

CHAPTER TWO

REVIEW OF LITERATURE AND STATEMENT OF OBJECTIVES

This review of literature has been undertaken to provide a framework of contemporary scientific knowledge within which to (a) design and carry out a series of studies and (b) evaluate, discuss and apply the results of these studies. It is structured around the two major themes of this thesis - **spatial** and **temporal** patterns in Australian dry rainforests.

I firstly define Australian dry seasonal rainforests and review their origins and affinities with seasonal rainforests in other continents. Secondly, I review the classificatory systems developed for Australian vegetation and rainforest in particular. These two sections provide the spatial framework for my studies.

I outline the history and results of studies in Australian dry rainforest communities, and then briefly review concepts relating to temporal processes in vegetation, with particular reference to Australian rainforests. Finally, I highlight the relative lack of knowledge of patterns and processes in dry seasonal rainforests, both in Australia and globally, and define my objectives and questions to be addressed in this thesis.

2.1 Australian “dry” rainforests - definition, origins and affinities.

2.1.1 A definition of “dry” rainforest.

The term "dry seasonal" or more simply "dry" rainforest is applied collectively to those communities in areas of relatively low and highly seasonal rainfall in eastern and northern Australia.

Species in these rainforests exhibit a range of adaptations to seasonal moisture stress, with deciduous or semi-deciduous species being particularly prominent. Smaller leaf sizes, sclerophylly, and prickles and thorns are also characteristic.

Dry rainforests include communities variously referred to as "monsoon forests, brigalow/softwood ("bottle-tree") scrubs, araucarian vine forests ("hoop pine scrubs") and the

deciduous and semi-evergreen vine thickets" (Gillison 1987), although these categories are not mutually exclusive.

2.1.2 Origins of Australian dry rainforests.

Australian dry seasonal rainforests are believed, in common with other Australian rainforests, to have evolved through climatic and edaphic sifting of a widespread palaeotropical rainforest flora that covered most of the Australian continent in the Late Cretaceous to early Tertiary period, 80-60 million years ago (80-60 Ma). At the time this concept was first put forward by Herbert (1932, 1935) and until relatively recently (e.g. Burbidge 1960), Australian rainforests were seen as comprising two (invasive) elements, the Indo-Malayan and the Antarctic elements, a view originating with Hooker (1860).

A contemporary interpretation of the development of Australian rainforests, based on palynological and (limited) macrofossil records, has been presented by Truswell (1990) (see below), who also concluded that no major influx of plant species occurred after contact with southeast Asia in the middle Miocene. Records appeared in fact to suggest that there have been sporadic interchanges between Australia and regions to the north since the Late Cretaceous - perhaps as early as 100 million years ago.

Four broad Australian vegetation systems were inferred by Truswell for the Eocene (58-37 Ma), with "complex rainforest," distinguished by a range of broad-leaved angiosperms and conifers, occupying lowland sites along the coast and in the Murray Basin, and "closed forest with *Nothofagus*" growing perhaps on better-drained areas, away from the lowlands.

Fossil information for the Oligocene (37-23.5 Ma) is confined to south-eastern Australia. There was considerable cooling during this period, which may have been associated with widespread drying. Truswell suggested that areas of *Nothofagus* increased, and there was a decrease in complex rainforest. She also suggested there existed extensive "swamp forests" in the Murray Basin, which may have been derived from the "complex rainforests" of the Eocene.

These Murray Basin swamp forests persisted into the Miocene (23.5-5 Ma). Forest with *Nothofagus* remained widespread in eastern Australia, extending into central Australia and also occurring in north-western Australia. There also appears to have been considerable variation

from region to region within the forests: in south-eastern Australia, for example, species of *Araucaria* and Myrtaceae were more abundant in inland areas than nearer the coast where *Nothofagus* was dominant (Truswell 1990)..

Considerable climatic fluctuations occurred during the Pliocene (5-1.3 Ma), which probably began with a warm, wet phase but later became drier and cooler. Open vegetation became more widespread. Fluctuations between rainforest and open vegetation were recorded at some sites, including Lake George, where the last rainforest phases occurred during the Early Pliocene (Singh and Geissler 1985).

By the beginning of the Pleistocene, Truswell asserted, rainforests had probably contracted to about their present area of distribution along the eastern fringe of Australia. During the Quaternary the extent and composition of rainforests were affected markedly by episodes of glaciation and associated drought and increased fire frequency. On the Atherton Tableland, for example, evidence from Lynch's Crater (Kershaw 1985) indicated that rainforests in the area were replaced by *Eucalyptus* forests between 34 000 and 26 000 years ago, which persisted until approximately 8 000 years ago, when fire frequencies declined and rainforests began to recolonize (Walker 1990). Supporting evidence has been provided by Hopkins, Ash, Graham, Head and Hewett (1993) from radiocarbon-dated charcoal samples.

Past climatic changes have also produced arid-adapted members of many rainforest genera, several of which are present in the more inland vine thickets (*Geijera parviflora*, *Ventilago viminalis*, *Owenia acidula*, *Atalaya hemiglauca*, *Parsonsia eucalyptophylla*). These species, most of which are tall shrubs and trees, occur widely in eucalypt and acacia woodlands and also are scattered emergents in many grasslands, for example the *Astrebla* wooded downs (Beadle 1981).

Gillison (1987) has drawn attention to the marked floristic and structural/physiognomic similarities between coastal vine thickets (littoral rainforest) and the inland communities. He proposed a common origin for these communities in the prograding coastlines of the Holocene and migrational pathways corresponding to the dry coastal corridors of Webb and Tracey (1981), but there is little evidence to support this theory (Adam 1992).

2.1.3 Affinities with seasonal rainforests in other continents.

One of the major difficulties in identifying analogous seasonal communities in other regions of the world lies in the definition of rainforest. As Gillison (1987) noted, many Australian "dry" rainforests are excluded from the accepted global (IUCN) definition of rainforest because of their relatively low heights and/or open canopies. Australian communities fall within categories ranging from "scrubland or thickets" to "mainly deciduous forests" (IUCN 1973). In contrast to the extensive literature on wetter rainforest communities, there is relatively little published data on the structure, composition and dynamics of the drier forms of seasonal rainforest (Murphy and Lugo 1986a). These latter categories have been largely ignored in recent reviews of African, American and southeast Asian rainforests (Hamilton 1989, Prance 1989, Whitmore 1989).

Structural/physiognomic classifications such as those of Beard (1944, 1955) and Webb (1959, 1968 and 1978a) (see 2.2.1.2 below) offer the most satisfactory basis for comparison between the rainforests of different continents. Beard (1967) compared Australian and African tropical vegetation types (omitting monsoon forests, however) and Webb *et al.* matched Australian rainforests with those of New Zealand, New Guinea and Thailand (Webb 1978b, Webb, Tracey and Williams 1976, 1985).

In his pioneering paper on the evolution of Australian plant communities, Herbert (1935) based his comparison of Australia and other southern hemisphere landmasses on climatic maps prepared by Thornthwaite (1933). These used a combination of two major indices, temperature efficiency (T-E) and precipitation effectiveness (P-E). The climatic regime occupied by brigalow communities (and associated vine thickets) (CB'w - subhumid, warm mesothermal, moisture deficit in winter) was matched in central and southern Africa (Kenya, Tanzania, Mozambique and Natal).

The floristic affinities between these regions and Australia were demonstrated by Webb and Tracey (1981). Nearly 20% of the Australian rainforest genera (103/545) also occur in Indomalesia, Africa and Madagascar.

Richards (1952) only briefly discussed seasonal rainforests, citing examples from Trinidad, Burma and West Africa. He drew a clear distinction between the evergreen seasonal rainforests (which he regarded as a subformation of the tropical rain forest formation-type) and semi-evergreen and deciduous seasonal forests, which were equivalent to the monsoon forest of Schimper (1903).

The review of tropical dry forest by Murphy and Lugo (1986a) drew on data from 18 study sites, including Kakadu/Kapalga in northern Australia. Most sites, such as Costa Rica, Mexico, northern Thailand, India, Sri Lanka, Nigeria and Ivory Coast, are north of the equator, and few receive less than 1000mm rainfall annually. Some areas have two wet seasons per year, compared with the single wet and dry seasons in northern Australia.

Swaine, Lieberman and Hall (1990) described the structure and dynamics of a dry forest community in Ghana, the most abundant tree species being *Diospyros abyssinica*, *D. mespiliformis*, *Millettia thonningii*, *Drypetes parvifolia* and *Vepris heterophylla*. Most species are evergreen except the emergents, for example *Ceiba pentandra*.

The main differences between West African dry forest and savanna vegetation (which are not always made clear in the literature) are the closed canopy, lack of a grass-dominated ground layer and different floristic composition (Swaine *et al.* 1990). Swaine *et al.* also noted marked physiognomic and floristic similarities between the Shai Hills forest and forest near Port Moresby, Papua New Guinea.

Semi-deciduous to deciduous woodlands and thickets occupy large areas in eastern Africa (the Zambezi floristic province of White (1983)). They include *Brachystegia - Julbernardia - Isoberlina* woodlands (miombo) and *Colophospermum mopane* woodlands (mopane). Miombo has a low (9-12m), relatively dense canopy (60-80% crown cover), has no grass layer and is not fire-resistant. Mopane is more open, with a denser grassy understorey. The dominants in these two communities rarely occur together and their associated floras are almost totally dissimilar (White 1983). These communities appear to bear more resemblance ecologically to tropical eucalypt woodlands than to Australian vine thickets.

White (1983) also described Zambezi dry deciduous forest (*Baikiaea plurijuga - Pterocarpus antunesii* forest) and dry scrub forest (*Adansonia digitata - Euphorbia conspicua*). Both communities have dense thicket-like understoreys. Boughey (1964) described a series of deciduous thickets on aeolian sands and sandstone in Northern Rhodesia (Zambia), which he concluded represented seral stages of dry deciduous forest types dominated by *Baikiaea plurijuga - Brachystegia spiciformis* and by *Entandrophragma caudatum* respectively. The thickets were the result of clearing and/or burning of the original seasonal forest communities.

In western Madagascar, the two most widespread types of primary vegetation are dry deciduous forest and deciduous thicket (White 1983). Eighty percent of the species are endemic, but many of the genera are also found in dry seasonal rainforest in Australia, for example *Diospyros*, *Hernandia*, *Grewia*, and *Terminalia*. Swollen-trunked trees are common and include *Adansonia* spp., *Gyrocarpus americanus* and *Bathiaea* spp..

Seasonal forests occur widely through Central America and northern South America, with deciduous forests represented in Venezuela, Brazil, Cuba, Trinidad (Beard 1944), Mexico, Costa Rica, Jamaica and Puerto Rico (Murphy and Lugo 1986a). Murphy and Lugo (1986b) described the structure and floristic composition of a subtropical dry (deciduous) forest on limestone in Guanica Forest, Puerto Rico. Major canopy species are *Gymnanthes lucida*, *Exostema caribaeum*, *Pisonia albida*, *Pictetia aculeata*, *Thouinia portoricensis*, *Coccoloba krugii* and *C. microstachya*. Genera shared with Australian dry rainforests include *Cassine*, *Erythroxylum*, *Pisonia* and *Zanthoxylum*.

