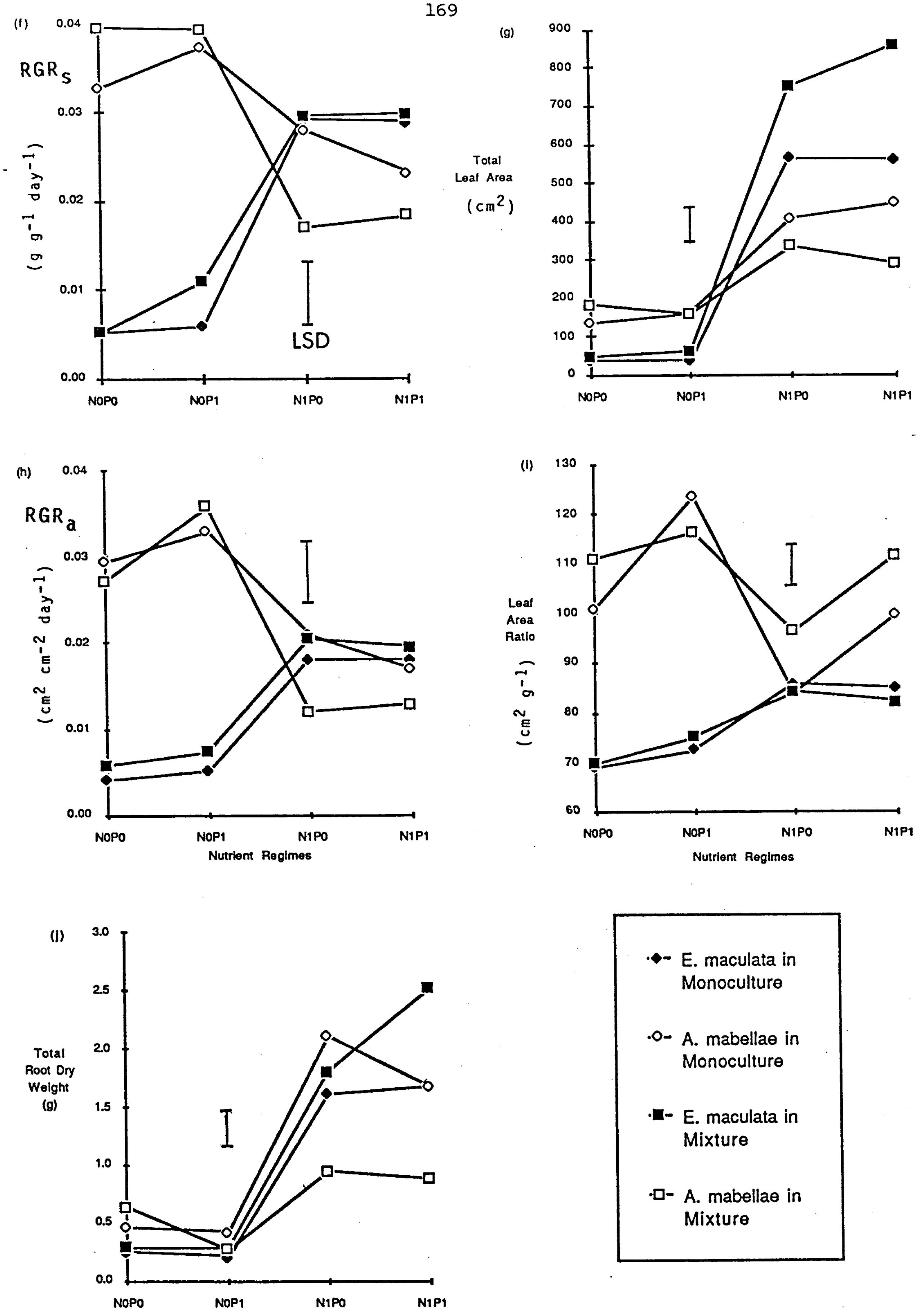

Figure 4.3 cont. The response to four nutrient regimes of (f) relative growth rate of shoot dry weight, (g) total leaf area, (h) relative growth rate of leaf area, (i) leaf area ratio and (j) total root dry weight of *E. maculata* and *E. pilularis* in monoculture and in mixture.

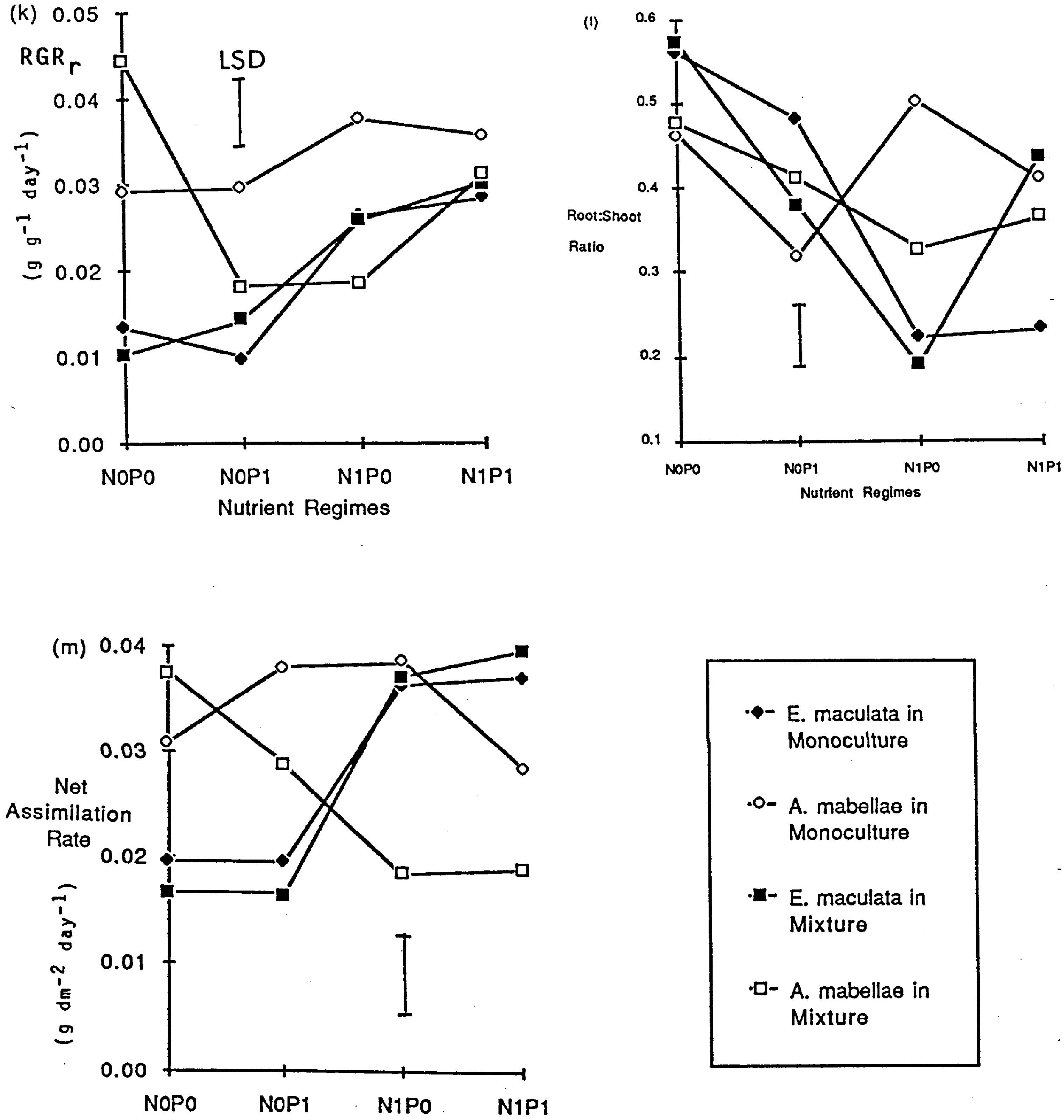

Figure 4.3 cont. The response to four nutrient regimes of (k) relative growth rate of root dry weight, (l) root:shoot ratio and (m) net assimilation rate of *E. maculata* and *E. pilularis* in monoculture and in mixture.

4.4.3 Discussion

The experiment shows throughout almost all of the measured plant attributes, that *E. maculata* performs poorly in relation to *A. mabellae* at a low nitrogen level, but *E. maculata* responds consistently to added nitrogen. While *A. mabellae* may also respond to added nitrogen, the response is not so great or consistent, so that at the higher nitrogen level, *E. maculata* out-performs the *Acacia* species. The greater response of *E. maculata* to nitrogen is also expressed in the different relative growth rate patterns. Those of *E. maculata* generally increase with added nitrogen while those of *A. mabellae* generally decline or are relatively unaffected. The same pattern applies to NAR.

There are possibly two components associated with the difference in response to nitrogen. Firstly, *A. mabellae* is likely to have a significant competitive advantage over *E. maculata* in the low nitrogen environments because of its ability to fix nitrogen. Secondly, *E. maculata* has grown consistently better than *A. mabellae* when both are subjected to high nitrogen treatments, demonstrating *E. maculata's* capacity to perform well in a nitrogen rich environment. Thus, while both species responded to nitrogen, the magnitude of the response has differed markedly. This tends to suggest that for optimum growth, *A. mabellae's* absolute requirement for nitrogen from the soil pool may be less than that for *E. maculata*. This view is supported by several field fertilizer studies involving *Acacia* species, and particularly *A. mearnsii*, and which have been reviewed by Schonau (1984). These have shown almost exclusively that *Acacia* responded strongly to phosphorus but weakly or not at all to nitrogen. Similar conclusions were made by Waki (1984) for *Acacia* species grown in Japan. The response to nitrogen in this experiment may therefore reflect the particularly low levels of nitrogen (205 ppm) in the unamended soil.

The total growth response of these two species to phosphorus is weaker and less consistent than is their response to nitrogen. This may be due in part to the already reasonable concentrations of phosphorus in the unamended soil (162 ppm). Neither species responded to phosphorus when it was added to a soil low in nitrogen. For *E. maculata*, this is perhaps not unusual since its growth rate in the absence of nitrogen was almost zero between harvest 1 and harvest 2, that is, the species is unable to respond to phosphorus where the primary limiting nutrient (nitrogen) is absent. For *A. mabellae*, growth was reasonable in the low nitrogen-low phosphorus treatment. There was no further response when phosphorus was added, suggesting the level of phosphorus in the unamended soil was already adequate for growth.

There were more variable responses to phosphorus where it was added to a soil high in nitrogen - governed in part by the type of competition involved. In the presence of intra-specific competition, neither species tended to respond to added phosphorus where the nitrogen level was already high, and there was even a slight decline in the growth of *A. mabellae*. However, where *E. maculata* and *A. mabellae* were grown in mixtures (inter-specific competition), there were contrasting responses to the addition of phosphorus. The growth of *E. maculata* was substantially enhanced while the growth of *A. mabellae* was substantially depressed. This suggests that at high nitrogen-high phosphorus levels, *E. maculata* is either photosynthetically more efficient than *A. mabellae*, or is able to gain access to a greater proportion of available nutrients. Once this dominance is established, it is possible that *E. maculata* is able to maintain or even improve its competitive advantage by continuing to harvest more of a limiting resource.

An examination of relative growth rates shows that *A. mabellae* growing in mixture with *E. maculata* at the low nitrogen level was superior to all other nutrient-species treatment combinations for the attributes assessed, with the exception of the relative rate of root dry weight production. The differences between *E. maculata* and *A. mabellae* at the low nitrogen levels are particularly striking, the latter species having relative growth rates five to ten times greater than those of *E. maculata*. Thus, for similar sized plants, *A. mabellae* must have a strong competitive advantage on sites where available soil nitrogen is either in limited supply or because of intense competition, is in high demand. Both these situations may exist on sites within the regrowth stands on Kioloa State Forest. Alternatively, *E. maculata* is often superior to *A. mabellae* in relative growth rates where nitrogen is added. Thus, the competitive ability of the two species may change sharply along a gradient of increasing nitrogen supply.

There are some notable differences in NAR between the nutrient-species treatment combinations. At the low nitrogen levels, *E. maculata* had relatively low NARs whereas *A. mabellae* performed much better. At the high nitrogen levels, *E. maculata* doubled its NAR whereas the NAR of *A. mabellae* tended to decline. Thus the photosynthetic efficiency of *E. maculata* is dramatically increased in nitrogen rich environments. In comparison, *A. mabellae* was slightly less efficient in the high as opposed to the low nitrogen treatments. In addition, where *A. mabellae* is grown in direct competition with vigorous *E. maculata*, there is a substantial decline in NAR. Otherwise the NAR of *A. mabellae* is less affected than *E. maculata* by variations in nutrient supply and may indicate that *Acacia* may be capable of reasonable growth on a wider range of soil fertility types. In contrast, early success of *E. maculata* may be limited to sites where there is rapid access to moderate to high levels of mineral nitrogen and possibly other nutrients as well. The requirement for nitrogen to give *E. maculata* a competitive advantage may be reflected in the way this species dominates soils at the upper end of the south coast soil fertility gradient (Chapter 3).

The range of NAR values reported in this study (0.0165 to 0.0298 g dm^{-2} day^{-1}) are higher than those reported by Turnbull (1979) for *E. cloeziana* grown under varying light conditions (0.0043 to 0.0286 g dm^{-2} day^{-1}), but lower than those reported by Awang (1977) for a number of eucalypt species grown at a range of nutrient levels (0.0329 to 0.0615 g dm^{-2} day^{-1} for *E. microcorys* and *E. pilularis* respectively).

4.5 SUMMARY

This group of three glasshouse experiments was designed to determine whether there are any inherent growth differences between a number of species found extensively within the cutover forest, and whether there are any differences in the way they respond to nutrients. The first experiment showed that the size of seedlings of four eucalypt species did not differ markedly at the end of 20 weeks, but that there were some differences in the rates of growth through this period. *E. pilularis* and *E. maculata* tended to have the fastest early growth, but slowed relative to *E. globoidea* and *E. gummifera* later in the experiment. The patterns of shoot height growth differed between species - *E. pilularis* and *E. maculata* were taller throughout the experiment. Similarly, *E. pilularis* had greater stem diameter and root dry weight over the 20 week period.

The second experiment showed the response of two of the species (*E. maculata, E. pilularis*) to variations in nutrient supply, and to intra- and inter-specific competition. For almost all plant attributes measured, both species responded positively to increasing nutrient supply whether grown in monoculture or in mixture. While there was little difference between species in shoot dry weight at any nutrient concentration, the species did differ in other ways in their response to nutrients. For example, *E. pilularis* in monoculture and in mixture with *E. maculata* had greater total shoot height, total leaf area and a larger leaf area ratio at virtually all nutrient concentrations than *E. maculata*. These could indicate a competitive advantage for *E. pilularis* over *E. maculata* over a wide range in soil fertility. On the other hand, for the attribute relative growth rate of shoot height, *E. pilularis* declined and *E. maculata* increased with increasing nutrient supply; and *E. maculata* had a greater NAR than *E. pilularis* at the higher nutrient concentrations. This now suggests that relative to *E. pilularis*, *E. maculata* could become more competitive on higher fertility soils.

The third glasshouse study showed very distinctive differences between *E. maculata* and *A. mabellae* in the way they responded to nutrients. Seedling *A. mabellae* had a clear competitive advantage over *E. maculata* in an environment low in available nitrogen, but the situation was reversed in a high nitrogen environment, and particularly where a high level of phosphorus was also present. In this case, seedling *E. maculata* had superior growth and competitive ability.

The varying growth responses of *A. mabellae* and *E. maculata* to nutrient addition suggests that in the early establishment phase after clearfelling of *E. maculata* forest, there may need to be a substantial pool of mineral nutrients and particularly nitrogen, which is sufficient to give *E. maculata* the necessary growth stimulation to beat concomitantly developing vegetation. Alternatively, in the situations described in Chapter 2 (Link Road and Livingstone Creek Road sites), the nitrogen pool may have been inadequate for this, allowing other perhaps less nutrient demanding species to gain an initial competitive advantage over *E. maculata*. These possibilities are examined further in Chapter 5, which deals with field responses of eucalypt species to nutrients and competition.

CHAPTER 5

THE EFFECTS OF NUTRIENTS AND COMPETITION ON THE DEVELOPMENT OF FOREST SPECIES

5.1 INTRODUCTION

The glasshouse studies in Chapter 4 establish an experimental basis for the hypothesis that nutritional factors are involved in the variable response of *E. maculata* in the regrowth stands on Kioloa State Forest. This theme is developed further in Chapter 5, in two field studies which examine the effects of nutrients and competition on the growth of *E. maculata*. In the first study, the response of seedling *E. maculata* and *E. pilularis* to additions of nitrogen, phosphorus and calcium is examined on a site that had been clearfelled about 13 years ago, and was subsequently dominated by *Acacia* species. The second study involves subjecting regrowth *E. maculata* which is overtopped by *Acacia*, to release from surrounding competition, to fertilizer, and to a combination of these two treatments. A trenching treatment was also superimposed at a later date. Both studies were designed to elucidate factors which may be currently limiting the development of *E. maculata* within the clearfelled area. The results of these two studies are discussed in the light of a series of field fertilizer experiments conducted by J.D. Williams and D.M. Halsall of the CSIRO Division of Plant Industry, on a site on the south coast which was cleared of mature *E. maculata* forest specifically for the purpose.

5.2 EXPERIMENT 1 : FIELD RESPONSES OF SEEDLING EUCALYPTS ON A REGROWTH SITE

This experiment compares the responses of *E. maculata* and *E. pilularis* to all combinations of nitrogen, phosphorus and calcium on a regrowth site on Kioloa State Forest. The species were grown in monoculture and in mixture to assess the effects of inter- and intra-specific competition.

5.2.1 Materials and Methods

The Experimental Site

The study site was located within Kioloa State Forest and was adjacent to Higgins Creek Road in Forestry Commission Compartment 168 (Department of Lands Map 1970).* Prior to clearfelling in 1972, the dominant overstorey species were *E. maculata*, *E. pilularis* and other eucalypt species. The site experienced a low intensity fire soon after clearfelling which may have produced a temporary increase in mineral nutrients, and especially soil nitrogen. However, because nitrogen levels may return to pre-burn levels within a year or two of a fire event (Dunn and Debano 1977; Grove *et al.* 1986), it was likely there would be little or any residual nutritional effect 13 years later.

In April 1984, the site was prepared for the fertilizer study by clearing all regrowth and erecting a wire exclosure to exclude grazing mammals. A rotary hoe was used to break up the surface soil to a depth of 10 cm, and weeds were sprayed with herbicide (Round-up). Subsequent weeding of the site was by hand.

The soil was derived from Ordovician parent material and consisted of a fine sandy loam surface horizon grading to a sandy clay and then to a medium clay at 70cm. The percentage of shale fragments increased with depth, and with the use of drainage ditches, the site was well drained. The mean concentrations of total nitrogen, phosphorus and calcium in the 0-10 cm section soil were 3214, 218 and 958 ppm respectively. The relatively high nitrogen concentration may be due to the contribution by nitrogen-fixing *Acacia* species on the site.

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* site situated at mid to lower end of a short slope running perpendicular to the main slope; along the main slope the site can be considered to be at a 'mid to lower' position

Experimental Design and Method

The study was initially designed to compare field responses of open-root planted *E. maculata* and *E. globoidea* to fertilizing. However, a large proportion of the *E. globoidea* seedlings, and to a lesser extent the *E. maculata* seedlings, died in the first two months following planting. An examination of several root systems showed that the main tap root had consistently turned upwards, apparently unable to penetrate deeper into the soil. This may have been due to the weakness of open-root planted seedlings, or perhaps to a high level of compaction of soil on the particular experimental site 13 years earlier.

The study was re-established in September 1984. To improve the establishment success, seedlings were raised in jiffy pots prior to planting in the field, and *E. globoidea* was replaced by *E. pilularis*. This latter species was chosen because it was then being used in a number of glasshouse studies (Chapters 4 and 7).

Experience with *E. pilularis* had shown that it tends to have more variable rates of germination than *E. maculata*. Establishment procedures were therefore as follows. Seed of *E. maculata* was sown directly in jiffy pots in a growth medium of equal parts peat, sand and soil. Seed of *E. pilularis* was sown in plastic trays in a growth medium of equal parts of perlite and vermiculite. About 12 days after germination, uniformly sized *E. pilularis* seedlings were transplanted into jiffy pots containing the peat-sand-soil mixture.

About 45 days after germination (30.10.84), seedlings of the two species were planted into the field. The site, soon after planting, is illustrated in Plate 5.1. The initial and subsequent fertilization rates and intervals, including an application relating to the abandoned trial, are shown in Table (5.1). One month after outplanting, seedlings were hand-watered and sprayed with insecticide (Malathion). In the early stages, periodic seedling deaths were replaced with spare jiffy pot stock.

Plate 5.1 The site used for the field seedling study, soon after planting.

Table 5.1 Rates and dates of fertilizer application to seedlings of *E. maculata* and *E. pilularis*. Each compound was given as a broadcast application to a plot of 36 or 18 (thinned) seedlings.

Date of Application	Elemental Quantity ($kg\ ha^{-1}$)		
	Nitrogen	Phosphorus	Calcium
14.6.84	50	15	10
30.10.84	50	15	20
7.11.84	101	45	50
11.4.85	101	45	50
10.9.85	101	45	50

NOTE: (i) Nitrogen added as NH_4NO_3

(ii) Phosphorus added as $NaH_2PO_4.2H_2O$

(iii) Calcium added as $CaCl_2$

The experiment was arranged as a randomized complete block design in the field with four species treatments, eight nutrient treatments and three replications. The species treatments were:

1. *E. maculata* in monoculture.
2. *E. pilularis* in monoculture.
3. *E. maculata* in mixture with *E. pilularis*.
4. *E. pilularis* in mixture with *E. maculata*.

Treatments 3 and 4 were obtained by interplanting the two species in equal numbers.

The nutrient treatments involved application of all combinations of nitrogen, phosphorus and calcium in a 2^3 factorial arrangement. The fertilizer treatments (Table 5.1) were based on previous fertilizer trials with eucalypts (Cromer *et al.* 1975; Cromer *et al.* 1981; Schönau 1984). Calcium was included in the treatments because relatively high concentrations of the element had been found in mature *E. maculata* foliage (Mak 1982). Applications were made at several intervals including one at planting, after the benefits of this had been reported by Sinha (1970) and Schönau (1983). The most practical application of fertilizer was in the form of a surface dressing. Schuster (1982) found little difference between this method and burying the fertilizer in shallow holes.

Each plot (treatment) initially consisted of 36 seedlings (6 x 6) planted at 0.15 x 0.15 m spacing, with 0.5 m separating each plot. 9.5 months after outplanting, plots were thinned to 18 seedlings. Because only 0.5 m separated each plot, it was initially decided to ignore any edge effect because it was likely to be minimal. Consequently, for the two height measurements, all 18 plants within each plot were measured. However, observations at the end of the second growing season suggested that the stem diameter of some of the edge plants were larger than the inner plants of the plots. Therefore assessment of basal stem diameter in June 1986 was carried out on only the inner eight trees of each plot.

Height growth was measured 10.5 and 15 months after outplanting, in September 1985 and February 1986 respectively. Because a fungal pathogen affected the apical extension of *E. maculata*, the basal stem diameter of plants was also assessed. This was done late in the second growing season, in June 1986.

All data were subjected to two-way analyses of variance, the factors being nutrients (in 2^3 factorial arrangement) and species treatments. Three data sets were analysed: first year height growth (September 1985), second year height growth (February 1986) and second year basal stem diameter growth (June 1986).

5.2.2 Results

The analysis of variance of first year height, second year height and second year diameter growth are shown in Table 5.2. The ranked order of means for particular treatment contrasts are shown in Tables 5.3 to 5.8. In both the first and second growing seasons, all *E. maculata* seedlings, irrespective of treatment, were infected with the fungal pathogen *Ramularia pitereka*. Walker and Bertus (1971) describe this as a stem and leaf canker which is restricted to *Eucalyptus* species found in the subgenus *Corymbia*. *E. pilularis*, from the genus *Monocalyptus*, was unaffected. There was a 100% infection level associated with *E. maculata* and the intensity of infection was visually assessed as being severe but variable. In all cases, apical growing tips and the younger leaves were damaged.

Shoot Height - September 1985

The results of analysis of variance of first year height growth are shown in Table 5.2. The main effect of phosphorus was highly significant ($P<0.001$). The mean height of seedlings without added phosphorus was 107.9 cm and with added phosphorus, 137.2 cm. The main species effect was also highly significant ($P<0.001$). *E. pilularis* in monoculture (144.5 cm) was significantly taller than all of the other species combinations. The heights of *E. maculata* in monoculture (105.3 cm) and *E. maculata* in mixture (106.0 cm) were significantly less than the height of *E. pilularis* in mixture (129.3 cm). Because the growth rate of *E. maculata* had been adversely affected by the fungus *Ramularia pitereka*, it was not possible to determine whether these differences were due to the influence of the pathogen, or to superior height growth of *E. pilularis* at all fertilizer treatments.

The first order interaction of calcium and species treatment was significant at the 5% level of probability. Where grown in mixture, height growth of *E. maculata* and *E. pilularis* were depressed in the presence of added calcium. In contrast, where grown in monoculture, both species had enhanced growth in the presence of added calcium (Table 5.3). However, none of these increases or decreases was significant.

The interaction between phosphorus and species treatment was not significant, that is, each species treatment responded to phosphorus in much the same way as the total seedling response (main effect). It is useful, however, to examine the relative variation in height growth of the individual species treatments to phosphorus addition (Table 5.4). This shows that *E. maculata*, and especially this species in mixture, had greater relative height growth than *E. pilularis* in response to added phosphorus. The percentage increases in first year height growth as a result of phosphorus addition were 17.5% (*E. pilularis* in mixture), 22.1% (*E. pilularis* in monoculture), 24.1% (*E. maculata* in monoculture) and 41.2% (*E. maculata* in mixture). Thus, *E. maculata* in mixture, has been better able to improve its relative competitive ability in the presence of added phosphorus than the other three species mixes. The relative response of *E. pilularis* has been less than either of the *E. maculata* treatments, even though the total height growth of *E. pilularis* was considerably greater.

Shoot Height - February 1986

The patterns of height growth over the two year period are similar to those for the first year, and are summarized in Table 5.2. The main effect of phosphorus was highly significant ($P<0.001$). The mean height of seedlings without added phosphorus was 189.9 cm and with added phosphorus, 221.9 cm. The main effect of species treatment was also highly significant ($P<0.001$). *E. maculata* in mixture (146.3 cm) and *E. maculata* in monoculture (147.0 cm) were now significantly and considerably shorter than *E. pilularis* in mixture (260.5 cm) and *E. pilularis* in monoculture (265.7 cm).

Although none of the interaction terms was significant, it is again useful to examine the individual responses of the four species mixes to phosphorus addition (Table 5.5). The relative increases in height growth for *E. pilularis* in mixture, *E. pilularis* in monoculture, *E. maculata* in monoculture and *E. maculata* in mixture were 9.9%, 12.7%, 22.2% and 42.7% respectively. Thus the two *E. maculata* treatments, and especially *E. maculata* in mixture had, as a proportion of their size, substantially greater height growth as a result of phosphorus addition than either of the *E. pilularis* treatments. *E. pilularis*, however, still had greater absolute height growth. This suggests that *E. pilularis* was forging ahead, but with added phosphorus, *E. maculata* could catch up in time.

Basal Stem Diameter - June 1986

To remove heterogeneity of variances, the analysis of basal stem diameter data uses values that have been log transformed. In the text, only the untransformed values are cited. The summary of analysis of variance is given in Table 5.2. As with shoot height, the main effect of phosphorus and species treatment were both highly significant ($P<0.001$). The diameter of seedlings with and without phosphorus was 1.60 and 1.31 cm respectively. The four species treatments all had significantly different diameters; the ranked order being *E. maculata* in mixture (0.96 cm) < *E. maculata* in monoculture (1.12 cm) < *E. pilularis* in monoculture (1.76 cm) < *E. pilularis* in mixture (1.99 cm). The main effect of nitrogen was also significant, at the 5% level of probability. Seedlings without added nitrogen had a mean basal stem diameter of 1.40 cm and those with added nitrogen, 1.50 cm. Neither of the shoot height measurements had shown a significant main effect of nitrogen.

Two first order interactions were significant (P<0.05) and both involved phosphorus. The interaction between phosphorus and species (Table 5.6) shows that three of the four species treatments had considerable increases in diameter growth as a result of phosphorus addition. The fourth, *E. pilularis* in mixture, had only a small increase in growth. The relative increases in diameter of the four species treatments in response to phosphorus (based on untransformed means) were 6.2% (*E. pilularis* in mixture), 20.0% (*E. pilularis* in monoculture), 34.7% (*E. maculata* in monoculture) and 41.2% (*E. maculata* in mixture). As with the two height analyses, *E. maculata*, and particularly this species in mixture, has in a relative sense, responded very much better than *E. pilularis* to additions of phosphorus.

The interaction between phosphorus and calcium (Table 5.7) shows that added calcium depressed diameter growth where phosphorus was not added, but enhanced diameter growth where phosphorus was added. Neither the decrease or increase, however, was significant.

The response of individual species treatments to nitrogen (Table 5.8) was more variable than that to phosphorus. *E. maculata* in monoculture and *E. pilularis* in mixture had significantly (P<0.05) enhanced diameter growth as a result of nitrogen addition. The diameter of *E. pilularis* in monoculture was unchanged by nitrogen addition while that of *E. maculata* in mixture was slightly depressed.

Table 5.2 Summary of the differences between attribute means associated with nutrient elements, species treatment and the interaction between these as derived from analyses of variance. No second or third order interactions were significant.

	Attribute		
Factor	Height Growth Year 1	Height Growth Year 2	Diameter Growth Year 2
Nitrogen	NS	NS	*
Phosphorus	***	***	***
Calcium	NS	NS	NS
Species treatment	***	***	***
Nitrogen . Phosphorus	NS	NS	NS
Nitrogen . Calcium	NS	NS	NS
Phosphorus . Calcium	NS	NS	*
Nitrogen . Species tmt	NS	NS	NS
Phosphorus . Species tmt	NS	NS	*
Calcium . Species tmt	*	NS	NS

* $P<0.05$; ** $P<0.01$: *** $P<0.001$; NS = not significant

Table 5.3 First year mean height (cm) of four species treatments in response to calcium.

Nutrient Treatment	Species Treatments			
	E. maculata in Monoculture	*E. maculata* in Mixture	*E. pilularis* in Monoculture	*E. pilularis* in Mixture
No Added Calcium	102.6	113.8	139.9	136.3
Added Calcium	108.0	98.3	149.2	122.3

NOTE: For each species treatment the change in growth in response to added calcium is not significant ($P<0.05$).

Table 5.4 First year mean height (cm) of four species treatments in response to phosphorus.

Nutrient Treatment	Species Treatments			
	E. maculata in Monoculture	*E. maculata* in Mixture	*E. pilularis* in Monoculture	*E. pilularis* in Mixture
No Added Phosphorus	90.0	87.9	130.1	118.9
Added Phosphorus	120.7 (34.1)	124.1 (41.2)	158.9 (22.1)	139.7 (17.5)

NOTE: For each species treatment, the increase in response to added phosphorus is significant ($P<0.05$). Percentage increases are given in brackets.

Table 5.5 Second year mean height (cm) of four species treatments in response to phosphorus.

Nutrient Treatment	Species Treatments			
	E. maculata in Monoculture	*E. maculata* in Mixture	*E. pilularis* in Monoculture	*E. pilularis* in Mixture
No Added Phosphorus	132.3	120.6	249.8	248.4
Added Phosphorus	161.7 (22.2)	172.1 (42.7)	281.6 (12.7)	272.6 (9.9)

NOTE: For each species treatment, the increase in response to added phosphorus is significant ($P< 0.05$). Percentage increases are given in brackets.

Table 5.6 Second year mean diameter (cm) of four species treatments in response to phosphorus.

Nutrient Treatment	Species Treatments			
	E. maculata in Monoculture	*E. maculata* in Mixture	*E. pilularis* in Monoculture	*E. pilularis* in Mixture
No Added Phosphorus	-0.057(0.95)	-0.252(0.80)	0.462(1.60)	0.645(1.93)
Added Phosphorus	0.232(1.28) [34.7]	0.119(1.13) [41.2]	0.640(1.92) [20.0]	0.695(2.05) [6.2]

NOTE: (i) Only *E. pilularis* in mixture does not differ significantly ($P<0.05$) between nutrient treatments.

(ii) Untransformed means are given in brackets.

(iii) Percentage changes in growth based on untransformed means are given in square brackets.

Table 5.7 Second year mean diameter (cm) of seedlings for all combinations of phosphorus and calcium.

	Calcium Absent	Calcium Present
Phosphorus Absent	0.240 (1.35)	0.161 (1.26)
Phosphorus Present	0.403 (1.57)	0.449 (1.62)

NOTE: (i) Neither of the changes in seedling growth in response to calcium addition are significant. Both changes in growth in response to phosphorus addition are significant ($P<0.05$).

(ii) Untransformed means are given in brakcets.

Table 5.8 Second year mean diameter (cm) of four species treatments in response to nitrogen.

	Species Treatments			
Nutrient Treatment	*E. maculata* in Monoculture	*E. maculata* in Mixture	*E. pilularis* in Monoculture	*E. pilularis* in Mixture
No Added Nitrogen	0.020(1.04)	-0.042(0.98)	0.547(1.74)	0.586(1.83)
Added Nitrogen	0.155(1.19) [14.4]	-0.091(0.94) [-4.1]	0.554(1.77) [1.7]	0.754(2.15) [17.5]

NOTE: (i) *E. maculata* in monoculture and *E. pilularis* in mixture differ signifcantly ($P<0.05$) between nutrient treatments. The other two species treatments do not.

(ii) Untransformed means are given in brackets.

(iii) Percentage changes in growth based on untransformed means are given in square brackets.

5.2.3 Discussion

The aim of this study was to identify some of the factors which may currently be limiting the development of eucalypt species within regrowth stands on Kioloa State Forest, and to determine whether there are any differences in growth, in response to inter- or intra-specific competition. It should be appreciated, however, that the experiment was established on a site that had carried dense *Acacia* regrowth for 13 years. Thus the site may differ in important ways from that immediately after the clearfelling of an old growth forest. Of the three nutrient elements examined, phosphorus was most limiting to the growth of seedling *E. maculata* and *E. pilularis* on this site. The height and diameter responses were all highly significant ($P<0.001$) with all four species treatments showing a positive response to the addition of phosphorus. Nitrogen significantly ($P<0.05$) influenced the second year diameter growth of seedlings, but the effect on individual species mixes was both less consistent and less pronounced than for phosphorus.

Differences between the species treatments were substantial. These were associated with differences between species rather than differences in the type of competition present (i.e. inter- or intra-specific). *E. pilularis* whether planted in monoculture or in mixture, had considerably greater height and diameter growth than *E. maculata*. These differences were to a large extent unaffected by the nutrient treatment applied. That is, *E. pilularis* had grown better in height and diameter regardless of the combination of elements added. This contrasts somewhat with the results in Experiment 2 Chapter 4, in which *E. pilularis* and *E. maculata* in a glasshouse environment tended to grow at similar rates where adequate nutrients were supplied. Other factors influencing the growth response are undoubtedly involved in a field study.

At least part of the reason for the depressed response of *E. maculata* relative to *E. pilularis* has been due to the adverse effect of the species specific fungus, *Ramularia pitereka*. This disease infects the stems and leaves, and particularly the region of apical extension, of *Eucalyptus* species from the subgenus *Corymbia* (Walker and Bertus 1971). By the end of the first growing season, 100% of *E. maculata* (*Corymbia*) seedlings in the trial had been infected by *R. pitereka*. Re-infection occurred in the second year of the trial. There did not appear to be a consistent relationship between the intensity of infection and treatment, but rather intensity varied between individual seedlings.

The infection of the apical growing tips affected the height growth of *E. maculata* while the loss of photosynthetic tissue was likely to have indirectly affected diameter growth. It was therefore not possible to assign the differences in the growth of the two species to inherently superior growth of *E. pilularis* at all nutrient treatments, or to the affect of *R. pitereka*. From the glasshouse experiments in Chapter 4, however, the heights of the two species were similar. On the other hand, it may be accepted that *E. pilularis* has a greater capacity to direct photosynthates to height production than other eucalypt species. Awang (1977) found in a large number of glasshouse experiments that while *E. pilularis* produced no more biomass than other eucalypt species, it consistently outgrew the others in height.

