2 LITERATURE REVIEW AND THEORETICAL PERSPECTIVES

2.1 Forest ecological research in Australia

2.1.1 Old-growth systems and wet sclerophyll forests

The WSF and the WTRF in the study area are forests of old-growth. The oldest trees in the WSF are possibly 250-300 years old (a professional guess by regional foresters) and the trees of the WTRF are presumably as old or more so. In tall wet sclerophyll old-growth forest systems, the canopy can range from one comprising a mix of species of variable age to one primarily comprised of an even-aged single species. The understorey tends to be more a reflection of processes and perturbation and can vary from a grassy or low herb layer to incipient rainforest. Old-growth forest represents a complex of forest structural types to which most of the Australian forest fauna have adapted (Scotts 1991) and, among the range of WSF formations, the one in which the greatest diversity of K-selected fauna will be supported (MacFarlane 1988 (mammals); Loyn 1980, Smith 1985, Kavanagh *et al.* 1985 (birds); Brown and Nelson 1993 (reptiles)). Because of the economic value of the timber resources of these forests as well as the suitability of their locations for plantation forests in contradistinction to their high conservation value, there is, inevitably, a range of opinion as to the appropriate definition of old-growth forest (Fig. 2.1, but also Dyne 1992 Appendix 2, Woodgate *et al.* 1994). For the purposes of this thesis my definition of old-growth forest is a forest that (a) has not been significantly disturbed by the results of European human activity and (b) contains predominantly aged trees in the canopy layer.

Concerted research specifically into the ecology of old-growth forests has been a relatively recent development (Resource Assessment Commission (RAC) 1992 (Chap. 6); Dyne 1992; Love *et al.* 1993; Woodgate *et al.* 1994) which has paralleled, and perhaps been fuelled by, a concomitant community-based concern for their future (Blakers 1987; Cameron and Penna 1988; Clark and Blakers 1989; Kirkpatrick *et al.* 1990; Norton *et al.* 1991). This concern has sprung from the move by forest managers to extend operations into areas of previously uncut forests in order for them to not only meet continuing demands for

Box 6.3 A conceptual structure for old-growth forests

Undisturbed

Negligible

Disturbance

Low

High

Forest age

Ecologically
mature forest

Forest and Timber Inquiry

Australian Conservation
Foundation

Australian Heritage
Commission

Forestry Commission
of NSW and Victorian
Government

Forestry
Commission of
Tasmania (1984)

Western Australian
Government

North East Forest
Alliance

Note: The uppermost graph illustrates the Forest and Timber Inquiry's definition of 'old growth'.
A selection of definitions and descriptions of old-growth forest received by the Inquiry is
interpreted graphically to illustrate their variability in relation to the extent of disturbance
and forest age.

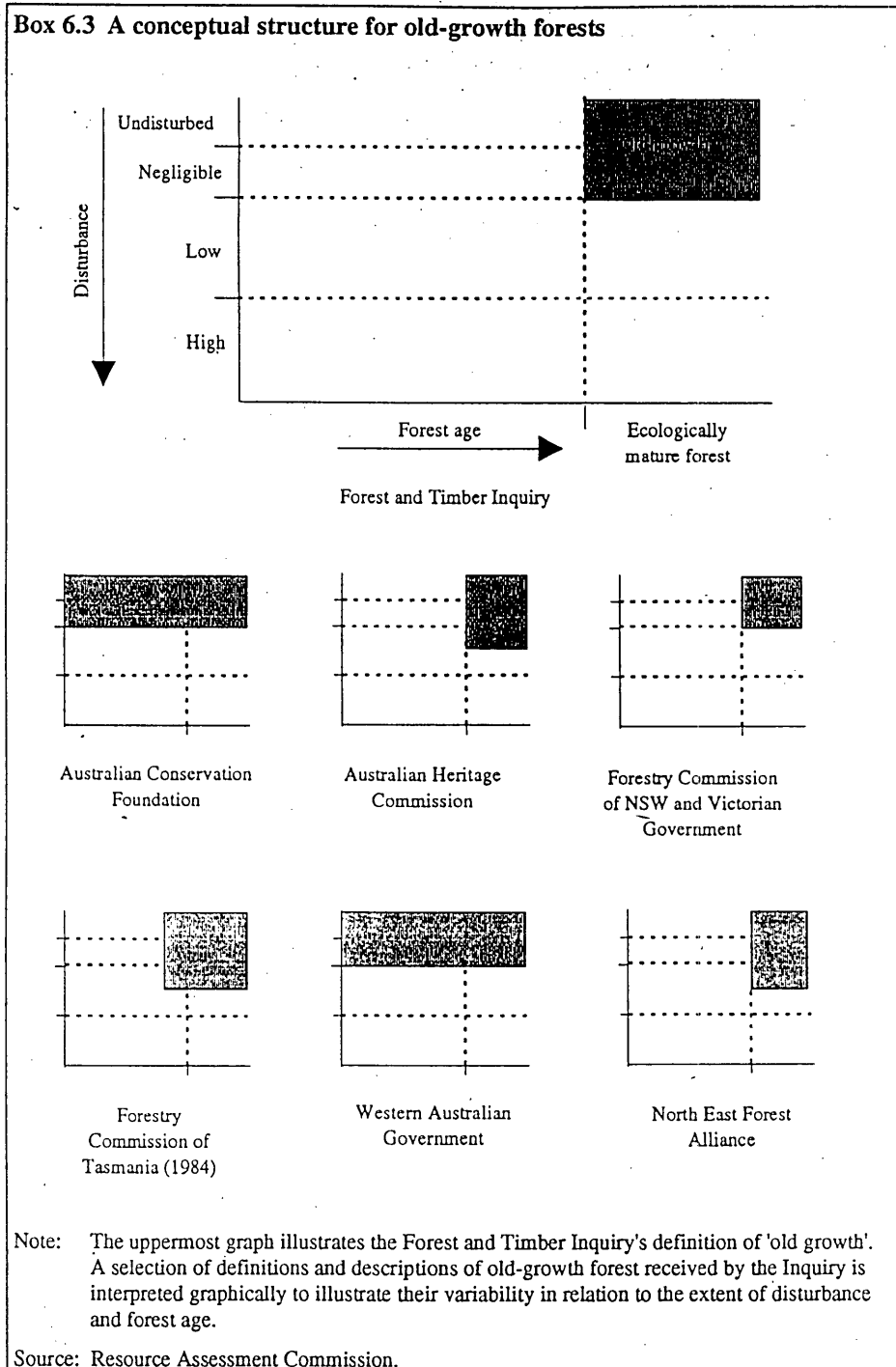Source: Resource Assessment Commission.

Figure 2.1 The range of definitions of old-growth forest as
interpreted by the Resource Assessment Commission.
(RAC 1992, p 141).

timber (Bigsby 1993), but also to replace forests that have been removed from production for inclusion in national parks (Gibbs 1992). The community attention was so sharply focussed on forest managers during the 1970s and early 1980s during the debate over the future management of rainforests in Australia, that when that issue was essentially resolved, the focus switched easily to the management practices employed in the old, commercially unproductive eucalypt forests (Squire 1993).

Notwithstanding the paucity of work specifically concerned with the old-growth forests, there has been a great deal of research into the ecology of WSF generally which has encompassed the old-growth forests. Of that work which has relevance to this study are the contributions to an understanding of WSF ecosystem processes and those investigations which have led to a better understanding of the ecology of the genus *Eucalyptus* in general and *E. pilularis* in particular.

With respect to WSF ecosystem processes, the significant work began with Beadle (1954, 1962) who pioneered the re-evaluation that soil processes were significantly associated with the vegetation. Baur's work (1957, 1962, 1965) further emphasised the importance of environmental processes in the understanding of the distribution of vegetation. From these beginnings research has developed in soil-vegetation relationships with studies on nitrification, nutrient cycling and litterfall and decomposition rates. Important contributions relevant to this work include Ashton (1975), Bevege (1978), Webb *et al.* (1969), Richards *et al.* (unpubl.) and a synthesis of this branch of study in Attiwill and Leeper (1987).

Jacobs (1955) presented the first comprehensive study of the life and growth of the genus *Eucalyptus*. His work was produced to assist foresters of the day and has since become a standard reference.

