CHAPTER 1

Introduction

1.1 Scope of the thesis

This thesis is about dynamic processes observed in some of the tropical rainforests of north-east Australia. The aims are to show that the essential features of these rainforest assemblages - their structure and floristics - appear to be largely the result of the characteristics of individual plant species available at each site and the history and nature of disturbance at that site. The ultimate objective is to provide information which will help forest managers reach perceived goals.

The characteristics of species which are of greatest importance are those relating to their regeneration strategies and establishment requirements. Figure 1 illustrates the nature, but not the magnitude, of what are believed to be some of the essential interactions amongst rainforest features, dynamic factors and the environment.

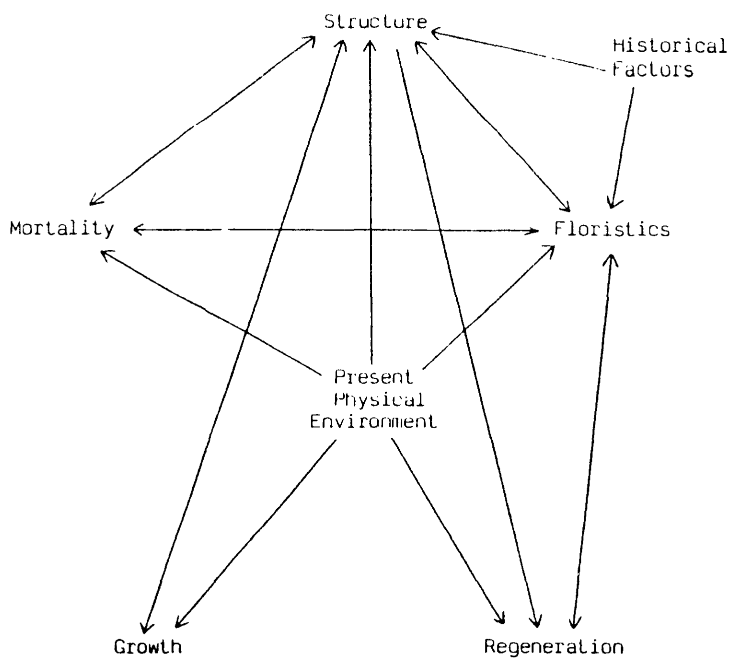

Figure 1. Some of the suspected relationships among rainforest features, dynamic factors and the environment are shown.

The general approach has been to link studies of assemblage structure and floristics in a series of unlogged sample plots with observations on the frequency and nature of forest disturbances and on aspects of the reproductive and growth patterns of their component tree species.

While this thesis does not examine directly the effects of disturbances introduced by European man (e.g. clearing and logging), it does contribute to an understanding of the mechanisms responsible for determining the direction of successional trends, and the development and maintenance of stability and diversity in rainforests. To use "undisturbed" rainforests as the basis for an important part of these studies might seem perverse. However, it must be remembered that even though much of our interest in the applied sphere centres on assemblages disturbed by man, their component species evolved in somewhat different circumstances.

The significance of the characteristics of successions initiated by man cannot however, be underestimated. Ewel (1980a) observed that:-

> "Just as successional communities reflect human destruction, they also signify high productivity and potential for net yield. They are quite literally the ecosystems that feed us."

Whether we like it or not, successional assemblages resulting from human disturbance will become more and more the norm everywhere, but especially in the tropics where the pressures of increasing human demands for timber, food and other agricultural products are making great in-roads into the remaining tropical forests. Although social, economic and political factors will determine how much of the tropical rainforest survives, any knowledge of the basic factors controlling diversity, succession and stability in the variety of tropical plant assemblages now used by man, will be to his benefit. This knowledge will also be of value in the challenging task of restoring the productivity of huge areas of degraded lands in the tropics to a useful level.

In the context of Australian rainforests, it is important to note that shifting cultivation has, as far as is known, never been practiced. The absence of this feature enables studies of the dynamics of rainforests to proceed with the knowledge that this environment is free from the variable which, on other continents, often seems to have caused observations relating to forest dynamics to be misinterpreted. Areas of rainforest as undisturbed as those of this region, may be rare in the tropics. For example evidence of past human activities led Sauer (1958) and Richards (1973) to suspect that there may be no virgin rainforest in the African or American tropics respectively.

1.2 Nomenclature

The terminology used in this thesis needs to be explained for it does not necessarily correspond with either recent or traditional use. Indeed most of the terms associated specifically with the descriptions of dynamic processes in plant assemblages have either a wide spectrum of meaning or a meaning which has gradually changed with time, often as further work brings out subtleties not appreciated at first. Divergent use is particularly noticeable between specialists in either animal or plant assemblages. However, the nomenclatural problems discussed below are not confined to the description of dynamic processes for even the meaning of the word "rainforest" is somewhat controversial and must be explained. The failure on the part of some authors in this field to clearly define the meanings of the terms they used has, I believe, led to some unnecessary controversy and confusion. Unfortunately, this problem has sometimes been compounded when the temporal and spatial parameters and the context of the study or discussion, were not described adequately. Where these parameters are described they are often useful, if unintended, indicators of their authors' experience, approach and perhaps prejudice. Miles (1979) claimed that:-

> "A researcher's basic attitudes and assumptions about vegetation govern his objectives and approach to any problem. These predispose him towards using particular kinds of data with their own special inherent limitations of interpretation."

Assemblage- In this thesis I use the term "assemblage" where others might use "community" or "ecosystem". In so doing, I follow the advice of McIntosh (1967) and Miles (1979) for the alternatives appear to imply a certain degree of spatial discreteness and internal interdependence between species which I cannot currently accept for the want of further experimental evidence. This judgement would not have the universal support of all those involved in the ecology of rainforests. For example the outlook of Webb and Tracey (1981) in relation to the development of rainforest "communities" seems apparent in the following sentence :-

> "Consequently, although the elementary units of vegetation change are species populations, the species tend to cohere in characteristic interdependent aggregates which are still recognizable during allogenic change as fragmentary associations derived from the original community-type."

<u>Canopy gap</u> - Brokaw (1982) discussed the problems associated with the definition of gaps created by treefalls in forests. He defined a canopy gap as :-

> "a hole in the forest extending through all levels to an average height of 2 m above the ground."

While this appears to be a useful definition, it is observed that the pattern of regeneration in a gap may be greatly influenced by the degree to which the forest floor is exposed by the disturbance creating the gap. Although the measurement of gap size presents problems (discussed in Chapter 4), the term "large gap" is used to indicate that the ratio of gap height/ gap diameter is < 3. This parameter for a "small gap" is > 4.

<u>Disturbance</u>- Disturbance is used in the sense of any change in the structure of an assemblage or part of an assemblage that is not part of a normal phenological cycle.

<u>Diversity</u>- This parameter is often used in a comparative fashion to compare the richness, in terms of species present, in two or more assemblages separated in time or space (e.g. Connell 1978). It is also used to reflect both the species richness and the evenness of the distribution of species in an assemblage (Pielou 1969). After examining floristic data from

this study (Appendix A) in relation to the 16 different indices of richness, evenness and diversity (sensu Pielou), Stocker, Unwin and West (1985) concluded that species number was the best index of richness. They also found that while the finite sample version of the Shannon-Weaver index of diversity (Brillioun 1962) appeared to be a good compromise between richness and diversity, Simpson's index (Simpson 1949; Peet 1974) emphasized evenness.

Normal phenological cycle- In this context, this term refers to those cyclic changes in crown characteristics associated with reproduction and foliage replacement.

Rainforest- It has often been pointed out that the terms "rain-forest", "rainforest" or "rain forest" are quite unsatisfactory (e.g. Baur 1964a) for all forests need some rain but not all are regarded as rainforests. Furthermore, neither the total amount nor seasonal distribution of rainfall necessarily determines whether a forest can be called a rainforest, although it must be said that rainforests are often found towards the wetter end of the climatic spectrum. The word appears to have had its origin in the pioneering work of Schimper (1903). The definition he gave for tropical rain-forest, "Evergreen, hygrophilous in character, at least 30 m high, but usually much taller, rich in thick-stemmed lianes and in woody as well as herbaceous epiphytes" would almost encompass the assemblages called rainforests in this thesis. However, the rainforests of this region all grow in a climate with a marked summer rainfall distribution (Table 1; Figures 5 and 6) and some deciduousness is apparent at a few sites. Nevertheless their close structural relationships with rainforests of the ever-wet tropics are quite obvious.

The use of the single word "rainforest" follows that of Baur (1964a), and more recently Webb and Tracey (1981). Baur adopted this word in an attempt to indicate :-

> "---the community's status as a fully independent plant formation and to avoid undue emphasis on rain as the sole determining environmental factor."

Baur reasoned that despite its inadequacies, the term rainforest was so well entrenched in the popular and scientific literature that it was impossible to remove. Alternative terms such as "vine forest" (Webb 1959) and "tropical forest" (Longman and Jenik 1974) have been suggested as the basis for a new terminology to describe assemblages currently thought of as rainforests but they have not been widely adopted. Sommer (1976) reviewed these nomenclatural problems and to meet the needs of large scale tropical forest inventories suggested the term "tropical moist forest" to encompass evergreen and partly evergreen forests together with certain savanna woodland mosaics.

For the purposes of this thesis the term "rainforest" is used in a fairly narrow sense. Specifically excluded are the transitional assemblages containing typical open forest tree species (particularly _Eucalyptus_ _spp._) in the upper canopy and a lower canopy in which rainforest species are prominent. Also excluded are assemblages at the drier extreme of the closed forest continuum i.e. the monsoon forest or vine thickets (_sensu_ Webb 1959) and the small areas of closed swamp forest found on parts of the coastal lowlands.

Regeneration- This word may be used to describe either the recovery process within a forest following disturbance or the immature plants which are, or could become, part of the recovery process. These plants may have been derived from seeds, coppice shoots or root suckers.

Regeneration _niche_- The meaning of this term follows that used by Grubb (1977). He defined a plant's niche as its total relationship with its environment, both physico-chemical and biotic. Further he stated that such a definition necessarily includes a statement of the role played by the plant as well as its tolerance. Within a complete definition four component niches were recognized:-

a) the habitat niche i.e. the physical and chemical limits tolerated by the mature plant.

b) the life-form niche i.e. productivity and three dimensional pattern.

c) the phenological niche i.e. the pattern of seasonal development.

d) the regeneration niche i.e. an expression of the requirements for a high chance of success in the replacement of one mature individual by a new mature individual of the next generation.

Shade tolerance- This term is used as an expression of the ability of trees to survive and grow beneath a forest canopy (Spurr and Barnes 1980). Tree species are often thought of as being either "shade tolerant" or "shade intolerant" (e.g. Acevedo 1980). However, in tropical rainforests at least, a continuum of response appears to exist (e.g. see Whitmore 1975; Augspurger 1984). In this thesis, species near the extremes are described as "small gap" and "large gap" species. Alternative descriptions used by other workers have included "primary" and "secondary" (e.g. Swaine and Hall 1983) "dryads" and "nomads" (van Steenis 1958b) "light-demanders" and "shade-bearers" (Whitmore 1975). "Large gap" species are also sometimes called "pioneer" or "seral" species. "Early" and "late" are sometimes used as adjectives to indicate intermediate positions e.g. "late secondary" species (Hopkins *et al.* 1977).

