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# PHYSIOLOGICAL ECOLOGY
# AND
# VEGETATION DYNAMICS
# OF
# NORTH QUEENSLAND UPLAND RAINFOREST – OPEN FOREST ECOTONES

Thesis submitted by
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in August, 1987
for the Degree of
**DOCTOR OF PHILOSOPHY**
in the Department of Botany
at James Cook University of North Queensland.

Plate 1. Boundary between rainforest (left) and tall open forest dominated by *Eucalyptus grandis* (right) at the eastern end of Lake Tinaroo on the Atherton Tablelands.

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Gordon A. Duff, 28/5/87.

# DEDICATION

I dedicate this thesis to the memory of

**WILLIAM R. BIRCH**

Who supervised this project during the initial years.

May he rest in peace.

# ABSTRACT

The transition between rainforest and open forest in the highlands of north Queensland is marked by an ecotonal assemblage dominated by the tall open forest species *Eucalyptus grandis*. This thesis examines the autecologies of a range of species from open forest, ecotone and rainforest assemblages, in relation to the dynamics of the rainforest - open forest boundary.

Rainforest - open forest transitions were investigated at Kirrama (18° 10' S, 145° 40' E) and Paluma (19° 01' S, 146° 15' E) in the highland rainforest belt of north Queensland. Structure and floristic composition were investigated at these sites, and changes in light intensity, soil moisture and microclimate across the rainforest boundary were recorded. In the transition from rainforest to open forest, photon flux density increased dramatically. Temperature range and saturation deficit also increased, while humidity and soil moisture availability decreased under most climatic conditions.

Water relations of a range of species were studied by measuring plant water potential ($\psi$) of mature forest trees in the field, and $\psi$, growth and competition of seedlings in the glasshouse. The greatest degree of drought tolerance was found in medium open forest species such as *Eucalyptus intermedia*, which also showed the lowest water potential values in the field. Water relations were identified as one factor limiting the movement of tall open forest and rainforest species into open forest.

Responses of a range of medium open forest, tall open forest, secondary and primary rainforest species seedlings to variations in light and mineral nutrient availability were investigated in the glasshouse. Growth experiments were conducted on these seedlings along shade gradients using three different nutrient treatments. Seedlings were grown in isolation and in species mixtures in separate experiments. Open forest species proved to be the most shade intolerant, and primary rainforest species exhibited the slowest growth rates and the greatest shade tolerance. Tall open forest and secondary rainforest species had the highest growth rates and the most substantial responses to variations in mineral nutrient concentrations. Rainforest species were more variable in their responses to light availability, and a hypothesis relating this variability to the heterogeneity of the light environment in rainforest or in the ecotone was proposed. Competition experiments conducted under shade gradients determined which species were most likely to become established at different positions on the ecotone, according to growth rate and shade tolerance. Resource allocation in seedlings was used to classify the species studied into groups, and this classification corresponded closely with the shade tolerances and growth characteristics discovered in the growth experiments.

Regrowth and regeneration after a low intensity fire at one of the study sites was investigated, demonstrating the resilience of the rainforest margin against the intrusion of fire. Open forest species recovered rapidly from the effects of fire, with coppicing as the main form of regeneration by fire damaged individuals. The effects of frost on rainforest and open forest species were examined, showing the faster growing rainforest pioneer and edge species to be the most susceptible to sub zero temperatures. An interaction between frost and subsequent fire was proposed, and evidence for this effect discussed.

Germination characteristics were investigated for a range of species. Open forest species had the most rapid germination and the greatest susceptibility to fungal attack. Dormancy was found in the seeds of rainforest pioneer species, while the secondary rainforest species investigated germinated rapidly and were successful in both rainforest and open forest substrates.

A model of vegetation dynamics on the ecotone incorporating the effects of disturbance (through fire, cyclones, frost and drought), climate, microenvironment, light, germination and dispersal was formulated. The model showed the mechanisms by which the rainforest edge advances into open forest, remains stationary or retreats as a result of severe disturbance. Fire was the critical factor controlling the position of the ecotone, while light intensity and water relations regulated the establishment and distribution of species across the ecotone.

These conclusions can be coupled with the results of previous investigations by other researchers to formulate forest management strategies for forest boundary systems and small rainforest isolates in highland areas of north Queensland.

# ACKNOWLEDGEMENTS

According to the rules and regulations dictated by the powers that be, a thesis such as this must be the sole work of the candidiate. This, I'm sure, is only partly true of any such dissertation. This thesis would not have reached completion in it's present form but for the invaluable contributions made by the following people.

Firstly, I would like to thank my supervisors, Betsy Jackes and Geoff Stocker, for their patience, friendship, generosity, enthusism, guidance and perserverance. I have enjoyed working with these two people immensely, and hope to continue the association in the future.

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Mrs Elaine Sommer gave generously of her time and energy to type this thesis, and I am especially grateful for her accuracy, and tolerance of my handwriting.

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"Winnie-the-Pooh sat down at the foot of the tree, put his head between his paws, and began to think."
(Milne, 1926).

## 1.1 OBJECTIVES

The abrupt transition between rainforest and open forest in the Queensland tropics is an unrivalled example of the dynamic nature of tropical plant communities. Domin (1911) was so impressed with the rainforest - open forest boundary that he wrote "The line of demarkation between them is most distinct, a fascinating phenomenon unique in the whole world."

It was the objective of this study to A:-examine the transition zone environment, B:-to identify the physical and biotic factors controlling the dynamics of the transition zone vegetation, C:-to quantify the responses of the plants in open forest, ecotone and rainforest communities to changes in key environmental factors and D:- to model the vegetation dynamics of the ecotone. Species used in this study were chosen as examples of medium open forest, tall open forest and early and late successional rainforest assemblages, representing the range of plant types found across the ecotone.

Unwin (1983) used a synecological approach in studying the dynamics of the rainforest - open forest transition. This study differs from that of Unwin by examining the autecologies of species found in plant assemblages making up the transition from mature rainforest at one extreme of the ecotone to medium open forest at the other.

In the light of current resource utilization in north-east Queensland, management of forests is becoming increasingly important, and may be critical to the survival of some of our unique plant communities in the near future. A viable model of rainforest boundary dynamics should provide useful insights for forest managers, who need to know the relative stability of natural and artificial ecotones.

## 1.2 THE RAINFOREST OPEN FOREST ECOTONE: DEFINITION, AND TERMINOLOGY USED IN THIS THESIS

'Rainforest' as used in this thesis follows the definition given by Webb and Tracey (1981) viz. "The canopy is closed and the trees densely spaced, in contrast to the open and generally scattered sclerophyllous vegetation that covers most of the forested areas of the continent in the moister coastal and subcoastal zones, but mainly in the east. In tropical and subtropical rainforests there are three or more tree layers, with or without emergents." Webb and Tracey (1981) identified characteristic life forms distinguishing rainforest from other forests including combinations of epiphytes, lianes, certain root and stem structures, certain tree ferns and palms, and the absence of annual herbs on the forest floor. All assemblages containing species of *Eucalyptus*, *Allocasuarina* and *Melaleuca*, and all but a few species of *Callitris*, *Acacia* and *Tristania*, i.e. species which do not regenerate within a well developed or slightly disturbed canopy of closed forest, are excluded by the definition.

Specht (1970) defined "open eucalypt forest", abbreviated in this thesis to "open forest", as being characterized by tree heights from 10 m to 30 m +, with a foliage projective cover of 30 to 70% in the upper stratum over a grassy understorey. *Eucalyptus* is, by definition, the dominant genus. Open forest in this study is subdivided into "medium open forest", with tree heights from 10 to 30 m, dominated by *Eucalyptus intermedia* and including *E. tereticornis*, *Allocasuarina torulosa*, *Banksia integrifolia* and *Lophostemon suaveolens*, and "tall open forest" dominated by *Eucalyptus grandis* with tree heights from 30 to >50 m. Tall open forest understorey is usually grass dominated with varying proportions of sclerophyllous shrubs and young rainforest species.

"Ecotone", "boundary" and "transition" are terms used to describe the interface between rainforest and open forest. Because of the dynamic and variable nature of this interface, a more rigid definition is neither possible nor practical. An ecotone is understood to be the transition zone between two different community types, but it could be argued that the ecotone itself is a third and distinct community type, often containing species found in neither rainforest nor open forest. A more detailed description is given in Chapter 2 which contains physical and floristic descriptions of ecotones found at two study sites.

Tree species names used in this thesis follow those of Hyland (1982). Classification of rainforest types follow those used by Tracey (1982).

The geographical region covered by the title of this thesis, the upland areas of north Queensland, includes forested areas between Townsville and Cooktown (fig. 1.1) at altitudes greater than 500 m above sea level.

## GLOSSARY OF ABBREVIATIONS:

dbh: Diameter at breast height (1.3 m)
dbhob: Diameter at breast height over bark
FSU: Full sunlight
PAR: Photosynthetically active radiation (400-700 nm wavelength)
PMS: Plant moisture stress
PPFD: Photosynthetic photon flux density
RH: Relative humidity
$\psi$: Total matric water potential

## 1.3 DISTRIBUTION OF RAINFOREST IN NORTH QUEENSLAND

Tropical rainforest in north Queensland occurs in a series of scattered and isolated patches of various sizes surrounded by open forest and land modified for grazing and agriculture (fig. 1.1). Because of the small size of many of these isolated pockets, a high proportion of the overall area under closed forest is accounted for by transition zone assemblages. Unwin (1983) noted that proper management of boundary dynamics may be critical to the maintenance and, in the case of the smaller patches, survival of these closed forest communities.

Differentiation between rainforest and open forest was originally attributed to either soil parent material or soil nutrient status (Baur, 1957; Moore, 1959; Tracey, 1969; Webb, 1969). However, Webb and Tracey (1981) concluded that although rainforest vegetation favoured high fertility, basaltic soils, closed forests could be found on a wide range of soil types and fertility levels. Stocker and Unwin (1986) proposed that fertility differences

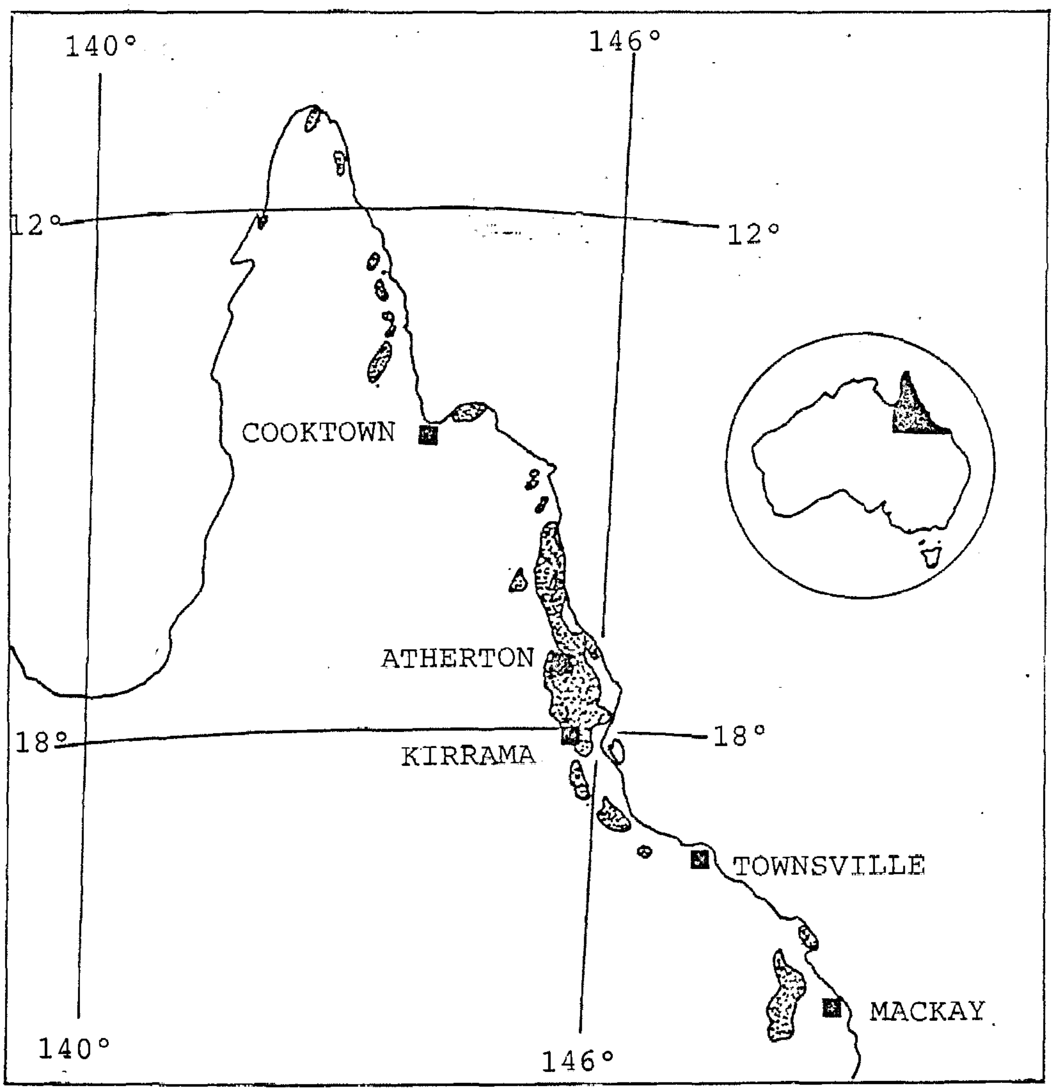

Figure 1.1. Map of north Queensland showing the distribution of rainforest (shaded areas) Scale 1:10,000,000. Adapted from Unwin (1983).

were more likely to influence vegetation dynamics on the rainforest edge by influencing fire behaviour. They concluded that poorer soils favoured regeneration of flammable vegetation and drier microenvironments, and regeneration on richer soils was less prone to subsequent fire. Results from this study indicated that neither edaphic factors (Chapter 2) nor rainfall (Chapter 3) can account for the fine scale differentiation between rainforest and open forest in north Queensland.

In southern mainland Australia and Tasmania, Jackson (1968) and Mount (1964) both identified fire as the main factor controlling the respective distributions of cool temperate rainforest and open eucalypt forest. In northern Australia, fire and the effects of the seasonal climate on fuel were recognized as important in controlling the distribution of closed and open forest types (Stocker, 1966; Stocker and Mott, 1981; Gillison, 1983; Unwin, 1983) (Chapter 5). Interactions between topography and fire were identified by Unwin (1983) as being important in determining the distribution of closed forest with respect to open forest.

## 1.4 EXPERIMENTAL APPROACH AND PRINCIPLE EXPERIMENTAL SPECIES

Factors controlling the dynamics of rainforest and open forest are many and interrelated, so that a number of different approaches were needed to derive a comprehensive model of the ecotone. Ideally, studies carried out over at least a number of decades of selected sites would provide all the information necessary to predict changes in the species composition, position and structure of the ecotone, but the lifespans of the organisms involved mostly exceed that of the average ecologist, so short term experimental work was the only available compromise. Unwin (1983) provided data covering the factors controlling the behaviour and effects of fire on the ecotone and the mechanisms of reestablishment in the ecotone following disturbance by fire. In this study, the autecologies of some of the species mentioned by Unwin (1983) were examined with respect to light, water relations, nutrient availability, competition and other forms of disturbance such as drought and frost.

Sites selected for pilot studies of the floristics and structure of the rainforest - open forest ecotone were also used to examine microclimatic changes accompanying the transition in vegetation types. From the floristic data obtained from these sites and from discussions with CSIRO personnel (G.C. Stocker, G.L. Unwin and J.G. Tracey) species were selected for detailed autecological studies.

Two species chosen as being representative of medium open forest were *Eucalyptus intermedia*, the dominant tree species, and *Imperata cylindrica*, one of the main grass species. *E. grandis* was the obvious candidate representing tall open forest. *Acacia mangium*, a prominent tree species from young rainforest growing on low nutrient soils, and *Eucalyptus torelliana*, a eucalypt species restricted in distribution to the rainforest edge, also generally found on low nutrient soils, were also selected.

*Alphitonia petriei* is an almost ubiquitous pioneer tree species common on disturbed rainforest margins such as road edges, and frequently forms relatively short lived almost monospecific stands on recently cleared rainforest sites. *Toona australis* is a fast growing secondary rainforest canopy species, commonly found on high fertility soils in ecotones and rainforest on the Atherton tablelands. *Flindersia brayleyana* is another fast growing secondary rainforest species found in the rainforest canopy on a range of soil types. *Neolitsea dealbata* is a conspicuous small tree species, common in both the rainforest understorey and on the rainforest edge on a large range of sites.

*Argyrodendron peralatum*, *Syzygium fibrosum* and *Syzygium wesa*, three primary rainforest canopy species were studied, . All are slow growing, shade tolerant species and can reach heights in excess of 30 m in areas of high rainfall and intermediate to high soil fertility.

Experiments were carried out mainly on these species, depending on seed or seedling availability and the presence and accessibility of adult trees in field experiments. When space for experiments in the glasshouse was limited, or experimental design reduced the number of species that could be examined, representatives of each group of species were selected. The species described are all trees, with the exception of *Imperata cylindrica*, and represent the complete range from medium open forest to mature rainforest. While it is recognized that shrubs, herbs, vines, ferns, epiphytes and lianes are all important elements of the main forest types, it was impractical to include a greater number of species in the experiments. The high species diversity of rainforest in particular meant that selection of species to be examined in the experiments was somewhat arbitrary, but it was beyond the scope of this study to examine the ecophysiological responses of >800 tree species.

Studies of water relations were conducted in the field on adult trees and under glasshouse conditions on tree seedlings. Plant water potential was measured using the "pressure bomb" described by Waring and Cleary (1967), and these experiments are described in Chapter 3.

Experiments on seedling growth under a range of light and nutrient regimes were conducted in the glasshouse (Chapter 4). A new approach to light intensity experiments was adopted, using a continuous shade gradient rather than several discrete shade regimes. These experiments studied seedling growth rates, survival, interspecific competition and species variability. The results obtained are applicable to the studies of both ecotone dynamics and gap phase regeneration in rainforest.

Germination and establishment experiments were conducted under laboratory conditions, and the effects of frost and fire were studied in the field (Chapter 5). While these experiments and field observations are diverse, they are all interrelated and the results combine to form a picture of the factors controlling the vegetation dynamics of north Queensland upland forest types, and the species responses to variations in these factors. The final chapter of this thesis ties the various aspects examined together in a model of rainforest - open forest ecotone dynamics.

# CHAPTER 2

# PHYSICAL CHARACTERISTICS AND AND FLORISTICS OF THE RAINFOREST - OPEN FOREST ECOTONE

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"I've been finding things in the Forest," said Tigger importantly. "I've found a pooh and a piglet and an eeyore, but I can't find any breakfast."
(Milne, 1926)

## 2.1 INTRODUCTION

This chapter describes the physical, structural and floristic characteristics of the study sites used for experiments and data collection in the field. Although most of this thesis evaluates the eco-physiological attributes of the species found in and bordering on the upland rainforest - open forest interface, a complete understanding of the vegetation dynamics of this ecotone requires a community / environment study as well as mechanistic analysis of the processes which take place within component species of each community.

Only one major study on the floristics, physical parameters and community dynamics of the Australian tropical rainforest - open forest ecotone has been attempted (Unwin 1983). However, many studies have been conducted in temperate Australia, where the emphasis has been on the effects of climate, edaphic factors and disturbance regime on the distributions of rainforest and open forest, and changes in these communities through time (Chapter 1).

Rainforest - open forest across boundaries are accompanied by marked changes in the environment as well as the more obvious variations in floristics and structure. Microclimatic factors such as light intensity, temperature maxima and minima, cold air drainage patterns and incidence of frost, local wind speed, relative humidity and soil moisture availability, vary as a direct result of the changes in vegetation. Physical properties of the soil, surface nutrient content and quantity and nature of litter also differ. In some cases, topography, soil type and parent material also vary with the transition in vegetation, as can rainfall and other macroclimatic factors in the case of broad ecotones. Finally, the nature and quantity of combustible fuel, and the probability and intensity of fire, also change dramatically in the transition from closed to open forest.

Comprehensive descriptions of physical environmental changes, vegetation structure and floristic changes across rainforest ecotones near Herberton (17° 23' S, 145° 23' E) were given by Unwin (1983).

## 2.2 DESCRIPTION OF STUDY SITES

Several criteria were used to select suitable sites for field studies; they had to be close to Townsville and accessible by road during the tropical "wet season". They were also selected so as to provide a degree of contrast with sites described by Unwin (1983).

The main area chosen for this study was located on the western side of the Kirrama Range (18° 40' S, 145° 44' E) (fig. 2.1) where three sites were selected (Kirrama Sites 1,2 and 3)(fig 2.2). A second study area was located near Paluma (19° 14' S, 146° 17' E) (figs 2.1 and 2.3).

Kirrama site 1 was located on an eastern facing 5° slope with the rainforest on the western side, the ecotone running along an approximate north - south line. Site 2 was similar in aspect and vegetation distribution, but on a steeper 7 - 10° slope. Site 3 was located on a 5° north-eastern slope with the transition from rainforest to open forest occurring from south east to north west (fig. 2.2). At all three sites the transition from rainforest to open forest occurs over a narrow ecotone, generally between 5 and 20 m in width.

Soils in the area are derived from granites, acid brownish yellow to brown loams to clay loams with weak to moderate structure. Rock outcrops are rare, and soil type is uniform throughout. Forests in the area were selectively logged on several occasions between 1945 (when vehicle access was first established) and 1965 (Queensland Department of Forestry, Cardwell).

The Paluma site was located approximately 5 km west north west of Paluma on the road to Hidden Valley. The Paluma ecotone represented a broader transition from rainforest, through tall *Eucalyptus grandis* over a closed subcanopy of rainforest species, to tall open forest and finally open forest. The ecotonal area dominated by *Eucalyptus grandis* is approximately 600 m in width on a gentle western facing slope. Soils are acidic loams and acidic clay loams which show little profile differentiation. They overlie rock at shallow depths with occasional granite outcrops. Again, no major change in soil type occurs in the transition from rainforest to open forest.

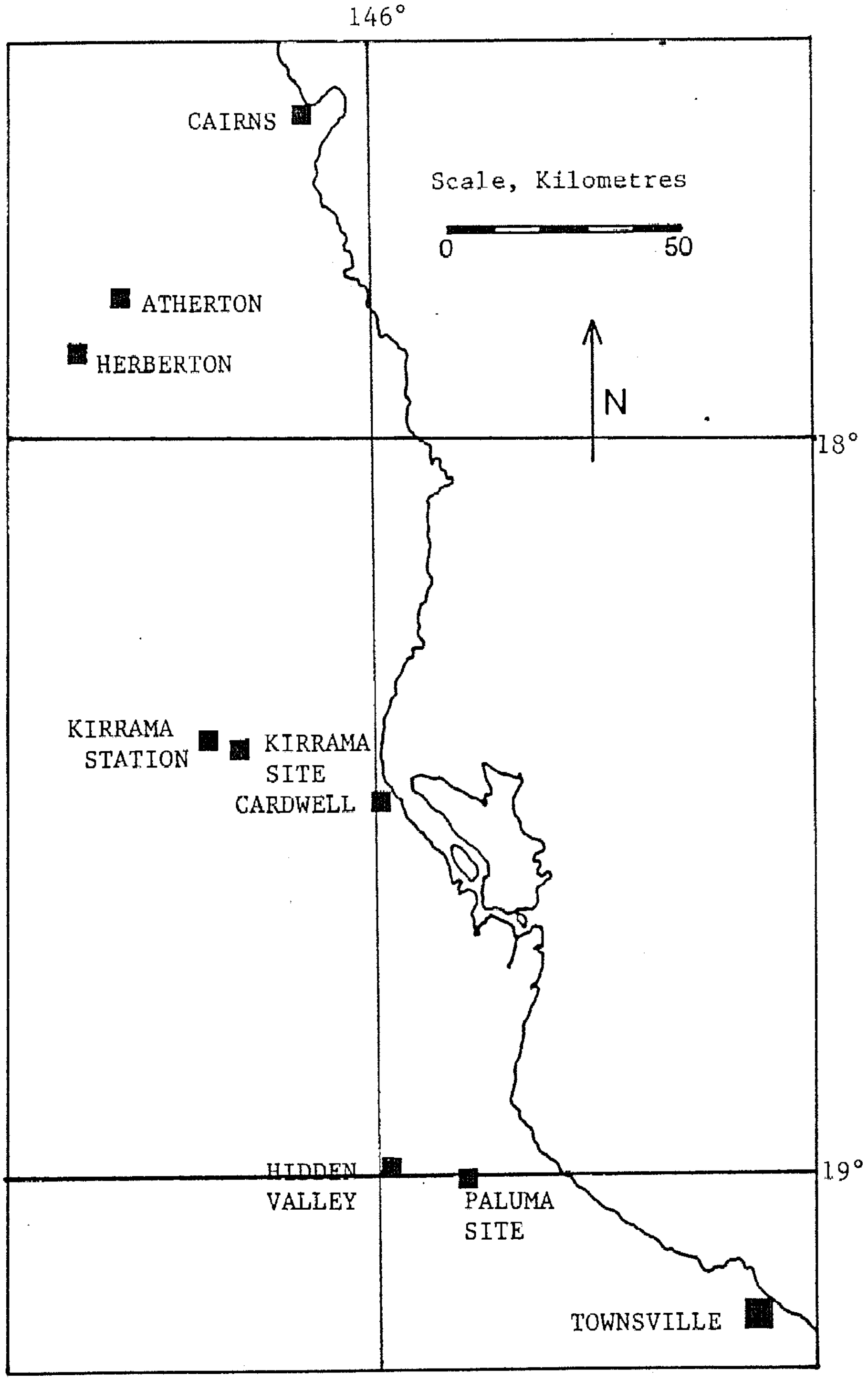


Figure 2.1 Map of North Queensland showing the location of study sites and areas mentioned in text.

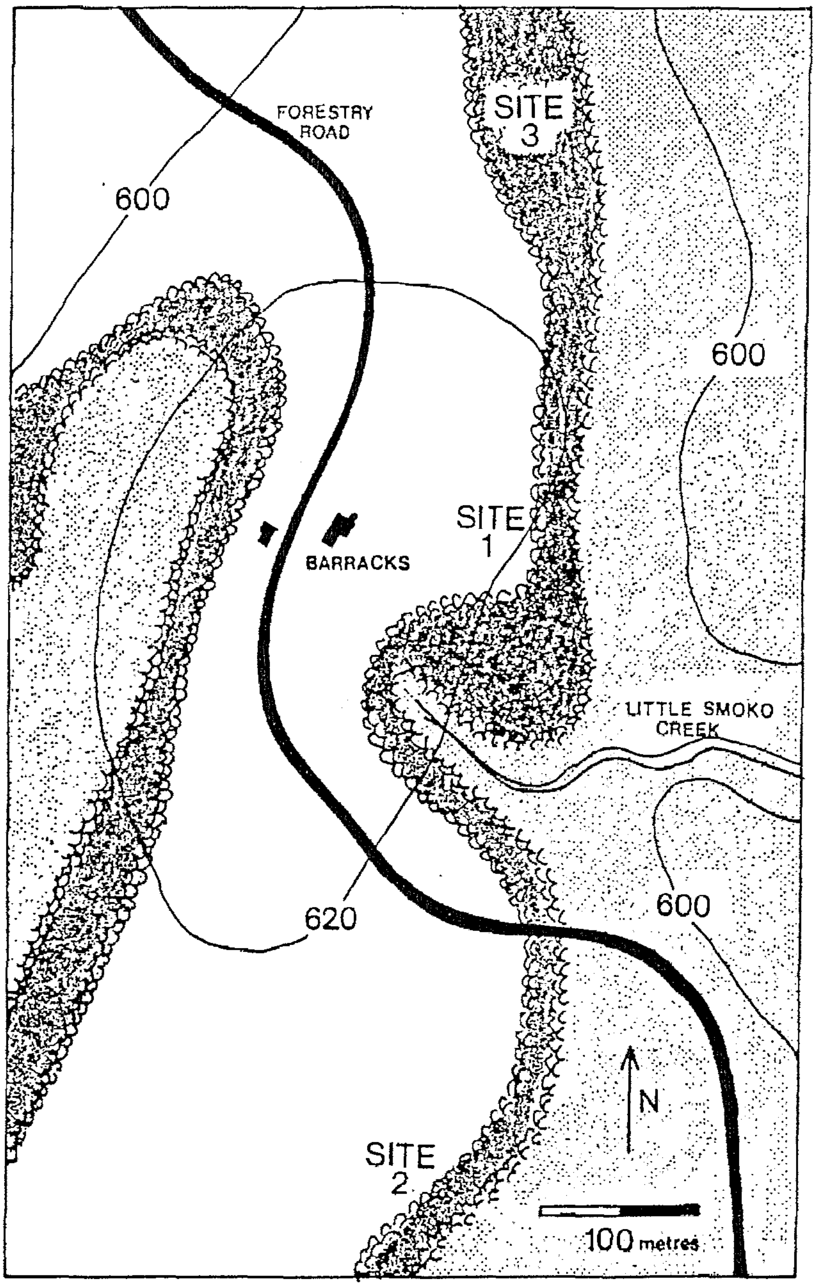


Figure 2.2 Location of Kirrama Study Sites showing distribution of Rainforest (light stippling), Tall open forest (heavy stippling) and Medium open forest (no stippling). Contour lines in metres.
Map compiled from RASC sheet 8061 Kirrama, 1:100 000 Forestry Map 8061-4 Kirrama, 1:50 000 and aerial photographs.

Lat. 18° 40' S Long. 145° 44' E

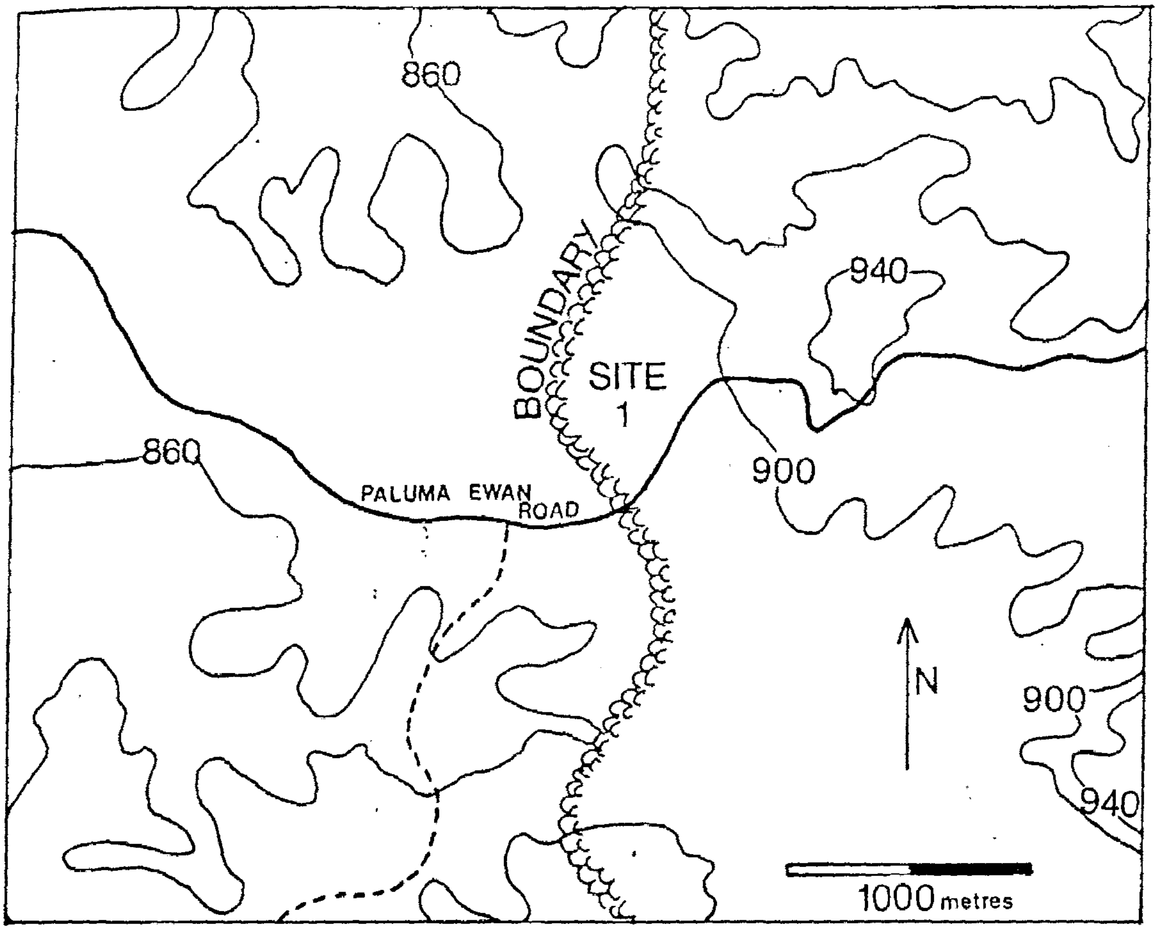


Figure 2.3 Location of Paluma Study Site showing distribution of Medium open forest (left of boundary) and a mosaic of Tall open forest, Tall open forest with rainforest understorey and Rainforest (right of boundary). Contour lines in metres. From RASC Sheet R 733 Paluma, 1:50 000.
Lat. 19° 14' S Long. 146° 17' E.

## 2.3 RAINFALL

Rainfall on the eastern seaboard of tropical Queensland is both strongly seasonal and spatially variable (fig. 2.4). Consequently, water availability plays a major role in determining vegetation distribution. Moisture availability is controlled by rainfall, topography, soil structure and microclimate. Microclimate is largely determined in turn by vegetation structure. The timing of rainfall can also be highly significant, especially in the case of dry season rainfall. A few centimetres of rain in the midst of the tropical "dry" is likely to be of greater benefit to the survival of moisture stressed plants than the equivalent amount during the "wet". Evaporation rates may also be lower during the cooler months of the dry season.

Unwin (1983) examined rainfall over a three year period at fortnightly intervals on twenty two sites along transects in the Herberton district. These sites were divided into three categories according to topography and vegetation structure. The categories were (1) open forest and woodland on high, exposed western slopes, (2) highland rainforest and margins with tall open forest, and (3) eastern slopes with open forest descending to the Atherton plateau. He noted that the intensity and duration of rainfall varied markedly from year to year, resulting in irregular seasonal and annual totals despite the apparent annual wet/dry cycle.

The topography in the Herberton district gives rise to an increase in precipitation with the movement of a moist south easterly airflow ascending the eastern slopes, which support open eucalypt forest. Maximum rainfall occurred on peak eastern elevations supporting rainforest and tall open forest ecotones. Rainfall was lower on western slopes, with the vegetation reverting to open eucalypt forest and woodland of decreasing structure and stand density.

A similar trend is noticeable in the Paluma district. The lower eastern slopes of the Paluma Range support woodland dominated by *Eucalyptus, Allocasuarina and Acacia* species. Stem density and diversity of woody species increase with altitude, culminating in rainforest at approximately 600 m on the eastern side of the range, although closed forest types descend considerably lower in gullies and creek beds. The land slopes downwards from 900 m at

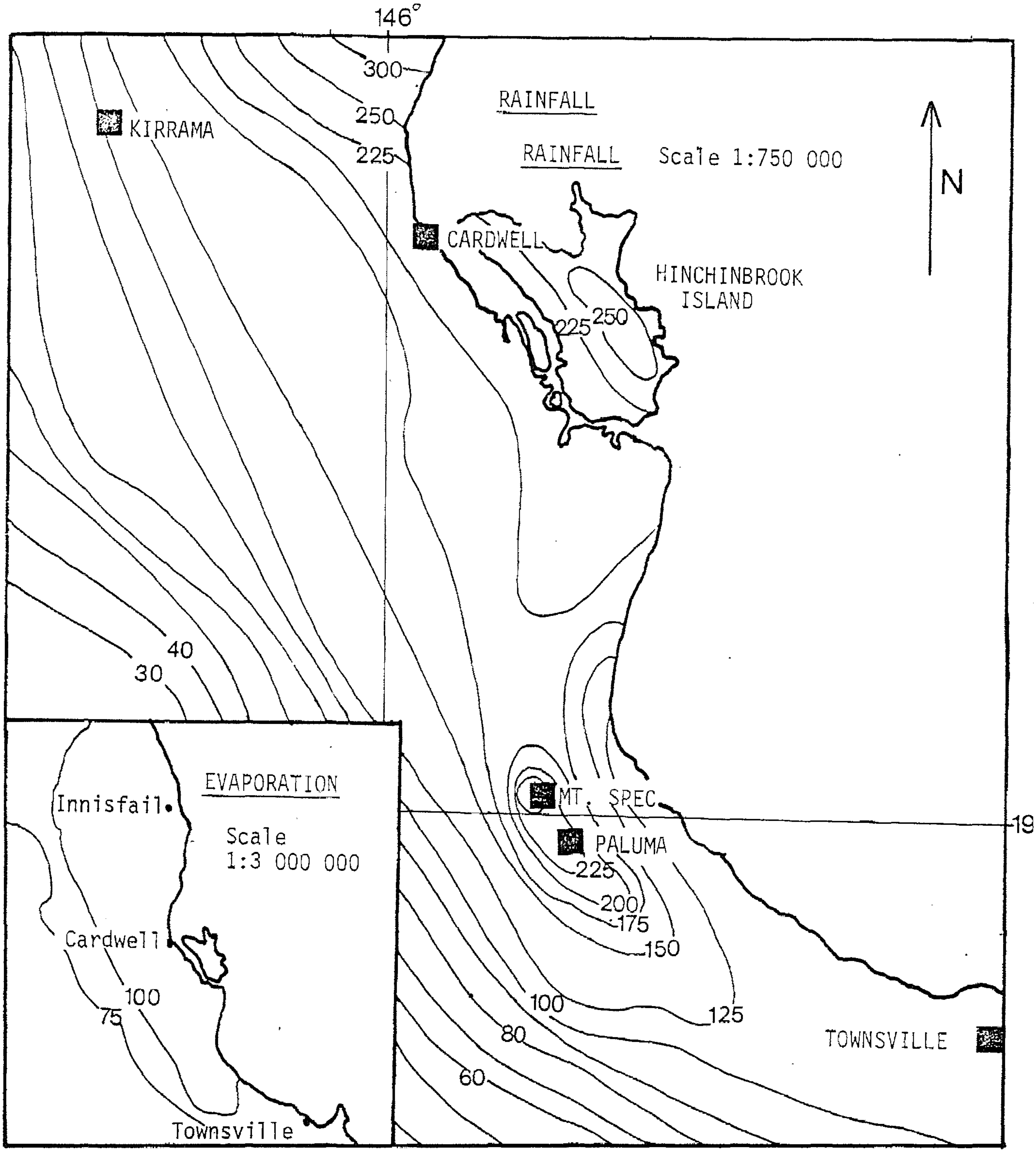


Figure 2.4 Mean annual rainfall (isohyets in cm) and mean annual evaporation (isohyets in cm) from Townsville to Kirrama.
From Department of National Development, Canberra, 1970. Resource Series, Climate, Burdekin Townsville Region.

Paluma to 620 m at Hidden Valley (18° 59' S, 146° 02' E) 20 km to the west north west. The vegetation changes from rainforest at Paluma to a wide belt (500 m to 2000 m) of tall open forest dominated by *Eucalyptus grandis* with a developing rainforest understorey (Paluma, Site 2). As altitude decreases and distance west of the range increases, the vegetation reverts to open forest.

Similar trends in rainfall, topography and vegetation occur on the Kirrama Range, with an overall open forest - rainforest - open forest transition moving from east to west. Records of rainfall for Cardwell (18° 16' S, 146° 02' E,) and Kirrama Station (18° 09' S, 145° 37' E) were taken from Bureau of Meteorology Records (1977) and cover periods of 122 and 90 years respectively; Kirrama Site 1 data were collected by Crowley (unpub.) from August, 1982 to April 1985 (Table 2.2). Cardwell is located at the base of the Kirrama Range (alt. 5 m), and Kirrama station (alt. 460 m) is 12 km west of Kirrama. The vegetation at Kirrama station is largely open forest with tall open forest and rainforest elements restricted to nearby gullies.

## 2.4 MICROCLIMATE

The transition from rainforest to open forest is accompanied by an obvious microclimatic change. The literature contains many descriptions of the microclimatic parameters within either closed forest or open forest, but direct comparisons between the two are rare.

Richards (1952) describes the microclimate at different strata within tropical rainforests, and subsequent authors have covered the spatial and temporal variation of microclimate within closed forests in detail (Leigh, 1975; Longman and Jenik, 1974; Walter, 1974 and Whitmore, 1973). Although closed forest has a strong "buffering" effect, reducing the extremes of temperature and moisture saturation deficit which may occur outside the forest, these studies emphasize the seasonality of humid tropical forest environments. Closed forests are spatially heterogeneous;solar radiation levels, temperature extremes, humidity, air circulation, evaporation and evapotranspiration rates can vary substantially between patches with full canopy cover and those with canopy gaps

MONTHLY AVERAGE (RAINFALL IN mm)

| LOCATION | LAT (S) | LONG (E) | ALTITUDE (m) | YEARS OF RECORD | Jan | Feb | Mar | Apr | May | June | Jul | Aug | Sep | Oct | Nov | Dec | AVERAGE (mm) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ATHERTON | 17°16' | 145°29' | 760 | 72 | 287 | 305 | 268 | 105 | 60 | 46 | 30 | 25 | 22 | 28 | 76 | 173 | 1425 |
| CARDWELL | 18°16' | 146°02' | 5 | 103 | 451 | 461 | 423 | 205 | 92 | 50 | 32 | 30 | 35 | 51 | 105 | 194 | 2129 |
| HERBERTON | 17°23' | 145°23' | 900 | 87 | 238 | 232 | 215 | 84 | 42 | 33 | 22 | 17 | 15 | 25 | 73 | 136 | 1132 |
| HIDDEN VALLEY | 18°59' | 146°02' | 620 | 3 | - | - | - | - | - | - | - | - | - | - | - | - | 1240 |
| KIRRAMA STATION | 18°09' | 145°37' | 457 | 40 | 231 | 269 | 204 | 75 | 58 | 44 | 28 | 29 | 19 | 27 | 59 | 108 | 1142 |
| KIRRAMA STUDY SITE | 18°40' | 145°44' | 620 | 2.5 | 130 | 202 | 338 | 57 | 125 | 11 | 8 | 29 | 9 | 25 | 54 | 98 | 1086 |
| MT. SPEC | 18°56' | 146°11' | 900 | 32 | 649 | 809 | 604 | 213 | 96 | 103 | 62 | 54 | 57 | 91 | 171 | 260 | 3169 |
| PALUMA | 19°00' | 146°12' | 892 | 13 | 726 | 567 | 443 | 150 | 135 | 44 | 34 | 38 | 54 | 89 | 134 | 429 | 2835 |

Table 2.1 Rainfall records for selected sites. Records for Kirrama study site from Crowley (unpub.). Records for Hidden Valley from the proprietor, Hidden Valley Pub. All other records from Bureau of Meteorology, 1981.
No monthly records are available for the Hidden Valley site.

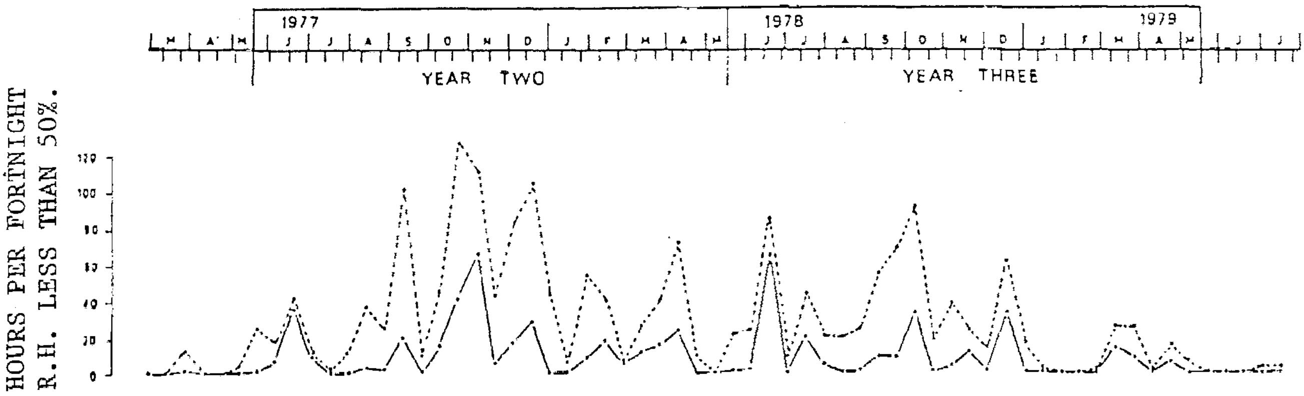


Figure 2.5 Persistence of low relative humidity in the understoreys of rainforest (----) and eucalypt forest (....) for a site on the Herberton Range. Curves indicate the number of hours per fortnight with relative humidity less than 50% (screen height 1.3 m). From Unwin (1983) Reproduced with permission.

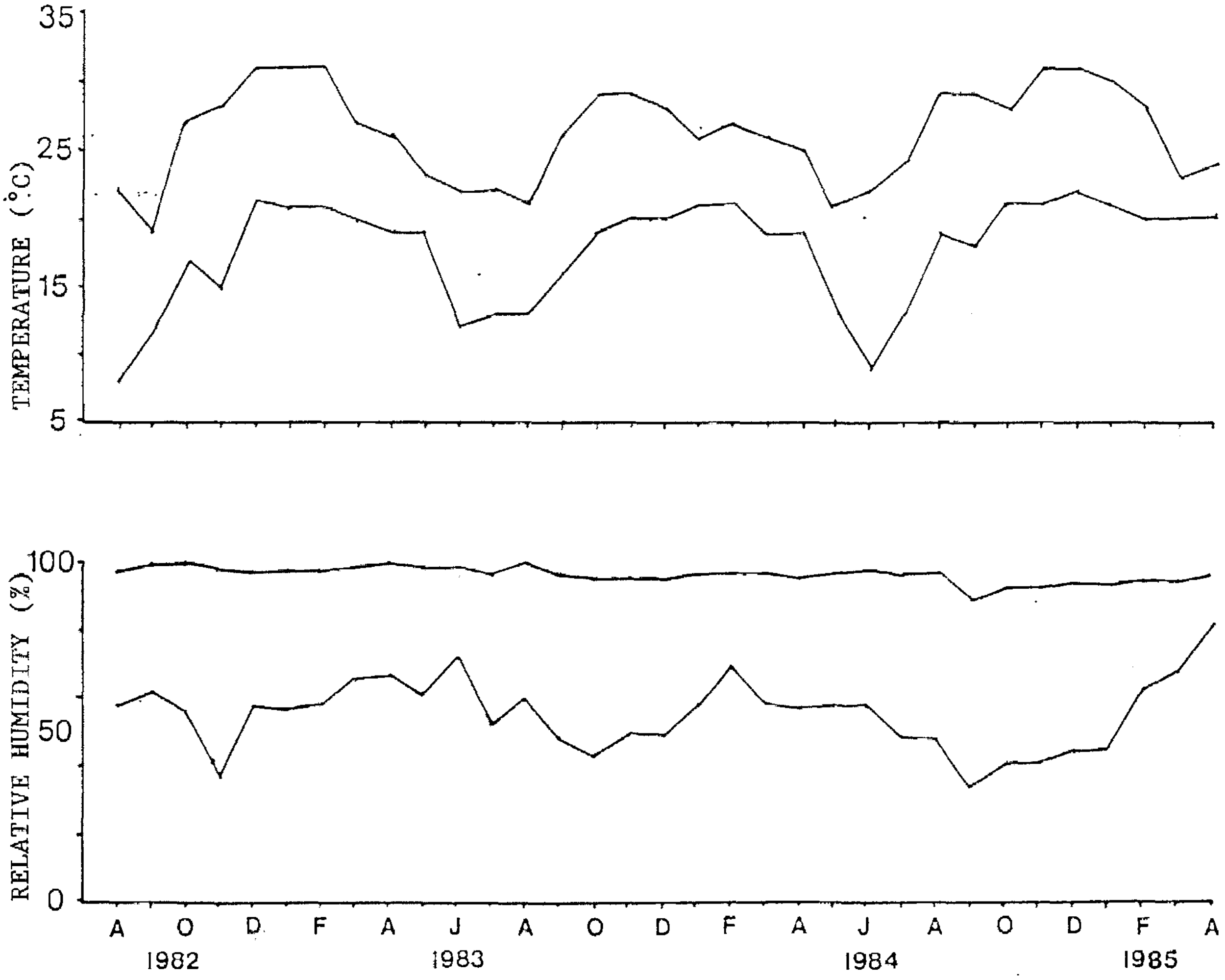


Figure 2.6 Maximum and minimum values for temperature (top) and relative humidity (bottom) collated at monthly intervals in open forest at Kirrama. From G. Crowley (unpub.).

of different sizes. Walter (1971) stated that only 0.5 to 1.0 % of sunlight reaches the forest floor under a closed canopy, but individual sunflecks may reach five times this level. These sunflecks represent the smallest class of "gap", and the larger the gap, the closer microclimate approaches the external extremes. Microclimate will also approach that of the external environment in the upper levels of the canopy.

By contrast, Dale (1973) found that the region of the crowns of eucalypt forests at Daylesford, Victoria tended to be the coolest parts of these forests during most of the diurnal and seasonal cycles. The exposure of the forest floor to sunlight during the day and long wave radiation from the forest floor at night meant that temperatures were highest at ground level.

Stocker (1968) discusses the variations in temperature and humidity between tall open forest and monsoon forest on Melville Island, Northern Territory. High humidity levels and hence reduced transpiration rates are maintained in the understorey of this closed monsoon forest. Litter decomposes more quickly under the closed forest canopy than in tall open forest, because of reduced moisture loss and lower temperatures. These conditions will also reduce the probability of fire in the closed monsoon forest : moist fuel and less of it.

Hopkins (1974) examined the differences between "external" and "internal" microclimate when comparing lowland closed forest and open savanna in West Africa. He concluded that the constant microclimate range and reduced moisture saturation deficit near the floor of closed forest occurred because the forest multiple canopy structure decreased air movement and radiation. The more open structure of the woodland, analogous to that of Australian open forest, had little effect on the ground level microclimate. Only beneath the herb layer was the microclimate altered.

Thermohygrograph data were collected across rainforest boundaries at two sites near Herberton (Unwin 1983) for 30 months at site 1 and 12 months at site 2. Eucalypt forests at both sites were warmer and drier than the adjacent rainforests, while rainforest sites showed lower levels of diurnal fluctuation during all weather conditions except tropical cyclones. Site 1, on a steep south easterly facing slope, was more exposed than the shallow north easterly aspect of site 2. The microclimates in both forest types at site 2 were more mesic than the corresponding forest types at site 1.

Figure 2.5 taken from Unwin (1983) shows the number of hours per fortnight registered as less than 50% relative humidity on hygrograph charts. The hygrographs were located 1.3 m above the forest floor, so the figure gives an indication of the length of periods of atmospheric "dryness" likely to be encountered by developing seedlings in each forest type. The duration and number of "dry" periods is predictably greater in eucalypt forests for both sites, and greater at site 1 than at site 2 for both forest types.

Thermohygrograph records were collected by Crowley (unpub.) over a 33 month period near the Kirrama study site (figure 2.6). The thermohygrograph was located in an area adjacent to open forest, and data were collated at monthly intervals.

## 2.5 LIGHT

### 2.5.1 INTRODUCTION

In the transition from rainforest to open forest, the one physical factor that varies more markedly than any other is light. A considerable amount of recent work assesses the spectral quality, energy flux and variability of light regimes in tropical forests (Anderson, 1964, 1971, Bjorkman and Ludlow, 1972, Chazdon and Fetcher, 1984, Evans 1968 ). These authors all agree that light in tropical forests is still not well understood. "All light measurement involves some compromise between accuracy and possibility." (Anderson, 1964). Bjorkman and Ludlow (1972) also emphasize the difficulties encountered in light measurements in tropical forests due to the "high level of heterogeneity" in these environments. Furthermore, Chazdon and Fetcher (1984) commented that "... of the above ground environmental factors affecting the life of tropical rainforest plants, light is undoubtedly the most variable, most complex and least readily quantified."

Floors of tropical rainforests probably constitute the lower limit of available light at which vascular plants are able to carry out sufficient photosynthesis for growth and survival (Bjorkman and Ludlow, 1972). The worldwide percentage transmission of diffuse radiation under closed forest canopies lies between 0.4% and 3.8% of available sunlight, representing a total daily photon flux of between 0.15 and 1.0 mol $m^{-2}$ $d^{-1}$.

Measurements have been made of both direct radiation and diffuse radiation. Anderson (1964) coined the term "diffuse site factor" which means the average percentage of available diffuse light of specified wavelengths transmitted through a canopy of vegetation over a specified time period. She also pioneered the use of hemispherical canopy photographs for determining the percentage of light penetration through a forest canopy. This technique was utilised at Kirrama and will be described in detail later in this chapter.

Light measurement in closed forest environments is complex because so many factors need to be examined. In order to gain a true impression of the light environment of a plant within a forest environment, the following points must be considered:

(1) Temporal variation, both seasonal and diurnal, in total radiation reaching the forest canopy. This will be affected by atmospheric and climatic conditions, as well as latitude and hence solar angle and sunlight intensity.

(2) Variation in proportions of wavelengths of light reaching the plants in question, particularly in the PAR range (photosynthetically active radiation, i.e. 400 to 700 nm).

(3) Spatial heterogeneity of the light environment within the forest due to the structure of the vegetation itself (e.g. degree of canopy closure, stratification, height of peripheral vegetation). These factors are particularly important when considering "sunflecks" or gaps of various sizes.

Bjorkman and Ludlow (1972) assessed the solar radiation environment on the floor of an area of virgin rainforest in Lamington National Park in southern Queensland, in sites with minimum gap canopy frequencies, ranging from 1.3 to 1.6%. The daily course of diffuse radiation (i.e. total radiation in the range of 300 to 2400 nm minus direct radiation contributed by sunflecks) closely matched that of the radiation above the canopy, reaching its peak at noon. The average diffuse radiation on the floor was 2.2% of that above the canopy. The total contribution by sunflecks in the course of the same day was

2.5% of the radiation above the canopy. This resulted from three major bursts of sunfleck activity, which were readily predicted from the hemispherical canopy photographs on which solar tracks had been superimposed.

However, when Bjorkman and Ludlow (1972) examined the photosynthetically active radiation levels at the same site, they found that the proportion of diffuse light energy of useable wavelengths reaching the forest floor was only 0.15% of that reaching the forest canopy, because of the filtering effect of the leaves in the canopy depleting the total quantum flux of those wavelengths that can be utilized for photosynthesis. Sunflecks contributed some two thirds of the photosynthetically active radiation reaching the forest floor as opposed to only one tenth of the total daily energy.

Based on the available data, Bjorkman and Ludlow (1972) estimated the average radiation reaching the forest floor annually to be 47.2 joule $cm^{-2}$ $day^{-1}$ or 2.58% of the energy in the wavelength range 300 to 2400 nm. Of this energy, 22.0 µmol $cm^{-2}$ $day^{-1}$ or 0.44% of PAR reaches the forest floor. Approximately 63% of this latter component was contributed by sunflecks and 37% was the diffuse radiation component.

In lowland tropical forest in Costa Rica, Chazdon and Fetcher (1984) examined the "photosynthetic photon flux density" (PPFD) i.e. the total PAR during a 12 month period under canopy gaps of different sizes. They found that under an unbroken canopy, 1-2% of the external PPFD reached the forest floor. In the centre of a $200m^2$ canopy gap, 9% reached the floor, and 20-35% in a 400 $m^2$ gap. Only in a $5000m^2$ gap did the external PPFD equate to that inside the gap. Only in this large gap did seasonal variation lead to any signifcant temporal variation inside the gap, producing higher PPFD's in the dry season.

Chazdon and Fetcher (1984) found that on the forest floor under an unbroken canopy, sunflecks contributed 55-77% of the total quantum flux, while >70% of daily 10min averages were less than 10 µmol $m^{-2}$ $s^{-1}$. (NB 1 µmol = 1 µE or microEinstein). The 200 $m^2$ gap centre received little direct radiation with total daily PPFD values of between 1.52 and 3.07 mol $m^{-2}$ $d^{-1}$. The $400m^2$ gap centre received 3.86 to 13.6 mol $m^{-2}$ $d^{-1}$ with 11% of 10 min averages on a clear day exceeding 1000 µmol $m^{-2}$ $s^{-1}$. In the clearing, total daily PPFD ranged from 13.7 to 33.9 mol $m^{-2}$ $d^{-1}$ and >40% of 10 min averages were > 1000 $\mu molm^{-2}$ $s^{-1}$.

The rainforest to open forest transition may vary, in the space of a few metres, from the extremes of those light intensities found in a large clearing to those found under a closed canopy. This change is most rapid close to the forest floor, and thus is likely to exert a strong influence on the distribution, establishment and success of seedlings in the early stages of recruitment. Subsequent chapters will examine the responses of seedlings of a range of species to extreme conditions of sunlight and shade, in both isolation and competition with seedlings of other species. This section will quantify the light environments likely to be encountered by seedlings in the field in order to place any subsequent light related experiments in context.

### 2.5.2 MATERIALS AND METHODS

Measurements of PAR using a Licor portable integrating light meter were carried out on three transects at Kirrama site 1 in May 1983, September 1983 and November 1984. Transects 30 m long ran perpendicular to the rainforest - tall open forest interface, including rainforest, tall open forest with rainforest elements in the understorey and open forest vegetation types . Measurements of PAR were made at 5 m intervals between morning (8.00 - 10.00 am), mid-day (11.30 - 1.00 pm) and afternoon (4.00 - 5.30 pm) periods at ground (0 m) and head (1.8 m) heights. PAR was integrated over a 10 second interval, and a mean of 4 PAR measurements from each corner of a 1 $m^2$ quadrat was calculated at each point along the transect. Temperature and humidity were recorded using a whirling hygrometer at three points along each transect, one in each vegetation type. Cloud cover and prevailing weather conditions were also noted.

Evaporimeters were also set up along these transects, but results from these proved to be highly inconsistent and were rejected as being unreliable. Other temperature, PAR and humidity records have been made at this and other sites as an adjunct to plant moisture stress measurements. These results are reported in Chapter 3.