While absolute comparisons of growth for the two species are not particularly satisfactory, relative growth comparisons are useful. The response of the four species treatments to phosphorus provides a valuable comparison because the main effects of these two factors were highly significant. For both the height and diameter, the percentage increase in growth in response to phosphorus was greater for *E. maculata* than for *E. pilularis*, despite the fungal infection. In particular, the response of *E. maculata* in mixture was consistently greater than that of the other treatments, showing about a 40% increase in both height and diameter. *E. pilularis* in mixture, on the other hand, had the smallest percentage increase in height and diameter, ranging between 6% and 18%. It is possible that the enhanced relative growth of *E. maculata* in mixture in the high phosphorus treatments was influential in depressing the relative growth of *E. pilularis*. It must be remembered, however, that in absolute terms, *E. pilularis* had both considerably greater shoot height and stem diameter than *E. maculata* at every nutrient treatment. Alternatively, it is possible that *E. pilularis* has shown a smaller relative response to phosphorus than *E. maculata* because it is able to harvest the soil phosphorus reserve more effectively or has less of an absolute requirement for soil phosphorus. Heinrich (1985) suggested that *E. pilularis* is able to grow on phosphorus deficient sand-dunes because of a well designed root system for the acquisition of phosphorus. Others (Mulligan and Patrick 1985a, 1985b; Heinrich and Patrick 1986) have shown that *E. pilularis* seedlings are able to maintain high levels of growth by gaining phosphorus from efficient mycorrhizal associations and by redeploying phosphorus from cotyledons to areas of growth.

In a glasshouse experiment in Chapter 4 (Experiment 3), it was shown that the major growth response of *E. maculata* seedlings was to nitrogen, with a smaller and more variable response to phosphorus. Other field studies (Darrow 1985) including one on a site adjacent to the Kioloa regrowth forest (J.D. Williams and D.M. Halsall unpublished) have shown similar trends, that is, the greatest growth response of *E. maculata* is to the element nitrogen. However, the present trial has shown that on a site which had carried regrowth *Acacia* species for 13 years, the major growth response of *E. maculata* (and *E. pilularis*) seedlings is to phosphorus, with a much smaller and less consistent response to nitrogen. It is possible that the nitrogen fixing *Acacia* species have made a substantial contribution to the available soil nitrogen pool over the 13 year period, to the extent that other nutrient elements may become growth limiting. Certainly, the high concentration of total soil nitrogen on this site (3214 ppm) supports this view. There is also some possibility of a residual nutritional effect of the low intensity burn which occurred 13 years previously, although others have shown that nitrogen levels may return to pre-burn levels within a year or two of a fire (Dunn and Debano 1977; Grove *et al.* 1986).

In Chapter 3, it was shown that mature *E. maculata* is most likely to occur on sites of higher fertility status (including phosphorus) on the south coast; and in Chapter 4, that *E. maculata* was more competitive where fertility was increased, and that it could respond to added phosphorus in an already high nitrogen environment. The present study supports the latter finding, that is, that *E. maculata* is able to respond positively to added phosphorus where nitrogen is not limiting. Given these facts, it is possible that *E. maculata* has an inherently greater requirement for phosphorus for adequate growth, or it can continue to respond to increasing supply of this nutrient. It may also mean *E. maculata* may be at a continuing disadvantage within regrowth stands where plant available phosphorus is limited and where competitive influences from other successional species remain substantial. If this is the case, then one of the reasons that *E. maculata* continues to occupy a sub-dominant position within regrowth stands may be an inability to acquire sufficient phosphorus to meet its requirements. Where *E. pilularis* and other successional species occupy dominant and co-dominant canopy positions within the same regrowth stands, they may have an inherently smaller requirement for phosphorus, or may have more efficient means of acquiring it than *E. maculata*. The question of the relative ability of south coast forest species to compete for phosphorus is taken up in Chapter 7.

The Possible Importance of *Ramularia pitereka* Following Clearfelling

The occurrence of the species specific fungus *R. pitereka* at high infection levels, and with such adverse effects on the growth of *E. maculata*, provides another possible reason for the lack of vigour of *E. maculata* on many sites within the regrowth forest. J. Walker (pers. comm.) has observed that a distinct relationship exists between the level of vegetation disturbance and the intensity of *R. pitereka* infection on south coast *E. maculata* forests. There may be very low levels in the undisturbed forest but increasingly high levels where there has been vegetation disturbance, for example, along power line easements. He suggests that where disturbance has occurred, conditions appear to swing in favour of the pathogen and quite severe damage can be observed.

The circumstances under which *R. pitereka* proliferated for two successive growing seasons in the present field trial cannot be considered entirely natural, yet some of the more important conditions associated with this outbreak may have been repeated in the years following clearfelling.

It is likely that conditions of above average rainfall and associated higher humidities will increase the probability of fungal outbreak (J. Walker pers. comm.). The rainfall data at Kioloa Meteorological Station for the two years in which this experiment took place (1984 and 1985) are presented in Table 5.9 (Commonwealth Bureau of Meteorology Records), along with statistics on rainfall for the years in which clearfelling took place (1967 to 1973) and for a period of three years afterwards. The mean average rainfall for the Kioloa Station since records were started (1958) is 1277 mm. The table shows that rainfall substantially above the average occurred in the years following clearfelling (1974, 1975, 1976) and for at least part of the duration of the field fertilizer experiment (1984). Thus in the present field trial, an outbreak of *R. pitereka* may have been associated with higher than average rainfall, a condition which also existed in the early years following clearfelling.

Table 5.9 Rainfall data from Kioloa Meteorological Station (Source: Commonwealth Bureau of Meteorology Records). Mean annual rainfall from 1958 to 1985 is 1277 mm.

Year	Annual Rainfall (mm)
Years in which clearfelling took place	
1967	1044
1968	686
1969	1511
1970	1065
1971	1084
1972	991
1973	1289
Three years following clearfelling	
1974	1854
1975	1674
1976	1924
Years of the field fertilizer experiment	
1984	1578
1985	1177

The high stocking rates in the present field experiment are likely to have been conducive to the rapid spread of air-borne *R. pitereka*. Increased contact between susceptible plants may also have enhanced the rate of spread. High stocking levels will also raise the humidity within the seedling canopy, providing conditions favourable for fungal outbreak. It can be argued that although stocking of *E. maculata* regeneration following clearfelling would not have been as high as that encountered in this field trial, certainly the total stocking of regrowth species on some sites would have been particularly high, providing conditions of high humidity that may have enhanced outbreaks of *R. pitereka* infection.

Any reduction in the shoot height or leaf area of *E. maculata* as a result of fungal infection, in the critical establishment phase, may have reduced its competitive ability, and will have been particularly important where other successional species developed rapidly and competition for resources was intense.

5.3 EXPERIMENT 2 : THE RESPONSE OF REGROWTH *E. MACULATA* TO FERTILIZER AND COMPETITION REMOVAL

This field trial examines factors which may be continuing to restrict the development of *E. maculata* regrowth beneath a canopy of concomitantly developing *Acacia*, 13 years after the forest was clearfelled. These factors may be the same as those which influenced the development of *E. maculata* in the establishment and early successional stages of stand development. Alternatively, environmental conditions may have been altered by biological processes in the course of stand development, to the extent that other growth factors may have become limiting. Thus in this experiment, the response of restricted or sub-dominant *E. maculata* to several treatments have been examined. These treatments include the removal of grasses around the *E. maculata* stem, the removal of the competing *Acacia* overwood, and the application of fertilizer to the plant.

5.3.1 Materials and Methods

Experimental Design

The experiment was arranged as a randomized complete block design in the field with five treatments and five replications (each stem representing a replication). Stems were selected which occupied a sub-dominant position within the regrowth canopy, and were allocated to the treatments to give sets of stems matched for diameter. The competitive influence from adjacent eucalypts (including two residual *E. maculata* seed trees) was unable to be controlled, and therefore differed between the treated *E. maculata* stems. This is likely to add to the variability of the growth response. The associated regrowth species on the site consisted mainly of *Acacia*, and were on average, about 6 m taller than the *E. maculata* stems. The five treatments were:

1. True Control (TC) - stems not treated in any way.
2. Basal Level Control (BLC) - all grasses within a two metre radius from the base of the stem cleared.
3. Basal Level Control plus Fertilizer (BLC+F) - as for No. 2, together with fertilizer addition at several (six) time intervals.
4. Basal Level Control plus Competition Removal (BLC+CR) - as for No. 2, together with clearing of all competing stems (almost exclusively *Acacia* species) within a two to three metre radius from the base of the stem. Competition between root systems of *E. maculata* and the remaining *Acacia* would still apply.
5. Basal Level Control plus Competition Removal plus Fertilizer (BLC+CR+F) - as for No. 4, together with fertilizer addition at six intervals.

After the selected *E. maculata* stems had been treated in this way for 17 months, two further treatments were superimposed. Firstly, where *Acacia* had been removed from around the *E. maculata* stems (BLC+CR, BLC+CR+F), a circular trench was dug to a depth of 20 cm at a radius of two metres from the base of the stem. This treatment severed the majority of fine roots in the upper soil profile mainly of *Acacia* species continuing to compete with *E. maculata*. It was designed to separate the possible influences of above and below ground competition on the growth of *E. maculata*. Secondly, any physical impediment directly restricting the height growth of any *E. maculata* stem, for example, an overtopping *Acacia* branch, was removed to ensure this was not the primary cause of its sub-dominant canopy position.

Experimental Method

This experiment was commenced at much the same time (August 1984) as the field based seedling-fertilizer experiment (Section 5.2), and it was therefore not possible at the time to identify which nutrient elements might be most critical for eucalypt growth. Consequently, the nutrient treatment was 'broad based' in that all elements considered important for plant growth were added. The fertilizer was applied six times over a 27 month period. The fertilizer compounds used, and the amounts applied are given in Table 5.10. These quantities tend to be greater than those used for seedling fertilizer studies, and are based on amounts used by R.G. Florence and J.P. Marsh (unpublished) for a fertilizer experiment with similarly aged regrowth *E. maculata*. For each application, part of the fertilizer was buried at four points close to the base of the stem. The remainder was applied as a surface dressing within a one to two metre radius and lightly raked in.

The trees were measured seven times, at 3, 6, 13, 17, 21, 24 and 27 months after initiation of the experiment in August 1984. Shoot height and stem diameter at breast height over bark (dbhob) were assessed. Bark shedding occurred in the summer months and affected stem diameter increment, but was consistent for all treatments. Despite the bark

Table 5.10 Elemental nutrient concentrations applied to regrowth *E. maculata* on six separate occasions over a 27 month period.

Nutrient Element	Concentration (g) per stem
Nitrogen	33.19
Phosphorus	10.16
Potassium	9.96
Calcium	52.31
Sulphur	26.07
Magnesium	2.081
Iron	1.236
Manganese	0.258
Zinc	0.103
Copper	0.0515
Boron	0.0103
Molybdenum	0.000515

NOTE: Four compounds were used; Banana Special (commercial fertilizer containing N, P, K and S), calcium nitrate, magnesium sulphate and Micromax (containing micro-nutrients).*

shedding, variation within each treatment was greater for shoot height than for stem diameter. This may have been due to errors in sighting the height sticks, and to the effects of insect grazing commonly observed in the sample trees. Invariably, this occurred on the apical growing shoots where the height measurements were taken. Because of these factors, diameter growth is considered a more reliable index of tree response.

* all nutrients added were in inorganic form

Initially, the two data sets were analysed using one-way analysis of covariance. The covariates were shoot height and stem diameter respectively, at the start of the experiment. In a second covariate analysis, the shoot height or stem diameter from the previous measurement was used as the covariate for the analysis of data for the current measurement, i.e. the covariate value was updated successively because of growth differences in response to the effect of treatments. Neither of the covariate analysis effects was significant. Consequently, one-way analysis of variance was used on all shoot height and stem diameter data at each of the seven measurements.

5.3.2 Results

The results of analysis of variance for the attributes stem diameter and shoot height, and the mutiple range comparisons of individual treatment means are given in Table 5.11. The initial size of the trees, the seven increments and the total growth over the period of the experiment are analysed.

Stem Diameter

The mean stem diameters for the five treatments at the start of the experiment were not significantly different (Table 5.11). Significant treatment effects were recorded for the first five increment periods, and for total growth. However, the differences for the last two increment periods were not significant.

The ranking of treatment means for the seven increment periods, and total growth are shown in Table 5.11, while the cumulative stem diameter increment over the period of the experiment is illustrated in Figure 5.1a. Prior to the trenching treatment in January 1986, there were no differences in mean stem diameter increments between the true control (TC), basal level control (BLC) and the basal level control plus fertilizer (BLC+F) treatments (Table 5.11). Alternatively, there was a strong effect of competition removal; the mean stem diameter increments of the basal level control plus competition removal (BLC+CR) treatment were significantly greater than those of the TC, BLC and BLC+F treatments at each measurement except the fourth (16.1.86). Where fertilizer was added following competition removal (BLC+CR+F), there was a further increase in stem diameter increment (Figure 5.1a). This additional response to fertilizer was maintained throughout the pre-trenching period, although the difference failed to reach statistical significance ($P<0.05$). The lack of response of *E. maculata* to fertilizing alone (BLC+F) compared to the control (TC and BLC) trees suggests that they were unable to utilize the added nutrients, and were able to response only where competition from surrounding trees was partially removed.

At the first measurement following the imposition of trenching (Increment 5), the difference in increment between competition removal only (BLC+CR) and competition removal plus fertilizer (BLC+CR+F) became significant for the first time (Table 5.11), that is, the effect of severing any remaining or re-invading *Acacia* roots (trenching) enhanced the stem diameter response of *E. maculata* where nutrients had also been added. The difference is illustrated in Figure 5.1a. This suggests that *E. maculata* may have had greater access to the fertilizer once root access by adjacent competing species was almost completely prevented by trenching. The differences between the TC, BLC and BLC+F treatments remained non-significant and the differences between these three treatments and the BLC+CR treatment remained significant (Table 5.11). None of the individual stems responded unusually following removal of any physical impediments to the development of leading shoots.

For the final two measurements (covering the period from May to November 1986), there were small increments in stem diameter for all treatments. The least growth would be expected in the majority of these months, and was a pattern that was repeated in the same months in 1985.

Shoot Height

There were no significant differences between the five treatments in tree heights at the beginning of the experiment (Table 5.11). The pattern of response in shoot height over the period of the experiment was broadly similar to that of stem diameter. However, greater variation within treatments meant there were fewer significant differences; there were significant differences between treatments for the second and fifth increments, and for total growth.

The ranking of treatment means for the seven increment periods, and for total growth, is shown in Table 5.11, and the cumulative shoot height increment over the period of the experiment is illustrated in Figure 5.1b. Up to the time when the trenching treatment was imposed (January 1986), there had been only one period (Increment 2) which produced a significant ($P<0.001$) difference between treatments (Table 5.11). Competition removal plus fertilizer (BLC+CR+F) had the greatest mean shoot height increment, followed by competition removal only (BLC+CR)*. The TC, BLC and BLC+F treatments had the least shoot height increment. These differences tended to be maintained, or increased slightly at the subsequent measurements (Figure 5.1b).

As was the case with stem diameter, the difference between the BLC+CR and BLC+CR+F treatments widened following the imposition of trenching in January 1986 (Figure 5.1b), but the difference was not significant (Table 5.11). In addition, the trenched stems continued to grow in height, but those without trenching did not (Figure 5.1b). However, this pattern had been repeated to some extent, in the same months of 1985 (i.e. prior to trenching), and it is not possible to say definitively whether the effect of severing any remaining or re-invading roots stimulated shoot height growth.*

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* A later measurement suggests there has been a delayed effect of trenching. It may be necessary to consider this could result, in part, from nutrients derived from severed roots.

Table 5.11 Summary of the differences between treatment means associated with 13-year-old regrowth E. maculata, and the ranking of means for each treatment contrast. Analyses are based on the diameter and height increment between each measurement. Measurement dates are given in brackets.

Attribute	DIAMETER (cm)						HEIGHT (m)					
	Significance	Ranked Order of Means					Significance	Ranked order of Means				
Initial Size (3.8.84)	NS	4.68 BLC+CR	4.78 BLC	4.98 BLC+CR+F	5.12 TC	5.14 BLC+F	NS	7.18 BLC+CR	7.48 TC	7.70 BLC+F	7.77 BLC+CR+F	7.89 BLC
Increment 1 (19.11.84)	***	0.14 BLC+F	0.15 BLC	0.18 TC	0.25 BLC+CR	0.30 BLC+CR+F	NS	0.08 TC	0.14 BLC+CR	0.15 BLC	0.16 BLC+F	0.19 BLC+CR+F
Increment 2 (11.2.85)	***	0.05 TC	0.05 BLC	0.06 BLC+F	0.23 BLC+CR	0.33 BLC+CR+F	***	0.03 BLC+F	0.06 BLC	0.13 TC	0.33 BLC+CR	0.49 BLC+CR+F
Increment 3 (10.9.85)	***	0.15 TC	0.17 BLC	0.18 BLC+F	0.41 BLC+CR	0.52 BLC+CR+F	NS	-0.11 BLC	0.02 BLC+F	0.04 TC	0.29 BLC+CR+F	0.31 BLC+CR
Increment 4 (16.1.86)	*	0.03 BLC+F	0.05 BLC	0.12 TC	0.15 BLC+CR	0.27 BLC+CR+F	NS	0.15 BLC+F	0.30 BLC	0.33 TC	0.36 BLC+CR	0.39 BLC+CR+F
Increment 5 (14.5.86)	***	0.15 TC	0.24 BLC+F	0.26 BLC	0.34 BLC+CR	0.59 BLC+CR+F	*	0.03 TC	0.04 BLC+F	0.09 BLC	0.30 BLC+CR	0.49 BLC+CR+F
Increment 6 (14.8.86)	NS	0.01 BLC	0.04 TC	0.04 BLC+F	0.04 CR	0.07 BLC+CR+F	NS	-0.05 TC	-0.03 BLC+CR+F	0.00 BLC	0.03 BLC+CR	0.08 BLC+F
Increment 7 (12.11.86)	NS	0.10 BLC+F	0.11 TC	0.13 BLC+CR+F	0.14 BLC	0.18 BLC+CR	NS	-0.16 BLC+CR+F	-0.11 BLC+F	-0.04 TC	-0.02 BLC	0.02 BLC+CR
Total Growth Increment	***	0.79 BLC+F	0.80 TC	0.83 BLC	1.60 BLC+CR	2.21 BLC+CR+F	*	0.37 BLC+F	0.46 BLC	0.51 TC	1.49 BLC+CR	1.65 BLC+CR+F

NOTE: i) Treatments: TC = True Control; BLC = Basal Level Control; BLC+F = Basal Level Control plus Fertilizer; BLC+CR = Basal Level Control plus Competition Release; BLC+CR+F = Basal level Control plus Competition Release plus Fertilizer.

ii) Treatments are ranked in increasing order of magnitude, horizontal bars span means which do not differ significantly using LSD ($P<0.05$).

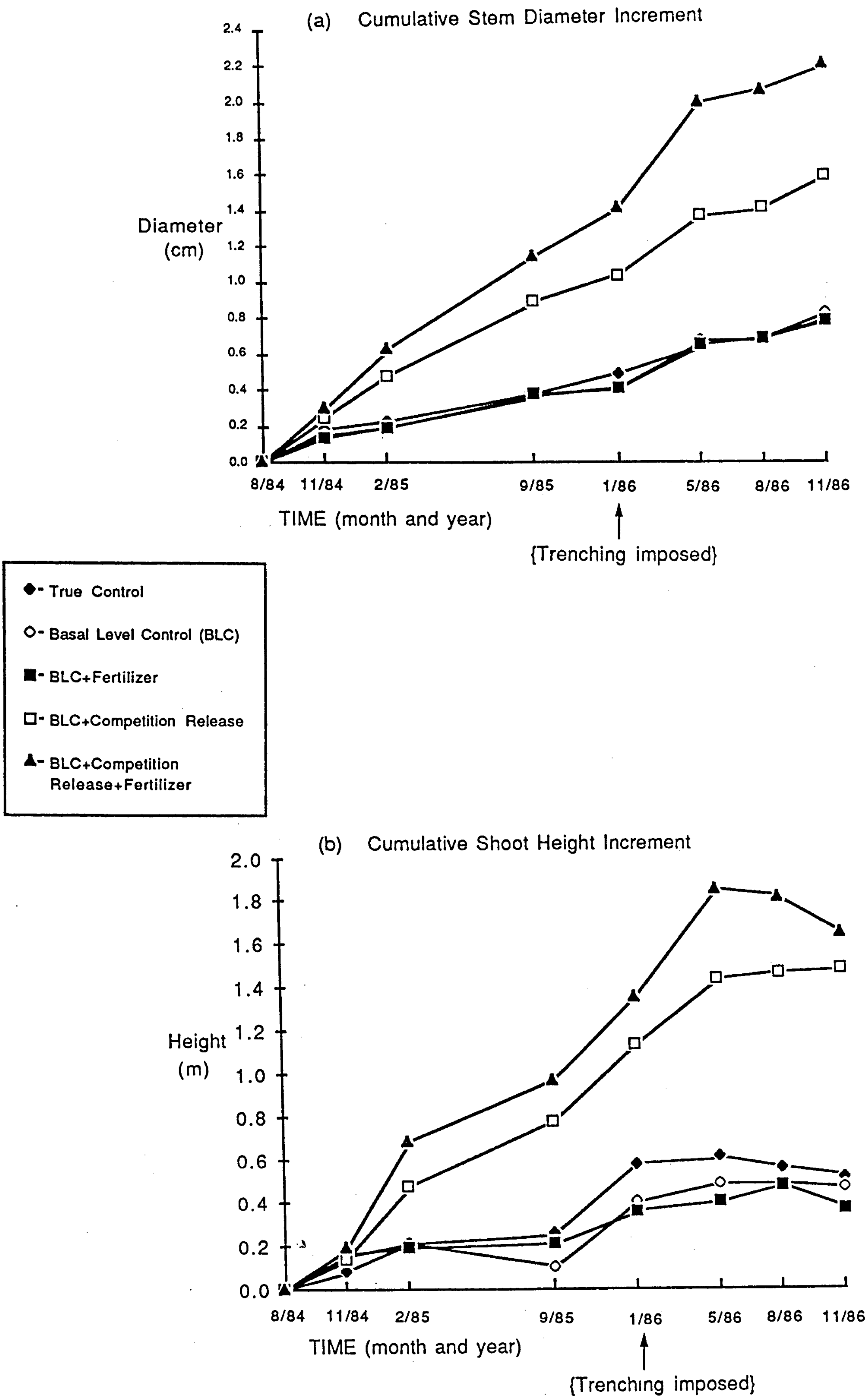

Figure 5.1 Cumulative (a) diameter and (b) height increment over 27 months of 13-year-old regrowth *E. maculata* subjected to five treatments.

As with stem diameter, there was little or no height increment at the last two measurements (August and November 1986) for any of the five treatments. In fact, at the final measurement, most responses were negative. Insect grazing on new leaves during the spring had been heavy, and it is likely this caused the reduction in height. The two fertilized treatments lost the most height at this measurement, suggesting preferential insect grazing on leaves of greater nutrient status. The severe insect grazing may thus have restricted the rate of diameter increment in the trenched and fertilized treatments as well.

5.3.3 Discussion

The restriction of *E. maculata* below the regrowth canopy may have two possible causes. Once subordinate to *Acacia*, there may have been insufficient light to permit development of *E. maculata* through the canopy. The other possibility is that *E. maculata* may be restricted by limiting soil factors (e.g. water, nutrients), or by the capacity to compete for these.

The possibility that insufficient light may be restricting *E. maculata* regrowth on this site, has not been investigated. However, there is some circumstantial evidence to suggest that the effect of shading may not be the critical factor. Unlike *E. maculata*, *E. pilularis* regrowth on the study site is now emergent over the *Acacia* canopy, suggesting it has had little difficulty harvesting sufficient light to maintain good growth rates. Part of this may have been due to the somewhat greater leaf area of *E. pilularis* (Chapter 4). *E. pilularis* is one of the more shade intolerant eucalypts (Jacobs 1955; Awang 1977), whereas *E. maculata* may be regarded as somewhat more tolerant (R.G. Florence, pers. comm.). It follows that because *E. pilularis* has performed substantially better than *E. maculata* in developing through the *Acacia* stand, it seems unlikely that the poor performance of *E. maculata* has been due primarily to inadequate light.

Nevertheless, it is appreciated that the role of light could have been a complementary factor, and warrants further investigation.* Given this qualification, it seems that limiting soil factors and root competition are the major contributors to the poor performance of *E. maculata.*

The broad patterns of diameter and height increment in response to the five treatments are clear. Where competition from immediately adjacent *Acacia* regrowth was removed or substantially reduced, *E. maculata* responded appreciably. This indicates a strong restrictive influence of *Acacia* species over *E. maculata* in this successional environment. There was no affect of fertilizer alone on diameter and height growth of *E. maculata,* but a response to fertilizer where competition had also been removed. Since *E. maculata* did not respond to fertilizer alone, some sort of release from competition is required before it is able to take advantage of added nutrients. However, it was not possible to determine directly from these results, what competitive influence may be involved.

Clearing grasses from around the base of the stem had no affect on the growth of *E. maculata.* However, because there was only a relatively light grass cover on the experimental site, this was perhaps not unexpected. The adverse influence of grasses on eucalypt growth may be quite substantial where development is more prolific (Bowen 1981; Webb *et al.* 1983; Ellis *et al.* 1985).

The trenching treatment was introduced in January 1986, to determine firstly whether any remaining or re-invading roots from adjacent *Acacia* might be affecting access to, or uptake of fertilizer by *E. maculata,* and secondly, whether the enhanced growth associated with the removal of immediately adjacent *Acacia* may have been due to a reduction in below or above ground competition (i.e. competition from roots or competition for light and growing space).**

* It is also possible that lowered light intensity will impair the growth of roots, and this should be included in further investigation.

** It is also possible there has been some inhibitory effect from prior occupation by Acacia - however, prior to the original clearfelling there would not have been a marked effect of Acacia on the site.

There is some evidence that where immediate overwood competition was removed and the site fertilized, *E. maculata* was still being affected by residual root competition from the nearest *Acacia* stems. Where the roots of the surrounding *Acacia* stems were partially severed (trenching) and the site re-fertilized, there was, after four months, a significant growth response in stem diameter - a response to fertilizer which had not been significant at any previous measurement. The response in shoot height to trenching and re-fertilizing is also seen to diverge from the other trenched treatment (Figure 5.1b), but the difference was not significant. This may have much to do with the heavy foliar grazing of fertilized trees. Thus overall, it is appreciated that the case for a response to trenching is not conclusive, and the experiment will be maintained until mid 1987 to monitor any further responses.

The responses to treatments in this experiment are similar to those obtained where a eucalypt (*E. grandis*) was planted in grassveld in South Africa (Poden 1984). While there was a relatively small response to partial removal of grass competition (pitting, ripping, spraying and weeding), and to fertilizer, a major response was obtained only with 'complete cultivation', in which it may be presumed the intense competitive influence of the dense fine root system of the grass was broken (Figure 5.2). Where this was done, there was a substantial additional response to fertilizer. The comparability between the responses of planted eucalypt seedlings in a grassveld, and that of *E. maculata* to removal of *Acacia* on Kioloa State Forest, suggest the same factors are operating, that is, a sensitivity to competition from a plant with a well developed surface root system.

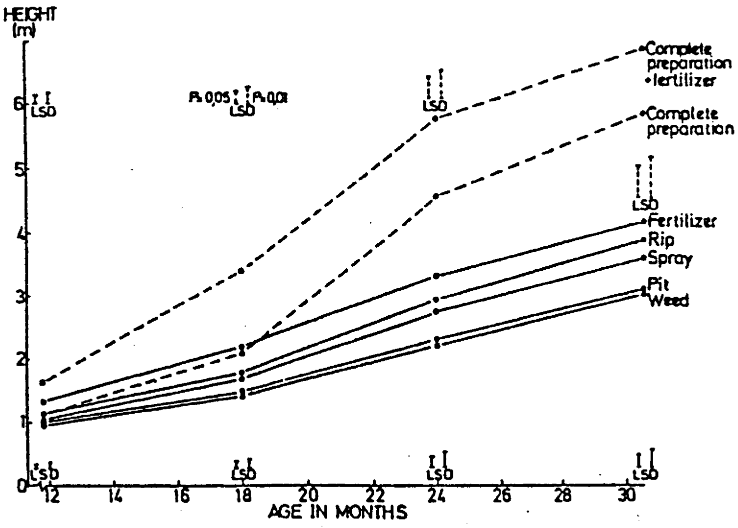

Figure 5.2 Heights of *E. grandis* planted in virgin grassveld for various site preparation treatments (after Boden 1984).

5.4 GENERAL DISCUSSION

The first experiment in this chapter has shown that phosphorus rather than nitrogen limits the growth of seedling eucalypts on a site which has carried a heavy *Acacia* stocking for 13 years. Native legumes are likely to have made a significant contribution to the nitrogen economy of the site, through the fixation of atmospheric nitrogen and the cycling of nitrogen rich litter (Feller 1980; Adams and Attiwill 1984a; Grove and Malajczuk 1985). The regrowth site is therefore unlikely to represent the condition of the nutrient pool, and particularly the nitrogen pool, in the soils at the time of clearfelling.

In an independent (unpublished) study, J.D. Williams and D.M. Halsall of the CSIRO examined the response of eucalypts to nutrients on a site adjacent to the regrowth stands on Kioloa State Forest. It is quite likely the nutrition of this site was similar to many of those at clearfelling. In a study based on factorial combinations of nitrogen, phosphorus and calcium, the height growth of *E. maculata* and

E. pilularis responded only where nitrogen and phosphorus were added together. This is in contrast to the fertilizer trial on the regrowth site, where the major response was to phosphorus - with or without added nitrogen. The experiment of J.D. Williams and D.M. Halsall demonstrates that nitrogen as well as phosphorus is important for the growth of seedling eucalypts on a site recently cleared. In their trial, as with that reported in this chapter, *E. pilularis* grew consistently better than *E. maculata*, regardless of nutrient treatment. The effects of an unidentified species specific pathogen, possibly *R. pitereka*, was also attributed in part to *E. maculata's* poor response.

In a further trial, J.D. Williams and D.M. Halsall examined the effect on height growth of establishing various mixtures of *E. maculata* and *Acacia longifolia* under conditions of 'nil' and 'high' added nitrogen (Figure 5.3). Without addition of nitrogen, *E. maculata* occupied either a sub-dominant or co-dominant position in the stand, depending on the species mix ratio. However, where nitrogen was added, E. maculata showed a marked increase in height growth at the expense of *Acacia*. Under this treatment, *A. longifolia* put on less height increment than for the 'nil' nitrogen treatment. This experiment clearly demonstrates the outstanding contribution of nitrogen supply to *E. maculata's* competitive ability in the early establishment phase, at least on some of the 'Kioloa' soils.

The second experiment described in this chapter has demonstrated the restrictive role that *Acacia* may play in the competitive relations of *E. maculata*. Only where the adjacent *Acacia* stems had been removed was *E. maculata* able to respond and its growth was further enhanced where fertilizer was added. However, without the benefit of 'competition release', *E. maculata* was unable to respond to fertilizer. The precise nature of this restrictive competitive effect was not identified.

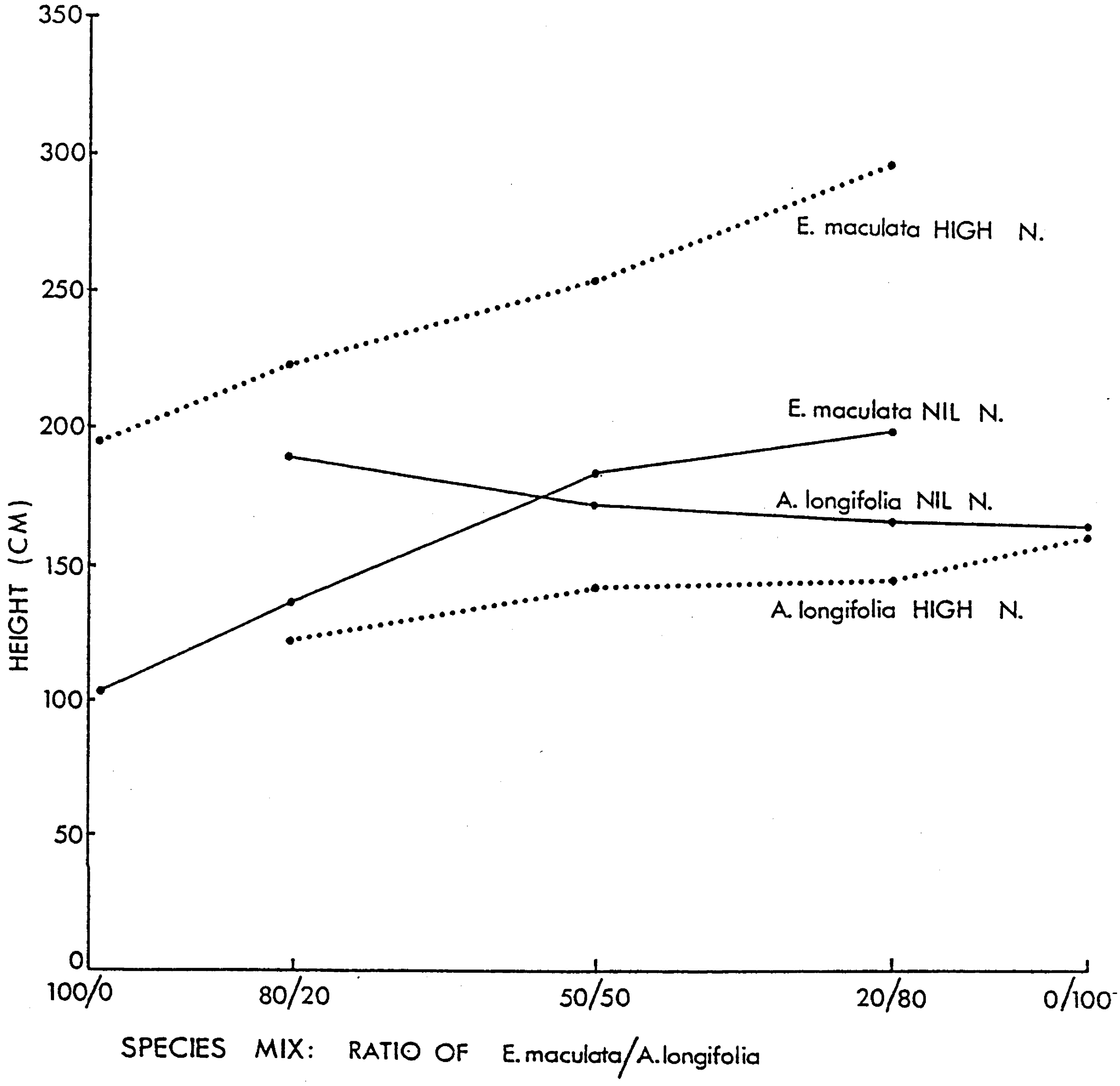

Figure 5.3 Effect on height growth of establishing mixtures of *E. maculata* and *Acacia longifolia* under conditions of nil and high added nitrogen (after J.D. Williams and D.M. Halsall unpublished).

The growth responses in this chapter highlight the importance of nutrition and competition on the successful development of *E. maculata*, and support the hypothesis that within the study area, sites may be nutritionally marginal for this species - at least in terms of its vigour and competitive ability at the regrowth phase, and under the conditions of clearfelling investigated in the study.

Throughout the study, nitrogen has been identified as one of the most important elements affecting the growth of *E. maculata*, particularly in the early seedling stage of development. The availability of nitrogen in the establishment stage of stand development may therefore have been critical in determining the success or otherwise of this species. In order to develop this theme further, it seemed desirable to establish the size and characteristics of the available nitrogen pool and the nature of nitrogen mineralization in a range of *E. maculata* soils. The study is described in Chapter 6. It also seemed desirable to ask whether it is a limited pool *per se* which is the only factor limiting the competitive ability of a species with an apparent high nutrient requirement, or whether differences between species in gaining access to nutrients may also be critical. A study on the form of the seedling roots of south coast species was established to help determine this (Chapter 7).