The work on *E. pilularis* has been led by Florence (1961, 1963, 1964, 1968, 1969a, 1969b, 1980) while Florence and Crocker (1962) and Floyd (1962) have explained the germination ecology of the species. *E. pilularis* is distributed down the Australian east coast for over 1300 km from 25.5°S to 37.5°S (Boland *et al.* 1984; although Florence (1964)

names the distribution limits as Fraser Island and the Victoria-N.S.W. border which extends those limits), such that the stands of *E. pilularis* in the study area are placed 300 km from the northern limit of the species. The morphological profile of the taxon that Florence has presented is complex as there are many local variations to the general description (Florence 1969a). The ecology of the species is also subject to variations dependent on the local suite of conditions including those historical. In essence, Florence highlights the ecology of the species as follows:

- It is outstanding among all the other members of the subgenus *Monocalyptus* in that it is never a minor component of the canopy except at the boundary of a local distribution (Florence 1963);
- it is separated from rainforest by congeners, usually members of the subgenus *Symphyomyrtus* (e.g. *E. saligna, E. grandis, E. microcorys*) but occasionally the monocalypts, *E. acmenioides* or *E. carnea* (*E. umbra* ssp. *carnea* (old name) in Florence 1963);
- it is often associated with a substrate high in quartz content and with high percentages of chlorite, mica and magnetite (Florence 1964);
- it is not suited to anaerobic and compacted soils and it requires higher soil moisture levels than other monocalypts (Florence 1964).

Much of the topical work on forest ecology is in the area of numerical analysis and the recent and historical work relevant to this study is referred to below.

2.1.2 Warm temperate rainforests

Australia's rainforests represent just 0.3% of the land mass (Baur 1989) being about 6% of the forested component of the country (RAC 1992). Research into aspects of Australia's rainforests work has escalated in recent years, building on the formidable pioneering work of L.J. Webb and his collaborators in north Queensland. The consequence of this escalation is that now much more than 6% of the literature which pertains to Australia's forest resources has dealt with rainforests. The

extent to which recent research efforts have been attracted to rainforests is indicated by Adam's (1992) comprehensive review of such work in which 75% of his over 700 references were published since 1980. In that period one of the most significant contributors to an understanding of rainforests in southeast Australia has been A.G. Floyd.

Floyd (1990a) has noted that the four major rainforest subformations in New South Wales can be identified in terms of rainfall, soil fertility, vegetation structure, leaf characteristics and the range of plant life forms. One of these subformations is WTRF and his definition of this type is:

> "Warm temperate rainforest contains less [canopy] diversity than subtropical and dry rainforests, with three to 15 tree species commonly present, forming a more uniform canopy of only two strata. Most leaves are simple, many of them toothed and ranging up to 12.5 cm long. This subformation occurs in cool, moist areas which favour lichens and ground ferns rather than large epiphytic ferns and orchids. Tropical features such as stranglers, palms, plank buttresses and woody vines are rare or absent" (Floyd 1990a, p.4-5).

Adam (1992) regards WTRF as simply:

> "an edaphically determined derivative of the subtropical complex...with distinctive structural and floristic composition" (Adam 1992, p. 78).

According to Webb's (1978) classification, WTRF is equivalent to simple notophyll evergreen vine-forest (SNEVF). WTRF, or a structural equivalent, occurs at suitable sites throughout almost the latitudinal range of rainforest in Australia on the less fertile soils, commonly the acid volcanics, and in situations of high rainfall. The subformation occurs on the upper slopes of Mts Bellenden Ker and Bartle Frere in North Queensland and south to Victoria. Floyd (1990b) has produced a classification of WTRF and this and other classifications are discussed below.

2.2   Forest boundaries

2.2.1   Introduction

The existence of zones of connection, separation, delimitation or transition, between adjacent stands of differing vegetation, often called ecotones or boundaries, has been recognised in ecological textbooks for a long time. With the mounting credibility of the continuum theory of vegetation distribution, the definition of these transition zones needs to be somewhat more circumspect. That they are clearly visible in the vegetated landscape justifies an ecological and nomenclatural recognition, even though the exact limits of the transition zones on the ground are sometimes difficult to determine.

In the face of the growing discipline of landscape ecology, which is evolving its own vocabulary, as opposed to that of traditional vegetation scientists, in the field of ecotonal studies, van der Maarel (1990) has attempted to differentiate the boundary types by separating boundaries of stress (ecotones) from those of gradation (ecoclines). This concept was first outlined by Whittaker (1960) and van der Maarel and Westhoff (1964) and the two conditions were later described as *limes convergens* (ecotone) and *limes divergens* (ecocline) in an erudite paper by van Leeuwen (1966). The *limes divergens* is marked by fuzzy demarcation, stability and high species richness.

Using van der Maarel's (1990) definition, the boundaries with which this study has been concerned should be regarded as ecoclines. I will, nevertheless, continue to use ecotone as it is more commonly in use in the Australian context. Also, throughout this thesis, my use of the term "boundary" is synonymous with ecotone as I am content with the notion that not only do forest ecotones represent the boundary region of associations of species with similar net responses to the prevailing environmental gradients but also that they include the transitional zone of vegetation gradation between the associations.

The identification and description of boundaries communicates a great deal about the forest communities they circumscribe in particular and the forest ecosystem in general. Note that in some quarters the term

"transition zone" is preferred to ecotone when referring to the boundary zone between forest types, a preference with which I have no difficulties such that the two terms and specifically, "transition zone forest" are used interchangeably in this thesis. Allen and Starr (1982, p.267) provide a most satisfactory definition of the ecotone:

> "A narrow ecological zone which possesses a mixture of floristic and faunal characteristics in between two different and relatively homogeneous ecological community types. Ecotones often represent gradients between two vegetations with different physiognomies."

The investigation of the extent to which the ecotones in the study area might represent identifiable vegetational assemblages was one of the objectives of this study.

When arguing the case for the continuum concept of vegetation, Whittaker (1956) opined that ecotones are indeed distinct vegetational groupings:

> "Ecotones are not in any very real sense boundaries between communities; they are communities themselves and may often be characterised by commodal groupings of smaller woody species". (Whittaker 1956, p 63)

Whittaker (1956) argued that forest ecotones should not be thought of as intermediate assemblages between the forest stands on either side. He pointed out that they have their own diagnostic species some of which occur in other transitional zones thus providing an ecological link between otherwise differing transitions.

2.2.2   Rainforest - wet sclerophyll forest ecotones

Until recently, most work in this area has had only indirect relevance to ecotone studies insofar as the published papers have been mainly concerned with either the distribution of patterns in the vegetation or with the nature and mechanisms of succession. This paucity of concentration on ecotones also exists in the international literature

generally (van der Maarel 1989). Early Australian work on the nature of the boundary between rainforest and eucalypt forest was initiated by Fraser and Vickery (1938) who discussed the advance of the cool temperate rainforest tree, *Nothofagus moorei*, into adjoining upland eucalypt forest. They also identified "true margin communities" comprising a number of rainforest species and these communities attained their best expression when the rainforest boundary appeared to be stable. Their contribution was followed by Cromer and Pryor (1942) who worked near Gympie using transects across the boundary zone in order to identify not only the species which were characteristic of the ecotone but also which of the canopy rainforest species were genuine climax species. The first significant publications on succession and the dynamics of the rainforest-WSF interface emanated from Tasmania (Gilbert 1959, 1963; Cremer 1960; Mount 1964, 1969; and Jackson 1968). Their polemic was mainly concerned with the role of fire in the structure, pattern and distribution of forests in that State. While that debate was further developed in more recent years (Jackson 1978; Mount 1979, 1982; Ashton 1981a, 1981b; Brown and Podger 1982; Bell, 1983; Ellis 1985), there was another line of argument which centred on the role of edaphic factors in delimiting the distribution of vegetation types. Beadle (1954, 1962) and Baur (1957) both pointed out the importance of the substrate and soil properties and the argument was refined by Florence (1964) and Webb (1968). Hogg and Kirkpatrick (1974) and Turner and Kelly (1981) also found that forest boundaries coincided with substrate junctions. In North Queensland Stocker (1981), Unwin *et al.* (1985, 1988) and Unwin (1989) worked on the controlling effect of fire intensity and frequency over the location and form of rainforest boundaries. Also in North Queensland, House (1986) evaluated the capacity for boundary movement by studying the seed banks and propagule exchange across rainforest-sclerophyll boundaries. Another line of inquiry was suggested by Smith and Guyer (1983) that the tall species of the WSF were boundary-adapted flora, for which further evidence was presented by Bell *et al.* (1987), and Bale (1980) investigated the importance of topography as an agent of ecotone control.