In southeast Asia, as elsewhere, the drier deciduous forests and thickets have been generally overlooked in favour of the moist evergreen and semi-deciduous (wet monsoon) rainforests. Studies on deciduous forest in southern India have been reported by Sukumar, Dattaraja, Suresh, Radhakrishnan, Vasudeva, Nirmala and Joshi (1992) and Murali and Sukumar (1994). In common with other deciduous communities in this region, the understorey of this forest is dominated by grasses, viz. *Themeda triandra*.

Dittus (1977) compared species compositions of five Sri Lankan forests. The driest of these, Madhu (1270mm rainfall), was dominated by *Drypetes sepiaria*, and also included *Memecylon* spp., *Diospyros ebenum*, *Manilkara hexandra* and *Vitex pinnata*.

A recurrent theme in the discussion of seasonal forests of Asia and Africa has been the widespread replacement of these communities by disclimax woodlands and grasslands. Walter (1971), for example, considered most or all of the grassland in India to have been derived from seasonal or dry forest. The grassy understoreys in many of these communities would render them particularly vulnerable to damage from fire. Seasonal rainforests in Australia, on the other hand, have only a minor component of grasses or other graminoids.

2.2 Classificatory systems and frameworks for Australian rainforests.

Early writings on Australian rainforests refer to them as "brush", "jungles" or "scrub" - the latter term being applied also to other relatively dense plant communities such as mallee (*Eucalyptus* spp.) or brigalow (*Acacia harpophylla*) (the "bricklow scrub" of Leichhardt (1847)). They were recognised as distinct from the eucalypt-dominated forest and woodland vegetation, but little effort was made to differentiate between types except where certain commercially important species were predominant, such as hoop pine (*Araucaria cunninghamii*) and red cedar (*Toona ciliata*) (pine scrubs, cedar brushes). A notable exception was Mueller's (1858) recognition of "bottle-tree scrubs" as a subunit of brigalow vegetation "-- where *Delarbechea*, *Bauhinia* and *Brachychiton* prevail --".

Schimper's (1903) definitions of rainforest communities appear to have been overlooked or ignored by early Australian rainforest ecologists. For example, Fraser and Vickery (1938) in their studies of the Barrington Tops rainforests distinguished a subtropical rainforest type, regarded as a depauperate form of tropical ("Indo-Malaysian") rainforest, and an upland "subantarctic rainforest" (i.e. the *Nothofagus moorei* community). These categories were essentially those of Hooker (1860).

Adam (1992) reviewed the development of classificatory systems for Australian rainforests. These are derived from structural features, floristic composition or a combination of both structure and floristics.

2.2.1 Structural classifications

2.2.1.1 Structural/floristic approach

Beadle and Costin (1952) proposed a classification system based on structure and floristics, which was intended to provide a continental framework for ecological studies. They used structure to define major vegetation formations and subformations, which were by and large units which were in established use, for example sclerophyll forest and woodland. Within subformations, the various subdivisions (alliances and associations) were based on the floristics of the dominant stratum, rather than overall composition.

The basic unit was the association, defined as "a climax community of which the dominant stratum has a qualitatively uniform floristic composition and which exhibits a uniform structure"

(Beadle and Costin 1952). Associations were amalgamated into alliances, defined as groups of "floristically-related associations of similar structure" and then into subformations.

Rainforest in Australia was recognised by Beadle and Costin (1952) and Baur (1957) as a single formation, comprising four subformations; temperate rainforest, subtropical rainforest, tropical rainforest and dry rainforest. This classification was modified by Baur (1965) - Beadle and Costin's "subtropical rainforest" is now known as warm temperate rainforest and their "tropical rainforest" as subtropical rainforest. Five subformations are now recognised, tropical rainforest being regarded as a more luxuriant equivalent of subtropical rainforest that is found in tropical north-eastern Australia. This modified classification was used by Beadle (1981) in his treatment of Australian vegetation and by Floyd (1990) in studies of New South Wales rainforests.

The dry rainforest subformation (in New South Wales) was defined by Floyd (1990) as follows:

"Occurs where rainfall is low for rainforest development, with only 600-1 100 mm annually and a markedly dry spring. Two tree strata, the upper being scattered emergents such as *Araucaria cunninghamii*, *Brachychiton discolor* and *Flindersia australis*. The lower, dense main layer may contain 10 to 30 species. Leaves or leaflets are characteristically hard and small, usually less than 7.5 cm long. Woody vines are very common, and stranglers may be prevalent also. Other tropical features such as plank buttressing, palms and large epiphytes are rare, however. There is a well-developed, prickly shrub layer and very sparse herbaceous ground cover."

There are several perceived weaknesses of the Beadle and Costin classification, particularly in the definition of associations. The presumption of climax state in stands and the difficulty of defining species associations (or equating stands to recognised associations) in all but the simplest rainforest types are probably the major practical limitations. Another point of criticism is the incongruence of climatically-named subformations frequently occurring in close proximity, for example subtropical, warm temperate and cool temperate rainforest on the Dorrigo Plateau.

The nomenclature aside, Floyd (1990) pointed out the detailed correlation between the subformations and the structural-physiognomic units proposed by Webb (see 2.2.1.2 below). The relative simplicity and established usage of the existing names are a major reason for their continued acceptance.

Floyd (1990) acknowledged the difficulties of defining species associations in rainforest communities, and favoured the term "suballiance" as used by Beadle (1981), because it "permits the absence of some of the key species with the exception of the alliance key species."

The dry rainforest subformation includes considerable structural variation. Floyd (1990) noted that the taller forests are sometimes referred to as "monsoon forest" while the lower stands have been variously called "dry scrub", "vine thicket" or "softwood scrub"

Floyd also expressed some concern about the classification of the littoral rainforests. These communities are placed within the subtropical rainforest subformation, with which they share most of their species. Structurally and physiognomically, however, littoral rainforests have more in common with dry rainforests (cf. Gillison 1987).

Floyd (1990) proposed 4 alliances within New South Wales dry rainforests:

1. *Drypetes - Araucaria* (3 suballiances)
2. *Waterhousea - Castanospermum* (3 suballiances)
3. *Choricarpia - Backhousia* (4 suballiances)
4. Vine thickets (2 suballiances).

This is a more conservative approach than that of Beadle (1981), who defined 10 alliances within the vine thickets and other related semi-arid communities, concluding that they "are difficult to classify, but are regarded as climaxes." However, it should be noted that Beadle was reviewing a much larger region (Australia) than Floyd and that several of Beadles's alliances (see below) do not occur in New South Wales.

1. *Cadellia pentastylis* alliance
2. *Brachychiton* spp. alliance
 - (i) *Brachychiton rupestris* suballiance
 - (ii) *Brachychiton australis* suballiance
 - (iii) *Brachychiton grandiflorus* suballiance
3. Mixed stands
4. *Erythrophleum chlorostachys* alliance
5. *Adansonia gregorii* alliance

6. *Terminalia - Lysiphyllum cunninghamii* alliance

(i) *Terminalia* spp. suballiance

(ii) *Lysiphyllum cunninghamii* suballiance

7. *Macropteranthes* spp. alliance

8. *Excoecaria parvifolia* alliance

9. *Geijera parviflora - Flindersia maculosa - Alectryon oleifolius* alliance

10. *Atalaya hemiglauca - Grevillea striata - Ventilago viminalis* alliance

2.2.1.2 Structural/physiognomic approach.

An alternative classificatory scheme for rainforest, based on both structural and physiognomic features, has been developed by Webb (1959, 1968, 1978a). He has argued that this approach may be more appropriate than floristics for developing a framework for Australian rainforests. There are major problems with floristic sampling and identification. Structural/physiognomic characters may be applicable over wider geographical areas and have the advantage that they can be recorded rapidly by workers lacking taxonomic expertise.

As noted above, Schimper (1903) and other early workers recognised that there were recurrent patterns of variation in physiognomic/structural features that could be correlated with environmental conditions, and their importance for rainforest classification were emphasised by Richards, Tansley and Watt (1940) and by Beard (1955).

Four categories of structural/physiognomic features were utilised by Webb (Webb 1978a):

(i) height and depth of canopy closure (prominence of different tree storeys or layers, evenness of canopy surface, presence and type of emergents, regularity of distribution of trunks of upper canopy trees, crown shapes, vertical extension of crowns in relation to length of trunks, etc.);

(ii) leaves (size, shape, texture, periodicity of leaf-fall, etc.);

(iii) trunks (texture and colour of bark, extent of covering by epiphytes, cauliflory, stilt roots, buttresses, spreading surface roots, club-like base, etc.);

(iv) special life-forms or growth forms (types of palm-like, fern-like, pandan-like, banana-like, bamboo-like, grass-like plants; stranglers; banyans; thorns, prickles and hooks; robust, slender and wiry vines; types of epiphytes and their vertical extension, etc.).

These features were discussed in detail by Webb, Tracey and Williams (1976) who provided a *pro forma* for field use. The prominence of each feature is scored on a four-point scale, and these data can be subject to numerical analysis. Webb, Tracey, Williams and Lance (1970) acknowledged, however that scores for particular features could vary according to the field experience of the recorder(s).

Leaf size classes are based on those of Raunkiaer (1934). Only tree species are assessed, and sizes should be determined from sun leaves. Stocker and Unwin (1989) have warned that cursory assessment of leaf size can be quite deceptive and Walker and Hopkins (1984) recommended that estimates should be standardised by collecting sun leaves from ten adjacent canopy trees.

Webb (1959) recognised three formations within Australian rainforests: tropical, subtropical and temperate (including cool and warm facies). Using structural and physiognomic features, he defined twelve rainforest subformations and provided a key for field recognition.

Webb's (1968) paper on the environmental relationships of Australian rainforests (see 2.2.2 below) recognised 20 structural types, seven of which may also have araucarian emergents. The term "mixed" was introduced for certain types of intermediate structural complexity, and seasonal mesophyll/notophyll communities were classed as "semi-deciduous" (rather than semi-evergreen).

Further modifications have been made to the classification and Webb (1978a) published a field key to the currently accepted Australian rainforest types. This is included as **Appendix 1**. Categories represented in dry rainforests include **low microphyll vine forest (LMVF)**, **araucarian microphyll vine forest (AMVF)**, **semi-evergreen vine thicket (SEVT)** and **deciduous vine thicket (DVT)**.

The unfamiliarity and relative complexity of the concepts and terminology introduced in Webb's classification have no doubt delayed its acceptance into general usage. Some confusion and resistance may also have arisen because of the considerable differences between successive early published versions of the classification (Webb 1959, 1968).

At the formation or subformation level it is possible to match most previously recognised rainforest categories with structural/physiognomic units (Floyd 1990, Winter, Atherton, Bell and Pahl 1987). The classification has been applied successfully in rainforest in New Zealand, New Guinea and Thailand (Webb 1978b, Webb *et al.* 1976, 1985).

2.2.1.3 Other structural classifications.

The most widely used vegetation classification in Australia during the past two decades has been the scheme developed by Specht (1970, 1981), which uses two structural categories, the projective foliage cover of the tallest stratum and the life-form and height of the tallest stratum.

There are several problems in applying this classification (Adam 1992). Objective measurement of projective foliage cover is extremely time-consuming, and most field botanists use a quick visual estimate which probably approximates canopy cover. In communities with deciduous canopy species, where part or all of the foliage is lost during the dry season, canopy cover would be a more appropriate measure.

