The Foliar Physiognomic Analysis and Taphonomy of Leaf Beds Derived from Modern Australian Rainforest.

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APPENDICES.

ABSTRACT

Previous foliar physiognomic analyses of fossil floras are criticised for comparing the characteristics of vegetation, and often particular synusiae, to what is not fossilised vegetation but leaf beds. The use of the proportion of species represented in foliar physiognomic classes is criticised for introducing further sources of error. Leaf beds are predicted to contain leaves from all forest synusiae, and taphonomic processes are predicted to produce a bias towards a different foliar physiognomic character than observed for canopy trees.

Many of the Tertiary floras reported from Australia are considered to have a "Tropical character". Webb's physiognomic classification of Australian rainforest has been used in this study as a framework to determine the taphonomic bias of leaf assemblages derived from Australian tropical rainforests, and interpret the "Physiognomic Signature" retained in these leaf assemblages.

Leaf litter was used as an analogue of fossil leaf beds, and collections were made from four of Webb's types of Australian rainforest — Microphyll Fern Forest (MFF), Simple Notophyll Vine Forest (SNVF), Complex Notophyll Vine Forest (CNVF), and Complex Mesophyll Vine Forest (CMVF). Replicate samples were collected at each of three sites for each forest type. Collections in NE Queensland allowed comparison between all four types from within a small geographic area, while collections from New South Wales were used to compare CNVF and SNVF from the latitudinal extremes of their modern distribution.

Leaf litter from each of these forest types was found to retain a unique "Physiognomic Signature" reflected in the frequency distribution of leaf length, width, and the position of greatest width. Leaf length for the litter was strongly correlated with the mean annual temperature of the collection sites, whereas leaf width for CNVF and MFF appeared to be interacting with a complex of factors.

The physiognomic signature of SNVF leaf litter was found to be distorted by stream transport by a decrease in the proportion of larger leaves in the leaf assemblages. The higher proportion of individuals with non-entire leaf margins for SNVF in New South Wales was thought to provide a sensitive indicator of a physiognomically distinct streamside vegetation. However, there was no sig-

nificant difference between the physiognomic character of streamside plants and litter samples from the forest interior.

The effects of tree position and size on the representation of local taxa in leaf litter was tested. Frequency of occurrence of taxa as leaves in the samples was compared to the position and size of the source trees to the litter collection points. Leaves were found to be very resticted in their ability to travel far from their source tree.

Analysis of the level of variation of leaf morphology within species found that the predicted dimorphism for rainforest trees between the 'sun' and 'shade' leaves represented two poles of a continuum. The idea that the physiognomy of the leaves of particular species could be used to predict their synusial origin was tested and rejected.

This study concluded that leaf beds retain a unique physiognomic signature which must be corrected for the streamside taphonomic bias to allow identification of the type of forest and the climatic characteristics of the source vegetation of fossil leaf beds.

This study has therefore demonstrated that by studying analogues of fossil leaf beds — leaf litter from the forest floor and from stream beds — it is possible to measure the transformations wrought by taphonomic processes. By understanding these transformations, or biases, it is then possible to analyse fossil leaf beds and extract a high level of information about the ecology and nature of past vegetation, and in turn reconstruct past climates and test existing models of ecological processes.

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma and, to the best of my knowledge, contains no material previously published or written by any other person except where due reference is made.

David R. Greenwood.

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Chapter 1

INTRODUCTION

1.1 The Palaeoecological Analysis of Australian Tertiary Vegetation.

One of the major purposes of palaeobotanical studies is to determine the character and composition of plant communities in the past. Analysis of plant fossil beds may proceed in several often interrelated directions, and may utilise macrofossils — vegetative and reproductive parts — and/or microfossils — e.g. pollen. A fossil flora is then usually interpreted by analogy to modern vegetation.

Palaeoecology is primarily concerned with the interpretation of community interactions, either between organisms within palaeocommunities, or between communities and the environment. However, often palaeoecological studies have been primarily concerned with determining the climatic relationships of a fossil flora, the palaeoclimate, in order to interpret regional and temporal variation in climate (e.g. Axelrod and Bailey, 1969). However, fossil plant beds can also be used as tests of ecological theories as they represent "natural experiments" (Knoll, 1986).

Within Australia, Tertiary plant beds have generally been considered as collections of fossil taxa. By this I mean that the approach has been to describe individual taxa from fossil localities separately, with little consideration given to the associations of taxa present or the character of the assemblage (e.g. Cookson and Duigan, 1950; Cookson and Pike, 1956; Blackburn, 1978; Hill, 1978; Christophel, 1984). This approach could be termed the "catalogue approach" as its central aim was to describe the material and identify the modern (or otherwise) affinities of the fossil taxa; producing "catalogues" of fossil taxa (e.g. Duigan, 1951).

These studies extend the known temporal and spatial distribution of some modern groups (e.g. Cookson and Pike, 1956; Hill, 1978 1987a; Christophel, 1984; Christophel and Basinger, 1985; Greenwood, 1987) and so add to the understanding of the phytogeography of the Australian Flora. However, they provide only general interpretations of the communities from which the plant material is sourced.

A second and important source of information has been palynological studies. These, however, have been the source of much confusion about Australian Tertiary vegetation. For example, until recently the vegetation of southern Australia during the Early Tertiary was considered to have been dominated by the southern beeches (*Nothofagus* Blume Fagaceae) and the austral conifers (Podocarpaceae and Araucariaceae) on the basis of the dominance of sediments of this age by palynomorphs of these taxa (e.g. Kemp, 1977 1981; Barlow, 1981 1982).

Until recently however, reliable macrofossil evidence for the presence of *Nothofagus* in southern Australia in the Early Tertiary has been lacking (Christophel, 1981 1986; Hill, 1984 1987a & b; Hill and Macphail, 1984). The majority of Australian Early Tertiary macrofossil floras have indicated a diverse association of taxa with affinities primarily to modern genera found in rainforest (Cookson and Pike, 1953; Christophel and Blackburn, 1978; Blackburn, 1981; Christophel, 1981 1984). These associations have generally been interpreted to indicate the presence of subtropical to tropical rainforest (Duigan, 1966; Christophel, 1981), vegetation types in which *Nothofagus* is absent today.

More recently, Australian Tertiary plant beds have begun to be examined with the intention of interpreting the character and composition of Tertiary vegetation, rather than adding to the "catalogue" (e.g. Christophel, 1981; Christophel, et al., 1987; Hill and Macphail, 1984). This situation reflects a world trend towards more quantitative approaches to the analysis of fossil plant beds (Spicer and Hill, 1979; Birks, 1985), and incorporates the use of parallel studies on the process and circumstances of fossilisation, or taphonomy (e.g. Scheihing and Pfefferkorn, 1984). These latter studies in particular, are altering the methodologies of collection and analysis (Birks, 1985; Knoll, 1986).

1.2 Palaeoecological Methods.

The ecology and climate of fossil vegetation is usually predicted by one of two methods (Axelrod and Bailey, 1969; Dorf, 1970; Wolfe, 1971; Roth and Dilcher, 1978; Martin, 1986):

1. the extrapolation of the ecological and climatic requirements of modern species to identified close relatives in a fossil flora;
2. the extrapolation of correlations between the prevailing leaf morphology, or physiognomy, of modern forests, to the physiognomy of the leaves in a fossil flora.

The first approach may be termed "floristic analysis" (Wolfe, 1971) as it relies on the observed correlations of modern floristic associations and climate. The second approach is usually termed "foliar physiognomic analysis" (Wolfe, 1971 1980a & b; Dolph, 1978; Roth and Dilcher, 1978) or "leaf physiognomic analysis" (Davis and Taylor, 1980; Christophel, 1981; Christophel and Greenwood, 1988). Both methods require uniformitarian assumptions and it is the application of these assumptions which draws criticism for both methods (Axelrod and Bailey, 1969; Dorf, 1970; Wolfe, 1971; Dolph, 1978; Martin, 1986).

Several other methods have also been employed to predict climate from plant fossils. For example, Lange proposed a system for determining precipitation from epiphyllous fungal structures. Lange found correlations between precipitation and the level of morphological complexity (grade) of both epiphyllous fungal "germlings" and Manginuloid hyphae found on leaf cuticles in a "standard search" (Lange, 1976; 1978). This method however, seems to have been largely ignored by the palaeobotanical community.

More recently, tree-ring analyses of rainfall and climatic seasonality have been applied to Mesozoic and Cenozoic woods (Creber and Chaloner, 1985; Francis, 1986). This method, however, has a restricted use as most Australian Tertiary wood lacks clearly defined rings (pers. observ.).

1.2.1 Floristic Analysis.

Floristic analysis is based on the uniformitarian assumption that fossil species closely related to modern species would have had the same ecological requirements (primarily thermal) as the modern species (MacGinitie, 1969; Axelrod and Bailey, 1969; Wolfe, 1971). The main determinants of plant distribution are thought to be the prevailing thermal regime, characterised by the annual average temperature, and the annual range of temperature (Axelrod and Bailey, 1969; Wolfe, 1971). Correct determination of the thermal characteristics of a fossil species are therefore dependant on the accurate determination of the closest modern relative, and accurate determination of the thermal requirements of the nearest modern relative. The closeness of the relationship between the fossil and the modern species is also critical (MacGinitie, 1969; Axelrod and Bailey, 1969; Wolfe, 1971; Roth and Dilcher, 1978).

Generally, floristic comparisons are of a vague nature, with imprecise definitions of the thermal requirements of modern species and by infer/ence related fossil species. This is exemplified by the use of terms such as; 'tropical', 'temperate', or 'frigid', to describe the climatic characteristics of species (Axelrod and Bailey, 1969; e.g. Bigwood and Hill, 1985). Axelrod and Bailey, however, proposed a system for accurately determining the thermal requirements or "thermal field" of modern species as an aid to predicting the thermal characteristics of fossil vegetation (Axelrod and Bailey, 1969).

Under their scheme, the thermal characteristics of all known areas where a species occurs, the annual average temperature, the annual range of temperature, and the "equability" of the climate, are plotted on a "nomogram" (Axelrod and Bailey, 1969). This graphical device allows the prediction of other important climatic characteristics such as the temperature of the warmest and coldest months and the length of frost-free periods.

The plotting of the characteristics of a series of sites covering the known range of the species will define it's "thermal field" (Axelrod and Bailey, 1969).

The detection of a closely related fossil species indicates that the choice of possible climates is restricted to this "thermal field". They made the suggestion, though, that it is necessary to consider as many species from a flora as possible, as the zone of overlap between the thermal fields of all the species will best define the characteristics of the palaeovegetation.

This approach makes a number of assumptions which, while perhaps not invalidating the approach altogether, suggest caution in its application. Fossil plants are generally represented by leaf remains alone. Attached reproductive structures, particularly flowers, are rare. Identification is therefore based on comparisons between the leaf morphology of the modern and fossil species (Dilcher, 1974; Hickey, 1977).

This restriction creates special problems as, in many environments there is a tendency towards convergence in gross leaf form (e.g. Tropical Rainforest; Richards, 1952). Leaf comparisons are therefore often based on fine detail of venation and the epidermis, usually represented by the cuticle (Dilcher, 1974; Hickey, 1977). In many cases no organic material remains and so identification must rely on gross form and venation detail alone.

These factors favour the identification of highly characteristic taxa over others. For example, Hill initially described the distinctive foliar remains of three species of cycad from the Eocene Nerriga locality (Hill, 1978), but referred the bulk of the flora to "parataxa" (Hill, 1983) or form genera (Hill, 1986).

The very large number of comparisons that are necessary, and the high level of convergence seen in gross leaf form, increase the possibility of the erroneous identification of Tertiary leaf taxa. Historically many floras, particularly in Australia, have been described on only cursory examination, and the identifications presented by early workers have either undergone major revisions, or remain highly suspect (Dilcher, 1971 1973; Christophel, 1981; Hill, 1987b). Clearly, floristic analyses of climate based on these floras are invalid (Dilcher, 1973; Roth and Dilcher, 1978).

The next major assumption of floristic analysis is the association of the thermal requirements of modern species to fossil close relatives. This assumes that there has been no change in their thermal requirements over time, and that the modern and fossil species are as close physiologically as they are morphologically (MacGinitie, 1969; Wolfe, 1971). Neither assumption is reasonable without supporting evidence.

Christophel and Greenwood (1988) have highlighted the danger of assumptions over the modern affinity of Early Tertiary taxa. *Banksiaephyllum* Cookson is a common macrofossil taxon in Eocene floras of southern Australia (e.g. Cookson and Duigan, 1950; Blackburn, 1981; Hill and Christophel, work in progress). Traditionally this taxon has been used for Tertiary leaves considered intermediate in morphology between *Banksia* L.f. and *Dryandra* R.Br. (Proteaceae; tribe Banksiaeae ; subtribe Banksiinae; Cookson and Duigan, 1950; Blackburn, 1981).

These genera are today characteristic of swamp vegetation or sclerophyllous heaths and woodlands (Johnson and Briggs, 1975). Spicer and Wolfe (1987) suggested that organ genera consistently associated in quiet water deposition have a very high probability of being conspecific. Leaves of *Banksiaephyllum* are generally found in association with the floral organ taxon, *Musgravinanthus* Christophel (Christophel, 1984; Christophel and Greenwood, 1988; Hill and Christophel, work in progress).

Musgravinanthus is intermediate in morphology between two modern rainforest genera closely related to *Banksia; Austromuellera* C.White and *Musgravea* F.Muell. (Proteaceae; tribe Banksiaeae subtribe Musgraveinae; Christophel, 1984). Christophel and Greenwood (1988) suggest that *Banksiaephyllum* may represent the foliar organ of *Musgravinanthus*, and by inference, a rainforest plant and not a sclerophyll heath plant.

The possibility for erroneous climatic inference is particularly high for taxonomic groups which were highly diverse and wide spread in the Early Tertiary, yet today are represented by only a few, or only a single species with a restricted distribution. The degree of affinity between fossil and modern species decreases with increasing age of the deposit (and increasing time for evolution), and correspondingly, the confidence in the prediction of common thermal requirements (MacGinitie, 1969).

The genus *Dacrycarpus* Endl. (Podocarpaceae), for example, is common in Tertiary sediments in southern Australia (Greenwood, 1987), and also in Antarctica and South America (Florin, 1963). However *Dacrycarpus* is now absent from Australia, and is represented by single species in both New Zealand and New Caledonia, and a small number of species in Malesia, each with very different and very narrow ecological requirements (de Laubenfels, 1969; Greenwood, 1987). The morphology of Early Tertiary Araucariaceae from localities in Tasmania are intermediate between *Agathis* R.A.Salisb. and *Araucaria* Juss., yet these two modern genera occur in quite different environments (Bigwood and Hill, 1985).

Floristic predictions based on such groups must be viewed with caution, as it is not known whether the extinct members occupied a much wider range of potential thermal regimes than the surviving species. It has also been shown that many Tertiary floras contain mixtures of taxa with close modern relatives represented in quite separate climates (Daley, 1972; Hill, 1987a). These floristic associations have been interpreted by some as suggesting that Early Tertiary climates have no modern analogue (Daley, 1972; Kemp, 1978: Bigwood and Hill, 1985; Hill, 1987a).

1.2.2 Foliar Physiognomic Analysis.

Foliar Physiognomy is defined as the characteristic form of the leaves of the plant — e.g. leaf margin type, shape, the presence of characteristic leaf features (e.g. 'drip tips', strongly acuminate leaf apices), and leaf size. The use of the physiognomy of fossil leaves to predict vegetation type and climates originates with Bailey and Sinnott (1915 1916) who found a correlation between the proportion of species with non-entire margins in regional floras, and regional climate.

Specifically, Bailey and Sinnott (1916) found that in equable environments the proportion of species with non-entire margins increased with increasing latitude, and to a similar extent with increasing altitude. Arid and "physiologically dry" habitats in the cold-temperate zone however, were also characterised by entire margins. The implication was that for equable habitats the proportion of species in a flora with non-entire margins was linked to the temperature characteristics of the region.

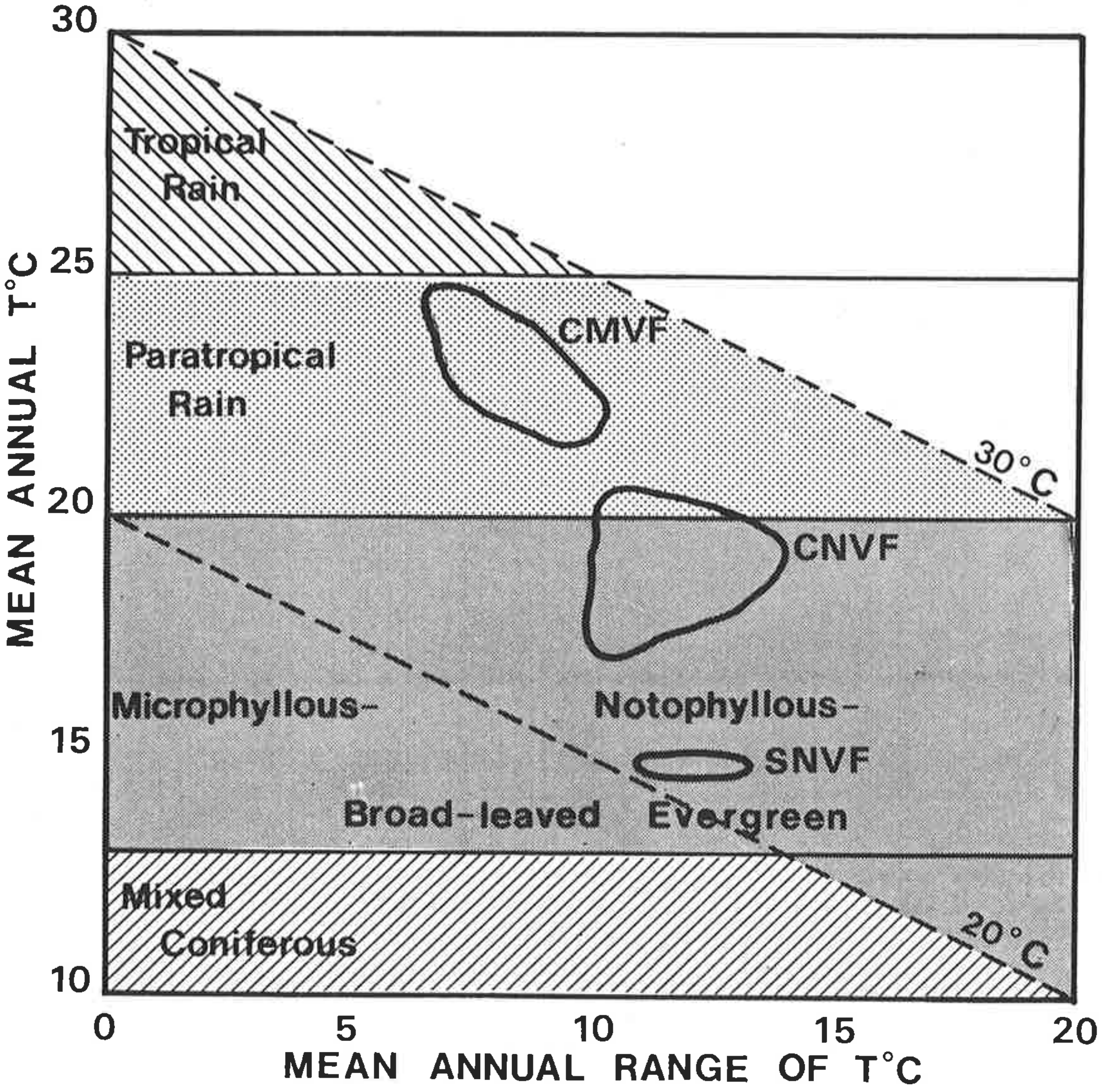
Bailey and Sinnott used these observations to determine the broad climatic characteristics of a number of Cretaceous and Tertiary leaf floras (Bailey and Sinnott, 1916). These broad climatic correlations were adopted by a number of palaeobotanists (e.g. Chaney and Sanborn, 1933; MacGinitie, 1969 1974), although floristic analysis has generally been the preferred method (Axelrod and Bailey, 1969; Dorf, 1970; Dolph, 1978).

Wolfe's physiognomic classification of the moist forests of East Asia used regional floras to determine correlations of annual average temperature and the annual range of temperature, with structural and foliar physiognomic features (Wolfe, 1980a). His main diagnostic feature was a correlation between the proportion of canopy tree species with non-entire margins and the annual average temperature (Fig. 1.1), which seems to offer an accurate source of comparison between Tertiary leaf floras and modern vegetation (e.g. Wolfe, 1980b, 1985, 1987).

The Australasian region (Australia and New Zealand), however, has a higher proportion of entire margined species than comparable regions, and it was suggested by Bailey and Sinnott (1916) that this situation reflected historical factors and the isolation of the Australasian region from potential immigration of non-entire forms from cooler regions. Much later, Wolfe has suggested that the cause is the preferential survival in the Northern Hemisphere cool Temperate zone of deciduous species (which predominantly have leaves with non-entire margins) after a major catastrophic cooling at the Cretaceous / Tertiary boundary (Wolfe, 1985 1987).

The prevailing leaf size in vegetation is also thought to be determined by climate (Bailey and Sinnott, 1915; Chaney and Sanborn, 1933; Raunkiaer, 1934). Bailey and Sinnott (1915) commented that on the basis of herbarium collections, leaves in moist tropical regions are "comparatively large". Chaney and Sanborn however, used leaf litter in their analysis of two Early Tertiary floras, and found a higher proportion of leaves over 10 cm length in litter from tropical forests than in leaf litter from temperate forests (Chaney, 1924; Chaney and Sanborn, 1933).

Fig.1.1 Wolfe's forest classification contrasted to Webb's forest types (from Wolfe, 1980).



Raunkiaer proposed a series of leaf size classes based on leaf area and noted that the prevailing leaf size class was successively smaller in cooler or drier climates than the optimum humid tropical climate (Raunkiaer, 1934). His proposal was that vegetation communities could be characterised by the relative proportions of species with leaves in these leaf size classes.

Beard used the characteristic Raunkiaer leaf size class of each species in a vegetation to derive the proportion of species in each leaf size class, in combination with structural features, to classify tropical American forests (Beard, 1944 1955). Beard's argument was that physiognomic and structural features reflected the immediate adaptation of vegetation to macroclimate, whereas floristic associations reflected historical factors (Beard, 1944 1955).

Following Beard's classification (1944, 1955), the prevailing leaf size of each species, and from this the proportion of species with leaves in each of Raunkiaer's leaf size classes, was used as a diagnostic tool to indicate the environmental determinants of vegetation structure and physiognomy (e.g. Richards, 1952; Cain, et al., 1956; Webb, 1959 1968; Grubb, et al., 1963a & b; Howard, 1969).

There is some debate however, over the relative roles of edaphic and climatic determinants of leaf physiognomy (e.g. Webb, 1959 1968; Loveless, 1961 1962; Kapos and Tanner, 1985). A chief issue is whether the characteristic smaller and thicker sun leaves of the canopy of tropical rainforests, and in particular, montane rainforests, represent adaptation to soil infertility, or to water stress (e.g. Kapos and Tanner, 1985; Sugden, 1985).

Vegetation structure is defined as the spatial arrangement of the trees and other synusiae; for example, the stratification of tropical forests (Richards, 1952; Webb, et al., 1970). Physiognomy in general includes both the foliar physiognomy and the characteristics of the plants themselves, usually indicated by the presence of particular life forms. These include, vines/lianes, strangler figs, epiphytes, cauliflory, buttressed tree trunks (Webb, et al., 1970). Thus "Foliar Physiognomy" may be distinguished as solely concerning the physiognomy of the leaves.

Richards (1952) modified Beard's classification, adopting a broader definition of 'Tropical Rainforest' as he included all evergreen tropical forests, whereas Beard made a distinction between seasonally dry 'Evergreen Seasonal Rainforest', and the non-seasonal 'Tropical Rainforest' (Beard, 1944, 1955). Important points on foliar physiognomy were added by Richards, who reiterated the common observation of the preponderence of tree species with elliptic leaves, with prominent drip tips and entire margins, and the dimorphism between leaves borne in the canopy ('sun leaves') and below the canopy ('shade leaves') in tropical rainforests (Richards, 1952).

Webb's physiognomic classification of Australian rainforest (1959, 1968) also uses a combination of structural features — principally the number of tree layers or strata — and physiognomic features — both the presence of characteristic life-forms and foliar physiognomy. Webb also adopted Raunkiaer's leaf size classes, adding a new class — "Notophyll" — for the "small mesophyll class" of Raunkiaer (1934; Webb, 1959; Fig. 1.2). Unlike Beard, however, Webb also considered the proportion of individuals, as well as species, represented in each leaf size class.

In each of these physiognomic classifications, direct correlation was suggested between the structure and physiognomy of the vegetation and the climate — "climatic climaxes" (Beard, 1944 1955; Richards, 1952; Webb, 1959). Webb however, placed a much greater emphasis on the influence of edaphic factors (mainly soil fertility) in determining structural characteristics, but suggested that some aspects of the foliar physiognomy were primarily under the control of the climate, mainly leaf size by temperature (Webb, 1959 1968).

However, it is rarely possible to infer structural features of vegetation and the life-forms of plants from plant fossil beds. For example, Kelly noted that *Clusia flava* (Clusiaceae) may develop as a normal tree, a protero-epiphyte, or a strangler, depending on the conditions of the site (Kelly, 1985). The presence of leaves of taxa often associated with particular life-forms therefore, can not always be used to suggest the presence of that life form. The foliar physiognomy however, can be directly observed.

The correlations between the foliar physiognomy of the forest types recognised under these classifications and (macro)climate offered an opportunity to improve

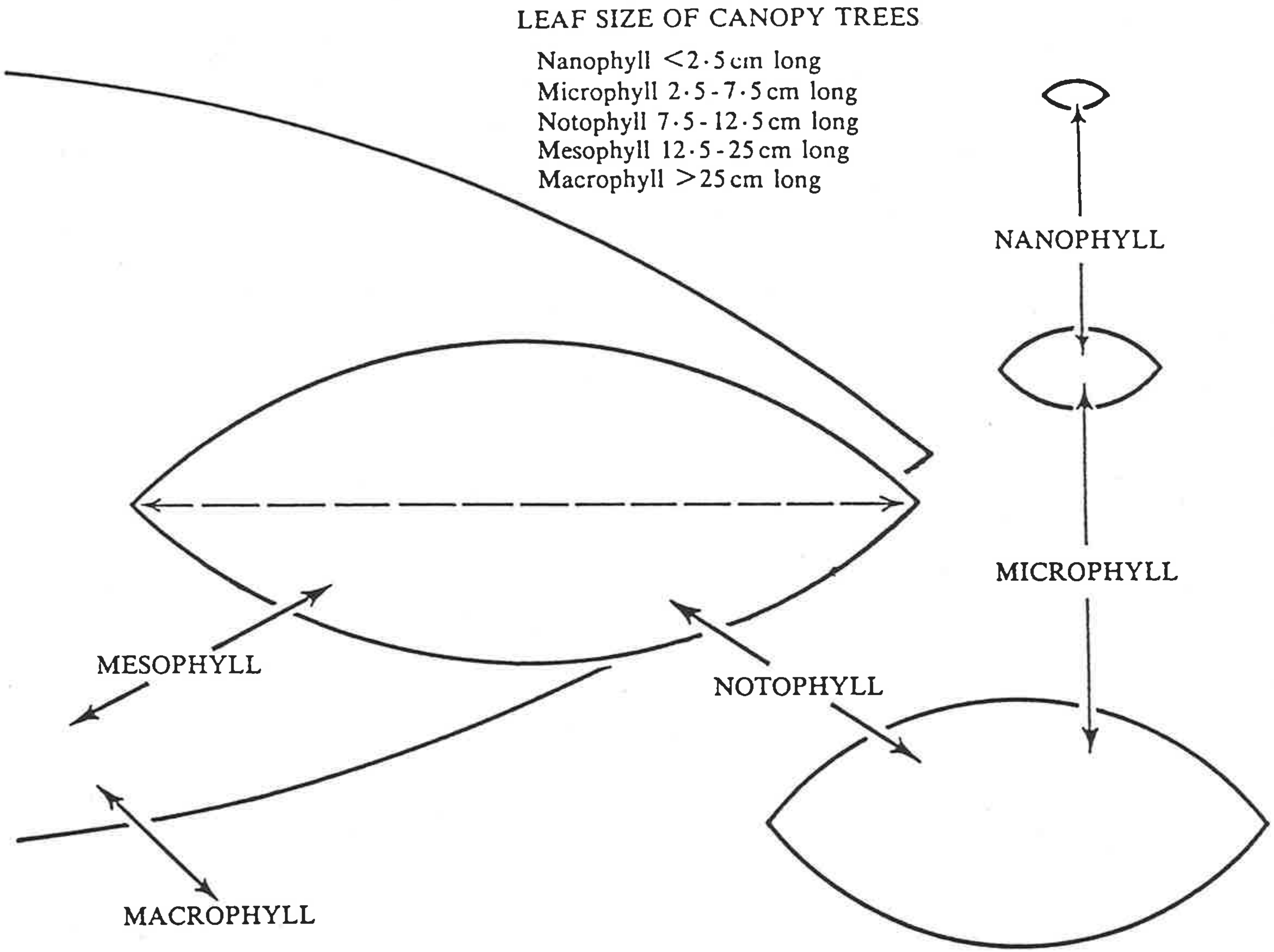


Fig: 1.2 Leaf size classes of Webb (1959), from a figure in Tracey (1982).

upon the crude estimation of temperature for Tertiary floras offered by Bailey and Sinnott's work. However the pioneering approach of Chaney and Sanborn (1933) of using the characteristics of leaf litter, rather than the actual forests, has been largely ignored.

Dissatisfaction with the floristic approach led MacGinitie to use the predominant leaf size of each species in the Eocene Green River Flora to determine the proportion of species within each of Raunkiaer's leaf size classes (as modified by Webb, 1959) as a method of comparison between the fossil flora and modern vegetation (MacGinitie, 1969).

This method continues to be used with studies by Christophel (1981) on southern Australian Early Tertiary floras, and by Zastawniak et al. (1985) on Antarctic Miocene floras contrasting the percentage of individual leaves in each of Webb's modified leaf size classes to the values given by Webb for each of the Australian Rainforest types.

In a series of studies, Dolph (1978, 1984), and Dolph and Dilcher (1979a & b) used the proportion of species with 'large leaves' (Dilcher, 1973) and entire margins (after Wolfe, 1971), to test correlations between foliar physiognomy and climate at sub-regional scale. They found no close correlation with a number of climatic variables (Dolph and Dilcher, 1979a), and suggested that local site differences are a possible source of the greater than expected variation (Dolph, 1979 1984; Dolph and Dilcher, 1979a & b).

Chaney and Sanborn's comparison of leaf litter with two Early Tertiary fossil leaf beds (Chaney and Sanborn, 1933) was in direct contrast to the approach used by later studies. In most instances, the characteristics of the actual modern forests has been compared to the fossil flora (e.g. MacGinitie, 1969 1974; Wolfe, 1971 1980b 1987; Christophel, 1981; Zastawniak, et al., et al., 1985), or used to measure correlations with climate (e.g. Wolfe, 1980a; Dolph, 1979 1984; Dolph and Dilcher, 1979a & b) .

The assumption of the later studies was that the foliar physiognomic characteristics of the forest would be represented essentially unaltered in the fossil leaf beds (Roth and Dilcher, 1978). In common with the later studies however, Chaney and Sanborn used the characteristics of species i.e. the average state for each species, to assess the relative proportion of the flora (both fossil and modern) in each foliar physiognomic class.

Roth and Dilcher (1978), and more recently, Ferguson (1985) and Martin (1986) have queried the direct application of the foliar physiognomic characteristics of modern vegetation to the interpretation of the vegetation which produced fossil leaf beds. Roth and Dilcher (1978) suggested that it is more appropriate to study the foliar physiognomic characteristics of neo-fossil leaf beds, thus avoiding problems associated with contrasting vegetation to leaf beds.

In the following section, it will be briefly discussed how different aspects of leaf physiognomy are determined by the interplay of environmental factors, and how these factors alter over very small distances in the forest environment. The corollary of this is that leaf litter, and by inference, fossil leaf beds, will contain a diverse assemblage of leaf physiognomies.

1.3 The Determinants of Leaf Physiognomy.

A number of features of foliar physiognomy are generally considered to vary according to environmental determinants. The main features however were listed by Dolph (1978);

1. size (often as area in Raunkiaer's classes)
2. margin type (entire or other)
3. texture (coriaceous - membranous)
4. presence or absence of drip-tips
5. density of stomata
6. organisation (compound or simple)
7. major type of venation (palmate or pinnate)

The expression of these characteristics in leaves is attributed to prevailing environmental factors — temperature, rainfall, soil fertility, light (Bailey and

Sinnott, 1916; Grubb, et al., 1963b; Taylor, 1975; Davis and Taylor, 1980; Lichtenthaler, 1985; Jones, 1985). Individual plants (and perhaps individual leaves; Davis and Taylor, 1980) will respond to the prevaling environment according to their inherent phenotypic plasticity (Schlichting and Levin, 1986), and the degree to which particular aspects of leaf physiognomy vary will also be dependent on inherited factors.

However, it is reasonable to expect that the net response of the community of plants (and the population of leaves on individual plants) in a particular locale will be in a dynamic equillibrium with the environment. The consequence of this is that the average response, i.e. the average physiognomy, will be tied to the characteristics of the macro-environment. Thus it is not surprising that Richards (1952) was able to characterise tropical rainforest trees as having leaves with a particular physiognomy which reflected their adaptation to the tropical rainforest environment.

The characteristic size and margin type of leaves has been usually attributed to temperature and precipitation (e.g. Bailey and Sinnott, 1916; Raunkiaer, 1934; Beard, 1944; Webb, 1959). However while leaf shape has often been used in taxonomic studies (e.g. Dickinson, et al., 1987; Herman, et al., 1987), it has also been demonstrated that some aspects of leaf shape seem to be primarily under environmental control (e.g. Hu Chia-Chi, et al., 1985; Rood, et al., 1986; Sokal, et al., 1986).

Givnish and Vermeij (1976) for example, demonstrated that the constraints of the liane life-form favoured the characteristic 'heart-shaped' leaves of tropical vines. The width of leaves also may reflect environmental control as stream-side leaves in temperate and some tropical forests are typically ‘stenophylls’, or ‘willow-form’ - i.e. have a high L/W ratio (van Steenis, 1981; Whitmore, 1984). Both van Steenis and Whitmore suggested that stenophylls may be an adaptation to times of high water (i.e. floods) and or high speed air flow associated with the water flow in fast flowing streams (van Steenis, 1981; Whitmore, 1984).

Theoretical modelling by Vogel (1970), Parkhurst and Loucks (1972), Taylor (1975), Givnish (1978 1984), and Chiariello (1984) suggests that the final shape and size of a leaf represents an adaptive compromise between maximising photosynthesis, and minimising the potentially destructive effects of excessive transpiration and thermal load. The leaf offsets the costs and benefits of maximising leaf area (maximising photosynthetic capacity), maximising the efficiency of photosynthesis (cost-benefits of producing and maintaining the leaf), and minimising the potential inefficiencies in the functioning of the leaf.

