CHAPTER 5

Propagule production, predation, dispersal and germination

Sexual reproduction provides almost all rainforest plants with their best means of dispersal to other sites and the mechanism allowing their evolution. While regeneration from vegetative material may be conspicuous in rainforest successions (e.g. the study described in Section 4.9), most regenerating plants of vegetative origin develop from root stocks which were formed by seedlings in the recent past i.e. they were probably no older than the age of the larger trees and in most cases much younger. In this Chapter aspects of the production, dispersal, predation and germination of seeds will be examined with emphasis on the relevance of these characteristics to rainforest dynamics.

5.1 Production

5.1.1 Precociousness

The age of first fruiting of rainforest trees is of interest since, in situations where vegetative regeneration is not possible (usually because past disturbance has totally killed or removed the prexisting vegetation), it provides an indication of the ability of a species to survive frequent perturbations (Noble and Slayter 1980). For example, early seed production would seem to be an advantage to a species colonizing sites which are frequently and often severely disturbed (e.g. stream banks). Indeed the arboretum data (Appendix F) and general observations revealed that the few "large gap" tree species in this region produce their first seed crop within 3-5 years of the perturbation which enabled them to establish. However, the arboretum data also revealed that species other than those which would normally be regarded as "large gap" species, may also produce fruit crops at an early age in open environments. Many of these were "small gap" species (e.g. <u>Acmena hemilampra</u> and <u>Lomatia fraxinifolia</u>) and would not normally produce seed until they were large enough to reach the higher light levels characteristic of the

upper canopy. Nevertheless this group were in a minority and seed production in the remainder may be initiated by an age dependent factor rather than the availability of surplus photosynthetic products or perhaps the presence of a spectral trigger (J. Norman pers. comm.). It may be observed that in situations where reproductive activity is at the expense of vegetative growth, a long lived species could be expected to have a competitive advantage by maximizing early growth, provided of course that its environment was relatively free of catastrophic disturbance.

5.1.2 Frequency

Very little phenological information of any kind is available for rainforest species in north-east Queensland. Furthermore the scattered information which is available is qualitative and its significance is difficult to interpret from the viewpoint of forest dynamics. For example, it is well known among forestry personnel that _Agathis robusta_ produces "reasonable" seed crops every two or three years. Here "reasonable" is related to the amount available to seed collectors. However, from the viewpoint of forest dynamics it has been observed that virtually all seeds of this species are eaten almost as quickly as they reach the ground (see Section 5.2) and that in reality there is only enough seed for effective regeneration following exceptionally heavy seed falls which may occur at intervals of perhaps 20-100 years. The link between frequency and predation is an important one and is discussed further in the final Chapter.

Observations made while collecting seed for experimental plantings suggested that in general only the few "large gap" tree species, such as the _Acacia_ spp., _Alphitonia petriei_, _Commersonia bartramia_ and _Trema orientalis_, were capable of producing seed crops every year. _T. orientalis_ and some of the hemiepiphytic _Ficus_ spp. appeared to produce almost continuous crops. For the "large gap" species this observation appears consistent with the normal pantropic pattern (see review by Whitmore 1983). Bazzaz and Pickett (1980) supposed that "large gap" species fruit annually because they are freed from competition. Denslow (1980a)

suggested that since large gaps were rare, "large gap" species must produce frequent crops of numerous seeds to survive (another hypothesis based on the net photosynthetic rate characteristic of "large gap" species, is discussed in Section 6.1.1c). However, the ability of the seeds of at least several of these species (e.g. A. petriei and Acacia melanoxylon) to remain viable in the soil for many years (see Section 5.4) suggests that annual production might also be the most effective means of maximizing seed quantity and maintaining a sufficiently extensive seed rain to colonize rare "large gap" situations. Interestingly, Toona australis was observed to produce regular annual seed crops. Despite this characteristic, its shade tolerance (Section 4.6) and large size at maturity (presumably implying long life), separate it from typical "large gap" species. A few species, such as Flindersia brayleyana and Cardwellia sublimis, which seem to be of intermediate shade tolerance, usually have a good crop every two, or occasionally three, years. Most other species (by far the majority) have seed crops at 3 year or longer intervals (Baur 1964b; B. Hyland unpublished).

Some information on fruiting frequency was also provided by data obtained from the litter collections of H. Brasell and G. Stocker (unpublished) and from the composition of dung samples collected during a study of seed dispersal by Cassowaries. The first study used 10 randomly arranged litter traps (each 0.7 m^2 in area) to sample the fortnightly litterfall in two rainforest plots (each 50 x 50 m) on the east and west sides of the Atherton Tableland (the methods and localities were described by Brasell et al. 1980). For a period of 18 months, the litter collected was sorted into reproductive and vegetative components. When the fruit component was considered (Table 45) it was observed that of the 31 species shedding vegetative material, 12 did not fruit, 19 fruited once and 3 fruited twice, during the 18 month collection period. In the second study (for methods see Section 5.3.1) seeds of 65 species were found during the two year study period (Table 46). Of these, seeds of 54 species were found during only one of the two fruiting seasons sampled. The data from both experiments must be interpreted with caution for they are very limited samples, both spatially and temporally.

However, observations by Crome (1975b) of species important in the diet of fruit eating pigeons, yielded similar data.

Table 45. Periods of fruit production for selected rainforest tree species on two undisturbed sites on the Atherton Tableland (adapted from H. Brasell and G. Stocker unpublished).

Site 1 — Period of mature fruit production

Species	1977 J	F	M	A	M	J	J	A	S	O	N	D	1978 J	F	M	A	M	J
Aleurites moluccana													x	x				
Argyrodendron trifoliolatum																		
Castanospermum australe																		
Castanospora alphandii													x					
Dendrocnide photinophylla													x					
Diploglottis diphyllostegia									x									
Ficus watkinsiana	x	x	x										x	x				
Flindersia schottiana													x					
Melia azedarach																x	x	
Planchonella obovoidea																		
Pseudocarapa nitidula																x	x	

Site 2

Species	1977 J	F	M	A	M	J	J	A	S	O	N	D	1978 J	F	M	A	M	J
Argyrodendron peralatum											x							
Cryptocarya angulata																		
Doryphora aromatica	x												x					
Elaeocarpus angustifolius							x											
E. ruminatus																		
Endiandra muelleri																		
E. tooram																		
Euodia bonwickii																		
Ficus obliqua var. obliqua													x					
F. pleurocarpa	x	x	x										x	x	x			
Hylandia dockrillii																		
Litsea leefeana						x	x	x										
Macaranga inamoena																		
Mallotus polyadenos													x	x				
Melicope fareana														x				
Myristica insipida											x		x	x	x			
Polyscias elegans						x	x	x										
P. murrayi																		
Rockinghamia angustifolia																		
Sloanea langii						x	x	x										

One of the most interesting aspects of the many species which fruit at intervals of two or more years was the synchronization which was observed amongst individuals of the same species; species within the same genus and even species within the same family. Individuals and taxa in the Lauraceae provided some good examples (see the genera Beilschmiedia, Cryptocarya and Endiandra in Table 46). It was also observed that years of high Avocado production (Persea americana Mill.) in the region tended to follow the pattern established by the native taxa of the Lauraceae and therefore it seems possible that the fruiting of most members of this family may be triggered by the same stimulus. While synchronization of

Table 46 .   The occurrence of viable seeds of rainforest plants in cassowary
dung samples which were collected monthly from July 1977 to July
1979.

Trees and mid to upper
canopy level vines.

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                                   1977      -            1978            -      1979
                                   J A S O N D J F M A M J J A S O N D J F M A M J J
Acmena divaricata                  x         x x x x x x x x                   x
A. graveolens                                            x x
Acronychia acronychioides                                    x
Amoora ferruginea                                  x
Barringtonia calyptrata                          x x
Beilschmiedia oligandra            x x x
B. sp. (Hyland 1982 #288)            x x
Calamus australis                                  x
C. moti                                              x
C. radicalis                                     x x   x
Chrysophyllum chartaceum                         x x
Corynocarpus cribbianus                                      x
Cryptocarya hypospodia             x
C. mackinnoniana                                                             x x x
C. oblata                          x
Davidsonia puriens                                 x     x
Diploglottis pedleyi                 x   x
Dysoxylum sp.                                                x
Elaeocarpus augustifolius                              x x
E. foveolatus                        x x
Endiandra compressa                  x
E. cowleyana                         x
E. sp. aff. E. impressicosta         x
E. montana                         x x x
E. sankeyana                       x x x
E. sp. aff. hypotephra             x x
Eugenia cormiflora                   x x x
Eugenia kuranda                      x x
Faradaya splendida                          x
Ficus congesta                                                               x
F. crassipes                       x x x x   x x x x x x   x   x x x x x x     x
F. obliqua var. petiolaris                  x
F. variegata                                     x x x         x       x x     x
F. virens                                   x                                   x
Ganophyllum falcatum                               x
Gmelina fasciculiflora                           x x
Irvingbaileya australis                            x
Myristica insipida                     x x
Nauclea orientalis                                           x
Piper sp.                            x
Pittosporum rubiginosum                              x
Podocarpus dispermus               x
Polyalthia michaelii                               x   x   x
Prunus turnerana                             x x
Rhysotoechia robertsonii                           x
Strychnos minor                                                 x
Syzygium dictyophlebium                              x          x
Terminalia sericocarpa                             x
Xanthophyllum octandrum                                x
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Understorey shrubs and herbs.

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                                   J A S O N D J F M A M J J A S O N D J F M A M J J
Alpinea coerulea                                     x
A. modesta                                       x x
A. sp.                                               x   x       x   x
Ardisia pachyrrachis                               x x
Cordyline terminalis                             x x x
Linospadix microcarya                    x     x x x x           x
Psychotria dallachyana                             x
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Secondary weeds

