2.2 Characteristics of the region's rainforests

2.2.1 Present day flora

The first extensive collections of the rainforest flora of
north-east Australia were those of Sir Joseph Banks and Dr
Daniel Solander during an enforced stay near what is now
Cooktown, to repair their ship the "Endeavour". While on this
epic voyage of discovery along the east coast of Australia,
this ship, commanded by Captain James Cook, had called briefly
at several other localities. However, after 6 weeks this was
by far the best collected area and Banks was able to report on
the 28th of August 1770 that :-

> "Botanizing with no kind of success. The Plants
> were now intirely compleated and nothing new to be
> found, so that sailing is all we wish for if the
> wind would but allow us." (Banks in Beaglehole
> 1962).

Other botanists associated with the early exploration of the
coast included Robert Brown during 1802 and Allan Cunningham
from 1819 to 1821 (Brass 1953). The first expedition to
proceed far inland was that commenced in 1848 by Edmund
Kennedy. Although the botanist William Carron was one of the
survivors of this ill fated journey, all botanical material,
except for a few seeds, was lost.

European settlement began in earnest in the region during
the 1860s. The following notes on later 19th century
collections have been extracted from Roberts and Whitten
(undated).

One of the first and perhaps the most systematic of the
early collectors in the region was John Dallachy. He lived in
Cardwell from about 1863 to 1871 and made many important
collections which were initially sent to F. von Mueller in
Melbourne. F.M. Bailey, Queensland Colonial Botanist
(1881-1915) made several extended collecting excursions into
the region. The first during 1873 was to Rockingham Bay and
the region of the upper Herbert River. This was followed by a
visit in 1877 to the Cairns and Barron River areas, in 1889 to
Mt Bellenden Ker and in 1897 to the islands of Torres Strait.

These expeditions provided Bailey with additional material for his flora of Queensland (Bailey 1899-1902). J.F. Bailey (F.M's son) collected on the Atherton Tablelands during 1890. Other minor collections from this period included those of Christie Palmerston (about 1870-1880) and W.A. Sayer (1886-1887 on Mt Bellenden Ker). Later visitors to the region included K. Domin (Prague) (1909-1910) and L.S. Gibbs (1914). The latter collected on Mt Bellenden Ker and later published a note on the phytogeography of this mountain (Gibbs 1917).

Despite the early collections, the rainforest flora was still poorly known until the 1950s. For instance W.D. Francis, in preparing his first edition of Australian Rain Forest Trees (Francis 1929), observed that he did not know enough about those species restricted to north Queensland to include them in that volume. Some were included in the following edition (Francis 1951) but even here a count revealed only about 250 of the 800 tree species recorded by Hyland (1982) for the rainforests of this region. The credit for much of our new knowledge of this flora must go to C.T. White, L.S. Smith, S.T. Blake, F.W. Whitehouse and other members of the staff of the Queensland Government Botanist. Forestry Department officers, especially E. Volck and B.P.M. Hyland and CSIRO personnel who were involved first in a phytochemical survey and later in ecological studies of the rainforests of this region (L.J. Webb, J.G. Tracey, W. Jones and others) also made important contributions. Other significant additions to the flora were made by H. Flecker (Cairns physician and amateur biologist) and L. Brass (the leader of many of the celebrated Archbold Scientific Expeditions of the 1930s and 40s and who later retired to Cairns).

Although the rate of discovery of new tree species has declined somewhat in recent years, much fundamental work on the taxonomy of rainforest plants remains to be done. At the present time there is no consolidated flora of practical value and many species are either still to be described or in obvious need of revision. The basic tool for identifying tree species in this region is Hyland's recently revised field key (Hyland 1982). This key uses vegetative characteristics (mainly leaf and blaze features) with species notes to assist

the user to reduce the possibilities to a single species. Hyland and Henry (1974) described the construction and operation of this key.

Tracey (1981), in reviewing the problems associated with the conservation of the Australian rainforest flora, emphasized the need to include as many habitat types as possible in the national park system.

2.2.2 Phytogeography

In retrospect the notion, first formalized by Hooker (1860), of an Indo-Malaysian origin for the rainforest flora, would have been readily accepted. The closed tropical forests were seen to belong to the Indian and Malaysian regions - open eucalypt forests and woodlands were the characteristic Australian vegetation! Initially there was little to argue about for, as indicated in the previous section, the floristics of the rainforests of this region were poorly known until comparatively recently. While it is now obvious that much of the rainforest flora has strong affinities with that normally considered to be typically Australian, most of the available evidence (discussed below) suggests that the recent popular notion of a purely endemic origin for Australian rainforest plants cannot be sustained.

The idea that there were at least some Australian elements in the rainforests is not entirely new. In one of the early studies of Queensland's vegetation, Domin (1911) saw the wet tropics of this region as having a truly Malayan - Papuan flora. He also noted that there were many endemic Australian genera and species in this flora and concluded that it must have separated at an early epoch to enable numerous endemics to develop independently. Swain (1928) viewed the "Malayan flora" as having displaced the eucalypts and araucarias from more favourable sites. Richards (1952) in his survey of the rainforests of the world, noted that :-

> "In tropical Queensland this forest closely resembles the rainforest of Indo-Malaysia in general aspect and except for the complete absence of Dipterocarpaceae in floristic composition."

Herbert (1960) suggested that Australia was the co-inheritor

of an ancient and widespread flora and although he was the first to really emphasize the endemic nature of many rainforest plant species, he still saw the tropical forests (meaning I presume, the rainforests) of this region as being basically Indo-Malayan. Burbidge (1960) extended these thoughts by recognizing that there were plants both in the tropic zone and the "Eremaea" which though not sclerophyllous were genuinely endemic elements in a floristic and phytogeographic sense. She also noted the close affinity of the flora of the region first with New Guinea and a longstanding, but lesser, relationship with that of Malaysia, New Caledonia and New Zealand.

Thorne (1963) placed the tropical and subtropical rainforests of east Queensland into the Torresian Province of the Papuan Subregion of the Oriental Region (Figure 12) even though he saw this area as a zone of heavy overlap with the Australian Region. Aspects of this overlap were examined by Barlow (1972), Carr (1972), Hoogland (1972), Wace (1972) and Webb and Tracey (1972). Although mainly concerned with the phytogeography of the Pacific Islands, Balgooy (1971) considered Thorne's subdivision to be one of the most acceptable biogeographically. Aubreville (1975) thought that the vegetation of the Western Pacific was derived from two old floras which were now well mixed. He also suggested that this region might be the cradle of the angiosperms.

Beadle (1981) analysed the rainforest flora of tropical and subtropical eastern Australia and detected an Asian - Australian relationship. He noted that 120 genera of dicotyledons were represented in Australia by a single species and in Asia by several to many (up to 200). Another 100 were represented in Australia by a few species and in Asia by several to many. The typical rainforest families Meliaceae and Lauraceae provide many examples of genera which are represented in Australia but have many more species in Malesia.

Johnson (1983) reviewed the general relationships between the floras of north Queensland and other regions of the continent. He observed that the rainforests contained most of
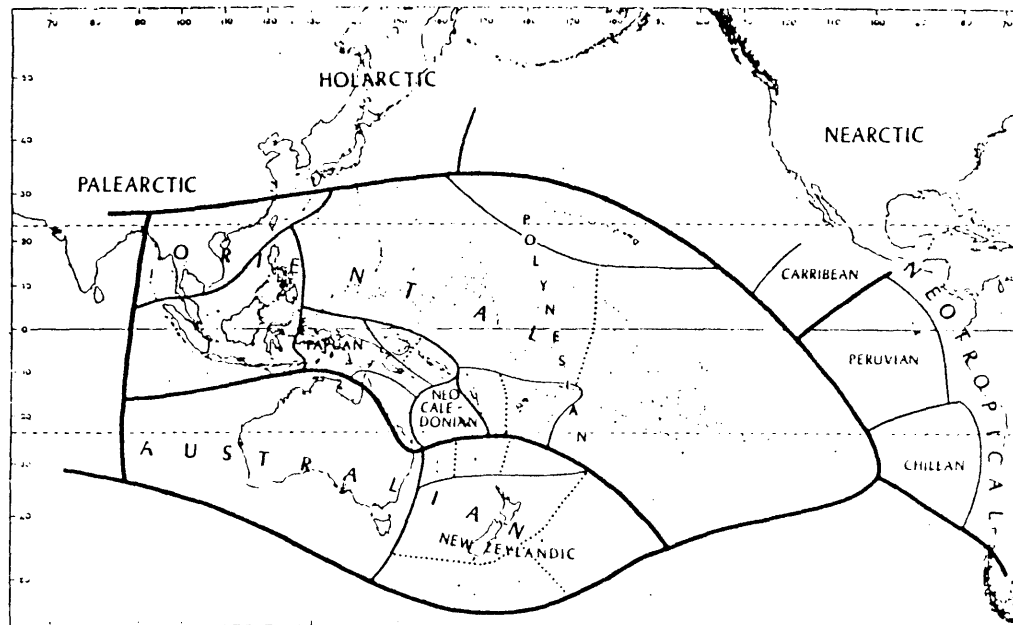
Figure 12. The south-west Pacific region showing the phytogeographical divisions according to Thorne (1963) (from Balgooy 1971).
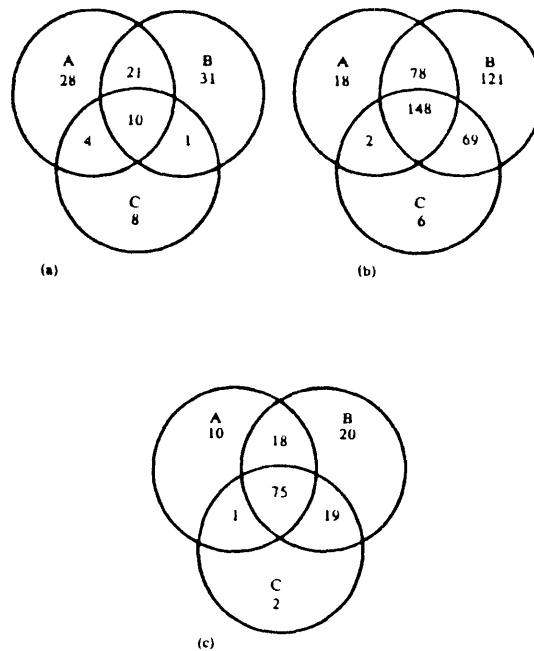

Figure 13. The distribution of (a) 103 endemic rainforest genera, (b) 442 nonendemic genera, and (c) 145 rainforest families among the three floristic regions identified by Webb and Tracey (1981) (from Webb and Tracey 1981).

the primitive plants and suggested that within the rainforest region, a dampening of climatic change had led to lower rates of extinction and provided an environment for slow evolution.

Within Australian rainforests Webb and Tracey (1981) recognized three floristic regions and nine provinces. The tropical rainforests discussed in this thesis are all found in their region B. The rainforests of subtropical and temperate Australia are included in region A, while the rainforests (sensu Webb 1959) of drier areas of east and north Australia are contained in region C. The authors claimed that the floras of A and C developed separately from B. There does, however, seem to be a degree of overlap when generic and family occurrences in these regions are compared (Figure 13). Although Webb and Tracey list eight rainforest families as being endemic to Australia, it has been suggested that one, Idiospermaceae, more properly belongs within Calycanthaceae and no others, except Austrobaileyaceae, are strictly endemic to the rainforests of north-east Australia.

Webb and Tracey (1981) divided their region B into three floristic provinces. B1 was described as :-

> "a scattered province extending from Cape York to south of Gladstone with outliers interwoven on drier coastal sites with B2 and A1. Its core areas are Bamaga - Lockerbie at Cape York, the riverine alluvia of the Iron Range area (e.g. Claudie, Pascoe and Lockhart Rivers), and the alluvia, upper slopes and gorges of the McIlwraith Range. It is tropical moist seasonal but unlike B3 occurs on a variety of soil parent materials and contains rain-green elements. It is separated from B2 by a wide corridor between Coen and Cooktown."

A description of two sample plots from within B1 may be found in Chapter 3.

> "B2 characterizes the humid tropical region between Cooktown and Cairns, north Queensland, from near sea level to highlands approximately 1600 m altitude and inland to a mean annual rainfall of approximately 1300 mm. It ranges from tropical wet and moist seasonal to subtropical moist seasonal and cool subtropical cloudy wet marginal-submontane to submontane. There are several outliers southwards near Mackay in central Queensland."

Most of the sample plots described in Chapter 3 are located in this province which contains by far the largest proportion of

this region's rainforests.

> "B3 is tropical moist seasonal (evergreen
> oligotrophic) and restricted to a few special niches
> on the sand dunes of north-eastern Cape York
> Peninsula, and some sandstone areas of Arnhem Land.
> Its core area, so far as is known, is between the
> Olive River and Newcastle Bay, with outliers at
> least as far south as Oombungi beach south-east of
> Cairns."

This province is not represented in the sample plot series.

2.2.3 Prehistory of the flora

The object of this section is to review our current
knowledge of the origins of the rainforest flora of the region
and to attempt to determine the effects of past environments
on the structure and floristics of present day rainforests.

Current hypotheses on the origins of the flora of north
Queensland's rainforests are based on studies of plant fossils
both within Australia and elsewhere, our present understanding
of continental drift and some notions of the possibilities for
long distance dispersal. From the point of view of the
development of the Australian flora, most of the arguments
surrounding continental drift now seem resolved. This theory
has provided a much more satisfactory explanation for the
distribution of the Australian flora than did those in the
past which had involved the idea of mass invasions of species
from Asia (e.g. Hooker 1860). Although long distance dispersal
is sometimes dismissed as unimportant (and indeed this may be
so for some floras - c.f. Webb and Tracey 1981) there are
enough instances (e.g. the flora of Hawaii) where there seem
to be no alternatives (Carlquist 1974). Long distance
dispersal must at least be seriously considered in any
discussion of the origins of a flora.