The latter particularly, relates to the thermal characteristics of the leaf shape and size (Vogel, 1970; Givnish, 1978). Large thin leaves heat-up more quickly in bright sunlight than small thick leaves, and cool more quickly in the absence of direct sunlight and/or in cooler temperatures. Photosynthesis is optimal at different temperatures for different species (Givnish, 1978 1984) and even different individuals (Chiariello, 1984; Jones, 1985). However as a generality, at high leaf temperatures photosynthesis ceases, either through the closure of the stomata (and hence cessation of gas exchange: C3 plants) or through thermal inhibition of biochemical processes.

Davis and Taylor found that the range of potential microclimatic regimes in a forest environment produce a range of potential leaf physiognomic types, and that quite different forest communities may share some types (Davis and Taylor, 1980). Tropical rainforest has been shown to exhibit extreme changes in humidity, temperature, light levels, and CO_2 concentration at various levels in the forest (Richards, 1952; Aoki, et al., 1975; Bourgeron, 1983; Whitmore, 1984). Richards (1952) and Whitmore (1984) pointed out that this vertical variation is reflected in a parallel transition in leaf form from the forest floor to the canopy.

A survey by Roth (1984) characterised the leaf forms of each layer (i.e. the leaf physiognomic types of Davis and Taylor, 1980), and demonstrated a transition in leaf form from types adapted to low light levels and high humidity (large membranous leaves; 'shade leaves'), to leaves adapted to high light levels and low humidity (small and coriaceous; 'sun leaves').

The convergence in leaf form in rainforest leaves from quite unrelated species has attracted considerable comment by numerous researchers as has the distinctive leaf form of the various synusiae in rainforest, and between leaves of various stages in the growth of large trees (Richards, 1952). This last point is of particular importance as it has often been commented that there are often quite extreme differences between the size and general morphology of 'sun' and 'shade' leaves from rainforest trees (Richards, 1952; Roth, 1984; Fig. 1.3).

It is reasonable to expect that leaves of both types from a single species (if not individual) may occur together in a fossil leaf bed. Similar heterophylly in *Populus* L. (Salicaceae) prompted Eckenwalder to caution against the setting of very strict morphological boundaries when describing Tertiary fossil species from leaves (Eckenwalder, 1986).

1.4 The Taphonomy of Leaf Beds.

An understanding of the influences on the input and transportation of dead plant (or animal) parts to places of deposition (Taphonomy) is important in any analysis of fossil beds to interpret the ecology of the community from which the plant parts were derived. Fossil deposits rarely preserve plant communities, rather, they preserve populations of plant organs (usually leaves).

Considerable comment has been made of the possible distortions caused by taphonomic processes to the proportional representation of these physiognomic classes in fossil leaf beds, particularly leaf size (MacGinitie, 1969; Dolph, 1978; Roth and Dilcher, 1978; Spicer, 1981). The research of Spicer (1981), and others on neofossil leaf beds (McQueen, 1969; Roth and Dilcher, 1978; Drake and Burrows, 1980; Holyoak, 1984; Hill and Gibson, 1986) suggests that fossil leaf beds are generally only representative of a local area and often distinctly biased towards the vegetation of the water's edge. Most foliar physiognomic analyses however, have paid little attention to this taphonomic bias, and contrasted the physiognomic characteristics of the fossil flora directly to published accounts of the foliar physiognomy of modern vegetation (e.g. Christophel, 1981; Zastawniak, et al., 1985), an approach which was criticised by Roth and Dilcher (1978), and Hill (1982), and most recently by Martin (1986).

Both Webb's classification of Australian rainforest (Webb, 1959 1968) and Wolfe's classification of East Asian forests (Wolfe, 1971 1980a) are based on the

SUN and SHADE leaves.

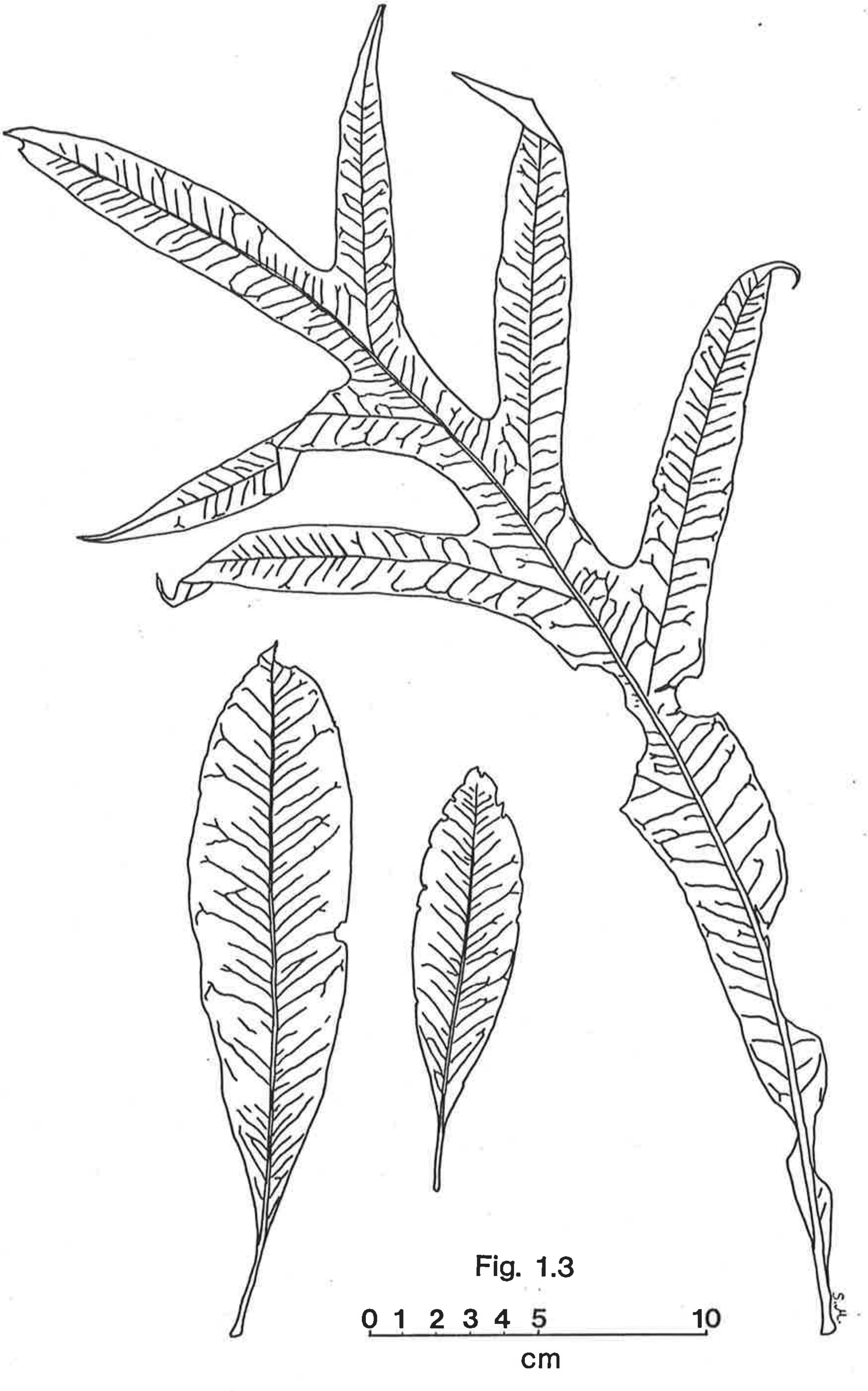


Fig. 1.3

foliar physiognomic characteristics of the canopy species. However, leaf beds will contain leaves from many synusiae, and not solely the canopy (Roth and Dilcher, 1978; Dolph, 1984; Ferguson, 1985). For example, Dolph found that while the proportion of canopy species with non-entire margins in the forests of Indiana was correlated with the annual average temperature, the proportion of species in the subordinate trees and shrubs was not (Dolph, 1984).

Many Eocene leaf beds in southern Australia and in southern USA are thought to have formed in the cut off branches of meandering rivers or braided streams (Christophel, Harris, and Syber, 1987; Potter and Dilcher, 1981). However comparatively little is known about the taphonomic bias created by deposition in stream-beds.

Studies on the input of leaves into lakes (e.g. Rau, 1976; Drake and Burrows, 1980; Hill and Gibson, 1986), and work in Arctic streams (Holyoak, 1984) suggests that leaf input into stream-beds will represent very local sources, and that significant shifts in the size representation of leaves will occur as the smaller sun leaves of the canopy are usually over-represented in lake and stream deposits. Foliar physiognomic interpretation of these deposits based on canopy characteristics would have suggested a cooler climate than actually prevailed (Roth and Dilcher, 1978; Spicer, 1981).

The degree of lignification of leaves appears to be an important factor controlling the rate of decay of leaves in streams (Kaushik and Hynes, 1971; Dudgeon, 1982), and may also be a source of bias towards the smaller, more lignified leaves of the upper canopy.

The relative influence of a physiognomically distinct streamside flora has also been suggested as a source of bias in the foliar physiognomic analysis of leaf beds (MacGinitie, 1969; Wolfe, 1971). In apparent contradiction to the previous example, it is suggested that the stream edge will favour the growth of species and individuals with on average larger leaves (MacGinitie, 1969), and perhaps fewer non-entire leaf margins (Wolfe, 1971 1980). Foliar physiognomic analysis of such a biased fossil flora would give a much warmer and or equable palaeoclimate than actually prevailed.

The relative leaf width of species associated with stream banks may also vary from the norm in tropical rainforest (van Steenis, 1981; Whitmore, 1984. It would be expected therefore, that leaf beds derived from such a vegetation would have much narrower leaves than the main forest.

In summary, there are clearly a number of factors which potentially may contribute to a bias in the foliar physiognomic characteristics of a streambed leaf deposit.

1. the preferential input of the smaller, more coriaceous, sun leaves of the canopy through the combined effects of; a) distance effects, b) differential survival of larger (thinner) leaves and smaller (thicker) leaves, and c) the screening effect of intervening vegetation.
2. the preferential survival of the smaller sun leaves during stream transport through variable rates of mechanical destruction and biological degradation.
3. the input of larger leaves, perhaps from a vegetation with a higher proportion of species and individuals with entire margined leaves than the main forest; in part in contradiction to points 1) and 2).
4. in some instances, the input of much narrower leaves due to the presence of a high proportion of species with stenophylls in the riparian vegetation.

Roth and Dilcher (1978) suggested that before foliar physiognomy can be applied to the analysis of the palaeoclimate of fossil floras, many modern leaf deposits must be studied to determine the relationship between the foliar characteristics of leaf beds derived from particular forest types under specific depositional circumstances (i.e. taphonomic studies). They proposed a uniform format for these studies and provided a sample catalog sheet for the collation of a register of such studies (Roth and Dilcher, 1978).

1.5 Aims of the Study.

The discussion above has highlighted several main areas of uncertainty with the usage of foliar physiognomic analysis for the prediction of palaeoclimate from

Tertiary leaf beds. These in turn may be defined as five main aims for this study:

1) to illustrate the distinction between the foliar physiognomic characteristics of vegetation and leaf beds from that vegetation.

Most of the previous studies of foliar physiognomy have considered either the characteristics of regional floras, with little or no account being taken of local variation in either vegetation or environment, or they have considered solely the characteristics of particular components of vegetation, usually the canopy trees (e.g. Webb, 1959; Wolfe, 1980a; cf. Dolph, 1984).

In either circumstance, the simple fact has been ignored that fossil leaf beds are assemblages of plant parts (i.e. leaves), not preserved vegetation. These assemblages generally represent localised deposition, and will consequently reflect only the local vegetation, including leaves from all potential source plants (Ferguson, 1985).

2) to determine whether leaf beds formed from physiognomically distinct vegetation types retain unique "physiognomic signatures".

Several studies on the taphonomy of leaf beds have been reported from Temperate (e.g. Drake and Burrows, 1980; Spicer, 1981; Hill and Gibson, 1986) and Arctic vegetation (Holyoak, 1984), however to date there has been only one study of taphonomic processes in a Tropical environment (Scheihing and Pfefferkorn, 1984). Further, most of these studies have considered the taphonomic influences on species representation in a leaf assemblage and few have considered the effects on the physiognomic characteristics of the assemblage.

Many of the Tertiary floras reported from Australia have a "Tropical character", that is the gross physiognomy of the fossil leaves and the taxonomic composition of these floras is reminiscent of the Rainforest vegetation of the Tropical region of Australia (Christophel, 1981 1984; Greenwood, 1987). It was important therefore to have an understanding of the nature of the taphonomic influences on the physiognomy of leaf assemblages derived from tropical Australian forests prior to using Foliar Physiognomic Analysis on the Tertiary fossil leaf beds.

3) to measure the taphonomic bias introduced by a) streamside vegetation,

and b) stream transport.

An important consideration is the influence on the foliar physiognomic characteristics of leaf beds due to streamside vegetation and taphonomic processes in the stream itself. In this study, the effects of these two factors have been considered as one question; i.e. how does the foliar physiognomic characteristics of streambed litter differ from that of leaf litter from the forest floor. Each is however, addressed in turn in the discussion.

4) to measure the morphological variation found within species in leaf beds — the affect on recorded diversity and species presence based observations.

Generally, Tertiary fossil species are described and identified from leaf material alone. Comparisons are made between selected specimens from the fossil flora and individual leaves usually taken from herbarium collections. Both sets of specimens run the risk of introducing considerable bias due to the possible (unrecognised) presence of heteromorphic sun and shade leaves from individual species in the fossil material.

There are many modern species, particularly in rainforest, where the shade (or juvenile) leaves are lobed or serrate margined (or both) and much larger than the entire margined sun (or adult) leaves. Inadequate sampling in either the fossil or modern material may highlight extreme morphs (sun vs shade) promoting the recognition of the two extremes in the fossil material as separate species. The higher diversity recorded as a result may bias, for example, foliar physiognomic analyses based on the proportion of species present with particular distinctive physiognomic traits e.g. non-entire margins (Wolfe, 1980a & b).

An aim of this study, therefore, was to consider the level of variation in leaf morphology commonly found within species in leaf beds. This information will indicate the level of variation at which species boundaries should be drawn in fossil leaf beds, and also the level of diversity expected in these beds.

5) to detect correlations between local foliar physiognomic attributes and local climate.

The final area of interest concerns problems associated with the interpretation of the relationship between the foliar physiognomy of Australian rainforests (Tertiary and modern) and climate. Webb's physiognomic classification demonstrated a linkage between the dominant leaf size of canopy trees and annual average temperature. It is perhaps necessary however, to examine the relationship between the physiognomic characteristics of the leaf beds, and the local climate. From this base it might be possible to redefine the climatic determinants of the foliar physiognomy of Australian rainforests, providing a more powerful predictive tool for the interpretation of Tertiary leaf beds.

The procedure used to examine these questions is discussed in Chapter 2 with a discussion of the nature of the Australian rainforest environment to further place the study in context.

Chapter 2

THE PHYSICAL AND BIOLOGICAL CHARACTER OF AUSTRALIAN RAINFOREST

2.1 Australian Rainforest Classification and Biogeography.

Rainforest in Australia has been traditionally subdivided into a number of subformations; Tropical, Sub- tropical, and (warm and cool) Temperate (Beadle and Costin, 1952; Baur, 1957; Webb, 1959). These subformations were based on an intuitive recognition of discrete floristic groupings associated with these climates. Under this classification the Temperate Rainforest (or "subantarctic rainforest"; Fraser and Vickery, 1937) was considered to represent an archaic floristic association inherited in common with the other southern continents- the "Antarctic Element". The Tropical Rainforest however, was considered an immigrant floristic association from SE Asia- the "Indo-Malaysian Element" (Burbidge,1960).

Herbert challenged this view, and suggested that much of the subtropical and tropical rainforest flora was not immigrant, but autochthonous (Herbert, 1960; 1966). The autochthonous origin of the tropical and subtropical rainforest flora has come to be accepted by some Australian botanists (Webb and Tracey, 1981; Webb, Tracey, and Jessup, 1986). There is also support from the fossil record as taxa characteristic of Australia's Tropical Rainforests have been found to be present in Eocene floras of southern Australia (Christophel, 1984; Christophel and Greenwood, 1987 1988; Greenwood, 1987). The older view however, persists with recent commentaries on the evolution of the Australian Flora preferring to consider the bulk of the tropical rainforest flora as immigrant (e.g. Barlow, 1981; Thorne, 1986; Barlow, 1988).

The traditional Rainforest subformations largely correspond to the physiognomic forest classification developed by Webb (1959, 1968; Webb and Tracey, 1975; Tracey, 1982). Webb's physiognomic classification is based on a correlation of structural features and foliar physiognomic features of Australian Rainforests with climatic and edaphic factors. The main forest types recognised in Webb's classification are shown in Table 2.1, and are contrasted with the traditional subformations in Table 2.2.

The number of tree strata and the presence of characteristic lifeforms (e.g. vines, strangler figs, epiphytes), and both the prevailing leaf size (Table 2.3) and the prevailing type of leaf margin of canopy trees (Table 2.4), were used by Webb to recognise forest types (Webb, 1959; 1968). The characteristics of the forest types used in this study are discussed latter in this chapter. A full discussion can be found in Webb (1959, 1968) and Tracey (1982).

Webb's classification makes no direct connection between climatic classification and the forest classification, however he does suggest causal links with annual average temperature and annual rainfall (including seasonality). The influence of edaphic factors (soil fertility) is considered by Webb to be a major determinant of forest type in conjunction with the climate. However, Webb considered leaf size to be more strongly under the influence of temperature and rainfall than soil type (Webb, 1968).

Therefore, unlike other physiognomic classifications of vegetation (e.g. Beard, 1944; Wolfe, 1980a), Webb's forest types do not represent climatic-climax formations (Beard, 1944), but rather represent climatic-edaphic correlations between forest structure, leaf physiognomy, and the environment (Webb, 1959; 1968). Different forest types may grow side by side on different soils, and rainforest may persist under quite low rainfall on soils of high fertility (Webb, 1968; Webb and

Table 2.1

Forest nomenclature of Tracey and Webb for NE Queensland.

Complex Mesophyll Vine Forest		CMVF
	1a 1b 1c	
Mesophyll Vine Forest		MVF
	2a 2b	
Mesophyll Vine Forest (with dominant palms)		MFPVF
	3a 3b	
Semideciduous Mesophyll Vine Forest		SDMVF
	4	
Complex Notophyll Vine Forest		CNVF
	5a 5b	
Complex Notophyll Vine Forest (with Agathis robusta)		CNVF
	6	
Notophyll Vine Forest		NVF
	7a 7b	
Simple Notophyll Vine Forest		SNVF
	8	
Simple Microphyll Vine-Fern Forest		MFF
	9	
Simple Microphyll Vine-Fern Thicket		MFT
	10	
Deciduous Microphyll Vine Thicket		DEVT
	11	

NB number and letter code refers to sub-types in Tracey, 1982.

Table 2.2 A comparison of Webb's rainforest types and traditional classifications.

Physiognomic Classification	Floristic – Climatic Classification
Complex mesophyll Vine Forest	Tropical Rainforest
Complex Notophyll Vine Forest	Subtropical Rainforest (N.S.W.)
Simple Notophyll Vine Forest	Montane and Lower Montane Rainforest (N.E. Qld) Warm Temperate Rainforest (N.S.W.)
Microphyll Fern / Mossy Forest	Temperate Rainforest Subantarctic Rainforest

From, Beadle and Costin, 1952, Baur, 1957, Webb, 1959, and Tracey, 1982.

Table 2.3

The proportion of trees (species and individuals) in Australian rainforest with leaves in Raunkiaer's leaf size classes: modified from Webb (1959).*

Forest Type	Mesophyll % spp / ind	Notophyll % spp / ind	Microphyll % spp/ ind
CMVF	50–70 / 60–70	30–50 / 30–40	0–5 / 0–5
MVF	30–50 / 30–40	40–50 / 50–60	5–15 / 5–15
CNVF	15–30 / 5–20	50–70 / c.85	10–20 / c.10
SNVF	0–30 / 0–20	55–75 / 25–95	0–40 / 10–70
MFF/MMF	0 / 0	0–10 / c.5	90–100 / 95–100

* Forest nomenclature follows Webb (1968) in part, and Tracey (1982).

Table 2.4

The proportion of non–entire margins on the leaves of trees in Australian rainforest: modified from Webb (1959).*

Forest Type	% species	% individuals
CMVF	10 – 30	5 – 25
MVF	25 – 45	15 – 35
CNVF	15 – 30	c. 45
SNVF	30 – 60	30 – 90
MFF/MMF	100**	100**

* Forest nomenclature follows Webb (1968) in part, and Tracey, 1982.

** NB This probably represents temperate forests only.

Tracey, 1981; Fig. 2.1). This interpretation may be termed "edaphic compensation" (Webb, 1959; 1968). However, the strong correlation between leaf size and annual average temperature (Webb, 1959; 1968) suggests that the foliar physiognomy of Australian Rainforests will reflect the local climate, whereas structural features will be more strongly under the influence of edaphic factors.

2.2 The Modern Distribution of Rainforest in Australia.

In Australia, rainforest mainly occurs as isolated small pockets in suitable habitats in the ranges bordering the east coast (Fig. 2.2). Larger blocks or "massifs" of rainforest occur in the tropical northeast and in an area to the south of the border between the states of Queensland and New South Wales. Cool temperate rainforests similarly occur in small pockets in mountainous areas of the states of Victoria and Tasmania although in Tasmania broad scale areas of rainforest are also present (Fig. 2.2). Rainforest pockets are also found in the northwest of the state of Western Australia and in the Arnhemland escarpment area of the Northern Territory. These last two "rainforests" are mostly tropical monsoon forest, and in some cases these forests are deciduous (Webb, 1959 1968). They are not considered in this thesis.

A survey by Webb and Tracey (1982) of Australian Rainforest gives some indication of the distribution of the main forest types recognised by Webb (1959, 1968; Tracey and Webb, 1975; Tracey, 1981). The sites from each of the four main forest types (Tracey and Webb, 1975; Tracey, 1982; Table 2.1) have been mapped in Figure 2.3 (SDMVF/MVF/CMVF), 2.4 (CNVF) , 2.5 (SNVF) , and 2.6 (MFF/MMF).

The mesophyll vine forests (CMVF, SDMVF, MVF) occur discontinuously in the tropical lowlands of the east coast from the tip of Cape York Peninsula to the vicinity of Mackay (Fig. 2.3). According to Webb (1959), the southern limit of CMVF is near Sarina, a small town to the south of Mackay. A survey of rainforest in Papua New Guinea by Webb and Tracey (1972) also recorded CMVF. In the region of the main rainforest "massif" in N.E. Queensland (Fig. 2.2; 19°00' S

Fig. 2.1

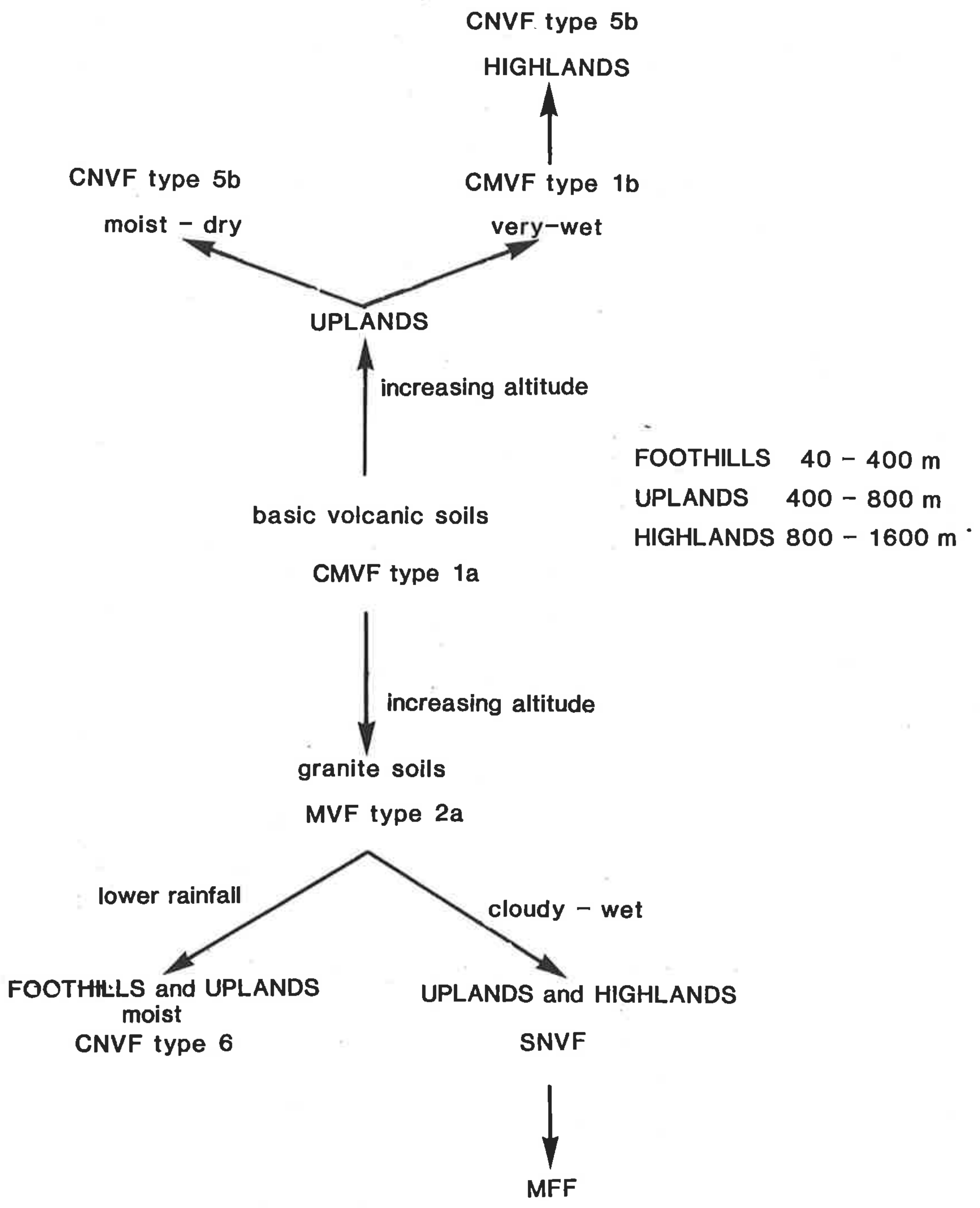


Figure 2.1 Environmental relationships of the principal rainforest types (sensu Webb, 1959 1968; Tracey, 1982) in the N.E. Queensland region. Modified from a figure in Tracey (1982). Forest nomenclature from Table 2.1.

Fig. 2.2

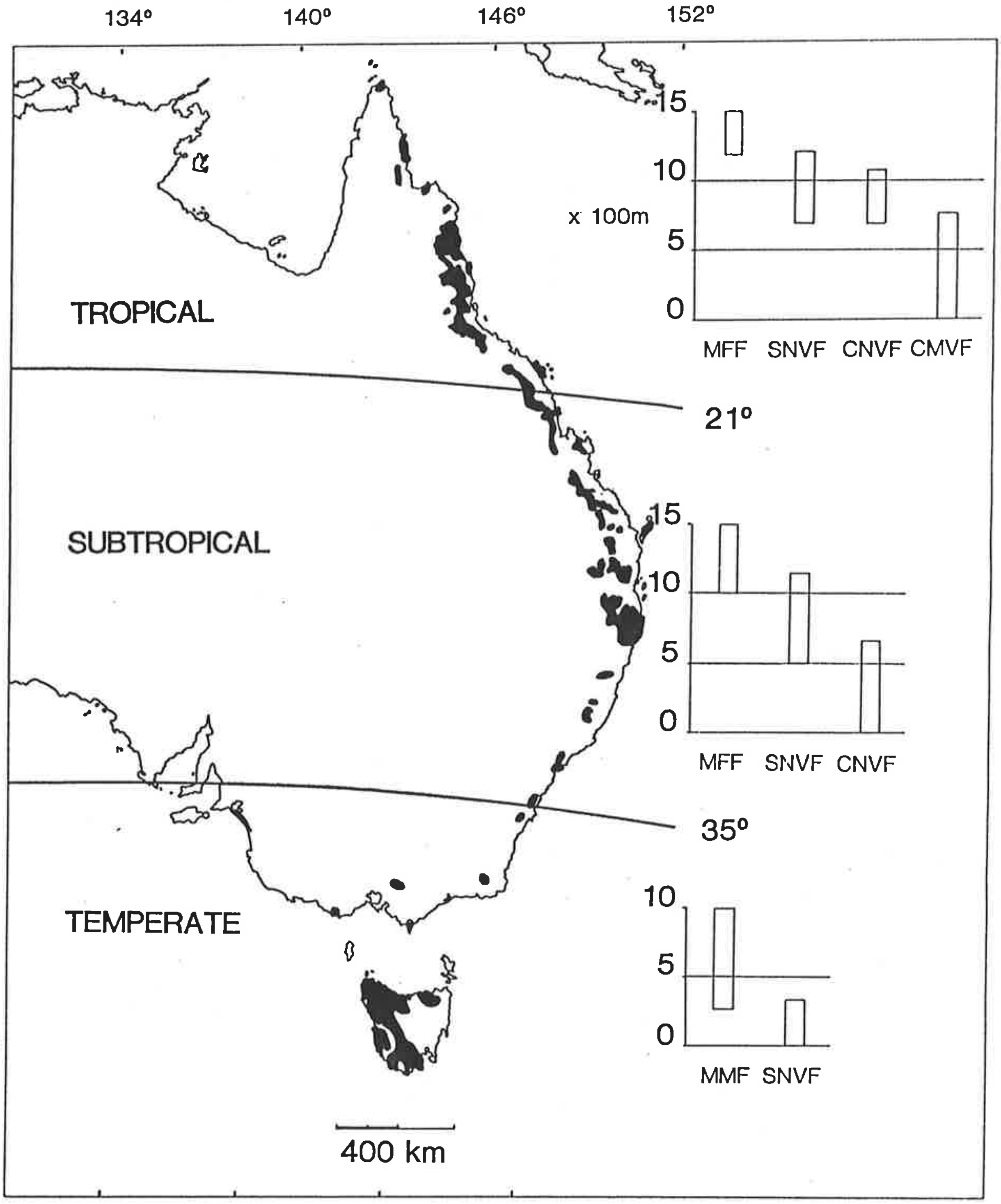


Figure 2.2 The modern distribution of rainforest in Australia. The areas indicated also include forest cleared since european settlement, and are slightly exaggerated as it was not possible at this scale to indicate the complex mosaic between rainforest and more open forest dominated by Eucalyptus spp. (Myrtaceae). The altitudinal range of the four principal rainforest types for the three climatic regions is indicated on the three graphs to the right of the figure. Data from Webb (1959, 1968), Tracey (1982), and Webb and Tracey (1982).

to 15°00' S), mesophyll vine forests are found up to an altitude of 750 metres (Tracey, 1982; Fig. 2.2).

The Complex Notophyll Vine Forests are most strongly represented in the subtropical lowlands of southern Queensland and northern New South Wales (Fig. 2.4). However, important outliers occur to the south in the Illawarra area near Woolongong, south of Sydney in New South Wales, and to the north on the Atherton Tableland (and nearby ranges) in N.E. Queensland in the wet tropic region. The occurrence of CNVF in N.E. Queensland is strongly controlled by edaphic factors (Fig. 2.1). In New South Wales and southern Queensland, CNVF generally occurs below 1000m, and usually below 500m altitude (Fig. 2.2).

Simple Notophyll Vine Forest occurs on suitable sites for most of the length of the coastal ranges of the east coast, however a major disjunction occurs in central coastal Queensland (Fig. 2.5). The main areas of occurrence are the higher ranges of the wet tropical region of N.E. Queensland, and the highlands of northern New South Wales and southern Queensland (Fig. 2.2, 2.5).

The distribution of the Microphyll Fern and Mossy Forests (including the Microphyll Vine-Fern Forests of N.E. Queensland) is less clear. These forests tend to occur as very small isolated pockets on high peaks (often stunted to a thicket, N.E. Queensland; Tracey, 1982), or within a vegetation mosaic on high plateaux and mountains (Fraser and Vickery, 1937; Baur, 1957). However, the main area of occurrence is the highlands of northern New South Wales and southern Queensland (Fig. 2.6; 28° – 33° S). Important outliers occur in ne Queensland, where MFF often grades into SNVF (Fig. 2.2), and in Victoria, where MFF is generally replaced by Nanophyll Mossy Forest.

2.3 Climate of the Rainforest Areas.

The climate of the humid tropical region of N.E. Queensland was discussed by Tracey (1982). However, some of the points can be usefully reiterated here. Additional information has been collected from the Australian Bureau of Meteorology to augment Tracey's comments (Gordon, 1971; Anon., 1983). This information is used later (Chapter 6) in an analysis of the climatic characteristics of Webb's

Figures 2.3 - 2.6 The modern distribution of the four principal rainforest types: CMVF/SDMVF/MVF, Fig. 2.3; CNVF, Fig. 2.4; SNVF, Fig. 2.5; MFF/MMF, Fig. 2.6. Each solid circle represents a Site from Webb and Tracey's survey (Webb and Tracey, 1982) representing the indicated forest type(s). At this scale some sites are almost coincident and so have been omitted. Many sites from S.E. Australia (mainly representing MMF in Tasmania) have been omitted due to inaccurate or incomplete location data.