There are also problems in defining the tallest stratum, for example at what density does *Araucaria cunninghamii* cease to be regarded as an emergent over closed-forest and become an open-woodland with a closed understorey? Walker and Hopkins (1984) (see below) set a limit of 5% canopy cover for emergents. An alternative approach is to choose the predominant, rather than the tallest, stratum (e.g. McDonald and Whiteman 1979).

The choice of height as the primary attribute for classification may also result in a failure to discriminate between rainforest communities of quite dissimilar structure and species composition. It may also result in artificial separation of very similar communities into, for example, tall closed-forests and (medium) closed-forest.

The structural classification proposed by Walker and Hopkins (1984) is based essentially upon that of Specht, but differs in using crown cover rather than projective foliage cover. It also includes a greater number of height classes and treats rainforest separately from other vegetation types in incorporating structural/physiognomic features (complexity, leaf size, floristic composition of the tallest stratum and indicator growth forms) (after Webb *et al.* 1976).

2.2.2 Floristic classifications

Webb, Tracey, Williams and Lance (1967a, b) explored the use of detailed floristic site lists in rainforest classification. They analysed data (18 sites X 818 species) from north-eastern Queensland and Cape York, using monothetic divisive and agglomerative polythetic classifications and Gower (PCoA) ordination. They found that the floristic classification closely reflected environmental factors, but there was only partial agreement between the floristic classification and the structural/physiognomic groups.

Webb *et al.* (1967b) also used various subsets of the floristic data and found that use of only the large tree species (269 species) gave exactly the same result as the full data set classification. Moreover, reduction of the data set to 65 species (by removing those which occurred at one site, for example) still allowed the major floristic divisions to be recovered. A similar result was obtained with the liane subset.

Webb *et al.* (1967a, b) suggested from these results that the rainforests comprise two vertically integrated elements. The canopy element (big trees, large vines and possibly vascular epiphytes) responds to the macroclimate and defines the floristic structure of the forest. The second element (the understorey plants) is buffered from the macroclimate by the canopy and the distribution of these species is more a reflection of edaphic factors and local disturbance history.

Because of the large proportion of single-site species in their data set, Webb *et al.* (1967b) concluded that floristic classifications (which generally used symmetrical methods) would be increasingly dominated by patterns of joint absences rather than joint occurrences of species. Floristic inventories, even if sampling was confined to the large trees, would involve collecting much unnecessary data and Webb *et al.* (1967b) suggested that a physiognomic/structural approach would be preferable for regional classifications.

Adam (1992) pointed out that the number of sites in this study (18) was insufficient to develop a practical regional classification and that numerical approaches to classification were only beginning to be developed at the time this research was undertaken. The disadvantages cited for agglomerative classification and ordination no longer apply with modern computing systems, although multi-dimensional scaling (see **Chapter 3**) may still require up to 15 minutes per ordination (5 dimensions) with a personal computer.

Williams, Lance, Webb and Tracey (1973) undertook subsequent studies on the use of quantitative data and the effect of plot size in differentiating between complex rainforest on basalt and structurally and floristically simple rainforest on rhyolite on the Nightcap Range in northern New South Wales. Their results suggested that the optimal sampling unit was a relatively large quadrat (0.1 ha) for which all trees were recorded. They also found that presence/absence data were as effective as quantitative data in determining the major patterns.

Because of the effort involved in collecting species data from large plots, Williams *et al.* (1973) recommended plotless sampling, recording a group of 20 or 25 contiguous trees. This approach (the “point clump” method) was shown by Williams, Lance, Webb, Tracey and Connell (1969) to be superior to plot sampling, and has been adopted in the present study (see 3.3.3).

Williams and Tracey (1984) successfully analysed a relatively large presence/absence data set (146 sites X 740 tree species) from north-eastern Queensland, using two-neighbour network analysis. The nineteen groups agreed closely with structural/physiognomic groupings recognised intuitively by Tracey and Webb (1975) and Tracey (1982).

Two recent studies of seasonal rainforest in northern Australia (see section 2.3.1) have involved the classification of large floristic (presence/absence) data sets. Russell-Smith (1991), in his study of Northern Territory rainforests, undertook a divisive classification (TWINSPAN) of a data set of 1219 sites X 559 taxa, deriving 16 floristic assemblages, while Kenneally, Keighery and Hyland (1991) used an agglomerative procedure to analyse data from 99 Kimberley sites.

Busby (1984) used a semi-quantitative floristic approach (Zurich-Montpellier method, see Mueller-Dombois and Ellenberg (1974)) in his classification of *Nothofagus cunninghamii* vegetation on Victoria and Tasmania. Agreement between floristic groups and structural forms was poor. Adam (1992) suggested that the relative low species diversity of woody plants in these rainforests compared with other rainforest types may be a reason why a phytosociological approach was successful. He concluded that although this approach could in theory be applicable to all rainforest types, the difficulties of recording total floristics and the complexity of the resulting data matrices would probably preclude its adoption.

2.2.2.1 A floristic framework for Australian rainforests

The first general floristic analysis of Australian rainforests by numerical methods was based on presence/absence data for 1147 tree species from 265 sites, mainly in eastern Australia. The results were discussed by Webb and Tracey (1981a). A second more comprehensive classification, using 1316 species from 561 sites, including some in northern and north-western Australia, was reported by Webb, Tracey and Williams (1984). At the highest level of the classification, three groups of sites were recognised as ecofloristic regions, which comprised in turn eight subgroups, known as ecofloristic provinces.

Webb *et al.* (1984) noted that these groupings, established from sampling different rainforest communities in particular habitats, differ from those in classical floristic geography in which the boundaries of units are derived from the geographic limits of combinations of species with approximately similar ranges.

The three site-groups making up the ecofloristic regions are more or less distinct geographically (see **Figure 2.1**, after Webb and Tracey 1994). Region A comprises temperate (microtherm) and subtropical (mesotherm) humid evergreen rainforests, region B tropical (megatherm) humid evergreen grading into highly seasonal raingreen (monsoon) forests and region C subtropical (mesotherm) moderately seasonal humid/subhumid raingreen forests.

The ecofloristic provinces, while having definable geographic ranges, may overlap considerably, both latitudinally and altitudinally. Webb *et al.* (1984) considered their provinces to be equivalent to the "class" level in the classical phytosociological (Zurich-Montpelier) hierarchy, but Adam (1992) commented that it would be difficult to make formal diagnoses because of the qualitative nature of the original data and the differences in sampling strategies between sites.

Webb *et al.* (1984) recognised three provinces within region A, three within region B and two in region C. Core areas (i.e. the densest and most characteristic aggregation of sites) were identified for each province. Floristic elements (and their diagnostic species) were identified within the provinces and related to structural types and climatic/edaphic factors.

The dry seasonal rainforest sites fell into two main groups, tropical northern Australia (province B₃) and subtropical eastern Australia (province C₂).

Province B_3 (regarded as a drier version of B_1) occurs across the Kimberley, Northern Territory and Cape York. Because of the extensive, patchy distribution, the concept of core areas was considered meaningless in this province. There are three main categories of habitat; coastal sands, alluvia along semi-permanent creeks and fire-proof bouldery outcrops and gullies in drier subcoastal sites (Webb *et al.* 1984). Floristic elements, all representing deciduous vine thicket, were described for each habitat on Cape York.

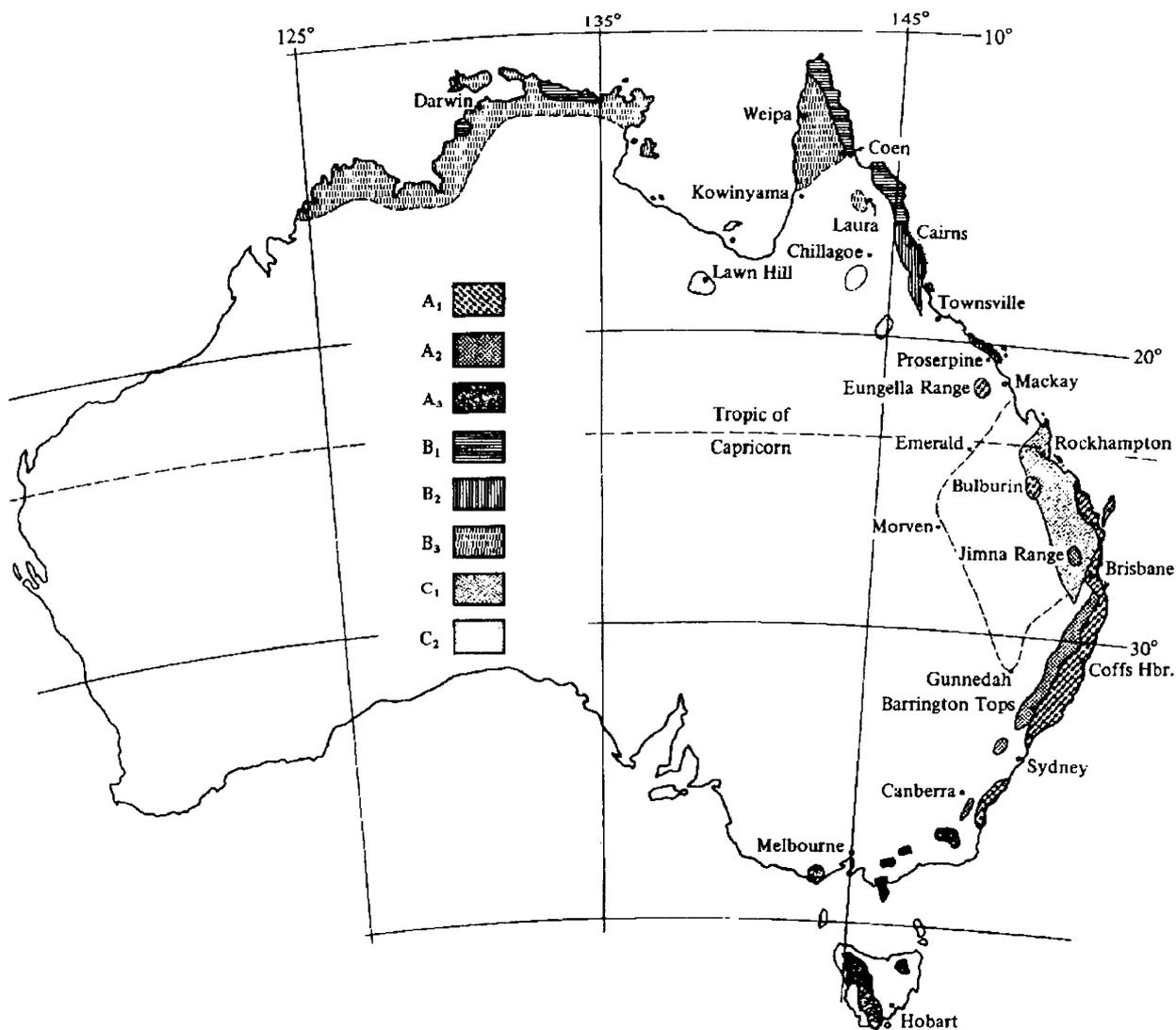


Figure 2.1 Distribution of floristic regions and provinces of Australian rainforests (after Webb and Tracey 1994)

Province C_2 was described as follows: "The core area is between Boonah and Biloela in subcoastal south and central Queensland, generally on soils from basic igneous rocks or calcareous sediments, but now practically all cleared:

(Indicator species are) *Alectryon connatus*, *Alstonia constricta*, *Atalaya salicifolia*, *Backhousia angustifolia*, *Brachychiton australis*, *B. rupestris*, *Cadellia pentastylis*, *Croton insularis*, *Ficus platypoda*, *Flindersia collina*.

