

CHAPTER 4

Regeneration: establishment, survival and early growth

4.1 Introduction

Field observations made during the establishment and maintenance of the plots, strongly suggested that an appreciation of the temporal and spatial nature of disturbance in the forest canopy was essential if the processes of regeneration, and therefore the factors affecting species composition, were to be understood. Indeed the contrast on the forest floor between disturbed areas, with vigorous abundant regeneration and weed growth, and the almost pervading gloom of a patch of long undisturbed forest, is frequently extreme and remarkably abrupt.

The significance of disturbance in rainforest dynamics has been examined frequently in recent years (e.g. see Section 2.3.1) probably as interest in ecology has shifted from a broad taxonomic and descriptive approach to an examination of basic mechanisms such as those controlling the regeneration, growth and mortality of the component species.

Although there now seems to be indisputable evidence that periodic catastrophes can have a reverberating influence on the structure and floristics of tropical rainforests (see Sections 2.1.5 and 2.3.2), the regeneration processes associated with relatively small canopy gaps, each created by the death or toppling of a single large tree, may have been of greater evolutionary significance. This suggestion, which is examined in some detail in this Chapter, is based on the hypothesis that diversity in tropical rainforests can largely be explained by the regeneration processes observable in relatively small gaps. Other factors influencing diversity are discussed in Chapters 5 and 6.

Regeneration processes within gaps have long been of interest to foresters who, in endeavouring to meet management objectives, have attempted to create gaps with specific characteristics to manipulate both the species composition

and the average growth rate of the most desirable tree species in stands (e.g. Baur 1964b). Indeed a knowledge of gap phenomena is the basis of any silvicultural system which depends on natural regeneration.

In this Chapter the mechanisms controlling the establishment, survival and growth of regeneration are examined. It commences with a largely theoretical discussion of aspects of disturbance and sunlight penetration to the forest floor, followed by field observations on disturbance and subsequent regeneration in the forests of this region. These observations are supplemented by field, greenhouse and arboretum trials. Although the main emphasis will be upon light regimes, other factors related to gap environments will be considered.

4.2 Sunflecks

Flecks of sunlight on the floors of rainforests have often attracted the attention of those interested in the regeneration of rainforest trees (Whitmore and Wong 1959; Whitmore 1966b). The small holes allowing beams of light to penetrate the canopy, usually appear to result from crown architecture, phenological processes and/or growth rather than from disturbance. Whitmore and Wong (1959) measured the light reflected upwards from a paper disc (0.14 m^2) held horizontally 70 cm above the ground and showed that in a Singapore rainforest sunflecks contributed substantially to the total amount of light reaching the forest floor. Bazzaz and Pickett (1980) noted that the light intensity at the centres of sunflecks often seems to have been overestimated. With the light measuring instruments now available, precise measurements of the characteristics of sunflecks are possible.

An examination of the geometry associated with sunflecks created by small holes in the canopy (B.A. Hutchinson 1975 in Galoux 1981) suggested that the light intensities in small sunflecks may be quite low. For example in Figure 45 I have assumed that the sun is in a vertical position subtending an angle of $32'$ above a gap in a closed canopy 30 m above the

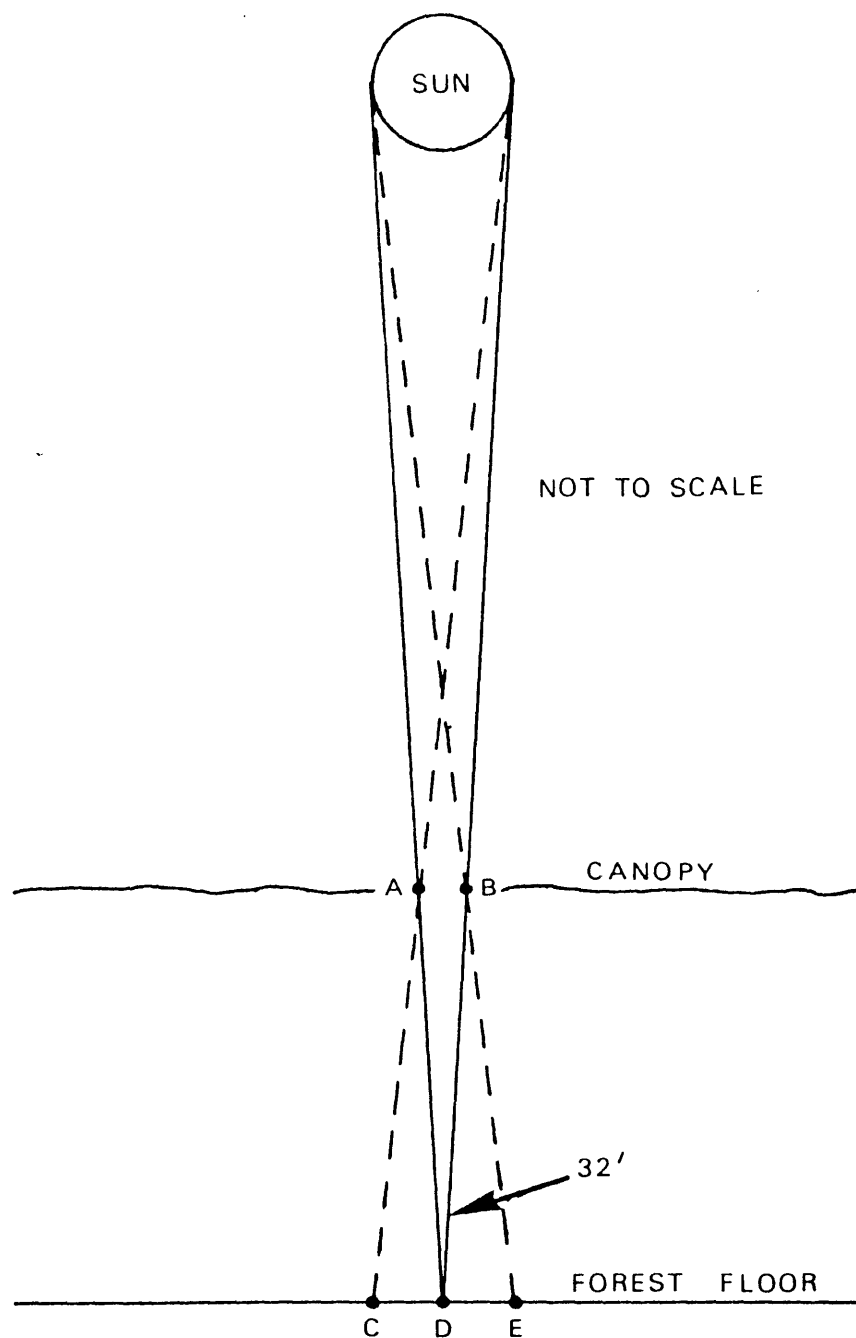


Figure 45. A diagrammatic illustration of a small canopy hole and the resulting sunfleck. Here the hole diameter (A - B) is only large enough for the very centre (D) of the sunfleck (C - E) to experience full sunlight intensity. The intensity of the sunlight in the sunfleck will decrease towards its perimeter.

ground. In these circumstances the gap must be 17 cm in diameter before the light at the very centre of a sunfleck approaches the intensity of that above the canopy. Light intensity across sunflecks is highest at their centres becoming less near their edges. In the example above, a 17 cm canopy gap would produce a sunfleck 34 cm across on the forest floor.

Unfortunately no detailed information is currently available on the intensity, spectral qualities and spatial and temporal distributions of sunflecks in the rainforests of this region. However, some preliminary information was obtained from quantum meter (Li-Cor Model LI-170; 20 mm sensor width) readings taken on the floor of plot 11 (see Section 3.2.2 for description). At the time the sun was almost vertically overhead and the sky was clear. Photosynthetically active radiation (PAR) levels outside the forest were $1850 \mu\text{E m}^{-2} \text{sec}^{-1}$. Spot measurements of PAR at the centres of flecks (3-10 cm in diameter on the forest floor) were often less than $40 \mu\text{E m}^{-2} \text{sec}^{-1}$ and sometimes as low as $4 \mu\text{E m}^{-2} \text{sec}^{-1}$. To gain an idea of the spatial distribution of sunflecks on the floor of this forest, PAR readings were taken at 25 regularly spaced points in a 10x10 m subplot. At most points the readings were too low ($< 1 \mu\text{E m}^{-2} \text{sec}^{-1}$) to register on the quantum meter. The maximum was $4 \mu\text{E m}^{-2} \text{sec}^{-1}$ at two points which happened to coincide with small sunflecks. Although the observations recorded seemed representative of undisturbed forest not subject to environmental extremes (such as very poor or very shallow soils or a severe dry season) the values are somewhat lower than those recorded by Bjorkman *et al.* (1972) in a south Queensland subtropical rainforest. This discrepancy will be commented upon later in this Chapter. Studies currently in progress on the photosynthesis of understorey plants (R. Pearcy pers. comm.) and the spectral qualities and spatial and temporal distributions of sunflecks (D. Yates and G. Stocker pers. comm.) should enable the role of sunflecks in maintaining the carbon balance of understorey species to be evaluated.

Although some rainforest plant species such as Alocasia macrorrhiza are reported to have compensation points as low as

from $0.05\text{--}0.2 \mu\text{E m}^{-2} \text{ sec}^{-1}$ (Bjorkman et al. 1972) it is usually thought (e.g. Longman and Jenik 1974) that only highly specialized understorey plants, such as this species, could live indefinitely on the floor of most undisturbed rainforest patches and that most green plants in these environments must be able to obtain additional energy from seed reserves (or possibly root grafts to individuals better placed to intercept sunlight) if they are to grow to where more PAR is available.

4.3 Disturbance gaps

Canopy gaps created by disturbance (see Section 1.2 for definitions) modify the microclimate and competitive environment on the forest floor beneath them in two ways. The first is that increased radiation reaching the forest floor not only increases the amount of light available to plants at lower levels but also heats up the soil's surface and may lower the moisture content of the surface soil and litter. The air temperature near the ground is increased and the humidity may be reduced. The second way is through the direct modification of the competitive environment by causing the death of, or damaging some individuals. As a consequence resources such as soil water and nutrients may become more readily available and allelopathic substances may be of less significance to others in the vicinity.

The size of an effective gap from a forest dynamics viewpoint (i.e. one which will allow seedlings or advanced growth on the forest floor to increase their growth rates appreciably) will depend on several factors besides gap diameter. They are the slope, aspect and latitude of the site and the height and nature of the forest canopy. Very small gaps may be closed by a minor extension of the crown of a single tree.

A feature of very large gaps in this region was the rapidity with which the vertical walls of gaps were "sealed", sometimes returning the light environment of the forest floor beneath adjacent undisturbed forest canopy to about the predisturbance level within a few months. This phenomenon was very noticeable when, on several occasions, attempts were made to

record photographically, structural features apparent at a freshly exposed rainforest face. If these photographs were not taken within a short time (typically 2 or 3 weeks) the features which had been so visible immediately after clearing were usually obscured by foliage derived from coppice shoots on trees, vines and saplings at the face, and herbs, shrubs and scramblers developed along the edge from seed (Plates 13 and 14).

The importance of gap geometry and its relationship with latitude does not appear to have been widely appreciated although several authors have provided models which predict shadow patterns adjacent to artificial forest edges, such as those created by clear cut coupes (Brown and Merritt 1971; Satterlund 1977; Halverson and Smith 1979). An interesting simulation model developed by Satterlund (1983) allowed the calculation of the shade cast on any site, at any time, by a randomly distributed conifer stand. However, the structural characteristics of rainforests limit its applicability to these assemblages. Unfortunately, the table established by Alexeyev (1970; in Galoux 1981) for PAR according to position in canopy gaps, sun elevation and diameters of gaps, was not accessible.

The following analyses of the effects of latitude on the light environments in gaps are based on standard astronomical formulae (Appendix D). Following Hartshorn (1980) I assumed that the canopy before disturbance was flat and opaque and that the disturbance formed a cylindrical gap right through to the forest floor. This model was used to illustrate the effects of latitude and gap size on the temporal and spatial distribution of sunlight on gap floors (for examples see Figure 46). While it showed that the amount of sunlight reaching the forest floor through small disturbance gaps was very limited, it was apparent that small gaps in the tropics provided a much more favourable environment for photosynthesis on the forest floor than did gaps of similar size in temperate environments. It was also apparent that while there was some spatial variability in the light regime across a gap (both E - W and N - S), the N - S variation was to some degree compensated for by seasonal shifts in the apparent sun



Plate 13. The wide range of species involved in edge closure along a newly exposed face includes the wild banana, Musa banksii F.Muell. and the climbing aroid, Raphidophora pinnata.



Plate 14. A natural rainforest edge bordering a stream. Note the role of the small trees, shrubs and particularly the climbers in sealing the forest edge.

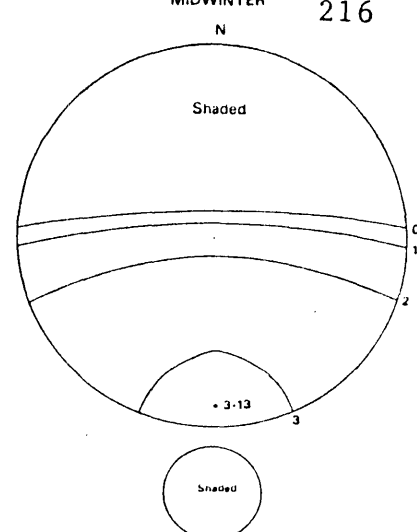
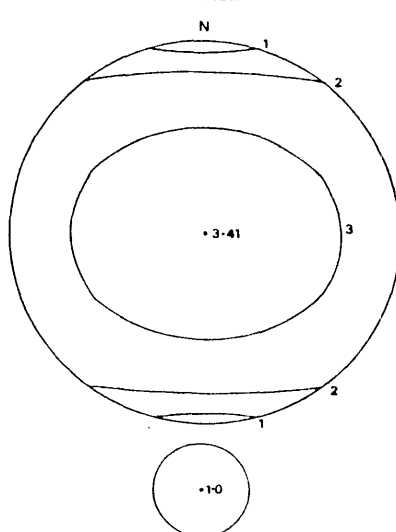
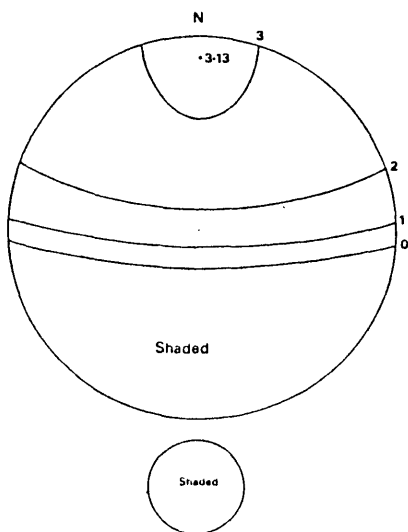
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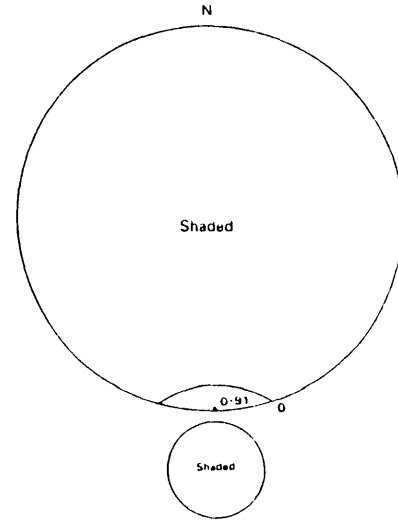
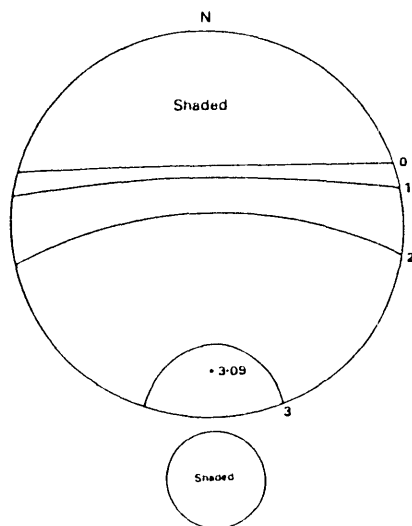
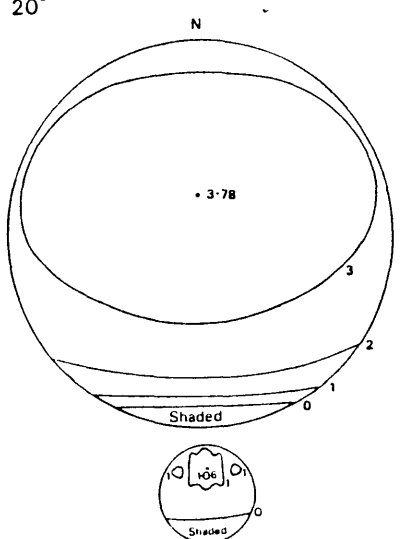
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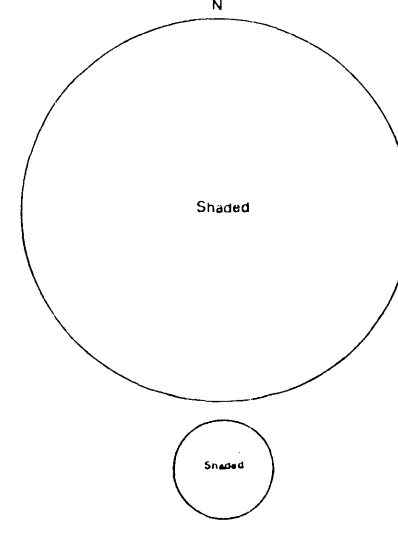
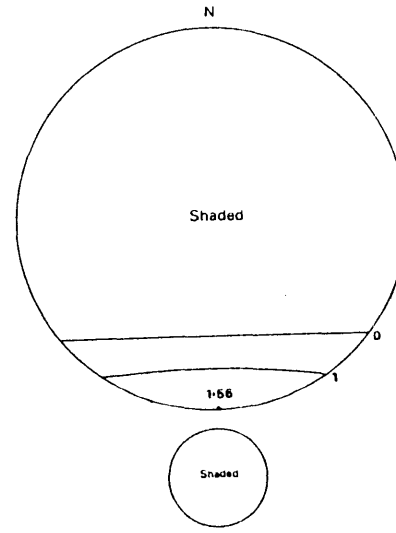
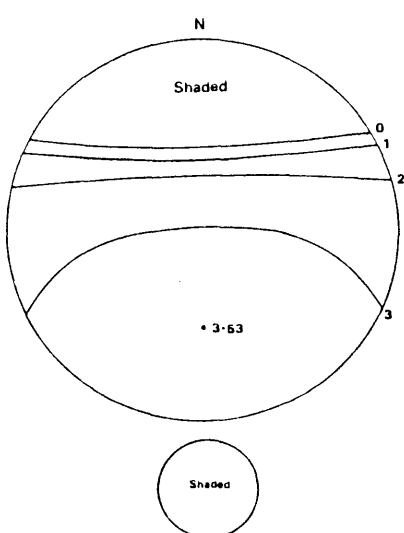


Figure 46. The spatial sunlight patterns on the floors of gaps at three different south latitudes, for two gap sizes and three contrasting days of the year are shown. The larger circles represent gaps of height/diameter = 1; the smaller, gaps with height/diameter = 4. Isopleths join points with 0, 1, 2 and 3 hours of direct sunlight on the days indicated (assuming cloud free conditions). Dot points indicate maxima (from G. Stocker and W. Taylor unpublished).

position.

Although the variability of the light regime within a gap may exert some control on regeneration pattern, differences among the light regimes in gaps of different sizes appear to be of great importance especially in the tropics for here sunlight can, on at least two days of each year, illuminate the floor of a gap of infinite height/diameter relationship. Outside the tropics the dimensions of the gap which will allow direct sunlight to penetrate to the floor of the gap are much more limited (Figure 47). Furthermore, the dimensions of gaps which would allow periodic photosynthesis for a range of plants on the forest floor beneath them are, in the tropics, of the size which could be produced by the death of a single tree or small group of trees. Figure 48 shows how relatively small variations in gap size in tropical closed forests could produce important differences in the light regime (and presumably that of related microclimatic elements) on the forest floor beneath gaps.