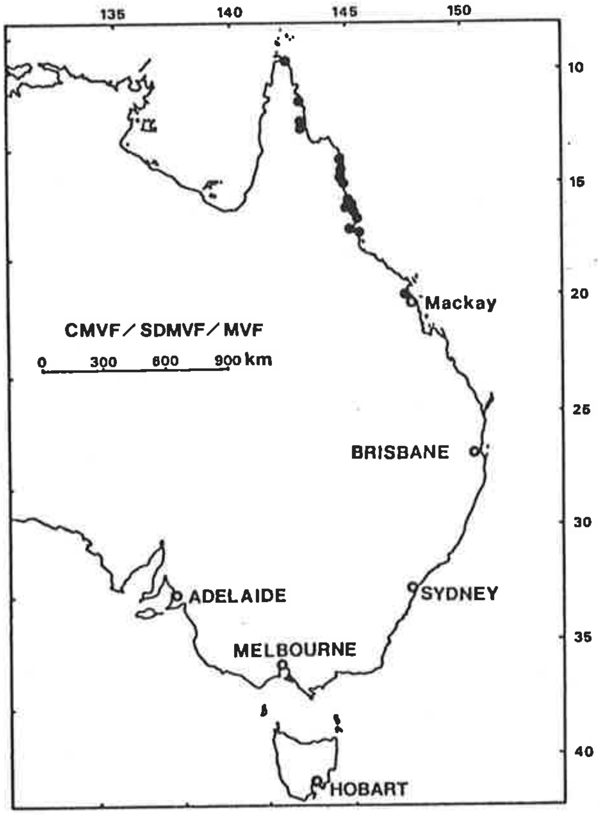


Fig. 2.3

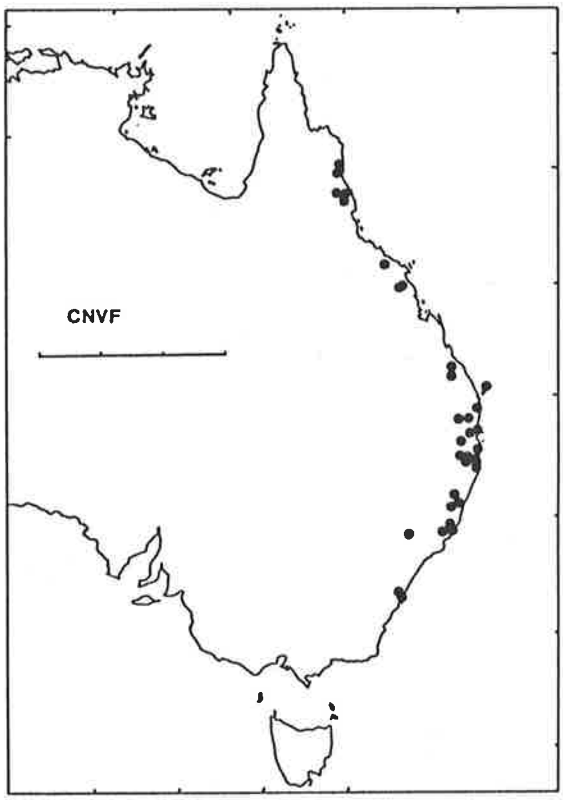


Fig. 2.4

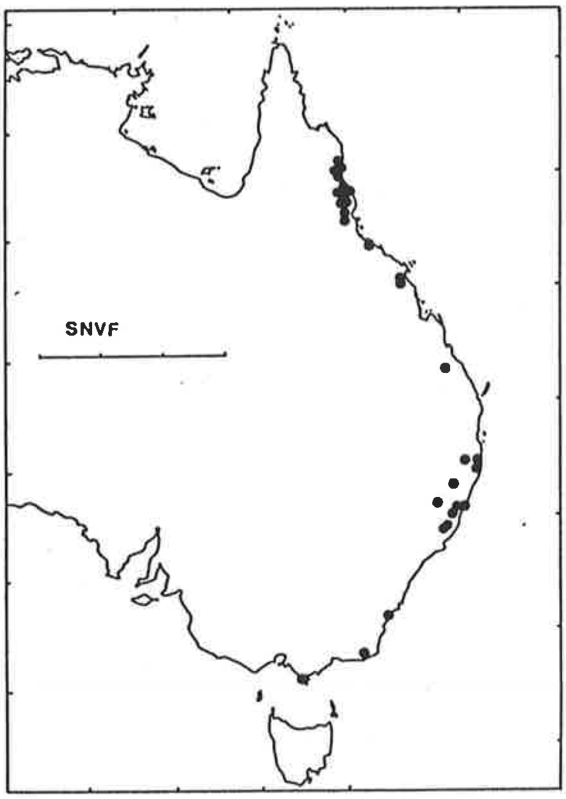


Fig. 2.5

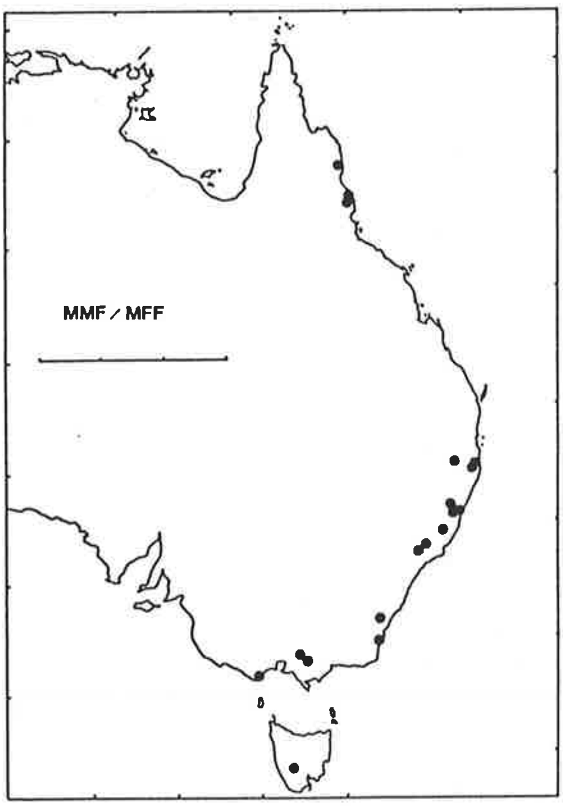
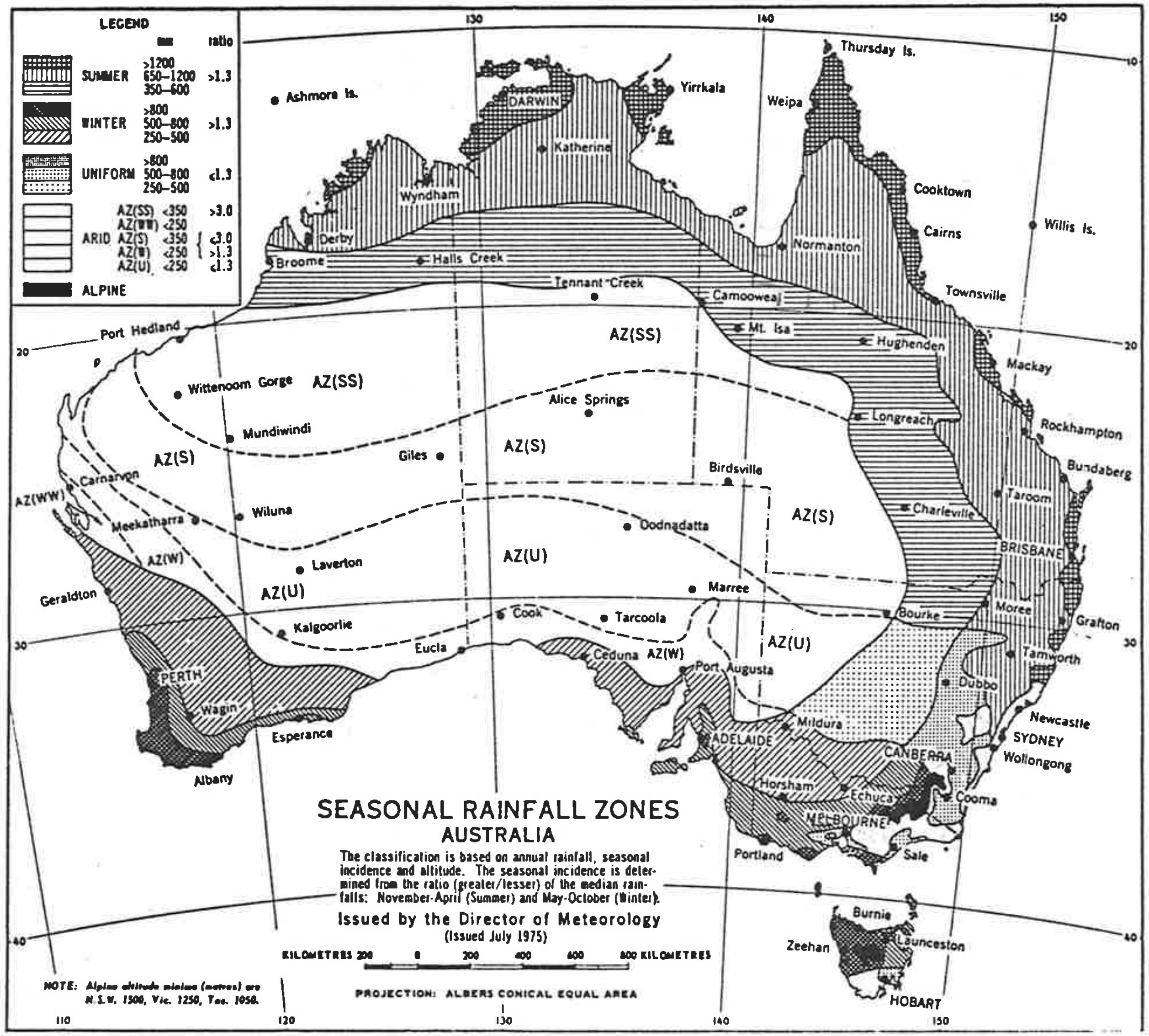


Fig. 2.6

Figure 2.7 The rainfall regimes of Australia. Rainforest occurs in the summer rainfall zone (>1200 mm) in N.E. Queensland, the uniform rainfall zones of New South Wales and eastern Victoria (>800 mm), and the winter rainfall zone of southern Victoria and Tasmania. From Anonymous (1982).

Fig. 2.7



forest types and the climatic classifications used by Holdridge (1967) and Wolfe (1980a).

The temperate rainforest areas (Fig. 2.2) of Victoria and Tasmania experience a short summer drought (usually February), although some areas are nearly nonseasonal, especially in the area of overlap between the summer and winter rainfall regimes (Fig. 2.7). All of the study sites are in the summer rainfall zone, and so the climatic characteristics of the winter rainfall temperate zone will not be considered in detail.

The subtropical rainforest areas (Fig. 2.2) of southern Queensland and northern New South Wales occur in the region of overlap between the summer and winter rainfall regimes, although in most areas there is a tendency towards higher summer rainfalls (Fig. 2.8). The climatic characteristics of meteorological recording stations from within the occurrence of CNVF, SNVF, and MFF, for this area are given in Figure 2.8. The seasonal range of temperature for any of the stations is not marked by world standards, and this is typical for the area. The seasonal range of temperature is greater than observed for the ne Queensland tropical region (Fig. 2.9).

The climate of Australia's tropical rainforest areas is monsoonal with a dry season from May through to November. The severity and actual length of this dry season varies over quite short distances due to topographic effects (Gordon, 1971; Sumner and Bonell, 1986). In most tropical rainforest areas rainfall increases with altitude (Whitmore, 1984). However, in N.E. Queensland it decreases markedly with increasing distance from the sea (Tracey, 1982; Spain, 1984; Sumner and Bonell, 1986). As a consequence, the western half of the Atherton Tableland area is more seasonal and much drier than the eastern half (Fig. 2.10).

2.4 The Rainforest Environment.

2.4.1 Rainforest Structure and Microclimates.

Rainforests, particularly 'Tropical rainforests', are noted for the apparent separation of the trees into a number of layers or strata (Richards, 1952 1983; Webb, 1959; Whitmore, 1984; Tracey, 1982). There is much debate however, over the

Figures 2.8 and 2.9 Climatic profiles of stations representing the principal rainforest types in N.S.W. (Fig. 2.8) and N.E. Queensland (Fig. 2.9). The bars of the histograms indicate monthly rainfall (mm), the squares the mean monthly maximum (solid squares) and minimum (open) temperature (T C). Anonymous, 1983.

Fig. 2.8 Climatic characteristics of stations representing 3 rainforest types in N.S.W.

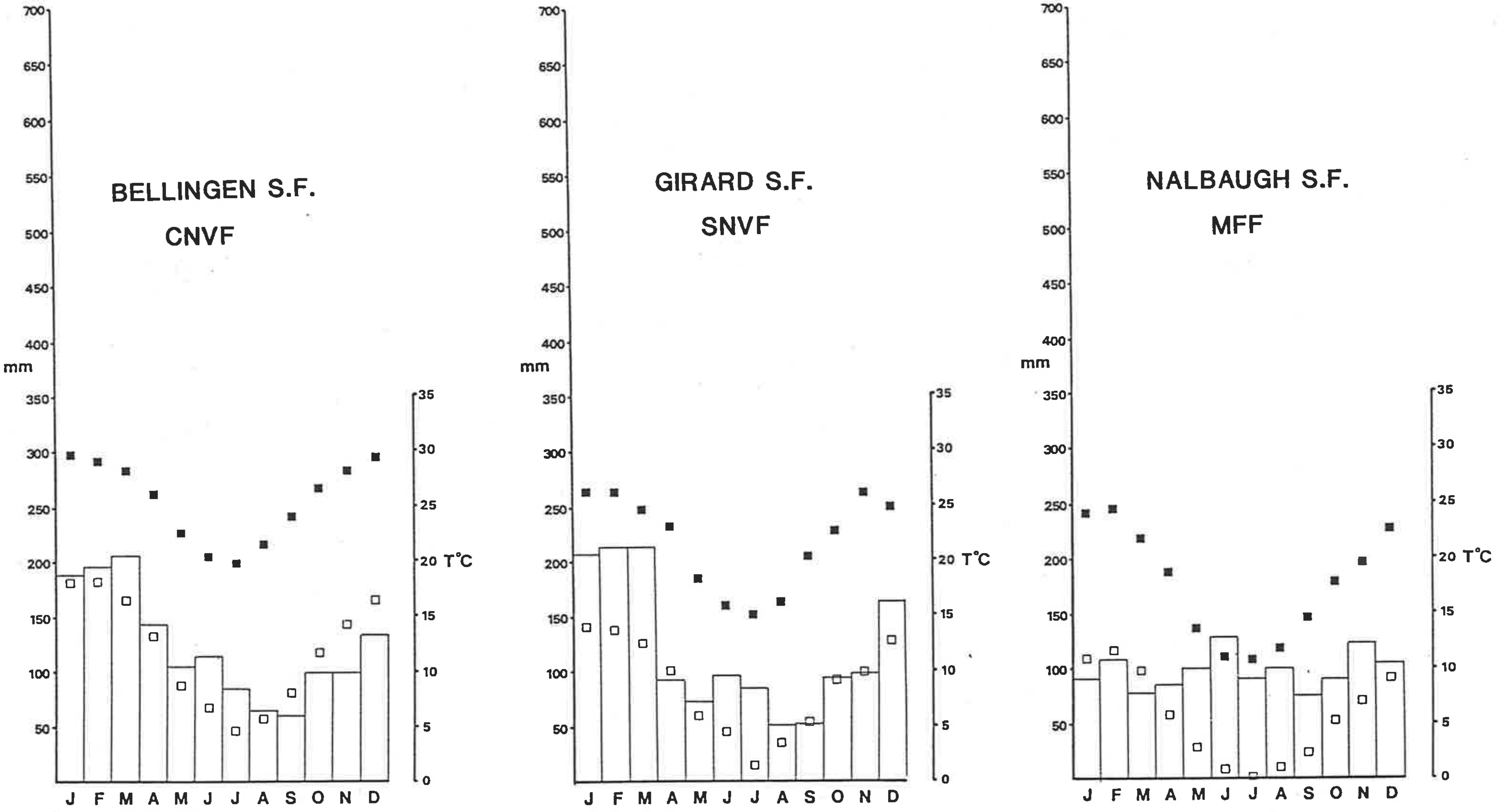


Fig. 2.9 Climatic characteristics of 3 stations representing rainforest types of N.E. Queensland.

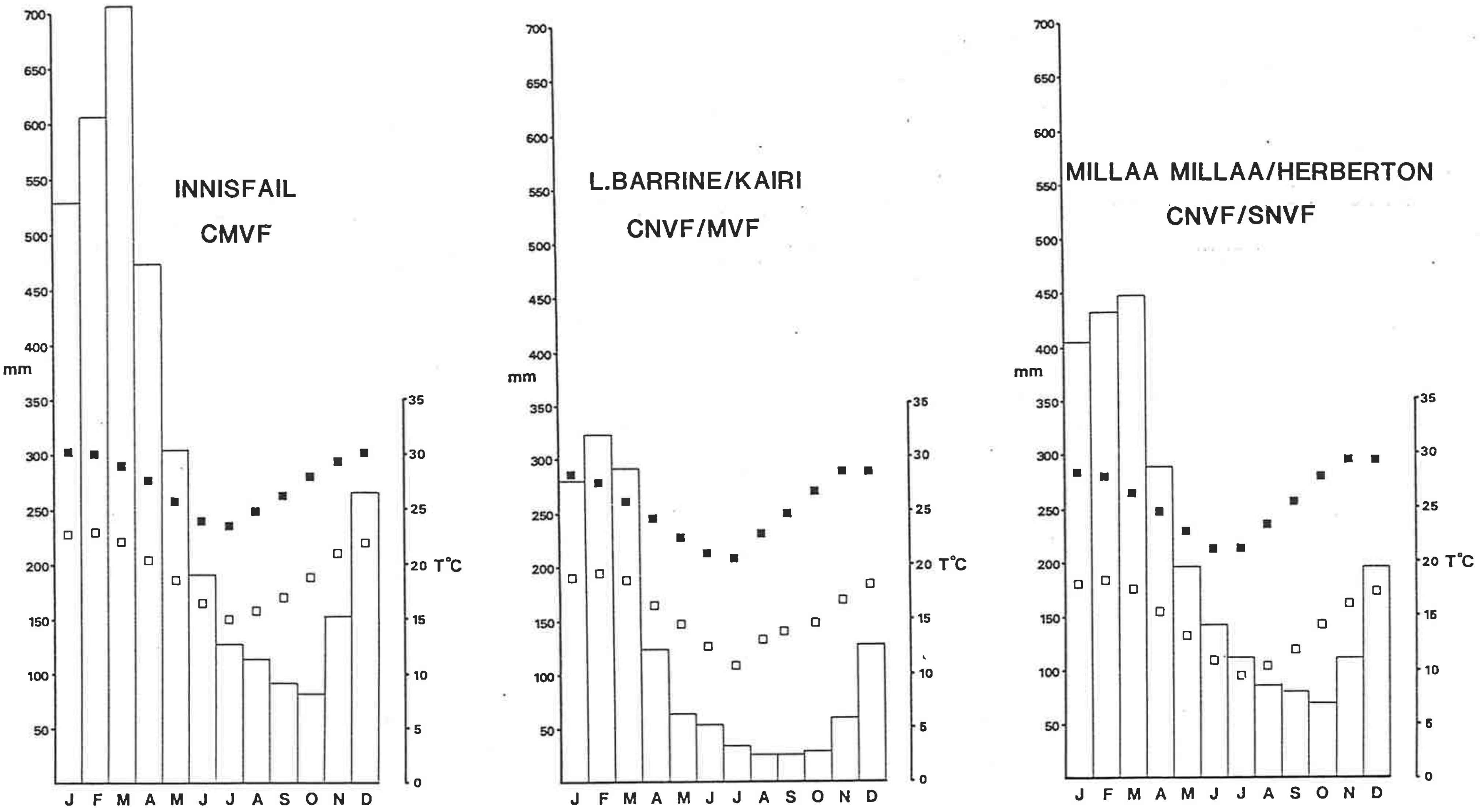


Fig. 2.10

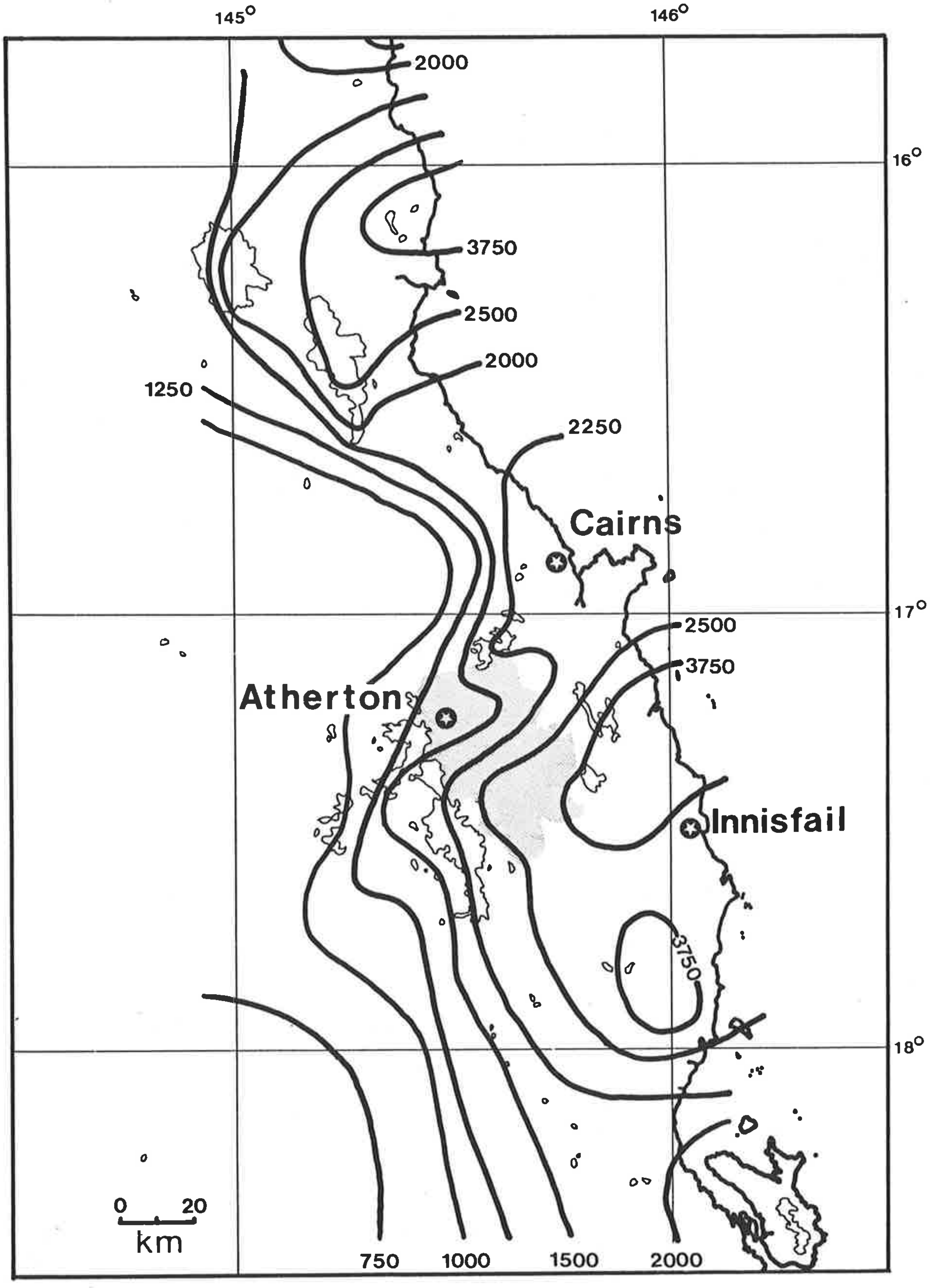


Figure 2.10 Rainfall map of the humid tropical region of N.E. Queensland. Isohyets in mm. The Atherton Tableland is stippled and the 1000m contour is indicated by a solid line. Slightly modified from a map in Tracey (1982).

usage and reality of stratification in tropical rainforests with some authors dismissing their utility in forest classifications (Whitmore, 1984; Bourgeron, 1983). According to Webb (1959) and Tracey (1982), these strata are not easily discerned in Australian rainforests due to the merging of the successive strata by 'transgressives'; saplings in the process of recruitment from a lower stratum into the next stratum (Tracey, 1982).

Although there is debate over rainforest "stratification", it is nevertheless apparent that tropical rainforests display a vertical structure with particular species ultimately occurring at different heights to others (Bourgeron, 1983; Richards, 1983; Whitmore, 1984). Each of these strata has a different microclimate with a progressive departure from the conditions experienced in the open to those experienced at the forest floor (Richards, 1952 1983; Aoki et al., 1975; Whitmore, 1984).

Generally the forest floor is much cooler and the atmospheric humidity much higher than experienced by the canopy, and the level of atmospheric CO_2 present may also vary (Aoki, et al., 1975; Bourgeron, 1983). The forest floor is also insulated from the drying and damaging effects of wind. The magnitude and direction of the difference between microclimates in the different levels of the forest also varies on a daily and annual basis (Whitmore, 1984).

Light levels at the forest floor are also very low, with many plants relying on occasional light flecks. The effect of the degree of structural complexity on the light environment in three Australian Rainforests — CNVF, SNVF, and MFF — was studied by Lowman for sites in New South Wales (Lowman, 1986). The thinner, less stratified canopy of MFF was found to allow more light to the forest floor than in the SNVF and CNVF examples, where the major light source appeared to be light flecks.

Theoretical modelling and experimental work (e.g. Givnish, 1978; Davis and Taylor, 1980) suggests that each microclimate within the successive strata will promote the growth of leaves of a different physiognomic character to the others (Roth, 1984). The canopy trees will require leaves adapted to resist dessication due to higher temperatures, light levels and wind speeds. Plants on the forest floor, including saplings of canopy and emergent species, will need larger leaves to take advantage of the lower light levels, and will not need to be adapted to prevent dessication due to the higher humidity and lower temperatures.

The number of tree strata has been used to differentiate between different rainforest types. Beard distinguished between 'Tropical Rainforest' with four tree layers, and 'Evergreen Seasonal Forest' with three layers (Beard, 1944; Richards, 1952). Similarly, Wolfe distinguishes his 'Tropical Rainforest' from 'Paratropical Rainforest' on the same basis (Wolfe, 1980a). The difference between Webb's 'Simple' and 'Complex' vine forests (rainforests) is the number of tree strata present (Webb, 1959, 1968; Tracey, 1982).

Each of the rainforest types used in this study possess different numbers of layers. Lowman (1986) found that CNVF, SNVF and MFF in New South Wales differed in the depth and complexity of the canopy layers. These differences can be considered to produce varying levels of complexity to the range of microclimates experienced by leaves over the whole forest. Webb's foliar physiognomic correlations were based on trees in the canopy alone, and so can be considered to be representative of only a part of the range of microclimates available in any of the rainforest types. Leaf litter, and by inference, fossil leaf deposits, will represent leaves from a range of strata and thus a range of microclimates.

2.4.2 Seasonality of Leaf Fall.

The longevity of the leaves of Australian rainforest trees is not well known (Rogers and Barnes, 1986). The longevity of leaves from two species in Indian monsoonal rainforest was found to be vary from 50 to just over 300 days (Shukla, 1984). Longevity was markedly different for leaves initiated at different times, and between species. Rogers and Barnes however, found that the leaves of the rainforest shrub, *Wilkiea macrophylla* (Monimiaceae), in CNVF in southern Queensland had a half-life of 6.84 years (Roger and Barnes, 1986). Leaf initiation in rainforest trees is usually associated with the commencement of the wet season (Richards, 1952; Webb et al., 1969). However, some species produce their leaves at other times (e.g. *Wilkiea macrophylla*, spring — summer dry period; Rogers and Barnes, 1986). The timing and volume of leaf fall is better known.

The essentially seasonal rainfall of Australia's tropical areas is reflected in the seasonality of leaf loss by most of the rainforest types in this area, although the degree of leaf loss varies according to the length and severity of the dry season (Webb et al., 1969). According to Webb et al. (1969) and Spain (1984), leaf loss in CMVF and CNVF in N.E. Queensland, and SNVF in New South Wales, occurs throughout the year, but with a marked peak in leaf loss from late September to late October. In the more seasonally dry forest types some trees will experience a complete loss of leaves (e.g. *Toona australis* (F.Muell.) Harms, Meliaceae). However most trees retain a full canopy and grow new leaves immediately after this peak in leaf loss, just before, or at the start of, the wet season. In contrast to these results, Proctor et al. (1983) and Brasell et al. (1980) found that rainforests in Sarawak and N.E. Queensland had a peak in litterfall at the time of highest rainfall.

Field surveys by the author in June 1982, and litter collections in August 1984, and September 1985 (Chapter 3), found moderate levels of leaf litter on the forest floor on each occasion. It is generally considered that decay rates of leaf litter are very high in tropical rainforests (Webb et al., 1969; Anderson and Swift, 1983). However, a survey of the literature on litter decay rates by Anderson and Swift (1983) found that most studies suggest that leaves may remain on the soil surface for up to a year in tropical lowland rainforests, and for slightly more than a year in tropical montane rainforests. From the data they list, it can be concluded that in tropical rainforests, leaf litter volumes at any one time generally represent leaf-fall over several months.

The commencement of the wet season is associated with sudden high rainfall (Gordon, 1971; Sumner and Bonell, 1986). I have also observed increased sediment load in streams at this time. These circumstances are very favourable for the inclusion of leaves in sedimentary structures such as cut-off stream meanders. High initial runoff will carry leaves beyond the main stream course into these structures. For example, Dudgeon found that a significant proportion of the leaf input into streams at the commencement of the monsoon in Hong Kong was from lateral transport of leaves from the forest floor by overwashing by surface runoff during heavy rain (Dudgeon, 1982). Therefore, from a taphonomic perspective, the litter loads at the commencement of the wet season (October — November) are of greatest interest as litter at this time is most likely to represent the input into depositional sites.

2.5 Descriptions of Forest Types.

2.5.1 Complex Mesophyll Vine Forest (CMVF).

Complex Mesophyll Vine Forest is perhaps equivalent to the 'Tropical Rainforest' of Beard (1944) or the 'Lowland Tropical Rainforest' of Richards (1952). Webb commented that 'Tropical Rainforest' as defined by Beard might be absent from Australia, and considered CMVF equivalent to the 'Evergreen Seasonal Forest' of Beard (1944; Webb, 1959). Wolfe considered CMVF equivalent to his 'Paratropical Rainforest', which is distinguished from 'Tropical Rainforest' on the basis of the presence of only three tree layers in 'Paratropical Rain Forest' compared to four layers in his 'Tropical Rainforest'. Paratropical Rainforest is also defined by the occurrence of this forest type in areas where the annual average temperature is between 20 and 25 degrees (Wolfe, 1980a).

Complex Mesophyll Vine Forest is typically species rich with no one species dominating the canopy although particular species of emergent may be characteristic of some areas (Tracey, 1982). The canopy of CMVF is generally dominated by species and individuals with mesophyll-sized leaves (Table 2.3), and there is usually three tree layers (Webb, 1959; Tracey, 1982). Species and individuals with non-entire margined leaves are rare or absent in the canopy (Table 2.4) and characteristic life-forms such as strangler figs and buttress roots are also prominent (Webb, 1959; Tracey, 1982). At slightly higher altitudes CMVF is replaced by Simple Mesophyll Vine Forest (MVF), which is the 'Lower Montane Rainforest' of Beard (1944; Webb, 1959) and would seem strictly analogous to Wolfe's 'Paratropical Rainforest' (Wolfe, 1980a). Simple Mesophyll Vine Forest is characterised by generally smaller leaf sizes than CMVF and other structural differences (Webb, 1959; Tracey, 1982).

2.5.2 Complex Notophyll Vine Forest (CNVF).

Complex Notophyll Vine Forest is equivalent to 'subtropical rainforest' and the 'Evergreen Seasonal Forest' of Beard's classification (Beard, 1944; Webb, 1959). In his physiognomic classification of east Asian mesic forests, Wolfe considered both CNVF and SNVF to be analogous to his Notophyllous Broad-leaved Evergreen Forest (Wolfe, 1980a). However, within Australia these two forest types are well differentiated and their occurrence is clearly delimited by separate climatic and edaphic factors (Webb, 1968).

In the humid tropical region of N.E. Queensland Complex Notophyll Vine Forest is restricted to areas where climatic and edaphic factors are suitable for its development (Tracey, 1982). Complex Notophyll Vine Forest (Type 5b; Tracey, 1982) occurs on high fertility soils (basalts and basic volcanics) under marginal rainfall regimes at intermediate altitudes (Figs 2.1 & 2.2). CNVF (Type 5a) also occurs at slightly higher altitudes on cool wet sites. In the Humid Tropical region CNVF is generally displaced by other rainforest types where rainfall is less seasonal, and higher, or soil fertility lower on higher (and wetter) sites (Webb, 1968; Tracey,1982: Fig. 2.1).

The basalt soils of the western half of the Atherton Tableland were once covered by Complex Notophyll Vine Forests (Tracey, 1982). Rapid clearance in the 1920-30's has left only a few small patches around old volcanic craters or in small State Forest reserves such as at Curtain Fig, where a large strangler fig (the "Curtain Fig")- *Ficus virens* (Moraceae) — and the surrounding rainforest, has been preserved as a tourist attraction.

The wetter, less seasonal eastern half of the Atherton Tableland supports Complex Mesophyll Vine Forest, grading into Mesophyll Vine Forest at slightly higher elevation (Fig. 2.10). Rainfall at the south eastern corner of the Atherton Tableland and in the Hugh Nelson Range to the west is also higher, however the cooler climate and edaphic factors (soil fertility) has produced a variant of CNVF (type 5a; Fig. 2.1). Complex Notophyll Vine Forest with *Agathis robusta* (Araucariaceae) (forest type 6) is also found in gullies on the south western edge of the Tinaroo Range to the north of the Atherton Tableland (Tracey, 1982;

Webb and Tracey, 1982).

The essentially edaphic-climatic determinants of N.E. Queensland CNVF (Fig. 2.1) are reflected in the floristic differences. For example, the more seasonal type of CNVF (type 5b) is characterised by semi-evergreen (i.e. leaf loss at times of severe moisture stress) and scattered deciduous trees, including *Melia adzedarach* var *australasica* and *Toona australis* (Meliaceae). The cool wet CNVF (type 5a) shares many species with SNVF, and also warmer wetter rainforest types. Deciduous species are rare in this type (Tracey, 1982).

In New South Wales and southern Queensland the transition from CNVF to SNVF is essentially climatically forced. Complex Notophyll Vine Forest is the dominant rainforest type in the subtropical lowlands between 20°S and 31°S, and formerly occurred as extensive stands in the region of the Clarence River in northern New South Wales. Extensive clearance in the late 1800's has left only scattered remnants in the more inaccessible areas where logging was not economic or occasionally forest was left for other reasons.

The CNVF of the lowlands of northern New South Wales shares many species with the Type 5a and Type 6 CNVF from N.E. Queensland, but retains a unique character (Webb, et al., 1984 Tracey, 1982). Local areas are of a lower species diversity than equivalent sites in N.E. Queensland.

There are several species shared between the New South Wales SNVF and the New South Wales CNVF including *Acradenia euodiiformis* (Rutaceae), *Orites excelsa* (Proteaceae), and *Syzygium crebinervis* (Myrtaceae; Fraser and Vickery, 1937; Baur, 1957). Often occasional individuals of species normally associated with one forest type will occur in the other, and the overlap seen in these lists partly reflects this. There are species, however, which occur equally in both forest types and others solely restricted to one forest type.

2.5.3 Simple Notophyll Vine Forest (SNVF).

Simple Notophyll Vine Forest incorporates the 'Warm Temperate Rainforest', 'Sub-Tropical Lower Montane Rainforest', and 'Tropical Sub-Montane Rainforest' of other classifications (Webb, 1959; Beard, 1944), and is physiognomically analogous to Wolfe's 'Notophyllous Broad-leaved Evergreen Forest' (Wolfe, 1980a). The canopy of SNVF is dominated by trees with notophyll-sized leaves with a moderate to high proportion of them with non-entire margins (Tables 2.3 & 2.4).

In N.E. Queensland (19°00' S to 15°00' S) SNVF principally occurs between 800-1000m but may occur between 400-1200m altitude (Webb, 1959; Tracey, 1982; pers. observ.). Simple Notophyll Vine Forest grades into Simple Microphyll Vine-Fern Forest at higher altitudes (800-1400m) as microphylls become more common with increasing altitude and exposure. At about 1200m on smaller peaks and 1400m on large mountain blocks Microphyll Fern Thicket replaces SNVF and MFF (Tracey, 1982; Fig. 2.1). In New South Wales SNVF occurs from sea level to 300m at 35°00' S, and from 300m to 1000m at 30°00' S and is replaced by MFF dominated by *Nothofagus moorei* (Fagaceae) at higher altitudes (Fig. 2.2).