CHAPTER 6

NITROGEN MINERALIZATION ALONG A VEGETATION GRADIENT

6.1 INTRODUCTION

Evidence now points strongly to the view that soil fertility delimits *E. maculata* and *E. piperita* communities, and that within its site range, *E. maculata's* competitive ability with other species will be a function of the size of the available nutrient pool during establishment. J.D. Williams and D.M. Halsall (unpublished) have shown that the element nitrogen severely limits the seedling growth of *E. maculata* on a site adjacent to the regrowth stands on Kioloa State Forest. The availability of soil nitrogen may therefore have been critical in the establishment and early successional stages of stand development. In order to investigate this possibility further, rates of mineralization of soil organic nitrogen were measured in soils taken from a range of sites in forest adjacent to the clearfelled stands. These had been selectively logged in much the same way as the stands chosen for clearfelling, and comprise the same range of species. Thus it is assumed that the study can lead to inferences about rates of mineralization on the sites which were subsequently clearfelled.

The sites chosen for the study represent a gradient in site quality from dry sclerophyll to wet sclerophyll forest, all with an *E. maculata* component. The main purpose of the study was to estimate the potential rates of nitrogen release in soils from four vegetation/site types, along this gradient. Soils were sampled, and three treatments ('undisturbed', 'physically disturbed' and 'heated') were imposed prior to laboratory incubation. Results were used to infer whether limited mineralization of nitrogen following logging could have restricted the development of some regrowth species, particularly *E. maculata*, and whether an intense regeneration burn (simulated by soil heating) may have provided a flush of nitrogen sufficient to give *E. maculata* a temporary advantage over other successional species.

6.2 PROCESSES OF NITROGEN MINERALIZATION

Mineralization of soil nitrogen is the term used for the process whereby nitrogen in organic compounds is converted into inorganic ions. The initial product is ammonium (NH_4-N), which in some instances is oxidised to form nitrate (NO_3-N). These transformations are driven by enzymes produced by the soil biota. Both fungi and bacteria readily decompose proteins, amino acids and other nitrogenous compounds, assimilating nitrogen into their own protoplasm. They release NH_4-N into the soil when available nitrogen is in excess of energy (carbon) available for new growth of microbes.

Two stages are involved in the oxidation of ammonium to nitrate. The first yields water and energy:

$$NH_4^+ + 1.5\ O_2 \longrightarrow NO_2^- + H_2O + 2H^+$$

$$G = -216.8 \times 10^3 \text{ Joules mol}^{-1}$$

and the second yields energy:

$$NO_2^- + 0.5\ O_2 \longrightarrow NO_3^-$$

$$G = -84.0 \times 10^3 \text{ Joules mol}^{-1}$$

(Delwiche 1981).

It has been suggested that the factor most likely to control the rate of nitrification is the rate of net ammonification (Jansson 1958; Wollum and Davey 1975). Ammonifying hetrotrophs may be better competitors for NH_4-N than nitrifying autotrophs (Jansson 1958; Jones and Richards 1977b), and only where there is abundant soil NH_4-N is the competitive control on nitrifying organisms removed (Carlyle and Malcolm 1986a). Mycorrhizae also compete for NH_4-N which can then be taken up by plants. Nitrification has been shown to be greater on soils where ammonification is greater. This occurs on sites where organic matter decomposition and nitrogen turnover is more rapid (DeRahm 1970, Pfadenhauer 1979, cited in Adams and Attiwill 1982; Adams and Attiwill 1982), on soils that have been fertilized (Popovic 1977; Adams and Attiwill 1984b), and on soils with higher fertility status (Youngberg 1978; Williams 1983). It has been argued that continued input of tree litter with a high C:N ratio (as is the case in many eucalypt forests) should effectively prevent mineralization of nitrogen from proceeding to the production of NO_3-N (Attiwill *et al.* 1981; Adams and Attiwill 1982; Adams and Attiwill 1986b).

Nitrification can be influenced by a number of environmental factors. It only proceeds rapidly in warm soils, and is reduced markedly where soil temperatures fall below 4 or 5°C. Optimum temperatures appear to be between 25 and 30°C. NO_3-N production was also thought to be inhibited in very acid soils, but more recent findings in which high NO_3-N contents have been found in very acid soils subject to acid rain, suggest this may not always be the case (R.J. Raison pers. comm.) This relationship is not clear because the effect of acidity is through the toxic effect of active aluminium ions (Russell 1973). Despite this, there seems to be little effect of pH on nitrification between the range 5 to 8. Ashton and Willis (1982) consider that microbial inhibitors may also be implicated in the production of NO_3-N, although their effect may only be short lived. It has also been suggested that mature successional vegetation may produce toxins inhibitory to nitrifying bacteria (Rice and Pancholy 1972, 1973, 1974) - a process which is thought to result in conservation of nitrogen and energy. However, Adams and Attiwill (1982) reported no evidence of this in older and higher quality forests of *E. obliqua* and *E. regnans* - a conclusion which was also reached by Lamb (1980) in relation to mature subtropical rainforest.

In addition to the gains of inorganic nitrogen associated with mineralization, soil can accumulate nitrogen through symbiotic and non-symbiotic fixation of atmospheric nitrogen, predominantly by bacteria. The bacteria associated with plants can only fix nitrogen actively if the plant is adequately supplied with the essential elements for growth. In successional communities, the input of nitrogen from nitrogen-fixing plants is often high in the early stages, but diminishes with time as these plants die out (Stephens and Walker 1970). Nitrogen inputs may also occur via rainfall (Attiwill *et al.* 1981; Lamb 1981).

Mineral nitrogen can be lost from the soil in a number of ways. It may be taken up by plants or assimilated into the cells or hyphae of soil micro-organisms (immobilization), both of which return nitrogen to the organic pool. Otherwise it may be converted into volatile compounds and lost to the air, or leached out of the soil. Gaseous losses of inorganic nitrogen may occur under conditions of poor aeration, where nitrates are reduced to oxides of nitrogen and free nitrogen gas (N_2) (denitrification). This process may be accelerated by the effects of plant roots - which contribute organic material from the high turnover of fine roots and reduce the oxygen concentrations through root respiration (Rolston *et al.* 1978). Transfer of nitrogen to the atmosphere may also occur in the combustion of organic matter or where the soil is heated (White *et al.* 1973; Ellis and Graley 1983; Raison *et al.* 1985a, 1985b). NO_3-N can be readily lost through leaching because it is usually dissolved in the soil solution (unless the soil dries out). NH_4-N is far more resistant to leaching than NO_3-N because it is held on the exchange complex.

The amount of mineral nitrogen found in the soil at any time represents the differences between inputs from mineralization and output processes described above.

In the decomposition of organic matter, celluloses and hemicelluloses are broken down first. The products of this process include energy and NH_4-N, which are synthesised by the micro-organisms. Excess NH_4-N may be released into the soil to contribute to the mineral nitrogen pool. The structural components of organic matter, for example lignin, are much more resistant to microbial attack and relatively few species can decompose them. Where this refractory material makes up a large proportion of organic matter, energy for microbial processes may become limiting. However, even energy will not lead to release of nitrogen where organic matter is composed of the more resistant structural components. This may be a problem in some eucalypt forest soils.

The cycling of nitrogen in eucalypt forests has been examined in some detail in two symposiums (Rummery and Hingston 1981; Turvey 1981). It is widely recognised that eucalypts efficiently redistribute nutrients within the plant to maintain tree growth on low fertility soils (Hatch 1955; Attiwill *et al.* 1978; Turner and Lambert 1981; Banks 1982). The withdrawal of nutrients prior to litterfall means that compared with litter in northern hemisphere hardwood forests, the eucalypt forest has litter with a high C:N ratio and low concentrations of nutrients (Jacobs 1955; Florence 1981). These features may restrict the mineralization of organic material on the forest floor. The process of incorporation of *E. pilularis* leaf litter into the soil has been described by Florence (1961). There was a rapid decline in litter dry weight as water soluble materials were leached, and more decomposable components utilized by micro-organisms. The rate of weight loss of litter then declined, and after 15-18 months, the leaf material was still essentially whole and forming a continuous litter mat. With time, this material became increasingly brittle, and at the soil-litter interface was progressively broken into small pieces and incorporated into the soil, possibly by larger litter fauna. This general pattern of decomposition of eucalypt leaf litter has also been reported by Hatch (1955) and McColl (1966). In contrast to eucalypt litter, the litter of the subtropical rainforest can be completely incorporated into the soil within a few months of its being shed (Florence 1961). In addition to leaf litter, the eucalypt sheds a large amount of woody material (twigs, capsules and bark). This may result ultimately in the immobilization of nitrogen within the more refractory components of the soil organic material (Florence and Crocker 1962), and in increased assimilation of a limited pool of soil mineral nitrogen by soil microbes.

The decomposition of eucalypt litter within the forest is affected by the quality of the eucalypt litter and the quality of the understorey litter. Eucalypt litter breakdown has been shown to be enhanced where there is a nitrogen rich understorey litter - which is typical of high quality wet sclerophyll forest (Florence 1961; Baker and Attiwill 1981; O'Connell 1981), and forest with a legume understorey (McColl 1966; Lamb *et al.* 1980). In contrast, O'Connell (1986) found little difference in decomposition rates of *E. marginata* litter located in forest with and without a legume understorey. The understorey may however, return a large amount of nitrogen to the forest floor relative to its above-ground biomass (Hingston 1981; O'Connell 1981). It has been shown that relative to organic matter, nitrogen may be held selectively in decomposing eucalypt litter (Hatch 1955; Baker and Attiwill 1981; O'Connell 1981; O'Connell and Menage 1983). In the presence of a legume understorey, the amount of nitrogen in eucalypt litter may even increase as decomposition proceeds (O'Connell 1986), but may eventually lead to an acceleration in the net mineralization of nitrogen. Adams and Attiwill (1986a) suggest that measures of litter quality such as lignin content may be of equal significance to nitrogen content and environmental conditions in determining degradability.

Nitrogen mineralization is often enhanced following some sort of perturbation, involving either physical soil disturbance or fire (Attiwill *et al.* 1981; Florence 1981; Vitousek 1981; Adams and Attiwill 1984b). Under field conditions, cycles of wetting and drying can stimulate microbial activity and enhance mineralization (Birch 1960, 1964; Russell 1973). The flush of mineral nitrogen is derived from the oxidation of organic material desorbed from the soil and rendered soluble by the drying process, and from the microbial cells killed as the soil dries out. On the other hand, van Schreven (1967) found soil wetting and drying had little effect on nitrogen mineralization after one month.

Intense fire, or heating of the soil, can also stimulate mineralization of nitrogen (see reviews by Raison 1979; O'Connell *et al.* 1981). Grove *et al.* (1986) reported a 182% increase in NH_4-N in the 1-3 cm soil immediately after an intense fire in *E. marginata* forest, but 1 year later, the concentration had returned close to pre-burn levels. Dunn and Debono (1977) also found similar patterns after fire. Khanna and Raison (1981) found elevated concentrations of NH_4-N at least two years after a prescribed burn, while Walker *et al.* (1986) reported that the amount of NH_4-N increases as soil heating increases. Others have reported increased NO_3-N following burning (Christensen 1973; Jones and Richards 1977a, 1977b; Mroz *et al.* 1980; Attiwill *et al.* 1981; Ellis 1981). However, fire can also cause losses of nitrogen contained in burned fuels and surface soils by volatilization and convective transfer of ash (Walker *et al.* 1986), and increase denitrification and leaching of NO_3-N (O'Connell *et al.* 1981).

Because of the influence of volatilization and particulate loss, total nitrogen often decreases following intense fire (White *et al.* 1973; Ellis and Graley, 1983; Raison *et al.* 1985a). Between 55% to 85% of the total nitrogen in the fuel load may be released to the atmosphere (Debell and Ralston 1970, Raison 1980, cited in O'Connell *et al.* 1981;

Raison *et al.* 1985b). However, others (Raison 1979; Grove *et al.* 1986) reported an increase in total nitrogen immediately after fire, and attributed this to incomplete combustion of some organic matter released in the fine ash material. Heating of the soil may also release some nitrogen immediately (Raison 1979), and increase mineralization of heat altered organic matter (Walker *et al.* 1986).

6.3 MATERIALS AND METHODS

Field Sites

Nitrogen mineralization studies were carried out on soils collected from four sites on Kioloa State Forest on the south coast of New South Wales. All sites carried an *E. maculata* component in the overstorey, but the quality of the forest and the composition of co-occurring species differed. The four sites, which are illustrated in Plate 6.1, represent a gradient from dry sclerophyll to high quality wet sclerophyll forest and are described below.

Site 1 Low quality mixed species forest with an *E. maculata, E. globoidea, E. gummifera* and *E. pilularis* overstorey and a sclerophyll/heath understorey. The main understorey species are *Leucopogon lanceolatus, Leptospermum flavescens, Acacia longifolia, Hibbertia aspera* and *Lepidosperma urophorum.* This will be referred to as the 'low quality dry sclerophyll' site.

Site 2 Moderate quality mixed species forest with *E. maculata* as the dominant overstorey species, but also containing *E. pilularis, E. globoidea* and *E. gummifera.* There is an open sclerophyll understorey with the main species being *Persoonia lanceolata, Leucopogon lanceolatus, Acacia ulicifolia* and *Lepidosperma urophorum.* This will be referred to as the 'moderate quality dry sclerophyll' site. The basal area of overstorey species on this, the Link Road site, is given in Section 2.3.1.

(1)

(2)

Plate 6.1 An illusstration of vegetation on (1) the low quality dry sclerophhyll site and (2) the moderate quality dry sclerophhyll site.

(3)

(4)

Plate 6.1 cont. An illustration of vegetation on (3) the intermediate sclerophyll site and (4) the wet sclerophyll site.

Site 3 High quality forest containing *E. maculata* and *E. pilularis*. The understorey contains both sclerophyll and mesophytic components, the main species being *Synoum glandulosum, Acacia floribunda, Pultenaea blakelyi* and *Entolasia marginata*. This will be referred to as the 'intermediate sclerophyll' site.

Site 4 High quality *E. maculata-E. pilularis* forest within a rainforest-eucalypt forest ecotone. The main mesophytic understorey species are *Callicoma serratifolia, Synoum glandulosum* and *Acmena smithii*. This will be referred to as the 'wet sclerophyll' site.

The level of *Acacia* stocking on Sites 1, 2 and 3 was not particularly high, and therefore may not have contributed greatly, in terms of nitrogen fixation, to the nitrogen economy of the sites.

Experimental Method

Soils were sampled one to two weeks after rainfall of 33 mm over a four day period, leaving the soils field moist (field capacity). Soils were sampled at each site within an area of 0.25 ha (50 x 50 m). The sampling area had not been disturbed in recent times. To ensure that the whole of the area was sampled adequately, each site was divided into four 25 x 25 m subsites. Within each of the subsites, 12 galvanized steel tubes (each 20 cm in length and with an internal diameter of 5 cm) were driven into the soil in pairs at randomly selected locations. All tubes (containing relatively undisturbed soil columns) were removed immediately and brought back to the laboratory. One core from each pair was set aside for incubation. This soil was untouched and formed the 'undisturbed' soil treatment. Soil from the second core of each pair was removed from the tubes, divided into depth segments (0-5, 5-10 and 10-20 cm), sieved (<5 mm) and bulked to produce two replications (each of four cores) for each subsite and depth, or eight replications for each site. These were subsampled for determination of initial mineral nitrogen and moisture content. The remainder of this soil was treated as described below and then incubated.

Soils from the four sites had three treatments applied prior to incubation in the dark at 20°C for 60 days. The treatments were:

1. Undisturbed - soil remaining undisturbed in the cores.
2. Disturbed - soil disturbed in the process of extracting and sieving soil cores; the aim was to simulate physical disturbance which may accompany logging operations. Four replications (each about a 200 g subsample) for each site and depth were used, and this was achieved by bulking the two replications from each subsite.
3. Disturbed and heated - disturbed (as for 2 above), with four replications per site and depth. The subsamples were heated for 3 h in an oven in sealed oven bags. Soil from the 0-5 cm depth was subjected to 100°C; from the 5-10 cm depth, 70°C; and from the 10-20 cm depth, 50°C. These temperatures aimed to simulate those experienced during slashburning after harvesting (Walker *et al.* 1986). After heating, soil was immediately subsampled to determine the immediate effect of heating on mineral nitrogen content.

Following the 60 day incubation, the undisturbed soil cores were processed as for the initial samples, and their mineral nitrogen contents determined. The disturbed, and disturbed and heated soils from the incubation were also subsampled for determination of moisture and mineral nitrogen content.

The laboratory processing of soils and measurements of mineral nitrogen content, pH, organic carbon and total nitrogen follow Raison *et al.* (in preparation). Field moist soils were stored at 4°C until they were processed, within a few days. After the soil cores were sectioned by depth and sieved, the fine and coarse earth fractions were weighed. A 10 g subsample of the fine earth was extracted by shaking with 50 ml 2N KCl for 1 h, followed by filtering. Filtrates were analysed by automated colorimetry following distillation of NH_4-N. Total mineral nitrogen was measured following reduction of NO_3-N using $Ti(SO_4)_2$ (Heffernan 1985). The difference between total mineral nitrogen and NH_4-N provided a measure of NO_3-N. The pH of the KCl extract was measured using a glass electrode, and soil moisture content determined by drying at 105°C to a constant weight. Bulk density was calculated from the mass of dry earth and the volume of the steel core. The mass of fine earth was used to convert soil mineral nitrogen concentrations to kg ha^{-1}. Organic carbon was determined following Walkley and Black (1934) wet digestion, and total nitrogen after Kjeldahl digestion.

Differences between the initial mineral nitrogen contents and the contents after 60 days incubation were used to calculate rates of net nitrogen mineralization, expressed as kg ha^{-1} $month^{-1}$. Two-way analyses of variance were used to separate the effects of soil treatment and site. The total mineral nitrogen contents for the 0-20 cm depth sections were analysed in this way - as were the total mineral nitrogen contents for the individual depth segments (0-5, 5-10, 10-20 cm). The same analyses were repeated for NH_4-N data. The production of NO_3-N was largely limited to one site.

6.4 RESULTS

The moisture content and bulk density of the soils, and the pH of the KCl extract are given in Table 6.1. The ranked order of means from analyses of variance of total mineral nitrogen and NH_4-N data for soil treatments and sites, are given in Table 6.2.

Table 6.1 Mean values (± standard error) of selected physical properties of soils from four sites.

Site	Soil Treatment	Percentage Moisture Content			Soil pH			Soil Bulk Density (g cm^{-3})		
		Soil Depth (cm)			Soil Depth (cm)			Soil Depth (cm)		
		0-5	5-10	10-20	0-5	5-10	10-20	0-5	5-10	10-20
Low Quality Dry Sclerophyll	Undisturbed	21.67 ± 2.04	17.00 ± 1.16	13.73 ± 1.04	3.34 ± 0.03	3.47 ± 0.03	3.73 ± 0.02	0.95 ± 0.04	1.36 ± 0.02	1.53 ± 0.02
	Disturbed	23.94 ± 3.32	18.09 ± 2.25	14.13 ± 1.58	3.21 ± 0.04	3.38 ± 0.03	3.58 ± 0.02			
	Heated	23.16 ± 2.96	17.00 ± 2.22	13.31 ± 1.59	3.24 ± 0.04	3.39 ± 0.03	3.60 ± 0.02			
Moderate Quality Dry Sclerophyll	Undisturbed	18.89 ± 0.65	16.28 ± 0.62	15.20 ± 0.69	3.33 ± 0.03	3.59 ± 0.04	3.80 ± 0.05	1.06 ± 0.02	1.49 ± 0.02	1.64 ± 0.04
	Disturbed	19.55 ± 0.51	15.68 ± 1.00	13.71 ± 0.92	3.23 ± 0.04	3.46 ± 0.04	3.66 ± 0.03			
	Heated	16.86 ± 0.70	15.01 ± 0.93	12.72 ± 0.90	3.26 ± 0.04	3.49 ± 0.05	3.68 ± 0.03			
Intermediate Sclerophyll	Undisturbed	17.59 ± 1.29	15.16 ± 1.15	11.76 ± 0.69	3.63 ± 0.04	3.63 ± 0.02	3.75 ± 0.01	0.88 ± 0.02	1.28 ± 0.03	1.51 ± 0.03
	Disturbed	18.72 ± 2.24	14.79 ± 1.52	11.30 ± 0.76	3.58 ± 0.06	3.61 ± 0.03	3.70 ± 0.01			
	Heated	17.13 ± 2.32	13.75 ± 1.43	10.55 ± 0.84	3.63 ± 0.06	3.67 ± 0.05	3.73 ± 0.01			
Wet Sclerophyll	Undisturbed	31.54 ± 0.94	22.15 ± 0.60	17.89 ± 0.53	3.20 ± 0.03	3.31 ± 0.04	3.53 ± 0.04	0.97 ± 0.05	1.31 ± 0.03	1.42 ± 0.03
	Disturbed	35.55 ± 1.31	23.55 ± 0.51	18.71 ± 0.38	3.15 ± 0.04	3.22 ± 0.04	3.40 ± 0.04			
	Heated	34.90 ± 1.48	22.72 ± 0.51	17.78 ± 0.25	3.24 ± 0.03	3.29 ± 0.04	3.45 ± 0.04			

NOTE: For undistubed soils, means are based on eight replications; for disturbed and heated soils, means are based on four replications. Soil bulk density was only determined in undisturbed soils.

Total Mineral Nitrogen

The initial mineral nitrogen contents of soils from the four sites are illustrated in Figure 6.1. The low and moderate quality dry sclerophyll soils (Sites 1 and 2) had the least, and the wet sclerophyll soil (Site 4) the greatest amounts of mineral nitrogen at the three soil depths. The intermediate sclerophyll soil (Site 3) had initial mineral nitrogen contents between these. Virtually no NO_3-N was present in any of these soils, although small amounts (<2 μg g^{-1}) were measured in three of the eight replications of soil from the wet sclerophyll site.

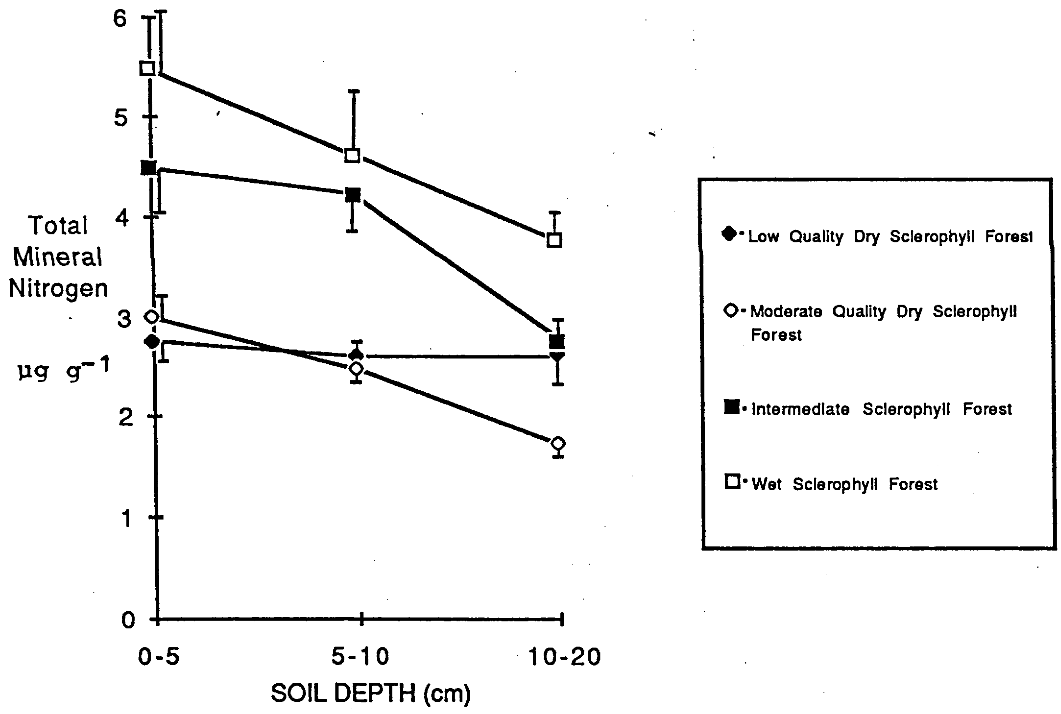

Figure 6.1 Initial mineral nitrogen content (μg g^{-1}) + or - standard error of soils from four sites prior to laboratory incubation.

The production of mineral nitrogen in soils from the four sites and for the various depths over the 60 day incubation, are shown in Figure 6.2. The undisturbed soil from the wet sclerophyll site produced nearly three times as much total mineral nitrogen in the 0-20 cm profile as did the soil from the intermediate sclerophyll, and the moderate and low quality dry sclerophyll sites. The rate of production in the four soils was 26.2, 8.7, 6.0 and 9.8 kg ha^{-1} month^{-1} respectively. Mineralization patterns within the three sections of the 0-20 cm profile are broadly similar (Figure 6.2), although, as might be expected, the quantity produced per unit depth of undisturbed soil was lower at 10-20 cm than at either 0-5 or 5-10 cm. Again, as might be expected, the rate of mineralization was better maintained in the wet sclerophyll soil at 10-20 cm than in the intermediate and dry sclerophyll soils.

Where compared with the undisturbed treatment, soil disturbance had little effect on the total mineral nitrogen produced in the wet sclerophyll and intermediate sclerophyll soils, and depressed that in the soils from the poorer quality sites. This may have been due to exposure of available carbon, resulting in immobilization. For example, in the 0-20 cm profile, the low quality dry sclerophyll soil produced 9.8 and 2.9 kg ha^{-1} month^{-1} in the undisturbed and disturbed treatments respectively. This pattern, in which mineral nitrogen production remained much the same, or was depressed in response to disturbance, was consistent for each soil depth.

In contrast to disturbance, mineral nitrogen production was markedly stimulated in all soils which had been heated. A proportion of this was an immediate response to heating (Table 6.3). The total production in the 0-20 cm section of the wet sclerophyll soil over the 60 day incubation (including mineral nitrogen produced immediately following heating) more than doubled (26.2 to 63.7 kg ha^{-1} month^{-1}), and the increase was proportionally greater in the other soils.

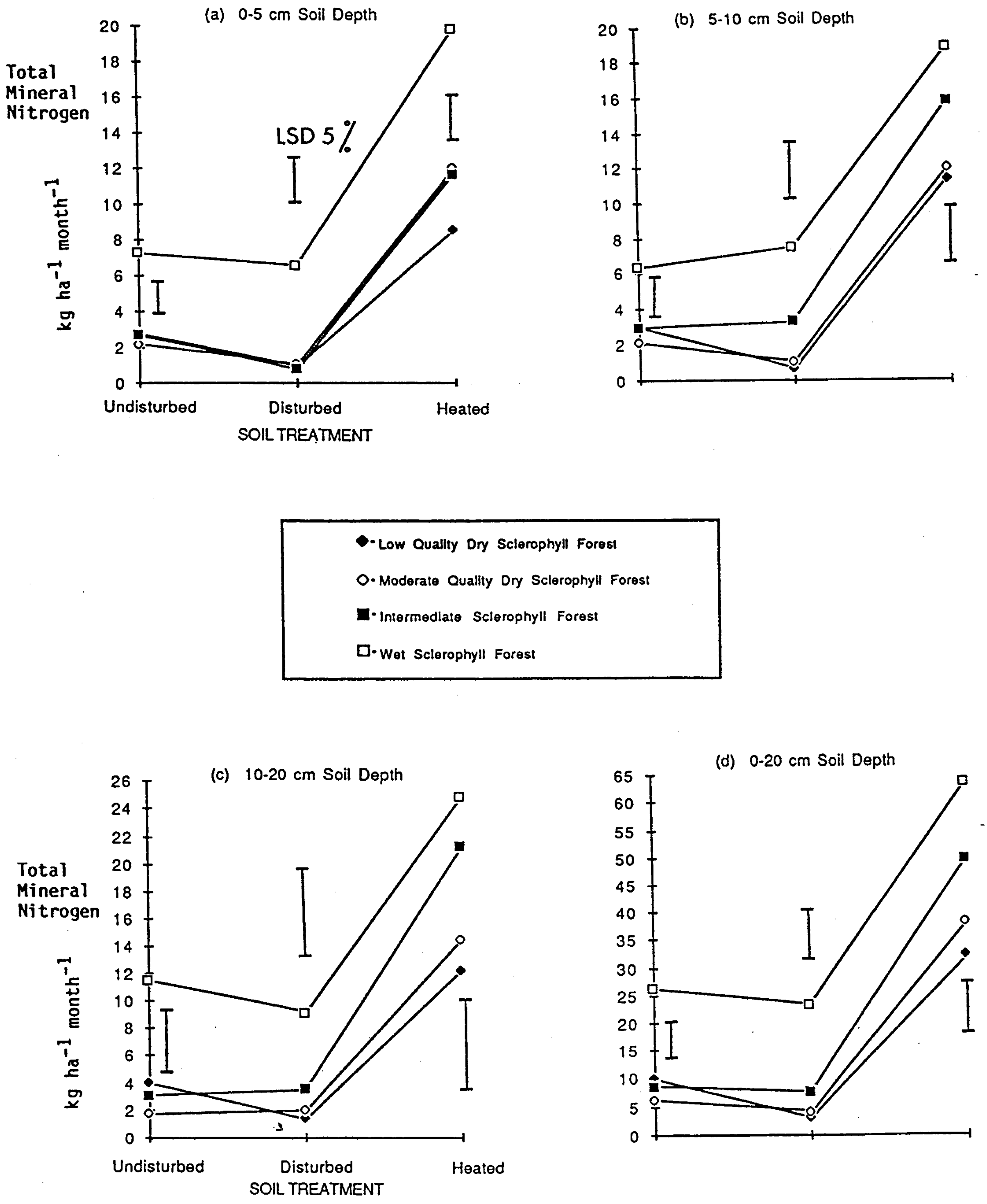

Figure 6.2 The rate of mineralization of soil nitrogen for different sites, treatments and depths during laboratory incubation at 20°C.

In the intermediate sclerophyll soil, production rose from 8.7 to 49.8 kg ha^{-1} month^{-1}, that is, potential mineralization is good, but is clearly restricted in the absence of an external stimulus. The individual depth segments from intermediate and dry sclerophyll soils also responded more to heating, in a relative sense, than the wet sclerophyll soil. Mineral nitrogen production responded particularly well in the intermediate sclerophyll soil. For example, at 5-10 cm, the intermediate sclerophyll soil produced 15.8 kg ha^{-1} month^{-1}, a quantity similar to that produced in the wet sclerophyll soil (18.9 kg ha^{-1} month^{-1}); and at 10-20 cm, total mineral nitrogen production in the intermediate sclerophyll soil rose from 3.1 to 21.3 kg ha^{-1} month^{-1} in response to heating while that in the wet sclerophyll soil rose from 11.5 to 24.8 kg ha^{-1} month^{-1}.

Heating produced an immediate response in mineral nitrogen production (Table 6.3), ranging from 3.83 μg g^{-1} in the 10-20 cm section of the moderate quality dry sclerophyll soil to 20.96 μg g^{-1} in the 0-5 cm section of the wet sclerophyll soil. This immediate release of mineral nitrogen (almost entirely NH_4-N) was probably a result of chemical oxidation of organic matter (Walker *et al.* 1986). As a percentage of the total nitrogen mineralized over the 60 day period, this was consistently greater in the 0-5 cm soil (Table 6.3). This might reflect both the nature of the more recently incorporated organic matter in the surface soil and the greater temperature at which this soil section was heated. The immediate release of nitrogen was as high as 29.5% of the total nitrogen mineralized in the low quality dry sclerophyll forest soil.

Table 6.2 Rate of mineralization of soil nitrogen and rate of NH_4-N production (kg ha^{-1} month^{-1}) in ranked order for soil treatments and sites.

Attribute	Soil Treatments			Sites			
Total Mineral N 0-5 cm	2.32	3.74	13.04	3.77	4.35	4.46	10.26
	Dist	Und	Heat	S1	S2	S3	S4
Total Mineral N 5-10 cm	3.10	3.58	14.54	4.29	4.48	6.26	9.78
	Dist	Und	Heat	S2	S1	S3	S4
Total Mineral N 10-20 cm	4.00	5.10	18.25	5.00	5.40	7.75	14.25
	Dist	Und	Heat	S2	S1	S3	S4
Total Mineral N 0-20 cm	9.45	12.7	46.05	13.60	13.65	18.70	34.85
	Dist	Und	Heat	S2	S1	S3	S4
NH_4-N 0-5 cm	0.86	2.52	12.22	3.62	4.14	4.24	6.11
	Dist	Und	Heat	S1	S3	S2	S4
NH_4-N 5-10 cm	1.20	2.24	14.16	4.31	4.48	5.28	5.78
	Dist	Und	Heat	S2	S1	S4	S3
NH_4-N 10-20 cm	3.50	0.80	17.70	5.05	5.15	6.90	8.35
	Dist	Und	Heat	S2	S1	S3	S4
NH_4-N 0-20 cm	2.85	8.25	44.25	13.25	13.65	17.00	19.75
	Dist	Und	Heat	S1	S2	S3	S4

NOTE: (i) Soil treatments: Und = Undisturbed; Dist = Disturbed; Heat = Heated.

(ii) Sites:
S1 = Low quality dry sclerophyll forest;
S2 = Moderate quality dry sclerophyll forest;
S3 = Intermediate sclerophyll forest;
S4 = Wet sclerophyll forest.

(iii) Treatments are ranked in increasing order of magnitude; horizontal bars span treatments whose means do not differ significantly using LSD ($P<0.05$).

Table 6.3 The amount of inorganic nitrogen ($\mu g\ g^{-1}$) produced from the immediate effect of heating. Values in brackets give this amount as a percentage of the combined mineral nitrogen produced from heating and over the the 60 day incubation period.

Site	Soil Depth (cm)		
	0-5	5-10	10-20
Low Quality Dry Sclerophyll (S1)	13.68 (29.5)	7.50 (14.4)	5.82 (21.6)
Moderate Quality Dry Sclerophyll (S2)	10.69 (16.7)	5.80 (10.2)	3.83 (12.6)
Intermediate Sclerophyll (S3)	19.72 (27.6)	12.72 (16.5)	6.89 (14.9)
Wet Sclerophyll (S4)	20.96 (18.4)	11.85 (12.2)	9.53 (17.1)

NH_4-N

At the end of the 60 day incubation period, the amount of NH_4-N present in the undisturbed soil in the 0-20 cm soil profile (Figure 6.3) represented a mineralization rate ranging from 6.0 kg ha^{-1} $month^{-1}$ in the moderate quality dry sclerophyll soil to 10.2 kg ha^{-1} $month^{-1}$ in the wet sclerophyll soil. The difference between the wet sclerophyll site and the other three sites in total mineral nitrogen was much greater than this, and therefore is due to differences in NO_3-N production.

The NH_4-N pattern shows the tendency to depression in response to disturbance. For the wet sclerophyll soil, this may be due to the substantial amount of NO_3-N produced (i.e. most of the NH_4-N was oxidised to form NO_3-N), but for the intermediate and dry sclerophyll soils, relatively little, or no NO_3-N was produced.