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                                   J A S O N D J F M A M J J A S O N D J F M A M J J
Cayratia clematidea                                             x
Octanthera sp.                               x x x x x       x   x x x     x x
Phytolacca octandra                                             x
Rubus alceaefolius                                 x   x                       x x
R. rosaefolius                                                  x
Solanum dallachii                          -                       x x       x
S. mauritianum                                     x
S. torvum                                   x x x x   x x       x x x       x   x
Trema orientalis                                                                 x
```

fruit production within species and between related taxa probably reflects similar physiological functioning, it would also appear to provide more seeds to satiate predators and perhaps, more conspicuous fruit crops to attract potential dispersers.

B. Hyland (unpublished) suggested that the average fruiting intervals in this region are not as long as those usually reported for the Malayan dipterocarps. R. Johns (unpublished) made a similar comment with regard to the lowland forest flora of Papua New Guinea. The fruit production data of the dipterocarp species they used to make this comparison may not, however, be typical of the majority of Malayan trees for Anon. (1927 in Barnard 1954); Mc Clure (1966); Medway (1972) and Burgess (1972) reported that most of the Malayan tree species they examined produced seed every 2 - 4 years.

There are several possible reasons why "small gap" species might be advantaged by having a fruit crop of consequence every two or more years. This strategy would, for instance, help these species avoid seed predation by short - lived specialized insects or rodents. It may also be related to efficient resource partitioning within the tree and enable it to produce a greater quantity of fruit in any one fruiting, thus being more likely to satiate predators, or if adapted to animal or bird dispersal, attract more potential dispersers. There is indeed no great need for "small gap" species to produce seed crops more often than every few years for most, if not all, are capable of establishing a pool of suppressed seedlings on the forest floor. These seedlings are ready to exploit additional resources made available from a canopy gap if one were to occur above them. It was also observed that those species which had seedlings of intermediate shade tolerance (e.g. _Toona_ _australis_ and _Flindersia_ _spp._), were more likely to produce annual or biennial seed crops than those shade tolerant species which had a pool of seedlings on the ground for several years after fruiting even when the forest canopy was intact.

5.1.3 Seasonality

Reich and Borchert (1984) thought that seasonal changes in the physiognomy of tropical rainforests were primarily caused by seasonal variation in rainfall rather than daylength or temperature. While the relative importance of these factors has still to be established for certain processes in many forest types, the examples below suggest that seasonal trends in fruiting in this region are associated with normal rainfall patterns.

Seasonality seemed most strongly developed in the group of wind dispersed species. The most prominent of these species belong to the genera _Flindersia, Argyrodendron, Toona, Cardwellia, Musgravea, Sterculia, Doryphora_ and _Atherosperma_ (an extended list is contained in Appendix A). Data collected for planning seed collections and from fruiting material in the CSIRO Atherton herbarium (QRS) indicated that almost all of these species shed their seeds during the late dry/early wet season period (November to February). An interesting partial exception was _Flindersia pimenteliana_. Although this species followed the normal pattern when it grew on the tablelands and highlands, seed shed occurred at lowland sites during June and July (early in the dry season). The reason for this shift in timing is not understood. Other _Flindersia spp._, with very similar seeds, retained their normal timing in lowland environments. Since seeds of _F. pimenteliana_ are short lived (maximum field life of 2-3 weeks) and this species is often common in lowland rainforests, the dry season of this part of the region cannot be so severe as to totally preclude the establishment of seedlings at this time.

Bird dispersed species showed much less seasonality, although again the late dry/early wet season seemed to provide the most variety (Tables 45 and 46). Studies reviewed by Howe and Smallwood (1982) indicated that in seasonal Neotropical rainforests, peak dispersal by animals was during the wetter months. It has been suggested that competition for dispersers may be responsible for spreading the fruiting season among bird dispersed plants (e.g. Howe 1977; McKey 1975). If this mechanism is operating here then the data in Tables 45 and 46

suggest that the spread has mainly occurred during that part of the year which appears most favourable for seedling establishment (see also Smythe 1970). During seed collecting activities some variability (one or two months) was observed in the time of maximum fruit production for the same species in different geographic areas and from one fruiting year to the next.

5.1.4 Duration

The wind dispersed species again appeared to have rather different characteristics from those which were bird dispersed. Since wind dispersed species do not have to compete with other species for dispersers, the only advantage to them of an extended fruiting season would be to improve their chances of establishing seedlings under favourable weather condition. This strategy does not seem to have been followed for almost all individuals of wind dispersed species were observed to shed their seed over a relatively short period, typically within a few days but always within a few weeks. Rapid dispersal could have advantages in circumstances where high seed predation rates were more of an obstacle to successful establishment than adverse weather conditions. It could also be a useful strategy to facilitate seedling establishment in favourable, if ephemeral environments and although these conditions do not seem to occur in rainforests, this strategy has been observed in species of fire prone environments e.g. some _Pinus_ and _Eucalyptus_ species.

The duration of dispersal for animal dispersed species appears to present divergent possibilities, for having all the fruit ripen at once may attract large numbers of nomadic dispersers whereas a spread over time may maximize dispersal opportunities by a smaller population of localised dispersers. The former may achieve a wider distribution but the latter provides more opportunities for a species to re-establish somewhere within its present distribution. Specific examples of the former strategy were not observed but are suspected amongst some species especially those of _Syzygium_ and closely allied genera.

Most bird dispersed species were observed to have mature fruit available for weeks, and in some cases months, of each fruiting year. For example, closely watched individuals of Cinnamomum laubatii, Arytera divaricata and Litsea leefeana progressively produced ripe fruit over periods of 10, 13 and 10 weeks respectively in 1980. Other species e.g. Acronychia acidula seemed able to hold mature fruit in their crowns for periods of a month or more. Frankie et al. (1974) observed similar phenomena in a Costa Rican rainforest.

While Howe and Eastabrook (1977) predicted that "small gap" species should have regular extended fruit crops which are dispersed by specialist frugivores, irregular extended fruiting (probably to avoid predation – Janzen 1976) was found to be the usual mode within this group of species. In fact in this region regular extended fruiting appeared to be more characteristic of "large gap" than "small gap" species.

5.1.5 Quantity

Very little quantitative data are available on the numbers of seed produced by rainforest trees in this region. However, B. Hyland (unpublished) estimated that a large tree of Cardwellia sublimis yielded 12,800 seeds and that a similar sized tree of Flindersia pimenteliana produced 144,000 seeds. An exceptionally large seed crop of Agathis robusta in the Bridle Creek area (25 km west of Cairns) during 1975 resulted in seedling densities of 50-100 m^{-2} over several hundred hectares of forest. The great importance of occasional very heavy seed crops in relation to the satiation of seed predators and assemblage diversity, has been mentioned by Janzen (1971; 1974; 1976) and Newman (1982) and will be discussed in the final Chapter.

While B. Hyland (unpublished) found indications that emergents and trees in silviculturally treated forests in this region, may have larger fruit crops than others of that species grown in restricted situations, quantitative data are not available. In contrast Chan (1980) found that individuals of some Shorea spp. in Malaya produced less seed in isolated situations (perhaps because cross pollination was obligatory

for these species).

Phenological data relating to the fruiting frequency, seasonality, duration and quantity characteristic of the component species, appear to be essential if predictive models of rainforest dynamics are to be developed. However, experience here has been that to be of value these data must be collected over a considerable period (5 years would seem to be an absolute minimum) and obtained from individual trees as well as on a species and area basis. They must also be closely linked to studies of germination and seed predation. Observations aimed at providing this information are in progress but are not yet far enough advanced to add significantly to our understanding of this complex topic.

5.2 Predation

The importance of seed predation in the dynamics of rainforest trees has been widely recognized and has, for some species, been closely examined (e.g. Janzen 1980). Indeed Janzen (1970), Connell (1971) and others have advanced the theory (previously mentioned in Section 2.3.1) that density dependent seed predation is an important mechanism in the establishment and maintenance of diversity and pattern in tropical forests. However, Connell now seems to have moved away from this theory (Connell 1978).

Two preliminary experiments were carried out to provide some information on the role of small mammals and birds in the predation of seeds on the forest floor. In the first trial seeds of a number of species were placed on the floor of an undisturbed rainforest in Wongabel forest 5 km south of Atherton. Half the seeds of each species were covered with a wire mesh (1.5 cm) screen; the other half were exposed. An assessment of predation was made 24 hours later. While those under the screen were invariably untouched, many of those exposed had disappeared (Table 47). The few chewed up remains suggested that most of those missing had been consumed on the spot, presumably by rodents. Some of the larger seeds (e.g. those of Triunia sp.) had obviously been carried a few metres

so that they could be wedged between convenient stones or roots while they were being eaten. As a result of some recent small mammal trapping in similar areas by F. Crome (pers. comm.), I now suspect that rodent populations here may have been relatively high, as they seem to be wherever the large seeds of Aleurites moluccana, a prominent species in this stand, are readily available as a food source.

The second predation trial was carried out in conjunction with the third establishment and growth trial (described in Section 4.6). Here seeds were placed on disturbed sites as well as those in the open. Predation rates (Table 48) were in general lower than those recorded in the previous trial. Again they suggested that there are important interspecific differences. There was also a tendency (sometimes significant at the 5% probability level) for predation to be greater under an intact canopy than on disturbed sites. The high palatability of Agathis robusta seed was very apparent in these results. Similar observations by B. Hyland (unpublished) had led him to believe that this species would not persist in logged forest. However, it is now apparent that a mast seed crop, such as that reported in the previous Section, can overcome this problem.

The role of insects in seed predation has not been closely examined although some observations were made. Already mentioned in the discussion of the third establishment and growth trial (Section 4.6) were the effects that ants had on the seed of some species on the forest floor. The fruits of a few rainforest tree species almost invariably appeared to be galled and lacked fully developed seeds. In one species, Halfordia scleroxyla, several hundred fruit, from different trees and over different fruiting seasons, were examined and only two seeds which appeared viable, were found. However, insect predation does not seem to be as important here as it is in those Central American forests described by Janzen (1980).

Some birds appeared to be predators both of fallen seeds and immature seeds contained within unripe fruit. The large megapods, Alectura lathami and Megapodius freycinet are

Table 47. The number of seeds of some rainforest tree species remaining after 24 hours exposure on the forest floor beneath an intact rainforest canopy.

Species	No. seeds at start	No. remaining
Argyrodendron polyandrum	20	13
Cryptocarya mackinnoniana	20	19
Cryptocarya sp. aff. C. corrugata	20	6
Elaeocarpus bancroftii	7	0
E. ruminatus	16	0
Endiandra montana	25	25
Triunia sp.	10	0
Maytenus disperma	20	0
Pittosporum·sp.	20	8
Rhodamnia argentea	19	0

Table 48. The mean number (from 8 replicates) of seeds remaining on the forest floor under different canopy treatments.

Species (seeds/replicate)	Exposure duration (days)	Canopy treatment		
		Intact	Small gap	Large gap
Agathis robusta (10)	1	4.0(3.0)	4.2(4.0)	8(1.6)
	6	1.6(2.1)	2.0(1.9)	4.3(3.2)
	17	0	0	0.6(1.6)
Argyrodendron polyandrum (10)	1	8.6(1.6)	8.8(1.4)	8.8(2.3)
	6	8.3(1.7)	8.6(1.3)	8.1(2.8)
	17	0	4.4(3.0)	1.0(2.6)
Flindersia brayleyana (15)	1	15(0)	13.9(2.0)	14.5(0.5)
	6	13.5(1.5)	13.5(2.2)	14.1(0.9)
	17	9.3(3.3)	12.1(2.1)	13.0(1.5)
Cardwellia sublimis (10)	1	9.9(0.3)	9.0(1.2)	9.7(0.4)
	6	8.4(2.5)	7.6(2.1)	8.4(1.0)
	17	2.0(2.0)	2.3(2.0)	4.1(3.3)

(standard deviation)

probably the most important of the ground dwelling seed predators. <u>Acacia</u> <u>aulacocarpa</u> seeds were recovered from the crop of <u>A.</u> <u>lathami</u>. Since this bird has a well developed gizzard, it is unlikely to be effective in seed dispersal. Local Aborigines have also reported that this bird can peck open the large hard shelled seeds (4 cm dia.) of <u>Endiandra</u> <u>palmerstonii</u> and eat the cotyledons and embryo within.

The other conspicuous group of avian seed predators are the parrots and cockatoos. These specialize in extracting seed from fruit approaching maturity. Species often affected were <u>Flindersia</u> and <u>Alphitonia</u> <u>spp.</u>.

The immature fruit of many species have characteristics which would make them unattractive to predators and potential dispersers alike. Their defences included non signalling colours (green or brown are widespread), spines (e.g. <u>Flindersia</u> <u>spp.</u>) and chemical irritants (e.g. the volatile oils present in the fruit of many Rutaceous species and stinging hairs on the stems and leaves of <u>Dendrocnide</u> <u>spp.</u>).

Overall the impression was gained that seed predation can be an important factor in determining the composition and number of seedlings becoming established on the forest floor. However, casual observations suggested that density dependent predation in the so-called "seed-shadow" may not be important for most tree species in this region. Indeed a common feature of these forests were the dense stands of suppressed seedlings beneath large trees of "small gap" species especially where these belonged to the families Sterculiaceae, Lauraceae and Myrtaceae. Although some overseas studies (e.g. Clark and Clark 1984) have provided data showing that density dependent predation (the basic mechanism of the "escape hypothesis" - Janzen 1970; Connell 1971) might play a role in the dynamics of some rainforests, other studies reviewed by Howe and Smallwood (1982) indicate that it may not be nearly as important as once thought.

5.3 Dispersal

Dispersal is usually seen as the mechanism which allows a

species a chance of occupying new sites which are unpredictable in time and space (Howe and Smallwood 1982), of establishing without being in direct competition with the parent and of avoiding other aspects of density dependent mortality (Regal 1977; Howe and Vande Kerckhove 1979; Janzen 1971). It may also be an important mechanism for promoting gene flow within a species (Cruz 1981) and of escaping from certain chronic diseases such as some root rots and viruses.

After many early observations of the dispersal mechanisms used by tropical plants (e.g. Ridley 1930) interest in this topic seems to have waned. There are, however, signs of renewed activity in this field especially by avian biologists (e.g. Proctor 1968; Snow 1981; Howe 1977; 1983) and plant biogeographers interested in the development of regional floras (e.g. Carlquist 1974). The review of the ecology of seed dispersal by Howe and Smallwood (1982) provided many examples for tropical rainforests.

Although little information on the dispersal of Australian rainforest species has been compiled, much can be inferred from the ornithological literature (e.g. Crome 1975a and b; 1976) and from botanical descriptions and the characteristics of fruit and seeds preserved as botanical specimens. Using information of this kind Webb and Tracey (1981) were able to draw up "dispersal spectra" for some selected rainforest sites in this region. They noted that 75-95% of the plants in the rainforests they examined were apparently bird dispersed.

An indication of the primary dispersal mechanisms of the tree species encountered in the permanent plots is given in Appendix A. The summary in Table 49 shows that the overwhelming majority of these species are also bird dispersed. In the first part of the following Section, bird dispersal, and in particular, dispersal by the Cassowary, Casuarius casuarius, is examined.

5.3.1 Birds

Of all the rainforest bird species, those which were most conspicuous as seed dispersal agents were the pigeons. All

Table 49. The primary dispersal agents of 421 of the tree species encountered in the permanent plots.

Agent	Proportion %
birds	79.6
wind	12.8
gravity	5.0
bats	1.7
other animals	0.9

Table 50. Rainforest plant species observed on Green Island as small seedlings but not as adult plants.

Trees

    Archontophoenix alexandrae

    Carallia brachiata

    Calophyllum sil

    Dysoxylum muelleri

    Eugenia sp.

    Glochidion sp.

    Melia azedarach

    Podocarpus neriifolius

    Pseudocarapa nitidula

    Ptychosperma elegans

Vines and shrubs

    Alyxia spicata

    Calamus australis

    Cayratia sp.

the rainforest members of this group are obligate frugivores
(Crome 1975a and b). Most species are usually restricted to
intact rainforests although the Brown Pigeon (<u>Macropygia</u>
<u>amboinensis</u>) was often seen in secondary vegetation and
appeared to be responsible for the spread of many "large gap"
weeds such as <u>Solanum</u> and <u>Rubus</u> <u>spp.</u> Others, particularly the
Flock Pigeon (<u>Lopholaimus</u> <u>antarcticus</u>) and the Torres Strait
Pigeon (<u>Ducula</u> <u>spilorrhoa</u>) were sometimes observed to feed in
rainforest remnants which were surrounded by pasture land.
This was especially noticeable on parts of the Atherton
Tableland where the heavy fruit crops often found on isolated
trees of·<u>Acronychia</u> <u>acidula</u>, were eagerly consumed by Flock
Pigeons.

Torres Strait Pigeons are migratory birds with flocks
leaving Papua New Guinea in July each year and making their
way southwards along the coast of north-east Queensland.
Although they feed on fruit in coastal lowland rainforests,
they usually nest on offshore islands before returning
northwards to Papua New Guinea in January. This species can
swallow quite large fruit and is known to carry seeds of many
species from the mainland to offshore islands (Crome 1975a).
Indeed the presence of many rainforest species observed on
Green Island (13 km from the nearest mainland) as seedlings
but not as adult plants (Table 50) can probably be attributed
to this species of pigeon (G. Stocker and B. Hyland
unpublished). The seasonally dry sandy calcareous soils on