In central Queensland - - - outliers mainly on limestones also link this province with C₁. All the elements represent semi-evergreen vine thickets, which have stunted *Araucaria cunninghamii* emergents towards the C₁ overlap.

In addition there are scattered outliers of deciduous vine thickets on limestone in the North Queensland hinterland, and of semi-evergreen vine thicket in drier areas further inland (i.e. Morven) in south Queensland and northern New South Wales (e.g. Gunnedah)" (Webb *et al.* 1984).

Although Webb *et al.* (1984) made reference (see above) to floristic elements within the C₂ province, all representing semi-evergreen vine thicket, they provided no descriptions of these elements, in contrast to those recognised within province B₃.

2.2.3 Environmental relationships of Australian rainforests

The influence of climate and other environmental factors such as soils in determining the distribution of Australian rainforest communities was recognised more than 60 years ago by Herbert (1935). He identified (Herbert 1960) three major environmental variables; temperature (altitudinal or latitudinal), rainfall and variations in soil conditions.

On the basis of the close correlation between structural/physiognomic features and climate and edaphic factors, Webb (1968) defined, and provided a field key to, habitat types associated with the structural types. Changes in rainforest structure along moisture and temperature gradients were also illustrated, for example see **Figure 2.2** .

It was noted by Webb (1968, 1969) that at the climatic extremes of rainforest distribution (tropical monsoonal and cool temperate rainforest for example) soil nutrients are far less critical than climatic and topographic factors. Stocker and Unwin (1989) have also suggested that relationships between soil and rainforest structure in the Wet Tropics may not be as clear cut as indicated by Webb. Adam (1992) commented that there was little measured data available to test these concepts, although Turner and Kelly (1981) showed significant differences in the chemistry of soils under complex notophyll vine forest (on basalt) and those under simple notophyll evergreen vine forest (on rhyolite) on the Nightcap Range in northern New South Wales.

Ceratopetalum apetalum (the dominant in SNEVF above) is one of a suite of rainforest species which are well-adapted to nutrient-poor sites, but in the absence of competition from

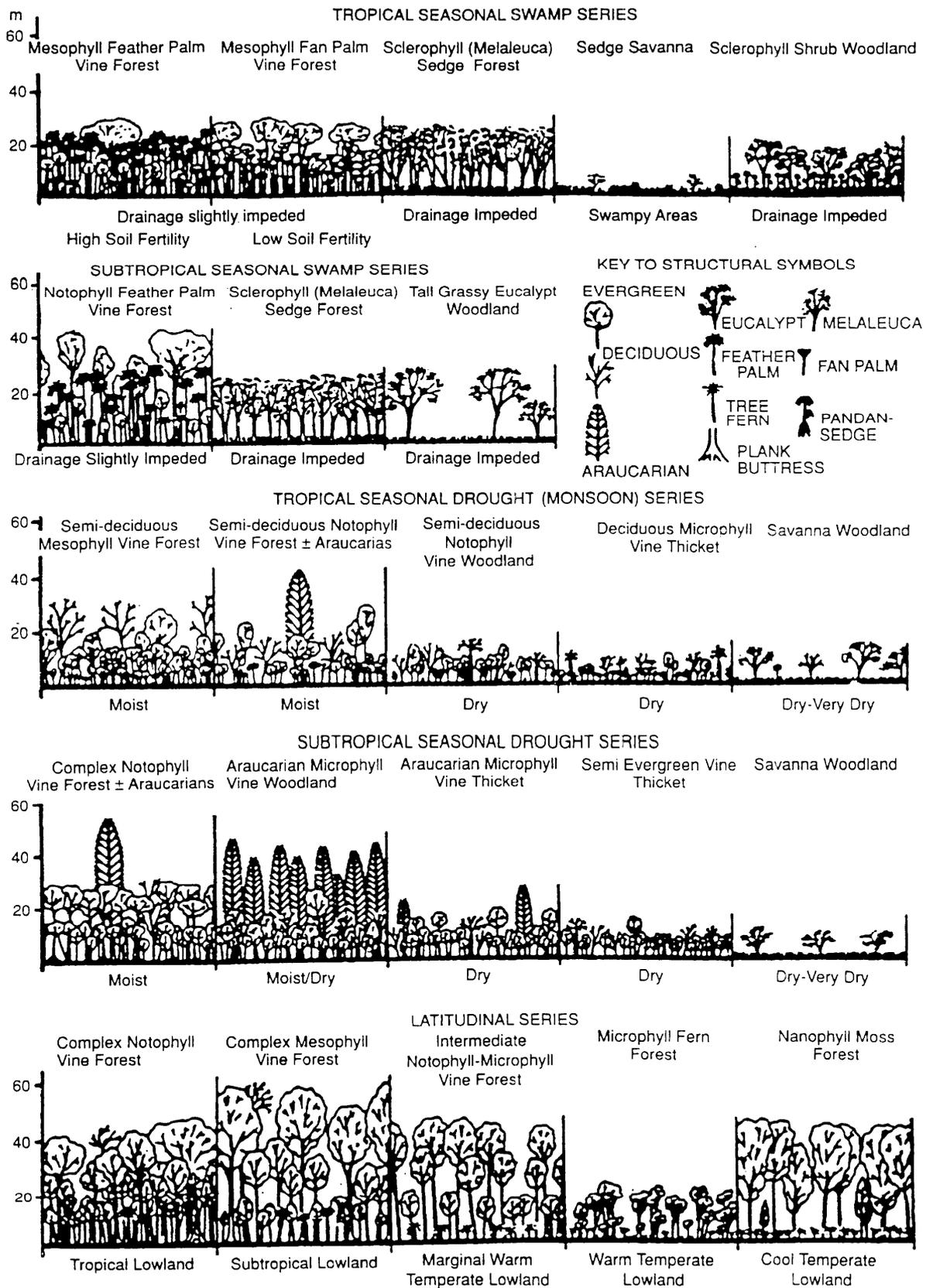


Figure 2.2 Structural changes in rainforest along different environmental gradients (after Webb 1968).

subtropical (CNVF) species, it forms an association on basalt at Mt Wilson and Robertson (McLuckie and Petrie 1927, Mills 1987).

Tracey (1969) classified soil physical data and lists of canopy trees from 49 forest sites (including 32 vine forest sites) throughout eastern Australia. Floristic groups were correlated with geographic and climatic regions rather than with soil groupings.

Relationships between climate and rainforest structure and floristic composition were further explored by Nix (1991), using the Webb *et al.* (1984) data base with some additional sites from southern New South Wales and Tasmania (matrix of 644 sites X 1422 species). For each site a series of twelve bioclimatic indices (6 temperature, 6 precipitation) was generated from the BIOCLIM [ystem (Busby 1991) (see also **Chapter 3**). The analyses also attempted to take soil nutrient status into account, with parent material given a potential plant nutrient supply rating on a 0-10 scale.

The analysis of structural classes produced 8 primary rainforest types within three main groups, megatherm, mesotherm and microtherm. Subdivisions within the first two groups reflected firstly water regime and then nutrient regimes, while the subdivision within the microtherm group reflected significantly lower temperatures. Nix used bioclimatic profiles for each group to generate maps of potential distributions.

The results of the analysis (see below) generally supported the structural/physiognomic typology of Webb (1958, 1968) (structural abbreviations follow Webb 1968).

(Megatherm)

1. Evergreen mesophyll vine forest (CMVF, MVF)
2. Semi-deciduous notophyll/mesophyll vine forest (SDMVF, SDNVF)
3. Deciduous microphyll vine thicket (DVT, SSENVF, SSENVT)

(Mesotherm)

4. Evergreen notophyll vine forest (CNVF, NVF, SNEVF)
5. Evergreen notophyll/microphyll vine forest (ANVF, AMVF, LMVF)
6. Semi-evergreen microphyll vine thicket (SEVT)

(Microtherm)

7. Evergreen microphyll fern forest (MFF)
8. Evergreen microphyll/nanophyll mossy forest (MMF, NMT)

Group 3 occurs across northern Australia as a series of isolates. The deciduous vine thickets have a lower rainfall regime, whereas the semi-evergreen communities (SSENVF/T) occur on sites with a much lower nutrient supply rating than DVT.

Group 6 comprises a single Webb category, semi-evergreen vine thicket, which occurs on soils of high nutrient status under relatively low rainfall conditions.. Nix found close floristic affinities between this group and the moister seasonal subtropical communities of group 5 (araucarian notophyll and microphyll vine forest and low microphyll vine forest). He drew attention to the marked climatic differences and lack of shared taxa between SEVT and DVT (group 3), which Webb *et al.* (1984) had regarded as closely related .

2.3 Studies in Australian dry seasonal rainforest communities.

This review is organised into two geographic sections, corresponding to floristic provinces defined by Webb *et al.* (1984) (a) northern Australia (the Kimberleys, Northern Territory and Cape York) (provinces B₁ and B₃) and (b) eastern (tropical (excluding Cape York) and subtropical) Australia (province C₂).

2.3.1 Northern Australia

Early studies in this region (and the Northern Territory in particular) were reviewed by Dunlop and Webb (1991). Blake (1953) referred to small rainforest patches (locally known as "jungles") as monsoon forests, and identified five types of habitat (on spring-fed creeks, on levees, in open forest, on rocky outcrops and behind coastal foredunes). Specht (1958) noted that monsoon forest grew on a variety of substrates provided moisture levels were high and identified seven habitat types. He considered that the moist habitats near swamps and streams supported a more mesophytic community (cf. evergreen rainforest).

These early surveys also identified woodland communities with an upper stratum of *Eucalyptus* species (the monsoon woodland of Gardiner (1942), the "deciduous low mixed open forest" of Blake (1953)), which had understoreys of broad-leaved deciduous species with affinities to the monsoon forests. CSIRO studies in the Kimberley region described similar mixed communities and also communities dominated by broad-leaved deciduous species, but at this time monsoon

forests equivalent to those described by Blake and Specht had not been recorded (although references were made to "jungle" north of Broome by Brockman in 1888 (McKenzie 1991)). The first accounts of rainforest in the Kimberley region were published by Miles and Burbidge (1975) (Prince Regent River) and Beard (1976) (the Mitchell plateau).

Story (1969, 1976) in surveys of the Alligator and Adelaide Rivers areas distinguished both rainforest (unbroken canopy, evergreen, to 25m high) and "semi-deciduous forest" or monsoon forest (broken canopy, up to 12m high).

Stocker and Hyland (1981) briefly described floristic assemblages in the deciduous monsoon forests ("semi-evergreen vine forests") of northern Australia.. They concluded "the communities cannot be regarded as a distinctive alliance comparable to the eastern stands."

Summary papers on the monsoon rainforests of northern Australia were prepared by Kenneally and Beard (1987) (Kimberley region) and by Russell-Smith and Dunlop (1987) (Northern Territory).

Under the National Rainforest Conservation Program during the late 1980s, detailed floristic surveys of monsoon forests were undertaken in the Northern Territory (1219 sites X 559 rainforest taxa) (Russell-Smith 1991) and in the Kimberleys (99 sites X 453 species) (Kenneally, Keighery and Hyland 1991).