There were very large increases in NH_4-N in response to soil heating. For example, the low quality dry sclerophyll site contained

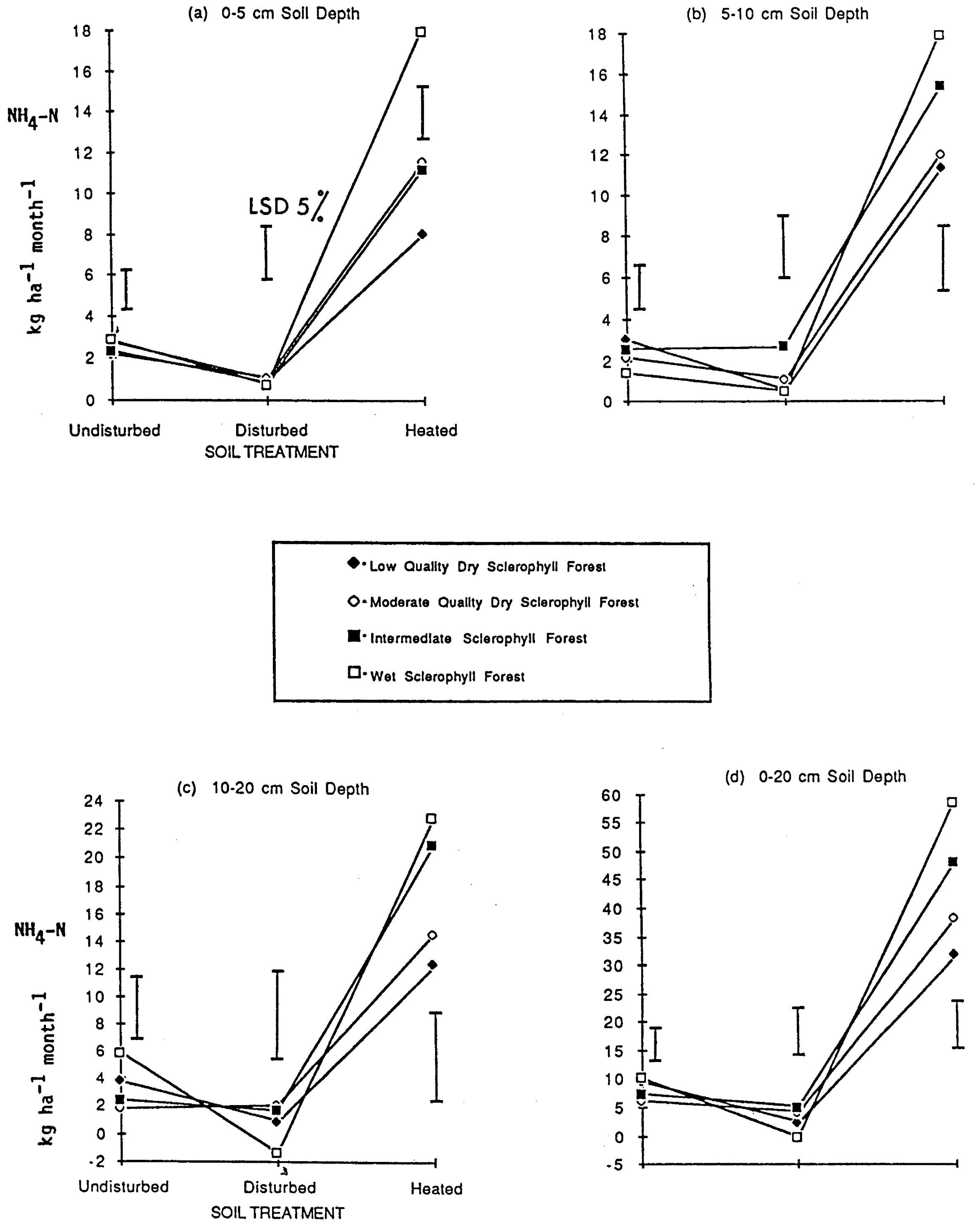

Figure 6.3 The rate of NH_4-N production in soils for different sites, treatments and depths during laboratory incubation at 20°C.

9.6 kg.ha^{-1}.month^{-1} of NH_4-N in the 0-20 cm section of the undisturbed soil, 2.4 in the disturbed soil, and 31.8 in the heated soil; and the intermediate sclerophyll site produced 7.3, 5.1 and 48.3 kg.ha^{-1}.month^{-1} in the undisturbed, disturbed and heated soils respectively.

The ammonification patterns were broadly similar at the three depths (Figure 6.3). It is noted that the intermediate sclerophyll soil responded better to disturbance and heating at 5-10 cm than at 0-5 cm. For example, at 0-5 cm, 11.2 kg.ha^{-1}.month^{-1} of NH_4-N was produced in the heated soil, and at 5-10 cm, 15.4 kg.ha^{-1}.month^{-1}. The reason for this is not known. At 10-20 cm, the wet sclerophyll soil produced more NH_4-N than the other three sites in the undisturbed soil, and less in the disturbed soil. The wet and intermediate sclerophyll soils were closely similar in NH_4-N production following heating at this depth.

NO_3-N

By far the greatest amounts of NO_3-N were produced in the wet sclerophyll soil (Table 6.4), although the quantity varied with the soil treatment. In the 0-20 cm profile, the undisturbed soil produced 16.05 kg.ha^{-1}.month^{-1} of NO_3-N or 61% of total mineral nitrogen; in the disturbed soil, it produced 23.48 kg.ha^{-1}.month^{-1} or 100% of total mineral nitrogen; and in the heated soil 4.90 kg.ha^{-1}.month^{-1} or 7.7% of total mineral nitrogen. In this soil, disturbance has markedly stimulated, and heating markedly depressed nitrification.

Soils from the intermediate sclerophyll site produced a small amount NO_3-N, but considerably less than the wet sclerophyll soils. In the 0-20 cm profile, 1.40 (16.1%), 2.50 (33.0%) and 1.18 (2.4%) kg.ha^{-1}.month^{-1} of NO_3-N were produced in the undisturbed, disturbed and heated soils respectively. As with the wet sclerophyll site, disturbance stimulated and heating depressed nitrification. Neither of the dry sclerophyll soils produced any significant amounts of NO_3-N.

Table 6.4 Rate of NO_3-N production (kg ha^{-1} month^{-1}) ± standard error in soils for different sites, treatments and depths during laboratory incubation at 20°C. Values in brackets give proportion of mineral nitrogen present as NO_3-N following incubation.

		Soil treatment		
Site	Soil Depth (cm)	Undisturbed	Disturbed	Heated
Low Quality Dry Sclerophyll (S1)	0-5	0.04 ± 0.04 (1.4)	0.00 ± 0.00 (0.0)	0.49 ± 0.17 (5.7)
	5-10	0.00 ± 0.00 (0.0)	0.00 ± 0.00 (0.0)	0.00 ± 0.00 (0.0)
	10-20	0.27 ± 0.27 (6.9)	0.54 ± 0.54 (40.4)	0.00 ± 0.00 (0.0)
	0-20	0.31 (3.2)	0.54 (18.8)	0.49 (1.5)
Moderate Quality Dry Sclerophyll (S2)	0-5	0.06 ± 0.06 (2.5)	0.01 ± 0.01 (0.5)	0.32 ± 0.18 (2.7)
	5-10	-0.02 ± 0.02 (0.0)	0.00 ± 0.00 (0.0)	-0.02 ± 0.02 (0.0)
	10-20	-0.09 ± 0.04 (0.0)	0.00 ± 0.00 (0.0)	0.00 ± 0.00 (0.0)
	0-20	-0.05 (0.0)	0.01 (0.1)	0.30 (0.8)
Intermediate Sclerophyll (S3)	0-5	0.34 ± 0.34 (13.0)	0.00 ± 0.00 (0.0)	0.45 ± 0.45 (3.8)
	5-10	0.40 ± 0.18 (13.8)	0.61 ± 0.36 (18.5)	0.46 ± 0.26 (2.9)
	10-20	0.65 ± 0.28 (21.0)	1.88 ± 0.82 (53.0)	0.26 ± 0.26 (1.2)
	0-20	1.40 (16.1)	2.50 (33.0)	1.18 (2.4)
Wet Sclerophyll (S4)	0-5	5.58 ± 0.63 (76.7)	5.84 ± 1.03 (88.6)	1.88 ± 0.24 (9.5)
	5-10	4.96 ± 0.92 (78.5)	7.04 ± 0.48 (93.3)	1.04 ± 0.28 (5.5)
	10-20	5.52 ± 0.80 (48.0)	10.60 ± 0.60 (100.0)	1.98 ± 1.34 (8.0)
	0-20	16.05 (61.3)	23.48 (100.0)	4.90 (7.7)

Other Chemical Soil Attributes

Organic carbon, total nitrogen and the C:N ratio of the soils, and the percentage of total nitrogen mineralized over the 60 day incubation in the undisturbed soil, are given in Table 6.5.

The organic carbon percentage tended to be greatest in the wet sclerophyll soil and least in the low quality dry sclerophyll soil, for example 7.75% and 5.79% respectively, in the 0-5 cm soil. For all sites, there was a regular decline in organic carbon with soil depth.

Table 6.5 Mean values (± standard error) of selected chemical properties of soils from four sites.

Site	Soil Depth (cm)	Carbon* (%)	Total Nitrogen ($\mu g\ g^{-1}$)	C:N ratio	% of Total Nitrogen Mineralized
Low Quality Dry Sclerophyll	0-5	5.79 ± 0.57	1934 ± 150	29.8 ± 0.8	0.62 ± 0.12
	5-10	3.38 ± 0.28	1264 ± 83	26.6 ± 0.5	0.73 ± 0.21
	10-20	1.87 ± 0.11	754 ± 61	24.9 ± 0.5	0.63 ± 0.09
Moderate Quality Dry Sclerophyll	0-5	7.36 ± 0.62	2314 ± 235	32.0 ± 1.2	0.38 ± 0.05
	5-10	5.98 ± 0.98	1578 ± 255	29.0 ± 1.2	0.38 ± 0.05
	10-20	1.95 ± 0.17	725 ± 58	26.9 ± 1.2	0.28 ± 0.05
Inter-mediate Sclerophyll	0-5	6.58 ± 0.37	2470 ± 181	26.8 ± 0.9	0.50 ± 0.12
	5-10	4.10 ± 0.24	1864 ± 88	22.0 ± 0.4	0.51 ± 0.16
	10-20	2.70 ± 0.17	1251 ± 75	21.6 ± 0.6	0.32 ± 0.07
Wet Sclerophyll	0-5	7.75 ± 0.60	2985 ± 197	25.9 ± 0.4	1.22 ± 0.23
	5-10	4.83 ± 0.20	2100 ± 89	23.0 ± 0.3	0.95 ± 0.19
	10-20	3.33 ± 0.16	1406 ± 62	23.6 ± 0.4	1.11 ± 0.28

NOTE: Means are based on four replications.

* organic carbon (Walkley-Black)

The patterns were similar for total soil nitrogen. For example, the wet sclerophyll soil had the greatest nitrogen concentration in the 0-5 cm soil (2985 $\mu g\ g^{-1}$), and the low quality dry sclerophyll soil the least (1934 $\mu g\ g^{-1}$). The differences between sites in total nitrogen are relatively greater than for organic carbon. Total nitrogen declined in a regular way with depth.

Given the similarity in carbon and nitrogen patterns, there was no great range in C:N ratios, although the ratios were somewhat lower in the soils from the two better quality sites. For example, the low and moderate quality dry sclerophyll soils had C:N ratios of 29.8 and 32.0 respectively, at the 0-5 cm soil depth; the intermediate and wet sclerophyll soils had ratios of 26.8 and 25.9. For all sites, the C:N ratios declined with depth, the lowest value being 21.6 in the 10-20 cm soil from the intermediate sclerophyll site.

Where the soils were undisturbed, soil from the high quality wet sclerophyll site had a substantially greater percentage of total nitrogen mineralized than any other site, for example, 1.22% and 0.50% in the 0-5 cm soil of the wet and intermediate sclerophyll sites respectively. Beyond this however, the pattern does not appear to be directly related to the quality of the site. For example, soil from the low quality dry sclerophyll site had a higher percentage of total nitrogen mineralized than the moderate quality dry sclerophyll and intermediate sclerophyll soils.

6.5 DISCUSSION

Nitrogen Mineralization Along a Vegetation Gradient

Although all of the forest soils examined mineralized, there was a distinct change in these processes at the wet sclerophyll end of the vegetation gradient. Not only was the mineralization of nitrogen considerably greater in this soil than in soils supporting the intermediate and dry sclerophyll forests, but the process proceeded more completely to the NO_3-N stage.

This does not appear to be related to soil pH, which was little different in the KCl extracts of the four soils (Table 6.1). The wet sclerophyll soil had in general, slightly lower, and the intermediate sclerophyll soil, slightly higher pHs than the soils from the two dry sclerophyll sites, however the pH for all sites and soil depths was quite low and ranged between 3.15 and 3.80.

The moisture contents of soils from the four sites varied somewhat (Table 6.1). While the soil which produced the greatest amount of mineral nitrogen (the wet sclerophyll soil) also had the highest moisture content, all four soils were close to field capacity or above. For example, the soil samples from the moderate quality dry sclerophyll site had moisture contents between 12.72 and 19.55%. Field capacity for this soil was determined to be 15% using pressure plate apparatus. Moisture contents are unlikely to have limited nitrogen mineralization.

In the undisturbed soil, nitrogen mineralization rates ranged from 2.2 to 7.3 kg ha^{-1} $month^{-1}$ in the 0-5 cm soil section, and from 6.0 to 26.2 kg ha^{-1} $month^{-1}$ in the 0-20 cm soil section, under the favourable conditions of the study (20°C, field capacity). Although these rates cannot be extrapolated to the whole year, they would, if maintained for six months, indicate rates of nitrogen supply to the vegetation which range from a low 13.2 (dry sclerophyll site), to a high 43.8 kg ha^{-1} yr^{-1} (wet sclerophyll site) in the 0-5 cm soil, and 36.0 to 157.2 kg ha^{-1} yr^{-1} in the total 0-20 cm soil. From in situ incubations, Adams and Attiwill (1986b) estimated annual uptake of nitrogen from the surface 5 cm of soil for a range of low and high productivity eucalypt forests to be between 27 and 160 kg ha^{-1} yr^{-1}. Turner and Lambert (1981) estimated uptake from a 27-year-old *E. grandis* stand to be about 60 kg ha^{-1} yr^{-1}. In selected northern hemisphere forests, total uptake of nitrogen has been estimated to be in the range 23.1 to 124 kg ha^{-1} yr^{-1} (Keeney 1980). Although not directly comparable and somewhat speculative, these nitrogen mineralization and uptake figures indicate that soils from the dry sclerophyll end of the south coast vegetation gradient may be incapable of producing sufficient mineral nitrogen to satisfy the demands made by some selected vegetation types. In contrast, soils from the wet sclerophyll end of the vegetation gradient may be more capable of satisifying those same nitrogen demands.

The mild disturbance treatment (i.e. without cycles of wetting and drying) had little effect on the mineralization of nitrogen, and even depressed mineralization in some soils, particularly those at the dry sclerophyll end of the vegetation gradient. Carlyle and Malcolm (1986a) also found little difference in nitrogen mineralization rates between intact and homogenised samples. Soil disturbance associated with mechanical harvesting operations has been shown to stimulate the production of mineral nitrogen (Attiwill *et al.* 1981; Vitousek 1981). Much of this increase may be due to the effects of repeated wetting and drying, which is known to stimulate microbial activity (Birch 1960, 1964). Nevertheless, van Schreven (1967) found that the total amount of nitrogen mineralized after one month under stable moisture conditions was equal to that obtained under fluctuating moisture conditions.

Mineralization of nitrogen responded substantially to heating of the soil, and this was consistent for all sites. Even a temperature of 50°C (10-20 cm soil depth) was sufficient to stimulate mineralization. Measurements of mineral nitrogen immediately after heating showed that between 10 and 30% of the increase was due to the immediate physical effects of heating, and may have been induced by protein decomposition (Walker *et al.* 1986), and release of NH_4-N from soil minerals (Raison 1979). The remainder of the nitrogen mineralized could have resulted from accelerated decomposition of heat-altered organic matter over the 60 day incubation. Similar effects of soil heating or fire on nitrogen mineralization have been reported by Dunn and Debano (1977), Raison (1979), Grove *et al.* (1986) and Walker *et al.* (1986).

Although all soils responded to heating, the greater relative responses were in the intermediate and dry sclerophyll soils. For example, total mineral nitrogen content in the wet sclerophyll soil increased from 26.2 to 63.7 kg ha^{-1} $month^{-1}$ (143% increase); in the intermediate sclerophyll soil, from 8.7 to 49.8 (473% increase); in the moderate quality dry sclerophyll soil from 6.0 to 38.4 (541% increase); and in the low quality dry sclerophyll soil from 9.8 to 32.2 (229% increase). This shows that while the more open sclerophyll forest types have restricted soil mineralization rates, the release of mineral nitrogen can be markedly stimulated by soil heating.

The reasons for the restricted mineralization may be related to the refractory nature of eucalypt sclerophyll organic matter. A characteristic of this is the high C:N ratio of the more lignified component of the organic matter which accumulates in the soil (Hingston 1981), and may be highly resistant to biological decay (Florence 1961, 1981). The long term incorporation of this material into the soil organic matter may lead to immobilization of nitrogen, and cause changes in the microbial population which reduces the capacity of soil to mineralize nitrogen (Florence and Crocker 1962; Florence 1981). An external stimulus such as heating may therefore be required to alter chemically the organic matter pool, rendering it more easily mineralized.

At the wet sclerophyll end of the vegetation gradient containing *E. maculata*, the nitrogen mineralization rate was high in comparison to the dry and intermediate sclerophyll sites. This may reflect both the greater nitrogen capital of the site (Table 6.5), and the more rapid breakdown of some components of the root and above-ground litter. In addition, the production of mineral nitrogen per unit of total nitrogen in the wet sclerophyll soil was somewhat higher, indicating perhaps, as Lamb (1980) has suggested, a larger pool of organic nitrogen participating in the nitrogen turnover process. The quantity and quality of the litter may differ appreciably between the wet and dry sclerophyll forest sites; this will apply to the greater diversity of organic matter within the wet sclerophyll soil, especially that derived from the more mesophytic components of the vegetation. Decomposition rates of litter on wet sclerophyll forest sites may be more rapid than rates for dry sclerophyll forest litter (Ashton 1975a; Woods and Raison 1983). This may be largely due to differences in the understorey components, although the rate of eucalypt litter breakdown has, in some cases, also been shown to be stimulated where there is a nitrogen rich understorey (Florence 1961; Lamb *et al.* 1980; Baker and Attiwill 1981). On all four sites in this study, the species in the overstorey consisted of *E. maculata* and a mixture of other eucalypt species, so that the amount of eucalypt litter accumulating on the forest floor may have been similar. Therefore, differences in nitrogen mineralization rates may be due largely to the more rapid decomposition of the litter of mesophytic understorey elements on the wet sclerophyll site, than to differences in eucalypt litter quality. Work done in Western Australia shows that the understorey litter in *E. diversicolor* forest is of major importance in recycling nitrogen and phosphorus (A.M. O'Connell unpublished). The more favourable moisture relations on the wet sclerophyll sites may also stimulate mineralization through accelerated litter decomposition.

The C:N ratios in the 0-5 cm soil from these four sites ranged from 25.9 to 32.0; and in the 10-20 cm soil, from 21.6 to 26.9. By comparison, the C:N ratio of the topsoil in mature *E. regnans* forest is given as 12 (Ashton 1975a), and in dry sclerophyll *E. marginata* forest, around 40 (Wallace and Hatch 1952). For nitrogen, little mineralization occurs until the C:N ratios fall within the range 30 to 20 or below (Lutz and Chandler 1946; Paul and Juma 1981; Vitousek 1981; O'Connell 1986).

The large differences in nitrogen mineralization rates between some of these soils occurred in spite of the relatively small differences in C:N ratios. It is possible that the C:N ratios in the wet sclerophyll soils are largely determined by the more slowly decomposing eucalypt components; it is also possible that the nitrogen and carbon contained in these understorey litter components is mineralized more rapidly and taken up by plants. On the dry sclerophyll sites, the C:N ratios may again be dominated by inputs of eucalypt litter, although there may be a greater contribution from some of the more slowly decomposing sclerophyllous understorey components.

The wet sclerophyll soil, in addition to mineralizing strongly, was capable of producing substantial amounts of NO_3-N. Several studies have suggested that the rate of net mineralization is the major factor determining the rate of nitrification (Jansson 1958; Wollum and Davey 1975; Popovic 1977; Youngberg 1978; Lamb 1980; Adams and Attiwill 1982; Williams 1983; Adams and Attiwill 1986b; Carlyle and Malcolm 1986a). Sites with rapid decomposition of litter and a favourable nitrogen capital tend to produce more mineral nitrogen, which in turn stimulates the production of NO_3-N.

This hypothesis is supported by the results of this study. The undisturbed wet sclerophyll soil produced substantially more mineral nitrogen than the intermediate and dry sclerophyll soils, and was also the only soil which produced very substantial amounts of NO_3-N. Nitrate production was stimulated further where the soil was disturbed, even though net mineralization declined, that is, virtually none of the mineralized nitrogen remained as NH_4-N. Soil disturbance appears to have altered the competitive relations between the ammonifying and nitrifying organisms, favouring the latter. Heating of the wet sclerophyll soil had the reverse effect on nitrification. Almost all of the very substantial amount of mineral nitrogen produced remained as NH_4-N. Nitrifying bacteria have thin-walled cells and are killed between 53 and 58°C, but some ammonifiers produce thick walls or spores, enabling them to survive at 100°C (Raison 1979). Consequently, it is likely that the nitrifiers were killed by the heat treatments, but some of the ammonifiers survived, and under the conditions of the experiment, there was no chance for re-inoculation. Others have reported increases in NO_3-N production following burning (Christensen 1973; Jones and Richards 1977a, 1977b; Mroz *et al.* 1980; Attiwill *et al.* 1981; Ellis 1981). Under these field conditions however, re-inoculation of the soil with nitrifying organisms after the fire may have allowed nitrification to proceed.

There was some nitrification in the intermediate sclerophyll soil, and this followed the same pattern in response to disturbance and heating as the wet sclerophyll soil. This soil did not, however, produce any more total mineral nitrogen than the two dry sclerophyll sites - neither of which produced NO_3-N.

Nitrogen Mineralization in Relation to Clearfelling

The differences in inorganic nitrogen production along the vegetation gradient suggest that forest quality and rate of nitrogen mineralization are related. Following clearfelling, the higher quality sites may have had a greater capacity to supply mineral nitrogen to the regenerating stand, in both NH_4-N and NO_3-N forms. Where competition was not overwhelming, *E. maculata* may have had access to sufficient of the mineral nitrogen pool to develop into a vigorous component of the regrowth forest. However, following clearfelling of lower forest quality sites, there may have been insufficient mineral nitrogen (and this predominantly in the NH_4-N form) for *E. maculata* to develop regrowth vigour, particularly where competition from other successional species was severe. Little is known of species preference for nitrogen in different forms, although there is some evidence that many plant species can use NH_4-N as effectively as NO_3-N (McFee and Stone 1968; Moore and Keraitis 1971; Chandler 1981; Ashton and Willis 1982). The ecological effect of limited NO_3-N in the dry sclerophyll forest soils must remain largely speculative.

In this study, the soil from the moderate quality dry sclerophyll forest was collected from the Link Road site. An analysis of vegetation on this site (Section 2.3.1) showed *E. maculata* to be a large-boled dominant in the mature forest and a weakly vigorous sub-dominant in the cutover forest. Moreover, there was a massive proliferation of healthy (dark green) graminoids predominantly, *Lepidosperma urophorum*, on the regrowth site compared to the adjacent mature forest. Thus, it is possible that the availability of nitrogen on these dry and intermediate sclerophyll forest sites may be limiting the competitive ability of *E. maculata* regrowth in the presence of strong competition from successional species.

The soil physical disturbance treatment in this study failed to stimulate the production of mineral nitrogen, although this may have been due in part to the absence of wetting and drying cycles which would occur under field conditions. Several authors have reported a rapid accumulation of mineral nitrogen, and particularly NO_3-N, following clearing and disturbance (Popovic 1975; Tamm 1979; Charley 1981; Freney 1981). The possible processes leading to this have been outlined by Attiwill *et al.* (1981). Following clearfelling, accession of litter is halted, and through better aeration and increased soil temperatures, decomposition of organic matter is accelerated. The lowering of the C:N ratio leads to an accumulation of mineral nitrogen, and from this, NO_3-N is produced. However, losses of mineral nitrogen may result because vegetation at the pioneer stage may not be sufficiently well developed to cycle nitrogen within the soil-plant system, and nitrate is easily leached.

From the response to the soil disturbance treatment in this study, it is possible that the mechanical disturbance associated with the clearfelling operations on the south coast was insufficient to stimulate the release of significant amounts of mineral nitrogen on low to intermediate sclerophyll sites. It is also possible that the mineral nitrogen which was produced was quickly and preferentially taken up by successional species, or in the case of NO_3-N, leached out of the upper soil profile. If this were the case, those species like *E. maculata*, which appear to have a greater competitive ability on more fertile sites (Chapters 3, 4 and 5) may be the first to lose their competitive advantage, and hence their ability to maintain rates of growth comparable with other successional species. The rapid growing *Acacia* species on the other hand, may be particularly well adapted to an environment where the availability of soil nitrogen is limited since they may have a lower requirement for nitrogen for competitive growth than *E. maculata* (Chapters 4 and 5), and related to this, are able to fix atmospheric nitrogen.

The soil heating treatment in this experiment was included to assess the possible contribution fire could make to the pool of mineral nitrogen in a range of these south coast soils. Without exception, a mild heat treatment substantially increased the soil mineral nitrogen content both immediately and during subsequent incubation. An intense regeneration burn may therefore have produced a substantially larger pool of plant-available nitrogen. On many regrowth sites, this could have provided *E. maculata* with the necessary stimulation to beat concomitantly developing species, and particularly the rapid-growing *Acacia* component. However, in the absence of a flush of nitrogen associated with burning, *E. maculata* may have had insufficient vigour to maintain growth at the same rate as some of the other, better adapted species. There is also however, a cost associated with fire in terms of volatile loss of nutrients and convective transfer of ash, including nitrogen and phosphorus (Raison *et al.* 1985a, 1985b). This may have important consequences on subsequent nutrient cycling processes within the regrowth stands.

As well as the possibility of limited nitrogen mineralization in some of these south coast forests, it is also stressed that losses of nutrients are associated with removal of logs in the harvesting operations, and through subsequent erosion and leaching (Crane 1978; Crane and Raison 1980; Turner 1981; Vitousek 1981; Richards and Charley 1983; Turner and Lambert 1986). The magnitude of these losses are unknown, but their effects could have further restricted the development of *E. maculata* in the regrowth forest.

A limited pool of soil nutrients *per se* may have been a contributory, but not necessarily the only factor restricting the competitive ability of a species with an apparent high nutrient requirement. Differences between species in gaining access to nutrients could also be critical in this situation, and this could involve consideration of the form of the *E. maculata* root system and that of its competitors. A study on the form of roots of south coast forest species was established to help determine this, and this is reported in Chapter 7.

CHAPTER 7

STUDIES ON THE FORM OF ROOT SYSTEMS

7.1 INTRODUCTION

The root system of a plant is probably of comparable significance to the shoot in the determination of ecological relationships (Chilvers 1972b). Root development is influenced by a range of soil factors. To succeed, plants must be able to efficiently exploit the soil horizons for resources in the face of competition from other plants. Soil factors have frequently been studied in order to explain pattern in vegetation (Beadle 1962; McColl and Humphreys 1967, Turner *et al.* 1978) and competitive plant interactions (Park 1975; Richards and Charley 1983; Ellis *et al.* 1985)

Differences in the early patterns of root system development may be particularly important in determining the competitive ability and therefore the success of species in an environment where competition is intense, such as that resulting from the development of highly stocked regrowth stands. It is in this context that the biomass and morphology of roots of some forest species have been investigated.

The three studies reported in this chapter examine the root morphology of a number of eucalypt species, and an *Acacia* species from Kioloa State Forest, and the effect of environmental variables (soil moisture supply and soil bulk density) on seedling development. In two glasshouse studies, the patterns of seedling root development are examined in 1 m long soil columns; and in a field study, root production is examined in the upper soil horizons of a site within the regrowth forest. The field study was done to establish whether the patterns of root development in the field are consistent with those shown in the glasshouse.

7.2 THE SIGNIFICANCE OF THE FORM OF ROOT SYSTEMS

The development and activity of root systems strongly influence the growth of trees (Squire *et al.* 1978). Böhm (1979) considers that root physiology and root ecology are the two main fields of root research. The former examines physiological processes in the roots, for example, cell division and transport mechanisms of ions within the root. The latter investigates the influence of environmental factors on the development of plant root systems. Some of the more important of these factors are likely to be moisture, temperature, oxygen supply, fertility, mechanical impedence, pathogens and predators (Sutton 1969).

Tree roots can be divided into coarse (structural) and fine (absorptive) roots (Moir and Bachelard 1969). The coarse roots of a plant provide anchorage, accumulate and store nutrients (Kolesnikov 1971), and connect fine roots both vertically and horizontally within the soil (Kimber 1974). The fine roots absorb water and mineral substances, interact with mycorrhizae, and excrete into the soil various substances such as sugars, organic acids and mineral compounds which contribute to the dissolution of mineral substances and the development of rhizospheric micro-organisms (Kolesnikov 1971).

An understanding of the dynamics of root system development may be of particular importance in ecological studies. In these, it may be necessary to distinguish between the biomass of the root system and the configuration (or morphology) of roots (Nambiar 1981). Biomass may be considered as a measure of quantity while configuration describes the arrangement of distribution of roots within the soil profile.

Biomass studies of root systems have been numerous (Feller 1980; Jackson and Chittenden 1981; McClaugherty *et al.* 1982; Foster 1985; Monk and Day 1985; Santantonio and Hermann 1985). These may, for example, examine the contribution roots make to the dynamic portion of the below ground biomass and nutrient capital (McClaugherty *et al.* 1982), or be used to construct equations to predict root biomass (Jackson and Chittenden 1981).

The configuration of roots affects paths of nutrient and water transfer from soil to roots (Barley 1970), which in turn affects the competitive ability of species. There have been many studies on the root development and morphology of tree species in the northern hemisphere (Toumey 1929; Sutton 1969; Reynolds 1970; Kolesnikov 1972; Ford and Deans 1977; Harris *et al.* 1979; Feret and Kreh 1985; Strong and LaRoi 1985). Within an Australian context, many studies have focused on the rooting relationships of introduced species and particularly *Pinus radiata* (Bowen 1964; Moir and Bachelard 1969; Squire *et al.* 1978; Nambiar 1980, 1983, 1984). These examine the effect of fertilizing and soil bulk density on the root development in a radiata pine plantation (Squire *et al.* 1978), the importance of first-order lateral roots on the growth of seedling radiata pine under environmental stress (Nambiar 1984), and other attributes of root systems.

There have been relatively few studies on the significance of root configuration and development in eucalypt ecology. There have been some controlled environment studies which have looked at: differences in root:shoot ratios between 14 Victorian eucalypts (Zimmer and Grose 1958); root distribution patterns in *E. camaldulensis* (Awe *et al.* 1976) and *E. delegatensis* (Webb *et al.* 1983); and the phosphorus acquisition by *E. pilularis* (Heinrich and Patrick 1986) and several Western Australian eucalypts (Barrow 1977).

Little is known of the morphology of root systems and the rooting densities of different species in native forest communities. Florence (1981) has given a generalized account of the role of root competition in eucalypt ecology. In Western Australia, a number of independent studies have examined the root system of *E. marginata* (jarrah). Kimber (1974) showed this species to have a dense lateral feeder root system in the top 0.9 m of soil, with a secondary dense layer of feeder roots at considerable depth near the water table. The two systems were connected by vertical sinker roots with little branching. Carbon *et al.* (1980) found the sandy surface soil (0-1 m deep) contained most of *E. marginata's* total root length - in the top 10 cm, the root density was 7 cm cm^{-3} , but declined for the rest of the surface horizon. In contrast, Zohar (1985) found the roots of an *E. camaldulensis* shelterbelt to be concentrated at a depth of 40-80 cm. In the sandy loam horizon (1-4 m deep) of the *E. marginata* soil, the root density was consistently about 0.2 cm cm^{-3}, and in the clay horizon above the water table (4-15+ m deep), 0.07 cm cm^{-3} (Carbon *et al.* 1980). On the granitic soils, the major descending roots of *E. marginata* were confined to channels that extended vertically from fissures and conduits, but only fine roots (<1 mm) penetrated the clay matrix. In profiles derived from dolerite, occupation of the deep clay by large and fine roots was diffuse and root channels were absent (Dell *et al.* 1983a). The characteristic deep feeder root system of *E. marginata* maintains supplies of moisture to the tree in the dry summer period (Kimber 1974). Dell and Wallace (1983) showed that the root growth of *E. marginata* was in two peak periods - in spring (September-October) and following autumn rain (May-June), although short roots may develop after very light showers of rain. In a comparative study, Shea *et al.* (1975) examined the root development of six species of eucalypt including *E. maculata*, but none had root development characteristics equivalent to that of *E. marginata*.

Nambiar (1981) reviewed what little is known about the root development of a number of native species. Ashton (1975b) has given a generalized account of the root development of *E. regnans* from the seedling, through the thicket, sapling, pole and spar stages, to the mature tree. The radial extent of lateral root spread usually exceeds the crown by 2 to 4.5 times (Ashton 1975b; Incoll 1979). The depth-wise distribution of roots in native forests seems similar to that found in pines, with nearly 75 percent of the roots in the 1.2 m profile being in the top 30 cm (Incoll 1979; Schuster 1979). Ashton (1975b) examined the fine roots in mature and pole *E. regnans* forest with *Pomaderris aspera* understoreys and found that eucalypts made up only 17 to 22% of the total fine root weight in the 0-15 cm soil compared to 76 to 78% for *P. aspera*. He concluded that the fine roots and mycorrhizae of *P. aspera* could be a very important factor in its competition with *E. regnans*, particularly in the first 5-6 years of development. This was later questioned by Nambiar (1981) who suggested, on the basis of observations by Barley (1970), that the absolute rooting densities (1-2 cm cm^{-3}) of the species combined were likely to be too low for any significant competition between roots.

Chilvers (1972b) showed how approximately equal numbers of roots of *E. dalrympleana* and *E. fastigata* were closely intermingled in the surface soil of a mixed forest, so that the two species appeared to be deployed to similar advantage.

Foster (1979) found somewhat different rooting strategies for a natural dry sclerophyll eucalypt forest and a *Pinus radiata* plantation growing on the same soil type, and suggested this may be one reason why the pine is able to invade the native forest. He found that while the vertical root distribution patterns of the pine and the eucalypt forest were similar, that is, a high proportion of roots were concentrated in the top 10 to 20 cm of soil, there was a contrast between the two forest types in the number of fine roots (<0.5 cm diameter) in the upper soil horizon, and the number and location of the larger roots (>0.5 cm diameter). Foster used a ratio of fine:larger roots exposed on the surface of the soil profile to characterise the type of root system as 'intensive' or 'extensive'. The pine plantation had a high density of fine roots exploiting the soil close to the tree (intensive), and the eucalypt forest had fewer fine roots and more longer roots exploring the soil (extensive). Foster suggested that the need for the eucalypts to occupy a larger volume of soil could be related to their apparent intolerance of root competition.

Soil compaction has been shown to affect root growth of native species (Schuster 1979). Where previous logging activity in 10-year-old regenerated *E. diversicolor* forest had increased the bulk density of the surface 0-10 cm soil from 0.90 to 1.35 g cm^{-3}, there was a decrease in the weight of roots from 3 to 0.25 kg m^{-3}. Root growth was affected to a depth of 100 cm even though the effect of logging on soil bulk density was not noticeable below 40 cm.

The majority of forest trees form symbiotic associations with non-pathogenic fungi which mediate in the transfer of substances passing between soil and plant tissues (Chilvers and Pryor 1965). These mycorrhizae allow effective uptake of poorly mobile ions, and probably highly mobile resources such as water and nitrates as well, from the relatively large volumes of soil between roots. Uptake may be assisted by fungal hyphal penetration of soil and litter, absorption of nutrients, and translocation of nutrients to the plant (Bowen 1981). In return, the fungus draws on the root for its carbohydrate supply (Foster and Marks 1967). A comprehensive examination of the mineral nutrition of mycorrhizae is provided by Bowen (1973).

Ectomycorrhizae occur on most if not all eucalypt species (Samuel 1926; Chilvers and Pryor 1965), and also on many other woody forest species (Warcup 1980). A more vigorous growth response of seedlings of three species of eucalypt when inoculated with mycorrhizal spores was reported by Pryor (1956). More recent studies have shown that mycorrhizae enhance the uptake of phosphorus with a consequent increase in growth (Malajczuk *et al.* 1975; Barrow 1977; Lee *et al.* 1981; Heinrich and Patrick 1986). Initially it was thought that *Monocalyptus* species had an obligate requirement for mycorrhizal fungi as opposed to a facultative requirement shown by *Symphyomyrtus* species (Pryor 1959b). However, subsequent work showed no evidence of host specificity of mycorrhizal fungi for different eucalypt subgenera (Chilvers 1972a), or indeed of any obligate requirement for any fungus-root symbiosis (Hickey 1980). The abundance of mycorrhizae can be reduced by burning (Reddell and Malajczuk 1984), but the effect of soil disturbance on mycorrhizal populations is unclear (Perry *et al.* 1982).