Within N.E. Queensland and New South Wales SNVF maintains fairly consistent floristics. However, there are important differences in the floristic characters of the N.E. Queensland and New South Wales SNVF's. Simple Notophyll Vine Forest in N.E. Queensland is relatively species rich, and according to Tracey (1982), there is a fairly consistent species composition in the tree layer. The New South Wales SNVF is by contrast relatively species poor and often tend to single species dominance of the canopy, e.g. *Ceratopetalum apetalum* (Cunoniaceae). These latter forests are colloquially called "Coachwood forest" after the local name for the dominant species.

Webb suggested that the New South Wales SNVF's are floristically depleted due to continual recovery from repeating 'catastrophe' in the form of extensive and highly destructive forest fires over recent geological time (Webb, 1968). The exigencies of the Pleistocene glaciations and associated drier climates may also be a contributing or causal factor. The floristic richness of the N.E. Queensland SNVF's therefore suggests that they represent the ancestral condition of these forests, and the New South Wales forests a derived survivor. The fossil evidence indicates that highly diverse rainforests with species related to species now found in N.E. Queensland SNVF, formerly grew in SE Australia (Christophel, 1984;

Greenwood, 1987; Christophel and Greenwood, 1988), supporting this idea.

2.5.4 Microphyll Fern Forest / Moss Forest (MFF & MMF).

According to Webb (1959) there is no true equivalent to Microphyll Fern Forest in other physiognomic classifications, although the stunted Microphyll Fern and Moss Thickets (MFT and MMT) of N.E. Queensland are probably analogous to "Tropical Montane Rainforest" and "Elfin Woodland" (Beard, 1944). Similar forests however, are present in montane New Guinea (Pajimans, 1977), the South Island of New Zealand, and southern Chile (Godley, 1960).

Microphyll Fern Forests and Microphyll Moss Forests are best developed on tall wet mountains between 1200 – 1500m in New South Wales and at lower altitudes in Victoria and Tasmania (Fig. 2.2 & 2.6). The equivalent formation in N.E. Queensland is Simple Microphyll Vine-Fern Forest which occurs between 800 – 1300m and grades into Simple Notophyll Vine Forest at lower altitudes. In New South Wales Microphyll Fern Forest and Simple Notophyll Vine Forest usually remain as quite distinct entities. Diversity in the New South Wales forests is much lower than in their counterparts in N.E. Queensland, and the degree of overlap in the ecological requirements of the component species is not as great as it is in the submontane and montane tropical zone.

The canopy of the Microphyll Fern Forests of New South Wales and southernmost Queensland are dominated by *Nothofagus moorei* (Fagaceae), and the forest floor is often fairly clear with only occasional clumps of bushes which become more frequent near streams. Treeferns (*Dicksonia antarctica* Labill. Dicksoniaceae) often form a discrete stratum. Leaf sizes in the canopy are typically microphyll although nanophylls and notophylls are well represented (Webb, 1959; Tracey, 1982; Table 2.3).

The MFF of New South Wales is floristically very distinct to the species rich MFF of N.E. Queensland with no tree species in common between the two regions. The bush *Trochocarpa laurina* R.Br. (Epacridaceae) however, is found in MFF and MFT in both N.E. Queensland and New South Wales (Floyd, 1982) and at the generic level, *Doryphora* (Atherospermataceae), *Drimys* (Winteraceae), *Elaeocarpus* (Elaeocarpaceae) and *Quintinia* (Escalloniaceae) occur in MFF in both regions (Floyd, 1978 1981a & b; Tracey, 1982).

Webb (1959) did not distinguish between MFF from the two regions and so does not give physiognomic comparisons. My own observations suggest that the high proportion of species from MFF with non-entire margins quoted by Webb (1959; Table 2.4) reflects the situation in the New South Wales MFF only, as perhaps only 50 – 60% of individuals in N.E. Queensland MFF had non-entire margins compared to close to 100% in New South Wales.

It is interesting to note that *Doryphora aromatica* (F.M.Bailey) L.S.Smith occurs in the upland CMVF, the "cool wet" CNVF, and SNVF of N.E.Queensland (Tracey, 1982). It's sole sister species, the New South Wales species, *D. sassafras* Endl., is similarly tolerant of a wide range of conditions. I have observed it in MFF, SNVF, and rarely in CNVF. One would expect that the physiognomy of the leaves of these species varies between individuals from each of the forest types, and matches more or less the prevailing physiognomy of the leaves of the surrounding forest. This point is discussed later (Chapter 7) as these two species occurred at three of the litter collection sites.

Chapter 3

SAMPLING STRATEGY AND DESCRIPTION OF COLLECTION SITES.

3.1 Introduction.

Recent studies on the taxonomic composition of southern Australian Tertiary Floras have highlighted the humid tropics of N.E. Queensland as a region where the modern relatives of commonly occurring Tertiary taxa are concentrated (Christophel, 1984; Greenwood, 1987; Christophel and Greenwood, 1987; Christophel and Greenwood, 1988). It was further suggested on the basis of the presence of these taxa in N.E. Queensland, that analogues of the Tertiary vegetation of southern Australia may be best sought in the rainforest vegetation of this area (Christophel and Greenwood, 1988). It was thus considered important to understand taphonomic influences on leaf beds formed in a tropical environment before foliar physiognomic analysis could be reliably applied to many of the Tertiary floras.

However, in the modern environment there are few opportunities where natural vegetation occurs in a situation which simulates depositional basins of the character which gave rise to the most common Tertiary leaf beds. This is particularly true in tropical forests where most of the lowland forests are cleared or substantially altered by man's activities. Some of Spicer's work suggested that in situations of quiet leaf deposition, the resultant leaf bed is essentially the same as leaf litter from the forest floor (Spicer, 1981).

Earlier in this thesis, it was argued that for many of the common sedimentary environments where Tertiary leaf beds are found in Australia, the leaves can be considered to have fallen directly (or nearly so) into the entrapping sediments. The use of leaf litter as an analogue of a fossil leaf bed has several advantages. Some of these points have been discussed previously. Principally, the use of leaf litter allows greater flexibility in the sampling strategy and in the types of questions answered. Finer control is possible over the origins of the leaves in the leaf beds. For example, it is possible that in some sedimentary environments two or more physiognomically distinct vegetation types maybe contributing leaves over very short distances. An example of three physiognomically distinct forest types (MFF, SNVF, and CMVF) occurring closely within the catchment of two tropical streams (Oliver Creek and Noah Creek) is shown in Figure 3.1.

The physiognomic character of a leaf bed formed in this circumstance will not represent any one of these vegetation types, but rather some amalgam of them. While it might be argued that these "mixed leaf beds" better reflect a "natural" situation, and therefore the type of circumstance likely in a Tertiary leaf bed, this study has sought to identify whether a single forest type contributing to a leaf bed retains a "physiognomic signature" in that bed. Mixed source leaf beds represent a more complex situation which can be studied subsequent to this study.

The decision was therefore made to use leaf litter as an analogue of recently deposited leafbeds in streams. It must be stressed however, that according to earlier studies on lake sediments (McQueen, 1969; Drake and Burrows, 1981; Hill and Gibson, 1986), leaf litter would not be a good approximation of fossil leafbeds formed in large lakes.

Using leaf litter as an analogue however, does not answer some other important questions on the taphonomy of leaf beds. Mechanical breakdown and differential decay during stream transport may selectively remove larger leaves prior to deposition (MacGinitie, 1969; Kaushik and Hynes, 1971; Wolfe, 1971; Spicer, 1981). It has also been suggested that streamside vegetation may have different physiognomic characteristics to the main forest, producing a biased interpretation (MacGinitie, 1969; Wolfe. 1971 1980a & b). Two examples of 'neofossil'

Fig. 3.1

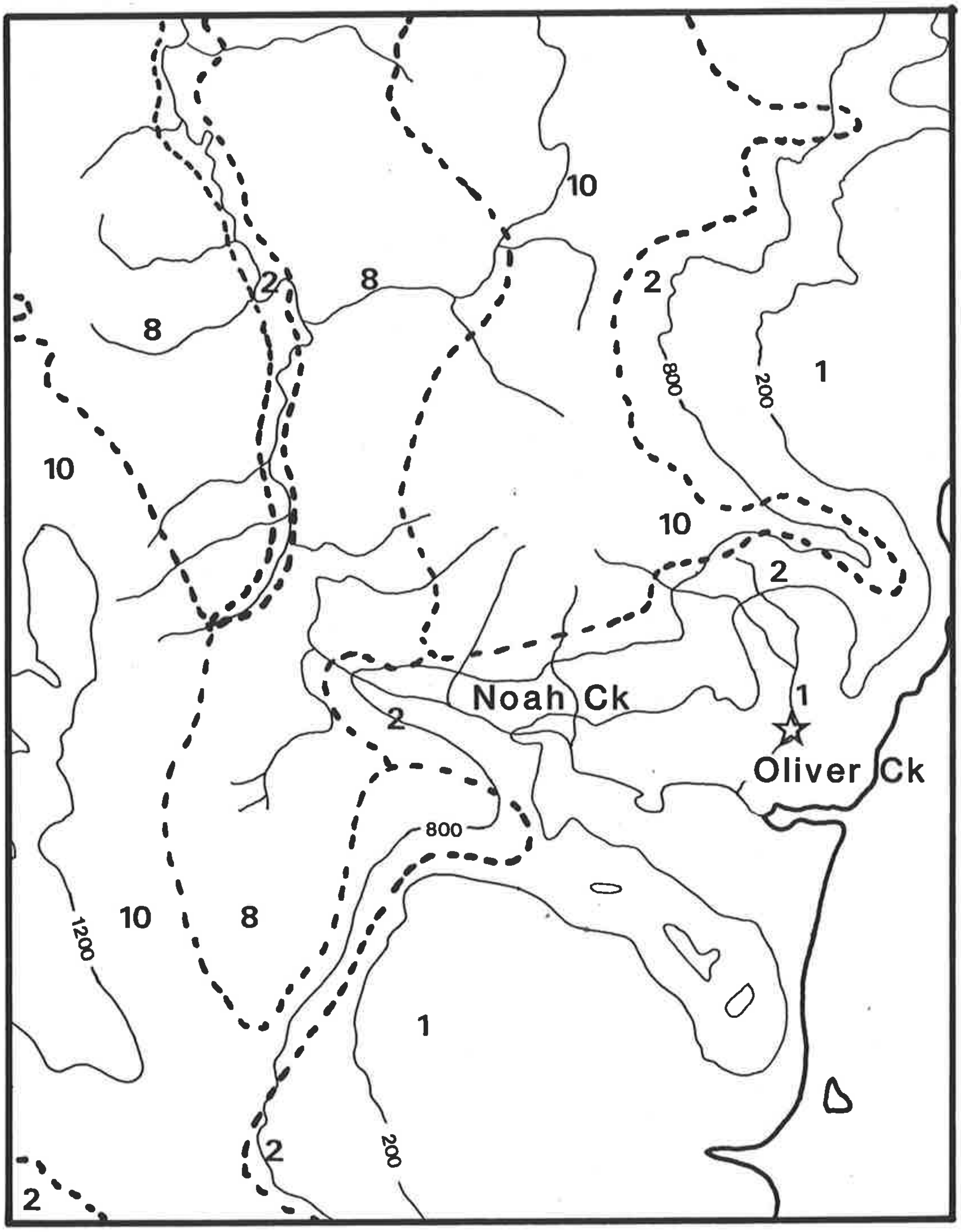


Figure 3.1 Vegetation map (simplified) of a small region north of Cairns, N.E. Queensland. See Fig. 3.2 for exact location. Boundaries of forest types indicated by dashed lines, numbers indicate forest types in Table 3.1. The leaf litter collection site, Oliver Ck (CMVF), is indicated by an open star. Forest types can be seen to more-or-less change with increasing elevation, producing a mosaic of four forest types within the catchment of Noah and Oliver Creeks.

leaf beds were incorporated into the study to measure the effect of this bias on "physiognomic signatures". They are further discussed later.

3.2 Approach Used in the Study.

Many previous studies on foliar physiognomic analysis considered regional differentiation of vegetation and sought to link this to large scale regional climatic variation (Dolph and Dilcher, 1978; e.g. Wolfe, 1971 1980a), or considered the role of climate (or microclimate) in determining the physiognomy of individual leaves (Davis and Taylor, 1980). Any study which seeks to correlate large scale pattern in one system (climate) to that in another (physiognomy of vegetation), requires an understanding of the processes and the factors determining the interactions between the two systems. Therefore, choice of the study area had to satisfy the demands of the questions asked as well as the available sources of information on the interacting systems under study.

The Webb physiognomic classification of Australian rainforest (Webb, 1959, 1968; Tracey 1982) provided a logical framework to test the presence of physiognomic signatures in leaf beds as it is already in part based on interactions between climate and leaf physiognomy. This classification system is in wide use in Australia, and furthermore Webb and Tracey have created a data base identifying 624 localities where a patch of rainforest has been classified and the component species at the site recorded (Webb and Tracey, 1982). In addition, much of the vegetation of the humid tropical region of N.E. Queensland (19° to 15°S 144°30' to 146°30' E, Tracey,1982) has been mapped using Webb's classification (Tracey and Webb, 1975).

This data base presented an opportunity where physiognomic analysis of leaf beds could be directly related to the known physiognomic characteristics of forest types. Forest typology and nomenclature for the N.E. Queensland rainforests follows Tracey (Tracey and Webb, 1975; Tracey, 1982) throughout this thesis unless otherwise stated. This nomenclature is repeated in Table 3.1. Forest typology and nomenclature for the rest of Australia follows Webb (1968), however SNVF (Simple Notophyll Vine Forest) is substituted for SNEVF ("Evergreen")

Table 3.1

Forest nomenclature of Tracey and Webb for NE Queensland.

Complex Mesophyll Vine Forest	1a 1b 1c	CMVF
Mesophyll Vine Forest	2a 2b	MVF
Mesophyll Vine Forest (with dominant palms)	3a 3b	MFPVF
Semideciduous Mesophyll Vine Forest	4	SDMVF
Complex Notophyll Vine Forest	5a 5b	CNVF
Complex Notophyll Vine Forest (with Agathis robusta)	6	CNVF
Notophyll Vine Forest	7a 7b	NVF
Simple Notophyll Vine Forest	8	SNVF
Simple Microphyll Vine-Fern Forest	9	MFF
Simple Microphyll Vine-Fern Thicket	10	MFT
Deciduous Microphyll Vine Thicket	11	DEVT

NB number and letter code refers to sub-types in Tracey, 1982.

in accordance with the usage in Tracey and Webb (1975) and Tracey (1982).

Only the main or 'core' forest types from Webb's classification, which reflect the major climatic divisions — Tropical, Subtropical, Warm and Cool Temperate (Fig. 2.2), were considered in this study. All of these forest types — Complex Mesophyll Vine Forest, Complex Notophyll Vine Forest, Simple Notophyll Vine Forest, and Microphyll Fern Forest (or Simple Microphyll Vine-Fern Forest, see later) — occur together within only one area, the humid tropical region of N.E. Queensland Webb, 1959, 1968; Tracey, 1982; Figs 2.3 - 2.6).

Three sites were selected to represent each major forest type (Table 3.2; Fig. 3.2), however each of the CNVF sites was selected to represent the subtypes recognised in Tracey and Webb's vegetation maps of the region (Tracey and Webb, 1975; Tracey, 1982). The three CMVF sites were chosen to cover the altitudinal range of this forest type, with a true lowland example (type 1a of Tracey, 1982), a 'foothills' example (type 1b), and a 'uplands' example (type 2a). The SNVF sites were similarly staggered to cover a range of site characteristics (Table 3.2; Fig. 3.2).

Late in the study, it was decided that regional differences within a particular forest type might also be significant as floristically, Australian rainforest displays a distinct regionalism (Webb, et al., 1986). A number of sites were selected in New South Wales (Fig. 3.3) to allow comparison of Complex Notophyll Vine Forest and Simple Notophyll Vine Forest from near the latitudinal extremes of their range within Australia (Fig. 2.2). The New South Wales CNVF site was substituted for the equivalent type in N.E. Queensland (type 6; Tracey, 1982).

An additional site of Microphyll Fern Forest (MFF) in New South Wales was also included. The MFF of New South Wales has *Nothofagus moorei* (Fagaceae) as the dominant canopy tree. *Nothofagus* species are absent from Microphyll Fern Forest (the Simple Microphyll Vine-Fern Forest of Tracey, 1982) in N.E. Queensland, and these forests are more species-rich than MFF dominated by *Nothofagus* in Australia.

Recently reported Australian Tertiary macrofossil deposits containing *Nothofagus* leaves (morphologically similar to *N. moorei* leaves) are thought in part to

Fig. 3.2

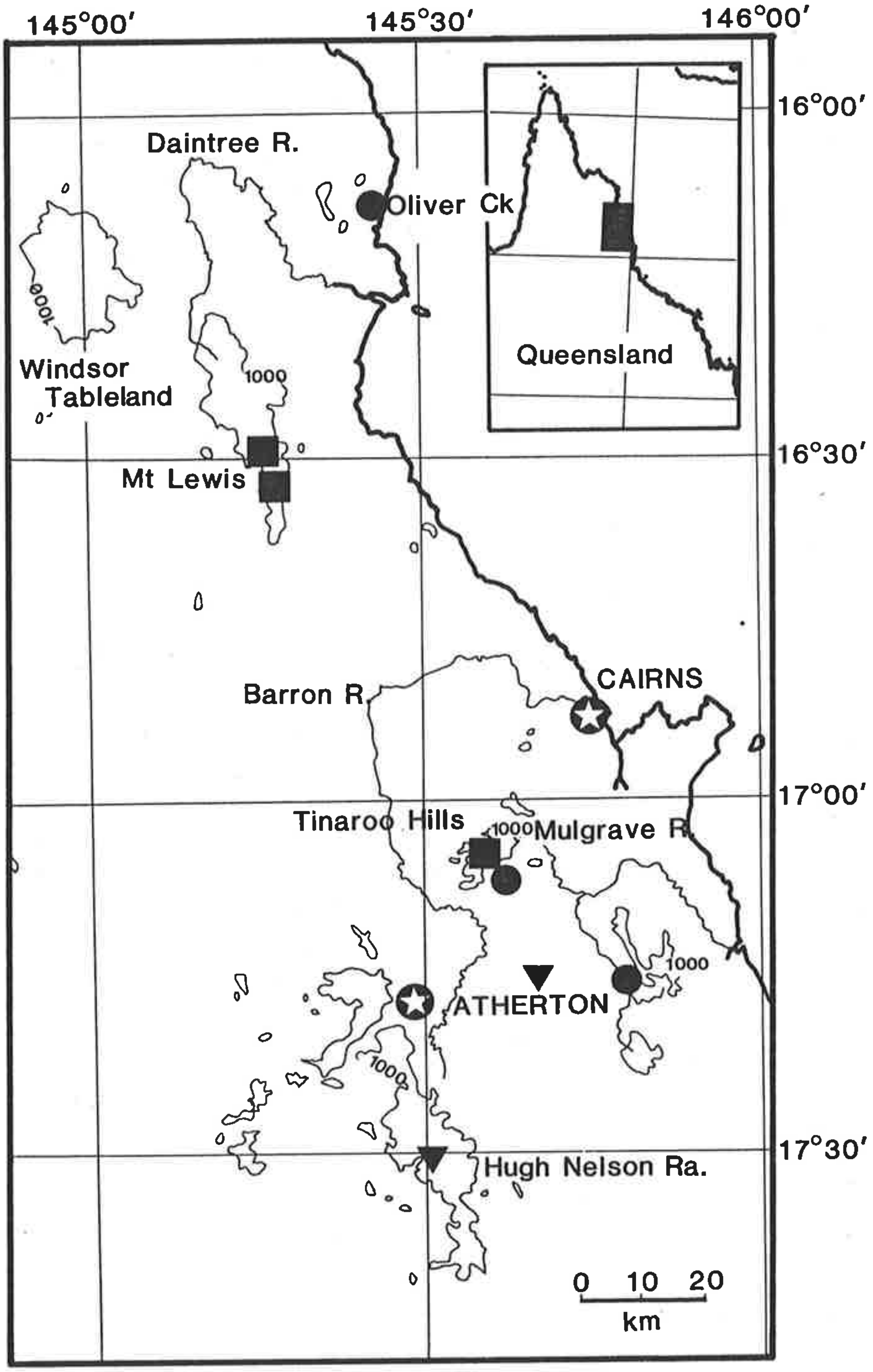


Figure 3.2 Location of leaf-litter collection sites in N.E. Queensland. The 1000m contour and the principal rivers of the region are indicated. The CMVF sites are indicated by solid circles, CNVF sites solid inverted triangles, and SNVF sites by solid squares. The CSIRO Tropical Forest Research Centre, at Atherton, was used as the base for the collecting.

Fig. 3.3

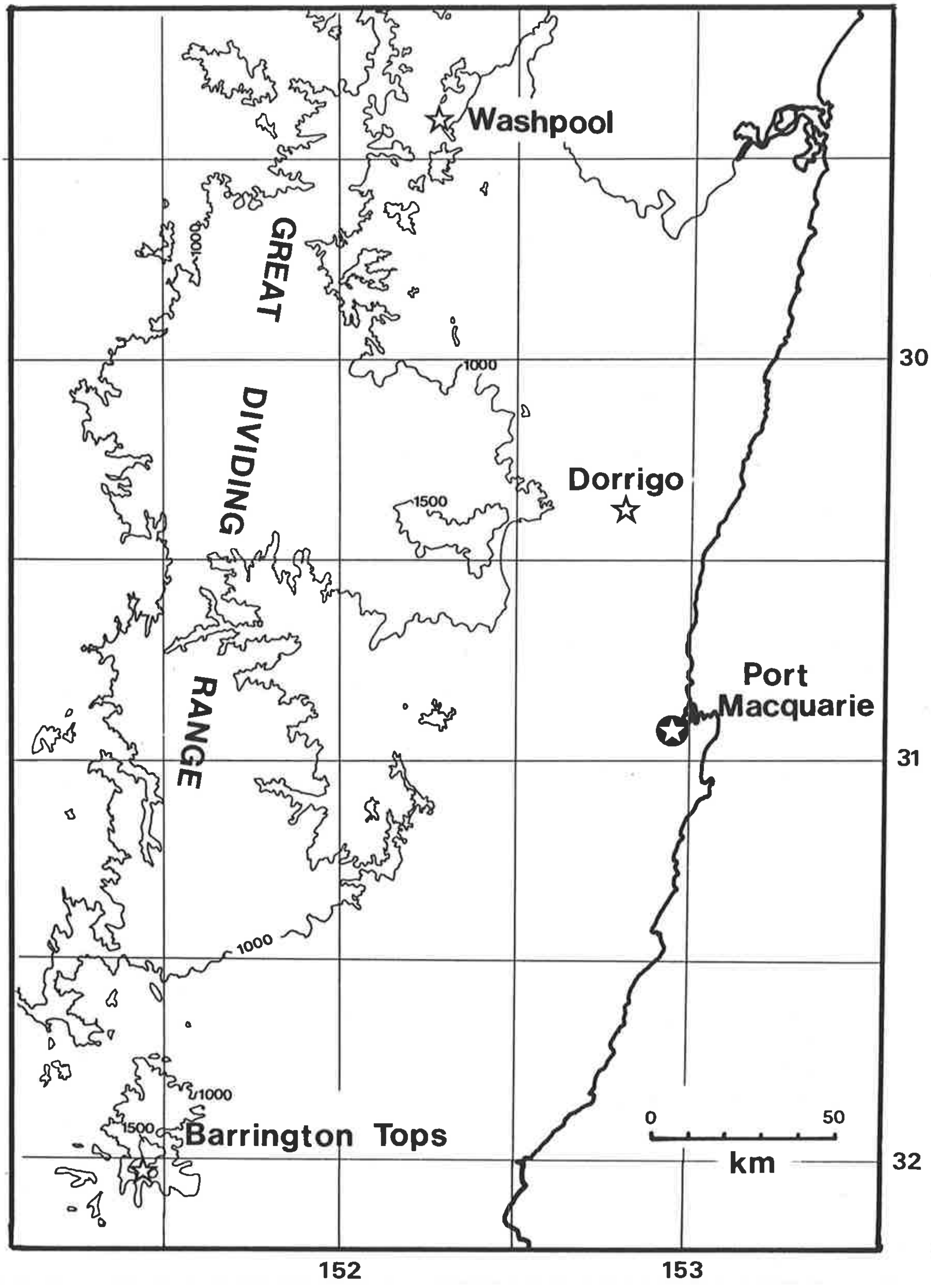


Figure 3.3 Location of leaf-litter collection sites in northern New South Wales (N.S.W.). The 1000m and 1500m contours are indicated, as is the Clarence River (not labelled). The area around the Clarence River was covered by CNVF prior to european settlement. Each litter collection site is indicated by an open star.

represent Microphyll Fern Forest (Hill, 1983a & b, 1987; Christophel, 1985), and fossil pollen attributable to *Nothofagus* often dominates southern Australian Early Tertiary deposits (Kemp, 1978). An understanding of the taphonomy and physiognomy of litter from the *Nothofagus* dominated forest-type is therefore critical to the palaeoecological interpretation of these fossil deposits.

3.3 Sampling Methods.

For each site an identifiable tree was chosen as a marker. Five sample points were then chosen arbitrarily within a 20 metre square with the tree at its centre. Placement of the sample points was arbitrary rather than random due to the need to avoid scattered clumps of ground level plants and fallen tree trunks. Care was taken to avoid regular placement of the sample points around the tree or close grouping of the sample points at one corner of the square. A typical layout is presented in Figure 3.4.

The samples were then collected by clearing a square metre of ground of all litter at each sample point, leaving only the bare mineral soil (Figs 3.5 & 3.6). This material was placed in labelled large plastic bags for transport to the base camp (CSIRO Atherton for the N.E. Qld sites) where it was sterilised by freezing for 48 hours prior to transport to Adelaide for analysis.

3.3.1 Sample treatment.

It was necessary to pretreat each sample prior to data collection as most leaves in most samples were curled, preventing easy measurement. In addition, only a subsample of leaves was required from some samples from SNVF and MFF as the smaller average leaf size of the litter from these forest types contributed up to 500 leaves from a single square metre sample in some cases, against the typical sample size of 224 leaves.

Each sample was air-dried in large trays for several days prior to initial sorting. All of the complete leaves (i.e. both tip and base intact and margin intact or nearly so) from each sample were transferred to separate shallow plastic trays. Each tray was then filled with hot water to which detergent had been added to

Fig. 3.4

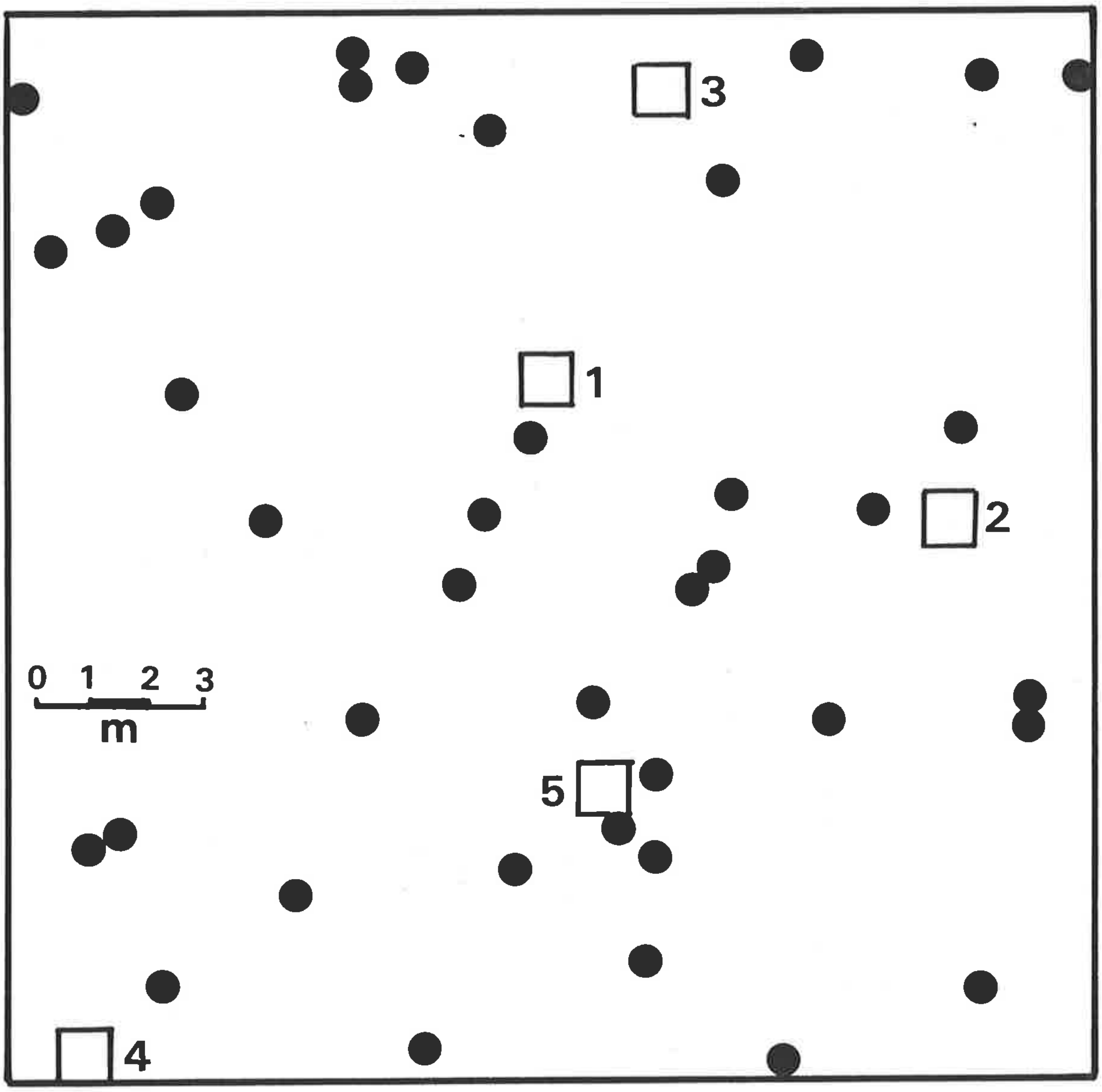


Figure 3.4 An example of the layout of sample points at a site in N.E. Queensland (Mt Lewis EP 18). Each of the solid circles represents the position of a tree (DBH > 10cm), and the open squares the 1 x 1 m sample plots.

Fig. 3.5 Leaves were removed by hand and transferred to bags. The author and assistant, Ms S Lys, Botany Dept., Adel. Univ.

Fig. 3.6 Each collection removed all litter from a square metre.

facilitate wetting of the leaves. Full wetting and softening was achieved after a few hours. The leaves were then transferred to plant presses for drying. In most cases, over 200 leaves were treated for analysis, however a small number of samples from early collections (3/50 or 6%) contained as few as 139 leaves due to fragmentation during transport.

In the CMVF and CNVF samples no subsampling was required. However, in about half of the SNVF and 1 of the 4 MFF samples, subsampling was used. In each of these cases, leaves were randomly removed from the soaking trays until a total of 250 leaves were in a press. After some initial trials it was found that around 200 leaves gave a consistent result in the determination of the range of variation of the metric physiognomic characters. The arrangement of the data sheets gave an arbitrary cutoff of 224 leaves, and for most samples this is the number measured.

3.3.2 Methods of Data Collection.

While computer-aided data collection is possible in measuring the physiognomic characters used in this study (e.g. West and Noble 1984), all measurements were made by hand and were recorded to the nearest millimetre. This approach was employed to allow parallel collection of data from fossil material not presented in this thesis which would have negated the potential time savings of computer-aided measurement. However, recent developments would indicate that future work will employ digitisation of leaf images for data extraction, as a considerable array of highly flexible software and compatible video-based digitisers have become recently available.

Leaf areas for a limited number of samples were measured using an image analyser (Delta-T Area Meter; Delta-T, Cambridge, England) to assess the degree of accuracy of leaf area estimation techniques. The majority of samples use estimated leaf areas. The validity of this approach is discussed in more detail in Chapter 4. The taxonomic identity of the leaves in some samples was determined in order to assess the influence of taxonomic bias in foliar physiognomic analysis and the effects of taphonomic processes on taxonomic representation in leaf-beds.

The leaves were primarily identified through comparison with herbarium specimens held in Adelaide (Palaeobotany Reference collection, Botany Dept., Adelaide Univ.) and at the Herbarium at the CSIRO Tropical Forest Research Centre in Atherton, N.E. Queensland (part of Herbarium Australiensis). Nomenclature follows Hyland (1977, 1983, and pers com.), Floyd (1977a & b, 1978, 1979a, b, c & d, 1980, 1981a, b & c, 1982), Boland et al. (1984), and Morley and Toelken (1983). Unless otherwise stated, all taxonomic identifications are the author's.

3.3.3 Physiognomic Characters Used in the Study.

According to Dolph and Dilcher (1979) eight main leaf characteristics are considered to be determined by climate:

1. leaf size (usually as leaf area)
2. leaf margin type (non-entire vs entire)
3. presence or absence of drip tips
4. the leaf organisation (simple vs compound)
5. major venation pattern
6. venation density
7. leaf texture
8. leaf base shape.

Of these, leaf size (as area) and margin type have been most commonly used in the foliar physiognomic analysis of fossil leaf beds.

For this study, physiognomic characteristics not easily determined from fossil leaves were discounted. Leaf texture is not measurable on an impression, and while the presence of pulvini can been used to demonstrate the presence of compound leaves (Richards, 1952), personal experience with both leaf litter and Tertiary mummified floras has shown that a large proportion of leaves are broken at or near to the point of insertion of the petiole into the lamina, and hence the presence or absence of pulvini can not be determined.

Several workers have commented on the prevalence of driptips on the leaves of rainforest plants (Richards, 1952; Hall and Swaine, 1984). A casual survey of litter on the rainforest floor will demonstrate the variable presence of this feature on the leaves of any given species, or the whole set of leaves present (Fig. 3.7). Juvenile and / or shade leaves seem more likely to possess this feature and there seems to be no measurable difference in the relative abundance of leaves with driptips between evergreen rainforest types, although Hall and Swaine (1984) found a decrease in the proportion of species with driptips along a rainfall gradient. At a gross level, the presence of leaves with driptips may be used to indicate 'rainforest', however within this forest type, the frequency of occurrence has little utility in physiognomic analyses.

Only fairly broadly defined characters were used as fine detail will tend to highlight phenetic differences, (e.g. venation, although see Macginitie, 1969), rather than adaptive differences. The rationale behind selection of each character is discussed later in this chapter. The following characters were used:

1. Leaf Length; to the nearest mm
2. Leaf Width; to the nearest mm
3. Leaf Width / Leaf Length x 100
4. Leaf Area; A = 0.667 x length x width (but see later)
5. Position of Greatest Width; to the nearest mm
6. Position of Greatest Width / Length x 100
7. Margin Type; entire or non-entire

These characters were measured for every leaf from each sample and the taxonomic identity of most leaves was also determined where possible. From this data it was possible to determine the characteristics for the leaf populations represented in the litter samples from each of the examples of the forest types. These are presented in the following chapter.