The situation in temperate closed forests is quite different, for with increasing latitude beyond the tropics, the critical gap size becomes larger and larger (Figure 47). Here regeneration in gaps from the death of one or two trees must usually be very shade tolerant to survive. One would expect perhaps that "large gap" species in temperate closed forests would be more dependent on very large gaps created by catastrophes (such as severe storms or forest fires) than would "large gap" species in the tropics. Indeed Fairbairn (1966), largely on the basis of the known regeneration strategies of forest trees in the United Kingdom, calculated that gaps would have to be from 0.4-2.0 ha in extent if cut-over forests in that country were to regenerate adequately.

The relationships among gap dimensions, latitude and the diversity of closed forest are explored further in the final Chapter. The following Section of this Chapter describes field investigations into some of the ways in which the forests of this region are disturbed and natural gaps created.

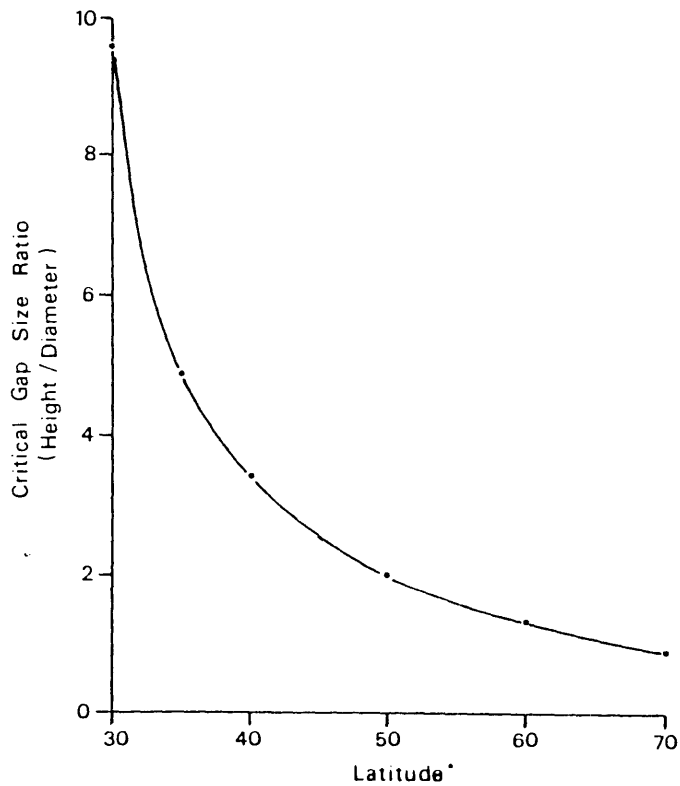


Figure 47. Plotted for various southern latitudes are the minimum sizes of idealized gaps which would allow direct sunlight to strike the gap floor.

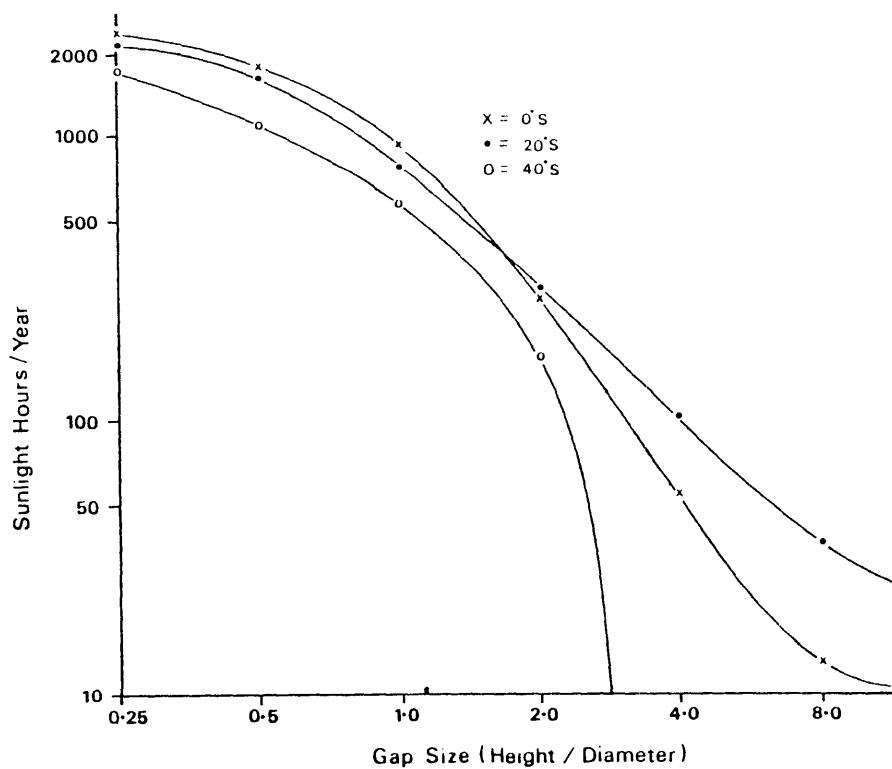


Figure 48. The maximum potential number of annual sunlight hours received on the floors of idealized gaps of various sizes, are plotted for latitudes 0, 20 and 40 degrees south (from G. Stocker and W. Taylor unpublished).

4.4 Forest disturbances - field observations

The range of recorded disturbance types and some notions of their frequency, extent and influence on the rainforests of this region were briefly discussed in Section 2.1.5. In the following parts of this Section, the effects of disturbance resulting from the death of a single tree due to competitive or ageing processes are compared with several disturbances of the catastrophic type.

4.4.1 Individual tree deaths

The dimensions of a gap created by the death of a tree due to the processes associated with competition or ageing, will largely be related to the size of the tree although individual species characteristics do play a role. For example, species with wood which decays rapidly in contact with the ground while the upper parts are relatively durable, will usually fall in one piece. Emergents also seem more likely to be wind-thrown because of the exposure of their upper limbs to wind, their weight and their characteristically high epiphyte loads. (While epiphytes have this role in the dynamics of the region's rainforests, they do not appear to be as important here as they are in the forests examined by Strong 1977.) Trees at lower canopy levels are more inclined to die and shed their parts while erect, for decay often proceeds according to part thickness (i.e. first leaves, then twigs, branches and finally the bole collapsing to the ground).

The differences between these two modes of death and decay are of great importance in determining the silvigenic process leading to the restoration of the structure of an assemblage. The toppling of a large tree usually causes the death of several other trees and the opening of a canopy gap. A range of new establishment sites is created and many species have the opportunity to seize the newly available resources (particularly light) by either vegetative means using advanced growth (e.g. existing seedlings or coppice shoots) or by germinating from seed.

The death of a single tree and its decay while standing usually results in minimal alteration to the structure of the assemblage. While some seedlings on the forest floor may gain temporary benefit from the additional light and other resources, the gap is often closed by saplings in the gap and adjoining individuals extending their crowns. In the temperate rainforests of South Africa, a survey of disturbance gaps by Geldenhuys and Maliepoard (1983) revealed that the average size of gaps formed in this way was less than half those created by the toppling of a live tree (151 compared with 342 m²).

In examining mortality data from the plot series (Table 9) it is tempting to assume that most of the deaths in the smaller size classes are the result of competitive interaction (i.e. resource starvation). However, the plots contained a number of species which have never been observed to grow into the larger size classes and thus some deaths in small size classes, as well as large, may be attributed to senility. For the reasons discussed above, the high tree mortality in the smaller size classes does not appear to have much effect on the remainder of the stand except for allowing the remaining trees to grow larger. In most of the sample plots, the creation of an effective regeneration gap would require the death of a tree larger than 30-40 cm dbh. Trees in this group die at a rate of roughly 1.5 (> 30 cm dbh) to 1 (> 40 cm dbh) ha⁻¹ annum⁻¹. Volck (1968) suggested that for stems over 29 cm dbh, 0.5% annual mortality (about 0.8 stems ha⁻¹ annum⁻¹) was a useful working figure for the rainforests of this region. However, most of Volck's data would have been derived from logged and silviculturally treated stands where one might expect fewer deaths from causes linked with senility and competitive displacement. Putz and Milton (1982) found that in old forest on Barro Colorado Island the annual mortality rate for stems above 19 cm dbh was 1%.

Although some attempts have been made (e.g. Lang and Knight 1983), problems of estimating gap size make it difficult to measure the rate of gap formation in tropical rainforests. The calculation of the disturbed area when a tree falls, seems to be rather more complicated for mature rainforests than for

temperate forests (Brokaw 1982) or for secondary rainforests (e.g. that examined by Lang and Knight 1983). The main difficulty appears to be the greater number of foliage layers usually found in mature rainforests. This problem became apparent when an attempt was made to delineate a series of gaps created by the toppling of a large tree of Aleurites moluccana (Figure 49). This tree, which was just outside the boundary of plot no. 11, was decayed at the butt, although it still had some living branches in its crown at the time it fell. In crashing to the ground it also knocked over a large tree of Toona australis and several smaller trees. In attempting to assess some characteristics of the canopy gaps created by this tree-fall, photographic and standard survey techniques similar to those discussed by Geldenhuys and Maliepoard (1983) were either unsatisfactory or difficult to use because of the presence of foliage of surviving trees at many different levels on the edge of the gap. The most satisfactory result was obtained by calculating the date on which the sun would be in a vertical position and at solar noon on that day plotting the extent of sunlight patches on the forest floor. It appears from Figure 49 that the area of holes may be rather smaller than the combined areas of crowns removed. The main holes are also well removed from the stump of the tree which caused this catastrophe. Immediately above this stump was a small hole just large enough for the bole when the tree was standing (Plates 15-19).

Observations of several other tree-falls in the surrounding forest suggested that the small gap above the stump was a reflection of the light tolerance status of A. moluccana. This is a "large gap" species and has a crown which is basically single layered. The toppling, about 100 m to the north, of a "small gap" species (Argyrodendron peralatum) of similar size, left a substantial gap above the stump. The latter species has a deep multilayered crown. It was also observed that each gap, or series of gaps, was often elongated in the direction of toppling. This can have an important influence at this latitude for the regeneration in gaps with a north-south orientation tended to behave as if the gaps were larger than those of equal size but of east-west orientation. "Large gap" weed species such as Dendrocnide moroides were

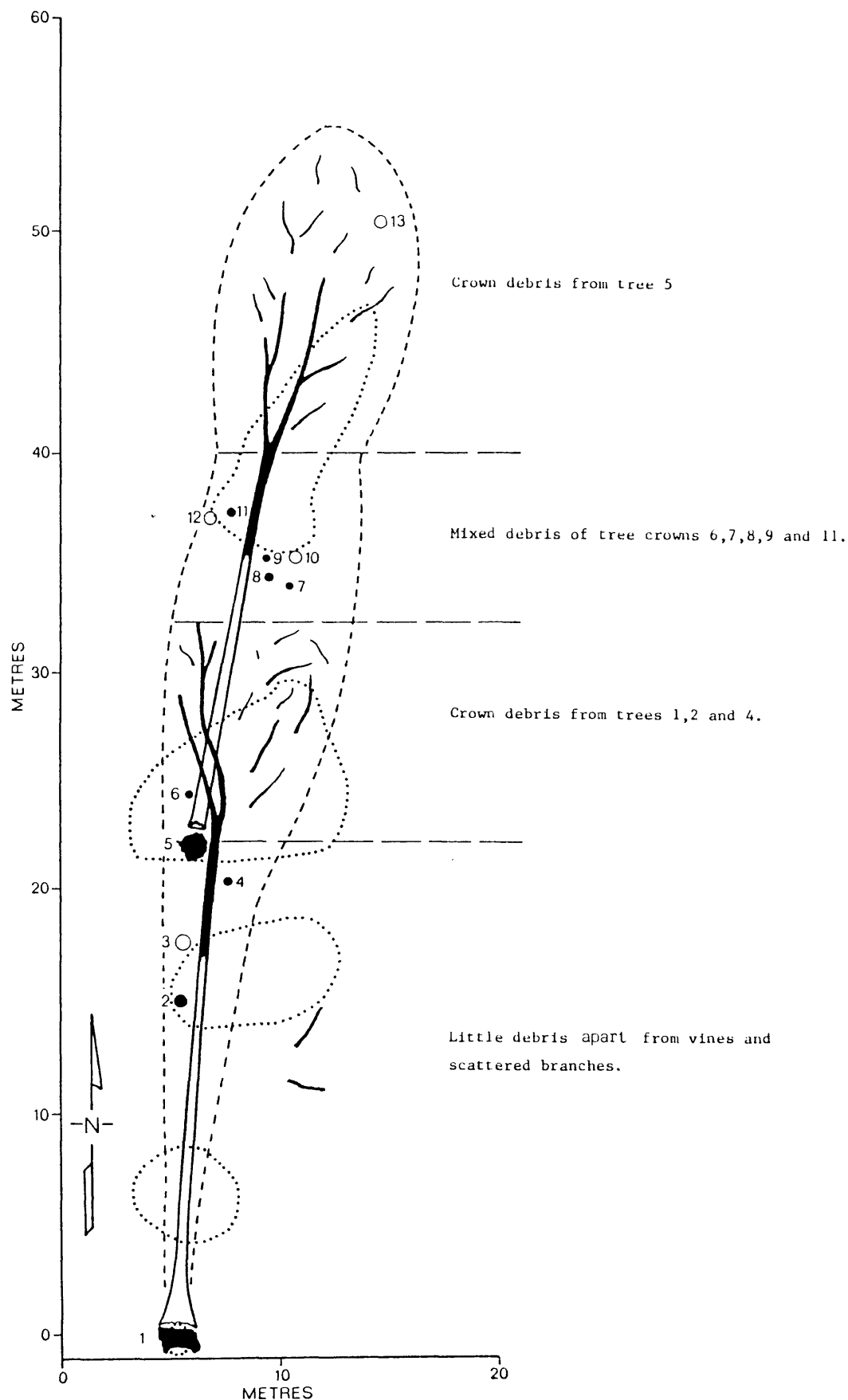


Figure 49. The area of ground disturbance (dashed line) and the projected area of the canopy gaps (dotted lines) created by the toppling of a large tree of *Aleurites moluccana* (no. 1), are shown. As this tree fell it carried with it a large tree of *Toona australis* (no. 5). While other trees in the vicinity had their crowns smashed (solid circles), some suffered only relatively minor damage (open circles).



Plate 15. The decayed butt of a large fallen Aleurites moluccana tree just outside plot 11. The following photographs illustrate some features of the canopy gap created by the toppling of this tree.

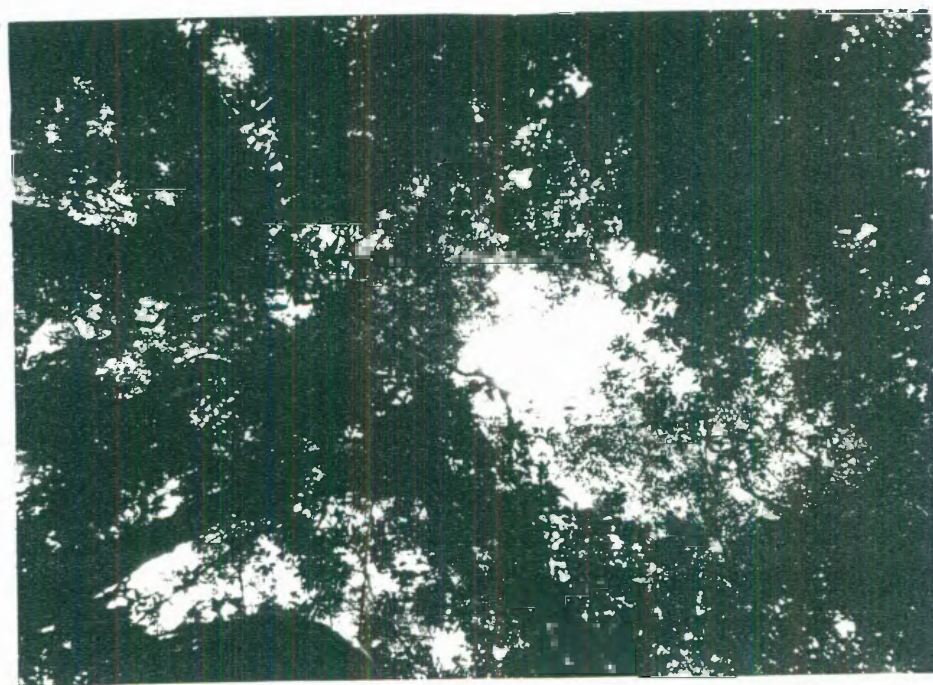


Plate 16. The small gap (about 1 m across) immediately above the stump of the fallen tree.

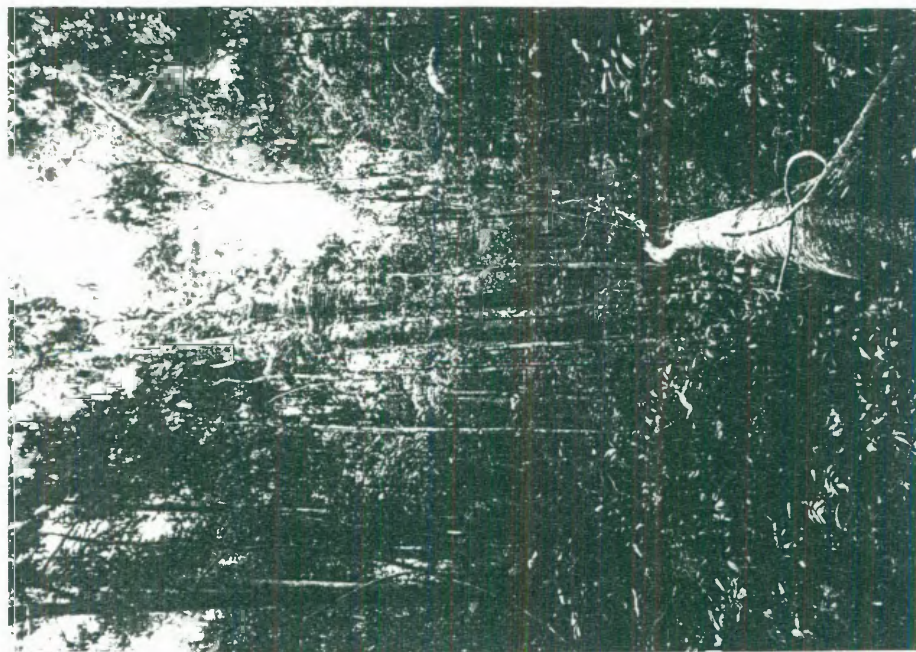


Plate 17. Looking along the log as it lay on the ground. Note the rather elongated, if discontinuous canopy gap created by the falling crown of the tree.



Plate 18. The smashed stump of a relatively large tree of Toona australis - one of the trees obliterated when its crown became entangled in that of the falling tree.



Plate 19. The resulting canopy gap.

certainly far more conspicuous in natural tree-fall gaps with a predominantly north-south orientation.

Overall this brief study revealed the highly variable nature of gap environments and the important role of chance in determining which species and individuals are able to benefit from the resources released. For instance while some surviving saplings suddenly received much more light, others in the vicinity appeared little better off than they were before the disturbance. Many others were smashed and some were buried beneath the crown debris from larger fallen trees. Some sites also became available for seed germination and seedling establishment. These sites also appeared to be quite variable in their light regimes (and related temperature and humidity characteristics) and substrate conditions (particularly litter type and depth).

4.4.2 Cyclone damage

The discussion in Section 2.1.5 suggested that wind damage to rainforests during cyclones could play an important role in their dynamics. Unfortunately there were no opportunities to examine in detail the effects of severe cyclone damage during the study period. However, some first hand impressions were gained from visits to the Darwin region after cyclone Tracey (Stocker 1976) and an examination of the vegetation on the Paluma Range after cyclone Althea (see Section 2.1.5 for general observations). From the viewpoint of forest dynamics, the most interesting feature of cyclone disturbance was the depth of branch and leaf material on the forest floor. Even though some trees had been toppled, little of the forest floor was exposed. Structural recovery appeared to come primarily from coppice on still standing stems and the growth of smaller trees which had escaped virtually unscathed. Regenerating "large gap" species were not conspicuous.

Further, more detailed observations of the effects of cyclones would be of great value to future studies of rainforest dynamics in this region.