Russell-Smith grouped the NT sites into 16 floristic assemblages using a polythetic divisive procedure (TWINSPAN) and detrended correspondence analysis (DCA) ordination. Eight groups comprised perennially moist sites, while the other eight groups were associated with seasonally dry landforms (included in this latter group, however, were sites associated with small springs and seepages in southern inland regions). Two major environmental gradients were identified; a primary latitudinal-moisture gradient and a secondary topographic-drainage gradient.

In the second tier of Russell-Smith's classification, the perennially moist sites were further divided into those associated typically with lowland floodplains and limestone formations (the "basic" sites) and those associated with sandstone formations (the "acidic" sites). The seasonally dry sites were divided into northern ("coastal/subcoastal") and southern communities ("inland"). The latter communities included semi-deciduous/deciduous rainforests and thickets on sandstone and

limestone outcrops and deep coastal calcareous sands (group 12) and deciduous vine thickets on talus slopes derived from sandstone and basalt and (less frequently) limestone (group 14). Both these groups extend south-east around the Gulf of Carpentaria.

Included in Russell-Smith's group 16 were a series of sites in low closed vegetation on residual (lateritic) land surfaces. The canopy is commonly dominated by lancewood (*Acacia shirleyi*) and/or bullwaddy (*Macropteranthes kekwickii*). The latter community covers more than 5000 km² (Wilson, Brocklehurst, Clark and Dickinson 1990). Whilst most of this vegetation could not be considered to be vine thicket, Russell-Smith noted that in certain situations the community contained many typically vine thicket species.

Russell-Smith also related his classification to the floristic groups ("ecofloristic provinces") defined by Webb *et al.* (1984). They placed Northern Territory rainforests mostly within provinces B₁ and B₃ and these do encompass most of the groups defined by Russell-Smith (i.e. groups 3-7 and 13 correspond with ecofloristic province B₁ and groups 8-12 and 14-16 with province B₃). Russell-Smith suggested that the deciduous vine thickets (groups 14-16) could equally represent a northern extension of province C₂. The affinities of the remaining groups (1-2, the "basic" sites) were considered by Russell-Smith to lie with province B₂.

Russell-Smith experienced difficulties in applying Webb's physiognomic-structural typology in many rainforest stands. Inconsistencies arose in the use of leaf size characters and also in applying the terms evergreen, semi-evergreen, semi-deciduous and deciduous.

The results of the Kimberley rainforest survey and analysis (Kenneally *et al.* 1991) agreed in many respects with those of the Northern Territory survey. In both studies, species richness was generally limited by size of each rainforest patch.

The Kimberley sites were classified on the basis of their perennial plant species, using a clustering procedure. Two major groups of sites were again distinguished, slope thickets (equivalent to Russell-Smith's seasonally dry sites) and riverine/swamp forests (i.e. perennially moist sites).

The slope patches further segregated on locality, size and soil-type (viz. Holocene dune sites and Tertiary surfaces), whereas the riverine/swamp communities segregated on site characteristics (gorges, swamps, riverine banks) and geographical locality.

In all, eighteen site groups were distinguished, of which nine represented single sites. The largest group (group 2) contained 41 sites, comprising the major rainforest patches on a variety of soils ranging from laterite to basalt and sandstone.

Only one rainforest species (the shrub *Hibiscus peralbus*) is endemic to the Kimberleys. Kenneally *et al.* (1991) commented on the general trend across the rainforests of northern Australia (the "Top End") of high taxonomic diversity of families and genera but low species-level diversity.

Affinities were discussed by Russell-Smith (1991) and Kenneally *et al.* (1991), who concluded that the monsoon rainforests form a floristic continuum across northern Australia. Many species have fleshy fruits adapted for bird or bat dispersal (see below) and rainforest patches can become established wherever suitable habitats are available. The concept of the monsoon rainforests as relictual (Webb and Tracey 1981) was challenged by Russell-Smith. Much rainforest is of Recent origin (the many patches on Holocene landforms, for example) and Russell-Smith posed the fundamental question: why is the distribution of rainforest so restricted? He considered this might be a result of past climates, particularly the Pliocene-Pleistocene aridity, combined with the effects of fire and the impact of burning practices by Aboriginal people over at least the past 60 000 years.

During the Northern Territory survey, plant population data were recorded in 394 mostly small rainforest patches. Russell-Smith and Lee (1992) reported that only 20% of common rainforest species typically occurred in populations of more than 50 adults per patch. Species with small populations are characteristically tree species with fruit which are dispersed by birds or bats, and it was suggested that significant gene flow occurs between rainforest patches.

Aspects of the ecology of monsoon rainforest communities including successional trends and the influence of fire, have been studied by Stocker (1971), Bowman and Dunlop (1986), Bowman (1991a, b, 1992) and Bowman, Wilson and McDonough (1991).

In a review of the conservation status of Northern Territory rainforests, Russell-Smith and Bowman (1992) concluded that most damage to vine thicket patches was attributable to inadequately controlled fires and introduced livestock, often in combination.

Liddle, Russell-Smith, Brock, Leach and Connors (1994) published distribution maps for 604 species of Northern Territory rainforest plants. The maps were based on herbarium records and

data from the 1219 sites surveyed by Russell-Smith, plus a further 25 sites on Tiwi (Melville) Island (Fensham and Woinarski 1992). Extra-regional distributional data were summarised, showing strong floristic connections with a broad region from Africa to the Pacific, but particularly the Indo-Malesian region.

As yet there are no comprehensive published accounts of the monsoon rainforests of northern Queensland, although a National Rainforest Conservation Program-funded survey of the Cape York Peninsula rainforests was completed recently by Stanton and Fell (QDE unpublished data). Pedley and Isbell (1971) mapped the rainforests of Cape York at 1:2 000 000 scale, and their report contained a brief description of Peninsula rainforests by L.J. Webb.

Lavarack and Godwin (1987) divided the Peninsula into seven regions and reviewed the distribution and status of rainforest in each. Cape York has a strongly monsoonal climate and all the rainforests are seasonal to some degree. Of particular relevance to the present discussion are the drier communities, the semi-deciduous and deciduous notophyll/microphyll vine forests and thickets. These are represented in three regions in particular;

Region 1. Iron Range-McIlwraith Range

Region 5. Rainforests of the western sand dunes

Region 7. Mid-Peninsula vine forests.

In the Iron Range/McIlwraith area, deciduous vine thicket occurs on the western slopes of the McIlwraith Range near Coen and in small patches in the Pascoe River headwaters south and west of Tozers Gap. This community typically occupies steep rocky hillsides with shallow soils, and characteristic species include *Cochlospermum gillivraei*, *Bombax ceiba* and *Brachychiton* spp..

A narrow band of sand dunes (up to 20km wide in the south) lines the Gulf of Carpentaria coast. The siliceous sands are frequently enriched with shell material and the water table is usually close to the surface. The rainforest may be divided into two areas - those of the Mapoon Plain (north of Weipa) and those of the Karumba Plain (south of Weipa). Lavarack and Godwin (1987) found the Mapoon Plain rainforests hard to classify according to the Webb system, but concluded that they probably best fitted into simple semi-evergreen notophyll vine forest and thicket.

The Karumba Plain has a lower rainfall and the community is classed as deciduous vine thicket. Deciduous and semi-deciduous canopy species include *Bombax ceiba*, *Cochlospermum*

gillivraei, *Sterculia quadrifida*, *Gyrocarpus americanus* and *Terminalia* spp..

Scattered patches of (?semi-deciduous) notophyll vine forest occur on deep red earths derived from laterite or bauxite in the area between Weipa, Moreton and the Jardine River. Lavarack and Godwin (1987) suggested that these patches may represent relict areas.

The significance of fire and changes in burning regimes following European settlement were also discussed by Lavarack and Godwin, who pointed to evidence, particularly on the east coast, of rainforest boundaries expanding. Bowman and Fensham (1991) undertook transect studies across a monsoon forest boundary near Weipa and noted the development after 15 years' fire protection of an ecotone with a shrub layer dominated by seedlings of monsoon forest species.

2.3.2 Eastern Australia.

The vine thicket communities of the brigalow region were first documented by Mitchell (1848) during his exploration north into the headwaters of the Nogoia River in 1845. Included among his collections was the type specimen of *Brachychiton rupestris*. Cunningham had earlier (1829) referred to "thick brushes from fifteen to twenty feet in height" in the headwaters of Lockyer Creek below the present site of Toowoomba (Steele 1972).

In his early account of the plant communities of western Queensland, Blake (1938) documented an area of ooline (*Cadellia pentastylis*) west of Mitchell, citing reports of other occurrences south of Morven. He noted the prominent shrubby understorey of *Acalypha eremorum* and the coarse grasses *Stipa ramosissima*, *Eragrostis megalosperma* and *Ancistrachne uncinulata*.

Blake also referred to the widespread invasion of grasslands and eucalypt woodlands by brigalow communities, which he placed with ooline in a "closed forest formation". This formation, he noted, was extensively developed east of his study area and included "true rainforest" (Blake 1938).

The Fitzroy River region was surveyed during 1962-64 by three CSIRO Land Research teams. Accounts of the vegetation of each survey area were reported by Story (1967), Pedley (1967) and Speck (1968), and all included descriptions of vine thicket communities, although classificatory systems and detail varied between authors. Gunn and Nix (1977) integrated the land system and

and unit data from the three studies and from this, Nix (1977) identified and briefly described three groups of vine thicket (low closed-forest) communities, (i) those on relatively fresh rock material, principally labile sediments, (ii) those on deeply weathered basalt and secondary carbonates (which are typically dominated by bonewood (*Macropteranthes leichhardtii*)) and (iii) vine thickets on deeply weathered sediments (many of which have emergent ooline (*Cadellia pentastylis*)).

In his review of the vegetation of the brigalow belt, Johnson (1984) provided a summary of structural and floristic variation in the semi-evergreen vine thickets and the associated brigalow/softwood communities. Johnson (1970) mapped vine thickets and other vegetation of the Brigalow Research Station near Theodore, central Queensland and also (Johnson 1980) described vegetation patterns along a 3.7 km transect at Brigalow.

Coaldrake, Tohill, McHarg and Hargreaves (1972) mapped and briefly described vine thicket communities on the CSIRO Narayen Research Station west of Mundubbera.

Kahn and Lawrie (1987) compiled plant and animal data for vine thickets in the Townsville hinterland (i.e. the northern C₂ floristic province), drawing mainly on data for the Forty Mile Scrub, Kinrara Crater, Toomba Basalt Flow (all basaltic substrates) and Barrabas Scrub near Charters Towers (deep coarse sands). They noted that favoured sites for vine thicket development included (a) rocky areas, but not precipitous slopes, (b) basalt, limestone and deep coarse sandy substrates and (c) certain topographic situations such as the base of small cliffs, gully heads and perennial springs or soaks. They discussed the role of fire, water availability and nutrient status as major factors influencing vine thicket structure and floristic composition, noting that many vine thicket species are quite fire tolerant. They also noted that thickets on contrasting nutrient-rich basalt and nutrient-poor sands had similar species compositions.

Kahn and Lawrie also commented on the apparent structural and floristic continuum between deciduous vine thicket and semi-evergreen vine thicket, even within a single vine thicket patch.. Examples quoted were the "typical" DVT species *Gyrocarpus americanus* and *Croton arnhemicus* and the SEVT species *Brachychiton australis* and *Flindersia collina*.