Fig. 3.7

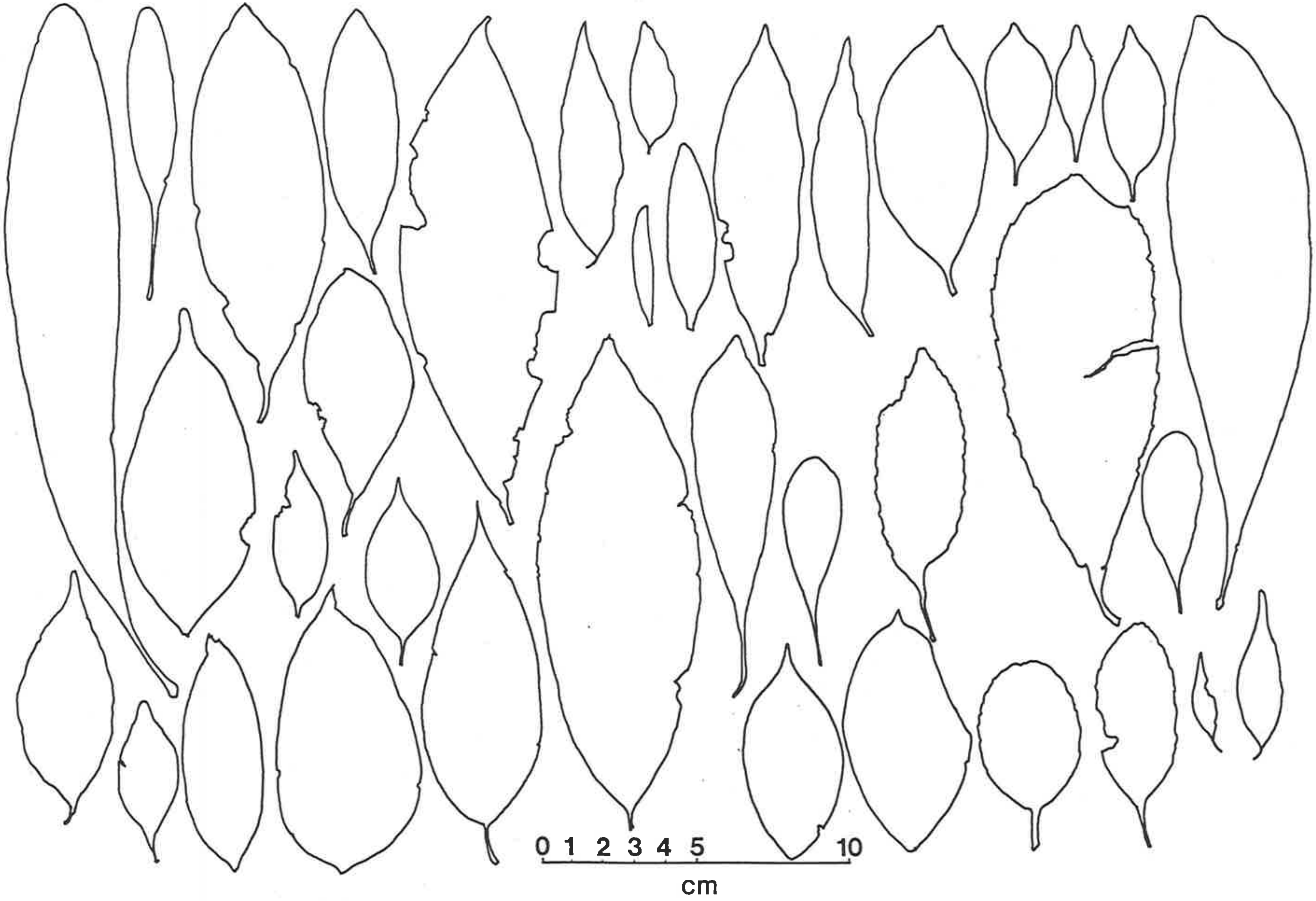


Figure 3.7 Silhouettes of a sample of leaves from leaf-litter of SNVF in N.E. Queensland (Mt Haig). Well developed "drip tips" are only present on a few leaves.

3.4 Description of Sites.

The study was broken into two phases with the first phase concentrated on collecting litter from N.E. Queensland sites over the months of August (1984) and September (1985). The second phase involved collecting litter samples from New South Wales sites during September 1986. However the data will be presented as one unit, and the various hypotheses considered as separate units. The samples from each of the sites in both regions are used to determine "physiognomic signatures for each of the sites and from these, the physiognomic signatures of each of the four forest types.

Each collection locality was either on a site used by Webb and Tracey (1982) for their survey of 624 sites, or was as close as possible to one of their original sites. This ensured that each leaf litter collection locality was in forest classified by Webb, and therefore definitive of the type. Also, their species lists reduced the number of comparisons necessary to identify leaves in some samples (see Chapter 7).

Their data has been used to give an indication of the number of species present at the litter sites. Unfortunately Webb and Tracey did not use a standard size for each site, and so the values given should only be taken as a guide to the diversity in the local area of the sample sites. The physical characteristics and a brief account of the forest community for all of the litter collection sites for each of the forest types is presented below.

3.4.1 Description of CMVF Litter Collection Sites.

Mobo Creek 17°10' S, 145°39' E.

Mobo Creek drains from the southern slopes of the Lamb Range (Fig. 3.8) which is mainly covered by Vine Forests overtopped by *Eucalyptus* spp., however the lower slopes on the western sides and leading up to the base of the Tinaroo Hills is covered by Complex Mesophyll Vine Forest (type 1b, Tracey, 1982) although much has been cleared, with Simple Mesophyll Vine Forest (type 2a) at slightly higher elevation. Simple Notophyll Vine Forests and Complex Notophyll Vine Forests occur on suitable sites nearby (Fig. 3.8). Mobo Creek drains through

Fig. 3.8

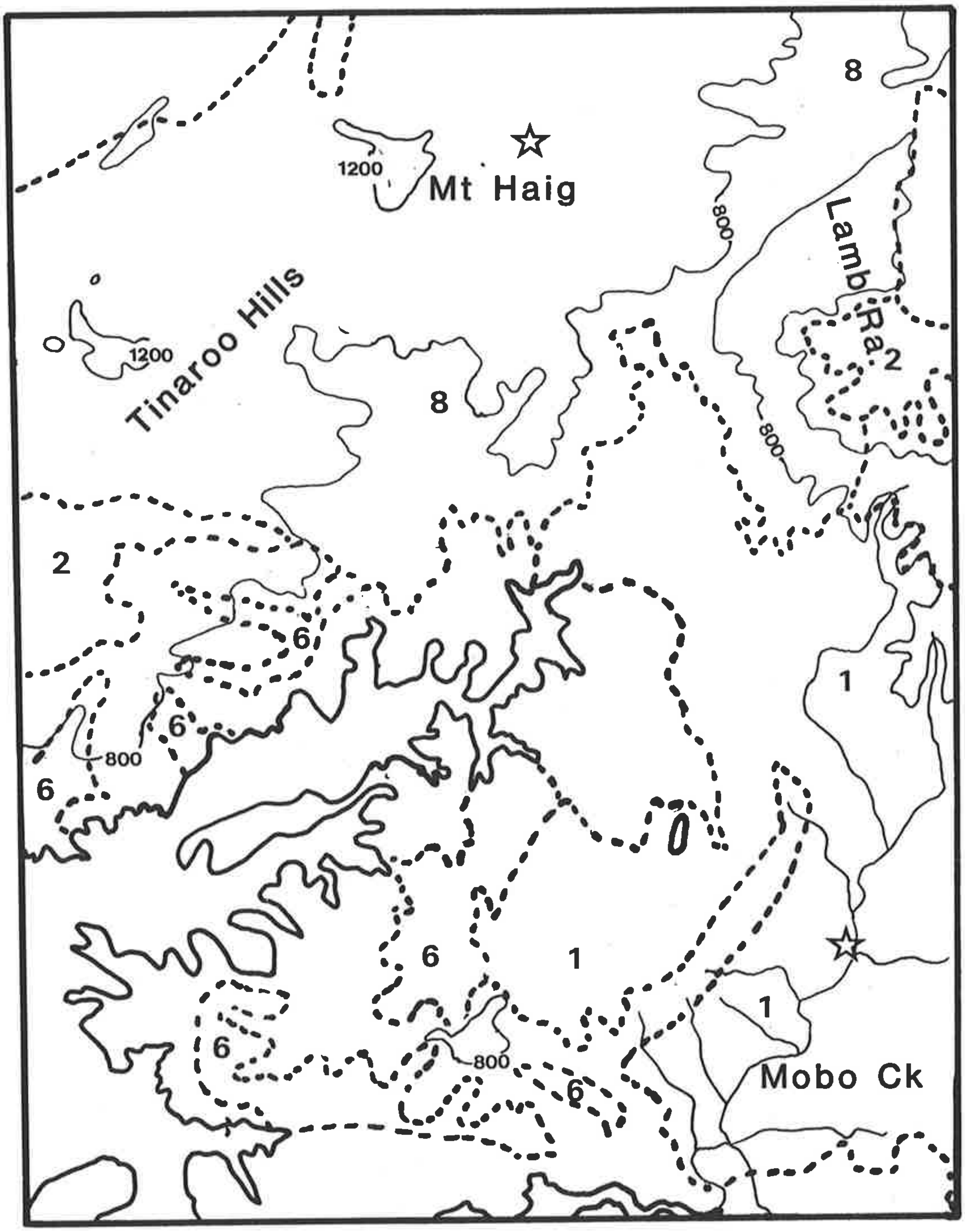


Figure 3.8 Vegetation map of the Mobo Ck (CMVF) and Mt Haig (SNVF) leaf-litter collection areas. Litter collection sites are indicated by open stars and vegetation boundaries by dashed lines. Number code refers to Table 3.1.

an old basalt flow and the litter site represents CMVF at its altitudinal limit in the region. An extinct volcano near Mobo Creek, Lake Euramoo, was used in a study on Quaternary pollen (Kershaw and Hyland, 1975).

There is no CMVF site surveyed by Webb and Tracey close to Mobo Creek, however, they recorded 87 species at their site 315 (Mt Chujeba Ridge) which is at a similar elevation and on similar soils (Webb and Tracey, 1982).

Mulgrave River 17°18' S, 145°48' E.

The Mulgrave River drains from the western slopes of Mount Bellenden Ker and the eastern edge of the Atherton Tableland (Fig. 3.9). Mt Bellenden Ker at 1561 metres elevation is the second tallest mountain in Queensland, with the adjacent Mt Bartle Frere the tallest at 1622 metres. The lower slopes of both mountains, including the floor of the Mulgrave River valley, are covered by Complex Mesophyll Vine Forest which grades into Simple Mesophyll Vine Forest at slightly higher elevations. Simple Notophyll Vine Forest grades into Simple Microphyll Vine-Fern Forest between 700 and 1300 m elevation (Fig. 3.9). The litter collection site was placed 100 metres from the river near a crossing over the river at about 120 m elevation. A large individual of *Citronella* aff. *C. moorei* (F.Muell. ex Benth.) Howard (Icacinaceae) was used as the centre tree.

The litter collection site is close to Webb and Tracey's site no. 331. They recorded 136 species at their site.

Oliver Creek 16°08' S, 145°27' E.

The area around the mouth of the Daintree River has elicited considerable attention as a centre of endemism for primitive angiosperms (e.g. Endress, 1983) with species such as *Idiospermum australiensis* S.T.Blake (Idiospermaceae) occurring only in the immediate area (Tracey, 1982; Webb, et al., 1986). Oliver Creek is the type locality of *Idiospermum australiensis* S.T.Blake and a large specimen of this species 50 m from the bank of Oliver creek was chosen as the centre tree.

This site represents the original lowland rainforest which has been cleared for the planting of sugar cane over much of the lowlands of the Humid Tropical

Fig. 3.9

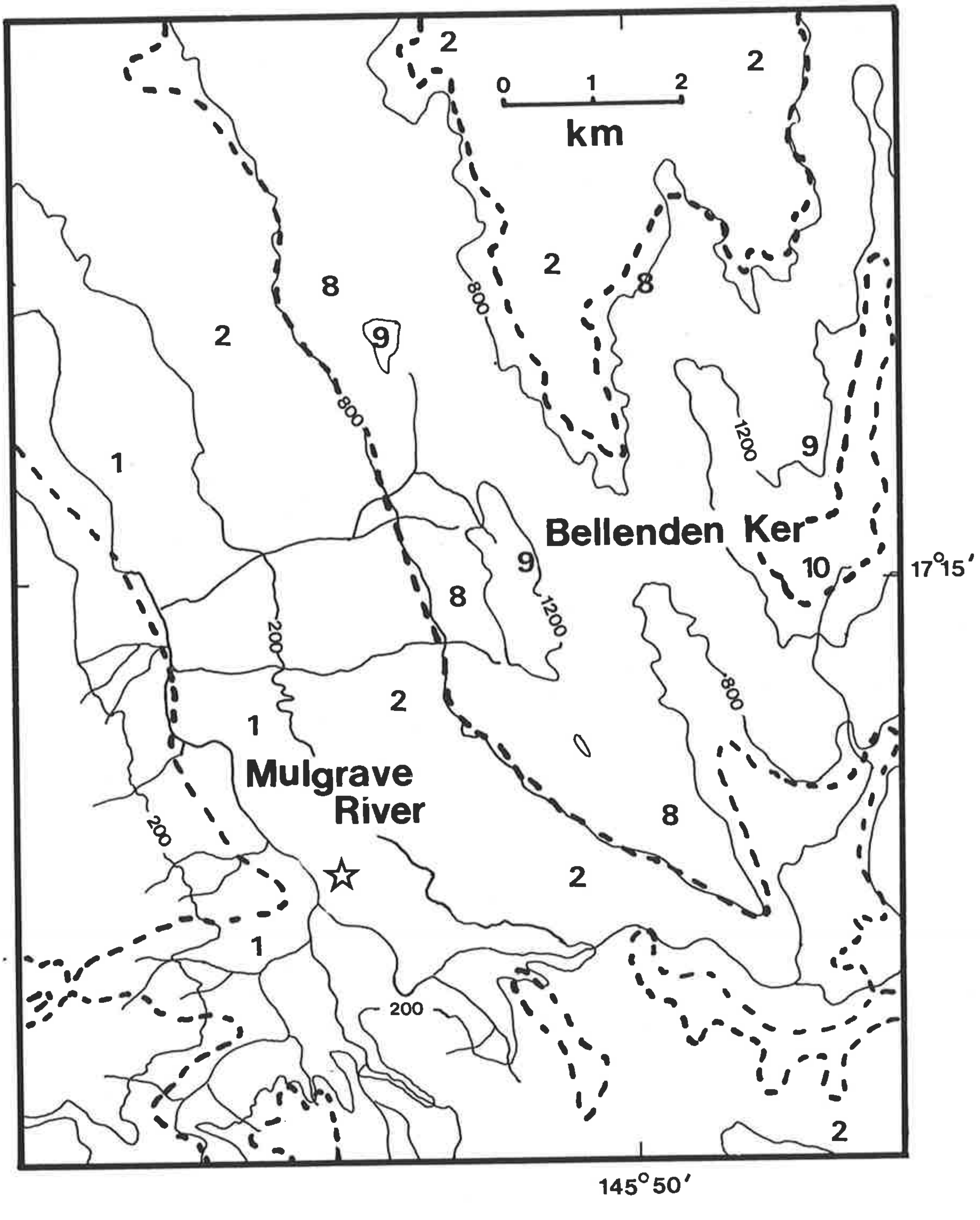


Figure 3.9 Vegetation map of the area around the Mulgrave River (CMVF) leaf-litter collection site. See Figures 3.1 and 3.8 for explanation.

Region of N.E. Queensland. To the south of Oliver Creek the CMVF forms a mosaic with other forest associations (Fig. 3.10) although there is also a large area which is cleared. At slightly higher elevations the CMVF grades into Simple Mesophyll Vine Forest.

Along the banks of the nearby Noah Creek (Fig. 3.10) a remnant population of *Gymnostoma* L.A.S. Johnson (Casuarinaceae) forms a riverine association which is considered by Christophel to be a possible analogue of a floristic association detected in the Eocene fossil flora of Anglesea, in Victoria, some 4000 km south at 38° south (Christophel and Greenwood, 1988). At higher elevations at the head of Noah Creek Simple Notophyll Vine Forest replaces the MVF, however the MVF is directly replaced by Microphyll Vine Thicket (MVT) in the slopes above Oliver Creek on Mt Hemmant due to wind shear and exposure effects (Tracey, 1982). The litter collection site is adjacent to Webb and Tracey's site no. 578. They recorded a total of only 91 species, however, they do not indicate the area sampled.

3.4.2 Descriptions of CNVF Litter Collection Sites.

Curtain Fig 17°18' S, 145°34' E.

The Curtain Fig State Forest park represents a remnant of formerly more extensive stands of CNVF on the Atherton Tableland (Fig. 3.11). The CNVF here is the more seasonal variant (type 5b) and contains many canopy trees which are semi-evergreen. This means they lose most of their leaves at times of extreme moisture stress. Similar patches occur to the west (Fig. 3.11), and near Atherton.

The litter collection site at Curtain Fig was in a patch of CNVF monitored by CSIRO, Experimental Plot 33 (G. Stocker and G. Unwin, CSIRO Atherton Tropical Forest Research Centre, pers. com., 1985). This area was also surveyed by Webb and Tracey (site no. 573). A large Red Cedar, *Toona australis* (F.Muell.) Harms (Meliaceae), was chosen as the centre tree. An important vine species at this site was *Cissus antarctica* Vent. (Vitaceae), which was evidenced by this leaf being the most common taxon in some litter samples from this site. A few individuals of *Flindersia pimenteliana* F.Muell. (Rutaceae or Flindersiaceae), were

Fig. 3.10

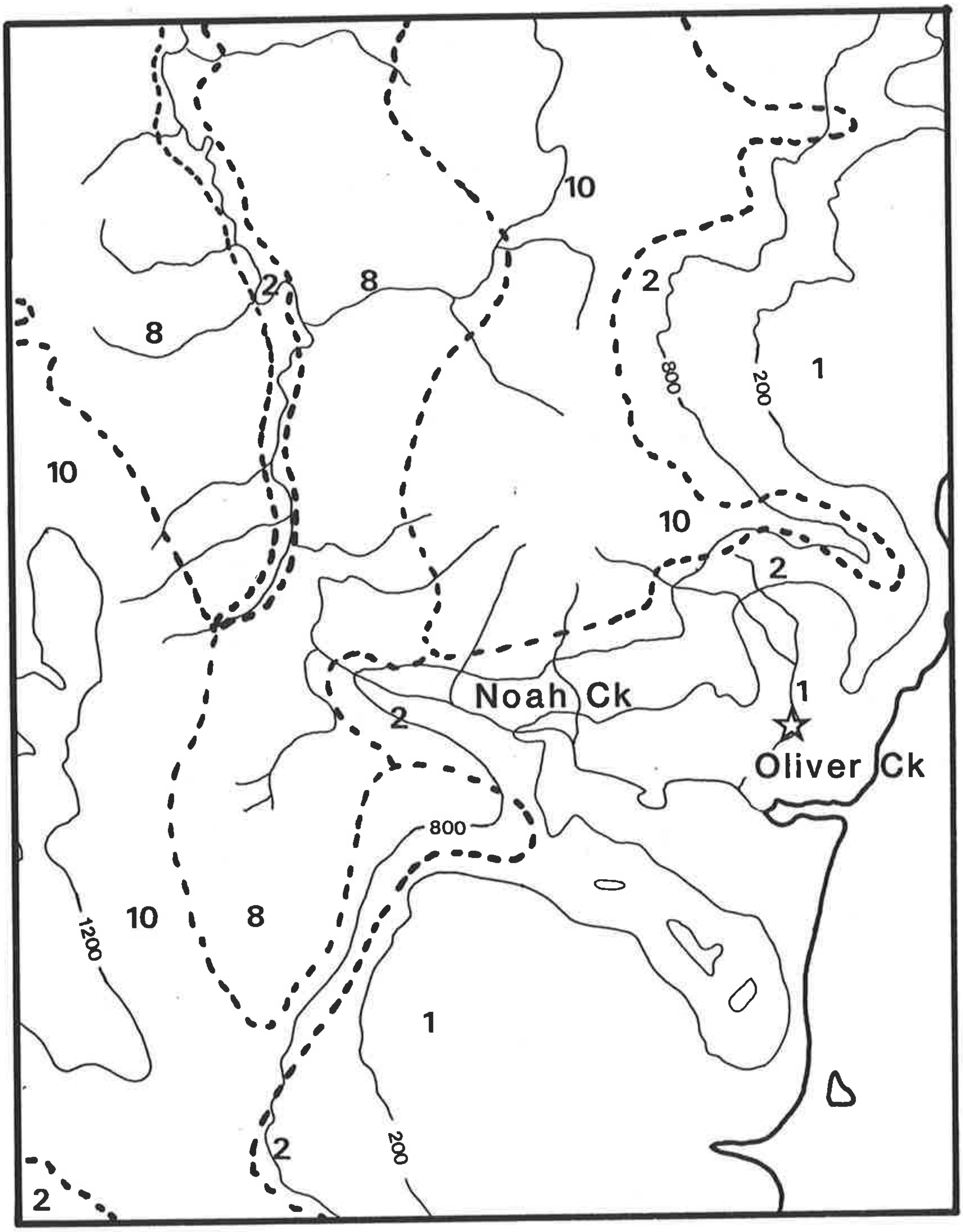


Figure 3.10 Vegetation map of the area around the Oliver Ck leaf-litter collection site. See Figs 3.1 and 3.8 for explanation.

Fig. 3.11

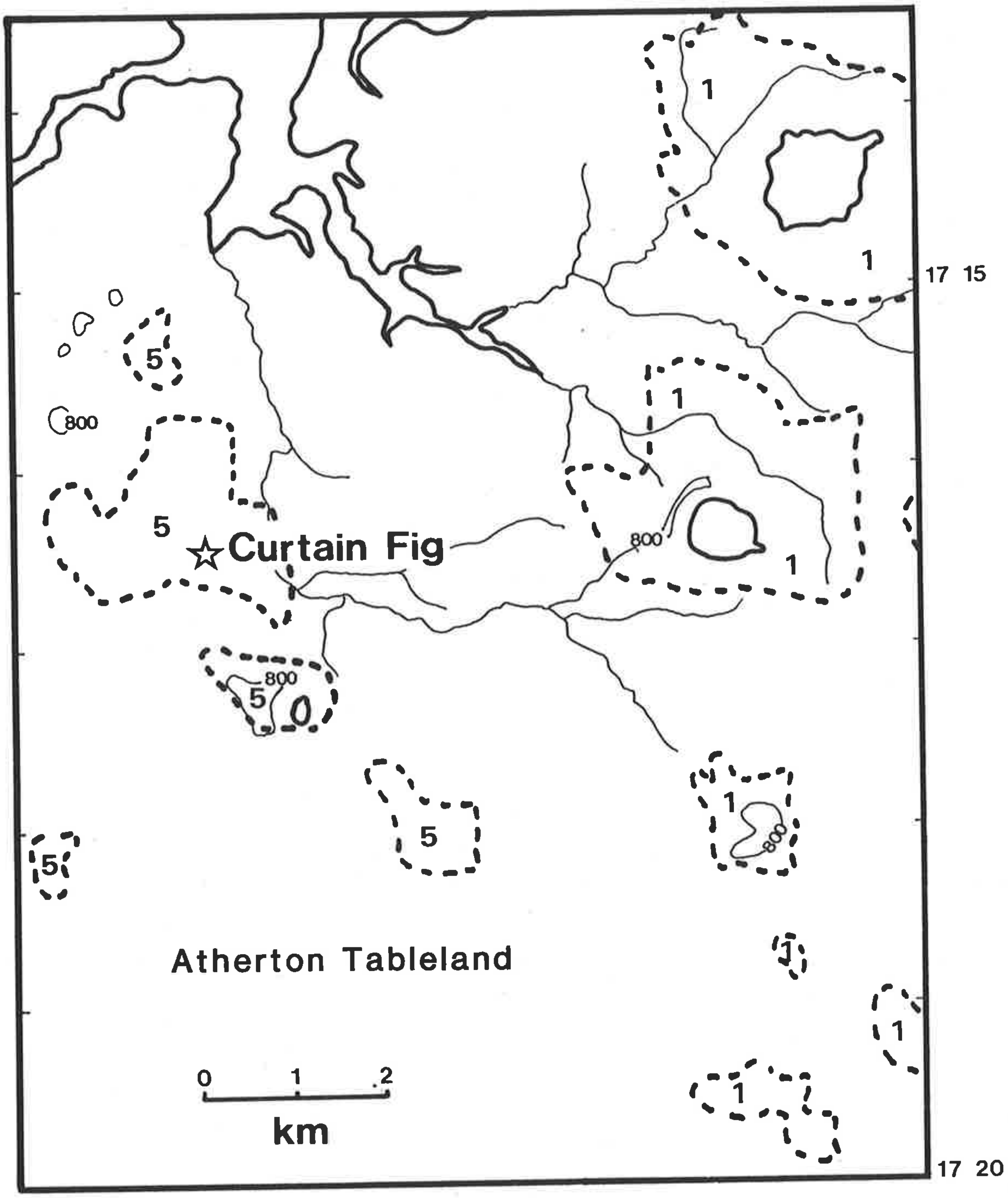


Figure 3.11 Vegetation map of the area around the Curtain Fig (CNVF) leaf-litter collection site. The Atherton Tableland is essentially flat with occasional volcanic craters producing relief (the 800m contours). Much of the original rainforest has been cleared, however, some rainforest has been retained around these craters and their lakes. See Figs 3.1 and 3.8 for explanation.

also present in the canopy at the site. Webb and tracey recorded a total of 85 species in their site at Curtain Fig (Webb and Tracey, 1982).

The Crater 17°25' S, 145°29' E.

The Crater National Park is an extinct volcanic crater at the southern end of the Herberton Range which borders the western edge of the Atherton Tableland (Fig. 3.12). Most of the National Park is Microphyll Vine-Fern Forest (MFF) and Simple Notophyll Vine Forest. A large patch of Complex Notophyll Vine Forest (type 5a, Tracey, 1982) occurs on the eastern edge of the Park some of which has been cleared (Fig. 3.12). The higher elevation and more regular rainfall of this site compared to Curtain Fig (Fig. 2.10), has produced significant floristic differences. The conifer *Prumnopitys amara* (Blume) Laubenf. (Podocarpaceae) is a conspicuous member of the canopy in the CNVF, with *Geissois biagiana* (F.Muell.) F.Muell. (Cunoniaceae). Deciduous trees are rare or absent in the canopy of this type of forest (Tracey, 1982).

An isolated individual of *Neolitsea dealbata* (R.Br.) Merr. (Lauraceae) was chosen as the centre tree near a small creek. The canopy here was dominated by an extremely large individual of *Geissois biagiana.* Webb and Tracey's site no. 72 is close to the litter collection site and they recorded a total of 183 species (Webb and Tracey, 1982).

Dorrigo (New South Wales) 30°20' S, 152°45' E.

The Dorrigo National Park represents a survivor from once extensive tracts of subtropical rainforest (Complex Notophyll Vine Forest) which were cleared from the lowlands of northern New South Wales in the late 1800's and early 1900's. Complex Notophyll Vine Forest in New South Wales and southern Queensland is structurally distinct from the more seasonal CNVF (type 5a & 5b of Tracey, 1982) typical of parts of the Atherton Tableland in N.E. Queensland, but has many species in common with the "CNVF with *Agathis robusta*" (type 6) of the latter region (Tracey, 1982). Complex Notophyll Vine Forest could be considered the "climatic climax" (in the sense of Beard, 1944) of the subtropical lowlands

Fig. 3.12

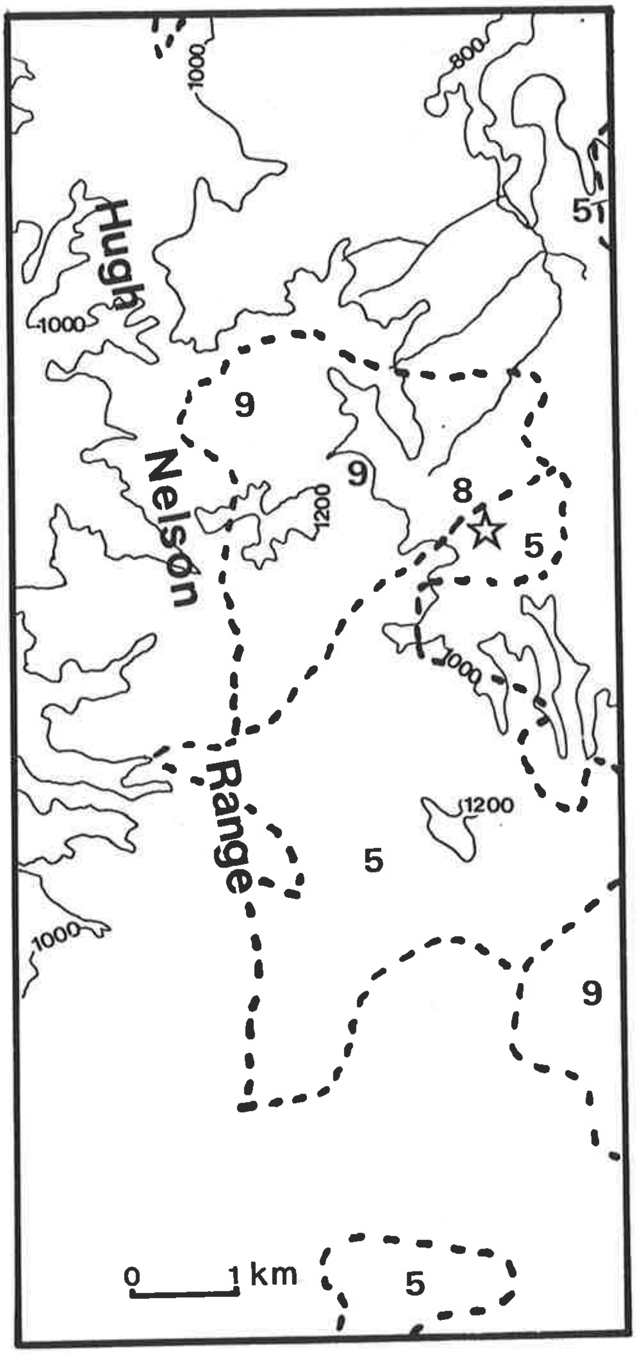


Figure 3.12 Vegetation map of the area around The Crater (CNVF) leaf-litter collection site. See Figs 3.1 and 3.8 for explanation.

of northern New South Wales and southern Queensland, and the Dorrigo site is close to the latitudinal limit of this forest type (Figs 2.2 & 3.3).

Two tree species were common at the litter collection site; *Sloanea woolsii* F.Muell. (Elaeocarpaceae) and *Dysoxylum fraseranum* (A.Juss.) Benth. (Meliaceae). A large flat area 100 m from a walking trail was chosen as the litter site with a mature specimen of *S. woolsii* as the centre tree. The original Webb and Tracey site (no. 165) could not be located however the Dorrigo forest area is small. They recorded a total of only 19 species in their Dorrigo site (Webb and Tracey, 1982).

3.4.3 Description of SNVF Litter Collection Sites.

Mount Haig 17°05' S, 145°35' E.

Mount Haig is part of a spur of the Lamb Range (the Tinaroo Ranges) bordering the northern edge of the Atherton Tableland and is mostly covered by Simple Notophyll Vine Forest (Fig. 3.8) with Simple Microphyll Vine-Fern Forest (MFF) on the highest parts. Complex Notophyll Vine Forest (type 6) and Complex Mesophyll Vine Forest (type 1b) occur in gullies at the southern foot of the range and Mesophyll Vine Forest (type 2a) occurs on the lower slopes of the eastern and northeastern sides of the range. The northern slopes grade quickly into Tall Open Forest through an ecotone of forest dominated by *Eucalyptus grandis* Hill ex Maiden (type 13c). This forest is similar in character to the Tall Wet Sclerophyll Forest of SE Australia, as it retains some rainforest species in its understory (Tracey, 1982).

Much of the area is in State Forests 607 and 185 and a Forestry road provides access to the ridge between Mt Haig and Mt Edith. The litter site was chosen several hundred metres off the road on a flatter area on the saddle between these two mountains in forest on a south east slope near Webb and Tracey's site no. 562 and CSIRO's Experimental Plot No. 3. The soil is granite derived and rainfall is in excess of 3000mm pa, and cloud often envelopes the ranges (Webb and Tracey, 1982).

Webb and Tracey recorded 114 species for site 562. *Agathis atropurpurea*

B.P.M.Hyland (Araucariaceae) was an emergent above the canopy in Webb and Tracey's site and a mature specimen of this species overtopping the litter collection site was chosen as the centre tree. The canopy was predominantly a small leaved species of *Syzygium* (Myrtaceae), *Ceratopetalum succirubrum* C.White (Cunoniaceae), *Balanops australiana* F.Muell. (Balanopsidaceae) and several species of *Elaeocarpus* (Elaeocarpaceae).

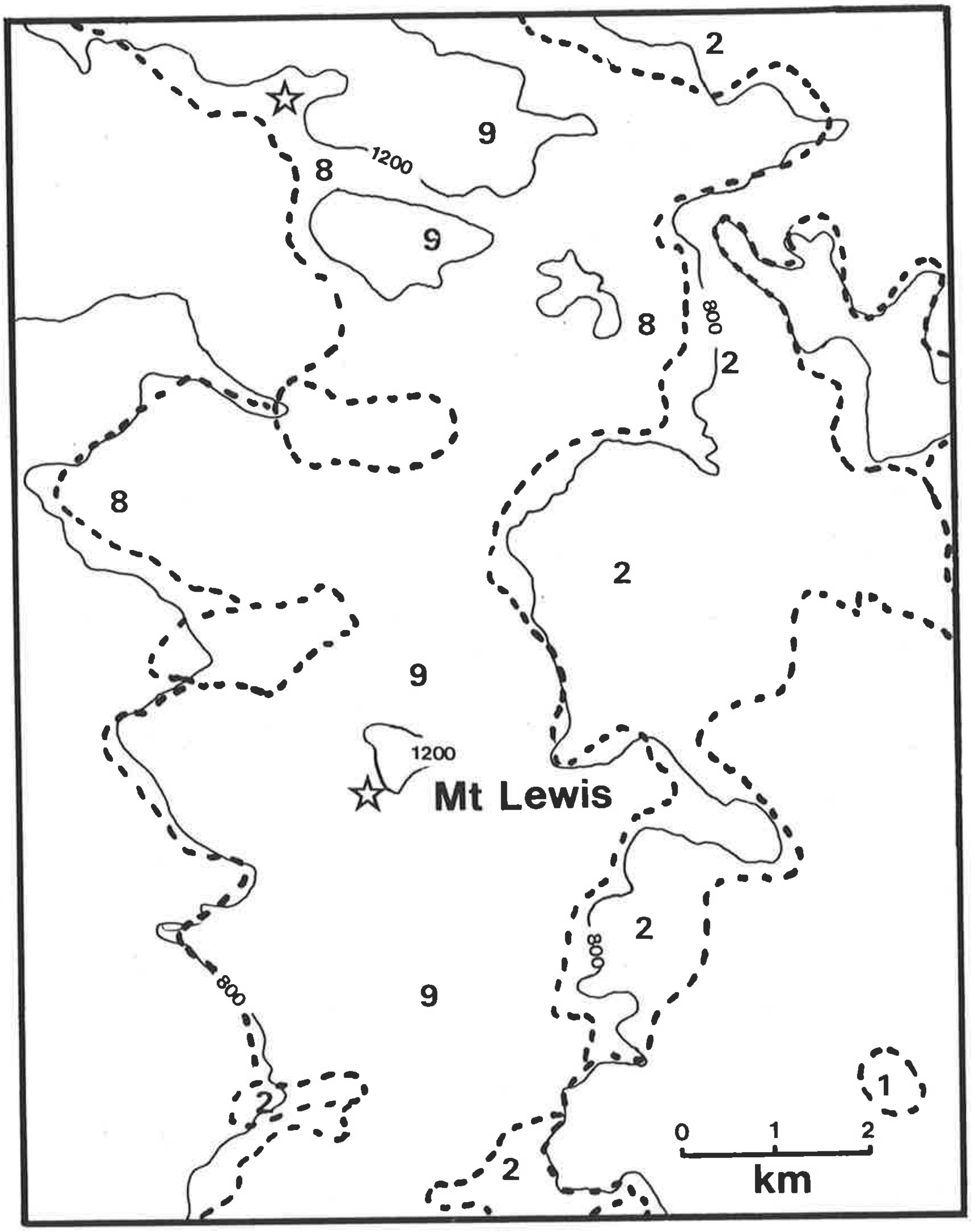
Mt Lewis Road 16°33' S, 145°17' E.