- Fossil evidence

Plant fossils may consist of either large plant fragments
(leaves, stems, flowers etc.) or microscopic particles
especially fossil pollen or spores. Although microfossils are
more easily preserved, their interpretation in terms of
taxonomic affinity, source, associated species and

environments is fraught with difficulties. Although these problems are often discussed (e.g. Walker 1978) they frequently seem to be overlooked by workers in this field. Christophel (1981) summed up the main problem as follows :-

> "The presence of a suite of palynomorphs at a given location, therefore supports the existence of the source plants within their pollen dispersal range but says nothing reliable about the vegetation at the actual deposition site".

Furthermore since the morphology of pollen grains is not affected in a consistent manner by environmental factors, recognition of their taxonomic affinities is essential if any assumptions are to be made about their environmental tolerances. Unfortunately reliable identification is by no means certain and the validity of assuming uniform climatic tolerances for taxa over periods of say 100 million years has yet to be adequately demonstrated (Christophel 1981).

Studies of macrofossils have their own set of problems. For example, it has seldom been possible to link satisfactorily material of Tertiary age with modern taxa at generic or specific level. The material itself is not commonly found and is not usually available from bore holes. It does, however, seem to be deposited much closer to its source than pollen and even if the taxa present cannot be related to extant taxa, it has been suggested that the general morphology of the material should enable some reconstruction in terms of the physiognomy (and thus the environment) of the original vegetation. However, Dolph and Dilcher (1980) warn that even these reconstructions should not be relied upon. Other problems in interpreting plant fossil data include the establishment of reliable chronologies and the difficulty of obtaining a comprehensive picture of the vegetation when the fossil record inevitably shows a bias towards wet environments (Truswell and Harris 1982).

To be realistic we are only at the beginnings of a knowledge of the history of the region's rainforests. The outline below must be regarded as merely looking at some of the problems and indicating the possibilities.

- Cretaceous

Although a significant part of the present rainforest flora (the conifers and ferns) had already evolved to forms close to those of the present day, the Cretaceous is a convenient time to begin. As well as heralding the beginnings of the angiosperms, this epoch also marked the rift between the southern continents, especially that between Antarctica and Australia. There were some significant features of the initial separation as reconstructed by Powell et al (1981). These were :-

i) a slow early separation of India from a combined Australia - Antarctica which commenced about 125 million years ago (myo),

ii) a rapid northern movement of India from 80 myo to about 53 myo,

iii) slower northern convergence of India and Australia with Asia from 53 myo to present.

During the Cretaceous, India moved away leaving Australia (and incidently South America) in close contact with Antarctica at a time when it is usually presumed that the angiosperms were rapidly evolving. The early Cretaceous flora of Australia seems to have been dominated by conifers allied to the Podocarpaceae and Araucariaceae (Dettmann 1981). Powell et al. (1981) estimated that by mid Cretaceous (100 myo) India was over 1,000 km from Australia and thus for most organisms an effective dispersal barrier had been created. The timing of the break-up was such that the southern conifers - Agathis, Podocarpus, and Dacrydium - could have found their way northwards into northern South East Asia (with Podocarpus now extending to Japan) via this route. However, Whitmore and Page (1980) suggested that Agathis was more likely to have invaded the Malay archipelago and Melanesian Islands from north-east Australia and New Caledonia.

The possibility that India could have been carrying a significant complement of Gondwanaland flora northwards has only recently been explored (e.g. Schuster 1976; Barlow 1981;

Specht 1981; Meijer 1982; Walker 1982). Although the introduction of angiosperms into Australia appears to have been an Albian event (108-100 myo)(up to 13 myo later than their inception in southern South America or southern Laurasia - Dettmann 1981), it is possible that some angiosperms became established on, or dispersed to, the India block while it was still within range. Interestingly current evidence suggests that an appreciable part of India would have had a warm wet climate immediately before and since its departure from the main part of Gondwanaland. In contrast Australia had a later start and may not have reached tropical latitudes in time for the whole continent to escape the periodic cooler and drier climates postulated by Martin (1981) for the later part of the Tertiary.

Although it is obvious that further evidence is required, this topic is of considerable interest in the context of Australian rainforests for it presents the possibility that some angiosperm taxa with southern affinities could have had a direct route to Asia other than through Australia. Certainly the presence of pollen of Proteaceae from deposits of Eocene age in India (Johnson and Briggs 1975), the extant Dipterocarps of the Seychelles (Raven 1979) and the groups of plants of Gondwanic origin now found scattered through Malesia on certain sites (such as dry serpentine soils) (Meijer 1982), raise some interesting questions.

A feature of the late Cretaceous in Australia was the appearance of angiosperm pollen from taxa related to <u>Nothofagus brassii</u> and the Proteaceae.

- Tertiary

Palynologists and geophysicists usually suggest that during the Palaeocene and Eocene, Australia and Antarctica were very close together (if not still joined) at about 60-70° south latitude (e.g. Crook 1981; Powell <u>et al.</u> 1981) and that at this time most of the southern part of the continent had a moist climate and a sea surface temperature of 18-20°C (Kemp 1981). However, it must be remembered that the continent has a latitudinal range of 43° (more if it is rotated about 45°

clockwise as has sometimes been suggested e.g. Beadle 1981).
It seems quite probable that such a large land mass would have
had a wide range of environments. It should also be observed
that, at high latitudes, the light levels characteristic of
the forest floor beneath canopy gaps in closed forests, may
have severely limited the diversity of the extensive
rainforests which might be expected in the postulated warm,
wet environment (see Section 4.3 for an explanation). The
diversity of assemblages of lesser stature e.g. shrublands
(if they existed at that time) need not have been so
restricted.

The fossil record in south-east Australia (Figure 14) showed
increasing diversity through the Tertiary (Martin 1981). A
feature of the oldest part of this assemblage is the number of
taxa which one would regard as being typically tropical.
However, Kemp (1981) reported that many in this group
disappeared from the fossil record after the Middle Eocene.
She suggested that the loss of "tropical" species from the
fossil record (and isotopic data) indicated a general cooling
of the climate.

The Australian continent moved steadily northwards during
the Oligocene. The climate appears to have cooled especially
towards the end of the Oligocene when Drake passage between
Antarctica and South America opened (Kemp 1981). There is
however, still evidence of vegetation on Antarctica at this
time. The Australian continent's move northwards continued
during the Miocene. The early part of this epoch may have been
wet but there are indications that drier conditions were
widespread. However, Martin (1981) suggested that "open
savannah woodland/forests and grasslands" did not become
widespread until the Pleistocene.

Australia was sufficiently far north for floristic exchange
with Asia to become a possibility in the Pliocene (Galloway
and Kemp 1981). Unfortunately very little is known about the
vegetation of the Pliocene except that it appeared to be a
time of sudden change. Galloway and Kemp (1981) suggested
that the deeply weathered soils of some basalts of this age
indicate that at least part of this epoch was warm and moist

UPPER CRETACEOUS	PALAEOCENE EOCENE	OLIGOCENE	MIOCENE	PLIOCENE

ARAUCARIACEAE

MICROCACHRYS

PODOCARPUS type 2

PHYLLOCLADUS type 2

ILEX

DACRYDIUM type 1

NOTHOFAGUS, brassii type

PROTEACEOUS type

WINTERACEAE

BANKSIEAE

AUSTROBUXUS - DISSILIARIA

CASUARINA

DACRYDIUM type 2

NOTHOFAGUS, fusca type

MYRTACEAE

XYLOMELUM type

PHYLLOCLADUS type 1

? PODOCARPUS sec. Dacrycarpus

? ANACOLOSA

SANTALUM

CUPANIEAE

RESTIONACEAE

GRAMINEAE

NOTHOFAGUS, menziesii type

LORANTHACEAE

SPARGANIUM

MACARANGA - MALLOTUS

CUPRESSACEAE

? MICRANTHEUM

? CHENOPOD - type

? EUCALYPTUS - type

ACACIA

SYMPLOCACEAE

'RANDIA'

COMPOSITAE

HALORAGIS

MONTIA?
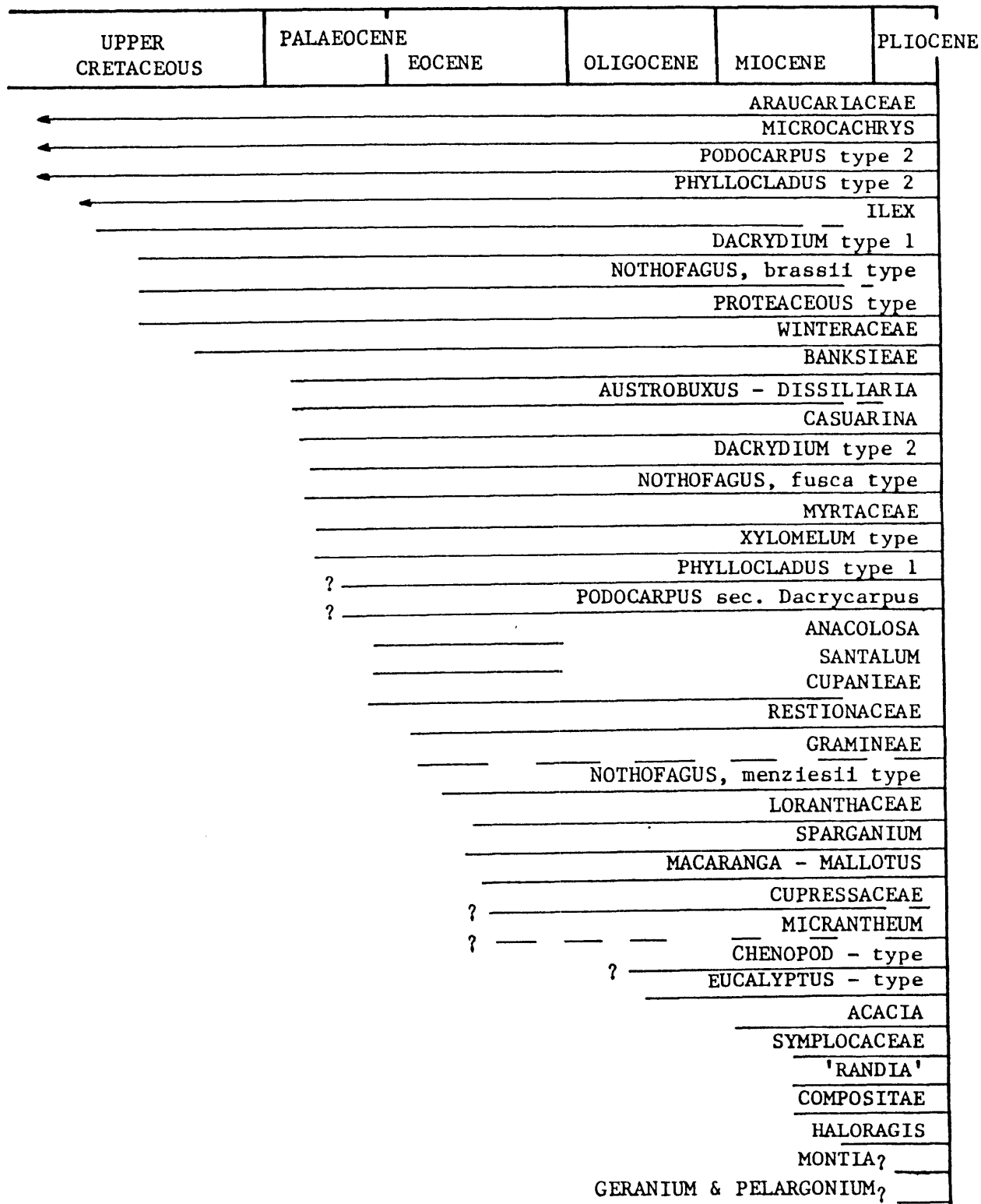
GERANIUM & PELARGONIUM?

Figure 14. A pollen assemblage showing increasing diversity through the Tertiary (from Martin 1981).

in south-east Australia. They also saw the Pliocene as an epoch when a major change occurred in the vegetation and the widespread rainforest cover of the Early Tertiary gave way to the predominantly xerophytic vegetation now so characteristic of Australia. Bowler (1982) showed how the Early Tertiary climate may have been modified to that of the present by an intensification and equatorial movement of the southern high pressure cells and the developing Antarctic ice sheet.

An examination of the Tertiary macrofossil record by Christophel (1981) painted a rather less certain picture and casts doubts over some interpretations of the palynological record. While the macrofossil record is rather scanty, much more material appears to await examination. The three assemblages examined by Christophel are of Eocene age. The Maslin Bay assemblage (near Adelaide, South Australia) has over 200 identifiable leaf types with no evidence of dominants. Only five taxa have been assigned to families with any confidence :- Araliaceae, Proteaceae (2), Podocarpaceae and Araucariaceae. Although over 25% of the pollen found with the macrofossils had affinities with Proteaceae and Nothofagus spp., less than 1% of the leaves belonged to Proteaceae and only one leaf even vaguely resembled those of extant Nothofagus spp. Further, no leaves recognizable as Myrtaceae were found although this family was reported for 5% of the pollen. Overall the size and shape of the leaves suggested to Christophel that they were derived from either a simple mesophyll vine forest or a complex notophyll vine forest (after the structural classification of Webb 1959).

The second macrofossil assemblage was the Nerriga assemblage (120 km north-east of Canberra). About 120 leaves have been recovered and sorted into almost 40 taxa. Only one has been assigned to a specific taxon (Cycadaceae). In contrast to the Maslin Bay assemblage, seven or eight leaf forms occurred more frequently than most of the others. Pollen extracted from samples of this exposure yielded Nothofagidites (2.5-10.5%), Proteaceae (15-23%) and Myrtaceae (2-7.5%). As yet no leaves attributable to either Nothofagus or Myrtaceae have been recorded although one or two may have proteaceous affinities.