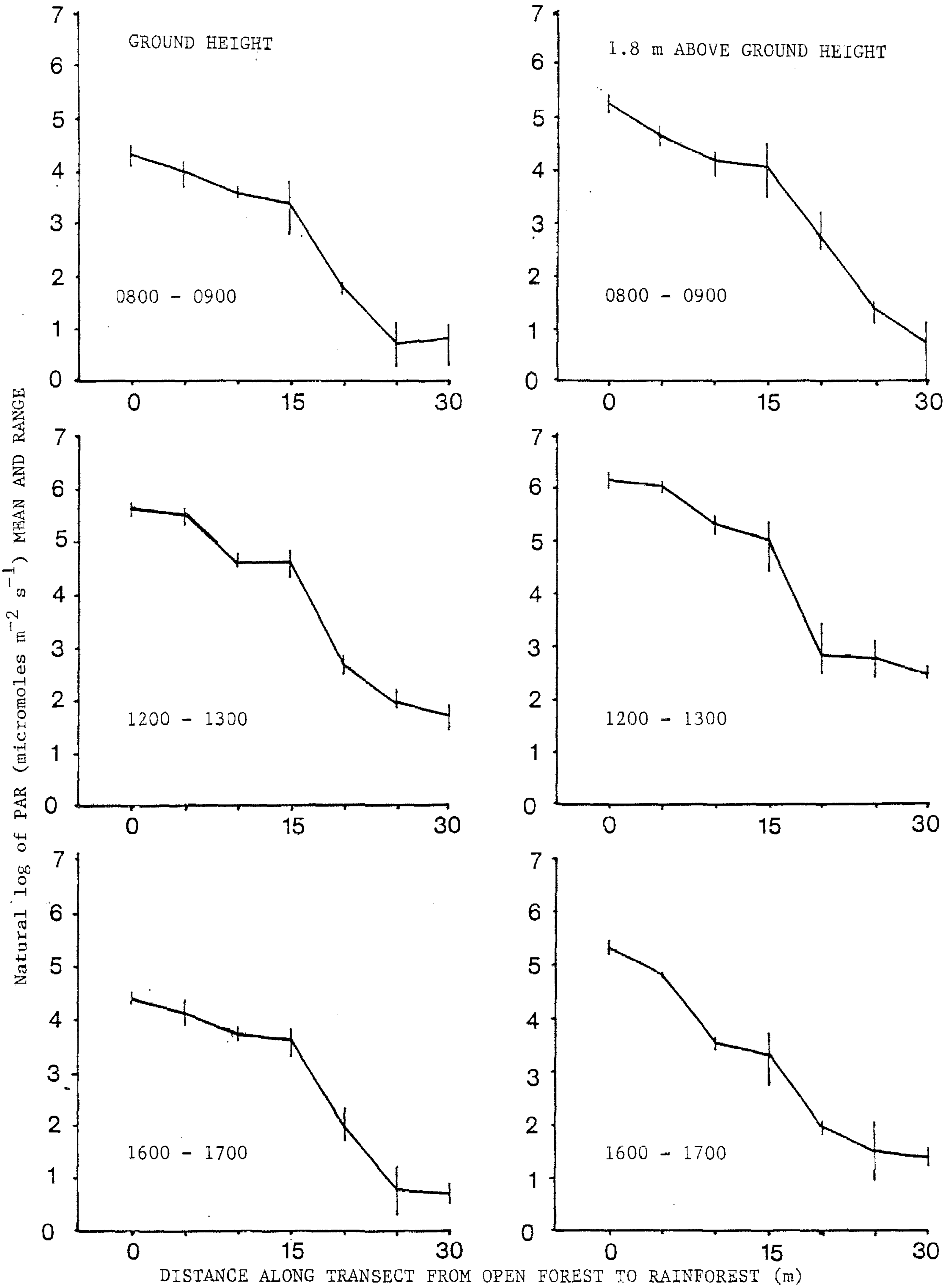
### 2.5.3 RESULTS AND DISCUSSION

Table 2.2 shows weather conditions and changes in temperature and humidity across the ecotone at Kirrama site 1 for the days when light meter measurements were made on the ecotone transects. In all cases, a sharp drop in temperature was accompanied by an increase in humidity in the transition from open forest to rainforest. Temperature changed by as much as 4.0°C and relative humidity by as much as 10%. Figures 2.7.1 to 2.7.18 show the natural log of mean and range of PAR at ground and 1.8m heights for morning, noon and late afternoon measurements in May 1983, September 1983 and November 1984. The lower light intensities ground level resulted from additional shading effects of low shrubs, ferns and herbs.

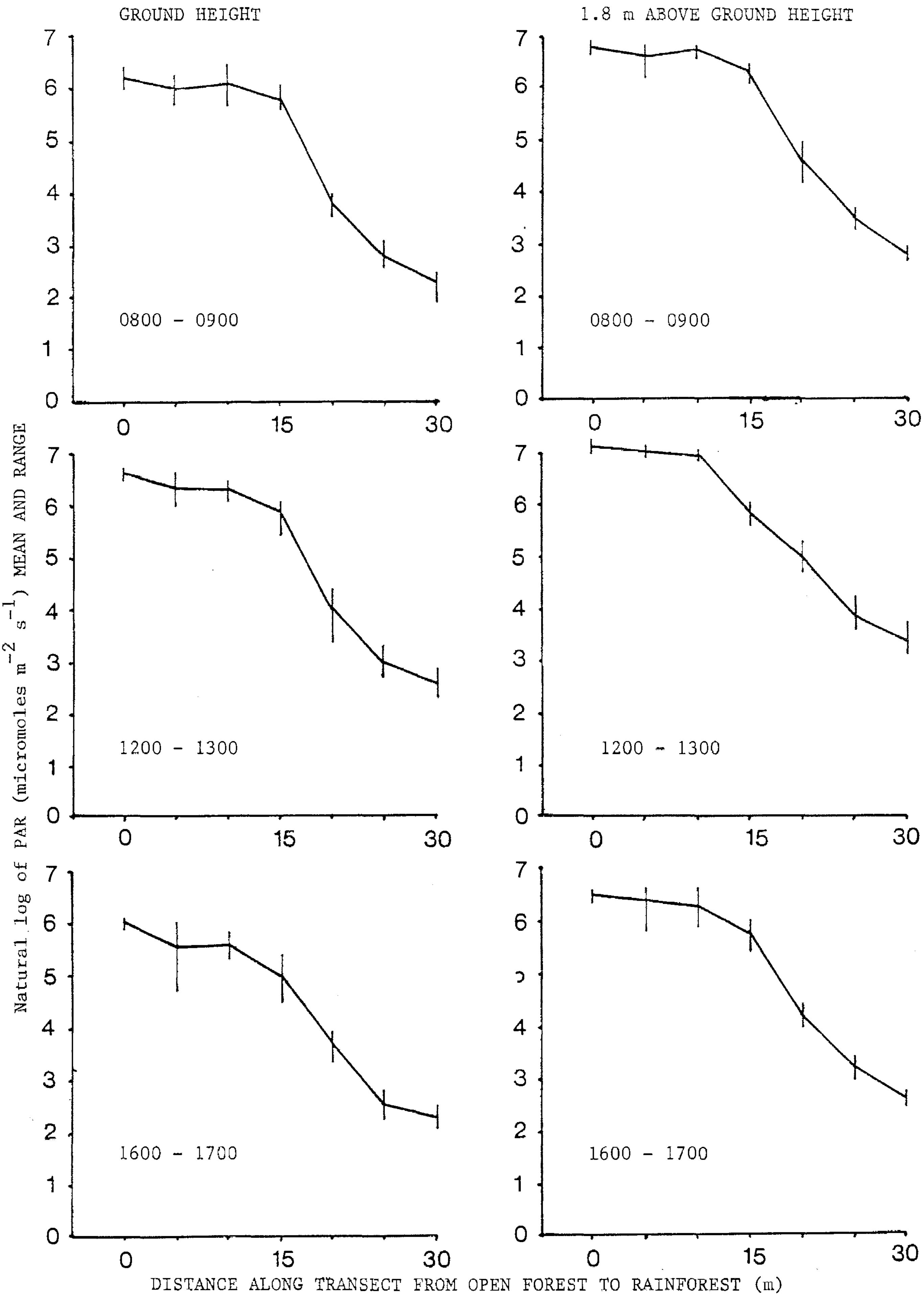
Maximum mean PAR recorded at any point was 1350 µmol $m^{-2}$ $s^{-1}$ at midday with 15% high cloud cover in medium open forest in September. The lowest record of mean PAR was 1.00 µmol $m^{-2}$ $s^{-1}$ on an overcast and drizzling morning in rainforest in May. It should be noted that the PAR sensor attached to the light meter measures both direct and diffuse light intensities, the latter sensed through 180° of arc.

PAR varied from rainforest to open forest by a factor of 46.80 ± 3.23 (mean ratio of all PAR measurements in rainforest to those in open forest ± standard error). PAR in medium open forest was approximately twice that in the tall open forest, and approximately ten times that in the ecotone. The most marked decrease in PAR occurs with the increase in shrub density under the tall open forest canopy. Relative PAR in the ecotone was marginally higher in the afternoon than in the morning due to the rainforest canopy blocking out a higher proportion of afternoon than morning sunlight at this site.

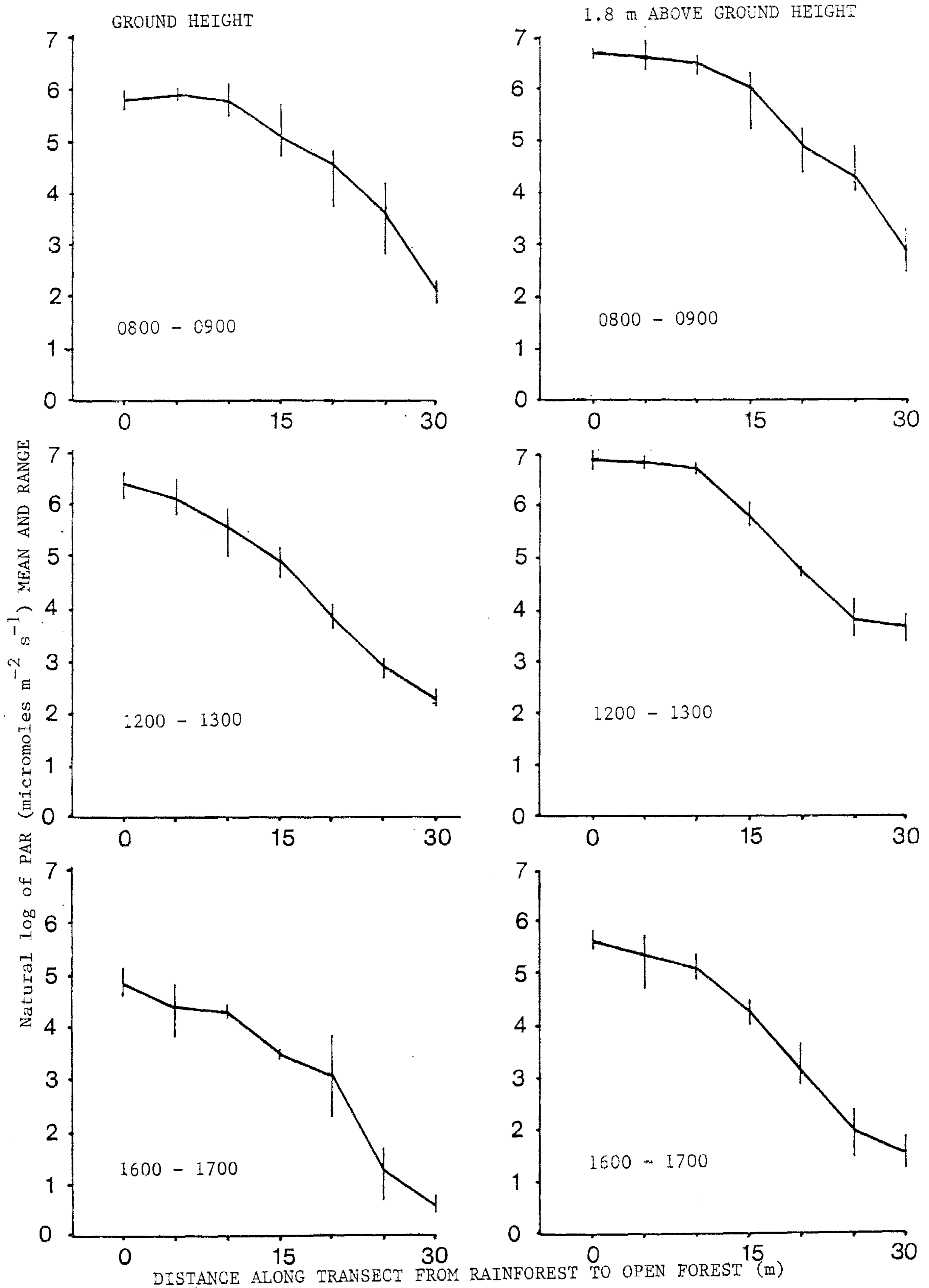
Overcast conditions reduced PAR values in open forest by a factor of 3.36 (mean of all open forest readings during one clear and one overcast day) and in



Figures 2.7.1 to 2.7.6 PAR across the ecotone at Kirrama site 1, May, 1983. Morning, noon and afternoon measurements at ground height and head height. PAR expressed as a natural logarithm.



Figures 2.7.7 to 2.7.12 PAR across the ecotone at Kirrama site 1, September 1983. Morning, noon and afternoon measurements at ground height and head height. PAR expressed as a natural logarithm.



Figures 2.7.13 to 2.7.18 PAR across the ecotone at Kirrama site 1, November, 1984. Morning, noon and afternoon measurements at ground height and head height. PAR expressed as a natural logarithm.

| MONTH | YEAR | TIME | WEATHER CONDITIONS | ΔRH (%) | ΔTEMP (°C) |
|---|---|---|---|---|---|
| MAY | 1983 | 0800 | Light drizzle, 100% low cloud | 6 | 2.0 |
| | | 1200 | 100% low cloud | 8 | 2.0 |
| | | 1600 | 100% low cloud | 8 | 1.5 |
| SEPT | 1983 | 0800 | 40% high cloud | 8 | 3.0 |
| | | 1200 | 15% high cloud | 8 | 3.0 |
| | | 1600 | Clear | 6 | 4.0 |
| NOV | 1984 | 0800 | 60% medium - high cloud | 10 | 3.0 |
| | | 1230 | 60% medium - high cloud | 8 | 2.5 |
| | | 1600 | 100% medium cloud | 8 | 3.5 |

Table 2.2 Weather conditions and changes in temperature and humidity across the ecotone at Kirrama Site 1.

rainforest by a factor of 2.56, the latter lower due to the higher proportion of diffuse as opposed to direct sunlight in the rainforest. Overcast conditions characteristically reduce the effects of small canopy gaps, by eliminating the influence of sunfleck events.

## 2.6 STRUCTURE AND FLORISTICS

### 2.6.1 INTRODUCTION

In characterising the structure and floristics of rainforest, tall open forest medium open forest, it is necessary to note that these vegetation types are seldom represented as discrete entities in the ecotone, but tend to form a continuum, however rapid the transition from one community to the next. The ecotone itself is often temporally and spatially unstable, and must be regarded as a dynamic boundary system. Nevertheless, in order to best describe the ecotone structurally, architecturally and floristically it is necessary to divide the transition into its component parts and describe these separately.

In his description of the structure and composition of rainforest and eucalypt forest, Unwin (1983) raises a number of questions about the distribution of species in the ecotone and comments "...the autecologies of these dominant tree species are fundamental to the complex forest - environment relations of the rainforest - eucalypt forest boundary. Why is an otherwise widely dispersed species (*Eucalyptus grandis*) so definitely restricted and yet so successfully established along the abrupt rainforest edge? Why does *Eucalyptus grandis* command such a prominent position in the narrow margin of tall open forest and yet disappear so abruptly in the adjoining medium forests of *E. intermedia*, *E. tereticornis* and/or *Allocasuarina torulosa*? Clues to the unique success of *Eucalyptus grandis* in this narrowly defined ecotonal niche are likely to offer a major contribution to the understanding of forest dynamics at the rainforest eucalypt forest boundary."

Similar questions arose upon the examination of the structure and species distribution of the ecotones observed in this study, and subsequent chapters concentrating on the autecologies of dominant and characteristic species,provide some of the answers to these and related questions.

A variety of different types of rainforest - open forest ecotone are found in northern Queensland, and these may be classified into a range of subtypes and intermediate forms. Smith and Guyer (1983) drew the distinction between what they describe as a "sharp edge" as opposed to an "ecotone" or more gradual transition in New South Wales rainforests. Unwin (1983) recognised five different types of transition zone. For this study, the transitions will be classified into one of the following three categories:

(A) An abrupt and apparently stationary rainforest margin with a complete transition occurring from rainforest to open forest through an ecotone not more than 30m wide.

(B) Ecotones in which rainforest species can be found extending out beneath a canopy of eucalypts or other typical open forest species, implying rainforest advance. The ecotone is generally less than 100 m wide.

(C) Extensive tracts of *Eucalyptus grandis* dominated tall open forest with a dense understorey of rainforest species.

It is not proposed that this classification be universally adopted; it is merely a convenience for the purpose of defining and comparing ecotones encountered in this study. Moreover, these classifications are based on the extent of a transition zone at a given time. A transition zone might eventually pass through all three categories as well as changing in position.

Unwin (1983) divided the rainforest ecotones into discrete community types and described each community in detail. The sites studied near Herberton include 0.5 ha plots of mature rainforest on the steep eastern slopes, young rainforest of the Hugh Nelson Range, two rainforest boundary plots, tall open eucalypt forest, tall open eucalypt forest with a closed understorey and medium open eucalypt forest. In these plots he examined canopy and understorey floristics, relative dominance and basal area of tree species, diversity and forest structure.

In the two boundary sites Unwin (1983) found an abrupt decrease in plant species richness in the transition from rainforest to open forest. The high diversity found in the species rich rainforest was maintained through the rainforest edge in all strata, and species numbers decreased only at the open forest end of the continuum. However, the boundary did contain a greater proportion of fast growing species than the rainforest (e.g. *Flindersia spp., Aleurites moluccana, Toona australis, Acacia aulacocarpa and Neolitsea dealbata*). Beneath this canopy of early secondary or large gap species is a dense barrier of shade intolerant shrubs, vines and "aggressive early successional species" (Unwin, 1983). This wall of vegetation acts as a protective buffer of relatively low flammability and has the capacity to regenerate rapidly following a disturbance such as a fire in the open forest. The exotic weed *Lantana camara* was evident at this ecotone site as at many others, contributing to the density and vigour of the edge vegetation but increasing the probability of dry season fire penetrating the rainforest boundary (Stocker, pers. comm.).

Smith and Guyer (1983) also noted two distinct zones in the rainforest contiguous with eucalypt forest in New South Wales. They examined species distribution in warm temperate rainforest - eucalypt forest margins at Barrington Tops and Girard State Forest, and described two vegetation assemblages within the rainforest. The outer zone, closer to the interface with open forest contained smaller, more closely spaced and younger trees. The inner zone contained fewer, larger and older trees. Only the outer zone contained any evidence of past fires. They proposed that the rainforest at both sites is advancing into the eucalypt forest, but that another severe fire would kill an area of rainforest and lead to its temporary replacement by eucalypt forest. The frequency of summer droughts, combined with high temperatures and strong dry winds results in a greater incidence of fires penetrating into and destroying rainforest in temperate Australia than in the tropics.

Unwin (1983) likened the undisturbed rainforest boundary to the edge of an expansive and semi-permanent forest gap, in which the processes of succession and regeneration parallel those which occur in a large internal opening in the rainforest canopy. This study will suggest that the principles which apply to dynamics and succession within tropical forests are interchangeable with those that govern the spatial and temporal changes in the ecotone.

Plate 2.1 Tall open forest with a rainforest understorey at Kirrama. Young stems of *Eucalyptus grandis* are evident in the centre of the photograph.

Plate 2.2 Tall open forest with an understorey of *Imperata cylindrica* at Paluma Site 1. The area was burnt in 1983, and photographed in 1987.

## 2.6.2 MATERIALS AND METHODS

### (a) KIRRAMA

A 50 m x 50 m quadrat was pegged out at Kirrama site 2, extending approximately 10 m past the ecotone into mature rainforest (fig 2.8). Vegetation types included in this 0.25 ha plot were medium open forest dominated by *Eucalyptus intermedia*, tall open forest dominated by *Eucalyptus grandis*, ecotonal vegetation with a high density of small trees and shrubs under a canopy of *Eucalyptus grandis*, and closed canopy rainforest with a relatively sparse understorey. The medium open forest and tall open forest understoreys were burnt by a "cool" grass fire in August 1982, but little damage to the trees was evident.

The quadrat was subdivided into 625 2 m x 2 m subplots, and the presence, species and girths of all trees >10 cm girth were recorded. In addition to these data, the girths of all trees >10 cm dbhob were recorded from an adjacent 50 m x 50 m quadrat, but positions were not recorded. Two transects 5 m x 50 m were laid out inside the first quadrat, spaced 25 m apart and oriented perpendicular to the rainforest edge (fig. 2.8). In these transects, species presence/absence was recorded at 5 m intervals, together with percentage estimated ground cover of grasses and shrubs <5 m in height, and careful note was made of any evidence of post fire eucalypt and acacia regeneration. Any evidence of past fire was recorded and the distribution of charcoal was noted. A species list for the general area of Kirrama site 2 was compiled.

A canopy profile diagram was prepared for a 50 m line transect at Kirrama site 1. Tree heights were measured using an inclinometer, and drawings were made of the architecture of all tree species found on the transect. Photographs were also used in preparation of the profile diagram.

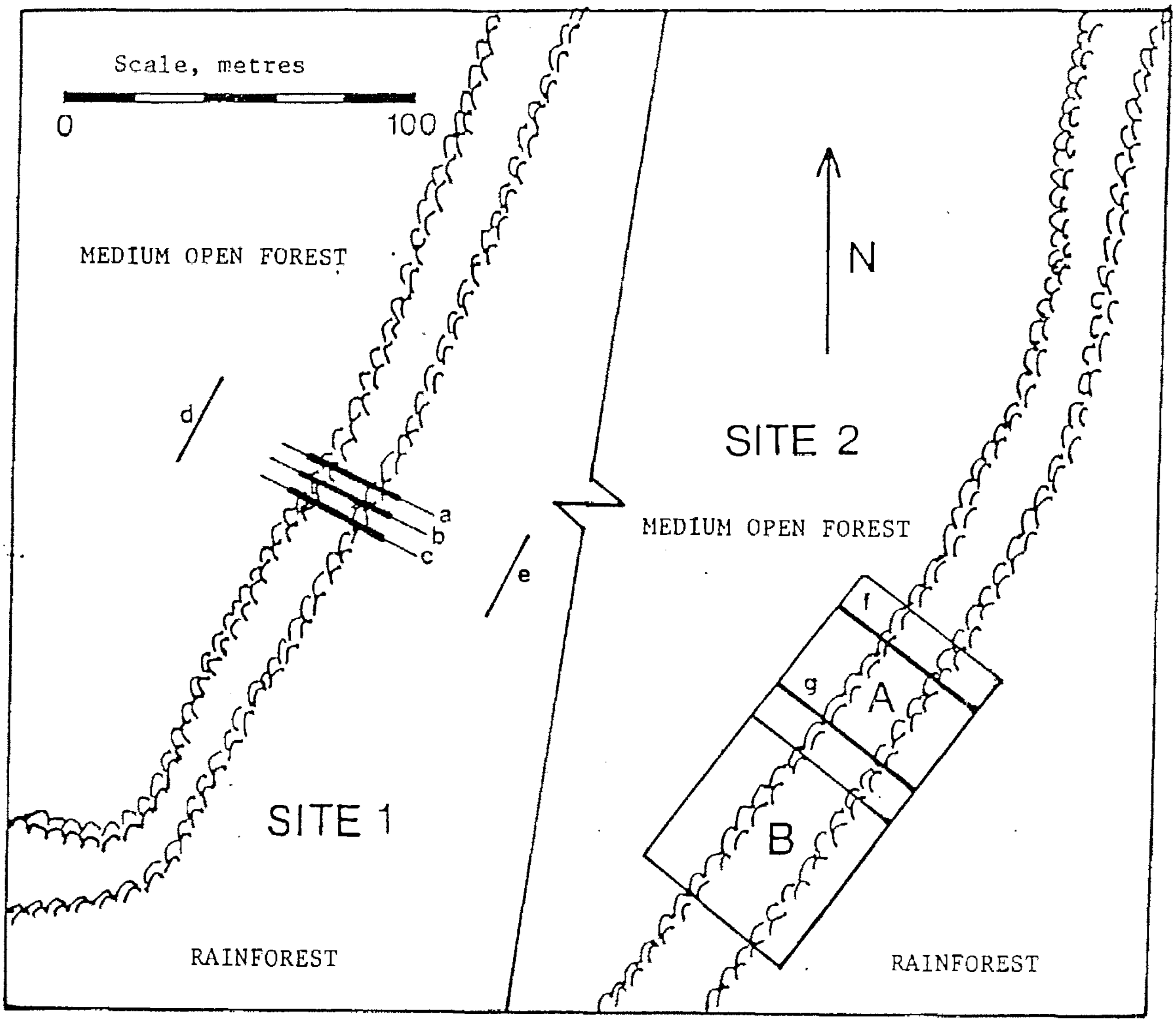


Figure 2.8 Quadrat and transect location at Kirrama sites 1 and 2.

KEY:

| | |
|---|---|
| a, b and c : | 30 m X 1 m Transects for PAR measurements and hemispherical canopy photographs. |
| b: | 50 m canopy profile diagram transect. |
| d and e: | 25 m hemispherical photograph transects. |
| A: | 50 m X 50 m quadrat for tree species mapping and dbh measurement. |
| B: | 50 m X 50 m quadrat for dbh measurements only. |
| f and g: | 50 m X 5 m strips for grass and shrub cover estimations. |

Refer to Figure 2.2 for site locations.

### (b) PALUMA

Species lists were made and species distribution was noted in the type "C" tall open forest with rainforest understorey at the Paluma site. Heights and girths of dominant tree species in an area of approximately 0.5 ha were recorded in order to compare this area with the rainforest ecotones at Kirrama. Evidence of past fires in the form of fire scars on tree trunks and the presence of charcoal in the soil was recorded.

## 2.6.3 RESULTS AND DISCUSSION

### (a) KIRRAMA

The canopy profile diagram (fig. 2.9) for a 50 m line transect at Kirrama Site 1 demonstrates the transition in vegetation at this ecotone. The figure is an idealised diagram showing the relative density, species architecture, heights and canopy layering of species along the transect. Only the dominant species are represented. The diagram is divided into 5 zones:

(A) Medium open forest.
(B) Tall open forest.
(C) Tall open forest with rainforest species in the understorey.
(D) Young rainforest with early successsional species.
(E) Mature rainforest late successional species.

The actual distinction between these zones in the field is not as readily obvious as in the diagram, and the relative area of each zone varies according to topography and disturbance history, but the diagram does provide a basic reference and is included for this purpose.

Floristics and species distribution are essentially similar at Kirrama sites 1,2 and 3, with the following exceptions. *Eucalyptus grandis* and *E. torelliana* are found up to 25 m into the "D" zone (young rainforest) at site 2, and this zone is more extensive at this site, indicating a greater incursion of rainforest into eucalypt forest in recent years. Individuals of *Alphitonia petriei* and *Argyrodendron polyandrum* are also found at site 2 but were not recorded at the other sites. *A. petriei* is restricted to the road edge, where it is codominant with *Acacia aulacocarpa*, *A. mangium* and *Eucalyptus torelliana*. At site 3, the edge is more disturbed due to more recent logging activities, and the "C" zone is more extensive. The "A" zone also contains a higher proportion of *Allocasuarina littoralis*, *A. torulosa*, *Eucalyptus tereticornis* , and *Neolitsea dealbata* occurs in the "C", "D" and "E" zones.

Medium open forest (zone "A") in the Kirrama study area is dominated by *Eucalyptus intermedia*, over a grassy understorey with *Imperata cylindrica* var.

Figure 2.9 Canopy profile diagram (next page) for the ecotone at Kirrama site 1. Zones A, B, C, D and E are described on the previous page.

SPECIES SHOWN IN THE DIAGRAM:

1. *Eucalyptus intermedia*
2. *Banksia integrifolia*
3. *Eucalyptus grandis*
4. *Eucalyptus torelliana*
5. *Alyxia thyrsifolia*
6. *Cupaniopsis serrata*
7. *Rhodomyrtus trineura*
8. *Alectryon tomentosus*
9. *Canarium australasicum*
10. *Glochidion ferdinandii*
11. *Alstonia muellerana*
12. *Schizomera ovata*
13. *Syzygium wilsonii*
14. *Euodia elleryana*
15. *Albizia toona*
16. *Cryptocarya mackinnoniana*
17. *Acacia aulacocarpa*
18. *Cryptocarya rigida*
19. *Melicope* sp.
20. *Darlingia darlingiana*
21. *Syzygium smithii*
22. *Agathis robusta*
23. *Flindersia brayleyana*
24. *Austromyrtus hillii*
25. *Gahnia* sp.


HEIGHT (m)
0
10
20
30
1
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
0
10
20
30
40
50
A
B
C
D
E
DISTANCE ALONG TRANSECT (m)

*major, Panicum maximum* and *Themeda australis.* Other woody species are less common and include *Acacia aulacocarpa, Alstonia muellerana, Banksia integrifolia, Cassia floribunda, Eucalyptus tereticornis, E. resinifera, Lophostemon suaveolens, and Xanthorroea sp. Maesa dependens, Pteridium esculentum* and *Guioa acutifolia* occur in the understorey. Tree heights seldom exceed 30 m, and density of trees of all tree species was estimated from quadrat data at 348 trees per hectare.

*Eucalyptus grandis* is the most obvious element of the "B" zone with individuals up to 50 m in height and in excess of 4m in girth. The understorey of the tall open forest varies from that found in the medium open forest to dense shrub - and vine thicket characteristic of the "C" zone. The latter is composed of shrubs, vines and herbs and some tree saplings up to 5 m in height, seldom exceeding 10cm in girth. A high proportion of the shrubs and saplings are members of the family Sapindaceae. Species found in this zone include *Alyxia thyrsifolia, Alstonia muellerana, Aglaia ferruginea, Alectryon tomentosus, Cupaniopsis serrata, Canarium australasicum, Euodia elleryana, Glochidion ferdinandii, Rhodomyrtus trineura, Rhodamnia sp., Schizomera ovata, Symplocos sp. and Zanthoxylum brachyacanthum.* The herb *Solanum torvum* and *Gahnia sp.* sedge were found in gaps in the shrub layer.

Tree species in the rainforest margin have a distinctive architecture, with branches spreading horizontally to maximise light interception. The most obvious example of this phenomenon is *Alphitonia petriei*, which frequently has a crown diameter in excess of its height in mature individuals, and an unusually small amount of canopy overlap. Canopy heights in the forest margins at Kirrama vary between 20 and 30 m, although individuals of *Eucalyptus torelliana* and *Acacia mangium* may reach heights of 40 m. The young rainforest margin (zone "D") contains *Acacia aulacocarpa, A. mangium, Albizia toona, Canthium* sp. aff. *C. odoratum, Eucalyptus torelliana, Flindersia brayleyana, Podocarpus neriifolius and Polyscias sp.* Sapindaceous shrubs, vines and saplings from zone "C" are still present but less common.

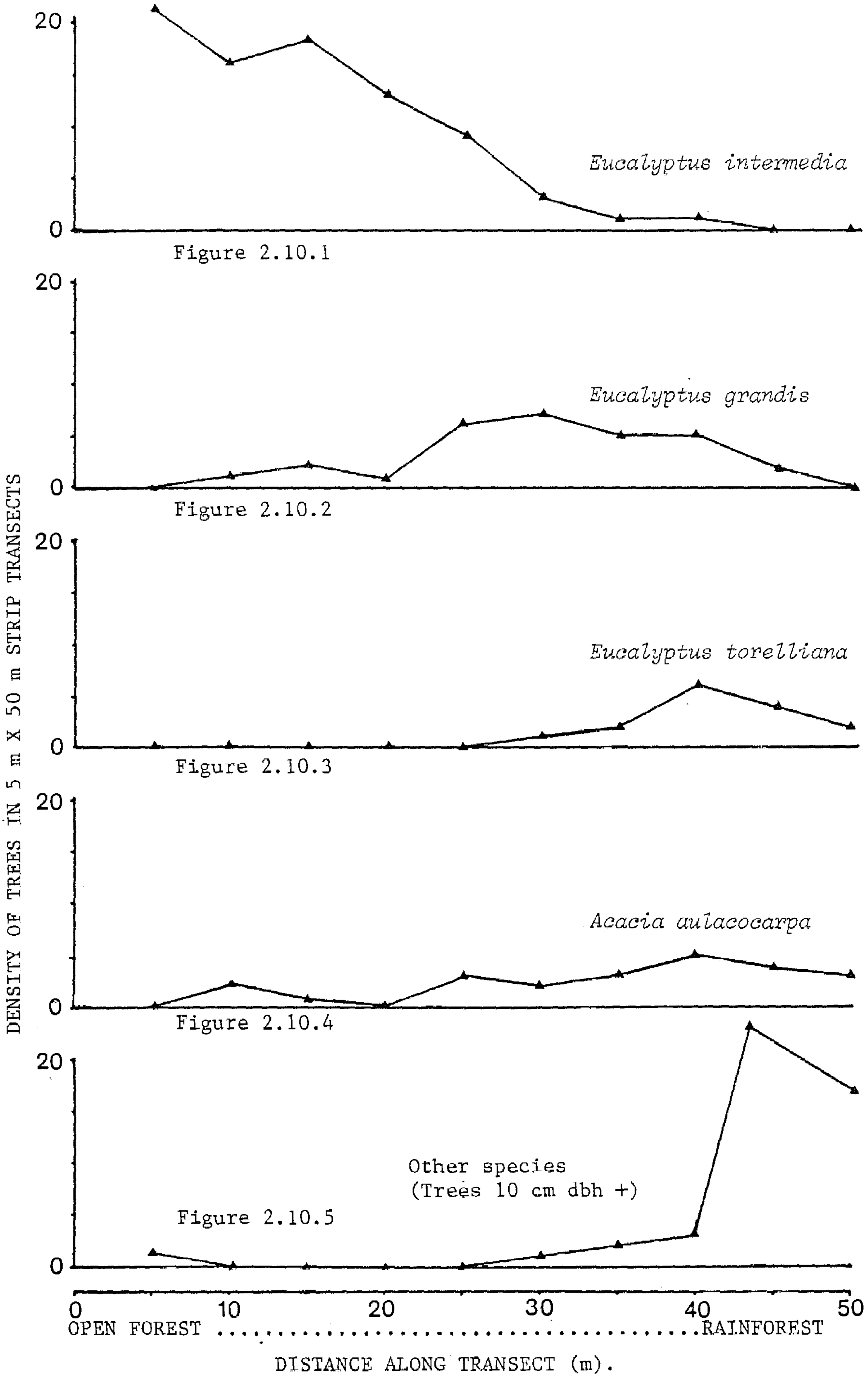
The mature rainforest has an irregular canopy 25 to 30 m in height with emergent *Acacia aulacocarpa, A. mangium* and *Agathis robusta* to 40 m. Canopy species include *Alstonia muellerana, Argyrodendron polyandrum, Austromyrtus* *hillii, Canarium australasicum, Cryptocarya mackinnoniana, C. putida, C.*sp., aff. *C. rigida, Darlingia darlingiana, Elaeocarpus* sp. nov. (BRI 126145), *Flindersia brayleyana, Glochidion ferdinandii, Melicope* sp., *Symplocos* sp., and *Syzygium smithii*. Understorey species such as *Bowenia spectabile, Dendrocnide moroides* and *Syzygium wilsonii* occur throughout, but the forest floor behind the ecotone is nevertheless relatively open, and dense low level vegetation occurs only under gaps in the canopy. Lianes and vascular epiphytes were present but uncommon. Plank buttresses occur only in a few species in the area. Vines such as *Calamus spp.* and *Smilax* sp. were also in evidence. With the exception of emergents, tree girths were less than 60 cm dbhob. The rainforest was classified according to Tracey (1982) as simple notophyll vine forest with *Agathis* emergents, although some discrepancies exist between the rainforest described in this reference and that found in the Kirrama study area.

The results for the 50 m x 50 m quadrat and the two 5 m x 50 m transects are shown in figures 2.10.1 to 2.10.10. The quadrat was divided into ten 5 m x 50 m strips running parallel to the rainforest boundary (fig. 2.8). Figures 2.10.1 to 2.10.4 show the densities of the four main tree species in each of the 5 m x 50 m strips for individuals >10 cm in girth.

The density of *Eucalyptus intermedia* is at a maximum furthest from the rainforest, and gradually diminishes to zero inside the rainforest (fig. 2.10.1). *E. intermedia* is replaced as the dominant tree species by *Eucalyptus grandis* in the tall open forest adjacent to the rainforest edge (fig. 2.10.2). Although tree density is not as high as that for *E. intermedia* in the medium open forest, the mean girth of *Eucalyptus grandis* (mean ± SE = 175.5 cm ± 12.817) is substantially greater than that for *E. intermedia* (58.0 cm ± 2.95).

*E. torelliana* is restricted to the rainforest ecotone (fig. 2.10.3) whereas *Acacia aulacocarpa* is found in small numbers in medium open forest, tall open forest and in slightly greater numbers in the ecotone and the rainforest (fig. 2.10.4). Figure 2.10.5 shows that tree species, other than the four dominants, with girths >10 cm are mainly restricted to the ecotone and the rainforest; very few of these species are fire tolerant open forest species.

Grasses species (mainly *Imperata cylindrica, Panicum maximum* and *Themeda australis*) are distributed in a similar pattern to *E. intermedia* (fig. 2.10.6)



Figures 2.10.1 to 2.10.5 Densities of trees greater than 10 cm dbh in 5 m X 50 m strips in a 50 m X 50 m quadrat at Kirrama site 2.

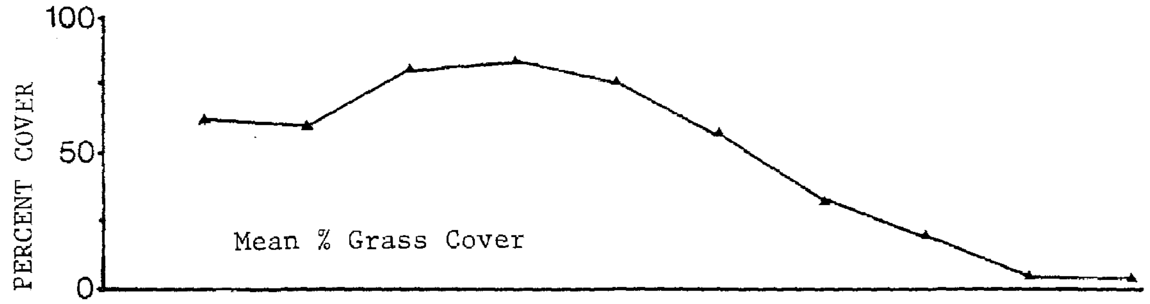


Figure 2.10.6

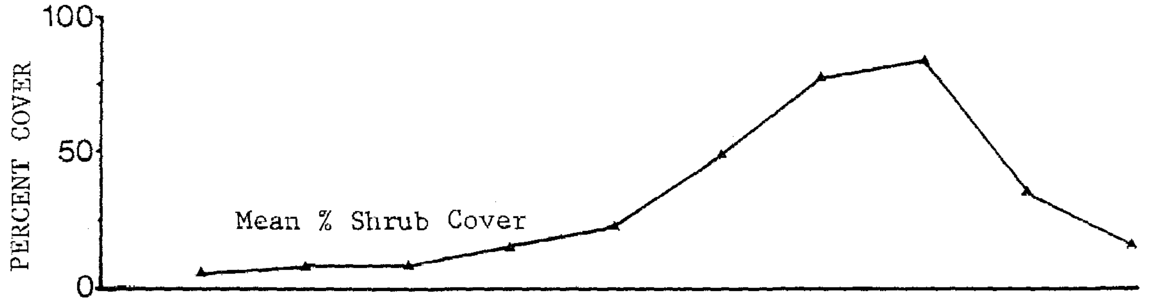


Figure 2.10.7

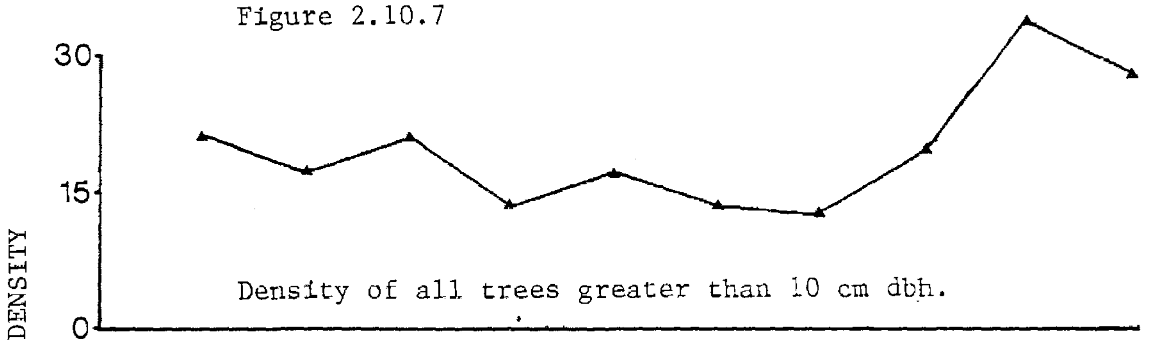


Figure 2.10.8

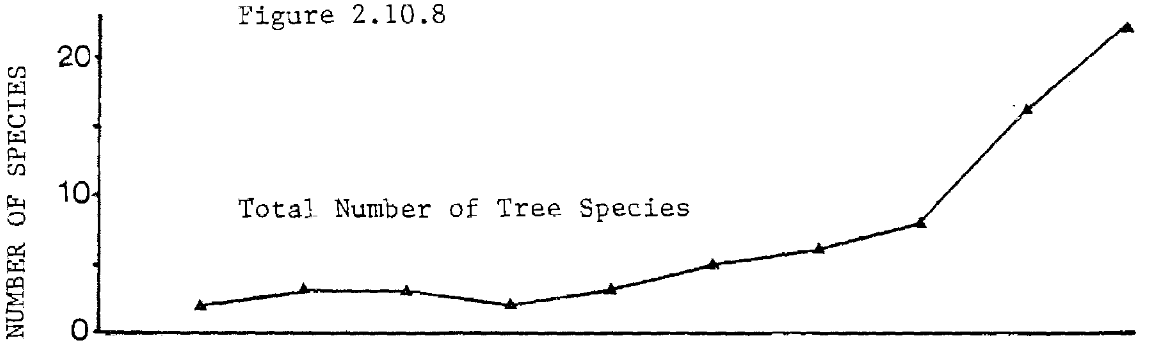


Figure 2.10.9

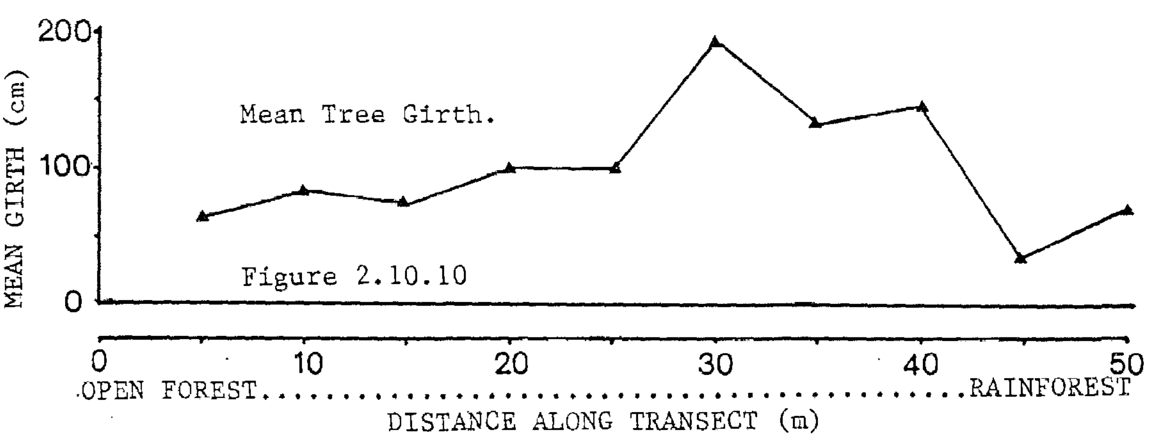


Figure 2.10.10

Figures 2.10.6 to 2.10.10 Grass cover, shrub cover, tree density, number of tree species and mean tree girth in 5 m X 50 m strips in a 50 m X 50 m quadrat at Kirrama site 2.

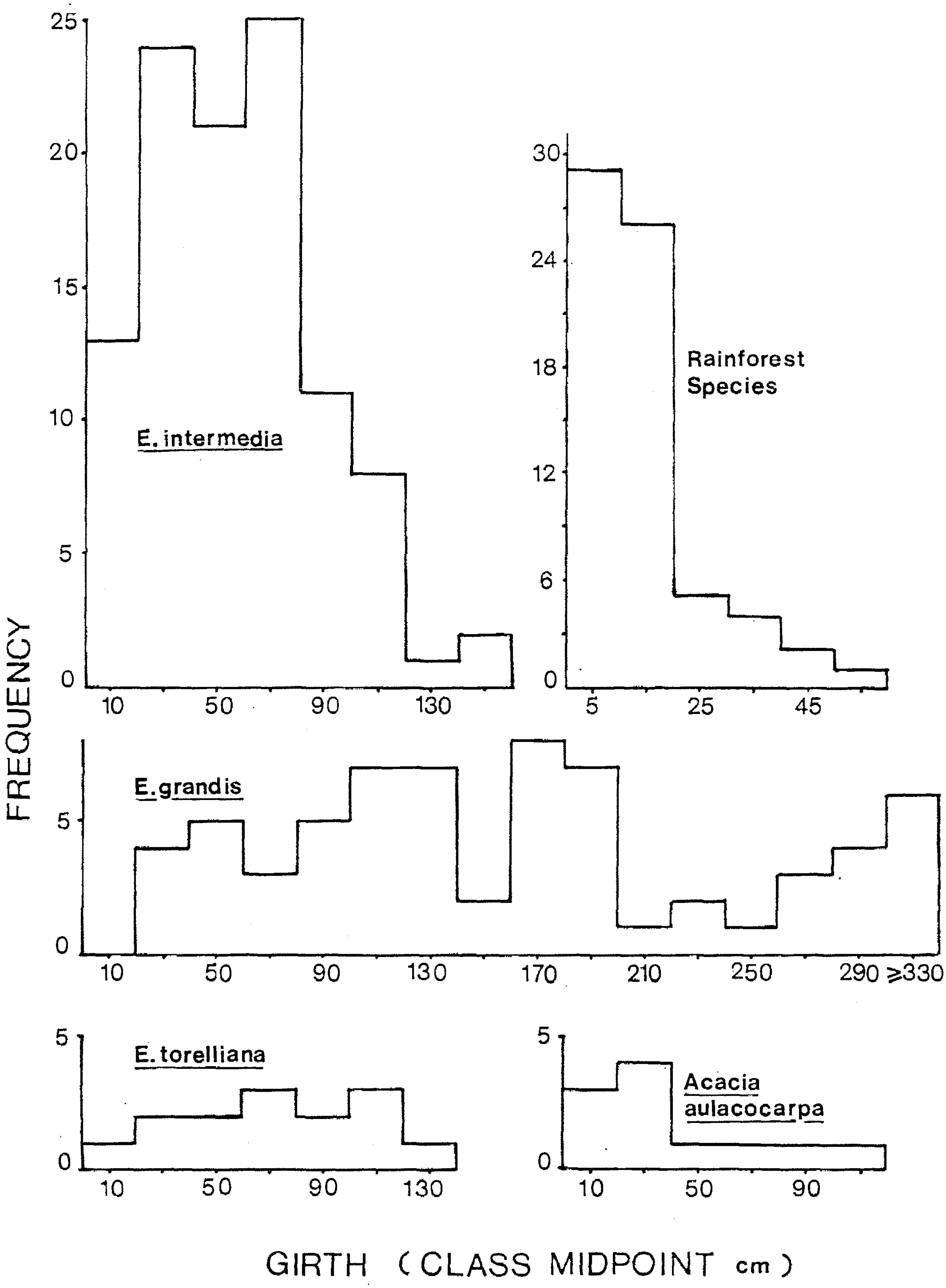


Figure 2.11 Girth frequency histograms for the four dominant tree species and miscellaneous rainforest species in a 50 m X 100 m quadrat at Kirrama site 2. Class midpoints in cm.

Under the denser vegetation cover of the ecotone these are replaced by more shade tolerant herbs and sedges. Grass cover varies seasonally with rainfall and fire frequency, but it is unlikely that the relative density deviates from the pattern shown in the figure. Mean percentage cover of shrubs and saplings <5 m in height varies inversely with grass cover, and reaches a peak in the ecotone, forming the dense barrier of vegetation on the rainforest described previously (fig 2.10.7).

Density of trees of all species >10 cm in girth reaches a minimum in the tall open forest belt, the low density here resulting from the presence of large individuals of *Eucalyptus grandis*. Maximum tree density occurs in the ecotone where there are large numbers of young rainforest trees. Tree density decreases inside the mature rainforest (fig. 2.10.8), where trees are larger, older and less densely spaced. Actual numbers of tree species per unit area reaches a maximum in the rainforest (fig. 2.10.9). Mean tree girth is highest in the tall open forest and lowest in the ecotone (fig. 2.10.10).

### (b) PALUMA

Vegetation at the Paluma site did not show the obvious zonation found on the Kirrama ecotones, but formed a complex mosaic of rainforest, tall open forest, sometimes with a rainforest understorey. An overall transition from rainforest to open forest took place from east to west, although pockets of tall open forest occurred within rainforest, and rainforest elements were found in gullies surrounded by medium open forest. A number of relatively dense, apparently even aged stands of young *Eucalyptus grandis* with vigorous understoreys of rainforest shrubs and saplings occurred throughout the area, indicating that at these sites, rainforest has moved into the open forest relatively recently. Elsewhere in the tall open forest, fire scars on boles and fire damaged or killed rainforest shrubs and saplings indicate that fire has slowed or halted the westward movement of the rainforest margin.

Medium open forest at the Paluma site was dominated by *Eucalyptus intermedia*, *Syncarpia glomulifera* and on higher ground, *Allocasuarina torulosa*. Other tree and shrub species included *Alphitonia excelsa*, *Banksia integrifolia* and *Rhodomyrtus trineura*. The forb layer was composed of the grasses *Imperata cylindrica* and *Panicum maximum*, *Pteridium* spp., and *Alpinia caerulea*, *Gahnia sp.* *Helichrysum rupicola* and *Pimelia* sp..

Tall open forest was dominated by *Eucalyptus grandis* with individuals exceeding 5 m in girth and 55 m in height. Other elements in tall open forest varied widely, and included *Acacia aulacocarpa*, *A. melanoxylon*, *Alectryon tomentosus*, *Alphitonia petriei*, *A. whitei*, *Alstonia muellerana*, *Breynia cernua*, *Dodonea tenuifolia*, *Glochidion sp.*, *Neolitsea dealbata*, *Pomaderris argyrophylla*, *Polyscias australianum*, *Rhodomyrtus trineura* and *Sloanea langii*, as well as a range of tree and shrub species in common with the rainforest proper. In more open areas dominated by *Eucalyptus grandis*, *Alpinia* spp., *Gahnia* spp., *Imperata cylindrica*, *Maesa dependens* and *Panicum maximum* were evident, along with pockets of *Lantana camara*.

In areas of rainforest without a dominant eucalypt canopy, some of the more common tree and shrub species were *Acacia melanoxylon*, *Acmena smithii*, *Baloghia* sp., *Buchanania* sp., *Cryptocarya* sp., *Endiandra discolor*, *Ficus rubiginosa*, *Elaeocarpus largiflorens*, *Guioa acutifolia*, *Mischiocarpus lachnocarpus*, *Neolitsea dealbata*, *Pittosporum ferugineum*, *Sloanea australis*, *S. langii* and *Syzygium australe*.

Canopy heights and stem densities varied greatly throughout the area, indicating a wide range of stand ages and therefore a complex history of disturbance and regrowth.

## 2.7 CONCLUSIONS AND SUMMARY

Few areas in the world contain examples of vegetation and microenvironmental transitions as abrupt and as contrasting as the north Queensland rainforest - open forest interface (Domin, 1911). The two plant assemblages are distinguishable in terms of vegetation structure, biomass, regeneration and successional processes, susceptibility to disturbance, and microenvironmental factors including temperature, humidity (and hence saturation deficit), light and exposure to environmental extremes. The transition from one set of environmental parameters to the other takes place in some cases over only a few metres. A similar change in environment occurs vertically, particularly in the rainforest. The differences between the environment on the forest floor and that in or above the canopy should not be overlooked, as these can logically be expected to be as great or greater than the differences found in the horizontal transition from closed to open forest, particularly with respect to the light environment.

The future vegetation of an area is largely determined by the success or failure of plants of different species to disseminate propagules, germinate, establish, grow and compete successfully with other plants. However,the most extreme habitat changes in the ecotone occur at or just above ground level. This is the environment encountered by propagules and seedlings of all plant species except for epiphytes, hence the pressure of environmental extremes on the forest floor will determine the eventual species distribution.

# CHAPTER 3

# WATER RELATIONS ON THE RAINFOREST - OPEN FOREST ECOTONE

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"It rained and it rained and it rained. Piglet told himself that never in his life, and he was goodness knows how old - three, was it, or four? - never had he seen so much rain."
(Milne, 1936)

## 3.1 INTRODUCTION

The humid tropical coast and adjacent uplands of north Queensland are traversed by acute topographic rainfall gradients running both east - west and north - south (Chapter 2). The discontinuous distribution of rainforest in this region is influenced by topography, fire and moisture regime as well as by agricultural land use. However, no causal relationship has been demonstrated between rainfall pattern and rainforest distribution (Unwin, 1983). It is believed that Australian tropical rainforests are restricted to areas with greater than 1200 mm mean annual rainfall and with no less than 25 mm mean monthly rainfall in the driest month (B.R. Jackes, pers. comm.) but discontinuous patches of rainforest occur westward from the coast as far as the 800 mm isohyet (Webb and Tracey, 1981). As no studies have ever been carried out to investigate the processes which relate forest growth to moisture availability in the Australian tropics, it remains to be proved that water relations determine the areas in which tropical rainforest can grow.

Unwin (1983) observed that in various parts of the Atherton Tablelands, rainforest and eucalypt forest coexist across a wide range of rainfall conditions. On the northern shore of Tinaroo Falls Dam with a mean annual rainfall of 1200 mm, tall open forest with *Eucalyptus grandis* occurs adjacent to seasonally dry upland rainforest. At the other extreme, Gadgarra State Forest, with a MAR of 2028 mm, contains examples of moist upland rainforest and open forest with *E. grandis* and *E. pellita*. Two further sites in coastal areas (Mission Beach, MAR = 3037 mm, and South Johnstone, MAR = 3302 mm) contain examples of both lowland rainforest and medium open forest (Unwin, 1983).

Stocker and Unwin (1986) proposed an ancient continuum in north-eastern Australia between tall coastal rainforest and semi arid thicket assemblages further inland, distributed according to rainfall variation. They suggested that this vegetation gradient was disrupted by an increase in fire frequency following the arrival of aboriginal man approximately 40000 years before present, and many of these closed forest assemblages have been replaced by fire tolerant, eucalypt dominated assemblages.

Webb and Tracey (1981) attempted to correlate climatic factors with particular rainforest types, but their conclusions related only to "core" areas, outside which there are "...many extraneous floristic elements as the result of past climatic changes." Table 3.1 shows the average climatic parameters for closed forest types on optimum sites throughout Australia as suggested by Webb and Tracey (1981).

| | | | Rainfall | | | Temperature | |
|---|---|---|---|---|---|---|---|
| Floristic element or province (climate type) | Structural type (on optimal site) | 'Average' climate station | mean annual (mm) | mean annual raindays | mean for driest six consecutive months (mm) | mean minimum, coldest month (°C) | Soil fertility |
| Tropical seasonal wet | complex mesophyll vine forest | Innisfail, Qld | 3644 | 155 | 760 | 15.1 | High |
| Tropical strongly seasonal moist | semi-deciduous mesophyll vine forest | Iron Range, Qld | 2049 | 202 | 215 | 18.4 | High/medium often riverine alluvium |
| Tropical strongly seasonal dry | deciduous microphyll vine forest | Kowanyama, Qld | 1222 | 71 | 36 | 14.8 | High/medium/low |
| Tropical extreme seasonal (monsoonal) moist | semi-deciduous notophyll vine forest | Darwin, NT | 1534 | 109 | 110 | 18.9 | Medium generally enriched coast sand |
| Warm sub-tropical seasonal moist | complex notophyll vine forest ± araucarians | Condong, NSW | 1722 | 142 | 550 | 5.8 | High |
| Sub-tropical seasonal dry | semi-evergreen microphyll vine thicket | Biloela, Qld | 699 | 75 | 187 | 5.1 | High/medium |
| Cool sub-tropical cloudy moist | notophyll vine forest | Cloud's Creek, Qld | 1397 | 138 | 413 | −0.3 | High/medium |
| Submontane cloudy moist | microphyll fern forest | Wentworth Falls, NSW | 1374 | 149 | 405 | 1.5 | High/medium |
| Warm temperate moist | microphyll vine-fern forest | Cann River, Victoria | 1004 | 146 | 448 | 2.0 | High/medium |
| Cool temperate wet | nanophyll fern or moss forest | Waratah, Tasmania | 2201 | 252 | 820 | 1.5 | High/medium/low |

Table 3.1 Environmental relationships between climatic types and structural types of rainforest, using selected meteorological data. from Webb and Tracey, 1981 (Copied with permission).

Plant moisture stress can be evaluated by looking at water relations under natural and artificial conditions. Measurements of transpiration compared to absorption rates are the ideal, but are difficult to carry out on a whole plant in the field with any reliability. Leaf conductance measurements with a diffusion porometer can be done on leaves still attached to the plant, but they only give an indication of transpiration on one leaf at a particular time. However, water potential determinations can be used to assess the water status of the whole plant in the field, water potential given as:

( $\psi$ ) = pressure (turgor) potential - osmotic potential - matric potential (Slatyer, 1967). Note that ( $\psi$ ) is always considered to be negative. The latter is the most widely used measurement.