An important review of the factors affecting the WSF-rainforest ecotone has been that of Ash (1988). Although his study was limited to

the situation in North Queensland, he concluded that the main factors controlling the location and form of the rainforest-WSF boundaries are fire factors, rainfall patterns, soil fertility and topography. The extent to which my findings support or conflict with the work in North Queensland and elsewhere is indicated and discussed in Chapter 5.

2.3 Ecological concepts addressed in this study

2.3.1 Vegetation dynamics

2.3.1.1 Introduction

Plant ecologists have long been fascinated by observations suggesting that vegetation occupying any particular location has recently changed, is currently changing or appears not to be changing. Many early papers in the field of vegetation science dealt with this subject and a considerable polemic has persisted in the literature for most of this century. This section briefly traces the history of that polemic and shows how the new thinkers in this area are drawing together all the hitherto competing strains of argument in the field of vegetation dynamics. The findings of this study will be presented in terms that utilise contemporary viewpoints.

2.3.1.2 Community concept

The community concept of vegetation science emanated from Clements' theory of the mechanism of vegetational succession (Clements 1905, 1916,1936). The theory was intuitively acceptable to most plant ecologists in the first part of the century because of the obvious patterns of vegetation distribution across the landscape. The theory holds that

- assemblages of plant species can be identified;
- these assemblages occur in recognisable combinations which can be referred to as ecosystem units; and
- ecosystem units occur in response to certain configurations of environmental factors.

The assemblages, or communities, are identified by the presence of key dominant and sub-dominant species. The community is regarded as an entity, almost organismal, as being more than the sum of its parts.

Watt (1947) used his study of the spatial and temporal dynamics of heather *Calluna vulgaris* communities to develop community theory away from the notion of community development proceeding to and ending at a climax condition by suggesting that the progression was in fact cyclic. He proposed that the climax situation was followed by a stage of degeneration and renewal such that the pattern observable in the landscape represented the range of states in which a community could be in the developmental cycle.

The community concept implied an interaction between the component species. This interaction existed not only between current members (e.g. character displacement in order to accommodate competition) but also between current and former members (e.g. site amelioration by the former members which suited current members). These considerations gave the community not only a spatial dynamic but a temporal one as well. Allen and Hoekstra (1992) argue that the nature of the community is derived from these past processes of accommodation rather than the past processes controlling the state of the community:

> "A quite separate set of historical accidents are the determinants of the state in which we happen to find a community. These local events are the equivalent of past erosion on a landscape. They are differently scaled from the ancient accommodations between species that have given the community its status as a community." (Allen and Hoekstra 1992, p. 128).

The community concept of vegetation has its support base mainly among the European ecologists who have evolved a number of schools of phytosociology based on the concept of discrete communities in vegetation. A summary of the various European schools of phytosociology is contained in Mueller-Dombois and Ellenberg (1974).

2.3.1.3 Continuum concept

During the 1920s and 1930s the germ of an alternative hypothesis to the community explanation of vegetation dynamics emerged. Gleason (1926, 1939) proposed that each species has evolved a unique set of responses to environmental changes. He argued that the vegetation that occupied any particular location at any particular time was a chance outcome of the availability of local flora to provide the successful propagules and the suitability of the site environment at the time, in terms of the evolved responses, for those propagules. The theory was supported by the many field examples of species joining or disappearing from an assemblage along environmental gradients.

Post-war researchers, notably John Curtis, who subscribed to Gleason's individualistic viewpoint, began turning to the notion that vegetation was not made up of discrete units but represented a continuum of change such that sharp boundaries between units should not occur. This change in thinking emerged when they experienced difficulty (e.g. Curtis and Greene 1949) defining the Clementsian communities. The fact that communities had been identified and named in Europe (e.g. Braun-Blanquet 1932) caused a philosophical split between European plant ecologists and their Anglo-American counterparts which is still a serious impediment to the development of a unified theory of vegetation dynamics (van der Maarel 1989). Curtis developed the concept of gradient analysis (Curtis and McIntosh 1951; Bray and Curtis 1957) that explicitly adopted the Gleasonian approach. The theory gained popularity for developers of ordination techniques beginning with Goodall (1953, 1954), Whittaker (1951, 1953, 1956) and Curtis (1959) who preceded a rapid expansion of analytical options that were based on the assumption that the continuum concept was correct.

By 1990, Austin (1990) proclaimed the community concept "out-dated" and asserted that most ecologists now accept the continuum concept. The continuum theory does appear to be the pragmatic explanation for the distribution of species but there remain problems with this theory when explaining the apparent occurrence of boundaries. The occasional very sharp boundaries between species groups, which occur in the study region and throughout the range of rainforests in Australia, is usually

argued as being a fire threshold. Unwin *et al.* (1985) describe sharp rainforest boundaries as due to regular low intensity burning and diffuse boundaries as due to irregular, intense fire.

In support of the continuum approach to vegetation analysis, Florence (1964) has described how, in Australian east coast forests, communities can be aligned on a soil fertility gradient, and the local variations of soil moisture and soil physical condition can enable species to grow in what would normally be prohibitively low soil nutrient levels. The effect of this is to allow penetration of rainforest species into WSF and the occupation of highly fertile soils by *E. pilularis.* Florence (1964) has described this as the complete expression of the WSF-rainforest continuum.

2.3.1.4 Switching

The continuum concept described above denies that sharp boundaries occur in vegetation patterns unless there is an associated sharp change in the environment. But as sharp boundaries often do occur in situations where the 'causal' environmental change is not apparent, Wilson and Agnew (1992) have proposed the concept of an ecological switching mechanism whereby plants modify their environment either to their advantage or else to the disadvantage of other species. This is not a novel idea as others have suggested such things (Wilson and Agnew (1992) provide examples) but they have distilled the ideas into a workable hypothesis. Typically for Australia, they suggest, there exist examples of fire-mediated switches. These switches could operate in different ways for different conditions across the country. For example, fire tolerant eucalypts produce a highly flammable litter layer which facilitates the intensity of a fire while fire intolerant rainforests reduce light levels and maintain higher humidity levels which serve to suppress fire.

Of the several types of switching mechanism described by Wilson and Agnew (1992) they do not canvass a situation that exists in old-growth WSF in Australia. This is an auto-allelopathy switch operated by the mature members of the community to suppress competition from seedlings of the same species (Jacobs 1955; Florence and Crocker 1962;

Incoll 1979). Florence has suggested that this switch (not his term), in conjunction with an imposed irregular fire regime, could give rise to stability in terms of sharp discontinuities between mature eucalypt forests and rainforest.

In both Tasmania (Mount 1964) and North Queensland (Stocker 1981; House 1986; Ash 1988; Unwin 1989) forest boundaries are apparently controlled by fire which tends to maintain very sharp boundaries between the pyrophytic and nonpyrophytic, or pyrophobic, vegetation. In northern New South Wales, however, the incidence of variable width boundaries suggests that the fire pattern and frequency is different or else there are other factors to consider. One factor might be the presence of a different suite of species in this region. A suite that contains (a) several species adapted to the conditions of the forest ecotone and (b) long-lived species which are able to persist long after the exigencies of forest dynamics have separated them from their original association. The following chapters will explore such factors. The incidence of sharp boundaries between forest types in the study area is assessed in Chapter 5.

2.3.1.5   Hierarchical continuum concept

As indicated above, modern workers in vegetation science are gradually constructing explanations for the nature of vegetation dynamics that are likely to be acceptable to the main disparate schools of thought. It is to be hoped that the outcome, by drawing on the various competing theories will be workable from an analytical point of view. Various authors have suggested that such a synthesis ought to be possible (Goodall 1963; van der Maarel 1989; Allen and Hoekstra 1992). European ecologists are compromising their Clementsian position by considering fuzzy systems vegetation theory (Marsili-Libelli 1989; De Patta Pillar and Orlóci 1991; Boryslawski and Krusinska 1991; but note also the American, Roberts 1986, 1989) while the Americans are developing an accommodation with hierarchy theory (Allen and Starr 1982; O'Neill *et al.* 1986; Kolasa 1989).

The recognition of the differing scales within both biological and environmental processes (Allen and Hoekstra 1992) and the

incorporation of hierarchy theory in the distribution of species have led to a new capacity to interpret vegetation patterns and change. The hierarchical continuum (HC) approach (Collins *et al.* 1993) to the interpretation of vegetation pattern requires data for all species including their abundance and distribution, and it requires these data along a temporal gradient. The advocates of the HC argue that it:

- overcomes the inadequacies of single sample classifications;
- enables the inclusion of both rare and common species in the model (Hanski 1991) when these are commonly discarded in other analyses because they either add little extra information or else they add noise (Mueller-Dombois and Ellenberg 1974; Gauch 1982);
- will discern species dynamics at either small or large scales; and
- enables modelling of possible improvements in competitive abilities and prediction of correlation between a species rank abundance at small and large scales (Collins *et al.* 1993).