4.4.3 Deaths attributed to Phytophthora cinnamomi

Phytophthora cinnamomi appears to have caused the death of patches of rainforest west of Mackay and Ingham (Anon. 1979). The debate as to whether its presence is the result of recent introductions or if it has been part of the native flora for a long time, has not been resolved. Shepherd (1975) proposed that P. cinnamomi entered north Australia with Malesian floristic elements during Pleistocene - Holocene times from the New Guinea/Celebes region. This hypothesis was based in part on rather meagre evidence that the Malesian component of the Australian flora is resistant to P. cinnamomi. Although the division of the region's flora in this way now seems rather suspect (Section 2.2.3) the conventional grouping of taxa shown in Table 33 reveals that many genera with strong Malesian affinities have also been found to contain susceptible species and perhaps claims by Newhook and Podger (1972) that this organism was transported to this continent during European settlement must be taken seriously.

Despite the controversy surrounding its origins, discussion on the effects of this organism has been included for it is obvious that even if it was not a factor in pre-European times, it is now present in virgin as well as modified rainforests. The problem was first noticed in 1975 and although patch deaths have now been recorded from many parts of the region, they only seem to be an important problem in the Eungella (near Mackay) and Oak Hills (near Ingham) areas in the southern part of the region. Investigations in the Eungella area by Brown and others (Anon. 1979) showed that patch deaths due to P. cinnamomi were confined to heavy clay soils and were often on the tops of broad ridges. Logged as well as virgin stands were affected. In some of the worst areas the extent of the visibly affected forest was reported to have almost doubled in the period December 1976 to August 1978 and while a series of transects which sampled 750 trees over 5 cm dbh in affected areas, did not produce quite such dramatic data (Figure 50), the illustrated trends must be cause for concern.

During a brief reconnaissance to the Eungella area, I

Table 33. The centre of origin and current distribution of genera of rainforest trees killed^a in north-east Queensland by Phytophthora cinnamomi.

<u>Genus</u>	<u>Possible centre of origin^b</u>	<u>Current distribution</u>
Ackama	Australia	Australia, New Zealand
Acronychia	c	Asia, Malesia, Australia
Cardwellia	Australia	Australia
Carnarvonia	Australia	Australia
Cinnamomum	c	East Asia to Australia, South America
Cryptocarya	c	Widespread ^d
Diospyros	c	Widespread
Elaeocarpus	Malesia/New Guinea	Old World
Flindersia	Australia/New Guinea	Australia, New Guinea
Melicope	c	India to Australia
Pilidiostigma	Australia	Australia
Planchonella	New Guinea/Australia	Widespread
Podocarpus (Sect. Podocarpus)	c	E. Asia, Southern Hemisphere
Sloanea	c	Widespread
Symplocos	S.E. Asia/Malesia/S.America	Widespread
Syzygium	S.E. Asia/Malesia/New Guinea	Widespread
	S. America	
Xanthophyllum	S.E. Asia/Malesia	India to Australia

a) from Brown (1976) and Table 34.

b) the localities given as possible centres of origin are in reality those where the genus is best represented at the present time. It is quite conceivable that the true centre of origin could be elsewhere. The data used have been taken from Balgooy (1971) and Willis and Airy Shaw (1973).

c) the current distribution of species in the genus provides no real clue as to its centre of origin.

d) the term "widespread" implies that the distribution of that genus is at least pantropic.

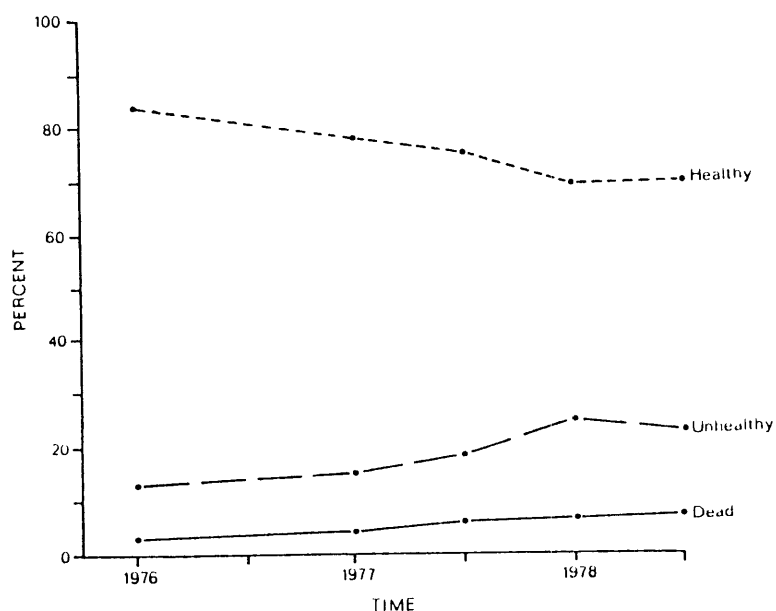


Figure 50. Trends in tree health and survival in a series of plots in areas infested by Phytophthora cinnamomi are shown. The total sample size was 750 trees all over 5 cm dbh. Based on data from Anon. (1975).

observed very little tree regeneration on badly affected sites. Where large groups of trees had died, the area supported a dense growth of sedges, mainly Gahnia spp. These will create a severe fire hazard during any future dry period. While there are some puzzling aspects of the origin and dispersal of this disease, observations associating dead patches with the wallows of wild pigs, have suggested that the latter may be a vector and although P. cinnamomi has been found in apparently healthy forest in this area, all positive isolations have been made close to or within infected areas (Anon. 1979).

By contrast the extent of forest disturbed by this disease in the Oak Hills area seemed more restricted and its effects more ephemeral. The following records were made when, in 1978, unexplained patch deaths commenced to occur in plot no. 6 of the series described in the previous Chapter. This plot was established during 1975 on the upper slope of a ridge which runs in a north-easterly direction. A normally dry gully crossed the plot from subplots I to L (Figure 51). At the time of establishment there was a small dead patch containing a large dead tree on a ridge a few metres to the south of the plot and it was assumed then that the death of these trees had been caused by lightning. The remaining forest seemed healthy and vigorous. During plot remeasurement in 1977 it was observed that patches of the understorey were starting to die and P. cinnamomi was isolated by B.N. Brown (pers. comm.) from affected areas. A decision was made to monitor the spread of this disease in the plot and notes on the extent of unhealthy and dead trees and shrubs were made during 1978, 1979 and 1981.

Areas marked 78 on Figure 51 were those first observed to be affected. An examination on the 22/2/78 indicated that deaths had probably commenced soon after plot establishment in 1975. Understorey recovery commenced in these areas during 1979 and by 1981 parts of these areas (especially those in subplot H) contained vigorous regeneration of understorey and tree species. The enclosed area in subplot L remained healthy throughout this period. The infected areas all seemed to be contiguous with a larger area on the slope below the plot.

Areas marked 79 were first observed to have been affected during that year. The canopy was open and the understorey generally dead. One large tree, a Flindersia brayleyana, and several smaller trees were either dead or dying. By 1981 the understorey had shown some signs of recovery. Vines, especially Calamus spp. and some "large gap" species such as the shrub, Dendrocnide moroides, were certainly very evident. Area 81 is a more recent extension of area 79.

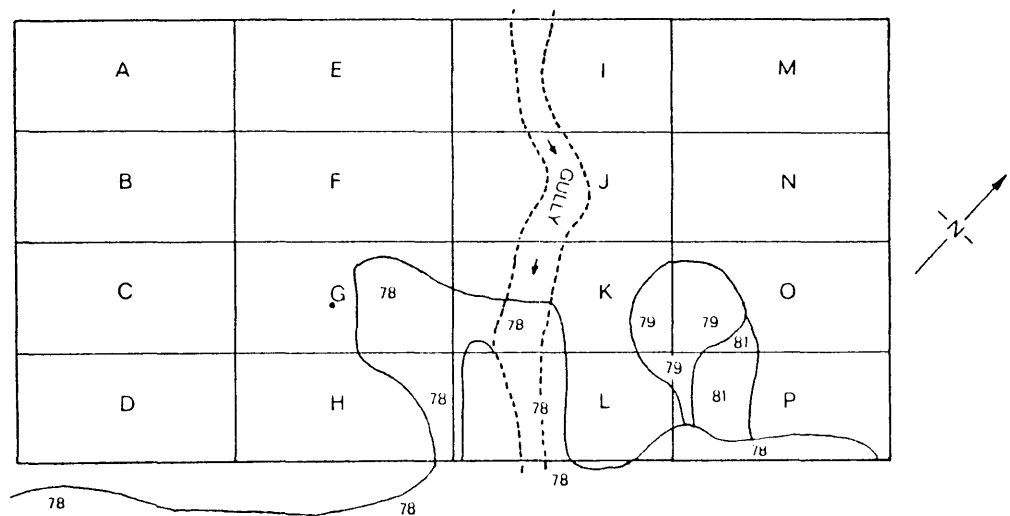


Figure 51. Plot 6 showing the subplot layout and the apparent extent of dieback due to Phytophthora cinnamomi.

Different tree species appeared to have different reactions to P. cinnamomi on this site (Table 34). For example, some such as Pullea stutzeri declined very slowly; others such as the Flindersia and Elaeocarpus spp. died quite quickly although they maintained relatively high diameter increment rates until shortly before their deaths; a few, such as Cryptocarya corrugata, did not appear to be affected and indeed some showed signs of benefiting by the additional resources freed from those competitors which were either ailing or dead.

The disturbance characteristics produced by this disease, were very variable and were probably dependent on a range of factors particularly stand floristics and soil physical characteristics. The initial impact appeared to be severe enough to remove, or at least facilitate the removal of rainforests from many sites at Eungella. At Oak Hills, it seemed that while some trees of all sizes died, the recovery of assemblage structure commenced within a few years of the initial attack. In both areas a secondary pulse of disturbance, the collapse of the dead spars, is still to occur. The main feature which distinguishes this disturbance type from the effects of cyclonic disturbance, is the widespread collapse of dead stems some time after the primary disturbance and the conspicuous "large gap" component among regenerating species.

4.4.4 Podocarpus neriifolius decline

In contrast to the widespread tree deaths caused by P. cinnamomi, the study described below is of the decline of a single species, Podocarpus neriifolius, in what appeared to be an otherwise unaffected block of rainforest on the McIlwraith Range north-east of Coen. This problem has not been observed in other parts of this species' range in north-east Queensland. However, a disease with some similar symptoms has affected two P. spp. in New Zealand (Anon. 1982).

P. neriifolius is a widely distributed rainforest conifer which is found in South East Asia from the east Himalayas,

Table 34. The survival and growth of trees over 10 cm dbh in areas of patch death within sample plot 6 - Oak Hills.

Species	dbh cm 1975	1977	Increment dbh cm 1979	1981
<i>Acronychia haplophylla</i>	14.7	0.1*	0.1	0
	21.0	dead*	-	-
	12.9	0.1	0.1*	dead
	14.9	0.1	dead*	-
	18.0	dead	-*	-
	21.9	0	0.1	0.1*
<i>Antidesma erostre</i>	11.6	0.1*	0.2	0.1
	11.8	0*	0.3	0
<i>Antirhea tenuiflora</i>	18.6	0.2*	0	0.2
	14.3	0.5*	0	0
	14.6	0	0.2*	0
<i>Apodytes brachystylis</i>	14.2	0.6*	0.7	0.4
	19.1	0.1	0.2	0
<i>Brackenridgea australiana</i>	12.1	0.1*	0	0.1
	14.8	0*	0	0
<i>Canarium muelleri</i>	34.1	0.2	0.1*	-0.1
<i>Cardwellia sublimis</i>	11.4	0.8	0.8*	0
<i>Carnarvonia aralifolia</i>	35.9	0.4	0.6	0.7*
<i>Cryptocarya corrugata</i>	23.6	0.6	0.5*	1.1
<i>C. mackinnoniana</i>	30.2	dead	-*	-
<i>Elaeocarpus arhemicus</i>	27.7	0.6	1.2*	dead
<i>E. angustifolius</i>	16.1	0.9	dead*	-
<i>Flindersia bourjotiana</i>	51.5	0.4	0.3*	dead
	14.1	0.6	0.7*	0.2
<i>F. brayleyana</i>	76.2	0.5	dead*	-
<i>Glochidion</i> sp.	21.5	1.0	1.4	1.8
<i>Kissodendron australianum</i>	18.1	0.1*	0.1	0
<i>Melicope fareana</i>	13.7	0.3*	0.2	-0.1
	10.1	dead*	-	-
	13.7	0.2	0.3	0.1*
<i>Pilidiostigma tropicum</i>	10.9	0.5	0.3*	dead
	20.9	0.5	0.3	0.3*
<i>Pullea stutzeri</i>	10.1	0.6*	0.4	0.2
	15.0	0.6*	0.4	0.2
	16.5	0.7*	0.6	0.4
	15.1	0.8*	0.4	0.4
<i>Sloanea macbrydei</i>	75.0	dead*	-	-
<i>Syzygium cormiflora</i>	16.1	0.6*	1.3	0.6
<i>S. johnsoni</i>	14.0	0.3*	0.3	0.1
<i>S. sp. (RFK 2511)</i>	11.0	0.1	0.4	0.8*
<i>Toechima lanceolatum</i>	15.4	0.5*	0.7	0.6
<i>Xanthophyllum octandrum</i>	13.1	dead*	-	-

*indicates first occasion on which deaths in the surrounding understorey became obvious.

through Burma, Malaya and the Andaman Islands to the East Indies, Fiji Islands and as far north as China (Dallimore and Jackson 1966). It is also found in north-east Australia where it is often a common species in lowland rainforests. Dead trees of this species had been observed in the McIlwraith Range area during 1972. However, because of the scattered occurrence of the species, mixed as it is with a wide variety of other rainforest trees, and the inaccessibility of the region, the number of large trees of this species which had been killed and the extent of the area affected, were not appreciated until a low level helicopter flight across the area during 1974. Ground visits in 1975, 1977, 1979 and 1981 to establish and maintain plot no. 10 (see previous Chapter) enabled further observations to be made. Reconnaissance of this area indicated that the only plant species visibly affected was P. neriifolius. While large dead trees were the most obvious, all size classes seemed to have been afflicted. Some of the dead trees had shed their bark and larger branches indicating that they had died several years previously. Others still held some foliage, often of coppice origin and usually chlorotic. A few appeared quite healthy.

When established, plot no. 10 contained six living trees over 10 cm dbh of this species. The subsequent diameter growth and survival of these individuals is shown in Table 35.

Table 35. The growth and survival of individual trees of Podocarpus neriifolius (> 10 cm dbh) in sample plot 10 - McIlwraith Range 1975-81.

Tree no.	dbh Sept 1975 (mm)	dbh increment (mm)		
		75-77	77-79	79-81
3/21	113	0	0	1
4/3	225	2*	1	0
8/20	121	dead	-	-
8/23	280	dead	-	-
9/30	263	2*	0	-1
15/5	313	-4	0	0

*Noticed as nearly dead at time of the 1977 measure.

In order to supplement the data from the plot, two transects each 400 x 10 m, were established in 1977. One extended north from the reference plot; the other to the east. On these transects observations were made of the diameter and health status of all individuals of P. neriifolius encountered. The following health states were recognized for those individuals over 1.3 m high :-

- a) healthy - complete green crown, normal stem form;
- b) necrotic - growing shoot dead and/or death of part of the crown, stem malformation or general discolouration of leaf tissues;
- c) near dead - advanced state of (b) often few green leaves remaining, crown very thin;
- d) recently dead - small branches, twigs and bark attached (estimated to have died within the last two years);
- e) long dead - dead stag without small branches or twigs, bark usually shed or shedding (estimated to have died 2-5 years ago).

Smaller individuals were described as either healthy, necrotic or dead.

Reassessments were made in 1979 and 1981. At the time of the first measurement about half of the larger (> 5 cm dbh) trees were described as long dead (Figure 52). All trees of this size which were described as necrotic in 1977 looked healthier in 1979 and even better in 1981. Some deaths did, however, continue in the 0-5 cm dbh size class during the period 1979-81. However, there was some active recruitment into this class during this period and it is thought that these deaths may be due to normal interspecific competition in the forest. The rate of decline of this species seems to have peaked about 1977.

The pattern of health in the seedlings (< 1.3 m high) is more difficult to interpret for the counts were often inconsistent mainly due to an inability to find small

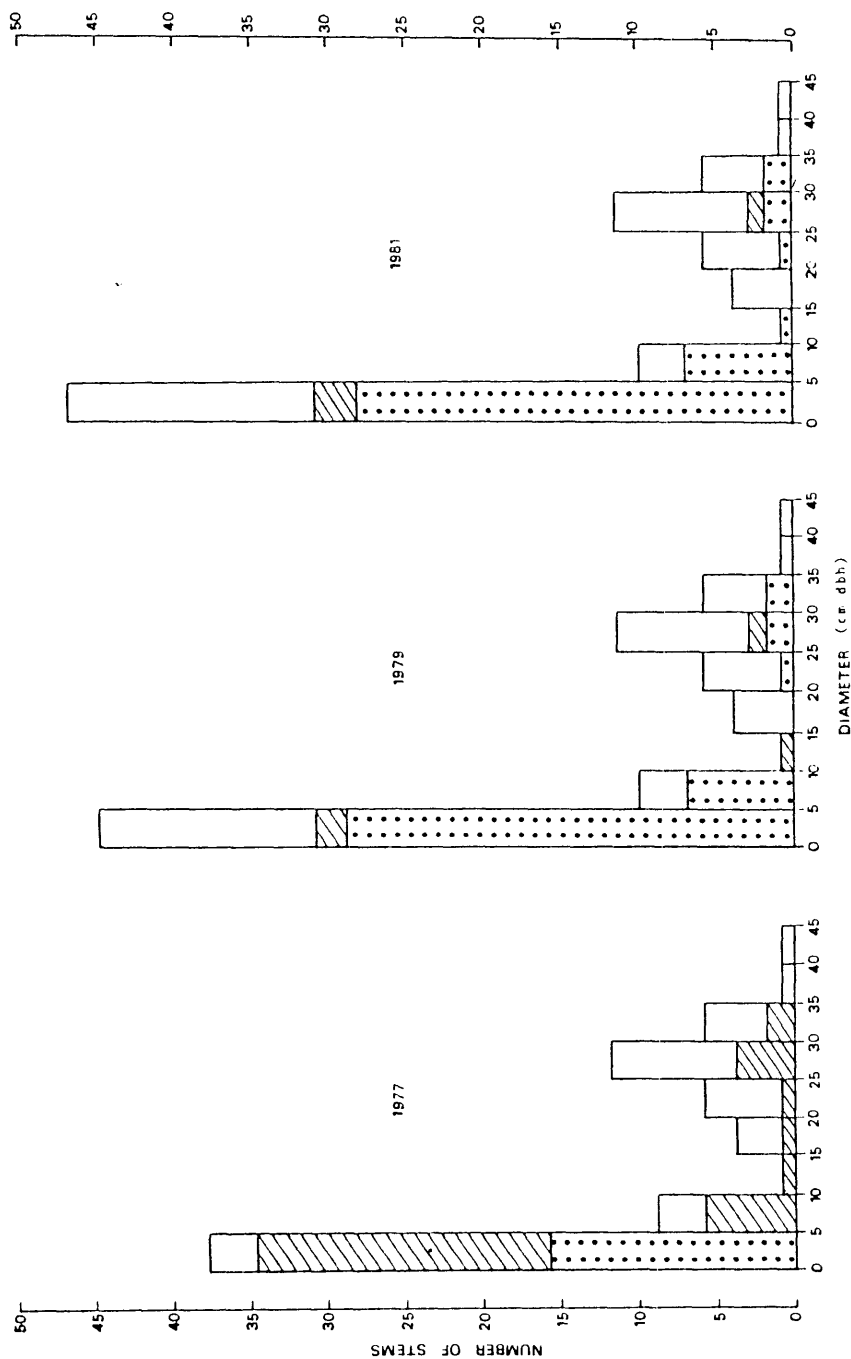


Figure 52. The three histograms illustrate the changing health status of *Podocarpus neriifolius* trees of various sizes along transects in the McIlwraith Range. The open bars show the number of dead trees, the bars with oblique lines the number of unhealthy trees and the dotted bars the number of healthy trees.

seedlings that had died and to distinguish the few which had grown from seed since the last observation. It can be observed, however, that in 1977 10% were classed as unhealthy. In later records, seedlings of this size class were observed to be either healthy or missing, presumed dead.