Fensham (1995, 1996a) carried out a comprehensive survey of the tropical component of the C₂ vine thickets, collecting species data from 358 sites between Chillagoe and the Rockhampton district. Existing areas of vine thicket were mapped at 1: 100 000 scale and their original extent

determined from early air photography and other historical records. Fensham's results are reviewed and discussed in relation to the present study in **Chapter 4**.

Forster, Bostock, Bird and Bean (1991) collated species lists for 232 rainforest sites in south-eastern Queensland to produce distribution maps and assessments of conservation status for 817 taxa. Sites ranged from semi-evergreen vine thicket to complex notophyll vine forest, with the main emphasis on the drier rainforest types. 92 sites were classed as semi-evergreen vine thicket or intergrades between semi-evergreen vine thicket and araucarian microphyll vine thicket.

In his account of the rainforests of New South Wales, Floyd (1990) recognized two vine thicket suballiances within the **Dry Rainforest** formation; (a) *Alectryon forsythii* - *A. subdentatus* - *Notelaea microcarpa* (suballiance no. 31) and (b) *Notelaea microcarpa* - *Ehretia membranifolia* - *Geijera parviflora* (suballiance no. 32).

The first suballiance (31) includes the communities on metasediments in the gorges of the upper Macleay and Guy Fawkes Rivers. They are classed as microphyll vine thickets or microphyll mossy thickets (King 1980), and on areas of greater soil depth and moisture, grade into a low microphyll mossy vine forest, the *Backhousia sciadophora* - *Dendrocnide* - *Drypetes* suballiance (Floyd 1990). Rainfall is low (<900 mm) and markedly seasonal with a summer peak. King (1980) noted the prevalence of fogs in the gorges, which may significantly increase total precipitation.

Mills (1987) cited examples of vine thicket vegetation in relatively dry locations on Devonian sediments in the Shoalhaven River Gorge in southern New South Wales, terming them "semi-evergreen notophyll vine thickets". They were placed by Floyd (1990) in suballiance 30 (*Backhousia myrtifolia* - *Acmena smithii*), occurring between the Hunter and Tuross Rivers.

Floyd's suballiance 32 is found mainly on rocky sites with basalt as the parent material, but may also occur on sediments. It occurs in the upper Hunter Valley at Mt Dangar and Glenbawn Dam and along the North-western Slopes from the Liverpool Range to north of Moree. It is classed (Floyd 1990) as semi-evergreen vine thicket, though lacking the characteristic bottle-tree (*Brachychiton australis* and *B. rupestris*) emergents of the Queensland vine thickets. The communities tend to be somewhat open and frequently have emergent eucalypts as well as *Casuarina cristata* and, in some examples, *Acacia harpophylla*. Areas of ooline (*Cadellia pentastylis*) occur south-east of Moree, east of Narrabri and north-west of Tenterfield.

Turner (1976b) reported on a survey of approx. 2.5 ha of vine thicket (4-8m high) on the Brushy Hill Range near Glenbawn Dam, upper Hunter River. Other areas of dry rainforest in the Hunter Valley described by Turner and Vernon (1994) are better-developed structurally ((low) notophyll vine forest often with emergent *Ficus* spp. and *Brachychiton discolor*) and are certainly more floristically diverse.

2.4 Temporal processes, with particular reference to Australian rainforests.

There is an extensive body of literature on the topic of ecological (community) succession. This review is aimed at presenting an outline only of the more significant developments in successional theory and at summarising current terminology and concepts. These provide a background for reviewing the literature relating to the dynamics of Australian rainforests in general, and to particular aspects of succession (soil seed-banks, vegetative regeneration and single-species dominance). Finally I review the limited published data on the dynamics of dry seasonal rainforests.

2.4.1 Definition of succession

Succession is generally defined as the changes in species composition and abundance during or following disturbance of a site. It may often involve directional changes such as an increase in biomass and/or a particular sequence of replacements in species abundances. Other patterns of abundance may occur, including convergence, divergence, total suppression and cyclic patterns (Drury and Nisbet 1973, Huston and Smith 1987).

Successions are commonly classified as primary or secondary, depending on the severity of disturbance to the vegetation. A disturbance severe enough to remove or bury all biotic material initiates primary succession; all others initiate secondary succession. Webb and Tracey (1981) also drew a distinction between the relatively short-term changes involved in succession and long-term changes in vegetation patterns resulting, for example, from climatic changes.

2.4.2 Development of successional theory

An early view of succession, proposed by Clements (1916, 1928) and Weaver and Clements (1938) was that at any site a community would progress by sequential succession ("relay floristics")

until it reached a climax of stable composition. Successions with different starting points would reach the same climax (i.e. climatic climax) within a particular region. Clements also proposed the concept of a community functioning cohesively as an organism - "the reaction of the community is regularly more than the sum of the reactions of the component species and individuals" (Clements 1928).

His concepts were vigorously opposed by Gleason (1926), who argued that successions and communities were the result of the spread and establishment of individual species (the individualistic model), and their composition was determined by the interaction of species properties and environmental conditions. Gleason's argument was extended by Egler (1954) who proposed that succession was largely the result of different rates of growth of species that were initially present ("initial floristic composition") following a disturbance, rather than a sequence of successively invading species.

Drury and Nisbet (1973) showed that patterns of abundance following disturbance included not only sequential replacements but also cycles and divergences. They noted the similarities between vegetation sequences in temporal successions and sequences along environmental gradients, and related succession to the "known correlation between stress tolerance, rapid growth, small size, short life and wide dispersal of seed" (Drury and Nisbet 1973), i.e. to plant life history strategies.

These concepts were further developed by Grime (1977), who proposed a classification scheme of life history strategies, based on adaptation to particular levels of disturbance and stress (i.e. low levels of resources). Three environmental categories were defined (low disturbance/low stress, high disturbance/low stress and low disturbance/high stress) and 3 life history strategies (competitor, ruderal and stress tolerator). Changes during succession alter the environment from high disturbance/low stress (high resources) to low disturbance/high stress, with associated change in dominant plant strategies from ruderal to stress tolerators. In more productive systems, there is a middle phase of high competition (low disturbance/low stress).

The main shortcoming of this model is the assumption of fixed life history strategies and therefore constant successional relationships between any two species of plants. As Smith and Huston (1989) pointed out, the relative adaptive ability of two species may vary depending on the particular environmental circumstances.

Connell and Slatyer (1977) proposed three alternative successional pathways; facilitation, inhibition and tolerance. Facilitation is essentially the classical, relay floristic pathway in which the presence of earlier species facilitates the entry of successive suites of species. Tolerance describes the situation in which later species are successful whether or not earlier species have preceded them.

The inhibition pathway is one in which early species exclude or suppress subsequent colonists (both early and late successional species), and continue to dominate the site, for example, *Acacia melanoxylon* and *A. aulacocarpa* (Hopkins 1990).

These different processes may interact, and the strengths and directions of these interactions could vary within a successional sequence. Thus an earlier species may have both facilitative and inhibitory effects on later species, and the primary concern is the overall net effect (Connell, Noble and Slatyer 1987).

Noble and Slatyer (1980) provided the following generalizations about major factors affecting succession:

1. Species composition immediately after disturbance is dependent upon propagules (which have dispersed from elsewhere or persisted through the disturbance at the site) or vegetative re-sprouting from organs surviving the disturbance.
2. Immediately after a disturbance, there is a pulse of recruitment or growth under conditions of little competition for space or other resources.
3. After the initial pulse, recruitment slows, since once an individual plant is established it is very difficult to displace (this applies particularly to perennial plants).
4. Subsequent recruitment of additional species is sometimes facilitated by prior occupancy, but is frequently restricted and may be inhibited.
5. In the absence of further disturbances, long-lived species and those which can regenerate in the presence of their own adults will finally become dominant.

Noble and Slatyer (1979, 1980) developed a scheme for predicting changes in species composition and dominance in communities subject to recurrent disturbance. The scheme utilised a small number of life history attributes (termed “vital attributes”) pertaining to the potentially dominant species in a community.

Three main groups of vital attributes were recognised, relating to:

1. the method of arrival or persistence of species at site during and after a disturbance
2. their ability to establish and grow to maturity in the developing community
3. the time taken for the species to reach critical life stages.

Each major species was categorised into a “species type”, based on the first two groups of vital attributes, and the interaction between the species types over time produced a replacement sequence which showed the major shifts in composition and dominance following a disturbance. Noble and Slatyer (1980) provided an example of a replacement sequence in a Tasmanian wet sclerophyll-rainforest system, which predicts the replacement of *Nothofagus* by *Atherosperma*.

In a somewhat similar approach, Huston and Smith (1987) carried out a series of simulations of competition between two species, using combinations of five different life history traits, maximum growth rate, maximum size, maximum longevity, maximum rate of sapling establishment and shade tolerance. They were able to produce 5 groups of successions: sequential successional replacement, divergence, convergence, total suppression and pseudo-cyclic replacements.

These simulations used an individual-based plant model, modified from the JABOWA/FORET forest simulation model (Botkin, Janek and Wallis 1972, Shugart, West and Emanuel 1981). This model simulates the annual tree-population dynamics of a defined area (scaled to the maximum size of the largest species present) by considering the birth, growth and death of all individuals in that area. Shugart, Hopkins, Burgess and Mortlock (1980) applied a version (the KIAMBRAM model) to a study of selective logging in CNVF on the Tweed Range (Wiangarie State Forest).

Huston and Smith (1987) compared their model with the resource-competition model of Tilman (1985) (a population-level model) Critical differences were seen to be: (i) interactions among individuals rather than among populations, (ii) competitive ability as an individual characteristic based on the interactions of life history characters with the individual’s environment, rather than a set of abstract parameters for an entire population and average environmental conditions, (iii) non-equilibrium dynamics; and (iv) autogenic changes, that is changes induced by the plants themselves, in the critical resources (light or soil nutrients) for competition.

Swaine and Whitmore (1988) briefly reviewed ecological classification systems (life history groups) for rainforest species and commented on the confusing terminology, much of which they considered lacked precise definition. They proposed a simple division into two groups or guilds (pioneer and non-pioneer/climax species), based on seed germination and seedling establishment characters. Within each guild there is continuous variation and an arbitrary subdivision was recommended, based on height at maturity (using Raunkier classes). Examples of height class subgroups were given and the diagnostic characters of pioneer tree species were tabulated.

Swaine and Whitmore rejected the concept of a group of late seral/late secondary species, i.e. species that germinate and establish below a pioneer canopy but not under a climax one. They argued that these “late secondary” species include both long-lived pioneers and certain climax (non-pioneer) species that need substantial canopy openings for regeneration.

2.4.3 Studies of disturbance and succession in Australian rainforests.

Most of the detailed studies of regeneration in Australian rainforests have involved the effects of logging in moist rainforest types (Adam 1992). These include subtropical rainforest (CNVF) on the Tweed Range (Wiangarie State Forest)(Burgess, Floyd, Kikkawa and Pattenmore 1975, Horne and Gwalter 1982) and warm temperate rainforest (SNEVF) in the Hastings region of New South Wales (King and Chapman 1983). Regeneration in an experimentally cleared area of CNVF at Mt Glorious was documented by Williams, Lance, Webb, Tracey and Dale (1969a) and Webb, Tracey and Williams (1972), who noted the impact on succession of the introduced shrub *Lantana camara*. Stocker (1981) also described regrowth following the felling and burning of CNVF on the Atherton Tableland.