Scientific names- The names applied to taxa in this thesis are consistent with their use as indicated below :-

a) north Queensland rainforest trees- Hyland (1982)

b) other seed plants:- i) Backer and Bakhuizen van der Brink (1963-68)(first priority) or ii) Bailey (1909)(if absent from i). The authority is named in the text if the species is not listed in any of the above.

c) ferns- Jones and Clemesha (1976).

d) mammals- Anon. (1980).

e) birds- Anon. (1969).

Stability- In reality it seems improbable that any biological system ever achieves true stability for most, if not all, organisms grow, reproduce and die in an unsteady environment. The results are changes in population characteristics which may be continuous. Stability must therefore be seen as a relative state when rates of change are at their lowest ebb.

Strategy- Strategy is used in a narrow sense to facilitate the description and comparison of parts of the life history of plant species. For example the regeneration strategy of a tree species could be related to some characteristics of its seed production and the optimal environmental and biological levels and limits for the growth and survival of the resulting seedlings. The use of the word "strategy" in studies of vegetation dynamics has been criticized by some who claim that it can imply deliberate planning on the part of the plant (e.g. McClendon and McMillen 1982; Whitmore 1978). Whitmore (1978) replaced the word by a neutral term "character syndrome" but like the word "rainforest" the term "strategy" appears well established despite the objections (see also Harper 1982).

Structure- Structure relates to the distribution of biomass making up a plant assemblage. Stand height, basal area and stem density are structural parameters which are often referred to in this thesis.

Succession- Succession is used in a broad sense to denote the occurrence in an assemblage of structural and/or floristic changes other than changes which are phenologically based. Thus its use here encompasses terms such as fluctuations, regeneration and long term cyclic changes (*sensu* Miles 1979; MacMahon 1979) as well as the general terms, primary and secondary succession. This approach is undertaken because it appears that the same basic principles apply to all these previously recognized types of vegetational change.

CHAPTER 2

Review

2.1 The natural environment of rainforests in north-east Australia

2.1.1 Geographic limits

The distribution of rainforests in tropical north-east Australia (Figure 2) is reportedly influenced by climate, soil fertility (Webb 1969), soil water regimes (Tracey 1969), historical factors especially Pleistocene climatic change (Webb and Tracey 1981), and fire regimes established by the Aborigines (Stocker and Mott 1981). They are found from sea level to almost the top of the highest mountain in the region (Mt Bartle Frere, 1622 m). It has been estimated that at the time Europeans arrived there were about 1.2×10^6 ha of rainforest in this region. About 80% remains, mostly in State Forests which have been logged or virtually untouched in National Parks and inaccessible portions of State Forests (Winter et al. 1984).

2.1.2 Climate

General aspects of the climate of the region have been described by Anon. (1965; 1971; 1977a). The following notes concentrate on those aspects relevant to the dynamics of the rainforests of the region.

a) Temperature

Mean monthly temperature data (Table 1) for selected sites in the region indicate a predictable drop in winter temperatures at higher latitudes and elevations but that summer temperatures are more influenced by elevation than by latitude. While winter temperatures are low enough to have a measurable effect on plant growth in areas above about 500 m elevation, a more important aspect of the temperature regime is the occurrence of frost. The frequency and severity of

Figure 2. The distribution of rainforests (as defined in Section 1.2) at the time of the commencement of European settlement is shown by the shaded areas (adapted from Stocker and Hyland 1981).

this phenomenon are discussed in Section 2.1.5.

b) Rainfall

The major features of the rainfall from the viewpoint of this study, are the very high annual averages recorded for some localities (the region contains the wettest part of Australia) and its seasonality (there is a marked summer maximum). Rainfall can usually be linked with one of three general synoptic patterns (Bonell and Gilmour 1980). In summary they are :-

i) convectional storms - these mostly occur during November, December and January. They appear to be of greater frequency on the western edge of the Atherton Tablelands[1] than elsewhere. As a result Malanda has a slightly lower December and January average rainfall than Atherton 14 km to the west even though its mean annual rainfall is 19% higher than that of Atherton. The "thunder-day" map (Figure 3) provides an indication of the relative importance of storm rains in different parts of the region. Storm rains are often heavy but isolated and of short duration. They occur late in the year when rain from other sources is infrequent.

ii) tropical interconvergence zone - this feature usually moves far enough south to bring heavy rain for one or two weeks, several times each year in the period January to March. This weather pattern often creates minor flooding. Associated winds are usually from the south-east and rainfall is heaviest along the east coast and on the slopes of the coastal ranges. This influence also brings persistent rains to the drier areas west of the Great Dividing Range. Sometimes a tropical low pressure system will form within the associated monsoonal trough, causing continuous heavy rain and high winds for as long as a week. These tropical lows often develop into cyclones (hurricanes). The destructive winds generated by cyclones are discussed later in this Section.

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1. This term includes the Mareeba, Atherton and Evelyn Tablelands.

iii) south-east trades - as anti-cyclones move across southern Australia they generate a south-easterly air stream which, although shallow, is occasionally sufficiently moist to produce showers in coastal areas and rain and drizzle on the mountains and eastern parts of the tablelands. Rain from the trades can occur at almost any time of the year but it is most prominent in the period March to August when the southern anti-cyclones direct the trade-winds across a more distant ocean fetch. Falls are generally light but persistent. Instability of the upper atmosphere may increase rainfall intensity and falls are then heavier and more widespread.

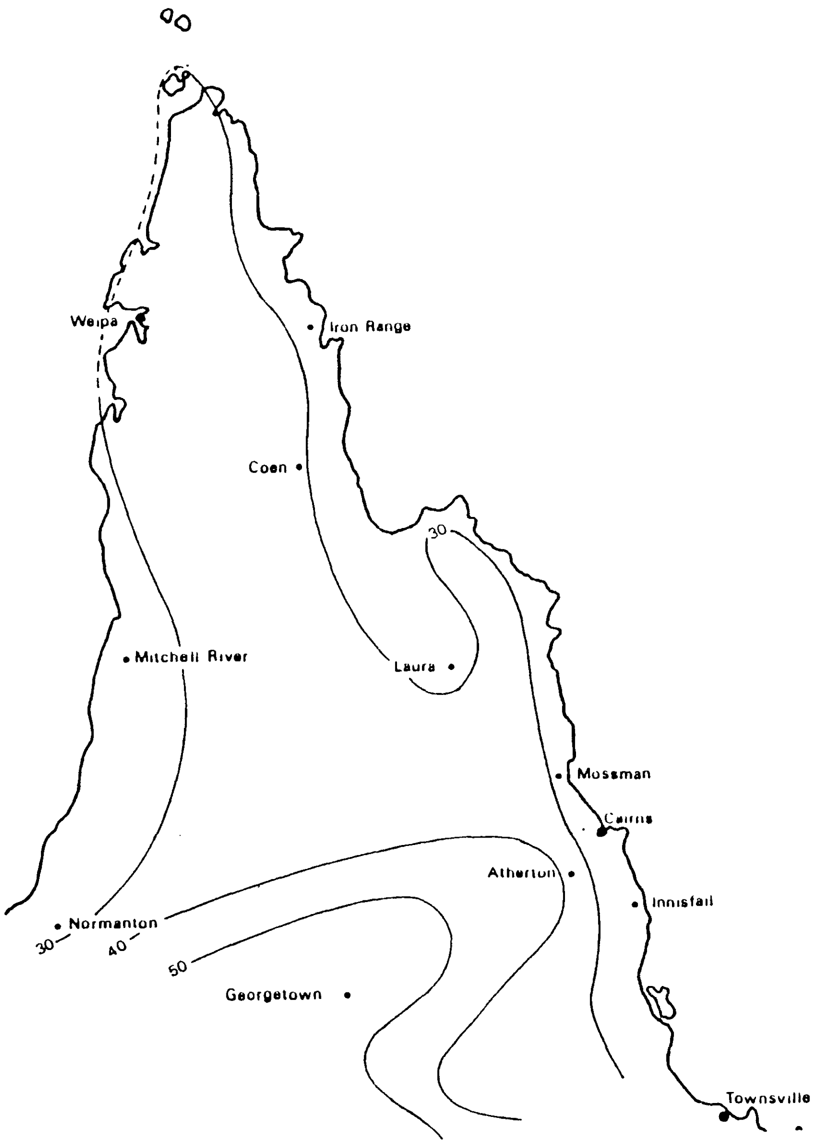

Figure 3. A "thunder-day" map of north-east Queensland (adapted from Anon. 1971).

Table 1. Meteorological data for selected localities within or near the rainforests of north Queensland (from Anon. 1965; 1971).

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
THURSDAY ISLAND 10 36' S 142 12' E 8m														
Mean monthly rainfall (mm)		441	409	345	202	48	16	11	6	3	9	46	193	1729
Temperature C	Mean Max.	30.5	30.0	29.5	29.5	29.0	28.5	27.5	27.5	28.5	29.5	31.0	31.5	29.5
	Mean Min.	25.0	25.0	25.0	25.0	24.5	23.5	22.5	22.5	23.0	24.0	25.0	25.5	24.0
Humidity %	0900 hrs.	82	83	82	80	79	79	80	77	74	72	71	74	78
	1500 hrs.	77	78	76	74	72	71	71	68	68	66	67	69	71
COOKTOWN 15 28' S 145 15' E 2m														
Mean monthly rainfall (mm)		368	367	396	208	75	52	27	29	16	23	64	159	1784
Temperature C	Mean Max.	31.5	31.0	30.5	29.0	27.5	26.5	26.0	26.5	28.0	29.5	31.0	32.0	29.0
	Mean Min.	24.0	24.0	23.5	23.0	21.5	20.0	19.0	19.5	21.0	22.5	23.5	24.0	22.0
Humidity %	0900 hrs.	79	81	80	77	76	77	76	72	71	69	70	73	75
	1500 hrs.	72	72	73	73	72	71	69	65	65	64	65	69	69
CAIRNS 16 55' S 145 46' E 2m														
Mean monthly rainfall (mm)		421	422	460	264	110	72	39	42	43	50	98	203	2224
Temperature C	Mean Max.	32.0	31.5	30.5	29.5	27.5	26.0	25.5	26.5	28.0	30.0	31.0	32.0	29.0
	Mean Min.	23.0	23.0	22.5	21.0	19.0	17.5	16.0	16.0	17.5	19.5	21.0	22.5	20.0
Humidity %	0900 hrs.	74	76	78	78	77	77	75	72	69	67	68	69	73
	1500 hrs.	69	68	70	68	68	67	63	61	61	62	63	66	66
ATHERTON 17 16' S 145 29' E 760m														
Mean monthly rainfall (mm)		287	305	268	105	60	46	30	25	22	28	76	173	1425
Temperature C	Mean Max.	28.5	28.0	27.0	25.0	23.0	22.0	21.5	22.5	25.0	27.5	29.0	29.5	26.0
	Mean Min.	18.0	18.0	17.5	15.0	13.0	10.5	10.0	10.0	11.0	13.5	16.0	17.0	14.0
Humidity %	0900 hrs.	78	83	82	83	83	82	80	75	67	62	65	68	75
INNISFAIL 17 31' S 146 2' E 7m														
Mean monthly rainfall (mm)		530	606	706	470	309	190	126	113	92	81	153	265	3641
Temperature C	Mean Max.	31.0	30.5	29.5	28.0	26.5	24.5	24.0	25.0	27.0	2 .5	30.0	31.0	28.0
	Mean Min.	22.0	22.0	21.5	19.5	17.5	15.5	14.0	14.0	16.0	18.0	19.5	21.0	18.5
Humidity %	0900 hrs.	80	84	86	86	87	87	85	83	80	77	77	76	82
	1500 hrs.	73	72	72	70	70	69	69	65	64	63	66	68	68
INGHAM 18 42' S 146 12' E 13m														
Mean monthly rainfall (mm)		421	457	418	181	93	57	38	34	36	47	87	165	2034
MACKAY 21 6' S 149 6' E 11m														
Mean monthly rainfall (mm)		335	321	306	152	94	67	41	26	40	46	74	164	1666
Temperature C	Mean Max.	30.0	29.5	28.5	27.0	24.5	22.0	21.5	23.0	25.0	27.5	29.0	30.0	26.5
	Mean Min.	23.0	23.0	21.5	19.5	16.0	13.5	12.0	12.5	15.0	18.5	21.0	22.5	18.0
Humidity %	0900 hrs.	75	76	78	77	77	78	76	73	69	67	67	69	73
	1500 hrs.	68	71	72	69	67	68	64	64	64	65	65	67	67