Still living trees accounted for 1.8% of the basal area of plot no. 10 in 1975. By 1979 the representation had fallen to 1.2%. More may die but the overall impression was that the health of the survivors had considerably improved. The transect data suggested about half the deaths of larger trees had occurred before 1975. Thus the original representation of P. neriifolius in the sample plot (where only living trees were recorded) may have been 2-3% of the total basal area. Despite the difficulties of reconnaissance, the data obtained from the transects and plot seemed typical of the affected area.

The cause of this decline remains a mystery. Examination of foliage, bark and wood yielded no useful information. W. Heather (pers. comm.) isolated a Verticillium sp. from soil surrounding roots of affected seedlings but since this species is a conifer and Verticillium generally affects only angiosperms (it acts by moving through the vessels of the current year's sapwood) it was unlikely to be the primary pathogen. Unfortunately further pathological tests could not be carried out.

The possibility that drought or excessive rain was responsible, appeared unlikely. However, the region is so remote that there are no rainfall stations from which useful data could be gathered. Drought, at least, seemed doubtful for in 1977 healthy trees of this species were observed in the dry semi-deciduous rainforest in the rain shadow area on the western slopes of the range.

From the point of view of forest dynamics, the disturbance had some unusual features for all size classes of a single species were affected. Larger trees seem to have died or lost the greater part of their foliage over a number of years. Distinct phases in the disturbance process were again identified. As trees died they gradually lost leaves, limbs

and bark. Healthy crowns of this species are relatively dense and the gaps created by the death of larger trees would have enabled many plants in the immediate vicinity to respond to additional available resources. The second phase of disturbance (caused by the rotting of the base of the dead spars and their fall) was frequently noted during the 1981 visit. Although some regeneration may be damaged by the falling stem or smothered under debris, the primary gap was generally enlarged and the amount of light available to species in the lower canopy increased. The size and shape of the secondary gap was observed to depend very much on the size of the dead spar and the degree of interlinking by vines of the spar with surrounding crowns.

These examples of different disturbances illustrate some variables of apparent significance in rainforest dynamics. Small disturbance patches caused by tree deaths due to senility and competitive displacement are a continuing feature of rainforests. The spatial and temporal arrangement of these patches largely depends on some characteristics of the component species. Catastrophic events vary greatly in their impact. They may be selective in their effects on species, disadvantaging one to many and occasionally favouring a few. Cyclones, perhaps the most widespread and frequent of the catastrophic disturbances influencing the rainforests of this region, may not cause the sudden change in floristics which, at first sight, might be expected. However, they may exert some overall influence in areas where they are particularly frequent (see Section 3.3.1) and the presence of "cyclone scrubs" indicates that there are limits to disturbance frequency and/or severity beyond which rainforests lose their basic structural and floristic features.

Although it appears that an understanding of the mechanisms controlling regeneration in small gaps will explain many aspects of the structure and floristics of rainforests, the relevance of the various theories so far proposed needs to be examined by seedling establishment experiments in the field and glasshouse. However, before field studies can be carried out, ways of quantifying what appears to be the most important of gap environmental variables, PAR, need to be devised.

4.5 Light measurement in gaps

Although it has long been known that light is essential for the growth of green plants, the measurement of available light is beset with many difficulties (M. Anderson 1966). This is particularly so if it is desired to measure the amount of light available to plants on the forest floor where the temporal and spatial variation is such that adequate replication and long periods of integrated measurements are highly desirable. However, recent advances in technology have considerably reduced the size and power requirement, as well as improving the ruggedness and accuracy, of many of the instruments available for direct measurements in the field. In undertaking this study a number of potentially useful techniques were examined. The most promising appeared to be either direct integrated sensing or an indirect method based on vertical canopy photographs (M. Anderson 1966; Jupp *et al.* 1980). After some experimentation the latter method was abandoned due to rapid and largely unpredictable changes in the structure of the rainforest canopy and an inability to measure the direct and diffuse radiation components above the canopy because of the absence of a tower or large clearing close to the experiment site. As currently available commercial instruments were too costly to replicate adequately and not appropriately designed for continuous use in a rainforest environment, the simple device described below was developed. Its low cost (in 1980 about A\$7/unit) and reliability suggest that it may, with little modification, have wide application for providing integrated light measurements.

In designing the device, it was considered that the ideal light integrator for studies of the growth of seedlings on the forest floor should have the following characteristics :-

a) capacity to provide linear integration of PAR within a wide range ($0-2000 \mu\text{E m}^{-2} \text{ sec}^{-1}$) for periods of at least two weeks;

b) built-in cosine correction;

c) the integration characteristics should be unaffected by temperature change or the passage of time;

d) the device should be robust enough to operate reliably in a tropical environment and be independent of external power supplies;

e) the unit cost should be low enough to allow adequate replication to sample the wide variation in the light environment on the forest floor.

The device developed is based on silicon photodiodes to generate a current which is stored in a microcoulometer. A circuit diagram and sketch of the device are shown in Figure 53.

Initially, 18 mm soda glass rimless test tubes were used for the body of the device but it was found that irregularities in the curved closed end produced a lensing effect on the incoming light. This problem was largely overcome by having tubes specially blown and the inside of each hemisphere sand-blasted so that it would act as a diffuser.

The photodiodes (Philips BPX41) measured approximately 4.5x2.2 mm. They were mounted with silicon sealant at the centre of the upper surface of a disc (18 mm diameter) of encapsulating material (Dow Corning 9161). The disc was cut from a 10 mm thick sheet of this material with a wad punch. A 5 ohm resistor was inserted into the centre of the disc and its leads were soldered to the lead wires of the photodiode so that they were in parallel. An insulated copper wire, a little longer than the tube, was also soldered to each of the leads. A miniature two-pin plug and a 1000 ohm resistor were attached to the other ends. The microcoulometer (Plessey 560-0002) was mounted on a two-pin socket compatible with the plug used above.

The device was assembled by pushing the disc with the photodiode uppermost, into the tube until it reached the base of the hemisphere. The disc was then held in place with silicon sealant. After checking that the microcoulometer was at zero, it was attached and pushed into the tube which was

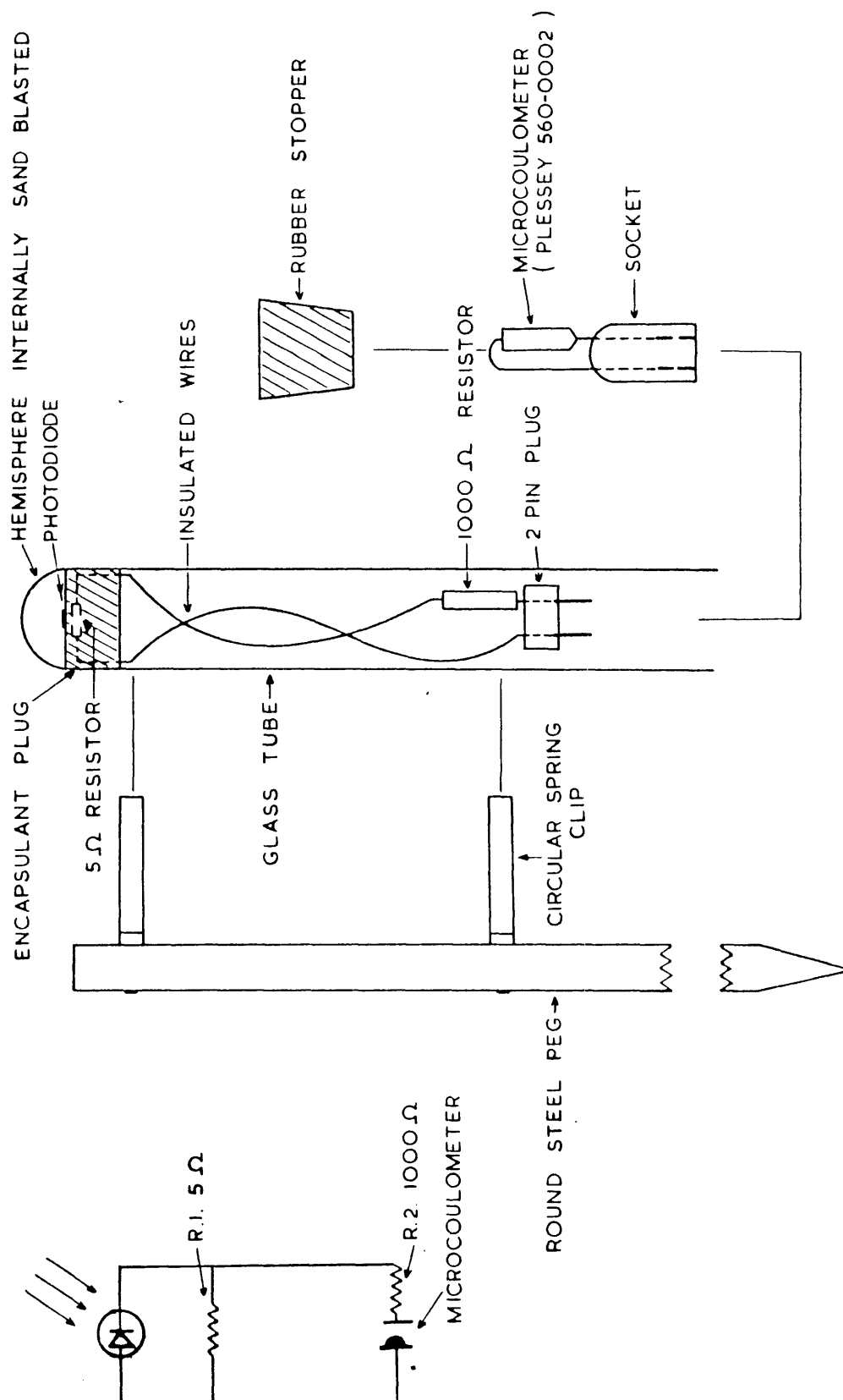


Figure 53. A circuit diagram and a sketch of the simple light integrator designed to characterize the light environments of treatments in seedling establishment and growth trials.

sealed with a rubber stopper. In the field, the device was held in place by two spring clips attached to a 6 mm diameter iron spike driven into the ground.

The microcoulometer was read with a Plessey Electro-products E-cell digital readout device, model EDR500. Simpler readout devices can be easily constructed but have not been so easy to use. The EDR500 also incorporated a circuit for testing this type of microcoulometer.

There proved to be approximately 10% variation in the output of these sensors. The main sources of this variation appeared to be differences in the light collecting areas of the photodiodes, irregularities in the glass hemispheres and variations from the nominal values of the resistors. Calibration by means of a variable resistor at R2 would make the device somewhat easier to use. Samples of these devices were tested against a LI-170 Li-Cor Quantum sensor. The effect of the angle of incidence of radiation was examined by allowing the sun rays to impinge the sensory surfaces of both instruments at various known angles of incidence (Figure 54).

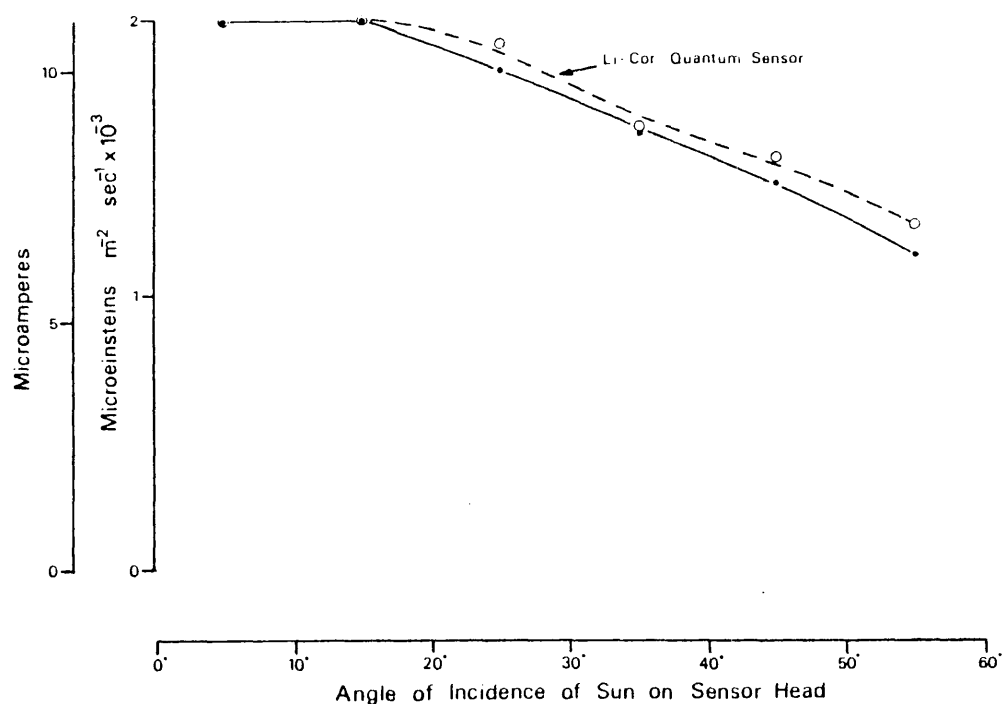


Figure 54. Comparison of the outputs with various angles of incident radiation from the integrating solarimeter described in the text and a commercial instrument (Li-Cor LI-170).

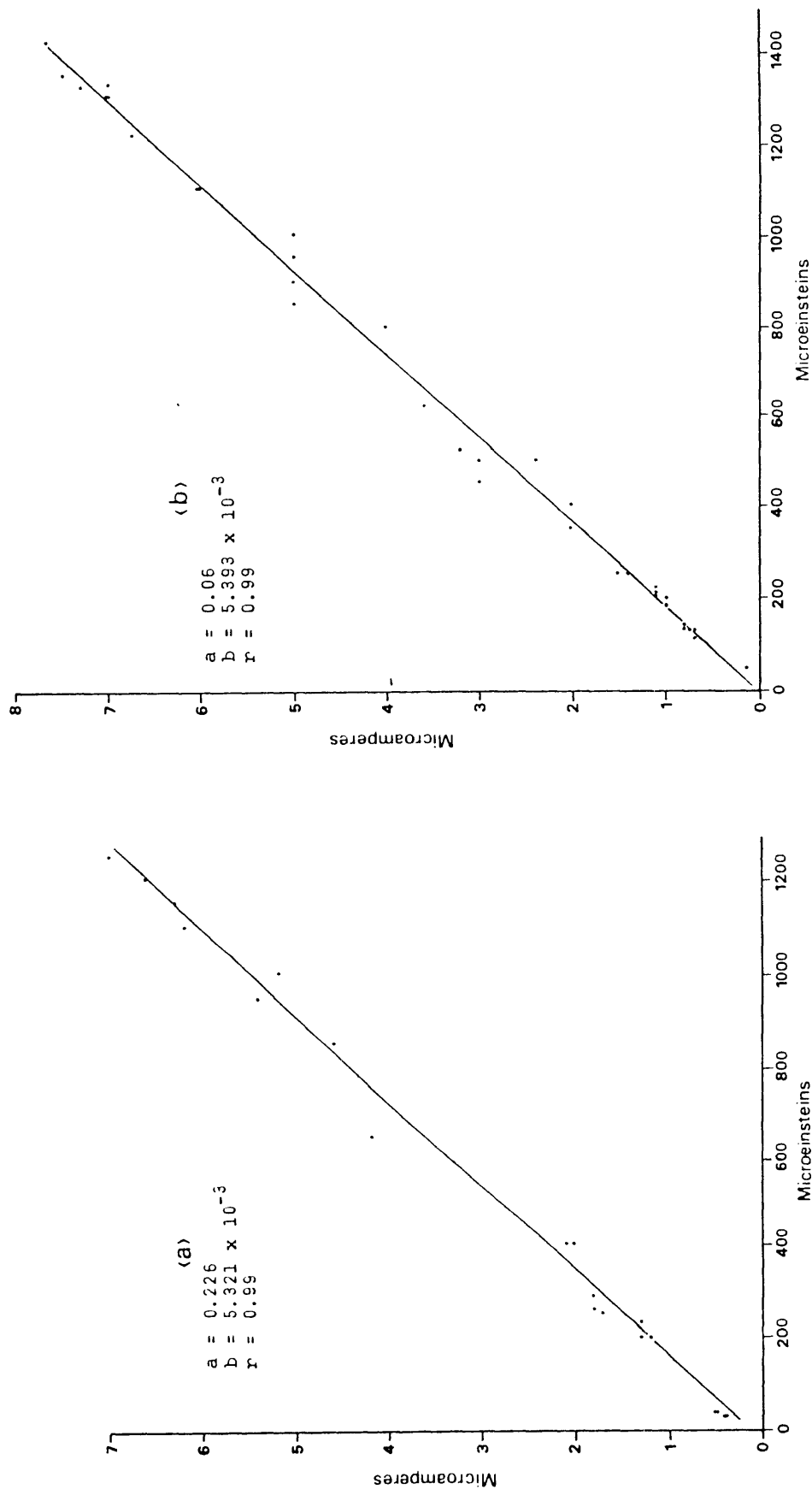


Figure 55. The outputs of the solarimeter described in the text are compared with a Li-Cor quantum sensor. The readings were taken in rainforest around noon using small gaps and sunflecks to provide a range of light intensities. In a) the sky was clear. In b) scattered cumulus clouds periodically obscured the sun and a proportion of the readings were taken during these intervals.

It was observed that usually readings for both instruments were either high or low. Intermediate readings were difficult to obtain except at gap edges. Here light intensities tended to change rapidly and much of the spread which is apparent in the mid sections of the graphs appeared due to the physical difficulty of reading both instruments simultaneously.

The calibration of the devices to enable their output to be converted to $\mu\text{E m}^{-2} \text{ sec}^{-1}$ (Figure 55) was carried out using gaps and sunflecks on the forest floor to provide a range of light environments which could be simultaneously monitored with both instruments. It is interesting to note that the relationship is almost linear and thus it can be concluded that in this particular environment, the high response to radiation in the 0.7-1.0 micron range by the silicon photodiode used, was not of great consequence.

The near linear response at low light levels was rather unexpected for Bjorkman and Ludlow (1972) had found, in a southern Queensland rainforest, that while the quantum flux on the forest floor was only 0.15% of that above the canopy, the total radiant energy flux on the forest floor was 2.3% of that above. This observation suggested that transmitted and reflected radiation makes up a considerable component of the total radiant energy flux reaching the forest floor. Assuming that the measurements of Bjorkman and Ludlow were accurate, there are several possible explanations for the results recorded here :-

a) the response of the instrument described here was distorted at very low light levels;

b) the conditions under which Bjorkman and Ludlow (1972) made their measurements were not comparable with those experienced during this study.

In the absence of a high precision, standard light measuring device the first hypothesis could not be tested. However, the manufacturer's specifications for the photodiode used, suggested that a response distortion was an unlikely cause. It is possible that aspects of the environment, particularly that a lower mean sun angle (Bjorkman and Ludlow's experiments were at 27° south latitude) may have increased the amount of reflected radiation or that thinner canopy leaves (perhaps from deciduous species) provided a high transmitted component to the total radiation flux observed on the forest floor at Bjorkman and Ludlow's study site.

While the above problem is almost totally irrelevant to the interpretation of the data relating to the survival and growth of seedlings in the field (next Section), the composition of the light within these forests should be examined more closely with a spectrophotometer. If, for some other purpose, more precise readings were required, the integrator described here could be modified to conform more closely to the PAR spectrum by the addition of appropriate absorption or interference filters (Woodward and Yaqub 1979; Woodward 1983) and the use of blue silicon photocells (Fitter et al. 1980). This would, however, increase their cost and complexity substantially.

The integrators described above were used in the field for 3 years and proved very reliable. It did, however, seem advisable to test the microcoulometers every 12 months and replace them if their response was not in accordance with their specifications.

4.6 Seedling establishment and growth in gaps

The series of three trials described below was established to determine the effects of gap characteristics, especially the light environment, on the survival and growth of selected tree species. They were established during January of the years 1979, 80 and 81. The species chosen were widespread species with a range of shade tolerances and a readily available supply of fresh seed of good quality. The trials were established in an easily accessible area of upland rainforest 25 km south of Atherton. The altitude of the site was about 1000 m and the red clayey soils appeared to be derived from rhyolitic rocks. Despite reports by local loggers that this area had been selectively logged on several occasions over the past 50 years, the upper canopy level was fairly regular and about 30 m high. The current logging cycle began in the area during 1977 and continued through the study period. Each trial was established in an area which had been selectively logged a few months previously and although forest logged in this way has some artificial features (these are discussed below), its use was the only feasible way of obtaining a variety of gap environments in a reasonably compact area.