this Island (which is essentially a coral cay) appeared to
prevent many rainforest species from becoming established.
The potential of the Torres Strait Pigeon for dispersing plant
species between Australia and Papua New Guinea is considerable
and it would appear advisable, both from a scientific and a
quarantine viewpoint, to examine the biology (including the
seed dispersal potential) of this species more closely.

Investigations, as yet unpublished, have also been carried
out on a group of more sedentary frugivores - the Bower Birds
(<u>Ptilonorhynchus</u>, <u>Prionodura</u> and <u>Scenopocetes</u> <u>spp.</u>) (D. Frith
pers. comm.). I suspect that members of this group will
prove to be important local dispersal agents. Of the other
frugivorous birds in the region the Cassowary is the most

conspicuous and a study of aspects of seed dispersal by this species is described below. Although many other species of frugivorous birds live in the rainforest, little if anything is known of their dispersal potential. Investigations elsewhere by Howe (1977; 1984) suggests that it is probably very variable. Howe (1984) maintained that the identification of "pivotal species", both of plants and dispersal agents, is a challenge which must be met if the long term management of rainforest patches is to be soundly based.

5.3.1.1 Cassowary dispersal

Cassowaries are very conspicuous frugivores in this region and could be "pivotal species". They are large (standing to 1.5 m high), powerfully built, flightless birds which are found in or near rainforests in north-east Australia, New Guinea and some adjacent islands (Rand and Gilliard 1967) (Figure 63). Of the three extant species recognized, C. casuarius is the most widespread and is the only species now found in Australia. They are reasonably common in lowland rainforests north of Ingham where their presence is indicated by tracks and piles of dung (Plate 31). The latter are readily recognizable, each consisting of up to 1 kg of seeds and fruit fragments. Crome (1976) used these dung components to identify the plant species contributing to their diet. The observation that seeds frequently germinated within the dung piles (Plate 32) prompted the present study. Although Ridley (1930) provided several reports of Cassowaries dispersing seeds of some forest species on Ceram and the Aru Islands, the Cassowary was not included in Snow's world survey of tropical frugivorous birds and their food plants (Snow 1981) and except for the notes of Crome (1976) and Frizelle (in White 1913) very little seems to be known of this bird's biology.

Site and methods - The study area was within Barong Logging Area on State Forest Reserve 755 (Lat. 17° 32' S; Long. 145° 50' E) at about 60-120 m above sea level. It lies 15 km to the south-east of the highest mountain (Mt Bartle Frere - 1622 m) in this region and about 55 km north-west of the study areas of Crome and Frizelle. Plot no. 9 (see Chapter 3 for details) lies within the study area and appears reasonably
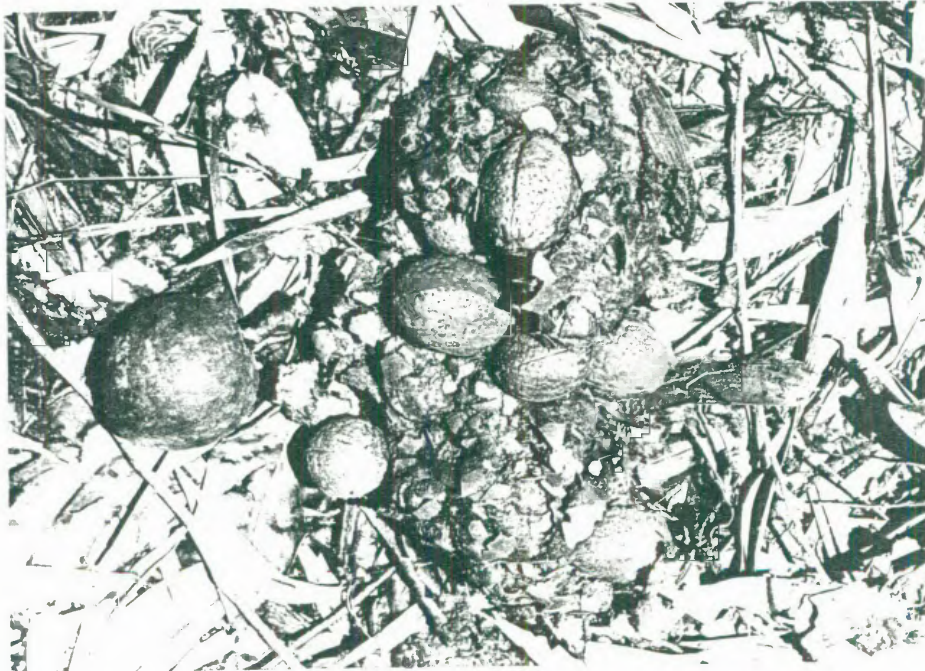
Plate 28. A fresh pile of Cassowary dung. The large seeds are from the fruit of Elaeocarpus bancroftii. A whole fruit (dia. 4.5 cm) of this species has been placed to one side for comparison.

Plate 29. A clump of Elaeocarpus augustifolius seedlings from an old Cassowary dung pile.

representative of the surrounding vegetation.

Collections of dung piles were made once every month from July 1977 to July 1979 inclusive, along and adjacent to, the final 10 km of a logging road. Although most were made from open areas such as roads, logging tracks and loading ramps, many were also found on the floor of undisturbed parts of the forest. At each visit an attempt was made to collect a minimum of six fresh undisturbed droppings. They were placed in plastic bags and transported back to the laboratory in Atherton. As soon as possible, usually the following day, each dropping was washed and for convenience, sorted into 3 size fractions. The origins and fresh weight of the different materials in each fraction were noted. The numbers of larger (> 0.5 cm dia.) seeds were also recorded. All the collected material was then placed in pots on a steam pasturized sand/peat potting medium (U.C. mix type B; Baker 1957) in a heated (minimum 18°C) glasshouse. After a minimum of 7 months the resulting seedlings were identified and the numbers of each species present recorded.

Results - The number of droppings examined each month averaged 5.5 (range 0-8, see Table 50). They were usually easily found except during the first four months of 1979 when a total of only seven were collected. The number of species of diaspore (as defined by van der Pijl 1969) recorded in each month's collection averaged 9.5 (range 2-21). There was a tendency for the number of species in the collections to follow a seasonal pattern with the minimum coinciding with the early part of the dry season (Table 50). The species contributing to the Cassowaries' diet during the study period are listed in Table 51. This Table also includes an indication of diaspore characteristics and some features of the parent plant. In this Table the boundary between medium and large diaspore size was placed at the estimated upper limit of fruit size (8 ml) which can be swallowed by the large fruit pigeons of New Guinea (Frith et al. 1976). About one third of the species of diaspores recorded, fell into the large category. Whole fruit either as drupes, berries or syconiums contributed much more to Cassowary diets than arillate seeds or other form of diaspore.

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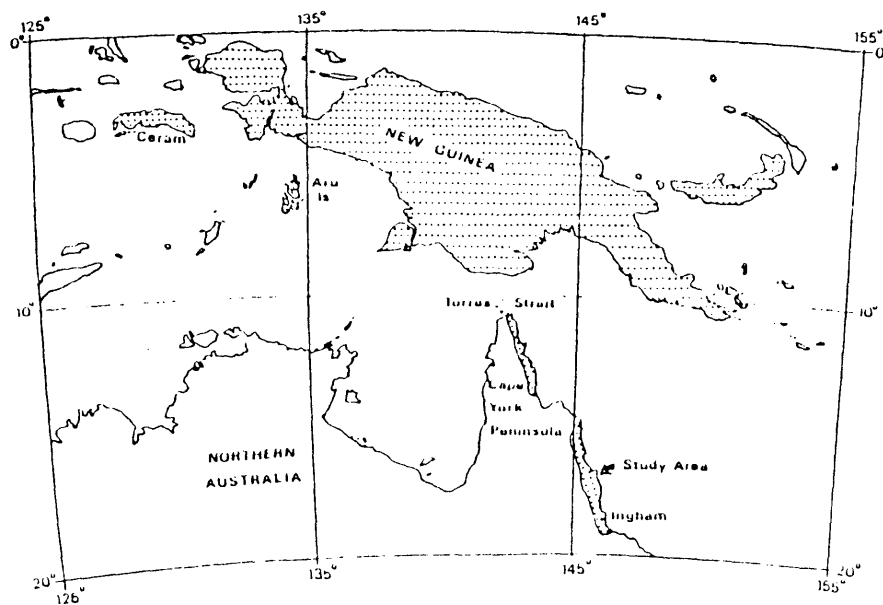
Figure 64. The shaded areas indicate the distribution of the three extant Casuarius spp.. C. casuarius is found in north-east Australia, southern and western New Guinea and on Ceram and the Aru Islands. C. unappendiculatus occurs in the northern lowlands of New Guinea while C. bennetti is found in the highlands (Rand and Gilliard 1967).

Table 51. Dung sample size and the total number of species of diaspore recorded in each monthly sample.

Month/Year		No. collections	Number spp. recorded
July	1977	3	4
August		6	9
September		6	17
October		6	20
November		6	10
December		8	10
January	1978	7	10
February		6	21
March		6	13
April		7	16
May		6	4
June		6	7
July		6	7
August		6	4
September		6	5
October		6	12
November		2	5
December		8	10
January	1979	3	11
February		2	7
March		2	2
April		0	0
May		6	8
June		7	7
July		5	9

Species of Cyperaceae, Poaceae and Compositae which appeared in the germination pots were not included in the Tables 50 and 51 for they were almost certainly derived from wind dispersed seeds blown onto the dung piles before they were collected. Two suspect species were, however, included. Both were recorded only once. The first, Castanospermum australe, is a common leguminous tree which has a simple diaspore of a large brown seed devoid of a fleshy pericarp or aril. Its presence probably reflects either the rather non selective nature of the Cassowaries' foraging habits or an accidental inclusion in the dung sample by the collector. The second, Trema orientalis, has a small fleshy drupe about 2 mm in diameter. It seems unlikely that Cassowaries would deliberately eat a fruit this small and it may have become attached to the dung after dispersal by a smaller frugivore.

The largest fruits consumed by Cassowaries in this study were those of Beilschmiedia sp. RFK 288. One dropping contained 13 of these fruit which had passed through the digestive system more or less intact. Their average diameter was 6 cm and average weight 52 g. In addition to fruit and fruit derived materials, other objects were occasionally observed in the droppings. These included bracket fungi, land snail shells, portions of tree fern (Cyathea sp.) fronds and fragments of Freycinetia sp. inflorescences.

An indication of the germination percentage of seeds individually identifiable in the dung samples is given in Table 51. Only 9 of the 78 species recorded failed to produce some seedlings. In general species in the Lauraceae and Myrtaceae germinated well. The best result was obtained from the large fruited laurel, Beilschmiedia oligandra, where only 3 of 400 seeds failed to germinate. One of the worst results was with Elaeocarpus foveolatus with only 6 of 1851 seeds germinating. Other Elaeocarpus and Acronychia spp. also germinated very poorly. The germination of several species improved as the fruiting season progressed. Collections of Prunus turnerana for example, had germination percentages of 0 for October, 6 for November and 86 for December 1978. With the possible exception of a few species, e.g. Rubus alceaefolius,

Table 52. Some characteristics of plant propagules collected in Cassowary dung

Taxa	Parent plant			Dispersal unit				Collection	
	Life form[a]	Habitat	Fruit type	Type	Size[b]	Colour	No.seeds	Frequency (months)	Germination[c]
Agavaceae									
Cordyline terminalis	pachycaul L	rainforest	berry	berry	small	red	4	3	n.a.
Annonaceae									
Polyalthia michaelii	tree M	rainforest	berry	berry	large	yellow	1	4	good
sp.	-	-	-	-	-	-	1	1	good
Apocynaceae									
Cerbera floribunda	tree M	rainforest	drupe	drupe	large	blue	2	3	nil
Barringtoniaceae									
Barringtonia calyptrata	tree U	rainforest	drupe	drupe	large	blue	1	3	good
Burseraceae									
Canarium muelleri	tree M	rainforest	drupe	drupe	medium	blue	1-2	1	nil
Combretaceae									
Terminalia sericocarpa	tree U	rainforest	drupe	drupe	small	purple	1	1	n.a.
Corynocarpaceae									
Corynocarpus cribbianus	tree L	rainforest	drupe	drupe	large	red	1	1	moderate
Davidsoniaceae									
Davidsonia pruriens	tree L	rainforest	berry	berry	large	purple	1-2	6	moderate
Elaeocarpaceae									
Elaeocarpus angustifolius	tree U	rainforest	drupe	drupe	medium	blue	1-4	3	moderate
E. foveolatus	tree U	rainforest	drupe	drupe	small	blue	1	4	poor
E. stellaris	tree M	rainforest	drupe	drupe	large	blue	2-4	2	nil
Himantandraceae									
Galbulimima belgraveana	tree U	rainforest	berry	berry	medium	red	7-10	1	nil
Icacinaceae									
Irvingbaileya australis	tree L	rainforest	drupe	drupe	large	white	1	6	moderate
Lauraceae									
Beilschmeidia sp.(Byland 1982, #288)	tree U	rainforest	berry	berry	large	black	1	2	good
B. oligandra	tree U	rainforest	berry	berry	large	black	1	4	good
Cryptocarya glabella	tree M	rainforest	drupe	drupe	large	red	1	3	nil
C. hypospodia	tree M	rainforest	berry	berry	medium	black	1	2	moderate
C. mackinnoniana	tree M	rainforest	berry	berry	medium	black	1	4	good
C. oblata	tree M	rainforest	berry	berry	large	orange	1	1	good
C. sp. aff. C. rigida	tree L	rainforest	berry	berry	small	black	1	2	nil
Endiandra compressa	tree M	rainforest	berry	berry	large	yellow	1	1	moderate

Species	Life form	Habitat	Fruit	Dispersal unit	Size	Colour	Seeds	No.	Rating
E. cowleyana	tree U	rainforest	berry	berry	medium	black	1	3	good
E. sp. aff. E. impressicosta	tree M	rainforest	berry	berry	large	black	1	1	good
E. montana	tree M	rainforest	berry	berry	large	orange	1	3	good
E. sankeyana	tree M	rainforest	berry	berry	large	black	1	3	good
E. sp. aff. E. hypotephra	tree M	rainforest	berry	berry	medium	black	1	3	good
Leguminosae									
Castanospermum australe	tree U	rainforest	legume	seed	large	brown	1	1	nil
Melastomataceae									
Octanthera sp.	shrub	riparian forest	berry	berry	medium	pink	10	12	n.a.
Meliaceae									
Amoora ferruginea	tree L	rainforest	berry	berry	medium	yellow	1-3	1	good
Dysoxylum sp.	-	-	-	-	-	-	-	1	moderate
Menispermaceae									
sp.	-	-	-	-	-	-	-	1	moderate
Moraceae									
Ficus congesta	tree L	rainforest	syconium	syconium	medium	cream	>10	2	n.a.
F. crassipes	strangler U	rainforest	syconium	syconium	large	yellow	>10	5	n.a.
F. obliqua var. petiolaris	strangler U	rainforest	syconium	syconium	small	red	>10	1	n.a.
F. triradiata	strangler U	rainforest	syconium	syconium	medium	yellow	>10	14	n.a.
F. variegata	tree U	rainforest	syconium	syconium	medium	cream	>10	7	n.a.
F. virens	strangler U	rainforest	syconium	syconium	medium	yellow	>10	2	n.a.
Myristicaceae									
Myristica insipida	tree M	rainforest	dehiscent drupe	arillate seed	medium	red	1	3	moderate
Myrsinaceae									
Ardisia pachyrrachis	shrub L	rainforest	berry	berry	small	red	1	2	n.a.
Myrtaceae									
Acmena divaricata	tree M	rainforest	berry	berry	large	red	1	13	good
A. graveolens	tree M	rainforest	berry	berry	large	red	1	2	moderate
Eugenia cormiflora	tree M	rainforest	berry	berry	large	white	1	3	good
Eugenia kuranda	tree M	rainforest	berry	berry	large	brown	1	2	good
Syzygium dictyophlebium	tree U	rainforest	berry	berry	medium	cream	1	3	good
Palmae									
Calamus australis	liane U	rainforest	drupe	drupe	medium	yellow	1	1	n.a.
C. moti	liane U	rainforest	drupe	drupe	medium	yellow	1	1	good
C. radicalis	liane U	rainforest	drupe	drupe	medium	yellow	1	7	moderate
Linospadix microcarya	pachycaul L	rainforest	drupe	drupe	small	red	1	8	good
Phytolaccaceae									
Phytolacca octandra*	herb	disturbed areas	berry	berry	small	black	6-8	1	n.a.
Piperaceae									
Piper sp.	vine M	rainforest	berry	berry	small	red	1	1	moderate
Pittosporaceae									
Pittosporum rubiginosum	tree L	rainforest	capsule	arillate	medium	red	2-4	1	n.a.

Species	Habit	Habitat	Megasporophyll	Fruit type	Size	Colour	Seeds/fruit	No.	Dispersal
Podocarpaceae									
Podocarpus dispermus	tree L	rainforest	drupe	arillate seeds	medium	red aril, black seed	1	1	n.a.
Rosaceae									
Prunus turnerana	tree M	rainforest	drupe	drupe	large	black	1	3	good
Rubus alceaefolius	scrambler	disturbed areas	aggregate fruit	aggregate fruit	medium	red	>10	4	n.a.
R. rosaefolius	scrambler	disturbed areas	aggregate fruit	aggregate fruit	medium	red	>10	1	n.a.
Rubiaceae									
Antirhea tenuiflora	tree L	rainforest	berry	berry	small	red	1-3	4	n.a.
Nauclea orientalis	tree U	rainforest	aggregate fruit	aggregate fruit	large	yellow	>10	1	n.a.
Psychotria dallachyana	shrub L	rainforest	berry	berry	small	cream	2	4	n.a.
Rutaceae									
Acronychia acronychioides	tree L	rainforest	drupe	drupe	medium	yellow	1-4	5	poor
A. vestita	tree M	rainforest	drupe	drupe	medium	cream	1-4	4	nil
Sapindaceae									
Diploglottis pedleyi	tree L	rainforest	capsule	arillate seed	large	red	1	1	good
Ganophyllum falcatum	tree M	rainforest	drupe	drupe	small	orange	1	2	n.a.
Rhysotoechia robertsonii	tree L	rainforest	capsule	arillate seed	medium	yellow aril black seed	1-3	1	good
Sapotaceae									
Chrysophyllum chartaceum	tree L	rainforest	berry	berry	medium	purple	1-2	2	n.a.
Planchonella sp.	tree	rainforest	berry	berry				3	nil
Siphonodontaceae									
Siphonodon membranaceous	tree M	rainforest	berry	berry	large	orange	>10	1	nil
Solanaceae									
Solanum dallachii	shrub	disturbed areas	berry	berry	medium	green	>10	3	n.a.
Solanum mauritianum*	shrub	disturbed areas	berry	berry	medium	yellow	>10	1	n.a.
S. torvum*	shrub	disturbed areas	berry	berry	medium	yellow	>10	10	n.a.
Strychnaceae									
Strychnos minor	vine U	rainforest	berry	berry	medium	yellow	1-4	1	moderate
Ulmaceae									
Trema orientalis	tree U	disturbed areas	drupe	drupe	small	black	1	1	n.a.

Verbenaceae								
Gmelina fasculiflora	tree M	rainforest	drupe	drupe	medium	blue	1	3	moderate
Faradaya splendida	vine U	rainforest	berry	berry	large	white	1	1	good
Vitidaceae								
Cayratia clematidea	liane M	disturbed areas	berry	berry	small	black	3	1	n.a.
Xanthophyllaceae								
Xanthophyllum octandrum	tree M	rainforest	capsule	capsule	small	black	1-2	1	n.a.
Zingiberaceae								
Alpinea caerulea	tall herb	disturbed area	berry	berry	small	blue	>10	1	n.a.
A. modesta	herb L	rainforest	berry	berry	small	blue	>10	3	n.a.
sp.	-	-	-	-	-	-	-	2	n.a.

a. L,M and U denote that the species is typically found in either the lower(L), middle(M) or upper(U) levels of forest canopy.

b. size based on volume calculated from propagule dimensions.

    small - <1 ml
    medium - 1-8 ml
    large - >8 ml

c. n.a. - germination occurred but no data on seed numbers in the collection(s) are available.

    poor - 0 - 3%
    moderate - 3-30%
    good - >30%

* introduced weeds

Ficus _spp._ and _Elaeocarpus_ _spp._, observations of the remaining seeds at the time of germination assessment indicated that germination was complete.

Discussion - Results confirmed previous observations (Crome 1976) that Cassowaries were primarily dependent on fruit from rainforest trees for their survival. They also showed that many of the seeds passed by Cassowaries retained their viability and that this bird is potentially an important dispersal agent for many rainforest plant species.

Cassowaries seemed to feed mainly on fruit which has fallen from the middle and upper canopy levels of "primary" rainforests. Only 14 of the species listed in Table 52 normally bear fruit within their reach. Three of these species are trees (e.g. see Plates 30 and 31); the remainder herbs, shrubs and scramblers. Furthermore fruit production from understorey species was observed to be low except on recently disturbed sites where "large gap" weed species, such as _Solanum_ _torvum_, may produce heavy fruit crops. Although droppings generally contained a mixture of several species, there were occasions when seeds and fruit fragments of a single species made up most of a month's collections. Taxa in this latter category included _Beilschmiedia_ _oligandra_, _Cryptocarya_ _mackinnoniana_, _Elaeocarpus_ _foveolatus_, _Prunus_ _turnerana_ and several individual species of _Ficus_, _Acronychia_ and _Calamus_. There were no indications that Cassowaries were selective about the site they choose for defecation for, although most of the collections were made from disturbed sites, it appeared that this only reflected the greater visibility of dung piles on these areas.

During the initial sorting process it was observed that many fruits with firm pericarps, especially those not fully mature, appeared to pass through Cassowaries almost unaltered. An apparently gentle digestive tract has been reported for other specialized frugivores and probably serves to protect them from poisonous compounds in seeds (McKey 1975). In this study it also appeared to ensure that a large percentage of seed with even the thinnest of seed coats could pass through a Cassowary undamaged. However, while Cassowaries are

Plate 30 and 31. The <u>Ficus</u> species have evolved several specialized fruiting displays. The upper photograph shows fruit developed from the roots of <u>F. congesta</u>. The lower species (<u>F. variegata</u>) has infrutescences from the small twigs to the base of the bole.

undoubtedly specialized frugivores, the incidental component of their diet recorded here and in Crome (1976), suggested that they are also forest floor scavengers.

There were some indications from simple glasshouse germination trials (Section 5.4) that the germination characteristics of seeds which have passed through Cassowaries were little different from those of seeds which have had externally adhering fleshy material either left intact or removed manually. However, this question cannot be adequately answered without controlled studies using captive birds. While there appears to be some debate as to the effects of passage through the gut on the germination characteristics of seeds, Howe and Smallwood (1982) also observed that most animal dispersed seeds germinated without handling or achieved only slight advantage by handling. The failure of nine of the 79 species eaten to germinate cannot positively be attributed to passage through a Cassowary for seven of them were represented by less than six seeds. Furthermore, it was suspected that the seeds of some species may not have been viable because of immaturity or insect damage and that, in some months (especially October and November), hot dry weather conditions may have adversely affected the germination of seeds from some droppings collected from open areas such as roads and logging ramps. One of the remaining species, Acronychia vestita, was found in larger numbers but has rarely germinated reliably under glasshouse conditions (see Section 5.4).

Even if passage of seeds through a Cassowary does not directly alter their germination characteristics, the digested flesh passed with them may affect germination and seedling establishment by retaining enough moisture to prevent seeds with thin and presumably pervious seed coats, from being killed by desiccation (Section 5.4). Moisture retained by this fine digested material may also enable seedlings to progress beyond the critical early establishment phase. This material also appeared to deter seed predating rodents for several small piles of Beilschmiedia oligandra seeds, from which adhering flesh had been removed by hand, were much more rapidly scattered and predated than dung piles containing the