The Anglesea assemblage (about 100 km south-west of Melbourne) appeared to be slightly older (? Upper Eocene) than the two previous finds. The several lenses located varied somewhat in composition. Casuarina and a Cycad dominate one but the others were more diverse e.g. an analysis of 81 specimens indicated 41 taxa. Again there did not seem to be any leaves of Nothofagus or Myrtaceae even though these species were again prominent in the palynological record.

When the macrofossils from all three sites were examined there was not a single leaf species common to all three floras. At the generic level the only taxon definitely found in all three was Casuarina. Christophel (1981) concluded that the Tertiary rainforests were composed mainly of genera now extinct. The questions which must be asked are where are the supposed forests of Nothofagus, Proteaceae and Myrtaceae and what does the pollen of these extinct macrofossil species look like? Although the species mix and leaf sizes suggested rainforests, the only taxa confidently identified was Casuarina - a genus most palaeobotanists associate with dry sclerophyll assemblages but which is also known from some rainforests.

The work of Christophel and others on the macrofossils of the Tertiary must raise many doubts about the validity of established hypotheses on the distribution and nature of Australia's Tertiary flora and Tertiary environments. It also has some relevance for ideas on the origins of the angiosperms as well as the reconstruction of floras and climates of epochs as recent as the Quaternary.

- Pleistocene

The Pleistocene is a convenient time to switch emphasis from speculation on the distant origins of the Australian tropical rainforest flora to an examination of the available evidence for the development of present day rainforests in north-east Australia. This should not be interpreted as meaning that there have been no significant losses from and/or additions to this flora since the Tertiary. It must also be realized that New Guinea cannot be considered separately from this region as

during this epoch, sea levels were often so low that a land bridge existed across Torres Strait.

It is apparent from the brief description of the region's geomorphology (Section 2.1.3) that the characteristic landscape of the region did not develop until late in the Tertiary. From the viewpoint of the flora, the Early Tertiary habitat seemed relatively uniform with little opportunity for significant refugia until the end of this period when block faulting provided considerable relief. However, it should be noted that the highlands of New Guinea began to develop much earlier (during the Late Eocene).

Our first glimpse of the recent flora came from a small coal seam of either Early Quaternary or Late Pliocene age, on the eastern edge of the Atherton Tableland. Kershaw and Sluiter (1982) reported that it contained pollen of Symplocos, Podocarpus, Elaeocarpus, Dacrydium, Cunoniaceae, Casuarinaceae, Myrtaceae and Nothofagus as common dry land taxa. All the taxa recognized, except for Nothofagus and Dacrydium, have extant species in or near the present day rainforests of north Queensland. Plant macrofossils of this age have also been found in this area (Reid 1926 and Denmead 1947 in de Keyser 1972) but these do not appear to have been critically examined.

Craters formed by Quaternary volcanism have provided suitable sites for long pollen sequences (ca. 120,000 years for Lynch's Crater) extensively studied by Kershaw, Walker and associates (for a useful summary see Kershaw 1981, 1983).

Kershaw's analyses have indicated that there have been great changes in the composition of the pollen rain (Figure 15). Several pollen types (e.g. those attributed to Nothofagus and Dacrydium) were not found in the upper levels of the deposits. The closest occurrences of species of these genera are now in New Guinea. Araucaria pollen also became less apparent in the upper portion of the record but two species may still be found in isolated pockets within the region's rainforests. The presumed decline of Araucaria has been linked to the suggestion that fire frequencies would have increased with the arrival of man on the continent. The
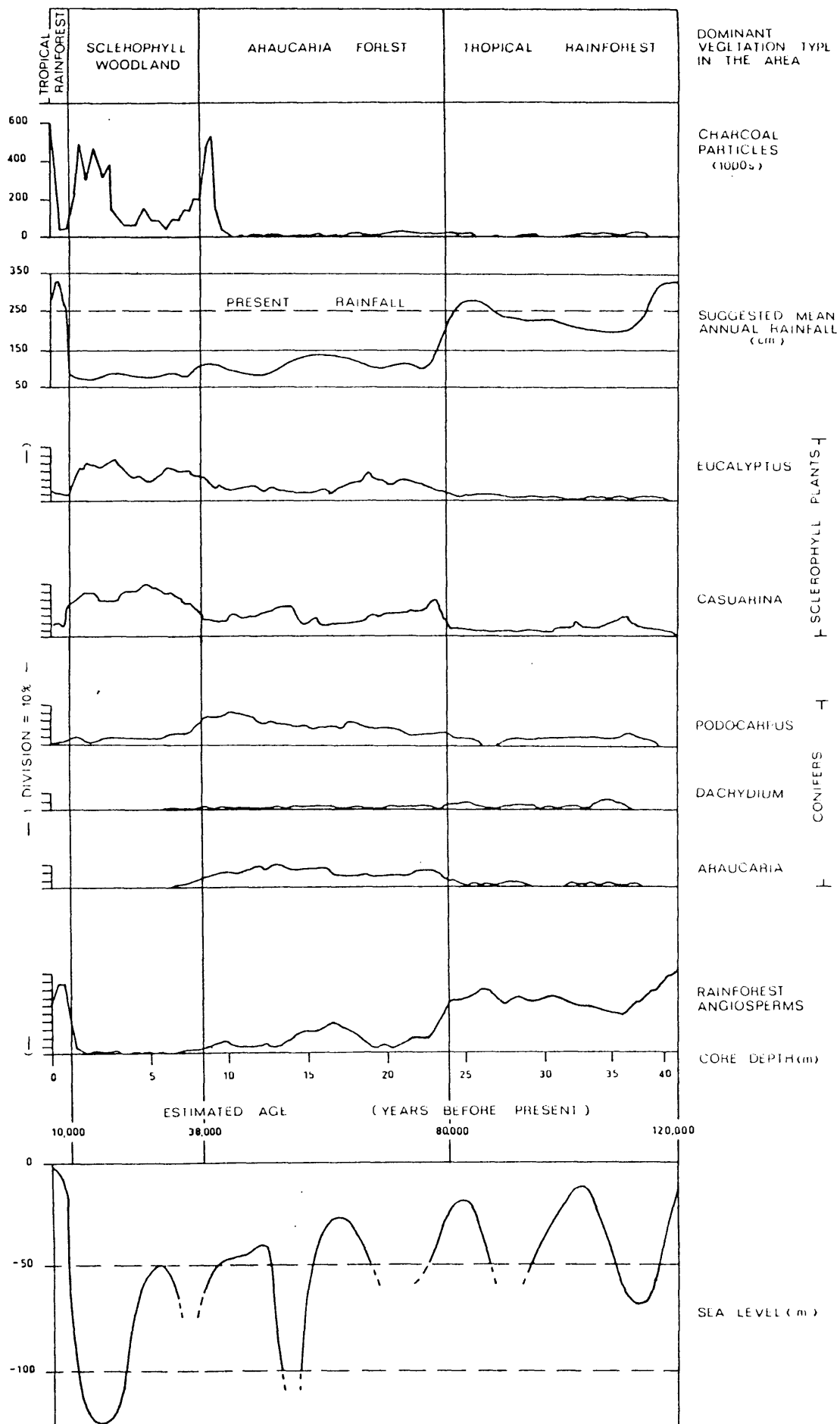
TROPICAL RAINFOREST | SCLEROPHYLL WOODLAND | ARAUCARIA FOREST | TROPICAL RAINFOREST | DOMINANT VEGETATION TYPE IN THE AREA

CHARCOAL PARTICLES (1000s)

600
400
200
0

350
250
150
50

PRESENT RAINFALL

SUGGESTED MEAN ANNUAL RAINFALL (cm)

EUCALYPTUS

CASUARINA

SCLEROPHYLL PLANTS

1 DIVISION = 10%

PODOCARPUS

DACRYDIUM

CONIFERS

ARAUCARIA

RAINFOREST ANGIOSPERMS

CORE DEPTH (m)

0   5   10   15   20   25   30   35   40

ESTIMATED AGE   (YEARS BEFORE PRESENT)

10,000   38,000   80,000   120,000

0

-50

-100

SEA LEVEL (m)

Figure 15. On the basis of the pollen and charcoal sequences summarized for the Atherton Tableland above, Kershaw (1980) suggested that there had been great changes in the vegetation and climate of this region during the past 120,000 years. The sea level data are from Kikkawa et al. (1981).

density of charcoal particles in these deposits tended to support this hypothesis.

Kershaw also suggested that changes in the relative quantities of various pollen types, especially the "Eucalyptus" component, indicated that there have been great changes in the floristics and structure of the plant assemblages contributing to the pollen rain and that these changes were a reflection of a changing climate. For example he saw open eucalypt forests as replacing rainforests during dry intervals. Indeed he postulated that the mean annual rainfall at Lynch's Crater (now about 2,600 mm) was generally less than 1,500 mm and sometimes as low as 600 mm during the period 8,000 to 75,000 years B.P. There may, however, be some alternative explanations which would account for the changes in the proportions of different pollen types in the sediment profile. For instance :-

a) the pollen assigned to Eucalyptus may belong to a rainforest member(s) of the Myrtaceae for there are problems in precisely allocating fossil pollen of this family to genera (Ambrose et al. 1979). Rainforest Myrtaceae of the genera Eugenia (sens. lat.), Backhousia, Xanthostemon, Lindsayomyrtus and Tristania are common dominants in the present day rainforests of the region (see Section 3.2). Other rainforest Myrtaceae such as Eucalyptopsis are now rare but may have once been numerous. Furthermore data from Kershaw and Sluiter (1982) indicated that in this region there may be a direct relationship between the percentage of Myrtaceae in the modern pollen rain and the average annual rainfall (Figure 16). Salas (1983) noted that pollen of Myrtaceae can also be very widely dispersed.

b) the other pollen type used as an indicator of open forest conditions, Casuarina (sens. lat.), can also be very widely dispersed (Flenley and King 1984). A further problem is that some casuarinas (more strictly the group now included by Johnson 1980 in Gymnostoma) tend to behave as a rainforest species in some areas of north Australia (e.g. on Thorton Peak) and New Guinea. Kershaw and Sluiter (1982) recently recognized the difficulties of distinguishing between
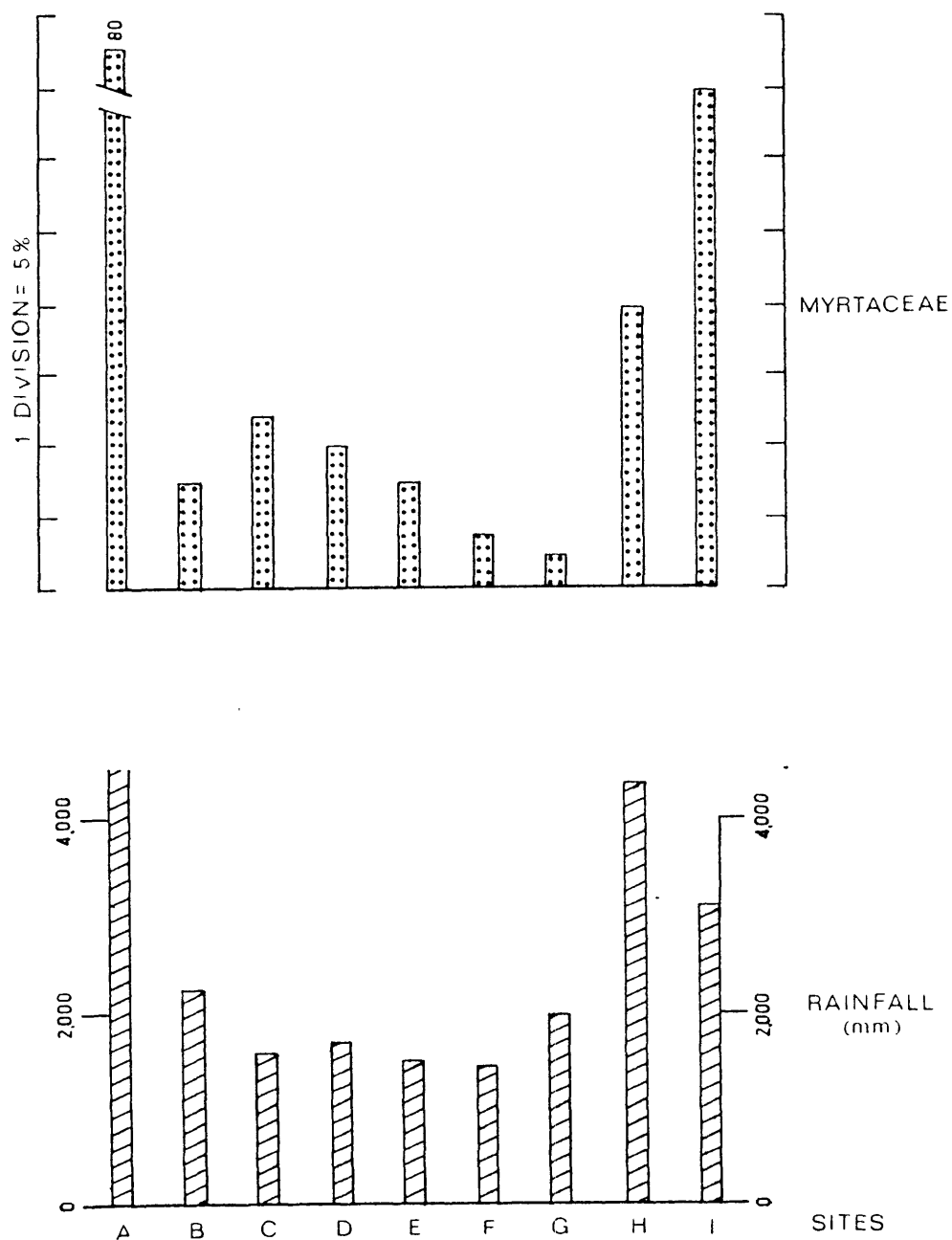

Figure 16. The occurrence of modern Myrtaceae pollen in moss polsters and the average annual rainfall at various sites in north Queensland (from Kershaw and Sluiter 1982).