Mount Lewis is part of the Mount Carbine Tableland (part of the Great Dividing Range; Fig. 3.13) which extends northward to the Daintree River. This range forms the majority of the catchment of the Daintree River. Much of the range is covered by rainforest, mainly Simple Microphyll Vine-Fern Forest and Simple Notophyll Vine Forest (Fig. 3.13), although Mesophyll Vine Forest (type 2a) occurs in some large patches on the lower slopes on the eastern side with small patches in gullies on the western and southern slopes. Complex Mesophyll Vine Forest occurs in gallery Forests and in small patches at lower elevations towards the coast (east).

The Simple Notophyll Vine Forest of this area contains two species of conifer (Podocarpaceae) which, in the case of one species, *Prumnopitys ladei* (Bailey) Laubenf., is restricted in occurrence to the area, and in the other, *Podocarpus smithii* Laubenf., is restricted to a few mountain areas in the Humid Tropical Region of N.E. Queensland. The latter is of particular interest as it's leaves are very close in morphology to the Eocene species, *Podocarpus platyphyllum* Greenwood (Greenwood, 1987). This species is now known from several southern Australian Eocene localities.

A site near a Webb and Tracey site (no. 255) was chosen where *P. smithii* was fairly common. A mature specimen of *P. smithii* was chosen as the centre tree on a SW facing slope 100m from a small stream. At slightly higher elevation (1200m) upslope the forest underwent a transition into MFF and then into stunted Microphyll Vine-Fern Thicket (MFT). Webb and Tracey (1983) recorded only 52 species in their nearby site, however they do not indicate the size of the

Fig. 3.13



area sampled.

Mt Lewis EP18 16° 31' S, 145° 16' E.

A second site was chosen in the Mt Lewis area as a CSIRO permanent Experimental Plot (EP 18) was available. This site had all of the trees in a quarter hectare numbered and identified. By recording the exact position the samples were collected relative to the trees, it was hoped to study the movement of the leaves relative to their source trees prior to settlement in the litter. This data is presented and analysed in Chapter 4.

EP18 is on a fairly flat area above a westerly facing gully. It is of particular interest as just out of the CSIRO plot on the edge of the gully is a small grove of Prumnopitys ladei, which as mentioned above, is restricted to the Mt Lewis — Mt Carbine Tableland area. A central tree was not chosen for this site due to the recording of the actual litter collection points.

The canopy of the area where litter was collected contained several individuals of *Planchonella euphlebia* (F.Muell.) Francis (Sapotaceae) and a large individual of both *Prumnopitys ladei* and *Stenocarpus* sp. nov. (Sterculiaceae). Several isolated large individuals of other species were close to the litter collection; these are discussed in more detail in Chapter 7. Webb and Tracey (1982) recorded 132 species at this site (no. 567). The total number in the local area considered, however, is probably much lower.

Washpool/Coombadjha Creek 29°28' S, 152°22' E.

The Simple Notophyll Vine Forest in New South Wales is floristically and qualitatively different to the SNVF from N.E. Queensland. The Washpool/Coombadjha Creek site occurs in a patch of "Coachwood forest", i.e. Simple Notophyll Vine Forest dominated by *Ceratopetalum apetalum* D.Don. (Cunoniaceae), at the edge of a large tract of this forest type in the catchment of Washpool Creek on Coombadjha Creek (Fig. 3.3). The Gibralter Ranges form an amphitheatre around the Washpool catchment, much of which is covered by Tall Open Forest (Eucalyptus spp). The Washpool / Coombadjha Creek site was characterised by low species diversity with *Ceratopetalum apetalum*, and *Doryphora sassafras* Endl. (Atherospermataceae) dominating the highset tree stratum with occasional individuals of *Orites excelsa* R.Br. (Proteaceae). *Quintinia sieberi* DC. (Escalloniaceae) and *Acmena smithii* (Poiret) Merr. & Perry (Myrtaceae) were common members of the middle stratum with saplings of the canopy species. A small tree, *Callicoma serratifolia* Andr. (Cunoniaceae), was common along the stream-bank. The survey site of Webb and Tracey in the Washpool area (site no. 426) recorded only 10 species, however a list for the Coombadjha Creek area prepared by the New South Wales NPWS lists 21 species.

The Coombadjha Creek area has several marked "nature trails" frequented by tourists, and so it was necessary to collect the litter away from the trail and as far as possible from past human interference of the litter layer. A flat area 100m from a large pool in Coombadjha Creek was selected with a large *Ceratopetalum apetalum* as the centre tree. The canopy here contained more individuals of *Doryphora sassafras* than elsewhere in the local area. However, as both *Ceratopetalum apetalum* and *D. sassafras* have serrate margins, this would not have affected the physiognomy of the litter. This area was essentially undisturbed as access was difficult across the creek, making it unlikely that the litter had been recently disturbed by people.

3.4.4 Description of MFF Litter Collection Site.

Barrington Tops 32°00' S, 151°29' E.

The Barrington Tops area is a large plateau of volcanic origin between 1000 and 1500 m elevation (Fig. 3.3). At lower elevation, Complex Notophyll Vine Forest occurs in gullies and occasional larger patches and Simple Notophyll Vine Forest also can be found at intermediate elevations in protected areas (Fraser and Vickery, 1937; Fig. 2.2). At between 1000 m and 1500m, Microphyll Fern Forest and Microphyll Mossy Forest ("cool temperate rain forest" with or without treeferns) forms a mosaic with snow-gum woodland (*Eucalyptus pauciflora* Sieber ex Sprengel, Myrtaceae).

The litter collection site was within a large patch of MFF (about 5 hectares) on the Barrington Tops plateau along a flowing stream. This patch was surrounded by snowgum woodland, and was in close proximity to several other patches of MFF. Many of the trees within the rainforest were fairly large with a dbh in excess of 2 m, suggesting that it had remained undisturbed for some time. Trees of *Nothofagus moorei* (F.Muell.) Krasser formed a continuous canopy with only a few scattered individuals of *Doryphora sassafras*. The shrub layer consisted of scattered individuals of *Trochocarpa laurina* (Epacridaceae) and *Elaeocarpus reticulatus* Smith (Elaeocarpaceae) with occasional stands of the treefern *Dicksonia antarctica* Labill. (Dicksoniaceae). Individuals of *Vesselowskya rubrifolia* (F.Muell.) Pampan. (Cunoniaceae) were restricted to the stream banks. The vine, *Smilax australis* R.Br. (Smilacaceae), was also rarely present.

A large specimen of *Nothofagus moorei* some 150 m from a track in the centre of the forest patch was chosen as the centre tree. Four bags of litter were collected at random locations spread about the tree over an area of 20 square metres. The site surveyed by Webb and Tracey (1982) at Barrington Tops (site no. 195) recorded 7 species, not including *Vesselowskya rubrifolia* or *Smilax australis*. The diversity recorded by them is comparable to that observed at the litter collection site.

3.5 Overview.

From the above descriptions a number of points need to be emphasised. The selection of sites for each of three of the four forest types (i.e. excluding MFF) encompases the full climatic range of their modern distribution.

Three of the SNVF sites are in N.E. Queensland, and one site is in New South Wales. The three N.E. Queensland sites (Mt Haig, Mt Lewis Rd, Mt Lewis EP18) cover the altitudinal range for that area (Table 3.2), and as will be explained in Chapter 6, the sites also cover the total range of annual average temperature. The New South Wales SNVF site (Washpool/Coombadjha Ck) is floristically distinct from the N.E. Queensland SNVF, with a higher seasonal range of temperature than the N.E. Queensland counterparts. The main foliar physiognomic difference is a predicted higher proportion of serrate margined species.

The CNVF sites were divided to cover the three main divisions of this forest type, which reflect varying degrees and type of seasonality. The two N.E.Queensland sites (Curtain Fig and The Crater) represent Webb and Tracey's types 5a & 5b (seasonally dry, and seasonally cold; Webb and Tracey, 1975; Tracey, 1982). The New South Wales site (Dorrigo) is essentially non-seasonal, and represents the "climatic-climax" (Beard, 1944 1955; Webb, 1968) of the subtropical lowlands of northern New South Wales and southern Queensland.

The Complex Mesophyll Vine Forest sites cover the full range of elevation (and hence annual average temperature) for the type in the region, with one site at sea level (Oliver Ck), another at 120 m (Mulgrave River), and the last at the altitudinal limit, 720 m (Mobo Ck; Table 3.2). All of the sites have essentially similar rainfall regimes, although Oliver Creek may be wetter (see Fig. 2.10).

The sole MMF/MFF site was in New South Wales. These forests are floristically distinct from the N.E. Queensland equivalent forests, and are very species poor. The climate is marked by higher extremes between seasons than for any of the other forest types examined. MFF may represent a possible analogue for some Tertiary vegetation containing *Nothofagus* spp.

These points have important predictions. In the first instance, the prediction is that the primary foliar physiognomic differences given by Webb (1959, 1968) for each of these forest types will be represented in the foliar physiognomic characteristics of the litter. The extent to which the leaf size distributions of the litter and Webb's canopy data differ is the subject of the first part of the following chapter.

The main prediction, however, is that the four forest types will possess a set of unique foliar physiognomic characteristics, defined by the relative contribution of each of the physiognomic characters, which allows the description of a "physiognomic signature" for each of the forest types. The method of defining these "physiognomic signatures" is described in Chapter 4, and the signature of all sites for each forest type is first contrasted prior to the signature for each forest type.

The different climatic characteristics of some of the forest examples may be reflected in small differences in the physiognomic signatures between sites of the one forest type. In addition, particular physiognomic characteristics maybe separate from the predicted main determinants of forest type (e.g. leaf size and annual average temperature; Webb, 1959 1968). Correlations between these characteristics and climatic variables other than annual temperature will provide finer resolution for palaeoclimatic prediction from foliar physiognomic analysis. This is the subject of Chapter 6.

Chapter 4

PHYSIOGNOMIC ANALYSIS OF LEAF LITTER

4.1 Physiognomic Signatures.

Earlier I argued that leaf litter is (in part) analogous to small local fossil leaf beds. Leaf litter, and more particularly stream-bed deposited leaf litter, will reflect a similar degree of taphonomic bias as the fossil leaf beds and will, it is proposed, reflect similar foliar physiognomic characteristics — at the population level — as fossil leaf beds derived from similar forests.

It was also argued that, where possible, fossil leaf beds must not be considered as a whole flora but rather, stratigraphically discrete samples must be treated separately (e.g. Spicer and Hill, 1979; Knoll, 1986). Comparison between samples will record the inherent variability of the whole leaf population contained within each leaf-bed. Individual samples of leaf litter can be considered as analogous to the stratigraphically discrete samples from a fossil leaf-bed, or more specifically, to those leaves collected from a single layer in a single rock.

The uneven size of fossil floras and variable occurrence of fossils within layers of a fossil deposit introduces an extra taphonomic bias which must be considered in any analysis. The use of taphonomically equivalent sample sets will partly redress this bias. The leaves within a sample must therefore be treated as a subset of the overall leaf population. The population can therefore be characterised by the mean of the population descriptors extracted from each sample. Proportions of small numbers of classes are crude examples of these descriptors, but obscure much useful information.

The approach used in this study has been to divide the data from the metric physiognomic characters — length, area, width and position of width — into a large number of arbitrary classes for fairly large numbers of individual leaves from the discrete samples. This data is presented graphically as histograms which display the spectrum of response and the relative contribution (frequency distribution) of different classes to the overall spectrum. Statistics which describe the frequency distribution — percentiles, maximum and minimum values (and hence the range), mean and median (50 th percentile) — act then as population descriptors and can be used to approximate the physiognomic "signature" of discrete sets of samples which can be used in multivariate analyses.

In this chapter, the "physiognomic signature" of each of the forest types (and the individual sites for each forest type) used in the study — CMVF, CNVF, SNVF, and MFF — are presented, and then subjected to analysis to test the discriminating and predictive power of these signatures. The data for each forest type is presented as frequency histograms (frequency distributions) for three of the metric physiognomic characters; leaf length, width, and area. These "signatures" are then compared based on the cumulative frequency distributions.

Four samples were used from each site, however the number of leaves extracted was not consistent for samples from CMVF due to unexpectedly high losses of intact leaves in transit from the collection points to Adelaide. Sample sizes are given in Table 4.1. The Raw Scores for each sample are in Appendices 1.1 – 1.11, and are summed in tabular form where appropriate.

4.2 Canopy Versus Litter.

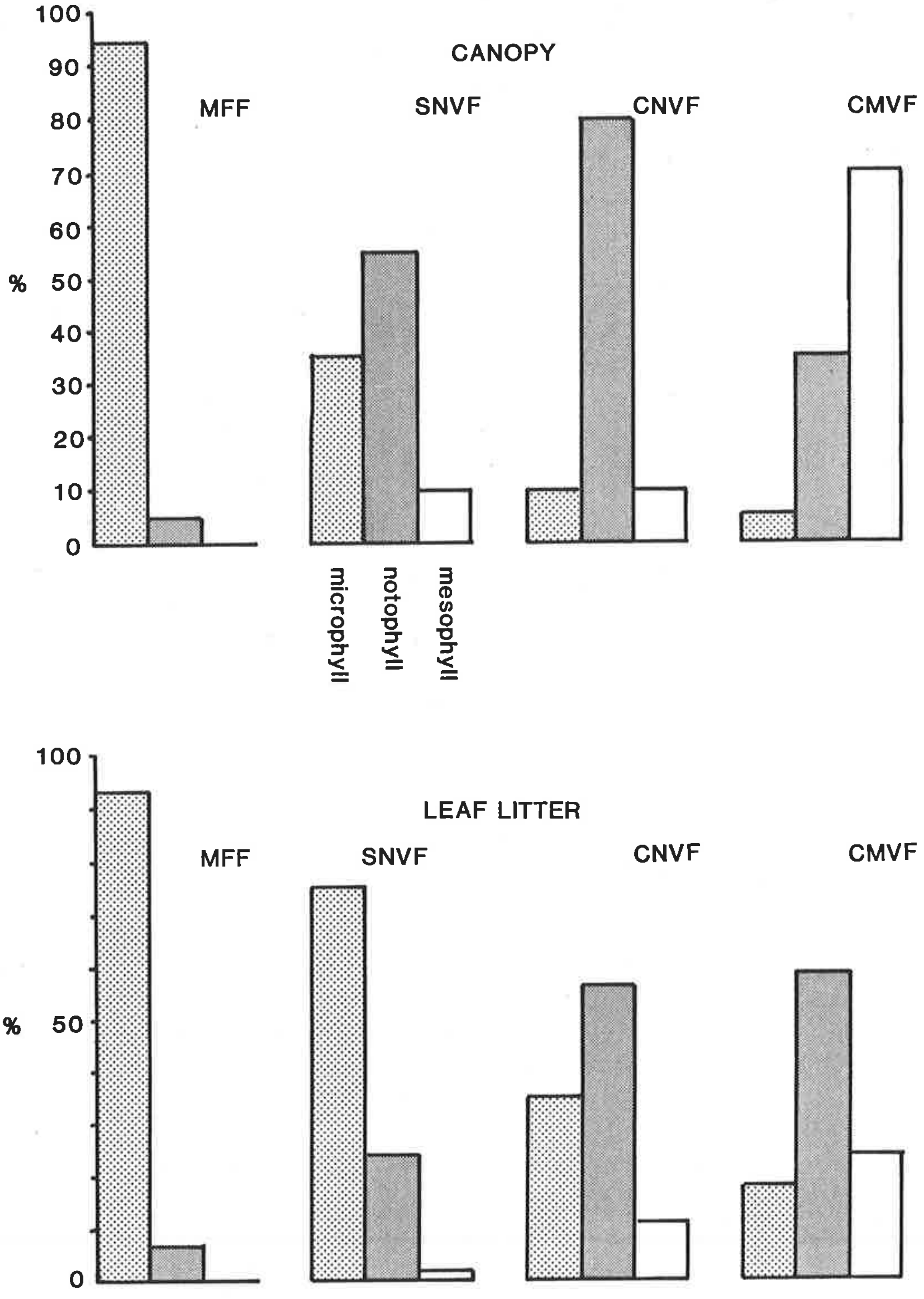
The proportions of Raunkiaer's and Webb's leaf size classes for litter samples are contrasted to Webb's data for the canopy (Webb, 1959) in Figure 4.1 (length defined classes for all samples and all sites pooled). As can be seen from the histograms, the SNVF, CNVF, and CMVF leaf litter has different proportions of the respective Raunkiaerian leaf size classes than recorded by Webb (1959)

Table 4.1

Number of leaves in each sample

Forest	Site	Sample			
		1	2	3	4
CMVF	Oliver Ck.	217	224	224	213
	Mulgrave R.	141	196	155	153
	Mobo Ck.	204	224	224	224
CNVF	Curtain Fig	224	224	224	224
	The Crater	224	224	224	224
	Dorrigo	224	224	224	224
SNVF	Mt. Haig	224	224	224	224
	Mt. Lewis Rd.	–	224	224	224
	Mt. Lewis EP18	224	224	224	224
	Washpool	224	224	224	224
MFF	Barrington Tops	224	213	224	224

Fig. 4.1 A comparison of the relative proportions of Webb's leaf size classes from canopy (Webb, 1959) and litter collections from four types of Australian rainforest.



for the canopy of the same forest types. In the absence of prior data for leaf litter, based on Webb's canopy data, it is likely that an unknown sample of leaf litter from CMVF would be interpreted as coming from CNVF, and litter from CNVF would be interpreted as coming from SNVF (Fig. 4.1). Perhaps surprisingly, MFF/MMF litter has almost the same proportions of leaves in the Raunkiaer/Webb leaf size classes as given by Webb for the canopy and SNVF litter is intermediate between MFF/MMF and SNVF canopy.

A clear implication of this data is that comparisons between the physiognomic characteristics of whole vegetation based on leaf size, and leaf beds (represented by leaf litter), will give an interpretation cooler than the source forest. The degree of the shift to smaller leaf sizes in litter from that recorded for the canopy does however seem to decrease for the cooler (and hence smaller average leaf size) forest types. Roth and Dilcher (1978) found a similar shift to smaller leaf sizes in their examination of lake-bed leaf deposits.

Webb's data was based on 'herbarium-type' collections from the canopy (Webb, 1959). The collection of leaf material from tropical rainforest trees is a difficult procedure due to the height of the trees and the intervening sub-canopy trees. Collection in Australia is often by one of two methods; either the severing of smaller branches at some juncture by a rifle shot, or by sending a line over the branch by sling-shot and pulling the branch down with a stronger line hoisted into place by the first. The differences seen between Webb's data and the litter samples may therefore reflect the different sources of the leaves as the more accessible lower branches would have been sampled.

Rainforests, particularly tropical forests, consist of a series of layers (Richards, 1956; Webb, 1959; Fig. 4.2), and Webb's samples (and those of most researchers) probably represent the mid-crown of individual trees, and not the topmost canopy or the lower layers. The different tree or shrub layers can be expected to produce leaves of different physiognomic character (e.g. Dolph, 1984). Litter will contain a collection of leaves from all layers and parts of the trees and most synusiae within the forest (Ferguson, 1985).

An additional factor is the mechanical damage and decay of leaves. Larger

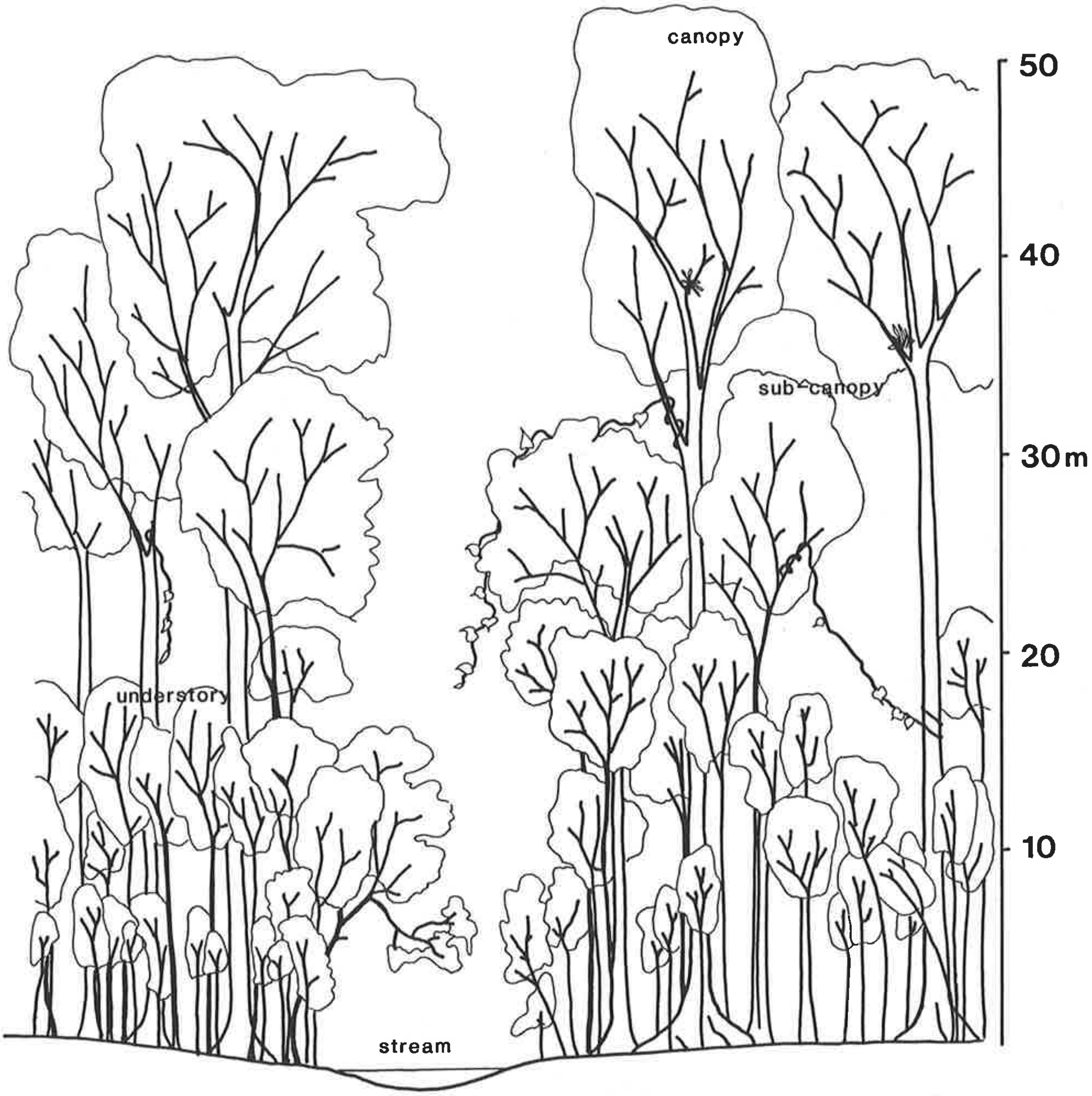


Fig. 4.2 Cross-section through CNVF in N.E. Queensland showing the stratification of the forest and the streamside vegetation (greatly modified from Tracey, 1982).

leaves are more susceptible to mechanical damage, and have a greatly reduced chance of reaching the forest floor intact than the smaller, coriaceous leaves of the topmost part of the canopy (Ferguson, 1985). Of lesser importance is the fact that larger leaves tend to be less lignified, and will therefore decay more quickly than the smaller leaves (Kaushik and Hynes, 1971; Spicer, 1981; Dudgeon, 1982; Ferguson, 1985). This is thought to be of reduced importance in this study however, as the litter was collected at the end of the dry season when litter volumes on the forest floor are at a peak and decay rates are low due to the reduced rainfall.

4.3 Physiognomic Characters.

4.3.1 Leaf Size

Leaf length has been commonly used in taxonomic studies (e.g. Hua Chia, et al., 1986; Eckenwalder, 1986), including fossil leaves (e.g. Hill, 1982; Burnham, 1986), although the use of leaf features in taxonomy has been considered a 'special purpose' approach until relatively recently by neobotanists. However, there has also been considerable caution voiced with regard to the use of leaf length as a taxonomic character due to the observed highly labile response to environmental factors.

However leaf area has generally been used in foliar physiognomic studies, following from Raunkiaer's work and generally using his leaf size classes (Raunkiaer, 1934; Beard, 1944; Cain, et al., 1956; Webb, 1959). Ideally, leaf area would be measured from a planimeter or more recently, by digitising the leaf for computer analysis (e.g. West and Crisp, 1984). However, leaf area has been generally estimated using the formula;

$A = 0.667 \times \text{length} \times \text{width}$ (Cain, et al., 1956).

Dolph investigated the use of this estimation measure and found that lobed and strongly ovate leaves were poorly estimated (Dolph, 1976). Figures 4.3, 4.4, & 4.5 show linear regressions of the estimated area and the measured area for a random selection of 50 leaves from a single sample from a site from three of the forest types (SNVF, CNVF and CMVF). Estimated and measured leaf area was

Figs. 4.3 – 4.5. Linear regressions of leaf area measured using an area meter, and estimated for three samples of 50 leaves from CMVF (Mobo Ck, 4.3), CNVF (Curtain Fig, 4.4), and SNVF (Mt Haig, 4.5).

Fig. 4.3

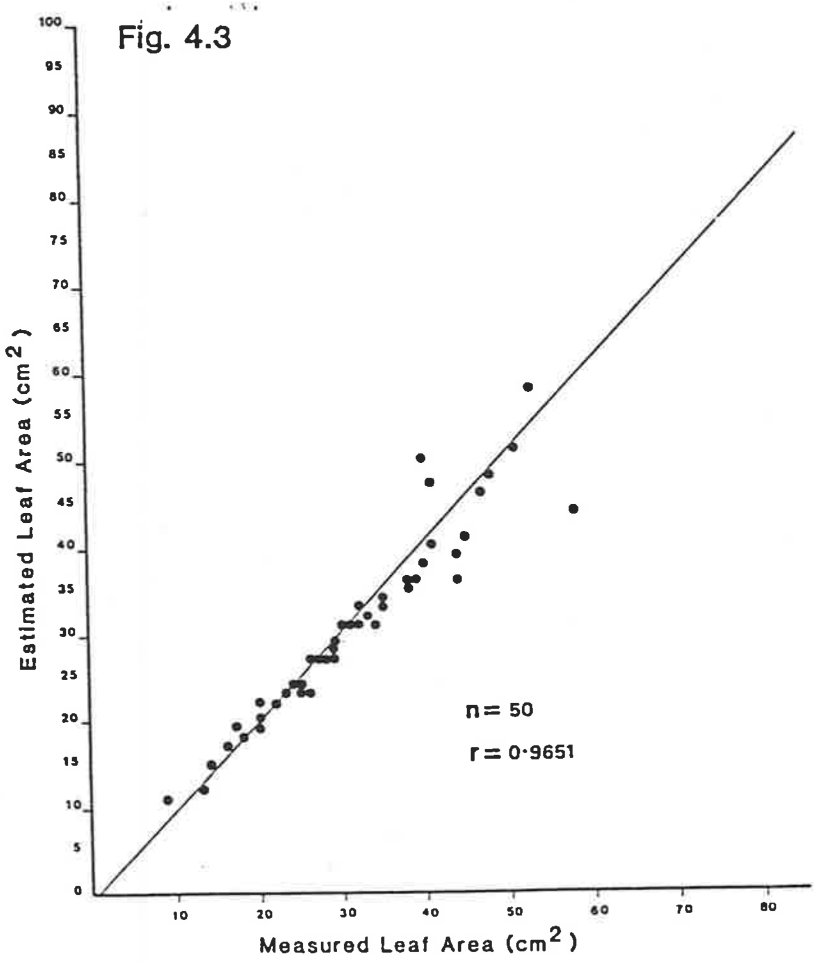


Fig. 4.4

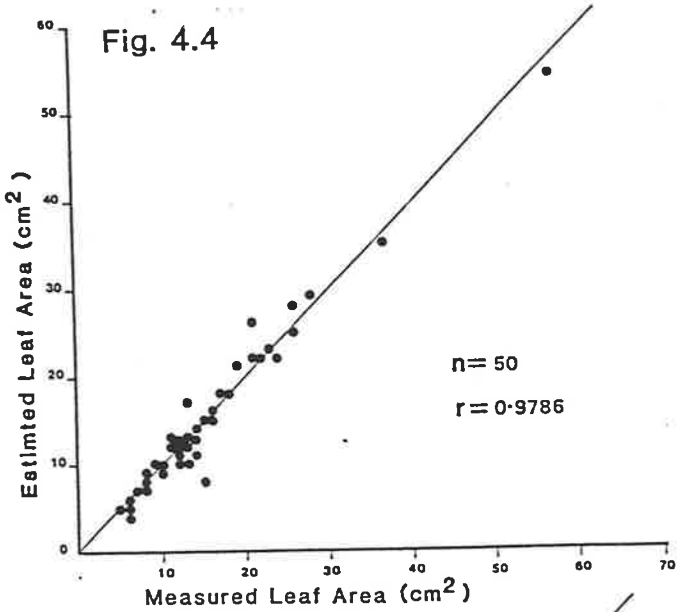
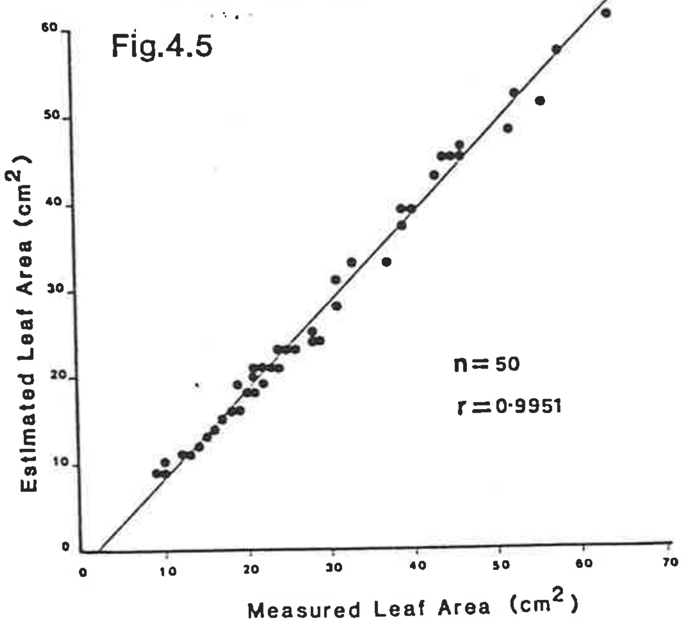


Fig.4.5



strongly correlated in each case.

This data suggests that the correction factor 0.667 gives an accurate measure of the frequency distribution of leaf area for the litter samples. This situation reflects the overall dominance by elliptic leaves in the samples of SNVF and CMVF leaf litter, and the general absence of lobed leaves in the litter. The area estimation correction factor used (0.667 or 2/3) gives an adequate indication of the leaf area frequency distribution for litter from these forests.

Webb (1959) considered leaf length a suitable substitute to area for field determination of his forest types. Length is an easier character to directly measure from impression fossils than area (although a digitised image overcomes this handicap), and the measurement of leaf area is susceptible to inaccuracy in cases where the matrix and or the fossil have been distorted after fossilisation. Most of the studies using leaf size for physiognomic analyses of modern forests have used leaf area, and so it is therefore important to determine the exact relationship between leaf area and length, and in turn, the relationship between these characters and environmental factors.

Unless otherwise stated, leaf length is used as the measure of leaf size for the rest of the thesis.

4.3.2 Leaf width

Leaf width is often considered to vary proportionally with length, and has not been seriously considered as a physiognomic character in isolation for ecological studies, except as a component of the overall leaf size. Trees which grow on stream banks in tropical rainforest, however, often have much narrower leaves (stenophylls) than the trees of the surrounding forest (Richards, 1952; Van Steenis, 1981; Whitmore, 1984). It is also a general observation that the leaves of plants in extreme environments, in addition to being of a smaller length, are often relatively narrower then leaves from the same species from milder environments (West and Noble 1984; Conran, 1987). Potts and Jackson (1986) also found that the leaves of *Eucalyptus* spp in Tasmania displayed a morphological cline with increasing altitude (and hence decreasing temperature) with leaf width (proportionally and absolutely) increasing for the altitudinal upper limit of the species.

The overall shape of a leaf is also considered to be an environmental adaptation (Vogel, 1970; Givnish and Vermeij, 1976). The "wideness" of a leaf, that is the width relative to the length, is an indication of one component of shape, other components being the degree of incision or other of the edge of the leaf blade (lobed / not lobed), the degree of symmetry along the long and short axes of the leaf blade, and the form of the leaf apex and base. Relative width can be expressed either as a ratio or a percentage of width to length.

Some research into the linkage between leaf physiognomy and climate has suggested that leaf length and width were too strongly correlated to be useful as separate characters (Dolph, 1979). However, this work was not based on natural populations of leaves, and the relationship of length to width, as a measure of shape, has been explored in this study to test the idea that leaf shape (as expressed in the relative width) is an important component of the physiognomic signature of some of the forest types studied, and also to test for the presence of a physiognomically distinct streamside vegetation.

4.3.3 Position of greatest width

The degree of symmetry between the top and bottom halves of a leaf can be expressed as a ratio between the length of the leaf blade, and the distance from the leaf base (usually the point of insertion of the petiole into the blade) to the point along the midvein where width is maximal (Fig. 4.6). This ratio can also be expressed as a percentage (length / position of > width x 100).