2.3.2   Diversity

One aspect of the analysis of vegetation data (Chapter 4) is the evaluation of the diversity of plant species at both the extremes of the vegetation gradients as well as within the transition zones. The uses of diversity terms in this thesis follow the definitions presented by Whittaker (1977) and Scheiner (1992). When I refer to diversity I do not mean species richness which is simply the count of species for a survey site. In Chapter 4, the exploratory data analysis includes the calculation of the species diversity within each forest type (alpha diversity) and the change of diversity along the transects (beta diversity). Pattern diversity (Scheiner 1992), specifically its subset, compositional pattern diversity, which is the arrangement of the plot data in the mathematical space defined by the site-species matrix, and which, by its nature, often produces a similar result to ordination, provides a measure of the mosaic diversity for the study area.

Various measures of diversity are used by ecologists (e.g. the Shannon-Weiner index and McIntosh's diversity index) although these are essentially measures of equitability in that they are derived from species richness and species abundance. I agree with Whittaker (1977) that specific measures of equitability or evenness, such as Pielou's (1966) index, which is calculated by dividing the Shannon index by the logarithm of species richness, are of little additional value because they are sample-size dependent. The Shannon index makes two assumptions (Magurran 1988) that need some accommodation. Firstly, it assumes that the data represent a random sample from an "infinitely large" population and, secondly, it assumes that all species in the population are present in the sample. Therefore, it, too, is sample-size dependent. The difficulties with these assumptions can be overcome by utilising the bias eliminating technique called the jackknife as done by Adams and McClune (1979). This procedure derives a normally distributed set of pseudodiversity indices which are obtained by leaving out each sample in turn for the calculation of each pseudo index. The mean of the set of jackknifed indices provides the diversity index.

2.3.3   Competition

The mechanisms of competition within the plant community are still not nearly as well defined as that for the animal world. There exists a number of competing paradigms (Shipley and Keddy 1994), which reflects the difficulty of conducting field experiments to resolve the numerous questions (Goldberg and Barton 1992). Most of the literature discussing plant competition assumes the superimposition of the principal of competitive exclusion. The reality that many species co-exist, sometimes in profusion, suggests that an additional theory of competitive combining ability may apply (Aarssen 1989). Aarssen (1989, p 397) writes:

"Selection for competitive combining ability is an evolutionary mechanism of coexistence, i.e. it involves evolutionary changes as a consequence of selection from competition and depends upon within-species genotypic variation."

This is an idea which was approached from a different perspective by Allen and Hoekstra (1992) when they referred to "ancient accommodations" between species (see quote above). Such an idea is required to interpret the stability of certain plant associations in the absence of perturbation. A major feature of the study area is the absence of recent evidence of perturbation in conjunction with an apparent stability of the forest boundaries (see Chapter 5). This apparent stability of boundaries is a function of the temporal scales which apply to change at the edges of these forest types. Connell and Slatyer (1977) could find no evidence of stability within a community of sexually reproducing individuals such that the species composition had reached a steady-state equilibrium. They concluded, therefore, that succession never stops. Yet Lewontin (1969, quoted by Connell and Slatyer 1977; Wilson and Agnew 1992) described the incidence of temporal and spatial stable points in vegetation distribution. These spatial stable points can be likened to resource-concentrated refugia or "hot spots" (Diamond (1975).

Florence (1969b) lamented the lack of basic studies concerned with the nature of competition between and within species comprising the eucalypt forest. While some limited work has been conducted on the mechanisms of intra- and interspecific competition (e.g. Chilvers and Brittain 1972; Burdon and Pryor 1975; Incoll 1979; Ashton 1981c), that situation is essentially unchanged.

2.4 Analysis of floristics

2.4.1 Background

One of the most interesting aspects of modern interpretation of ecological data is the extent to which statistical and mathematical tools can be utilised. Since the mid 1970s when the power of personal computers became such that they began performing a significant and increasing range of tasks previously left to main-frames, the options for experimenters have developed accordingly. Already a huge literature has accrued in the field of ecological data analysis and much of it has relevance to this study.

Ecological data analysis is a field of applied statistical analysis in which Australian researchers have made a significant contribution. D.W. Goodall coined the term ordination (Goodall 1954) and has continued to stimulate thinking in this area (Goodall 1964, 1966a, 1966b, 1969; Goodall and Johnson 1982; Goodall and Feoli 1991). In the 1960s, bioanalysts W.T. Williams, J.M. Lambert, G.N. Lance and M.B. Dale in various joint papers provided important contributions to the understanding of classificatory tools, similarity indexes and analytical theory (Williams and Lambert 1959, 1960, 1961; Lambert and Williams 1962, 1966; Lambert and Dale 1964; Lance and Williams 1965, 1966, 1967a, 1967b, 1977; Williams and Dale 1965; Williams and Lance 1965; Williams *et al.*1966; Dale and Anderson 1972, 1973; Dale and Webb 1975). Dale is still contributing to pattern analytical theory (e.g. Dale 1988).

More recently, M.P. Austin, through his efforts toward accurately modelling the vegetation continuum, has effected a major advance with his models portraying the shape of response curves of individual *Eucalyptus* species to environmental variables (Austin 1976, 1980, 1985, 1987,1992; Austin *et al.* 1984; Austin and Smith 1989). P.R. Minchin (1987a, 1987b, 1989) has assessed ordination techniques and modelled complex community patterns. D.P. Faith (1983, 1984; Faith *et al.* 1987) has made very helpful evaluations of similarity measures and gradient analyses while L. Belbin (1993) has developed an internationally applied software package for pattern analysis.

2.4.2   Validity of the classification approach to vegetation
            analysis

Classification, or cluster analysis, of vegetation on the basis of similarity of distribution across sampling sites or, alternatively, classification of sites on the basis of the similarity of their floristics has become a standard, almost mandatory, outcome of most vegetation survey work since suitable techniques became available in the 1950s. Nevertheless, many workers, particularly those who are convinced that vegetation is distributed as a continuum, have had difficulty with these outcomes which impose arbitrary divisions in order to derive the relationships that may exist. For example, Whittaker (1956, p.31)

wrote: "it has not proved possible to establish the existence of associations as natural units by statistical means"; McIntosh (1967) also indicated that numerical classification was still on trial; and Florence (1969b, p.84) wrote: "The eucalypt forest is frequently far too complex to be readily subdivided into a small number of distinctive units". Goodall (1953), an advocate of the advantages of numerical classification of vegetation data, had anticipated such problems by reminding workers that numerical classifications classify the sample areas chosen, not the entire vegetation.

There are two major technical problems associated with numerical classification procedures. The first is that the algorithms operate until the data is exhausted. That is, they will find classes in any data regardless of whether such classes exist in nature or not and every datum ultimately becomes a class. A typical divisive classification system, however, does produce results with decreasing error estimates for its initial divisions. Unfortunately, these low errors reach a limit such that as division continues past this point, the error associated with each division begins to rise. The consequence is that classifications can become untrustworthy at their lowest levels. To counter the classification *ad absurdum*, uniformly-applied stopping rules have to be devised and imposed. The ideal classification should terminate each branch at the point when the error is at a minimum. The second difficulty was alluded to in Section 2.3.1.5 above and that is that classification algorithms do not take into account the fuzzy nature of natural divisions. In other words, they do not permit a class to have multiple group membership or for groups to overlap in vegetation space. This problem is essentially the basis of the difficulty that advocates of continuum theory have with numerical classification.