Casuarina and Gymnostoma and of problems associated with interpreting their significance in the pollen rain.

c) the link between mean annual rainfall and the position of the boundary between eucalypt forest and rainforest is not as close as often assumed and while Lynch's Crater was surrounded by rainforest at the time of European settlement, there were small pockets of open eucalypt forest within a few kilometres.

d) after the arrival of man, frost-killed vegetation below the crater rim may have been regularly burnt. In these circumstances the structure and floristics of the affected vegetation would be greatly altered irrespective of any long term trends in temperature or precipitation (see Section 2.1.5c).

e) the nature of the pollen rain could have been influenced by successional vegetation on ash deposits and lava flows from the intermittent volcanic activity which, in this region, extended from the Tertiary to 10-20,000 years ago. Paijmans (1973) found that on recent volcanic landscapes in New Britain (average annual rainfall over 4,000 mm) Casuarina papuana and Eucalyptus deglupta were prominent species in the early successional stages.

If Kershaw's reconstruction of past climatic conditions is correct, then it seems important to determine if the postulated long dry period between 8,000 and 75,000 years B.P. was a widespread or purely local phenomenon. If widespread, it is doubtful whether local refuges would have been large enough to hold more than a fraction of the mesic flora needed to recolonize the region on the return of more favourable conditions.

There are some indications that there could have been a dry interval in the region during this period. For instance Hopley (1973) found geomorphological evidence of dry conditions about 15,000 years ago in the Townsville area. A little further afield studies of sediments from the north-west shelf suggested an arid maximum 17,000 years B.P. (Bowler et al. 1976). Saline deposits from the floor of the Gulf of

Carpentaria indicated very dry conditions during the period 19,000 - 15,000 years B.P. (Coventry et al. 1980). Whitehouse (1963) suggested that the sand dune systems found on Cape York Peninsula may have been formed during a period when the climate was drier and the sea level was lower. However, Pye (1983) found that dune formation in this region was largely controlled by sediment sorting and wind energy near the shoreline. The present climate was not necessarily unfavourable.

The distribution of plant species also provides some clues as to past climatic conditions. For instance Burbidge (1960) suggested that the eucalypts which reached New Guinea would not have been able to migrate from north Australia without a land bridge across Torres Strait. A rather radical drying up of the currently very wet Papuan Gulf area would also seem necessary. However, the movement of eucalypts into New Guinea may not have been possible without the assistance of man, for as well as having limited dispersal ability (by wind or gravity), eucalypts do not regenerate well unless fires have removed competing vegetation and created a suitable seed bed.

The links between north Australia and New Guinea could not however, have always been through open forests for both areas share some wind dispersed rainforest species, notably Flindersia pimenteliana, F. pubescens, F. iffliana, Grevillea pinnatifida and Oreocallis wickhamii. It is difficult to imagine how the large winged seeds of these species could have traversed the present gap without the presence of a continuous corridor of mesic closed forest sometime during the Quaternary.

The presence of small, apparently relic patches of fire sensitive closed forest (or monsoon forest) across north Australia (discussed above) suggests that the very dry period postulated may not have been entirely regional in extent, for it is assumed that the fragmentation commenced during, or before, the postulated dry interval. In this circumstance the patches would have had difficulty maintaining their integrity under conditions much more adverse than those of the present day. Once these fire sensitive assemblages were eliminated

from sites, they would not have been able to regain them on the return of more mesic conditions because of the generally unavoidable addition of fire to their original environment.

The origins of rainforest organisms other than plants were also examined for clues as to whether the current flora invaded from the north or has been here throughout the Tertiary and Quaternary. Unfortunately, useful data in terms of fossils of known ages and taxonomic relationships are even harder to find for other organisms than for plants. However, Kikkawa et al. (1981) observed that more than 98% of the land birds of the region "are immigrants from the north or radiants of early immigrants". The postulated arid periods could account for the low level of typically Australian species in the rainforest bird fauna for Mayr (1969a) noted that birds would face high extinction rates in refuges under a deteriorating climate. The presence of the Cassowary (Casuarius casuarius) is an enigma for it is a large flightless bird, a specialized rainforest frugivore and related to other ratites – a group of southern affinity with other representatives in Africa and South America. Assuming that it and its ancestors always fed on the fruit of rainforest plants, it would seem particularly susceptible to extinction if there were marked reductions in rainforest areas.

Reptiles are not numerous in the region's rainforests and after an examination of the origins, biogeography, distribution patterns and island evolution of this group in Australia, Cogger and Heatwole (1981) made the following observations :-

> "In reptiles, the virtual failure of any of the older endemic elements to invade the wetter forests of the East and North (despite the contention that such forests were much more widespread during the Pleistocene interglacials) suggests that such forests in Australia are not only young, but that their expansion during the Pleistocene was quite short-lived if not transient. Conversely, the Pleistocene invasion of these forests by Indo-Papuan elements across the Torres Strait land bridge is simply a measure of their pre-adaptation to this moist, tropical climatic regime."

The lack of specialized rainforest mammals (especially

frugivores - see Chapter 5) is also rather surprising.

Except for the major problem of the presence of the Cassowary most of the biotic evidence seems to point to the decimation of Tertiary rainforests during dry epochs with a residue of survivors (mainly within the plant component) supplemented by recent invasions of birds and probably plants, through New Guinea.

Another approach to predicting Late Quaternary vegetation patterns is through palaeoclimatic prediction based on a study of the phenomena responsible for the region's climate. While not disputing these attempts, Oliver (in Coventry et al. 1980) cautioned that the atmospheric balance is such that quite small shifts in our physical assumptions may even make it possible to establish two almost opposed models.

The model used by Nix and Kalma (1972) attempted to reconstruct the Quaternary climate of this region by relating temporal variations in temperature and precipitation to atmospheric circulation and sea level fluctuations. In very broad terms they suggested that world wide cooling to produce a slightly lower sea level (13-50 m below present) may have made north-east Australia somewhat wetter than it is at present. However, further lowering made this region cooler and drier. The region's sensitivity to sea level is related to the depth of Torres Strait. A fall of 13 m in the present sea level would bridge the Strait preventing the circulation of cooler water through the Gulf of Carpentaria and across the Sunda and Sahul shelves. Furthermore they thought that a drop greater than 50 m would drastically reduce the area of shallow sea available for rapid heating and the consequent generation of atmospheric instability along the intertropical convergence zone. Examples of the changes predicted by Nix and Kalma are illustrated in Figure 17. Current estimates of sea levels during recent glacials and interglacials are shown in Figure 15. Nix and Kalma's model suggests that the rainfall regimes derived from atmospheric instability along the intertropical convergence zone, would not consistently follow the glacials (dry), inter-glacials (wet), pattern suggested by Kershaw (1978).
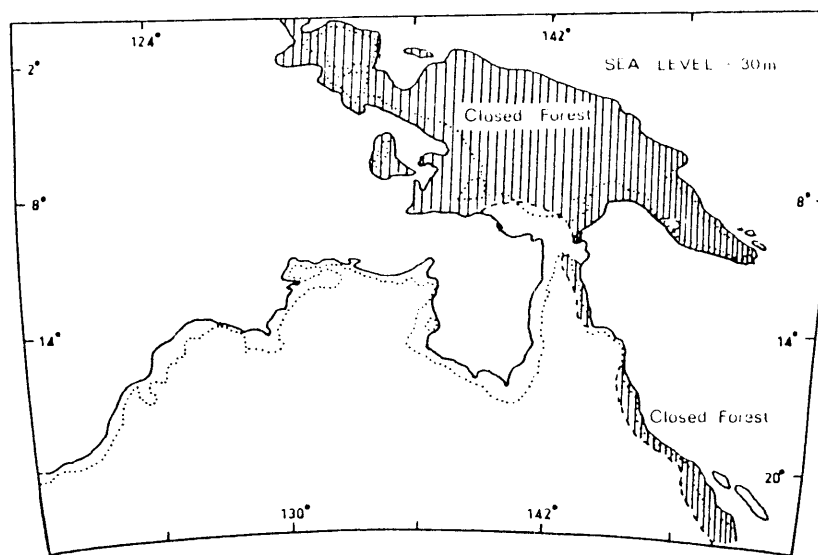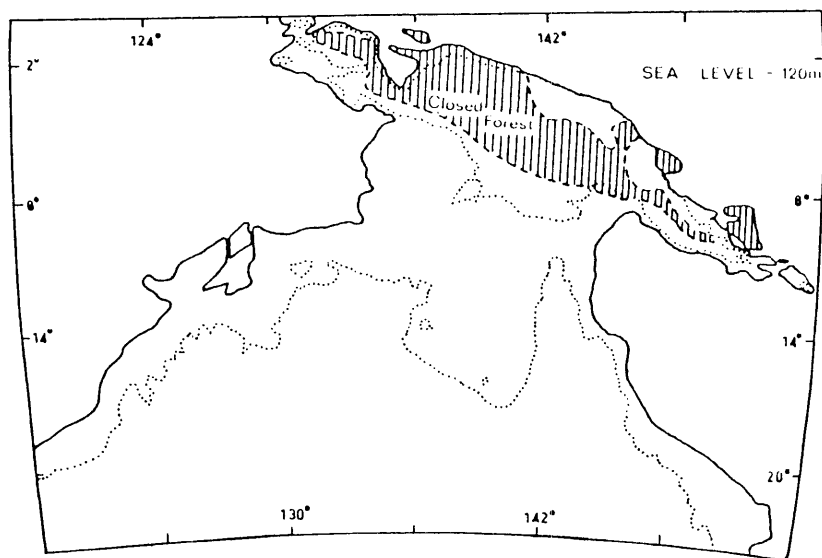
Figure 17. Examples of how Nix and Kalma (1971) thought that sea level changes affected the climate and consequently the distribution of tropical closed forests during Pleistocene glacial epochs. The sea levels in the upper map existed between 17,000 and 14,000 years ago. Nix and Kalma suggested that at this time the precipitation would have been 0.5x present, evaporation 1.25x present and air temperature 1°C below present. The sea levels in the lower map existed 8,000 years ago. They estimated that at this time the precipitation was 1.5x present, evaporation the same and the air temperature about 1°C above present.

As well as rain from moist unstable air associated with the southern movement of the intertropical convergence zone during summer, rain brought by the south-east trades is of great importance in determining the composition and structure of plant assemblages in this region (Section 2.1.2). The effects of glacial epochs on rain from this source, seem uncertain. Cooler seas may have reduced the ability of the trades to accumulate moisture and a more northern mean path for anticyclones during the winter (Webster and Streten 1972) may not have allowed them to pick up as much moisture while passing over the ocean as they do at the present time.

On the whole it is difficult to say much more than that the climate seems to have fluctuated during the Quaternary. The amplitude and timing of the fluctuations still seem very much to be open questions. The effects of these climatic changes on the vegetation are even more uncertain, complicated as they are by the arrival of man sometime during this period. His use of fire in vegetation management would have disrupted the ancient closed forest continuum, forever altering the ability of fire sensitive rainforest assemblages to regain ground lost during any arid epochs. In particular it is thought that his use of fire could have prevented the redevelopment of a corridor of mesic closed forest linking Australia and New Guinea.

In the context of the Tertiary origins of the rainforest flora of north-east Australia, the situation regarding Australian elements may not be as clear as previously believed (e.g. Stocker and Hyland 1981; Webb and Tracey 1981). The possibility that much of the Tertiary pollen identified as extant taxa, is in reality from unrelated extinct genera, must be seriously considered. It also seems quite possible that some Gondwanic angiosperm floristic elements were introduced into Asia via the Indian subcontinent 40-60 myo before Australia's near collision with Sundaland 15 myo. Typical southern elements could have arrived in north Australia by an Asian route as well as directly. Tertiary and Late Quaternary plant macrofossil assemblages from north Australia are available and must be closely examined before the questions surrounding the origins of the region's flora can be

satisfactorily answered.

The uncertainties expressed above contrast with the views of Webb and Tracey (1981). They argued strongly for an ancient, essentially Australian, origin for our rainforest flora and claimed that the extent of migration of flora to and from Australia remained conjectural. To use their precise words :-

> "The efficacy of long distance dispersal should not be exaggerated because of the low vagility of many rainforest plants that would be involved in 'communal colonization' particularly species occurring late in succession in rainforest ecosystems, e.g. species with large seeds of short viability or with heavy wind-dispersed seeds."

However, it does not seem necessary to invoke long distance dispersal arguments to account for the comparatively short ocean crossings which could have been made by plants migrating to this region from the north during the last 15 myo. The argument of "communal colonization" has also been advanced by van Steenis (1971) in an attempt to explain the current and past distribution of Nothofagus without resort to continental drift. While this holistic argument is interesting it seems somewhat contradictory to another concept, that of "species sifting", which has also been used by Webb and Tracey (1981) in their discussion of the origins of the Australian rainforest flora.