same species. However, even in dung piles, seeds which had not germinated were eventually scattered and their contents eaten after one or two months of washing by rain. The observation of seeds in dung piles being less liable to predation contrasts with those of Janzen (1982) who found the opposite effect in his studies of seed predation by rodents in Central American rainforests.

Species germinating in dung piles must usually, because of their proximity, face strong inter- and intra-specific competition. As a result large seeded species appear to have an advantage over smaller ones in the dung pile environment as their additional seed reserves may allow them to produce a taller seedling in the period immediately following germination (see Section 4.7) and thus shade out competitors with smaller seeds. This may account for the dominance of single seeded diaspores recorded for those large fruited species primarily dependent on Cassowaries for dispersal. Most of the many seeded diaspores are of small to medium size (see Table 52) and appear to be widely dispersed by a variety of frugivores.

Unfortunately not enough is known about the biology of the Cassowary to make an assessment of its role in long distance dispersal but it must be important over shorter distances and in particular in ensuring that large diaspores reach higher ground. It is hoped that further work can be undertaken to provide data on the time taken for seeds to pass through their digestive tract and the extent of their daily and seasonal movements. At the present time there is no information beyond the following brief observations :- Ridley (1930) found that a captive Cassowary fed fruits of <u>Chrysobalanus</u> <u>icaco</u> L. retained the seeds for at least 10 hours 40 minutes; Frizelle (in White 1913) thought that they might have territories from 0.5-2 square miles (1.3-5 km^2). Although it has also been suggested that they shift in response to seasonal conditions, the evidence is largely circumstantial. For example, Crome (1976) found low numbers of droppings in the February to May period and suggested that during this time the birds had either left the area, considerably extended their foraging ranges, or were starving. I also noted one period early in

1979 when droppings were difficult to find and concluded, rather tentatively, that they had moved from the study area.

While the efficiency of Cassowaries as long distance dispersers of seed cannot be critically assessed, I have seen them moving through open eucalypt woodland on northern Cape York Peninsula. Thus they may be important in moving large seeds across areas of unfavourable environment, for example from the gallery rainforest of one river system to the next. In prehistoric times it is conceivable that they could have carried plant species between Australia and New Guinea for Torres Strait is very shallow and was dry as recently as 8,000 years ago (Nix and Kalma 1972; also Section 2.2.3).

5.3.2 Bats

Unfortunately very little is known of the biology of bats in this region and much research will be required before their role in plant dispersal can be critically assessed. It has, however, been reported (Fleming and Heithaus 1981) that bats were important in dispersing species for "secondary" successions as well as maintaining the heterogeneity of "primary" forest in Costa Rica. In north-east Australia the fruit bats, Pteropus spp., may be important dispersers especially of species which have medium sized fruit (see Table 51 for a definition of fruit sizes) and fruit with many small seeds which they are forced to swallow (e.g. Ficus spp.). They also seemed to be short distance dispersers of some species having relatively large seeds (Eugenia kuranda and Barringtonia calyptrata). However, few plants in the flora have characteristics specifically associated with bat dispersal (e.g. dull coloured and strongly smelling fruits - van der Pijl 1969).

5.3.3 Other mammals

None of the larger terrestrial or arboreal mammals inhabiting the region's rainforests are specialized frugivores. The arboreal tree kangaroos, Dendrolagus spp. and most of the possums Trichosurus, Pseudocheirus and

Dactylopsila spp. are strictly herbivorous. However, the indigenous rodents (Rattus, Melomys and Uromys spp.) appear to disperse some fallen fruit. For example white tailed rats (U. caudimaculatus) were caught in box traps baited with clusters of the fruit of Dendrocnide moroides. Seeds of D. moroides which were recovered from the dung of captured rats, germinated readily. It was also of interest to observe that small patches (< 0.5 ha) of rainforest isolated by farmland seldom contained the otherwise ubiquitous D. moroides. This suggests that these patches were not large enough to contain a rodent population sufficient to maintain a seed rain of this short lived shrubby species.

Despite the comments above, I suspect that the general role of rodents is more often that of seed predators and that, except for a few species with small hard seeds (such as those of D. moroides), effective dispersal only occurs as an accident when the seed is lost before it can be eaten. While this mode of dispersal is somewhat akin to that of the "scatter hoarders" of other regions, the seed hoarding habit has not yet been observed in this region. A few large fruit species such as Aleurites moluccana, Castanospermum australe (in some localities only) and Macadamia spp. may be dependent on the rodents for dispersal for they lacked characteristics which suggested dispersal by other vectors except perhaps water and gravity.

5.3.4 Wind

Although relatively few (13%) of the tree species found in the permanent plot series were wind dispersed (Table 49), this group does account for a relatively high percentage of the larger trees within the forests of the region. Wind dispersal is sometimes thought of as a primitive characteristic probably because many of the conifers (but not all e.g. Podocarpus spp.) are wind dispersed. It is also often associated with "large gap" species (McKey 1975) but again there are many exceptions both of "small gap" species being wind dispersed (Argyrodendron spp.) and "large gap" species being bird dispersed (Trema spp.). One generalization which can be made is that "primary" forest species which are wind dispersed, are

all found in the upper canopy or as emergents (see also Baur 1964b). Similar trends have been observed in other tropical rainforests by Howe and Smallwood (1982).

The wind dispersed seeds examined were mainly of the autogyrating or plate type. The relative effectiveness of these types were examined by McCutchen (1977) who suggested that autogyrating types would be better adapted to open forests. Both types are, however, well represented in the rainforests of this region by, for example, the seeds of Argyrodendron (autogyrating) and Flindersia (plate type) species. It is suspected that the morphology of plate type seeds may provide their seedlings with an advantage in the initial phase of establishment. This possibility is further examined in Section 6.1.1.

5.3.5 Water

Very few species appear to rely upon water transport and even then alternative modes seem to be available. For instance while Castanospermum australe is apparently water dispersed over much of its range, it seems to be dispersed by rodents in forests well away from streams on the Atherton Tablelands. Syzygium tierneyanum, a common stream side species, appears to be as well adapted for dispersal by birds (or even fish) as by water.

5.3.6 Gravity

While gravity alone is probably the sole dispersal agent for only a few species (notably Idiospermum australe) it is an important secondary mechanism for most and large masses of seedlings originating from seed which has simply fallen to the ground can be observed beneath many parent trees in years when the fruit crop has been so heavy that it has satiated both predators and dispersers. However, the observation by Budowski (1963) that, in the rainforests of Panama and Costa Rica, large numbers of species were dependent on gravity for dispersal, does not seem to have any parallels in this region.

5.3.7 General discussion of dispersal

It is of interest to compare the dispersal patterns observed here and those found elsewhere in the tropics. Most large diaspores in Australian rainforests have signalling colours and do not have a conspicuous smell or closed hard rind. Signalling colours are the characteristics of diaspores dispersed by frugivorous birds (Snow 1971) rather than mammals (van der Pijl 1969) and although it has been stated that some of the extinct marsupials may have dispersed large seeds (Janzen and Martin 1982), there appears to be no conclusive evidence for this suggestion. Certainly none of the extant mammals of the Australian – New Guinea region (with the exception of the fruit bats) are as frugivorous as many of those in the American or African tropics or those parts of the Asian tropics west and north of Wallace's line.

A comparison of Figures 63 and 64 reveals that most of the large fruited rainforest plant species which appeared suitable for consumption by Cassowaries, are found within their present range. Cassowaries may not, however, be the primary dispersers of all these species, for a few are also carried by fruit bats. Thus the possibility that the Cassowary might be a "pivotal species" (Howe 1984) requires further examination. A study of the distribution and reproductive ecology of some rainforest species which occur in south-east Australia and have large diaspores with features characteristic of those which are bird dispersed, could be rewarding for there is fossil evidence that Cassowaries (Miller 1962) or at least their near relatives (the extinct Dromornithidae) (Rich 1979) were present in southern Australia during the Pleistocene.

Since the tastes of man seem more closely related to those of frugivorous mammals than birds, the apparent absence from this region of plants whose dispersal is linked with large mammals may help explain the frequent observation (e.g. Boland and Turnbull 1981) that there are few, if any, indigenous fruit species which might be developed for horticulture. Alternatively, it may be that those of European background (i.e. most of the present inhabitants of the continent) are unappreciative of the numerous fruits eaten by the Aborigines

who, in evolutionary terms, are also recent arrivals.
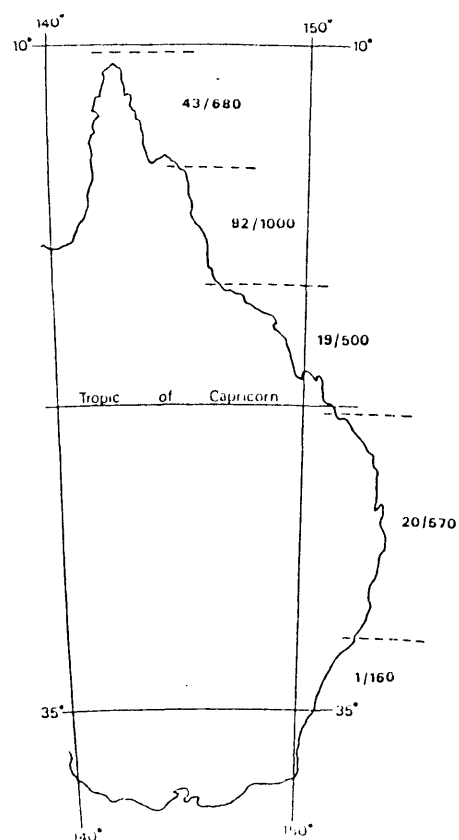
Figure 65. The east coast of Australia showing estimates of
the proportion of large fruited species in the woody flora of
different regions. Cassowaries are now only found in the two
northern regions (see Figure 64). The estimates were made
using data from Beadle et al. (1962), Hyland (1982), A.
Irvine (pers. comm.), Tracey (1982 and pers. comm.) and
Williams (1980).

5.4 Germination

Some problems were encountered when attempting to assess the
germination characteristics of a range of this region's
rainforest plants. The most important were the long intervals
between fruit crops of most species, difficulties in obtaining
enough seed for adequate replication of experiments, an
inability to store the seed of more than a few species for
supplementary experiments and the low germination percentages
apparently characteristic of many species. Nevertheless,
whenever rainforest plant species were observed to be in
mature fruit, seeds and voucher botanical specimens were
collected and the seeds germinated in the glasshouse to
provide seedlings for the development of the arboretum and for

preservation in the herbarium.

Fleshy parts adhering to the seeds were usually removed
before sowing them in pots on U.C. mix type B (Baker 1957).
They were lightly covered with about 1 cm of basalt scoria to
prevent them being dislodged during watering. Records were
kept of the times taken for the seeds to germinate. From
these records (summarized in Table 53 and Appendix A) it was
possible to determine which species produced seeds apparently
capable of remaining dormant in the soil. Although a degree
of dormancy was a conspicuous feature of the seeds of some
"large gap" species (notably Alphitonia petriei and some
Acacia spp.), the seeds of very few other tree species seemed
able to remain viable in the surface soil from one fruiting
period to the next (see Section 5.1.2). This finding is in
broad agreement with the results obtained by germinating seeds
in soil samples taken from a variety of "primary" and
disturbed lowland forest sites in this region by Hopkins and
Graham (1983) and overseas experience in similar environments
(e.g. Budowski 1970; Gomez-Pompa et al. 1972; Liew 1973;
Cheke et al. 1979; Prevost 1981; Uhl and Clark 1983; see
Whitmore 1983 for a review).

Table 53. The time taken for the complete germination in the
glasshouse of seeds of 318 of the tree species encountered in
the permanent plots.

Months for complete germination	Proportion %
< 6	87.7
6 - 24	11.0
> 24	1.3

An interesting exception to the generalization above was the "small gap" species <u>Beilschmiedia bancroftii</u>. This species has large seeds (about 4 cm in diameter) protected by a hard woody endocarp. About 30 were placed on a tray of moist potting mix in the greenhouse during 1972 and for the next 11 years they germinated at the rate of two or three a year. In this particular species seed coat permeability seemed to be the factor controlling germination, for when the endocarp was cut, the seeds germinated rapidly. Rapid rather than sporadic germination could be effected in several of the most prominent of the "large gap" species (<u>Alphitonia petriei</u> and some <u>Acacia spp</u>.) by applying moist heat (80°C) for an hour.

While May (1975b) considered that seed dormancy was generally absent from tropical species because they tended to be selected for their ability to compete rather than be opportunistic, the rainforest environment is such that it is rather difficult to think of any advantage that seed dormancy could bring to a "small gap" species. Indeed predation, and in particular, the problem of protecting the relatively large seeds common to many "small gap" species from predation, would seem to limit any possible advantage seed dormancy would give to most species. Although the rapid germination of seeds may only shift the predator problem from the seed eaters to the grazers, seedlings have a chance of recovering from grazing and in any event, are in a better position to detect and take advantage of additional resources which may become available through canopy disturbance.

Attempts were made both in the glasshouse and germination cabinet to see if the germination of bird dispersed fruits was inhibited, as has sometimes been suggested (e.g. Lieberman <u>et al.</u> 1979), by leaving the fleshy parts attached. The species examined were <u>Arytera divaricata, Neolitsea dealbata, Canarium vitiense, Ganophyllum falcatum, Wilkiea sp. GS 1524, Eugenia kuranda, Syzygium tierneyanum, Acronychia acidula, Podocarpus ladei, Rhodamnia argentea</u> and <u>Securinega melanthesoides</u>. In the glasshouse the methods previously described were used. The germination cabinet was run on cycles of 12 hours light at 30°C and 12 hours dark at 20°C. The seeds were placed on

filter paper moistened with distilled water in petri dishes and germinations were recorded daily. Each treatment contained 25-100 seeds (the number depending upon their availability). While some differences were observed, they were from the viewpoint of forest dynamics, minor and usually in the form of a delay of a day or so in the development of maximum germination rate for those lots of seed with adhering flesh. The usual pattern is illustrated in Figure 66 by the behaviour of A. divaricata. However, the results of this experiment can only be regarded as a preliminary guide and the experiments should be repeated using seed obtained from fruit fed to captive birds.

Some trials in a germination cabinet were also undertaken to examine the germination responses of two "large gap" species (Dendrocnide moroides and Alphitonia petriei) and several "intermediate" to "small gap" species (Toona australis, Alstonia scholaris and Neolitsea dealbata) to total darkness as well as the 12 hour light regime. The petri dishes containing the seeds for the dark treatments were wrapped in aluminium foil. While no important differences in germination characteristics were detected, numerous studies elsewhere (e.g. Vazquez-Yanes 1976; 1977; Bazzaz and Pickett 1980; Cresswell and Grime 1981 and Aminuddin and Ng 1982) have shown that the germination of seeds of some other "large gap" species was affected by both light quantity and quality. The results for T. australis (Figure 66) appeared to be representative of those for the species examined in this study.

The frequency of recalcitrant seeds (those which lose their viability on partial dehydration) amongst rainforest plants has recently been commented upon by Whitmore (1983). Some physiological properties of these seeds were discussed by King and Roberts (1979). Recalcitrant seeds are generally very difficult to artificially store although some advances have been made by carefully controlling seed moisture content and the storage atmosphere and temperature (P. Tompsett pers. comm.). It is perhaps no accident that so many seeds of tropical rainforest species, particularly "small gap" species, are recalcitrant. Seeds which are not harmed on drying to

lower moisture content, may be better adapted to remain viable
for long periods in the soil. However, this attribute is
probably unnecessary, if not disadvantageous, for those
species whose seeds will usually fall into an environment
where relative humidities are consistently high. Furthermore,
as Harper et al. (1970) have pointed out, a large dehydrated
seed lying on the forest floor could have some difficulty
absorbing enough water to germinate.

In an attempt to make a preliminary assessment of the role
of this characteristic in the regeneration of this region's
rainforests, the seeds of some species were dehydrated at room
temperature in a desiccator containing silica gel. The
effects of this treatment on their characteristics (Figure 67
and Table 54) suggested that seeds of those species examined,
may not be as readily dehydrated (and thus killed) as some of
those in Malaysia where Mori et al. (1980) reported that
leaving Calamus manan seed to air dry for 4 days was
sufficient to dehydrate them to below the 40-50% moisture
content which was the lethal level for this species.

The influence of soil surface temperature on the failure of
certain species to establish on the forest floor beneath large
canopy gaps was briefly examined. On hot dry days surface
temperatures (measured with thermocouples) in these situations
occasionally reached 60°C. However, seeds of all the species
listed in Table 54 were able to endure 60°C for 3 days in a
laboratory oven without affecting their germination.
Temperatures of 70°C for the same period did have an adverse
influence on some species as did desiccation over silica gel
at room temperature for 12 days (Table 54). Overall the
results suggested that seeds of at least some recalcitrant
species (typified by Castanospora alphandii and Pouteria
castanospora) may be able to withstand the high soil surface
temperatures and low humidities experienced in large gap
environments for a few days and possibly longer. The seeds of
some species (especially those in the Sterculiaceae) were able
to modify the establishment microsite by producing mucilage
just before the radical emerged. Harper et al. (1970) noted
that this ability improved the chance of seedling
establishment, for it increased the area of seed/surface water
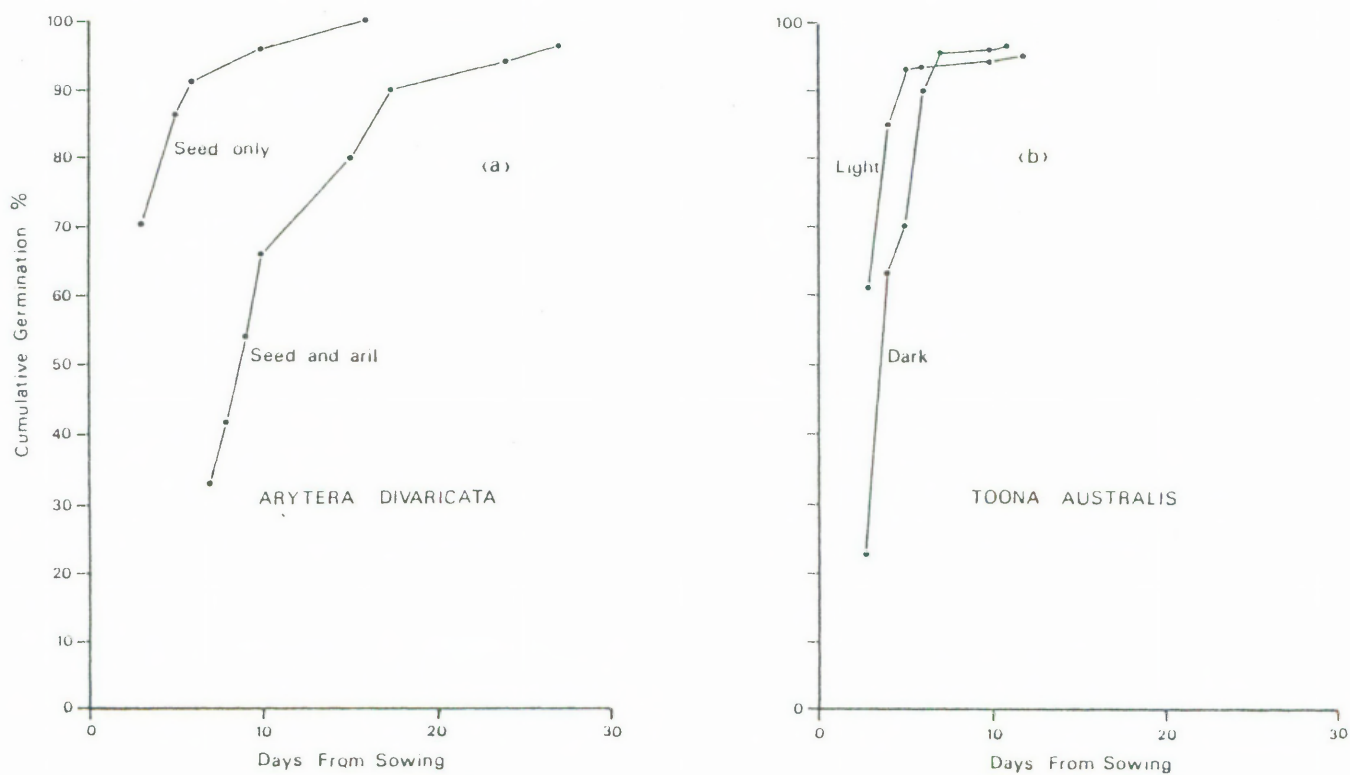
Figure 66. Illustrated are the progressive germination percentages for :- a) <u>Arytera divaricata</u> seeds with and without arils, b) <u>Toona australis</u> seeds exposed to light and kept in darkness.
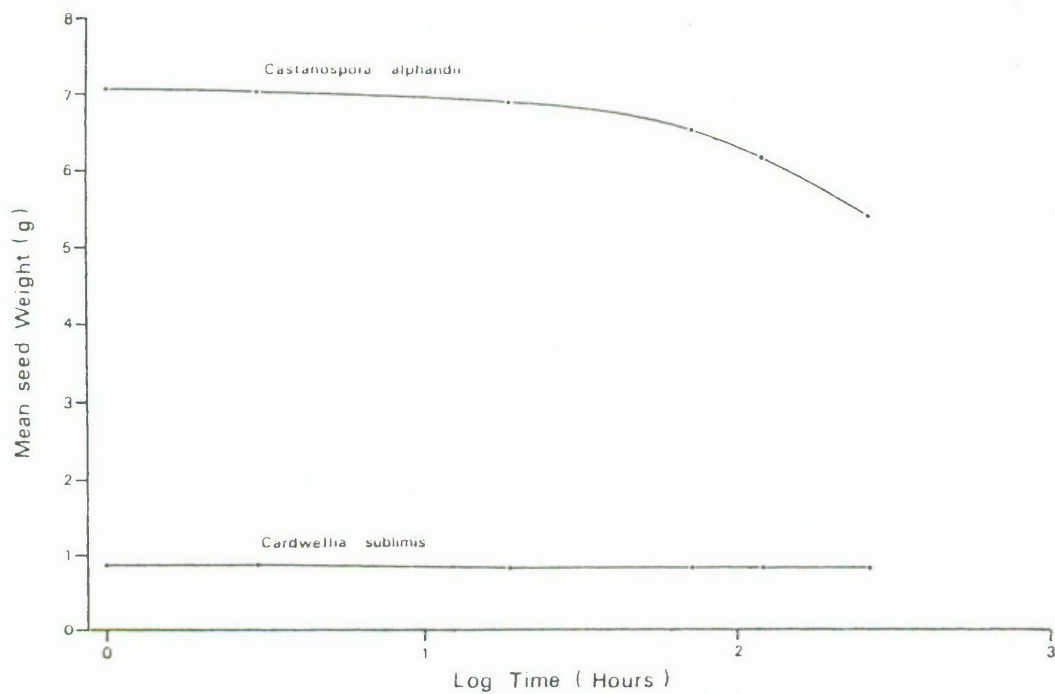
Figure 67. Weight losses of seeds of <u>Castanospora alphandii</u> and <u>Cardwellia sublimis</u> when stored at room temperature in a silica gel desiccator are shown.

Table 54. The effects of heat (3 days at 60°C and 70°C) and desiccation (12 days over silica gel at room temperature) on some characteristics of seed of selected rainforest tree species.

Species	no. seeds/ treatment	mean fresh seed weight (g)	% water loss			Germination %			
			after desiccation	after heating 60°C	70°C	fresh	desiccated	heat treated 60°C	heat treated 70°C
Castanospora alphandii	16	7.06	23	11	44	100	0	100	0
Cardwellia sublimis	30	0.87	4.3	4.1	7.3	77	93	81	83
Flindersia brayleyana	40	0.08	4.0	4.5	7.3	97	90	97	25
F. pimenteliana	40	0.09	5.4	5.4	6.3	100	100	100	85