Total water potential and osmotic potential are the most commonly used parameters to determine plant water status, but the meaning and interpretation of each one under natural conditions is sometimes open to speculation. Medina (1983) interprets total water potential as a direct indicator of total water status in a plant, thus minimum values of healthy leaves during periods of water stress can be used to indicate drought tolerance. Plant water potential can be measured using the "pressure bomb" technique pioneered by Scholander *et al* (1965) and described in detail by Waring and Cleary (1967). So called PMS (plant moisture stress) measurements are dependent on soil moisture potential, atmospheric conditions and the ability of the plant to control water loss (Waring and Cleary, 1967). Predawn PMS measurements give the best indication of the soil moisture potential, as the plant is most likely to be at equilibrium with the soil at this time. Midday to early afternoon measurements will show the minimum water potential, and hence the maximum level of water stress, attained by the plant.

When considering water relations, two groups of plants are recognised, drought tolerators and drought avoiders. Species in the first group have a plasmatic tolerance to low water potentials and osmotic potentials in their vacuolar sap. Drought avoiders present several characteristics that allow them to overcome water stress without reducing water potential to any great extent. These include deep root systems which guarantee adequate water supply during dry periods; efficient stomatal regulation of transpiration; and shedding of transpiring organs when water losses cannot be recovered. These adaptations all involve an energy cost to the plant.

In tropical forests, the adaptations to water stress include (a) an increase in deciduous behaviour, (b) dominance of microphylly and compound deciduous leaves, (c) greater development of underground organs and deeper root systems, (d) tolerance to low water potential and low osmotic potential of the vacuolar sap in evergreens and (e) mechanisms for reducing the amount of absorbed radiation such as a high degree of leaf inclination, leaf roughness and hairiness (Medina, 1983).

Bazazz and Pickett (1980) reviewed ecophysiological studies on trees in tropical forests, and concluded that whilst little work has been carried out on transpiration in tropical forest trees, there are no good reasons to expect transpiration rates to be different between tropical and temperate trees under similar conditions. There is little difference in stomatal densities between the two, and available data indicate that a range in transpiration rates of 2.2 to 22.0 mg $H_2O$ $dm^{-2}s^{-1}$ is common to both (Walter, 1971). Understorey plants tend to have lower stomatal densities than emergent trees or plants growing in the open (Bazazz and Pickett, 1980).

Differences between early and late successional tree species with respect to cellular anatomy and stomatal behaviour have been found to occur in a number of instances (Bazazz and Pickett, 1980). Earlier successional trees have larger vessels, and hence a lower resistance to water movement, than do mature forest trees. Late successional and understorey species are sensitive to water limitation and close their stomata quickly when they experience water deficit, thus lowering photosynthetic and transpiration rates (Bazazz and Pickett (1980). However, few measurements have been carried out on photosynthesis in moisture stressed tropical tree species.

Very few measurements of tissue water potential have been reported for plants growing in tropical environments (Robichaux *et al*, 1984). Fetcher (1979) measured the water potential of five tree species in wet lowland forests in Panama. At the end of a prolonged dry season, diurnal water potentials varied between -0.5 and -2.5 MPa for most species, but *Trichilia tuberculata* reached values as low as -3.9 MPa. These results indicate that plants in even the wet tropical environments may be subjected to severe tissue water deficits during prolonged dry periods (Robichaux *et al*, 1984).

Water potential values of between -0.2 and -0.4 MPa in the wet season and -0.8 to -1.2 MPa in the dry season were reported by Robichaux and Pearcy (1980) for understorey *Euphorbia* spp. in Hawaiian mesic forests. Oberbauer (1982) measured water potentials in *Pentaclethra macroloba*, a common tree species growing in lowland wet forests in Costa Rica. While water potentials reached -1.7 MPa in the upper canopy, the minimum values in the understorey leaves of the same species were often up to 0.5 MPa higher. Medina (1983) reported a range of -0.1 to -1.0 MPa in three montane wet forest species in Costa Rica on an exceptionally clear day.

Leaf area indices of forests have been shown to have a significant effect on plant water potentials. Unpublished data by Rundel (Robichaux *et al.* 1984) that predawn water potentials for tree species growing in undisturbed forest with a leaf area index of 6 $m^2/m^2$ were up to 3.5 times lower than those growing in a large gap with a low leaf area index. Higher levels of moisture available to plants in gaps because of lower transpiration rates per unit area of forest would account for these results, but the greater degree of exposure to sunlight and air movement in gaps might tend to counter the effect. Insufficient data are available to draw any valid conclusion at this point.

Parrish and Bazazz (1982) investigated niche responses of early and late successional tree species along light, nutrient and moisture gradients. They found that seedling of the early successional species (*Pinus taeda*, *Crataegus mollis* and *Gleditsea triacanthos*) had greater niche breadths than the late successional species (*Acer saccharum*, *Quercus rubra* and *Tilia americana*). As well as being able to grow in a greater range of moisture regimes, the early successional species showed greater tolerance of dry conditions.

Ladiges (1974) examined the drought tolerance of four populations of *Eucalyptus viminalis* grown from seed under glasshouse conditions. The seedlings taken from populations in low rainfall areas showed greater resistance to desiccation and were less damaged by sustained drought than the seedlings from the two high rainfall populations. The more resistant seedlings did not simply avoid drought by quickly closing stomata, but were capable of maintaining relatively high rates of transpiration under moderate moisture stress. Wilting occurred in the high rainfall populations at higher water potentials and higher relative leaf turgidity than in the low rainfall populations. Jarvis and Jarvis (1963) determined that a linear relationship exists between water potential and relative turgidity, in four species of varying degrees of drought tolerance.

Two eucalypt species, *E. behriana* and *E. microcarpa*, investigated by Myers and Neales (1984), produced a mean dawn water potential at three sites of -3.07 MPa. Seasonal variation ranged from -2.0 ± 0.1 to 4.4 ± 0.1 Mpa, depending on rainfall. Dawn water potential for the lower rainfall site dominated by *E. behriana* was frequently lower than that at the moister site with *E. microcarpa*. Myers and Neales (1984) concluded that the smaller and slower growing individuals of *E. behriana* were more drought tolerant than those of *E. microcarpa*, and that the two species intermingle in mixed stands in areas of intermediate drought stress. In these areas a broad ecotone occurs between mallee and woodland vegetation.

This chapter describes experiments carried out in the field and under glasshouse conditions to determine the nature of the change in water relations across the rainforest - open forest boundary. Measurements of soil moisture and plant water potential in the field showed marked changes in water availability and levels of plant moisture stress through the ecotone, and the results confirm water relations as an important factor in determining the establishment and distribution of species and ultimately vegetation types. Glasshouse experiments were used to establish the relative levels of drought tolerance in seedlings of tree species from rainforest, ecotone and open forest, and the trends observed in these experiments closely mirror the respective distributions of the same and similar species in the field.

## 3.2 MATERIALS AND METHODS

### 3.2.1 FIELD EXPERIMENTS

Soil moisture determinations were carried out at Kirrama Site 1 on three 50 m transects running perpendicular to the rainforest margin (Chapter 2) in February, August and November, 1984. Two soil samples were collected every 5 m along each transect at depths of 0 - 10 cm (litter excluded) and 40 - 50 cm below ground level. The samples were placed in glass jars sealed with parafilm and a screw cap. Previous trials with this method have shown no discernable change in soil wet weight for periods of up to 2 months provided the seal remains undamaged. The samples were individually weighed, oven dried at 90°C for 10 days and then reweighed to determine pecentage soil moisture.

Water potential measurements were conducted at Kirrama sites 1, 2 and 3 from 1983 to 1986 to examine variations in plant water relations according to species, diurnal and seasonal changes, topography and surrounding vegetation type. A "pressure bomb" leaf chamber was used for all measurements.

Eleven tree species were selected from rainforest, ecotone and open forest habitats. Table 3.3 shows the species used and the number of replicates for each. Water potential measurements were carried out on five successive days in May 1983, and on four successive days in August 1983 between 11:30 and 14:00 hours. One healthy branch was brought down from an unshaded portion of the crown of each tree using a rifle with a telescopic sight. A twig with at least three intact leaves was removed from the branch and placed in the pressure chamber within 2 minutes of the branch reaching the ground.[1] In most cases, three measurements were made on different twigs from each branch, and the mean water potentail of these was recorded. Temperature, relative humidity, light intensity and estimated cloud cover were also recorded. The height of each tree used in the experiment was estimated using a clinometer.

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[1] Preliminary trials carried out with accessible branches removed from trees showed that water potential in leaves from the ends of large branches remained constant for periods of no less than 2 minutes and up to 10 minutes from the time the branch was removed, depending on air temperature and relative humidity. Water potential then began to decrease steadily.

Measurements of water potential for saplings between 2 and 3 m in height were also made for five species during the course of the experiment. These are also shown in table 3.3.

Five individuals of *Eucalyptus intermedia* were selected to determine the effects of topography and associated vegetation on the predawn water potential of a single species. These trees were located along a 200 m transect on a gradual slope at Kirrama Site 1. Tree 1 was located on level ground at the top of the slope in medium open forest. Tree 2 was also located in medium open forest 50 m downslope from tree 1 and an estimated 2.5 m lower. Trees 3 and 4 were 150 m downslope from tree 1, growing in tall open forest in association with *Eucalyptus grandis*. Tree 5 was 30 m further downslope and surrounded by immature rainforest 5 m inside the rainforest ecotone. All trees were between 25 and 30 m in height. The trees were selected and marked during daylight. Branches were removed from the crowns between 04:00 and 05:30 hours using a spotlight and a 12 guage shotgun. An assistant was required to hold the spotlight and trace the descent of the branch. Water potential was recorded as described previously. This procedure was carried out on two successive mornings in February, August and November, 1984.

Measurements of water potential were made at 2 hourly intervals on two trees of *Eucalyptus grandis* and two of *E. intermedia* from 05:00 to 18:00 hours in August, 1984, June and May, 1985. The two *E. intermedia* individuals used were trees 1 and 4 from the previous experiment. Both *E. grandis* trees were approximately 35 m in height, one growing in tall open forest near the rainforest boundary, the other 40 m upslope from the first and largely surrounded by medium open forest. All measurements were made on unshaded leaves from the top part of the crown. Only the downslope *E. grandis* was recorded in May, 1986.

### 3.2.3 GLASSHOUSE EXPERIMENTS

Twelve seedlings of each of *Eucalyptus grandis*, *E. intermedia* and *E. torelliana* were grown from seed under glasshouse conditions. They were placed in 4.5 l pots containing a 3:1 sand : peat potting mix, watered 3 times weekly to field capacity and treated with 200 ml of standard strength 'Aquasol' fertilizer every two weeks. Light levels in the glasshouse were maintained at approximately 60% full sunlight. The pots were arranged on a 1 x 3 m bench in a randomised pattern.

Gypsum block soil moisture potential probes were buried 5cm below the soil surface in 12 pots containing seedlings and in 2 pots containing only soil. The experiment was conducted in November, 1983 when glasshouse temperature and relative humidity ranged between 20°C and 35°C, and 60% and 90% respectively. Temperature, relative humidity and cloud cover were recorded daily during the course of the experiment.

On the morning of day 1 of the experiment, each pot was watered to field capacity. Electrical conductance was measured in each gypsum block at 12:00 hours, and subsamples of soil from the two control pots were removed, weighed, oven dried and then reweighed to determine the correlation between conductance and percentage soil moisture. After the initial saturation, the pots were given no further water during the course of the experiment.

Midday measurements of water potential were carried out for 9 days. On each day, six seedlings of each species were selected, and three leaves were removed from each. Water potential measurements were recorded for each leaf, and the mean water potential was calculated for each seedling. The seedlings were rotated from day to day, so that leaves were removed from each seedling on every second day. No more than an estimated 10% of the foliage was removed from any seedling during the course of the experiment. Notes were made on the condition of each seedling, particularly with respect to wilting, at daily intervals. The experiment was terminated after 9 days, when the seedlings were destructively harvested, oven dried at 70°C for 5 days together with all leaves previously removed, then weighed. Total leaf areas were calculated using photocopies of all leaves from each seedling, which were cut out, weighed and compared with a series of standards. Attempts were made to obtain root dry weights, but it proved impossible to separate the roots from the potting mix with any degree of certainty.

A pilot moisture competition experiment between *Eucalyptus grandis* and *E. intermedia* was commenced in February, 1984. 33 seedlings of each species were grown from seed in 20 cm standard pots for. Watering, fertilization and potting mix were as previously described. Two seedlings were grown in each pot. The arrangement of seedlings and the number of replicates in each case are shown in table 3.2.

Table 3.2 shows the species and numbers of replicates used in the moisture competition experiments. Treatments were commenced in the pilot trial after 8 weeks of normal growth, and in the main trial after 10 weeks.

In both experiments, the "wet" treatment involved daily watering to field capacity of each pot to field capacity. In the "dry" treatment, no water was applied to any of the pots until the first signs of wilting became apparent, at which time all pots were watered to field capacity. This generally meant watering the "dry" pots at 5 day intervals, although towards the end of the experiments this interval was shortened to 3 days as the seedlings became larger and required more water.

| SPECIES PAIR | NUMBER OF REPLICATES | |
|---|---|---|
| | WET | DRY |
| *Pilot Trial* | | |
| *Eucalyptus grandis X 2* | 6 | 6 |
| *Eucalyptus intermedia X 2* | 6 | 6 |
| *Eucalyptus grandis + E. intermedia* | 9 | 9 |
| *Main Trial* | | |
| *Eucalyptus grandis X 2* | 4 | 4 |
| *Eucalyptus intermedia X 2* | 4 | 4 |
| *Eucalyptus torelliana X 2* | 4 | 4 |
| *Alphitonia petriei X 2* | 4 | 4 |
| *Syzygium fibrosum X 2* | 4 | 4 |
| *Toona australis X 2* | 4 | 4 |
| *Eucalyptus grandis + E. intermedia* | 8 | 8 |
| *Eucalyptus grandis + E. torelliana* | 8 | 8 |
| *Eucalyptus grandis + Toona australis* | 8 | 8 |
| *Toona australis + Syzygium fibrosum* | 8 | 8 |
| *Toona australis + Eucalyptus torelliana* | 8 | 8 |
| *Toona australis + Alphitonia petriei* | 8 | 8 |

Table 3.2 Numbers of pots used in the pilot and main moisture competition trials. Two seedlings were grown in each pot.

Heights of the seedlings were measured at the start of the experiment and at monthly intervals during the course of the experiment. All seedlings were harvested, dried and weighed after 10 weeks in the pilot trial and after 12 weeks in the main trial. Half way throught the experiment, 10 ml samples of soil were removed from 20 of the dry treatment pots at daily intervals for 5 days, weighed, dried and reweighed. The samples were taken from 5cm below the soil surface. Care was taken to avoid root damage.

Twenty seedlings of each of *Alphitonia petriei, Eucalyptus grandis, E. intermedia, E. torelliana, Flindersia brayleyana, F. pimenteliana, Neolitsea dealbata, Syzygium fibrosum, S. wesa and Toona australis* were grown from seed in 20 cm standard pots for 3 months, one seedling per pot. Ten of each were subjected to the wet treatment during the course of the main competition trial, and 10 to the dry treatment. At the end of 12 weeks of these treatments, all pots were watered to field capacity. The seedlings were then left for 10 days without water. Notes were made on the onset and severity of wilting in these seedlings. After 10 days the seedlings were rewatered, and watering was maintained until recovery occurred or until seedling death was established.

## 3.3 RESULTS AND DISCUSSION

### 3.3.1 FIELD EXPERIMENTS

Soil moisture percentages were higher in rainforest than in open forest in both dry and rainy conditions (figs. 3.1.1-3.1.3), and formed a gradient across the ecotone. In terms of seedling establishment, there is up to two times as much water available under a closed canopy in the rainforest than in medium open forest at the Kirrama study site. In the rainforest and ecotone areas, surface soil moisture was higher than in the subsurface (40 - 50 cm), while the opposite occurs in the open forest area, probably due to the greater coverage of shallow rooted grasses and herbs, and their high rate of transpiration.

The highest soil moisture contents occurred in February, while there is little apparent difference between the August and November results. Rainfall readings for Kirrama for the two months preceding each soil collection were 740.7 mm for January and February, 47.9 mm for July and August and 42.8 mm for October and November (Crowley, unpub.).

Table 3.3 shows mean midday water potentials for 11 species at the Kirrama study sites from periods during wet and dry seasons. Results from this data were divided into three site classes, rainforest, ecotone and open forest, according to the location of the individuals sampled. Two way analysis of variance showed a highly significant effect of site (F = 41.38, df = 2,25, p = 0.0000) and of season (F = 11.57, df = 2,25, p = 0.0003) but no significant interaction. It should be noted that since there is no species overlap between sites in this data set, the effect of site may be interpreted as an effect of species. Water potentials were highest in the rainforest in the wet season sample, lowest in the open forest and in the dry season, and intermediate in the ecotone. Mean water potentials for the three sites and two seasons are shown in table 3.4

These data suggest a gradient in the degree of drought tolernce between rainforest and open forest tree species, coincident with the changes in soil moisture availability and microclimate across the ecotone.

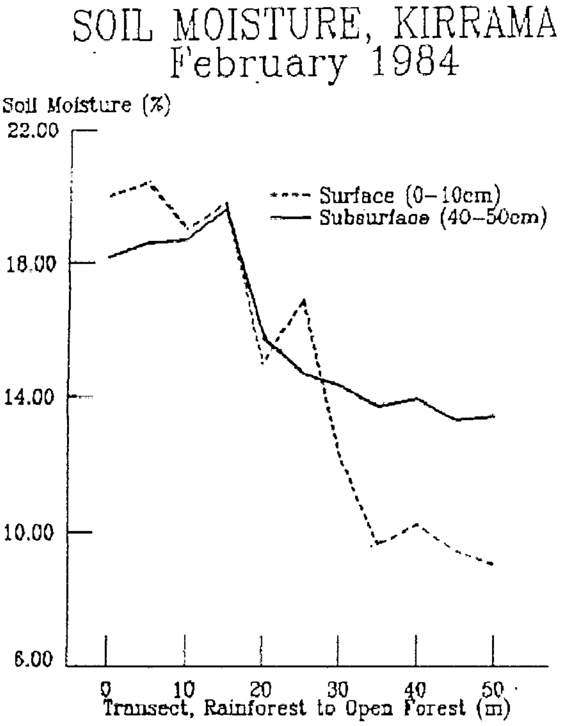

Figure 3.1.1

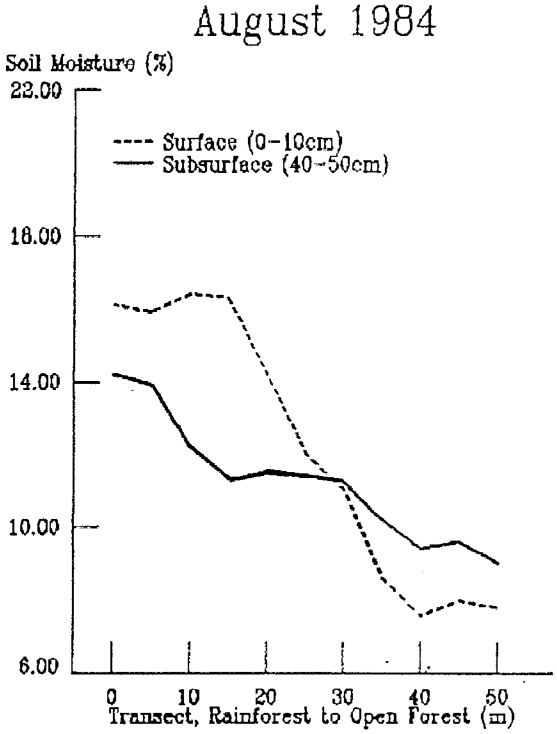

Figure 3.1.2

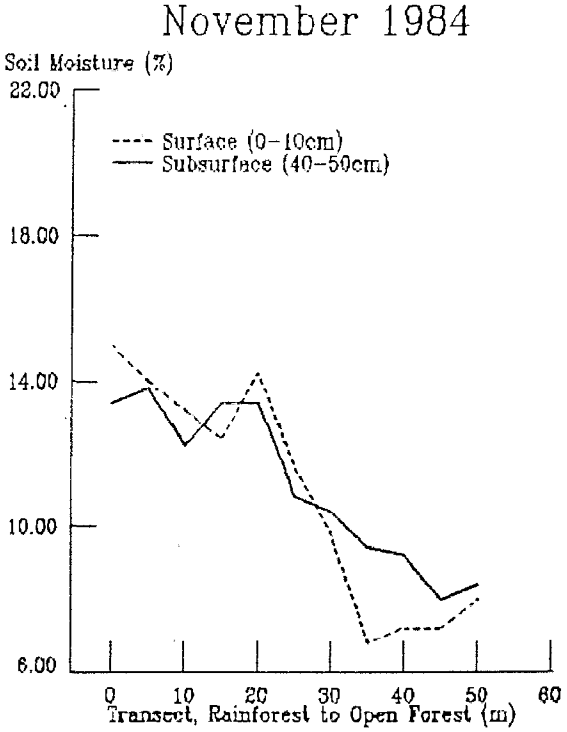

Figure 3.1.3

Figures 3.1.1 - 3.1.3 Percentage soil moisture at Kirrama in February August and November,1984. Broken lines show mean surface soil moisture (0 - 10 cm); unbroken lines show mean subsurface soil moisture (40 - 50 cm). Means calculted from 3 parallel 50m transects running from rainforest (left) to open forest (right).

|  |  |  |  | WATER POTENTIAL (-MPa) |  |  |  |
|---|---|---|---|---|---|---|---|
| SPECIES | LOCATION | TREE/ SAPLING | N | MAY 1983 |  | AUGUST 1983 |  |
|  |  |  |  | MEAN | ± SE | MEAN | ± SE |
| *Cardwellia sublimis* | R | T | 3 | 0.42 | 0.097 | 0.97 | 0.036 |
| *Cardwellia sublimis* | R | S | 2 | 0.29 | 0.098 | 0.73 | 0.047 |
| *Cryptocarya rigida* | R | T | 4 | 0.43 | 0.033 | 1.14 | 0.079 |
| *Darlingia darlingiana* | R | T | 3 | 0.36 | 0.018 | 0.99 | 0.011 |
| *Acacia aulacocarpa* | E | T | 5 | 0.72 | 0.009 | 1.86 | 0.106 |
| *Acacia aulacocarpa* | E | S | 5 | 0.51 | 0.007 | 1.16 | 0.065 |
| *Alphitonia petriei* | E | T | 5 | 0.68 | 0.047 | 1.57 | 0.135 |
| *Eucalyptus grandis* | E | T | 10 | 0.65 | 0.029 | 1.87 | 0.090 |
| *Eucalyptus grandis* | E | S | 5 | 0.48 | 0.017 | 1.45 | 0.048 |
| *Eucalyptus torelliana* | E | T | 5 | 0.48 | 0.028 | 1.49 | 0.056 |
| *Eucalyptus torelliana* | E | S | 5 | 0.37 | 0.035 | 1.15 | 0.071 |
| *Neolitsea dealbata* | E | T | 5 | 0.44 | 0.012 | 0.97 | 0.055 |
| *Allocasuarina torulosa* | O | T | 5 | 0.36 | 0.012 | 1.49 | 0.143 |
| *Eucalyptus intermedia* | O | T | 10 | 0.75 | 0.013 | 2.47 | 0.082 |
| *Eucalyptus intermedia* | O | S | 5 | 0.66 | 0.060 | 1.79 | 0.145 |
| *Eucalyptus tereticornis* | O | T | 10 | 0.98 | 0.024 | 2.52 | 0.161 |

Table 3.3 Mean midday water potentials for trees >15 m in height (T) and saplings <3 m in height (S) in rainforest (R), ecotone and tall open forest (E) and medium open forest (O). N is the number of plants sampled. Mean and standard error water potentials are given in -MPa.

|  | MAY 1983 | AUGUST 1983 |
|---|---|---|
| RAINFOREST | - 0.46 ± 0.061 | - 0.95 ± 0.053 |
| ECOTONE | - 0.54 ± 0.022 | - 1.44 ± 0.056 |
| OPEN FOREST | - 0.68 ± 0.510 | - 2.07 ± 0.102 |

Table 3.4 Mean ± standard error midday water potential (MPa) for a range of species in three different vegetation types at Kirrama.

The lowest midday water potentials occurred in *Eucalyptus intermedia* (-3.5 MPa, Mean ± SE = -2.47 ± 0.082 MPa) and in *E. tereticornis* (-4.0 MPa, Mean ± SE = -2.52 ± 0.161 MPa) in dry conditions. These two species also recorded the lowest water potentials in wet conditions. Highest water potentials occurred in the rainforest species *Cardwellia sublimis* and *Darlingia darlingiana* in both wet and dry conditions. The ecotone and rainforest understorey species *Neolitsea dealbata* also maintained a relatively high water potential in both the wet and dry season samples.

A paired t test showed a significant difference ($p < 0.01$) between water potentials of five tree species >15 m in height compared to saplings of the same species <3 m in height. Tree height must also be taken into consideration when considering moisture stress. The microenvironmental gradient of the ecotone is complicated by variations in canopy height, and an emergent tree in rainforest may suffer the same levels of moisture stress as an open forest tree of similar height. Water potential measurements recorded in relatively hot, dry conditions on 30m emergent rainforest trees were as low as -2.5 MPa (G.L. Unwin, pers.comm.). These data were collected with the aid of a 30 m permanent tower located in Curtain Fig State Forest. Equivalent data proved impossible to obtain at Kirrama due to the inaccessibility of emergent crowns.

The effects of site and topography on predawn water potential in *Eucalyptus intermedia* (table 3.5) showed water potentials of downslope trees closer to the rainforest margin are higher for August and November, but appear to be relatively uniform in the wet season sample. Assuming that predawn water potential accurately reflects soil water potential, the soil water potential is higher downslope and close to the rainforest edge in the dry season.

| | February | | August | | November | |
|---|---|---|---|---|---|---|
| Morning | #1 | #2 | #1 | #2 | #1 | #2 |
| Tree # | | | | | | |
| 1 | -0.2 | -0.25 | -0.6 | -0.5 | -0.5 | -0.45 |
| 2 | -0.25 | -0.15 | -0.55 | -0.6 | -0.6 | -0.55 |
| 3 | -0.2 | -0.2 | -0.7 | -0.65 | -0.5 | -0.45 |
| 4 | -0.25 | -0.2 | -0.4 | -0.55 | -0.35 | -0.4 |
| 5 | -0.2 | -0.25 | -0.35 | -0.35 | -0.4 | -0.35 |

Table 3.5 Predawn water potentials (MPa) for *Eucalyptus intermedia* on two successsive mornings in February, August and November, 1984. Trees numbered sequentially from 1 (upslope, 200m from the rainforest edge) to 5 (downslope, inside the rainforest edge).

These trends are verified by the diurnal water potential data shown in figures 3.2.1 to 3.2.3. The individuals of *E. intermedia* and *E. grandis* located upslope tended to maintain lower water potentials during the course of the day than those close to the rainforest edge. Water potentials in *E. intermedia* were consistently lower at each site than those for *E. grandis* on all occasions. The downslope *E. grandis* tree tended to reach its minimum water potential later in the day than the other trees, probably because of partial shading by the adjacent rainforest on the eastern side of this tree.

## GLASSHOUSE EXPERIMENTS

Percentage soil moistures estimated from electrical conductance in the gypsum blocks during the course of the glasshouse water potential trial are shown in figure 3.3. The readings from the two control pots containing soil only, lay within the 95% confidence limits of the other readings, indicating that the major component of water loss from the pots was through evaporation from the soil surface. It was therefore assumed that soil

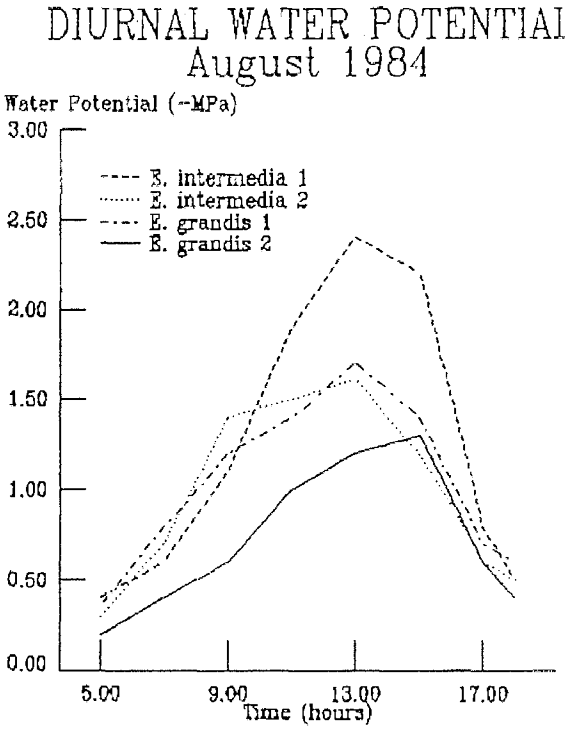
DIURNAL WATER POTENTIAL
August 1984

Figure 3.2.1

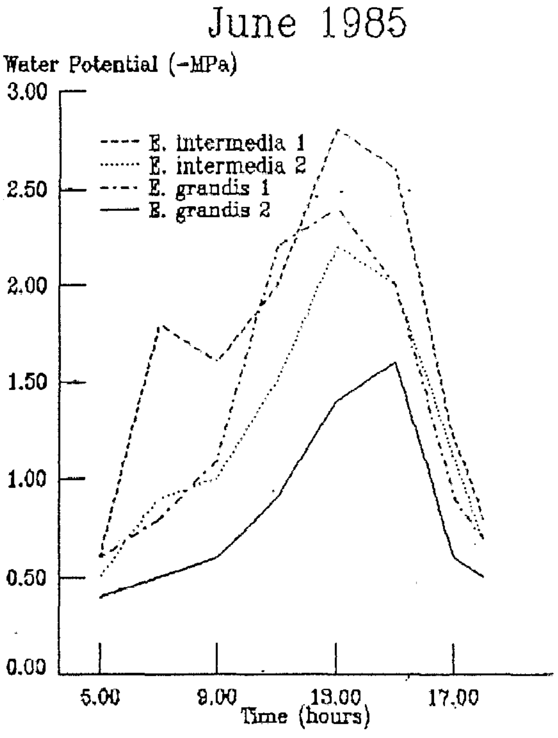
June 1985

Figure 3.2.2

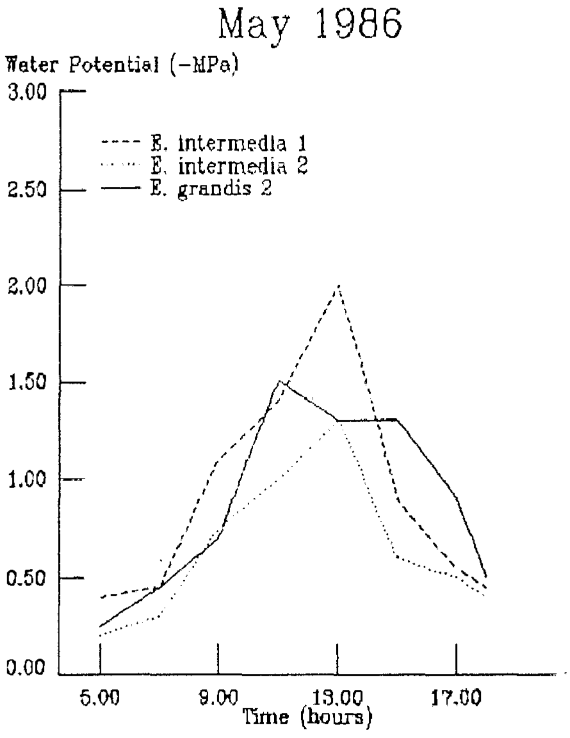
May 1986

Figure 3.2.3

Figures 3.2.1 - 3.2.3 Variations in water potential (-MPa) in August 1984, June, 1985 and May, 1986 in individual trees of *Eucalyptus grandis* and *E. intermedia* located upslope in medium open forest (1) and downslope, near the rainforest edge (2). Water potential measurements were carried out at two hourly intervals from 0500 to 1800.

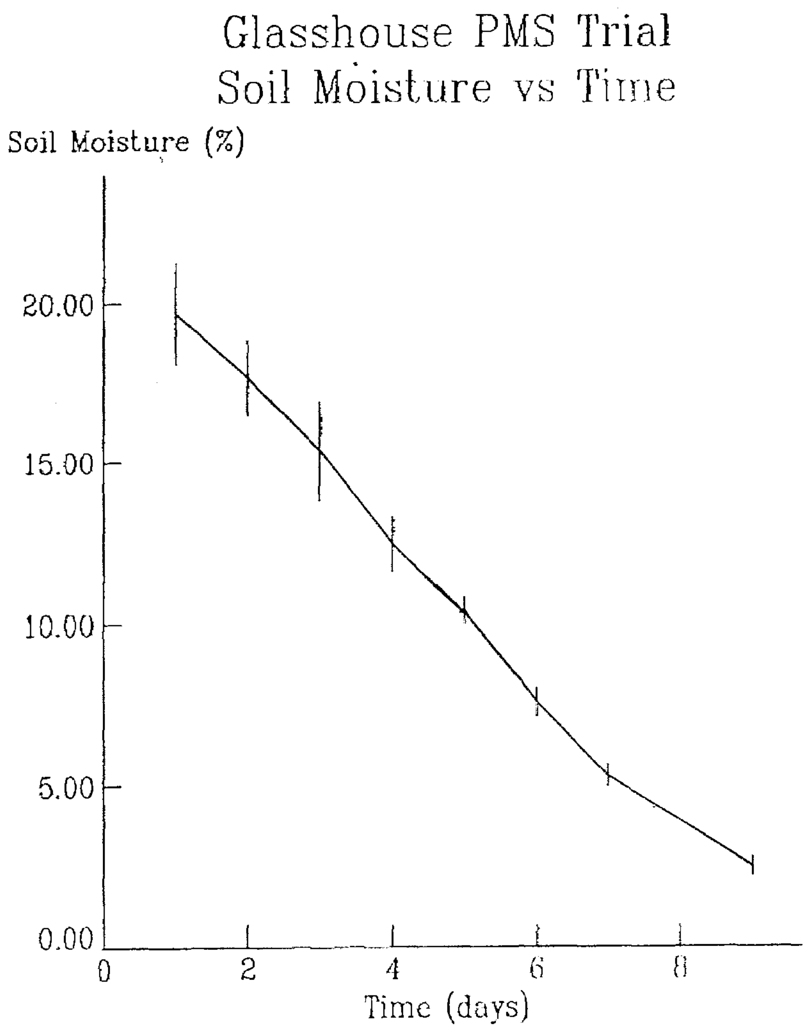

Figure 3.3

Figure 3.3 Mean and standard error soil moisture against time in the glasshouse moisture stress trial. Soil moisture in percent, time in days.

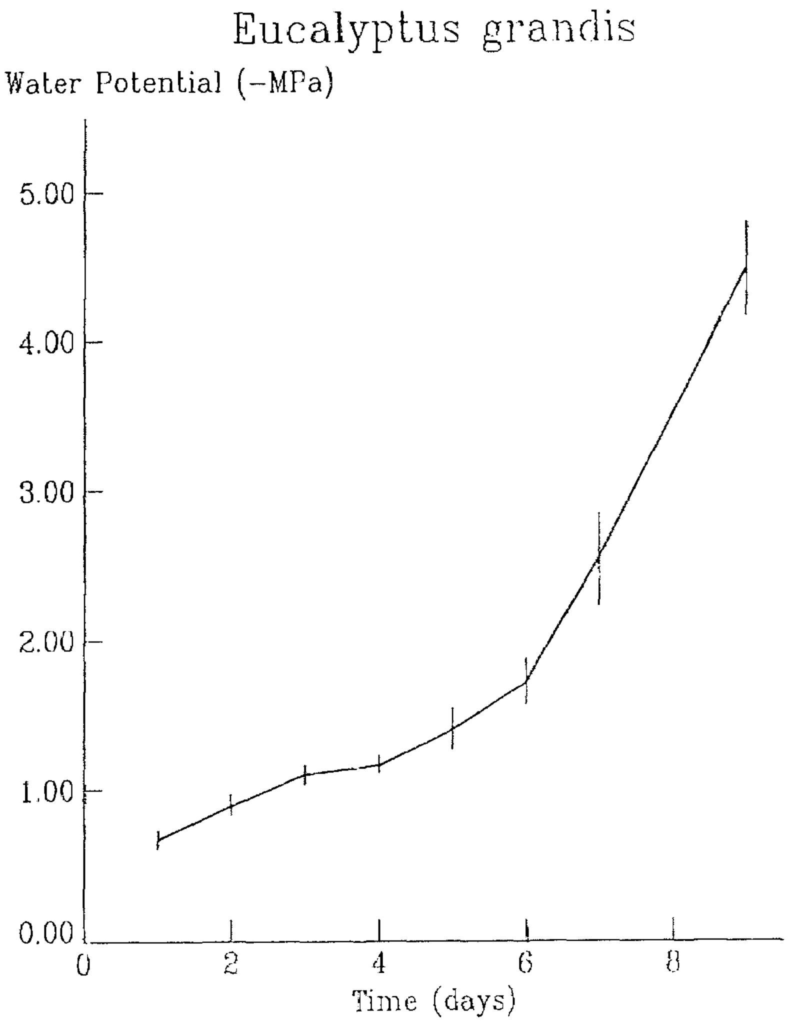

Figure 3.4.1

Figure 3.4.1 Mean and standard error water potential (-MPa) against time (days) in seedlings of *Eucalyptus grandis*.

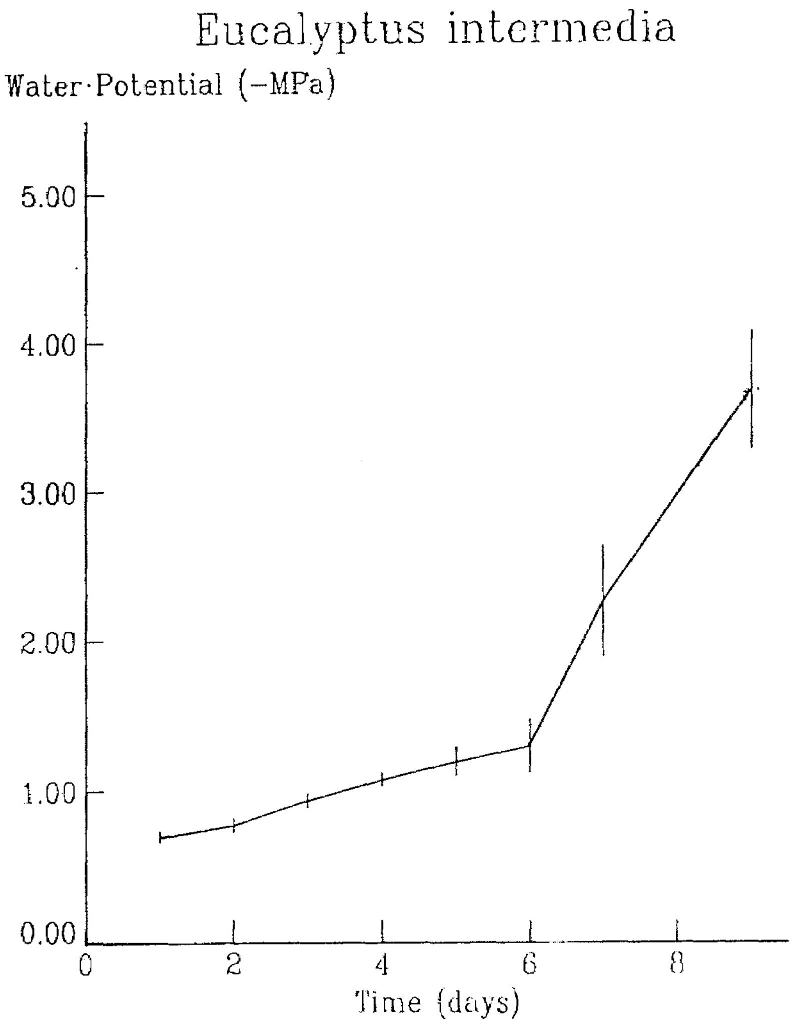
Eucalyptus intermedia

Figure 3.4.2

Figure 3.4.2 Mean and standard error water potential (-MPa) against time (days) in seedlings of *Eucalyptus intermedia*.

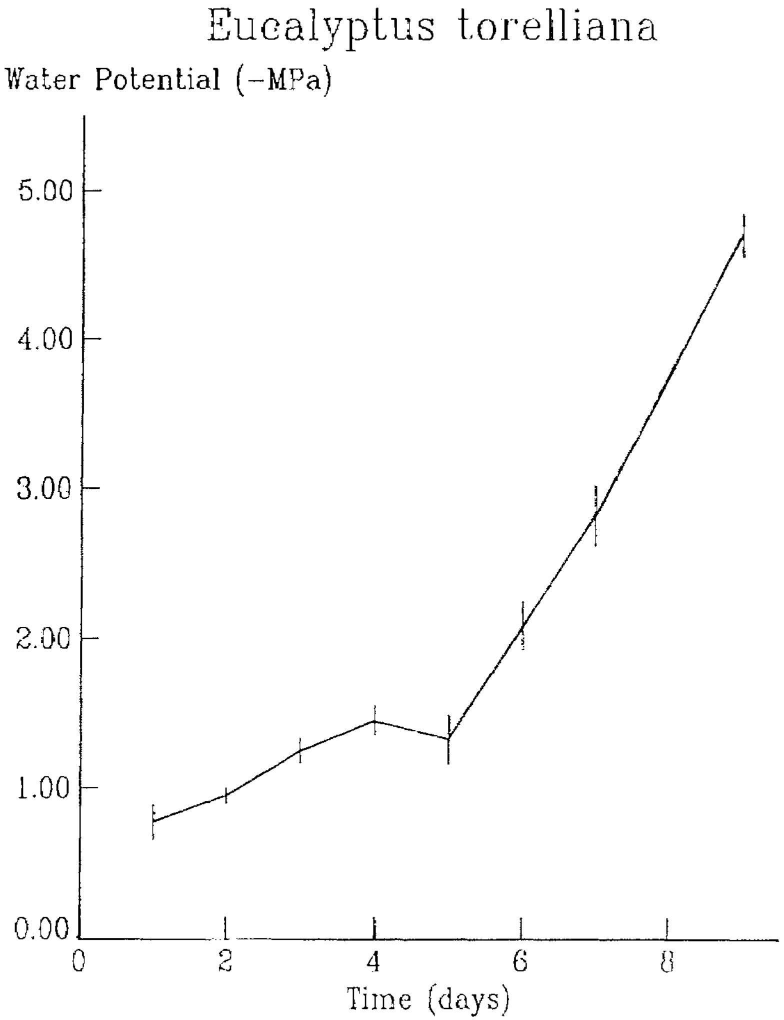
Eucalyptus torelliana

Figure 3.4.3

Figure 3.4.3 Mean and standard error water potential (-MPa) against time (days) in seedlings of *Eucalyptus torelliana*.

| SPECIES | MEAN DRY WEIGHT (g)<br>95% Conf. Limits | MEAN LEAF AREA ($cm^2$)<br>95% Conf Limits |
|---|---|---|
| *E. grandis* | 3.66 | 704.2 |
| | 2.71 to 4.61 | 512.7 to 895.7 |
| *E. intermedia* | 4.50 | 691.1 |
| | 2.85 to 6.15 | 538.6 to 843.6 |
| *E. torelliana* | 3.68 | 501.4 |
| | 2.56 to 4.80 | 360.8 to 642.0 |

Table 3.6. Mean and 95% confidence limits for dry weights and leaf areas of seedlings used in the glasshouse moisture stress trial.

| SPECIES | N | $R^2$ | SLOPE | S.E. SLOPE | INTERCEPT | S.E. INTERCEPT |
|---|---|---|---|---|---|---|
| *E. grandis* | 48 | 0.88 | -17.66 | 1.159 | 57.42 | 4.56 |
| 95% Conf. limits | | | -19.99 to -15.33 | | 48.24 to 66.60 | |
| *E. intermedia* | 48 | 0.81 | -15.13 | 1.230 | 49.86 | 5.17 |
| 95% Conf. limits | | | -17.60 to -12.66 | | 39.46 to 61.26 | |
| *E. torelliana* | 48 | 0.89 | -18.16 | 1.097 | 59.92 | 4.14 |
| 95% Conf. limits | | | -20.37 to -15.95 | | 51.59 to 68.25 | |

Table 3.7 Results of analysis of variance of regression for water potential against log soil moisture for three eucalypt species in the glasshouse moisture stress trial.

moisture potential did not vary significantly between pots at any given time. Mean dry weights did not vary significantly between species, nor did mean leaf areas (Table 3.6).

Analysis of variance of regression was performed on water potential for the three species against log soil moisture. The results are shown in table 3.7. It can be seen from the overlap of 95% confidence limits that there is no significant difference between the slopes or intercepts of these three lines. Figures 3.4.1 to 3.4.3 show daily midday water potentials for the three species in the glasshouse.

Seedlings of *E. torelliana* wilted at lower soil moisture levels than seedlings of *E. grandis*, while *E. intermedia* seedlings wilted only slightly (fig. 3.5). Leaf loss also occurred earlier in the experiment in E. torelliana than in *E. grandis*, and there was no leaf damage or loss to *E. intermedia*. While the water potential results themselves appear to be inconclusive, it is nevertheless obvious that a distinct ranking of drought tolerance exists within the three eucalypt species studied. *E. intermedia* is evidently the most drought tolerant of the three, while *E. torelliana* is the least able to cope with moisture stress. This ranking of species coincides with the distribution of adult trees of the same species on the Kirrama ecotones, with *E. intermedia* found in the areas of most severe drought stress, and *E. torelliana* in the most protected sites. The results of the two sets of competition experiments were analysed using a series of t tests. The mean dry weight for each species grown in monoculture was compared with that of the same species grown together with one other. The results of the analyses are shown in table 3.8. Replacement series diagrams for each species pair are shown in figures 3.5.1 to 3.5.7.

The growth of *E. intermedia* is inhibited in the presence of *E. grandis* in well watered conditions, while the reverse occurs in drought stressed conditions. This indicates that *E. grandis* is a superior competitor for resources to *E. intermedia* as long as there is adequate water available. *E. intermedia* will tend to dominate if water is the limiting factor. The results also indicate a tendency for *E. grandis* to outcompete *Toona australis* when adequate moisture is available (a trend confirmed by a later experiment - chapter 4), and *Toona* shows a significantly higher growth rate in the presence of *E. grandis* under drought stressed conditions than it does in monoculture (table 3.8). Finally, *Toona* supresses the growth of

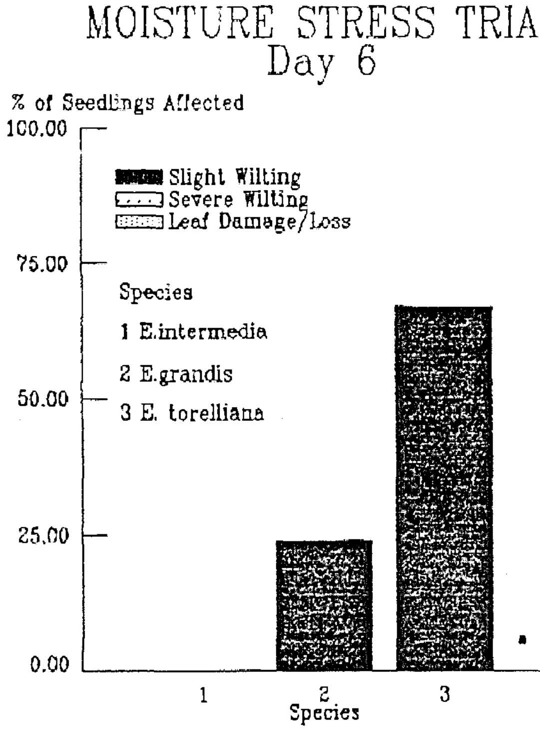

Figure 3.5.1

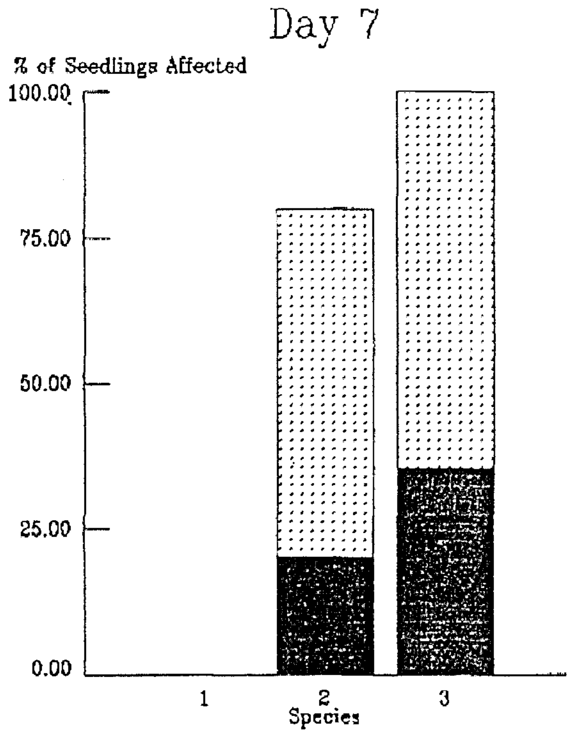

Figure 3.5.2

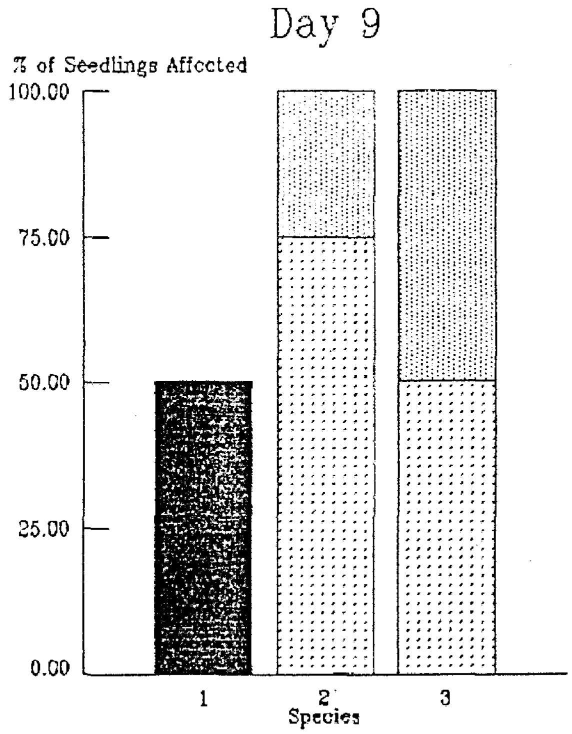

Figure 3.5.3

Figures 3.5.1 - 3.5.3 Degrees of wilting and leaf damage in seedlings of *Eucalyptus intermedia (1), E. grandis (2)* and *E. torelliana (3)* after 6, 7 and 9 days without water. Vertical axis shows the proportion of each group of 12 seedlings affected. Black represents slight wilting and loss of turgidity, light stippling represents severe wilting and heavy stippling represents permanent leaf damage or leaf loss.

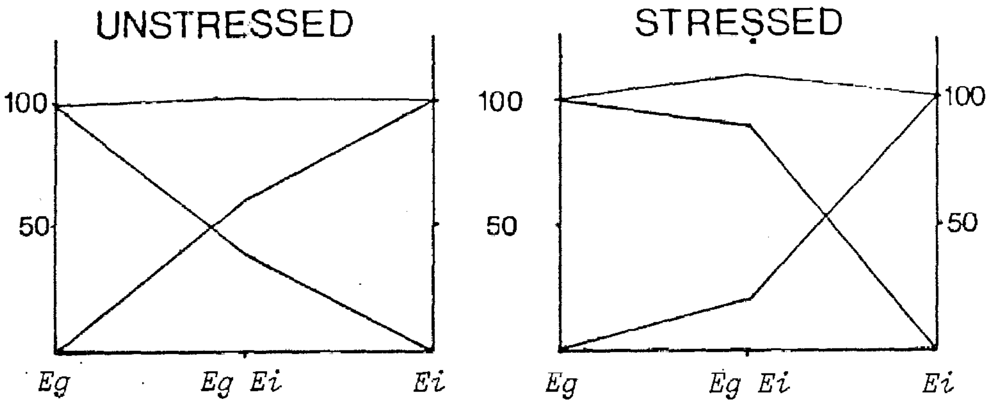

*Fig 3.6.1 Pilot Trial*

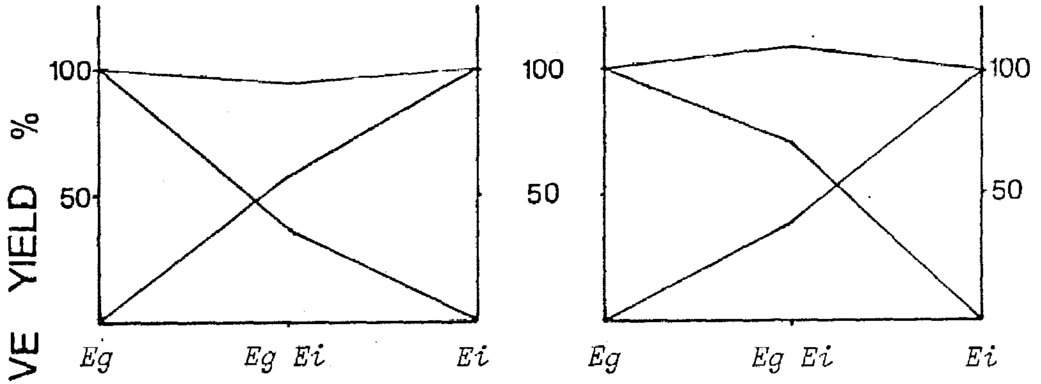

*Fig 3.6.2*

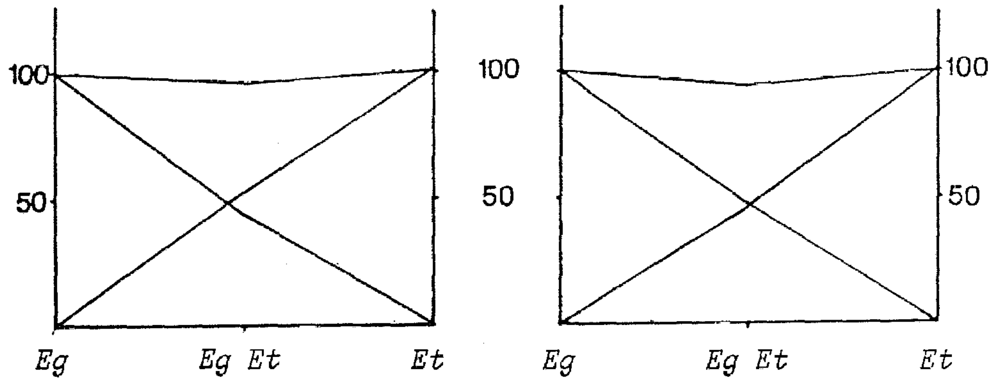

*Fig 3.6.3*

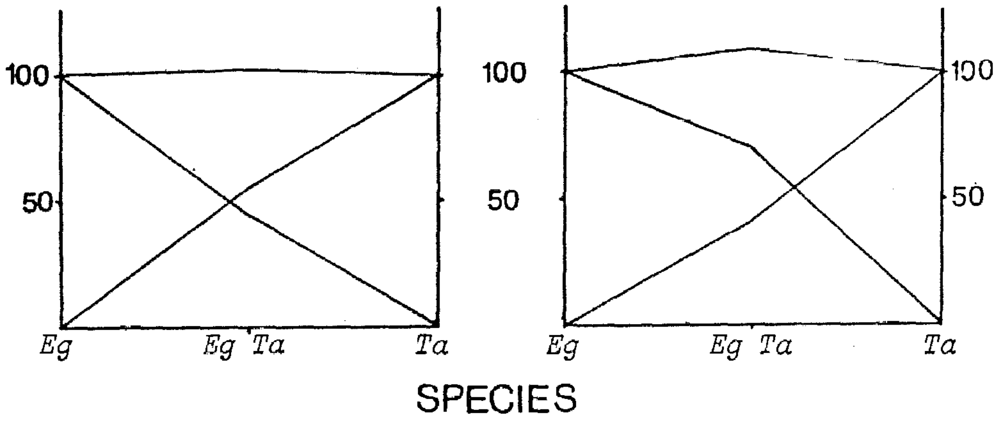

*Fig 3.6.4*

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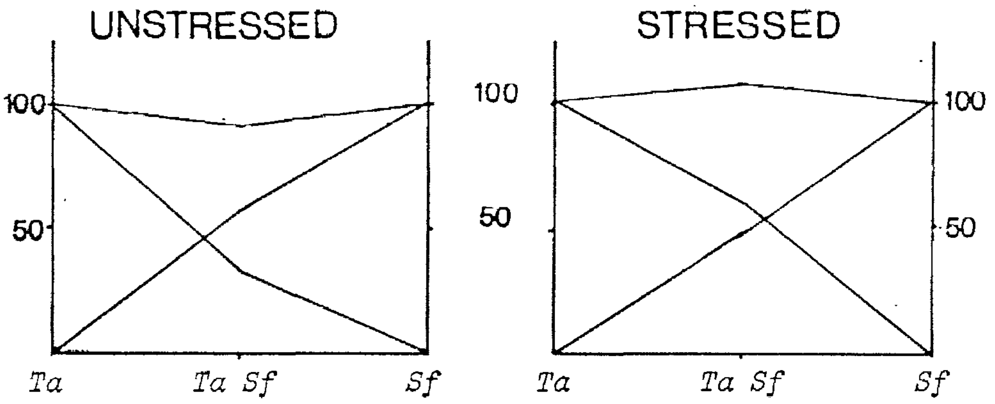

Fig 3.6.5

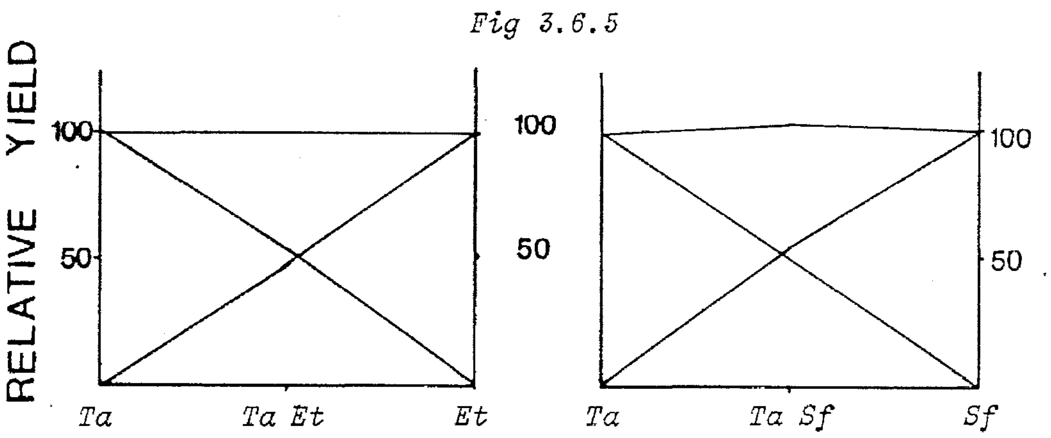

Fig 3.6.6

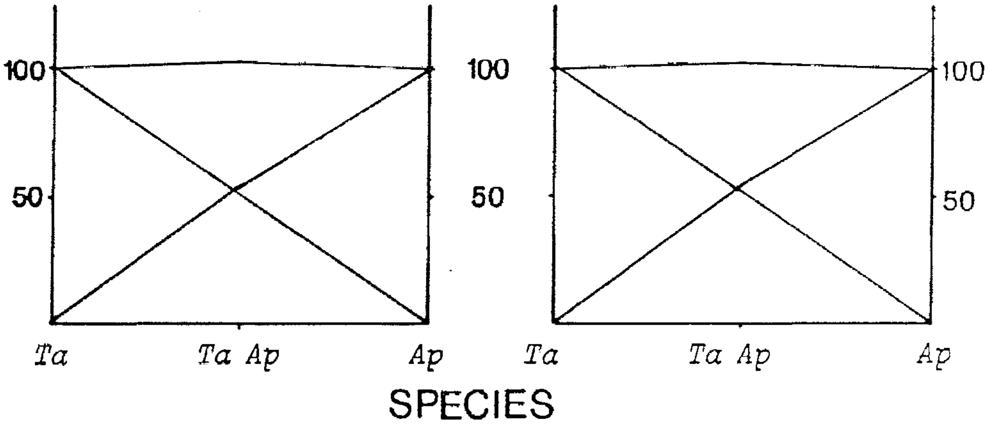

Fig 3.6.7

*Species Code:* *Ap Alphitonia petriei*
*Eg Eucalyptus grandis*
*Ei E. intermedia*
*Et E. torelliana*
*Sf Syzygium fibrosum*
*Ta Toona australis*

Figures 3.6.1 to 3.6.7 Replacement series diagrams showing mean relative yields under drought stressed and stress free conditions for six species pairs. Relative yields in percent.

|  | DROUGHT STRESSED SEEDLINGS |  |  |  |  |  |  | UNSTRESSED SEEDLINGS |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SPECIES PAIR | $\bar{x}$ MONO s.d(g) | $\bar{x}$ MIX s.d(g) | $s^2_p$ | S.E. | d.f. | t | prob. | $\bar{x}$ MONO s.d(g) | $\bar{x}$ MIX s.d(g) | $s^2_p$ | S.E. | d.f. | t | prob |
| Eucalyptus grandis | 0.481 | 0.210 | 0.011 | 0.046 | 19 | 5.89 | <0.001 | 2.68 | 3.06 | 0.088 | 0.131 | 19 | 2.916 | 0.005- |
| PILOT TRIAL | 0.428 | 0.181 |  |  |  |  |  | 0.892 | 0.934 |  |  |  |  | 0.01 |
| Eucalyptus intermedia | 1.30 | 2.21 | 0.039 | 0.087 | 19 | 10.46 | <0.001 | 2.72 | 2.20 | 0.051 | 0.099 | 19 | 5.253 | <0.001 |
|  | 0.520 | 0.691 |  |  |  |  |  | 0.342 | 0.921 |  |  |  |  |  |
| Eucalyptus grandis | 0.97 | 0.66 | 0.019 | 0.074 | 14 | 4.189 | <0.001 | 3.03 | 3.67 | 0.203 | 0.241 | 14 | 2.656 | 0.01- |
| MAIN TRIAL | 0.340 | 0.396 |  |  |  |  |  | 0.877 | 1.442 |  |  |  |  | 0.02 |
| Eucalyptus intermedia | 1.67 | 2.32 | 0.133 | 0.195 | 14 | 3.333 | <0.001 | 2.81 | 2.01 | 0.359 | 0.320 | 14 | 2.500 | 0.02- |
|  | 1.02 | 0.905 |  |  |  |  |  | 2.178 | 0.537 |  |  |  |  | 0.05 |
| Eucalyptus grandis | 0.97 | 0.92 | 0.033 | 0.097 | 14 | 0.515 | N.S. | 3.03 | 3.10 | 0.085 | 0.156 | 14 | 0.449 | N.S. |
|  | 0.340 | 0.494 |  |  |  |  |  | 0.877 | 0.651 |  |  |  |  |  |
| Eucalyptus torelliana | 1.12 | 1.03 | 0.042 | 0.110 | 14 | 0.818 | N.S. | 2.22 | 2.31 | 0.058 | 0.129 | 14 | 0.698 | N.S. |
|  | 0.593 | 0.481 |  |  |  |  |  | 0.764 | 0.481 |  |  |  |  |  |
| Eucalyptus grandis | 0.97 | 0.78 | 0.063 | 0.134 | 14 | 0.418 | 0.10 | 3.03 | 3.29 | 0.129 | 0.192 | 14 | 1.354 | 0.10 |
|  | 0.340 | 0.877 |  |  |  |  |  | 0.20 | 0.877 | 1.018 |  |  |  | 0.20 |
| Toona australis | 0.57 | 0.71 | 0.008 | 0.049 | 14 | 2.857 | 0.01- | 1.82 | 1.61 | 0.46 | 0.115 | 14 | 1.826 | 0.05 |
|  | 0.254 | 0.226 |  |  |  |  | 0.02 | 0.679 | 0.424 |  |  |  |  | -0.10 |
| Toona australis | 0.57 | 0.54 | 0.010 | 0.053 | 14 | 0.566 | N.S. | 1.82 | 2.07 | 0.039 | 0.106 | 14 | 2.358 | 0.02- |
|  | 0.254 | 0.282 |  |  |  |  |  | 0.679 | 0.283 |  |  |  |  | 0.05 |
| Syzygium fibrosum | 0.39 | 0.45 | 0.003 | 0.029 | 14 | 1.538 | 0.10 | 1.15 | 0.76 | 0.023 | 0.081 | 14 | 4.815 | <0.001 |
|  | 0.085 | 0.170 |  |  |  |  | -0.20 | 0.453 | 0.340 |  |  |  |  |  |
| Toona australis | 0.57 | 0.60 | 0.012 | 0.059 | 14 | 0.508 | N.S. | 1.82 | 1.74 | 0.046 | 0.115 | 14 | 0.696 | N.S. |
|  | 0.254 | 0.311 |  |  |  |  |  | 0.679 | 0.424 |  |  |  |  |  |
| Eucalyptus torelliana | 1.12 | 1.13 | 0.033 | 0.097 | 14 | 0.103 | N.S. | 2.22 | 2.37 | 0.080 | 0.151 | 14 | 0.993 | N.S. |
|  | 0.594 | 0.340 |  |  |  |  |  | 0.767 | 0.735 |  |  |  |  |  |
| Toona australis | 0.57 | 0.62 | 0.025 | 0.085 | 14 | 0.588 | N.S. | 1.82 | 1.96 | 0.075 | 0.146 | 14 | 0.959 | N.S. |
|  | 0.254 | 0.537 |  |  |  |  |  | 0.679 | 0.764 |  |  |  |  |  |
| Alphitonia petriei | 0.84 | 0.87 | 0.033 | 0.097 | 14 | 0.344 | N.S. | 2.42 | 2.52 | 0.142 | 0.201 | 14 | 0.498 | N.S. |
|  | 0.651 | 0.198 |  |  |  |  |  | 1.103 | 0.877 |  |  |  |  |  |

Table 3.8 Results of two competition trials with moisture stressed and stress free seedlings. The table shows mean dry weights for seedlings grown in monoculture (x MONO) and in combination with another species (x MIX), and the results of a series of t tests comparing these two mean values for each species pair. The probability (prob.) that there is no significant difference between the two means is given for each species pair. N.S. signifies a probability greater than 0.05 i.e. not significant.