2.4.3 Existing classifications

Ever since Schimper's (1903) work, ecologists have been devising ways to classify vegetation. In Australia, a great many techniques have been described for a wide range of vegetation types and regions. The production of these techniques is mainly driven by a dissatisfaction with the application of pre-existing classifications to the range of the Australian vegetation. Johnston and Lacey (1984), in the course of

proposing yet another system, presented an excellent history of Australian work in this area. They pointed out that most of the systems proposed had not been trialled by other workers and by 1984 there were only three systems which were being used at all regularly. These were those of Webb (1959), Beard (1969) and Specht (1970). Johnston and Lacey (1984) however, in comments with which I concur, find fault with all these systems. Webb's (1959) has worked only with rainforest vegetation, Beard's (1969) has regional applicability only and with increasing use Specht's (1970) has been found to improperly classify too many particular associations. Even the system of Johnston and Lacey (1984) is limited to the consideration of the woody canopy layer only. Johnston and Lacey (1984) however, have identified the three basic requirements for a classification to be viable. These are that the classes are (1) based on intrinsic vegetational attributes only (Webb *et al.* (1970) had suggested that a structural-floristic classification might be possible and eventually Webb and Tracey (1981a) produced such a classification but this still was restricted to northern Australian rainforests), (2) valid at varying scales or depth of cluster, and (3) able to accommodate any community of the designated plant group.

More recently, Floyd (1990a, 1990b), drawing in part on the work of Baur (1965), has produced a classification of rainforests in New South Wales which has potential for application to the rainforest patches evaluated in this study. Floyd's (1990a, 1990b) classification is the current standard work but this system requires extensive field experience to operate with confidence. Floyd's rules require that at least one but no more than six species be rated as very common for the site (Floyd 1990a p 23) which can sometimes be an uncomfortable constraint, particularly when the species rated as very common are not necessarily Floyd's indicator species. The difficulty lies in the fact that his proposed classification is essentially intuitive rather than objective. This means that although each class is characterised by the abundance of one or more key indicator species, the intuitive classifier can accurately place a site into a particular class even in the absence of all the key species! Such flexibility is beyond the capacity of numerical classification algorithms.

2.4.4   Identification of vegetation patterns

The fundamental objective of this project was to study the vegetational response to the environment in terms of the resultant patterns that can be mapped in the vegetational mosaic. The extent of fuzziness of this mosaic is a measure of the variability of the boundaries of the mosaic components. It is also an indication of the response surface induced by the controlling factors for vegetation distribution. Pattern in the vegetation of a forest system has both horizontal and vertical expression. That is, the mix of species present at each point of observation indicates the horizontal pattern while the mix of size classes of those species gives rise to the vertical pattern. Vertical pattern is generally called structure. Structural patterns in vegetation are described in the next Section and will be analysed and discussed in the Chapter 4.

Horizontal pattern in Australian forests has two distinct manifestations. The first is the globally recognised pattern of co-occurrences of the same suite of species (albeit a disagreement about the causal mechanisms) and the second is the hierarchical organisation of pattern whereby an apparently homogeneous mix of forest canopy species overstand a range of understorey assemblages. This was observed by Ashton (1981b) who noted that there is no immutable association between eucalypt forest and any particular understorey which begs the question of interest to this project: is there an immutable association between the boundaries of eucalypt forest and those of the understorey at those locations? The mapping of understorey not only determined the range of associations that exist in that stratum but was also used to investigate the question of the concurrence of layer boundaries. The possibility, then, of a third manifestation of pattern which is layer oriented and not hierarchical was a question which was addressed by the data collection strategy which is described in Chapter 3.

The controlling factors for vegetation distribution may be allogenic, that is, those relating to the physical environment including chance exogenous perturbation such as fires and cyclones or they may be autogenic such as availability of propagules, growth related feedback

mechanisms (*sensu* Wilson and Agnew 1992), and random autogenic perturbation such as old-growth treefall. Various aspects of the physical environment were mapped in conjunction with the vegetation in order to model, not so much the extent to which they match the response surfaces of the vegetation, which I expected to be fuzzy, if not inconclusive, but to establish an appreciation of the *probability* of the relevance of the physical environment to the nature and location of the forest boundaries.

I noted that Webb *et al.* (1972) suggest caution when modelling small scale patchiness using environmental factors because the relevance of those factors may be difficult to establish. Modelling and hence making predictions from autogenic factors is much more difficult although it is attempted in this study by incorporating the interactions in both vegetation space and environmental space. Allen and Hoekstra (1992) have contributed significantly to an understanding of this difficulty of predicting community behaviour, a difficulty which is due to the often misunderstood lack of a "one-to-one mapping of community composition onto environment".

Allen and Hoekstra (1992), using terms drawn from the work of D.W. Roberts, point out that there is a relation between environmental and species spaces (Roberts 1989). A change in vegetation may induce an immediate change in one or more environmental factors (elastic factors) or a very slow change (plastic factors) or none at all. Hence the state of the environmental factors at any point in time is a consequence of past vegetation processes. They describe environmental space in terms of a response surface which may be dissected by areas of strong positive feedback or may be relatively flat and thereby not constrained to any particular vegetational trend. The flat areas would suit the continuum theorists while the dissected surface indicates a high reliability of vegetation prediction for such environments as expected by the supporters of the Clementsian theory of communities.

> "Both positive and negative feedback play important roles in the [visible] pattern. Add to this the complications of differences between elastic and plastic site factors. It then becomes clear how the same vegetation can occur in different physical

environments, and how different vegetation can occur in separate sites that replicate site factors. Therefore, vegetation is not a *function* of the environment, rather it has a *relation* to its environment." (Allen and Hoekstra 1992, p 150, emphasis added).

Associations of species are observable within main vegetation formations. The conventional pattern analysis techniques separate these groups whereupon their relevance, in terms of their incidence and distribution, to the nature of boundary variation can be evaluated. The problem with these conventional classificatory techniques is that they do not take into account the above relation between environment and species space such that there is no provision for multiple group membership as implied by the relation. There is also no indication of how much variation in environment is possible within any derived group. The explorations in pattern analysis refinement below which attempt to deal with this and other technical problems in numerical classification draw, in part, on the ideas of Allen and Hoekstra (1992), Roberts (1989) and Collins *et al.* (1993).

2.4.5   Transition zone vegetation pattern

Other researchers (Smith and Guyer 1983; Bell *et al.* 1987; Ash 1988; Unwin 1989) have reported a band of vegetation of distinct structure around identifiable rainforest stands. Bell *et al.* (1987) noted the dominance in the transition zone of *Eucalyptus grandis* or *E. resinifera.* and Unwin (1989) recorded only three species over 6 m in height. Still in Queensland but further south, Cromer and Pryor (1942) recorded less than ten species growing as trees in the transition zone. Unwin (1989) further indicated that the structure and composition of the rainforest became more homogeneous near and at the boundary of the formation. From those findings it is apparent that in north Queensland the transition zone is comprised of only a few canopy species.

None of the above researchers, however, specifically identified the existence of a vegetation association that could be categorised as a boundary community. If such a community was identifiable, it should exhibit the following characteristics:

- contain a set of species of sufficient longevity to not be regarded as secondary successional species;

- its diagnostic species should be able to reproduce under their own canopy.

2.5 Analysis of vegetation structure

2.5.1 Introduction

One of the analytically useful and easily measurable facets of vegetation change along the gradient from one community to another, is the concomitant change in vegetation structure. The onset of change in structure along the gradient has been shown to herald the transition from one community to another. Unwin (1989) noted the change in rainforest structure close to the boundary and Bell *et al.* (1987), Ash (1988) and Unwin (1989) have noted the increased size of sclerophyllous species when adjacent to the boundary with rainforest. The extent to which the structure of the vegetation in the transition zone differs from that at the extremes of the gradient may be used to evaluate the dynamics of the transition zone itself. An analysis of the variation in structure between separate transition zones and between the transition zone and the adjacent WSF and WTRF was thought would indicate whether there is a relationship between other boundary characteristics and the vegetation structure within the boundary region.

2.5.2 Identification of the range of structural types

The forest is comprised of a taxonomy of growth forms. The Orders could be regarded as the trees, the lianes, the shrubs, the herbs, and the lower flora. Within the trees we can think of Families split according to crown shape, crown density and average plant height and basal area. The lianes can be split on the basis of their height preference; shrubs by shape and crown density; herbs by habit, substrate preference, and population density. Lower levels of this "taxonomy" are separated by other aspects of plant architecture. In the case of trees, such aspects

include branch angle, the proclivity to form multiple stems and regenerative capabilities.

Tree architecture has much to do with the growing environment, the microclimate, which is likely to vary for each vegetation formation and which is a subject of this study. Honda and Fisher (1978) showed that branch architecture is designed to maximise the effective leaf surface area and Hallé *et al.* (1978) have developed a much more sophisticated taxonomy of plant architecture than that outlined above. In a useful paper, Porter (1989) has followed up some of the ideas of Hallé *et al.* (1978) with respect to the canopy phenology. For the purposes of developing an appreciation of the structural variation I wanted to know the extent of the range of the various architectural types within each growth form across the vegetation gradient.