A distinctive feature of the rainforests of north-east Australia is the presence in the upper canopy of the following endemic or near endemic genera :- Flindersia, Cardwellia, Musgravea, Placospermum, Buckinghamia, Darlingia, Backhousia, Blepharocarya, Castanospermum, Ceratopetalum and Doryphora. The presence of other primitive and restricted angiosperm genera - Idiospermum, Austrobaileya, Sphenostemon, Bubbia, Ostrearia, Neostrearia, Eupomatia and Galbulimima adds to their uniqueness. However, these floristic features should not be allowed to overshadow the very large number of genera (over 200) which are basically South East Asian and represented in this region by a small number of species (see Section 2.2.2). The suspected Laurasian floristic components appear to be mixed more thoroughly with Gondwanic elements than in New Guinea where Whitmore (1981) observed that lowland rainforests had been massively invaded by Laurasian elements

and that Gondwanic elements were more conspicuous at higher elevations and on poor soils.

From the viewpoint of rainforest floristics and dynamics, the studies reviewed above are not particularly conclusive. For example we cannot really determine whether the rainforests of this region have been fluctuating in extent in only a minor way since the Tertiary or whether they are on relatively new ground after recent expansion from local refuges (as postulated by Webb and Tracey 1981). Perhaps many or most of their component species have only recently come from refuges as far away as the foothills of the Owen Stanley Range in Papua New Guinea. If their species have been restricted to refuges, it is probable that some present day assemblages might not contain species with slow dispersal rates. Indeed some may be so recent that the entrance of slowly dispersing species is a major source of floristic change. Although some "invasion fronts" (Whitmore 1977) seem recognizable, the only contemporary evidence we have that species may have recently expanded from refuges, is some rather tentative information from an examination of the chemistry of the volatile oils of Flindersia bourjotiana (Wiffin 1978). Studies of the distribution of isozymes within selected plant species appear to offer some new possibilities for a closer look at these interesting problems.

2.2.4 Ecological studies

A useful point to commence a review of ecological research in the region's rainforests is with the visit of Dr Karel Domin of Prague during 1909-1910. His paper on Queensland's plant associations (Domin 1911) showed a remarkable insight for those times. Domin referred to the rainforests as "vine scrubs". He was the first to observe that, in north-east Australia, these assemblages are found on a variety of soils noting that :-

> "They prefer, of course, always a rich, deep soil, especially alluvial and basaltic, but in those portions where the rainfall reaches a very high range, we find them on a very poor, almost innutritious soil, as on Bellenden Ker or Bartle Frere, on a poor granitic soil."

Domin recognized five different types of rainforest; one on lowland alluvials, three on "non basalts" and one on the basalts of the Atherton Tableland as well as other types he calls "coastal scrubs". Unfortunately he provided few other details of his types. Domin was also impressed by the sharp boundary between open eucalypt forests and rainforests, emphasising the first part of the following sentence in his paper by the use of italics :-

> "The line of demarcation between them is most distinct, a phenomenon which is unique in the whole world."

Domin explained many of the boundaries in terms of soil-water and nutrient regimes and appeared close to understanding the role of fire in preventing rainforest species from invading the eucalypt forest. He was however, unable to explain some of the other boundaries he saw especially those on the Atherton Tableland.

Local interest in the relationships between structural and floristic features and the environment of the region's rainforests began in earnest with the publication of papers by Francis (1928; 1939) and Swain (1928). Francis (1928) had examined the rainforests of the Eungella Range west of Mackay. As well as noting the favourable climatic conditions for rainforests in this region, he observed that :-

> "As the equator is approached the relative

        importance of soil is not so evident, because the
        increasing temperature and humidity in combination
        with heavy rainfall appear to be sufficient to
        maintain rain forest growth on comparatively poor
        soils."

This observation paralleled that which Domin (1911) made 18
years earlier. Francis (1939) also thought that the diversity
of the rainforests of the Atherton Tablelands might be due to
the fertile basaltic soil.

Swain, who was Conservator of Forests in Queensland from
1920 to 1931, prepared an overview of the forests of
Queensland for a British Empire Forestry Conference (Swain
1928). He attempted to resolve the problem of what to call the
closed forests of this region :- "jungles", "rain forests" or
"scrubs". He decided that none of these terms was really
suitable as the word "jungles" came from a Sanskrit word
meaning open woodland; "rain forest" he thought could not
exist in a seasonally dry climate; while "scrub", a local name
still extensively used, implied an assemblage of much lower
stature than the forests in question.

Although Swain assumed that rainforest soils were all of
high fertility, he had a relatively good appreciation of the
role of fire in the dynamics of the rainforest edge. He
emphasised what he called "topographic and vegetation shelter"
in the development of rainforests claiming that "Climax indeed
is reached by piling shelter upon shelter."

Swain seems to have been the first to attempt to divide,
along traditional lines, the northern rainforests into
floristic associations by naming three major and six minor
units. In the light of present day experience, these
associations seem to reflect the then limited accessibility of
these rainforests rather than natural species groupings.

While journals such as those of Jack (1921) had provided
some information on the vegetation of the more isolated
northern part of this region, little was really known until
the 1948 Archbold expedition. L.J. Brass, the leader of this
expedition recorded for the first time much of the biology of
this region (Brass 1953). It is interesting to observe his
occasional problem in distinguishing monsoon forests from

rainforests and also his prediction that the dry Cooktown to Coen area would be an important break in the distribution of many rainforest plants and mammals.

Herbert (1960) in reviewing the tropical and subtropical rainforests of Australia suggested that while these assemblages were the "climatic climax" on the most favourable soils, they also formed an "edaphic climax" in those regions where high temperature, humidity and rainfall showed little variation throughout the year. Herbert, like Swain before him, took care to point to the seasonality of the north-east environment and to the effects of fire but he did not seem to share Swain's doubts about the use of the term "rain forest".

From the late 1950s to the present, L.J. Webb and his co-workers (primarily J.G. Tracey and W.T. Williams) have dominated ecological research in the rainforests of Australia. To a large degree this group pioneered the use of numerical methods for studies in rainforest synecology. While the following brief review attempts to provide some perspective of this group's work, it concentrates on key papers and research in the tropics rather than that restricted to rainforests of subtropical and temperate Australia.

In one of his early papers, Webb (1959) attempted to overcome some of the problems of using floristics as a starting point for subdividing rainforests into more manageable units by choosing as a basis for their characterization, physiognomic features, especially the average size of the leaves of the larger trees. Using this system most of the rainforests of north-east Australia would be described as either complex notophyll vine forests or complex mesophyll vine forests. The original classification was revised (Webb 1968; 1978) and the number of types recognized increased from 18 in the original, to 23 in Webb (1978). Of the 18 types first recognized, six were transitional assemblages. The 23 types in the latest revised list were based on the old list with some splitting of old types, the recognition of several entirely new types and the incorporation of some types previously regarded as transitional.

Webb also explored the possibilities of using floristic techniques for forest typing and in the first of two related papers (Webb et al. 1967a) on the use of numerical methods to analyse floristic data from tropical rainforests, Webb and his co-authors compared methods applicable to site/species data. The 18 sites used were relatively small (0.1 ha). The total number of vascular plant species found in them was 818. Webb and co-workers found that the 18 sites could be classified into six groups each of three sites and that the 818 species could be divided into nine groups (plus a residual). These nine groups in various combinations appeared to define the six site groups. However, after consideration of the results of their second study, which examined problems of species sampling using the same data set (Webb et al. 1967b), they were forced to conclude that the status of these species groups was, in part at least, an artifact of the method of numerical analysis used.

In the second study (Webb et al. 1967b) the species were divided into ten subsets on the basis of their life form (e.g. big trees, shrubs etc). They concluded that species of the big tree group carried the whole of the classificatory information reproducing the original classification of the first paper down to the ultimate division of the hierarchy. No other subset possessed this property. This study was also claimed to illustrate the "problem" of the tendency for big tree species to be confined to a single site or at least be very restricted in their distribution. The question which must be asked is whether this phenomenon is real or only the result of the small plot size used to gather the data. Species area curves, such as those of Richards (1952), suggest that if they had lifted the plot size from 0.1 to 0.5 ha they would increase the number of tree species over 10 cm dbh by 2 to 4 fold. At the conclusion of this study, however, the authors appeared to have definitely decided that "some form of physiognomic structural classification will be essential" for typing the region's rainforests.

The value of a physiognomic - structural classification in mapping rainforest types was tested when Tracey and Webb (1975) used a modification of the system initially described

by Webb (1959) to map, at a scale of 1:100,000, the rainforests from Cooktown to Ingham. The forests were segregated into 11 major types. Two or three subdivisions were made in five of these types. While the major types are primarily based on physiognomic features, soils and/or soil parent materials were often used to delineate subdivisions. The vegetation typing was primarily undertaken from aerial photographs with some ground checking. An examination of the maps suggested that in practice, boundaries between some types could not be distinguished (especially the boundary between simple notophyll vine forest and simple microphyll vine-fern forest). In other places the boundary was rather arbitrary (e.g. that between complex mesophyll vine forests and complex notophyll vine forests on the Atherton Tableland) while in a few localities the typing was conspicuously in error (e.g. eucalypt dominated forest mapped as complex notophyll vine forest).

Despite these criticisms the maps have proved useful to those concerned with broad aspects of land use planning, particularly for the delineation of conservation areas. Tracey (1982) provided useful supplementary material examining some of the environmental relationships among the forest types recognized on this series of maps. Tracey's arguments relating to the general relationships among types followed those of Webb (1968)(see below).

Further developments to forest typing techniques based on physiognomic features were made when Webb et al. (1976) used a "proforma" to collect structural data from 44 sites in Papua New Guinea and 45 sites in the Bloomfield-Mareeba area of north-east Australia. The information required at each site included features such as :- locality, canopy characteristics (mainly height, surface configuration, depth, density, presence of layering and emergents), density of ground cover, uniformity of stems of main canopy, rooting features, bark texture and colour, leaf sizes of canopy trees, special shapes and textures of all leaves, deciduousness, presence and characteristics of special life forms (e.g. palms, tree ferns, strangler trees, banyans, trees and shrubs with special appendages, pandans, bamboos, shrubs with broad rigid toothed

leaves, epiphyllae and other epiphytes, and vines with palm leaves, spiny appendages, and robust or wiry stems), leaf characteristics of herbs, presence of ground ferns, evidence of disturbance, the physical environment and an optional survey of trees in a 20x20 m plot.

Their classificatory analysis of the data collected during this study suggested that their methodology was in general unsatisfactory for simple forests, regrowth rainforests, forests under extremely limiting conditions and eucalypt woodlands. Under the above circumstances the use of supplementary floristic information seemed inevitable. However, their approach seemed useful in complex rainforests where floristic information is much harder to obtain. The authors claimed that in these complex forests their use of structural features produced ecologically meaningful divisions below the subformation level.

Williams and Tracey (1984) used network analysis to establish floristic relationships among 146 sites within the main rainforest belt (Cooktown to Townsville). Their "two neighbour" analysis was based on the presence or absence from each site of 740 tree species. They established 19 network groups of which 8 corresponded exactly with one of the 20 map types of Tracey and Webb (1975). The usual pattern for the remaining types was that one network group would transcend two intuitive groups or vice versa. An exception was the map unit "mesophyll vine forest" which straddled seven network groups. The authors concluded that the floristic diversity of this unit was unacceptably wide.

Webb's physiognomic classifications seem to have been most useful for broad scale comparisons of rainforests by conservation planners. However, studies elsewhere in the tropics (e.g. Dolph and Dilcher 1980) have suggested that the use of leaf size characteristics at such a high level in a forest type classification could present some problems for trends in leaf size may not follow expected patterns (e.g. a decrease in average leaf size with increasing elevation). A cursory assessment of the dominant leaf size of an assemblage can be deceptively difficult and quantitative checks have

sometimes yielded very different results (G. Stocker unpublished data).

Webb (1968) endeavoured to relate his structural types to environmental parameters. His 400 study sites covered a wide latitudinal and altitudinal range along the east Australian coast. In summary he claimed that the following relationships exist between physiognomic features and environmental parameters :-

a) deciduousness -
i.   fewer available species with increasing latitude,
ii. more numerous on eutrophic soils,
iii. more numerous with lower rainfall especially on eutrophic soils,
iv. fewer deciduous species with increasing altitude.

b) leaf size - the proportion of species with microphyll sizes generally increases while those with mesophyll sizes decrease with -
i.   increasing altitude,
ii. increasing latitude,
iii. decreasing rainfall,
iv. decreasing soil mineral nutrient status.

c) selected life forms (robust woody lianes, palms, plank buttresses and tree ferns) - the number of available species generally decreases with -
i.   increasing latitude,
ii. increasing altitude,
iii. decreasing annual rainfall.

In this study Webb used parent rock types as indicators of soil fertility and suggested that eucalypt forest is the climatic type in the higher rainfall areas only on oligotrophic soils and nowhere else. Overall his conclusions were similar to those he had already drawn (Webb 1966) in discussing the relationships between selected habitat sites on the wet tropical lowlands of this region although, in the 1966 study, some additional emphasis was placed on internal drainage as a significant attribute of a site.

In a later study Webb (1969) examined the relationships among some forest types of east Australia and soil chemical characteristics, on 27 different sites using numerical classification and ordination techniques. He claimed that :-

> "Over a range of fifteen degrees of latitude along
> the wet coast of eastern Australia the distribution
> of different structural types of vegetation is

> broadly correlated with different soil nutrient
> levels as grouped by numerical methods provided the
> soils are well drained."

However, it should be noted that there were only four sites which were clearly not rainforest. They were all on Frazer Island which originated as a large mass of wind deposited sand and is separated from the northern rainforest sites by over 1400 km. In view of earlier statements (going back to Domin 1911) that soil characteristics are less important in determining rainforest distribution in the tropics, it is surprising that Webb (1969) did not sample a wider range of different structural types of vegetation in this region. Had he done so, he may have observed that both rainforest and open eucalypt forest types occur along most, if not all, of the fertility gradient.