*Syzygium fibrosum* to its own advantage when supplied with adequate water, but loses this advantage under drought stressed conditions. No other species pairs in the experiment demonstrated significant competition. It is probable that the trends shown in this experiment would become more pronounced if the seedlings were grown for longer periods of time.

Figure 3.6 shows the change in percentage moisture in the 20 subsampled pots over a 6 day period during the course of this experiment. Field capacity (mean ± SE) was 12.4 ± 0.82% water. After 1 day the moisture content dropped to one third of this value, after which the rate of drying out dropped off exponentially.

Table 3.9 shows the time to first wilting and the percentage mortality of the ten species subjected to severe drought stress. Mortality was highest in the late secondary successional species *Flindersia brayleyana* and *F. pimenteliana*. Both species lost all their foliage after wilting, and recovery was between 0 and 40 %. Recovery was much higher in the other late secondary species *Toona australis*, probably because this species is dry season deciduous and therefore better able to cope with drought induced leaf loss. The two primary rainforest species *Syzygium fibrosum* and *S. wesa* showed relatively high tolerance of moisture stress, recovering in 80 - 90% of cases.

*Eucalyptus grandis*, *E. torelliana* and *Alphitonia petriei* all shed foliage after wilting but recovered in the majority of cases. *E. intermedia* maintained leaf turgidity for the longest period, lost few leaves and recovered in 100% of cases.

Most species showed a greater degree of drought tolerance after pretreatment under dry conditions. The exceptions were *Flindersia brayleyana* and *Toona australis*. The latter actually showed marginally higher mortality in the prestressed group. Since preconditioning improves the level of drought tolerance, it is reasonable to assume that these species would be more drought tolerant when growing in sites with lower soil moisture and/or greater water vapour deficits as a result of climatic conditions.

| SPECIES | NORMAL SEEDLINGS<br>WILTING (days) | <br>RECOVERY (%) | PRESTRESSED SEEDLINGS<br>WILTING (days) | <br>RECOVERY (%) |
|---|---|---|---|---|
| *Alphitonia petriei* | *4* | *60* | *5* | *80* |
| *Eucalyptus grandis* | *4* | *80* | *5* | *100* |
| *E. intermedia* | *7* | *100* | *8* | *100* |
| *E. torelliana* | *3* | *70* | *5* | *70* |
| *Flindersia brayleyana* | *4* | *40* | *4* | *40* |
| *F. pimenteliana* | *3* | *0* | *3* | *20* |
| *Neolitsea dealbata* | *4* | *60* | *5* | *100* |
| *Syzygium fibrosum* | *4* | *80* | *5* | *80* |
| *S. wesa* | *4* | *80* | *5* | *90* |
| *Toona australis* | *3* | *100* | *4* | *90* |

Table 3.9. Effects of prolonged drought stress on normal and prestressed seedlings showing the mean number of days taken for each species to start wilting, and the percentage recovery of each species after re-watering.

## 3.4 CONCLUSIONS AND SUMMARY

The field data from Kirrama show there is an acute gradient in moisture availability in the top 50 cm of soil. In dry conditions, the soil moisture content of rainforest soil can be more than twice that in open forest. This is reflected in the water relations of trees growing in and on either side of the ecotone. Plants growing in medium open forest have been shown to reach water potentials as low as -4.0 MPa in the case of tall eucalypts at midday in dry conditions. Dominance of these species in the canopy of medium open forests indicates a high degree of drought tolerance.

Drought stress conditions are less frequent and less intense in the rainforest. The higher leaf area index in closed forest must be compensated for by reduced transpiration rates and soil evaporation, as a result of the more humid, cooler and more stable microclimate. While it is possible that rainforest emergents suffer levels of drought stress almost as severe as those of open forest species, rainforest species certainly encounter a more benign water regime in the establishment phase.

Experimental evidence suggests that shade tolerant rainforest tree species seedlings are more drought tolerant than secondary species. This may be due to superior stomatal control in the slower growing primary species. However, secondary species are more likely to encounter higher light intensities, greater air movement, higher temperatures and therefore greater moisture stress in large gaps and on the ecotone.

The distribution of the two rainforest margin eucalypt species *E. grandis* and *E. torelliana* at Kirrama can be partly accounted for by water relations. These two species evidently require the greater moisture availability offered by the microenvironment of the rainforest edge, and are not as tolerant of moisture stress conditions as the medium open forest species *E. intermedia* and *E. tereticornis*. It is difficult to judge how much the distribution of these eucalypts is accounted for by water relations as opposed to fire regime, although there is no doubt that both factors play important and interdependent roles.

Moisture stress conditions in open forest will reduce the chances of rainforest species establishing, althought he effects of fire must again be taken into consideration (chapter 5). Competition with species better adapted to a high light regime is another possible cause for the exclusion of rainforest species from medium open forest. Whatever the cause or causes, few orthophyllous species become established in open forest more than a few metres from the ecotone at Kirrama (chapter 2). Those that do are mostly shrub species seldom attaining heights in excess of 5 m.

At sites such as the Kirrama and Paluma ecotones where the rainfall regime is at the low end of the rainfall requirements for tropical rainforest growth, relatively dry years will shift the competitive balance in favour of open forest species. A sequence of relatively wet years will favour the incursion of rainforest into open forest, assisted by the greater moisture availability and the reduced frequency and intensity of fires. Unwin (1983) concluded that rainforest in the Atherton Tableland is either stable or moving out into open forest now, because of changes in fire regime implemented since the arrival of European man in the area.

Further studies of moisture availability and plant water relations in the field will allow researchers to more accurately pinpoint the climatic, edaphic and disturbance conditions which will favour or suppress the establishment of closed forest species in the open forest environment. That this establishment will take place at or near the rainforest boundary is beyond doubt in most cases.

# CHAPTER 4

# REQUIREMENTS OF SEEDLINGS FROM RAINFOREST, ECOTONE AND OPEN FOREST

## THE EFFECTS OF LIGHT AND NUTRIENT ON GROWTH, COMPETITION, VARIABILITY AND RESOURCE ALLOCATION

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"What shall we do about poor little Tigger?
If he never eats nothin he'll never get bigger
He doesn't like honey and haycorns and thistles
Because of the taste and because of the bristles
And all the good things that an animal likes
Have the wrong sort of swallow or too many spikes...
... But whatever his weight in pounds, shillings and ounces
He always seems bigger because of the bounces"

(Bear P. *loc. cit.* Milne 1928)

## 4.1 INTRODUCTION

Processes influencing seedling establishment and growth are of great importance to the population structure of forests. Using data from Hartshorn (1975), Caswell (1978) showed that the annual growth rate of a population of *Pentaclethra macroloba* in Costa Rica was more sensitive to changes in growth and survival of seedlings, saplings, and small trees than to changes in adult reproduction. Piñero et al. (1984) performed a similar type of analysis of the factors that influence population growth in *Astrocaryum mexicanum*. They concluded that fecundity was less important than survival which in turn was less important than growth in the life history of tropical trees. Thus, selection for increased growth and survival as seedlings, saplings, and small trees should produce greater increases in population growth rate than selection for increased reproduction by adults.

For this chapter, experiments were conducted dealing with the responses of seedlings to varying light and nutrient levels. The effects of competition on light responses were examined, and growth of seedlings in various light and nutrient regimes was compared with seedling morphology and resource allocation. The species studied were characteristic of either closed forests, open forests or ecotonal assemblages (table 4.1).

Of all the physical factors that change across the rainforest - open forest boundary, light is the most variable. Irradiance at ground level in open forest may be more than 100 times higher than those on the rainforest floor (chapter 2, fig. 2.7). The gradient in available light is even steeper in the vertical plane between the floor and canopy of a closed forest. PAR in gaps and on the rainforest boundary lies between these two extremes. Since a wide range of light regimes occur on the many available regeneration sites in closed forest and closed forest - open forest ecotones, the successful establishment of one of the many available species largely depends on its adaptation to the light regime prevailing on a particular site.

It has long been recognized that different tropical forest species have different gap requirements (Richards, 1952; Whitmore, 1975; Bazazz and Pickett, 1980; Bazazz, 1984; Brokaw, 1984). In chapter 2, a comparison was made between the rainforest edge and a large gap, and with respect to light environments, this is a valid analogy. Performance of species in different gap types requires a range of strategies. Different species of tropical forest plants are thought to specialize on different gap types (Bazazz, 1984) and this specialization may contribute to the high species diversity of tropical forests (Connell, 1978).

Four main groups of plants with different gap requirements were recognized by Whitmore (1975), viz: (1) species that establish and grow beneath closed canopies, (2) species that establish and grow beneath closed canopies but benefit from gaps, (3) species that establish under closed canopies but require gaps to mature and reproduce, and (4) species that establish, grow and reproduce only in gaps. However, these are points on a continuum of gap preferences and each species may be unique in its preference (Bazazz, 1984).

Experiments examining the responses of tropical rainforest seedlings to light availability have been carried out by a number of researchers (e.g. Cunningham, 1959; Bjorkman *et al.*, 1972; Parrish and Bazazz, 1982; Fetcher *et al.*, 1983; Whitmore and Bowen, 1983; Pearcy, 1983; Pearcy and Calkin, 1983; Whitmore and Wooi-Khoon, 1983; Augspurger, 1984a; Langenheim *et al.*, 1984; Oberbauer and Strain, 1984 and Aylett, 1985). These experiments utilized one of two basic approaches; either direct measurement of seedling growth in different light regimes, or analysis of photosynthetic rates by measuring $CO_2$ uptake at different light intensities.

Data from the literature on photosynthesis of tropical forest species are difficult to interpret because of different methods, nonstandardized expression of results, different growth conditions, varying duration of measurements and varying age of plants and leaves. Moreover, few species have been studied and there are no detailed comparisons of photosynthesis, respiration and transpiration of "successional" and "mature forest" species (Bazazz and Pickett, 1980). $CO_2$ and water exchange have been compared in temperate species at different stages of succession, but the comparisons are based on the sun-adapted/shade-adapted dichotomy (Bazazz, 1979). This division is simplistic and may be misleading, especially in tropical forests (Bazazz and Pickett, 1980, Brokaw, 1985). The differences between sun-adapted and shade-adapted species in tropical forests are not clear. An individual may germinate in one light environment but develop in another or even a series of contrasting light regimes before entering the canopy. Moreover, morphological, physiological and biochemical properties of leaves may change with tree development (Bazazz and Pickett, 1980).

Photosynthetic responses of plants to the low light levels of the rainforest floor were studied by Bjorkman et al. (1972), Pearcy (1983) and Pearcy and Calkin (1983). Bjorkman et al. (1972) reported that nearly half the total carbon gain of the understorey herb, *Alocasia macrorrhiza*, occurred during brief periods of sunfleck activity. Pearcy and Calkin (1983) noted the rapid photosynthetic response of understorey saplings of *Claoxylon sandwicense*, allowing it to make use of short duration sunflecks. This species had a very low respiration rate and saturated at about 10% full sunlight. The light compensation point was less than 0.1% full sunlight (2 $\mu$mol $m^{-2}$ $s^{-1}$), one tenth of the diffuse PAR at the study site (20 $\mu$mol $m^{-2}$ $s^{-1}$). PAR measured in sunflecks at this site was approximately 200 $\mu$mol $m^{-2}$ $s^{-1}$, equivalent to the saturation point of *Claoxylon* (Pearcy and Calkin, 1983).

Oberbauer (1983 loc. cit. Mooney et al., 1984) found the light requirement of the Costa Rican canopy species *Pentaclethra macroloba* to be relatively low, with no increase in growth observed at PAR levels above 20% full sunlight. The species showed low acclimation potential, and light interception was reduced following leaflet closure at light levels higher than 20% full sunlight.

Whitmore and Bowen (1983) found that growth rates of *Agathis macrophylla* and *A. robusta* ssp. *nesophila* were reduced to 70% of the maximum rate at 12% of full sunlight, and concluded that both species could persist and grow under small canopy gaps in the rainforest. They compared the net assimilation rates (rate of weight increase per unit leaf area) of the two *Agathis* species with *Helianthus annuus* (sunflower) under full sunlight conditions, and found these rates to be 3 - 5 times greater in the herb than in the rainforest seedlings.

Whitmore and Wooi-Khoon (1983) also used *Helianthus* as a comparative means of assessing the net assimilation rate of balsa (*Ochroma lagopus*) under simulated "large gap" conditions. *Ochroma*, an "...archetypal pioneer species..." (Whitmore and Wooi-Khoon, 1983), had a net assimilation rate of 75% of that of *Helianthus*, in contrast to the 26 - 34% reported for *Agathis* species (Whitmore and Bowen, 1983).

Photosynthetic responses to light and the effects of acclimation in seedlings of three Amazonian rainforest canopy species (*Hymenaea courbaril, H. parvifolia* and *Copaifera venezuelana*) and two Australian *Agathis* species (*A. robusta* and *A. microstachya*) were examined by Langenheim *et al.* (1984). Seedlings were grown in 6% and 100% full sunlight, and their $CO_2$ assimilation was measured at different PAR levels. Although light compensation points were lower in seedlings grown in shade for all five species, only *A. robusta* showed any significant increase in light saturated assimilation rates when grown in full sunlight, making this species more competitive when gaps occur (Langenheim *et al.*, 1984). The light compensation points ranging from 5 to 9 μmol $m^{-2}$ $s^{-1}$ in shaded seedlings and 13 to 24 μmol $m^{-2}s^{-1}$ in unshaded seedlings are typical of those of shade tolerant rainforest seedlings.

The value of light compensation point as an indicator of species success under shade is, however, only of limited value (Ashton and Turner, 1979). A comparison of seedlings of *Eucalyptus regnans*, a tall open forest tree species, and *Nothofagus cunninghamii*, a cool temperate rainforest tree species produced light compensation points of 1.5% and 1.15% full sunlight respectively. Although young *E. regnans* seedlings are tolerant of shade, their ability to cope with herbivores and parasites is weak under shaded conditions, while *N. cunninghamii* is far more persistent (Howard, 1973).

The effects of light regime on seedlings of *Heliocarpus appendiculatus*, a pioneer tree species and *Dipteryx panamensis*, a small gap species, both from moist tropical forests in Costa Rica, were compared by Fetcher *et al.* (1983). The seedlings were grown in full sunlight, 80% shade and 98% shade for one month and then switched between environments and grown for a further two months.

Survival of *Heliocarpus* in 98% shade was 49%, while all seedlings of *Dipteryx* survived in all three light regimes. Both species acclimatized completely when transferred from one light regime to another, although *Heliocarpus* exhibited greater plasticity of leaf morphology. Fetcher *et. al.* (1983) consider it to be a characteristic of early successional species such as *Heliocarpus* that they will be better adapted to sudden increases in irradiance, temperature and atmospheric humidity deficits.

Parrish and Bazazz (1982) also noted greater plasticity, or greater "niche breadths", in early successional species compared to late successional species on three resource gradients. The responses of early and late successional tree seedlings to gradients of light, moisture and nutrients showed greater plasticity of early successional species with respect to moisture and nutrients, but similar broad responses were found in all species along the light gradient (Parrish and Bazazz, 1982).

Bazazz and Pickett (1980) concluded that, in general, early successional species have high light compensation points and high rates of maximum photosynthesis, while leaves of the lower canopy and of understorey saplings have low light compensation and saturation points and high quantum efficiencies. Stephens and Waggoner (1970) compared the photosynthetic characteristics of *Cecropia*, a pioneer species with *Goethalsia*, a canopy species, and two understorey species *Croton glabellus* and *Protium glabrum*. Light saturation points were 0.8 g cal $cm^{-2}s^{-1}$ for *Cecropia*, 0.4 g cal $cm^{-2}s^{-1}$ for *Goethalsia* and 0.2 g cal $cm^{-2}s^{-1}$ for the two understorey species.

Aylett (1985) assembled data from a number of studies and found that the maximum rate of photosynthesis in terms of $CO_2$ fixation per unit area per unit time is consistently higher in fast growing secondary forest tree species than in primary forest tree species.

Augspurger (1984a) investigated the light requirements of eighteen tree species seedlings from Barro Colorado island, Panama. All had wind dispersed seeds, and species ranged from large gap pioneers to shade tolerant primary trees. Most species germinated rapidly, within 1-2 weeks from planting. No correlation was found between seed size and shade tolerance, although previous studies have shown that such correlations occur in some cases (Grime and Jeffrey, 1965, Rabinowitz, 1978) including those described later in this chapter. Instead, shade tolerance was more closely correlated with resistance to disease (Augspurger, 1984a). The more shade tolerant seedlings proved to be more resistant to pathogen and herbivore attack in shaded conditions, possibly as a result of their having greater seed reserves.

No relationship was found between initial seed reserves and seedling size after one year of growth, although seedlings grown from small seeds were smaller after the initial 4 weeks of growth (Augspurger, 1984b). Growth rates in unshaded conditions were not correlated with shade tolerance, while most of the species grew little in shade (1 - 2 % full sunlight) during the course of one year. Only seedlings of the pioneer species *Ochroma pyramidale* showed noticeable etiolation in shade (Augspurger, 1984b). These results seem to contradict those of Brokaw (1980, loc. cit. Augspurger, 1984b) who found that saplings of more shade tolerant species grew slower than gap requiring species in high light environments.

Nutrient and water availability may alter the responses of seedlings to light, although the interactions between water relations, fertilization and light availability in tropical tree species have yet to be analysed. Cunningham (1959) looked at the separate effects of shade and fertilization in cocoa production, but failed to draw any conclusions about the interaction effect.

Succession following clear felling of a humid tropical forest in Costa Rica was examined by Harcombe (1977). He found that fertilization of some plots produced no increase in biomass in artificially seeded plots. When natural regeneration was allowed to take place, addition of fertilizer enhanced the dominance of grass and herb species at the expense of tree seedlings. Biomass and nutrient standing crop were lower in the forb dominated plots, so fertilization retarded succession, and reduced nutrient and biomass accumulation rates.

Bazazz (1984) mentioned nutrient pulses in gap environments, referring to relatively high concentrations of nutrients released into the soil after gap creating disturbances. He stated "It is expected" (although not proven) "that seedlings in areas of high nutrient pulses will be more able to use the newly available light energy than would seedlings that experience no nutrient pulse". Some species may be able to utilize released resources better than others, and varying resource allocation to roots, stems or leaves may alter this advantage under different circumstances. Unfortunately, there appears to be no experimental evidence for this in the literature, relating to tropical forests.

Shukla and Ramakrishnan (1984) observed differences in resource allocation strategies in two early and two late successional tropical tree species from north-eastern India. They found that the early successional species allocated more resources to the shoot, especially the bole, while the late successional species had higher allocation to the roots. Late successional species had higher leaf area indices, although early successional species had wider, deeper crowns. This study demonstrated that morphological characteristics are often as useful as physiological responses in determining successional status of forest tree species.

On the north Queensland upland rainforest - open forest ecotone, soil surface, nutrients vary as much according to topography as to vegetation type (Unwin, 1983). At one site near Herberton, soil cations and total phosphorus were higher in the surface soil of open forest than rainforest. Nitrogen varied in the opposite direction, possibly due to the loss of nitrogen to the atmosphere during fires. At another site, mineral element contents were higher in the top 0.5 m of rainforest soil, but the differences were overshadowed by variations in nutrient caused by topography and drainage patterns. Moreover, rainforest growth and species richness remained unaffected by the loss of surface soil nutrients via drainage. Of seven vegetation strata examined through the ecotone at the second site, the highest stand density and forest cover occurred in a rainforested gully, which had the poorest soil nutrient status (Unwin, 1983).

Seedling trials carried out by Unwin (1983) showed that soil nutrient levels do not determine the initial outcome of regeneration across the ecotone. *Eucalyptus* seedlings grew better in eucalypt forest soil, even when the mineral element content of the rainforest soil was higher. Growth of rainforest seedlings did not vary between soil types. When he added nutrients to the soils, the greatest increases in growth were observed in *E. grandis* (17 fold) and *E. intermedia* (26 fold), compared with far more modest growth rate increases in *Toona australis*, *Flindersia brayleyana* and *F. bourjotiana*, all of which showed approximately 2 fold increases.

Unwin (1983) concluded that survival and regeneration of plant species in the ecotone were not dependent on variations in surface soil nutrients. Soil nutrients vary more according to topography than to differences between rainforest and eucalypt forest nutrient systems, and that seedling growth and establishment is largely independent of superficial soil differences.

Austin and Austin (1980) used an experimental nutrient gradient to compare the performances of thirteen temperate grass species in monoculture and in competition with one another. The nutrient gradients varied logarithmically from 1/64 to 16 times the recommended concentration. Sixteen treatment levels were used, with no replication. While the data of Austin and Austin (1980) is not directly relevant to this discussion, the experimental design they used is of considerable interest, as it proved to be highly efficient at determining the performance and tolerance limits of a species, in monoculture or in competition with others. It is the performance of species on ecological gradients that determines the dynamics and floristics of vegetation boundary systems such as the rainforest - open forest ecotone.

## 4.2 MATERIALS AND METHODS

Three major glasshouse experiments were conducted to determine the effects of light and nutrient regimes on seedling growth, resource allocation, competition and variability. Seedling growth rates were studied of nine species from rainforest, ecotone and open forest communities in three nutrient regimes along PAR gradients. Above ground resource allocation in each species was also studied in this experiment. The second experiment was designed to investigate trends in species variability observed in the first experiment. The third experiment looked at species growth along the same resource gradients as the first, and included the effects of competition.

### 4.2.1. EXPERIMENT 1

The species used and their sources are listed in table 4.1. Seeds from each species were placed in trays containing a 3:1 mixture of washed river sand and peat. Although sowing times were staggered in order to obtain approximately synchronous germination of species, seeds of *Argyrodendron peralatum*, germinated somewhat earlier than expected and were kept in the glasshouse under a double layer of 90% "Sarlon" shade cloth until potted out.

Twenty seedlings of each species were selected at random immediately after germination, oven dried at 90°C for two days, and weighed to provide values for initial dry weights.

Seedlings were potted out over two days in 20 cm diameter pots with a capacity of 4.5 l. The potting mix used was a steam pasturized 3:1 mixture of washed river sand and peat, with gypsum and dolomite added according to a standard U.C. potting mix formula (Baker 1957). The seedlings were grown for 20 days in the glasshouse with no additional shading. Three seedlings of the same species were placed in each pot, and after 20 days the smaller or less robust seedlings were removed leaving one seedling per pot. During the initial 20 days dead or obviously unhealthy seedlings were replaced by seedlings from the seed trays. Any subsequent deaths were attributed to experimental treatment, and no seedlings were replaced after 20 days.

The trial was established in a glasshouse with heating and cooling systems able to maintain temperatures between 18°C and 30°C. Seedlings were

| SPECIES | DAYS TO INITIAL GERMINATION | DAYS TO >50% GERMINATION | INITIAL MEAN SEEDLING DRY WEIGHT (mg) | SEED SOURCE | | NUMBER OF PARENT TREES |
|---|---|---|---|---|---|---|
| | | | | SITE | LATITUDE LONGITUDE | |
| *Acacia mangium* Willd. | 9 | 10 | 9.8 | Atherton | 17°16'S<br>145°29'E | 1 |
| *Alphitonia petriei* Braid & C.T. White | 7 | 14 | 6.2 | Paluma | 19°01'S<br>146°15'E | 3 |
| *Argyrodendren peralatum* F.M. Bail. | 16 | 21 | 209 | Curtain Fig N.P. | 17°25'S<br>14°25'E | 1 |
| *Eucalyptus grandis* W. Hill ex Maiden | 4 | 8 | 1.2 | 2.4 km East of Atherton | 17°16'S<br>145°21'E | 1 |
| *Eucaluptus intermedia* R.T. Baker | 4 | 7 | 5.1 | Julatten | 16°37'S<br>145°20'E | 1 |
| *Flindersia brayleyana* F. Muell. | 11 | 13 | 101 | Atherton | 17°16'S<br>145°29'E | 1 |
| *Imperata cylindrica* (Nees) C.E. Hubbard | 9 | 12 | 1.3 | Atherton | 17°16'S<br>145°29'E | - |
| *Syzygum wesa* Hyland | 7 | 13 | 369 | Atherton | 17°16'S<br>145°29'E | 1 |
| *Toona australis* F. Muell | 12 | 14 | 47 | Malanda | 17°21'S<br>145°30'E | 1 |

Table 4.1 Species used, sources of seed, germination times, numbers of parent trees and initial seedling dry weights in experiment 1.

arranged in three 9 by 16 matrices, with one plant of each species represented in each row. Species/rows were arranged randomly. 2 - 3 g of freshly collected rainforest soil from Wongabel State Forest was added to each pot to provide a source of any necessary mycorrhizal fungi or bacteria. No additional nutrient was provided during the first 20 days. Pots were watered daily using a fine misting nozzle and tap water. The glasshouse was sprayed with "Carbaryl" insecticide and "Captan" fungicide at approximate 2 monthly intervals.

Shading for the seedlings was provided by 3.5 cm wide aluminium slats arranged parallel to the rows of pots, oriented east-west, and mounted on three steel 3 x 3.4 m frames (fig 4.1). Gaps between the slats were calculated to provide a logarithmic gradient of PAR varying in a direction perpendicular to the rows of pots (fig 4.2, plate 4.1). The frames were suspended 20 cm above the tallest seedling, and were moved upwards throughout the course of the experiment so as to maintain at least 10 cm separation from the frame to the top of the tallest seedling. Black plastic sheeting was hung from the sides of the frame to the ground to exclude any reflected side-light. To maintain air movement around the pots and help keep the temperature of all treatments as uniform as possible, the pots were supported on wire mesh 5 cm above the glasshouse floor.

PAR under the shade frames was measured using a "Li-Cor" light meter attached to a chart recorder, with a photosynthetically active radiation[1] sensor (400 - 700 mm) mounted on a small trolley and moved at a steady rate under the frame by an electric winch. These measurements were carried out at midday on one clear and one overcast day. A 20 cm gap was maintained from the plastic to the outside pots to reduce edge effects. The entire frame could be raised for watering and measurements made during the course of the experiment. 200 ml of a balanced commercial fertilizer, "Aquasol", was applied once weekly to each pot. The concentrations used for the "low", "medium" and "high" blocks are shown in table 4.2. The "Aquasol" powder was oven dried before weighing and then dissolved in tap water.

During the experiment, photon flux density in the glasshouse was recorded using a "Li-Cor" integrating meter fitted with a photosynthetically active radiation sensor. Readings were made once weekly.

Seedling heights and the number of developed leaf nodes were recorded for each seedling at 20, 41, 72, 105, 162 and 181 days after commencement of the

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[1] A 180 degree cosine corrected sensor was used.

Plate 4.1 Shade frames in the Atherton CSIRO glasshouse. The frames provided a logarithmic PAR gradient.

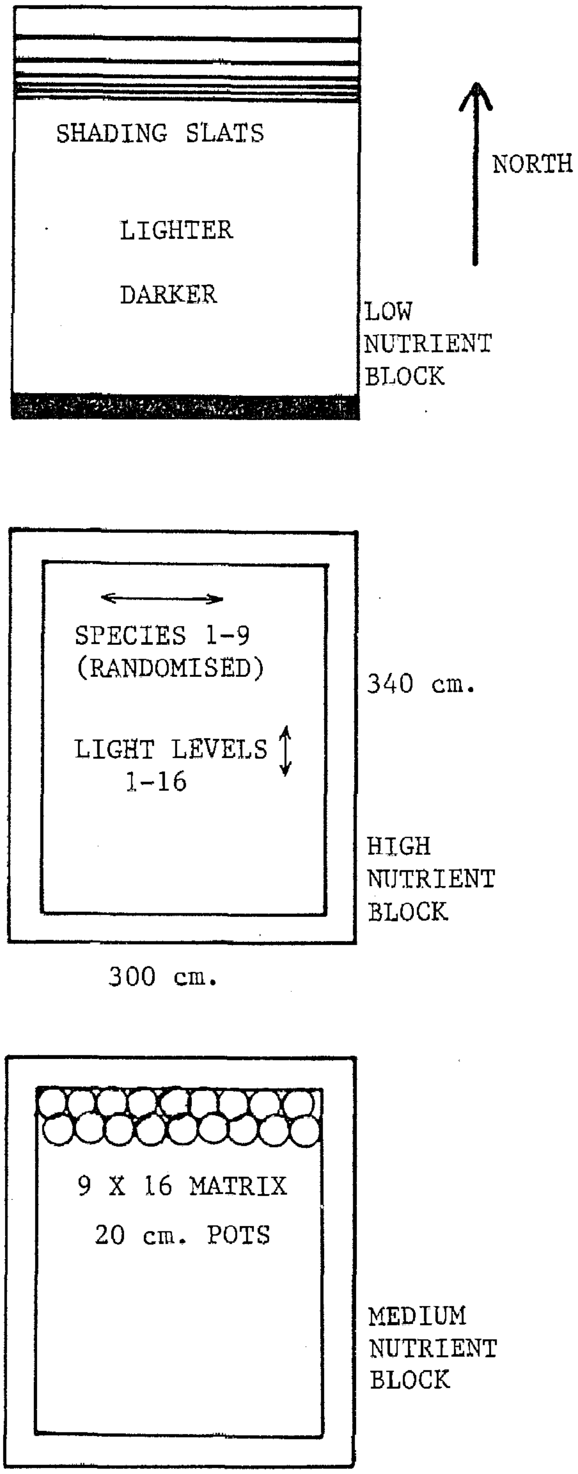

Figure 4.1 Arrangement of pots and shading frames in the glasshouse (Atherton CSIRO) for experiment 1. Similar arrangements were used in experiments 2 and 3. Pot size and nutrient treatment were altered in experiment 2, giving a 10 X 18 matrix, and an 8 X 16 matrix was used in experiment 3 (see text).

MINERAL NUTRIENT CONCENTRATIONS (mg/l)

| MINERAL | LOW | MEDIUM | HIGH |
|---|---|---|---|
| Nitrogen | 15.33 | 62.32 | 306.6 |
| Phosphorus | 2.67 | 10.68 | 53.4 |
| Potassium | 12.00 | 48.00 | 240.0 |
| Zinc | 0.033 | 0.132 | 0.667 |
| Copper | 0.040 | 0.160 | 0.800 |
| Molybdenum | 0.0087 | 0.0384 | 0.174 |
| Manganese | 0.100 | 0.400 | 2.00 |
| Iron (FeEDTA) | 0.040 | 0.132 | 0.667 |
| Sulphur | 0.0267 | 0.107 | 0.534 |
| Boron | 0.0073 | 0.0292 | 0.146 |

Table 4.2 Concentrations of mineral nutrients used in experiments 1, 2 and 3, shown in mg/l.

| SPECIES | NUTRIENT | SLOPE ($\times 10^{-4}$) | INTERCEPT | F | PROB. | $r^2$ |
|---|---|---|---|---|---|---|
| *Alphitonia petriei* | LOW | 2.35 | -0.002 | 119.7 | 0.0000 | 0.90 |
| | MEDIUM | 3.38 | -0.113 | 124.1 | 0.0000 | 0.90 |
| | HIGH | 12.70 | 0.0078 | 244.6 | 0.0000 | 0.95 |
| *Eucalyptus grandis* | LOW | 4.28 | 0.0472 | 49.3 | 0.0000 | 0.80 |
| | MEDIUM | 5.63 | 0.0951 | 168.1 | 0.0000 | 0.93 |
| | HIGH | 7.04 | -0.0287 | 2330.1 | 0.0000 | 0.99 |
| *Toona australis* | LOW | 2.01 | -0.0380 | 92.7 | 0.0000 | 0.88 |
| | MEDIUM | 3.50 | 0.189 | 194.9 | 0.0000 | 0.93 |
| | HIGH | 4.95 | -0.108 | 171.8 | 0.0000 | 0.92 |

Table 4.3 Regression analysis of projected leaf area ($cm^2$) against dry weight (g) for experiment 1.

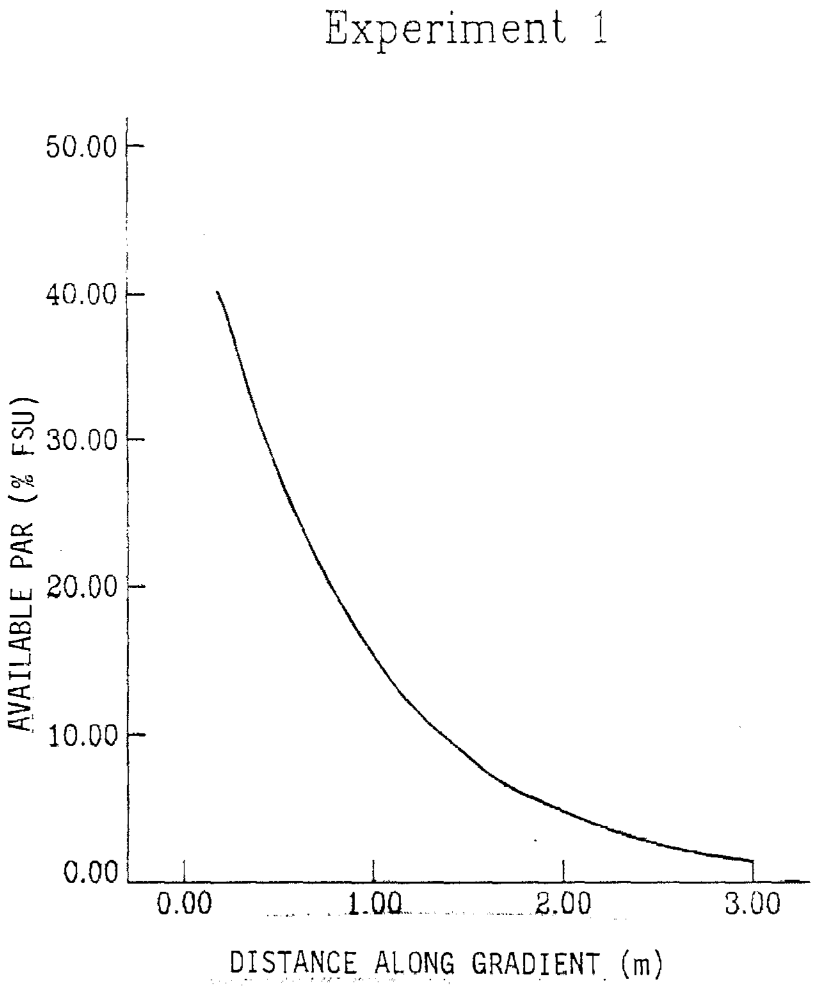

Figure 4.2 Available PAR (% full sunlight) against distance along the shade gradient (m) in experiment 1.

experiment. At day 105 a series of vertical photographs were taken to enable projected leaf area for each plant to be estimated.

Damage due to insect or fungal attack was noted as it occurred. In *Acacia mangium* the time of first phyllode development was recorded.

In order to maintain sufficient space to avoid mutual shading, at day 110 the seedlings of *Alphitonia petriei*, *Eucalyptus grandis* and *Toona australis* were harvested, instead of day 181. In addition to previously recorded variables, stem dry weight, leaf dry weight and total leaf area were recorded for each seedling.

Dry weight measurements were carried out after oven drying at 90°C for 5 days. Leaf area measurements were made with a "Li-Cor" LI3000 portable area meter.

### 4.2.2. EXPERIMENT 2

Experimental procedure for experiments 2 and 3 was in many ways similar to experiment 1, with some exceptions. As experiment 2 was designed to determine the degree of variability of open forest species compared to rainforest species with respect to light, a greater number of replicates were used. Four species were studied (*Eucalyptus grandis, E. intermedia, Neolitsea dealbata* and *Toona australis*) and grown in only one nutrient level, the medium nutrient concentration used in experiment 1. The shade gradient was steeper than that used in experiment 1, with light levels ranging from 2.5% to 50% full sunlight (fig 4.3).

Seedlings were germinated from seed using the same techniques as those for experiment 1. Three seedlings of each species were placed in 14 cm x 14 cm square pots, with capacities of 2.5 l. Seedlings were thinned out to one per pot after 21 days. Pots were laid out in three 10 x 16 matrices, giving 16 different PAR levels under the shade gradients. Each row of pots contained two seedlings of two species and three seedlings of the other two, arranged at random within the rows. At each light level there were 8 replicates each of *Eucalyptus intermedia* and *Toona australis*, and 7 of *Eucalyptus grandis* and *Neolitsea dealbata*. Watering nutrient application, fungicide and insecticide treatments were carried out as in experiment 1.

Seedlings were harvested before they became large enough to have any shading effect on their neighbours. *E. grandis* and *T. australis* were harvested

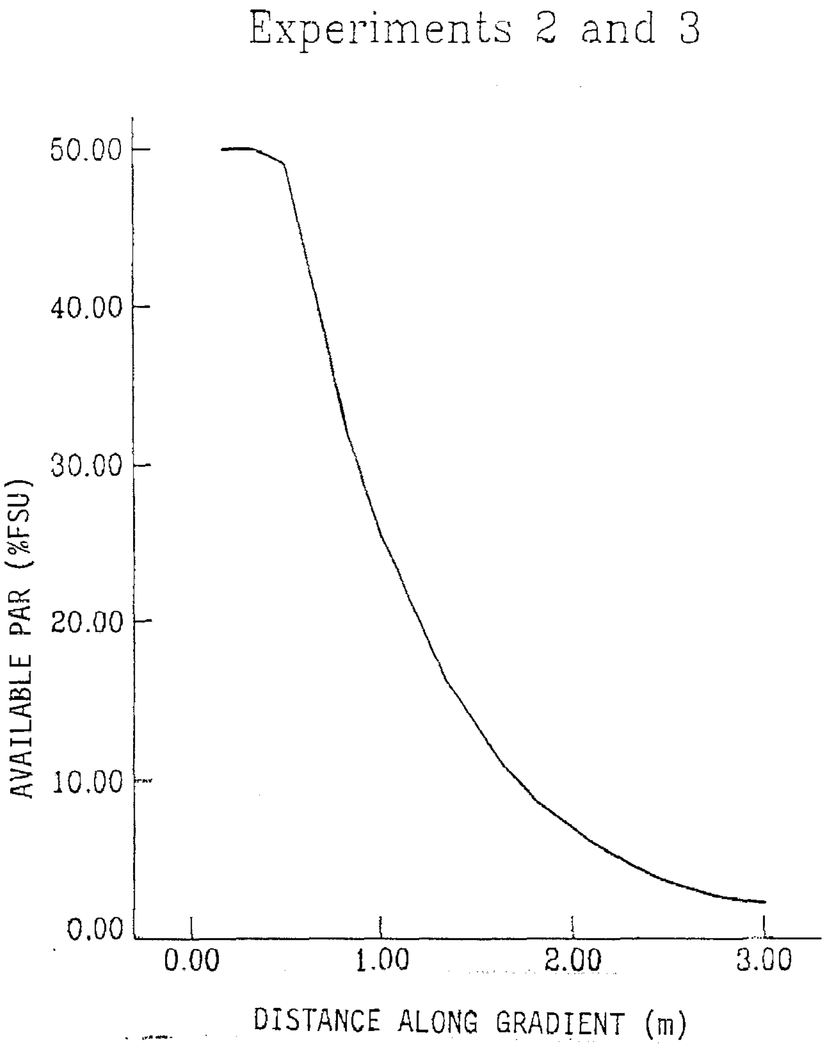

Figure 4.3 Available PAR (% full sunlight) against distance along the shade gradient (m) in experiments 2 and 3.

after 110 days, *E. intermedia* after 130 days and *N. dealbata* after 152 days. Seedlings were oven dried at 90°C for 5 to 7 days, and then weighed.

### 4.2.3. EXPERIMENT 3

Experiment 3 utilized the same shade gradient as experiment 2. Seedlings of *Acacia mangium, Argyrodendron peralatum, Eucalyptus grandis* and *Toona australis* were grown from seed and potted out in 4.5 l pots. Initially, two seedlings of each species were planted in each pot. After 18 days, seedlings were thinned out to one of each species per pot. Seedlings were arranged at each corner of an 8 cm square in the centre of each pot. Pots were arranged in three 8 x 13 matrices, with 13 light levels and 8 replicates per level. Nutrient application was the same as in experiment 1. Seedlings were grown in the high nutrient block for 96 days, and in the medium and low nutrient blocks for 128 days. Harvesting, drying and weighing were carried out as in the previous two experiments.

PAR under the shade frames was measured as in experiment 1, at midday on a clear day. PAR in the glasshouse was not recorded during the course of experiments 2 or 3 due to equipment failure.

## 4.3. RESULTS AND DISCUSSION

### 4.3.1. EXPERIMENT 1

The dates of sowing, initial germination and >50% germination for experiment 1 are shown in table 4.1. Photon flux density incident upon seedlings beneath shade frames on one clear and one cloudy day are shown in fig 4.4. Mean daily photon flux rates in the glasshouse were 158 $\mu Em^{-2}s^{-1}$ (fig 4.4). Glasshouse irradiance levels were approximately 50% of those outside.

Graphs of dry weight against PAR for the final harvest of all species in all three nutrient regimes, with regression lines and $r^2$ values are shown in figs 4.6 to 4.14. Dry weight results for *Alphitonia petriei*, *Eucalyptus grandis* and *Toona australis* from the high nutrient regime are not included in the figures. Because of their rapid growth these species were harvested on day 110 instead of day 181 with the rest of the seedlings. Graphs of projected leaf area against PAR for these three species are shown in figs 4.15 to 4.17. table 4.3 shows the results of regression analysis for projected leaf area against dry weight. $R^2$ values ranging from 0.80 to 0.99 indicate that projected leaf area provides a reasonable index for comparing growth at the intermediate stages of the experiment.

Data were analysed using the statistical software of Nie *et al.* (1975). A range of regression curves were fitted to each data set and the best fitting curve for each species/nutrient regime group was selected according to $r^2$ values (table 4.4).

Regression analyses were also carried out for the relationships between light and seedling height, total leaf area, projected leaf area and number of expanded leaf nodes for each species at each nutrient level. All trends observed in these analyses were the same as those observed for light against dry weight.

As indicated by the figures and statistical analyses, the responses of the species fall into three broad categories. Individuals of the most shade tolerant species *Argyrodendron peralatum* and *Syzygium wesa* (figs 4.6 and 4.7) persisted at the darkest end of the light gradient. Dry weight values for these species tend to level off or even decrease at the maximum light levels i.e. 80% ambient or approximately 40% full sunlight suggesting photoinhibition (Powles,

| SPECIES | NUT. | INTERCEPT (c) | SLOPE $(ax)X10^{-2}$ | SLOPE $(bx^{2})X10^{-3}$ | F | PROB. | $r^2$ | LINE |
|---|---|---|---|---|---|---|---|---|
| *Acacia mangium* | L | 0.0425 | 0.108 | 0.185 | 26.29 | <.001 | 0.81 | Q |
| | M | -0.306 | 5.45 | -0.557 | 7.12 | <.05 | 0.87 | Q |
| | H | -0.191 | 5.76 | -0.0904 | 7.29 | <.05 | 0.81 | Q |
| *Alphitonia petriei* | L | -0.0023 | 0.852 | - | 122.7 | <.001 | 0.95 | L |
| | M | 0.445 | 3.14 | - | 4.26 | NS | 0.38 | L |
| | H | -0.629 | 7.25 | - | 126.9 | <.001 | 0.89 | L |
| *Argyrodendron peralatum* | L | 0.190 | 0.425 | 0.0442 | 6.53 | <.05 | 0.50 | Q |
| | M | 0.225 | 0.926 | 0.0373 | 9.17 | <.02 | 0.59 | Q |
| | H | 0.0347 | 3.40 | 0.320 | 15.82 | <.002 | 0.71 | Q |
| *Eucalyptus grandis* | L | -0.161 | 2.30 | - | 65.46 | <.001 | 0.90 | L |
| | M | -0.105 | 9.14 | - | 60.99 | <.001 | 0.88 | L |
| | H | -0.121 | -0.250 | 1.180 | 39.80 | <.001 | 0.88 | Q |
| *Eucalyptus intermedia* | L | 0.0305 | -0.697 | 0.343 | 62.64 | <.001 | 0.92 | Q |
| | M | 0.177 | -0.267 | 0.917 | 33.27 | <.001 | 0.85 | Q |
| | H | -0.107 | 1.08 | 0.440 | 13.58 | <.002 | 0.73 | Q |
| *Flindersia brayleyana* | L | 0.271 | 1.25 | -0.153 | 3.00 | NS | 0.32 | Q |
| | M | 0.221 | 7.65 | -1.02 | 2.60 | NS | 0.30 | Q |
| | H | -0.210 | 9.57 | -0.338 | 45.49 | <.001 | 0.86 | Q |
| *Imperata cylindrica* | L | 0.056 | 0.665 | - | 16.69 | <.001 | 0.85 | L |
| | M | -6.261 | 1.775 | - | 106.1 | <.001 | 0.84 | E |
| | H | -10.439 | 2.918 | - | 86.62 | <.001 | 0.87 | E |
| *Syzygium wesa* | L | 0.106 | 0.752 | -0.119 | 8.03 | <.05 | 0.62 | Q |
| | M | -0.0761 | 2.83 | -0.295 | 10.31 | <.02 | 0.58 | Q |
| | H | 0.0692 | 1.62 | -0.0945 | 8.55 | <.05 | 0.65 | Q |
| *Toona australis* | L | 0.0698 | 0.180 | - | 2.09 | NS | 0.25 | L |
| | M | 0.691 | 0.595 | - | 1.03 | NS | 0.20 | L |
| | H | 0.0812 | 3.79 | - | 11.08 | <.01 | 0.53 | L |

Table 4.4 Results of regression analyses of 9 species in 3 nutrient treatments (L = low, M = medium, H = high) for dry weight (g) against PAR (% Full Sunlight) in experiment 1. The last column shows the type of curve which gave the best fit (L = straight line, Q = quadratic, E = exponential). Degrees of freedom = 1,14 in all cases.

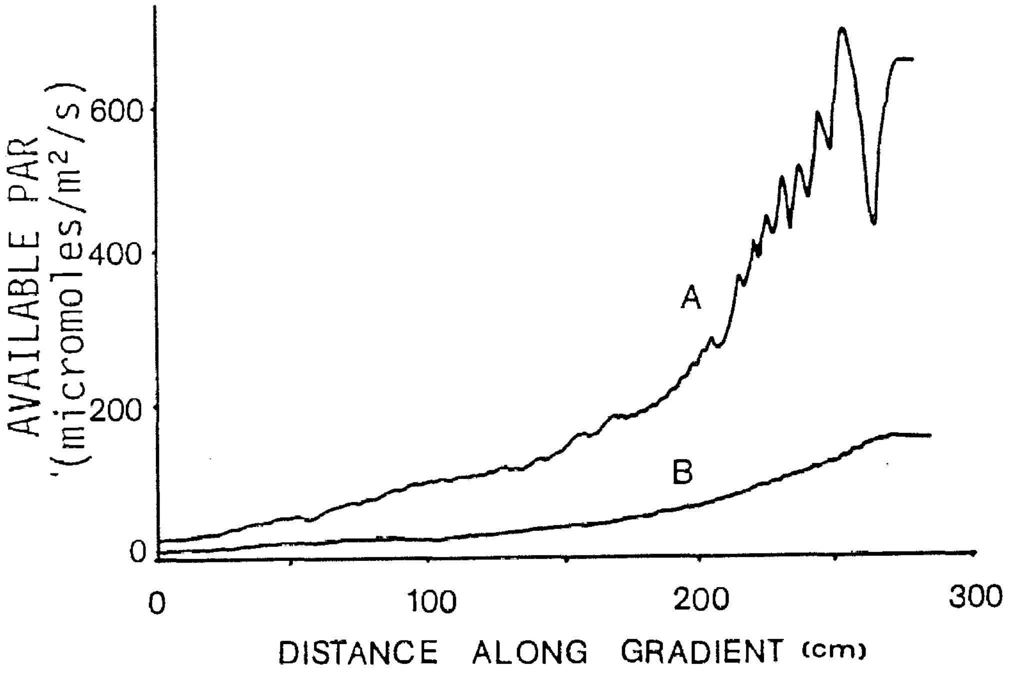

Figure 4.4 Available PAR measured under the shade frame in experiment 1 at midday on one clear day (A) and one overcast day (B). Par is given in μmoles $m^{-2}$ $s^{-1}$.

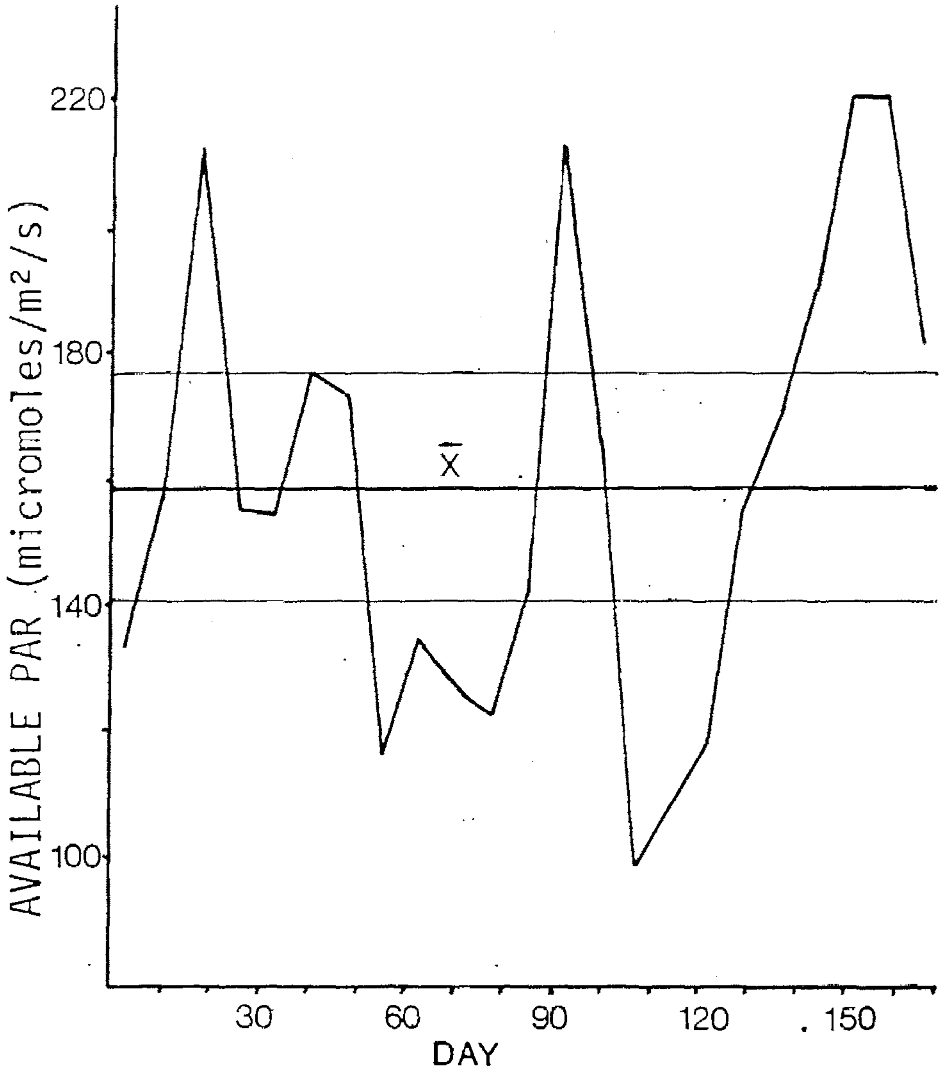

Figure 4.5 Available PAR measured in the glasshouse during the course of experiment 1. Mean PAR was calculated weekly and is shown in μmoles $m^{-2}$ $s^{-1}$. Also shown are the overall mean (heavy line) and standard error (fine lines).