Pithecellobium grandiflorum	40	0.13	7.5	7.4	9.8	83	50	85	0
Pouteria castanosperma	12	13.6	33	15	50	83	8	91	0
Toona australis	100	0.05	8.5	6.0	6.7	74	85	81	12

contact.

Although the germination of large recalcitrant seeds in large newly created gaps would not normally be of great importance in rainforest dynamics (regeneration of most of these species would already be established on the forest floor), future investigations of the environmental factors controlling the successful establishment of seedlings should concentrate on the phase immediately after radical emergence (see also Kalkman 1979; Sarukhan 1978). It is suspected that at this time temperature and humidity parameters could be critical. Casual observations made during the establishment of the field establishment and growth trials (Section 4.6) indicated that soil surface features (litter nature and depth)(see also Barnard 1954) and subsurface characteristics (moisture content, structure and texture) could also be of importance in determining whether a species established successfully.

Putz (1983) suggested that in large gaps, the successful establishment of the small seeded "large gap" species was favoured by the patches of disturbed soil prevalent in gaps of this size. While this may be true, it is observed that the area of soil most likely to be disturbed is near the butt of the toppled tree and that the canopy gap above the butt may be rather insignificant when compared with the gap created by the falling crown (compare Plates 16 and 19; see also Figure 49).

A feature of the results of the germination trials in the glasshouse and laboratory, was the variability of the germination percentage data among species. Seeds of a number of species, especially those which were wind dispersed, invariably nearly all germinated. Several groups of species were however, notorious for either not germinating at all or producing very low germination percentages. These groups were prominent in the Elaeocarpaceae (Elaeocarpus and Aceratium spp.) and the Rutaceae (Acronychia and Halfordia spp.). While insect attack may be responsible for the low germination percentages observed in some species of the Rutaceae, seeds of most species in the Elaeocarpaceae usually showed no signs of damage and apparently good seed usually decayed in the potting

medium without germinating. Various treatments to induce germination, such as soaking the seeds in water and cracking seed coats, were tried without marked success.

In concluding this Chapter it is apparent that the processes determining which species is able to place its diaspores on a suitable establishment microhabitat, have many stochastic elements. Further comment on the roles of these processes in successions, and the establishment and maintenance of diversity and stability, will be made in the next Chapter.

CHAPTER 6

Synthesis

6.1 Introduction

This final chapter links species attributes, disturbance patterns and environmental features with the structural and floristic characteristics of succession. Implications for rainforest evolutionary patterns, diversity, stability and management are also examined. To facilitate discussion, relationships among these topics are outlined in Figure 68. The following résumé sets the scene.

It was apparent from the outset (see Chapter 1, especially Figure 1) that many factors could influence the structural and floristic characteristics of rainforest. Although past research had indicated the existence of broad structural and floristic patterns which could be related to some environmental features (Section 2.2.4), little was known of the role of individual species in rainforest dynamics. While a review of the history of rainforests in the region raised some uncertainties about its origins and past extent (Section 2.2.3) most of the evidence indicated constant change in its distribution and floristics during the Pleistocene and Recent. Size and density patterns for important tree species in study plots suggested that the floristics of some sites were in equilibrium. The presence of clearly transient species in others indicated that at least part of their floristic component was in a nonequilibrium state (Section 3.3.1).

Data from the plots also indicated that relationships between the distribution of species and broad scale features of the physical environment, were not particularly obvious (Section 3.2.1). This suggested that chance and local influences at establishment may be important in this forest type. Indeed discrete patches of the forest floor beneath canopy gaps have long been recognized as a major focus for rainforest regeneration (Section 2.3.2). When the temporal and spatial patterns of gaps in relation to the various disturbance types were examined (Section 4.4), it was found

that many small gaps were created at random intervals by the death and/or toppling of individual or small groups of trees. Although periodic catastrophes may sometimes create many gaps simultaneously, these disturbances do not often seem to exert a dominating influence on rainforest dynamics.

A model of the light environment on the floors of gaps revealed ways in which this environment might be partitioned by a range of species having different light requirements for optimal growth and survival (Sections 4.2 and 4.3). Field and glasshouse experiments confirmed that rainforest tree species have these characteristics (Sections 4.6 and 4.7). Additional supporting evidence was observed in growth data for tree species in the plots and arboretum (Sections 3.3 and 4.8). Available information indicated that most species were relatively shade tolerant and thus capable of surviving for some time in low light situations (i.e. beneath an undisturbed canopy).

Although an examination of regeneration modes following disturbance stressed the potential for most species to re-establish vegetatively (Section 4.9), sexual reproduction cannot be overlooked for seeds are the ultimate source of nearly all vegetative propagules. Observations recorded in Chapter 5 indicated that seeds of most shade tolerant species were produced at intervals of three or more years, adapted to bird dispersal, of medium to large size and of short viability. In contrast those of relatively shade intolerant species tended to be produced at one to two year intervals and be much smaller in size. A few were well adapted to survive for long periods in the soil.

SPECIES ATTRIBUTES

    Propagule availability
      - parental demography
      - reproductive biology

    Growth characteristics
      - shade tolerance

ENVIRONMENT

    Macro- and Gap
      - temperature
      - light
      - soil

    Biological
      - interacting species

    Catastrophic phenomenon

CHANCE
    - propagule availability
    - gap disturbance patterns
    - weather

SUCCESSIONAL CHARACTERISTICS

EVOLUTIONARY TRENDS

FLORISTICS

DIVERSITY

STRUCTURE

STABILITY

MANAGEMENT IMPLICATIONS

Figure 68. Flow chart outlining relationships among topics
discussed in Chapter 6.

6.2 Succession

The initial focus of this synthesis is on the processes of
regeneration following natural disturbance. Since these
processes determine stand structure and floristics, they must
also influence other stand properties, particularly diversity
and stability, and form the basis for forest management.

6.2.1 Basic features

Demographic and disturbance patterns (Sections 3.2.2 and 4.4
respectively) suggest the primary importance of regeneration
in gaps created by the death and /or toppling of a single tree
or small group of trees. Mortality data indicate that
individual tree deaths occur continuously at the rate of about
1% of the stems in any size class (Section 4.4.1 and Table 9).
However, periodic widespread catastrophes do occur and
regeneration following these disturbances may, on at least
some sites (e.g. plots 3, 11 and 13) be intermingled with that
resulting from more frequent, if scattered, gaps created
following individual, unrelated tree deaths.

It is obvious that all the available species could not
normally be contained on a patch of forest floor beneath a
typical canopy gap. The following section examines those
attributes (species, environment and site) which determine
whether propagules of a particular species will be available
to fill a canopy gap.

6.2.2 Species attributes

The attributes which make up the regeneration strategy of a
species are related to all four subdivisions of the species
niche as defined by Grubb (1977) (Section 1.2). Those
associated with propagule availability via the sexual
reproductive mode form 3 groups i.e. those of the parent,
those of the diaspore and those controlling the survival and
growth of the newly developing plant. Contrasts existing
between attributes of "large gap" and "small gap" species are
highlighted.

a) Parental characteristics

Precociousness - Observations of "large gap" species in the arboretum supported field observations that this group produced fruit at a younger age than most "small gap" species (Section 5.1.1). This may be an advantage since "large gap" species appear to be more dependent on seedling regeneration after disturbance than "small gap" species (Section 4.9).

Longevity - Connell and Slatyer (1970) noted that long life spans would be favoured if the "inhibition" model of succession operated. The possible importance of this model in rainforests is discussed in Sections 6.2.5 and 6.3.

Relationships are apparent between longevity and shade tolerance. For example radiocarbon dates (Table 32) indicate life spans for "intermediate" and "small gap" species of from about 400 to over 1000 years. The decline of the "large gap" species, Aleurites moluccana, in plot 11 suggests a life span for this species of about 80 years. General observations of areas for which the disturbance history is known and size class, growth and mortality data for plots (e.g. no. 3) indicate that other "large gap" species, such as Acacia aulacocarpa and Alphitonia petriei, have even shorter life spans.

Fruiting phenology - There are five attributes which are of importance:-

- the frequency of production of fruit crops (regular, annual crops are more likely to be produced by "large gap" species - Section 5.1.2),

- the degree of synchronization of fruiting within a species (generally marked - Section 5.1.2),

- the quantity of fruit produced (mast years may be particularly important for satiating seed predators - Section 5.1.5),

- the duration of the fruiting season (although variable, wind dispersed species tend to be dispersed over a short period while animal dispersed species may have extended

seasons - Section 5.1.4),

- the seasonal timing of fruiting (although there is a wide spread among species, a peak occurs at the beginning of the wet season - Section 5.1.3).

b) Diaspore characteristics

Morphology - The shape, colour, size and composition of a diaspore will usually indicate its primary dispersers (Section 5.3; van der Pijl 1969; Howe and Smallwood 1982).

The size of seeds observed in this study varied from the dust-like seeds of some of the epiphytes to the large (to 10 cm dia.), heavy (about 500 g) spherical seeds of Idiospermum australe. Suggested advantages of large seeds include :

- rapid production of large seedlings which have a better chance than those of smaller seeds in competition for light and other resources (Grubb 1977).

- establishment of extensive root systems to avoid drought (Grubb 1977).

- enabling seedling growth while waiting for mycorrhizal infection (Janos 1980).

- enabling substantial root development and thus stability and an ability to withstand dry periods when germinating on forest floor litter.

Disadvantages are presumably that for the same resource cost, a plant could produce more small seeds than large seeds and that these small seeds would be more densely dispersed thus improving the chances of locating a favourable microhabitat (Horn 1974). Although small propagules might have more available animal dispersers, the cassowary study (Section 5.3.1.1) indicated that even the largest propagules could be carried considerable distances. Some "large gap" species seemed to maximize the number of potential dispersers by having aggregate fruit which a smaller bird could pull apart or a larger one swallow whole e.g. Rubus spp.

Those rainforest plants with very small seeds were specialized species, usually either epiphytes (e.g. orchids) or commencing their lives as epiphytes (e.g. strangling figs). For the orchids, establishment is also dependent on the availability of a suitable fungal associate and often aided by their possession of a water conserving crassulacean acid metabolic pathway (Winter et al. 1983). In this group maximizing the probability of finding favourable sites appears paramount.

While a clear relationship between seed size and shade tolerance did not emerge from the glasshouse trials (Table 39), all "large gap" species (with one exception noted below), had small seeds. Thus seed dispersal generally seems of greater importance than seed size for members of this group. The exception, Aleurites moluccana, has large seeds which enable its seedlings to grow very rapidly (Table 39). This attribute may allow this species to compete with ephemeral grasses and herbs which often colonize large gaps (Table 38).[1]

The larger seeds of most "small gap" species indicate that survival and growth are more important than finding the optimum microsite. The single seeded characteristic of animal dispersed "small gap" diaspores (e.g. see Table 52) may have evolved to maximize seed size without reducing the range of potential dispersers. The few "small gap" species producing numerous small seeds (e.g. Antirhea tenuiflora) appear to require special microsites (such as bare soil exposed on the root ball of toppled stems) for seedling establishment.

Harper el al. (1970) observed that seed shape was a compromise between efficiency in packaging, dispersal and seedling establishment. In the rainforests of this region most seeds are round or oval in outline and presumably these are the most efficient shapes for animal dispersal and the encapsulation of the energy reserves required for a developing

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1. Although the glasshouse shading trial (Section 4.7) suggested that its large seed reserves could also provide some assistance in heavily shaded situations, small seedlings of this species have never been seen beneath undisturbed forest canopies.

seedling. There is, however, a small but important group of species in the Flindersiaceae and Proteaceae which have flat, wind dispersed seeds (the "plate" type of McCutchen 1977). While the flat outline improves the possibilities for wind dispersal over rounded shapes, it also enables the plant to produce a seed where, with a minimum of energy expended, the cotyledons can open and immediately present a relatively large area for photosynthesis (Plate 32). A few species have rounded, animal dispersed seeds in which the cotyledons are folded and expand rapidly on germination (e.g. Micromeleum minutum and Ganophyllum falcatum).

Plate 32. Young seedlings of a bird dispersed species Castanospora alphandii (A) and three wind dispersed species - Flindersia brayleyana (B), F. pimenteliana (C) and Cardwellia sublimis (D). All the wind dispersed species shown have large flat cotyledons which appear to enable a rapid start to photosynthesis after germination.

Dispersal - While dispersal of propagules away from parents has several potential advantages (see Section 5.3), a major consideration must be that it provides a chance for species to occupy new sites. Observations in north east Australia (summarized in Table 49) indicated that most rainforest tree species are bird dispersed. This mode would generally facilitate wider dispersal than other modes. In situations where rainforests are expanding, or have recently done so, it seems reasonable to assume that their floristics might be influenced by the different dispersal capabilities of potentially available species. However, although bird dispersal may be the most efficient mode of long distance, especially patch to patch dispersal, studies of rainforests expanding into eucalypt forests by Unwin (1983) showed that some wind dispersed species (e.g. Toona australis and Flindersia spp.) were prominent among the early invaders. As well as having some physiological attributes which enable them to establish successfully in open forest environments, these species are also independent of animal vectors which might see eucalypt forests as a relatively inhospitable habitat.

Dispersal and related attributes (especially production and predation) warrant detailed study. A theoretical model examining the efficacy of dispersal in relation to safe site area and seed production (Geritz et al. 1984) may provide a useful starting point.

Seed germination - The quality of the seed produced by the region's rainforest trees was very variable. Inexplicably low germination percentages were characteristic of some species (Sections 5.3.1 and 5.4). However, from a forest dynamics viewpoint, the observation that dormancy did not seem developed sufficiently (Table 53) for most species to establish a store of their seeds in the soil to bridge the period between fruit crops (Section 5.1.2), is probably of greater importance.

While dormancy is a conspicuous attribute among "large gap" species, a few "small gap" species also have dormant seeds (e.g. Beilschmiedia bancroftii). Periods of viability after seed shed were found to be as short as three weeks for spec⁃

such as <u>Castanospora</u> <u>alphandii</u> and <u>Sterculia</u> <u>laurifolia</u>. The general characteristic of rapid germination is thought to be related to greater predation pressure on seeds than seedlings and the ability of seedlings to respond rapidly to additional light following canopy disturbance. Seedlings are also better able to recover from being partially consumed (i.e. grazed) than seeds which usually rot following anything more serious than superficial damage. Dormant seeds would appear to be most effective for species which either occur on sites where unpredictable periods of severe stress (especially droughts) occur, are shade intolerant or have a poor ability to resprout vegetatively following damage.

c) Vegetative reproduction.

Most species examined in this thesis (Section 4.9) appeared capable of producing coppice shoots after damage and in some the root suckering mode occurs extensively. Capacity to coppice appears greatest in "small gap" species. While the ability to coppice may decline as stem size increases, vegetative reproduction appears to provide a means of enabling those species whose individuals have not reached reproductive maturity, to survive all but the most severe physical disturbance.

An important question is whether the ability of a species to produce root suckers (or to a lesser extent coppice shoots) permits that species to have a wider than normal shade tolerance range or even two distinct shade tolerance niches. This might be the case for at least two species, <u>Acacia</u> <u>melanoxylon</u> and <u>Alstonia</u> <u>muellerana</u> for root suckers of both species appear more shade tolerant than their seedlings. In view of these possibilities, it is surprising that the ability to produce root suckers is not found in many more species. Perhaps the problems of escaping from root rots and viral infections have prevented this attribute from becoming widespread.

The ability of damaged crowns to recover by coppicing also appears most frequent in "small gap" species. This process is of importance for it gradually alters the light regime in gaps

and may force a shift of dominance towards the more shade tolerant of the regenerating species.

d) Seedling growth and shade tolerance

Shade tolerance and growth - Although growth alone has been used in making an assessment of the shade tolerance of tree species (Kramer and Kozlowski 1960), survival is also included in most measures (Lorimer 1983). The usual classification of tree species into shade tolerants or shade intolerants has been recognized as a convenient oversimplification and a continuum of shade tolerance exists among both tropical and temperate tree species (e.g. Baker 1950, Grubb 1973, Whitmore 1975, Opler et al. 1980, Augspurger 1984). Studies reported in this thesis (notably Section 4.6, Figures 57 and 59; Section 4.7, Table 39) support this view.