Tracey (1969) did not use the same sites in his "parallel" study of soil physical properties. However, Tracey's 49 sites covered a similar geographic range and again most of the sites were in rainforest with only 17 in assemblages of other affinity. He concluded that the forest vegetation patterns in east Australia were not generally correlated, except under extreme conditions, with soil physical properties such as moisture availability and aeration, although some complex types of rainforest were, in the wet tropics and subtropics, restricted to soils with favourable aeration at field capacity.

Using multiple nearest neighbour techniques, Williams et al. (1969a) examined species distributions in a small patch (0.4 ha) of unlogged rainforest in north Queensland and detected what they saw as a striking and informative pattern. Furthermore, their study suggested that this pattern could not be obtained by plot sampling. In discussing the results, the authors seemed to have assumed that pattern in rainforest largely corresponds to environmental discontinuities or gradients. They did not appear to have considered the possibility that some pattern could arise from the characteristics of regeneration in treefall gaps (for instance the availability of seed of a certain species at the right time - Nicholson 1965). They did, however, claim to be able to explain some features in terms of the autecology of the

species involved. Although the scales of the Malaysian studies reported by Poore (1968), Wong and Whitmore (1970) and Austin et al. (1972) were rather different, these studies provide interesting comparisons and show how much the experimental approach used can influence conclusions about the causes of pattern in rainforests.

Aspects of pattern and succession were also examined by Williams et al. (1969b) in a subtropical rainforest in south Queensland. While perhaps not strictly applicable to the tropical rainforests further north, this study illustrated the value of new numerical techniques for this purpose. The site was re-examined 5 years later when different analytical methods were used (Webb et al. 1972). Unfortunately, I believe that the nature of their initial disturbance (the area was cleared by bulldozer) was very atypical when compared with any natural disturbance such as the damage caused by a cyclone. As a result some of the conclusions drawn from this study may not be of much value in gaining a general appreciation of the mechanisms underlying regeneration and pattern in rainforests. Nevertheless, this study brought forward some very basic questions concerning the nature of succession and these will be mentioned later in this Chapter.

In addition to their basic synecological studies Webb and his associates attempted to apply the methodology they had developed to practical problems such as assessing the suitability of certain sites for the establishment of plantations of the indigenous rainforest conifer Araucaria cunninghamii (Webb and Tracey 1967), predicting the agricultural potential of forest land (Webb et al. 1971) and selecting land for nature conservation (Webb 1966; Webb et al. 1973).

Webb and Tracey (1981) brought together much of the wealth of material and experience they had gathered during the four proceeding decades and provided a thought-provoking commentary on the origins of Australian rainforests. Of particular interest were the sections linking their synecological studies with the biogeographical relationships of the Australian rainforest flora (both within the continent and elsewhere);

the relationships among environments, rainforest structure and floristics and their views on successional processes in rainforests. These and other aspects of this important paper are discussed in relevant sections of this thesis. Overall one is left with the impression that Webb and Tracey have regarded rainforest species as being interdependent and that they saw rainforests in rather a Clementsian light - more or less as a super-organism.

Colleagues within the CSIRO group based at Atherton have also made contributions which are relevant to this thesis. Investigations of the dynamics of the rainforest/eucalypt forest ecotone (Unwin et al. 1984) were of special interest for these studies highlighted the role of established fire regimes and topography in determining the stability and position of the ecotone (see Section 2.1.5g). Other studies undertaken by members of the Atherton group included aspects of nutrient accession within rainforests and adjacent plantations (e.g. Brasell et al. 1980). An important conclusion of these studies was that site rather than forest type can have the most influence on flux rates. They also revealed strong seasonal patterns in phenological processes in the region's rainforests.

Mention must also be made of the silvicultural research which has been carried out over the past 70 years by Atherton based personnel of the Queensland Department of Forestry. While much of the data obtained is still to be published, papers by Volck (1968; 1975), Nicholson (1972), Anon. (1983) and various reports (especially Anon. 1977b; 1979) provide insights. Of special interest are the data relating to yield from rainforests subject to logging with or without various forms of silvicultural treatment. Volck (1975) produced some early results indicating that yield might be highest from the granitic soils but subsequent data suggested that this was not always so (Anon. 1979). From the point of view of forest dynamics one of the most important findings (M. Higgins pers. comm.) was that although the growth of trees in areas

silviculturally treated[1] increased initially, they were back to their predisturbance levels within 10 years. On the other hand the effects on growth of a much heavier disturbance – the selective logging of about 25% of the original stand basal area – lasted almost twenty years.

Other work which should be briefly mentioned here, even though relevant aspects will be discussed later in this thesis, is that of Hopkins (1981) and Hopkins and Graham (1983) on successional assemblages in this region and Connell (1978) and Connell et al. (1984) for contributions to theories relating to the establishment and maintenance of diversity in rainforests.

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1. Useless trees killed, some understorey shrubs and vines removed – see Baur (1964a) for details of these treatments.

2.3 Review of current concepts of diversity, succession and stability.

In establishing a logical pathway between the attributes of individual species and rainforest structure and floristics, the processes controlling diversity, succession and stability must be examined.

2.3.1 Diversity

The interest in diversity (<u>sens. lat.</u>) in tropical rainforests is long standing for diversity, both in terms of species richness and of life form, is a major feature which is immediately obvious to the visitor from temperate regions. So much so that Humboldt is reported (by Kurz 1875 in Richards 1952) to have to have written :-

> "The excessive diversity of the flora and its richness in flowering plants forbid one to ask what is the composition of this forest."

Most of the early workers attempted to explain the establishment of high diversity in rainforests by considering their presumed historical stability and the obvious reationship between diversity and the relative rates of evolution and extinction. For example Richards (1952) attributed the high floristic richness of rainforests to two factors. The first related to conditions in the tropics which favoured high rates of speciation. He made special mention of the climate which he saw as favourable to plant growth and reproduction in all seasons. The second reason was tied to the then current view that the tropical land masses were of great age and that they were supposed to have been climatically stable through long periods of geological time. Subsequent research has shown that while both these factors may influence diversity, they are unlikely to be its prime initiator. Some might even argue that the constantly favourable climate could impede rather than accelerate speciation. Studies of vegetational history in most parts of the tropics have established however, that there have been great changes in the nature and distribution of tropical rainforests and indeed some of the greatest changes appear to

have occurred during the last 14,000 to 7,000 years (Flenley 1979).

Van Steenis (1977) also used the tropical climate argument as the basis of his hypothesis. He claimed that :-

> "a congenial equable climate such as the tropical rainforest which has persisted ecologically unhampered for aeons, has the lowest competition pressure, hence the lowest survival level in all habitats for plants, hence for them the widest patio ludens[1]. Consequently the tropical rainforest offered the longest and largest opportunity towards form creation on the globe, for all kinds of structural developments which came up to survival conditions."

Van Steenis (1969, 1971) provided further argument to support this claim. While a wide "patio ludens" may be present (for reservations see Dobzhansky 1977), the presumed lack of competition pressure in rainforests is difficult to sustain and will be discussed later in this thesis.

Using similar if somewhat more controversial arguments, Fedorov (1977) attempted to explain the development of high diversity in tropical rainforests in terms of the evolutionary ability of the taxa there to form homologous series. He based his view on the assumption that in rainforests "natural selection does not eliminate indifferent characters; these characters remain in a population, their frequency being governed by genetic drift". Implicit in his argument was his earlier claim (Fedorov 1966) that no competitive relations ever develop within the populations of most species except where a species forms more or less dense associations and that there is no elimination of individuals within a population as would ensue from the over — population of any area by individuals of the same species.

Ashton (1969) in challenging aspects of the diversity hypothesis developed by Fedorov (1966), concluded that the complexity of rainforests could be explained by the seasonal and geological stability of the climate leading to selection

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1. Van Steenis (1977) uses this term in the sense of free space for the structural development of non adaptive characters.

for mutual avoidance and, through increasing specialization, to increasingly narrow ecological amplitudes and complex integrated systems of high productive efficiency. He noted that as the complexity increases, the number of biotic niches into which evolution can take place increases but each becomes increasingly narrow. In keeping with the general view of that time, Ashton also thought that the presumed great age of the tropical rainforests was important. Ashton also suggested that while the initial process of speciation among trees was usually, perhaps always, allopatric in response to conventional selection pressures, biochemical differences at generic and family level maintained these forests.

Several other minor possibilities, such as the effects of higher temperatures on biological activity, are discussed in a useful if brief review of the topic by Longman and Jenik (1974). These authors claimed that the reasons for species diversity in tropical forests are complex and show many interactions of environmental and evolutionary features. However, while many of their theories (and those of most others) may explain how the multitude of species came to occur in the tropics, they do not often provide any idea of the mechanisms which allow so many species to exist together.

An important hypothesis, contributing to the development of "mechanistic" theories, was that high floristic diversity is an essential attribute of tropical assemblages for it provides sufficient dilution for individual species to escape from predators that would otherwise kill them or prevent them reproducing. Janzen (1970) and Connell (1971) strongly pursued this, the "predation" theory and Janzen (1969) found many examples of quite specific predator/host relationships especially among the Brucid beetles and the leguminous tree flora of Central America. While the studies of spacing dynamics undertaken by Clark and Clark (1984) also provide some supporting evidence, the basic arguments depend to a large degree on host specificity and more evidence is required for a wider range of forests. Connell (1978) largely abandoned this theory for the "intermediate disturbance" hypothesis (mentioned below). I suspect that while the "predation" mechanism may contribute to the maintenance of

diversity, it cannot entirely account for the very high level of diversity usually observed in tropical rainforests.

The reasons for high species richness in the tropical rainforests have often been linked with conditions favouring high niche diversity. The basic aspect of niche theory, "competitive exclusion" or Gause's hypothesis (Gause 1934 in Harper 1977), can be traced back to before Darwin's time (G.E. Hutchinson 1975). Whittaker (1965) pioneered recent advances by recognizing that each species occupies that part of niche space to which it is best adapted - the part in which it has some competitive advantages over other species. He concluded that :-

> "Evolution of both niche and habitat differentiation permits many species to exist together in communities as partial competitors, with distributions broadly and continuously overlapping forming in the landscapes many intergrading communities."

However, Whittaker still saw the historical stability of tropical rainforests as the main reason for their high diversity.

Richards (1969) introduced the niche concept into the rainforest diversity arguments and enumerated a number of species characteristics which he thought could be of relevance. These were :- mature height, growth rate, life span, shade tolerance, reproductive strategy, type of dispersal mechanism and phenology of leafing, flowering and fruiting. Richards, however, seemed frustrated by an absence of autecological data which would enable the value of the niche theory to be tested in the context of rainforest diversity.

Brunig (1973) attributed the high diversity of the rainforests he studied in Sarawak and Brunei to "a strong tendency to endemism and a diverse flora and of a favourable and diverse but climatically continually favourable environment." He claimed that the large niche hyperspace so developed had been occupied by a great multitude of tree species each with an apparently narrow ecological range. The probability of a particular species occurring within its narrow niche was thought to be greater than for other regions

of niche space. He concluded that species richness, equitability and species distribution should be related to soil conditions which he apparently saw as providing the dominant niche axes.

The debate on whether fine divisions of soil niche axes play a significant role in tropical rainforest diversity continues with conflicting experimental support. Some of the arguments merely reflect a different scale of approach. For example the floristic differences observed by Davis and Richards (1933-34) at the boundary between brown and black sands, seem to have occurred at a much more pronounced soil boundary than those in Schulz's study area (Schulz 1960) where he was unable to detect significant relationships between soil characteristics and species occurrence. Ashton and Brunig (1975) concluded that while the local floristic variation appeared to be primarily related to soil chemistry, the variation of intrinsic structure, the dynamics of forest stands and the regional floristics, all related mainly to physical environmental factors, especially to the water and energy regimes.

Diversity in the relatively seasonal rainforests of Ghana, was found by Hall and Swaine (1976) to be highest on soils where total exchangeable bases were lowest. Huston (1980) also found a negative correlation between the level of available soil nutrients (except for magnesium, manganese and nitrogen) and species richness in Costa Rican forests. However, Proctor et al. (1983) did not find these relationships during their studies of forests in Sarawak. In other studies the methodology used may have been too insensitive to detect differences (e.g. Wong and Whitmore 1970). Whitmore (1977) concluded that "the variation in tropical forests related to soil variation is only one part of the total variation and must be viewed at the correct levels in the context of the overall hierarchy of variation."

In a broader context Ashton (1969) thought that tropical trees had very specialized adaptations to their biotic and physical environments but that a single micro-habitat could be filled by one of several species by historical accident.

Whittaker and Levin (1977) observed that differences in species distributions could be the result of subtle ecotype differences evolved by competing species.

Studies of diversity in temperate forests have also been rather unrewarding. Whittaker (1972) when commenting on attempts to correlate diversity with environmental features, concluded that for continental biotas :-

> "The complex effects of time, aspects of experimental rigor, historic differences in availability of species from adjacent areas, and effects of community structure may only be partly disentangled by correlations. Correlation analysis serves as an aid to conceptical interpretation, but not as a basis of formal statement and deductive predictions."

Glenn-Lewin (1977) met with little success when he attempted to use multiple regression techniques to determine the causes of species diversity in north American temperate forests. He was however, able to conclude that :-

a) on a continental scale diversity seemed to be related to mean annual temperature but not precipitation;

b) diversity is substantially greater in continental climates than maritime regions;

c) relationships between diversity and community structure are generally weak except that -

d) there is an inverse relationship between diversity and abundance of conifer tree species.