Figures 4.6 to 4.14 Plots of dry weight (g) against available PAR (% full sunlight) for the nine species used in experiment 1. Regression lines and $r^2$ values are shown on each graph. Low nutrient points (L) are represented by round dots, medium nutrient points (M) by squares and high nutrient points (H) by triangles. Species are shown at the base of each graph.

Figures 4.15 to 4.17 Plots of projected leaf area ($cm^2$) against available PAR (% full sunlight) for the three fastest growing species in experiment 1. Graphs are annotated as in figures 4.6 to 4.14.

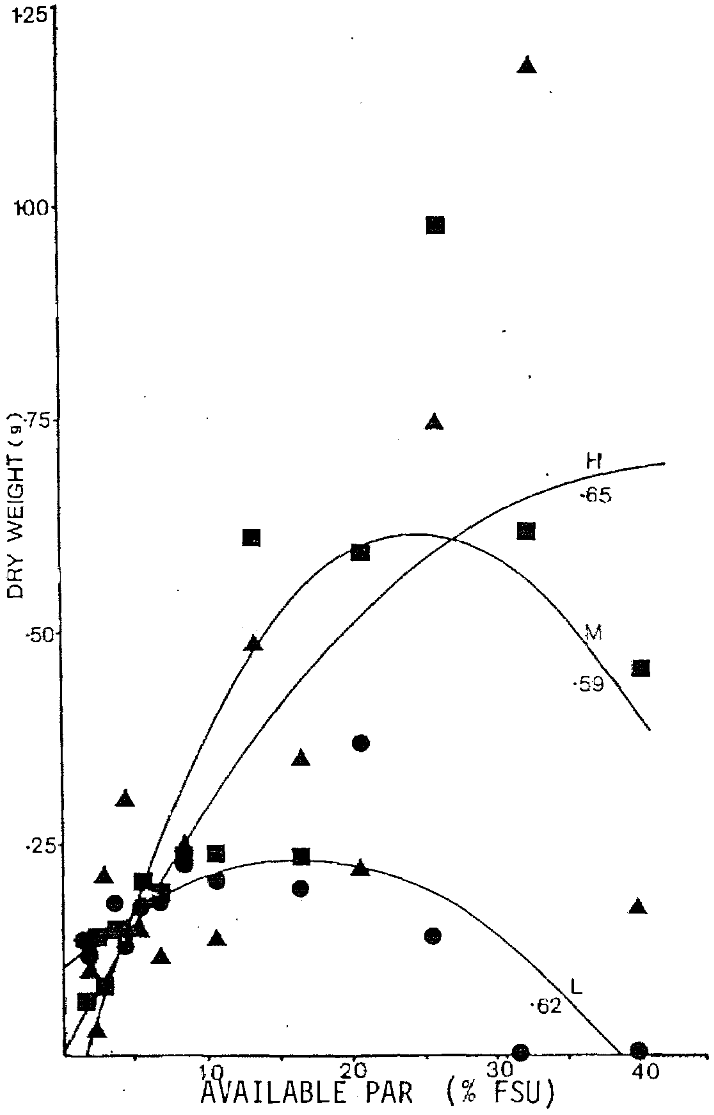

Figure 4.6 *Argyrodendron peralatum*

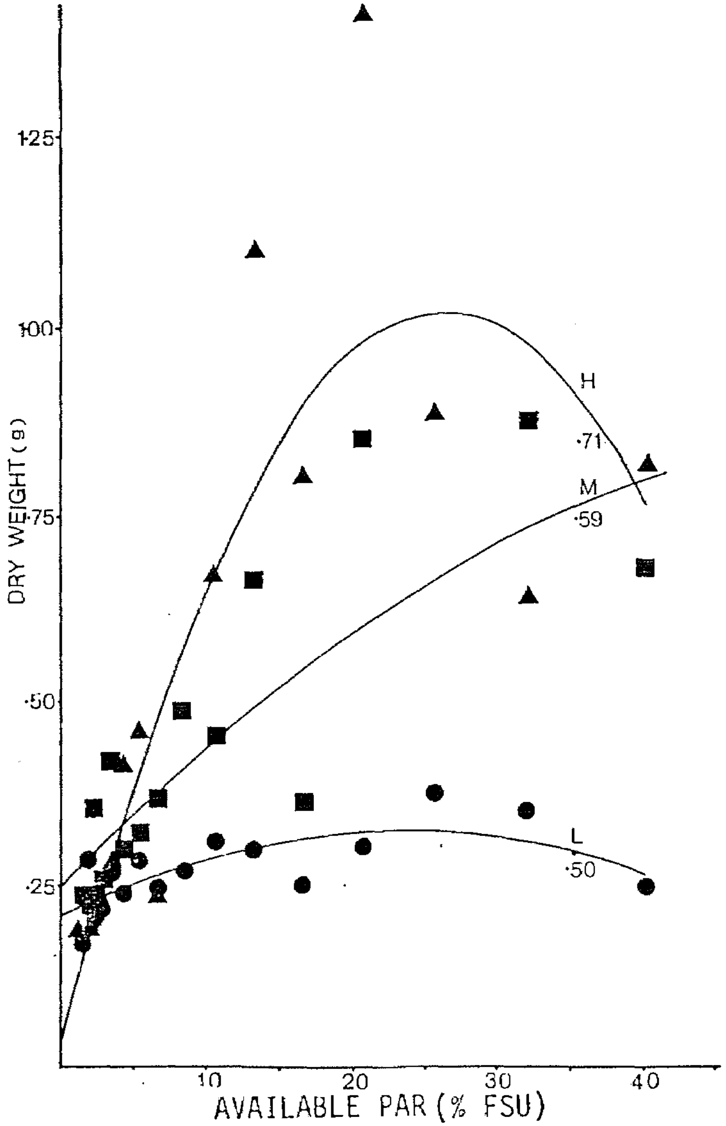

Figure 4.7 *Syzygium wesa*

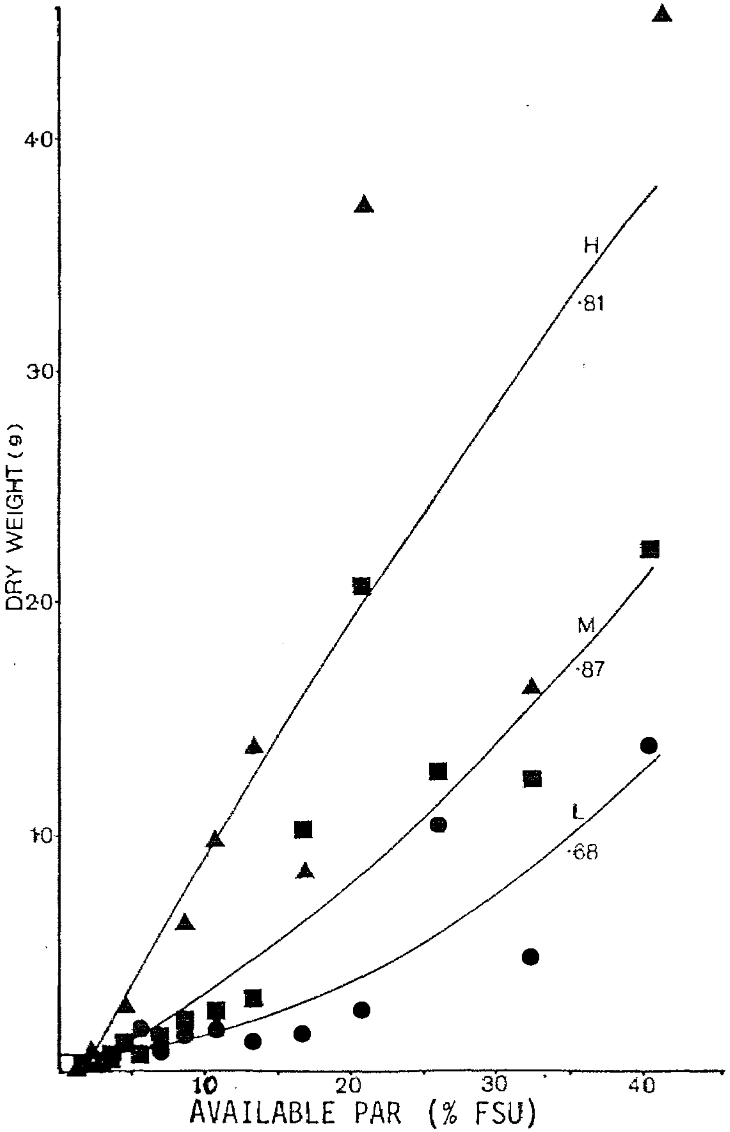

Figure 4.8 *Acacia mangium*

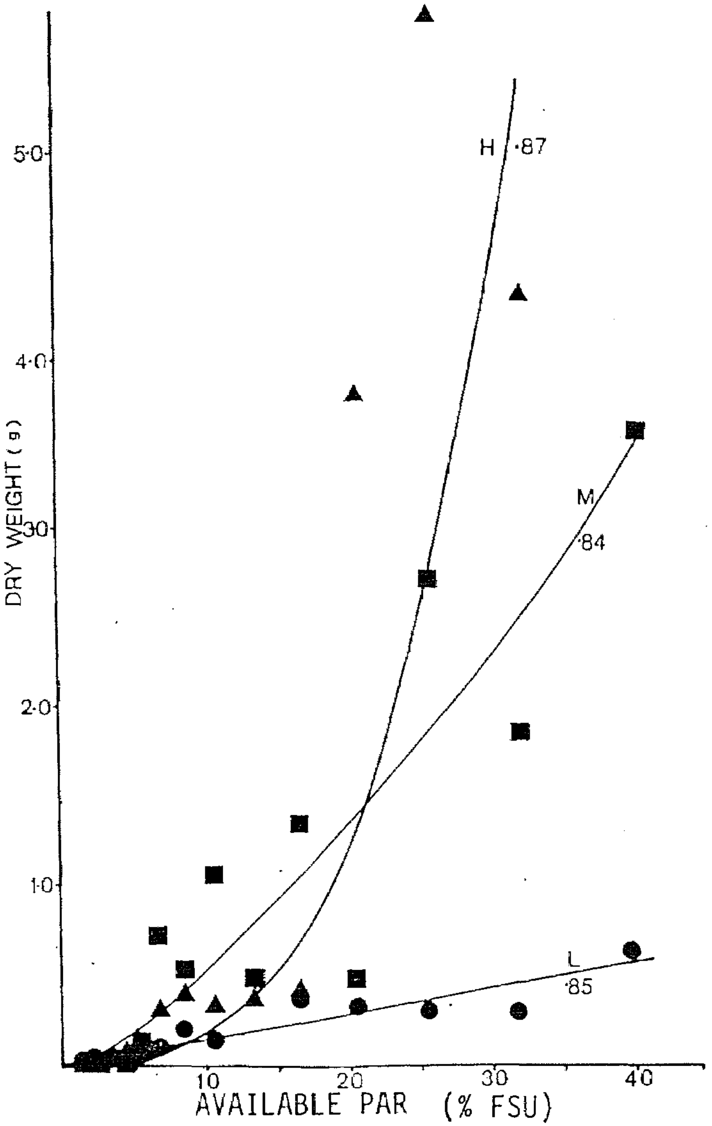

Figure 4.9 *Eucalyptus intermedia*

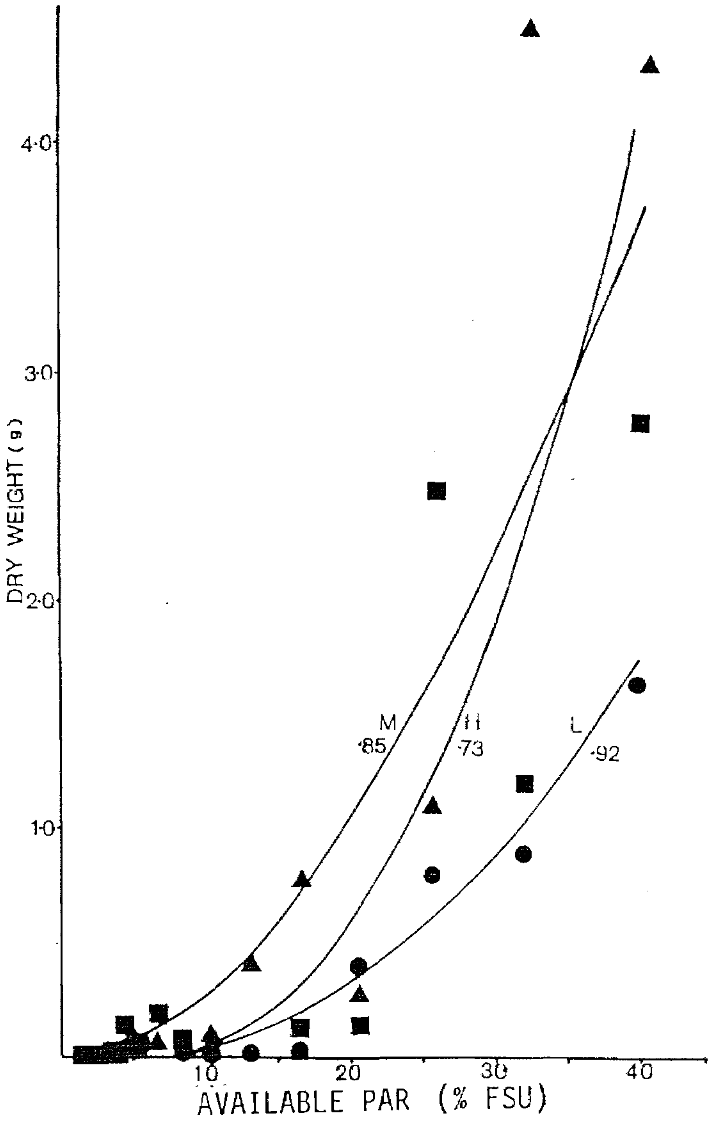

Figure 4.10 *Eucalyptus intermedia*

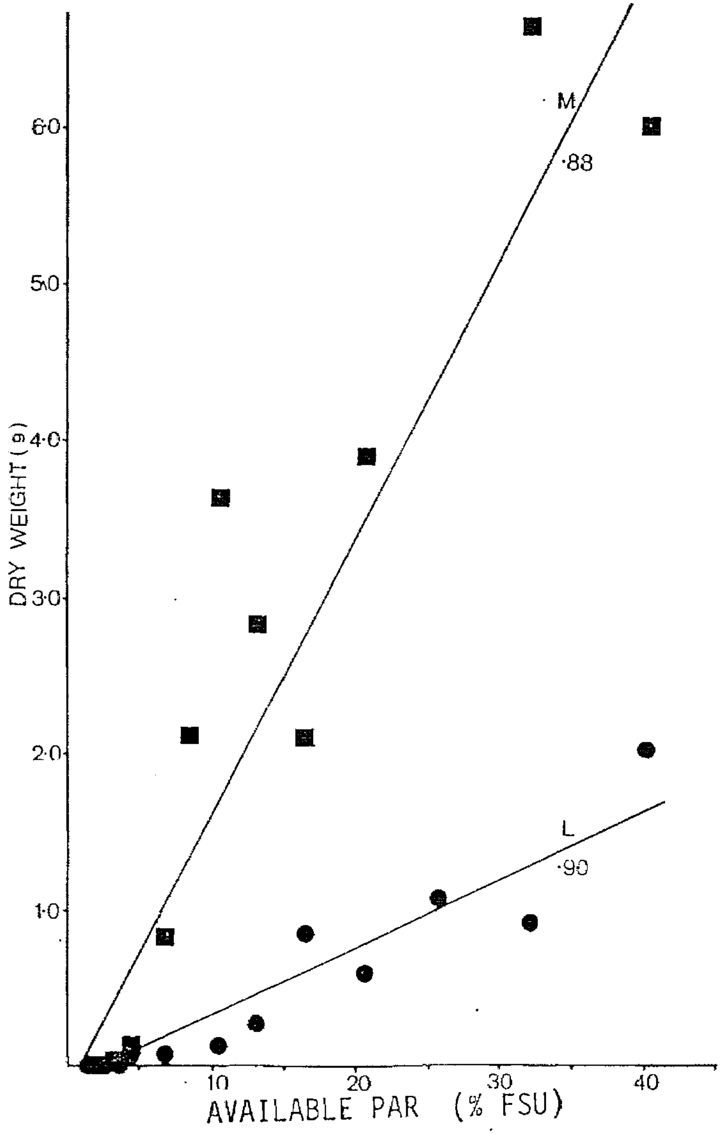

Figure 4.11 *Eucalyptus grandis*

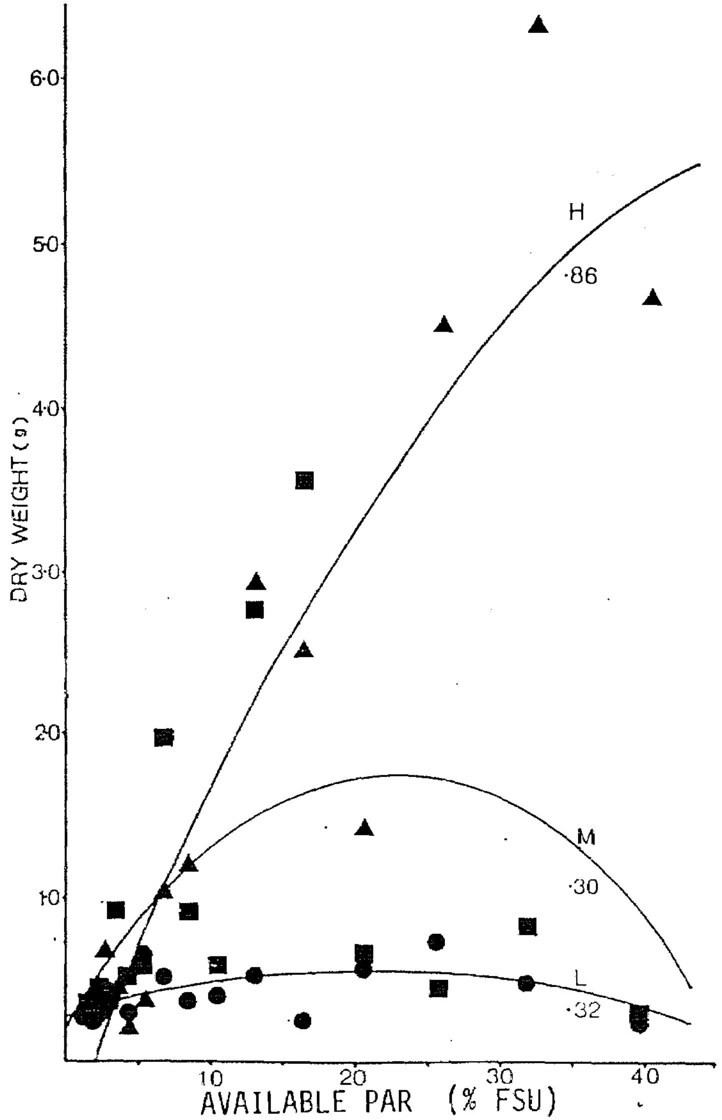

Figure 4.12 *Flindersia brayleyana*

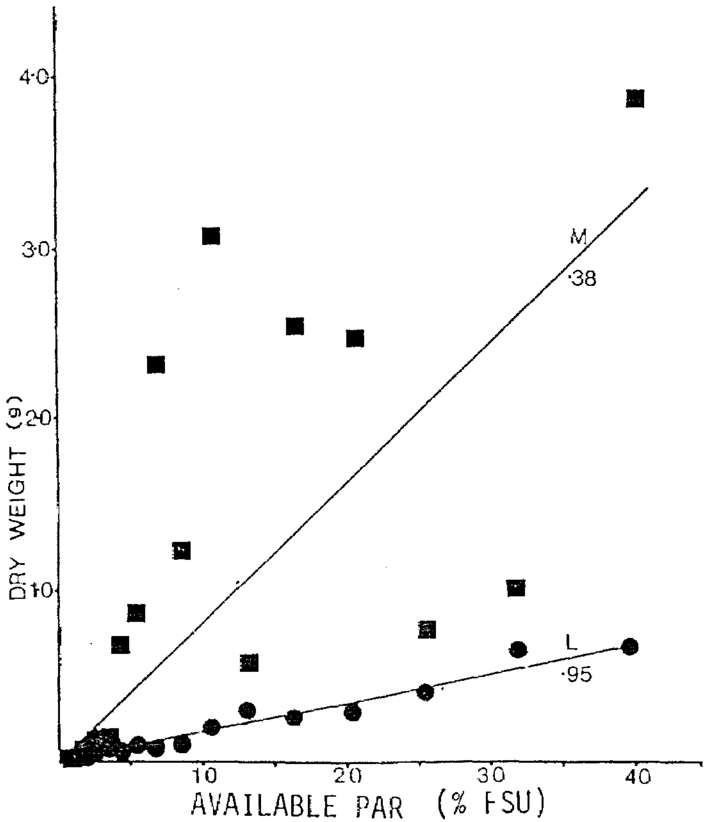

Figure 4.13 *Alphitonia petriei*

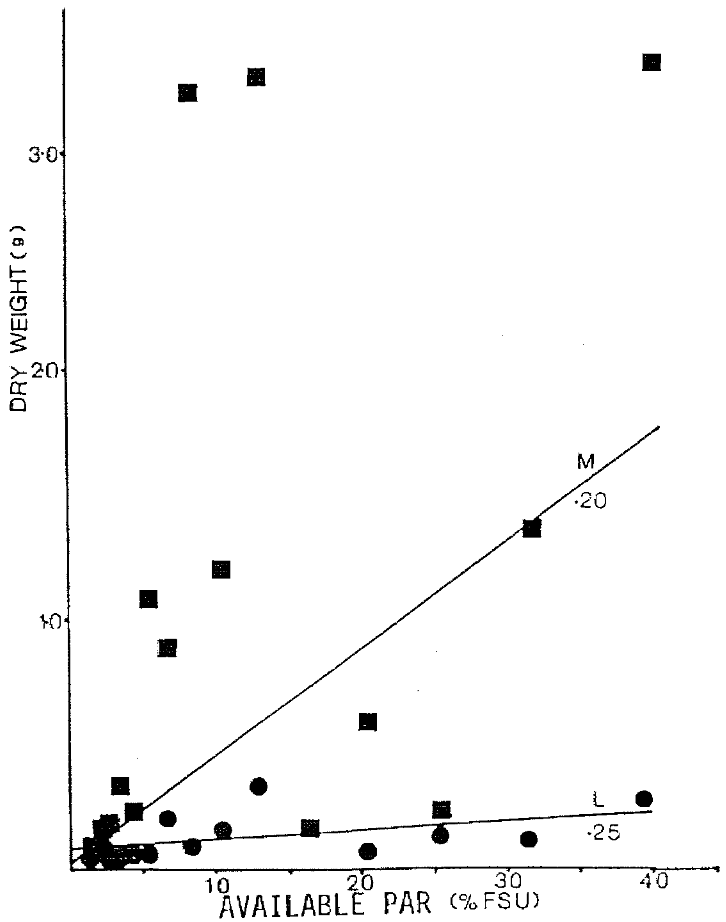

Figure 4.14 *Toona australis*

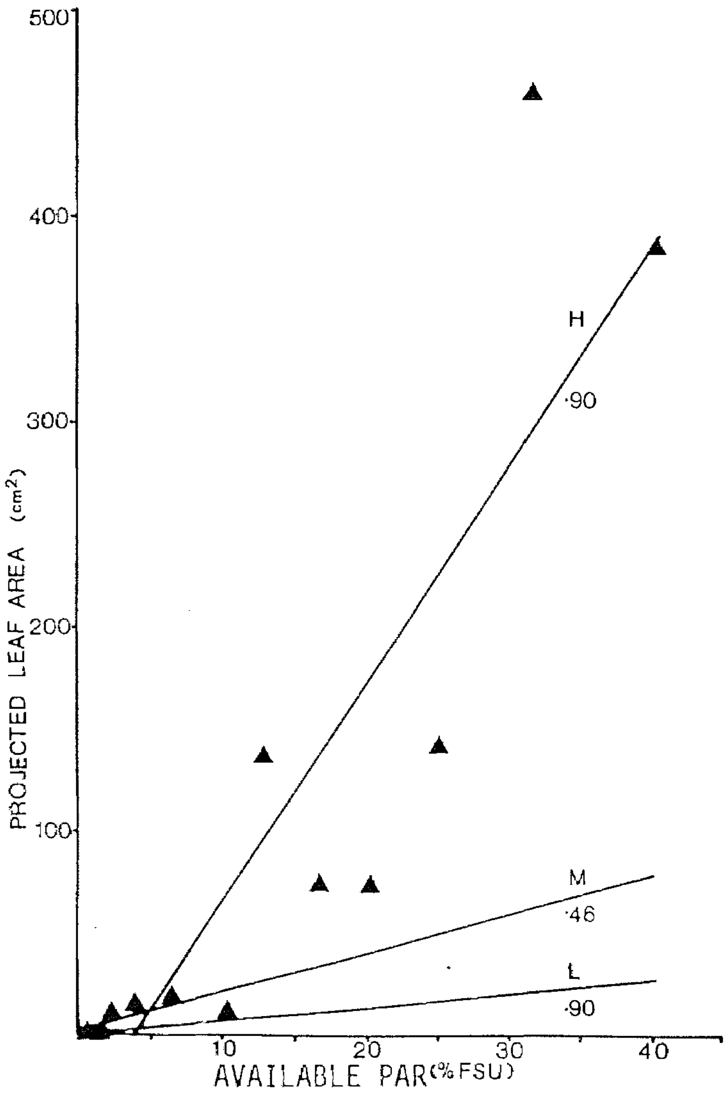

Figure 4.15 *Eucalyptus grandis*

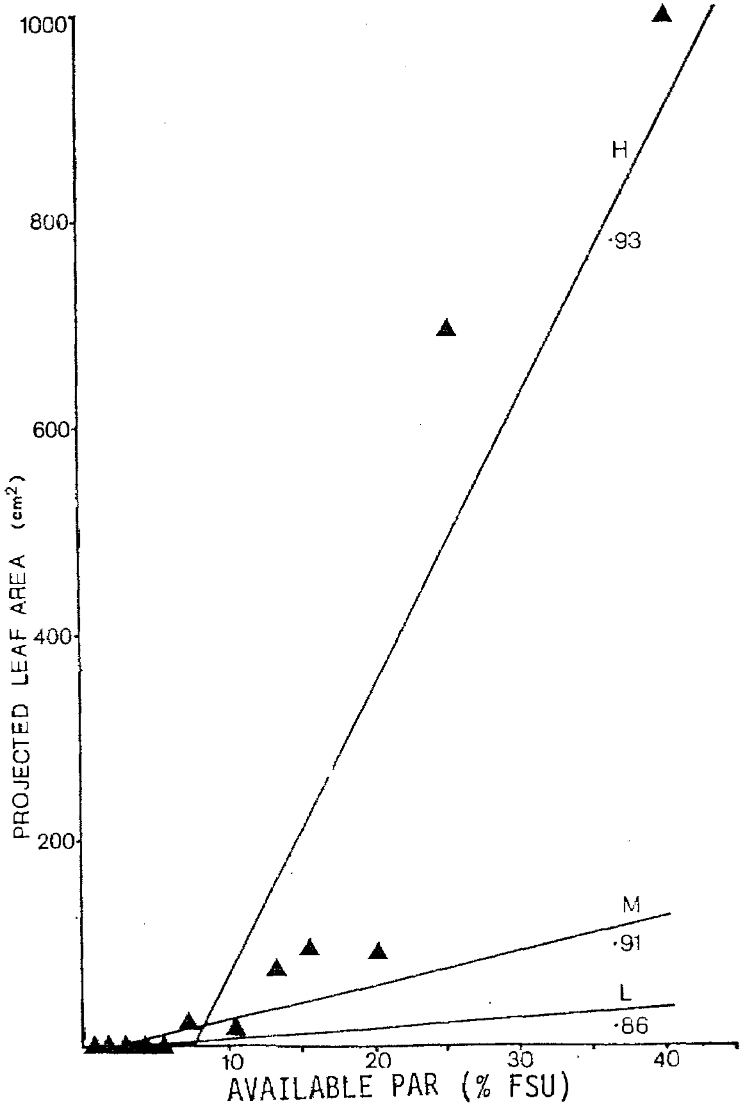

Figure 4.16 *Alphitonia petriei*

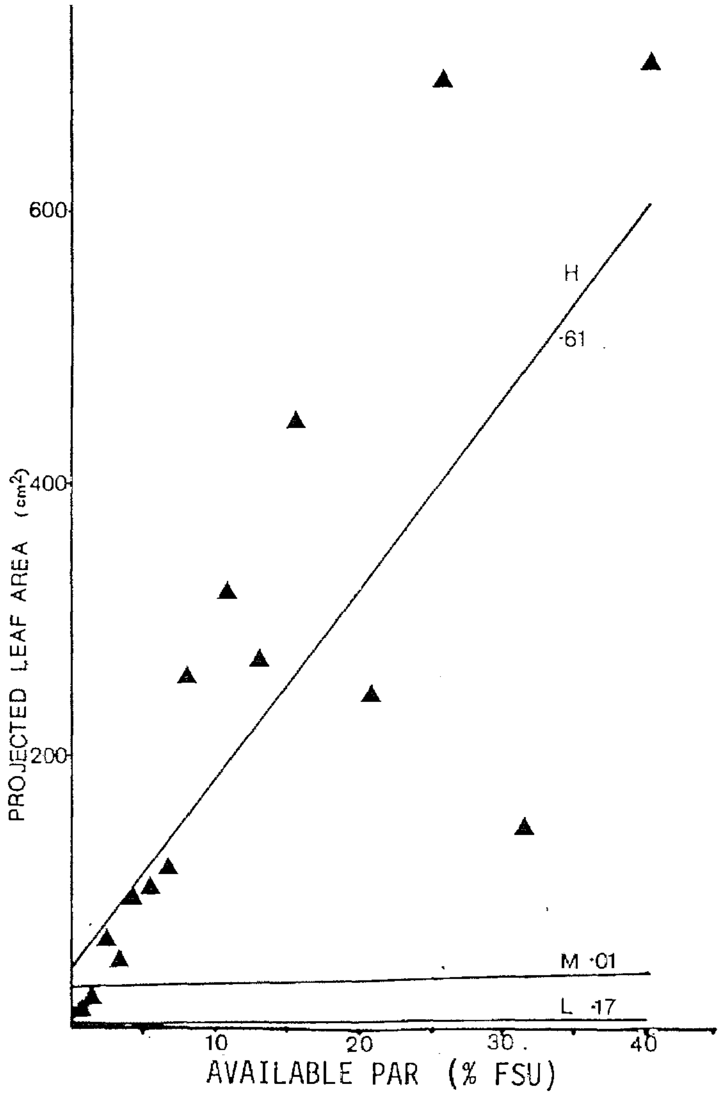

Figure 4.17 *Toona australis*

1984). Both these species achieved their maximum dry weight yields between 30% and 60% ambient PAR or 15% to 30% full sunlight. The trend towards diminished growth under strong irradiance was most pronounced at low nutrient levels. These responses are to be expected from "small gap" or primary rainforest species. It should be noted that nutrient effects are not as marked in these two species as in relatively shade intolerant species such as *Alphitonia petriei*, *Eucalyptus grandis*, *Flindersia brayleyana* or *Toona australia*.

The second group includes the open forest species *Eucalyptus grandis*, *E. intermedia*, *Imperata cylindrica* and *Acacia mangium* (figs. 4.8, 4.9, 4.10, 4.11 and 4.15). Almost all individuals of *Eucalyptus grandis*, *Eucalyptus intermedia* and *Imperata cylindrica* failed to persist in less than 10% ambient light or 5% full sunlight. Although fungicides and insecticides were used throughout the course of the experiment, many of these individuals apparently succumbed to insect or microbial attack, and their deaths can be partly attributed to insufficient light, and partly to herbivores and pathogens. In a natural situation the minimum tolerable light levels for seedlings of these species would probably be considerably higher due to the influence of low vigour on their sensitivity to herbivory and damping off. Although *Acacia mangium* individuals persisted at the lowest light levels in most cases, probably due to greater seed reserves, growth at low light levels was negligible (fig. 4.8). However, field observations indicate that *Acacia mangium* is capable of establishment in unburnt *I. cylindrica* grassland (G.C. Stocker, pers. comm.). *Acacia mangium* may prove to be more resistant to insects and pathogens than the other species in the group. First phyllode development in *Acacia mangium* occurred earlier at higher PAR levels and at higher nutrient concentrations.

The differences in growth between the "medium" and "high" nutrient treatments for *E. grandis* were substantially greater than for the other three species in this group (fig. 4.15). This indicates that *Acacia mangium*, *Eucalyptus intermedia* and *Imperata cylindrica* are probably more suited to soils of lower nutrient status than *Eucalyptus grandis*.

The third group includes those rainforest species which dominate large disturbance gaps, *Alphitonia petriei*, *Flindersia brayleyana* and *Toona australis*. At low and medium nutrient concentrations the growth of *F. brayleyana* tended to level off or decrease at the highest light levels, although the high degree of variability of the data makes it difficult to confirm this trend. Similar levels of variability are seen for medium nutrient levels in *Alphitonia petriei* and *Toona australis.* As growth of these species at low nutrient level is greatly reduced compared to medium and high levels, it is difficult to analyse any significant trends in these cases, although *Alphitonia petriei* does exhibit a significant linear response to increasing light at the low nutrient level ($r^2 = 0.86$).

All three of these species were found to persist at the lowest light levels (<5% FSU), although *Flindersia brayleyana* is evidently more shade tolerant than *Toona australis* which in turn appears to be more shade tolerant than *Alphitonia petriei.* Thus *Flindersia brayleyana* is closer to *Argyrodendron peralatum* or *Syzygium wesa* in its responses to light than *Alphitonia petriei* or *Toona australis.* These conclusions are based on the growth of the three species at the lower light levels, and do not appear to reflect the quantities of seed reserves available (fig. 4.18). Observations of growth and mortality of rainforest trees and of seedling growth and survival in gaps (G.C. Stocker unpublished) tend to confirm these shade tolerance rankings.

Initial dry weights compared with final dry weights (at the medium nutrient level) show a relationship between seed reserves and early growth rate (fig. 4.18). While only a small number of species are represented, this observation reflects the different dispersal strategies of small gap, large gap and open forest species. Richards (1952) suggested the strategy adopted by small gap species tends to be one of greater seed reserves but fewer seeds than either large gap or open forest species, allowing longer periods of persistence at low light levels.

Because the three fastest growing species, *Eucalyptus grandis*, *Alphitonia petriei* and *Toona australis* showed a substantially greater difference in growth between medium and high nutrient regimes than did any of the other species, it was necessary to harvest them prematurely (figs. 4.15 to 4.17). This requirement of high light and nutrient levels to attain maximum growth is a feature of fast growing, opportunistic species, and thus could partly explain the occurrence of *Eucalyptus grandis* in rainforest/open forest ecotones, and the presence of *Alphitonia petriei* and *Toona australis* on disturbed and undisturbed rainforest margins and in the larger rainforest gaps.

The high degree of variability shown by the rainforest species *Alphitonia petriei, Argyrodendron peralatum, Flindersia brayleyana, Syzygium wesa* and *Toona australis*, particularly at the medium nutrient level may well

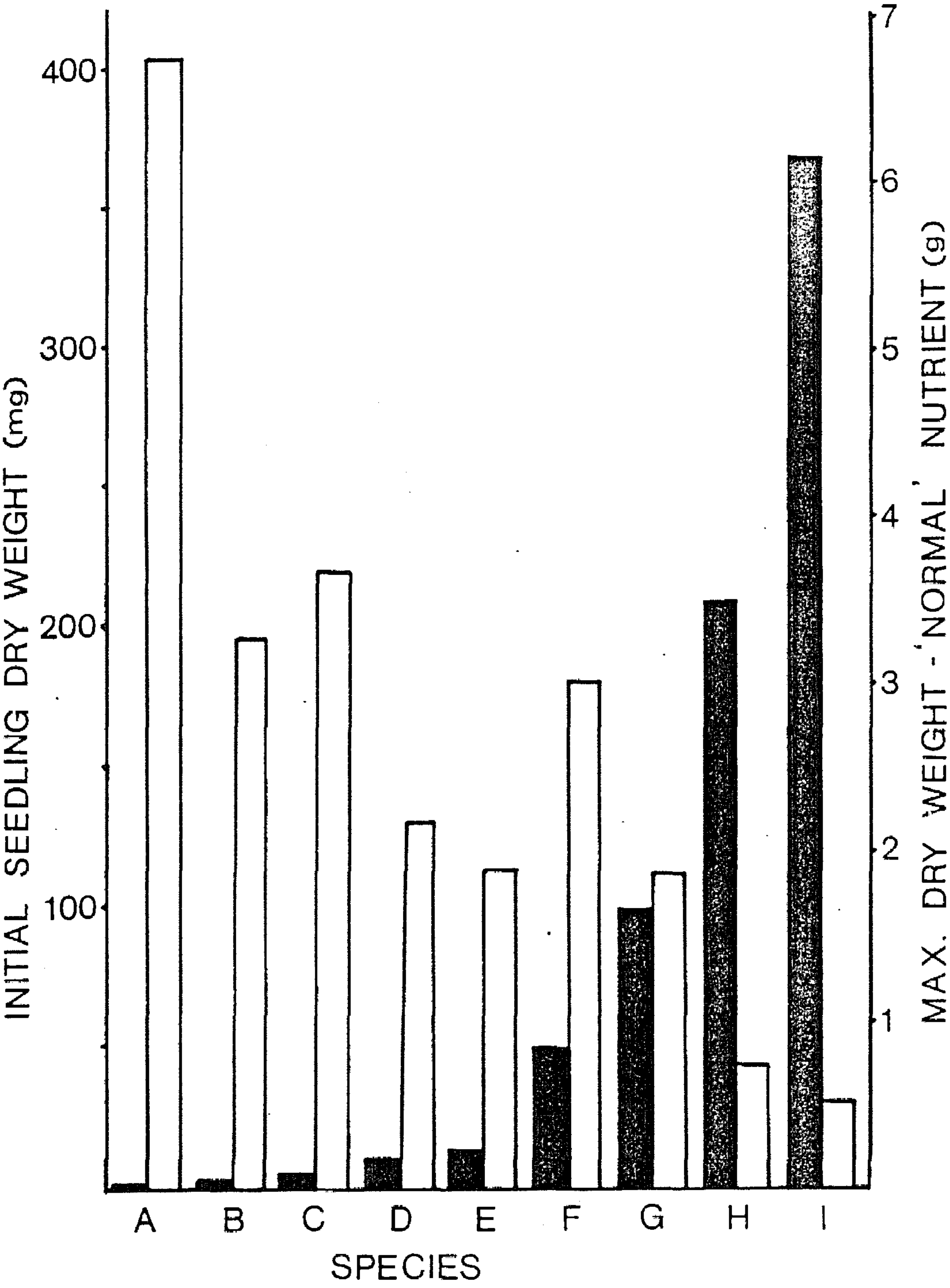

Figure 4.18. Initial seedling dry weights measured on the day of germination (shaded bars, mg) and maximum seedling dry weights 181 days after the commencement of the experiment at the medium nutrient level (open bars, g) calculated from the regression lines. Species: *A: Eucalyptus grandis, B: Imperata cylindrica; C: Eucalyptus intermedia, D: Alphitonia petriei, E: Acacia mangium, F: Toona australis, G: Flindersia brayleyana, H: Argyrodendron peralatum, I: Syzygium wesa.*

reflect an inherent genotypic heterogeneity with response to light. One outcome is that a species may have a greater range of potential gap sizes to colonize. Experiment 2 was designed to further test this hypothesis (Section 4.3.2).

An alternative explanation for the poor fit of some species to regression lines in the dry weight vs. light analyses is that some individuals of these species may have been genetically unfit and hence slower growing than other individuals in any light environments. However, when seedlings were selected at the start of the experiment, there was little indication of this variability, and all seedlings used appeared to be healthy. At the conclusion of the experiment, the slower growing individuals were no different in appearance to adjacent faster growing individuals, nor was there any evidence of competition for light amongst the seedlings. Although it is suspected that seedlings which grew slowly in the high light end of the gradient would have had higher survival rates in low light conditions than fast growing individuals of the same species, this has yet to be proved experimentally.

Although it may be convenient to think of shade tolerance in terms of discrete categories (e.g. large gap, small gap, etc.) into which all tropical forest species fit, it is likely that when data become available for a greater number of species, overlap between categories will increase, and the resultant continuum of physiological responses would range from light demanding open forest species to shade tolerant, small gap, "primary" rainforest species.

Above ground resource allocation was investigated for the nine species in experiment 1. Analysis of variance of regression was used on natural logs of each of the following variables to determine whether the relationship between each variable pair was isometric. Analyses were carried out separately for each species.

1. Stem dry weight: leaf dry weight
2. Height: total dry weight
3. Total dry weight: total leaf area
4. Total leaf area: projected leaf area
5. Total leaf area: leaf dry weight.

The log/log regression analysis (table 4.5) shows that for each species, all variable pairs except height: total dry weight are linearly related, as the slopes of the log/log regression lines do not deviate significantly from one. The relationships between height and total dry weight were all found to be

| SPECIES | n | t (0.05) | VARIABLE PAIR | SLOPE | S.E. SLOPE | 95% CONFIDENCE LIMITS, SLOPE | $R^2$ |
|---|---|---|---|---|---|---|---|
| Acacia mangium | 41 | 2.02 | SDW:LDW | 1.129 | 0.315 | 0.493-1.765 | 0.96 |
| | | | HEI:TDW | 0.324 | 0.222 | -0.124-0.772 | 0.82 |
| | | | TDW:TLA | 0.869 | 0.231 | 0.402-1.336 | 0.97 |
| | | | TLA:LDW | 0.829 | 0.245 | 0.334-1.324 | 0.96 |
| | | | TLA:PLA | 0.745 | 0.456 | -0.157-1.377 | 0.82 |
| Alphitonia petriei | 43 | 2.02 | SDW:LDW | 1.156 | 0.388 | 0.372-1.940 | 0.93 |
| | | | HEI:TDW | 0.314 | 0.238 | -0.167-0.795 | 0.78 |
| | | | TDW:TLA | 0.904 | 0.439 | 0.017-1.791 | 0.90 |
| | | | TLA:LDW | 0.865 | 0.448 | 0.040-1.770 | 0.89 |
| | | | TLA:PLA | 0.856 | 0.489 | -0.132-1.844 | 0.85 |
| Argyrodendron peralatum | 47 | 2.01 | SDW:LDW | 0.450 | 0.552 | -0.660-1.560 | 0.47 |
| | | | HEI:TDW | 0.279 | 0.144 | -0.010-0.568 | 0.51 |
| | | | TDW:TLA | 0.881 | 0.209 | 0.461-1.301 | 0.84 |
| | | | TLA:LDW | 0.800 | 0.144 | 0.511-1.089 | 0.92 |
| | | | TLA:PLA | 0.625 | 0.220 | 0.183-1.067 | 0.60 |
| Eucalyptus grandis | 37 | 2.03 | SDW:LDW | 0.911 | 0.460 | -0.023-1.845 | 0.92 |
| | | | HEI:TDW | 0.345 | 0.161 | 0.018-0.672 | 0.93 |
| | | | TDW:TLA | 0.711 | 0.450 | -0.203-1.625 | 0.87 |
| | | | TLA:LDW | 0.702 | 0.524 | -0.362-1.766 | 0.83 |
| | | | TLA:PLA | 1.056 | 0.700 | -0.365-2.477 | 0.69 |
| Eucalyptus intermedia | 39 | 2.02 | SDW:LDW | 1.056 | 0.533 | -0.026-2.138 | 0.93 |
| | | | HEI:TDW | 0.358 | 0.294 | -0.236-0.952 | 0.90 |
| | | | TDW:TLA | 1.024 | 0.467 | 0.081-1.967 | 0.95 |
| | | | TLA:LDW | 0.981 | 0.473 | 0.026-1.936 | 0.95 |
| | | | TLA:PLA | 0.762 | 0.483 | -0.214-1.738 | 0.92 |
| Flindersia brayleyana | 46 | 2.01 | LDW:SDW | 0.927 | 0.510 | -0.098-1.952 | 0.72 |
| | | | HEI:TDW | 0.285 | 0.160 | -0.037-0.607 | 0.72 |
| | | | TDW:TLA | 0.941 | 0.305 | 0.328-1.554 | 0.89 |
| | | | TLA:LDW | 0.903 | 0.261 | 0.378-1.428 | 0.92 |
| | | | TLA:PLA | 0.778 | 0.238 | 0.300-1.256 | 0.90 |
| Imperata cylindrica | 39 | 2.02 | LDW:SDW | - | - | - | - |
| | | | HEI:TDW | 0.295 | 0.221 | -0.151-0.741 | 0.75 |
| | | | TDW:TLA | 1.016 | 0.327 | 0.445-1.676 | 0.94 |
| | | | TLA:LDW | 1.016 | 0.327 | 0.445-1.676 | 0.94 |
| | | | TLA:PLA | 0.740 | 0.456 | -0.181-1.661 | 0.74 |
| Syzygium wesa | 39 | 2.02 | LDW:SDW | 1.000 | 0.352 | 0.289-1.711 | 0.74 |
| | | | HEI:TDW | 0.299 | 0.158 | -0.020-0.618 | 0.59 |
| | | | TDW:TLA | 0.979 | 0.178 | 0.619-1.339 | 0.92 |
| | | | TLA:LDW | 0.915 | 0.163 | 0.586-1.244 | 0.94 |
| | | | TLA:PLA | 0.805 | 0.390 | 0.017-1.593 | 0.64 |
| Toona australis | 46 | 2.01 | LDW:SDW | 1.064 | 0.337 | 0.387-1.741 | 0.94 |
| | | | HEI:TDW | 0.378 | 0.191 | -0.008-0.764 | 0.88 |
| | | | TDW:TLA | 1.011 | 0.418 | 0.167-1.855 | 0.91 |
| | | | TLA:LDW | 0.965 | 0.399 | 0.159-1.771 | 0.92 |
| | | | TLA:PLA | 1.106 | 0.820 | -0.550-2.762 | 0.79 |

Table 4.5 Log/log regression analysis of the variables used in seedling resource allocation analysis. The variables are isometrically related if the slope of the line does not differ significantly from 1. The table shows the the number of points, values of t, the slope of the regression line, standard error and 95% confidence limits of the slope and the $R^2$ for the regression for each species and each variable pair. The variables are stem dry weight (SDW), leaf dry weight (LDW), height (HEI), total dry weight (TDW), total leaf area (TLA) and projected leaf area (PLA). The analysis was carried out on the natural logarithms of these variables.

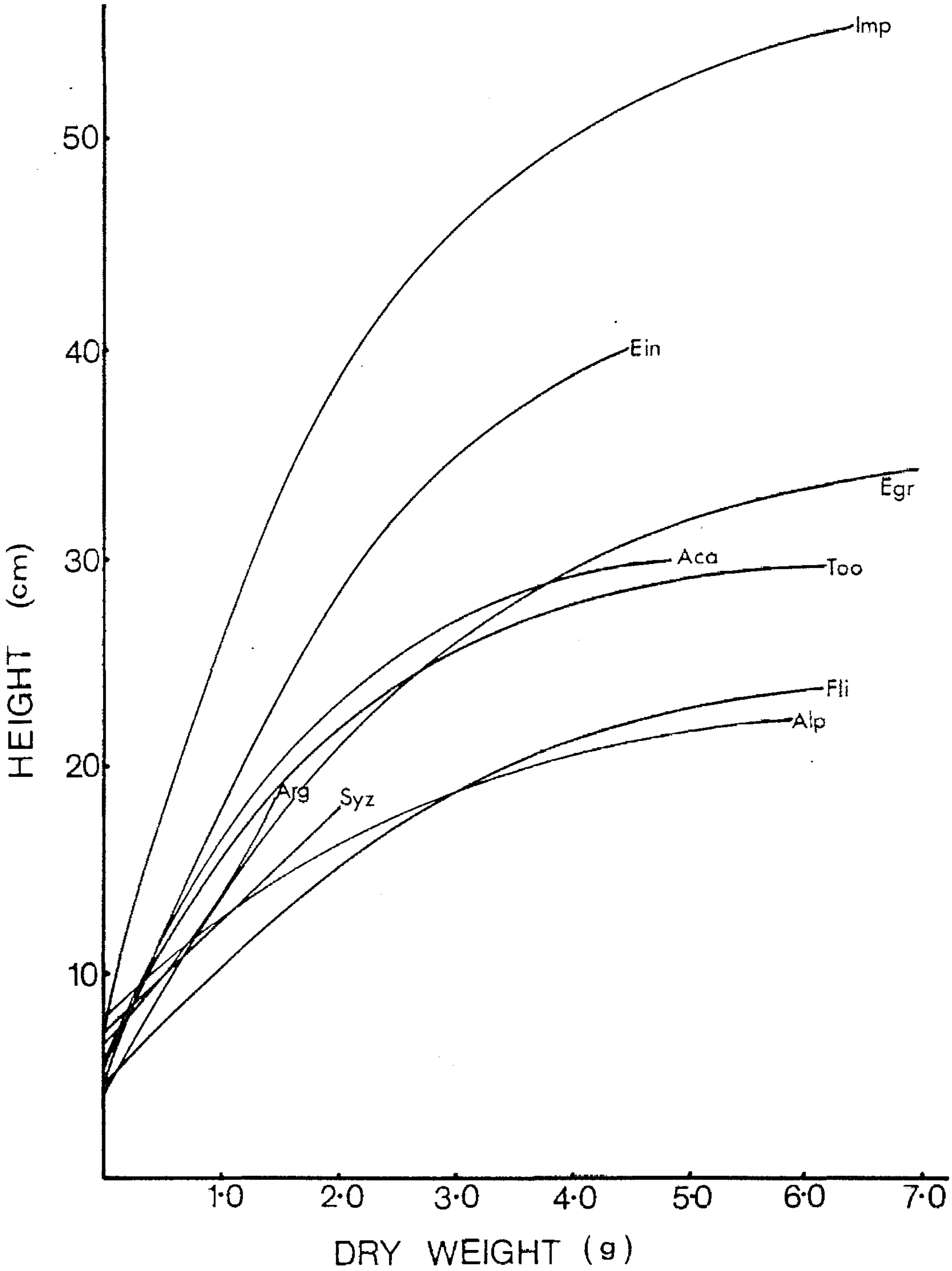

Figure 4.19 Regression lines for height (cm) against dry weight (g) for the nine species in experiment 1. *Aca: Acacia mangium, Alp: Alphitonia petriei, Arg: Argyrodendron peralatum, Egr: Eucalyptus grandis, Ein: Eucalyptus intermedia, Fli: Flindersia Brayleyana, Imp: Imperata cylindrica, Syz: Syzygium wesa, Too: Toona australis.*

quadratic (table 4.6, fig. 4.19). Ratios were calculated for each species between the four isometrically related variable pairs and height: (total dry weight)$^{-2}$. These are shown in figures 4.20 to 4.24.

The five resource allocation variables were analysed together using "Clustan-2" classification software (Wishart, 1978). Species were grouped using inverse Squared Euclidean Distance as a similarity measure. The resultant dendrogram is shown in figure 4.25. Four species groups are apparent in the figure. *Acacia mangium* and *Eucalyptus intermedia* form the first group at a high similarity level. Both species are shade intolerant, and are probably adapted to low nutrient status soils, as was noted previously. *Argyrodendron peralatum*, *Syzygium wesa* and *Flindersia brayleyana* form the second group of morphologically closely related species. Again, the physiological responses of *Argyrodendron peralatum* and *Syzygium wesa*, both small gap species, are similar, while *Flindersia brayleyana* showed physiological characteristics intermediate between the small and large gap species groups. *Imperata cylindrica* is isolated as the only non woody species included in the analysis. Finally, the three fastest growing species, *Alphitonia petriei*, *Eucalyptus grandis* and *Toona australis* form a morphological group. *Toona australis* is distinguished from the other two species in being deciduous and therefore allocating fewer resources to its leaves (fig. 4.20).

The high degree of similarity between the groups of species formed according to physiological responses and those based on resource allocation may be a coincidence, and a larger group of species should be tested. Nevertheless, this study demonstrates that resource allocation in seedlings may be a viable means of determining successional status, and future studies should incorporate this type of analysis.

### 4.3.2. EXPERIMENT 2

Analysis of variance of regression was carried out on dry weight against PAR for the four species examined in experiment 2. Table 4.7 shows the results of these analyses. The regression lines, means and standard errors are shown in figures 4.26 to 4.29. These results confirm the observations from experiment 1. The two open forest species, *Eucalyptus grandis* and *E. intermedia* are less variable in their response to light than the two rainforest species *Neolitsea dealbata* and *Toona australis*. Response curves are also of

Figures 4.20 to 4.24 Resource allocation ratios for the nine species used in experiment 1. The heavy blocks represent standard errors, and the lines represent the 95% confidence limits for each species and each ratio. The variable pairs are shown at the base of each graph. *Aca: Acacia mangium, Alp: Alphitonia petriei, Arg: Argyrodendron peralatum, Egr: Eucalyptus grandis, Ein: Eucalyptus intermedia, Fli: Flindersia brayleyana, Imp: Imperata cylindrica, Syz: Syzygium wesa, Too: Toona australis.*

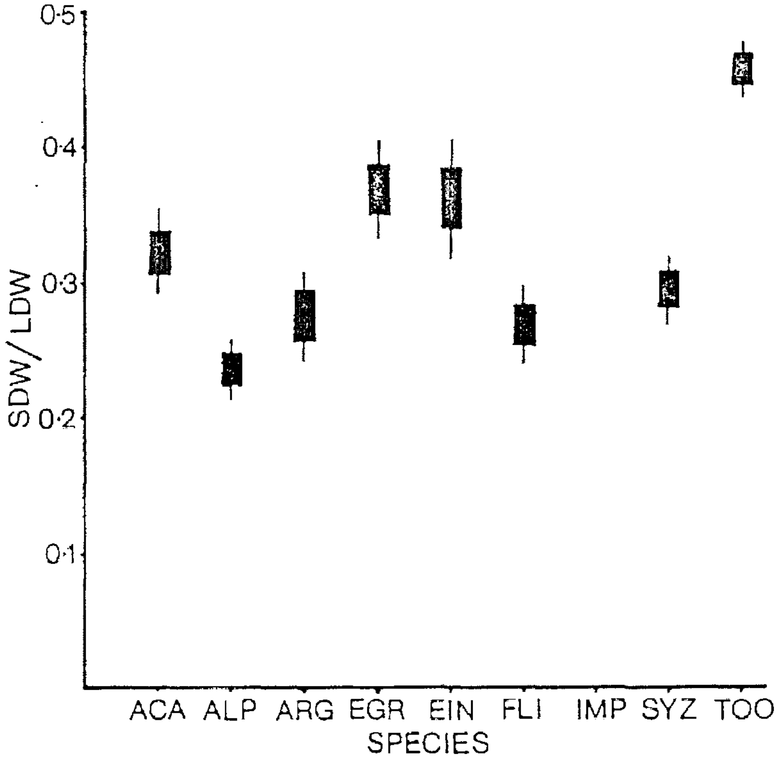

Figure 4.20 Mean ratios between stem dry weight (g) and leaf dry weight (g)

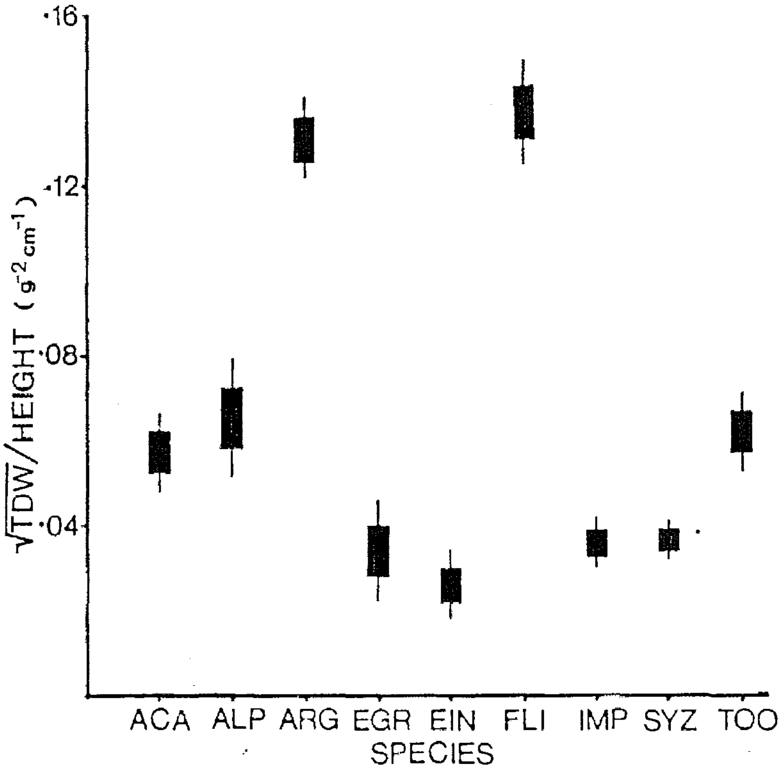

Figure 4.21 Mean ratios between (total dry weight)$^{-2}$ · (g) and height (cm).

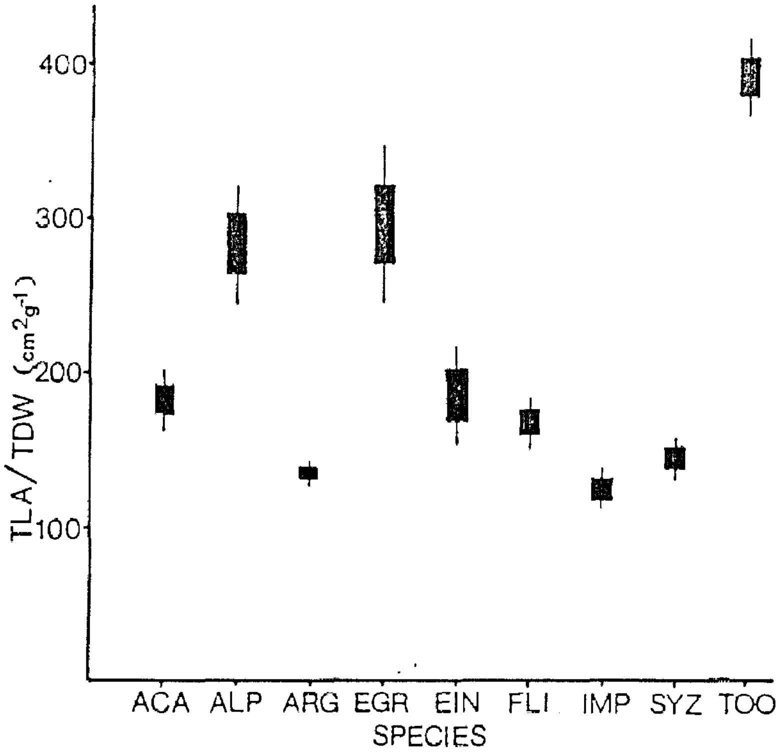

Figure 4.22 Mean ratios between total leaf area (cm$^2$) and total dry weight (g).