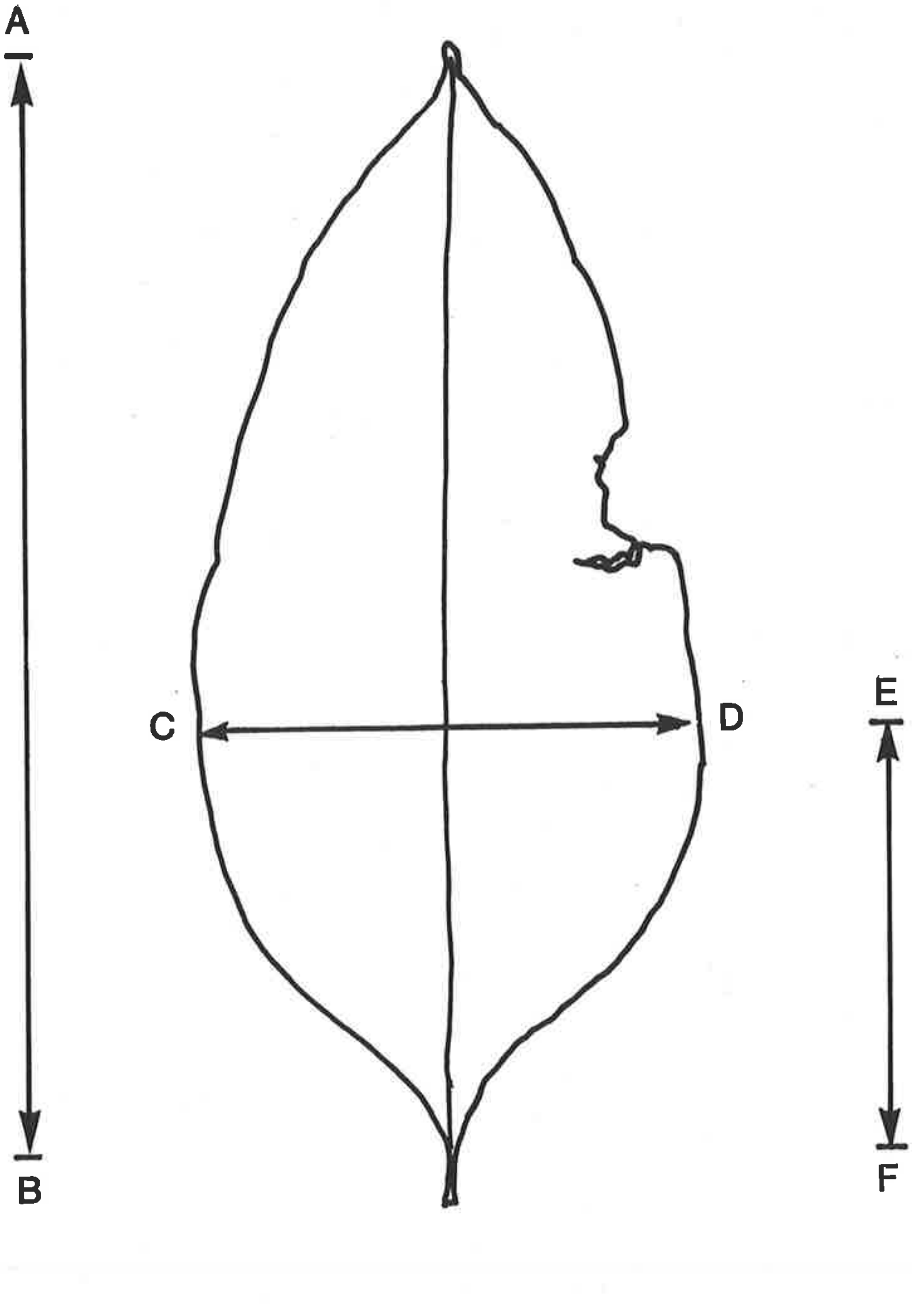
Leaf shape is generally quantified using the ratio of length to width (Hickey, 1984), although leaf shape can be more accurately defined using a series of reference points or "pseudolandmarks" (Dickinson, et al., 1987). However, departures from the elliptic shape are generally defined by a shift of the widest point from the midline of the leaf (Hickey, 1975). From a practical point of view, symmetric leaves with the widest point in the middle third of the leaf (Fig. 4.6) can be considered elliptic, whereas leaves with the widest point in the lower (ovate) or upper third (obovate) are not. For the purpose of this study, "elliptic" was defined as:

Fig. 4.6 leaf showing the measurement of the characters used.

A - B, length. C - D, width (at maximum).

E - F, position of maximal width (distance from insertion of petiole to point along midrib where width is maximal).

Fig. 4.6



symmetric leaves with the Position of Maximal Width within the range 34 – 65% of length.

The leaves of rainforest trees are considered to be typically elliptic (e.g. Richards, 1952). However, vine leaves are often ovate (or at least broader in the lower third of the leaf), and will be encountered in litter samples (and hence fossil beds). This character has often been used in taxonomic studies and has been shown to vary within species (Hill, 1978; Herman, et al., 1987), and may also reflect environmental influences (Givnish, 1978).

4.3.4 Margin type (entire or other)

Simple Notophyll Vine Forest has the highest variation in the proportion of species or individuals (canopy) with non-entire margins (Table 2.4). Microphyll Moss Forest has the highest proportion of species (100%) with non-entire margins quoted, but this is for populations in southern Australia as the proportion of individuals with non-entire margins in Queensland MFF is lower than 100% (c. 50 – 60%; pers. observ.). The high variation in the proportion of non- entire margins in SNVF, however, suggests that this forest type is sensitive to the environmental factors which favour non-entire margins, and would demonstrate the streamside bias discussed previously. Other forest types may not be sensitive enough (variable enough) to significantly detect differences in the proportion of non-entire margined leaves due to the streamside bias. Therefore, for the purpose of testing the streamside bias in margin type, SNVF sites with parallel collections from stream-beds were used. This information is discussed separately in Chapter 5.

4.4 Physiognomic Signatures of the Forest Types.

In most cases where leaf size (generally area) has been used in foliar physiognomic analysis, the relative proportions in the Raunkiaer/Webb size classes have been used (e.g. Beard, 1944; Grubb, et al., 1963a & b; Christophel, 1981; Zastawniak, et al., 1985). The use of smaller divisions however, displays more detail of the relative contribution of different sized leaves to the overall size character of leaf populations.

The values of the metric physiognomic characters (length, width, and position of maximal width) for the samples from each of the sites are presented in the following sections as frequency histograms, or frequency distributions. The mean value of the frequency of leaves in 10mm classes (0 – 10 mm, 11 – 20 mm, 21 – 30 mm, etc) is pooled for all samples for each site for each of the forest types for leaf width and the position of maximal width. Leaf length also uses 10 mm classes, however the boundaries have been staggered to start at 15 mm to allow the class intervals to coincide with the boundaries of Webbs leaf size classes (0 – 15, 16 – 25, 26 – 35mm, etc).

These frequency distributions and the subsequent data on leaf margins, constitute the "physiognomic signatures" of the four forest types at the sites used. The average of these "site signatures" for each forest type is then used as the "forest physiognomic signature". The "forest signatures" are contrasted in the concluding section of this chapter .

4.4.1 Complex Mesophyll Vine Forest

Three sites were used in the analysis of the physiognomic signatures of CMVF litter; Mobo Ck, Mulgrave R., and Oliver Ck (all N.E. Qld.). The frequency distributions of leaf length for these sites are shown in Figures 4.7, 4.8, and 4.9.

Maximum leaf length for the sites varied from 360 mm (Mobo Creek) to 315 mm (Mulgrave River), although within sites the variation was greater with maximum length varying from 210 to 316 mm between the Oliver Creek samples (Table 4.2). Minimum leaf length varied from 26 mm (Oliver Ck), to 33 mm (Mobo Ck), and within sites the variation was comparable with minimum length varying (for example) from 32 to 52 mm in the Mulgrave River samples (Table 4.2). Mean leaf length for each site varied between sites within a narrow range; 101.3 mm (Mobo Creek) to 111.7 mm (Mulgrave River). The variation between samples within sites was comparable, with mean length varying from 107.8 to 115.5 mm in the Mulgrave River samples. The median length value for the sites ranges from 97 mm (Mobo Ck) to 110 mm (Mulgrave R.), a range very close to that observed for within sites, and also for mean leaf length.

Figs 4.7 - 4.9 Frequency distributions of leaf length (mm) for CMVF - Mobo Ck (4.7), Mulgrave R. (4.8), Oliver Ck (4.9).

Class interval is 10 mm, the upper bound of each class is indicated.

Fig. 4.7

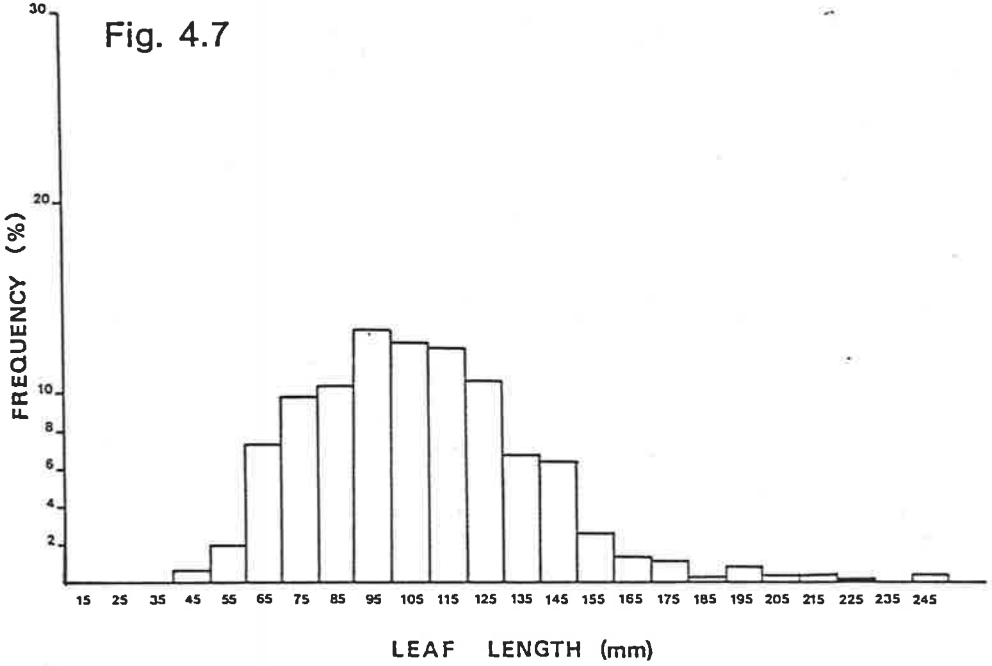


Fig. 4.8

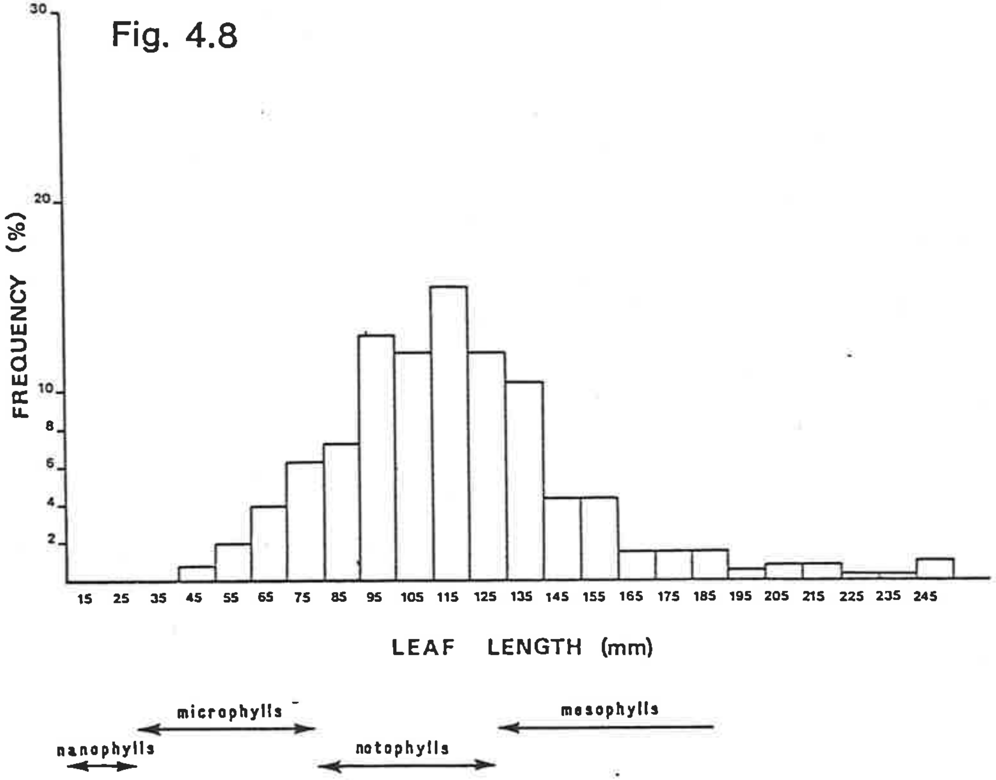
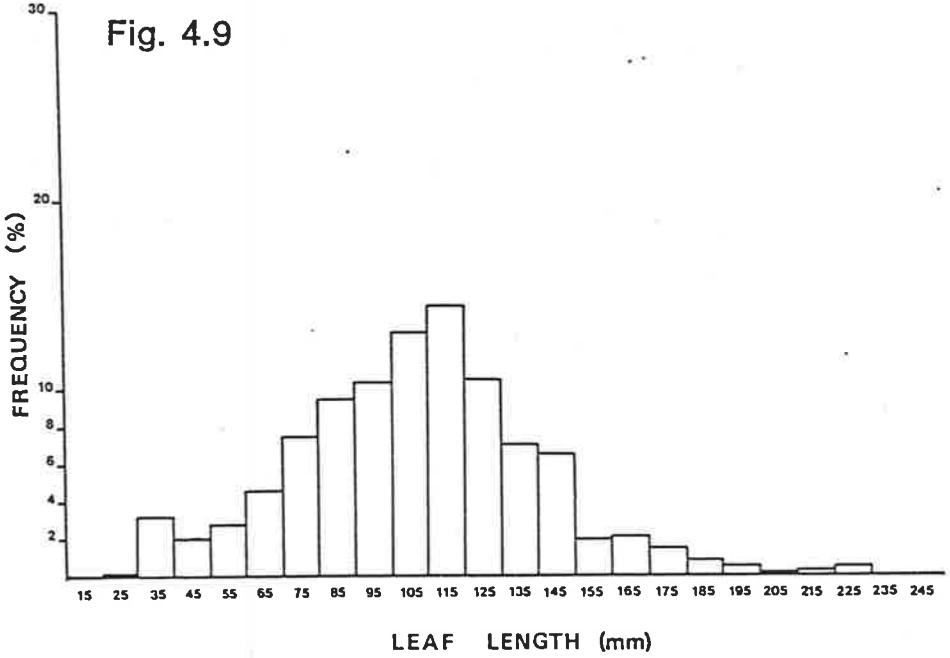


Fig. 4.9



sites	maximum		minimum		mean		percentiles				
			(range/samples)				10	20	50	80	90
Table 4.2 LEAF LENGTH											
Mobo Ck	360	(---)	33	(--)	101.3	(---,---)	65	75	97	122	136
Oliver Ck	316	(210)	26	(47)	103	(96,106)	65	76	102	126	141
Mulgrave R	315	(236)	32	(52)	111.7	(107,115)	72	86	110	132	150
Table 4.3 LEAF WIDTH											
	129	(9)	36.6	(--)	24	(--,--)	28	36	44	50	--
	98	(86)	9	(19)	41.1	(38,45)	26	30	40	52	58
	126	(105)	7	(9)	40.3	(38,41)	12	28	40	50	60
Table 4.4 RELATIVE LEAF WIDTH											
	87.7	(--)	8.1	(--)	37.2	(--,--)	29	31	35	42	48
	86.7	(63)	19.3	(25)	40.8	(37,43)	30	32	39	47	53
	107.1	(61)	4.7	(7)	37.5	(84,39)	10	29	39	47	52
Table 4.5 LEAF AREA											
	205	(--)	2.9	(--)	26.3	(--,--)	10	14	23	34	42
	137	(100)	1.6	(6)	30.3	(26,35)	12	16	27	41	54
	199	(160)	3.2	(6)	32	(30,33)	9	13	26	41	56

The high variation in maximum leaf length, and low variation in mean and median length (within sites, and between sites) reflects the occasional presence of very large leaves (Fig 4.10). These leaves are often the juveniles of canopy species, or "shade leaves", and in the case of the Proteaceae (e.g. *Darlingia darlingiana* (F.Muell.) L.A.S. Johnson, Fig. 4.11), they can be very large and membranous, and are often lobed. In contrast, the adult leaves are quite small and coriaceous, and are either much less lobed or entire.

This data suggests that if the rarer leaf sizes are excluded (i.e. the leaves in the upper and lower 20%), each site has characteristic leaf size spectra. The mean, median (50th percentile), 80th, and 20th percentiles, approximate this spectrum and can be used to represent the character of these sites.

The frequency distributions of leaf width are shown in Figures 4.12, 4.13, and 4.14. Maximum leaf width varies from 98 mm (Oliver Ck) to 129 mm (Mobo Ck), whereas minimum leaf width is more constant between sites varying from 7 mm (Mulgrave R.) to 9 mm (Mobo Ck & Oliver Ck; Table 4.3). The mean and median leaf widths for the three sites are however, within a narrow range; 36.6 mm (Mobo Ck) to 41.1 mm (Oliver Ck). The variation in maximum width further reflects the presence of the extra-large juvenile and 'shade' leaves discussed above, but also reflects the presence of the wide vine leaves (Fig. 4.12).

The leaf width frequency distributions and the upper percentiles of leaf width further reveal the presence of "unusual" sized leaves. The 10 th percentile for two of the sites varies within a narrow range (Mobo Ck; 24 mm & Oliver Ck; 26 mm), however the value for the Mulgrave River samples is much lower (Table 4.3) due to the presence of the very narrow leaves of *Prumnopitys amara* (Podocarpaceae). This also reflected in a minor peak of abundance of narrow leaves in the frequency distribution (Fig. 4.13).

The "relative width" of the leaves is also instructive (the ratio of width to length expressed as a percentage; Table 4.4). Vine leaves are characteristically very broad (i.e. have a large "relative width"), and the large variation between the maximum value for the Mulgrave River site (107.1%; Table 4.4) and the other two sites (86.7 – 87.7%) reflects the presence of quite large vine leaves in

Fig. 4.10 Silhouettes of a selection of leaves from a single sample of leaf litter from Oliver Creek (CMVF, NE Qld). The leaves labelled "A" & "B" represent the smallest and largest leaves of *Idiospermum australiensis* (Idiospermaceae) found in the sample.

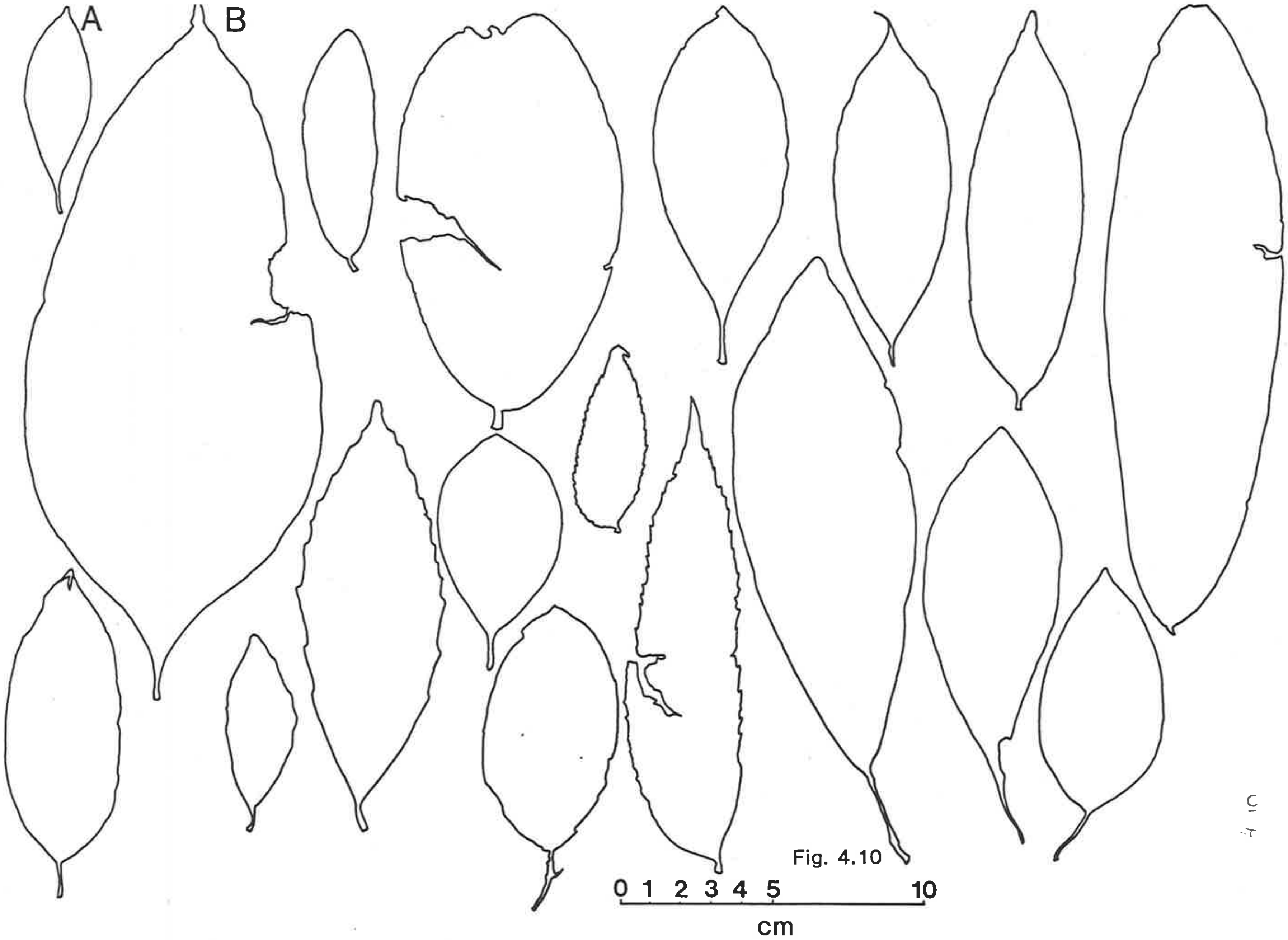
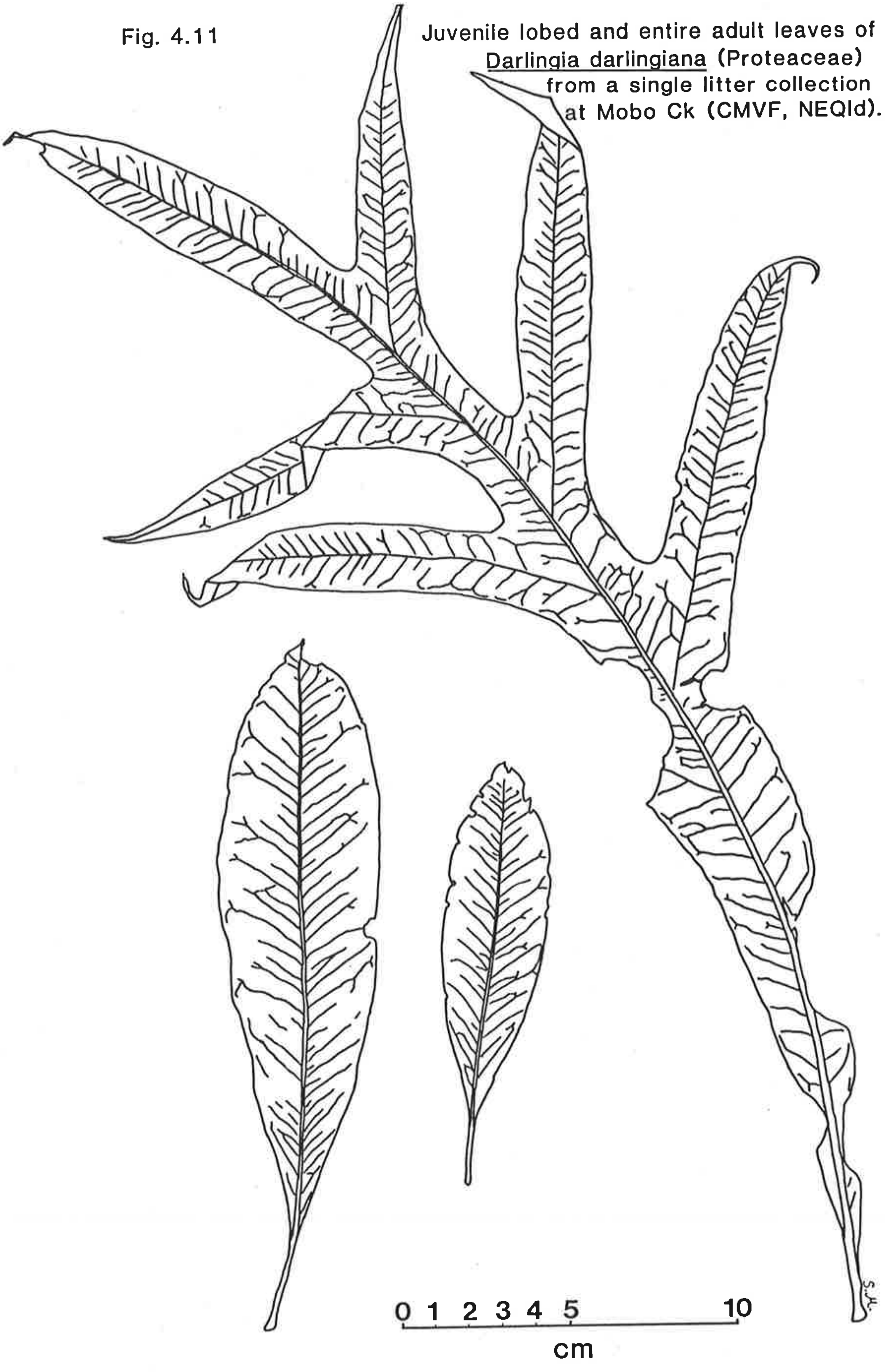


Fig. 4.10

Fig. 4.11

Juvenile lobed and entire adult leaves of Darlingia darlingiana (Proteaceae) from a single litter collection at Mobo Ck (CMVF, NEQld).



Figs 4.12 – 4.14 Frequency distributions of leaf width (mm) for CMVF – Mobo Ck (4.12), Mulgrave R. (4.13), Oliver Ck (4.14). Class interval is 5mm, the upper bound of each class is indicated.

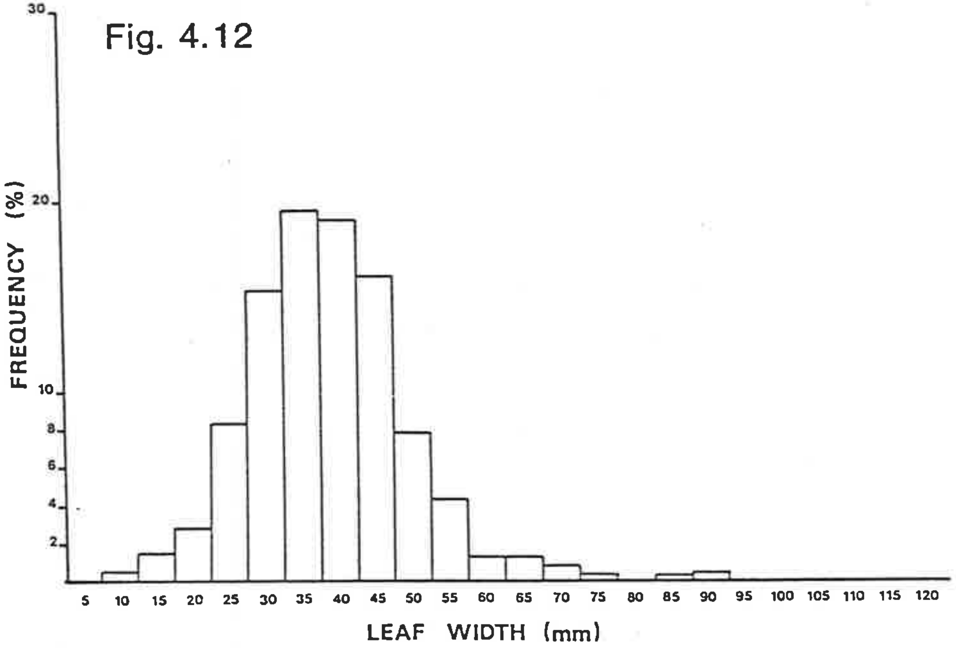


Fig. 4.12

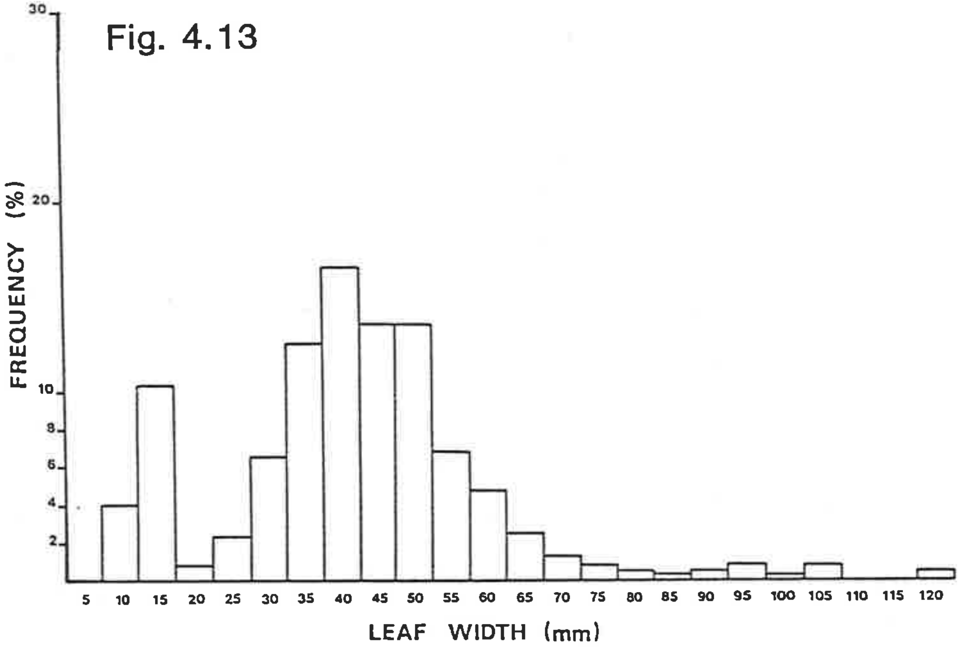


Fig. 4.13

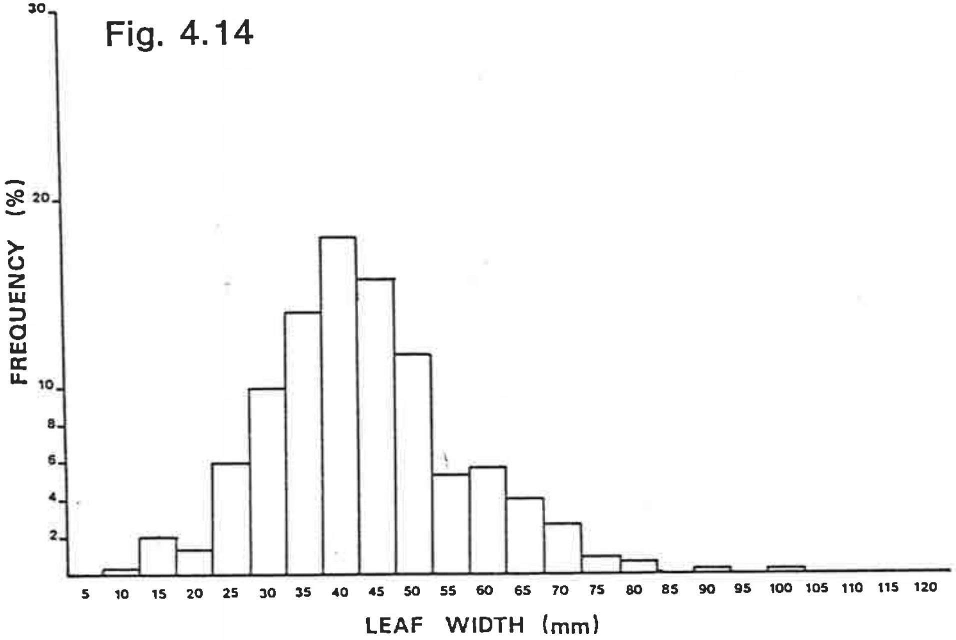


Fig. 4.14

the Mulgrave River samples. The presence of the very narrow leaves of *P. amara* are also indicated by the low value for the 10 th percentile of relative width for Mulgrave River (Table 4.4).

The Position of Maximal Width (Table 4.5) records the deviation from an elliptic shape. The high values for the 10 th percentile (38.5% – 40.4%) and the low values for the 90 th percentile (55.4% – 56.1%), suggest that the greater majority of leaves from all three sites were essentially elliptic (position of max. width less than 66%, greater than 33%). The mean and median values add support, being within 5% of 50% of length.

The frequency distributions of leaf area (from the equation: A = 2/3 Length x Width) are shown in Figs 4.15, 4.16, and 4.17. The narrow leaves of *Prumnopitys amara* have induced a higher representation of leaves of smaller area (Fig. 4.16), however the overall distribution of leaf area is similar to that of the other two sites (Figs 4.15 & 4.17).

The CMVF sites were overwhelmingly dominated by leaves with entire margins (Table 4.6). In most cases only one or two leaves with non-entire margins were present. The differences between or within sites are very small, with the frequency of leaves with non-entire margins below 16% in each sample, and generally below 5%.

4.4.2 Complex Notophyll Vine Forest

Three sites were used in the analysis of the physiognomic signatures of CNVF litter; Curtain Fig, The Crater (both N.E. Qld), and Dorrigo (NSW). This forest type was the most variable of those examined, as discussed later. The frequency distributions of leaf length for these sites are shown in Figures, 4.18, 4.19, and 4.20.

Maximum leaf length varied greatly between The Crater (301 mm) and the other two sites (Curtain Fig, 220 mm; and Dorrigo N.P., 227 mm: Table 4.7). Minimum leaf length varied from 27 mm (both The Crater & Curtain Fig), to 28 mm (Dorrigo). However, mean leaf length varied from 92.9 mm (Curtain Fig) to 82.6 mm (The Crater). The median leaf length showed a similar pattern.

The 80th and 90th percentiles of leaf length for each site are less variable

Table 4.6

Proportions of non-entire leaves

forest type	site	sample 1	2	3	4	(mean)
MFF/MMF		87	99	85	97	(92)
SNVF	(1)	5	3	43	11	(16)
	(2)	17	4	6	4	(8)
	(3)	5	11	4	--	(7)
	(4)	63	81	93	67	(76)
CNVF	(1)	46	45	39	46	(44)
	(2)	68	74	51	77	(68)
	(3)	37	38	50	50	(44)
CMVF	(1)	0	2	1	2	(1)
	(2)	--	16	13	1	(10)
	(3)	1	1	1	1	(1)

Figs 4.15 – 4.17 Frequency distributions of leaf area (cm^2) for CMVF – Mobo Ck (4.15), Mulgrave R. (4.16), Oliver Ck (4.17). Class interval is $5cm^2$, the upper bound of each class is indicated.