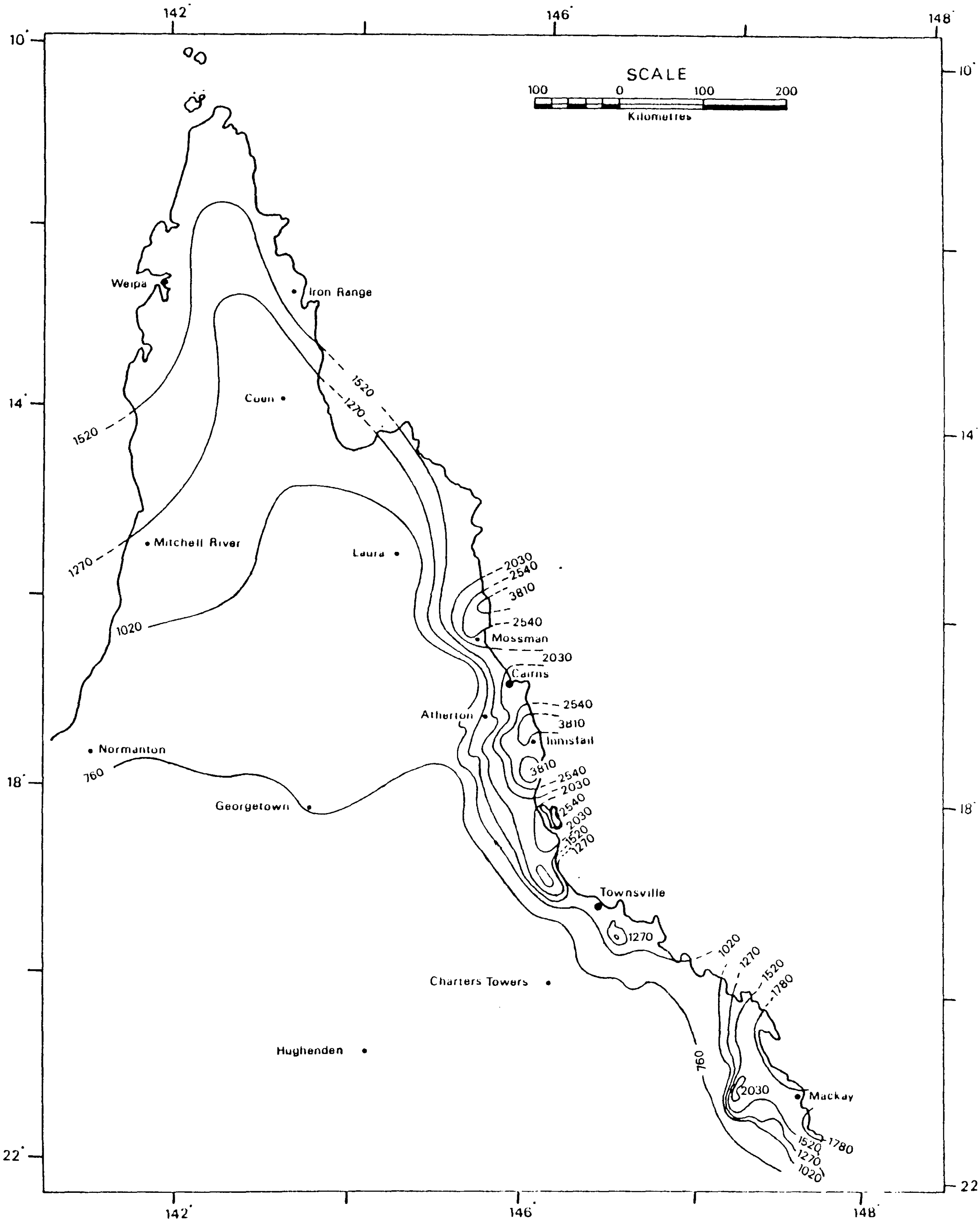

Figure 4. North-east Queensland showing average annual rainfall isohyets (mm) (adapted from Anon. 1965; 1971).

Annual rainfall isohyets for the region are shown in Figure 4. Mean monthly falls for selected localities (Table 1 and Figure 5) illustrate the strong seasonality of the rainfall, especially when compared with Lae (Papua New Guinea) or Brisbane (southern Queensland). Annual rainfall variability for sites listed in Table 1 range from 29% for Thursday Island to 43% for Cairns (Anon. 1971). Average annual rain-day frequency varies from 101 (Barrine) to 178 (South Johnstone). The significance and incidence of droughts are discussed later in this Section.

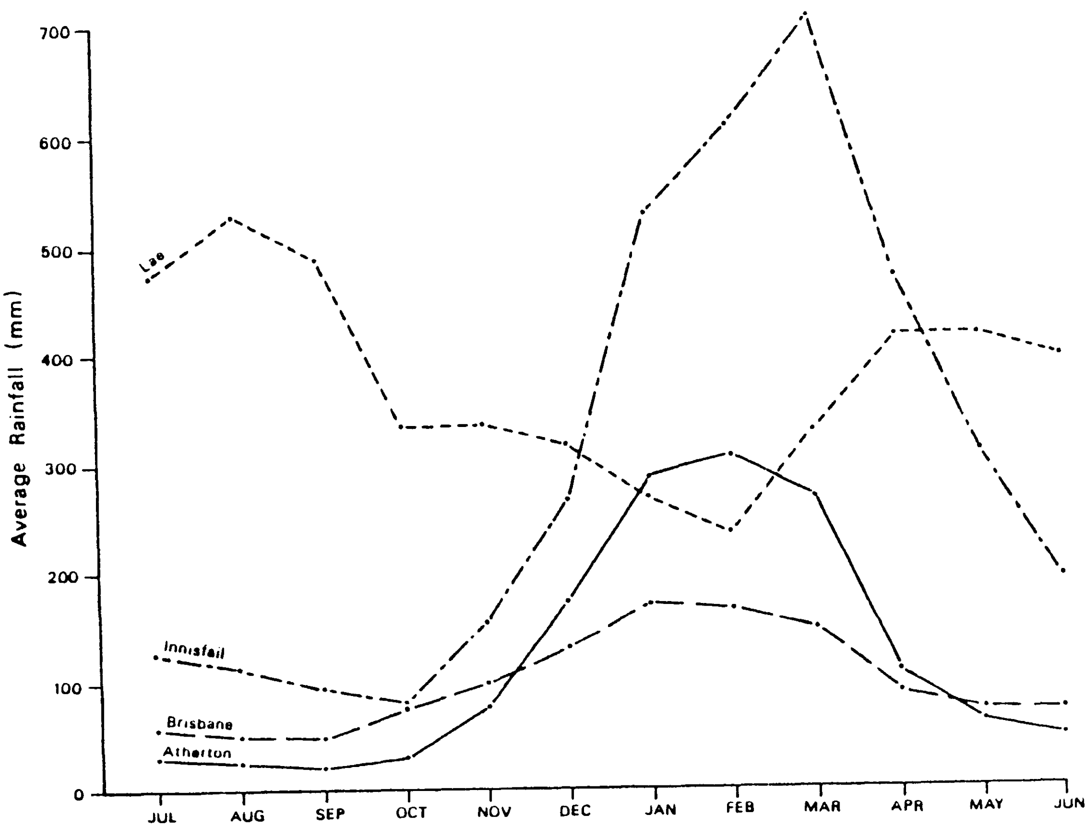

Figure 5. Monthly rainfall averages for some local regional centres are plotted and compared with similar values for Lae (Papua New Guinea) and Brisbane (south Queensland) to illustrate the seasonality of this region's rainfall (data from Anon. 1977a; McAlpine et al. 1975).

Whitmore (1981) considered the seasonality quotient developed by Schmidt and Ferguson (1951) to be the most useful from the viewpoint of relationships between vegetation types and rainfall. This quotient links rainfall quantity with seasonality in the following equation :-

$$Q = \frac{\text{no. of dry months } (< 60 \text{ mm})}{\text{no. of wet months } (> 100 \text{ mm})} \times 100$$

A plot of Q values for the main part of the region is shown in Figure 6.