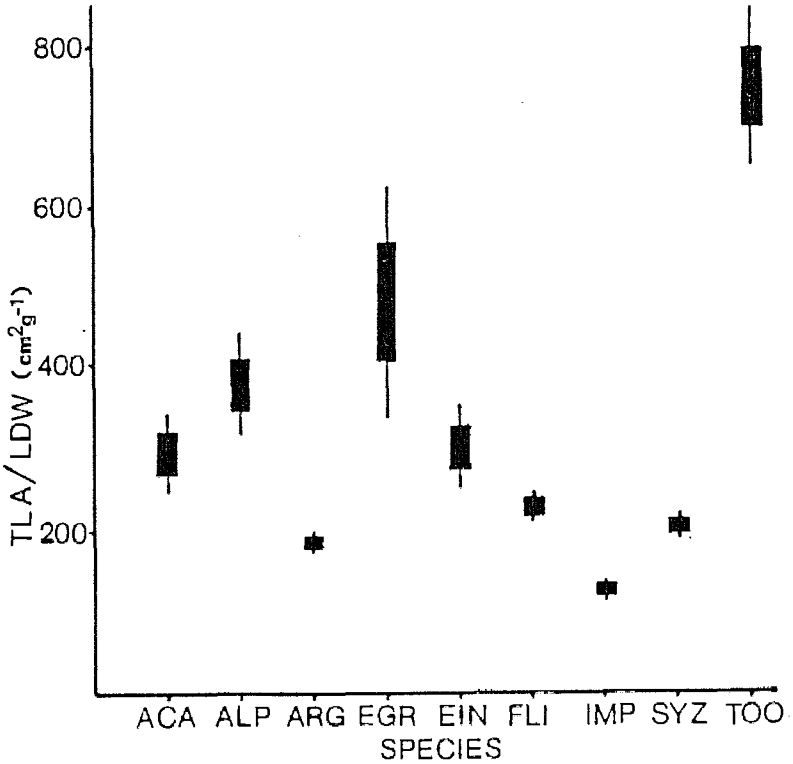

Figure 4.23 Mean ratios between total leaf area (cm$^2$) and leaf dry weight (g).

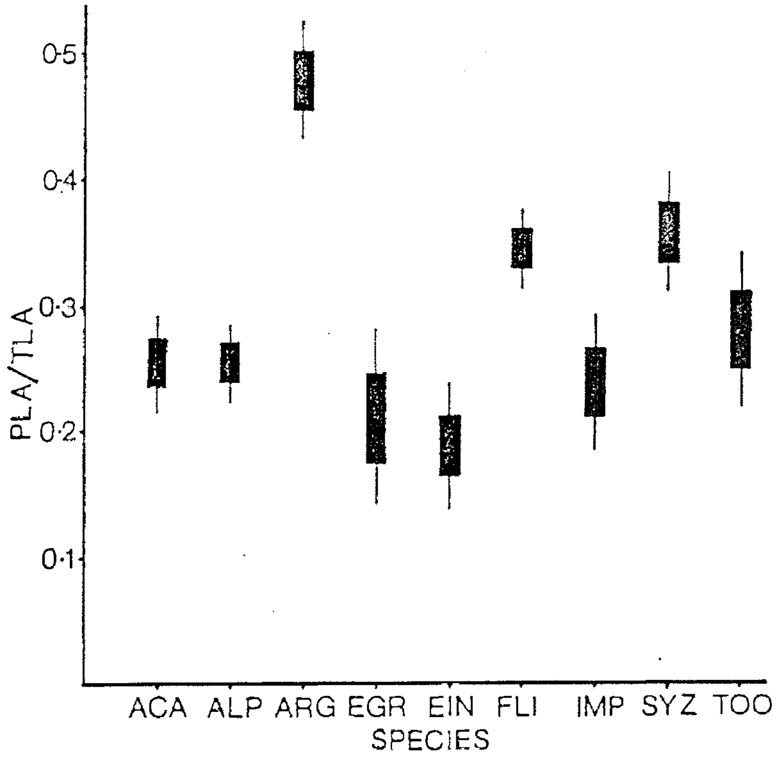

Figure 4.24 Mean ratios between projected leaf area ($cm^2$) and total leaf area ($cm^2$).

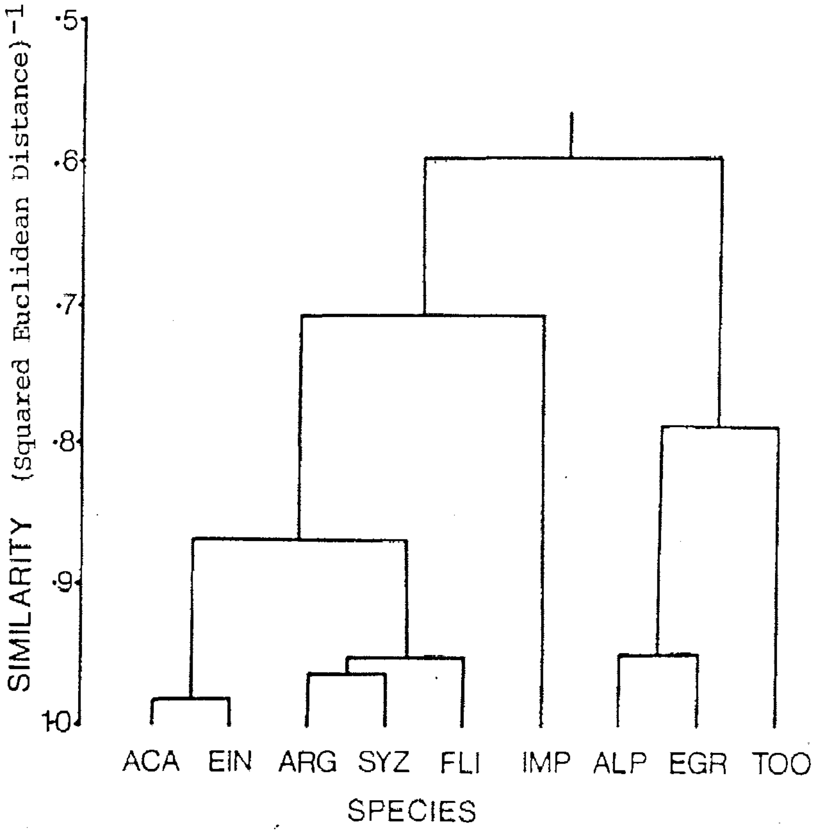

Figure 4.25 Results of the classification analysis of the resource allocation variables for the nine species used in experiment 1. Similarity is given on the vertical axis in inverse squared euclidean distance.

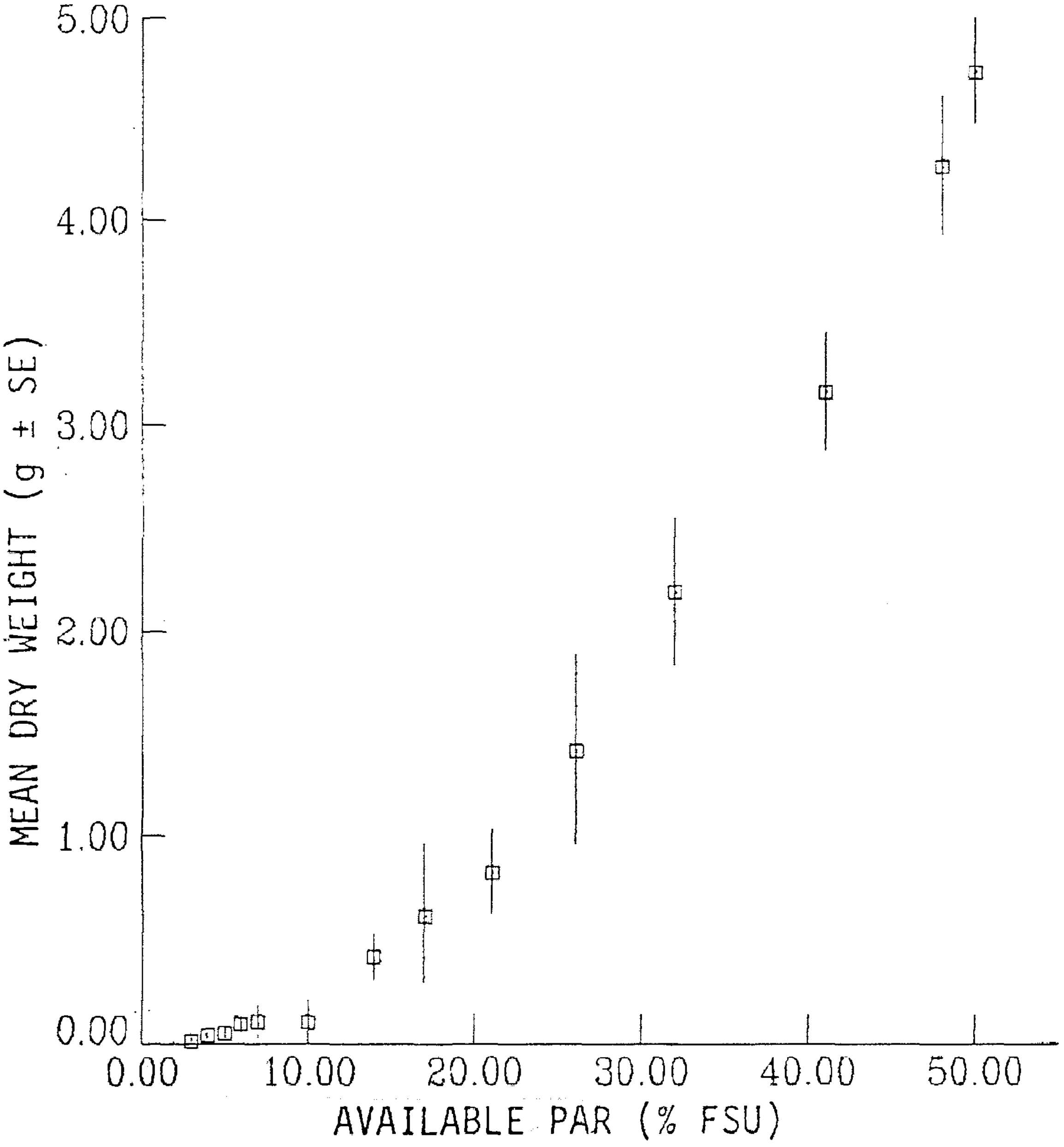

Figure 4.26 Dry weight (mean ± SE, g) against available PAR (% full sunlight) in experiment 2, for *Eucalyptus grandis*.

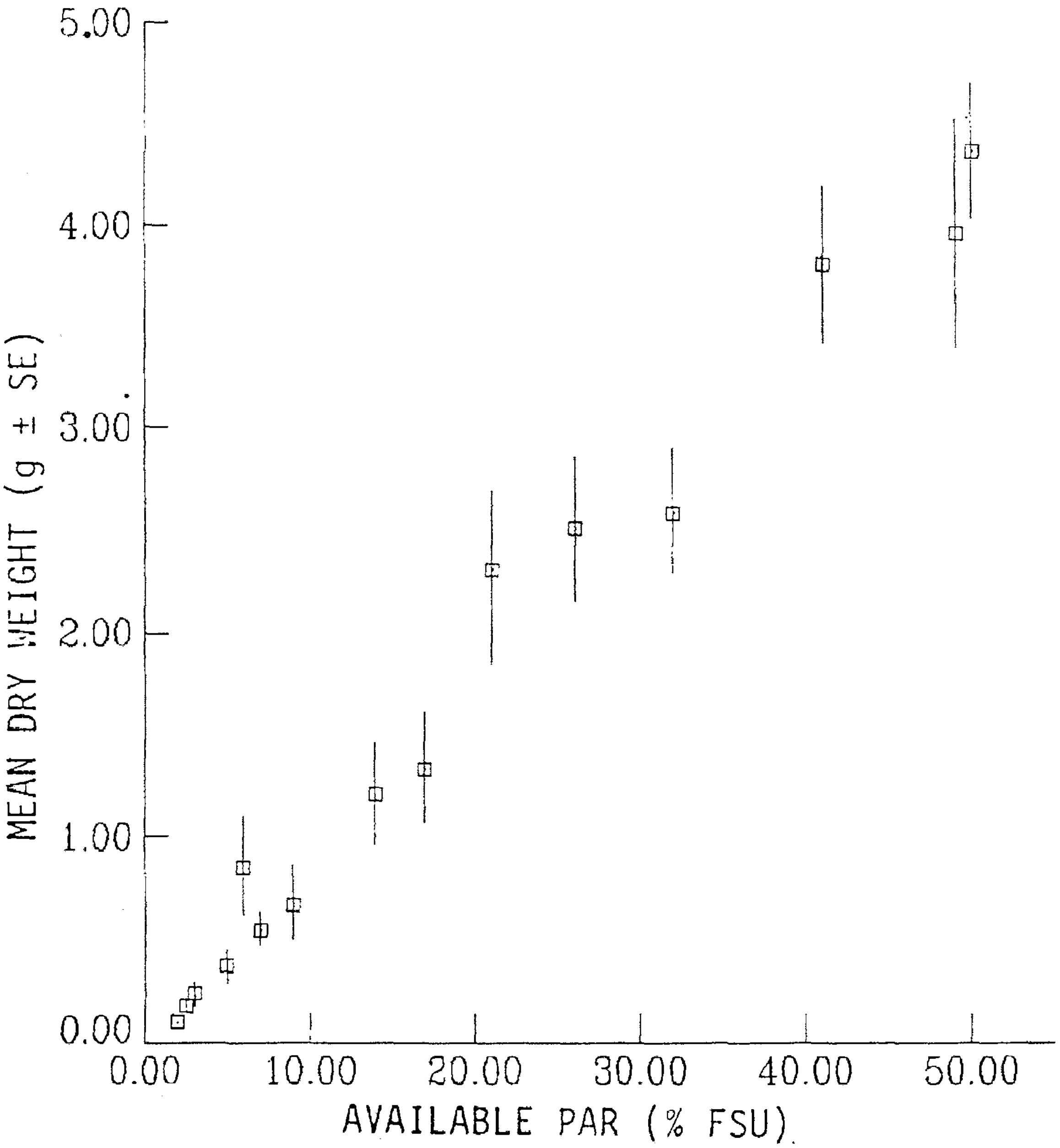

Figure 4.27 Dry weight (mean ± SE, g) against available PAR (% full sunlight) in experiment 2, for *Eucalyptus intermedia*.

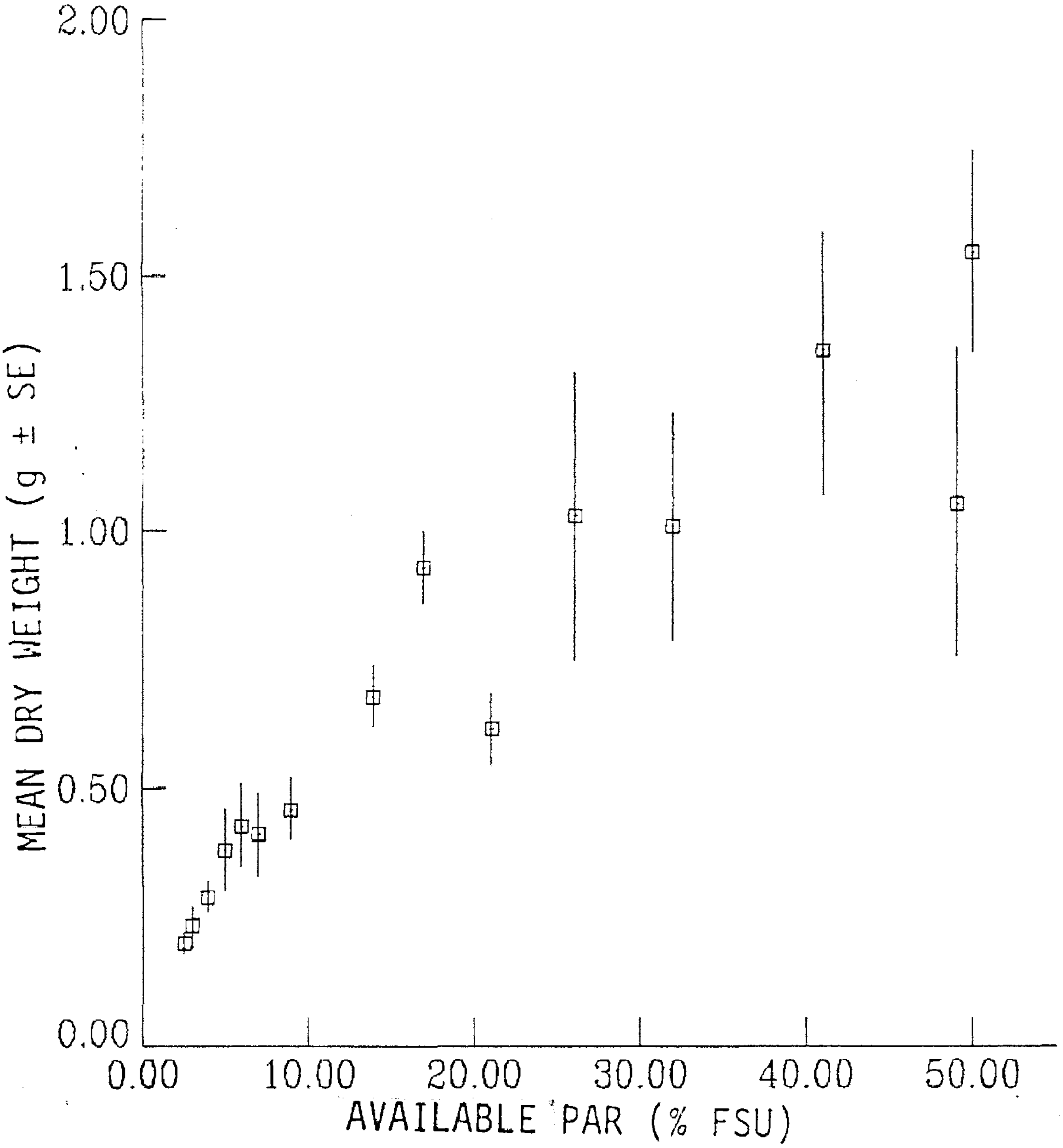

Figure 4.28 Dry weight (mean ± SE, g) against available PAR (% full sunlight) in experiment 2, for *Neolitsea dealbata*.

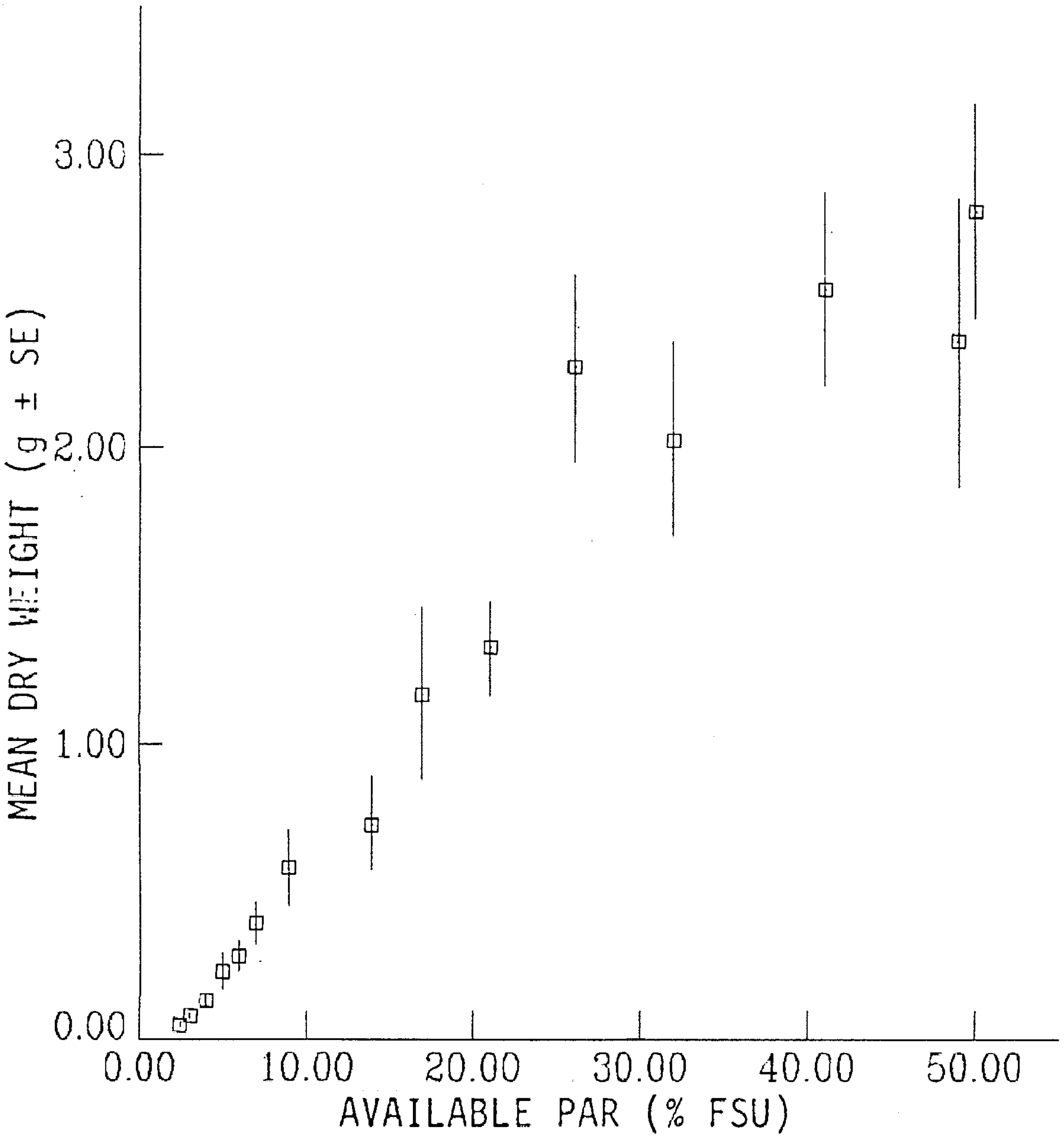

Figure 4.29 Dry weight (mean ± SE, g) against available PAR (% full sunlight) in experiment 2, for *Toona australis*.

| SPECIES | SLOPE (a) | SLOPE (b) | INTERCEPT (c) | $r^2$ |
|---|---|---|---|---|
| *Acacia mangium* | 12.153 | -1.726 | 6.566 | 0.83 |
| *Alphitonia petriei* | 7.133 | -0.737 | 4.686 | 0.80 |
| *Argyrodendron peralatum* | 3.935 | 1.969 | 7.471 | 0.74 |
| *Eucalyptus grandis* | 11.213 | -1.107 | 3.865 | 0.84 |
| *Eucalyptus intermedia* | 16.202 | -1.838 | 3.390 | 0.89 |
| *Flindersia brayleyana* | 4.549 | -0.325 | 8.728 | 0.81 |
| *Imperata cylindrica* | 21.747 | -2.924 | 9.238 | 0.81 |
| *Syzygium wesa* | 0.0913 | - | -0.372 | 0.84 |
| *Toona australis* | 12.356 | -2.001 | 6.210 | 0.84 |

Table 4.6 Regression equations for height (cm) against total dry weight (g) for 9 species in experiment 1. All equations are of the form $y = ax + bx^2 + c$ except for *Syzygium wesa*, which has a straight line relationship between the two variables.

| SPECIES | n | INTERCEPT (c) | SLOPE (ax)X10$^{-1}$ | SLOPE (bx$^2$)X10$^{-3}$ | F | PROB. | $r^2$ |
|---|---|---|---|---|---|---|---|
| *Eucalyptus grandis* | 111 | -0.051 | 0.0792 | 0.392 | 569.3 | <.001 | 0.91 |
| *Eucalyptus intermedia* | 128 | -0.118 | 0.546 | -0.105 | 247.6 | <.001 | 0.80 |
| *Neolitsea dealbata* | 108 | 0.164 | 0.194 | -0.0710 | 57.95 | <.001 | 0.51 |
| *Toona australis* | 143 | -0.224 | 0.509 | -0.215 | 128.9 | <.001 | 0.63 |

Table 4.7 Results of regression analysis of dry weight (g) against PAR (% Full Sunlight) for 4 species in experiment 2. Curves fitted are all quadratics ($y = ax + bx^2 + c$).

similar shape to those found in experiment 1. *Neolitsea dealbata* is the slowest growing and most shade tolerant of the four species, and shows the greatest degree of variability in its response to light. Observations carried out at Kirrama and Paluma indicate that *Neolitsea dealbata* occupies a wide range of different gap sizes. If given suitable openings it grows to a height of 15 m (B.P.M. Hyland, unpub.), although it also seems to persist in the understorey as a low shrub at many sites.

The open forest species are adapted to establish in more homogenous, high light environments and are not faced with a wide range of gap sizes to colonize. For this reason, their responses to light gradients are more uniform than rainforest species. The light environment in rainforest is highly heterogeneous, depending on the distribution, shape, orientation and sizes of gaps in the canopy. Consequently, rainforest species would have a greater range of potential sites in which to become established if each individual of a species produced a group of offspring with a high level of between seedling variability of shade tolerance. These trends could be confirmed by extensive analysis of photosynthesis of rainforest trees of different ages and in different gap sizes under field conditions, but the equipment to do so was not available for this study.

### 4.3.3. EXPERIMENT 3

The responses of the four species examined in the competition experiment to light and nutrient were substantially different to the results obtained in experiment 1 for the same species grown in monoculture. figures 4.30 to 4.32 show the means and standard errors of total dry weight/pot against PAR in each nutrient regime. The most rapid growth for all four species combined occurred at the high nutrient level, and the response to light is linear (fig. 4.30). As nutrient concentration was reduced, so the light level at which maximum dry weight/pot was reached tended to decrease, indicating that nutrient concentration became a limiting factor to growth in the medium and low nutrient treatments (figs. 4.31 and 4.32).

Relative proportions of the total dry weight in each pot were calculated for each species. Mean and standard error relative dry weights are plotted against light for each species in high, medium and low nutrient levels in figures 4.33 to 4.44.

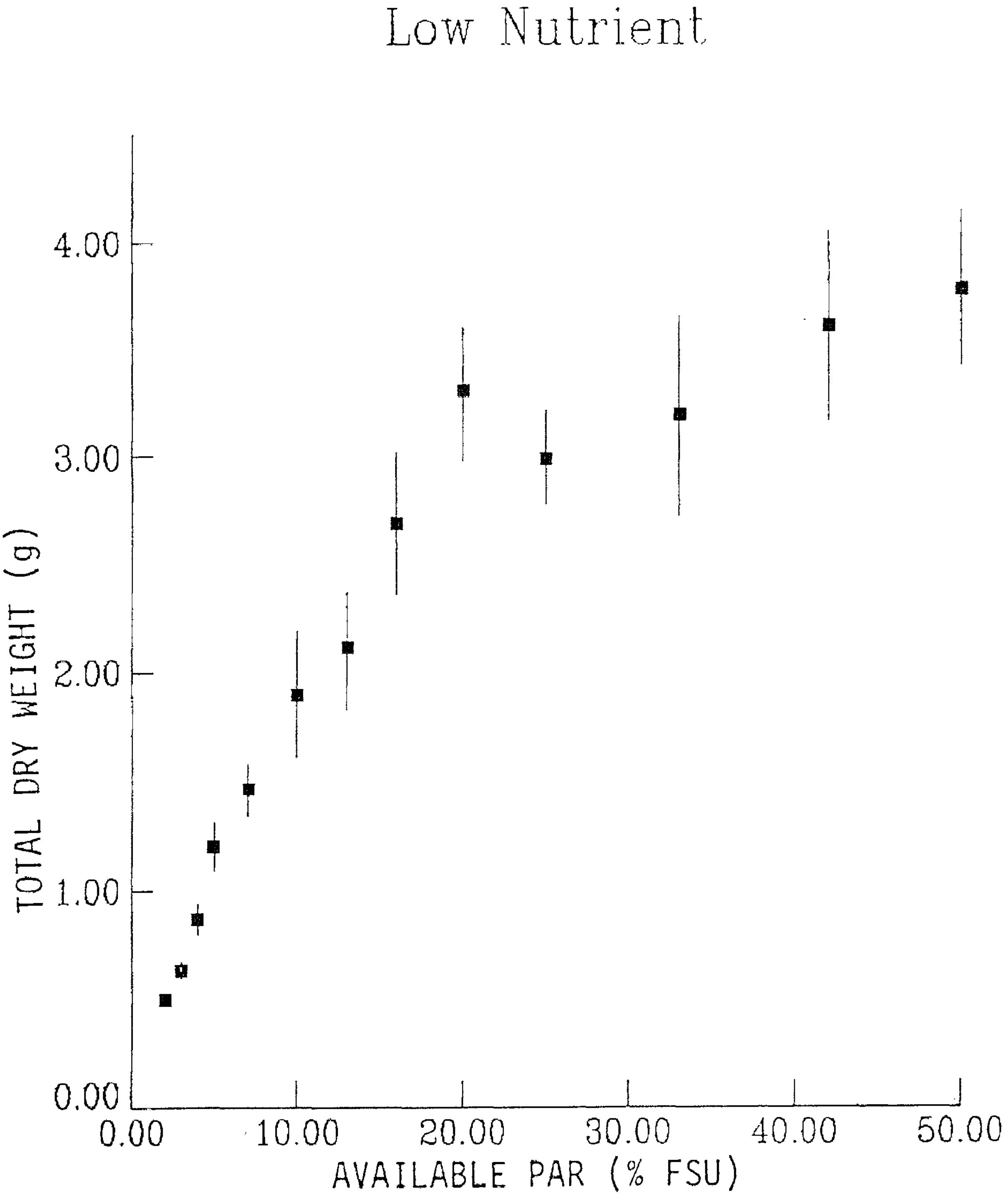

Figure 4.30 Total dry weight (mean ± SE, g) for four species combined against available PAR (% full sunlight) in experiment 3. Low nutrient.

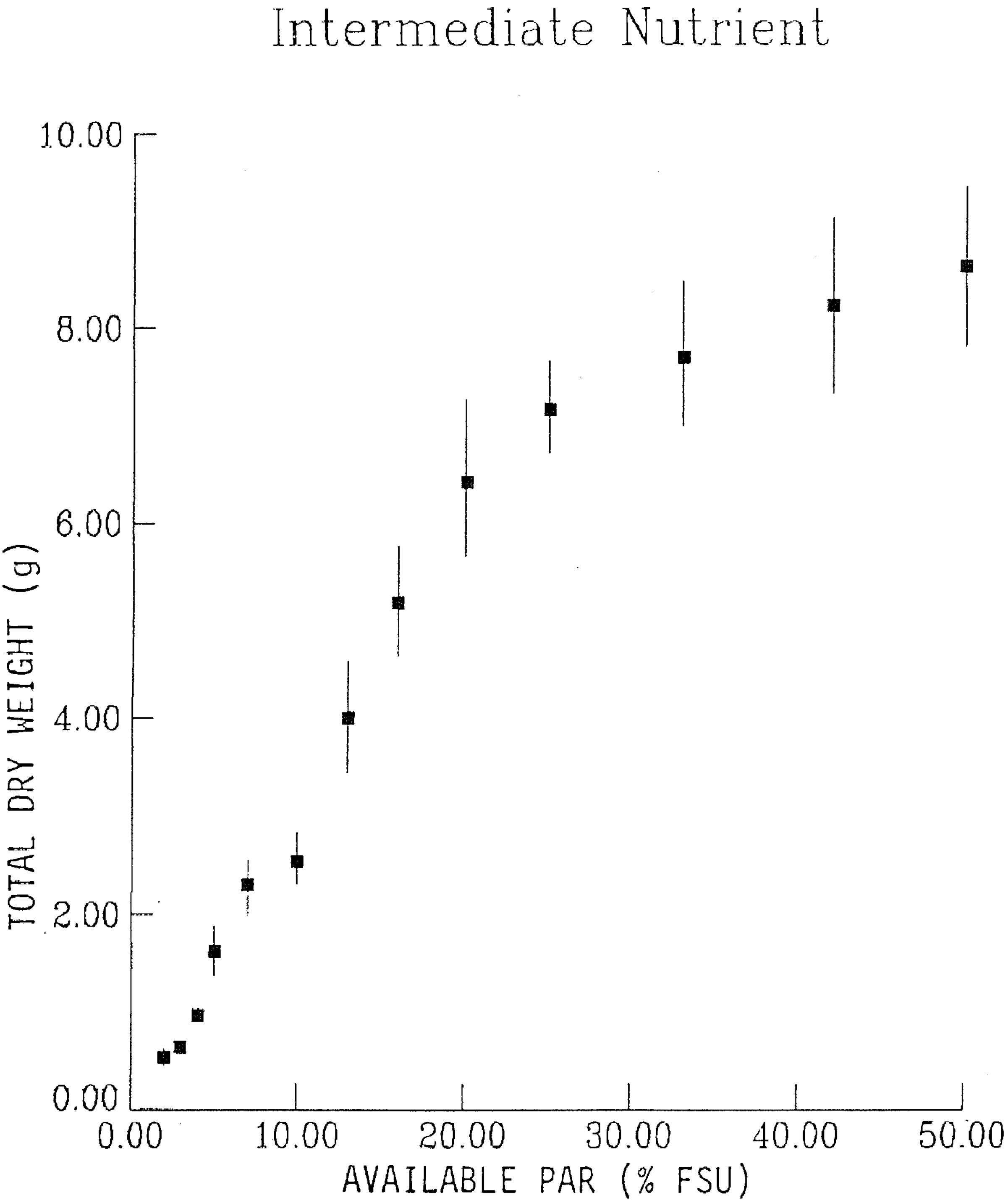

Figure 4.31 Total dry weight (mean ± SE, g) for four species combined against available PAR (% full sunlight) in experiment 3. Medium nutrient.

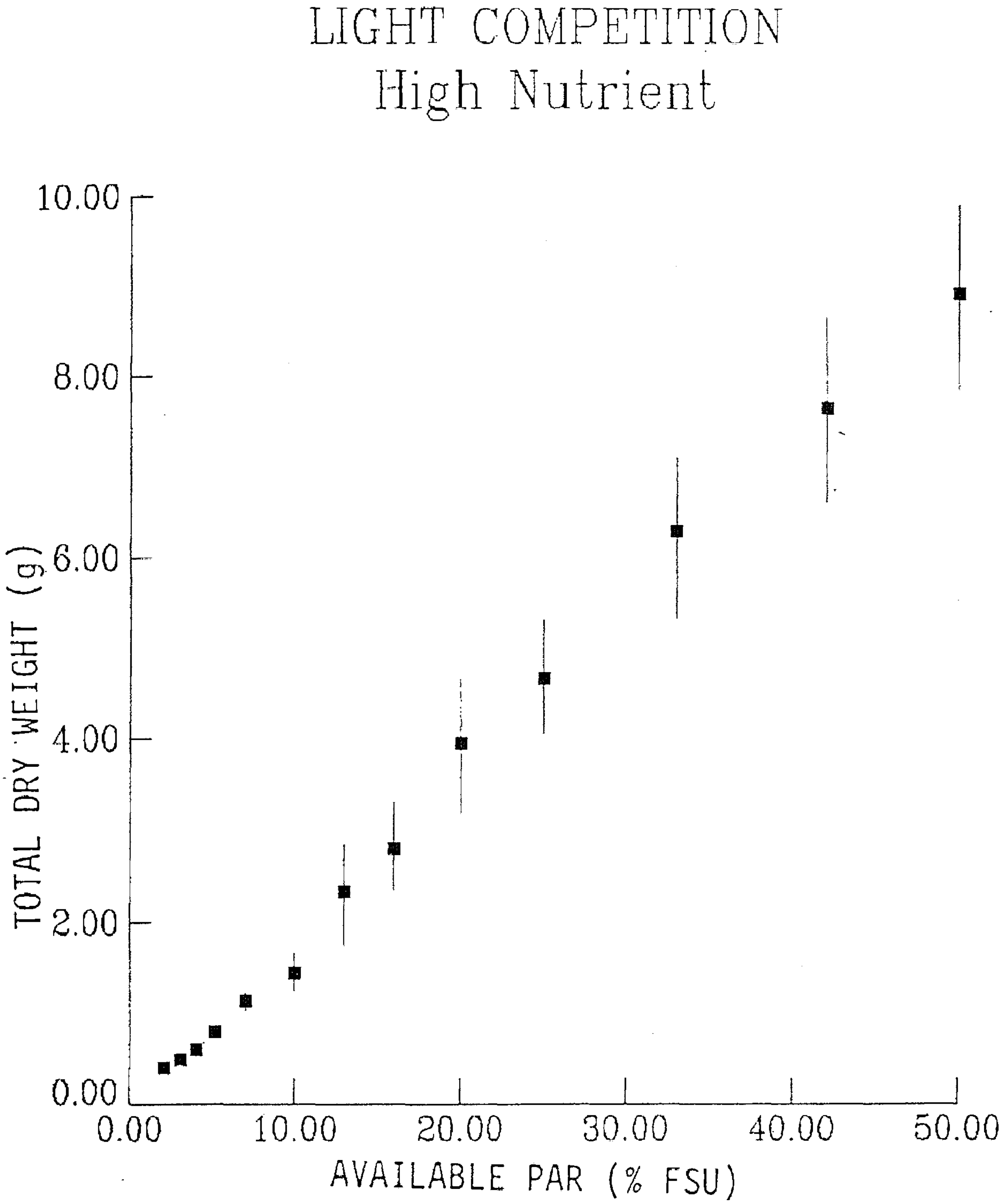

Figure 4.32 Total dry weight (mean ± SE, g) for four species combined against available PAR (% full sunlight) in experiment 3. High nutrient.

At low light levels, *Argyrodendron peralatum* is clearly the dominant species (figs. 4.33, 4.37 and 4.41), making up approximately 80% of the total dry weight at <5% full sunlight in all three nutrient regimes. The relative dominance of this species is highest in the low nutrient regime, probably as a result of greater seed reserves (fig. 4.19). The ability of *Argyrodendron peralatum* to persist and grow in low light environments, shown in experiment 1, gives this species the highest likelihood of success in competition with less shade tolerant species in a small gap or under a closed canopy.

As PAR is increased, *Eucalyptus grandis* emerges as the dominant species. It is evident (figs. 4.31, 4.35 and 4.39) that of the four species, this is the most able to take advantage of high PAR levels. Even at PAR levels around 20% FSU, *Eucalyptus grandis* makes up over 50% of the total dry weight in the medium and high nutrient regimes. In the field, this advantage may be reduced by herbivores or pathogens, to which *Eucalyptus grandis* appears to be more susceptible (experiment 1). Moreover, results described in chapter 5 show that *Eucalyptus grandis* is less likely to establish under a rainforest canopy due to small seed size and damping off effects.

At the low nutrient level, the competitive advantage of *Eucalyptus grandis* is reduced in the face of proportionally more vigorous growth of *Acacia mangium*. Experiment 1 indicated that *Acacia mangium* is more tolerant of nutrient poor soils, and while *Acacia mangium* does not grow as large as *Eucalyptus grandis* even at the low nutrient level, it approaches its full growth potential more closely than in the medium or high nutrient levels.Both *Acacia mangium* and *Toona australis* are clearly affected by competition from *Eucalyptus grandis*. Results from experiment 1 showed that these species, *Toona australis* in particular, grow nearly as fast as *Eucalyptus grandis* in high PAR levels. However, when competing for light and nutrients, *Toona australis* is evidently inferior to *Eucalyptus grandis*, indicated by the low proportional dry weight of *Toona australis* at all PAR values above approximately 10% FSU. In a few isolated cases throughout the range from 10% to 50% FSU, individuals of *Toona* grew much larger than the neighbouring *Eucalyptus grandis*, which in turn were greatly suppressed. From the results of this experiment, however, such cases were obviously exceptions. At between 5 and 10% FSU in the medium nutrient treatment, *Toona* is the dominant species, although it closely shares this dominance with *Eucalyptus grandis* and *Argyrodendron peralatum*.

Figures 4.33 to 4.44 Proportion of total dry weight per pot (proportion of TDW = dry weight of seedling / total dry weight of all seedlings in the pot, mean ± SE) against available PAR (% full sunlight) for the four species used in the competition experiment (experiment 3). Species and nutrient treatment are shown at the base of each graph.

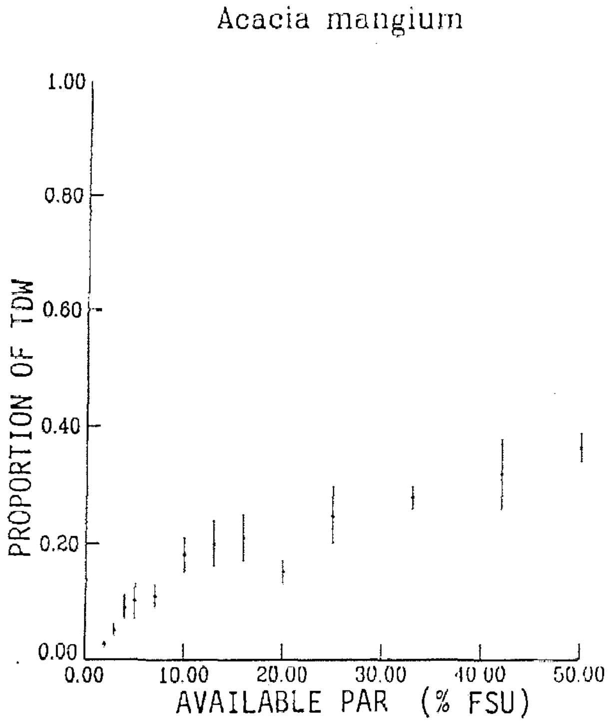

Figure 4.33 *Acacia mangium*, Low nutrient.

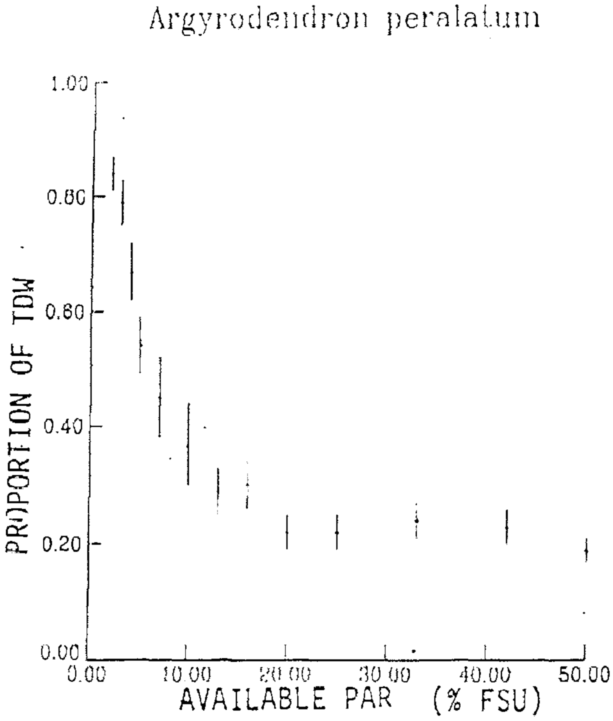

Figure 4.34 *Argyrodendron peralatum* Low nutrient.

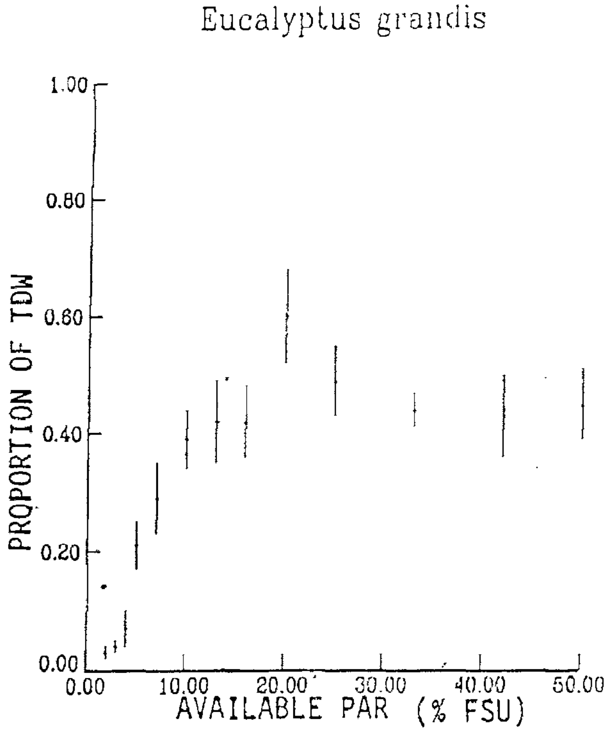

Figure 4.35 *Eucalyptus grandis*, Low nutrient.

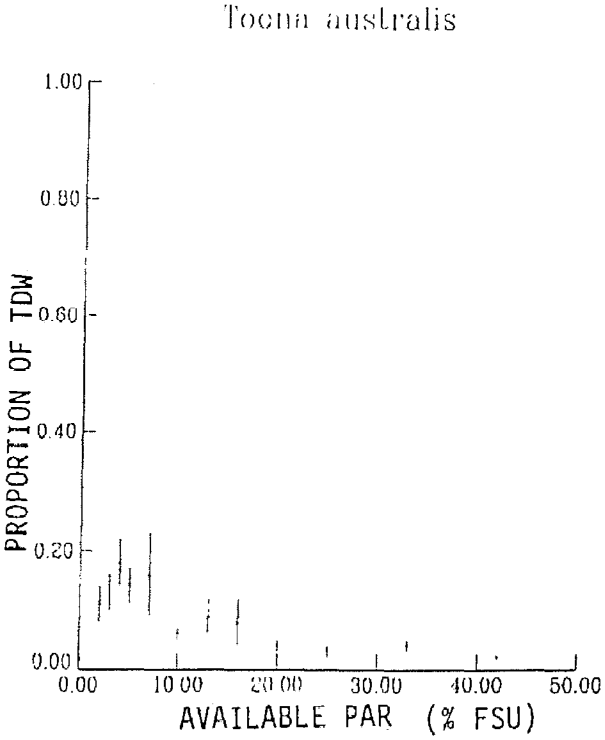

Figure 4.36 *Toona australis*, Low nutrient.

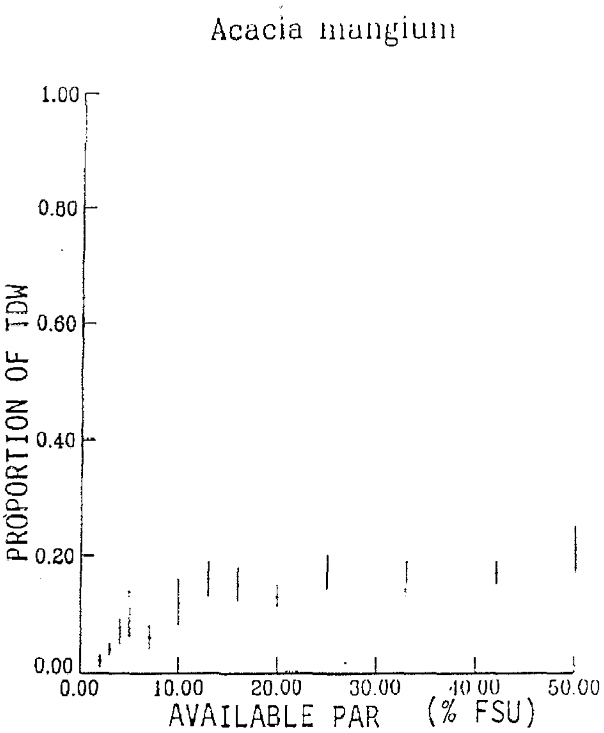

Figure 4.37 *Acacia mangium*, Medium nutrient.

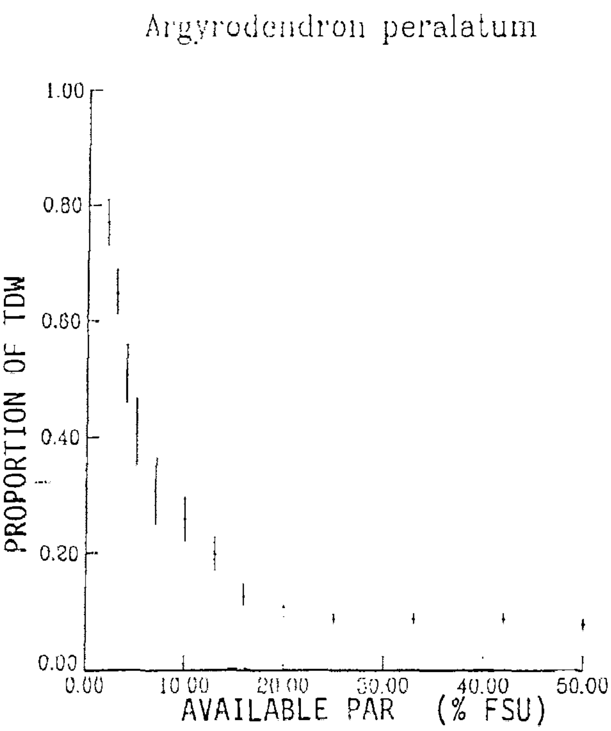

Figure 4.38 *Argyrodendron peralatum*, Medium nutrient.

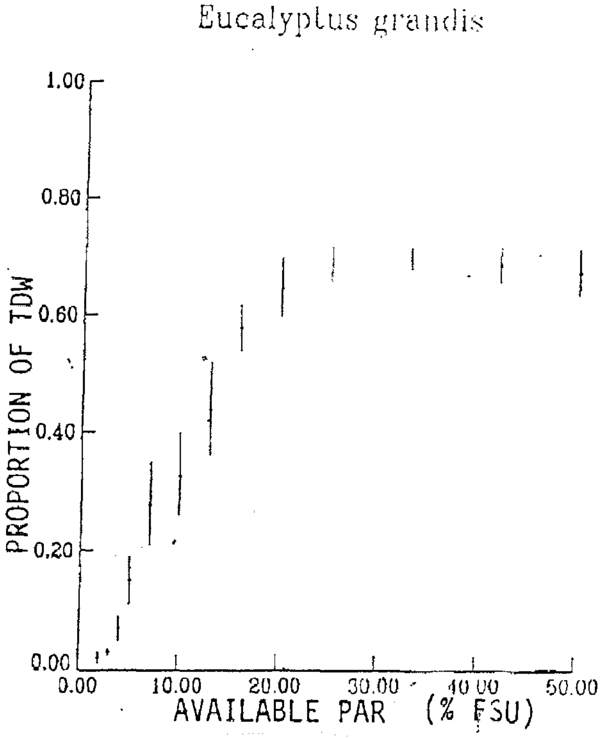

Figure 4.39 *Eucalyptus grandis*, Medium nutrient.

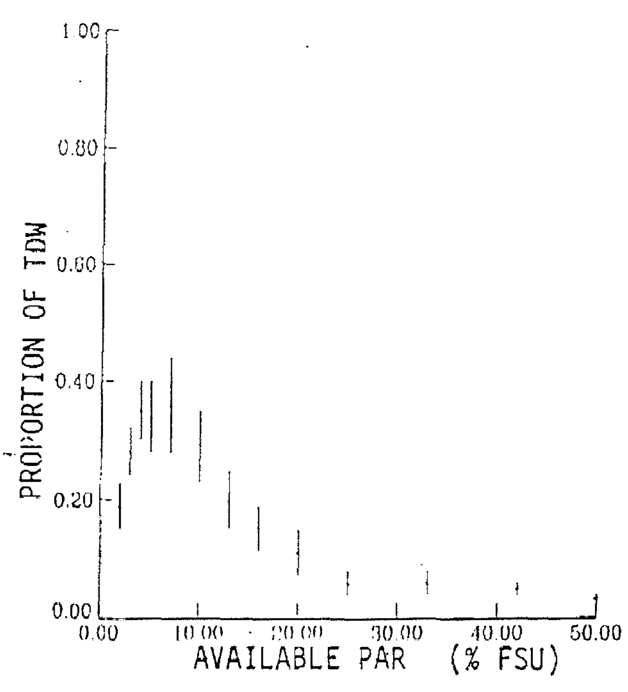

Figure 4.40 *Toona australis*, Medium nutrient.

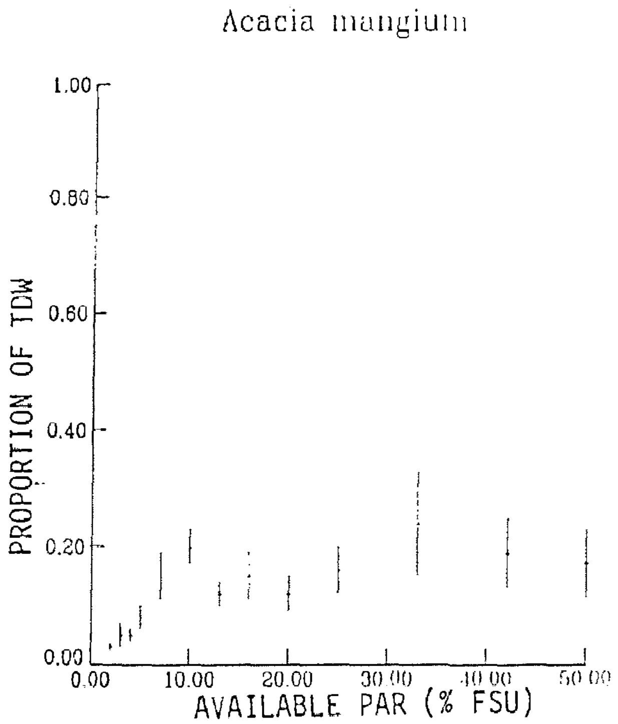

Figure 4.41 *Acacia mangium*, High nutrient.

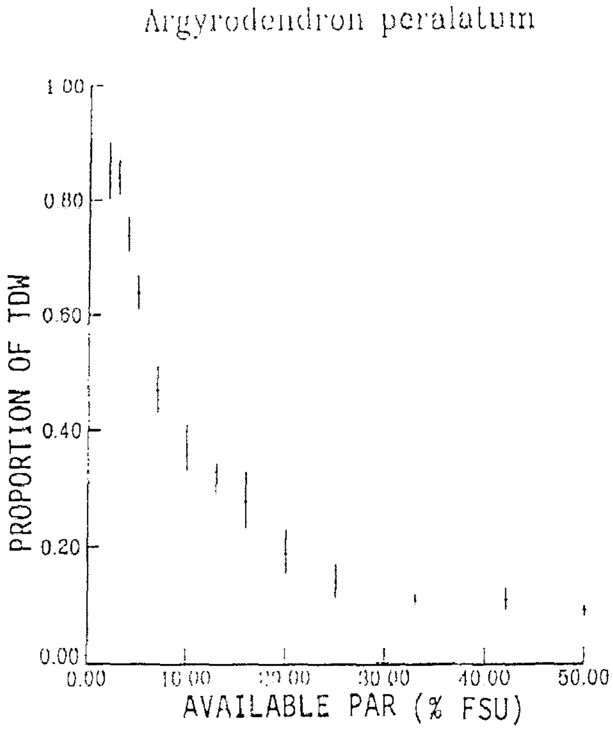

Figure 4.42 *Argyrodendron peralatum*, High nutrient.

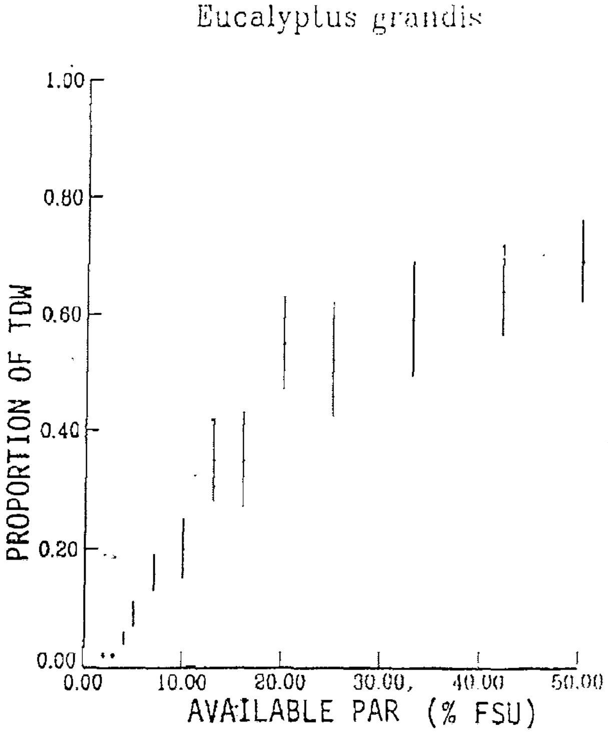

Figure 4.43 *Eucalyptus grandis*, High nutrient.

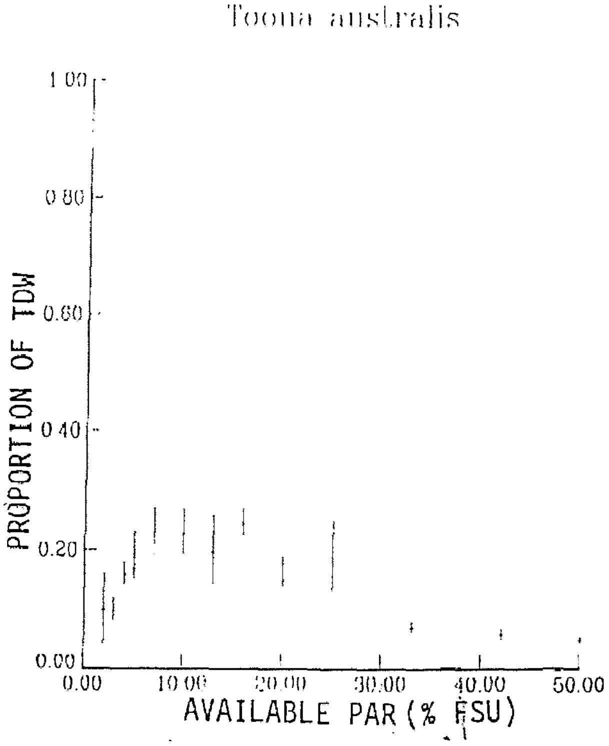

Figure 4.44 *Toona australis*, High nutrient.