Levin (1974; 1976) emphasized the possible effects of environmental heterogeneity and dispersal on diversity. The role of disturbance in increasing environmental heterogeneity was discussed by Levin and Paine (1974). Grubb (1977) suggested that diversity had more to do with the requirements for regeneration than with the tolerances of adults and that this matched the growing conviction amongst evolutionists that speciation was primarily related to adaptive changes in reproductive characteristics. Ricklefs (1977) suggested that local heterogeneity in soil properties and surface micro-environment, caused by the influence of physical factors

is a function of the total range of habitats and degree of specialization of the species to parts of that range (the "niche diversification" hypothesis).

e) at equilibrium each species uses interference mechanisms which cause it to win over some competitors but lose to others (the "circular network" hypothesis).

f) mortality from causes unrelated to the competitive interaction falls heaviest on whichever species ranks highest in competitive ability (the "compensatory mortality" hypothesis).

Connell concluded by observing that although all six hypotheses may contribute to maintaining high diversity, the relative importance of each was very different. In his view most local assemblages changed either as a result of frequent disturbance or more gradual climatic shifts and he thought that these changes maintained diversity by preventing the elimination of inferior competitors.

Connell et al. (1984) closely examined the "compensatory mortality" hypothesis. They showed that this mechanism sometimes operated but could not determine its importance relative to the other mechanisms suggested in Connell's earlier paper (Connell 1978). Connell's various hypotheses are discussed further in Chapter 6.

Nix (1982) suggested that the high regional diversity in the tropics could be largely attributed to the "vertical stacking of near-optimal environments for discrete thermal response elements." The role of this hypothesis in the establishment and maintenance of diversity will also be discussed in Chapter 6.

Many tropical biologists have been attracted to the "refuge theory" as a contributing mechanism to explain the development of high diversity in the tropics. The basis of this theory is the hypothesis that vegetational change during any period of the earth's history causes fragmentation of species ranges and the isolation of a portion of the respective biotas in ecological refuges. Here species populations either become

extinct, survive unchanged or differentiate to the level of subspecies or species (Haffer 1982). The theory largely arose from supposed speciation due to the isolation of taxa in Amazonian refuges during arid phases of the Pleistocene (Vanzolini 1973). While most of the evidence has been gathered in the Neotropics (for examples see Prance 1982), the observation by Ashton (1969) that many lowland trees in Borneo were limited to a single river system, could be interpreted as supporting evidence. However, there seem to be alternative explanations for many of these observations and I would agree with Endler (1982) and Simpson (1982) that the role of the "refuge theory" in the establishment of high diversity is still to be established.

The environmental heterogeneity created by canopy gaps has been studied by many workers whose primary interest has been in rainforest dynamics (e.g. Whitmore 1974; 1975; 1978; 1982; Hartshorn 1978; 1980; Hallé et al. 1978; Rollet 1983). Denslow (1980b) (apparently independently of Ricklefs 1977) advanced the hypothesis of gap partitioning as an important factor in the maintenance of high diversity in tropical rainforests. Oldeman (1983) attempted to establish links among diversity, succession and the architectural attributes of the component species in rainforests. In his view eco-unit^2 diversity and environmental gradients between eco-units co-determine the range of spatial niches, and hence the potential species diversity. Further discussion of the relationship between gap dynamics and diversity will be left to later Chapters.

Finally, Proctor et al. (1983) in their ecological studies of lowland rainforests in Sarawak, concluded that :-

> "Species richness depends on many factors which may interact and be limiting in different situations so that simple interpretations involving single factors are usually impossible."

While this conclusion may prove to be somewhat pessimistic, it certainly seems that the mechanisms controlling the

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2. Defined by Oldeman (1983) as "a vegetation unit which has started to grow on one surface at one moment".

establishment and maintenance of diversity are poorly understood. The only certainty appears to be that diversity is a self-augmenting evolutionary process (Bourgeron 1983 quoting Whittaker 1975).

2.3.2 Succession

Succession is used in a broad sense to denote changes which occur in an assemblage of plants over time, other than changes which are phenologically based. This use is explained in more detail in Section 1.2. The emphasis in this thesis is on what are usually described as secondary successions. Before commencing a discussion of successions in the tropics, some observation on the perceived nature of forest successions in general should be made.

Spurr (1952) reviewed the origins of the concept of forest succession and found that it went back to Roman times. He reported that the concept was well understood in its modern context in some European countries and North America by the middle of the nineteenth century and by the name "forest succession" from 1863. However, agreement on the mechanisms involved in succession has been elusive.

Many ecologists were greatly influenced by Clements and others who established the theory of succession leading to a climax. Their underlying philosophy appears to be best expressed by quoting the opening lines of Clements (1916).

> "The developmental study of vegetation necessarily rests on the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures and dies."

While Clements' assumption was seriously challenged by Gleason (1926) who proposed the individualistic concept of the plant association, Clements' ideas dominated ecological thought for almost half a century. However, it is obvious from the literature that many ecologists (e.g. Whittaker 1953) had reservations about the total validity of Clementsian dogma and modifications were made to accommodate field observations. Gleason's ideas were taken up by others, especially Egler (1954) and Drury and Nisbet (1973). Although Gleason's views now seem to have general acceptance, it is apparent from the

discussion in the previous Section that Clementsian philosophy still appeals to some workers. In the context of the tropical rainforest Ashton (1964b) claimed that his data and that of Schulz (1960) supported Gleason's individualistic concepts.

Connell and Slatyer (1977) brought together the conflicting views of succession noting that the divergence of opinion was based upon three quite different views of the way biotic assemblages are organized. They called their first model the "facilitation" model and as its name implies this model incorporated the Clementsian views of succession. The second - the "tolerance" model was 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. The third was the "inhibition" model. Here it was assumed 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 are released by the damage or death of the previous occupant. The net result was the favouring of long lived species. Overall they concluded that there was more evidence available to support the third model than the other two. The possible role of these three models in rainforest successions will be discussed in Chapter 6.

Using a similar approach van Hulst (1979a) argued that in established views of succession two kinds of habitat change are usually postulated - those due to reaction and those due to competition. Reaction implies that preceeding species prepared the site for future colonizers; competition that the direction of the succession depends only on instantaneous interactions. When he constructed successional models using each of these habitat change mechanisms and a third hybrid using both, he found that all three models produced the expected bell shaped species curves along a time axis. However, only one model (the competition model) realistically allowed the artificial halting of a succession. As a consequence van Hulst concluded that the replacement process of plant species can be entirely understood in terms of instantaneous interaction, chiefly competition. He also

concluded that stress intensity must be negatively correlated with competition intensity. Thus competition becomes increasingly intense as succession proceeds and poorly competitive early successional species are eventually ousted by more powerful competitors. The debate on the role of competition in rainforest dynamics was mentioned in the previous Section and will be discussed again in Chapter 6.

Van Hulst raised another important point in a later paper (van Hulst 1979b) when he examined the value of Markovian chain models of succession such as Horn (1975) used in his studies of succession in a North American temperate forest. Van Hulst was forced to conclude that :-

> "- - - the classical conceptions to the contrary, ecological succession appears to be highly indeterminate. This clearly calls for stochastic rather than deterministic descriptions."

May (1975a), Austin (1977), Binkley (1980) and van Hulst (1980) also raised some questions about assumptions commonly made by users of Markovian chain or differential equation models and noted the failure of several workers to test models with sets of data other than those used in their establishment. Van Hulst suggested that either the models be adequately tested or thrown out and attention focused on the direct effects of disturbance.

Noble and Slatyer (1980) developed the latter theme and examined the use of the "vital attributes" of individual species in predicting successional changes in plant communities subject to recurrent disturbance. "Vital attributes" are defined by Noble and Slatyer (1980) as the attributes of a species which are vital in determining its role in vegetation replacement sequences. They consider that the most important vital attributes of a species are found in each of three groups of a plant's characteristics. These groups are :-

a) the method of arrival or persistence at a site during or after a disturbance,

b) the ability to establish and grow to maturity in the developing community,

c) the time taken for a species to reach critical life stages.

Noble and Slatyer developed these ideas mainly from their experience with temperate forest assemblages where fire was the main disturbing factor. The potential for using this approach to gain an insight to successional sequences in rainforests, is discussed in Chapter 6.

Successional models of considerable theoretical and practical interest are the various adaptations of the gap replacement models pioneered by Botkin et al. (1970). These models have been used to simulate the development of rainforest stands and are discussed towards the end of this section.

Interest in tropical forest succession appears to have arisen early, apparently stimulated by the eruption of Krakatau in 1883 and the opportunities this provided to study a succession commencing on sterile volcanic ash (e.g. Treub 1888; Backer 1909; 1929; Docters van Leeuwen 1936). Richards (1952) reviewed the development of the vegetation on Krakatau and the controversy over whether any of the original vegetation survived on the island. Even if some did survive, most of the colonizing species would have probably come from elsewhere. Richards (quoting Docters van Leeuwen 1936) reported that 50 years after the explosion 271 species had become established and of these 41 were wind dispersed, 28 by sea, 25 by animal and 6 by man. Initial growth was rapid with closed forest already established after 14 years. Richards (1952) concluded that although the vegetation of Krakatau had not yet reached "a stable climax stage", the general course of future change could be predicted with some confidence, at least for the upper and middle regions of the island.

The widespread practice of shifting cultivation has provided many opportunities to study rainforest succession on large clearings. One of the earliest was that of Burkill (1919) who examined the floristics of a 30 year old patch of regenerating rainforest in the vicinity of Singapore. Following similar observations in a Malayan rainforest Symington (1933) noted that :-

> "After felling, coppice growth, if allowed to develop, will within a few years create a stand which, except for the presence of a few typical secondary species, shows little indication that the rainforest has been so recently cleared."

Many other useful observations have been made in the literature specifically examining aspects of shifting agriculture (e.g. Clayton 1958; Nye and Greenland 1960; Kunstadter et al. 1978; Adedeji 1984).

In recent years several studies had been made of regenerating stands arising from patches of tropical rainforest felled for various reasons. In Kalimantan, Kartawinata et al. (1980) examined regrowth following shifting cultivation and on areas were the forest was felled and the debris either physically removed or burnt. They showed that most pioneer species arose from seed whereas the primary forest species developed mainly from resprouts. Burning was detrimental to resprouting but since it increased the height growth of seedlings, they suggested that it might have a fertilizing effect. The area which had been subjected to shifting cultivation, had the lowest species richness, probably because of repeated burning. My studies of regeneration on a felled and burnt plot (described in detail in Section 4.9 and by Stocker 1981) also illustrated the importance of coppice in enabling the regeneration of primary forest species.

Another study of importance was that of the regeneration on 25 ha of cleared rainforest in French Guiana by Maury-Lechon (1982). Here it was observed that the factors influencing the heterogeneity of the regenerating stand were, in decreasing order of importance :- fire, drainage, the proportion of ground covered by debris, seed stored in the soil, seed dispersed to the clearing by animals and the proximity of undisturbed forest.

Although outside the tropics, the studies of succession and pattern by Williams, Webb and co-workers (Williams et al. 1969; Webb et al. 1972) were of interest. The basis for these studies was the regrowth on a small plot (58x28 m) they had cleared in subtropical rainforest on Mt Glorious in

south-east Queensland (lat. 27° 20` S, long. 152° 45` E). In many respects this work was a landmark in establishing the value of numerical techniques in successional studies. They used what I believe to be the best experimental strategy (i.e. that of disturbing an area of vegetation and following the progress of succession over a period of time) and the results appear to have some implications for studies of succession in similarly disturbed areas. However, I doubt that some of the conclusions drawn can be directly applied to natural successional sequences observed in rainforests. My reasons are based on the nature of the disturbance used. To quote from Williams et al. (1969b) :-

> "...; this (the plot) was felled and the logs and slash piled on the south western corner of the plot by a bulldozer. During this operation the blade of the bulldozer scraped away litter to expose mineral soil except in the vicinity of the stumps."

This kind of disturbance does not simulate any natural form of catastrophe except perhaps a landslip. Wind is the main factor causing disturbance to areas of this size or larger in the rainforests of this region (Section 2.1.5) and following wind disturbance the ground is covered with branches and litter to the extent that the area is almost impenetrable. Generally the only bare soil to be seen surrounds the roots of wind-thrown trees.

As a result of the treatment used in the Mt Glorious study, seedlings from seed, either in the soil at the time of the disturbance or arriving at the site soon afterwards, were very prominent and the coppice shoots present were initially ignored (Williams et al. 1969b). It was later realized (Webb et al. 1972) that in general the vegetative regrowth was growing faster than the remaining seedlings and thus was of some significance.

Similar studies would be of considerable interest if they were repeated on a site disturbed by high winds. Unfortunately satisfactory artificial simulation of this phenomena would seem impossible. However, suitable conditions to commence a study of this type occur about every 10 years somewhere in the rainforests of north-east Queensland (Section 2.1.5). It was also obvious from the results of the Mt

Glorious study that any new experiment would have to be studied intermittently for at least 10-20 years before really useful information about long term trends could be obtained.

While the conclusions drawn from the Mt Glorious study may not have been totally applicable to studies of successional processes in naturally disturbed rainforests, Webb et al. (1972) drew up an important list of questions concerning the general nature of successions in rainforests. These questions are examined in Chapter 6.

While studies of successions resulting from massive disturbance are of great interest to land managers in the tropics, an understanding of the processes of recovery from less spectacular events, such as tree falls in virgin forest, promises to provide many general insights of successional phenomena. The basis for this suggestion is that most of the species available for the recolonization of very large gaps, have evolved in circumstances where catastrophic disturbances, such as those initiated by man, have usually been either absent or so infrequent that they were of no evolutionary consequence. As a result it might be expected that an understanding of the mechanisms which control the structure and composition of regeneration in natural gaps, might allow a greater manipulation of the regeneration in very large man-made gaps.