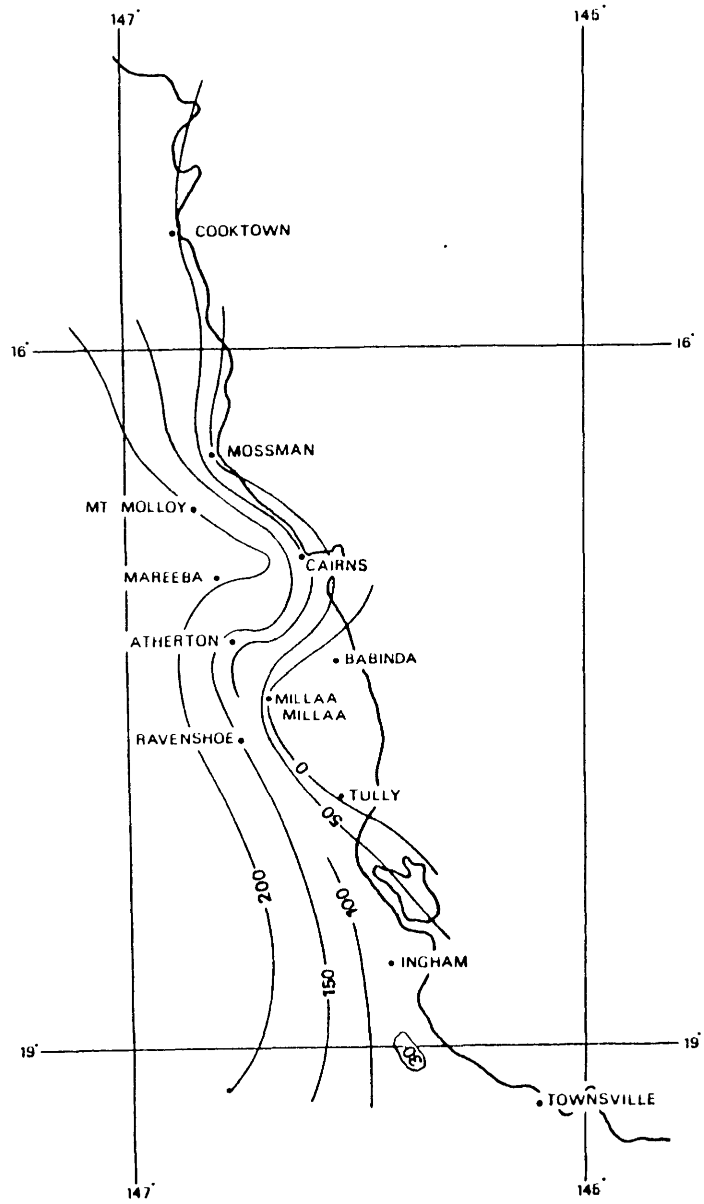

Figure 6. The seasonality of the environment (especially from the viewpoint of plant growth) decreases with falling values of the quotient Q of Schmidt and Ferguson (1951) (data derived from Anon. 1971).

c. Evaporation

There are few records of evaporation (E) for the region. Application of the Waite formula, E = 21.2(Saturation vapour deficit) (Anon. 1971) indicates that the annual evaporation in the eastern part of the region averages between 1270 and 1397 mm annum^{-1}. Evaporation appears to be highest during November and December when average monthly values for coastal areas exceed 150 mm.

d. Humidity

Humidity records are only available for a few localities in the region. Those for Cairns (Table 1) probably represent most of the coastal lowlands within the region.

e. Winds

Although winds are a very important part of the climate in this region, their characteristics are more appropriately discussed below under the heading of "Disturbances" (Section 2.1.5).

2.1.3. Geology and geomorphology

The landscapes of north-east Australia began to evolve into their present form during the latter part of the Tertiary. The following account of their development is based on that of de Keyser (1972) and although it refers to the Atherton Tablelands and adjacent areas, it is generally applicable to the remaining parts of the region.

Except for some probable faulting, most of the Mesozoic and Lower Tertiary was a period of denudation without deposition. Later in the Tertiary (? Pliocene) strong block faulting broke up the peneplain, uplifting the tablelands but causing the subsidence of the coastal plain and continental shelf. Some volcanism in the form of basalt flows commenced in parts of the region. The earliest flowed over an area of shallow lacustrine/fluviatile deposits. Volcanism reached its peak on the Atherton Tablelands during the Quaternary when basalt flowed down the deep valleys at the eastern edge and was accompanied and succeeded by pyroclastic deposits. Recurrent movement along some of the faults and differential erosion accentuated the relief. Alluvial deposits filled sunken coastal plain areas while littoral/marine sediments were being laid down on the shelf platform and the Great Barrier Reef was formed (Figure 7). The general physiography of the region is shown in Figure 8.

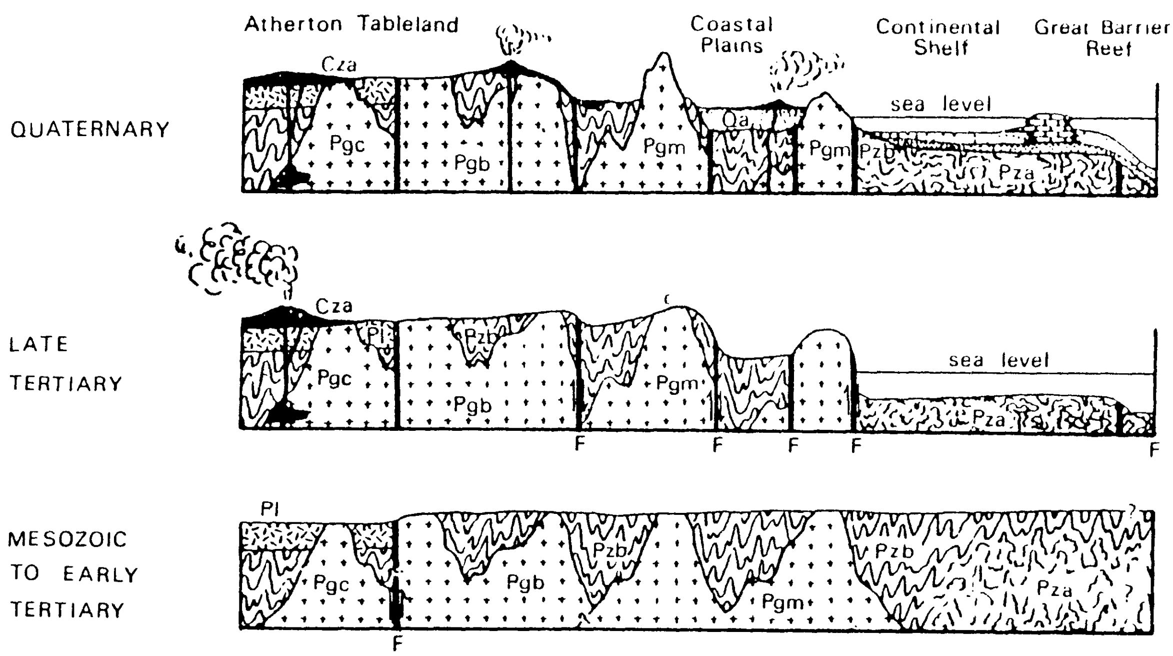

Figure 7. The stages in the development of the region's modern landscapes are illustrated. Qa - Quaternary deposits; Cza - Tertiary basalts; Pl - lake deposits; Pz - metamorphics; Pg - granites; F - faults (adapted from de Keyser 1972).

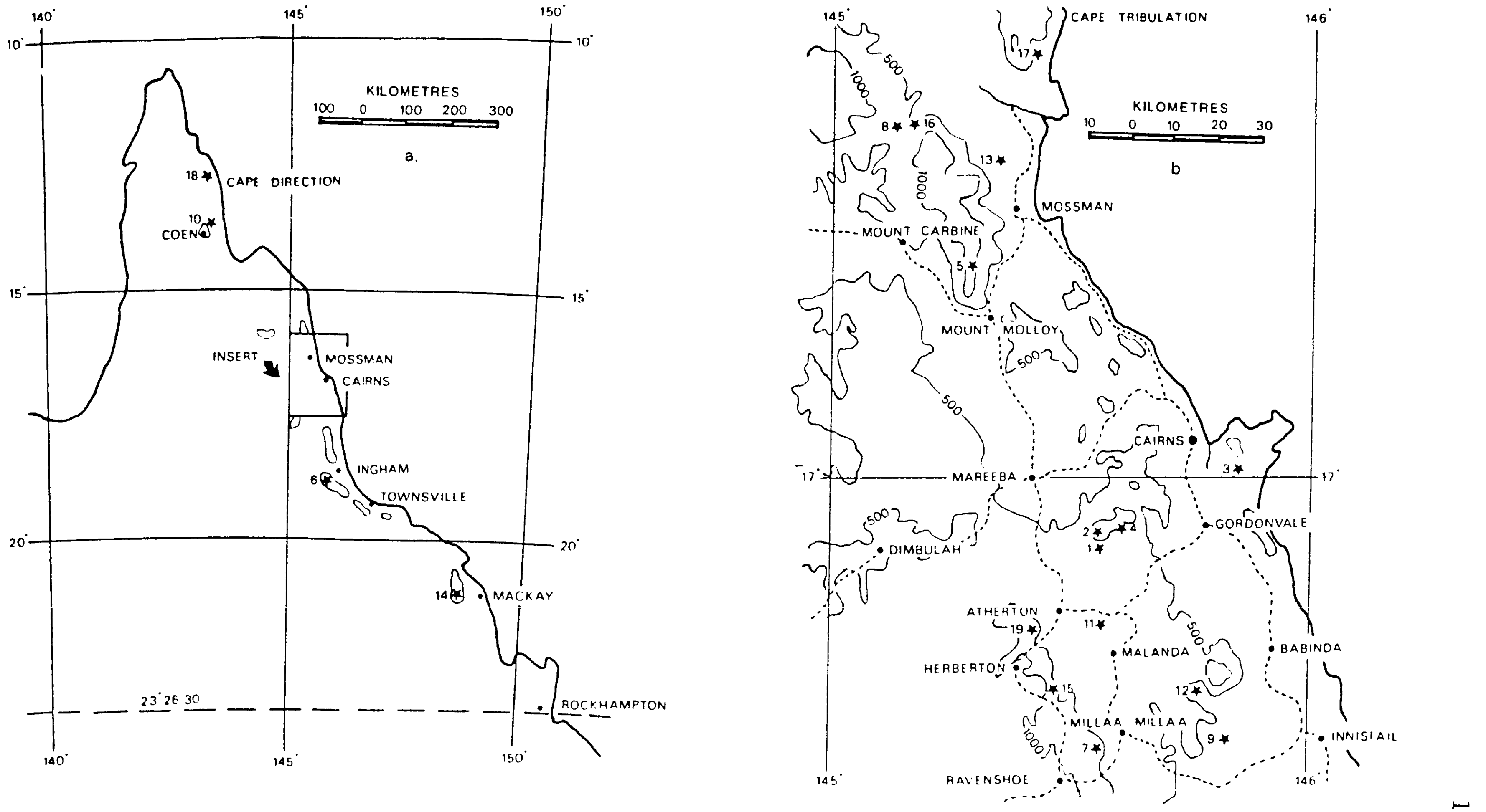

Figure 8. Maps of the region showing the 500 m contour (a. and b.) and the 1000 m contour (b.) together with the locations of the plots described in Chapter 3.

2.1.4 Soils

Most of the rainforest soils of north-east Australia have received little more than a cursory examination. However, in recognizing the strong relationships between certain soil characteristics and the parent rock, three main soil types were identified :-

a) the granitic soils on some of the foothills but more characteristic on the mountains,

b) the metamorphic soils primarily derived from shales at low and medium elevations,

c) the basaltic soils mainly on the tablelands.

The following notes provide some perspective of these broad soil "types". Examples of their chemical and physical characteristics may be found in Chapter 3.