It becomes clearer from this experiment why *Eucalyptus grandis* occupies such a dominant role on the rainforest ecotone. Given sufficient light to outgrow any damage incurred from herbivores and pathogens, and suitable conditions for establishment, seedlings of *Eucalyptus grandis* appear to be able to capitalize on the available resources more efficiently than species such as *Acacia mangium* and *Toona australis*.

## 4.4. CONCLUSIONS AND SUMMARY

PAR varies across the rainforest - open forest ecotone in a gradient, and the species growing along this gradient show a continuum of physiological responses to light, from shade intolerant, fast growing open forest species to shade tolerant, slow growing small gap and understorey species. The responses of many of these species to PAR varies according to the amount of available soil nutrients.

Open forest species establish in a relatively homogenous, high light environment, and their responses to variations in PAR are uniform. These species are sometimes capable of persisting, with little growth, in low light environments, but in field conditions they will quickly succumb to herbivores, fungi and bacteria.

Fast growing secondary and late secondary rainforest species are capable of rapid growth when supplied with sufficient light and nutrient, and are adapted to capitalize rapidly on these resources when they become available. Shade tolerant rainforest species succeed in establishing and growing in low light environments where faster growing species are unable to persist. Because of the heterogeneity of the light environment in the ecotone and under a rainforest canopy, rainforest species exhibit considerable variability in their responses to light and nutrient, so that each species is capable of colonizing a wide range of edge and gap environments. The species rich rainforest flora represents a continuum of degrees of shade tolerance, and classifying species according to light requirements is further complicated by the variability within species.

Of all species investigated, *Eucalyptus grandis* is the most capable of utilizing high PAR and nutrient concentrations. Although limited by water availability and possibly fire on one side of the ecotone, and shade, herbivores and damping off on the other, in the ecotone environment itself, *Eucalyptus grandis* is the largest and most numerous species. The next chapter describes the effects of disturbances on the ecotone environment, and investigates some of the factors controlling germination and seedling establishment, providing further explanations for the distribution of species such as *Eucalyptus grandis* across the rainforest boundary.

# CHAPTER 5
# DISTURBANCE AND RECRUITMENT ON THE ECOTONE

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"I'm planting a haycorn, Pooh, so that it can grow up into an oak-tree, and have lots of haycorns just outside the front door instead of having to walk miles and miles, do you see Pooh?"
(Milne, 1926)

## 5.1 INTRODUCTION

The two main agents of widespread disturbance on the upland rainforest - open forest ecotone in north Queensland, excluding man, are fire and cyclones. Extreme climatic conditions such as drought and frost may act as secondary sources of disturbance, both interacting with fire. Disturbance may also be caused by individual tree deaths as a result of senility or competition, accounting for up to 11% of the standing biomass per year in some Australian tropical forests (G.C. Stocker, unpub.). This chapter is a review of the effects of disturbance on the dynamics of the rainforest - open forest interface, and includes data from field observations on the effects of fire and frost, as well as results from germination and establishment experiments. Some aspects of regeneration in the ecotone following disturbance are discussed.

The effects of cyclones on the ecology of north Queensland lowland rainforest were discussed by Webb (1958). He noted that coastal rainforest structure and floristics could be greatly modified by cyclonic winds, interacting with local topography. The most extreme examples are the "cyclone scrubs", where the low, uneven canopy is dominated by vines, and the scattered emergents often form climber towers. In more sheltered areas, defoliation and wind throws lead to a dense understorey dominated by the vine species *Calamus australis* (Webb, 1958).

Webb (1958) also discussed the possibility of fires following "dry" cyclones, giving rise to Acacia, eucalypt and/or grass dominated corridors within coastal rainforest. Cyclones are regarded by many observers as a major contributing factor to the instability of sub-equatorial tropical rainforests.

Johns (1986) recognized a number of factors contributing to the instability of tropical forests in New Guinea. These natural phenomena included landslides, volcanic activity, drought, fires, frost, snow, lightning strikes and cyclonic winds. He concluded that these factors combine to maintain a constant state of disturbance and regeneration in areas throughout both the lowlands and uplands of New Guinea.

Unwin *et al.* (1986) studied the immediate effects of tropical cyclone "Winifred", which crossed the Queensland east coast just to the south of Innisfail on the 1st of February 1986. Wind speeds reaching up to 176 km $h^{-1}$ affected areas of forest north to Cairns, south to Cardwell and west to Ravenshoe. While boles of rainforest emergents and understorey trees were

Plate 5.1 Rainforest damaged by cyclone 'Winifred', February, 1986. The photograph was taken one month after the cyclone, when recovery had already commenced.

broken in severely affected areas, associated open forests dominated by *Eucalyptus* and *Melaleuca* spp. were not as severely damaged. Trees in open forest tended to lose branches, twigs and leaves rather than break off at the bole. Rainforest - eucalypt forest ecotones were altered structurally in affected sites, as the rainforest understorey was more severely damaged by high winds than the emergent eucalypts (Unwin *et al.*, 1986).

Stocker and Unwin (1986) suggested that repeated fires in cyclone damaged rainforest areas would eventually result in exposed areas such as ridgetops being dominated by eucalypts, grasses and other open forest species. The disruption of the rainforest canopy increases insolation and reduces humidity, and increased litter on the forest floor results in a large quantity of dry fuel, permitting the otherwise unlikely possibility of fire in rainforest. The probability of such a fire depends on post cyclone weather conditions, and will gradually become less as the rainforest canopy redevelops and the litter is broken down (Unwin *et al.*, 1986). Cyclones of such intensity are relatively rare in human experience, but in the lifespan of forest trees they are almost inevitable occurrences in most areas near the north Queensland coast. A cyclone - fire interaction could account for the occupation of sites available to rainforest by open forest species in many cases.

Unwin *et al* (1985) examined the behaviour and effects of an experimental fire in open forest adjacent to the rainforest boundary at an upland rainforest site near Herberton. Topography emerged as the main controlling factor in fire behaviour, which was also influenced by wind speed and direction in relation to topography, and fuel characteristics. The species in the rainforest ecotone showed considerable resilience to fire, and most species regenerated rapidly by coppicing. Unwin *et al.* (1985) concluded that periods of high intensity fires on the rainforest boundary, as a result of favourable climatic conditions, winds and fuel availability, would promote the incursion of open forest species into areas previously occupied by rainforest. Alternatively, a succession of years with low to moderate intensity fires or no fires at all would result in the advance of rainforest species into open forest. In recent years, reduction in fuel availability due to grazing by cattle has meant that fire intensity has been reduced in some areas, and the presence of young emergent *Eucalyptus grandis* above a rainforest understorey in many sites indicates that the rainforest margin is advancing in these sites.

Stocker (1981) also noted the ability of rainforest species to regenerate by coppicing and root suckering. Of 82 species observed in a felled and burnt rainforest site at Danbulla (17°10'S, 145°35'E), 74 regenerated by coppicing, 10 from root suckers and 34 species had established from seed 23 months after the disturbance. The species with the highest growth rates were those which developed from seed. However, only a few species are consistently able to regenerate from seed after a catastrophic disturbance of the original stand (Stocker, 1981). Low seed production in most years, seed consumption by animals and limited periods of seed viability limit seedling regeneration for most species. One exception is *Alphitonia petriei*, which can maintain a pool of viable seed in the forest soil for extended periods.

Stocker (1981) pointed out that fire following felling or cyclone damage might favour the regeneration of tree species, as fire excludes many vine species which would otherwise smother regenerating trees in many cases. However, repeated fires would tend to favour invasion by grass and eucalypt species (Stocker and Mott, 1981). The elimination of rainforest species and invasion by grass species following a second burn was also noted by Whitmore (1975) in discussing the effects of shifting cultivation in the Far East seasonal tropics.

Unwin (1983) carried out a series of seedling establishment trials on a rainforest ecotone site near Herberton, along burnt and unburnt open forest transects both extending into unburnt rainforest. He found that, in general, seedlings established more readily in the forest type with which they were normally associated. *Eucalyptus grandis*, *E. intermedia* and *Allocasuarina torulosa* germinated to a limited extent on leaf litter under a rainforest canopy, but no seedlings survived after 4 weeks. Seedling deaths were attributed to fungal damping off, and Unwin (1983) suggested that these species would require a severe disturbance (e.g. cyclone) followed by fire in order to establish within a rainforest. However, the rainforest species *Toona australis* showed the highest germination rate and seedling survival in burnt open forest, and after 38 weeks the performance of this species was lowest in the rainforest. Unwin (1983) suggested the success of *Toona australis* in burnt open forest, together with its ability to coppice after fire, explained its prominence in the rainforest margin.

The other two species studied by Unwin (1983) in this experiment, *Cardwellia sublimis* and *Flindersia brayleyana*, exhibited better germination and establishment in rainforest. These two species were limited by desiccation and lethally high temperatures when sown away from a closed canopy. Neither of these two species encountered the problem of suspension above the soil by leaf litter in the rainforest to the same extent as the other, smaller seeded species. Unwin (1983) also stressed the importance of burning to provide an ashbed in which *Eucalyptus* and *Allocasuarina* species can establish successfully. Few *Eucalyptus* and *Allocasuarina* seedlings survived after 38 weeks under grass and herb cover in unburnt open forest, in contrast to relatively high survival in burnt open forest.

In open forest, heavy seed loss was attributed to ants for the open forest species, and small mammals for the rainforest species, especially *Cardwellia sublimis* and *Flindersia brayleyana*. Physical damage to seedlings by scrub turkeys (*Alectura lathami*) also accounted for a large proportion of seedling death in the rainforest (Unwin, 1983).

Other studies of seed germination in tropical forests have been undertaken by Cheke *et al.*, 1979; Garwood, 1983; Hopkins and Graham, 1984; Vazquez-Yanes and Segovia, 1984, and Whitmore, 1983. All these authors recognize the short term viability of seeds of most primary rainforest species, which tend to be large, have high moisture contents and rapid germination. Dormancy is more common in secondary species, and rainforest soil seed banks contain a high proportion of these early successional species. Germination in many of these species can be triggered by increases in light intensity or temperature, the conditions encountered when a canopy gap is formed in the rainforest. Hopkins and Graham (1984) found that seeds of primary rainforest species were mostly destroyed by heating the soil containing the seeds to 60°C, while seeds of early successional species, including *Alphitonia petriei* and *Acacia aulacocarpa*, were unaffected by this treatment. Germination of *Acacia mangium* was actually enhanced by soil heating (Hopkins and Graham, 1984).

While germination characteristics of seeds are important in determining the species composition following disturbances such as fire or gap formation anywhere in rainforest or open forest, recolonization is not exclusively dependent on seed germination and seedling establishment. Vegetative regeneration from lignotubers, root suckers and coppicing also play an important role. The mode of recolonization of a disturbed site is influenced by the scale and severity of the disturbance. A small gap within the rainforest may be occupied by branches growing out from adjacent trees, while a high intensity fire in open forest leaves the area to be recolonized to a large extent by seeds dispersing in from areas outside the disturbed site.

## 5.2 MATERIALS AND METHODS

### 5.2.1 FIRE DAMAGE, KIRRAMA

A survey of post-fire recruitment and regeneration in tall and medium open forest was carried out at Kirrana, site 2 (Chapter 2) in April 1983 . A grass fire occurred here in November, 1982, burning approximately 5 ha of medium open forest understorey, and reaching into tall open forest, scorching shrubs and saplings on the rainforest margin. Two 5 x 30 m transects were laid out, one in unburnt forest and the other, parallel to the first, in recently burnt forest (in quadrats 'A' and 'B', Fig. 2.8. Chapter 2). Numbers and species of recently established seedlings, lignotuber and coppice regeneration and grass cover were recorded for the dominant species in each transect. In the transect through burnt forest, shrub and sapling death or regrowth were noted, and species identified where possible. Height of scorch damage was also recorded for shrubs and saplings.

### 5.2.2 FROST DAMAGE, ATHERTON TABLELANDS

Observations of rainforest/open forest distributions in the vicinity of low lying parts of the Atherton Tableland suggested that frosts may have been an important factor in determining their boundaries. Unusually cold temperatures experienced during July 1984 enabled the effects on plants along ecotones to be examined.

Frost is a seasonal feature of the environment on many sites above 700 m in humid tropical region of north Queensland (lat. 15°-19°S, long. 145°30'E). For example, Atherton (elevation 760 m) experiences an average of 3.5 light frosts (screen temperature 0-2°C) and 2.5 heavy frosts (screen temperature< 0°C) per annum (Anon, 1971). They occur overnight during May to September, when the atmosphere is dry, clear and still.

While the immediate effects of frosts on vegetation are most noticeable in cold air drainage channels and on exposed rainforest margins (particularly artificially created edges such as roadsides) damage to undisturbed forest has been observed. Occasional very heavy frosts can be quite devastating. For example the 1932 Queensland Forestry Department Annual Report noted that severe frosts in this region had "burnt jungle trees to a height of 70 feet and killed lantana (*Lantana camara*) outright."

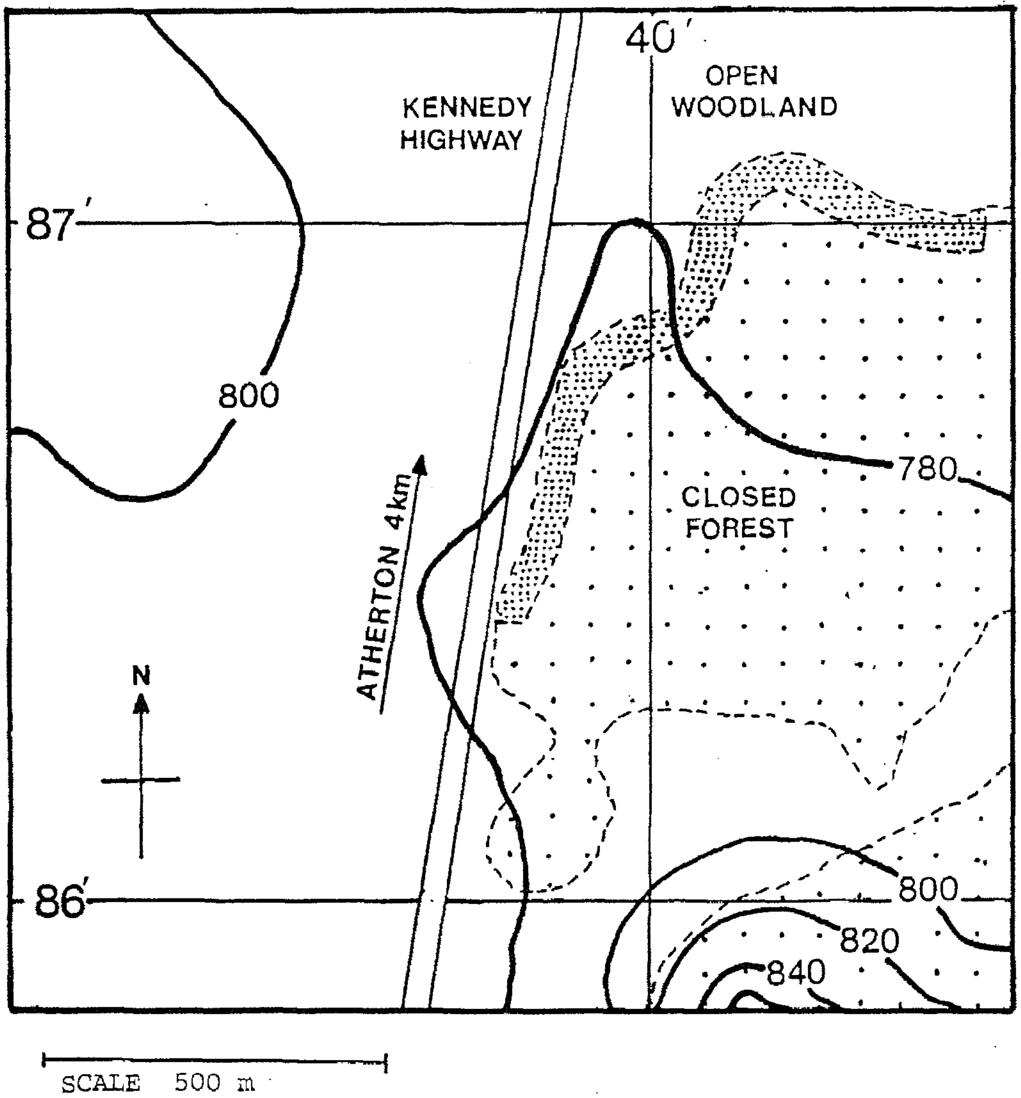


Figure 5.1 Map showing the location of the study site at Wongabel State Forest. Contour lines are in metres. Light stippling represents rainforest, heavy stippling shows the location of the edge where frost damage was assessed and unshaded areas represent open forest and cleared, pasture

Following nine days of recurring frost during July 1984 (Table 5.1), relative frost susceptibilities of typical rainforest, open forest and ecotonal species were assessed. The investigation centred on a well defined, though rather disturbed ecotone on the north-western edge of Wongabel State Forest (Fig. 5.1). Here foliage damage was very obvious, probably due to cold air drainage into the basin immediately to the west of this site. Data recorded included species, position and estimated crown height of all individuals encountered. The degree of frost damage to each tree was visually assessed using the following foliage death categories:

0 : No damage evident,

1 : 1% to 20%,

2 : 21% to 50%,

3 : 51% to 80% and

4 : 81% to 100% of the foliage killed.

At least one example of each species investigated was photographed for later comparison. The site was revisited in October 1984, December 1984, February 1985 and April 1985 to assess the extent of crown recovery of previously tagged individuals. In April 1985 (9 months after the frost) deep blazes were made into the trunks of trees still showing no evidence of new foliage to determine whether these individuals were still living.

An additional site at Herberton (17°23'S, 145°23'E, elevation 900 m) was also investigated in the week following this frost period, to determine the extent of damage to open forest species in that area. Notes were made of damaged foliage in a number of species although no trees were tagged. Recovery was assessed in October 1984.

| Date | Minimum Temperature (°C) | |
|---|---|---|
| | Screen | Grass |
| June 30 | 8.5 | 5.5 |
| July 1 | 1.0 | n.a. |
| 2 | 1.0 | -4.0 |
| 3 | 2.5 | -1.5 |
| 4 | 3.5 | -0.5 |
| 5 | 3.0 | -1.0 |
| 6 | 3.0 | -1.5 |
| 7 | 3.5 | n.a. |
| 8 | 5.0 | n.a. |
| 9 | 3.5 | -1.0 |
| 10 | 9.5 | 8.0 |

Table 5.1 Screen and grass temperatures at CSIRO Atherton laboratory, June 30 to July 10, 1984. Subsequent grass temperature readings at Wongabel indicated that on clear, still nights minima may be 2-3°C lower than those recorded at the Atherton laboratory.
n.a.: Not available. Although grass minimum temperatures were not recorded, widespread frosts were observed in the general area on these days.

### 5.2.3 GERMINATION TRIALS

A series of germination trials were carried out to determine the conditions required for seedling establishment from seed across the ecotone.

The effects of light and temperature on germination rate were investigated for seeds of nine species (table 5.2). Seeds were collected from trees by removing seed bearing branches with a long handled pruner or a .222 rifle with a telescopic sight. Table 5.2 also shows collection sites, and duration and conditions of seed storage.

Germination was carried out in petri dishes, on a disc of filter paper resting on a 3 - 5 mm deep layer of vermiculite. Petri dishes were kept

| SPECIES | COLLECTION SITE | LATITUDE LONGITUDE | DURATION OF STORAGE (months) | STORAGE CONDITIONS |
|---|---|---|---|---|
| *Acacia mangium* | ATHERTON | 17°16' S<br>145°29' E | 5 | ROOM TEMPERATURE |
| *Alphitonia petriei* | PALUMA | 19°01' S<br>146°15' E | 1 | ROOM TEMPERATURE |
| *Alpinia caerulea* | KIRRAMA | 18°40' S<br>145°44' E | - | FRESH SEED |
| *Eucalyptus grandis* | KIRRAMA | 18°40' S<br>145°44' E | 2 | ROOM TEMPERATURE |
| *Eucalyptus intermedia* | KIRRAMA | 18°40' S<br>145°44' E | 3 | ROOM TEMPERATURE |
| *Eucalyptus torelliana* | KIRRAMA | 18°40' S<br>145°44' E | 1 | ROOM TEMPERATURE |
| *Flindersia brayleyana* | ATHERTON | 17°16' S<br>145°29' E | 3 | REFRIDGERATED, 4°C |
| *Neolitsea dealbata* | HERBERTON | 17°23' S<br>145°23' E | - | FRESH SEED |
| *Toona australis* | MALANDA | 17°21' S<br>145°30' E | 3 | REFRIDGERATED, 4°C |

Table 5.2 Species used in the germination experiments, collection sites and storage conditions for the seeds.

closed, and moistened regularly with distilled water. Seeds were sprayed at 10 day intervals with a weak solution of 'Captan' fungicide. Twenty seeds of each species were placed on the filter paper in the dishes, which were kept in three growth cabinets at 18°C, 24°C and 30°C. Half of the petri dishes were kept in light proof containers inside the growth cabinets. The other half were subjected to a 14 hour light/10 hour dark photoperiod, with light intensities in the former case ranging between 27 and 50 µmol $m^{-2}$ $s^{-1}$.

The petri dishes were examined daily. Seeds were counted as germinated when either a hypocotyl or an epicotyl had emerged. Seeds were removed after germination. After 20 to 70 days (depending on species), ungerminated seeds were removed and dissected to determine whether they contained a viable embryo.

Germination and seedling establishment trials were used to determine the effects of substrate on establishment. Six 30 cm x 25 cm x 5 cm plastic seed trays were subdivided into three equal sections using wooden strips. Two trays were filled with open forest soil, and four with rainforest soil, two of which were covered with leaf litter. All soils were collected at Kirrama a few days before commencement of the experiment. Fifty seeds each of *Alphitonia petriei*, *Eucalyptus grandis*, *E. intermedia*, *E. torelliana*, *Neolitsea dealbata* and *Toona australia* were placed on the surface of each substrate. Trays were kept in the glasshouse, and watered three times per week. Temperatures in the glasshouse ranged between 19°C and 27°C during the course of the experiment. Numbers of surviving seedlings were recorded at weekly intervals for 10 weeks.

## 5.3 RESULTS AND DISCUSSION

### 5.3.1 FIELD OBSERVATIONS, KIRRAMA

The fire in open forest at Kirrama in November 1982 was of low to moderate intensity, scorching shrubs to a height of 2 m without damaging foliage on taller saplings or trees. The most apparent damage was in small sections of the rainforest margin, where small shrubs and saplings on the outside edge were killed to a distance of 1 to 3 m from the edge. The evidence suggests that these plants did not burn, but were scorched by burning grasses, litter and *Lantana camara*. Table 5.3 shows the eleven main shrub, sapling and understorey species found in the two transects. Also shown are either numbers of individuals or mean estimated ground cover of each species

| SPECIES | MEAN COVER (%) | | NUMBER OF INDIVIDUALS/150m$^2$ | |
|---|---|---|---|---|
| | BURNT | UNBURNT | BURNT | UNBURNT |
| *Acacia aulacocarpa* | | | 37 s | 6 |
| *Alectryon tomentosus* | | | 14 c | 24 |
| *Alstonia muellerana* | | | - | 6 |
| *Cupaniopsis serrata* | | | 21 c/s | 7 |
| *Eucalyptus intermedia* | | | 26 l | 19 |
| *Imperata cylindrica* | 27 r | 48 | | |
| *Lantana camara* | 7 c | 5 | | |
| *Maesa dependens* | 14 r | 6 | | |
| *Pteridium esculentum* | 15 r | 9 | | |
| *Rhodomyrtus trineura* | | | 58 c | 26 |
| *Themeda triandra* | - | 29 | | |

Table 5.3 Main species less than 2m in height in two 5m x 30m transects in open forest at Kirrama, one of which was burnt 5 months prior to the survey. Principle modes of regeneration are shown for species in the recently burnt transect. s = seedling, c = coppice, l = lignotuber and r = rhizome.

in both the "burnt" and "unburnt" transects, together with the principle modes of regeneration in each case.

The orthophyllous shrub species *Alectryon tomentosus*, *Cupaniopsis serrata* and *Rhodomyrtus trineura* all regenerated by coppicing, and plants of these species appeared healthy and to be growing rapidly, with new (5 month old) stems between 0.5 and 1.5 m in height. *Alstonia muellerana* was absent from the burnt transect, although the architecture of some of the dead saplings in this transect suggested that they may have been *Alstonia muellerana*. Seedlings of *Acacia aulacocarpa* were more than twice as frequent in the burnt transect compared with the unburnt transect, although the former were considerably smaller, reaching heights of up to 0.5 m in the burnt transect compared with heights of up to 3 m in the unburnt area. There was no evidence of coppice or underground regeneration in this species, and all new individuals appeared to be established from seed. By contrast, 19 of the 26 young plants of *Eucalyptus intermedia* in the burnt transect were resprouting from lignotubers, and only 7 appeared to be grown directly from seed. Heights of *E. intermedia* in the burnt transect were up to 0.8 m.

*Maesa dependens* and *Lantana camara* both appeared to regenerate successfully after the fire. *Maesa dependens* resprouted from rhizomes in all cases, while regrowth in *Lantana* occurred from the bases of burnt stems. The bracken ferm, *Pteridium esculentum* also resprouted from rhizones. These three species appeared to be favoured by the recent fire, contributing to a greater proportion of ground cover in the burnt transect, and appearing more vigorous in this area than in the unburnt area.

Of the two grass species, only *Imperata cylindrica* appeared to regenerate successfully after the fire. *Themeda triandra* does not seem to be favoured by disturbance, and may colonize after a sufficient period without fire: *Imperata cylindrica* regrowth was green and vigorous, and occurred mostly from burnt clumps rather than from seed.

There was no evidence of *Eucalyptus grandis* regrowth in either transect, and an exhaustive search of the burnt area turned up one seedling of *E. grandis* growing in a moist pocket of litter and charcoal in an old tree stump. The species does not produce a lignotuber, and does not regenerate from epicormic shoots, so it relies on seed for establishment following disturbance. *E. grandis* establishment is more likely to take place after a high intensity fire which would reduce the competitive advantage of vegetatively regenerating species, and the level of ant predation of seed. High intensity fire also results in high nutrient concentrations in the ashbed, leading to a competitive advantage for species such as *E. grandis* (chapter 4). Results reported in Chapter 3 showed that *E. grandis* seedlings are more susceptible to drought stress than seedlings of *E. intermedia* and other open forest species, so climatic conditions might also play an important role in *E. grandis* regeneration.

High intensity fires are rare in Australian tropical open forest (G.C. Stocker, pers. comm.). However, increased fuel availability following a tropical cyclone may lead to such a fire. Tropical cyclone Winifred, which crossed the Queensland east coast 100 km north of Kirrama in February 1986 caused considerable destruction at the Kirrama study site. Near the rainforest boundary at site 1, the ground was covered with large branches of *E. grandis* and *E. intermedia*, together with a much greater accumulation of leaf litter than normal. Leaves were stripped from the open forest trees by high winds, and the top parts of eucalypt crowns were broken off in a number of cases. The rainforest showed less damage, although a few of the emergent species (*Ficus* spp. and *Flindersia brayleyana*) were toppled over. Cyclone damage was not as severe at Kirrama as it was in the rainforests nearer to the coast, but the possibility of a post-cyclone fire of higher intensity than normal at sites such as Kirrama must not be overlooked. While there were no fires in 1986 at the Kirrama study sites, had post cyclone conditions been drier, and had a fire started, the increased fuel availability would probably have given rise to different modes of regeneration and recolonization on the rainforest margin.

### 5.3.2 FROST

The species investigated, numbers of individuals, degree of damage and approximate time of recovery are presented in table 5.4. The faster growing early secondary rainforest tree species (notably *Alphitonia petriei*, *Aleurites moluccana*, *Euodia vitiflora*, *Glochidion* sp., *Homolanthus papuana* and *Mallotus polyadenos*) were generally more frost susceptible than late secondary or primary species (mainly *Araucaria cunninghamii*, *Castanospermum australe*, *Flindersia brayleyana* and *F. schottiana*). Examples from the latter group were examined in positions immediately adjacent to affected trees of other species

| Site/Species | Numbers individuals examined | Estimated mean foliage height (m) | % Foliage lost (numbers in each category) | | | | | Recovery time (months) | Mortality (%) |
|---|---|---|---|---|---|---|---|---|---|
| | | | 0 | 1-20 | 21-50 | 51-80 | 81-100 | | |
| Wongabel | | | | | | | | | |
| Aleurites moluccana | 9 | 20 | - | - | - | 3 | 6 | 3-5 | 0 |
| Alphitonia petriei | 15 | 15 | - | - | - | 2 | 13 | 7 | 87 |
| Araucaria cunninghamii | 1 | 30 | 1 | - | - | - | - | - | 0 |
| Calamus caryotoides | 3 | 2 | 1 | 2 | - | - | - | 3 | 0 |
| Castanospermum australe | 2 | 25 | 2 | - | - | - | - | - | 0 |
| Castanospora alphandii | 2 | 10 | - | 2 | - | - | - | 3 | 0 |
| Eucalyptus tereticornis | 4 | 25 | 4 | - | - | - | - | - | 0 |
| Euodia vitiflora | 2 | 12 | - | - | - | 2 | - | 5 | 0 |
| Flindersia brayleyana | 1 | 20 | 1 | - | - | - | - | - | 0 |
| Flindersia schottiana | 1 | 20 | 1 | - | - | - | - | - | 0 |
| Glochidion sp. | 2 | 5 | - | - | 2 | - | - | 3 | 0 |
| Homolanthus papuana | 11 | 10 | - | - | - | 8 | 3 | 3 | 0 |
| Lantana camara | >10 | 1.5 | - | - | - | - | >10 | 3-5 | 0 |
| Litsea leafeana | 1 | 15 | - | - | 1 | - | - | 3 | 0 |
| Mallotus polyadenos | 5 | 5 | - | - | - | 2 | 3 | 3-5 | 0 |
| Mischocarpus exangulatus | 3 | 5 | - | - | 3 | - | - | 3 | 0 |
| Neolitsea dealbata | 1 | 5 | - | - | - | - | 1 | 3 | 0 |
| Panicum maximum | >10 | 1.5 | - | - | - | - | >10 | 3 | 0 |
| Pennisetum sp. | >10 | 1.5 | - | - | - | - | >10 | 3 | 0 |
| Platycerium superbum | 1 | 15 | - | - | - | 1 | - | 5 | 0 |
| Polyscias elengans | 3 | 10 | 3 | - | - | - | - | - | 0 |
| Solanum mauritianum | 10 | 2 | - | - | 10 | - | - | 3 | 0 |
| Terminalia sericocarpa | 8 | 10 | - | - | - | 2 | 6 | 5 | 75 |
| Tristania suaveolens | 2 | 5 | - | 2 | - | - | - | 3 | 0 |
| Herberton | | | | | | | | | |
| Casuarina littoralis | >5 | 6 | - | - | >5 | - | - | 3 | 0 |
| Cyathea cooperi | 6 | 2 | - | - | - | 2 | 4 | 3 | 0 |
| Eucalyptus alba | >5 | 20 | - | - | >5 | - | - | 3 | 0 |
| Eucalyptus citriodora | >5 | 20 | - | - | >5 | - | - | 3 | 0 |
| Eucalyptus grandis | >10 | 30 | >10 | - | - | - | - | - | 0 |
| Eucalyptus intermedia | >5 | 25 | - | >5 | - | - | - | 3 | 0 |

Table 5.4 Frost damage to species at Herberton and Wongabel State Forest. The table shows the estimated degree of damage attributed to frost, time taken for recovery in frost damaged species and percentage mortality in those species killed by the frost in July, 1984.

Plate 5.2 Rainforest trees and grass species growing on a road edge at Wongabel State Forest, following severe frosts in July, 1984. Frost damage is evident on the exposed rainforest margin, while trees away from the road edge are relatively undamaged.

and were thus presumably exposed to the same cold temperature extremes. Nevertheless, they showed no obvious signs of frost damage. Of the early successional species, only *Polyscias elegans* appeared to have any resistance to frost.

Although not a typical early successional tree species, *Terminalia sericocarpa* was also severely affected. This species is commonly found in relatively dry coastal rainforests and may be less well adapted to chilling than most other species in this assemblage.

The open forest species at the higher and presumably cooler Herberton site showed a range of responses. However, all affected individuals had produced new foliage within three months of the frost period and any evidence of frost damage had disappeared by this time. Immediately after the frost, foliage damage was greatest for *Allocasuarina littoralis*, *Eucalyptus alba* and *E. citriodora*. *E. grandis* showed little evidence of leaf injury.

Within the open forest portion of the ecotone at the Wongabel site, even the well protected lower leaves of the grasses and exotic weeds (mainly *Panicum maximum*, *Pennisetum sp.*, *Lantana camara* and *Solanum mauritianum*) became brown, dry and brittle less than two days after the initial frost. Thus flammability of the ecotone was greatly increased and an area (about 0.5 ha) of *Panicum* and *Pennisetum* pasture adjacent to the study site was accidentally burnt a week after the frost period. This fire also scorched foliage on a number of rainforest trees. Some of these trees eventually died.

Although severe frost is highly seasonal and infrequent, it can exert a controlling influence on rainforest edge dynamics in some upland areas of north Queensland. Its primary effects are to alter competitive balances among different species on the rainforest edge and it may even eliminate large proportions of particularly sensitive species (e.g. *Alphitonia petriei*) within limited areas. Due to the insulating properties of surrounding vegetation, it is unlikely that similar effects would often, if ever, be noticed in small gaps within undisturbed or secondary forest.

However, the most important influence of frost may lie in its influence on fuel curing, especially in frost hollows and on forest edges, because frosting increases the ease of ignition and resultant fire intensity. Since both these fire characteristics have an important role in controlling the position and nature of rainforest / eucalypt forest ecotones (Unwin, 1983), frost could have an important influence on natural vegetation patterns especially in wet upland environments where the dry season is neither extended nor severe. While on the Wongabel site some trees were killed following frost and fire, it is suspected that stresses imposed by drought, frost severity, the interval between frosting and fire (especially the degree to which crown recovery had occurred), fire intensity and genotypic characteristics of the species, all contribute to determine if an individual will survive.

Frost / fire interactions appear to be the most plausible explanation for observations that eucalypt forests frequently occurred on the western and north-western margins of swampy sites and that the vegetation on their other sides was usually (or had been until recent clearing) rainforest (G.C. Stocker, pers. comm.). Aborigines would have burnt these areas whenever severe frosts created sufficient fuel and the prevailing south-easterly winds would have carried fires to the north-west gradually eroding rainforest in that sector. The fire resistant eucalypts would have eventually colonized the area previously occupied by rainforest.

An alternative explanation is that rainforests have only recently expanded into the general area but have not been able to take over those parts of the eucalypt forest where frosts have influenced fuel curing sufficiently to cause ignition probabilities and fire intensities to be higher than in other areas.

The greater sensitivity of many early successional species to frost injury cannot be satisfactorily explained. While primary species do tend to have smaller leaves and multilayered crowns, it seems more probable that most of their relative resistance is due to other leaf and twig characteristics, especially cell sizes and solute concentrations.

### 5.3.3 GERMINATION EXPERIMENTS

The results of the effects of light and temperature on germination in the nine species described in the previous section are shown in figures 5.2 to 5.19. Table 5.5 shows a summary of these results.

The most rapid germination occurs in the three *Eucalyptus* species, *E. grandis*, *E. intermedia* and *E. torelliana*. Germination in these species was not inhibited by lack of light. *E. intermedia* seeds germinated most rapidly at 30°C, whereas *E. grandis* and *E. torelliana* showed similar rates of germination at 24°C and 30°C. The higher temperature requirement of *E. intermedia* corresponds with the conditions of the open forest environment which this species would be expected to colonize. *E. grandis* and *E. torelliana* seeds would germinate equally well in open forest or in the cooler, shaded environment of the rainforest margin. In all three eucalypt species, none of the ungerminated seeds appeared to contain viable embryos, indicating no dormancy mechanisms. The eucalypts are adapted for rapid germination in the event of favourable conditions occurring e.g. ashbeds. Seeds are small and susceptible to ant predation, so they would not be expected to last long on the ground after being released from their capsules.

Germination in the four secondary rainforest and edge species, *Acacia mangium*, *Alphitonia petriei*, *Alpinia caerulea* and *Toona australis* was enhanced by light and higher temperatures. Dormancy was found to occur in *Acacia*, *Alphitonia* and *Alpinia*, and is particularly obvious in the first two species. Table 5.5 shows that 96%, 94% and 89% respectively of all seeds examined of these species appeared to contain viable embryos, although germination was greatly reduced in dark conditions, especially at lower temperatures. Germination can be enhanced in *Acacia* seeds by heat treatment, and in *Alphitonia* by heat treatment or leaching. These three species will germinate in conditions following disturbance, as a result of the increased light intensities and temperatures on the ground resulting from gap formation in the rainforest or removal of vegetation by fire from the ecotone.

Germination in *Toona* was only delayed by a few days in darkness, and no dormancy was indicated for this species. Almost all the viable seeds had germinated after 20 days in all of the light and temperature conditions used. In this respect, the behaviour of *Toona* seeds is similar to that of the eucalypt seeds.

| SPECIES | OPTIMUM GERMINATION TEMPERATURE (°C) | MAXIMUM GERMINATION (%) | VIABILITY (ALL SEEDS) (%) | DAYS TO FIRST GERMINATION (OPTIMUM TEMP.) | DAYS TO 50% OF MAXIMUM GERMINATION | GERMINATION IMPROVED BY LIGHT ? |
|---|---|---|---|---|---|---|
| *Acacia mangium* | 30 | 85 | 96 | 8 | 18 | YES |
| *Alphitonia petriei* | 30 | 70 | 94 | 7 | 11 | YES |
| *Alpinia caerulea* | 30 | 90 | 89 | 11 | 16 | YES |
| *Eucalyptus grandis* | 24 - 30 | 95 | 92 | 3 | 6 | NO |
| *Eucalyptus intermedia* | 30 | 100 | 95 | 4 | 5 | NO |
| *Eucalyptus torelliana* | 24 - 30 | 100 | 98 | 2 | 2 | NO |
| *Flindersia brayleyana* | 24 - 30 | 100 | 97 | 9 | 12 | NO |
| *Neolitsea dealbata* | 30 | 45 | 87 | 10 | 12 | ? |
| *Toona australis* | 30 | 95 | 93 | 8 | 10 | YES |

Table 5.5 Optimum germination temperatures (18°C,24°C or 30°C), maximum percentage germination in any one petri dish, percentage viability of all seeds used, number of days to initial germination at the optimum temperature for the species, number of days to 50% of the maximum germination at the optimum temperature for the species and the effects of light on germination.

Figures 5.2 to 5.18 Results of germination trials on seeds of nine rainforest and open forest tree species. Each graph shows the number of seeds germinating out of a total of 20 at 18°C, 25°C and 30°C for seeds kept in both light and dark conditions. The horizontal axis gives time after initial sowing in days. Seed viability for each species based on squash tests of all ungerminated seeds is shown in table 5.5.

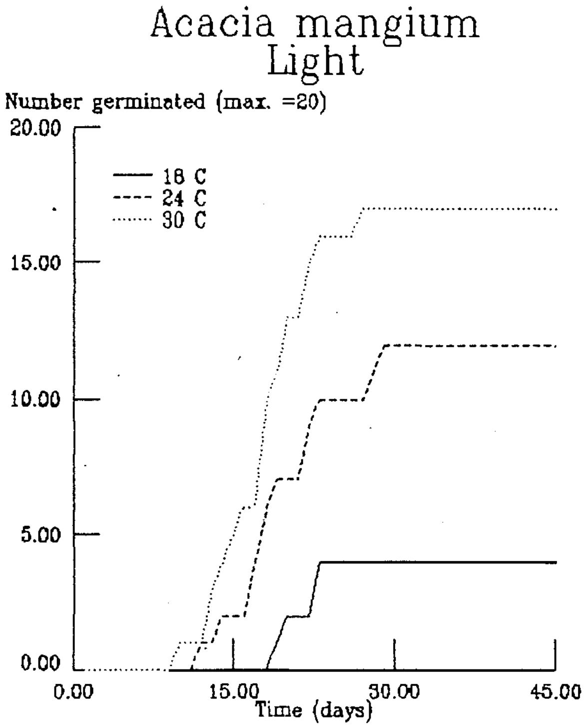


Figure 5.2

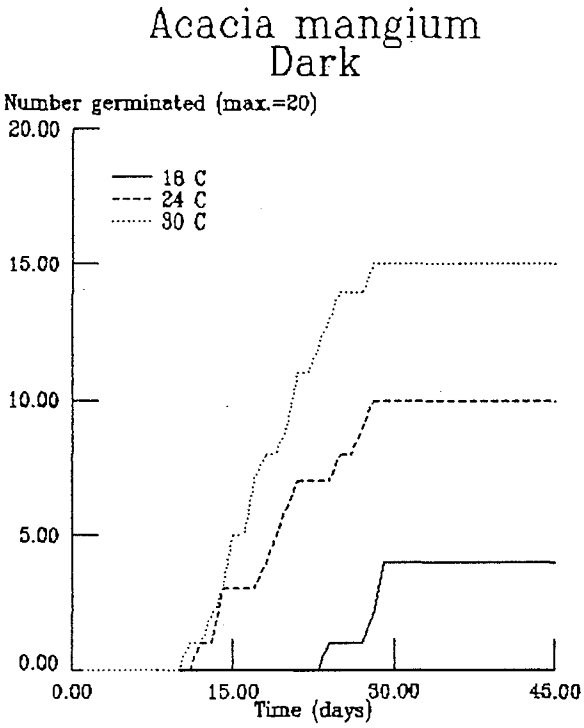


Figure 5.3

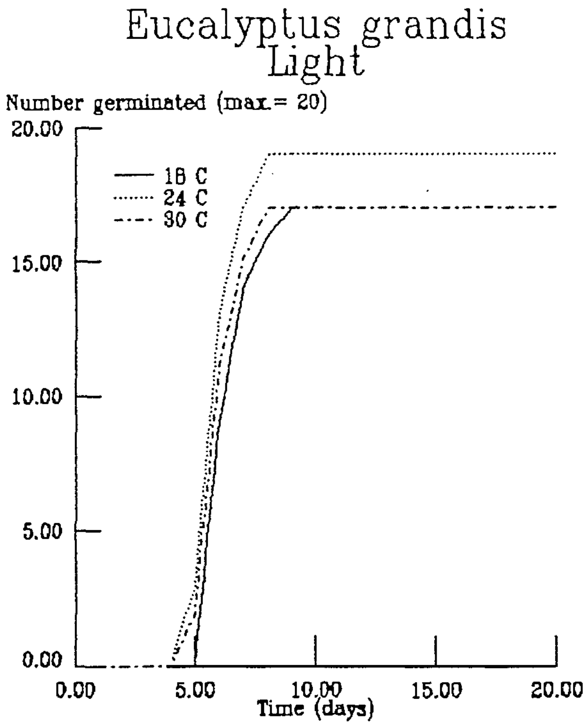

Eucalyptus grandis
Light

Figure 5.4

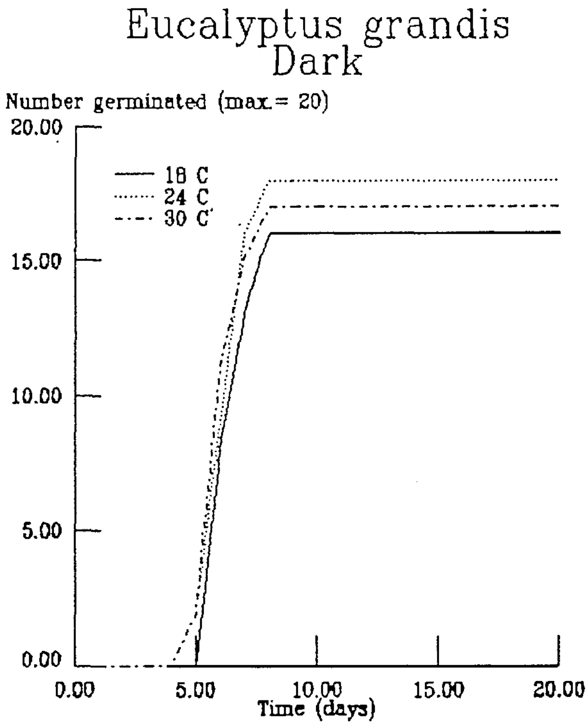

Eucalyptus grandis
Dark

Figure 5.5

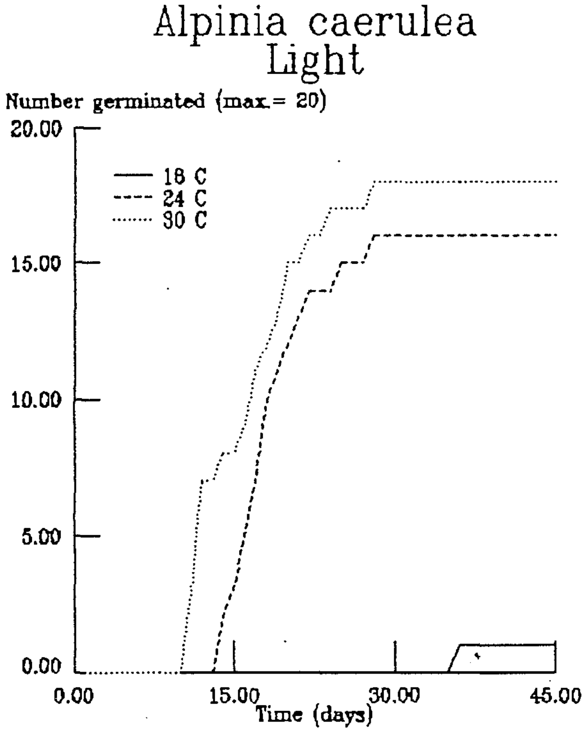

Alpinia caerulea
Light

Figure 5.6

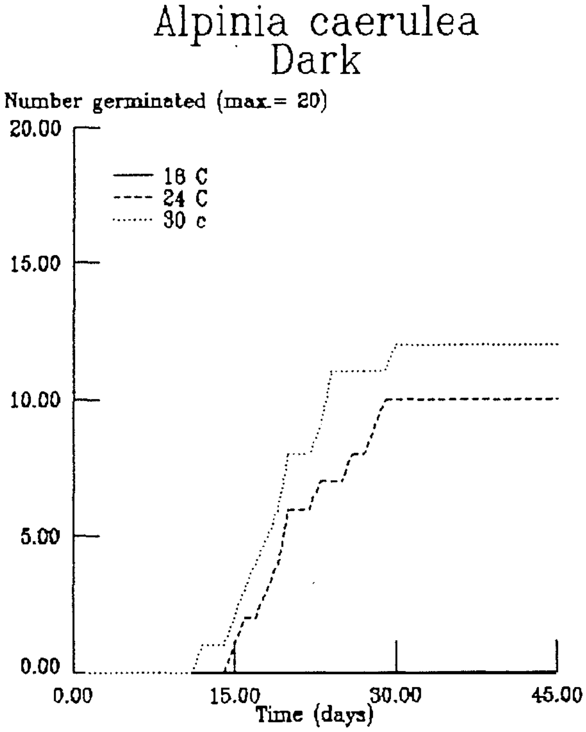

Alpinia caerulea
Dark

Figure 5.7

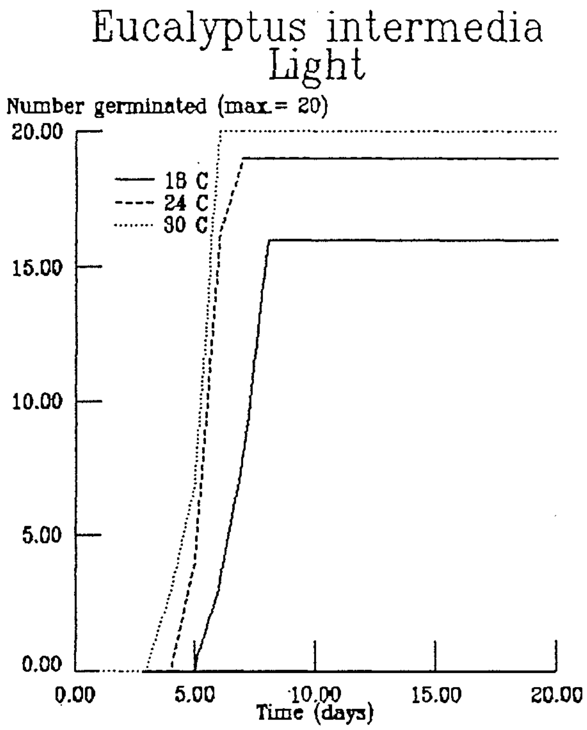


Figure 5.8

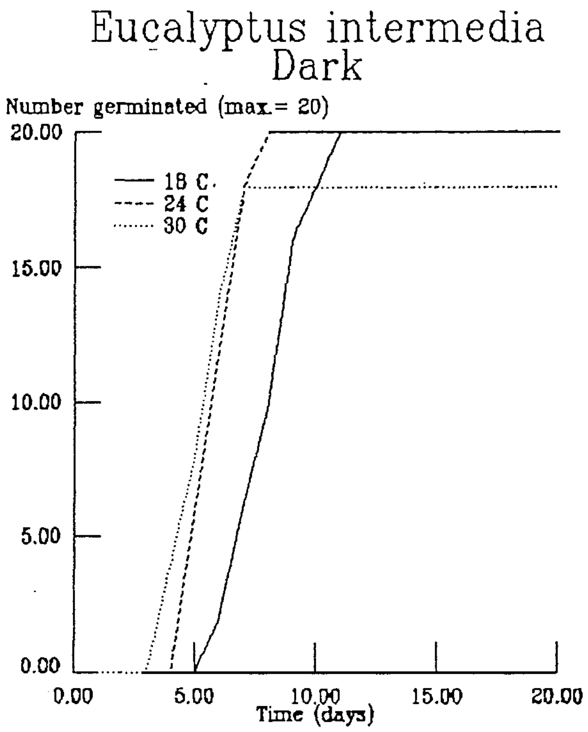


Figure 5.9

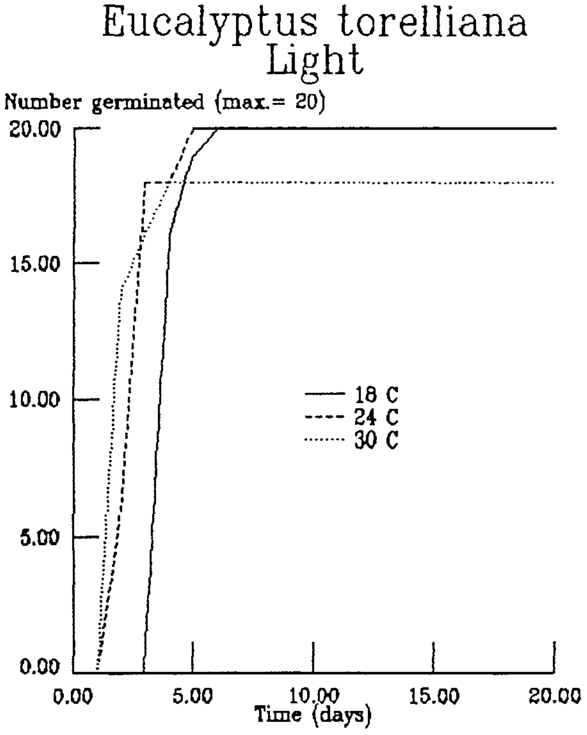


Figure 5.10

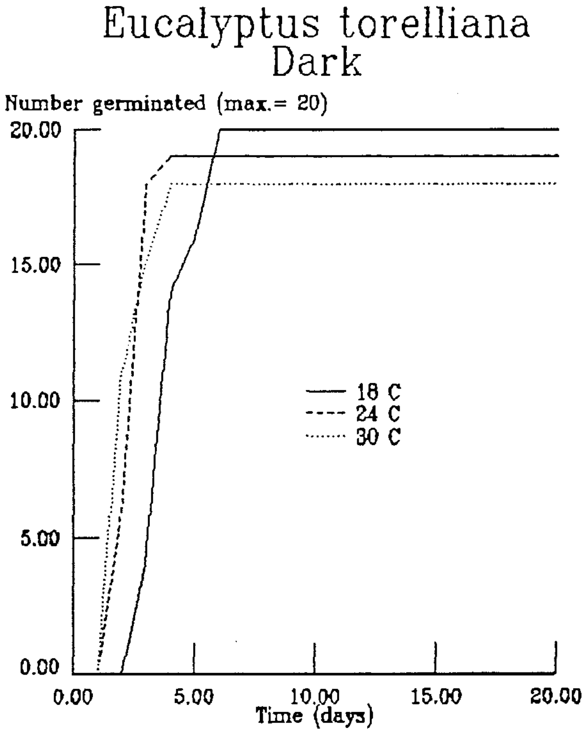


Figure 5.11

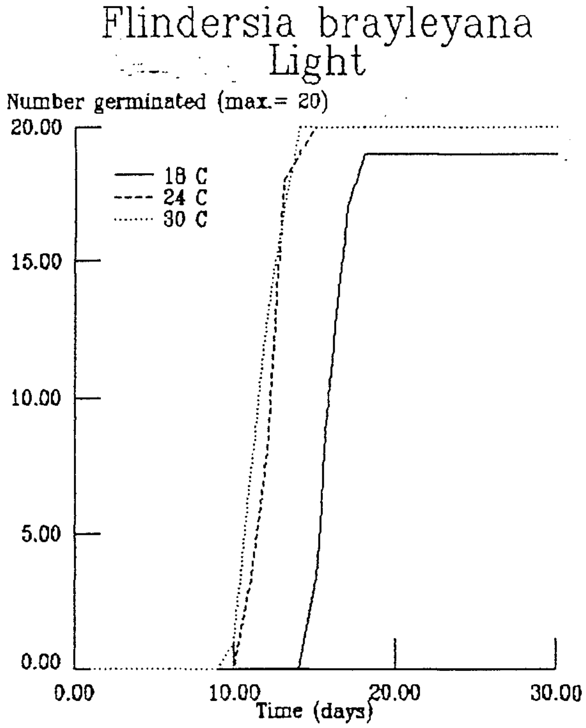

Flindersia brayleyana
Light

Figure 5.12

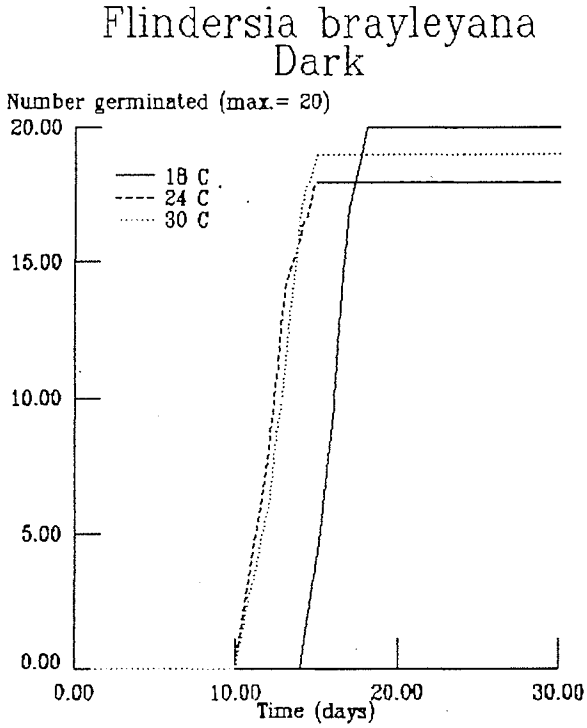

Flindersia brayleyana
Dark

Figure 5.13

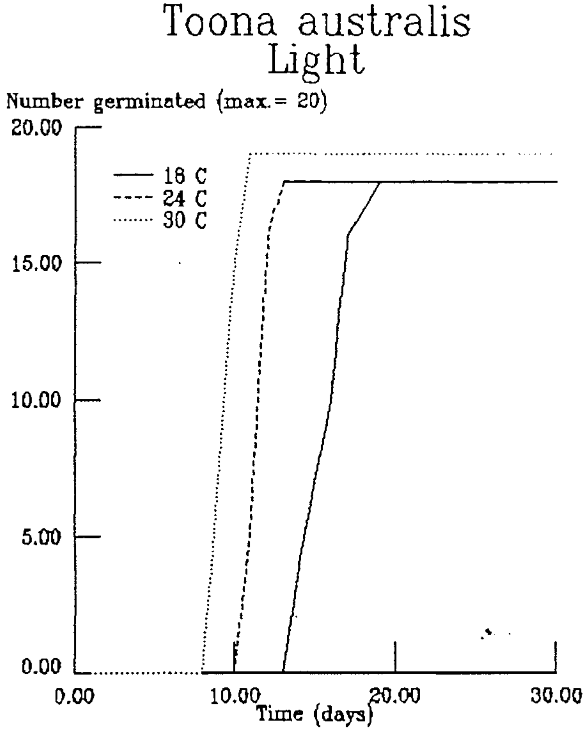

Toona australis
Light

Figure 5.14

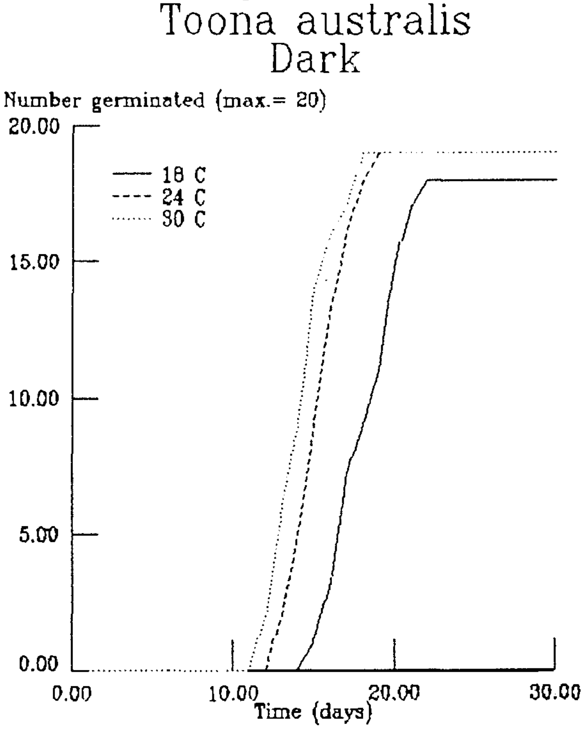

Toona australis
Dark

Figure 5.15

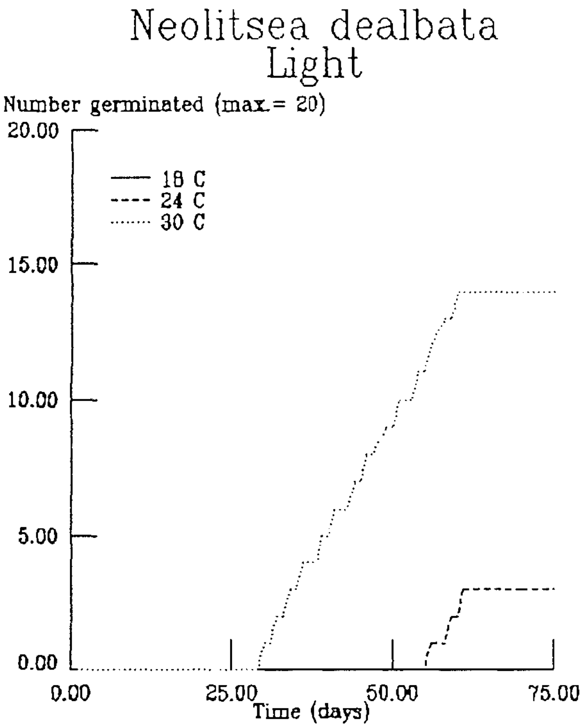


Figure 5.16

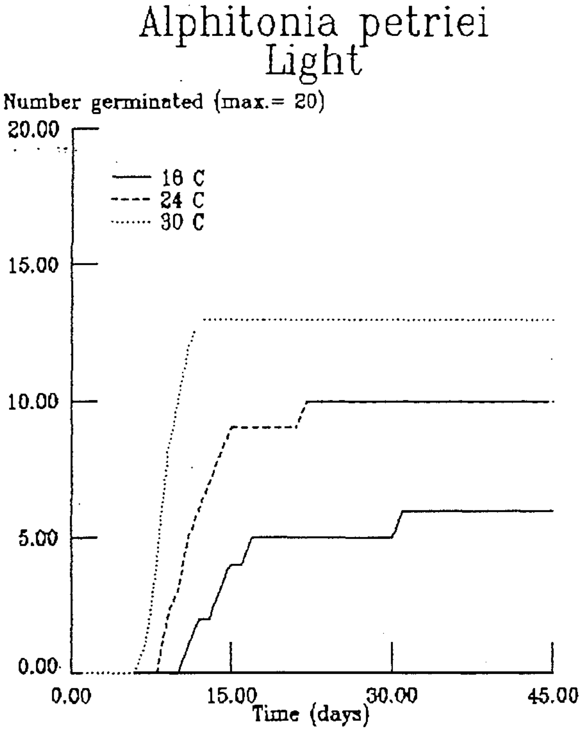


Figure 5.17

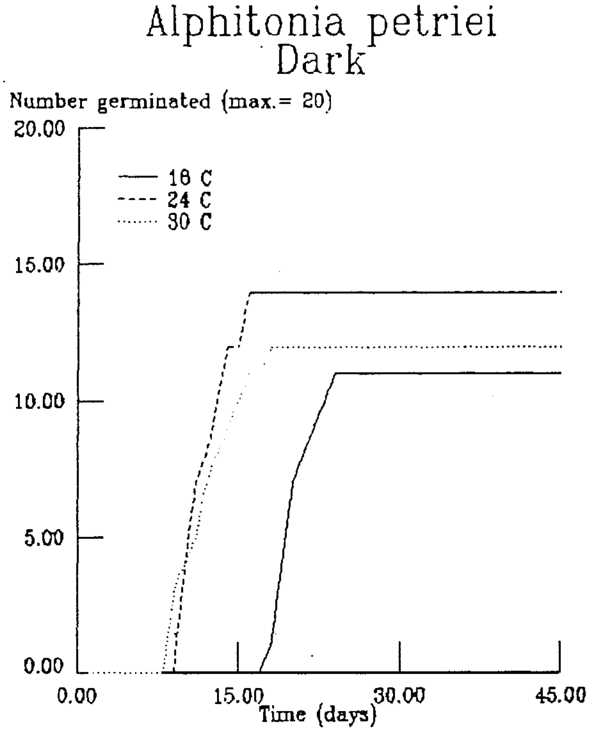


Figure 5.18

Accidental dehydration of the seeds of *Neolitsea dealbata* in the dark treatment rendered these results unusable. Nevertheless, *Neolitsea* showed considerable cool temperature induced dormancy, and slow, staggered germination. Germination of *Flindersia brayleyana* seeds was not inhibited by darkness, and germination rates in this species were similar at 24°C and 30°C. No dormancy was apparent in *Flindersia* and germination was relatively rapid. *Flindersia* seeds have a large, papery wing and are adapted for wind dispersal. *Neolitsea* seeds have a fleshy outer covering over a woody endocarp, and germination did not occur in this species until the fleshy covering was removed. *Neolitsea* appears to be adapted to dispersal by birds or mammals, and germination may be enhanced by passage of the seeds through their digestive tracts.