Studies of regeneration processes in natural gaps are also of relevance to forest managers, for a knowledge of the influence of gap characteristics on the floristics of the regenerating stand is essential to the successful operation of most silvicultural systems which rely on natural regeneration. Aspects of gap regeneration theory, particularly the notion that tree species differ in their ability to survive and grow in shady conditions, appear to be as old as the forestry profession. The historical outline of the development of silvicultural systems for Malayan forests given by Banard (1954), certainly suggests that the applicability of many aspects of gap regeneration theory to rainforest management, was appreciated at the beginning of this century.

Despite some early knowledge of rainforest dynamics, there were still some blind alleys to be trodden. For instance, in the forests of the Ivory Coast, Aubreville (1938) observed that there was little regeneration of the species which dominated the upper canopy. On this basis he suggested that the upper canopy of these forests might be made up of a mosaic of species associations and that the species within these associations were always replaced by different species from another association. While Richards (1952) provided some other examples which could be interpreted as supporting Aubreville's theory, most tropical ecologists would now accept that these patterns were probably the result of past catastrophic disturbances. The latter view is supported by evidence (Sauer 1958; Richards 1973) that most, if not all, the rainforests in Africa and South America have been affected by shifting cultivation. The patterns observed by Aubreville were most probably due to the replacement of long-lived "large gap" species (see Section 1.2) which had arisen following shifting cultivation, with species of greater shade tolerance.

Van Steenis (1958a and b) developed the gap regeneration theory further by observing that large gaps were invariably colonized by a small group of species he called "nomads" (van Steenis 1958b). He thought that once the "nomads" were established, "diffuse" regeneration of more shade tolerant species, the "dryads", would gradually take over. He also noted that fortuitous events could lead to the early establishment of shade tolerant species in large gaps (the "spotwise" process - van Steenis 1958a).

Gap regeneration theory has been considerably refined in recent years (e.g. Whitmore 1974; 1975; 1978; Rickleffs 1977; Hartshorn 1978; 1980; Denslow 1980b) and from the discussion in the previous section, it appears that this theory has as much to contribute to an explanation of the high species richness of tropical forests (see further discussion in Chapter 6) as it does to elucidate the mechanisms of regeneration. Further aspects of gap theory will be considered in subsequent chapters.

The recent development of several models of successional processes in rainforests has enabled profitable areas for further research to be more readily identified. The simple mathematical model of rainforest dynamics developed by Acevedo (1980) is based on the rate of light gap formation and the subsequent colonization rates of shade tolerant and intolerant classes of trees (Figure 18). Although Acevedo showed that his model could satisfactorily predict the overall composition of stands on Barro Colorado Island and at La Selva in Costa Rica, both these stands have probably been influenced by shifting agriculture. I suspect that wider applications of this model may be restricted by its simplicity. Obvious limitations were Acevedo's decision to allow only two classes of shade tolerance when in practice there appears to be a continuum (e.g. see Whitmore 1975) and his apparent failure to recognize the effects of gaps created by the deaths of shade intolerant species.
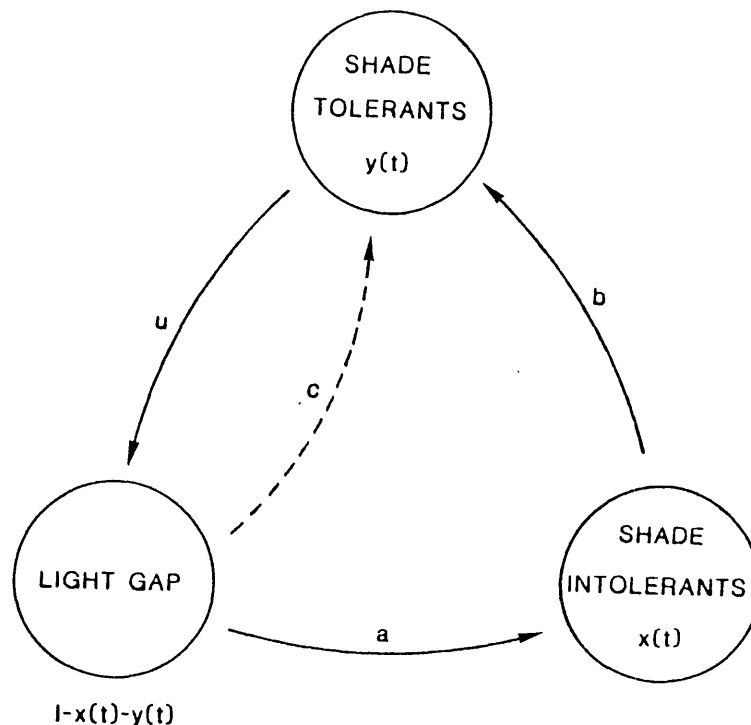

Figure 18. In the rainforest dynamics model of Acevedo (1980) the colonization rates of light gaps by shade intolerants and shade tolerants are represented by "a" and "c" respectively. "b" is the transition rate for shade intolerants to shade tolerants. At any time (t) the forest composition is given by the fractions x(t) (shade intolerants), y(t) (shade tolerants) and 1 - x(t) - y(t) (gaps). Acevedo suggested that "c" tends to be small when most light gaps are large.

Models which bring together the probability of a particular species establishing in an assemblage, with some characteristics of the regeneration, growth and mortality patterns of the component species, have been used to predict successional sequences in an Australian subtropical rainforest (Shugart et al. 1981a) and to study the role of disturbance in a montane rainforest in Costa Rica (Doyle 1981). The application of these models to stand prediction and questions of patterns and dynamics in forests was reviewed by Shugart et al. (1981b). They claimed that the Kiambram model (Shugart et al. 1981a) of succession in an Australian subtropical rainforest, could be verified from observations of successions in the same region by Webb et al. (1972) and Hopkins et al. (1977). They suggested that this model was validated by its ability to predict the abundances and basal areas of trees in Wiangree State Forest (the basic data were also from this forest) and that it would be useful for the evaluation of timber harvesting schemes in Australian subtropical rainforests.

In a broader context, Shugart et al. (1981b) noted that although certain species characteristics could greatly influence successional trends in assemblages where those species were important, there were some trends which were not simply a consequence of the component species. They also observed that computer models of succession form a basis of a theory of community dynamics that can be tested against observations, that can be manipulated to produce testable hypotheses, and that can provide long term predictions on assemblage behaviour.

Despite the variable quality of the autecological information used to operate models such as that of Shugart et al. (1981a), these models have produced quite plausible stand projections. Their value for forest management must increase with improvements in the quantity and quality of data relating to the dynamic characteristics of component species. The value, and enormity, of collecting information on all the species of interest in the tropics was commented upon by Gomes-Pompa and Vazques-Yanes (1981). They thought that the true nature of succession in the tropics would not become

apparent until the life cycles of important species were clearly understood.

2.3.3 Stability

In the popular literature it is often said that the existence of rainforests in many parts of the world is threatened because of the activities of man. The more emotive of these articles usually claim that rainforests are inherently very fragile and imply that minor incursions will sow the seeds of their destruction. The first statement is undoubtedly true. Some countries have already lost virtually all their rainforests. The social and economic situation in other countries is such that it appears inevitable that they will lose all their primary rainforests sooner or later. In other countries there is at least a chance that some rainforests will remain virtually untouched. This gloomy picture does not, however, mean that rainforests are inherently any more fragile than other assemblage types. It could just mean that man, having destroyed or replaced most of the world's temperate forests, is as a result of his experience and numbers, somewhat more efficient, and devastating, in extracting the resources of the tropics.

Unfortunately the word stability has been used in many different ways and measured by different assemblage functions or characteristics (Orians 1974). As a result the literature is confusing and at times apparently ambiguous. The widespread use of the term in zoological literature, where several trophic levels may be involved, does not make the topic any simpler.

The criteria used in evaluating stability have varied. Number of species, species diversity and species composition are the commonest but process measurements, such as aspects of nutrient cycling, have also been used. Recently the value of some of the process measures of stability have been questioned. For example Harcombe (1980) and Jordan and Herrera (1981) suggested that tight nutrient cycles may not be as important in rainforest stability as previously believed. It is also apparent that stability indicated by one criterion

does not necessarily mean that other assemblage features will be stable. For example, Brasell __et__ __al.__ (1980) compared aspects of the nutrient flow in an undisturbed rainforest with those in an adjacent Araucaria plantation. The great similarities observed between the systems suggested that since the rainforest was presumably stable, the Araucaria was also stable. In reality there is no chance that the Araucaria plantation could maintain itself in its present form for rainforest species make up an understorey which permit very few Araucaria seedlings to establish. Without human intervention, Araucaria would probably disappear from the site in a generation or two.

In considering stability Golley (1977) pointed out that there are problems of scale. He asked :-

> "What are the temporal and spatial scales used to
> determine persistence? And, what are the criteria
> used to determine equilibrium states of the
> community?"

The answer to the first question is that it depends on the observer's interest. Space can virtually vary from an establishment site for a seedling to a region; time from a few weeks (or even less) to hundreds of years. Thus we need to specify our temporal and spatial time frame in any discussion of stability. The second question can be answered more assertively, but first several aspects of stability must be recognized. In the sense of Lewontin (1969) they are :-

i) neighbourhood stability - concerning the ability of a system to return to the equilibrium point after a disturbance,

ii) global stability - systems converging towards one point from all other points,

iii) relative stability - measured by the magnitude of the perturbations required to disturb the system, the distance the system moves from the equilibrium and the time required to return to equilibrium.

There are two important aspects to relative stability :-

i) the resistance of a system to displacement,

ii) the resilience of a system i.e. its rate and direction of return to its original state.

It has been suggested by Webster, Alaide and Patler (in Golley 1977) that there is an inverse relationship between resistance and resilience.

Debate as to whether complex assemblages such as rainforests are more or less fragile than simpler systems has been confusing. Hutchinson (1959) suggested that stability of an assemblage increases as the number of links in its food chain increases. May (1974) took the view that in simple biological communities with only one trophic level, greater complexity in the form of more species more closely packed, made for less stability. May maintained that closer species packing was desirable from an evolutionary viewpoint, because it made far more efficient use of the resources available. However, it is very unlikely that niches can be narrowed indefinitely without loss of assemblage stability and in rainforests the complexity may not be created by a narrowing of niche widths but may be the result of a multitude of niche types and stochastic influences. May (1973) made another observation which is worth quoting :-

> "In nature we deal not with arbitrary complex systems, but rather with ones selected by a long and intricate process . . . What sets man-made monocultures aside is not so much their simplicity as their "unnaturalness", the community's lack of any significant evolutionary pedigree."

While this statement may be true, he obviously does not mean that natural assemblages have been stable throughout long periods of geological time. Natural adjustments through evolution, local extinction, migration and environmental change must have occurred without significant loss of stability. While niche width data for rainforest plants is generally lacking, Knight (1975) thought that the species he examined on Barro Colorado Island may have broader widths than temperate species. McNaughton (1978) found that highly diverse African grasslands were more stable than simple ones and suggested that both connectance and interaction strength[3]

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3. Nomenclature here follows Pimm (1984).

declined as diversity increased. Saunders (1976) also showed that the linear connectivity of complex tropical assemblages was low and thought that this accounted for their stability. Van Voris <u>et</u> <u>al.</u> (1980) however, maintained that their experimental evidence suggested that increasing functional complexity leads to increasing ecosystem stability.

The recent review by Pimm (1984) has done much to clarify complexity-stability questions. Pimm concluded that theoretically, the more species present in an assemblage :-

i) the less connected it should be, if it is to be stable,

ii) the less resilient will be its populations,

iii) the greater will be the change in species composition and biomass when a species is removed,

iv) the longer the persistence of species composition in the absence of species removal.

The more connected an assemblage :-

i) the fewer species it must have if it is to be stable,

ii) the more likely it is to lose other species if one is removed, but

iii) the more resilient will be its populations,

iv) the more persistent will be its populations,

v) the more resistant will be its biomass if a species is removed.

Pimm also concluded that progress in our understanding of the complexity and stability of assemblages will come from more theoretical and field studies, but is likely to come fastest when these studies consider questions which are both theoretically tractable and experimentally testable.

Despite the complexities of the largely theoretical arguments summarized by Pimm, a partial resolution of the practical problems of assessing stability might lie in studies of the mechanisms of succession, for both stability and

succession appear to be closely related and in a way stability could be viewed as a measure of the rate of succession.

Aspects of rainforest stability are discussed further in the last Chapter. At this point only one thing is certain and that is that the old idea of an ancient enduring tropical rainforest can no longer be upheld. The botanical research reviewed by Flenley (1979) (noted above) showed that the vegetation throughout the tropics was very different 4,000 to 7,000 years ago. Furthermore Flenley pointed out that for such changes to have been possible, the component species (which would have been present during this period of change) must have always acted in an individualistic rather than in a holistic manner.

In concluding this Chapter it is apparent that ecological research in Australia's tropical rainforests has only just begun. Although the ever-wet conditions of much of the equatorial zone are lacking, the region contains a wide range of forest types and enjoys socio-economic conditions which currently permit much of the rainforest resource to remain in a virgin state. Studies in the region's rainforests of the mechanisms responsible for the establishment and maintenance of diversity and stability, and the operation of succession, could contribute greatly to the theory and practice of tropical forest management. In Chapter 3 the floristics, structure and dynamics of rainforests in a series of plots are described in relation to environmental features. With planned continued measurement these plots will provide precise information on the recruitment, growth and mortality characteristics of the component species. These data are essential to the refinement and operation of successional models such as that used by Shugart et al. (1981a). In view of the importance of the regeneration strategies and establishment niche requirements of the available species in the mechanisms which seem to control diversity, succession and stability, Chapter 4 examines the establishment, survival and early growth of regeneration while Chapter 5 deals with aspects of propagule production, predation and germination. The final Chapter brings all these studies together.