Some granite soils are weathered very deeply even on steep slopes while others are quite shallow. They are usually well structured but are sometimes prone to erosion when destabilized by disturbance such as logging. The shallower granite soils tend to be yellowish at depth while the deeper ones are often pink to red.

The metamorphic soils are as variable as those derived from granites. They are often yellow in colour with massive clay subsoil close to the surface. Their internal drainage, and stability following disturbance, are usually poor. Soils from rhyolites and related ancient acid volcanic rocks (e.g. Glen Gordon volcanics) are occasionally interspersed and confused with metamorphic soils but generally their characteristics are similar.

Soils from weathered basalts are found scattered throughout most of the region. Basalt flows probably began late in the Pliocene (de Keyser 1972) and continued periodically to perhaps 10 or 20,000 years ago (Kershaw 1971). Differences in age and rainfall have affected weathering, providing a wide range of kraznozemic soils. Some of the youngest seem hardly more than lithosols - a little red brown clay between virtually unweathered vesicular basaltic boulders. Others are weathered to depths of 10 m or more and contain no rock except very occasional core stones.

While most of the rainforest soils in this region can be placed in one of these three "types", there are other soils of some importance. The most widespread and variable are those formed on Quaternary deposits near the coast. These vary from undifferentiated bouldery gravels and sands through silts and clays to peats and organic mucks. Perennial or seasonal water logging is a common feature of the clay and organic phases.

Although detailed studies of the soils of north Queensland have generally avoided areas of rainforest, those by Gillman (1976), Isbell et al. (1976) and Probert (1977) included some rainforest soils. As well as contributing to our knowledge of the characteristics of rainforest soils, these studies also made some interesting comparisons between rainforest and open eucalypt forest soils.

The most extensive studies undertaken were those of the red basaltic soils by Gillman (1976) and Isbell et al. (1976). Their primary aim was to examine a number of chemical and morphological properties with variation in mean annual rainfall. They examined 24 sites of which 13 were in open eucalypt forest (mainly in the drier part of the region to the west of the main rainforest belt) and 11 were in rainforest. Isbell et al. found that while profile morphology, clay content and clay mineralogy changed with rainfall, the marked vegetation contrasts at several sites with the same rainfall, were not associated with differences in any of these soil properties. Gillman (1976) examined some chemical properties of the same set of samples and observed that most of the variation could be attributed to the average rainfall of the sampling site. Gillman observed considerable overlap in the values for each soil property between vegetation types, indicating no association between these soil properties and vegetation.

The study by Probert (1977) of the carbon-nitrogen-sulphur relationships of a range of north Queensland soils, did not include sufficient rainforest soils to contribute much further to our understanding of the relationships between vegetation and soils. However, Probert noted that the carbon : nitrogen ratio tended to be wider under open eucalypt forests. He thought that this might be due to regular fires in these assemblages (see Section 2.1.5e) but was unable to suggest the precise mechanism.

A wide range of soil physical and chemical properties were examined by Unwin (1983) as part of a study of the rainforest/eucalypt forest ecotone in the hills immediately to the west of Atherton (see Unwin et al. 1984 for an outline). The soils here were derived mainly from rhyolites and in examining their characteristics, Unwin did not find consistent patterns which would have explained the distribution of these contrasting forest types. He concluded that the factors controlling the established fire regime were the most important of the wide range of environmental parameters studied (for further mention of this study see Section 2.2.4).

2.1.5 Disturbances

Disturbance as the initiator of secondary succession is a fundamental factor in forest dynamics. Its major characteristics are its intensity, extent and frequency. Its intensity will largely determine the starting point of the succession. Minor disturbance, for example that causing a large branch to be torn from a tree, may not result in any floristic change on the site as the gap could be rapidly filled by compensatory vegetative growth on existing plants. A moderate disturbance, as might be occasioned by the uprooting of a canopy tree, may induce floristic change through regeneration from seed on the forest floor as well as vegetative compensation. An extreme disturbance such as that caused by a landslip may require the arrival of propagules from some distance before vegetation can become re-established.

The extent of the disturbance (gap size) may have a profound effect on the initial floristics of a subsequent succession through the influence of gap size on the characteristics of the micro-habitats available for seedling establishment and growth. The size of the disturbed area may also influence the availability of propagules. Some environmental characteristics of forest gaps are of considerable importance to understanding forest diversity and are discussed in detail later in this thesis.

Disturbance may affect the floristics and structure of forest patches from very rarely (e.g. landslips once in a 1,000 years or more) to almost continually (e.g. foliage grazing). Some of the more frequent events are difficult to separate from regular seasonal cyclic events. Others, such as frosts at moderate altitude in the tropics, may be irregular catastrophes in that environment but part of the normal seasonal environmental cycle in temperate zones. While some disturbances may be so infrequent as to be inconsequential from an evolutionary viewpoint, they can have very important consequences for forest composition (Whitmore 1977; Hopkins 1981).

In the following sections some of the natural disturbances affecting rainforests are discussed in relation to their intensity, extent, frequency and predictability in north-east Australia.

a) Wind

Although the tropics in general do not experience the persistent winds of some temperate latitudes, occasional strong wind events appear to play an important role in the dynamics of most tropical rainforests. Damaging winds are usually created by either convectional storms or cyclones. Frontal storms of the type frequently encountered in temperate climates are very rare in this region (as they are in most other parts of the tropics). Although storms and cyclones are discussed separately below, the difference in the potential of each to disturb a forest is more a matter of frequency and extent than in their effects on individual trees. Convectional storms appear to be the main source of destructive winds within 5 degrees latitude of the Equator. At higher tropical latitudes their significance lessens and cyclones take the dominant role.

The most critical factor contributing to wind damage is wind speed, particularly as the force exerted is proportional to wind velocity squared e.g. a wind with a speed of 150 km hr^{-1} will exert twice the force of one of 106 km hr^{-1}. There is also some interaction between wind and rain for rain influences soil physical characteristics increasing the probability of windthrow. Rain may also saturate basket epiphytes in the crown of a tree and thus add to the total loading on the tree.

Unfortunately there are few data on the frequency and extent of convectional storm damage to tropical forests in this region. The record of "thunder-days" provides the only statistic of value. The drier region to the west of the rainforest belt has more "thunder-days" (and thus presumably more convectional storms) than the rainforest belt (Figure 3). The incidence of "thunder-days" in this region (20-50) is low compared with many other tropical localities. For example three localities in Borneo (Kuching, Bintulu and Miri) recorded annual averages of 163, 96 and 109 "thunder-days", respectively (Anderson 1964). In north Queensland, convectional storms mainly occur early in the wet season. While the winds associated with these storms occasionally reach hurricane force (63 km hr^{-1}), forest disturbance, such as crown damage and uprooted trees, is usually confined to narrow strips, no more than a few hundred metres wide. Although storm damage is not frequent enough in this region to enable useful statistics to be gathered in a short period, high winds from convectional storms must be considered a significant environmental factor during the life span of large trees. However, disturbance from this cause seems more extensive in many other parts of the tropics. For example in Borneo, Anderson (1964) found areas of severe forest damage of up to 80 ha attributable to storm damage.

When compared with convectional storms, the extent of forest disturbance resulting from a cyclone may be several orders of magnitude greater. Because they usually affect large numbers of people adversely, the influences of cyclones on forests are better (if sometimes incidentally) recorded. Forest damage from the large cyclone during 1956 in Puerto Rico extended over 2000 km^2 (Wadsworth and Englerth 1959). A similar area was devastated in Kelantan (northern Malaya) during 1883 (Browne 1949; Wyatt-Smith 1954). In contrast the area of severe damage caused by cyclone "Tracey" in the Darwin area during 1974 was estimated at 460 km^2 (Stocker 1976). Similar estimates of damage from cyclones in north Queensland have not been made but it is thought that the area usually affected is of the order of tens or hundreds rather than thousands of square kilometres. The data on cyclone frequency for this region (Figure 9) are more reliable and on average it appears that a cyclone would affect the vegetation of part of this region every year (Lourensz 1977; Dobson and Stewart 1974). The seasonal frequency peak corresponds with the summer wet season (Table 2). The highest wind velocity ever recorded for this region was in Cairns during 1956 when a gust reached 146 km hr^{-1} (Anon. 1971). Estimates of extreme gusts over the region for various return periods are given in Table 3.

Based on their Puerto Rican study, Wadsworth and Englerth (1959) came to the following conclusions :-

i) damage was as serious on sites protected from normal winds as on those exposed.

ii) forests on slopes are subjected to the hazard of cyclone damage regardless of aspect.

iii) forests on shallow soils have not proved to be less windfirm than those on deep soils.

iv) uprooting of trees indicating poor anchorage, is a common form of cyclone damage on soils which normally are very moist or wet.

v) all-aged mixed forests frequently suffer from slight and selective cyclone damage; even-aged pure forest generally suffers either no damage or very serious damage.

vi) heavy thinning of forest is conducive to wind damage.

vii) different tree species vary to a significant degree in their susceptibility to windthrow and breakage from cyclones.