Figures 5.20 to 5.25 show the rates of seedling survival in the three different substrates used in the substrate experiment. Germination in *Eucalyptus grandis, E. intermedia, E. torelliana* and *Toona australis* was higher in rainforest soil than in open forest soil, although rates of seedling survival in these two substrates appear similar. The greater organic matter content of the rainforest soil leading to higher moisture retention probably makes rainforest soil a better substrate for germination of these species. Seedling deaths on these two substrates appeared to result from overcrowding, mutual shading and fungal attack. Seeds of the three eucalypts and *Toona australis* dropped onto rainforest litter managed to germinate in most cases, but early seedling death occurred when the developing roots failed to penetrate the litter and reach the underlying soil. Later in the course of the experiment, many of the seedlings succumbed to fungal damping off, compounded by the humid environment and shading provided by the leaf litter. Additional shading in the field by the rainforest canopy would enhance the effects of damping off, leading to a low probability of establishment in rainforest for eucalypts and *Toona australis*.

*Alphitonia petriei* seeds also encountered problems in rainforest litter, but greater seed reserves (chapter 4, fig 4.18) allowed the seedlings more chance of establishment. Differences in seedling survival for *Alphitonia petriei* were not great, and the species did not appear to be susceptible to damping off. Seeds of *Neolitsea dealbata* performed equally well in all three substrates, the greater seed mass overcoming the problem of suspension above the soil in rainforest leaf litter.

Figures 5.19 to 5.24 Results of trials examining the effects of substrate (open forest soil, rainforest soil and rainforest soil with a covering of leaf litter) on germination and establishment of seeds of six rainforest and open forest tree species over a ten week period. Graphs show the numbers of surviving seedlings in each substrate at weekly intervals. Fifty seeds of each species were sown in each substrate.

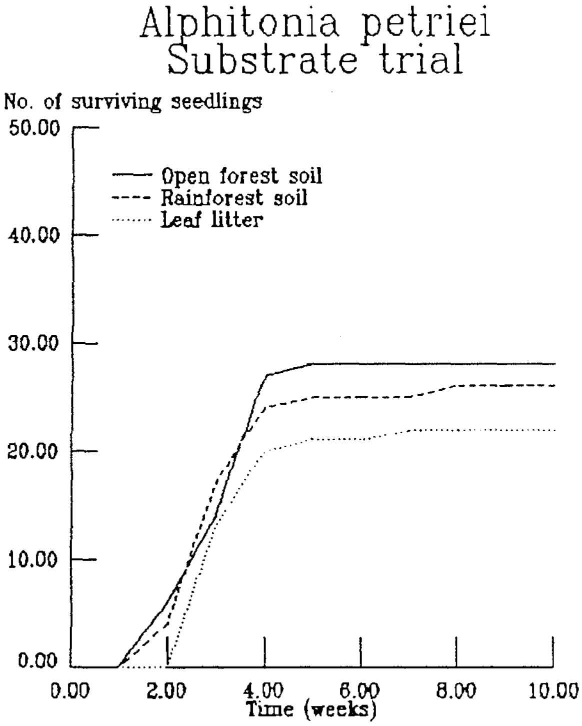


Figure 5.19

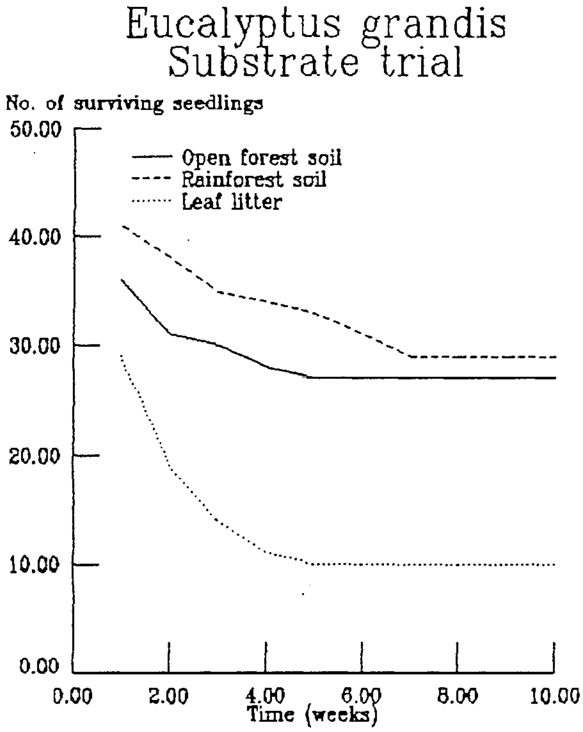


Figure 5.20

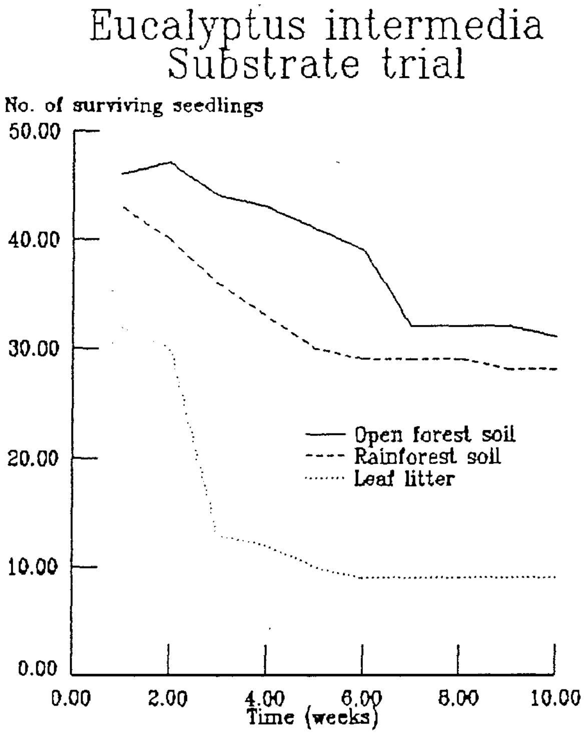


Figure 5.21

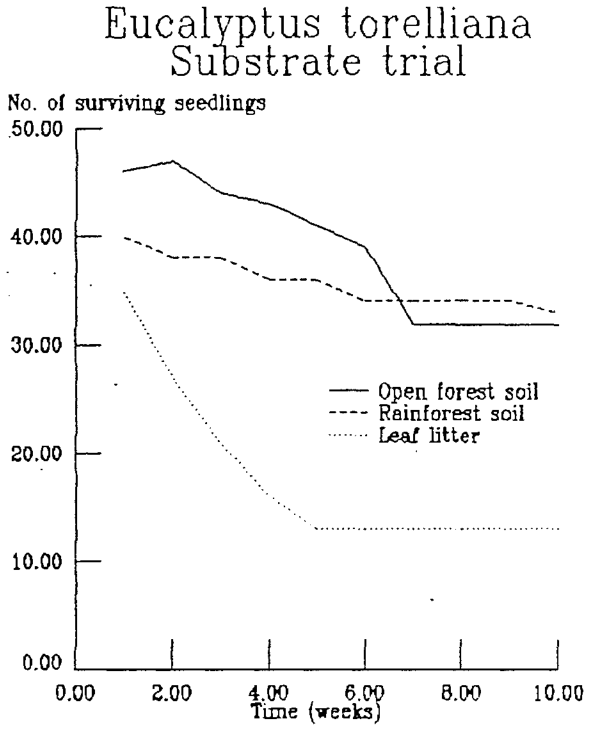


Figure 5.22

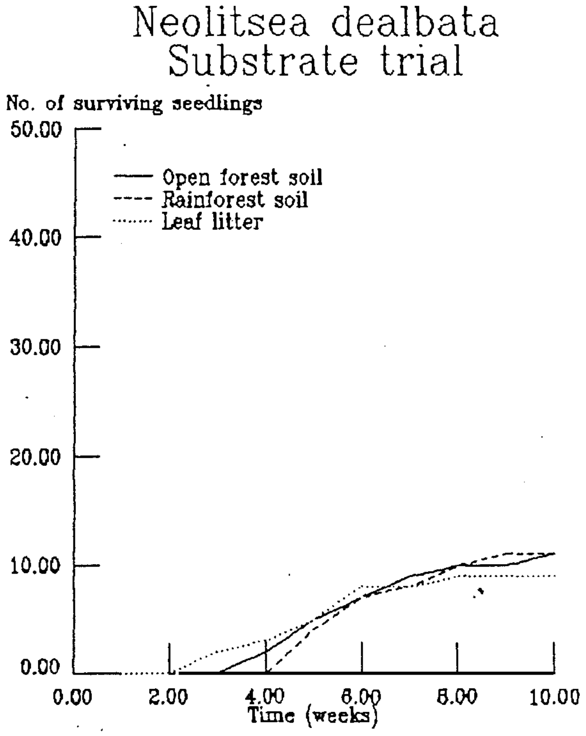


Figure 5.23

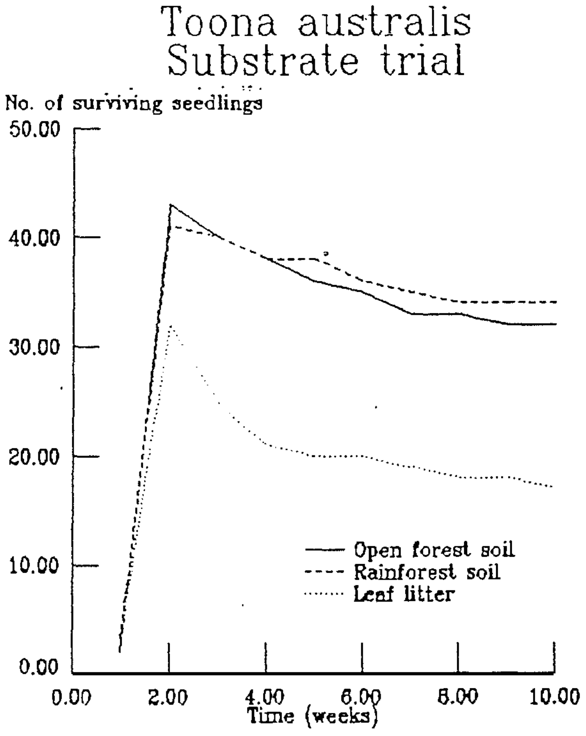


Figure 5.24

## 5.4 CONCLUSIONS AND SUMMARY

Fire emerges as the main disturbance factor controlling the distribution of species across the ecotone. Fire is controlled by a large range of physical, climatic and floristic factors. Topography, as well as wind strength and direction will influence the direction and intensity of fires in open forest. Intensity of fire is also controlled by the nature and condition of the available fuel, determined in turn by the predominant vegetation and climatic factors such as rainfall. Fires of exceptionally high intensity may occur after unusual climatic events such as drought, cyclones and frost. High intensity fires will favour the incursion of open forest species into rainforest, while the reverse will occur if fires are of low intensity, infrequent or non-existent. The rainforest margin is well protected against low intensity fires, as many of the edge species are capable of rapid regeneration following fire disturbance, and will form a dense, relatively fire proof buffer along the edge which is impervious to all but high intensity burns (Unwin, 1983).

Open forest species, particularly eucalypts, depend on fire to regenerate successfully. These species are incapable of regenerating under a closed canopy, and invasion of closed forest species into open forest will push the rainforest margin further into open forest. Rainforest species are generally able to establish under a closed canopy in the event of gap formation, and do not rely on large scale disturbances ;such as fire to maintain the vegetation type. Thus, control over the fire regime will allow management of the position of the rainforest margin, and an understanding of the regeneration requirements of the open forest and rainforest species gives the forest managers the opportunity to control and manipulate species composition in both forest types.

# CHAPTER 6
# CONCLUSIONS AND SUMMARY

## TABLE OF CONTENTS

"Supposing a tree fell down, Pooh, when we were underneath it?"

"Supposing it didn't," said Pooh after careful thought.
(Milne, 1926)

## 6.1 SUCCESSION IN TROPICAL FORESTS

A wealth of literature is available on succession in tropical forests the world over, and the dynamics of open forest in Australia have also been the subject of a vast number of published studies. Few authors, however, have compared the two or examined the cases where the two forest types meet. The patterns and processes in open and closed forest types in Australia are so radically different that any comparison would seem purely academic, but for the fact that open and closed forest boundaries do coincide and overlap, particularly in upland areas of north Queensland. Superficially, rainforest and open forest both appear to be self sustaining communities. The microenvironment produced by rainforest is suitable only for the regeneration of rainforest species, the low light levels therein excluding eucalypts and grasses. Moreover, the moisture stressed, fire prone environment of open forest lends an overwhelming competitive advantage to suitably adapted sclerophyllous open forest species, and here rainforest species have little hope of establishment and survival. Tall open forest also appears to be the province of *Eucalyptus grandis*, and neither rainforest nor medium open forest species are able to successfully establish or compete with *E. grandis* on its home ground. However, it is under a canopy of *E. grandis* that the boundary moves through time, and the movement of the boundary zone raises questions about the long term stability of both rainforest and open forest.

Species diversity in the open forests of tropical Australia is relatively low, and regeneration is dependent on disturbance by fire. Variations in species dominance may be brought about by alterations in fire frequency or intensity (Stocker and Mott, 1981) but the prevalence of *Eucalyptus intermedia* dominated grassland as the vegetation type adjacent to most of the rainforest boundaries in upland north Queensland suggests that the disturbance regime on these sites is within the tolerance limits of this vegetation type. Thus, medium open forest is in a state of dynamic equilibrium and follows a relatively simple, stable, cyclic successional pattern. The dominance of some open forest sites in the vicinity of the rainforest margin by *Allocasuarina torulosa* or *A. littoralis* may be related to variations in fire regime or edaphic factors (Crowley, pers. comm.) but this relationship does not fall within the scope of this study.

Succession in closed forest environments is greatly complicated by the high species diversity, so successional models in the literature deal with species groups rather than with individual species. Successional patterns also vary according to the scale of the initiating disturbance i.e. the size of the gap created in the closed canopy.

Bazazz (1984) recognized that the relative contribution of various gap filling guilds varied with the size of the gap created. The smallest gaps are occupied by increased growth of adjacent trees. As gap sizes increased the gaps were usually filled by suppressed seedlings that were present on the forest floor before the arrival of the gap (advance regeneration). Resprouting is also common in this type of gap (Stocker, 1981). In larger gaps, a significant contribution is made by secondary tree species with long lived seeds germinating in the seed bank. In very large gaps, immigrant species whose seeds arrive after gap formation tend to dominate. Where large scale clearing has occurred, these invading species may include herbs and grasses, possibly delaying the process of gap filling (Bazazz, 1984), especially when fire follows the forb invasion.

Ewel (1984) described the basic pattern of succession in moist tropical forests. The earliest colonizers, the herbaceous stage of the succession, usually die within a year, unless the process is arrested by the dry season and, in some cases on a long term basis by fires. These are succeeded by woody pioneer species which can usually be found in the understorey of the herbaceous layer in the first few months following clearing. Within a few years, these fast growing pioneer species form a nearly closed canopy, often dominated by a single species. As the pioneer species grow older, tree diversity increases and the frequency and distribution of the species reflect a complex interaction of seed abundance, seed predation, competition, herbivory and microsite differences (Ewel, 1984). There is no clearly defined end point for the process, and the theoretical mature forest composed of a diverse mixture of large-seeded, shade tolerant plants (Richards, 1952) is, in nature, constantly interrupted by tree falls and the reinitiation of species replacement at a range of points along the successional pathway depending on the size and nature of the gap created.

Whitmore (1982) proposed that forests throughout the world are fundamentally similar in their processes of succession and maintenance, and distinguished three arbitrary phases in the forest growth cycle: gap, building and mature. These phases can be identified by what he referred to as "tolerance classes" of the species making up the stand. Amongst tree species, he recognized two extremes: those which are adapted to regeneration in open sites and big gaps and those which are adapted to closed forest and small gaps. The two extremes are distinguished by the species responses to light. Bazazz (1984) listed other physiological characteristics of large gap and pioneer species (table 6.1).

---

1. Long seed and seedling dormancy.
2. Germination is enhanced by light, decreased by far red/red ratios, temperature fluctuations and nutrients.
3. Mostly epigeal germination; ~~photosynthetic~~ cotyledons.
4. High rates of photosynthesis, respiration, transpiration, high conductances, high N-contents.
5. Continuous production of leaves; fast leaf turnover rates; leaves arranged in flat crowns, and are not multilayered.
6. Rapid growth; low density wood; large leaves.
7. Highly branched, intensive deep root system; low dependence on mycorrhizae; mostly $NO_3$ users.
8. Early and long flowering time.
9. Rapid response to changes in resource levels.
10. High acclimation potential.
11. High susceptibility to herbivores and pathogens.

---

Table 6.1 Characteristics of pioneer or early successional rainforest species. From Bazazz, 1984.

Whitmore (1982) suggested three broad classes of tropical rainforest trees. Pioneer species are readily identified by having rapid seedling growth and copious, small, readily dispersed seeds which in many cases exhibit dormancy. He identified some of the principle genera of pioneer species: *Cecropia* (70 - 80 spp.) and *Ochroma* (monotypic) in the neotropics, *Macaranga* (80 spp.) and *Musanga* (2 spp.) in Africa, *Macaranga* (200 spp.) in the eastern tropics and *Trema* (30 spp.) which is pan tropical. *Alphitonia* (2 spp.) is an excellent example of a pioneer genus in the Australian tropics.

A broad class of species of intermediate tolerance (secondary and/or late secondary species) which cannot successfully colonize bare open sites but which become dominant at an intermediate stage of secondary succession and which do not perpetuate themselves *in situ* were recognized by Whitmore (1982) and Ewel (1984). Many of the commercially valuable timber species of the tropics belong to this group. *Cedrela*, *Swietenia*, *Bombacopsis*, *Cordia*, *Dialyanthera*, *Inyanthera* and *Vivola* are examples of these genera in the neotropics. In Africa the main ~~representatives~~ are *Entandro phrangra*, *Guarea*, *Khaya*, *Loxoa* and *Triplochiton*, while *Shorea* is a prominent example in Asia (Whitmore, 1982). *Toona* and *Flindersia* are two Australian tropical genera with valuable timber which fall into this category.

At the other end of the scale are the shade tolerant species which are able to regenerate in situ. According to Whitmore (1982) each part of the humid tropics has a large range of genera which fall into this class.

Jones (1956) recorded the pattern of forest succession in Nigeria, and noted that in forests dominated by 200 year old late secondary species (African mahoganies), these species were not regenerating but were being replaced by a self-perpetuating "climax" forest of fewer species growing up from the forest understorey.

Aubreville (1938) postulated a haphazard tree replacement rather than a succession in Ivory Coast rainforest, and this idea has found some merit in the eyes of later authors (Richards, 1952; Jones, 1956; Webb *et al.*, 1972, Whitmore, 1974). At the other extreme, Oldeman (1978) proposed five floristically and structurally different stages of succession in tropical forests. While purely random species replacement seems an unlikely mechanism, particularly in the light of the existence of differing degrees of shade tolerance in tropical trees, five sharply defined stages of succession would be difficult to demonstrate in most tropical forests.

Brokaw (1985) studied regeneration in a range of gap sizes (20 - 705 $m^2$) on Barro Colorado Island, dividing the colonizing species into two groups, pioneer and primary. Pioneer species were those found only in gaps, while primary species were found both in gaps and in the understorey of mature forest. Stem densities of pioneer and primary species were highest shortly after gap formation, and levelled off or declined after 3 to 6 years. In large gaps (> 150 $m^2$) pioneer species attained high densities and then experienced heavy mortality. Stem density of primary species did not vary with gap size. In larger gaps, pioneer species grew faster than primary species, and a larger range of size classes was exhibited by pioneer species.

Hopkins (1981) proposed a secondary successional pathway for complex mesophyll vine forest illustrated in figure 6.1. He recognized four groups of species: pioneers, early secondary or nomad species, late secondary species and mature phase species. He suggested that approximately 800 years would be required for mature phase rainforest to regenerate from a large clearing (e.g. 10 ha) of Australian tropical rainforest. This reconstructive or progressive secondary succession model passes through six phases between an area of bare ground and 'mature' forest, and can be interrupted at various points by fire and/or invasion of exotic species. He pointed out 4 main features of this proposed model of regeneration, viz.

"1. Disturbance is essential to the process of natural regeneration. Without disturbance there could be no change. The type of changes that occur are a product of the type, intensity, and frequency of disturbance.

2. The primary forest exists as an overlapping mosaic of regenerating units, localised reconstructive successions or microseres. The character of the forest at any particular point in time is a manifestation of the proportion of the forest area which is in particular stages of microsere development.

3. The physiognomic structure, floristic composition and structure, and dynamic ecological characteristics of the forest are as much a product of the disturbance regime to which it has been subjected as they are to the more commonly flaunted variations in climate, soils, and topography.

4. The effect of different types of disturbance on rainforest will depend on the disturbance regime within which it has evolved. Disturbance which, because of type, periodicity, or intensity, is unusual relative to a particular forest type, will have a far greater impact than that which falls within the usual disturbance regime and vice versa." (Hopkins, 1981)

Chapter 4 of this study examined a tendency for rainforest species seedlings to vary in their response to changes in PAR to a greater extent than open forest species. The models of forest succession in the literature all suggest a sequence of species replacement by progressively more shade tolerant individuals. In some cases, the species of these trees may not follow as predictable a pattern. Rainforest species individuals may exhibit a range of

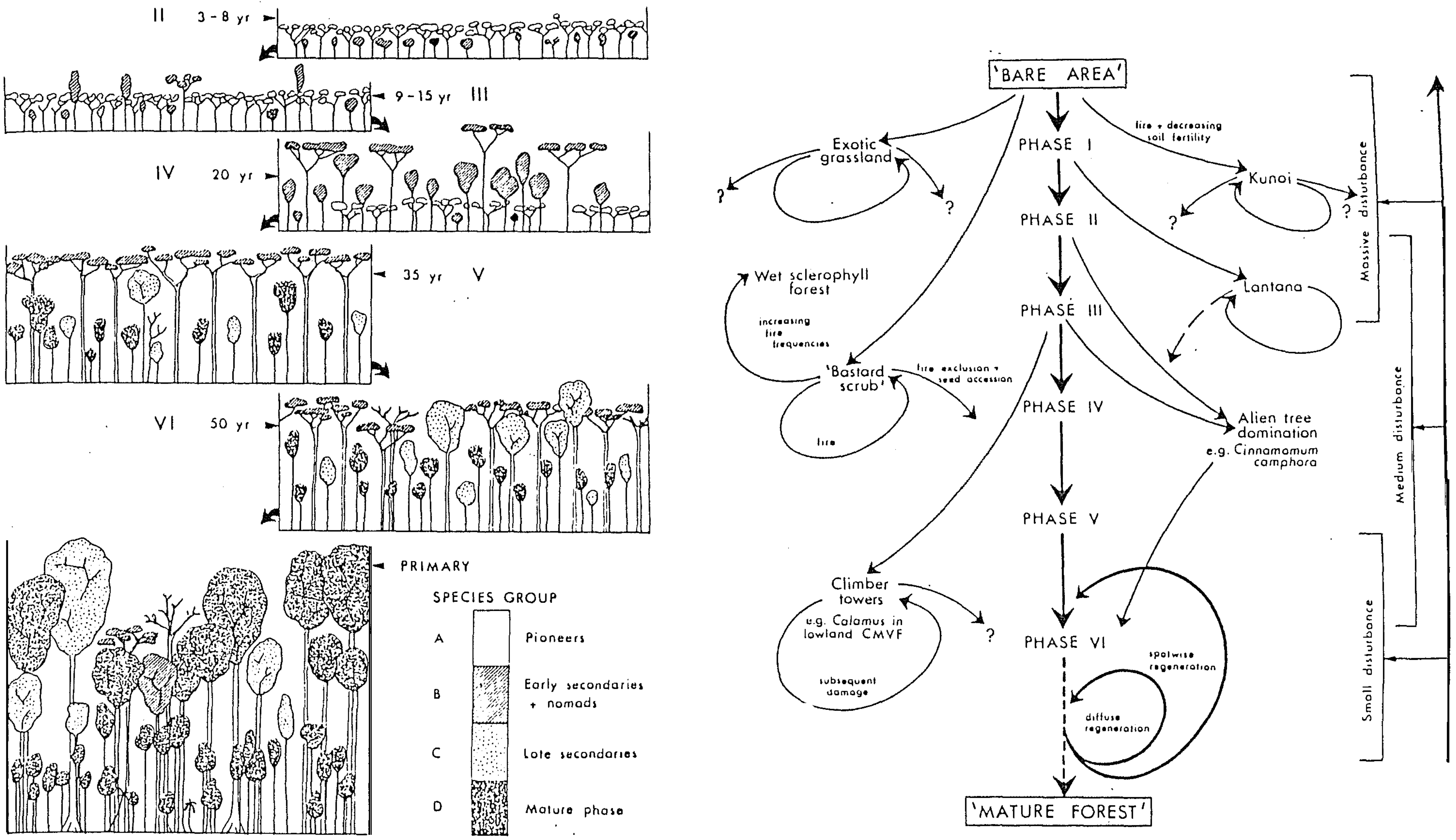


Figure 6.1 A model of secondary succession following clearing in complex mesophyll vine forest. From Hopkins (1981).

degrees of shade tolerance, and may thus occur throughout a range of phases during a secondary succession.

The postulated variable response of rainforest species is not to be confused with those species which, as individuals, exhibit a wide range of physiological tolerance (i.e. generalists). Rather, secondary rainforest species such as *Alphitonia petriei, Flindersia brayleyana, Neolitsea dealbata* and *Toona australis* contribute seeds to the pool of available colonizing plants, each of which will give rise to a seedling which is a specialist for a slightly different light regime or gap size. Evidence for this hypothesis does exist from field observations. Young saplings of *Alphitonia petriei* have been found under small canopy gaps ($\approx 50$ m$^2$) in rainforest at Paluma. This species is normally found growing in large clearings ($> 200$ m$^2$) or on road edges. *Neolitsea dealbata* appears to be a successful colonizing species in large gaps, but also occurs in the understorey beneath an undisturbed canopy at sites such as Longlands Gap State Forest, near Herberton. Dense sapling growth of *Toona australis* from seed co-occurs with stands of *Alphitonia petriei* on 2 - 3 m wide snig tracks on the Mt Winsor Tableland (plate 6.1), while 3 m high saplings of *Toona australis* were found under small canopy gaps at Curtain Fig State Forest on the Atherton Tableland.

The rainforest floor is a highly heterogeneous light environment, with PAR varying by several orders of magnitude from the closed canopy environment to the centres of large gaps. Species that are capable of producing large numbers of seeds will maximise their chances of establishment if their seedlings can compete successfully in a range of light environments. A consequence of this hypothesis is that species occupation of gap environments in rainforest may be largely stochastic. The "equal chance hypothesis" proposed by Connell (1978) as one of six possible explanations of the high diversity of tropical forests suggests that the individuals which first reach a gap through random processes of dispersal are the ones with the greatest chance of colonizing that gap. Arrival of a seed dispersed into a gap depends upon the mode and timing of dispersal. Wind dispersed seeds such as those of *Toona australis* or *Flindersia brayleyana*, which germinate within a few weeks of reaching the soil will need to be dispersed from nearby parent trees and at a time closely ~~corresponding~~ to that of the formation of the canopy gap. In order to become established in the gap, these species must be able to maintain growth in the light level of the gap, (i.e. exhibit a certain degree of shade

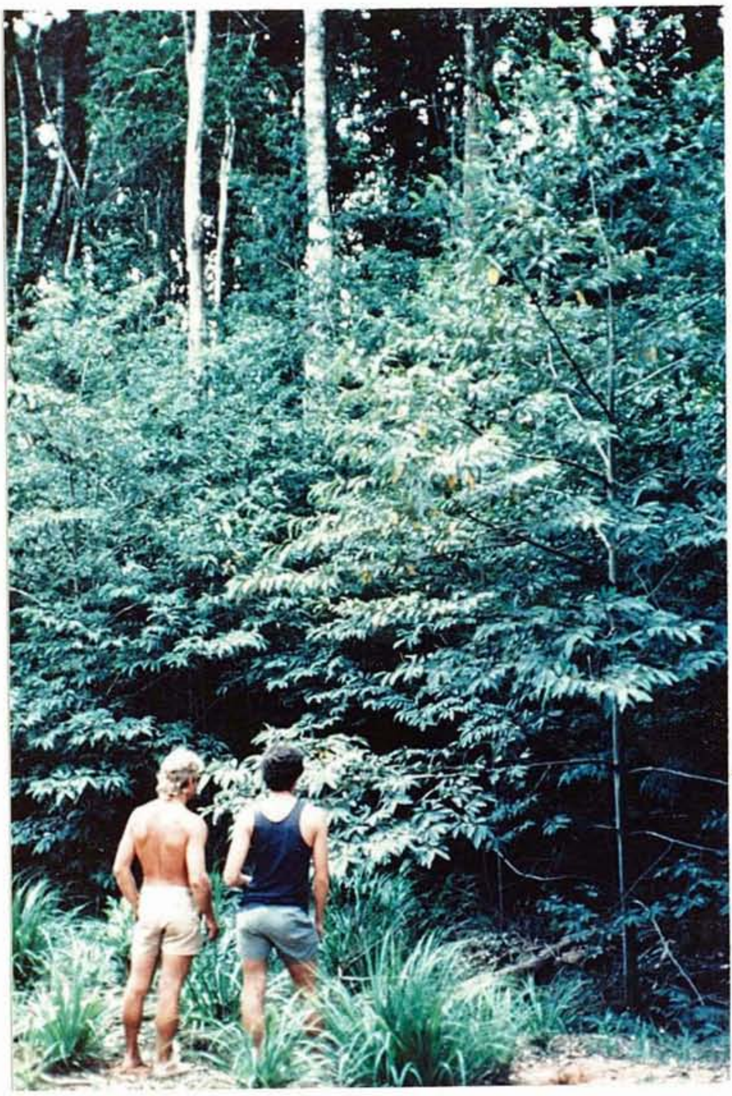


Plate 6.1 Regrowth of *Alphitonia petriei* and *Toona australis* on a 7 year old snig track on the Mt. Winsor Tableland.

tolerance) and at the same time grow rapidly enough to compete with the other seedlings in the gap for light and soil nutrients. The successful seedling or seedlings will thus be those whose optimum light requirements most closely correspond to the size of the canopy gap. A species whose seedlings exhibit a range of optimum light requirements will thus have a greater chance of eventually becoming established.

Variability of response to the light environment in rainforest species will allow them a similar range of potential niches in the rainforest ecotone. The floor on the rainforest margin is even more variable in light intensity than the rainforest floor. The prevalence of secondary rainforest species across the rainforest ecotone, such as *Toona* and *Flindersia* (Unwin, 1983) may be partly attributed to seedling variability in these species.

## 6.2 DYNAMICS OF THE RAINFOREST ECOTONE

The low PAR found under an undisturbed rainforest canopy is incompatible with eucalypt regeneration (Cremer, 1960). Hence "mixed forest" stands, with a eucalypt canopy over a rainforest understorey are a late stage in the fire initialized succession from eucalypt forest to rainforest (Cremer, 1968 and Jackson, 1968). Extensive areas of mixed forest occur in southern Australia, where rainforest is susceptible to high intensity forest fires (Jackson, 1968). In tropical Australia, mixed forest normally occurs only on rainforest margins or on exposed ridgetops as a result of cyclone fire interactions (Unwin, 1983). In these cases, *Eucalyptus grandis* is almost invariably the dominant eucalypt species. Both Unwin (1983) and Smith and Guyer (1983) recognized that, in historic times, rainforest at many sites has expanded into areas previously dominated by eucalypts, possibly as a result of recent changes in the fire regime at these sites. There is little doubt that fire is the factor which controls the position and movement of the rainforest - open forest ecotone (Chapter 5). It is intended in this section to review the effect of environmental variables such as PAR, water relations and seed bed conditions on the mechanisms controlling the dynamics of the ecotone. These variables are controlled largely by the predominant vegetation type, and hence, indirectly by the fire regime.

### 6.2.1 THE ROLE OF *Eucalyptus grandis*

The key to the rainforest ecotone lies in the autecology of the dominant tree species, *Eucalyptus grandis*. Unwin (1983) raised a number of questions about the role of this species (Chapter 2), in the dynamics of the rainforest boundary, and results obtained in this study suggest answers to some of these questions.

Field observations (Chapter 2) indicate that the medium open forest environment is unsuitable for the growth of *E. grandis*. There appear to be two main reasons for this. Firstly, *E. grandis* is not well adapted to withstand the effects of high frequency, low intensity fires which are common in tropical open forest. Although adult trees of *E. grandis* appear to be unaffected by low intensity fires, as the bases of these trees are well protected by heavy bark, repeated fires over a long period will eventually erode the butts of even the largest trees, leading to their eventual death. Moreover, young seedlings and saplings of *E. grandis* are susceptible to fire. Unlike young seedlings of *E. intermedia*, *E. grandis* does not produce a lignotuber and does not readily regenerate if the above ground portion of the plant is destroyed. Hence, *E. grandis* is less able to compete for resources following low intensity fires than *E. intermedia* or the grass species found in medium open forest. Secondly, moisture stress conditions are more severe in medium open forest than in the ecotone or the rainforest (Chapter 3). *E. grandis* is less drought resistant than its neighbouring counterpart, *E. intermedia*, and is less likely to withstand moisture stress, particularly in the seedling stages, during the protracted periods of low rainfall.

The inability of *E. grandis* to regenerate under a rainforest canopy is readily explained by its low degree of shade tolerance. At intermediate PAR levels such as those of the very edge of the rainforest ecotone, *E. grandis* may be capable of growth, but succumbs readily to attack by pathogens and herbivores. Moreover, the seedbed conditions provided by rainforest litter are unsuitable for *E. grandis* regeneration (Chapter 5).

Regeneration of *E. grandis* will be favoured following a fire of high intensity, particularly near the rainforest boundary, since the high nutrient content of the ashbed, high PAR because of the removal of shading vegetation and the relatively moist microclimate and soil of the rainforest boundary region following a high intensity fire are almost ideal conditions for the growth of any tree species. However under these conditions, *E. grandis* exhibits a higher rate of growth than any other species examined in this study.

Observations made in tall open forest at Gilbey State Forest (17° 26' S, 145° 28' E) on the Atherton Tablelands two months after a relatively high intensity fire in December 1986 indicated that germination and seedling survival for *Eucalyptus grandis* were substantially higher in the remaining ash from burnt out logs than on adjacent areas of burnt ground. The heat of the burning logs apparently killed the underground organs of grass species, and seedlings in the ash beds were almost exclusively *Eucalyptus grandis* and *E. resinifera*. In adjacent areas without the remains of burnt timber, grass regeneration appeared to have suppressed eucalypt seedlings, and very few were in evidence. Other reasons for this observation could include high moisture retention by the ash, high nutrient ~~concentrations~~ in the ash and heat sterilization reducing the effects of seedling damping off.

The competition experiment described in Chapter 4 illustrates the ability of *E. grandis* to effectively outcompete other fast growing species such as *Acacia mangium* or *Toona australia* under conditions of high seedling density. In nutrient poor soils, *Acacia* species may be able to compete on an equal footing, while secondary rainforest species such as *Toona, Flindersia* or *Alphitonia* will outcompete *E. grandis* at PAR levels less than 20% FSU. Further out from the rainforest edge, frequent fires and moisture stress will swing the competitive balance in favour of *E. intermedia*, but in the ecotone, *E. grandis* is inevitably dominant. Regrowth of rainforest species under the developing canopy of *E. grandis* is probably responsible for excluding low intensity fire from the ecotone, allowing *E. grandis* saplings to reach a sufficient size to resist the effects of the next fire to penetrate into the ecotone. This developing rainforest understorey prevents subsequent regeneration of *E. grandis in situ*, so the movement of the rainforest boundary is conveniently recorded by the presence of emergent *E. grandis* over a rainforest understorey. Individuals of *E. grandis* overtopping young rainforest at Kirrama up to 80 m behind the rainforest margin indicate that the rainforest at these sites has encroached at least 80 m into open forest since the last set of conditions allowing *E. grandis* regeneration on the boundary.

### 6.2.2 RAINFOREST EXPANSION INTO OPEN FOREST

The microenvironment of the tall open forest belt resembles that of closed forest more closely as the rainforest margin is approached. Soil moisture increases (Chapter 3) and saturation deficit is reduced, while PAR decreases (Chapter 2). Thus, conditions favouring the establishment of pioneer and secondary rainforest species occur in open forest near the rainforest boundary. In particular, PAR is reduced by the shading effect of adjacent rainforest, particularly on boundaries running north-south. Shaded conditions and litter accumulation will reduce the chances of eucalypts and grasses becoming established and thus favour establishment by rainforest secondary tree species, shrubs and vines. Patterns of succession and colonization on the rainforest boundary are similar to those encountered in large canopy gaps. Secondary rainforest tree species are capable of rapid growth in partially shaded conditions, particularly in soils with high nutrient concentrations such as ash beds. Rapid germination shown by these species (e.g. *Toona* and

*Flindersia*, Chapter 5) allow them to establish quickly on the rainforest margin following a disturbance. Subject to suitable conditions for dispersal, these secondary species will be followed, in time, by more shade tolerant primary rainforest species. Establishment of rainforest under tall open forest results, and the rainforest microenvironment will advance further into open forest, favouring in turn, further advance by rainforest species.

Rainforest species on the margin are protected to a certain extent from drought stress by increased humidity and decreased evaporation provided by the closed canopy, and from the effects of fire by the low combustibility and efficient vegetative regeneration of species on the edge, forming a buffer zone against subsequent fires. Thus, in the absence of high intensity fire penetrating inside the rainforest margin, rainforest species will gradually move out into open forest, creating a microenvironment favourable to the subsequent regeneration of rainforest species and excluding the more fire prone open forest grasses and eucalypts.

### 6.2.3 REPLACEMENT OF RAINFOREST BY OPEN FOREST

High intensity fire, which removes a large percentage of the rainforest canopy, is the only mechanism by which open forest species can colonize areas previously occupied by rainforest. The *Eucalyptus*, *Casuarina* and grass species of tropical open forest mostly produce wind dispersed seeds with rapid germination and limited viability, so in order for colonization of disturbed rainforest by open forest species to take place, a nearby seed source must be available. Generally, these conditions are fulfilled only near the rainforest boundary, so encroachment of open forest into rainforest also takes place across the ecotone.

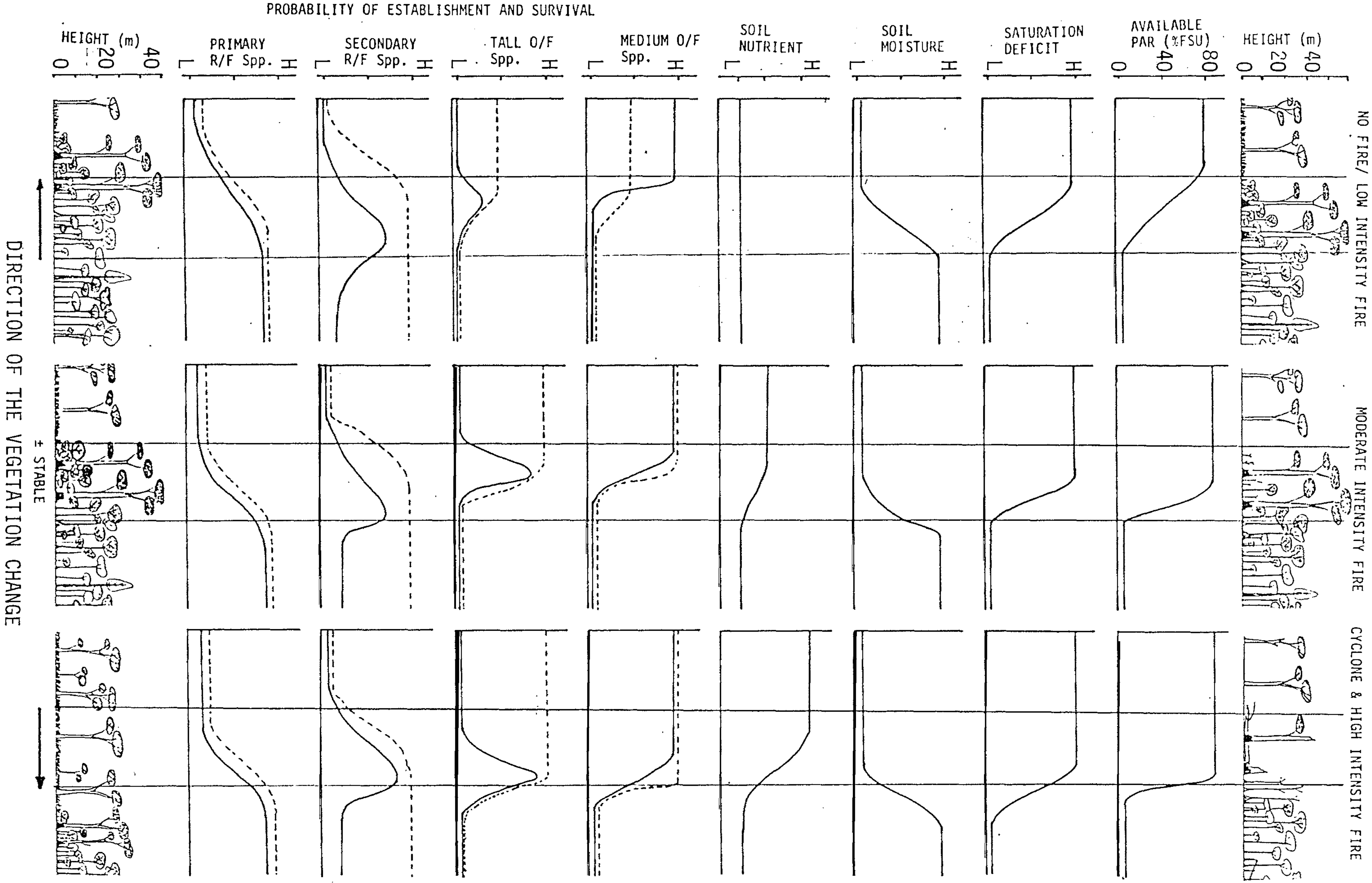
Conditions allowing fire in Australian tropical rainforests are relatively rare (Stocker, 1981). Under normal conditions, rainforest will not burn, so an initiating disturbance (cyclone, drought or frost) is required to modify fuel conditions and availability. Cyclone - fire interactions were noted by Webb, 1958; Unwin, 1983 and Unwin *et al.*, 1986 (Chapter 5). Reports of fire in rainforest following severe drought in Curtain Fig State Forest in 1915 exist in historical records (G.C. Stocker, pers. comm.) and large individuals of *Castanospermum australe* and *Litsea leefeana* in this area carry what appear to be old fire scars. However, since there is no evidence of emergent eucalypts in this forest, so open forest failed to become established in this case, possibly because the propagule source was too far away. The present 30 m + canopy at this site is composed of a mixture of primary and secondary rainforest species, including *Argyrodendron peralatum*, *Castanospermum australe*, *Aleurites moluccana*, *Litsea leefeana*, *Flindersia* spp. and *Toona australis*. Frost - fire interactions on rainforest boundaries were postulated in Chapter 5. The dry conditions associated with frosts at altitudes > 700 m on the Atherton Tablelands, coupled with the susceptibility of the leaves of pioneer and secondary rainforest trees on the forest boundary to frost scorching give rise to conditions in which fire could penetrate into rainforest. Distribution of rainforest and open forest in frost hollows on the Atherton Tablelands could be attributed to past frost-fire interactions (Duff and Stocker, in prep.).

Once open forest species become established, the probability of fire is increased, and subsequent repeated fires will prevent recovery by rainforest species. Thus, while encroachment of rainforest into open forest is a gradual process, replacement of rainforest by open forest will tend to take place on a more extensive scale, but only following unpredictable and relatively infrequent events such as severe disturbance by cyclones, drought and frost, all interacting with fire. Because of the limited dispersal capabilities of eucalypts compared to grasses, grassland is sometimes an intermediate stage in the displacement of rainforest by open forest (G.C. Stocker, pers. comm.).

### 6.2.4 A MODEL OF THE RAINFOREST ECOTONE

A simple model illustrating the probability of establishment on the rainforest margin of the four guilds of species is shown in figure 6.2. These are (1) Open forest species, including *Eucalyptus intermedia*, *Allocasuarina torulosa* and grass species; (2) Tall open forest species, especially *E. grandis* and *E. torelliana* (3) Pioneer and secondary rainforest species e.g. *Alphitonia petriei*, *Flindersia brayleyana* and *Toona australis*, and (4) Primary rainforest species and shade tolerant understorey species such as *Argyrodendron peralatum* and *Syzygium wesa*. Establishment probability is divided into high, intermediate and low categories, and represents the likelihood of seedlings of each guild establishing in a given position on the ecotone, and of these seedlings surviving to maturity. Three disturbance conditions are represented:

Figure 6.2 Model of the rainforest-open forest ecotone under three different disturbance regimes: 1. No fire or low intensity fire; 2. Moderate intensity fire; 3. High intensity fire following a cyclone or other major disturbance. The model shows the state of the ecotone immediately after the disturbance (top) and after recolonizing plants have reached maturity (bottom). Variations in microenvironment across the ecotone are represented graphically: Available PAR (% full sunlight), Saturation deficit (Relative; H=high, L=low), Soil moisture (Relative) and Soil nutrient availability (Relative). The relative probabilities of establishment (broken lines) and survival (solid lines) are shown for four guilds of plants: Medium open forest species; Tall open forest species; Secondary rainforest species and Primary rainforest species.


PROBABILITY OF ESTABLISHMENT AND SURVIVAL
HEIGHT (m)
0 20 40
PRIMARY R/F Spp.
SECONDARY R/F Spp.
TALL O/F Spp.
MEDIUM O/F Spp.
SOIL NUTRIENT
SOIL MOISTURE
SATURATION DEFICIT
AVAILABLE PAR (%FSU)
0 40 80
HEIGHT (m)
0 20 40
L
H
NO FIRE/ LOW INTENSITY FIRE
MODERATE INTENSITY FIRE
CYCLONE & HIGH INTENSITY FIRE
± STABLE
DIRECTION OF THE VEGETATION CHANGE

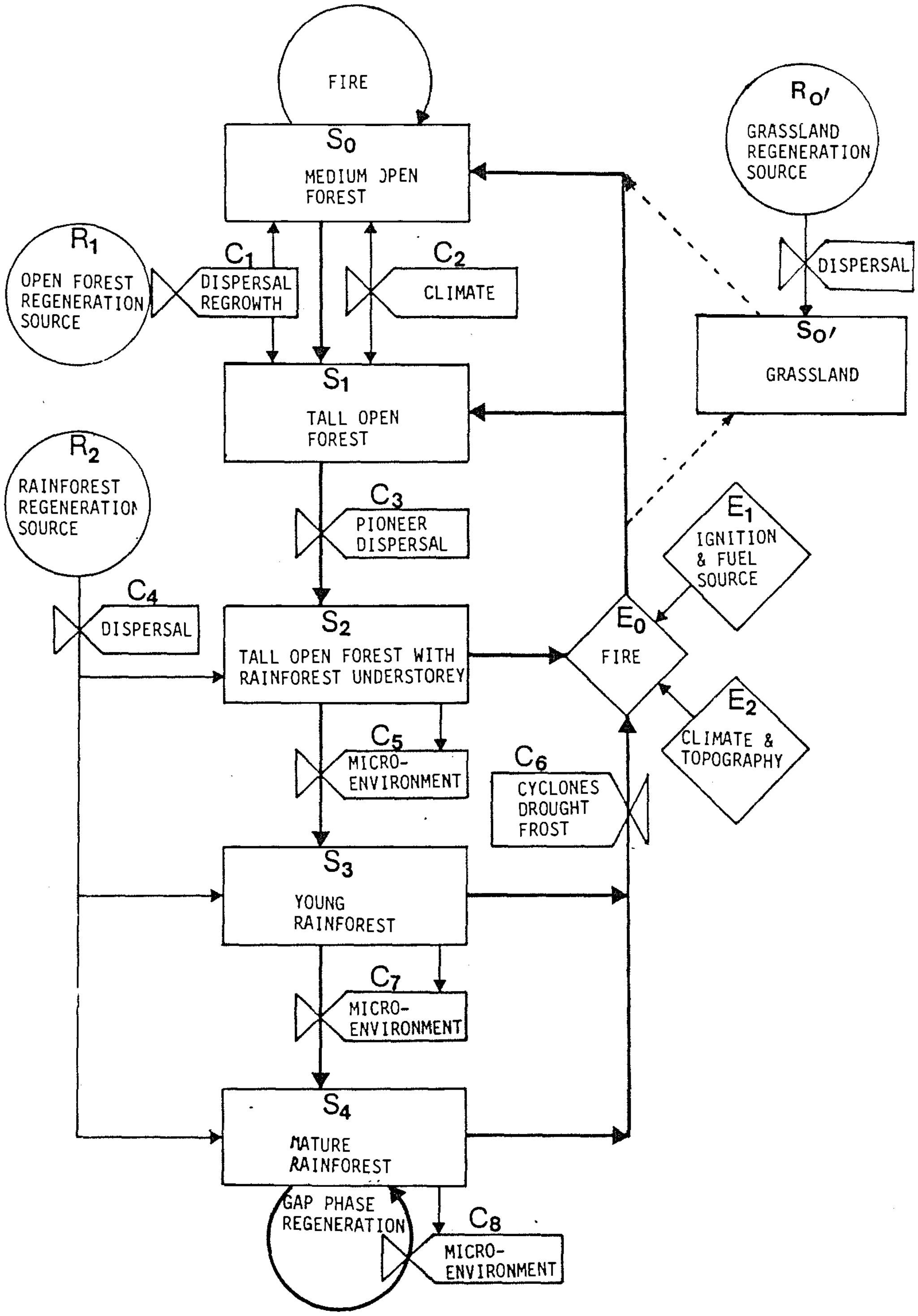


Figure 6.3 A model of the vegetation change on the rainforest boundary. Adapted from Macmahon (1979) and Unwin (1983).

no fire or low intensity fire, moderate intensity fire, and high intensity fire. In the absence of fire, rainforest will advance into open forest as a result of the favourable gradient in PAR, moisture regime and seed bed characteristics. Low intensity fire not penetrating into the ecotone will maintain the position of the ecotone, although rainforest will advance into open forest given a sufficient fire free interval. High intensity fire will allow penetration of open forest species into rainforest, and establishment of tall open forest species (*Eucalyptus grandis*) on the newly formed rainforest margin.

Figure 6.3 adapted from MacMahon (1979) is a model of the change in vegetation at a point on the rainforest margin through five different points in time. The transition from $S_0$ (medium open forest) to $S_1$ (tall open forest) occurs either as a result of changing climatic conditions, with increased rainfall favouring the establishment of tall open forest, or as a result of changes in microclimatic conditions caused by the developing rainforest edge (control gate $C_2$). Establishment of tall open forest is also dependent on an adjacent seed source ($R_1$), as *E. grandis* does not regenerate vegetatively (control gate $C_1$).

The transition from $S_1$ to $S_2$ (tall open forest with a rainforest understorey) occurs as a result of dispersal of pioneer and secondary rainforest species into tall open forest ($C_3$). As these develop they modify the microclimate in the tall open forest, favouring the establishment of primary rainforest species. The establishment of these rainforest species in tall open forest is dependent on dispersal ($C_4$) or vegetative regeneration of existing rainforest species following disturbance ($R_2$.

The presence of a closed subcanopy in $S_2$ reduces the light availability on the forest floor to such an extent that the *Eucalyptus* spp. are unable to regenerate *in situ* ($C_5$), so when the adult eucalypts die, they are not replaced, and the young rainforest understorey is left ($S_3$). The microenvironment of young rainforest ($C_7$) favours the establishment of primary rainforest species, leading to the development of mature rainforest ($S_4$). Mature rainforest is sustained in a state of dynamic equilibrium (in terms of structure if not floristics) through the processes of gap phase regeneration.

The dominant environmental factor ($E_0$) is fire, the intensity of which is controlled by climate and topography ($E_1$) and fuel availability ($E_2$). Fire frequency is controlled by fuel availability ($E_2$) and ignition sources ($E_3$). Fuel is available in transition states $S_0$ and $S_1$ during dry periods, and after exceptional climatic events such as cyclones, severe frosts and severe drought in $S_2$, $S_3$ and $S_4$, allowing the possibility of rainforest replacement by open forest. Grassland ($S_0$) may form an intermediate stage in the transition from rainforest to open forest in the absence of a nearby source of open forest tree species propagules. Mature rainforest may also be replaced by young rainforest following fire, as in the Curtain Fig State Forest fire in 1915.

Note that microenvironment (PAR and saturation deficit) is a product of the existing vegetation type. Vegetation types $S_1$ and $S_3$ are always transition states, while $S_0$, $S_2$ and $S_4$ are capable of remaining in a state of dynamic equilibrium for indefinite periods provided there are no major changes in the disturbance regime. Regeneration sources R1 and R2 include coppicing (R2), lignotuber resprouting (R1), soil seed banks (R2) and seed dispersed from outside (R1 and R2).

## 6.3 CONCLUDING REMARKS

The conclusion of Unwin (1983) that rainforest in upland areas of north Queensland is currently expanding into areas previously occupied by open forest is supported in this study. The results obtained in this thesis explain the ecophysiological mechanisms by which this transition occurs. Clearly, fire is the key element, but water relations, light availability and dispersal all play a role. Changes in light availability, macroclimate, microclimate and the disturbance regime are capable of causing rapid changes in the position and structure of rainforest - open forest ecotones. Many such boundaries probably arose as a result of the use of fire by aboriginals, and changes in the fire regime caused by the arrival of European man in the Australian tropics may be resulting in substantial changes to the distributions of rainforest and tall open forest assemblages. It is hoped that the results of this thesis will be useful in future management planning for north Queensland's forests.

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