After an initial reconnaissance of a freshly logged area, I decided to use 3 distinct logged forest conditions (Plates 20-22) to provide a range of light regimes on the forest floor. These were :-

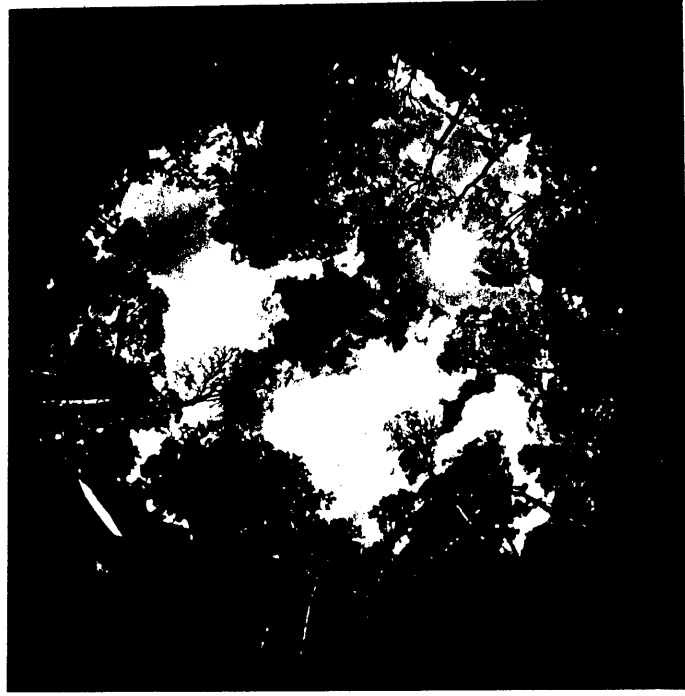
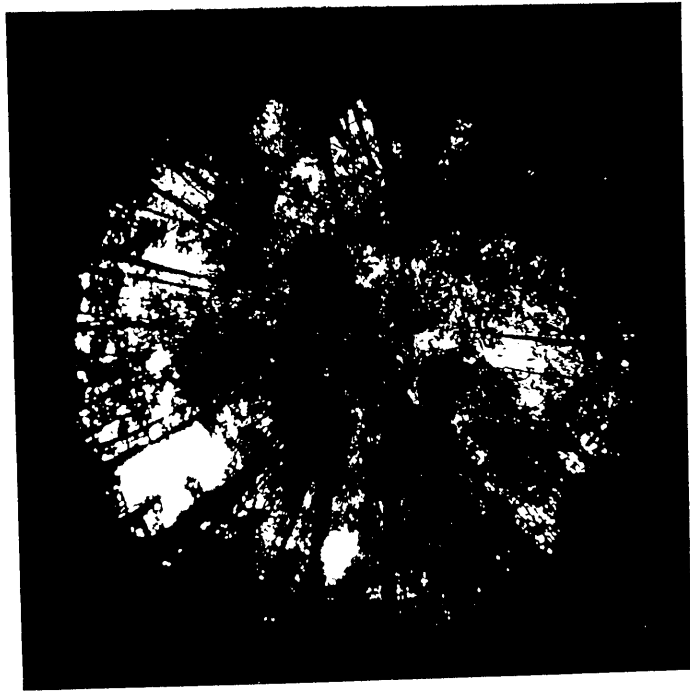
a) undisturbed patches - present as small islands through the selectively logged area.

b) patches where the upper canopy was partially removed, there had been heavy mid and lower canopy disruption and a variable degree of ground disturbance. The gap height : diameter ratios of these sites were estimated to be between 5:1 and 4:1.

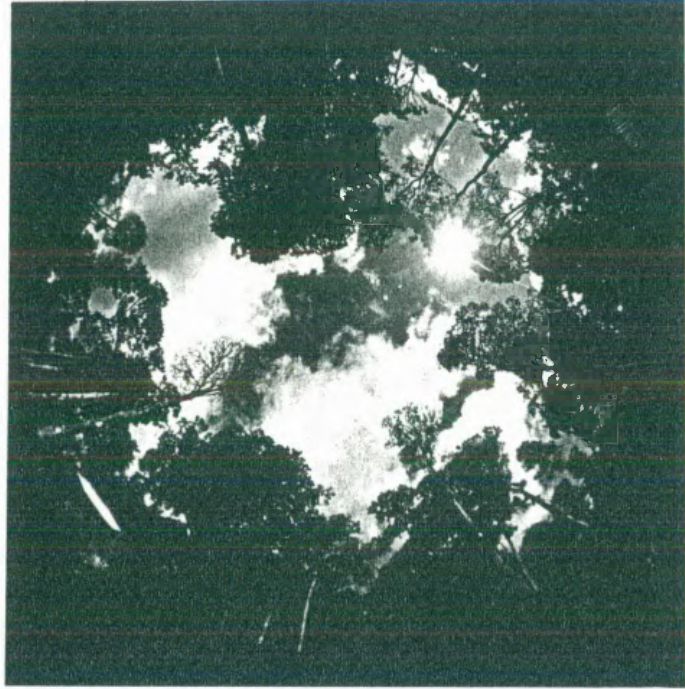
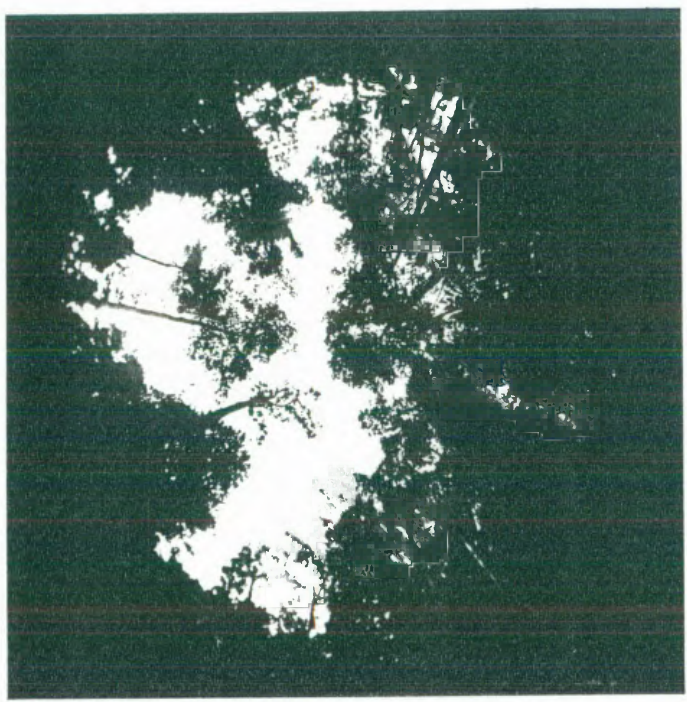
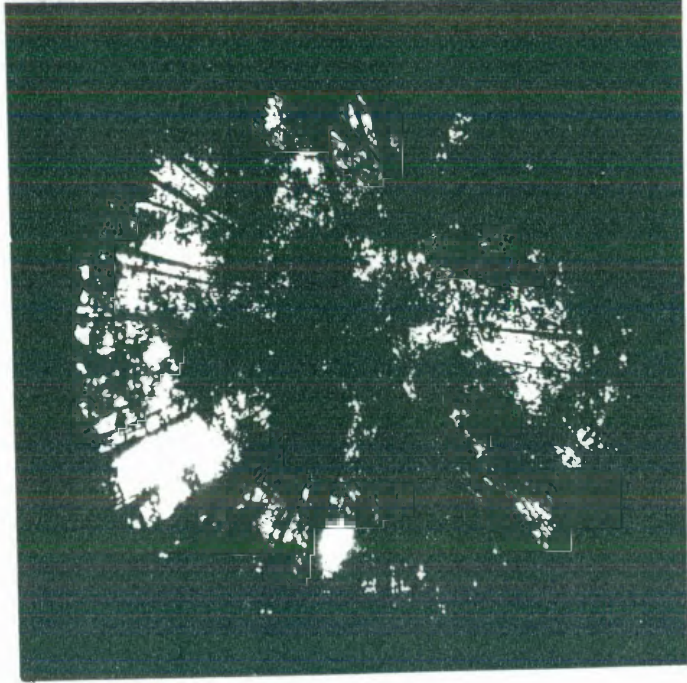
c) patches where full canopy removal with a moderate degree of ground disturbance had occurred. The gap height : diameter ratios were estimated to be between 3:1 and 2:1.

The first undisturbed treatment site was located near the centre of one of the intact patches. From this starting point sites for the second and third treatments were then located at the nearest point where the conditions outlined in b. and c. above, prevailed. This process was repeated to provide 4 replicates for the trial established in 1979 and 8 for those in the following two years. The seeds of species chosen for each trial were placed on the surface of the soil in equal sectors of a 1 x 1 m quadrat. They were protected from predation by rats and disturbance from litter-scratching birds (mainly Megapods) by a galvanized wire mesh cover (Plate 23). This was removed 6-12 months after the seeds had germinated. One of the light integrators, described in the previous Section, was positioned above each of the protective covers and read fortnightly. They were usually removed late one afternoon; read, cleaned and checked that night and returned early the following morning. The light readings were stopped after 12 months for by then it was no longer feasible to keep the sensors above the rapidly growing vegetation at the more open sites and it was felt that the light environment at each site was adequately characterized (Table 36).

In the first trial the species used were Darlingia



Plates 20, 21 & 22. These vertical 180 degree photographs illustrate typical canopy conditions (no disturbance, small gap, large gap) used in the seedling establishment and growth experiments.



There are many trees in the forest and a large number of them are very old. The trees are very tall and have many leaves. The forest is very green and the air is very fresh. The forest is very beautiful and I like to go there very much.

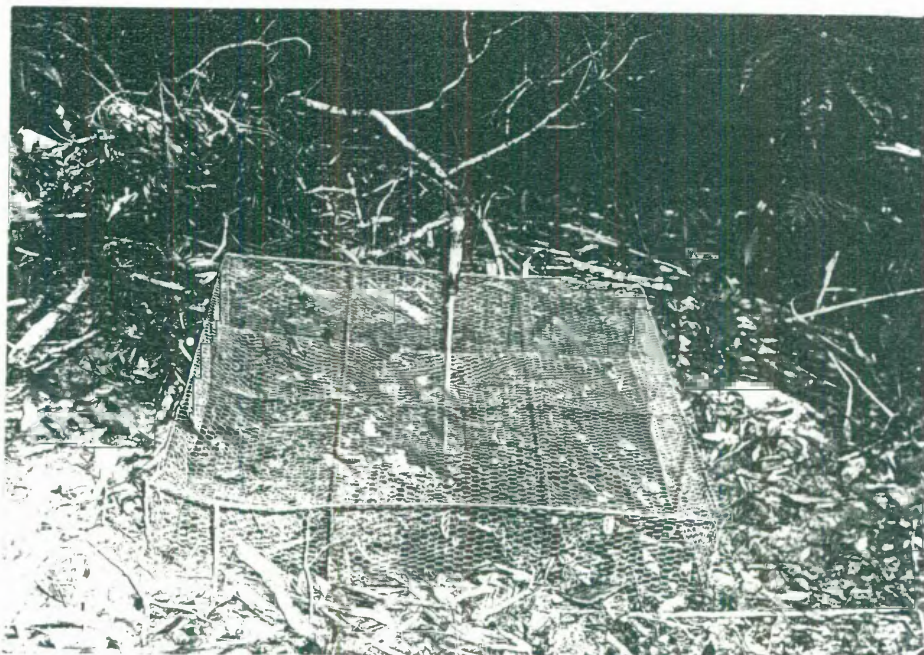


Plate 23. The 1 x 1 m protective cover used to prevent small mammals eating seeds in the seedling establishment and growth experiments. The light integrator can be seen mounted on a stake protruding from the centre of the cover.



Plate 24. Seedlings of Darlingia darlingiana after 4 years persistence under an intact canopy. It was by then the only surviving species in this treatment of the first seedling establishment and growth trial.



Plate 25. Seedlings of Darlingia darlingiana, 4 years old and a little over 1 m high in a small gap environment. The only other species to grow in this gap environment was Toona australis.

Plate 26. Seedlings of Acacia aulacocarpa and Alphitonia petriei 4 years old and about 6 m high in a large gap environment. Also growing in this gap are seedlings of Toona australis (3 m high) and Darlingia darlingiana (0.4 m high).

darlingiana, Acacia aulacocarpa, Toona australis and Alphitonia petriei. After 4 years the differences in mean height (Table 37) and survival (Figure 56) among the species were considerable. While gathering the height data it was observed that many seedlings were being shaded by other seedlings and therefore they were not receiving the measured PAR. Consequently in the regression analysis (Figure 57) only the heights of the tallest individual of each species in each plot were compared with the recorded PAR environment of that plot. Even so, it was necessary to ignore some values derived from individuals shaded by taller individuals of other species (Figure 57). The species with the most variable height growth rate was T. australis (Table 37). This was probably because its seedlings are initially very small and easily overshadowed if not obtaining get a head start. Unfortunately there were only sufficient data to calculate regressions for D. darlingiana and T. australis. Nevertheless the high growth rates for A. petriei and A. aulacocarpa in large gaps and their inability to survive in small gaps, are evident in Figures 56 and 57.

The results for D. darlingiana were somewhat unexpected for this species had given the impression of being a "large gap" species for it was often observed on roadsides. However, its performance in this trial suggested that it was relatively slow growing and shade tolerant. Its presence on road verges in rainforest areas may be due to some other characteristic such as an ability to establish in grass. The survival and early growth of T. australis appeared to be adversely affected by very low light and a continuous litter layer on the forest floor (damping off seemed to be an important problem). Loose mineral soil provided the best substrate for its establishment. The period of viability of seeds in the field for both D. darlingiana and T. australis only seemed to be for a few weeks. The other two species used in this trial, A. aulacocarpa and A. petriei, have small hard seeds which appeared to be able to remain dormant in the soil for much longer. Both seemed typical "large gap" tree species and only established and grew under high light conditions. Given a favourable environment they did, however, grow very quickly. In contrast D. darlingiana seemed incapable of very high

Table 36. Average PAR received in each treatment during the first year of the field establishment and growth trials
($\mu\text{E m}^{-2} \times 10^{-6}$)(1 standard deviation).

<u>Canopy treatment</u>	<u>Trial</u>		
	<u>1</u>	<u>2</u>	<u>3</u>
Intact	68(88)	17(25)	27(13)
Small gaps	896(392)	340(207)	1228(544)
Large gaps	4352(771)	1889(466)	2552(549)

Table 37. Mean heights (m) of survivors in the field species establishment and growth trials (as at February 1983).

Trial 1 - 4 years after establishment

Species	Intact	<u>Canopy treatment</u>	
		Small gap	Large gap
Darlingia darlingiana	0.2(0.1)	0.8(0.5)	0.4(0.4)
Toona australis	f	1.1(0.5)	3.1(2.0)
Alphitonia petriei	f	f	6.5(0)
Acacia aulacocarpa	f	f	6.3(0.7)

Trial 2 - 3 years after establishment

Species	Intact	<u>Canopy treatment</u>	
		Small gap	Large gap
Flindersia brayleyana	0.07(0.03)	0.4(0.2)	0.6(0)
Cardwellia sublimis	0.2(0.1)	0.4(0.05)	f
Argyrodendron polyandrum	0.05(0)	0.1(0.1)	0.05(0)
Toona australis	f	0.4(0.3)	1.2(0.1)

Trial 3 - 2 years after establishment

Species	Intact	<u>Canopy treatment</u>	
		Small gap	Large gap
Agathis robusta	0.06(0.01)	0.18(0.08)	0.18(0.06)
Argyrodendron peralatum	0.08(0.02)	0.17(0.07)	0.1(0.05)
Cryptocarya angulata	0.12(0.04)	0.19(0.04)	0.55(0)
Syzygium sp. (RFK 1891)	0.09(0.04)	0.51(0.30)	f
Toona australis	0.05(0)	0.59(0.34)	0.74(0.64)

f = failed to establish in any replication of that treatment.

(standard deviation)

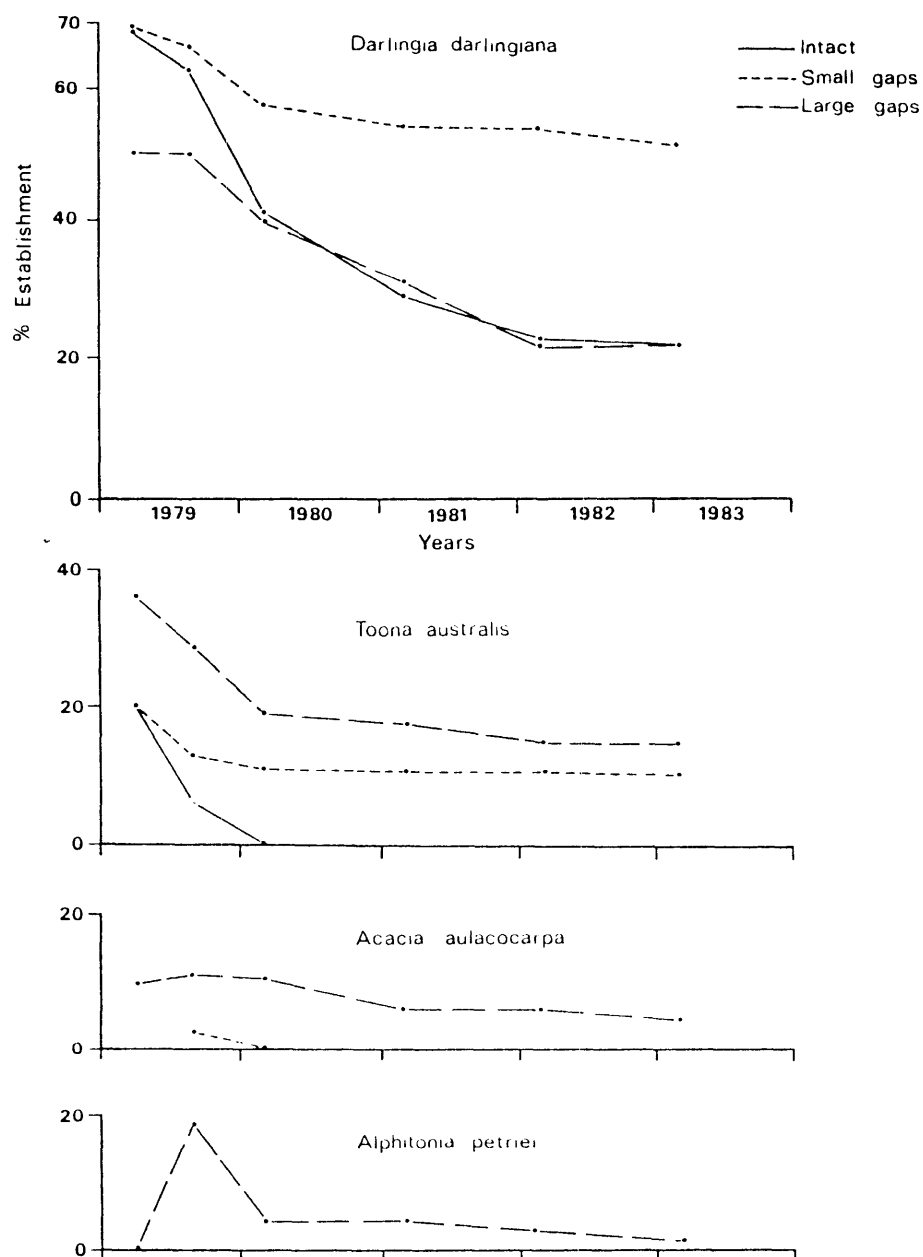


Figure 56. Progressive establishment percentages are shown for the species sown in the first seedling establishment and growth trial.

Table 38. Dry weights (g m^{-2}) of grasses, sedges and herbs competing with tree seedlings in the first field establishment and growth trial - six months after establishment.