The influence of shade tolerance on seedling survival was observed in the seedling establishment trial (Section 4.6) where, under a dense intact canopy, seedling numbers often declined steadily during the period immediately following germination (Figures 56 and 58). Seedling longevity under heavy shade may be as short as a few weeks (e.g. Toona australis with fresh seed weights of < 0.1 g); to 3-5 years for species such as Argyrodendron peralatum (seed weight about 1 g); to an expected 10-20 years for some of the larger seeded (> 5 g) species such as many of those in the families Sapindaceae, Lauraceae and Myrtaceae. The relative importance of reserves remaining in the cotyledons and of photosynthesis, in allowing shade tolerant seedlings to persist beneath a closed canopy, is not known but it is suspected that in most species the reserves in the cotyledons are used to provide seedlings with as large a leaf area as possible, soon after germination. Exceptions may include some very large seeded species, such as Idiospermum australe, where the cotyledons remain firm and apparently functional as storage organs for many years.

The link, observed between shade tolerance and seedling growth rate observed in the glasshouse and field establishment trials (Section 4.6, Figures 57 and 59; Section 4.7, Table

39), the arboretum planting (Section 4.8, Table 40) and the regrowth study (Section 4.9, Table 44) may be explained by various physiological and morphological attributes outlined below.

Mooney et al. (1980) noted that photosynthetic capacities were least for understorey species, intermediate for overstorey species and highest for pioneer species. (These categories appear to correspond with my "specialized understorey", "small gap" and "large gap" species respectively.) Whitmore and Gong (1983) and Oberbauer and Strain (1984) provided further evidence supporting these trends. The latter also noted that light saturation occurred at higher levels for "large gap" species than for those from more shaded environments and that stomatal conductances followed a pattern similar to photosynthetic rates. It also seems possible that the higher net photosynthetic rates observed for "large gap" species may account for the ability of species within this group to produce annual fruit crops (Section 5.1.2).

The respiration rates of tropical plants appear worthy of further examination. It is usually assumed that respiration rates for tropical trees are high (Evans 1972, Grubb 1973 and Kramer and Kozlowski 1960). While discussing temperate species Bazzaz (1979) observed that dark respiration declined with increasing shade tolerance, although the rate of decline was less than that of photosynthesis. Given the low potential for photosynthesis on the forest floor (due to the long periods when photon flux densities are very low – Section 4.2), the ability of a seedling to grow, or even the period for which it will be able to survive, will depend very much on its rate of respiration.

Other physiological characteristics suggested by Bazzaz (1979) as being of importance but for which little or no data are available for tropical species, are stomatal and mesophyll resistance (both probably increase with shade tolerance), rate of stomatal opening (may be faster in shade tolerant species – but see conflicting evidence discussed by Kozlowski 1979) and photosynthetic response to declining leaf water potential

(shade tolerant species seem more sensitive).

Few studies have been made of morphological attributes which contribute to shade tolerance. However, leaf structure (McClendon and McMillen 1982) and crown shape and density appear to be involved. Root development and distribution may contribute.

Several important aspects relating to the role of shade tolerance in rainforest succession have still to be addressed. Perhaps the most pressing is the degree to which shade tolerance within a species is altered by environmental features (such as soil chemistry or the established light regime) or the age of the individual plant. Another relates to the genetic variability of the characteristics controlling shade tolerance within species.

Although there is currently little information available which would help answer these questions, we might at least expect to see ranking changes on a fertility gradient where some of the component species are adapted to overcome a resource limitation. Species which are able to fix atmospheric nitrogen are obvious examples. The comparatively low growth rate of one of these specialized species, Acacia aulacocarpa, on the relatively fertile site of the regeneration trial (Section 4.9, Table 44), suggested that it was removed from its usual position in shade tolerance ranking.

e) Tree growth

The general trend for shade tolerance to be inversely related to growth rate has been recognized by foresters for a long time and this knowledge has formed the basis of many of the silvicultural systems which have been applied in rainforests (see Baur 1964a for examples). This trend has also been observed by other authors notably Grime (1966)(for temperate tree species), Fox (1976) and Rai (1983)(for tropical rainforest species). It was apparent in the relative increment rates of trees in the permanent plots (see discussions of tree growth in Sections 3.2.2 and 3.3.2, Table

30).

Species attributes characteristic of "large gap" and "small gap" species are summarized in Table 55.

Table 55. Some typical attributes of "small gap" and "large gap" species observed in the rainforests of north-east Australia.

Characteristic	Small gap species	Large gap species
Fruit	single seeded	many seeded or aggregate
Seed		
– type	recalcitrant	orthodox
– size	often large	usually small
– dormancy	rarely	often
– dispersal	no clear pattern	
– germination type	no clear pattern	
– frequency of production	3 or more years	annually
Seedlings		
– shade tolerance	high	low
– growth	slow	fast
– growth emphasis	leaf area	height
Trees		
– growth	slow	fast
– coppicing ability	good	poor
– apical dominance	variable	good
– leaf size	microphyll – mesophyll	notophyll – macrophyll
– wood density	moderate	low
– crown	many layered	single layered
– longevity	long	short

6.2.3 Regeneration niches - environmental attributes.

Critical environmental parameters of a plant's regeneration niche appear to be those influencing the transition from seed to seedling and early seedling growth. Three important categories are:

- atmospheric (mainly light and temperature regimes),

- edaphic (soil water status and chemical and physical characteristics),

- biological (especially the characteristics of interacting organisms).

Predictable temporal variations in these properties may be just as important in defining a niche type as the average condition. The effect of catastrophic events (e.g. cyclone and fire) must also be considered.

a) Temperature

Mean, seasonal variability and extremes are important characteristics. Altitude and latitude are the primary determinants of mean temperature. Nix (1982) suggested that plants could be divided into 5 groups based on their optimum temperatures for growth. He also observed that in the tropics, plants from all these groups could be found on an altitudinal gradient from sea level to the snow line of high mountains.

Latitude also has an important influence on seasonal variability (generally greater at higher latitudes). Its net effect is that there are fewer potential temperature response groups and a smaller fraction of each year available for optimal plant establishment and growth, with increasing latitude.

Temperature extremes resulting in plant mortality may be of regional importance e.g. frost on the Atherton Tablelands (Section 2.1.5c) and high soil surface temperatures (reaching $60^{o}C$) in large openings (Section 5.4).

b) Light

While light would not seem to be a factor limiting rainforest growth except perhaps in some cloudy mountainous regions (Nix 1982), it is apparent that its spatial and temporal patterns on the forest floor influence competitive interactions among plants regenerating in gaps (Chapter 4). The most important variables controlling these patterns are the size and shape of characteristic disturbance gaps and latitude (Sections 4.2 - 4.4). Figures 46-48 indicate that in those closed forests which primarily depend on seedling growth in scattered tree fall gaps for their regeneration, the niche axis relating to light availability, is very much truncated by increasing latitude. Thus it could be expected that temperate closed forests, in which regeneration characteristically occurs in relatively small gaps,[1] would have a higher percentage of shade tolerant "small gap" species than tropical closed forests.

Although differences have been observed between the spectral composition of light near the forest floor and that entering the assemblage (e.g. Bjorkman and Ludlow 1972), it seems improbable that light quality could contribute greatly to niche diversity because spectral composition would appear to be closely related to an overriding parameter, photon flux density. However, it has been found that the seeds of some rainforest species have different germination characteristics when exposed to light of different wavelengths (e.g. Aminuddin and Ng 1982).

c) Soil

Soil characteristics which seem important sources of regeneration niche diversity, relate to surface conditions and some physical and chemical properties.

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1. Other important types of temperate closed forest are formed by infrequent severe catastrophes particularly fire. These forests are usually dominated by shade intolerant species especially in their early stages of development.

Although there are indications that soil surface conditions
can be very important in determining the floristics of stands
regenerating in clearings (e.g. Williams et al. 1969b;
Boerboom 1974; Zwetsloot 1981; Maury-Lechon 1982) their
influence within tree-fall gaps appears to be unexplored.
Important factors probably include those which affect surface
temperatures (mainly surface soil colour and structure) and
the nature and depth of the litter. High surface temperatures
(and associated low humidities) may restrict the establishment
of some species but on the whole this problem, if not confined
to large gaps and clearings, is certainly much greater as gap
size increases. Litter conditions on the forest floor beneath
a canopy gap resulting from a toppled tree, were observed to
range from exposed mineral soil to deep beds of broken
branches, leaves and epiphytes from the crown of the toppled
tree (Section 4.4.1). The importance of seed size in relation
to establishment on forest floor litter was mentioned in
Section 6.2.2b.

Observations during the seedling establishment trial
(Section 4.6) illustrated the importance of adequate soil
moisture for initial establishment. The species examined here
behaved in the same way as those temperate species studied by
Pickett and Bazzaz (1978) i.e. all seemed to require similar
optimal soil moisture conditions for establishment and early
growth. Therefore it appears that both weather conditions and
soil properties restricting water availability, would limit
the total niche volume of that site.

While there is a relationship between latitude and rainfall
seasonality, it is not as simple as that between temperature
and latitude or even between the light environments in gaps
and latitude. For example if we consider a transect from
north Papua New Guinea down along the east coast of Australia
and ignored the local influences of topography, we would find
a relatively aseasonal rainfall regime to about $8^{o}S$.
Seasonality (heavy summer rainfall, winter/spring drought)
becomes increasingly prominent to about $12^{o}S$ and remains high
until about $25^{o}S$. Aseasonality returns between about $30-35^{o}S$,
although at higher latitudes seasonality again increases and

favourable soil water regimes are more likely to occur in winter than in summer months.

The role of spatial and temporal variations in nutrient availability of soil beneath a canopy gap, in influencing the outcome of competition amongst regenerating species, is largely a matter for conjecture. While pattern in soil chemical attributes seems to exist at this scale, there is little direct evidence that these patterns influence competitive processes. Methodologies used by Austin and Austin (1980) and Hartgerink and Bazzaz (1984) may provide an appropriate starting point.

At regional scales there is a greater chance that patterns in soil chemistry will provide opportunities for different suites of species to regenerate on what would otherwise appear to be similar sites and thus variability in soil chemistry might increase regional niche volume. However, the plot data (Section 3.3) indicated that soil chemistry may only exert important controls on floristics where soils have abnormal chemical features (such as very high or very low nutrient levels). In these circumstances specialized species often have mechanisms (e.g. the suspected nitrogen fixing abilities of _Acacia aulacocarpa_) which give them superior competitive abilities over species characteristic of normal sites. A similar conclusion was reached by Baillie and Ashton (1983) who envisaged that, in the mixed lowland dipterocarp forests of Sarawak, edaphic effects did not rigidly exclude ill-adapted species. Rather, they thought that such edaphic effects tended to improve the probability of survival of adapted species through the operation of a range of stochastic processes relating to reproductive biology and gap formation. Overall, the importance of soil chemistry in controlling species composition warrants further examination.

d) Biological.

While the importance of shading has already been discussed at length, two other biological processes should be considered - predation and chemical inhibition. Observations of seed predation (Section 5.2) and of seedling browsing during

initial establishment (Section 4.6) indicated that seed losses were usually greater and that species varied significantly in their susceptibility. Although earlier work had suggested that species specific predation played an important role in the maintenance of floristic diversity (e.g. Connell 1971, Janzen 1971), studies by Forman and Hahn (1980) in Caribbean semi-evergreen rainforest, revealed other factors (they suggested establishment microhabitats) could be more important. I suspect that the most important role of predation is that it decreases the frequency of effective seed crops and thus increases the importance of occasional mast crops for susceptible species.

Despite some work (e.g. Webb et al. 1967c) little is really known about the significance of inter- and intra-specific inhibition in forest assemblages (Bazzaz 1979; Rice 1979). However, it seems probable that chemicals secreted by the roots or leaves of some plants in an assemblage may affect the survival and vigour of some or many of their neighbours.

e) Catastrophic phenomena.

Severe disturbances such as those due to volcanic activity, landslips, cyclones and fires, create many new establishment sites. However, in contrast to those establishment sites formed by the death or toppling of a single tree (or small group of trees), these sites are all formed within a short time frame. They are also usually more extensive and are more uniform in their environmental characteristics. These factors would seem to promote dominance by those species with an existing pool of propagules and with shade tolerance attributes appropriate to the environment within the disturbed forest. If severe disturbance is frequent enough (using a time scale relating to the life span of a tree), catastrophic phenomena can exert a chronic influence on the structure and floristics of assemblages. The cyclone scrubs mentioned in Section 2.1.5 seem to be good examples.

In summary, the specific and environmental attributes described above indicate that:

- they may be divided into two groups according to their mode of influence on the floristics of regenerating gaps. Attributes such as those associated with the physical environment and species' shade tolerance provide an overall deterministic framework. Attributes relating to the spatial and temporal distribution of gaps and the availability of propagules introduce a stochastic component (see below).

- the total volume of the regeneration niche of tropical rainforests is greater than most, if not all, other plant assemblages. The implications for assemblage diversity are discussed in Section 6.4.

Figure 69 summarizes the main effects of gap size on the floristics and growth characteristics of a regenerating patch.

Figure 69. A summary of the main effects of gap size on the floristics and growth characteristics of a regenerating patch.

Gap size	large	small
Colonizers		
- species	large gap + small gap	small gap
- immediate origins	seed advanced growth	advanced growth
- growth rates	fast intermediate	slow
Diversity	fluctuating	stable
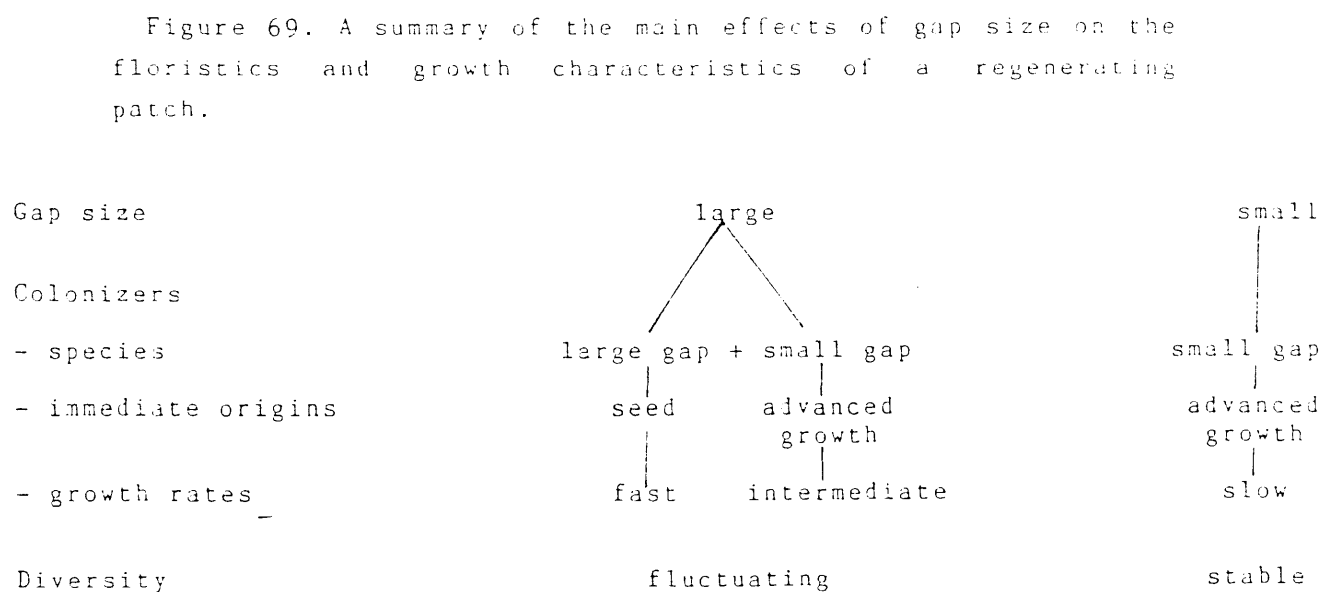
6.2.4 Role of chance

Many of the effects of chance on rainforest floristics have been mentioned during preceding discussions on species and environmental attributes and the course of succession. In summarizing the role of chance, it seems that its primary influences fall into two groups:

- those determining the availability of potentially successful species,

- those controlling the temporal and spatial patterns of disturbance.

Propagule availability is affected by the demography and reproductive biology of the available parent species. Chance elements in determining the actual density and spatial arrangement of advanced growth are introduced during propagule production, dispersal and predation and by weather during initial establishment. Subsequent survival and growth depend largely on chance in the patterns of disturbance which may increase the resources available to some individuals while smashing or smothering others with debris.

In the time frame similar to a reproductive cycle for a typical rainforest tree, disturbance patterns resulting from the collapse or toppling of mature and/or senescent trees seem almost unpredictable. It is only over more extensive areas and longer time scales that meaningful predictions might be made.

6.2.5. Successional models

Simple successional models often require information as to whether stand floristics are in an equilibrium or non-equilibrium state. Given the regeneration patterns outlined in this chapter and the consequences for stand floristics of differing dispersal abilities in an environment where rainforests are expanding, the region's rainforests would generally have to be regarded as being in a non-equilibrium condition. However, at the temporal and spatial scale of the plot studies, many species exhibited

equilibrium behaviour (discussed further in Section 6.5 below).

Another important consequence for successional models of rainforest regeneration following disturbance which primarily affects adults, is the influence of advanced growth (see especially Section 4.9). Surviving seedlings and shoots from damaged stems or roots permit the re-establishment of species existing before the disturbance. i.e. regeneration is not totally dependent on propagules from the survivors. Some of the species which are unable to maintain a pool of seedlings on the forest floor or recover readily by sprouting (several shade intolerants) have a long-lived seed store in the soil and so are also independent of propagules from survivors.

In the context of classical models of assemblage organization, as outlined by Connell and Slatyer (1977), the necessity for autogenic changes of the type implicit in the "facilitation" model, was not observed. The absence of this requirement was especially noteworthy in the study of regeneration after felling and burning (Section 4.9) and during the successful establishment of a wide range of "primary" species in the arboretum without first establishing "pioneer" species (Section 4.8). These changes may be more important on severely degraded sites, such as abandoned quarries, and these sites have often been used to provide examples of successional sequences which were consistent with this model (e.g. see Finegan 1984).

The "tolerance" model is based on the view that succession leads to an assemblage composed of those species most efficient in exploiting resources, presumably each specialized on different kinds or proportions of resources. This model appears to represent the main mechanism controlling succession in the rainforests of this region. The key resource is identified as the amount of light available during the regeneration and establishment phase of a plant's life cycle. Since there is a relationship between longevity and shade tolerance (Section 6.2.2a), progressive mortality (most shade intolerant first) provides opportunities for continued recruitment of shade tolerant species during the course of