2.5.3   Sources of variation

The local variation in structure of the various forest types is not necessarily an outcome of evolution and species competitive abilities. Although those factors are fundamental at the scale of the forest formation, at the within-forest scale the actual species occupying any particular location and the consequent forest structure at that point is commonly due to the environmental disturbance history. Variation in forest structure may also be partly influenced by the sporadic activities of invertebrates, although that possibility was not investigated during this study.

The most dramatic disturbance effects are chance allogenic events such as fire (fire as an autogenic event does not seem to be a factor in these forests), which at least seriously affects the understorey; cyclone, which can knock down or seriously damage the canopy; and landslip, which can result in the localised instant removal of the entire forest. All of these factors may cause short or long term alteration of forest structure. Sometimes the effects are delayed as often damage inflicted on a tree by such perturbations may go unnoticed for several years until the tree suddenly dies from the consequences of subsequent fungal or termite invasion and breakdown of its woody tissue.

Past disturbance at a forest study site can often be inferred from such data as the mix of species present at that location, the age classes of those species, the health of individuals, the comparative growth symmetry among conspecifics and the presence on trees of bole scars resulting from previous damage. The presence of pioneer or secondary successional species within a mature forest is a certain sign of a past disturbance which resulted in the removal of forest canopy. The date of such a disturbance can be fixed by the apparent age of the successional species present. In WTRF, there is a suite of species which are regarded as secondary species (Floyd 1989) and in WSF, a number of genera including *Banksia* and *Allocasuarina* (Beadle 1981) can be used to date fire in the understorey while the height (i.e. age) and species composition of the canopy of WSF essentially dates the last wildfire.

Minor disturbance events such as lightning strike and treefall are often indicated by either remnant logs; aged secondary species or vines; the proliferation of species which prefer to grow on exposed subsoil such as *Dawsonia* spp; and secondary impacts such as soil erosion. In some instances point disturbance can be inferred from the incidence of crookedness in tree trunk development or orthotropic growth away from the vertical.

The extent to which disturbance may have contributed to the current structure of the forest sample plots was addressed in the formulation of the study objectives.

2.5.4   Structural arrangement

Structural diversity present in the forest gives the forest its particular visual character. The arrangement of forest cover in forests generally has several dimensions. Firstly, there is the vertical organisation which is manifested as vegetation layers. Secondly, there is the variation in leaf densities within crown types. Thirdly, there is the packing density of similar crown types within the layers and fourthly, there is the pattern of spatial distribution of the tree architectural types. Consideration of all of these dimensions of structural diversity may lead to the possibility of developing a physiognomic classification of structural types within the forest formations.

The main effects of forest structure are on the rate at which the amount of available light diminishes from the canopy to the forest floor, on the patterns of air movement within the forest and on the hindrance of the progress of juvenile canopy plants from the understorey layer to the upper forest layers. The main impact of canopy crown characteristics is on the temperature and light levels within the forest. Chauvin (1967) noted that when solar radiation falls below 16% inside northern hemisphere forests, the forest floor will be bare and scattered bushes do not appear until it reaches about 25%. Turton and Duff (1992) demonstrated the concomitant change in light regimes with change in forest structure along the gradient from open forest to rainforest in north Queensland. The low airflow velocity within rainforests reduces dessication rates allowing the proliferation of bryophytes, lichens and fungi but also virtually eliminates the incidence of anemochorous understorey species in that formation.

The existence of vegetation layers within forests is well documented for many forest types (Hallé *et al.* 1978; Parker 1995) especially for rainforests where the mix of forest layers is most pronounced (Richards 1952,1983; Grubb *et al.* 1963) . Forest layers have also been recognised for the tall eucalypt forests of eastern Australia (Jacobs 1955). Forest layering is essentially the result of the physical arrangement of an aggregation of plant growth form types.

Terborgh (1985) presented a simple model of the phenomenon of forest layering. The model proposed that as light passed through the forest canopy an environment of mixed light and shade occurred immediately below the canopy. At a level slightly lower, the bases of the cones of light intersect such that the shaded area is at a minimum. It is at the height of this level that a non-canopy species maximises the amount of light available to it and hence the layer forms. The model postulates that a similar process controls the development of any subsequent layers. Pukkala *et al.* (1991) showed that light is a plausible factor in structuring vegetation but that the situation is somewhat more complicated than Terborgh's (1985) basic model, although they conceded that further investigation was still required.

Models of radiation penetration, however, often assume (1) there is a uniformity of leaf distribution within crowns, (2) that the shadow contribution of branches and stems can be ignored and (3) that penetration does not change with solar direction. Depending on which type of Australian forest is under consideration, at least one of these assumptions cannot be relied on with confidence when modelling radiation penetration. These same assumptions are perpetuated in this study with respect to the analysis of the distribution of packing arrangements of tree crowns and the predicted consequences in terms of the changes in amounts of light penetration along the vegetation gradient.

Pukkala *et al.* (1991) found that the number of shade level minima increase with the crown height/crown width ratio. Essentially, the number of minima increase with the packing density of crowns which suggests that for rainforest, in which canopy tree abundance is greater than the wet sclerophyll forest, the evidence of layering should be more apparent. At greater depths below the canopy however, light levels are often too low to support plant life yet the fact that even in the closed-canopy, putatively multi-layered rainforest, plant life persists on the forest floor indicates that the role of sunflecks in supporting plant growth processes is critical (Chazdon 1988) and may also be important to sub-canopy layers. Jacobs (1955) measured the light levels at the floor of a high quality WSF as being 2.5-5.0% of that above the canopy. Turton and Duff (1992) found direct light levels at 1.3 m in tropical rainforest to be 0.3-5.5%. The importance of sunflecks, emanating from microclimate-scale canopy movements, is indicated by those figures as the understorey in Australian wet sclerophyll forests is ubiquitous and often profuse. Although Turnbull and Yates (1993) believe that sunflecks, as representing direct, unfiltered sunlight, were fairly unlikely on the rainforest floor, my experience suggests that it is quite commonplace in WTRF. Chazdon (1988) found that the direct light from sunflecks contributed up to 78% of the total light reaching understorey plants. The incidence of sunflecks within the WTRF was not, however, measured in this study.

The typical structure of the WSF and WTRF, as well as the TZF, are shown in Plates 10 to 15 and these should be used as basic references throughout the discussion topics pertaining to forest structure.

2.6 Forest microclimate

2.6.1 Introduction

The climate of the forest, directly or indirectly, determines the timing and prospects of all stages of plant and animal development. In fact the vegetation of an area can be used as an integrated interpretation of all the climatic elements (Lee 1978). The climate can be divided into two distinct classes, the microclimate and the macroclimate. While both classes are concerned with the same components, namely, rainfall (absolute humidity), wind strength (air currents) and solar radiation (temperature), the differences are found in the intensity of changes that occur with time and elevation (Unwin 1978). The macroclimate is essentially the climate as measured by meteorologists. While the macroclimate is critical to the formation and maintenance of a forest environment, it is the microclimate which holds particular fascination for forest ecologists. Microclimatology is a branch of meteorology pioneered by Rudolph Geiger (e.g. Geiger 1965) which is concerned with analysis of the uniform climate in small areas. Ecologists are interested in the microclimate of the immediate environment of biological entities (Chauvin 1967). The main objective of microclimatology is to "describe the state of the atmosphere to which living organisms are exposed" (Elston and Monteith 1975, p.1).

Climate modification within the forest is due almost entirely to the depth, density and packing arrangements of the leafy crowns of the overstorey. The resultant magnitudes of the components of forest microclimate are a measure of the extent to which the forest structure modifies its external environment (Russell *et al.* 1989). These components importantly affect plant water stress which affects photosynthesis and the level of abscisic acid (Aba), the hormone involved in dormancy and abscission (Raven *et al.* 1981). Plants respond to the strength of the microclimate components in several ways.

Plate 10. Wet sclerophyll canopy structure. The upper canopy
is comprised of the open spreading limbs of very tall
individuals of *E. pilularis* (at left, right and middle
distance of photo). The midlayer is dominated by the
fine leaved *A. torulosa* (dark-leaved tree in centre)
while the thin stems of *Elaeocarpus*, *Persoonia* and
Cryptocarya are very common.

Plate 11.   Wet sclerophyll understorey structure.   The understorey is typically dominated by tall sedges (*Schoenus* and *Lepidosperma* spp) and the fern *Sticherus lobatus*.   At left is the large, common shrub *Acrotriche aggregata*, while scattered across the photo are the thin stems of *Elaeocarpus reticulatus* and *Persoonia media*.