Canopy treatment	Mean (standard deviation)
Intact	0.30(0.42)
Small gap	4.41(3.13)
Large gap	111.46(68.56)

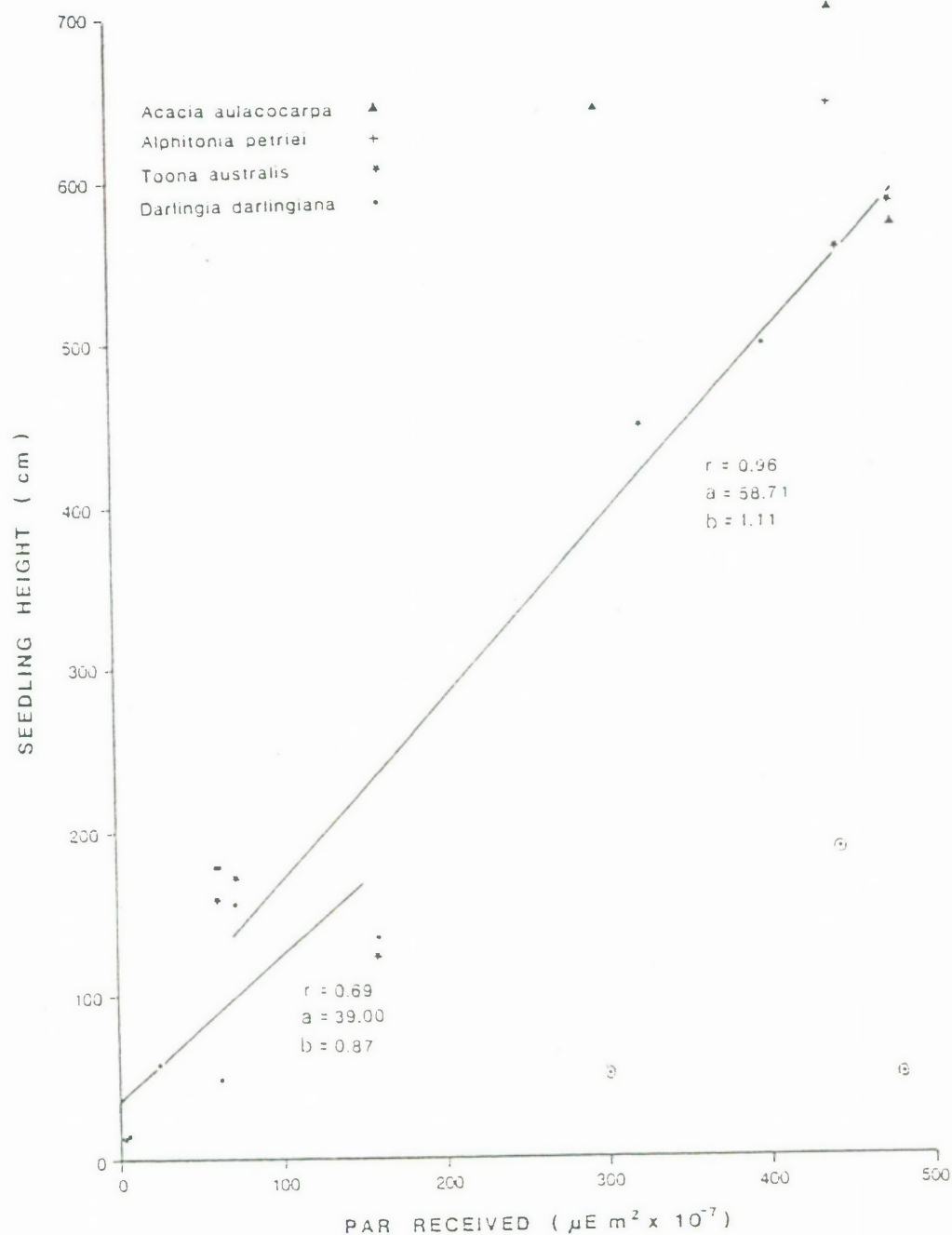


Figure 57. Relationships between height at age four years of the tallest individuals of Darlingia darlingiana and Toona australis in each plot and PAR received by the tallest individuals in that plot during the first year, are illustrated. Similar data for Acacia aulacocarpa and Alphitonia petriei are shown but are too few to establish meaningful regressions.

Circled values were derived from individuals overtopped by seedlings of other species or weeds. They were not used in the regression calculations.

growth rates, although it did show more rapid height growth in openings.

In the trial described above, competition from herbaceous weeds was particularly severe on the more open sites during the first six months (Table 38) and it was apparent that the best places for initial tree seedling establishment, if not growth, were in the smaller gaps.

In the second trial the species used were Flindersia brayleyana, Cardwellia sublimis, Argyrodendron polyandrum and Toona australis. The initial establishment in this trial was very poor because of an unusually late start to the wet season. Although the seeds were protected from animal predation, ants burrowed through the seed coats of many of them and ate the cotyledons (especially those of Cardwellia sublimis). This form of predation had not previously been observed in this region although there are several similar reports from Malayan rainforests (Burgess 1975; Duncan 1977). The mean heights of the survivors in each of the treatments are shown in Table 37. Most of the species (except for A. polyandrum) were taller in the large gaps. T. australis again failed to establish in the intact canopy treatment. The failure of Cardwellia sublimis to establish in the open was almost certainly due to the hot dry conditions which prevailed for several weeks after the seeds were sown. Although the overall effects of the unusual weather during establishment are suspected to be such that further discussion of the results might be more misleading than informative, this trial highlighted the importance of variations in weather patterns during the establishment phase, on the growth and survival of individual species.

The species used in the third trial were Agathis robusta, Argyrodendron peralatum, Cryptocarya angulata, Syzygium sp. (RFK 1891) and T. australis. The start of the wet season was again rather abnormal with storms separated by hot dry periods of 5-10 days lasting for about a month longer than usual. This weather regime affected the establishment of most species in the open but appeared to enable T. australis to survive in the intact canopy treatment (Figure 58) for much longer than

was observed in the two previous trials.

Overestimates of PAR levels reaching plants of slower growing species, where they were overtopped by weeds and faster growing species, were again observed. Consequently some values were ignored in regression calculations (Figure 59). Overall, growth and survival data (Figures 58 and 59) indicate that, except for T. australis, the species used in this trial were "small gap" species. Although T. australis has many attributes of "large gap" species (Section 5.1.2) it is more shade tolerant than typical "large gap" species such as A. aulacocarpa and A. petriei.

General observations made during these trials suggested that much of the variability in survival (and to a lesser degree growth) within treatments was attributable to microsite characteristics. This variation was greatest among the replicates of the large gap treatment and may have been caused by soil surface disturbance or compaction during the logging process. The degree of surface wash after heavy rain also appeared to be much more variable among large gap sites.

It was also interesting to observe (Figures 56 and 58) that mortality rates, following initial establishment, were often highest in the intact canopy treatment. This was even observed amongst "small gap" species which had established well in this treatment.

One of the difficulties of interpreting the field trials described above was to determine the relative importance of all the possible environmental variables. As has already been pointed out the formation of a gap primarily affects the radiation environment on the forest floor. Although the role of light (more accurately PAR) has more often been implied (e.g. Hartshorn 1980) than directly stated (e.g. Connell 1971) it has been widely accepted that light is the resource in shortest supply for the growth of regeneration on the floor of most, if not all, rainforests. However, the hypothesis has sometimes been advanced that it is not the additional light which causes the growth rate of regeneration to be higher in gap environments, but that the observed response is due to an increase in available soil based resources (e.g. Wilkinson

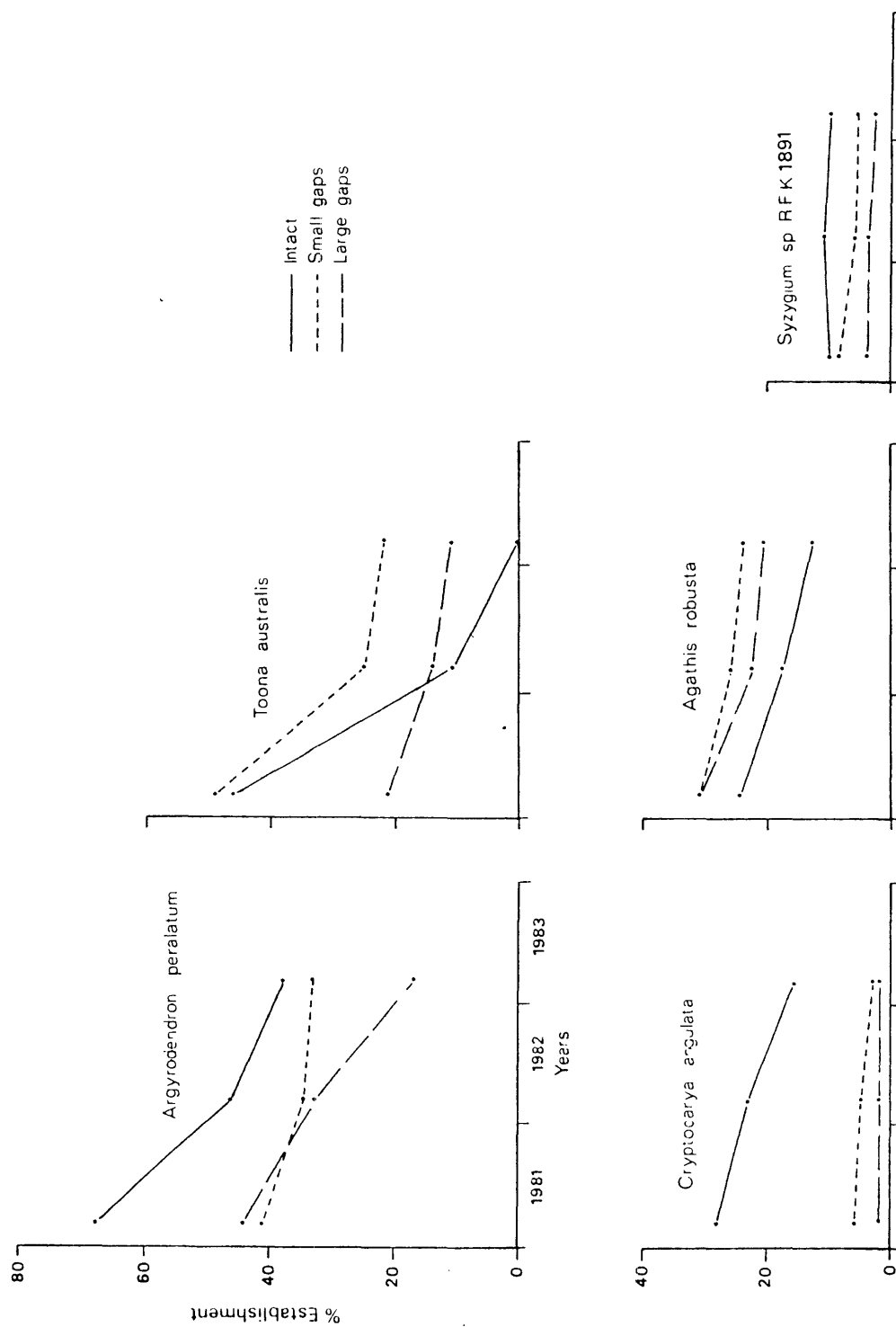


Figure 58. Progressive establishment percentages are shown for the species sown in the third seedling establishment and growth trial.

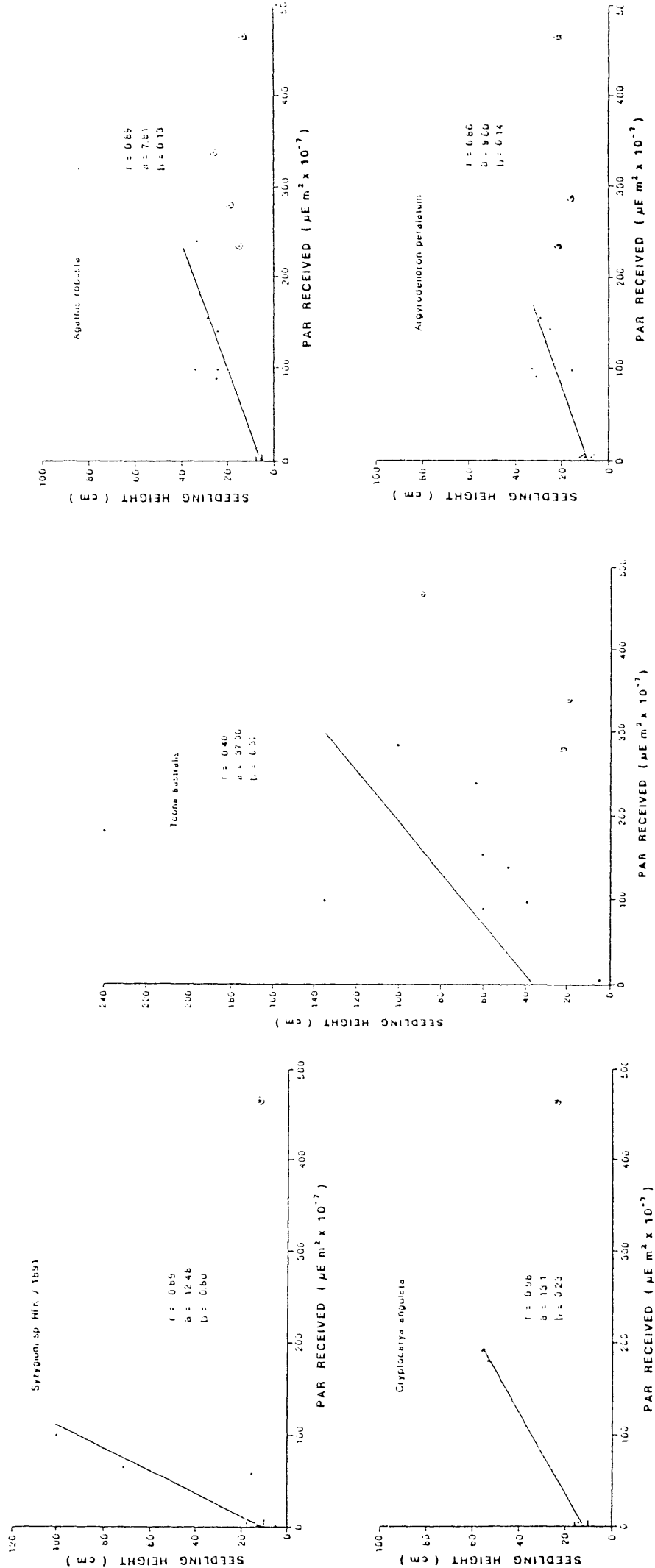


Figure 59. Relationships between height at age two years of the tallest surviving individuals in each plot of the third trial and PAR received by the tallest individuals in that plot during the first year, are shown. Circled values were derived from individuals overtopped by seedlings of other species or weeds. They were not used in the regression calculations.

1939) and perhaps a decrease in allelopathic influences. The classical experimental procedure is to observe the response of regeneration on the forest floor to trenching. Unfortunately most accounts of trenching experiments do not contain quantitative information about the light environment on the forest floor and it is therefore difficult to decide whether light was really a limiting factor in the environment studied. If it were, then one might expect no response to trenching and vice versa. While two trenching studies in rainforest (Connell 1971; Whitmore 1966b) did not, another (D.I. Nicholson pers. comm.) did reveal a growth response. The establishment of further trenching experiments to provide supplementary information for the previous experiment was considered but not carried out because of the difficulties of interpreting the results even when the light environment of the experimental area is known. For instance trenching must affect both soil water and nutrient availability, and it can be very difficult to adequately control these factors in field experiments. Some questions which must be considered in interpreting trenching experiments are :-

a) do deeper uncut roots under the trenched area tap its resources?

b) has trenching altered the natural soil water regime and either increased or decreased water availability to the trenched site?

c) does the decay of cut roots alter the nutrient status of the trenched area?

Rather than grapple with these uncertainties, I decided to see if the patterns of survival and growth observed in this trial, could be repeated in a glasshouse environment where light effects could be more easily distinguished from the influence of other factors. Another alternative may have been to provide additional water and nutrients to regeneration on a forest floor under an intact canopy and observe the results. Again it seemed that there would be difficulties of interpretation. However, it is of interest to observe that in an unrelated experiment in rainforest silviculture, I found that underplanted seedlings of Flindersia brayleyana showed no

significant response to fertilizer application even though the soils on the site appeared to be infertile and the canopy was somewhat reduced by the standard forest treatment technique (described by Baur 1964b) used for enrichment planting.

4.7 Glasshouse shading trials

The main difficulty with shading experiments is to provide various light treatments while minimizing variations between treatments in other environmental parameters especially temperature. The shading cylinder design used by Grime and Jeffrey (1965) seemed to have some advantages over those methods which use slats or shade cloth but the cylinders are difficult to use with large numbers of seedlings. With the notable exception of the recent study of Augspurger (1984), the few similar experiments of this nature undertaken by others (e.g. Nicholson 1960; Parrish and Bazzaz 1982) have generally used rather high minimal light intensities. For example the lowest light intensity used by Parrish and Bazzaz in their study of the effects of a range of light regimes on the growth of some temperate tree species, was 25% of that in the open. As noted earlier in this Chapter, the regeneration of many rainforest trees will grow at much lower levels. The design described below attempted to minimize temperature problems while providing the seedlings with PAR environments representative of the range found on the forest floor beneath canopy gaps.

The glasshouse in which the trial was established was ventilated by forced air evaporative coolers which generally were able to maintain internal air temperatures within 2°C of the external ambient. Air circulation within the house was assisted by 4 additional fans. Electric heaters prevented minimum temperatures from falling below 15°C. Whiting reduced the light transmitted into the glasshouse to an average of 25% of that outside. The internal light environment was monitored with a Li-Cor quantum sensor attached to a Li-Cor LI-500 integrator.

Three shading frames each containing 4 randomly arranged

shading treatments were constructed and secured to a similar number of mesh topped nursery benches (Figure 60). The shading material used was white aluminium venetian blind strip (34 mm wide) laid in a north-south direction and separated by gaps of 23, 6 or 1 mm. These configurations provided moving bands of light across the plants below. The overall result was that the plants in each replicate received either 100, 40, 15, or 2.8% of the light available in the open treatment.

Selected plants were grown on these benches as seed supplies and space permitted. The 22 species used represent a range of rainforest trees, a rainforest canopy level climber, Calamus radicalis, and a large open forest tree characteristic of rainforest margins, Eucalyptus grandis. Attempts to use several other species, notably Acacia spp. and Alphitonia petriei, in this trial were not successful mainly because their germination behaviour, growth characteristics or susceptibility to scale insects, made it difficult to obtain a uniform batch of seedlings. The procedure adopted was to germinate the seeds under normal glasshouse conditions and transplant 4 or 5 of each species to 18 cm diameter plastic pots. One of these pots was placed in each treatment replicate. The potting medium used was steam pasteurized U.C. mix type B (Baker 1957). Subsequent maintenance and foliar fertilizing was the same as that for the remainder of the glasshouse. The seedlings were removed when it became apparent that the larger of those in the fastest growing treatment were beginning to shade others in the same pot. The height and oven dried weight (105°C) of each seedling were recorded.