More recently, Olsen and Lamb (1988) and Unwin, Applegate, Stocker and Nicholson (1988) have studied early regeneration after major natural disturbances to rainforest (storm and cyclonic damage respectively).

Hopkins (1975) defined temporal patterns (phases) of regrowth in CNVF on the McPherson Range, based on a series of stands of known age, and incorporated these into a more general model of secondary succession in Australian tropical and subtropical rainforests (Hopkins 1981) (see **Figure 2.3**). Four broad species groups were documented (Hopkins, Kikkawa, Graham, Tracey and

Webb 1977), with groups A and B corresponding to the pioneer category of Swaine and Whitmore (1988)(see above) and group D the climax species. Group A comprises two sub-groups, herbaceous annuals or short-lived perennials (A_1) and short-lived shrubs and small trees (A_2). Group B species were termed "early secondary species" (Hopkins *et al.* 1977) and are fast-growing, shade-intolerant trees which produce large quantities of well-dispersed seeds.

Group C ("late secondary") species are "intermediate in most characteristics between groups B and D" (Hopkins *et al.* 1977), but this concept has been rejected by Swaine and Whitmore (1988) (see above). The climax (group D) species are slow-growing and long-lived, fruit irregularly, and seed is generally poorly-dispersed and often has a short period of viability.

The type of regeneration at a particular site depends upon the size of the canopy gap and the extent of exposure of mineral soil, i.e. the size and intensity of disturbance. Small gaps, caused by collapse of old trees or local wind-throws, are rapidly filled by expansion of the crowns of adjacent trees or by the growth of suppressed trees. Re-establishment of the more shade-tolerant (group D) species in these situations is called "diffuse" regeneration.

Larger gaps, caused for example by lightning strikes or the fall of a large tree, frequently bringing down other trees, provide suitable conditions for establishment and growth of early secondary (group B) species and at least some pioneer (group A) species. Conditions on gap margins, for example, are also suitable for germination and growth of mature-phase (climax) species, thus producing a probabilistic combination of all seral stages. The fast growth rate of group B species and the shade tolerance of group D species allow both groups to occupy the site over the short-term (an example of a tolerance pathway). The establishment of climax species in these large gaps is termed "spot-wise " regeneration (van Steenis 1958).

Primary subtropical and tropical rainforests thus comprise mosaics of regenerating units, termed microseres (Hopkins 1981), resulting from the continual production of gaps of varying sizes by natural disturbances. The structural and floristic composition of these forests are therefore as much a product of their disturbance regimes (type, intensity and frequency of disturbance) as they are related to variations in climate, soils and topography.

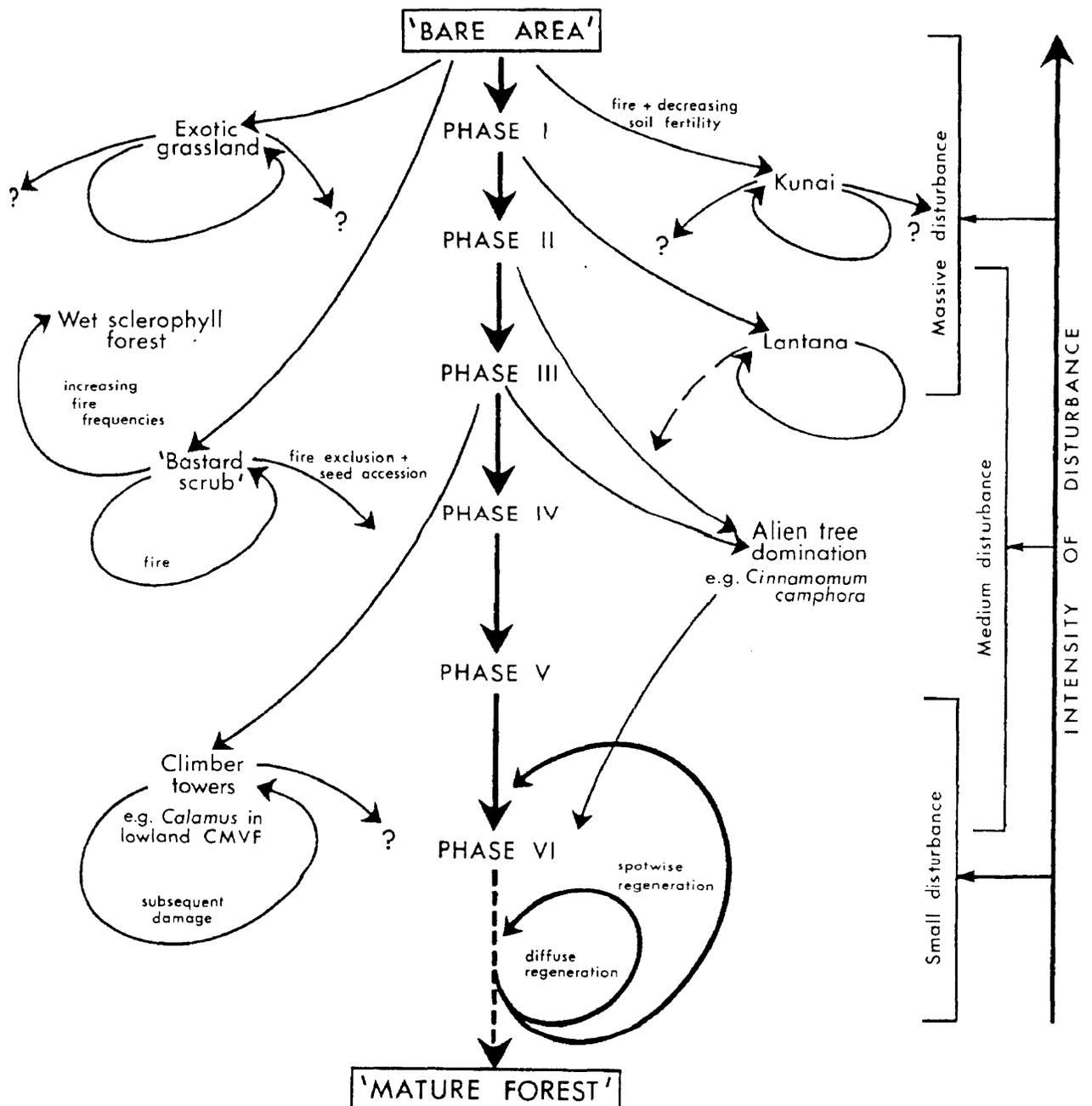


Figure 2.3 Schematic representation of secondary succession and natural regeneration in rainforest showing some of the variations that can occur in relation to intensity of disturbance (after Hopkins 1981).

Adam (1992) compared the above model with descriptions of succession in relatively species-poor temperate rainforests (MMF and SNEVF), and noted significant differences in Tasmanian *Nothofagus cunninghamii* communities. Read and Hill (1983) recorded the presence of a pioneer (group A) shrub stage in old field succession, but regeneration otherwise appears to involve

fewer groups of species and fewer phases than that of the more complex rainforests. There are relatively few group B (fast-growing tree) species (for example *Acacia dealbata*, *A. melanoxylon* and *Pomaderris apetala*) and the shade-intolerant *N. cunninghamii* and *Eucryphia lucida* are able to maintain their dominance (in the absence of major disturbance) through coppicing and seedling establishment in small gaps (Read and Hill 1985).

Ceratopetalum apetalum, which frequently dominates SNEVF, is able to germinate and survive in heavy shade, but can also establish in large open gaps. It also regenerates vegetatively (Adam 1992).

2.4.4 Some aspects of succession, with reference to Australian rainforests.

2.4.4.1 Vegetative regeneration.

Regeneration of temperate rainforest species by vegetative means (see above) has also been discussed by Johnston and Lacey (1983), who documented the ability of several MMF and SNEVF species to produce basal sprouts from undamaged stems. The swollen stem bases in these species were termed "basal burls" by Lacey and Johnston (1990), and also occur in *Dicymbe corymbosa* ("clump wallaba"), a leguminous tree dominant in rainforest in Guyana and the Rio Negro region of Amazonia (Richards 1952).

Acmena smithii, another common temperate rainforest species, is able to regenerate from a lignotuber (after fire, for example) (Ashton and Frankenberg 1976). In an area of rainforest (CNVF) felled and burnt in North Queensland, Stocker (1981) recorded 74 species coppicing from stumps and 10 producing root suckers. He also reported that the early growth of these plants was slower than that of trees regenerating from seed. In contrast, Webb *et al.* (1972) found that plants with coppice growth were taller than plants growing from seed.

Russell-Smith and Dunlop (1987) noted that many Northern Territory rainforest species regenerate vegetatively following fire, but may be killed by frequent and/or intense fires. Bowman (1991a) found that of 32 species affected by fire in 5 monsoon rainforests most recovered vegetatively and only 11 species had individuals killed. Resprouting did not occur in *Aidia racemosa* and *Ficus racemosa* and was rare in *Hibiscus tiliaceus*.

Olsen and Lamb (1988) reported vegetative regrowth in 35 out of an original 44 tree species in CNVF severely damaged by a storm in Lamington National Park. Similarly, Unwin *et al.* (1988) recorded widespread regrowth (leaf shoots and/or stem coppice) in lowland tropical rainforest trees 40 days after severe cyclonic damage.

2.4.4.2 Single-species dominance.

Richards (1952) documented examples of several tropical rainforest communities in which single species made up most of the stand. These included *Mora excelsa*, *M. gonggrijpii*, *Eperua falcata* and *Dicymbe corymbosa* (South America), also *Gilbertiodendron (Macrolobium) dewevrei* and *Cynometra alexandri* (central Africa). He noted that the South American communities were generally associated with non-optimal soil conditions; for example, *Eperua falcata* (wallaba) is restricted to bleached sandy soils (podzols) (Richards 1952).

Connell and Lowman (1989) collated data from 17 sites in moist tropical rainforest dominated by single species (see **Table 2.1**). These included a north Queensland (*Backhousia bancroftii*) site (type 2) and 3 sites studied by Richards (1952) at Moraballi in Guyana.

Table 2.1 Some mechanisms that could produce low diversity among canopy trees in tropical and subtropical rainforest (from Connell and Lowman 1989).

Type I. Dominant species persists beyond one generation

The juveniles of the dominant can establish and survive beneath unbroken canopy or in small tree-fall gaps. For several reasons, only a single species achieves dominance and persists.

A. Initial establishment of dominance

1. The dominant is the most common species first colonising a large open patch.
2. The dominant gradually invades an existing rainforest by tree by tree replacement. It replaces existing species because it is superior to all other local species for one of the following reasons:
 - a. it is the most resistant to deleterious physical conditions or natural enemies (e.g. pathogens, parasites, herbivores; or
 - b. it is the superior competitor either in interference or in exploitation of resources.

B. Persistence beyond one generation

Once established, the dominant species persists for one or both of two reasons.

1. Its juveniles are so much more abundant than those of other canopy species that it has a higher probability of replacement, all other things being equal.
2. It is superior to all other local tree species for one or both of the reasons under A2.

Type II: Dominant species does not persist beyond one generation

Early invaders of a large patch soon after it is cleared by a disturbance often do not persist because their juveniles cannot establish and survive beneath unbroken canopy or in small tree-fall gaps. These colonists are often members of a single species for two reasons.