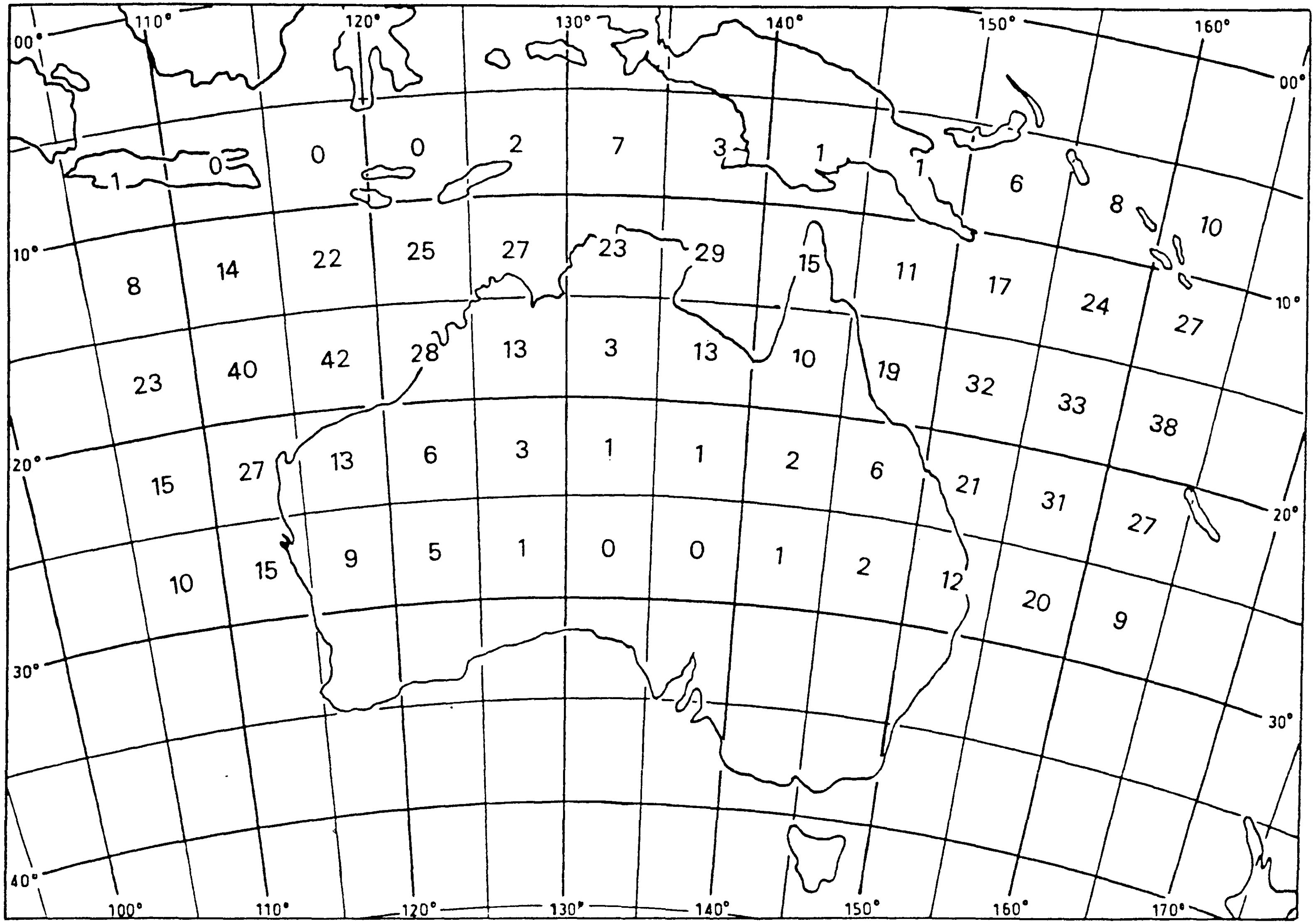

Figure 9. The average decadal incidence of cyclones in 5 degree latitude/longitude squares for north Australia and associated regions (data from July 1959 to June 1975 - Lourensz 1977).

Table 2. Number of tropical cyclones occurring in the north-east of Australia in the 50 years from 1911 to 1960 (adapted from Anon. 1971).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Queensland Gulf Coast	10	-	1	-	-	-	-	-	-	-	-	1	12
Thursday Is. to Cooktown	2	3	5	2	-	-	-	-	-	-	-	2	14
Cooktown to Townsville	6	14	7	2	-	-	-	-	-	-	-	-	29

Table 3. Estimated extreme wind gusts for north-east Australia (adapted from Anon. 1971).

East coast, south of 15°S				
Return period (years)	10	20	50	100
Extreme gusts (km hr^{-1})	120-130	130-140	150-160	165-185
Atherton Tablelands and south-west				
Return period (years)	10	20	50	100
Extreme gusts (km hr^{-1})	120	130	140-150	150-165
Northern peninsula, north of 15°S				
Return period (years)	10	20	50	100
Extreme gusts (km hr^{-1})	120	130	150-160	165

Unfortunately there is little information on the relative resistance of north Australian tree species to high winds. In the Northern Territory, Stocker (1976) observed that tree species of the littoral and eucalypt forests were better able to withstand high winds than those of the rainforests (more strictly monsoon forests). While some trees in the former group were windthrown or severely damaged (especially if weakened by rot or termites) most merely shed their leaves and recovered rapidly with the production of epicormic shoots. Although rainforest species were mostly windthrown or smashed, there were some exceptions, notably *Alstonia actinophylla*. Trees of this species appeared to have escaped relatively unscathed by shedding twigs and leaves before the wind loading was high enough to cause serious structural damage. A general feature was that some trees which initially appeared to have survived and showed normal signs of recovery, died within a year. The reasons for their deaths were not obvious but it was suspected that insect and fungal attack in damaged tissue and sun scald on exposed branches, may have been contributing factors.

The landfall of cyclones in this region is sometimes accompanied by tidal surges. The highest recorded was over 12 m in Bathurst Bay during 1899 (Anon. 1971). The effects of a surge of this magnitude on low lying coastal vegetation can only be imagined but they must be catastrophic.

The first hand accounts recorded below provide some insight into the nature and extent of disturbance to the rainforests of this region, by these infrequent but, from a forest dynamic viewpoint, potentially important phenomena.

The rainforests of the Atherton Tablelands had just started to be cleared when in 1918 a cyclone passed through the area. A settler, Mr T.D. McGreekam wrote (T.D. McGreekam unpublished data) his impressions of the effects of six hours of hurricane force winds :-

> "The uncut trees were stripped of leaves to the extent that buildings normally hidden behind 400 m of virgin rain forest could be seen quite plainly. In other places the trees had lost many branches or were windthrown to the extent that half were on the

> ground. The area affected seems to have extended in a wide belt from Atherton to Innisfail and Babinda. The subcoastal areas seemed to have been worst affected."

The effects of the 1920 cyclone were mentioned in the Annual Report of the Queensland Forestry Department (QFD) for that year and a letter from the Acting District Forester, J.M. Freyr, was quoted :-

> "On the 2nd February, 1920 a cyclone of great intensity swept all the coastal country from about Gordonvale north to Port Douglas and destroyed about 25 to 35% of timber, at least. From Oaklands to Mt Molloy and Port Douglas large areas of scrub were reduced to bare poles or were entirely uprooted or broken off."

This commentary is accompanied by some excellent photographs of the damage. This report also noted that the cyclone created "a highly inflammable trash which was productive of damaging fires in the Kuranda, Oaklands and Mt Molloy Districts". Further brief mentions of cyclone damage to forests in the region are contained in the QFD Annual Reports of 1927 and 1933.

The most recent occasion of widespread cyclone damage to rainforests in north Queensland, was in December 1971 when cyclone Althea (central pressure 952 mb and estimated maximum wind speed 106 km hr^{-1} - Anon. 1972) passed over the Paluma Range 40 km to the north of Townsville. Although access to the area was limited, observations made soon after indicated that the damage to the rainforest was very variable. Some trees were wind thrown, others were snapped off somewhere along the bole, some had branches of various sizes removed while still others stood apparently unaffected. The reaction to the high winds in the nearby eucalypt forest was similar to that observed by Stocker (1976) in the Darwin area.

Webb (1958) seems to have been the first to appreciate the general influence that cyclones have had on the characteristics of this region's rainforests. In describing the damage caused by the severe cyclone of 1956, he mentioned the development of cyclone related phenomena such as the vine tangles which are locally called "cyclone scrubs" (Plates 1 and 2). Webb estimated that none of the rainforests of the

Plates 1 and 2. Lowland rainforest showing evidence of cyclone damage. Many of the emergent trees are covered with climbers (<u>Bambusa moreheadiana</u> Bail. and <u>Merremia peltata</u> respectively).

Plates 1 and 2. Lowland rainforest showing evidence of cyclone damage. Many of the emergent trees are covered with climbers (_Bambusa moreheadiana_ Bail. and _Merremia peltata_ respectively).

lowlands and foothills of north Queensland could escape severe or general cyclone damage for more than 40 years and thought it unlikely that any rainforest area in Queensland would remain unaffected by cyclones for as long as 500 years.

In this study Webb also recognized the potential effects of fire in cyclone debris and attributed some of the grassland tongues on ascending spurs in the Babinda area to the combined effects of cyclones and fires. With this background it is somewhat surprising that Webb (1964) did not consider the possibility that the grassy balds of the Bunya Mountains in southern Queensland were the result of rainforest destruction by a cyclone/fire interaction with subsequent fire (aided perhaps by frost) maintaining the grassland. Similar though less spectacular balds are found in parts of north Queensland.

b) Droughts

Records from many parts of the tropics indicate that droughts, severe enough to affect the structure and floristics of tropical rainforests, appear to be sufficiently frequent to warrant close examination.

In Papua New Guinea, R. Johns (unpublished data) reported that twice during the last eighty years the Gogol Valley (near Madang) suffered from severe drought and subsequent fires. On the first occasion in the early 1900s the Gogol River ceased flowing for three years. During August 1980 I observed, on the summit of Mt Kaindi (2400 m) (near Wau, Papua New Guinea) that small patches of the normally saturated montane rainforest had been recently burnt by local villagers. It was not difficult to imagine that a continuation for another month of that drought would have resulted in the destruction of large areas of montane forest.

Brunig (1971) and Poore (1968) commented on the effects of drought in different parts of Malaysia. Severe droughts and associated fires (such as that during 1982/83 - P. Woods pers. comm.) appear to occur in Borneo several times each century (see also Ashton and Brunig 1975).

The most severe drought recorded in this region appears to have been during 1915 when the area surrounding Atherton received less than half the normal rainfall (Table 4). The Department of Forestry Annual Report for 1915 noted that in this part of the region :-

> ". . moist evergreen scrubs were rendered leafless, while the underwood and much of the overwood was killed, this allowing fires to spread in reserves which are usually considered quite safe from fire danger."

The report for the following year observed that inkweed (Phytolacca octandra) and stinging trees (Dendrocnide spp.) had invaded the forest damaged by drought. Herbert (1935) reported the death of many rainforest epiphytes in some parts of north Queensland during the drought of 1923.

Severe droughts, although infrequent on human time scales, may be very important in the dynamics of many rainforests and studies of their effects and associated recovery processes, should be made whenever the opportunity occurs.

c) Frost

Frost may be a significant part of the region's environment at elevations above 700 m. For example Atherton (elevation 760 m) experiences on average 3.5 light frosts (screen temperature 0 - 2^{o}C) and 2.5 heavy frosts (screen temperature < 0^{o}C) every year (Anon. 1971). Frosts may occur at night any time during the cooler period of the year (May to September) but only when the atmosphere is dry, clear and still. Frost effects on forest vegetation are mainly observed on artificially maintained forest edges (Plate 3) but there are records of severe frost damaging undisturbed forest. For example the Queensland Forestry Department Annual Report for 1932 observed that severe frosts in June of that year had, in some areas "burnt jungle trees to a height of 70 feet."