Plate 12.   Transition zone structure.   The canopy of this
formation is punctuated by the overtowering of a
scattering of very tall specimens of *E. pilularis*
(centre of photo).   Typically, a strong rainforest
element (commonly *Callicoma*) comprises the mid-
layer.   The understorey is often sparse and the photo
shows the evidence for this feature which is discussed
further in the text.

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Plate 13. Transition zone structure. The mid-layer is
sometimes a congestion of both rainforest and wet
sclerophyll elements. The photo shows a mixture of
the smooth stems of *Callicoma* and the rough trunks
of *Allocasuarina* Behind the tall sedge (*Lepidosperma
elatius*) in the foreground, the open understorey of
the transition zone is apparent.

Plate 14.   Warm temperate rainforest structure.   The main
canopy species in this formation is *Ceratopetalum*
(centre of photo).   The mid-layer is rich with many
species present.   Typical growth forms of rainforest
are present in the photo: the palms *Archontophoenix*
(tall stem on right) and *Linospadix* (centre).   The
treefern, *Cyathea leichhardtiana*, appears in the centre
background.

Plate 15. Warm temperate rainforest understorey structure.
The dense packing of a large number of mesophyllous
species typifies the understorey of this formation.
In the foreground are the fronds of the very common
climbing palm species *Calamus muelleri* which often
colonises forest gaps in such density that it forms
almost impenetrable thickets. The other two species
of palm are also present. At the centre of the
photograph is a young specimen of the large-leaved,
small tree *Anopterus macleayanus*.

Morphogenetic responses to higher temperatures may include rapid stem elongation, incorporating higher rates of photosynthesis and development of 'sun' and 'shade' leaves, that is, leaves varying from low to high specific leaf area. Phenotypic responses include the timing of dormancy, bud breaks, flowering and germination, leaf abscission, fruiting and several thermonastic and thermoperiodic responses. In fact most biological reactions have a clear optimum temperature. Plants can respond to changing light regimes in up to four ways (Jones 1983). These are phototrophism (including diaheliotrophism and paraheliotrophism), photonasty, photoperiodism and photomorphogenesis. The outcome of this relationship between plants and their microclimate occurs in a context of competition between species and individuals.

2.6.2   The status of forest microclimatic research

2.6.2.1   International work

Most of the modern international work in relation to forest microclimates flows from plant physiological studies concerned with assessing likely forest responses to the rising levels of CO_2 in the atmosphere. The already elevated levels are expected to double sometime early next century (Houghton and Woodwell 1989). Studies so far indicate that under the influence of a regime of elevated CO_2, plant responses to and utilisations of all other environmental variables are radically altered (e.g. Conroy 1992; Ball and Munns 1992) such that the value of past studies of forest microclimates is being diminished by the new climatic exigency. Nevertheless, since Geiger (1965) established the discipline of microclimatology, several outstanding contributions have been made. Monteith (1975) has edited the standard work while useful general textbooks have been produced by Yoshino (1975), Lee (1978) and Jones (1983).

2.5.2.2   Australian studies

Australian forest microclimatological studies in the past have been primarily concerned with the relevance of the work to production forestry. Consequently, there have been a number of papers reporting

the frost sensitivity of the seedlings of various timber species and the responses to other climatological aspects such as water stress and wind. These works have also been conducted in a research environment where the most fashionable general climatological topics have been in the presumed more economically relevant area of the recently

recognised (in the western Pacific region) El Niño and Southern Oscillation effects. Further, the past Australian studies have, to an extent, lost their relevance because, until very recently, there had been no hard evidence to justify taking into account the expected doubling of CO_2 concentrations. The relevance, therefore, of these previous works to natural unmanaged forests might be limited. Plant physiologists have also worked on the ecophysiology of certain species. Some of these include Connor *et al.* 1977 (*Eucalyptus regnans*); Doley 1978 (*E. grandis*); Körner and Cochrane 1985 (*E. pauciflora*) and Doley and Yates 1991 (rainforest trees). The latter workers, however, lamented the lack of physiological data for rainforest species from which their microclimatological preferences could be predicted.

Roberts (1964) was one of the early workers with his study of temperature and moisture variation across the air-litter-soil boundaries which pursued an understanding of the behaviour of forest fires. Dale (1972, 1973) undertook a comprehensive study of the temperature and air current profile in a eucalypt forest from above the canopy down through the canopy to the ground and, for temperature, up to 50 cm below ground. Bale (1980) proved a variation in microclimate could be attributed to a range of topographical parameters in WSF. Unwin (1983) reported on forest edge seedling and and sapling responses to light availability. Aston (1985) determined the heat storage capacities of the various components of the biomass of a eucalypt forest and the rates at which these components accumulated and discharged their heat store. Duff (1988) measured the changes in ground level light intensity from tropical rainforest to open woodland and more recently that work has been followed up by Turton and Duff (1992) who related the changes in available light to the structure and floristics of the tropical forests.

Recently attention has been turned to the modern climatic situation (e.g. Wong *et al.* 1992) but there have been no past attempts to study the

microclimate gradient from eucalypt forest to rainforest in subtropical Australia to relate to research on climate change. This project contributes a beginning to this topic.

2.7 Forest litterfall

2.7.1 Introduction

The production of vegetative litter is central in the process of nutrient and energy cycling, the maintenance of faunal habitat, the provision of the propagule germination environment (indirectly in the form of post-fire ash in the case of *Eucalyptus* and some other understorey WSF genera) and the amelioration of extremes of soil moisture and temperature. The presence of the standing litter crop has influence over the structure of ground herbs (Givnish 1982) and is pivotal with respect to the scale of the ecosystem processes of fire and surface erosion. In the mature forests of the study area, where the biomass has become more or less constant, the annual litterfall is also an index of the productivity of the forest (Attiwill and Leeper 1987). Bray and Gorham (1964, p 104) wrote that

> "the study of quantitative aspects of litter-fall [is] an important part of forest ecology, dealing with a major pathway for both energy and nutrient transfer in this type of ecosystem"

2.7.2 Status of litterfall research

2.7.2.1 Sclerophyll forests

Most studies of litter in Australian forests have occurred in the various types of sclerophyll forests which represent the major proportion of the forested landscape. These studies, while varying in their specific objectives, have generally been concerned with aspects of nutrient return via the plant litter to the soil and eventually to the standing forest. Few studies (e.g. Birk 1979) have been concerned about the subject of litterfall *per se* with the consequence that data tend not to

be analysed by species and rarely by the full range of component parts. Nevertheless, they have almost all addressed the question of what is the rate of litter accession such that there is now a useful body of literature portraying litterfall patterns across the continent. There is, however, a paucity of data from old-growth WSF in the high rainfall areas of northern NSW. Only Webb *et al.* (1969) have obtained litterfall data from a forest and environment comparable to that occurring in the study area. No work has been specifically carried out in forest transition zones (although Turnbull and Madden (1983, 1986) did study the litterfall in a transition site between forest and open sedgeland) let alone the old-growth WSF - WTRF transition zone of the high rainfall areas of northern NSW. Hutson and Veitch (1985) also lamented the paucity of litterfall data from sclerophyll forests with annual average rainfall exceeding 1800 mm.

The earliest reported work with *Eucalyptus* sclerophyll forest litterfall was Hatch (1955) who worked in the *E. marginata* forests of Western Australia. Hatch (1955) reported on the rates of accession and decomposition of the litter and also assessed the nutritional value of the litter layer. Aspects of this general pattern of study were pursued by many workers in the following years in New South Wales including Hannon (1958), Florence (1961), McColl (1966), van Loon (1969), Webb *et al.* (1969), Park (1975), Richards and Charley (1977), Watson (1977), Fox *et al.* (1979), Bale (1980), Pressland (1982), Briggs and Maher (1983), Turner and Lambert (1983), Pook (1984) and Lamb (1985); in Western Australia including O'Connell *et al.* (1979) and O'Connell and Menagé (1982); in Victoria including Gill (1964), Attiwill (1968), Ashton (1975), Attiwill *et al.* (1978) and Baker (1983); in A.C.T. including Hutchings and Oswald (1975), and Thomas *et al.* (1992); in Queensland including Rogers and Westman (1977), Birk (1979), Plowman (1979) and Burrows and Burrows (1992); in South Australia including Lee and Correll (1978) and Hutson (1985) and in Tasmania represented by Turnbull and Madden (1983, 1986).