Against this background, it was considered that it would be useful to compare the form of eucalypt and *Acacia* seedling root systems to see whether there were differences between them which might help explain a problem in stand dynamics.

7.3 EXPERIMENT 1 : ROOT SYSTEM DEVELOPMENT OF SOUTH COAST EUCALYPT SPECIES UNDER GLASSHOUSE CONDITIONS

This study examines root development patterns in 1 m long soil columns of several eucalypt species which are found within the regrowth stands on Kioloa State Forest. The effect of soil moisture on the species response is also examined. Its objective is to assess whether there are any basic differences in root systems of species which could help explain competitive relationships and distribution patterns of species.

7.3.1 Materials and Methods

Experimental Design

The experiment was arranged as a randomized complete block design in the glasshouse with seven eucalypt species from Kioloa State Forest and *E. camaldulensis*, two watering regimes and four replications (pots). Seven of the species occur either singly or in mixture in a mosaic pattern between Batemans Bay and Nowra on the south coast of N.S.W. These are *E. gummifera* and *E. maculata* (*Corymbia*), *E. globoidea* and *E. pilularis* (*Monocalyptus*), and *E. paniculata, E. pellita and E. saligna* (*Symphyomyrtus*). The *Symphyomyrtus* species *E. camaldulensis* was also included because its root development has been examined previously under similar conditions (Awe *et al.* 1976), and it would provide a known standard of root development. Two spare pots of *E. maculata* and *E. camaldulensis* were included to allow checks on the progress of root development in the main experiment. Information on the species and provenances of seed used in the experiments in this chapter are given in Table 1.1 (Chapter 1).

Experimental Method

White plastic pipe, of internal diameter 12 cm, was cut into 1 m lengths to form open-ended pots. The pipe was halved lengthwise then sealed back into place with packaging tape and fencing wire. One open end was enclosed with nylon mesh and secured with tape and wire. The pots were filled with a sandy loam from a commercial soil yard to about 11310 cm^3 volume. The pots are illustrated in Plate 7.1.

Nutrients (Nutricote, with an N:P:K ratio of 13.0:5.7:9.1 and 8-9 month release period) were mixed with the soil at a rate of 3 g per 1000 cm^3 of soil. Thus the following were added to each pot: 5.77 g of elemental nitrogen, 1.94 g of phosphorus, 3.09 g of potassium and 2.00 g of calcium. The pots were stood on thick gauge wire mesh for free drainage.

In July 1984, seed of the eight species were sown on a medium containing equal parts of perlite and vermiculite. The germinates were transplanted to the pots about 52 days after germination, at about the

Plate 7.1

The 1 m long pots used to examine root system development in Experiments 1 and 2.

three-leaf-pair stage, one seedling per pot. At about the five-leaf-pair stage (92 days after germination) two treatments were applied, (i) watering twice daily at a rate of two litres per hour for two minutes, to maintain approximate field capacity, and (ii) bringing pots to field capacity and then discontinuing watering. The two treatments will be referred to as the 'field capacity' and 'drying' treatments respectively. The experiment was harvested 65 days after treatments began. At harvest, the soil in the unwatered pots had an approximate mean moisture content (from five points down the pot) of 1.81%. Using pressure plate apparatus, the moisture content of this soil at approximate permanent wilting point (-15 bars) was estimated to be 3.24%.

Measurements were made at harvest of seedling height and shoot dry weight. The soil-root column was exposed, and the length of the root system of each seedling measured to its lowest point in the soil (root depth). The soil was carefully washed from the root system, and it was divided from the top into 20 cm sections. For each 20 cm section, roots were dried at 85°C until a constant weight was obtained. The weight in grams was converted to a value expressing the dry weight of roots per cubic decimetre of soil explored (g dm^{-3}). The lowest point in the pot in which roots had penetrated defined the extent of soil exploration. The use of the measure g dm^{-3} enabled a direct comparison of root production between pots, in the section of soil where root penetration had ceased. For example, in two separate pots where roots had penetrated to depths of 87 and 94 cm, a direct comparison of total root dry weight (g) for the 80-100 cm section would be invalid. However, if the root dry weight in the volume of soil contained in the 80-87 and 80-94 cm sections were assessed and expressed as g dm^{-3}, a direct comparison of values could be made. Total plant dry weight and the root:shoot ratios were also assessed.

All data were subjected to two-way analyses of variance, the factors being species and moisture. Where the plot of residuals versus fitted values indicated that there was heterogeneity of variance, a log or square root transformation was made. Only untransformed means are referred to in the text.

To assess root development, analyses were performed on the following attributes:

1. Rooting depth (cm).
2. Total root weight (g).
3. Root weight in each of the five 20 cm sections (g dm^{-3}).
4. A 'root allocation' ratio which expresses the mean weight (g dm^{-3}) of roots in the 0-40 cm section of the soil profile

and the mean weight (g dm^{-3}) of roots in the section of soil explored by roots below 40 cm. The ratio provides an indication of how species allocate photosynthates to root production throughout the soil profile.

7.3.2 Results

The results of analyses of variance are summarized in Table 7.1 and mutiple range comparisons of overall seedling means are presented in Table 7.2. Most of the attributes for seedlings showed significant differences between species means and for several, there were also significant differences between moisture regimes. For all assessed attributes, only one significant ($P<0.05$) interaction was recorded (root:shoot ratio), demonstrating that virtually all seedling attributes responded similarly to the separate 'field capacity' and 'drying' treatments. The following sections examine shoot production, root production, and root distribution patterns.

(i) Shoot Production

Shoot Height. Both species and moisture differences were highly significant ($P<0.001$). The 'field capacity' treatment produced greater shoot height (39.6 cm) than the 'drying' treatment (32.2 cm). Individual species means are ranked in order in Table 7.2. Seedlings of *E. camaldulensis* (63.7 cm) were considerably and significantly taller than all other species. Of the south coast species, *E. gummifera* (24.2 cm) and *E. pellita* (41.0 cm) were the shortest and tallest respectively.

Plant Dry Weight. There was a small effect of moisture on total dry weight production and there were also differences between species. Both factors were significant at the 5% level of probability. The plants receiving regular water produced more plant dry weight (6.73 g) than those where water was withheld (5.29 g). Of the species, *E. saligna* (9.22 g) was the most productive and *E. gummifera* (3.89 g) the least. *E. maculata* (6.24 g) had the third largest plant dry weight. Plant dry weight of the *Symphyomyrtus* species was in general, larger than that of the *Monocalyptus* species.

Shoot Dry Weight. There were no differences between species in shoot dry weight production. There was a significant ($P<0.01$) moisture effect in which the 'field capacity' treatment produced more shoot dry weight than the 'drying' treatment.

(ii) Root Production

Root Dry Weight. This attribute was not influenced by moisture but there were highly significant ($P<0.001$) differences between species. The ranked order of species is very similar to that of plant dry weight production with the *Symphyomyrtus* species having seedlings with larger root dry weights than the *Monocalyptus* species. *E. saligna* (4.09 g) had a particularly large root weight. Of the two *Corymbia* species, *E. maculata* (2.00 g) had an intermediate weight of roots while *E. gummifera* (1.17 g) had the least of all species.

Root:Shoot Ratio. The effect of moisture on the root:shoot ratio was highly significant ($P<0.001$), as was the difference between species. The 'drying' treatment produced a larger root:shoot ratio (0.678) than the 'field capacity' treatment (0.505). Overall, the ranked order of species (Table 7.2) shows that *E. gummifera* (0.436) and *E. maculata* (0.486) had significantly smaller root:shoot ratios than all other species. Of the remaining six species, *E. camaldulensis* (0.685), *E. saligna* (0.676), *E. pilularis* (0.639) and *E. pellita* (0.634) did not differ in their root:shoot ratios; and *E. paniculata* (0.594) and *E. globoidea* (0.580) had significantly smaller ratios than at least one of these four species.

The interaction between moisture and species was significant at the 5% level of probability. There were three species in which there was no difference between the root:shoot ratios in the 'field capacity' and 'drying' treatments. These were *E. gummifera*, *E. pilularis* and *E. globiodea*. All other species had significantly larger root:shoot ratios in the 'drying' treatment, increasing by about half.

Root Depth. The rooting depth was significantly ($P<0.05$) affected by moisture and also varied with species. The root systems of seedlings grown at field capacity were slightly shallower (86.4 cm) than those grown without regular water (92.3 cm). Differences between species again tend to be related to their subgeneric groups. The four *Symphyomyrtus* species rooted to a greater depth (range from 89.7 to 95.9 cm) than the two *Monocalyptus* species, *E. globoidea* (83.6 cm) and *E. pilularis* (83.7 cm). Of the *Corymbia* species, *E. maculata* (93.5 cm) had a rooting depth similar to the *Symphyomyrtus* species while *E. gummifera* (80.4 cm) had the smallest rooting depth of any species. This latter result is primarily a function of the low rooting depth for *E. gummifera* (67.5 cm) in the 'field capacity' treatment.

(iii) Root Distribution Patterns

The pattern of root distribution within the soil profile may have greater ecological significance than either total root dry weights or root:shoot ratios. Assessment of root distribution was done by dividing the root system of each plant into five 20 cm sections, determining dry weights and then converting each weight to g dm^{-3}. In their study of rooting patterns of *E. camaldulensis*, Awe *et al.* (1976) had used similar pots to those used in this experiment. They found unrealistic root distribution patterns because matting of roots had occured at the bottom of the 1 m tubes. In this experiment, matting of roots did not occur to any great extent, although one or two of the longer roots of some species had reached the bottom of the pot.

The root weight (g dm^{-3}) in each of the five 20 cm sections of soil was assessed separately using analysis of variance to determine whether the pattern of root production varied with moisture and between species down the profile. The root development patterns are also summarized in graphical form in (Figure 7.1).

Root Weight 0-20 cm. Soil moisture affected root dry weight production in the 0-20 cm section of the soil profile; root dry weights were significantly ($P<0.05$) greater in the 'field capacity' (0.41 g dm^{-3}) than the 'drying' treatment (0.30 g dm^{-3}). Highly significant ($P<0.001$) differences were recorded between species. The ranked order (Table 7.2) shows that the two *Corymbia* species *E. gummifera* (0.14 g dm^{-3}) and *E. maculata* (0.27 g dm^{-3}) had the lowest root weights in this section of the soil profile. *E. globoidea* (0.32 g dm^{-3}) and *E. paniculata* (0.32 g dm^{-3}) had intermediate root weights while three of the four *Symphyomyrtus* species (*E. camaldulensis*, *E. pellita*, *E. saligna*) and *E. pilularis* (*Monocalyptus*), produced the largest root weights.

Root Weight 20-40 cm. Root dry weight in the 20-40 cm section of soil was not influenced by moisture but there was a significant ($P<0.01$) difference between species. The ranked order (Table 7.2) is similar to that in the 0-20 cm section with the two *Corymbia* species again having the smallest root weights. The two *Monocalyptus* species had root weights that were bettered only by *E. saligna*, although *E. pellita* had equivalent weight to the *Monocalyptus* species.

Root Weight 40-60 cm. There were very few differences in the weight of roots in the 40-60 cm section of soil. The moisture effect was not significant while there was a slight but significant ($P<0.05$) difference between species. *E. saligna* again had a greater root weight than all other species.

Root Weight 60-80 cm. There was a significant (P<0.01) effect of both moisture and species on root dry weight in the 60-80 cm section of soil. A greater root weight (0.17 g dm^{-3}) was produced under the 'drying' treatment than under the 'field capacity' treatment (0.12 g dm^{-3}). The ranked order of species shows that relative to the 0-20 and 20-40 cm analyses, some species have altered their positions, while others remain unchanged. *E. globoidea* (0.08 g dm^{-3}) has replaced *E. gummifera* as the species with the smallest root dry weight while *E. saligna* (0.25 g dm^{-3}) has still produced the greatest root dry weight. While *E. maculata* had a low root weight in the upper sections of soil, its root weight in the 60-80 cm section (0.16 g dm^{-3}) was exceeded only by that of *E. saligna*. Nevertheless, most of the species had root weights not too different from that of *E. maculata*.

Table 7.1 Summary of the differences between attribute means associated with moisture, species and the interaction between these as derived from analyses of variance.

Attribute	Moisture	Species	Interaction
Shoot Height	***	***	NS
Plant Dry Weight	*	*	NS
Shoot Dry Weight	**	NS	NS
Root Dry Weight	NS	***	NS
Root:Shoot Ratio	***	***	*
Root Depth	*	*	NS
Root Dry Weight 0-20 cm	*	***	NS
Root Dry Weight 20-40 cm	NS	**	NS
Root Dry Weight 40-60 cm	NS	*	NS
Root Dry Weight 60-80 cm	**	**	NS
Root Dry Weight 80-100 cm	NS	*	NS
Root Allocation Ratio	***	***	NS

* $P<0.05$; ** $P<0.01$; *** $P<0.001$; NS = not significant

Table 7.2 Ranking of seedling means for moisture and species.

Attribute	Moisture		Species							
Shoot Height (cm)	32.2 Dry	39.6 Wet	24.2 Egum	27.8 Eglo	29.0 Epil	30.7 Emac	33.4 Epan	37.7 Esal	41.0 Epel	63.7 Ecam
Plant Dry Weight (g)	5.29 Dry	6.73 Wet	3.89 Egum	5.10 Eglo	5.41 Epan	5.48 Epil	6.07 Ecam	6.24 Emac	6.65 Epel	9.22 Esal
Shoot Dry Weight (g)	1.72 (3.11) Dry	2.05 (4.45) Wet	1.62 (2.73) Egum	1.75 (3.18) Epil	1.78 (3.27) Eglo	1.82 (3.49) Epan	1.84 (3.63) Ecam	1.97 (4.15) Epel	2.00 (4.24) Emac	2.33 (5.55) Esal
Root Dry Weight (g)	2.19 Dry	2.26 Wet	1.17 Egum	1.83 Eglo	1.86 Epil	1.92 Epan	2.00 Emac	2.44 Ecam	2.50 Epel	4.09 Esal
Root:Shoot Ratio	0.505 Wet	0.678 Dry	0.436 Egum	0.486 Emac	0.580 Eglo	0.594 Epan	0.634 Epel	0.639 Epil	0.676 Esal	0.685 Ecam
Root Depth (cm)	86.4 Wet	92.3 Dry	80.4 Egum	83.6 Eglo	83.7 Epil	89.7 Epan	93.5 Emac	93.8 Epel	94.0 Ecam	95.9 Esal
Root Dry Weight (0-20 cm) g dm^{-3}	-1.33 (0.30) Dry	-1.05 (0.41) Wet	-2.03 (0.14) Egum	-1.43 (0.27) Emac	-1.23 (0.32) Epan	1.16 (0.32) Eglo	-1.07 (0.41) Epil	-0.99 (0.42) Epel	-0.94 (0.44) Ecam	-0.67 (0.54) Esal
Root Dry Weight (20-40 cm)	0.44 (0.21) Dry	0.47 (0.24) Wet	0.34 (0.12) Egum	0.38 (0.16) Emac	0.42 (0.18) Epan	0.43 (0.21) Ecam	0.50 (0.26) Epel	0.50 (0.26) Epil	0.50 (0.25) Eglo	0.58 (0.34) Esal
Root Dry Weight (40-60 cm)	0.16 Dry	0.18 Wet	0.13 Ecam	0.13 Egum	0.15 Emac	0.16 Eglo	0.16 Epan	0.18 Epil	0.18 Epel	0.27 Esal
Root Dry Weight (60-80 cm)	0.12 Wet	0.17 Dry	0.08 Eglo	0.12 Epan	0.12 Egum	0.13 Ecam	0.15 Epil	0.15 Epel	0.16 Emac	0.25 Esal
Root Dry Weight (80-100 cm)	-2.15 (0.15) Wet	-1.83 (0.21) Dry	-2.63 (0.08) Eglo	-2.28 (0.13) Epil	-2.19 (0.13) Epel	-2.00 (0.16) Epan	-1.75 (0.22) Emac	-1.54 (0.28) Esal	-1.53 (0.24) Ecam	
Root Allocation Ratio	0.364 (1.58) Dry	0.810 (2.45) Wet	0.066 (1.11) Egum	0.222 (1.38) Emac	0.549 (1.84) Esal	0.568 (1.92) Epan	0.681(2.16) Epel	0.714 (2.19) Ecam	0.874 (2.69) Epil	1.022 (2.84) Eglo

NOTE: i) Moisture treatments: Wet = Field Capacity; Dry = Drying.

ii) Ecam = *Eucalyptus camaldulensis*; Eglo = *E. globoidea*; Egum = *E. gummifera*; Emac = *E. maculata*; Epan = *E. paniculata*; Epel = *E. pellita*; Epil = *E. pilularis*; Esal = *E. saligna*.

iii) Treatments are ranked in increasing order of magnitude; horizontal bars span treatments whose means do not differ significantly using LSD ($P<0.05$). Where transformations of the data have been made, the untransformed means are given in brackets.

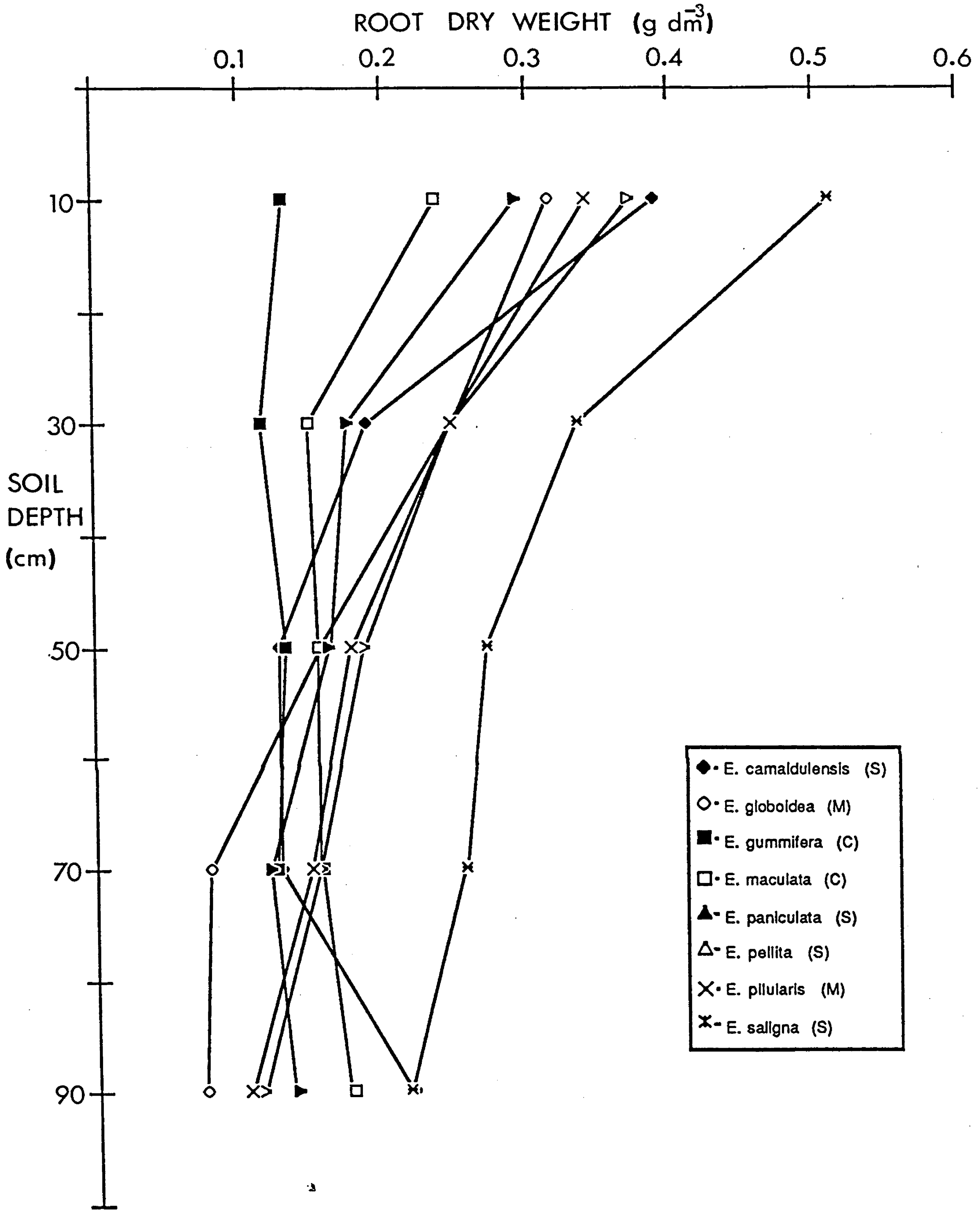

Figure 7.1 Root dry weight (g dm^{-3}) production of eight eucalypt species down a 1 m soil column.

Root Weight 80-100 cm. *E. gummifera* was not included in this analysis because all four seedlings in the 'field capacity' treatment had root systems which failed to reach 80 cm. The response of species in root dry weight production in the 80-100 cm section of soil was significant at the 5% level of probability while the effect of moisture was not significant. The root dry weight production of individual species is shown in ranked order in Table 7.2. The two *Monocalyptus* species *E. globoidea* (0.08 g dm^{-3}) and *E. pilularis* (0.13 g dm^{-3}) had the least root dry weight in the 80-100 cm section of soil, while *E. maculata* (0.22 g dm^{-3}) had a root weight which was bettered only by *E. camaldulensis* (0.24 g dm^{-3}) and *E. saligna* (0.28 g dm^{-3}). The last species produced more than double the root weight of *E. pilularis* and *E. globoidea* at this depth.

(iv) Root Allocation Ratio

A 'root allocation' ratio based on the mean weight of roots (g dm^{-3}) in the 0-40 cm section of the soil profile and the mean weight of roots in the exploited section of soil below 40 cm, can give a very good indication of the inherent morphological character of each species. It demonstrates, in particular, whether species tend to produce the majority of their roots in the upper soil horizon or deeper in the soil profile. A larger ratio indicates that relatively more root photosynthate is allocated to the upper rather than the lower section of the soil profile, and vice versa for a smaller ratio. The 'root allocation' ratio is useful as a standardizing procedure because it provides a measure of the pattern of root distribution without needing to consider absolute differences in root weight.

The influence of moisture on the 'root allocation' ratio was highly significant ($P<0.001$). Seedlings maintained at field capacity had a considerably larger 'root allocation' ratio (2.45) than those where water was withheld (1.58). The difference between species was also highly significant (P<0.001) and is related mainly to the distinctive response of species in different subgeneric groups. The ranked order of means (Table 7.2) shows that the two *Corymbia* species *E. maculata* (1.38) and *E. gummifera* (1.11) had significantly lower 'root allocation' ratios than all other species, that is, these two species direct more of the photosynthate allocated to root production deeper in the soil profile than any of the other species examined. Alternatively it can be said that these two species direct relatively less photosynthate to root production in the upper 40 cm of the soil profile than any other species. In contrast to the *Corymbia* species, the two *Monocalyptus* species *E. pilularis* (2.69) and *E. globoidea* (2.84) had significantly higher 'root allocation' ratios than all other species, i.e. these two species allocate relatively more photosynthate to the development of a root system higher in the soil profile. The four *Symphyomyrtus* species had 'root allocation' ratios that were intermediate between the *Corymbia* and *Monocalyptus* species and hence their pattern of root development is less distinct.

7.3.3 Discussion

The study has shown there are inherent differences between south coast eucalypt species in the morphology of seedling roots, and that for a number of the attributes, differences are apparent at the subgeneric level. Because most of the species examined co-occur and compete for the same resources within the regrowth stands on Kioloa State Forest, it is possible these differences may have a bearing on their relative success on different sites.

The study further shows that differences in soil moisture significantly affect the development of both the root system and the above ground components of eucalypt seedlings. The response to moisture varied according to the attribute measured, for example, where water was applied regularly, shoot height, plant dry weight and shoot dry weight were greater but depth of root penetration was less and root:shoot ratios lower. On the other hand, the total root weight was unaffected by the moisture regime, although the distribution of the root biomass within the soil profile was significantly affected. The seedlings in the drying pots had greater root:shoot ratios than those in the regularly watered pots. A similar response has been reported by Awe *et al.* (1976) for seedlings of *E. camaldulensis*. The drying pots also produced root systems that penetrated further down the soil profile, and had a smaller 'root allocation' ratio, i.e. greater root weight at depth. These plant responses might be expected if it is assumed that root extension is driven by a search for moisture when there is only a limited supply in the soil.

For many of the root attributes, *E. gummifera* had the smallest and least vigorous, and *E. saligna* the largest and most vigorous of the species' root systems. The other six species generally fell between these two extremes, although the ranked order varied with the attribute being assessed. The following discussion examines some of the more ecologically important of these attributes.

Root:Shoot Ratios. There were some differences between species in root:shoot ratios. The two *Corymbia* species *E. gummifera* (0.436) and *E. maculata* (0.486) had lower root:shoot ratios than all other species. The low root:shoot ratio for *E. maculata* in comparison to other species was surprising - given its adaptation to drier sites (Forestry Commission of N.S.W. 1985). However, *E. maculata's* low root:shoot ratio may be compensated for by other root attributes. This will be discussed later. Of the other species, *E. globoidea* (0.580) had the lowest and *E. camaldulensis* (0.685) the highest root:shoot ratios, although few differences were significant. Some of the species demonstrated moderately large differences in root:shoot ratios in response to moisture supply. *E. maculata, E. camaldulensis, E. saligna* and *E. pellita* all increased their root:shoot ratios by about half in the 'drying' treatment. A similar response has been reported for *E. maculata* (Bachelard 1986), and *E. camaldulensis* (Awe *et al.* 1976). Alternatively, *E. globoidea, E. pilularis* and *E. gummifera* did not respond appreciably to differences in moisture status, perhaps suggesting that these three species do not possess the same degree of physiological ability to vary the relative rate of root production in response to drought. Nevertheless, Bachelard (1986) found that *E. pilularis* had a greater root:shoot ratio in a 'dry' compared to a 'wet' soil.

Rooting Depth. The depth to which roots penetrated varied with species. However, because several of the seedlings of some species had at least a few roots which reached the bottom of the pot, differences were not particularly striking. *E. gummifera* (*Corymbia*) had a significantly shorter root system than several other species, including *E. maculata*. The *Monocalyptus* species *E. globoidea* and *E. pilularis* also had shorter root systems, but they differed significantly only from *E. saligna*. The three species with the shortest root systems were also those in which the root:shoot ratios did not increase in response to the 'drying' treatment. These two features suggest that *E. pilularis, E. globoidea* and *E. gummifera* may be the least able of the species examined to cope with a prolonged soil drying phase.

Root Weight Distribution. Patterns of root weight distribution within the soil profile may have ecological significance. For example, in the upper sections of the profile, the *Corymbia* species *E. maculata* and *E. gummifera* had the lowest, and *E. saligna* the greatest root weights, with the *Monocalyptus* species *E. globoidea* and *E. pilularis* intermediate. While *E. gummifera* and *E. saligna* maintained these positions down the soil profile, *E. maculata* did not. Within the lower sections of the soil profile, *E. maculata* now had, relative to other species, a greater root weight, being ranked second and third in root weight at 60-80 and 80-100 cm sections respectively. Alternatively, the root weights of *E. globoidea* and *E. pilularis* at these depths were the lowest recorded. Thus in the upper horizons, *E. maculata* appears to have a somewhat more poorly developed root system compared to several other south coast eucalypts. It is possible that where competition is severe and moisture not limiting, *E. maculata* may be disadvantaged in gaining access to important nutrients, particularly on sites where the fertility may already be marginal.

Root Allocation Ratios. The root allocation ratios (Table 7.2) provide a very good summary of the differences in the rooting patterns in that they are able to define in a broad way, the morphological character of root systems. Both *E. gummifera* and *E. maculata*, with 'root allocation' ratios of 1.11 and 1.38 respectively, were most effective at allocating a higher percentage of photosynthates to root development lower in a dimensionally restricted soil profile. This is in spite of the fact that these two species had significantly lower root:shoot ratios than the other south coast species examined. *E. maculata* appears to be conservative in its allocation of photosynthates to root production, but relatively efficient at distributing its photosynthetic allocation lower in the soil profile. *E. gummifera* may also conservatively allocate photosynthates to root production, but it differed from *E. maculata* in that its mean rooting depth was significantly less. The rooting characteristics described suggest that *E. maculata* could be more competitive than other species on sites where moisture is limited in the upper soil horizons - either because of periodic drought or a restricted soil volume and water holding capacity of the soil, but is accessible in some form at depth. J.R. Bartle (pers. comm.) found that compared to some other eucalypts, *E. maculata* had a reasonably well developed deep root system and a strong main tap root when planted on rehabilitated bauxite mines. *E. maculata's* distribution in drier regions of northern N.S.W. and southern Queensland confirms its adaptation to drier environments.

The two *Monocalyptus* species, *E. globoidea* and *E. pilularis*, with root allocation ratios of 2.84 and 2.69 respectively, differed markedly from *E. maculata* by allocating the majority of photosynthates to root development higher in the soil profile. The depth of root penetration for these two species was also less than for *E. maculata*. These characteristics may be advantageous on sites where soil moisture availability is not limiting and access to nutrients could be more critical in affecting a species competitive response.

The three south coast *Symphyomyrtus* species, had 'root allocation' ratios which were intermediate between the *Monocalyptus* and *Corymbia* species, and tended to be most closely aligned with *E. camaldulensis* in the way they distributed photosynthates to root development, but perhaps in response to different environmental conditions. *E. camaldulensis*, with a 'root allocation' ratio of 2.19, is a fast growing species known widely for its ability to tolerate periodically wet and dry environments (Awe *et al.* 1976). It would benefit by having a root system which can explore the upper horizons but also maintain access to moisture in a rapidly drying soil. *E. paniculata* (1.92) is generally found on drier ridge and top slope positions and would also benefit from a root system that is able to explore a reasonable volume of soil. *E. saligna* (1.84) is a rapid growing wet sclerophyll species which may tend to rely on a high rate of root (and shoot) production throughout the soil profile in the seedling stage to beat concomitantly developing vegetation. This rapid growth rate was demonstrated by the fact that *E. saligna* had significantly higher root and shoot dry weights than all other species examined. *E. pellita* (2.16) generally occurs on sites where soil drainage and aeration are relatively impeded. R.G. Florence (pers. comm.) has suggested that *E. pellita* and *E. pilularis* may form a replacement series on some sites on the south coast in which the occurrence of *E. pilularis* is taken to reflect well aerated soils in the upper horizons. Hence on poorly drained and aerated soils, a greater number of roots, relative to *E. pilularis*, may penetrate to depth where soil conditions are more favourable.

It is quite likely that differences in the seedling root morphology may be particularly important where species have overlapping ranges and therefore compete directly with one another for site resources. For example, the differences in the patterns of root development of *E. maculata* and *E. pilularis* suggest that where these two species occur in mixture, their ability to exploit different sections of the soil profile provides a means of niche differentiation within the same environment. This may be why, despite their rather distinctive geographic ranges at more northern latitudes, they co-occur so widely on Kioloa State Forest. Alternatively, these same differences may on another site, allow one species to compete more effectively, often to the extent that the second species eventually is excluded or occupies a sub-dominant position in the canopy.

Previous studies (Jacobs 1955; Zimmer and Grose 1958) on eucalypt root systems have shown that species from drier regions have generally larger root:shoot ratios. Alternatively, the present study shows that of the species examined, *E. maculata* is most commonly associated with dry conditions, but has one of the lowest root:shoot ratios. By examining the pattern of root allocation throughout the profile however, it is clear that a greater proportion of roots occur deeper in the soil profile than for the other species. Thus species adapted to drier environments may in some cases have relatively high root:shoot ratios but in others, the mechanism may be to distribute root photosynthate to where soil moisture may be more be accessible (e.g. at depth). The pattern of root development may be at least as important as more traditional measures (e.g. root:shoot ratios) in defining the significance of root systems in ecological studies. Alternatively, there may be inherent differences in root:shoot ratios between seedlings from different geographic locations. For example, a provenance of *E. maculata* seed from a drier environment may produce a seedling with an inherently higher root:shoot ratio than seed from a wetter environment, such as that experienced on the south coast. Hence the relatively low root:shoot ratio of *E. maculata* in this experiment may also reflect this natural source of variation.

The positive nature of these results suggest that studies on seedling root morphology may help to explain the problem in stand dynamics being examined in this thesis. It was appropriate therefore to extend this study by examining more critically the root development of two eucalypt species, and to compare root development of the eucalypts and *Acacia*. It was hoped in this way to better appreciate some of the competitive relationships between them.

7.4 EXPERIMENT 2 : ROOT SYSTEM DEVELOPMENT OF EUCALYPT AND *ACACIA* SPECIES UNDER GLASSHOUSE CONDITIONS

In this experiment, an examination is made of the root systems of *E. maculata* and *E. pilularis*, two of the species identified in Experiment 1 as having different seedling root morphologies. This is done both to confirm the results of that experiment, and to examine more precisely the nature of these differences. This is based on an assessment of the pattern of development of separate coarse and fine root components, and an examination of fine root length production. The root morphologies of the eucalypts are in turn compared with that of *Acacia mabellae*. This and several other *Acacia* species compete directly with *E. maculata* and *E. pilularis* on a wide range of sites within regrowth stands on Kioloa State Forest. The effects of soil bulk density on the development of the seedling root systems of each of the three species have also been examined. The level of soil compaction may influence the competitive response of species by altering the pattern and extent of root system development. This could be important on a heavily logged forest site.

7.4.1 Materials and Methods

This experiment was arranged as a randomized design in the glasshouse with three species, three compaction levels (bulk densities) and four replications.

The 1 m long pots used in this experiment were similar to those used in the previous root growth experiment. Soil for the pots was collected to a depth of 20 cm from a moderate quality *E. maculata* site on Kioloa State Forest. Soil from the same site had been used previously (Experiment 1, Chapter 4), and a fuller description of the soil characteristics is given there. The soil was passed through a 1 cm sieve before being placed in pots.

Three different soil compaction levels were used in the experiment, and were prepared in the following way:

1. Lowest Bulk Density - the pots were filled to the top with soil, tapped lightly on the ground 10 times, topped up and tapped lightly 20 times. The latter procedure was repeated two more times.
2. Medium Bulk Density - soil was placed in the pots in separate lots of 1200 cm^3. Between each placement, the pot was tapped firmly on the ground 10 times.
3. Highest Bulk Density - soil was placed in the pots in separate lots of 1200 cm^3. Between each placement, the soil was firmly tamped down with a steel soil coring hammer.

In July 1985, seed of *E. maculata*, *E. pilularis* and *A. mabellae* were sown on a substrate of equal parts of perlite and vermiculite. The *Acacia* seed was pretreated in boiling water for three one minute intervals, taking out each time those seed which had imbibed water. Seedlings of the three species were transplanted to the pots about 35 days after germination. Initially, four seedlings per pot were planted, and these were later thinned to one. Watering was done twice daily from above to maintain approximate field capacity. The pots were stood on thick wire mesh for free drainage. The experiment was harvested 178 days after the seedlings were transplanted.

At harvest, shoot height, leaf dry weight and leaf area were measured. It had been intended to measure stem dry weight to obtain a measure of total shoot dry weight, i.e. leaf dry weight + stem dry weight, but the harvested stem was stolen from the Forestry Department glasshouse. Accordingly, for each of the species, a regression equation was calculated which predicted stem dry weight from leaf dry weight. The data for each of the species came from experiments in Chapter 4. Only data within the range of leaf dry weights in the current experiment were used in the regression. In all cases, a quadratic term provided the best fit. The regression equations for *A. mabellae*, *E. maculata* and *E. pilularis* produced R^2 values of 0.983, 0.992 and 0.987 respectively.

The root system of each seedling was measured to its lowest point in the soil, washed out and divided into five possible sections: 0-15, 15-30, 30-50, 50-75 and 75-100 cm. For each section, roots were separated into fine (<0-1 mm diameter) and coarse (>1 mm diameter) components. Ford and Deans (1977), Feller (1980) and Nambiar (1983) used the same definitions for fine roots. Unless the total length of fine roots was to be assessed first, the roots were oven dried at 85°C until a constant weight was obtained. The weight in grams was converted to a value expressing the dry weight of roots per cubic decimetre of soil explored (g dm^{-3}). The lowest point to which roots had penetrated defined the extent of soil exploration.