The regressions of height and dry matter production on the total amount of PAR received by each species (Figures 60 and 61) showed some interesting trends. The most important were related to the slopes of the regression lines for height growth on PAR. The steepness of these slopes appeared to be inversely related to their perceived shade tolerance. In Table 39 the species (with regression constants and percentage survivals in each treatment) are listed in order of slope (steepest first) within each group. Three rather arbitrary divisions were made in this list. The two species in Group 1

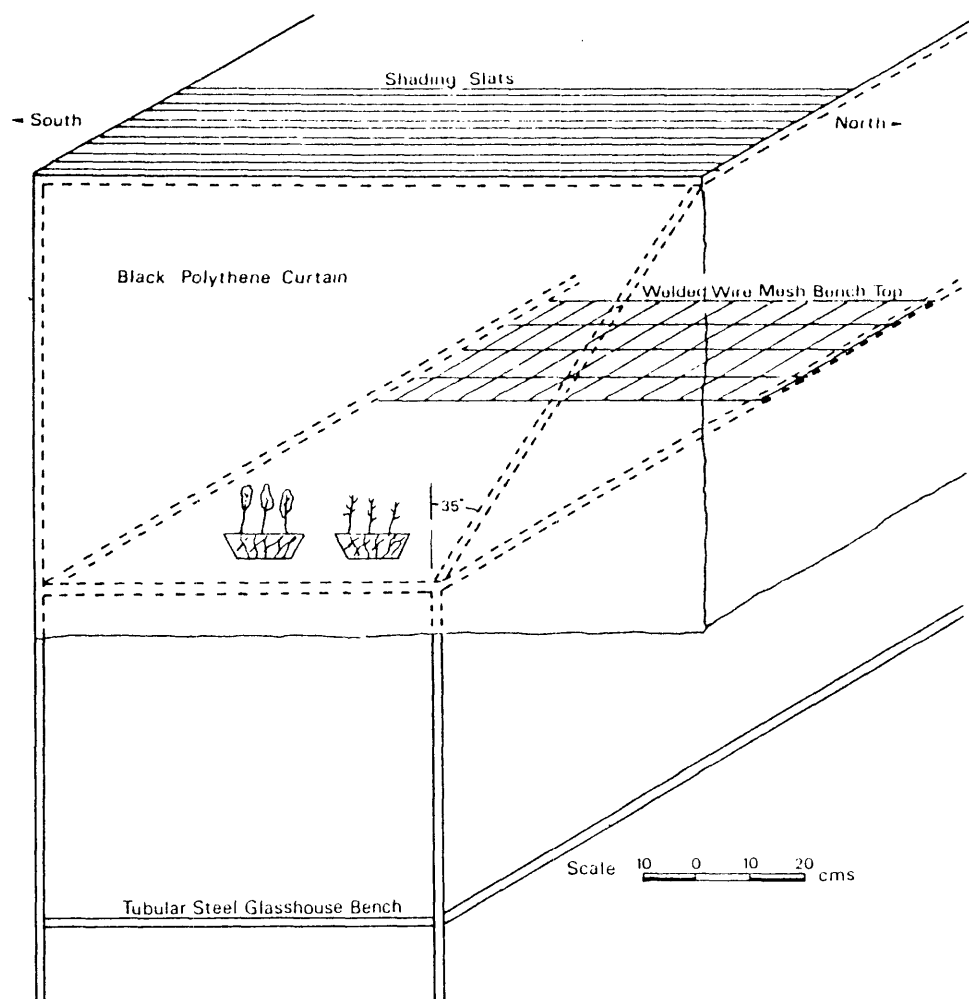


Figure 60. The design of the shading benches used in the glasshouse growth trial is illustrated.

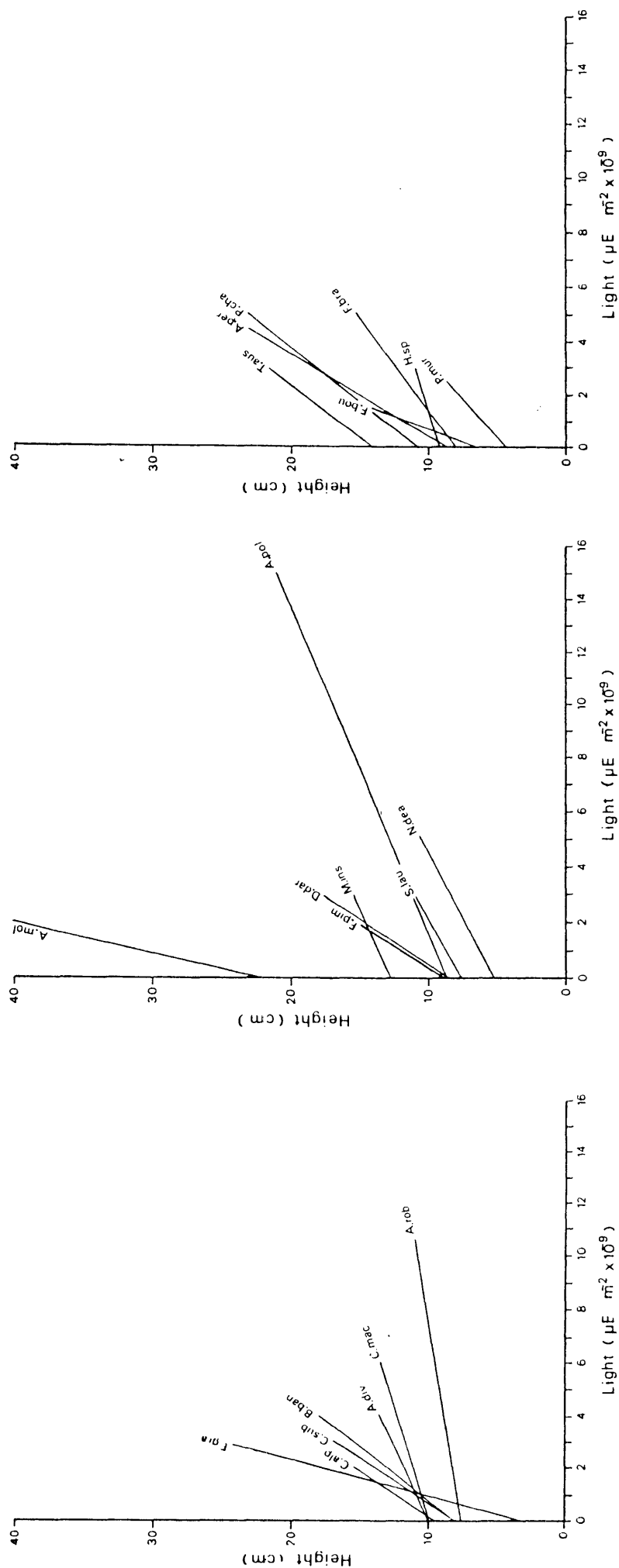


Figure 61. The regressions of height growth on PAR received in the glasshouse shading trial are illustrated (they are separated into three groups for clarity). Full species names and the characteristics of the regressions are included in Table 39. Regression points are shown in Appendix E.

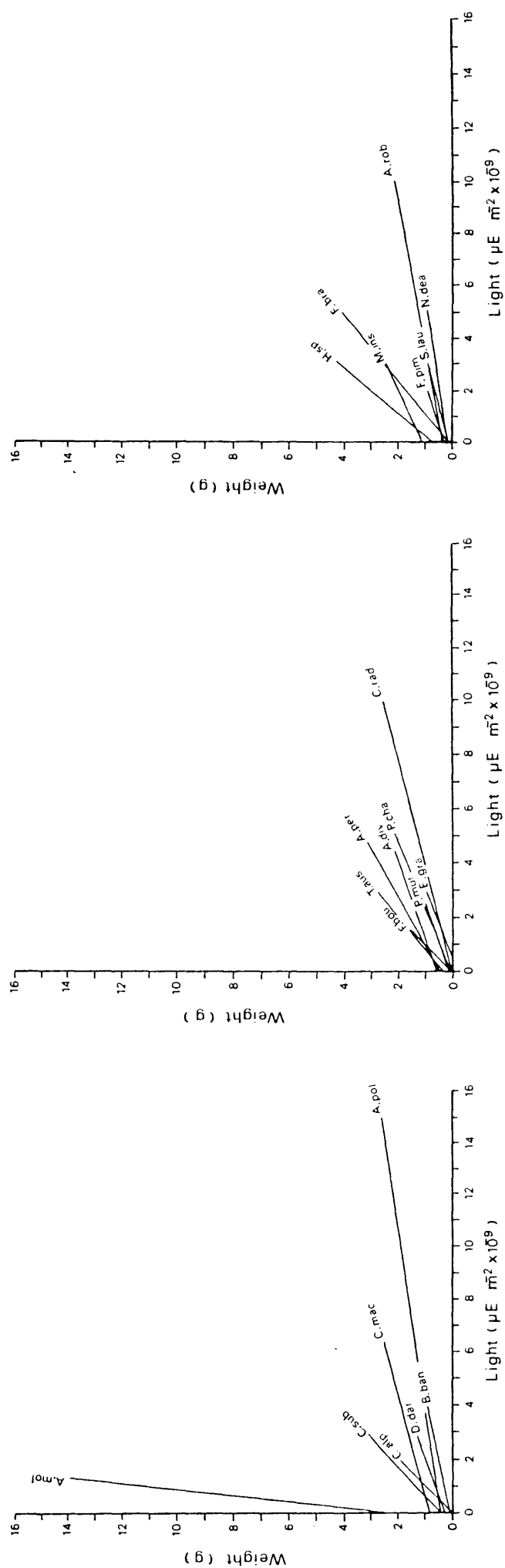


Figure 62. The regressions of dry matter production on PAR received in the glasshouse shading trial are illustrated (they are separated into three groups for clarity). Full species names and the characteristics of the regressions are included in Table 39. Regression points are shown in Appendix F.

Table 39. Height and dry matter regression constants (a and b) and correlation coefficients (r) with survivals (%) for the rainforest plant species grown under various light regimes in the glasshouse.

Treatment duration (days)	Heights		Regression		Weights b	r	% Survival (Decreasing light →)				Seed size*	
	a	b	r	a			L1	L2	L3	L4		
Group 1												
Aleurites moluccana	68	24.3	8.13	0.59	2.39	8.32	0.95	100	100	100	100	1
Eucalyptus grandis	182	3.70	6.80	0.86	-0.16	0.40	0.80	100	100	73	0	22
Group 2												
Flindersia bourjotiana	107	6.67	5.06	0.88	0.18	0.88	0.96	100	100	100	27	15
Argyrodendron perlatum	290	8.56	3.32	0.69	0.51	0.51	0.78	100	100	100	100	9
Darlingia darlingiana	208	8.40	3.14	0.83	0.23	0.34	0.86	100	100	100	93	12
Flindersia pimentaliana	155	9.00	3.09	0.93	0.29	0.28	0.91	73	93	87	7	16
Castanospora alphandii	160	9.34	3.07	0.93	0.25	0.77	0.99	100	100	93	53	2
Cardwellia sublimis	201	7.89	3.06	0.94	0.39	0.90	0.91	92	100	100	58	5
Backhousia bancroftii	230	8.09	2.51	0.72	0.06	0.22	0.90	97	87	90	0	20
Planchonella chartacea	331	10.71	2.51	0.67	0.05	0.42	0.73	100	100	100	92	6
Toona australis	199	14.2	2.45	0.59	0.47	0.75	0.91	100	100	100	0	19
Polyscias murrayi	188	4.59	1.70	0.81	0.03	0.41	0.89	100	80	87	0	21
Flindersia brayleyana	281	8.23	1.44	0.86	0.14	0.78	0.88	100	100	100	100	14
Sterculia laurifolia	210	7.67	1.13	0.61	0.15	0.25	0.91	92	100	75	33	7
Neolitsea dealbata	365	5.41	1.02	0.76	0.20	0.16	0.82	100	100	100	100	8
Group 3												
Arytera divaricata	265	9.87	0.96	0.84	0.53	0.36	0.80	100	100	92	85	17
Myristica insipida	215	12.8	0.96	0.40	1.01	0.47	0.81	100	100	100	100	3
Argyrodendron polyandrum	509	8.86	0.61	0.76	0.36	0.15	0.91	100	100	92	83	11
Cryptocarya mackinnoniana	392	9.32	0.72	0.69	0.86	0.26	0.80	92	100	100	75	4
Harpullia sp.	235	9.36	0.61	0.32	0.66	1.13	0.77	100	100	100	85	13
Agathis robusta	646	7.62	0.33	0.46	0.42	0.16	0.85	67	56	92	67	18
Calamus radialis	604	-	-	-	0.31	0.26	0.97	100	67	100	92	10

* Ranked in size from 30 mm dia. (*A. moluccana*) to 0.5 mm (*E. grandis*).

could be described as "large gap" species which grow rapidly but only in large gaps. Most species examined fell into Group 2 which appeared to be composed of species typically found in smaller gaps. These species generally grow more rapidly in gap situations than those of Group 3 which included some very shade tolerant species.

It can be observed (Table 39) that the correlation coefficients for height on PAR of species in Group 3 were generally lower than the remainder even though the coefficients for dry weight on PAR remained high. It is thought that in this group, the maximization of height growth does not provide such a competitive advantage as it does with species higher on the list. The Group 3 species seemed to be more prone to adopt the alternative strategy of producing more leaf area to capture as much as possible of the limited PAR available.

Variations among species (and perhaps between individuals) in partitioning photosynthetic production between height growth and leaf area probably account for the generally lower correlation coefficients observed for height on PAR than dry weight on PAR. Many of these interspecific differences appeared to be reflected in differences between the height and dry matter regressions for individual species (e.g. compare the regression lines of E. grandis and A. robusta. The former grew rapidly in height for a relatively small increase in dry matter; the latter increased in height and dry matter at about the same rate).

It is suspected that for some species, partitioning between height and leaf growth may change as their seedlings grow taller, for while most species in Group B appeared to favour the strategy of rapid early height growth, some such as P. brayleyana and A. robusta were lower on the list than expected. During early growth, species in the latter group appeared to be expanding their leaf area more than several other species, which from general observations (e.g. the arboretum growth rates in Appendix F), I would have thought had similar height growth rates as small trees and saplings. Similar trends in seedling development have been reported for

a range of temperate plants (e.g. Lodge 1981).

The value of the intercept on the "y" axis appeared to be related to seed size. Although survival at low light seemed, in very general terms, to be related to seed size (Table 39) it is suspected that some of the larger seeded species high on the list (especially A. moluccana) would have had low survival at low light levels if the shading chamber had been large enough for them to be grown for a longer period.

In considering the results of this experiment it should be noted that even the highest PAR level was only about a quarter of that of full sunlight and while the total PAR received by the plants was comparable to those in most gap environments, the plants in this experiment did not receive the periods of intense PAR which would sometimes be received by plants in large gaps. Again, probably because of the low mean PAR levels applied, none of the species showed signs of growth suppression, observed for example by Nicholson (1960) and Sasaki and Mori (1981), at high light levels. Indeed, in retrospect, it appears that some of the difficulties (irregular growth and susceptibility to insect and fungal attack) in establishing the "large gap" species (Acacia spp. and Alphitonia petriei) for use in this experiment, may have been related to poor seedling vigour resulting from the low levels of PAR in the glasshouse environment.

In the following Section some observations are made on the growth of a large number of rainforest tree species established in the open without the benefit of artificial or natural shading.

4.8 Survival and growth in a rainforest species arboretum

The CSIRO Forest Research laboratory at Atherton had its beginnings in 1971 when it was established on a 3.2 ha site on the outskirts of that town. The site had originally been rainforest but within several hundred metres of the drier western boundary of the main rainforest block. The forest was probably cleared around 1900 and regularly cropped (mainly for maize) until the laboratory was established in 1971. One of

the first projects undertaken was the establishment of an arboretum on that part of the land not occupied by buildings and other facilities. The main objectives of the arboretum were as follows:-

- a. to see if a rainforest could be established by planting a full range of species in an open, old field situation;
- b. to determine the survival and relative rates of growth of rainforest tree species established in the open;
- c. to provide a ready source of seed and other botanical material, especially of rarer species;
- d. to make a preliminary assessment of the horticultural and silvicultural value of the region's flora;
- e. to enable the methodology for studies of floral biology to be developed.
- f. to enable Station staff and visitors to familiarize themselves with the forest flora of the region.

The general policy has been to attempt to establish about three individuals of every tree species in the region. Almost all those established have been grown from seed and their origins can be traced through voucher specimens which were obtained with the seed. The development of the arboretum has been gradual with the establishment of new species continuing whenever seed becomes available. In order to prevent unnecessary mortality and improve growth some watering and a little fertilizing has been carried out. Water sprays were also occasionally used to provide frost protection but the topographic situation is such that this precaution never seems to have been absolutely necessary. Shading, either by artificial means or cover crops, has never been used although in recent years the shaded environment in the older section where the canopy has now closed, has been used to establish a range of understorey herbs, shrubs and epiphytes.

Even though the soils were somewhat degraded from erosion and almost continuous cropping, and the site drier than would be typical of the region's rainforests, it was found that most

species could be successfully established in full sunlight despite some predictions that successful establishment would only occur if a "successional sequence" along classical lines (the facilitation model) was established and the desired species introduced at appropriate stages. The few species which have failed, have usually belonged to that group of small tree species which never reach the upper canopy. The reason for their deaths usually seems to have been their very thin bark which was killed by exposure to long periods of full sunlight. Arytera lautererana is a good example of a species which seemed difficult to establish because of this problem.

From the viewpoint of forest dynamics some of the most interesting data derived from the arboretum are those relating to height growth rates. The species growing in the oldest part of the arboretum are listed with their mean annual height increments and other details in Appendix F. The frequency distribution of taxa in increment classes (Table 40) suggests that there are relatively few fast growing species but many of intermediate growth rate and even more of slow growth rate. However, it is possible that the local environment may not have been suitable for some of the latter. Comparisons of the growth rates of the species common to both the plot series (Appendix A) and the arboretum revealed that most of those listed as fast growing in the plots had height growth rates greater than 0.4 m annum^{-1} in the arboretum. However, many of those listed as slow growing in the plots had good height growth rates in the arboretum where many of the constraints (e.g. excessive shading) experienced in the field, were ameliorated. (Weaver 1983 observed that "small gap" species had proportionally, a greater growth response to the thinning of a Puerto Rican rainforest than less shade tolerant species.) Overall the plot and the arboretum data suggest that the average rainforest tree is rather slow growing in terms of both height and diameter increment with maximum growth rates about 3 to 4 times their average. Again the fastest growing species were those few which would be regarded as "large gap" species (Acacia spp., Commersonia bartramia and Aleurites moluccana).

Table 40. Numbers of rainforest tree species in mean height growth rate classes (m annum^{-1}) in the Atherton arboretum.

Growth rate (m annum^{-1})	>1.3	1.2	1.1	1.0	0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.2	<0.1
No. species	2	-	4	4	10	11	13	20	34	39	32	38	39



Plate 27. The oldest (12 years) section of the CSIRO Division of Forest Research arboretum. The tallest tree (14 m high) in this photograph is Aleurites moluccana.

4.9 The significance of the vegetative mode in regeneration

Most of the discussion in this Chapter so far has been concerned with the ability of seedlings to establish and grow in gaps. In the study described below attention was focussed on regeneration from vegetative sources such as roots and stems which existed before the gap was formed.

The 100 x 100 m felled and burnt plot forming the basis for this study was established as one treatment of an experiment examining the effects of various silvicultural alternatives on the growth of planted seedlings of Flindersia brayleyana and F. pimenteliana. The study was commenced when it was observed that many components of the original rainforest had regenerated by coppice. Although seedlings and root suckers of some tree species in the original stand were also present, they appeared to be of lesser overall significance. The study was located on State Forest Reserve 185, Danbulla, in Python Logging Area (Lat. 17° 10' S, Long. 145° 35' E) at 720 m altitude. The rainfall is estimated to average 1600 mm annum⁻¹. The soils are krasnozems and are similar to those described by Isbell et al. (1976). The topography is undulating with the study area sloping gently to the south. The most recent (and only) specific record of wind damage at this site was the observation of minor damage following cyclone Agnes in 1956 (Anon. undated).

Although selective logging would have commenced in the area of the site during the early 1900s, logging area records (Anon. undated) indicated that at the time of the commencement of the current experiment, the site had not been logged for at least 30 years. It may, however, have been silviculturally treated during the early 1950s to favour valuable timber species. This treatment would have involved slashing the understorey and killing useless or low-value tree species by girdling or poisoning (Volck 1968).

Despite the history of the site, there were few signs of past disturbance immediately before the establishment of the current experiment. Stumps and other logging residues had disappeared, "large gap" tree species were not very conspicuous and the observation of some low-value tree species

in the upper canopy suggested that any silvicultural treatment had had little effect on the overall floristics of the stand. The physiognomy of the stand at this time resembled that described by Webb (1959) as complex mesophyll vine forest with a few Agathis robusta emergents.

Before the commencement of the treatments an inventory of potentially marketable trees (mainly those over 1.2 m girth above buttress) on the plot was prepared to assist salvage logging. After logging, the remaining large trees were felled with a chainsaw and the site was cleared of small trees, shrubs and vines by slashing. The debris was burnt where it lay 3 months later.

In the 18 months following the burn, spot spraying with 2, 4-D-amine salt (0.4%) in water was used several times to kill Dendrocnide moroides, a dangerous stinging shrub which had to be controlled to maintain access to the area. E. Volck (pers. comm.) had previously used 2,4-D applications of this strength to control D. moroides with little or no visible effect on other species in the vicinity. Seedlings of the exotic shrubby weed Solanum mauritianum were also controlled by applying 2,4,5-T-ester (2%) in diesel fuel to cut stumps.