succession.

Although competition among individual plants is central to the "tolerance" model, its role has been questioned (van Steenis 1969; 1971, Fedorov 1966; 1977 and more generally by Lewin 1983a and b, see Section 2.3.1). In comparison with assemblages of low diversity, the dilution effect caused by the species richness characteristic of tropical rainforests, might reasonably be expected to result in low intra-specific competition and indeed this seems to provide a basis for the hypotheses of van Steenis and Fedorov. Given the nature of succession in rainforest, intra-specific competition should be greatest among "large gap" species since they are fewer in number and more likely to be growing in closer proximity than "small gap" species. However, even within the latter group, competition amongst individuals is conspicuous in the carpet of seedlings which usually follows mast seed crops.

In a broader context, inter-specific competition for light is a pervading phenomenon with only the few emergents escaping its influence. A critical feature of inter-specific competition for an establishment and growth site in small gap environments, is that the species competing and their size and spatial arrangement will almost certainly be unique even amongst sites which are otherwise similar.

While some problems were apparent in Acevedo's simple model of rainforest dynamics (Acevedo 1980, Section 2.3.2), further development of tolerance models of this type would seem rewarding.

The "inhibition" model assumes that no species necessarily has competitive superiority over another. Thus the first species to arrive and establish has an immense advantage over any others and replacement only occurs when resources were released by the death of, or damage to, the previous occupant. The net result is the favouring of long lived species. Although constrained by the operation of the "tolerance" model, the "inhibition" model may operate within guilds of species with similar shade tolerance.

The "vital attributes" approach (Noble and Slatyer 1980) to

predicting floristic and structural trends associated with
succession, was examined in relation to its usefulness in
rainforest situations. While the concepts outlined seemed
useful for defining key autecological parameters, its
application to developing a deterministic framework for
rainforest successions was found to be limited by current
problems of ranking many species with very similar
attributes.

The future use of probability models, such as that applied
to data from an Australian subtropical rainforest by Shugart
et al. (1981a), promises to provide some broad scale
predictions of floristic trends. Although a reasonable
conceptual basis for the operation of these models within
limited spatial scales, now seems clear, their application is
currently limited by a lack of data on the autecological
characteristics of the available species. On a broader scale
they might be limited by some problems in relating the
probability of successful establishment and growth to specific
environmental parameters (Ewel 1980b, Section 3.3).

A problem still to be examined is the extent of anomolous
behaviour among rainforest species. This trait was observed
by Glenn-Lewin (1980) when plant species took different roles
in a succession than those usually described for them. While
this behaviour might merely reflect inadequate data on the
subtleties of the regeneration niche characteristics of the
component species, it could be the result of some "emergent"
property of the assemblage (see Shugart et al. 1981b).
Further examination is warranted, for the value of
successional theory to problems in vegetation management
depends very much on the predictability of species behaviour.

6.3 Evolutionary trends

The view that evolution in rainforests need not favour rapid growth (Ashton and Brunig 1975), now appears to require modification especially as growth rate emerges as an important attribute in considerations of rainforest dynamics and management.

Growth which improves crown position, size and shape, provides a mechanism enabling an individual to capture a greater proportion of the most limiting resource - light. Rapid growth would seem especially advantageous for "large gap" species which do not usually survive if overtopped (for example see Section 4.6 especially Figure 56). Even among "small gap" species, the capacity to grow as rapidly as the light environment permitted, would place it in a stronger competitive position. However, the physiological attributes associated with rapid growth appear to decrease shade tolerance and thus the ability to survive for long periods under an undisturbed canopy.

In view of the above attributes, there would appear to be an evolutionary advantage for a species which was able to survive well for long periods in low light and then grow more rapidly than its competitors when released into bright conditions. Development of morphological and physiological refinements associated with efficient acclimatization could possibly have played a role in the switch from Gymnosperm to Angiosperm dominated rainforests early in the Tertiary. Evolutionary trends in this direction may also be responsible for the development of very successful groups such as the dipterocarps. However, while these developments may periodically act to reduce diversity by producing a species which is faster growing than others of equivalent or lesser shade tolerance, Tilman's models (Tilman 1982) indicate that the effect would be short lived for such "super species" would soon begin to specialize and then speciate, redressing the balance.

Evolutionary pressure may also account for the relationship between longevity and shade tolerance (Section 6.2.2a). Connell and Slayter (1977) observed that long lived species

would be favoured where the "inhibition" model of assemblage functioning operated. As noted in Section 6.2.5 this model was most likely to operate within species guilds of similar shade tolerance. Since it has often been observed that there are few intolerant tree species in tropical rainforests (e.g. van Steenis 1958b) these guilds could be expected to be most numerous towards the shade tolerant end of the tolerance continuum.

6.4 Diversity

Here, I follow the usual practice (e.g. Connell 1978; Leigh 1982) of equating "diversity" with "species richness". The scales used are "gap diversity" - that within an area of 10-1000 m^2 (e.g. the normal area available beneath a canopy gap for the establishment and growth of regeneration); "site diversity" - that within an area containing limited edaphic and topographic variability (e.g. the 0.5 ha plots described in Chapter 3) and "regional diversity" - large, relatively discrete rainforest blocks containing a wide range of environments (e.g. the sectors of the east coast of Australia identified in Figure 65).

While plot studies (Chapter 3) suggested that site diversities were lower in this region than in South East Asian rainforests, they provided few direct indications of the basis for this difference. Other observations of interest were that:-

i) plot diversity was inversely related to the level of exchangeable bases in the soil (Appendix C2).

ii) regional closed forest diversity in eastern Australia appears strongly and inversely related to latitude (e.g. Figure 70).

iii) regional and site diversities of other structural forms of plant assemblage (e.g. open forests, shrublands and grasslands) are not as influenced by latitude as closed forests (e.g. open eucalypt forest sites are dominated by one to a few species whether in tropical or temperate Australia).

iv) tree species appear to make up over half the total vascular plants in Australia's tropical rainforests (Table 8).

v) gap and site diversities appear higher in tropical and subtropical rainforests than in adjacent forests of other structural type (e.g. whereas rainforest sites in north Queensland may contain 52-135 tree species - Table 8, there might only be 3-5 tree species on nearby tall open forest sites - Unwin 1983).
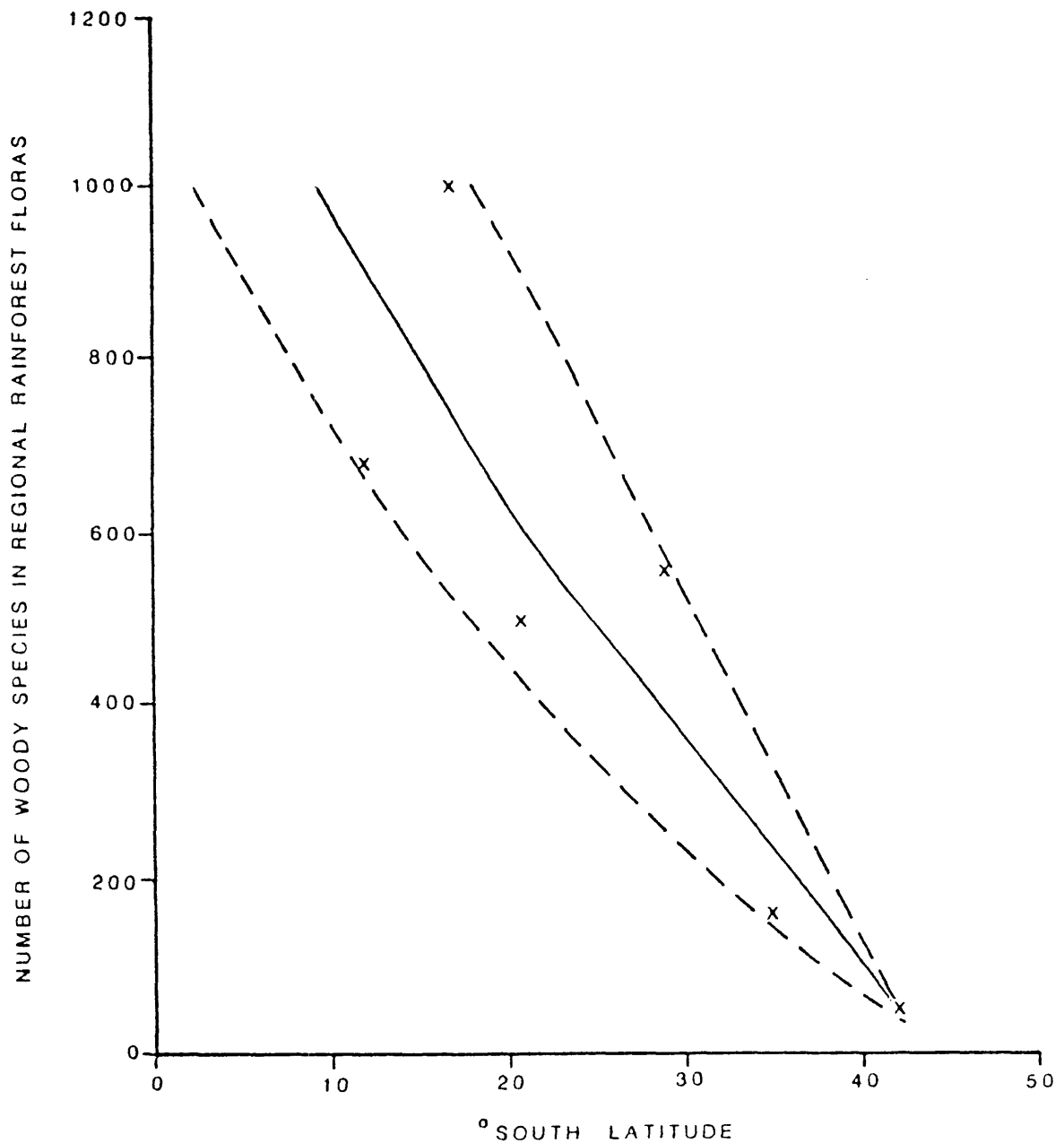
Figure 70. Regional latitudinal trends in the number of woody plant species in the rainforests of east Australia are indicated by the solid line. Crosses show the actual number of species for the regions indicated in Figure 65 with the addition of data for the region centred on 42°S (Tasmania) from Jarman and Brown (1983). The upper dashed line suggests the approximate upper species richness limit for regions where rainforests are very widespread and topographic and edaphic variability are considerable. The lower dashed line is thought to approximate the minimum level of species richness for regions where rainforests are restricted.

These observations suggested that while site diversity might be influenced by soil fertility, the diversity characteristic of rainforests seems linked with some basic element of their structure and a latitudinal control of resource partitioning during the establishment phase of the dominant life form i.e. the trees.

The most prominent of the structural and disturbance features characteristic of rainforests are closed canopies (Section 4.2) and a disturbance regime which continually provides relatively small discrete sites for regeneration to develop (Section 4.4.1). These features are generally absent from other forest types. Although small, these sites are environmentally heterogeneous, particularly with respect to the light regime (Sections 4.3). I believe that the factors controlling propagule availability (reproductive biology of the component species and attributes of the disturbance pattern - summarized in Section 6.2) and partitioning of the light regime by species establishing in gaps (Sections 4.6 and 4.7), have enabled the diversity characteristic of gaps in tropical rainforest to evolve and be maintained. Site diversity is the aggregation of many discrete regeneration events in gaps of varying size, created at varying times, with a varying population (both species and density) of available propagules establishing during a range of weather conditions. Regional diversity also includes species with different climatic requirements and specialists to particularly favourable or stressful sites e.g. soils from ultrabasic parent material.

The observed decrease in diversity with increasing latitude might be primarily explained by a tendency towards a more simplified light environment on the forest floor beneath small canopy gaps in rainforests at higher latitudes (Section 4.3). However, there are several other factors which might limit diversity at higher latitudes. They are seasonal limitations on the proportion of each year available for plant establishment and growth (due to soil water availability and temperature) and higher seasonal temperature ranges (Section 6.2.3a). Nix (1982) observed that latitude also influenced the range of altitudinally controlled thermal regimes which are

potentially available; the number of recognizable regimes decreasing from the warmer end of the range with increasing latitude. He argued that because of opportunities for chance establishment of species outside their normal thermal range, some additional enhancement of local diversity could be expected where a range of thermal response regimes is available in a restricted geographic area. However, it should be noted that in many parts of the tropics, the altitudinal range is insufficient to provide the cooler thermal regimes.

A rather hypothetical view of the way in which latitude influences the basic processes contributing to the regional diversity of closed forests in a latitudinal transect from New Guinea through east Australia, is illustrated in Figure 71. Here, controls imposed on the floristics of regeneration in gaps by the gap size characteristic of closed forests and gap geometry in relation to sun angle, are shown as the basic influence. The second lowest sector illustrates the effects of latitude on the range of altitudinally controlled thermal regimes potentially available. The third sector shows the influence of seasonally limiting temperature and soil water regimes. At this longitude the first influence is seasonal "winter" drought which intrudes rapidly at about $8^{o}S$. Although the rainfall is again aseasonal at around $30-35^{o}S$, summer drought is apparent at still higher latitudes. The latitudinal influence causing winter temperatures to be unfavourable for plant establishment or growth, follows a more consistent pattern.

The influence of soil fertility on site diversity has been noted by other workers. For example, Ashton (in Ashton et al. 1978) thought the highest diversity in the Bornean rainforests would be found on sites with average to somewhat infertile soils, while Huston (1979) and Budowski (1965) noted low assemblage diversity when soil conditions were extreme. These observations are supported by Tilman's graphical models of the competition amongst species for limiting resources. Using these models Tilman (1982) showed that diversity should be highest at low levels of limiting resources and that it should decrease at both high and very low levels. However, the data available from this region do not appear to support
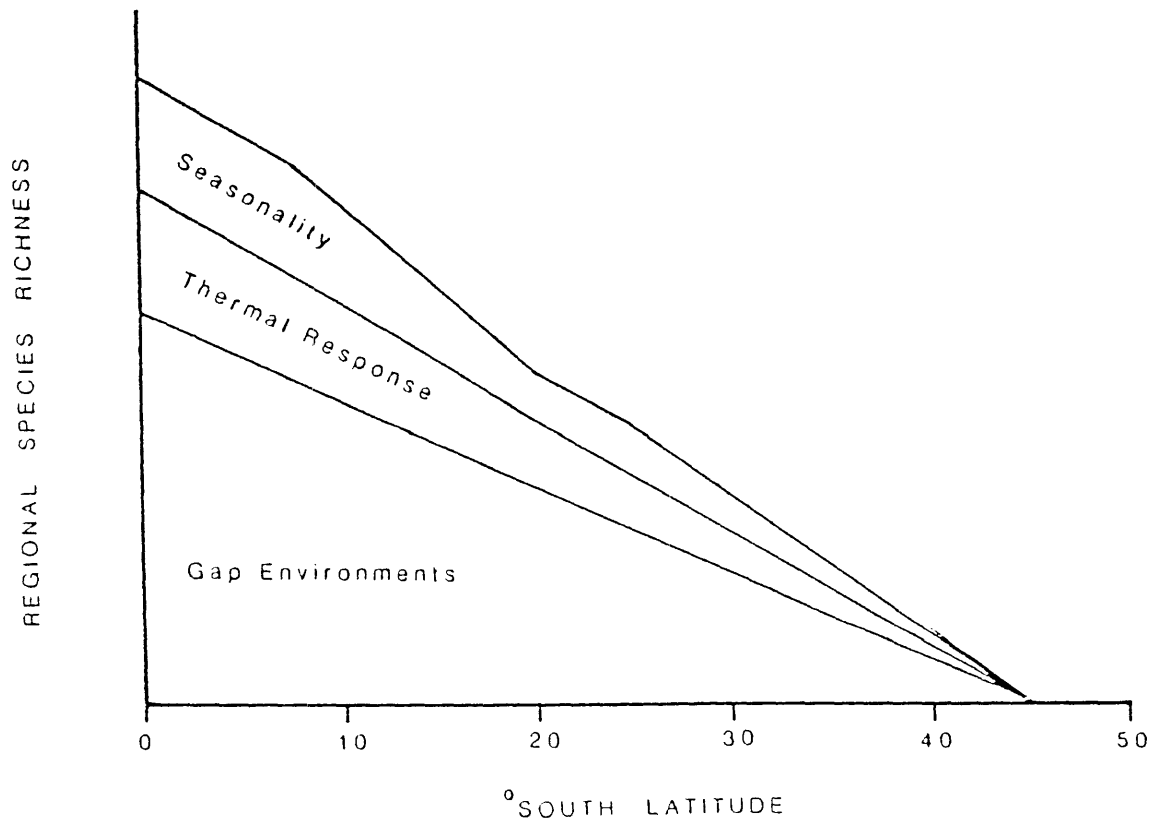
Figure 71. The ways in which latitude appears to influence the three basic processes contributing to regional diversity along a transect from New Guinea through eastern Australia, are illustrated. The bottom sector of the figure shows the effects of latitude on the variety of establishment sites created by spatial and temporal partitioning of gap environments; the second sector demonstrates the influence of the number of potentially available thermal regimes; the third sector indicates the effects of seasonality in determining the period of each year available for plant establishment and growth.

Fittkau's theory that diversity is an adaptation to continuous limitation of nutrients and food scarcity under otherwise optimal conditions for life (Fittkau 1983).

In relating my observations to current theories of the mechanisms responsible for the establishment and maintenance of diversity, I note that models based on equilibrium and non-equilibrium systems (e.g. Connell 1978) do not seem mutually exclusive for these states tend to be scale sensitive and appear species rather than assemblage attributes. For example whereas "small gap" species may exhibit equilibrium behaviour on a site as small as a sample plot, any "large gap" species present will usually show signs of becoming locally extinct even though they might be colonizing nearby sites.

Since the light regime on the forest floor beneath a canopy gap is an important habitat component, my observations could be regarded as an extension of the niche differentiation theory. Past interest in this theory has concentrated on those edaphic factors which were thought to enable a rainforest species to occupy that particular portion of the available habitat providing it with the best competitive edge (e.g. Ashton 1969; Ricklefs 1977; Whitmore 1978 and Denslow 1980a). Ricklefs (1977) suggested that tropical trees may have divided this niche axis finely. Although Connell (1978) saw variation along "niche axes" (such as food, habitat space and time of activity) as providing many individual niches for animal species to occupy, he saw plants as being less specialized for, along the food niche axis, they all have similar basic resource requirements (such as light, water, carbon dioxide and mineral nutrients). These outlooks do not appear to appreciate the significance of attributes relating to shade tolerance and the role of other niche characteristics, particularly those of the "phenological niche" which influences propagule availability and the "life form niche" which relates to productivity and growth form characteristics. Sugihara (1980) noted that competitive niche differentiation models produce a log normal distribution of species abundances. While this species distribution pattern is characteristic of both tropical and temperate forest assemblages (e.g. Leigh 1982; Section 3.3.1), it may also be

created by other models of forest dynamics (e.g. the "competitive equipoise" model described by Hubbell 1979).

Connell (1978) suggested that an "intermediate disturbance" mechanism maintained high diversity by preventing the elimination of inferior competitors. I would emphasize that typical temporal patterns of disturbance in rainforests result in regeneration strongly influenced by propagule availability and weather during establishment (Section 6.2.4; see also Alugov 1982). If disturbance was to prevent the elimination of inferior competitors, it would probably have to be frequent relative to the age of the dominant species in the assemblage, for plot demographic data (Section 3.2.2) and species survival in establishment trials (Section 4.6) indicate that the death of inferior competitors is most likely in the early stages of their life cycles (see also Webb 1968).

Although Connell (1978) cited some examples (Eggeling 1947 and Jones 1956) to support his hypothesis that diversity falls off with decreasing disturbance frequency, there appeared to be no direct relationships between the frequency with which sites are influenced by cyclones and diversity in north east Australia (Section 3.3.1). However, it is suspected that the diversity of the vine dominated "cyclone scrubs" (briefly mentioned in Sections 2.1.5 and in discussing plots 9 and 13 - Section 3.2), may be much lower than surrounding rainforest. These occur in coastal forests on sites subject to frequent and very severe wind disturbance. Basic forest structure appears to have been destroyed and vines cover the crowns of remaining trees. Normal gap recovery processes are therefore prevented. The low diversity of some of the surrounding forests dominated by Backhousia bancroftii and Lindsayomrytus brachyandrus may be attributed to the physical resistance of these species to wind disturbance (see discussion on Plots 9 and 17 and Section 3.3.1).

Outlined below are some other hypotheses mentioned by Connell (1978) or Leigh (1982). Although the mechanisms associated with these may contribute to the establishment and maintenance of diversity, none appears able to explain the contrasts in diversity between rainforests and adjacent open

forest and/or the unique latitudinal trends in rainforest diversity noted earlier in this section.

Hypotheses based on the assumption that species are approximately equal in ability to colonize, exclude invaders and resist environmental vicissitude (Connell 1978) may be relevant within guilds of similar species. Hubbell (1979) established a model based on these assumptions, to predict change in species numbers over time. Unfortunately this model appears inappropriate, at least for the rainforests of this region, for it ignores the role of advanced growth in succession (proposing that all regeneration following a disturbance is derived from the survivors of that disturbance) and assumes that all trees have similar regeneration, growth and survival characteristics.

The number of different life forms found in rainforests also appears to be of secondary importance, for while the physical environment of the tropics favours some life forms (e.g. epiphytes) more than do temperate climates, much of the unique latitudinal influence on rainforest diversity can be observed in its effects on the members of the dominant group - the tree species.

Chesson and Warner (1981) thought that species may coexist because their reproduction rates responded differently to environmental change. If the species were long lived, environmental variations would favour rare species because they gain far more from a year favourable to reproduction than they lose in an unfavourable year. Since variability in reproductive success from year to year and long life are typical characteristics of "small gap" species (Section 6.2.2) this mechanism may contribute. However, more data on species longevity and their reproductive patterns are required before the importance of this mechanism can be understood.

Studies by Connell et al. (1984) did not find unequivocal evidence to either support or refute the hypothesis that mortality from causes unrelated to competitive interaction falls heaviest on whichever species ranks highest in competitive ability. However, predation during seed and early seedling stages does increase the chance element in

determining the available propagules on a regeneration site at the time of disturbance.