An examination of fine root length was also undertaken. An initial attempt was made to establish a regression equation to predict fine root length for each species. A positive correlation between fine root length and fine root weight was demonstrated for each species, but due to variation in 'woodiness' of roots down the soil profile, the R^2 values were generally too low to rely on the estimate. As a result, fine root length was assessed by intercept counting (Newman 1966; Marsh 1971; Tennant 1975). In this method, the washed roots are spread on a tray containing grid squares of a known dimension, and a count is made of the number of intersections between the roots and the grid lines. One and a half centimetre grid squares were used in this assessment. Root length is derived from the formula:

$$\text{Root Length} = 11/14 \times \text{Number of Intercepts} \times \text{Grid Unit (cm)}$$

Fine root length was measured in the 0-15 cm section of each pot at each compaction level. In addition, the fine root length was measured in all five sections of each low bulk density pot. This enabled the pattern of fine root development to be assessed at all depths in a permeable soil. The seedlings grown in the low bulk density soil were chosen for this because the root systems in most of these pots had penetrated below 75 cm, making direct comparisons of root profile development for each of the three species possible. Seedlings in both the medium and high bulk density treatments produced shallower and more variable rooting depths.

Root length was estimated prior to oven drying the sample. The length in centimetres was converted to a value expressing the length of roots per cubic centimetre of soil explored (cm cm^{-3}). Again, this was a particularly useful measure in cases where the root system had explored less than the full section of soil, enabling a direct comparison between treatments for any particular section to be made.

The bulk density of the soil was measured at harvest. However, the conflicting requirements of determining bulk density and washing soil from the roots meant the bulk density was assessed only for soil where roots had not penetrated. Because *E. pilularis* roots generally had not reached the bottom of the pots, these were sampled for bulk density, when the pots were split open. Undisturbed cylinders of soil (varying in length from 10 to 20 cm) were extracted from varying positions in the pots, oven dried at 105°C until a constant weight was obtained. The volume of each cylinder was calculated and the bulk density determined. The mean bulk density and standard error for the low, medium and high compaction levels were 1.06 ± 0.03, 1.18 ± 0.02 and 1.38 ± 0.01 g cm^{-3} respectively. The value of 1.06 g cm^{-3} may be most closely associated with field bulk density in the surface soils (0-5 cm) of the regrowth forest. Measurements of soil bulk density over 11 sites along a slope gradient on the Livingstone Creek Road clearfelled area (Section 2.3.2) showed that the mean ± standard error was 1.05 ± 0.04 g cm^{-3}, while the bulk density of soil from the four sites used for the nitrogen mineralization study (Chapter 6) ranged from 0.88 ± 0.02 to 1.06 ± 0.02 g cm^{-3}. Bachelard (1986) found similar surface bulk densities (1.03 ± 0.03) in soil supporting *E. maculata* forest on the south coast. Soil bulk density, however, increases quite sharply in the sub-surface horizons (See Chapter 6; Bachelard 1986), up to 1.64 g cm^{-3} in the 10-20 cm soil section.

Data were analysed using one- or two-way analyses of variance. The factors were either species or species and bulk density. One-way analyses were used for attributes measured in the low bulk density pots and two-way analyses were used for attributes which were assessed in all

36 pots. Heterogeneity of variance was corrected by the use of log or square root transformations. Only untransformed means are referred to in the text.

7.4.2 Results

The results of two-way analyses of variance are summarized in Table 7.3 and mutiple range comparisons of overall seedling means are presented in Table 7.4. The response of each species at each soil bulk density for the range of attributes assessed are illustrated in Figure 7.2a-o.

(i) The Effect of Species and Soil Bulk Density on Shoot Growth

Shoot Height. Soil bulk density affected shoot height in a highly significant way (P<0.001), while the species effect and the interaction between species and bulk density were significant at the 95% level of probability (Table 7.3). Shoot height decreased significantly with increasing bulk density; and the height of *E. pilularis* was significantly lower than that of *E. maculata* and *A. mabellae* (Table 7.4).

The response of each species to soil bulk density is shown in Figure 7.2a. Shoot height of *A. mabellae* was similar in the low (52.5 cm) and medium (47.3 cm) bulk density treatments, but there was a dramatic decline (19.5 cm) in the high bulk density treatment. *E. maculata* had its greatest shoot height (51.8 cm) in the low bulk density treatment and was not affected by soil compaction to the same extent as the *Acacia* species. *E. pilularis* had consistently the lowest shoot height at each of the three bulk densities, but was also least affected by variation in soil compaction.

Plant and Shoot Dry Weight. There was a significant (P<0.001) decline in total plant dry weight production with increasing bulk density. There was also a significant (P<0.05) species effect; *E. maculata* and *A. mabellae* produced more plant dry weight than *E. pilularis*.

The interaction between bulk density and species (Figure 7.2b) was significant (P<0.05). There was an increase in plant dry weight with decreasing bulk density for all species. The plant dry weight of *A. mabellae* was particularly affected at high bulk density - this was not as pronounced for the two eucalypt species. *E. pilularis* produced less plant dry weight than *E. maculata* and *A. mabellae* at low and medium bulk density. At high bulk density, *E. maculata* produced more, and *A. mabellae* less, plant dry weight than *E. pilularis*.

The pattern of shoot dry weight production was very similar to that of plant dry weight production. There was a significant (P<0.001) decline in shoot dry weight with increasing bulk density and there was a significant (P<0.01) species effect. *E. maculata* produced the greatest, and *E. pilularis* the least shoot dry weight.

The interaction term was also significant (P<0.05). The description of plant dry weight production for each bulk density-species combination applies equally to the results of shoot dry weight production (Fig7.2c).

Leaf Area. Soil bulk density significantly (P<0.001) affected leaf area production - increasing bulk density corresponded with a decrease in leaf area. The species and interaction terms were not significant. The ranked order of means for species (Table 7.4), and the bulk density-species interaction (Figure 7.2d) for this attribute and plant dry weight are similar.

(ii) The Effect of Species and Soil Bulk Density on Root Growth

Root Depth. Bulk density significantly ($P<0.001$) affected rooting depth. With each increase in bulk density, there was a significant decrease in rooting depth (Table 7.4). However, the species effect was not significant nor was there a significant interaction term. Nevertheless, the extent of decline in rooting depth differed for the three species (Figure 7.2e). *A. mabellae* was most, and *E. pilularis* least affected by soil compaction. At low bulk density, rooting depths for *A. mabellae*, *E. maculata* and *E. pilularis* were 92, 90 and 72 cm respectively. At high bulk density, the rooting depths for the same order of species were 12, 39 and 40 cm respectively. The difference in the rooting depth of *E. maculata* as a result of differences in soil bulk density is illustrated in Plate 7.2.

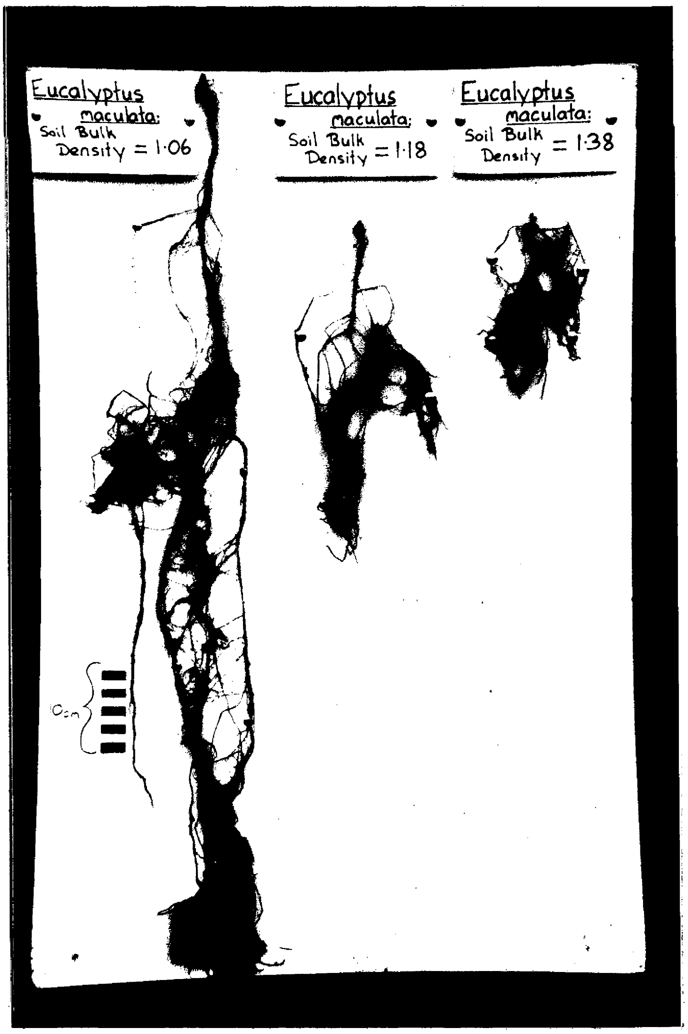

Plate 7.2

The effect of different soil bulk densities on the development of the seedling *E. maculata* root system.

Root Dry Weight - Fine, Coarse and Total. The effects of bulk density on each of fine, coarse and total root dry weight were all highly significant ($P<0.001$). As bulk density increased, all three measures of root dry weight declined. However, differences in the way species responded to bulk density were not so consistent. Coarse root dry weight production did not differ between species (Table 7.4). Alternatively, *A. mabellae* (1.26 g) produced twice as much fine root weight as *E. pilularis* (0.67 g), with *E. maculata* (0.97 g) intermediate. *E. pilularis* also produced significantly less total root weight than the other two species.

Fine, coarse and total root weights for each species at the three soil compaction levels are illustrated in Figure 7.2f-h. This shows that at low and medium bulk densities, *A. mabellae* produced most, and *E. pilularis* least weight of fine roots (Figure 7.2f). However, at high bulk density, *A. mabellae* produced substantially less fine root weight than *E. pilularis*, which in turn produced less than *E. maculata*. Thus *A. mabellae's* fine root production was superior to that of the eucalypts in soils of low to medium compaction, whereas *E. maculata* was relatively better at the higher compaction level. Coarse root production shows a different pattern of production (Figure 7.2g). *E. maculata* had greater coarse root weight than *E. pilularis* and *A. mabellae* in the low and high bulk density treatments, but less than these two species in the medium bulk density treatment. This is difficult to interpret. The pattern of total root weight production (Figure 7.2h) is similar to that of fine root weight.

The broad differences between species can be expressed in a fine root weight:coarse root weight ratio for the several bulk density-species combinations (Table 7.5). A larger ratio indicates that a species has more fine roots relative to coarse roots, and vice versa for a small ratio. At low and medium bulk densities, *A. mabellae* had a larger fine weight:coarse weight ratio than the eucalypt species; *E. maculata* had a particularly low ratio at low bulk density. *A. mabellae's* fine weight:coarse weight ratio declined at high bulk density, while the ratios for the two eucalypt species increased.

Table 7.3 Summary of the differences between attribute means associated with species, bulk density and the interaction between these as derived from analyses of variance.

	Species	Bulk Density	Interaction
Shoot Height	***	***	*
Plant Dry Weight	*	***	*
Shoot Dry Weight	**	***	*
Leaf Area	NS	***	NS
Root Depth	NS	***	NS
Root Dry Weight - Fine	**	***	**
Root Dry Weight - Coarse	NS	***	NS
Root Dry Weight - Total	NS	***	*
Root:Shoot Ratio	*	NS	*
Root Dry Weight (0-15 cm) - Fine	***	NS	***
Root Dry Weight (0-15 cm) - Coarse	NS	***	NS
Root Dry Weight (0-15 cm) - Total	***	***	*
Coarse Root Length:Coarse Root Weight Ratio (0-15 cm)	*	**	**
Coarse Root Length (0-15 cm)	*	***	***
Fine Root Length (0-15 cm)	**	NS	**

* $P<0.05$; ** $P<0.01$; *** $P<0.001$; NS = not significant

Table 7.4 Ranking of seedling means for bulk density and species.

Attribute	Bulk Density			Species		
Shoot Height (cm)	21.2 High	35.4 Medium	44.0 Low	23.0 Epil	37.7 Emac	39.8 Amab
Plant Dry Weight (g)	1.63 (2.98) High	2.32 (5.67) Medium	2.99 (9.54) Low	1.91 (3.93) Epil	2.44 (6.92) Amab	2.58 (7.33) Emac
Shoot Dry Weight	1.42 (2.27) High	2.01 (4.30) Medium	2.58 (7.17) Low	1.63 (2.88) Epil	2.10 (5.14) Amab	2.28 (5.73) Emac
Leaf Area (cm^2)	13.1 (196) High	19.0 (381) Medium	24.9 (656) Low	16.8 (310) Epil	19.8 (457) Amab	20.4 (467) Emac
Root Depth (cm)	30.2 High	52.5 Medium	84.6 Low	54.6 Amab	55.4 Epil	57.3 Emac
Fine Root Dry Weight (g)	0.50 High	0.93 Medium	1.47 Low	0.67 Epil	0.97 Emac	1.26 Amab
Coarse Root Dry Weight (g)	-1.80 (0.20) High	-0.89 (0.44) Medium	-0.27 (0.90) Low	-1.17 (0.39) Epil	-1.00 (0.52) Amab	-0.79 (0.63) Emac
Total Root Dry Weight (g)	0.78 (0.70) High	1.14 (1.34) Medium	1.50 (2.37) Low	0.98 (1.05) Epil	1.21 (1.60) Emac	1.22 (1.76) Amab
Root:Shoot Ratio	0.303 High	0.322 Medium	0.351 Low	0.289 Emac	0.337 Amab	0.350 Epil
Fine Root Dry Weight (0-15 cm) (g dm^{-3})	0.185 High	0.208 Low	0.210 Medium	0.141 Epil	0.161 Emac	0.301 Amab
Coarse Root Dry Weight (0-15 cm) (g dm^{-3})	0.336 (0.118) High	0.486 (0.244) Medium	0.605 (0.383) Low	0.435 (0.206) Epil	0.479 (0.249) Emac	0.514 (0.289) Amab
Total Root Dry Weight (0-15 cm) (g dm^{-3})	0.303 High	0.454 Medium	0.623 Low	0.347 Epil	0.410 Emac	0.623 Amab
Coarse Root Length: Coarse Root Weight Ratio (0-15 cm)	4.37 (100) Low	4.46 (101) High	5.00 (164) Medium	4.29 (85) Emac	4.68 (14.1) Amab	4.85 (1.40) Epil
Coarse Root Length (0-15 cm) (cm)	2.96 (33.1) High	3.87 (60.9) Low	4.06 (75.3) Medium	3.26 (27.5) Emac	3.64 (81.3) Amab	3.99 (60.6) Epil
Fine Root Length (0-15 cm) (cm cm^{-3})	1.35 High	1.48 Low	1.51 Medium	1.17 Epil	1.21 Emac	1.97 Amab

NOTE: i) Mean soil bulk density (g cm^{-3}): Low = 1.06; Medium = 1.18; High = 1.38.

ii) Species: Emac = *Eucalyptus maculata*; Epil = *E. pilularis*; Amac = *Acacia mabellae*

iii) Treatments are ranked in increasing order of magnitude: horizontal bars span treatments whose means do not differ significantly using LSD ($P<0.05$). Where transformations of the data have been made, the untransformed means are given in brackets.

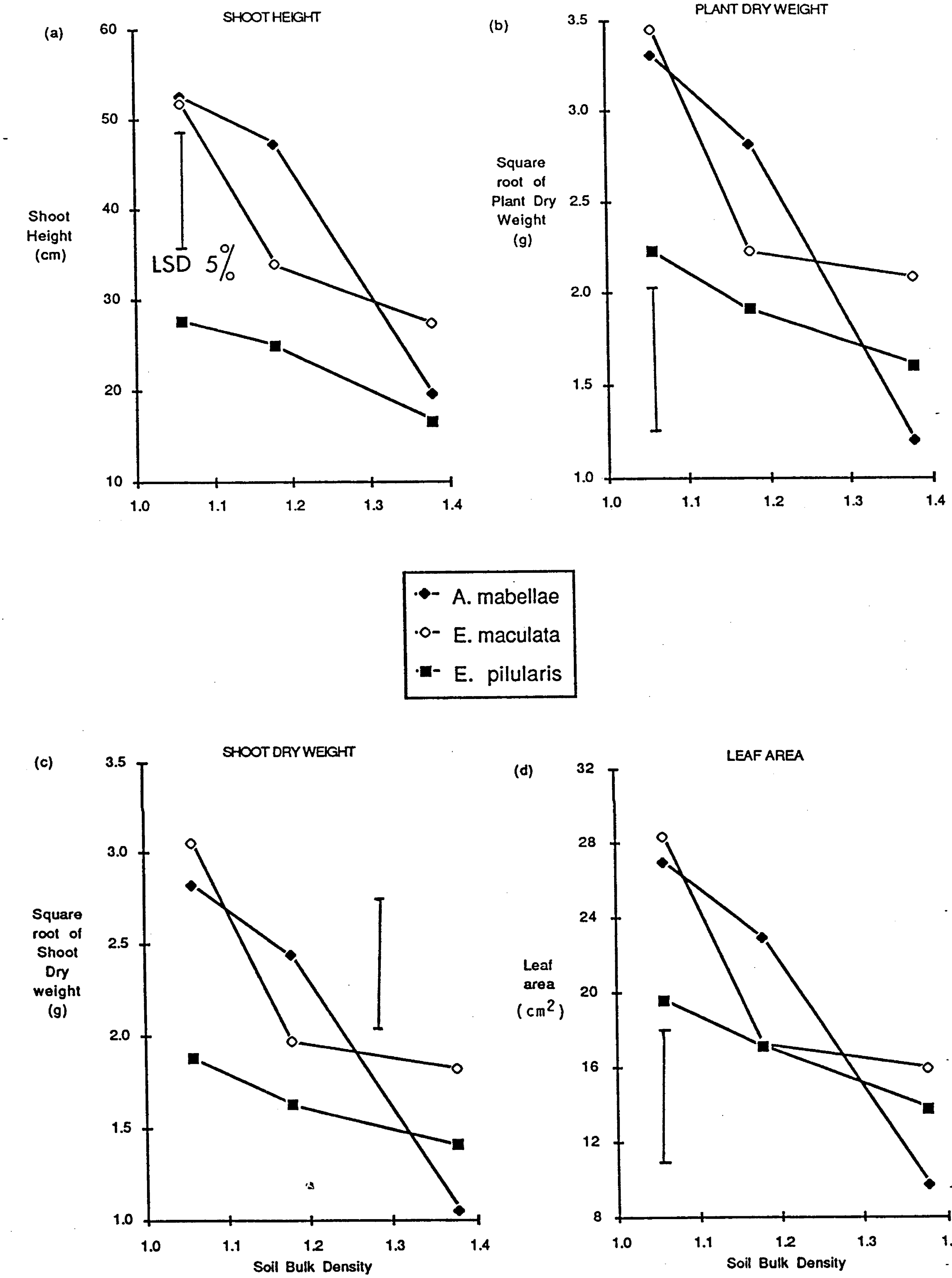

Figure 7.2 The response to soil bulk density (g cm^{-3}) of shoot attributes of two eucalypt species and an *Acacia* species.

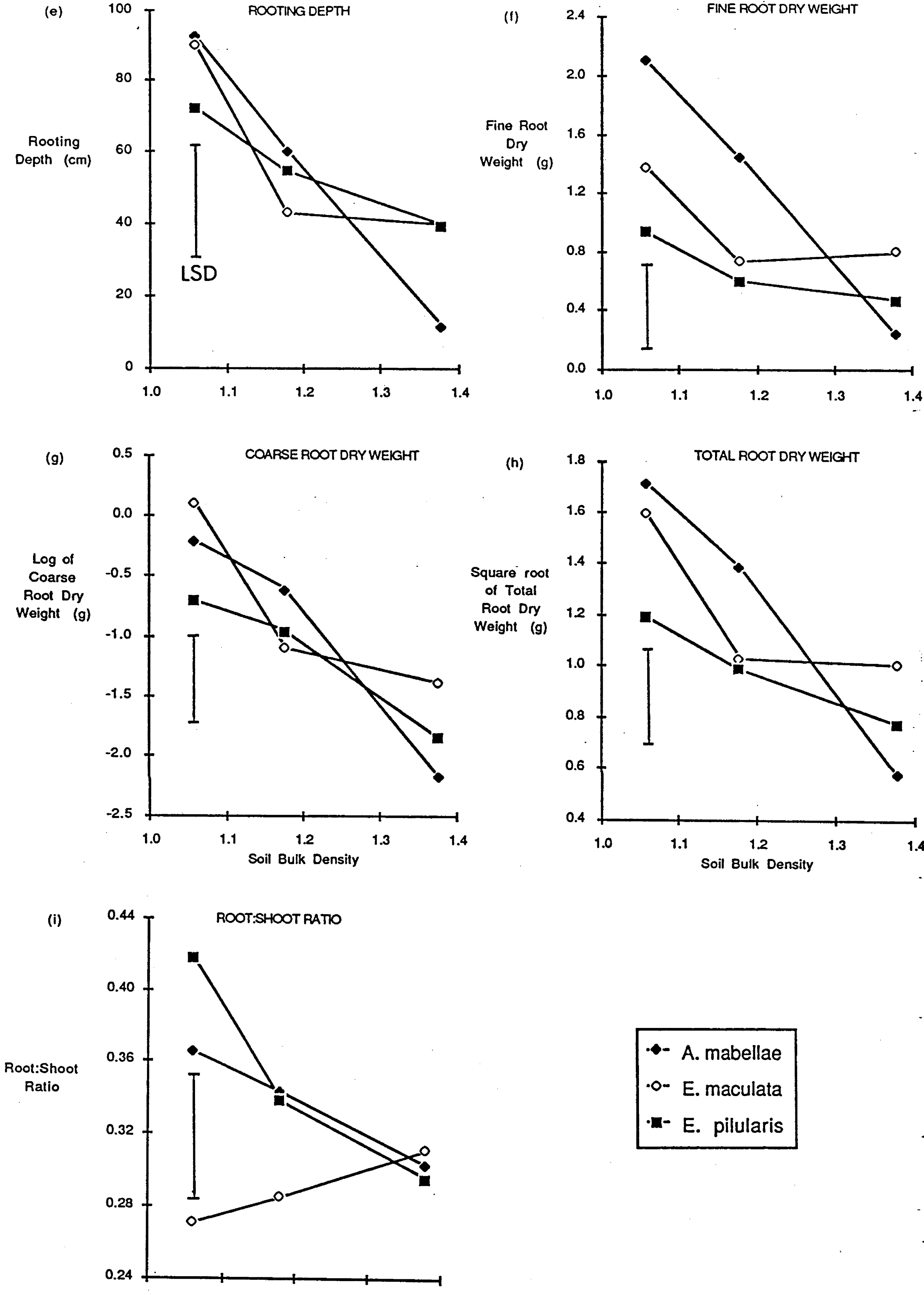

Figure 7.2 cont. The response to soil bulk density of root attributes in the total 1 m soil column of two eucalypt species and an *Acacia* species.

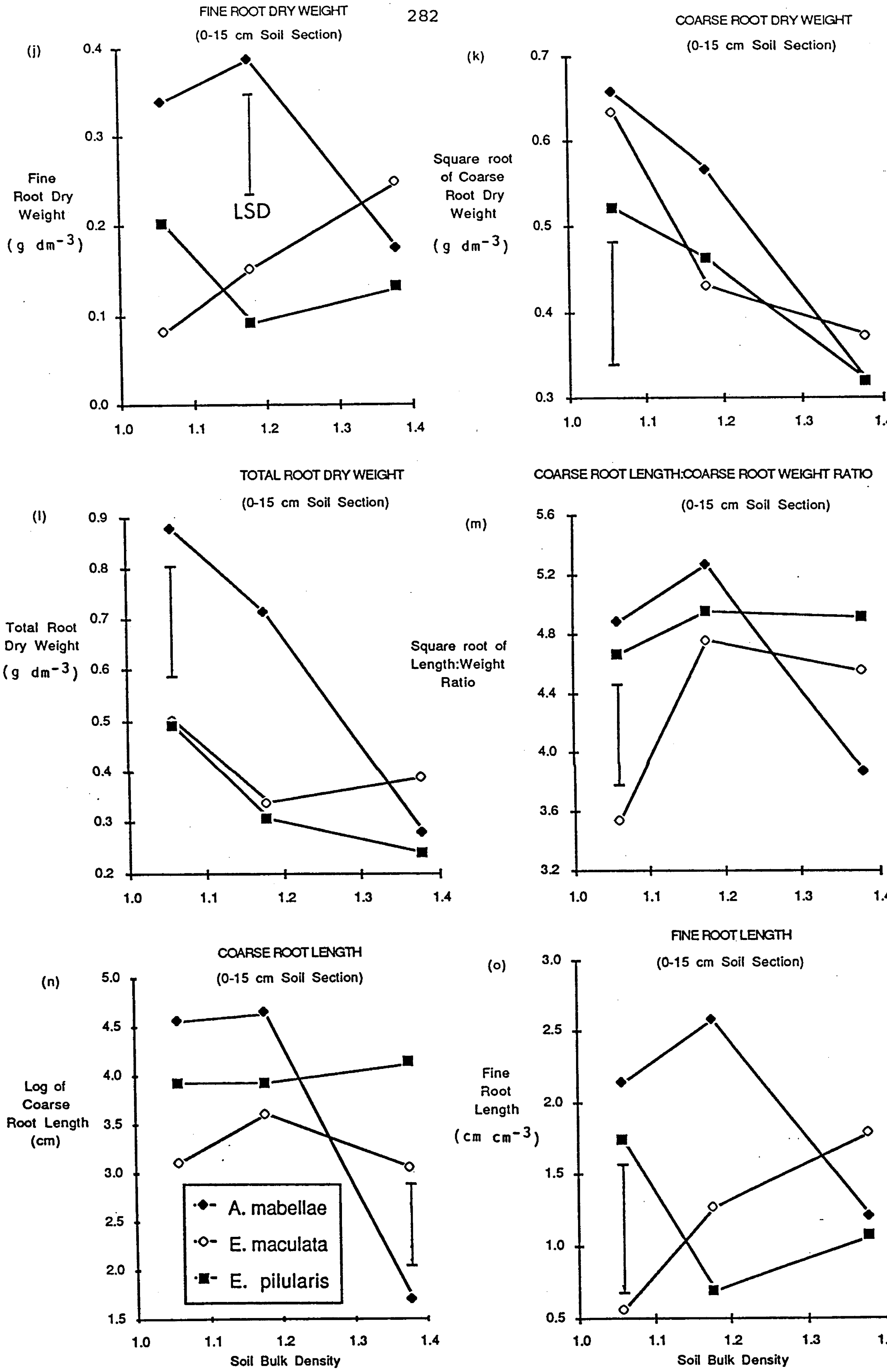

Figure 7.2 cont. The response to soil bulk density of root attributes in the 0-15 cm section of the soil column of two eucalypt species and an *Acacia* species.

Table 7.5 Ratio of fine root weight to coarse root weight for three species at three soil bulk densities.

Soil Bulk Density ($g\ cm^{-3}$)	Species		
	A. mabellae	*E. maculata*	*E. pilularis*
Low (1.06)	2.42	1.09	1.65
Medium (1.18)	2.58	2.11	1.47
High (1.38)	1.86	2.95	2.50

Root:Shoot Ratio. The effect of soil bulk density on the root:shoot ratio was not significant while the species effect was significant ($P<0.05$). *E. maculata* had a lower root:shoot ratio (0.289) than *A. mabellae* (0.337) and *E. pilularis* (0.350) (Table 7.4).

The interaction between bulk density and species was significant ($P<0.05$). Figure 7.2i shows decreasing root:shoot ratios for *E. pilularis* and *A. mabellae*, and an increasing ratio for *E. maculata* with increasing soil bulk density. At low bulk density, the root:shoot ratio of *E. maculata* was notably lower than those of *E. pilularis* and *A. mabellae*. Alternatively, at high bulk density, the ratios were similar. This means the root:shoot ratio of *E. maculata* is stimulated where grown on a high bulk density soil and could reflect a particular adaptation of *E. maculata* to a more poorly structured soil.

In Experiment 1, the root:shoot ratios of *E. maculata* and *E. pilularis* were much higher than those reported in this experiment, and may reflect differences in the structure and composition of the rooting medium.

(iii) Root Production in the Upper Part (0-15 cm) of the Soil Profile

The extent and characteristics of the root system in the upper section of the soil profile may be particularly important in determining the species ability to compete for nutrients in short supply. The following analyses examine a number of aspects of root development in the 0-15 cm section of the soil profile. This is based on an analysis of both root dry weight production and the length of fine nutrient and water absorbing roots.

Root Dry Weight - Fine, Coarse and Total. The effect of soil bulk density on coarse and total root dry weight (g dm^{-3}) in the 0-15 cm section of the soil profile was highly significant ($P<0.001$). Root weight increased with decreasing bulk density. Alternatively, bulk density did not have a significant effect on fine root weight. There were some significant differences associated with species. *A. mabellae* had greater fine and total root weight production than *E. maculata* and *E. pilularis* (Table 7.4). Coarse root weight for the three species was, however, similar.

Again it is useful to separately examine the fine, coarse and total root components for the bulk density-species combinations, this time in the 0-15 cm soil zone (Figs 7.2j-l). Fine root weight is considered first (Figure 7.2j). At low bulk density, *A. mabellae* (0.339 g dm^{-3}) and to a lesser extent *E. pilularis* (0.202 g dm^{-3}), produced substantially greater fine root weight than *E. maculata* (0.082 g dm^{-3}). *A. mabellae* had the greatest fine root weight at medium bulk density as well. In the high bulk density treatment, *E. maculata* produced the greatest fine root weight. Where compared with fine root weight, the production of coarse root weight for the three species was not markedly different (Figure 7.2k). Differences in total root weight in the 0-15 cm section (Figure 7.2l) are therefore a reflection of differences in fine root weight. At the lower soil compaction levels, both *E. maculata* and *E. pilularis* produced substantially less fine and total root weight than *A. mabellae.*

Coarse Root Length:Coarse Root Weight Ratio. This ratio provides a measure of the average thickness of coarse roots. A larger ratio indicates that the average thickness of coarse roots is smaller, and vice versa for a smaller ratio.

The effect of bulk density on the coarse root length:coarse root weight ratio in the upper 15 cm of the soil profile was significant ($P<0.01$), however the pattern is not consistent. At medium bulk density, there was a significantly larger ratio than at low and high bulk densities (Table 7.4). The species effect was also significant ($P<0.05$). *E. maculata* had a smaller ratio than *E. pilularis* while *A. mabellae* did not differ from either species.

There was a significant ($P<0.05$) interaction effect (Figure 7.2m). At low bulk density, *E. maculata* had a significantly smaller coarse length:coarse weight ratio than *E. pilularis* or *A. mabellae*, that is, *E. maculata* had on average, thicker coarse roots in the 0-15 cm section of the soil profile than the other two species. At medium bulk density, there were no obvious differences, while *A. mabellae* had the lowest ratio in the high bulk density treatment.

Coarse Root Length. When examined in conjunction with the previous analysis (coarse root length:coarse root weight ratio), this analysis is useful in demonstrating whether the upper horizon coarse root system is orientated towards producing a strong main tap root or several, finer first and second order laterals.

Both bulk density and species effects were significant ($P<0.01$), as was the interaction effect ($P<0.001$). The length of coarse roots in the 0-15 cm section of soil declined with increasing bulk density; and

E. maculata had a smaller length of coarse roots than *E. pilularis*.

The response of each species at each bulk density is shown in Figure 7.2n. At low bulk density, *E. maculata* (23.1 cm) had a small, and *A. mabellae* (101.4 cm) a large length of coarse roots in the 0-15 cm section of soil. *E. pilularis* (58.3 cm) was intermediate in this respect. The same pattern was apparent in the medium bulk density treatment, but the differences between the species were not as large. At high bulk density, *A. mabellae* had, by virtue of its very poor growth in this treatment, the lowest coarse root length. *E. maculata* had an intermediate length, and *E. pilularis* continued to produce an equivalent length of coarse roots regardless of soil compaction level.

The results from this and the coarse root length:coarse root weight analysis show that at low bulk density, *E. maculata* produced a shorter and thicker coarse root system than *E. pilularis* or *A. mabellae*. In the medium bulk density treatment, the differences between species were less, but still support the concept that *E. maculata* devotes photosynthates to a main tap root while *A. mabellae* and *E. pilularis* produce more radiating lateral roots. At high bulk density, *E. maculata* continued to have shorter and thicker coarse roots than *E. pilularis* while *A. mabellae* had very few coarse roots in this treatment.

Fine Root Length. Fine root length is perhaps a better indicator of a plant's ability to explore the soil volume and hence acquire nutrients than is fine root weight (Barley 1970). Therefore differences associated with this analysis may have greater ecological significance than differences in production of fine root weight.

The effect of soil bulk density and species on fine root length (cm cm^{-3}) in the 0-15 cm section of the soil profile was similar in many respects to that on fine root weight. The effect of bulk density was not significant, while the response of species was significant

($P<0.01$). *A. mabellae* produced greater fine root length than the eucalypt species.

The interaction between bulk density and species was significant ($P<0.01$) and is shown in Figure 7.2o. There were some important differences between this and the fine root weight analysis. At low bulk density, *A. mabellae* (2.13 cm cm^{-3}) and *E. pilularis* (1.74 cm cm^{-3}) did not differ with respect to fine root length, but both were significantly and considerably greater than *E. maculata* (0.56 cm cm^{-3}). In the analysis of fine root weight, *E. pilularis* produced significantly more than *E. maculata* but significantly less than *A. mabellae*. Two features are important here. Firstly, at low bulk density, *E. maculata* devoted considerably less photosynthate to fine root length production than *A. mabellae* or *E. pilularis* in the important upper 15 cm section of the soil profile. Secondly, *E. pilularis* produced less fine root weight than *A. mabellae*, but the species were more similar in production of fine root length. This indicates that the mean diameter of fine *E. pilularis* roots (i.e. roots 0-1 mm) is less than the mean diameter of fine *A. mabellae* roots, and/or the anatomical structure of the fine root system for the two species differs (i.e. for an equivalent root diameter, the weight is different). Observations while processing the samples suggest that the former may be the case, i.e. the mean diameter of fine roots differ.

At medium bulk density, *A. mabellae* produced substantially more fine root length than *E. maculata* and *E. pilularis*. The latter species was particularly depressed in this treatment. At high bulk density, *E. maculata* produced more fine root length than the other two species, although the differences were not significant.

(iv) Fine Root Length in the Total Soil Column at Low Bulk Density

The following one-way analyses of variance examine specifically fine root length (cm cm^{-3}) production in the total soil columns of the 12 low bulk density pots. Initially, fine root length in the total pot is assessed. In addition, fine root length in each of the five sections is examined to determine whether there are any differences in the way species allocate fine roots down the profile. Significant differences for each attribute and the ranking of species means are shown in Table 7.6. Because there are very few degrees of freedom, differences have to be quite large before a significant difference is recorded.

Total Fine Root Length. There was no difference between species in fine root length production in the total soil profile. The fine root lengths for *A. mabellae*, *E. maculata* and *E. pilularis* were 1.65, 1.48 and 1.37 cm cm^{-3} respectively.

Fine Root Length in the 0-15 cm Section. The effect of species and soil bulk density (including low bulk density) on fine root length in the 0-15 cm section of soil was examined in the previous section. In the present analysis, the difference between species still remained significant ($P<0.01$) even though the residual degrees of freedom had been reduced from 26 to 8. *A. mabellae* and *E. pilularis*, with fine root lengths of 2.13 and 1.74 cm cm^{-3} respectively, had significantly higher values than that of *E. maculata* (0.56 cm cm^{-3}).

Fine Root Length at 15-30 cm. The differences between species in fine root length in the 15-30 cm section of soil were not significant, but as with the previous analysis, *E. maculata* had less fine root length than the other two species. *A. mabellae*, *E. pilularis* and *E. maculata* had values of 1.71, 1.98 and 0.87 cm cm^{-3} respectively.