The height and mode of regeneration of all tree species was recorded on the whole plot in July 1976, 23 months after the burn. Three modes of regeneration were recognized:-

- a) by seedlings germinating after the burn;
- b) by stumps producing coppice shoots;
- c) by sucker shoots from roots.

Some difficulties were encountered in this assessment:-

- a) it was not possible to identify all species to a specific level with the sterile material available;
- b) the dense growth of short-lived weeds and grasses made finding individual regrowth stems less than 1 m tall extremely difficult and this class was therefore omitted from the assessment;

c) the lower stems of the shoots were examined to determine their origin. If necessary, they were removed from the soil. Nevertheless, it is thought that a few shoots assessed as post-fire seedlings could have originated from established roots and conversely some recorded as coppicing stumps could have originated from post-fire seedlings which had been damaged;

d) two species, Alstonia muellerana and Sloanea langii, produced root suckers in great profusion and, although some coppicing was observed, all the shoots were counted as root suckers as the few coppicing stumps were usually hidden by clumps of root suckers and were difficult to separate from them. The number of shoots recorded for these species was approximate and their mean heights were based on a visual assessment;

e) the division between tree and shrub species is somewhat arbitrary and thus some of the shorter-lived species (less than about 10 years) which occasionally develop an arborescent habit (e.g. Solanum mauritianum) were not included in the observations although some slightly longer-lived tree species were included (e.g. Duboisia myoporoides, Mallotus ricinoides, M. paniculatus and Homalanthus populifolius);

f) many species were not encountered often enough to make useful interspecific comparisons of their height growths and regeneration modes. The species were arbitrarily divided therefore into two groups according to their recorded density: $n =$ or > 10 and $n < 10$.

The only record of the floristics of the site before clearing was contained in the inventory prepared for salvage logging. The list of 20 tree species extracted from this document (Table 41) cannot be regarded as complete for trees assessed as of no commercial value because of small size, poor stem form, stem defect or unfavourable wood characteristics were not included. The species recorded are listed in silvicultural groups which are based on their wood values and silvicultural characteristics (Baur 1964a). Seven of the species listed did not reappear after the treatment.

Table 41. Potentially useful trees over 1.2 m girth above buttress in the original stand.

Species	Silvicultural group ^a	No. stems
<i>Agathis robusta</i> ^b	A	1
<i>Flindersia acuminata</i>	A	1
<i>F. brayleyana</i>	A	4
<i>Oreocallis wickhamii</i>	B	2
<i>Argyrodendron</i> spp.	C	24
<i>Blepharocarya involucrigera</i>	C	5
<i>Carnarvonia araliifolia</i> ^b	C	1
<i>Darlingia darlingiana</i>	C	2
<i>Sloanea langii</i>	C	1
<i>Acacia aulacocarpa</i>	D	1
<i>Aleurites moluccana</i>	D	2
<i>Beilschmiedia obtusifolia</i> ^b	D	1
<i>Eugenia leuhmannii</i> ^b	D	1
<i>Brachychiton acerifolium</i> ^b	Not listed	3
<i>Cerbera inflata</i> ^b	" "	1
<i>Cryptocarya mackinnoniana</i>	" "	1
<i>Elaeocarpus ruminatus</i>	" "	1
<i>Flindersia schottiana</i>	" "	3
<i>Homalium circumpinnatum</i> ^b	" "	1
<i>Stenocarpus sinuatus</i>	" "	1
	Total	57

^aGroup A more desirable than B, etc. (after Bauer 1964a).

^bNo regeneration observed after felling and burning.

The intensity of the burning treatment was observed to be quite variable. Nevertheless, the fire consumed the leaf litter and at least the small branches of the fallen trees over the whole plot.

Germination of weed species from seed commenced about a month after the burn. Prominent species for the first twelve months were Dendrocide moroides, Solanum mauritianum, Phytolacca octandra, Ageratum conyzoides, Erigeron sp. and a few grasses. Aside from its control of D. moroides the hormone spray did not appear to be strong enough to affect the growth or survival of either herbaceous or woody regeneration. During the second year, grass density increased so that 23 months after the burn, grasses dominated most of the area between the regenerating tree species. A significant feature of the grass layer during the second year was the appearance of a few small clumps of Imperata cylindrica. On this site there is no doubt that, if recurrent fires had occurred, they would have led to the replacement of the woody regeneration by I. cylindrica. This phenomenon appears to be as common in this region (Stocker and Mott 1981) as it is in the remainder of the tropics (e.g. Whitmore 1975; Adediji 1984).

Of the 82 tree species observed regenerating on the plot 23 months after the fire, 74 coppiced from stumps, 10 produced root suckers, while 34 regenerated from seed (Tables 42 and 43). It was observed that most of the coppicing stumps were 20 cm or less in diameter and although many larger stumps had coppiced immediately after felling, they did not subsequently recoppice to replace shoots destroyed by the fire. In contrast to the coppice and seedling regeneration, root suckers of the two main suckering species, Alstonia muellerana and Sloanea langii, were distributed in moderately dense clumps around the parent stumps and therefore it appeared unlikely that their density was indicative of their final representation in the regrowth stand.

The mean heights of the regenerating trees were compared with the regeneration mode (Table 44). The few species regenerating mainly from seed, have generally grown more

Table 42. Regeneration modes observed in species encountered 10 or more times.

Species	No. stems	Coppicing stumps (%)	Root suckers (%)	Seedlings (%)
Regeneration mainly by coppice				
<i>Austromyrtus shepherdii</i>	13	100		
<i>Austromyrtus</i> sp.	22	100		
<i>Cryptocarya hypospodia</i>	55	100		
<i>Daphnandra repandula</i>	15	100		
<i>Darlingia darlingiana</i>	14	100		
<i>Planchonella obovoidea</i>	25	100		
<i>Toeckia erythrocarpum</i>	15	100		
<i>Cryptocarya mackinnoniana</i>	44	98		2
<i>Litsea leefeana</i>	54	98		2
<i>Argyrodendron</i> spp.	67	97		3
<i>Mallotus polyandrus</i>	45	96		4
<i>Rhodomyrtus macrocarpa</i>	19	95	5	
<i>Castanospermum australe</i>	16	94		6
<i>Macaranga subdentata</i>	70	94	4	2
<i>Endiandra cowleyana</i>	67	91		9
<i>Guioa</i> sp.	10	90		10
<i>Davidsonia pruriens</i>	17	88		12
<i>Decaspermum fruticosum</i>	34	85	15	
<i>Stenocarpus sinuatus</i>	79	82	16	2
<i>Acronychia acidula</i>	52	73	19	8
<i>Diploglottis australis</i>	19	69	26	5
Total	752			
Regeneration mainly by root suckers				
<i>Alstonia muellerana</i>	500 ^a		100	
<i>Sloanea langii</i>	200 ^a		100	
Total	700			
Regeneration mainly from seed				
<i>Acacia aulacocarpa</i>	10			100
<i>Aleurites moluccana</i>	74	3		97
<i>Mallotus ricinoides</i>	28	3		97
<i>Tieghemopanax elegans</i>	108	6		94
<i>Mallotus paniculatus</i>	12	8		92
<i>Trema orientalis</i>	148	18		82
<i>Clerodendron cunninghamii</i>	18	22		78
<i>Ficus</i> sp.	13	31		69
<i>Alphitonia petriei</i>	25	36		64
Total	436			

a = Estimated (see text)

Table 43. Regeneration modes observed for species with fewer than 10 individual sightings.

Species	Coppicing stumps	Root suckers	Seedlings
<i>Ackama australiensis</i>	x		
<i>Acronychia vestita</i>	x		
<i>Alstonia scholaris</i>	x		
<i>Archidendron vaillantii</i>	x		
<i>Arytera divaricata</i>	x		
<i>A. lautererana</i>	x		
<i>Blepharocarya involucrigera</i>	x		x
<i>Canarium muelleri</i>	x	x	x
<i>Castanospora alphanthii</i>	x		
<i>Cryptocarya murrayi</i>	x		
<i>Cupaniopsis foveolata</i>	x		
<i>C. serrata</i>	x		
<i>Dendrocnide photinophylla</i>	x		
<i>Duboisia myoporoides</i>			x
<i>Dysoxylum</i> sp.	x		
<i>Elaeocarpus ruminatus</i>	x		
<i>Endiandra muelleri</i>	x		
<i>E. sankeyana</i>	x		
<i>Eugenia cormiflora</i>	x		
<i>Euodia bonwickii</i>	x		
<i>Eupomatia laurina</i>	x		
<i>Euroschinus falcata</i>	x		
<i>Ficus leptoclada</i>	x		
<i>F. septica</i>	x		
<i>Flindersia acuminata</i>	x		
<i>F. brayleyana</i>	x		
<i>F. schottiana</i>	x		x
<i>Gardenia ovularis</i>	x		
<i>Homalanthus populifolius</i>			x
<i>Mallotus philippinensis</i>	x		x
<i>Melia azedarach</i>			x
<i>Melicope erythrococca</i>	x		
<i>Mischocarpus pyriformis</i>	x		
<i>Neolitsea dealbata</i>			x
<i>Oreocallis wickhamii</i>	x		x
<i>Pilidiostigma tropicum</i>	x		
<i>Pisonia umbelliflora</i>	x		
<i>Pithecellobium grandiflorum</i>			x
<i>Premna acuminata</i>	x		
<i>Pseudoweinmannia lachnocarpa</i>	x	x	
<i>Randia fitzalanii</i>	x		
<i>Rhysotoechia robertsonii</i>	x		
<i>Rhodomyrtus trineura</i>	x		
<i>Scolopia brownii</i>	x		
<i>Tetrasynandra pubescens</i>	x		
<i>Tieghemopanax murrayi</i>			x
<i>Wilkiea</i> sp.	x		
<i>Xylopiya maccraei</i>	x		
<i>Zanthoxylum dominianum</i>	x		x
<i>Z. veneficum</i>			x

Table 44. Regeneration mode related to the mean height of species 23 months after the fire.

Species	Density stems ha ⁻¹	Mean height		Mode ^a
		m	s.d.	
<i>Alphitonia petriei</i>	16	3.1	0.9	S
<i>Mallotus paniculatus</i>	11	3.0	0.6	S
<i>M. ricinoides</i>	27	3.0	0.7	S
<i>Aleurites moluccana</i>	72	2.7	0.9	S
<i>Trema orientalis</i>	121 (27)	2.6 (2.5)	0.6 (0.9)	S (C)
<i>Alstonia muellerana</i>	500 ^b	2.5 ^b	-	R
<i>Sloanea langii</i>	200 ^b	2.5 ^b	-	R
<i>Rhodomyrtus macrocarpa</i>	18	2.4	0.5	C
<i>Macaranga subdentata</i>	66	2.3	0.6	C
<i>Tieghemopanax elegans</i>	101	2.3	0.8	S
<i>Litsea leefeana</i>	53	2.2	0.7	C
<i>Acronychia acidula</i>	38 (10)	2.1 (1.8)	0.6 (0.3)	C (R)
<i>Clerodendron cunninghamii</i>	14	2.1	0.6	S
<i>Diploglottis australis</i>	13	2.1	0.5	C
<i>Stenocarpus sinuatus</i>	65 (13)	2.1 (1.5)	0.6 (0.5)	C (R)
<i>Mallotus polyadenos</i>	43	2.0	0.6	C
<i>Planchonella brownlessiana</i>	25	2.0	0.6	C
<i>Argyrodendron</i> spp.	65	1.9	0.5	C
<i>Austromyrtus shepherdii</i>	13	1.9	0.6	C
<i>Castanospermum australe</i>	15	1.9	0.6	C
<i>Cryptocarya hypospodia</i>	55	1.9	0.5	C
<i>Davidsonia pruriens</i>	15	1.9	0.9	C
<i>Endiandra cowleyana</i>	61	1.9	0.5	C
<i>Acacia aulacocarpa</i>	10	1.8	0.8	S
<i>Austromyrtus</i> sp.	22	1.8	0.4	C
<i>Cryptocarya mackinnoniana</i>	43	1.8	0.5	C
<i>Decaspermum fruticosum</i>	29	1.8	0.6	C
<i>Toeckia erythrocarpum</i>	15	1.8	0.6	C
<i>Daphnandra repandula</i>	15	1.7	0.5	C
<i>Darlingia darlingiana</i>	14	1.7	0.4	C

^aS - seedlings; R - root suckers; C - coppiced stumps.

^bEstimated (see text)

quickly than species using vegetative modes. It was also observed that most of the species developing from seed were "large gap" species while most of those using vegetative modes were from the "small gap" end of the presumed shade tolerance continuum.

There are some difficulties in interpreting the observations made during this essentially fortuitous study. For instance :-

a) a detailed knowledge of the structure and floristics of the stand before clearing would have enabled comparisons of pre- and post-perturbation floristics to be made with greater precision;

b) although the silvicultural treatments carried out about 30 years ago may not have greatly affected the floristic composition of the forest, they would have increased the proportion of trees in the smaller size classes, i.e. those most likely to coppice following a slash and burn treatment;

c) the hormone spray used to control Dendrocnide moroides did not appear to affect regeneration of other species but the possibility that it may have unobtrusively altered survival and growth cannot be excluded altogether;

d) some regenerating species may have been excluded by the decision to ignore regeneration less than 1 m tall. However, stems observed in this category were usually so deeply buried in the dense growth of herbs and grasses that their chances of survival seemed low;

e) reduced competition following the control of D. moroides and Solanum mauritianum may have improved the survival and growth of the taller regeneration.

The total number of tree species regenerating (82) on the study site fell within the range of tree species numbers which could be expected on an undisturbed site of that size in this region (see Chapter 3). There are several possible explanations for the apparent absence of seven of the species recorded in the original stand :-

a) these species are unable to coppice following a felling and burning treatment;

b) coppice development did not occur because smaller sizes with strong coppicing ability were not present in the original stand;

c) seedling regeneration did not occur because there was either no seed stored in the soil, or no seed arrived on the site after the burn;

d) regeneration occurred but failed to develop sufficiently to be recorded.

Despite the problems discussed above, it appears that on the study site most tree species are not solely dependent on seed for their reappearance after felling and burning, for they are capable of vegetative regeneration. The ability of so many rainforest tree species to coppice after burning was somewhat unexpected, for fire is an infrequent phenomenon in the rainforest environment and rainforest tree species are usually thought of as being fire sensitive. In the absence of shifting cultivation, the only occasions when a catastrophe similar to the felling and burning treatments could have occurred would have been following severe cyclone damage and subsequent fire in the debris.

Considering the potential advantage of a species regenerating vegetatively on an established root system, a feature of the present study was the high growth rate exhibited by most of those species which regenerated largely from seed (Table 44). While high growth rates have been shown to be characteristic of "large gap" species (see previous Sections) fast growth could also be seen as a necessary attribute for species with limited coppicing ability that are forced to compete with vigorous coppice regeneration from other species. An apparent exception was Acacia aulacocarpa. However, this species is not usually encountered on soils of basaltic origin and is much more characteristic of disturbed vegetation on poorer soils derived from metamorphic parent material where perhaps its ability to fix nitrogen places it in a stronger competitive position.

Most references to the vegetative regeneration of rainforest species in other regions (e.g. Whitmore 1975) have suggested that this mechanism is most important in areas with one or more limiting factors e.g. the heath, swamp and monsoon forests. Ewel (1980b) suspected that the coppicing habit in drier forests may be because establishment from seed is less reliable and root decay not as prominent in drier regions. While this reasoning seems quite plausible, there have been other observations (e.g. Symington 1933, Clayton 1958, Kartawinata et al. 1980; Maury-Lechon 1982; King and Chapman 1983; Adedeji 1984) to suggest that coppice regeneration can be an important mechanism in many rainforest types. Kartawinata et al. also noted that, in a regenerating lowland dipterocarp forest in East Kalimantan, most primary species present had developed from coppice rather than seed. While some implications of the relationship between the regeneration mode and shade tolerance of a species are examined in Chapter 6, the vegetative regeneration mode certainly cannot be ignored in any consideration of the regeneration characteristics of rainforest tree species.

In summary, investigations described in this Chapter suggest that there are only a few specialized vascular rainforest plants capable of growing to reproductive size with the PAR levels typically found beneath undisturbed rainforest canopies. A model of the light environment on the forest floor beneath canopy gaps, showed temporal and spatial patterns which were greatly influenced by latitude and gap size. The survival and growth of rainforest tree seedlings were found to be specifically related to gap size, primarily because species' growth rates seemed inversely related to their shade tolerance. However, while the general relationship between growth rate and shade tolerance was maintained, most "small gap" species can be established and will usually grow faster in open than heavily shaded positions.

Figure 62 shows the probable relationships across the normal PAR range between PAR and growth rate and PAR and survival for "large gap" and "small gap" species. The growth advantage of "large gap" species was preserved even when, as seedlings,

they had to compete with "small gap" species arising from established root systems.

While effects attributable to photo-inhibition were not conspicuous in the field and glasshouse trials described, they have been observed where seedlings of "small gap" species were suddenly exposed to very high PAR levels by logging disturbance and in recent glasshouse trials (G. Duff and G. Stocker unpublished) where maximum PAR levels were almost twice those used in the experiment described above. They have also been widely reported from elsewhere (e.g. Nicholson 1966; Sasaki and Mori 1981). In practice deaths of "small gap" species due to the effects of severe photo-inhibition are probably rare because in very open situations these species are rapidly over-topped by "large gap" species which can tolerate very high PAR levels. Conspicuous tissue damage to leaves following their sudden exposure to high solar radiation levels may also be caused by desiccation and associated high leaf temperatures. The mechanisms permitting "small gap" species to outgrow sensitivity to high PAR levels (as they should if they are to become part of the upper canopy) do not seem to have been explored.

Although some of the mechanisms contributing to shade tolerance are now beginning to be understood, many field and laboratory studies seem necessary before this important property can be adequately quantified. Further research in this area will undoubtedly contribute greatly to improved models of forest dynamics. Other aspects of shade tolerance and possible directions for future research are discussed in Chapter 6.

While the basic mechanisms associated with competition among regenerating species in gaps seem as if they might be predictable, the seedling establishment and growth experiments carried out in the field suggested that weather patterns during early establishment can exert an important initial influence on seedling survival and growth. Furthermore, species vary in their response to less than favourable weather during establishment. However, a much greater stochastic element would seem to occur in the factors controlling the

arrival of a specific propagule at a suitable establishment microsite. In order to examine these factors more closely, the next Chapter discusses relevant events, from propagule development to germination, in the life cycles of rainforest plants.

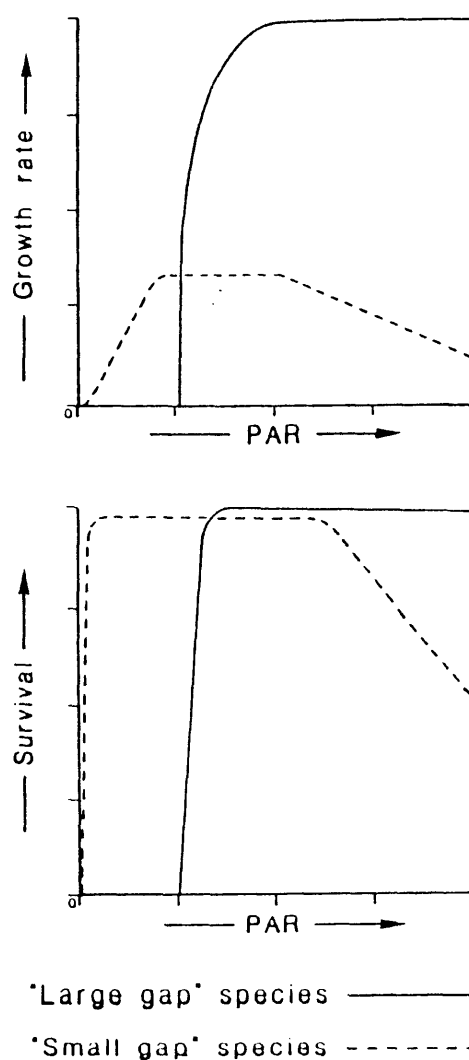


Figure 63. A diagrammatic illustration of the probable relationships across the normal PAR range between PAR and growth rate and PAR and survival for "large gap" and "small gap" species.