A. Only a short time is available for invasion before canopy closure.

B. Few species of trees are adapted to tolerate the conditions in a large, recently disturbed patch.

Connell and Lowman suggested a number of mechanisms by which single-species dominance could occur in otherwise complex rainforest communities (see **Table 2.1**), and discussed the possible role of mycorrhizal relationships. Some of these mechanisms might also operate in dry seasonal rainforests.

2.4.4.3 Seed banks in Australian rainforests

Results of Australian studies on soil seed banks have been consistent with overseas findings (Adam 1992). Most studies have been undertaken in tropical rainforest in north-eastern Queensland by Hopkins and Graham (1983, 1987), Graham and Hopkins (1990) and Hopkins, Tracey and Graham (1990), but data are also available from subtropical rainforest in Lamington National Park (Abdulhadi and Lamb 1988). Hopkins *et al.* (1990) compared the seed banks of three structural types of rainforest, which included semi-evergreen vine thicket (the Forty Mile Scrub) near Mt Garnet. Results from this site differed quite markedly from those from complex mesophyll and complex notophyll vine forest - there was a greater number of seeds but they were almost entirely of annual and short-lived perennial herbs, notably *Ageratum conyzoides*.

Tree and shrub species in the seed-bank at Forty Mile Scrub included *Geijera salicifolia*, *Flueggea leucopyrus*, *Ficus platypoda*, *Cassinia laevis*, *Trema aspera* and *Polyscias elegans*. *Alphitonia excelsa* and *Acacia aulacocarpa*, two common pioneer tree species in Forty Mile Scrub, were not recorded from the seed-bank.

Three possible reasons were offered for the different seed-bank structure in the semi-evergreen vine thicket; the seasonally open canopy allows short-lived species to establish and produce seed rapidly, seeds of long-lived species such as trees and shrubs would be unlikely to accumulate because they would be exposed annually to conditions suitable for germination (i.e. high light and soil temperatures) and (thirdly) the levels of disturbance caused by cattle and pigs in this site would favour the establishment and spread of "weedy" species (Hopkins *et al.* 1990).

2.4.5 Studies of dynamics in dry seasonal forests

The paucity of data from these communities was highlighted by Murphy and Lugo (1986a) (see above) who drew heavily on their results from Guanica, Puerto Rico. The community was found to have relatively low biomass, reflecting the overall smaller structure, but a much larger proportion of root biomass (50%) compared with moister rainforest types.

Because of the short growing seasons, trees generally have lower annual diameter growth, which may be less than their seasonal shrinkage and expansion (reflecting water availability) (Swaine *et al.* 1990). Murphy and Lugo noted that as annual rainfall decreases and/or drought periods increase, the upper tree stratum becomes deciduous and with even lower rainfall, some lower stratum species become deciduous also. Most dry forests are composed of numerous facultatively or obligately deciduous species. At Guanacaste (Costa Rica), 60-75% of all trees are deciduous. Janzen (1981) also recorded severe herbivory and defoliations with many plant species in various seasons or years in Costa Rican dry forest.

Because of their more rigorous and less predictable climate, dry forests are considered more vulnerable to stress during the successional process than are wet forests. Furthermore, succession is a generally slower process in terms of plant growth and other developmental features (Murphy and Lugo 1986a). On the other hand, because of the relative simplicity and small structure of many mature dry forests and because of the predominance of coppicing, dry forests have the potential to recover to a mature state more quickly than do wet forests, and they may therefore be considered more resilient. Recovery times of wet and dry forest ecosystems have been estimated as 1000 and 150 years respectively (Murphy and Lugo 1986a).

Coppicing is the primary regeneration mechanism in dry sites that have been cut (Murphy and Lugo 1986b). A consequence of this is the very patchy development of dry forest in the early stages of succession - this patchiness was also noted by Swaine *et al.* (1990) in the Shai Hills forest. Murphy and Lugo (1986b) found no evidence of a long-lived soil seed pool in the Puerto Rico dry forests.

2.5 Conclusions from review of literature.

2.5.1 Dry seasonal rainforests in a global context.

Dry seasonal rainforests are the most poorly known group of rainforests on a global basis. At the time the present study was being planned, the only review of this topic was the recently published paper by Murphy and Lugo (1986a). As noted above, this drew on data from a very limited number of research sites, including one from northern Australia. Little has been added since to our understanding of structural and floristic relationships within these communities, with most of

our current knowledge based on just two research sites, Shai Hills in Ghana and Guanica in Puerto Rico. There is a great need for collaborative research aimed at linking and increasing knowledge of dry seasonal rainforests between continents. Such an approach has been undertaken in recent years in the southern temperate rainforests, notably those dominated by *Nothofagus* species, of Australia, New Zealand and South America (Veblen, Hill and Read 1996).

Attempted comparisons between dry seasonal forests on the different continents are hampered by the lack of a common structural classification. No other classification appears to provide a comparable scale of resolution to the structural-physiognomic approach developed by Webb and co-workers in eastern Australia and applied to a limited extent in the south-east Asian region.

The commonly-used term "seasonal forest" covers a wide range of structural variation, and indeed could be applied to most tropical and subtropical Australian rainforests. As noted above, of the studies of dry seasonal forests reviewed by Murphy and Lugo, most involved sites with considerably higher annual rainfall than the drier Australian vine forests and thickets, which generally have less than 1000 mm per annum.

It would appear that in terms of structural features and climatic regimes, the dry seasonal rainforests of southern Africa and Madagascar most closely approach those of eastern Australia. Apart from an early study by Boughey (1964) in Zambia, little has been published on their structure, floristic composition and environmental relationships.

The disturbance regimes and associated temporal changes within the Australian dry seasonal rainforests may differ considerably from those documented for other continents and therefore limit the extent to which analogies may be drawn. The Australian Aborigines never practiced agriculture and hence Australian rainforests have not been cut for shifting agriculture as have those in most other regions of the world (Connell, Webb and Tracey 1984). The two major research sites in dry seasonal forest (Shai Hills and Guanica) both represent regrowth communities which have been logged or partly cleared in the past 100 years. The multi-stemmed habit of *Diospyros* spp. at Shai Hills, for example, is probably more a result of selective felling than a reflection of site or climatic factors (Swaine *et al.* 1990).

Reference has also been made (Walter 1971) to the widespread replacement of seasonal forests by grasslands in Africa and Asia. There is evidence (Stocker 1970, Russell-Smith 1991) that the distribution of Australian seasonal forests has been influenced by the fire regimes practiced by Aborigines, which would have tended to restrict the expansion of these communities under favourable environmental conditions. However, some burning practices are believed to have been specifically aimed at protecting individual vine forest and thicket patches (e.g. Jones 1980).

The Caribbean islands, including Puerto Rico, are subject to recurrent severe natural disturbance from hurricanes. Whilst cyclones are a major feature of northern Australian weather patterns, destructive winds generally affect only coastal and immediately subcoastal areas. The associated heavy rainfall usually has a far more extensive (and beneficial) influence on dry seasonal forests.

2.5.2 Spatial and temporal patterns in Australian dry seasonal rainforests.

The distribution and environmental relationships of the structural forms of Australian rainforests have been clarified in a series of papers by Webb (1959, 1968, 1978). The structural-physiognomic classification proposed by Webb is robust and has been shown to be able to accommodate other classifications such as that of Baur (1957). The dry seasonal rainforests comprise principally two structural/physiognomic forms, deciduous vine thicket (DVT) (northern Australia) and semi-evergreen vine thicket (SEVT) (eastern Australia).

Although the dry seasonal rainforests of eastern Australia are predominantly SEVT in structure, in north-eastern Queensland the distinctions between SEVT and DVT categories are not always clear. Many vine thickets in subcoastal districts of Queensland contain emergent *Araucaria cunninghamii* in addition to the characteristic *Brachychiton* emergents, and hence may be classified as araucarian microphyll vine thicket or woodland.

Floristic patterns in Australian rainforests have also been established at a continental scale (Webb, Tracey and Williams 1984), using presence/absence data for tree and shrub species. Dry seasonal rainforests are represented in three of the nine ecofloristic provinces defined by Webb *et al.* - B₃ (northern Australia), C₁ and C₂ (eastern Australia). Province C₁ includes some of the moister examples of SEVT, with most falling within the C₂ province (see **Figure 2.1**).

The C₂ floristic province therefore provides an appropriate broad geographical and ecological context for a study of pattern in dry rainforests in eastern Australia. It also coincides largely with the Brigalow Belt Biogeographic Region defined by Stanton and Morgan (1977), although the northern group of outliers falls within the Einasleigh Uplands Biogeographic Region.

Vine thickets occur on a range of landforms within the Brigalow Belt Biogeographic Region. Extensive clearing has occurred through much of the region and although many of the remaining areas of this community are protected within conservation reserves, it is not known how representative these are. A more detailed knowledge of patterns and relationships within vine thicket vegetation is needed to facilitate conservation planning for these communities within the Brigalow Belt Biogeographic Region.

Local (i.e. small-scale) species patterns and corresponding site factors have been studied in some moister subtropical rainforests in Australia, such as the Nightcap Range (Williams *et al.* 1973, Turner and Kelly 1981) and Barrington Tops (Turner 1976a). Whilst land survey reports for the Fitzroy region of central Queensland (Gunn *et al.* 1967, Story *et al.* 1967, Speck *et al.* 1968) illustrate broad relationships between vine thickets and associated communities and underlying landforms and soils, only Gunn (1974) and Johnson (1980) have explored these relationships further.

Johnson's study is particularly significant, since it involved the establishment of a continuous series of permanent plots. This provided an opportunity in the present study to explore temporal as well as spatial variation within an area of vine thicket dominated by *Macropteranthes leichhardtii*, a community which occurred extensively across the central Brigalow Belt Biogeographic Region and which has now been cleared from most areas of low relief. Knowledge of succession and other temporal processes in dry seasonal rainforests is almost completely lacking, with most of our concepts of rainforest succession having been developed in moist rainforest communities (see section 2.4).

2.6 Objectives of present study.

The major objective of this study is to explore floristic patterns in semi-evergreen vine thicket vegetation, with particular emphasis on the major remnants of this community which are found mainly in the Fitzroy and Burnett River catchments of central and southern Queensland. The

following questions are asked: **Are there broad-scale patterns of species distribution and abundance? If so, how are these related to climatic and other environmental factors? How robust are these patterns and relationships when applied over a broader region, i.e. the Brigalow Belt Biogeographic Region? How do these patterns and relationships conform with contemporary community concepts and relationships within Australian dry rainforests?**

These questions are addressed in **Chapters 3 and 4**. The first question forms the main theme of **Chapter 3**, addressed through the collection and analysis of stand data from vine thickets in central and southern Queensland. **Chapter 4** examines species patterns and climatic relationships within an expanded, bioregional context and relates these to the results of other regional studies in Australian vine thickets.

The second objective of the present study is to examine spatial and temporal patterns within an area of *Macropteranthes leichhardtii* - dominated vine thicket in central Queensland. The following questions are asked: **What local-scale patterns of species distribution and abundance occur within vine thicket and associated brigalow (*Acacia harpophylla*) - dominated vegetation? How are these patterns related to site factors? What temporal changes can be identified in these communities, i.e. what changes in species abundance have taken place since establishment of the transect? Can these changes be related to currently-accepted models of succession in rainforest vegetation?** The first two questions are addressed in **Chapter 5** and the latter two questions in **Chapter 6**, using data in both chapters from a permanent vegetation transect established at Brigalow Research Station by Johnson (1980).