Fine Root Length at 30-50 cm. There were significant ($P<0.05$) differences in fine root length in the 30-50 cm section of the soil profile. *E. pilularis* (1.55 cm cm^{-3}) had significantly more fine root length than *E. maculata* (0.92 cm cm^{-3}) and *A. mabellae* (1.00 cm cm^{-3}).

Fine Root Length at 50-75 cm. There were no differences in fine root length in the 50-75 cm section of soil. However, *E. pilularis* (0.78 cm cm^{-3}) had the smallest and *E. maculata* (1.23 cm cm^{-3}) the largest length, while *A. mabellae* (1.04 cm cm^{-3}) was intermediate.

Fine Root Length at 75-100 cm. In this analysis there were only 5 residual degrees of freedom. Two *E. pilularis* seedlings, one *A. mabellae* and one *E. maculata* seedling had not reached a depth of 75 cm. Despite this, differences were significant ($P<0.05$). *E. pilularis* had depressed fine root length (0.17 cm cm^{-3}) in comparison to *A. mabellae* (1.71 cm cm^{-3}) and particularly *E. maculata* (2.83 cm cm^{-3}).

In summary (Figure 7.3), *A. mabellae* had a relatively large length of fine roots in the 0-15 and 15-30 cm sections of the soil profile. This declined somewhat in the middle 30-50 cm section but increased again in the 50-75 and 75-100 cm sections. *E. maculata* had a small length of fine roots in both the 0-15 and 15-30 cm sections of the soil profile but increased in the 30-50 and 50-75 cm sections. In the lower (75-100 cm) section, there was another substantial increase in fine root length of *E. maculata*, and in fact this was the greatest value for any species at any depth. The pattern of fine root length production for *E. pilularis* contrasts with that of *E. maculata*. Fine root length was greatest in the 0-15 and 15-30 cm sections of the soil profile. Fine root length at 30-50 cm was smaller but not markedly so. At 50-75 and 75-100 cm, there was a substantial decline in the length of fine roots, and in fact the basal section of the profile had the smallest value for any species at any depth.

Table 7.6 Summary of the differences between attribute means associated with species (from the low bulk density treatment) as derived from analyses of variance, and ranking of means for the three species. Fine root length is measured in cm cm^{-3}.

Attribute	Species	Ranked Order of Means		
Total Fine Root Length	NS	1.37 Epil	1.48 Emac	1.65 Amab
Fine Root Length (0-15 cm)	**	0.56 Emac	1.74 Epil	2.13 Amab
Fine Root Length (15-30 cm)	NS	0.87 Emac	1.71 Amab	1.98 Epil
Fine Root Length (30-50 cm)	**	0.92 Emac	1.00 Amab	1.55 Epil
Fine Root Length (50-75 cm)	NS	0.78 Epil	1.04 Amab	1.23 Emac
Fine Root Length (75-100 cm)	*	0.17 Epil	1.71 Amab	2.83 Emac
Root Allocation Ratio	***	0.81 Emac	1.54 Amab	4.92 Epil

NOTE: (i) * $P<0.05$; ** $P<0.01$; *** $P<0.001$; NS = not significant.

(ii) Species: Emac = *Eucalyptus maculata*; Epil = *Eucalyptus pilularis*; Amab = *Acacia mabellae*.

(iii) Species are ranked in increasing order of magnitude; horizontal bars span the species whose means do not differ significantly using LSD ($P<0.05$). Where transformations of the data have been made, the untransformed means are given in brackets.

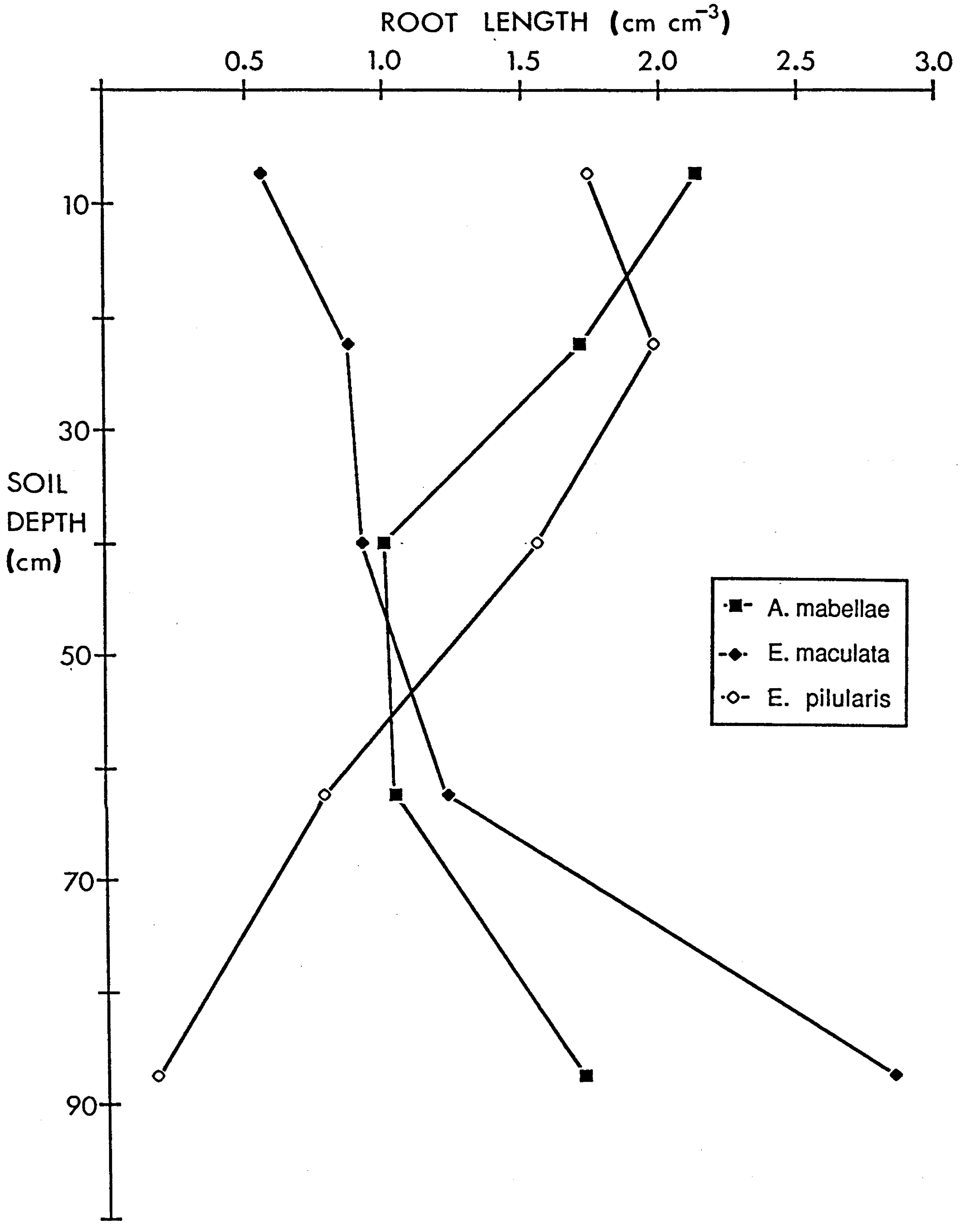

Figure 7.3 Root length (cm cm^{-3}) production of two eucalypt species and an *Acacia* species down a 1 m soil column.

(v) Root Allocation Ratio

As in the previous experiment, a 'root allocation' ratio is useful for succinctly describing the pattern of root distribution within the soil profile. Instead of using root weight however, this ratio is based on the mean length of fine roots (cm cm^{-3}) in the 0-50 cm section of the soil profile and the mean length of fine roots in the section of soil below 50 cm which roots have explored. A larger ratio indicates relatively more fine root length in the upper part of the soil profile, and vice versa for a smaller ratio.

The effect of species was considerable and highly significant ($P<0.001$). *E. pilularis* (4.92) had a significantly higher 'root allocation' ratio than *A. mabellae* (1.64) and *E. maculata* (0.81), the latter two species not differing. Thus, *E. pilularis* concentrated its fine root production in the top half of the soil profile by a factor of five. *A. mabellae* had a greater density of fine roots in the upper half of the soil profile - by a 'root allocation' factor approaching two. *E. maculata* on the other hand had a greater density of fine roots below 50 cm. Although *A. mabellae* had a higher 'root allocation' ratio than *E. maculata*, the difference was not significant, leading to the suggestion that there may be some similarities in the pattern of fine root distribution down the soil profile even though absolute root length differs.

In conclusion, at the lowest bulk density, while fine root lengths for the three species in the whole pot were similar, the patterns of fine root production down the soil profile were very different.

7.4.3 Discussion

The results of Experiment 2 show significant differences in the pattern of root development of the competing species *E. maculata*, *E. pilularis* and *A. mabellae*. In Experiment 1, it had been shown that

E. maculata allocated root weight deeper in the soil profile than several other competing eucalypt species. The present experiment confirms this. In addition, by examining more closely the partitioning of root biomass, it is now shown that the allocation to fine and coarse root production, and the distribution of these two components within the soil profile are features which differ substantially between the three species. It is possible these characteristics play an important role in the competitive response of species following clearfelling. The effects of soil bulk density on root development, and the distribution of roots down the soil profile are examined more critically in the following discussion.

Effect of Soil Compaction on Root Development of Species. Differences in the level of soil compaction had a marked effect on many of the root and shoot parameters. For many attributes (e.g. shoot height, plant dry weight, leaf area, root dry weight), the species responded in a similar way, showing a marked decline in growth with increasing soil bulk density. Soil compaction affects root growth and hence the plant by increasing soil strength and, at a constant volumetric water content, reducing air-filled porosity (Squire and Flinn 1981). For some of the attributes, the three species responded differently to different levels of soil compaction (e.g. root:shoot ratio, and fine root weight and length in the 0-15 cm section of soil profile).

Total root weight for the three species combined, declined from 2.37 g to 0.70 g as bulk density increased from 1.06 to 1.38 g cm^{-3}. A similar pattern of response has been recorded by Schuster (1979) in 10-year-old regenerated *E. diversicolor* forest. As bulk density increased from 0.90 to 1.35 g cm^{-3}, the amount of roots in the surface soil decreased from 3 to 0.25 kg m^{-3}. Other workers (Sands and Bowen 1978; Squire *et al.* 1978) have found a similar response in

Pinus radiata. Reduction in root growth with increased soil compaction is related to the extra resistance offered by soils of greater strength to root penetration (Sands *et al.* 1979), and results in restricted uptake of less mobile nutrients (Barley 1970).

Undoubtedly some soil compaction would have occurred as a result of the clearfelling operations on the south coast and this would almost certainly have affected the growth potential of regenerating species. However, in most cases it is impossible to isolate the effects of soil bulk density from other factors that may have affected regrowth. One possible exception concerns an area of failed regrowth on Higgins Creek Road. Neither *Acacia* or eucalypt species have successfully established. The history of operations on this compartment has been examined in some detail in a case study by Neave (1983). It suffices to say that the use of heavy machinery was more intensive on this than on many other sites in the cutover area and this almost certainly resulted in increased soil compaction. This may have been one factor precluding successful recolonization of the site.

This experiment serves to emphasize the need to carefully control soil bulk density when undertaking pot trials.

Root System Development Within the Upper Soil Horizon. Root system development in the 0-15 cm section of the soil profile has been examined in the greatest detail because of the importance of the upper horizons in providing resources for plant growth (Charley 1981; Strong and LaRoi 1985) and because the majority of roots, and particularly fine roots under field conditions occur in the upper soil horizons (Ashton 1975b; Feller 1980; Charley 1981; Nambiar 1983). At the soil compaction level which may be most closely associated with conditions in the upper soil horizon within the regrowth forest (bulk density 1.06 g cm^{-3}) (See Chapters 2 and 6), *Acacia* produced substantially more fine root weight than the two eucalypt species, and *E. maculata* in particular had a very low weight of fine roots. More importantly perhaps, the length of the fine roots was substantially different for the three species. *E. maculata*, with a fine root length of 0.56 cm cm^{-3} in the 0-15 cm section of soil, had a far less well developed fine root system than *E. pilularis* (1.74 cm cm^{-3}), and particularly *A. mabellae* (2.13 cm cm^{-3}). Under some conditions then, *E. maculata* could be at a great disadvantage compared to other regrowth species through a limited ability to explore the upper soil horizons. At medium bulk density, *A. mabellae*, *E. maculata* and *E. pilularis* had root lengths of 2.58, 1.27 and 0.69 cm cm^{-3} respectively in the 0-15 cm section while at high bulk density, the lengths were 1.21, 1.79 and 1.07 cm cm^{-3} respectively. Thus *A. mabellae* is also most prolific at the medium bulk density while *E. maculata* produces the greatest fine root length of the three species at the highest bulk density. The figure of 0.69 cm cm^{-3} for *E. pilularis* in the medium bulk density treatment is probably an underestimate, given that the root length for this species is appreciably larger at both higher and lower levels of soil compaction.

Root length of *A. mabellae* and *E. pilularis* were reduced at high soil bulk density, whereas *E. maculata* showed the reverse trend - that of increasing fine root length at the high soil bulk density. Thus where soil is compacted or of poor structure, *E. maculata* may be the best adapted of the three species in that it may continue to explore the upper soil horizons by producing a reasonable length of fine ramifying roots. In a similar way, *E. maculata* increased its root:shoot ratio in response to increasing soil bulk density, whereas that of *E. pilularis* and *A. mabellae* declined. An adaption of *E. maculata* to more difficult environmental conditions may also be expressed in the positive response of the *E. maculata* root system to a drying soil (Experiment 1), a response that was not evident for *E. pilularis*. Although the increased rooting density would benefit *E. maculata* at higher bulk densities, the total volume of soil explored is still severely localized and restricted (i.e. root depth restricted) compared to the lower bulk densities.

Where soil compaction is not unduly restrictive, the limited production of fine roots suggests *E. maculata* may have difficulty in gaining access to important nutrients in the upper soil horizons. In contrast, *A. mabellae* and possibly *E. pilularis*, will be able to explore a greater volume of soil in which to provide their nutrient requirements. In an environment of intense competition, these rooting differences in the upper soil profile may have a considerable and adverse bearing on the ability of *E. maculata* to gain access to nutrients.

While there are strong contrasts in fine root development of *E. maculata* and *A. mabellae*, that of *E. pilularis* and *A. mabellae* are more similar. Although *E. pilularis* had less fine root weight than *A. mabellae* in the 0-15 cm zone of the low bulk density pots, the fine root length of the two species was more equal. This suggests that the mean diameter of fine roots is less for *E. pilularis* than *A. mabellae*, and is supported by observations during the processing of samples. Elsewhere, Barrow (1977) found that the modal value of root diameter distribution for *Acacia pulchella* was greater than for *E. marginata*, *E. diversicolor*, *E. calophylla* and *Banksia grandis*, and suggested that plants with thin roots should be anatomically well-adapted for uptake because they can explore a large volume of soil with little expenditure of energy. However, while *E. pilularis* may in certain circumstances be able to explore an equivalent volume of soil to *A. mabellae* as a result of similarities in fine root length, the root surface area available for absorption, and hence the extent of the rhizosphere influence for the two species, will differ because of the differences in fine root diameter. Thus, *A. mabellae* may have greater root access to soil resources because it is able to provide a greater area of contact between the roots and the soil for a similar length of roots.

Two other root parameters were assessed in the 0-15 cm section of the soil profile. The coarse root length:coarse root weight ratio and coarse root length may together be taken to indicate whether the three species are orientated towards producing a single main tap root, or several branching first and second order lateral roots. An examination of these two parameters showed that *E. maculata* had a mean 'thickness' of coarse roots that was larger, and a length of coarse roots that was smaller than either *A. mabellae* or *E. pilularis*. Thus in the region of soil where the root system initially develops, *E. maculata* tends to produce fewer but thicker coarse roots. In effect, *E. maculata* has a better developed main tap root system and fewer lateral roots than the other two species. The coarse root system of a young *E. maculata* sapling is illustrated in Plate 7.3 to show the development of a strong main tap root and few first order laterals. Alternatively, *A. mabellae* and *E. pilularis* have more lateral surface spreading roots and a less well defined tap root than *E. maculata*. For *Acacia* at least, this conclusion is supported by Waki (1984) who states that in general, *Acacia* mainly develops a surface root system with a short tap root.

Root Development Down the Soil Profile. The pattern of fine root length production down the low bulk density soil profiles (Figure 7.3) has been summarized in the 'root allocation' ratios. This showed that *E. maculata* had a strong tendency to allocate the majority of fine root length in the lower part of the soil column. *E. pilularis* on the other hand produced a concentration of fine root length in the upper soil profile. *A. mabellae* differed from both the eucalypts by allocating a reasonable proportion of fine root length throughout the profile. These distinctive patterns of root distribution - surface orientated in the case of *E. pilularis*, more deeply directed in the case of *E. maculata*, and a more uniform distribution of fine roots in the case of *A. mabellae* - may influence the competitive response by providing

Plate 7.3

Tap root development of a young *E. maculata* sapling from Kioloa State Forest.

differential access to nutrients and water. Therefore, the environmental conditions on a particular site will determine which species are favoured.

Summary. This experiment has shown that *E. pilularis*, and particularly *A. mabellae*, develop a system of fine absorbing roots and lateral surface spreading roots in the upper soil horizon that are more substantial than that of *E. maculata* These features strongly suggest that in comparison to *E. maculata*, *A. mabellae* and *E. pilularis* could have greater access to the available soil nutrient pool. As a consequence, they may be more competitive on sites where stocking levels are high or where available soil nutrients are in limited supply, both of which may apply to many sites within the regrowth forest. On the other hand, *E. maculata* produces a more vertically orientated root system that is better developed in this respect than those of *A. mabellae* and *E. pilularis*. Such a root system may be involved in providing *E. maculata* with access to soil moisture at depth, and therefore a competitive advantage on sites where moisture becomes periodically limiting. As a rule, the faster the development of the tap root, the greater is the resistance of the plant to aridity (Mishra and Bhola 1967). This may help to explain why *E. maculata* is able to occupy both dominant and co-dominant canopy positions on many of the drier ridge and top slope sites within the regrowth forest. However the dominance of *E. pilularis* and *A. mabellae* species over *E. maculata* on many lower slope sites, where moisture is less likely to be limiting, suggests that for some reason, *E. maculata* becomes less competitive. The influence of differences in root development which have been demonstrated in this and the previous experiment, and particularly *E. maculata's* poorly developed fine surface root system, may be determining factors.

The two glasshouse studies have indicated that there are substantial differences in root system development of a number of competing species which are found in the regrowth stands. It remains to confirm that this applies as well to the root development patterns of the species in the regrowth stands.

7.5 EXPERIMENT 3 : THE FINE ROOT SYSTEMS OF EUCALYPT AND *ACACIA* SPECIES IN REGROWTH FOREST

In the third root study, soil coring techniques have been used to examine root development of *E. maculata*, *E. pilularis* and *Acacia* species in 13-year-old regrowth. This will determine whether the differences in root development of seedlings shown under controlled conditions are repeated under field conditions and at a later stage in the development (life cycle) of the plant.

7.5.1 Materials and Methods

Sampling Procedure

Root sampling was undertaken on a mid slope position adjacent to Livingstone Creek Road, and in close proximity to the sites where both the vegetation description (Section 2.3.2) and the regrowth competition-fertilizer experiment (Section 5.3) were undertaken. The site, on Ordovician parent material, was occupied by *E. maculata*, *E. pilularis* and *A. mabellae*, and to a lesser extent by *A. irrorata* and *A. floribunda*, and was one of the few areas within the regrowth forest which was devoid of a substantial understorey and grass component. Subsequent root identification was therefore facilitated.

On the study site, the *Acacia* species, *E. maculata* and *E. pilularis* sometimes occurred, either exclusively, or as the dominant component of a small 'regrowth patch'. Hence it was considered that sampling of roots from the soils supporting these patches would indicate the extent of root proliferation associated with each of the three species types. No attempt was made to identify roots from different species of *Acacia*. It was decided that root sampling would be carried out in both winter and spring periods to determine whether root growth showed any seasonal pattern.

A pilot sampling program was necessary to determine the extent of variation in the spatial distribution of roots, the minimum number of samples required and any time constraints. In mid June 1985, four soil cores were taken at 10 cm depth intervals to 30 cm from randomly selected positions in the *Acacia* patches. Using the same technique, three cores were each taken from the *E. maculata* and *E. pilularis* patches. The roots were subsequently washed, and length and weight measured.

Using data from the pilot sample, the required sample size to restrict the error to within a certain percentage of the mean was determined using the method of Snedecor and Cochran (1967). This method is described in Section 2.3.1. In order to obtain estimates of fine root length within 10% of the true mean with 90% confidence for the 0-10 cm soil section, 99, 509, and 164 core samples would be required for *Acacia* species, *E. maculata* and *E. pilularis* respectively. The large number of samples required probably reflects both the small pilot sample and the high natural variation in root distribution patterns. Sampling at this intensity was considered to be unrealistic given the large amount of time needed to wash and measure roots from each soil core.

Primarily because of time constraints, the first root sampling program consisted of taking four cores from the *Acacia*, and three from each of the *E. pilularis* and *E. maculata* patches in early August, and combining these with the pilot sample taken in June. This made up the winter sampling. Thus a total of eight holes were cored in the *Acacia* patches, and six each in the *E. maculata* and *E. pilularis* patches. This is comparable with McClaugherty *et al.* (1982) who estimated fine root dry matter from nine 19 mm diameter core samples. The spatial distribution of all stems by diameter classes within a three metre radius of cores taken in the winter sampling are shown in Figure 7.4a-c to give an indication of the size and composition of species making up the 'regrowth patches'.

The second root sampling program was modified slightly in the light of results from the winter sampling. In mid November 1985, six holes were cored within one metre of the previous core holes, in each of the three species patches. Because very few roots were found in the 20-30 cm cores from the winter sampling, cores were only taken to a depth of 20 cm.

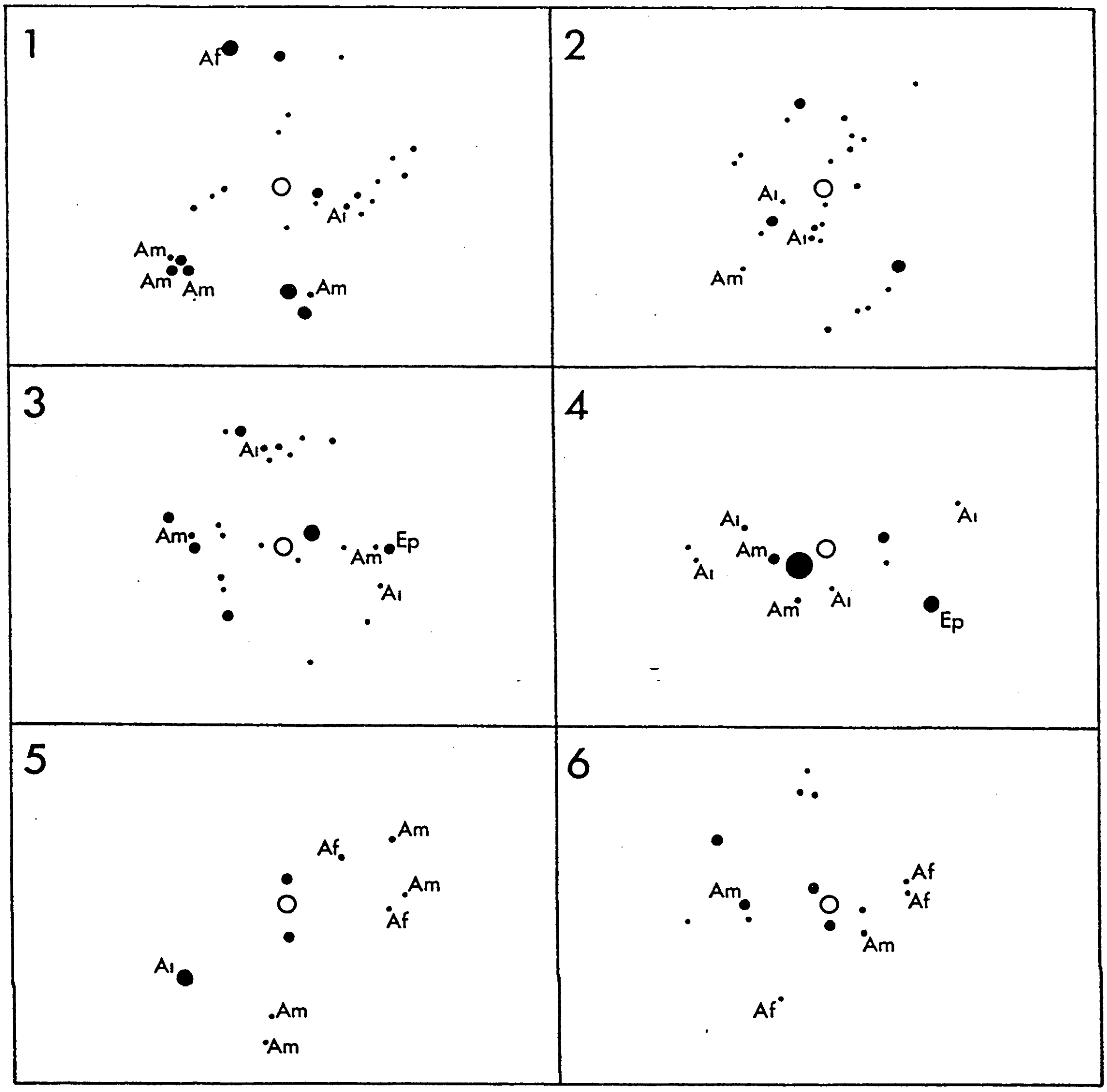

Figure 7.4a

Spatial distribution of all stems by diameter classes within a 3 m radius of soil cores taken from the '*E. maculata* regrowth patches' in the winter sampling period. Each unmarked dot represents an *E. maculata* stem. Soil cores for the spring sampling period were located within 1 m of these core positions.

(i) ○ Soil Core Location

(ii) Stem Diameter (cm)

. 0–4.9

. 5–9.9

• 10–14.9

● 15–19.9

⬤ 20–24.9

(iii) Am = *Acacia mabellae*
Ai = *A. irrorata*
Af = *A. floribunda*
Ep = *Eucalyptus pilularis*

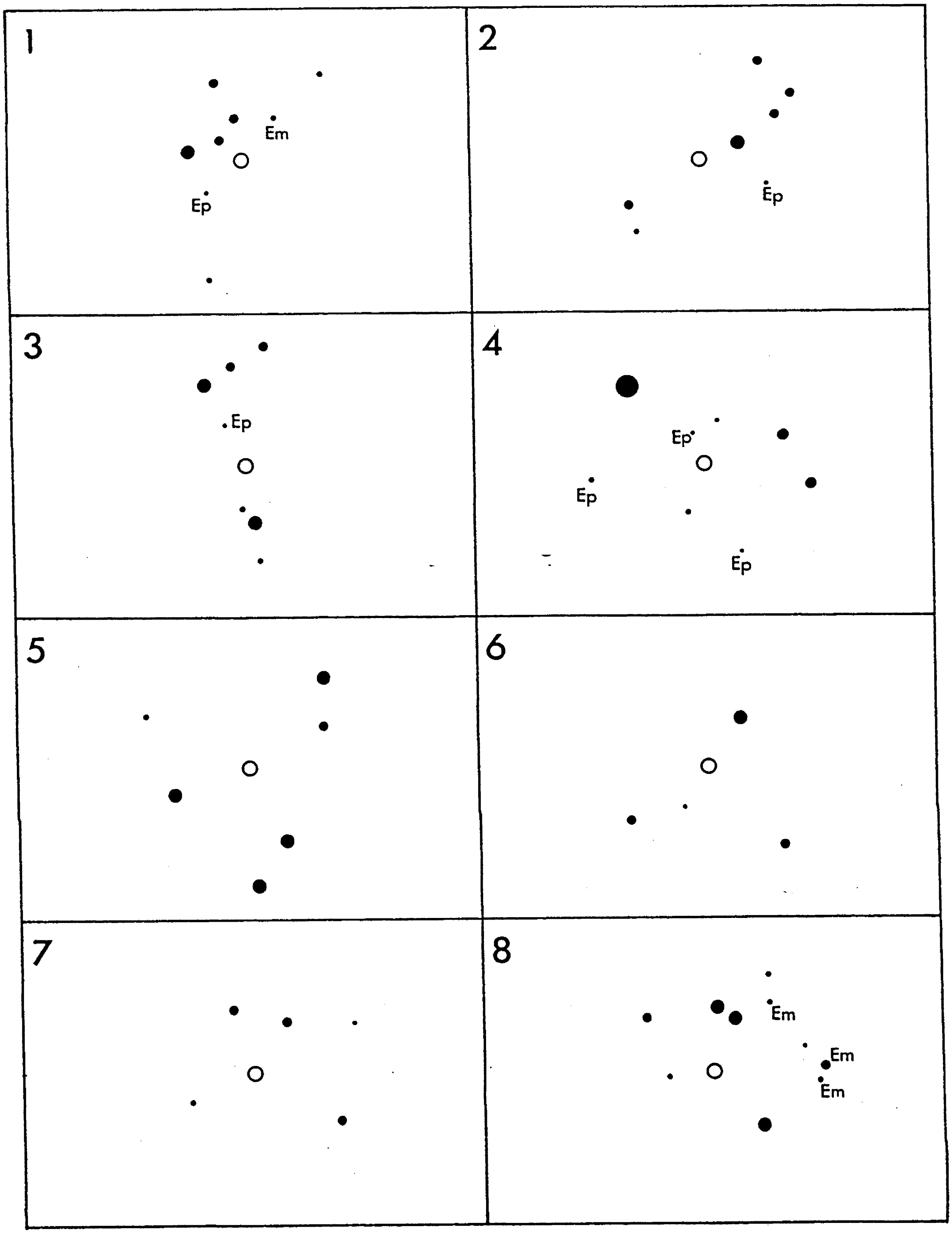

Figure 7.4b

Spatial distribution of all stems by diameter classes within a 3 m radius of soil cores taken from the '*Acacia* regrowth patches' in the winter sampling period. Each unmarked dot represents an *Acacia* stem. Soil cores for the spring sampling period were located within 1 m of these core positions.

(i) ○ Soil Core Location

(ii) Stem Diameter (cm)

· 0–4.9
· 5–9.9
• 10–14.9
• 15–19.9
● 20–24.9

(iii) Em = *Eucalyptus maculata*
Ep = *E. pilularis*

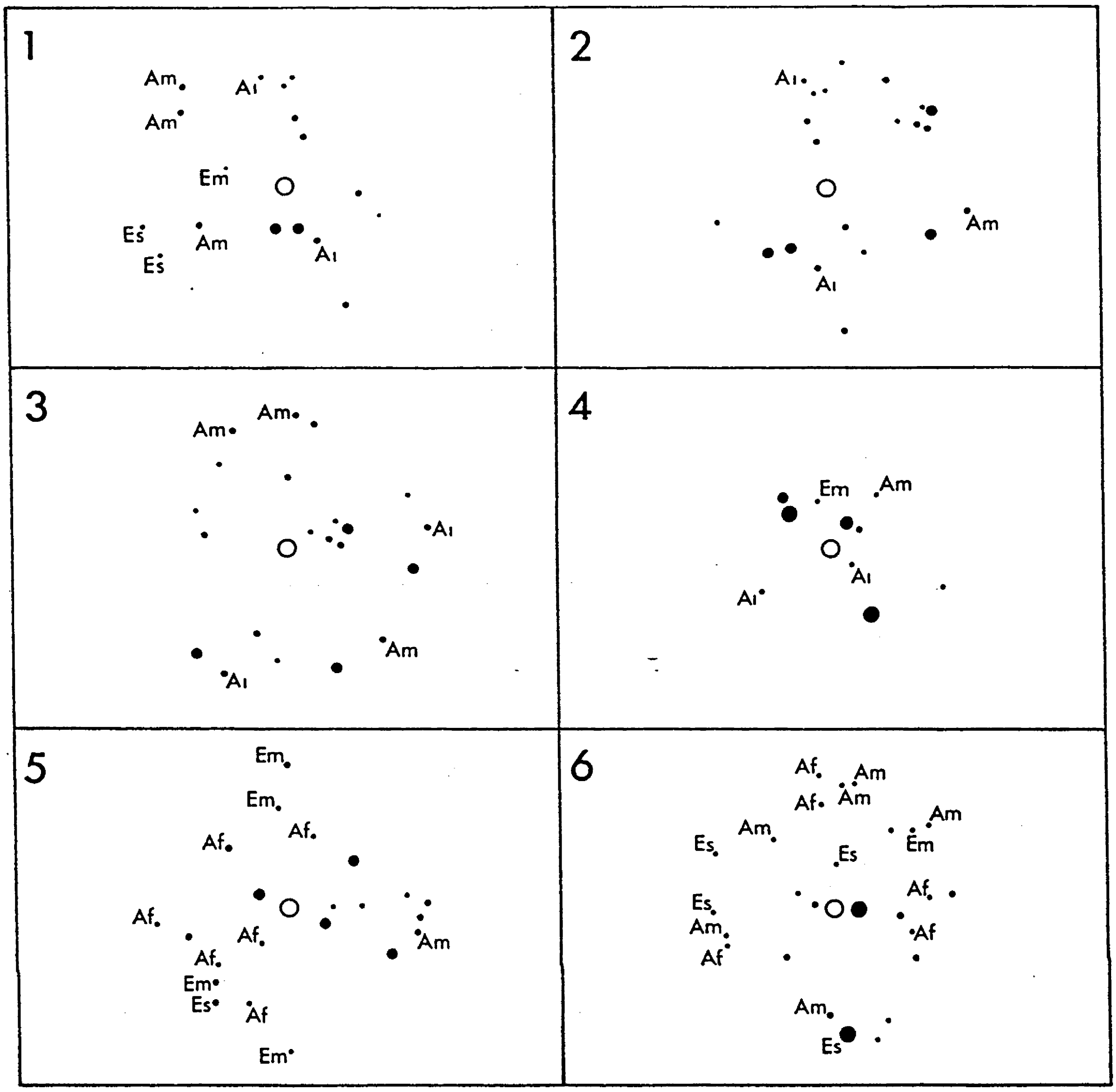

Figure 7.4c

Spatial distribution of all stems by diameter classes within a 3 m radius of soil cores taken from the '*E. pilularis* regrowth patches' in the winter sampling period. Each unmarked dot represents an *E. pilularis* stem. Soil cores for the spring sampling period were located within 1 m of these core positions.

(i) ○ Soil Core Location

(ii) Stem Diameter (cm)

- · 0–4.9
- • 5–9.9
- • 10–14.9
- ● 15–19.9
- ⬤ 20–24.9

(iii) Am = *Acacia mabellae*
Ai = *A. irrorata*
Af = *A. floribunda*
Em = *Eucalyptus maculata*
Es = *E. saligna*

Experimental Method

Root samples were collected at 10 cm intervals to either 20 cm (second sample) or 30 cm (first sample) using a hardened steel corer (internal diameter 75 mm, core volume per 10 cm length 441.8 cm^3) hammered into the ground with a sliding steel cylinder. Cores were placed in plastic bags and subsequently stored in a cold room (0°C) until processing.

Roots were washed from soil cores over successively smaller sieves to 1.4 mm. Fine roots are prone to loss during sample preparation in this way (Reynolds 1970; Nambiar 1981), and this study was probably no exception. No attempt was made to extract mycorrhizae, although it was observed that fungal associations appeared to be most extensive in the *E. pilularis* soil cores.* Coarse root length was measured directly while fine root length was measured by intercept counting (Newman 1966; Marsh 1971; Tennant 1975). This method is described in the previous experiment. Half centimetre grid squares were used for measuring fine root length of the 'winter' samples. For roots collected in spring, one and a half centimetre grid squares were used. This allowed a considerable time saving with only a small loss in precision of estimate (Tennant 1975). Root weight was measured after drying at 85°C to a constant weight.

The extracted roots were sorted into two size classes: 0-2 mm diameter for fine roots and >2 mm for coarse roots. In the previous experiment, fine roots were defined as those with diameters of 0-1 mm. This was because root diameters in a seedling study are more uniform than those found in the field. After processing several cores in the present study, it was decided on the basis of readily observable features, for example, secondary thickening and inflexibility, that 0-2 mm diameter would best represent the fine root component of these 13-year-old regrowth species. The sizes also follow the definitions by Ashton (1975b), and Jackson and Chittenden (1981).