It is also suspected that fires in frosted vegetation may have been a significant factor in converting some areas of rainforest to eucalypt forest and in maintaining and extending

Table 4. Atherton rainfall during the 1915 drought (from Atherton Post Office records).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Year
Absolute (mm)	65	75	18	15	15	19	10	0	0	6	43	232	498
% of mean annual rainfall	23	25	7	14	25	41	20	0	0	22	57	135	35

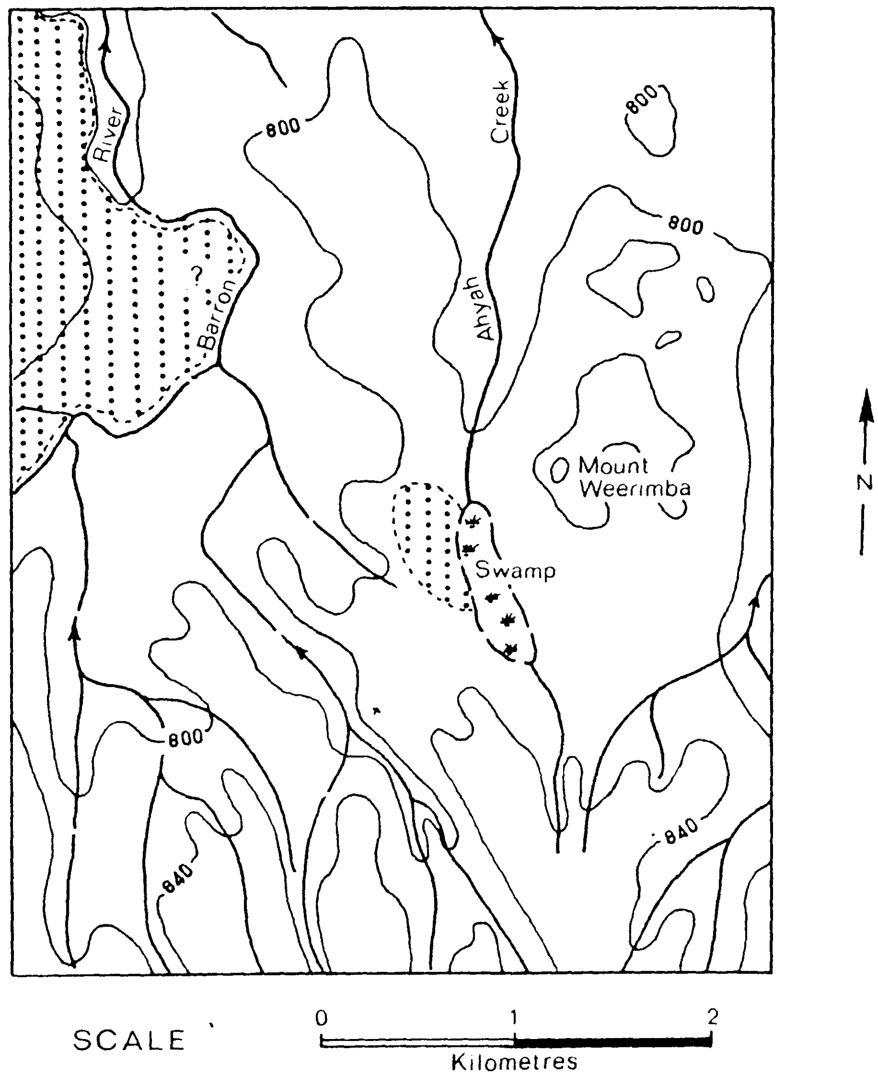

Figure 10. A sketch map of part of the Upper Barron area of the Atherton Tableland. Ahyah Creek has been partially blocked by a lava flow from Mt Werrimba to form a small lake which is now a peat filled swamp dominated by tall sedges. The dotted sections are tall open eucalypt forest. The patch described in the text lies immediately to the north-west of the swamp. The larger area of eucalypt forest to the west of the Barron River may also have been developed and maintained by frost/fire phenomena but here variable soil types and topography complicate the issue. The remaining area is, or was until recent clearing, rainforest. The contour interval is 40 m.

the eucalypt forest. The first clue to the development of the hypothesis came with the observation that many low lying swampy areas (especially those developed when basalt flows on the Atherton Tablelands dammed established drainage lines) frequently had eucalypt forest on their west and north-west margins but rarely on other sides. These swampy areas are frost hollows and perhaps Aborigines took the opportunity to burn them whenever severe frost provided sufficient fuel. The prevailing south-east winds would have carried the fires to the north-west, gradually eroding the rainforest in that sector. Eucalypt seed may have been inadvertently carried to the clearing by Aborigines who would have found these open areas quite attractive from the viewpoint of both food gathering and as camping sites.

A related alternative explanation is that rainforest has recently expanded into the general area but has not been able to take over that part of the eucalypt forest where fire ignition was more reliable because of the supplementary effects of frost on fuel curing. A sketch map of one of these sites is shown in Figure 10.

King and Chapman (1983) reported that frost alone may suppress for many years the revegetation of large gaps in the temperate rainforests of New South Wales. This phenomenon has not been observed in north-east Australia.

d) Lightning

Anderson (1964) considered lightning to be one of the most important factors causing mortality among rainforest dominants in regions where thunderstorms are frequent. He and Brunig (1964) noted that in Sarawak the peat swamps which are dominated by an even canopy of _Shorea albida_ Sym. are particularly susceptible. In these forests Anderson observed that as much as 0.6 ha (containing 70 trees) could be killed by a single strike. Brunig estimated that 2.6% of this forest type was obviously affected by lightning deaths. Although small gaps were often closed by undamaged neighbouring trees extending their branches into the gaps, they were frequently enlarged because some undamaged trees on their edges were windthrown. Both authors concluded that lightning damage was of special importance in the ecology of S. albida.

Anderson (1964) also noted the effects of lightning on forests growing on broken topography and with uneven canopies. In both these circumstances lightning seems to have less impact than it does on the S. albida forest. Usually only the emergents and closely associated species are affected. However, near the focal point all sizes down to small seedlings may be killed. He observed that some species are either more resistant to lightning damage or recover more often after damage.

In temperate and semi-arid tropical environments lightning is also important as a natural source of ignition for wild fires. Fires resulting from lightning strikes are very rare in the tropics although some instances have been reported (e.g. J.R.A. Anderson 1966). A model used to predict lightning fire ignition probabilities (Fuguay et al. 1979) suggests that in rainforests, even dry fuels resulting from hurricane force winds would be difficult to ignite by lightning because of their relatively high bulk density. Almost the only localities where lightning fires could be of significance in the wet tropics would be on some mountain tops especially those in karst areas which dry out rapidly and where the vegetation is often sclerophyllous in character.

Despite a lack of useful data, lightning appears to play a minor part in the dynamics of north Queensland rainforests. Small dead patches, which could be attributed to lightning strike, were occasionally seen in the forest. Sometimes lightning was the obvious cause, especially where strips of bark and wood had been torn from an emergent tree. On other occasions clear evidence was lacking. The only useful statistic is that of "thunder-days" (Figure 3).

e) Fire

Fire is not normally considered to be a factor causing either local or widespread disturbance to rainforests for although most rainforest species are relatively fire sensitive (but not as fire sensitive as often thought - see Section 4.5), the litter on the forest floor is usually too moist and sparse to support a fire (Stocker and Mott 1981). There are, however, several situations where fire can readily occur in rainforest assemblages. The most widespread are where rainforests have been greatly disturbed by hurricane force winds or severe drought. Fires in rainforests due to both these causes have been recorded in this region. Local fires also seem possible in areas defoliated by severe frost (see above).

The role of man in relation to fires has already been mentioned. Before his arrival in this part of the tropics the ignition of droughted or wind damaged forest was much more unlikely for lightning would have usually been the only feasible ignition source. While man may not have used shifting cultivation in this region, his ignition of frosted, droughted or wind damaged areas of rainforest could have had important consequences (see Section 2.1.5 g).

f) Geomorphological events

Catastrophic changes in landform seldom provide opportunities for successional events in this region and thus this factor provides a marked contrast with neighbouring New Guinea where successions on landslips (often following earth tremors), recent alluvial deposits and fresh volcanic landscapes are commonplace (White 1975). Small landslips do occasionally occur in otherwise undisturbed forest on steep slopes after unusually heavy rainfall in this region. For example several relatively small, if conspicuous, landslips occurred during January 1979 on the slopes of Mt Bartle Frere and Mt Bellenden Ker after several weeks of heavy rain (4.8 times the monthly mean). However, it is considered that their frequency and extent are such that they are relatively insignificant in forest dynamics.

g) Biotic factors - Man

The arrival of Aborigines on the continent created new disturbance possibilities and may have altered the vegetation very significantly. Their time of arrival is still very much a matter of debate. They were certainly well established in southern Australia at 32,000 B.P. (Barbetti and Allen 1972). More debatable evidence led Merrilees (1979) to suggest that they could have arrived 200,000 years ago. All agree that Aborigines came from the north and most (except for Abbie 1975) accept that there were at least two successive waves of invasion. The lower sea levels during most of the Quaternary would have allowed easy movements into the continent with minimal boating skills.

Views of the effects of man's arrival on the vegetation of Australia vary enormously. For example Specht (1975) saw the Aborigines as model conservationists lacking the technology to make any impact. Horton (1980) had similar views. Merrilees (1979), Jones (1975), Jones and Bowler (1980) and Tindale (1981) saw their impact mainly as new predators and efficient hunters although these authors were also aware that their use of fire may have been important. Stocker and Mott (1981) examined the role of fire in the ecology of the tropical forests and woodlands of north Australia and predicted that the introduction of a new fire regime by Aborigines would have had a most profound effect on the vegetation. Stocker and Mott noted that Aborigines used fire for hunting and access clearing. They suggested that even if its use for hunting was not well developed when Aborigines arrived, its significance for access clearing would have been obvious. Consequently great changes would have occurred in the fire regimes of those plant assemblages already adapted to fire as an occasional feature of the environment. For example :-

i) fires would have become more frequent.

ii) fires would have occurred more often early in the dry season rather than at the beginning of the wet when lightning from thunderstorms would have in the past been the primary source of ignition.

iii) fires under the new ignition regime would not have had so much available fuel (due mainly to increased frequency and fuel curing characteristics) and thus would have generally been less intense.

Overall the fire pattern in the grasslands and woodlands inhabited by the Aborigines would have changed from periodic catastrophes to a regular and often seasonal part of the environment.

The real significance of the change in fire ignition regime would have been its effect on a postulated ancient closed forest/thicket continuum (Figure 11) which appears to have existed over a wide rainfall range (4000 - 500 mm mean annual rainfall) on free draining soils in north Australia (Stocker 1980; Stocker and Mott 1981). This continuum seems to have been broken up by physical disturbance and subsequent fires and, except in certain fire protected sites, to have been largely replaced by fire adapted open forests and woodlands dominated by eucalypts. Once this happened the local retreat and reinvasion of the more mesic rainforest elements to and from refuges in response to climatic change, would have been much more difficult (in some cases virtually impossible) for the fire adapted assemblages are easily maintained, even in high rainfall environments, provided there is a short dry season and a reliable source of ignition.

The closed forest continuum hypothesis is supported by Sluiter and Kershaw (1982) who compared fossil and recent pollen spectra from a range of Australian sites and concluded that there may not have been any major disruption of Pliocene vegetation patterns until the late Quaternary. They noted that at this time there was a massive expansion of "open eucalypt vegetation" at the expense of "drier rainforest" and other "sclerophyll communities" in response to an increase in burning, most likely as a result of Aborigines. As well as having an influence on the vegetation, Hughes and Sullivan (1981) attributed the accelerated rate of natural erosion evident during the Late Holocene to burning by Aborigines.