Comparative summaries of most of the results from these studies have been presented by Bevege (1978), Walker (1979, 1981) and Hutson and Veitch (1985). In Chapter 4 the results of the litterfall measured

during this study will be related to those obtained by these other researchers.

2.7.2.2 Rainforests

Studies of rainforest litterfall have been greatly outnumbered by the work in sclerophyll forests. This is due not only to the smaller area occupied by rainforests but also by the complexity associated with the increased numbers of species and the concomitant variation in species distribution and range of chemical composition of the litter of each species. Lamb (1991) reported on the work carried out on rainforest litterfall such as it was. As would be expected, most of the work has been conducted in Queensland by Bailey (1976), Plowman (1979), Brasell *et al.* (1980), Spain (1984), House (1986), Hopkins and Graham (1989), Hegarty (1991) and Benson and Pearson (1993) but also in New South Wales by Webb *et al.* (1969), Watson (1977) and Lowman (1988) and in Tasmania by Turnbull and Madden (1983, 1986).

2.7.3 The role of litterfall and seedling survival

The extent of litterfall in the forests has the potential to significantly influence seedling success through the development of its standing crop state and also through its support of mycorrhizal and general microfloral ecology especially in the wet sclerophyll forests. The standing litter crop has been well recognised in the role that it plays in the spread of forest fires and it is the actuality of these forest fires which eliminate seedlings of the mesic, fire-intolerant rainforest species which might otherwise replace the pre-existing understorey leading to eventual permanent colonisation. So, by facilitating the spread of fire, the standing litter preserves a growing environment suitable to sclerophyllous species.

The second way in which the litter contributes to the control of seedling development is by virtue of the nutritional support it provides to microbial processes. Florence and Crocker (1962) have documented how the soil derived from the humus layer in Blackbutt forests is able to suppress the growth and survival of Blackbutt seedlings. The actual role of the humus is somewhat complicated as Incoll (1979) has shown

that it is limited to the zone of the root ecosystem of the mature canopy individuals.

A possible third seedling control consequence of litterfall was investigated by Wilson and Zammit (1992). They confirmed that the depth of litter on the ground does have the effect of suppressing germination. Wilson and Zammit (1992) recorded increased seedling densities at those sites from which litter was removed and decreased densities at those sites to which litter was added. They noted, however, that these trends did not persist into the second year due to the re-established influence of other factors.

It appears, therefore, that, particularly for WSFs, but also for the adjacent TZFs, the volume, and temporal distribution of litterfall have a significant influence on seedling establishment. It is the species range of seedling establishment in the TZF, of course, which determines the future make up of the boundary zone.

2.8   The role of fire

Fire is the major Australian agent of control of vegetation dynamics, vegetation structure, plant biology and even vegetation evolution. The establishment and distribution of *Eucalyptus* forests are generally agreed to be a function of local fire histories. In recent years, a number of researchers has begun to question this established wisdom, particularly with respect to the dependence of certain species on fire and that the so-called pyrophytic flora have selected in response to the presence of fire. This position has been questioned by Florence (1964, 1968) with particular reference to *Eucalyptus pilularis* forests. Florence argued that, in the case of *Eucalyptus pilularis*, fire is of secondary influence to the distribution of a species which was primarily responding to the distribution of particular suite of soil physical factors. While it is possible that the maintenance of the location and nature of boundaries of *Eucalyptus pilularis* forests may be realised through the periodic revisitation by fire, in this study area a typical range of boundary characteristics and dynamics have been maintained in the absence of, at least, short cycle periodic fire.

Mutch (1970) described the hypothesis of selection for fire which many writers (e.g. Carpenter and Recher 1979) have assumed to apply. Snyder (1984) has proposed an alternative explanation for the evolution by some species of attributes which render them less susceptible to elimination by fire. The analyses of Baur (1957) followed by Turner and Lambert (1983) of wet sclerophyll forests suggest that in the absence of fire they would be overtaken by rainforest. This is an assumption about which Florence (1964, 1968) has expressed doubts. He argued that if the rainforest was to overrun the WSF, the resulting arrangement would be unstable such that it would easily revert to the prior condition. A fresh aspect on the question was provided by Barrett and Ash (1992) who grew the key species which occur in the WTRF-WSF gradient under laboratory conditions. From differences recorded in growth and carbon partitioning, they determined that the separation in the distribution of these species on that vegetational gradient was primarily due to biological responses to the environmental gradients and that fire, as an agent of vegetation pattern, was a secondary factor. Fire histories and inadequate knowledge of fire behaviour where rainforests are involved can also serve to confound otherwise good explanations for the location of forest boundaries. Webb (1969), and later in Webb and Tracey (1981b), blamed the influence of fire for the breakdown of his correlation between forest type and soil nutrient levels which occurred in the submontane subtropics and Ridley and Gardner (1961) expressed the belief that the burning of rainforest in southeastern Australia is underestimated by botanists because of the similar result (i.e. vigorous colonisation by *Lantana camara*) to that of thickets developing on abandoned cultivated land.

The extent to which fire is an important contributive factor in the study of local vegetation dynamics is always a complex issue. The conditions at the time of a fire, in terms of available fuel, prevailing weather and recently past weather, the topography and the type of vegetation are variables which can profoundly effect what a fire actually burns. In general fire intensity increases with annual rainfall due to an increase in fuel availability but the frequency tends to decrease. The fuel quality, however, is modified by the soil nutrient content as poor soils tend to support a sclerophyllous understorey

which is low in mineral matter and therefore highly flammable. Eucalypts on poor soils benefit from an increase in fire frequency because of the nutrient release triggered by virtue of the high leaf oil content, low flashpoints of the oils and their decorticating bark.

Ridges and spurs exposed to dry winds are usually the sites of these poor soils such that they tend to burn hotter more easily. Barrett and Ash (1992) concluded that while fire was strongly controlled by vegetation type, it did not directly control vegetation distribution in their study area. In the absence of a pattern of regular fires, the data gathered during this project supports their thesis.

While nominating a range of climatic, topographic and edaphic variables that have relevance to vegetation distribution and hence boundary location, Ash (1988) concluded that a knowledge of these variables is still not enough to predict existing boundaries in tropical Australia because of the unknowable component of historical fire patterns in relation to historical vegetation patterns. Ash (1988) concluded that it was possible that in some locations there had "been a continuity in burning regime, with a fire at least every 10-20 years, maintained for 5000-10000 years". Such a fire frequency does not apply in this study area and, although there may be an underlying frequency with far greater fire-free intervals, a knowledge of a certain suite of predictor variables may indeed be adequate to predict boundary distribution for rugged terrain sites in subtropical Australia. Currently, researchers at the University of Melbourne are working on the derivation of just such a modelling process which achieves long term prediction of forest boundary locations for temperate Australia (A.Taplin pers. comm.).

2.9   Analytical techniques

A range of analyses and statistical tests were utilised to achieve the above objectives within the limits of the data available. Both pattern analysis and predictive modelling procedures are implemented wherever possible. As indicated above, pattern analysis has benefitted from a considerable research effort, particularly during the 1970s and 1980s with the result that there are always several options for analysis. The

particular options selected for classification and ordination will be discussed in the analysis section within each chapter.

Austin and Cunningham (1981) introduced logistic regression in the form of Generalized Linear Models (GLMs) to data analysis of vegetation. GLMs (McCullagh and Nelder 1983) assume a linear combination of all relevant variables in the predictive model and enable the specification of a non-linear form, but Austin and Cunningham (1981) echoed the call made earlier by Austin (1980) that there remained a need for an appropriate model for gradient analysis which specified an appropriate error function and response slope. They asserted that smoothed curves without data points were no longer enough. A new class of model, the Generalized Additive Model (GAM), which promised to overcome the limitations of GLMs, was published by Hastie and Tibshirani (1986), yet the only use of GAMs in vegetation science so far has been by Yee and Mitchell (1991) despite the greatly expanded theoretical contribution by Hastie and Tibshirani (1990). This may be due to the fact that the statistical establishment is still wary of GAMs because there is a concern that their theoretical validity has not yet been unequivocally established (Dr W Venables pers. comm.).

Notwithstanding that concern, GAMs are used extensively for predictive modelling in this study. GAMs are superior to GLMs for modelling ecological data in that (a) they do not assume some parametric form for the predictive variables and (b) the variables are smoothed and each term enters additively into the model. The GAM has the advantage of being able to reveal nonlinearity within the variables.