Only *Acacia* roots were recovered from soil cores taken from *Acacia* regrowth patches. Alternatively, *Acacia* roots were found in soil cores taken from both *E. maculata* and *E. pilularis* regrowth patches. It was therefore necessary to be able to distinguish between the *Acacia* and eucalypt roots within the one soil core, and was in fact for the most part, relatively simple.

Larger diameter roots (>2 mm) could be identified by examination of tissue features (eg vessel size and arrangement, colour) in cross-section under a low power binocular microscope. The occurrence of nitrogen fixing nodules on *Acacia* species was the single most important characteristic separating the fine roots of *Acacia* and eucalypt roots. In addition, most of the *Acacia* fine roots had easily recognisable external features which became familiar once the operator gained experience processing the soil cores. Chilvers (1972b) had similarly found that with only very little practice, eucalypt roots could be readily distinguished from the roots of *Acacia*. Nevertheless, some roots and especially those of *E. maculata* and *Acacia* were difficult to separate. Since this study is based on the hypothesis that *Acacia* roots may be more prolific than either *E. maculata* or *E. pilularis* roots in the upper soil horizon, it was decided that where there was any uncertainty, roots would be assigned to the eucalypt species being examined. In this way, if the eucalypt roots in a eucalypt regrowth patch still had less root length or weight than corresponding *Acacia* roots in an *Acacia* patch, it was more likely that those differences would be real.

Data Analysis

Root length and weight data for roots 0-2 mm in diameter and total roots, from 0-10 cm and 10-20 cm depths, and for winter and spring collection periods were analysed separately using one-way analyses of variance. T-tests were used to determine whether there were any differences in root data between sampling periods. For each species, fine root length and weight were compared for winter and spring sampling periods. None of the comparisons were significant so the data were also pooled to provide a greater sample size. Data transformations were made where heterogeneity of variance was indicated. Only untransformed means are referred to in the text.

7.5.2 Results

In the text, reference to *Acacia* roots implies they were collected from an *Acacia* 'regrowth patch'. Similarly, reference to *E. maculata* and *E. pilularis* roots implies they were collected from *E. maculata* and *E. pilularis* 'regrowth' patches respectively. It is also noted that because the length of roots >2 mm in diameter formed a very small proportion of total root length, the two analyses of variance produced the same result. For discussion purposes, reference will only be made to the analysis of root length 0-2 mm in diameter.

A summary of the results of analyses of variance and ranking of species means are shown in Table 7.7.

Root Length

For the winter sampling period, the length of *Acacia* fine roots (1.618 cm cm^{-3}) from the 0-10 cm soil horizon was significantly greater than that of either *E. pilularis* (0.937 cm cm^{-3}) or *E. maculata* (0.559 cm cm^{-3}) from an equivalent depth (Table 7.7). In the 10-20 cm zone, *Acacia* (0.738 cm cm^{-3}) again had significantly larger values than *E. pilularis* (0.299 cm cm^{-3}) and *E. maculata* (0.222 cm cm^{-3}). The differences between species in fine root length were even more striking at the spring sampling period (Table 7.7). For example, in the 0-10 cm soil, *Acacia* and *E. maculata* had fine root lengths of 2.173 and 0.353

cm cm^{-3} respectively. For both sampling periods, *E. pilularis* had a greater length of fine roots than *E. maculata* in the 0-10 cm zone, but perhaps because of the small sample size, the differences were not significant. In the 10-20 cm soil horizon, *E. maculata* roots had consistently greater fine root length than *E. pilularis*, but again the differences were not significant.

The analysis of pooled data from the winter and spring sampling periods highlights a difference that previously was not significant (Table 7.7). In the 0-10 cm zone, the length of *E. pilularis* (0.894 cm cm^{-3}) fine roots was significantly greater than that of *E. maculata* (0.466 cm cm^{-3}) fine roots, while the fine root length of *Acacia* (1.856 cm cm^{-3}) was significantly greater than both eucalypt species. In the 10-20 cm zone, the results from the pooled data were no different to the results from separate spring and winter samples.

Root Weight

At both winter and spring sampling, *E. maculata* consistently had the smallest weight of both fine and total roots in the 0-10 cm soil horizon (Table 7.7). By pooling the data, this difference became significant for roots 0-2 mm in diameter, but remained non-significant for total root weight. It is possible that many of the larger diameter and vertically penetrating roots would not have been sampled using a vertically inserted corer. Given that *E. maculata* may have a greater number of vertically orientated roots than *Acacia* species and *E. pilularis* (Experiments 1 and 2), it is possible this type of sampling may have underestimated the total root weight of *E. maculata* more than it did for the other species. The comparison between *E. pilularis* and *Acacia* roots 0-2 mm in diameter showed that the latter had the greater weight in both sampling periods although neither of the differences were significant. There were no consistent differences in root weight between the three species types in the 10-20 cm zone.

Table 7.7 Summary of the differences between attribute means of root data as derived from analyses of variance, and ranking of the means for the three species. Root length is measured in cm cm^{-3} and root weight is measured in g dm^{-3}.

Attribute	Root Diameter	Soil Depth	Species	Ranked Order of Means		
Winter Sampling Period						
Root length	< 2 mm	0-10 cm	**	0.559 Emac	0.937 Epil	1.618 Acspp
Root length	< 2 mm	10-20 cm	**	0.222 Emac	0.299 Epil	0.738 Acspp
Root weight	< 2 mm	0-10 cm	*	0.437 Emac	0.903 Epil	1.365 Acspp
Root weight	< 2 mm	10-20 cm	NS	0.308 Epil	0.437 Emac	0.620 Acspp
Root weight	total	0-10 cm	NS	1.403 Emac	2.037 Acspp	2.173 Epil
Root weight	total	10-20 cm	NS	0.593 E.pil	0.679 Acspp	0.688 Epil
Spring Sampling Period						
Root length	< 2 mm	0-10 cm	***	0.0111 (0.353) Emac	0.0127 (0.849) Epil	0.0154 (2.173) Acspp
Root length	< 2 mm	10-20 cm	**	0.0096 (0.168) Epil	0.0103 (0.247) Emac	0.0122 (0.561) Acspp
Root weight	< 2 mm	0-10 cm	*	0.385 Emac	1.204 EPil	1.496 Acspp
Root weight	< 2 mm	10-20 cm	NS	0.288 Epil	0.330 Emac	0.428 Acspp
Root weight	total	0-10 cm	NS	-4.323 (0.385) Emac	-2.037 (1.403) Epil	-0.837 (1.901) Acspp
Root weight	total	10-20 cm	NS	0.475 Emac	0.905 Acspp	1.154 Epil
Combined Winter and Spring Sampling Period						
Root length	< 2 mm	0-10 cm	***	0.0116 (0.466) Emac	0.0131 (0.894) Epil	0.0150 (1.856) Acspp
Root length	< 2 mm	10-20 cm	***	0.0099 (0.195) Epil	0.0101 (0.274) Emac	0.0126 (0.663) Acspp
Root weight	< 2 mm	0-10 cm	***	0.412 Emac	1.052 Epil	1.421 Acspp
Root weight	< 2 mm	10-20 cm	NS	0.296 Epil	0.389 Emac	0.532 Acspp
Root weight	total	0-10 cm	*	0.944 Emac	1.786 Epil	1.985 Acspp
Root weight	total	10-20 cm	NS	-4.572 (0.595) E.mac	-4.142 (0.774) Epil	-3.146 (0.878) Acspp

NOTE: i) * $P<0.05$; ** $P<0.01$; *** $P<0.001$; NS = not significant

ii) Species: Emac = *Eucalyptus maculata*; Epil = *E. pilularis*; Acspp = *Acacia* species

iii) Species are ranked in increasing order of magnitude; horizontal bars span the species whose means do not differ using LSD ($P<0.05$). Where transformations of the data have been made, the untransformed means are given in brackets.

For each species type, there were no differences in fine root length or weight between the winter and spring sampling periods. This may in part be due to the low number of degrees of freedom associated with each contrast.

7.5.3 Discussion

Given the spatial variability in root system development (Reynolds 1970), the field study confirms the conclusions of the glasshouse root growth studies. Within the important upper section of the soil profile, *Acacia* was more prolific in its production of fine roots than *E. pilularis* and *E. maculata*. Similarly, *E. pilularis* had more fine roots than *E. maculata*, and although this only occurred in the 0-10 cm soil horizon, it was in this section that the majority of fine roots were located. For example, the fine root length for combined winter and spring sampling in the 0-10 cm zone for *E. maculata*, *E. pilularis* and *A. mabellae* were 0.466, 0.894 and 1.856 cm cm^{-3} respectively. These values are likely to be underestimates because a proportion of the finer roots will have been lost when washing the soil cores. Carbon *et al.* (1980) found the mean rooting density in the sandy surface soils of *E. marginata* forest to be 7 cm cm^{-3}, but this included roots from all species present on the site. Rooting densities in young pine plantations are reported to be between 0.05 to 0.32 cm cm^{-3}, and in older plantations, 0.8 to 5.0 cm cm^{-3} (Nambiar 1983). Nambiar (1981) has speculated on the basis of a review of root configuration by Barley (1970), that rooting densities of less than 2 cm cm^{-3} do not provide significant competition between roots. However, the positive response of regrowth *E. maculata* to removal of surrounding *Acacia* competition (Chapter 5) was on the same site as this field root study, and suggests that rooting densities of the order reported here (2 cm cm^{-3}) may indeed influence the competitive ability of species. Similarly, Ashton (1975b) considered that the fine roots of the understorey species *Pomaderris aspera*, which appeared to have a rooting density of between 1-2 cm cm^{-3} (Nambiar 1981), could be a very important factor in its competition with *E. regnans*.

The study indicates that strategies for allocating photosynthates to root production for the three species may be different. Although based on a relatively small sample size and inherently variable data, this hypothesis is supported by comparing, from pooled data, the ratio of fine root weight to coarse root weight for the three species types in the 0-10 cm zone. For *E. maculata*, *E. pilularis* and *Acacia* species, the ratios were 0.77, 1.43 and 2.52 respectively. Thus, under field conditions *E. maculata* has, in addition to producing less absolute fine and coarse root weight, a tendency to produce relatively less fine root weight compared to coarse root weight than either *E. pilularis* or *Acacia*. The ratios suggest that there may be inherent morphological differences in the upper horizon root systems of the three species. This is supported by the pot trials which showed that in comparison to *E. pilularis* and *Acacia*, *E. maculata* developed a stronger vertical tap root, had fewer fine roots and first and second order laterals roots in the surface horizons, and allocated a higher proportion of photosynthates to root production at depth.

The distribution of fine roots in the regrowth stands further supports the view that *Acacia* may be better able than *E. pilularis* and *E. maculata* to acquire nutrients in limited supply, thus enhancing its competitive ability on such soils. Nambiar (1984) considers that even small variations in the size and vigour of roots during the establishment phase can have a large influence on growth. In a similar fashion, the quantitative pattern of root growth of barley is established during the first 2-3 weeks from planting (May *et al.* 1965). The differences in root systems may be particularly important where competition for resources has been intense - as is likely to have been the case on many sites following clearfelling. The sites where *Acacia* has proliferated and *E. maculata* occupies a sub-dominant canopy position could therefore reflect *E. maculata's* inability and *Acacia's* ability to gain rapid access to available soil nutrients.

While the vigour of regrowth *E. maculata* tends to be highly variable in the clearfelled forest, *E. pilularis* tends, in contrast, to form a dominant component of the regrowth forest wherever it occurs. Both the field and pot trials have shown that *E. pilularis* has a better developed upper horizon fine root system than *E. maculata*. Hence, the generally greater vigour of *E. pilularis* may in part be due to the ability of its root system to compete effectively with *Acacia* and other species for limited nutrients. As was stated in Chapter 5, Heinrich (1985) suggested that *E. pilularis* is able to compete effectively on phosphorus deficient soils because it is able to acquire phosphorus from an efficient network of fine roots and mycorrhizae. *E. pilularis* is also able to rapidly adjust both phosphorus deployment and growth rate to fluctuations in the soil phosphorus supply (Mulligan and Patrick 1985a).

In this study, there were no differences in fine root growth between the winter and spring sampling periods. Ashton (1976b) has suggested that the roots and mycorrhizae of *E. regnans* may grow throughout the year in central Victoria, provided that the soil does not dry out. Since temperatures on the south coast of N.S.W. are generally higher than in the *E. regnans* region, and rain may fall in any month, it is possible that root growth also continues through the winter months. Although root growth of *E. regnans* may occur at any time, there are two peak periods of production - in winter to spring, and in autumn after the break of the dry season (Ashton 1976b). Similarly, in *E. marginata* forest, root growth occurs in two peak periods - in spring (September-October) and following autumn rain (May-June) (Dell and

Wallace 1983). The sampling in the present study covered only the winter-spring period and may therefore be associated with continuing root growth.

The studies on root systems have necessarily been confined to relatively few species. Although not addressed in this study, the grasses are likely to have been strong competitors for soil nutrients and moisture following clearfelling. Bowen (1981) has suggested that the concentration of tree roots in the soil at any one time are usually an order of magnitude lower than for grasses, for example, some 2 cm cm^{-3} in soils for *Pinus radiata* and some 50 cm cm^{-3} in soil for *Poa pratense* in the surface soil. Both Webb *et al.* (1983) and Ellis *et al.* (1985) suggested that the growth check of *E. delegatensis* in highland Tasmania following clearfelling and burning is strongly influenced by the proliferation of grasses which, by virtue of dense root growth, compete strongly for plant resources. The development of grasses following the clearfelling operations on the south coast has been variable, but on many sites, intense. Part of this proliferation may have been due to the preference some grasses* show for wetter sites (e.g. *Lepidosperma*, *Lomandra*, *Gahnia*) and may have been induced by removal of a large transpiring leaf surface area which resulted in a rise in the water table. Because of *E. maculata's* relatively poorly developed upper horizon fine root system, this species may be at a greater disadvantage than others in its competition with grasses.

The role of mycorrhizae in the nutrition of the regrowth stands on Kioloa State Forest has not been examined. However, Chilvers and Pryor (1965) reported ectomycorrhizae on 147 species of *Eucalyptus* and suggested that all eucalypts are capable of forming mycorrhizae in association with suitable fungi. Other forest plants including species of *Acacia* and many woody shrubs may also be ectomycorrhizal (Warcup, 1980). Thus it is probable that many of the species in the regrowth stands, including *E. maculata*, formed associations with mycorrhizae.

* graminoids

7.6 SUMMARY OF CONCLUSIONS FROM ROOT STUDIES

The series of three root growth experiments in this chapter arose out of a need to identify some of the mechanisms which may have influenced the differential competitive responses of some of the more widely occurring regrowth species. In particular, whether there are any basic differences in root system development which might indicate differences in access to and acquisition of available soil nutrients and soil moisture.

The three root growth experiments have demonstrated clear differences in the root system configuration and morphology for a number of competing species found extensively in the regrowth forest. The major differences can be summarised as follows:

1. In long pots, *E. maculata* allocated relatively more of its root photosynthate deeper in the soil profile than several other south coast eucalypts and *A. mabellae*.
2. In long pots at the approximate field bulk density of surface soil, seedling *E. maculata* produced less fine root length and weight in the upper, and more in the lower part of the soil profile than either *E. pilularis* or *A. mabellae*.
3. In the upper 15 cm of long pots, seedling *E. maculata* produced a well defined main tap root and few first and second order laterals while *E. pilularis* and *A. mabellae* had a less well defined tap root and more lateral roots.
4. Under field conditions, *Acacia* regrowth species had considerably greater fine root length and weight than *E. maculata* in the important upper 20 cm of the soil profile. *E. pilularis* was intermediate between these two species.

The studies identify some of the component differences in root systems that may be of particular significance in determining differential competitive responses of species, and show that under field conditions, root development was consistent with that under glasshouse conditions. It is concluded that differences in the patterns of root growth associated with the south coast eucalypt species and an *Acacia* species may have an important bearing on their success in a highly competitive environment.

CHAPTER 8

GENERAL DISCUSSION AND CONCLUSIONS

It remains to draw together the findings of the study in order to assess whether the initial hypothesis can be accepted or rejected. Possible options for the continued management of these forests are discussed.

The hypothesis forming the basis of this study states that environmental factors and particularly soil nutrient supply, may be marginal for *E. maculata* at the establishment phase on some sites following clearfelling. This will be most critical where there is a rapidly developing stratum of secondary species. In order to investigate this, several questions have been addressed.

The first was that of regrowth stocking. Regrowth of *E. maculata* may be highly variable in response to logging. For example, the frequency of *E. maculata* regrowth stems may generally decline from upper to lower slopes, and in many cases, its vigour will as well. This may be due, in part, to the distribution of lignotuberous advance growth of *E. maculata*, which is less frequent, or absent, on lower slopes. Based on this observation, and on an examination of the physical features of the swelling at the base of the regrowth stem, it is likely that the stocking of *E. maculata* on lower slopes originated primarily from new seedlings, rather than from an advance growth pool. Alternatively, regrowth on upper slopes originated from both sources. The greater vigour and persistence of lignotuberous seedlings may be one reason why *E. maculata* has generally performed better on upper than lower slopes. Moreover, the eucalypt lignotuber may benefit from a period of 'preconditioning' under moisture stress. This effect may be most apparent on exposed upper slope sites - where, in general, the most vigorous *E. maculata* regrowth is found.

The second question addressed was that of spatial and environmental relationships of species and communities within the forest as a whole. The working hypothesis suggested that environmental factors delimiting species communities may be much the same as those responsible for the relatively poor performance of regrowth of *E. maculata* on some sites. Previous studies had suggested that the distribution of eucalypt species is associated with changes in soil fertility. A numerical analysis of site chemical information in this study confirmed this by showing that the vegetation gradient, rainforest → wet sclerophyll forest → dry sclerophyll forest → heath, is clearly associated with a decrease in soil nutrient concentrations. Within this generalized fertility gradient, *E. maculata* occupies a wide range of sites, extending from some of the higher fertility sites to those at the low to moderate fertility end of the spectrum. On the latter sites, there is an increasing occurrence of eucalypt species other than *E. maculata*, these perhaps being better adapted to soils of lower fertility.

Based on an appreciation of vegetation and environmental gradients, it was possible to establish that some of the clearfelled sites, and particularly those where regrowth of *E. maculata* has performed poorly, are towards the marginal end of *E. maculata's* fertility range; this is despite their occurrence on lower slopes where site fertility might be expected to be somewhat greater than on upper slopes. In this case, it seemed possible that, given the distribution and density of subsidiary species along the slope, competition for limited nutrients at the establishment and early successional stages might profoundly influence the way species responded to clearfelling. Thus, if it could be established that *E. maculata* tended to lose its competitive ability where nutrient supply is limited, it would lend validity to the concept that the nutrient status of the soil at the early development stage can influence the composition and dynamics of the stand. This concept was next examined in a series of glasshouse and field nutrient studies comparing the growth of *E. maculata* with other eucalypt species and an *Acacia* species. The glasshouse studies showed a number of important features.

1. There are few inherent growth differences between four south coast eucalypts - which might have helped to explain the much larger differences between species in the regrowth forest.
2. At lower nutrient levels, *E. pilularis* has a large, and *E. maculata* a small relative growth rate of height. However, with increasing nutrient supply, the relative growth rate of height of *E. maculata* increases while that of *E. pilularis* declines.
3. While the net assimilation rate of *E. maculata* and *E. pilularis* are similar where grown in a low nutrient medium, that of *E. maculata* is consistently better as nutrient supply increases.
4. While *Acacia mabellae* may grow substantially better than *E. maculata* in a low nitrogen environment, *E. maculata* will outgrow *A. mabellae* where nitrogen is added.

These studies point to the possibility that relative to other species in the regrowth forest, *E. maculata* has a poor competitive ability where nutrients are in limited supply, but that as nutrient supply improves, it becomes increasingly competitive.

A field study on the response of eucalypt seedlings to fertilizer also highlighted some points which may help to explain *E. maculata's* poor competitive ability on some sites.

1. Where *Acacia* has developed in conjunction with other regrowth species, nutrients other than nitrogen, and particularly phosphorus, may become factors limiting growth - as shown by the large responses of seedlings of *E. maculata* and

E. pilularis to phosphorus rather than nitrogen. This suggests that over a period of years, the nitrogen-fixing *Acacia* may have contributed substantially to the pool of available soil nitrogen.

2. In the field seedling study, irrespective of the nutrient treatment, *E. pilularis* grew substantially better than *E. maculata*. This may have been due in part to the superior growth of *E. pilularis* on these soils, and to the adverse effect on *E. maculata* of the fungus *Ramularia pitereka* - a pathogen specific to species from the subgenus *Corymbia*. It follows that the fungus may also have affected the growth of seedling *E. maculata* following clearfelling.

3. Although *E. pilularis* performed best in total growth, *E. maculata* responded consistently better, in relative terms, to additions of phosphorus, adding weight to the hypothesis that *E. maculata* requires a reasonable level of nutrients for adequate growth.

4. The results of this field seedling study contrast somewhat with the results of a study by J.D. Williams and D.M. Halsall on a site adjacent to the clearfelled area, and cleared specifically for the study. They found that seedling *E. maculata* responded very strongly to nitrogen, suggesting that this nutrient in particular, may have been very important in limiting the development of *E. maculata* following clearfelling.

The non-eucalypt component of the regrowth forest may have a large impact on the emergence of *E. maculata* through the regrowth canopy. This is demonstrated in a study which showed that *E. maculata* under an *Acacia* canopy could not respond to fertilizer alone, but could respond appreciably once released from the restrictive effect of surrounding *Acacia*. Moreover, once this was done, *E. maculata* was able to show a further response to fertilizer. It seemed that *E. maculata* may be highly sensitive to root competition, and only when this is removed is it able to respond to a good nutrient supply.

The findings of J.D. Williams and D.M. Halsall, and the large positive responses of *E. maculata* to nitrogen in the pot study, led to an examination of the potential rates of nitrogen mineralization in soils from a range of sites adjacent to the clearfelled stands. Because these sites may reflect the condition of the nitrogen pool prior to clearfelling, such a study may give clues about nitrogen availability to the emerging regrowth stands. The study showed that although all soils examined mineralized, those at the wet sclerophyll end of the vegetation gradient were capable of producing far more mineral nitrogen than those at the dry sclerophyll end, and the process proceeded more completely to the NO_3-N stage. In the hope of showing that mechanical site disturbance associated with logging may stimulate mineralization, the effect of soil disturbance was examined. However, this treatment failed to stimulate any further production of mineral nitrogen. The effect of soil heating was also examined to assess the possible contribution of a regeneration burn to mineralization processes. Heating markedly stimulated mineral nitrogen production in all soils, with the greater relative responses being in soils from the dry and intermediate sclerophyll sites. Thus the more open sclerophyll types have restricted mineralization which can be stimulated appreciably by soil heating. It may be concluded that in the absence of a regeneration burn, availability of soil nitrogen may have been an important factor limiting the development of regrowth *E. maculata*, particularly towards the nutritionally marginal range of this species, and on the lower slopes where advance growth does not accumulate.

Another and perhaps very important factor affecting the development of species in a regrowth stand concerns differential access of plants to soil resources. This may be related to differences in the form of species root systems. From an examination of the root morphology of a number of species from Kioloa State Forest, several factors have been determined which may have a bearing on the development of *E. maculata*.

1. *E. maculata* allocates relatively less root photosynthate in upper, and relatively more in lower sections of the soil profile, than several other south coast eucalypts.
2. *E. maculata* has less fine root length than *E. pilularis* and particularly *A. mabellae* in the surface soil horizons.
3. In the surface horizons, *E. maculata* develops a well-defined tap root, while *E. pilularis* and *A. mabellae* have more poorly defined tap roots and more coarse lateral roots.

The findings indicate that compared to other successional species in the regrowth forest, *E. maculata* may have limited access to soil nutrient elements in the surface soil, where most nutrients accumulate. In situations where competition for nutrients is severe, or where nutrients are in limited supply, for example within parts of the Kioloa regrowth forest, *E. maculata* could lose its competitive edge to other better adapted species. The deeper-rooting ability of *E. maculata* may however, provide it with a competitive advantage where moisture becomes periodically limiting in the surface soil.

In summary, *E. maculata* may be maintained as a dominant species in much of the undisturbed forest through a delicate balance of environmental factors and species interactions. However, the character of the *E. maculata* seedling may be largely unsuited to cope with the type of competitive environment created by clearfelling. In particular, it would appear that *E. maculata's* requirement for a reasonable nutrient supply, and its relatively poorly developed fine root system may restrict its potential for rapid development where available nutrients are limited, or competition for them is severe.

The Silvicultural Management of *E. maculata* Forests

The clearfelling of *E. maculata* stands on Kioloa State Forest was undertaken with the purpose of converting relatively stagnant forest into productive even-aged stands. However, in using this technique, there has been a failure to appreciate the possible variation in response of *E. maculata* to differences in site and other environmental factors.

In nature, the *E. maculata* type is one of those which normally relies on an established lignotuber pool, with occasional accession of new seedlings to maintain that pool, and thus the stand's regeneration potential. *E. maculata* is one of the more fire resistant species (McArthur 1968) and would rarely have been 'destroyed' over large areas. Regrowth probably developed periodically in patches following death or weakening of senescent trees. It may therefore be inappropriate to radically depart from natural processes by clearfelling. Under the clearfelling regime, reliance must be placed on both new seedlings and established lignotubers for regeneration. However, for many of the sites in the study area, this reliance was unjustified, and its consequences are reflected 12-18 years later in the highly variable distribution, stocking and vigour of regrowth.

It follows that in order to achieve the objective of improving the productivity of the forest, a silvicultural schedule is required which is more sympathetic to the ecological attributes of *E. maculata*. Added to this is the fact that these forests have recently been placed on the Register of the National Estate, and this might preclude the use of clearfelling techniques with associated intensive site disturbance.

Furrer (1971) suggests on the basis of his silvicultural studies on *E. maculata* that there is good reason for the separation of wet and dry sclerophyll forest into two distinct entities for silvicultural treatment. Within dry sclerophyll sites, silvicultural practice based on the presence of a lignotuber pool, and simple site treatments to release that pool, will give good results for many sites. This may not necessarily be the case on wet sclerophyll sites.

Given the silvicultural constraints imposed by the inclusion of these forests on the Register of the National Estate, it may be necessary to consider setting aside completely from logging, those wet sclerophyll areas where a lignotuberous advance growth pool is absent, and where new seedling establishment would be difficult to obtain from a mild site treatment. Alternatively, where the wet sclerophyll forest is to be harvested, a silvicultural regime might be required where logging is followed immediately by mechanical site disturbance to prepare an adequate seedbed, and to check the development of understorey species until the new seedling growth is well established. Even then, there is no guarantee that *E. maculata* will have the capacity to become sufficiently well established and to develop sufficient vigour to out-compete other developing species. Alternatively, it may be more appropriate to use a two-stage method of cutting, in which as much as half the overwood is retained, the site treated, and a lignotuber pool develops beneath the residual canopy. The retention of the overwood for some time may help suppress subsidiary species while seedlings become firmly established.

From a silvicultural perspective, the use of fire on wet sclerophyll sites may provide the necessary nutritional stimulus for *E. maculata* regeneration to gain and maintain dominance over concomitantly developing vegetation. Certainly the results from Chapter 6 support this view. However, in using fire, there is the very real danger of stimulating prolific fire weed species, suggesting that fire disturbance should be approached cautiously.

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Appendix I

A description of statistical procedures used in the thesis.

Analysis of Variance (ANOVA). ANOVA was performed using GENSTAT and is a procedure by which the variation embodied in the data of the sample may be resolved into component variations due to treatment effects. Each of the components yields an estimate of the population variance; and these estimates are tested for homogeneity by means of the *F* table (Weatherburn 1962). The basic assumptions of ANOVA, normality of the distribution of errors and homogeneity of variance (Neter and Wasserman 1974) were tested by examining the residual scatter plots, and if warranted, a $\log_e$ or square root transformation of the data was made. The transformed data reduces the errors due to scaling (Prakash 1985). Outliers in the data were identified from the residual analysis. These were removed and treated as missing values. Because the treatment levels were fixed, Model I of the ANOVA was used (Snedecor and Cochran 1967). Treatment means were compared by a least significance (LSD) test using the value of standard errors of difference of means (Steel and Torrie 1960) and two-tailed student's 't' value with a probability level of P<0.05.

Regression Analysis. The regression analysis was performed by least squares method using GLIM. The relationship between variables was tested by the deviation method (Neter and Wasserman 1974) which involves fitting models beginning with linear and testing the variation with higher models. The model selected was that which best explained the variation in the data and was aided by examining the magnitude of the R^2 value and the residual analysis. Simplicity of the model was also a criterion for selection.

Principal Coordinate Analysis (PCO). PCO was performed on GENSTAT and is an ordination technique which reduces the dimensionality of a set of attribute data with as little information loss as possible so that the configuration of the data can be examined readily (Turnbull 1979). Noy-Meir (1971) states that this method involves the replacement of a set of m variables, partly covarying over n individuals (sites), by a smaller set of p new variables or coordinates (vectors) which efficiently express most of the observed variation and covariation in the original variables. Most ordination methods simplify the relationships between the individuals and can be represented in simple graphical form (Turnbull 1979).

The operations of PCO can be summarized as follows - there is an m x n matrix say S where the (ik)th element a_{ik} is a measure of similarity between the ith and the kth individual. By a sequence of mathematical operations (involving extraction of latent roots and latent vectors) (Stiteler 1979), a simplified representation of individuals in a reduced number of dimensions is arrived at. The complexity of many attributes is simplified by attribute integration using standard mathematical functions. The differences between some of these functions have been summarized by Reddy (1983). The distance coefficients (measure of distance or dissimilarity) are of two types: non-standardized (e.g. Euclidean metric, Mean character distance) and standardized (e.g. Canberra metric, Gower metric). Where the similarity matrix is obtained with population range or standard deviation in the denominator (i.e. most standardized measures), there is no change in the original order obtained by the numerator. Therefore, it works as a true standardization procedure, retaining the original order shown by the matrix.

For analysis in Chapter 3, computational procedures followed those developed by Gower (1966). The method relies upon a similarity/dissimilarity matrix between individuals (sites). In contrast to the more commonly used principal components analysis, PCO relies on a data matrix other than the raw attributes matrix, and unlike the former technique, the analysis is invariant under changes of scale in the units measured. Thus, PCO has the advantage of being able to cope with qualitative as well as quantitative attributes. However both techniques suffer from difficulty in interpretation as vectors do not contain the physical meaning (Reddy 1983).

The Gower metric was used for the analysis primarily because this measure had been incorporated into the 'PCO' algorithm contained on the GENSTAT package. It takes the form:

$$S_{ij} - 1 - \mathrm{MOD}(x[i] - x[j])/\mathrm{Range}$$

Conjoint absences (zero matches) for any attribute do not contribute to the expression. This stems from the rationale that mutual absence is not considered to be evidence of similarity.

Output from the GENSTAT 'PCO' directive includes the percentage variance explained by each principal coordinate (calculated directly from the corresponding latent root value) up to the number of coordinates specified, and a list of the latent vectors (coordinate scores) for each of these principal coordinates. The latent roots are the variances of the principal coordinates and the latent vectors give the coordinates of individuals in the reduced space. Latent vectors are orthogonal (GENSTAT 1977).

A scatter diagram of individuals in two dimensional space is produced by plotting the first principal coordinate against the second principal coordinate, facilitating a visual representation and examination of the data. This can be done for any combination of principal coordinates, but the number of plots is usually determined by the percentage variance accounted for by each principal coordinate.

The graphs display the spatial relationship of individuals with respect to the data variables employed in the analysis. However, because this is a representation of a potentially complex multi-dimensional configuration of points, the gaps between individuals will always signify separation at least as large as the real separations, whereas the lack of such gaps will not necessarily mean a similar lack of real separations (Orloci 1978).

An additional facility used in PCO analysis relates a principal coordinate back to the original attributes so that principal coordinates obtained from a similarity matrix can be interpreted by relating them to the attributes of the data matrix. For each attribute, an approximated pseudo-F-statistic is computed, and serves to rank the attributes in order of importance of their contribution to the vector.

A common assumption of PCO is that the data structure is linear. It means that the method cannot respond to non-linear trends (Orloci 1978). Most ecologists would not expect species to interact or respond to an environmental gradient in a linear manner, though most ordination methods including PCO assume this (Austin 1971). In fact, the response of a species to environmental factors is more often a convex (or bell-shaped) curve with a maximum in the middle (the species optimum) (Noy-Meir 1971). Ordination tends to be inefficient in direct proportion to the degree and type of non-linearity present as it reproduces the original non-linear point configuration occurring in the full dimensions (Orloci 1978).

Appendix II

Mineral composition of full (i.e. single strength) Hoaglands (No. 2) solution (Hoagland and Arnon, 1938) applied in Experiment 1 Chapter 2, and Experiment 2 Chapter 4.

Compound Hoaglands No. 2	Conc. of stock	ml. stock/litre
$NH_4H_2PO_4$	1M	1
KNO_3	1M	6
$Ca(NO_3)_2.4H_2O$	1M	4
$MgSO_4.7H_2O$	1M	2
Micro-nutrients		1
Fe Edta		1
NaOH	0.1M	5

NOTE: (i) Micro-nutrient Stock Solution

2.86g boric acid H_3BO_3; 1.81g manganese chloride $MnCl_2.4H_2O$; 0.22g zinc sulphate $ZnSO_4.7H_2O$; 0.08g copper sulphate $CuSO_4.5H_2O$; 0.02g molybdic acid $H_2MoO_4.H_2O$; 1000 ml mineral free water.

(ii) Chelated ferric iron stock solution (Fe Edta)

Dissolve 16.65g diamino-ethane-tetra-acetic acid disodium salt in 250 ml mineral-free water. Dissolve 12.45g AR grade ferrous sulphate ($FeSO_4.7H_2O$) in 250 ml mineral-free water. Mix the two solutions and aerate overnight to produce the stable ferric complex.

(iii) Hoaglands No. 2 solution contains the following concentrations (mg/l) of elements: N 211.7, P 32.2, K 235.9, Ca 160.9, Mg 48.3, Na 3.61, S 66.7, Cl 0.143, Fe 5.007, B 0.105, Co 0.005, Mn 0.111, Cu 0.013, Zn 0.02, Mo 0.012.

(iv) Hoaglands No. 1 solution has nitrogen in nitrate (NO_3-) form only. KH_2PO_4 is substituted for $NH_4H_2PO_4$. Otherwise the compounds are the same as for the Hoaglands No. 2 solution, although amounts of stock/litre vary: 1 ml KH_2PO_4, 5 ml KNO_3, 5 ml $Ca(NO_3)_2$.

(v) References:

1. Hoagland and Arnon (1938); 2. Hewitt (1966); 3. Awang (1977); 4. Asher (1978); 5. Mowatt (1981).

Appendix III

Mineral composition of nutrient solution applied in Experiment 3 Chapter 4. Based on compounds used by Halsall *et al.* (1983). Minor elements were supplied according to Hoagland and Arnon's No. 2 solution (Hewitt, 1966).

Compound	Conc. of stock	ml stock/litre	mg/l (ppm) of each element
NH_4NO_3	1M	4.5	N 126
$NaNO_3$	1M	6.0	N 84, Na 138
$NaH_2PO_4.2H_2O$	1M	1.0	P 31, Na 23
$CaCl_2$	1M	4.0	Ca 160, Cl 284
K_2SO_4	0.5M	6.0	K 235, S 96.4
$Mg\ SO_4.7H_2O$	1M	2.02	Mg 49, S 64.6
Micronutrients			
Fe Edta			

NOTE: (i) Elements for micro-nutrient and Fe Edta solutions are described in Appendix II

(ii) The compounds NH_4NO_3 and $NaNO_3$ were excluded for solutions not containing nitrogen. $NaH_2PO_4.2H_2O$ was excluded for solutions not containing phosphorus.

(iii) The concentration of sodium varied where nitrogen or phosphorus was excluded from the nutrient solution. Hewitt (1966) states that variations in sodium above minimal concentrations are considered likely to have the least effect of the possible variants that might be used to obtain the desired nutrient composites.

(iv) 0.1M NaOH was used to adjust the ph of each solution to about 6.5.