After comparing tropical and temperate forests, Jordan and Murphy (1978) thought that the low diversity of temperate forests might be a reflection of a supposed evolutionary requirement for temperate tree species to be more efficient producers of wood and were thus better competitors than their tropical counterparts. In Section 6.6, I propose an alternative hypothesis to account for their basic observation.

I conclude that an explanation of rainforest diversity need not incorporate their supposed great age (e.g. Richards 1952), or even their youth (Lewin 1984). In my view it can be most satisfactorily explained by studying the regeneration, growth and mortality patterns of the component species in natural forest. It also seems possible from the discussions here and in Whitehead (1982) that claims, such as those of Hill (1973), that diversity can be related to assemblage features such as stability, maturity, productivity, evolutionary time and predation pressure, may not be generally applicable.

6.5 Stability

In assessing the various views on the stability of rainforests, there are problems of philosophical approach, measurement and scale.

The results of studies described in this thesis generally support reductionist theories which hold that most of the basic properties of a plant assemblage can be predicted if the properties of the individual species which are either present in, or available to make up an assemblage, are known. In contrast to alternate holist interpretations, this view does not emphasize or perhaps even acknowledge, interdependence among component plant species. Thus removal or modification of part of an assemblage will cause some adjustment which will be seen to be almost directly in proportion to the changes made. Holists often see such modifications as causing a chain reaction with extensive unforeseen implications (Harper 1982). The question as to whether truly "pivotal species" (Howe 1984) occur in rainforests cannot yet be satisfactorily answered, although the Cassowary must be a contender (Section 5.3.1.1).

Measures used to assess the stability of rainforests will depend on the purpose of the study. For example those concerned with the preservation of rainforest biota will study trends in individual species abundances, while those interested in continuing wood production might study changes in floristic composition or nutrient pools and fluxes.

Because of the nature of regenerative processes in rainforests, patches of small size may appear to have low stability (in terms of both resistance and resilience) when individual species abundances are used as the measure. However, an assessment, using the same measure, of the stability of a larger area surrounding this patch, might show stable characteristics. A possible example of this phenomenon is given below. Differing temporal scales can lead to similar problems when the influence of cyclic successional patterns dominates assemblage floristics.

An examination of the growth rates and size class distributions of individual important tree species in the data

derived from the plots described in Chapter 3, suggested that many of these sites could not be described as in equilibrium in terms of individual species abundances, even though they were undisturbed by human influence. In some instances the apparent lack of stability may be a problem of scale i.e. the plots may not be large enough to hold adequate samples of all the species in the area and while species movement into and out of the plots could be taking place, these shifts may be balanced by opposite movements on adjacent sites. The floristic richness and stem size distributions of individual species in the Mt Lewis plot (no 5) may be symptomatic of this phenomenon for the apparent changes were not suggestive of any particular successional trend.

On other sites trends in plot floristics may be a reflection of long term cyclic changes due to infrequent severe disturbances (especially cyclones). Several of the plots (e.g. 3 and 13), containing relatively high densities of "large gap" species such as Acacia aulacocarpa, appeared to provide good examples of this type of cyclic succession.

The nearness of open forest and the relatively high proportion of species of intermediate shade tolerance (e.g. Flindersia spp.) in the important species lists for a third and relatively large group of plots (particularly 6, 8, 11, 14 and 19) leads me to suspect that there may not yet have been time for all the potential species to have become established in the area. Although direct evidence for this supposition is not currently available, there are indications of a general rainforest expansion which began about 10,000 years ago in this region (Kershaw 1981). The sensitivity of the rainforest / eucalypt forest ecotone to environmental shifts is illustrated by the marked expansion of rainforests during the past 50-100 years in areas where fires lit by Aborigines no longer acted as a constraint (Section 2.1.5g). It is to be expected that the floristics of these new rainforests would be influenced by differences in the dispersal efficiency of the available rainforest species (Section 5.3) and the probability of long term persistence especially among the first of the "small gap" species to invade the site. Floristic instability due to similar factors appears to have occurred in some high

latitude North American forests (Botkin 1979; Davis 1981). The probability of long term species persistence led Hopkins (1981) to suggest that the rainforests of this region may be thousands of years behind climatic change and that many types were enmeshed in a spatial framework laid down in the past.

The proposition that rainforests in north east Australia might be in retrogressive successional stages because of gradual losses of critical nutrients, should also be examined. Walker et al. (1983) have proposed that such successions might be common on the old landscapes characteristic of this continent and that disturbance of such systems is likely to increase the rate of nutrient loss causing a decline in the vegetation. Stark (1978) suggested that natural retrogressive successions accounted for the vegetation patterns he observed in part of Amazonia. While similar patterns were not obvious in this region, the preparation of nutrient budgets for a range of representative sites (a task beyond the scope of this study) is essential for evaluating this proposition. It is, however, observed that most of the landscapes occupied by rainforests in this region were rejuvenated by block faulting and volcanism during the latter part of the Tertiary and throughout the Quaternary. Parent material weathering could therefore, still be providing significant nutrient input. It is also noteworthy that, in this region, the fire regime, rather than soil nutrients, usually appears to determine the relative distributions of closed and open forest. Although this regime is in a state of flux, recent trends appear to favour an expansion rather than a contraction of the area under rainforest (Section 2.1.5).

In terms of individual species abundances, much of the region's rainforests appears naturally unstable, at least on spatial scales relevant to forest management or within temporal scales akin to human lifespans. Effects of human interference on both the rate and direction of floristic change are therefore not easily forecast. Some apparent trends are discussed in Section 6.6.

6.6 Forest management implications

Although tropical rainforests yield many products, forest managers' major concerns are usually with wood production. Important questions relate to the stability of logged or silviculturally treated forests and the productivity (both quantity and quality) of managed stands. The following observations of probable stability following selective logging in the rainforests of north east Australia, assume that about 25% of the standing basal area is removed at intervals of 30-50 years. (This prescription would be close to that envisaged for this region's logged forests.)

Although selective logging creates some soil and litter disturbance not observed when gaps are created naturally (Whitmore 1983), some first approximations of its effects can be made on the basis of a knowledge of the regeneration strategies and other niche characteristics of individual species and insights into the dynamics of some stands gained through the plot studies.

At the first logging cycle most of the trees cut would be large emergents. The gaps created by removing these trees and constructing logging roads and loading ramps would initially allow proliferation of previously restricted "large gap" species such as Alphitonia petriei and Commersonia bartramia. Gaps created during subsequent logging cycles would generally be smaller as the average size of the trees harvested would be less than during the initial cut. Disturbance created by the re-opening of logging roads and tracks, and loading ramps would not be as great as that during their initial construction and it should generally be possible to use lighter equipment than in the initial logging. The most important long term change in the disturbance regime would be that gap formation mainly occurred during harvesting (i.e. at intervals of about 30 years) rather than more or less randomly. Mean size and long term average rate of gap formation could be expected to be slightly greater than in unlogged forest.

The new disturbance regime (described above) would favour an increase in the representation of species (such as Flindersia

brayleyana, Toona australis and Cardwellia sublimis) which tend to dominate gaps of intermediate size. The inability of these species to survive for long periods on the forest floor beneath an undisturbed canopy should not disadvantage them because the interval between effective seed crops (1-3 years depending upon species) appears to approximate the time that their seedlings can survive under heavy shade (Sections 4.6 and 5.1.2). The proportion of "large gap" species would decline following recut cycles to a relatively constant level which would probably be somewhat higher than that in unlogged forest. Opportunities for "small gap" species to establish and grow would seem to be little different from those in natural forest.

Denslow (1980b) predicted that logging would cause a gradual loss of species from rainforests. My impression for these forests is that while the selective logging regime envisaged may alter some of their floristic and structural features, if any loss of species occurs, it is likely to be over very long periods. Such losses would probably be obscured by floristic changes resulting from influences such as climatic fluctuations and other human activities especially the introduction of alien species and interference (often unconsciously) with propagule dispersal. Of all the rainforests examined, those represented by lowland plots dominated by a single species (9 and 17) may be the least resilient from the viewpoint of recovery after logging, especially if large gaps were created. These stands appear the result of adaptation of the dominant species to cyclonic winds (Section 3.3.1). The recovery of these forest types would probably be exceedingly slow whenever exploitation resulted in the formation of large gaps, for the dominant species are both "small gap" types. Attempts by these species to regenerate in large gaps would result in their being swamped by fast growing "large gap" vines, particularly Merremia peltata. Support for this prediction is found in "cyclone scrubs" which occur naturally within these forest types (Section 2.1.5). In these assemblages trees rarely seem able to break through the low liane dominated canopy and restoration of forest structure would appear to be a very lengthy process. It also seems possible that increased vine

loadings on any remaining stems could reduce their ability to withstand wind from subsequent cyclones. Kochummen and Ng (1977) and Rico-Gray (1980) also observed that prolific liane growth could have a considerable influence on the course of successions.

Questions surrounding the long term productivity of rainforests may be of greater immediate concern than those of their stability, for managed forests which are not seen to pay their way are more liable to be converted to other forms of land use.

In logged and silviculturally treated rainforests of north east Australia, volume increments range from 1.6-2.3 m^3 ha^{-1} $annum^{-1}$ (Volck 1975). Typical values for the tropics generally appear to be 1-3 m^3 ha^{-1} $annum^{-1}$ with a maximum of 8-9 m^3 ha^{-1} $annum^{-1}$ (Johnson 1976; Wadsworth 1983). However, sites yielding growth rates as high as 21 m^3 ha^{-1} $annum^{-1}$ have also been reported (Weidelt 1984). In contrast, plantations of shade intolerant species, such as some _Acacia_, _Pinus_ and _Eucalyptus_ _spp._, frequently yield 20-50 m^3 ha^{-1} $annum^{-1}$ (Johnson 1976; Wadsworth 1983).

Although complicated by factors such as wood density (Jordan and Farnworth 1980), biomass allocation (Johnson 1976; Shukla and Ramakrishnan 1984) and tree architecture (Dawkins 1959; Whitmore 1975), the generally low wood production rates noted above appear to be primarily a reflection of the low maximum growth rates which can be achieved by the "small gap" species which dominate most rainforests. Although these species are unable to grow as rapidly as the few shade intolerant "large gap" species even when supplied with adequate resources, they do seem to be able to respond proportionally more than those species whose behaviour tends towards the "large gap" group (Section 4.8; Weaver 1983).

Although Ashton and Brunig (1975) suggested that the processes of natural selection which lead to enhanced rates of production, were not normally favoured in rainforests, growth does appear to be an important species attribute (Section 6.3). Another different view was that of Jordan and Murphy (1978) who claimed that trees having the greatest rate of wood

production were the most successful competitors. However, longevity can mollify any advantages from rapid growth especially when linked with shade tolerance.

Jordan (1971; 1983) and Jordan and Murphy (1978) noted that temperate tree species were generally faster growing than those of tropical forests. They suggested that tropical trees might be less efficient in utilizing available light for growth than trees of temperate regions. I believe their generalization may be the result of the widespread presence in temperate regions of open forests and forests formed by catastrophic events, especially fire. Because of the regeneration environments characteristic of these temperate forests, they might be expected to have a higher proportion of faster growing, shade intolerant species than most tropical forests.

If the capacity of rainforests to produce wood is largely dependent on the shade tolerance of the trees within it, then the theoretical model relating the light regime on the forest floor to canopy gap size and site latitude has some important implications for forest management. This model indicates that there will be proportionally more trees tending towards the faster growing "large gap" type in equatorial rainforests than in rainforests at higher latitudes (Section 4.3). Provided the faster growing species are commercially desirable, silvicultural treatments aimed at reducing the proportion of slower growing species should therefore be more practical in rainforests at low than at high latitudes. However, if the "large gap" species group contains weed species which are difficult to control, silvicultural treatment may only confound undesirable floristic changes associated with logging.

6.7 Concluding remarks

The basic premise adopted in these studies has been that the essential features of rainforests - their floristics and structure - are largely the result of the characteristics of the available species and the history and nature of disturbance at that site. An improved understanding of the processes controlling succession was obtained during studies described in this thesis. This has enabled some evolutionary trends in rainforests to be predicted. Factors influencing rainforest stability and the establishment and maintenance of diversity have been clarified. An improved understanding of the role of tree growth in succession should enable refinements to the methodology for manipulating the species composition of modified forests and for selecting species for plantations. The supposition that rainforest productivity (in terms of wood) is inherently restricted, also has very important implications for the management of rainforests.

Finegan (1984) would view my approach as reductionist (in which chance and Darwinian interpretations dominate) and would contrast it with holism (the view emphasising unity and integration in nature). In his discussion of forest succession Finegan concluded that :-

> ". . the reductionist story fails, as it stands, for two reasons: it neglects the nature of seed dispersal, and its generalizations about environmental change and exploitative and conservative species are untenable."

In my view Finegan takes too narrow a view of the reductionist approach and links it too closely with the "initial floristic composition" model of succession. A reductionist approach need not neglect the nature of seed dispersal - a topic discussed at some length in this thesis. I also believe that Finegan places too much emphasis on autogenic changes which are apparent during the revegetation of severely disturbed sites. There is much less scope for such changes during the regeneration of rainforest gaps of typical size. I suspect that data derived from disturbance types which are so rare as to be insignificant from an evolutionary viewpoint, might be meaningless, if not misleading, in developing general models of successional processes. Phenomena which required the

postulation of "emergent properties" (sensu Shugart et al. 1981b) were not observed during these studies.

Gomez-Pompa and Vazquez-Yanes (1981) also found that the individualistic concept was the only helpful general model of plant association to be of value in their studies of a Mexican rainforest and noted the enormous amount of data on individual species characteristics which will have to be collected before the true nature of succession in the tropics will be established. Recent advances in ecophysiological research, when combined with studies of population biology have, as predicted by Bazzaz and Pickett (1980), improved our general understanding of rainforest dynamics. Future ecophysiological studies of relationships among attributes linked with shade tolerance may permit some short cuts in developing successional models.

The approach used in this thesis also appears capable of providing information which the silviculturalist could confidently use in rainforest management. At this stage it does not seem feasible to reduce the amount of data which must be collected. For example, long term observation of the vegetation in plots appears to be as essential as the collection of data relating to the regeneration strategies of the component species. As a next step in refining silvicultural practice for the rainforests of north east Australia, models predicting future stand development should be tested using data from plots established in logged and silviculturally treated forests by the Queensland Department of Forestry.

In a global context, the devastation of many tropical rainforests appears to be the result of an inability to bridge the gap between socio-economic demands and desirable silvicultural practices. This conflict appears to have been an important factor in leading Webb (1983), Myers (1983) and many others to advocate the management of tropical forests primarily for their non-wood values (chemical products, rattans, genetic resources, water, erosion control, research etc.). The supposition in this thesis that there are significant limitations to the capacity of well managed,

silviculturally treated rainforests to produce anywhere near as much wood as plantations, tends to support this conviction. Unfortunately the same socio-economic factors would also appear to preclude any important change in typical patterns of forest exploitation. Indeed studies by Wadsworth (1983) showed that even with a greatly expanded plantation program, the logging of rainforests will have to continue if the projected world demands for wood are to be met. A better understanding of rainforest dynamics is essential for even rudimentary management of this resource. While an holistic research approach may prove to be of some benefit to forest managers, I believe that studies of the ways in which individual species contribute to assemblage functioning, must be accorded the highest priority.