Although Aborigines may have established fruit trees around regularly used camp sites (Hynes and Chase 1982), they never practiced shifting cultivation except on some of the islands in northern Torres Strait. Golson (1972) and Harris (1976; 1977) in attempting to explain this phenomenon suggested that population pressures did not demand a more sophisticated life

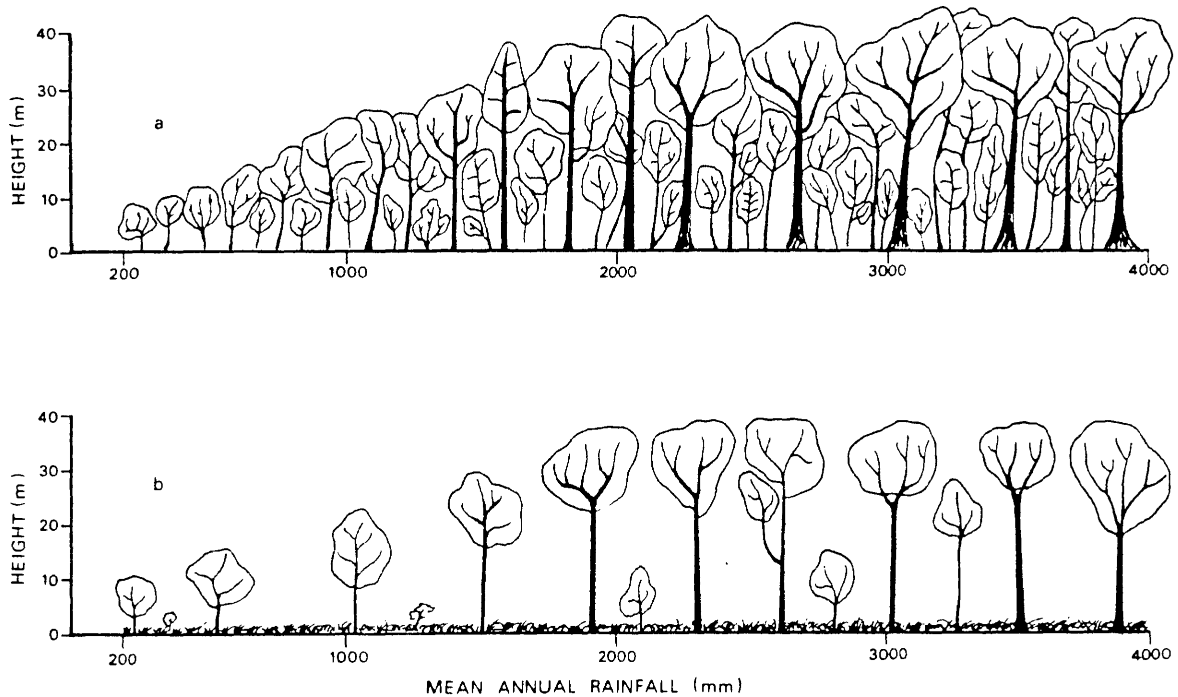

Figure 11. The postulated ancient closed forest and woodland continuum along the rainfall gradient in north Australia is diagrammatically illustrated (a). This continuum appears to have dominated freely drained soils in this region before the Aborigines arrived and to have been disrupted by fires lit by them. The closed forests and woodlands are now mainly found near the rainfall extremes. Elsewhere they have been replaced by open forests and woodlands which are usually dominated by eucalypts (b).

style than that of the hunter gatherer from the Islanders and Aborigines inhabiting the southern islands and the tip of Cape York Peninsula. They cited evidence that in times of hardship these people would establish temporary gardens but revert to hunter gathering when conditions improved. In my view these authors neglected the effects which the longer dry season would have had on the cultivation of the available food plants (primarily *Ipomoea batatas* and *Colocasia esculenta*). For example Thursday Island in the south of Torres Strait has seven months with an average rainfall of less than 50 mm. Records are scanty for northern islands but nearby Daru (Papua New Guinea) has only one month with less than 50 mm although the mean annual rainfall on Daru is a little higher (2063 c.f. 1740 mm).

If shifting agriculture had found its way further south into the main rainforest block, I believe the climate and soils are such that it would have been very successful. However, under a climate similar to that now prevailing, repeated fires in abandoned garden areas would have resulted in the development of extensive areas of grassland and eventually the development of open eucalypt forest over almost the whole of the area. The latter prediction is based on observations of the effects of shifting agriculture in other parts of the tropics with a similar degree of rainfall seasonality and a study of the effects of cyclones and fire on the hillslope vegetation near Cairns (Stocker and Mott 1981).

There are, in many areas of north Australia, indications that closed forests have expanded since the breakdown of traditional Aboriginal lifestyles 50-150 years ago (Stocker 1981). Blake (1939) noted a recent advancement of rainforests in this region but does not seem to have appreciated the role of fire in the dynamics of the eucalypt/rainforest boundary.

It should be observed that some authors have claimed that other factors such as soil water availability (Specht 1981) or soil fertility (Webb 1969) are the primary determinants of the relative distributions of the contrasting open and closed forest types. However, recent studies, reviewed by Unwin *et al.* (1984) and Stocker and Unwin (1985), have suggested that where these factors appear to exert a control, they do so through their influence on the floristics, and thus the flammability, of the vegetation regenerating along fire damaged rainforest ecotones.

-Other vertebrates

In pre-European times mammals, with the possible exception of fruit bats, do not seem to have been significant factors in disturbing the rainforests of this region. However, it is possible that some of the now extinct larger marsupials could have been rainforest inhabitants and played an important role in rainforest dynamics during the Pleistocene and earlier epochs.

The largest of the extant indigenous mammals are the tree kangaroos (Dendrolagus lumholtzi and D. bennettianus) and the pademelon (Thylogale stigmatica). Tree kangaroos are only found in the central part of the main rainforest belt and although they appear to live mainly on leaves in the rainforest canopy, B. Hyland (unpublished data) reported that they often graze tree seedlings as tall as 1 m high on the forest floor. T. stigmatica and other species of pademelon are commonly found in the rainforests of east Australia. It is suspected that they are favoured by forest disturbance for the effects of their browsing activities were often very noticeable in areas which were recently logged. They also appeared to be responsible for bark stripping on some regenerating shrubs and trees (Plate 4). This activity was observed regularly in the period May to July, but the reasons for it are obscure. No shredded material was seen on the ground beneath attacked plants and it is not known whether the bark is used to fill a seasonal food demand or for some other purpose such as a nest. The species most affected was the introduced shrubby weed Solanum mauritianum although small trees of species such as Flindersia pimenteliana may also be damaged in this way. While bark stripping usually ring-barks plants, they often coppice from the base and are attacked again during the following year. Where T. stigmatica are numerous they could influence the early direction and rate of succession following severe disturbance.

Plate 3. Frost damage to an artificially maintained rainforest edge near "The Crater" 30 km south of Atherton at an elevation of 1000 m. Almost all the understorey and many of the larger trees have been killed.

Plate 4. The pademelon, Thylogale stigmatica, appeared responsible for the bark stripping often seen on saplings and here on the introduced shrubby weed Solanum mauritianum.

There are some smaller rainforest mammals such as the possums (Trichosurus, Pseudocheirus and Dactylopsila species), the musky rat-kangaroo (Hypsiprymnodon) and the rats (Rattus, Uromys and Melomys). Although the possums are mainly arboreal grazers, none appears to disturb rainforests significantly. Rats appear to eat the seeds of many species and thus may have an important role in rainforest dynamics.

In many parts of the region, fruit bats (alternatively flying foxes) occur in colonies which may contain thousands of individuals. The commonest species is Pteropus conspicillatus. It appears that their camps are seasonally occupied over long periods of time. For example, several of those reported by Ratcliffe (1938) in his visit to north Queensland, still seem to be in existence. However, it seems unlikely that some of the easily accessible camps would have been occupied in pre-European times for Aborigines would have killed (for food) as many flying foxes as they could, whenever they had the opportunity. In parts of the Northern Territory where flying foxes are still actively hunted, most of their camps are on relatively inaccessible mangrove islands.

A characteristic of most flying fox camps is that many of the larger trees are dead or dying. In one camp near the Barron River, Ratcliffe (1938) equated the effects of the flying foxes to that of a cyclone as the localized devastation was so great. Physical damage, such as injury to the bark on the branches and limbs broken off due to the weight of sometimes hundreds of these animals, may provide an explanation for the damage. Ridley (1930) reported that flying foxes with young in a camp in the Singapore Botanic Gardens' did not fly off with the rest in the evening but stayed behind eating buds and leaves from trees in the vicinity of the camp until the trees there were almost leafless. As far as is known this herbivorous habit has not been reported elsewhere but if widespread, may be the explanation for much of the defoliation usually seen in camps.

The photograph (Plate 5) illustrates damage in the Tolga Scrub created by a large flying fox camp during 1980. This

Plate 5. Tree deaths (Argyrodendron peralatum) and damage (Castanospermum australe) in a flying fox camp in the "Tolga Scrub" 4 km north of Atherton.

Plate 6. The stinging shrub, Dendrocnide moroides, grew vigorously in the gaps created by the disturbance illustrated in Plate 5.

Plate 5. Tree deaths (Argyrodendron peralatum) and damage (Castanospermum australe) in a flying fox camp in the "Tolga Scrub" 4 km north of Atherton.

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small strip of rainforest is a remnant of the rainforest which once covered a large part of the Atherton Tableland. The main species killed was Argyrodendron peralatum. Trees of several other prominent species, such as Aleurites moluccana and Castanospermum australe, were badly damaged but most seem to be recovering. The photograph was taken 18 months after local residents forced the flying foxes to vacate this camp. In general only the upper canopy and emergent trees were affected. Gaps, created by damage to or the deaths of these trees, are being filled by a rapid development of small trees, shrubs and vines. Dendrocnide moroides and Calamus caryotoides are particularly conspicuous (Plate 6). Further gaps will be formed in a few years by the collapse of the many dead spars now standing.

With the coming of Europeans, wild pigs and cattle have occasionally taken up residence in rainforests. Wild pigs may eventually cause some significant changes in the floristics of the forests, for their rooting severely disturbs, often eliminating, many herbs, shrubs and seedlings. Low lying areas are most affected and the surface soil, on patches over 0.2 ha, is often found completely upturned. Wild pigs may also be a vector for the spread of the root pathogen Phytophthora cinnamomi (further details in Section 4.1).

Two of the indigenous megapods, Megapodius freycinet and Alectura lathami, have also been observed to disturb small seedlings as they scratch through the litter searching for food. They are probably a significant destroyer of seedlings under about 10 cm high. Larger seedlings may be damaged by their activities but seem better able to survive.

Insect pests and disease also play a role in forest disturbance. Although insect droppings occasionally made up a significant part of the litter fall in a lowland rainforest near Cairns (G. Stocker and A. Irvine unpublished data) insect grazing, leading to tree death, has not been recorded in north Queensland's rainforests. However, Anderson (1961) attributed the death of 12,000 ha of Shorea albida swamp forest in Borneo to this cause. Detailed discussions on the effects of one, perhaps two, pathogenic micro-organisms in the forests of this region are contained in Section 4.4.