Fig. 4.15

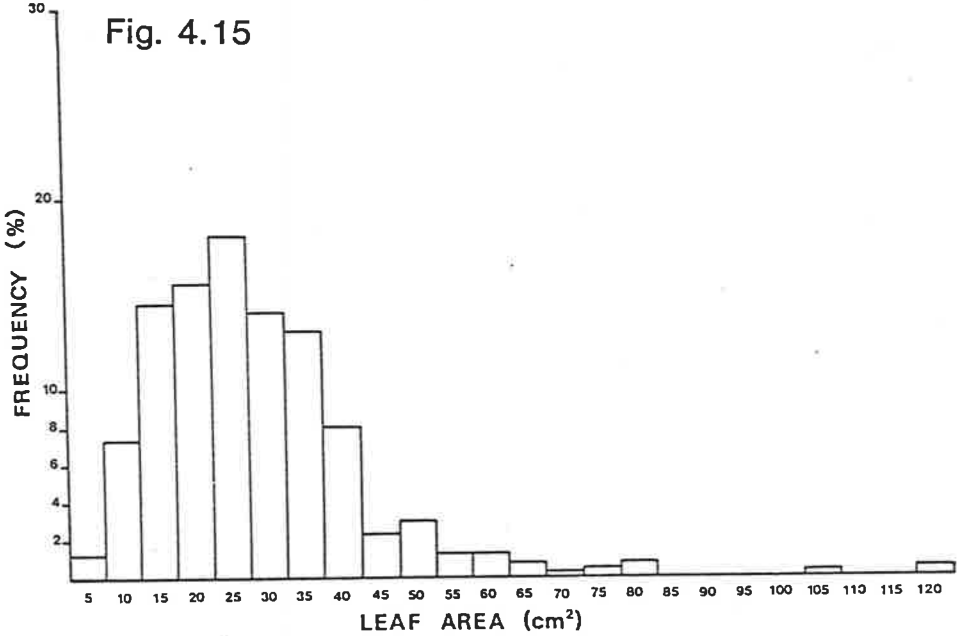


Fig. 4.16

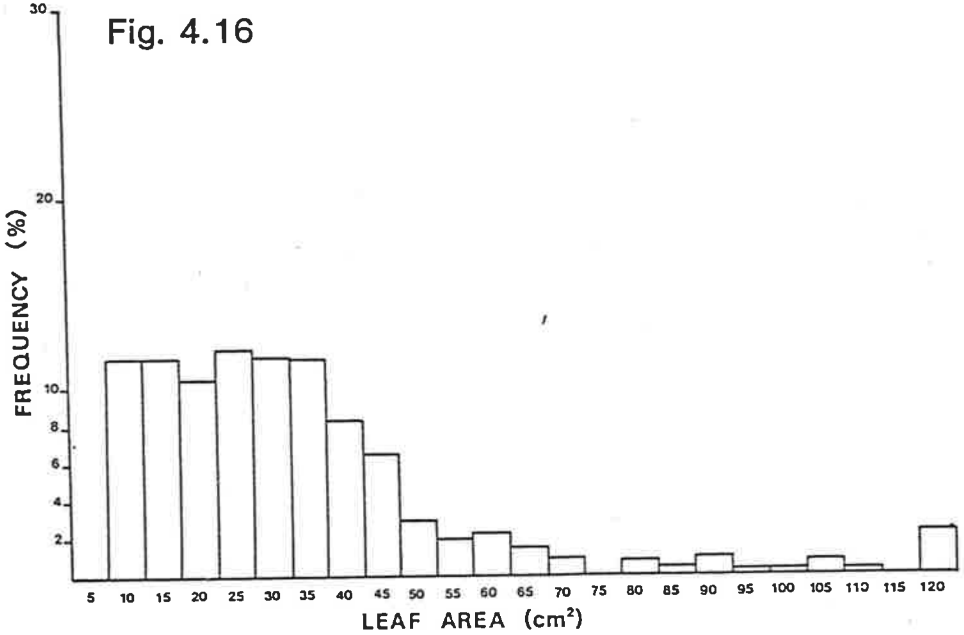
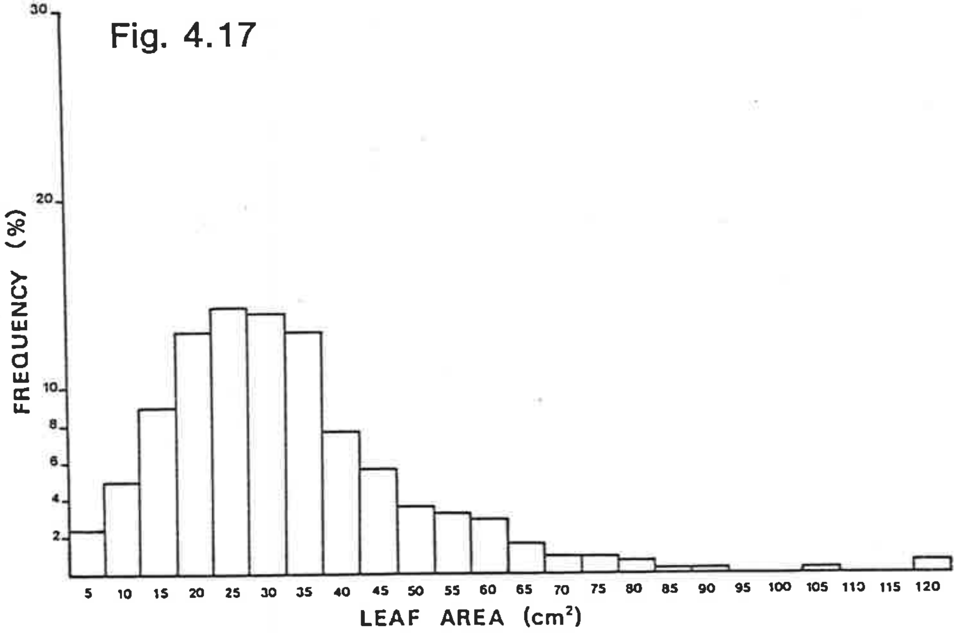


Fig. 4.17



Figs 4.18 – 4.20 Frequency distributions of leaf length for CNVF – Curtain Fig (4.18), The Crater (4.19), Dorrigo (4.20).

Fig. 4.18

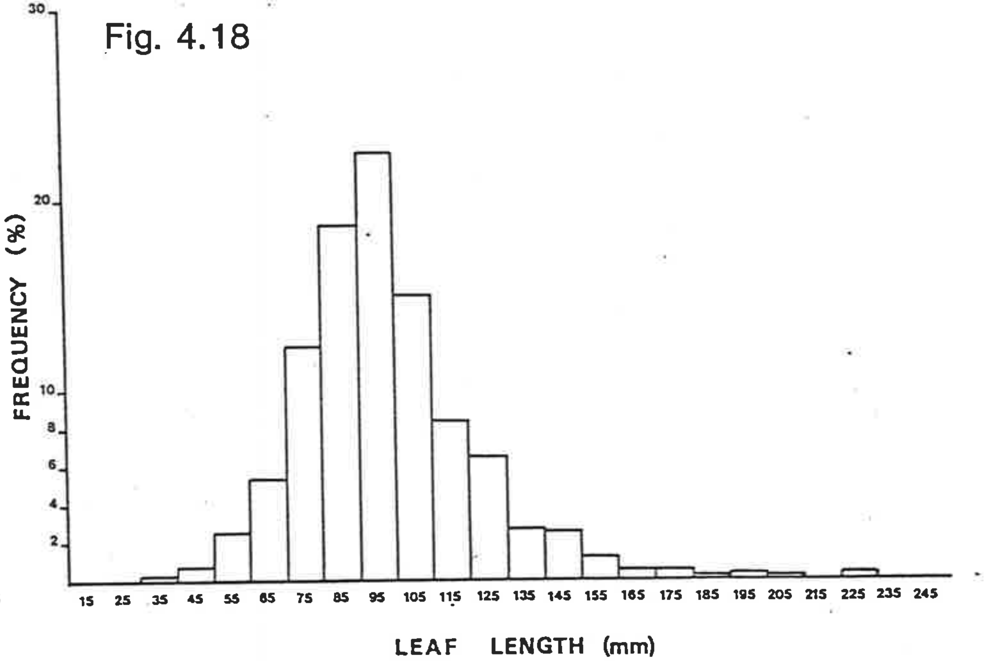


Fig. 4.19

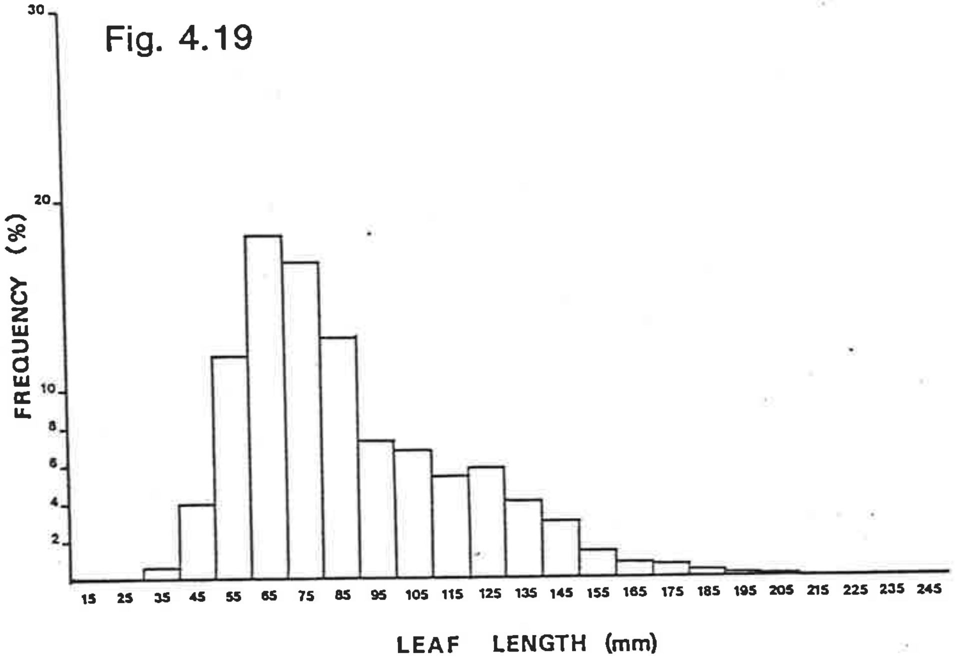
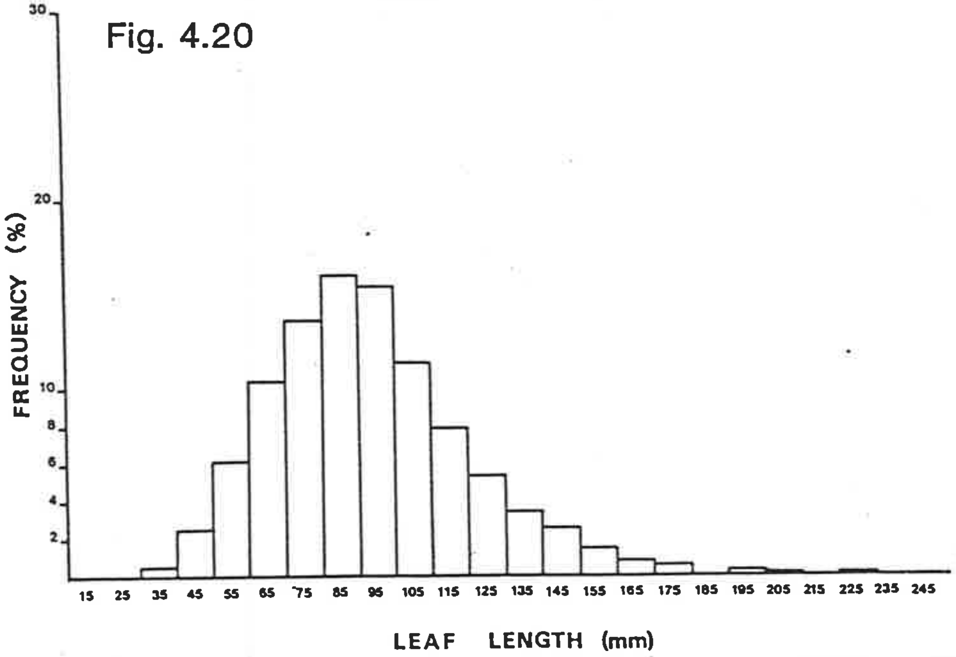


Fig. 4.20



sites	maximum	minimum	mean	percentiles				
	(range/samples)			10	20	50	80	90
Table 4.7 LEAF LENGTH								
Curtain Fig	220 (155)	27 (45)	92.9 (88,101)	67	75	90	108	121
The Crater	301 (163)	27 (40)	82.6 (80,85)	51	57	74	109	128
Dorrigo	227 (190)	28 (42)	88.4 (83,90)	56	65	85	109	125
Table 4.8 LEAF WIDTH								
	142 (107)	11 (17)	41.5 (39,42)	27	31	40	50	56
	134 (89)	7 (25)	39.7 (37,43)	24	28	38	51	57
	87 (60)	9 (10)	28.2 (27,28)	18	21	27	35	39
Table 4.9 RELATIVE LEAF WIDTH								
	105 (77)	22.6 (26)	45.5 (43,47)	30	34	45	55	60
	100 (69)	5.2 (27)	49.6 (45,55)	35	40	51	59	62
	96.7 (51)	18.5 (21)	32.5 (31,32)	26	28	31	36	38

than the maximum and minimum lengths (Table 4.7), varying from 108 and 121 mm (Curtain Fig) to 109 mm (Dorrigo) and 128 mm (The Crater). This implies that the extreme differences in maximum leaf length between The Crater and the other two sites reflects the presence of a few individual very large leaves. Previous discussion (above for CMVF) suggested that a likely explanation was the presence of over-sized juvenile or 'shade' leaves of some species. This would also seem to be the case in this instance (e.g. Fig. 21).

This data suggests that if the rarer leaf sizes are excluded (i.e. the leaves in the upper and lower 10%), each site has characteristic leaf size spectra. The mean, median (50th percentile), 80th, and 20th percentiles, approximate this spectrum and can be used to represent the character of these sites.

The Frequency distributions of Leaf Width for the CNVF sites reveal a large variation between the N.E. Queensland sites (Curtain Fig, Fig. 4.22; & The Crater, Fig. 4.23) and the N.S.W. site (Dorrigo, Fig. 4.24). The leaves of the Dorrigo site are much narrower than the leaves of either The Crater or Curtain Fig (Table 4.8). This is demonstrated by the maximal width (142 mm Curtain Fig, 134 mm The Crater; 87 mm Dorrigo), the much lower value of the mean and median width (Dorrigo 28.2 & 27 mm; 39.7 – 41.5 mm & 38 – 40 mm for the N.E. Qld sites), and the 10 th and 90 th percentiles of width (Table 4.8).

The relative width values further emphasise the differences between the ne Queensland and the N.S.W. CNVF sites (Table 4.9). The maximum values are within a common small range (96.7 – 105%), however the lower and upper percentiles of relative width vary greatly between the N.E. Queensland and the New South Wales site (Dorrigo). The mean and median values also reflect these differences.

Further differences between the CNVF sites are reflected in the Position of Maximal Width (Table 4.10). In contrast to leaf width and relative width, position of maximum width varies the greatest between the seasonally-dry Curtain Fig site, and the sites at Dorrigo and The Crater. This point is further discussed in Chapter 6.

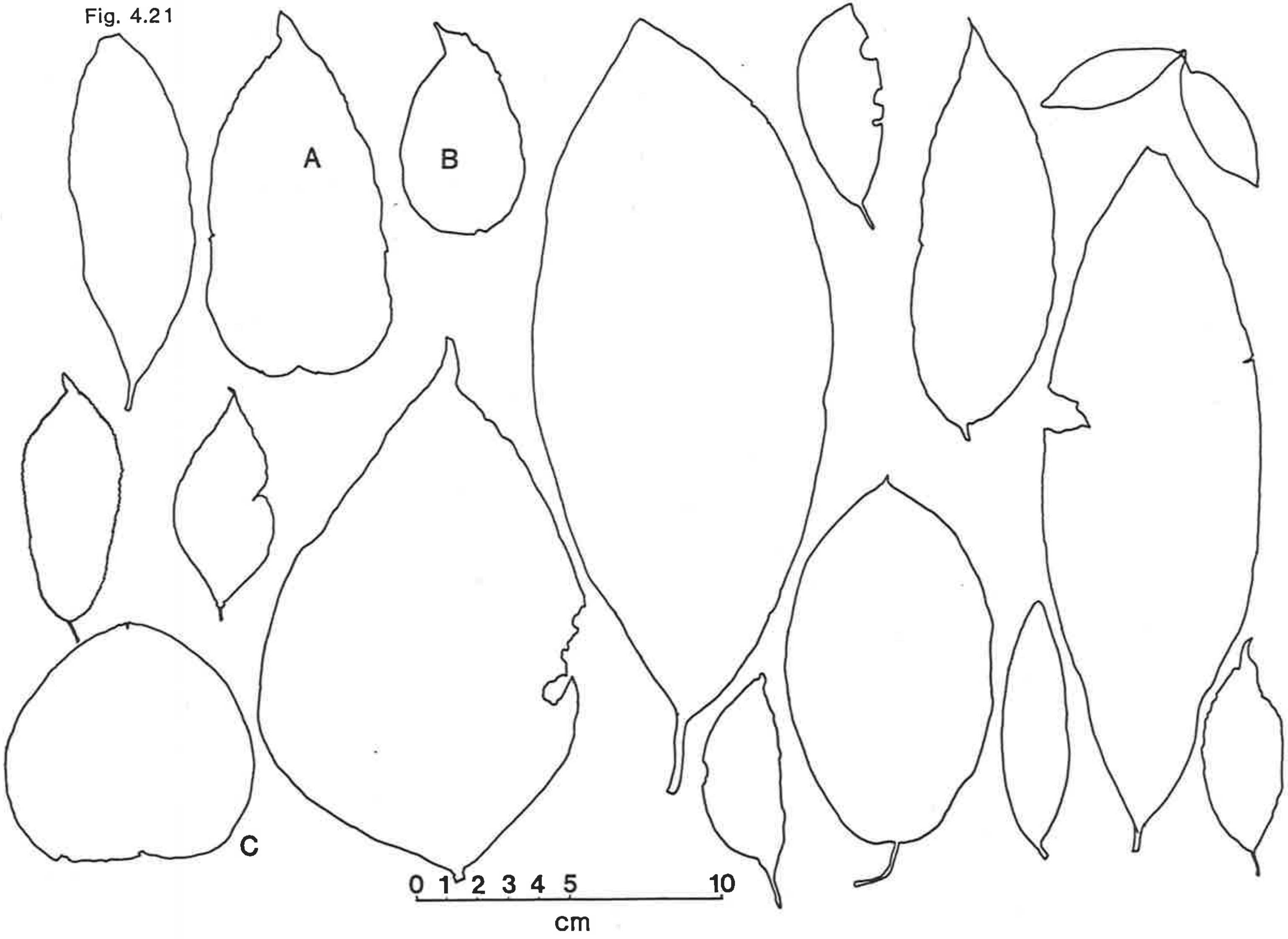
The Frequency distributions of Leaf Area (A = 2/3 Length x Width) show

Table 4.10 POSITION OF MAXIMAL WIDTH (% of length)

sites	maximum		minimum		mean		percentiles				
	(range/samples)						10	20	50	80	90
Mobo Ck	84.8	(--)	12.7	(--)	47.4	(--,--)	40	42	47	52	55
Oliver Ck	65.8	(63)	16.3	(28)	47.8	(45,50)	39	42	47	52	55
Mulgrave R	75.6	(63)	22.7	(26)	47.1	(45,48)	38	41	47	52	56
Curtain Fig	69	(53)	15	(22)	35.2	(33,37)	24	27	36	--	--
The Crater	72.4	(59)	11.6	(20)	42.7	(37,49)	27	33	44	50	54
Dorrigo	71	(64)	23.9	(37)	50	(48,51)	42	44	49	55	59

Fig. 4.21 Silhouettes of a selection of leaves from a single sample of leaf litter from Curtain Fig (CNVF, NE Qld). The leaves labelled "A" & "B" represent the largest and smallest leaves of _Cissus_ _antarctica_ (Vitaceae), a vine. The leaf "C" is also a vine (Menispermaceae).

Fig. 4.21



Figs 4.22 – 4.24 Frequency distributions of leaf width for CNVF – Curtain Fig (4.22), The Crater (4.23), Dorrigo (4.24).

Fig. 4.22

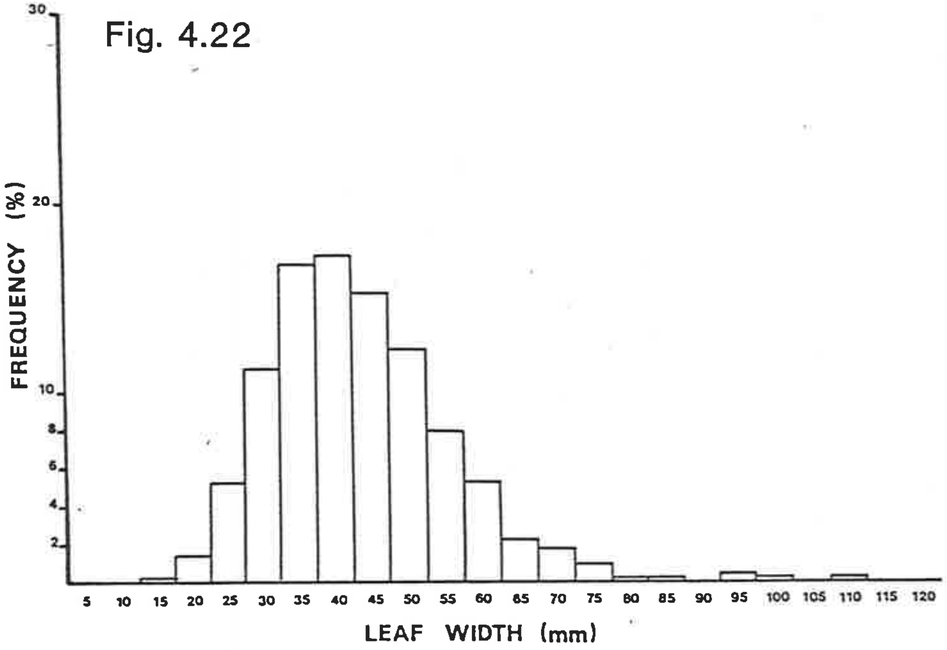


Fig. 4.23

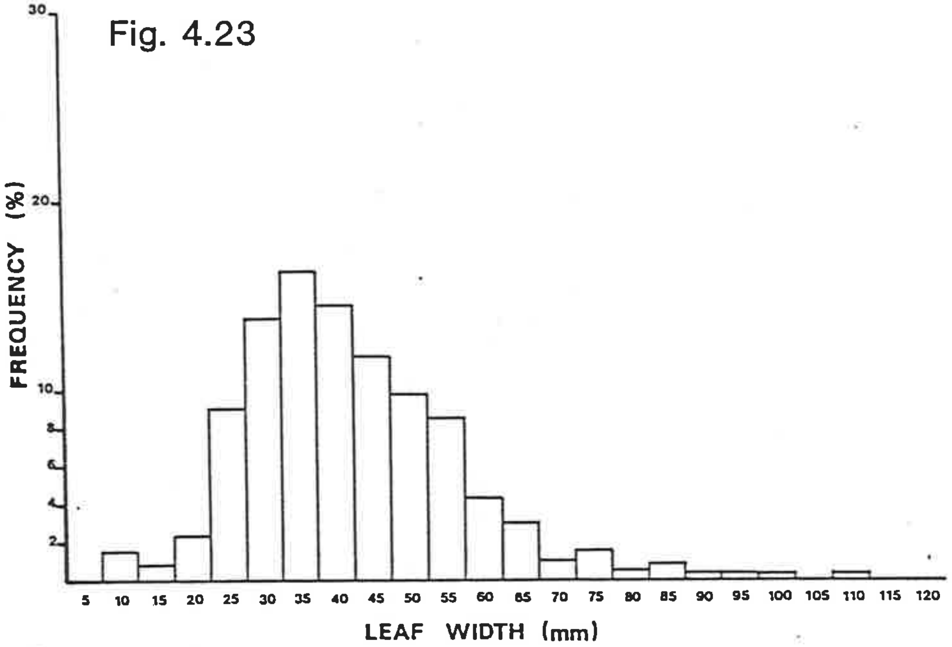
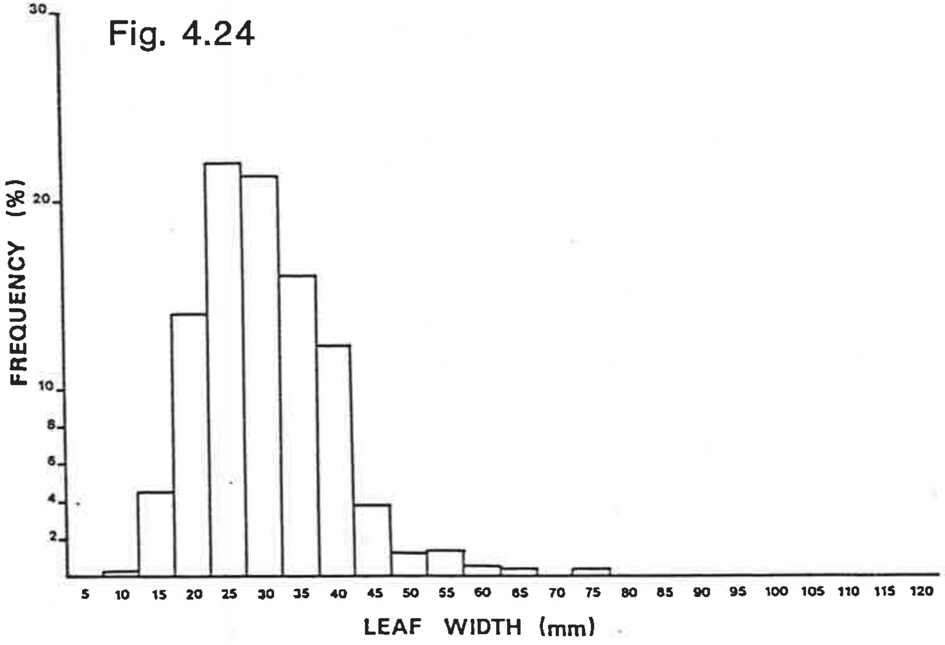


Fig. 4.24



a higher proportion of smaller leaves in the Dorrigo site litter (Figs 4.25, 4.26, & 4.27). In contrast to the leaf length data, based on leaf area, The Crater has smaller leaves than the Curtain Fig site (Figs 4.26 & 4.25). The more ovate leaves of the Curtain Fig site however, may have over-estimated leaf area for this site (Dolph, 1979). The results of the earlier linear regressions of estimated and measured leaf area suggest that this is probably not the case.

The proportion of leaves with non-entire margins was quite variable both within and between sites (Table 4.6). The Curtain Fig site was most variable (51 – 77%), with the other sites falling into a smaller range (Dorrigo N.P. 37 — 50%; The Crater 39 – 46%). The range of individual leaves with non-entire margins overlapped for the three sites, however the Curtain Fig site litter generally had higher proportions of non-entire leaves. This is clearly demonstrated by the mean value for each site: Dorrigo and The Crater, both 44%; Curtain Fig, 68% (Table 4.6). The main difference between the Curtain Fig site and the other sites is the strongly seasonal rainfall of the former.

4.4.3 Simple Notophyll Vine Forest

Four sites were used in the analysis of physiognomic signatures from SNVF; Mt Haig, Mt Lewis Rd, Mt Lewis EP18 (all from N.E. Qld), and Coombadjha Ck (NSW). The frequency distributions of leaf length for these sites are shown in Figures 4.28, 4.29, 4.30, and 4.31.

Maximum leaf length for the sites varied from 276 mm (Mt Lewis EP18) to 156 mm (Coombadjha Ck: Figs 4.30 to 4.31; Table 4.11). The minimum length for each site varied from 13 mm (Mt Haig) to 28 mm (Mt Lewis EP18).

Within site variation was however of a similar magnitude with maximum length varying from 270 to 147 mm in the Mt Haig samples, and minimum length varying from 13 to 30 mm (Table 4.11). The mean and median lengths were uniform between sites, although the Mt Lewis EP18 site had generally much larger leaves (mean length 71.8 mm; Coombadjha Ck mean length 62.8 mm). The Mt Haig site however, was found to be quite variable with mean length ranging from 58.2 to 74.5 mm.

The leaf length frequency distributions of the sites serve to emphasise the

Figs 4.25 - 4.27 Frequency distributions of leaf area for CNVF - Curtain Fig (4.25), The Crater (4.26), Dorrigo (4.27).

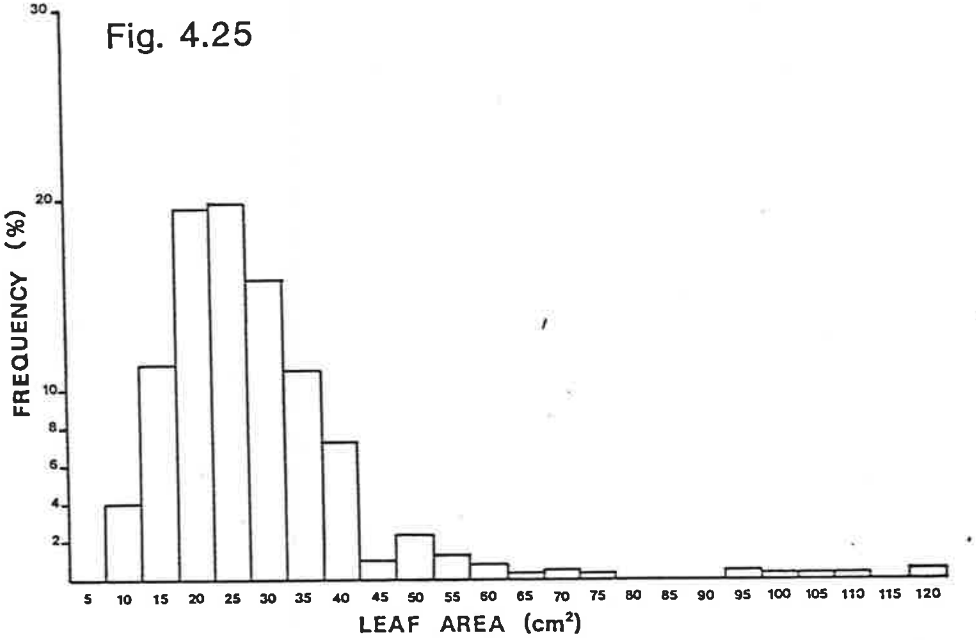


Fig. 4.25

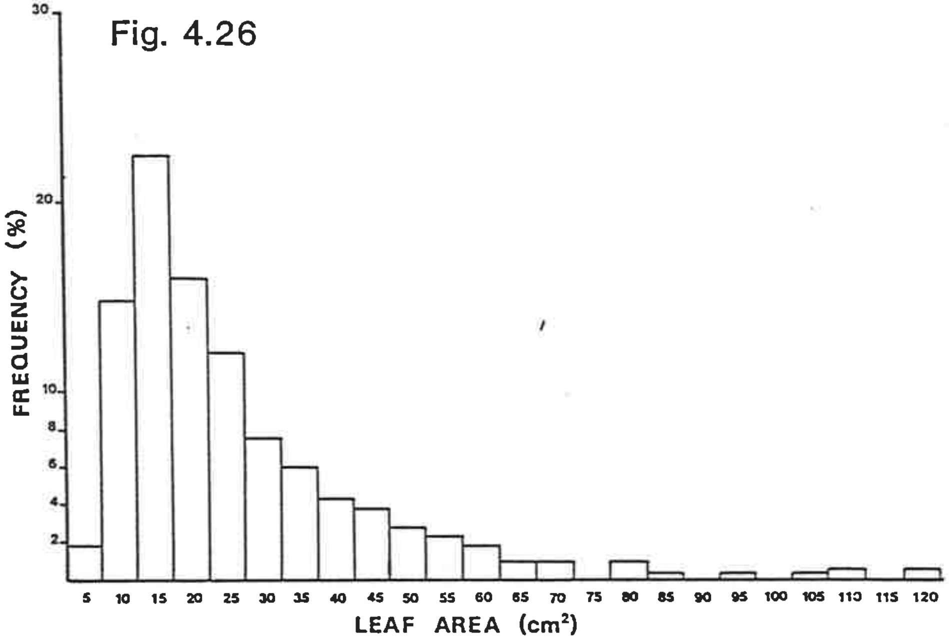


Fig. 4.26

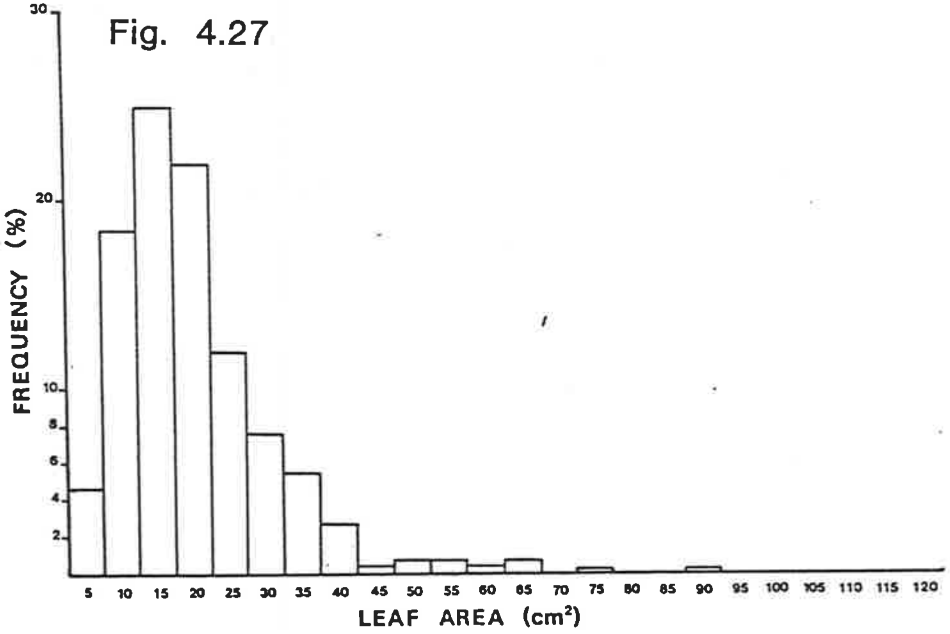


Fig. 4.27

Figs 4.28 – 4.31 Frequency distributions of leaf length (mm) for SNVF – Mt Haig (4.28), Mt Lewis Rd (4.29), Mt Lewis EP18 (4.30), Washpool (4.31).

Fig. 4.28

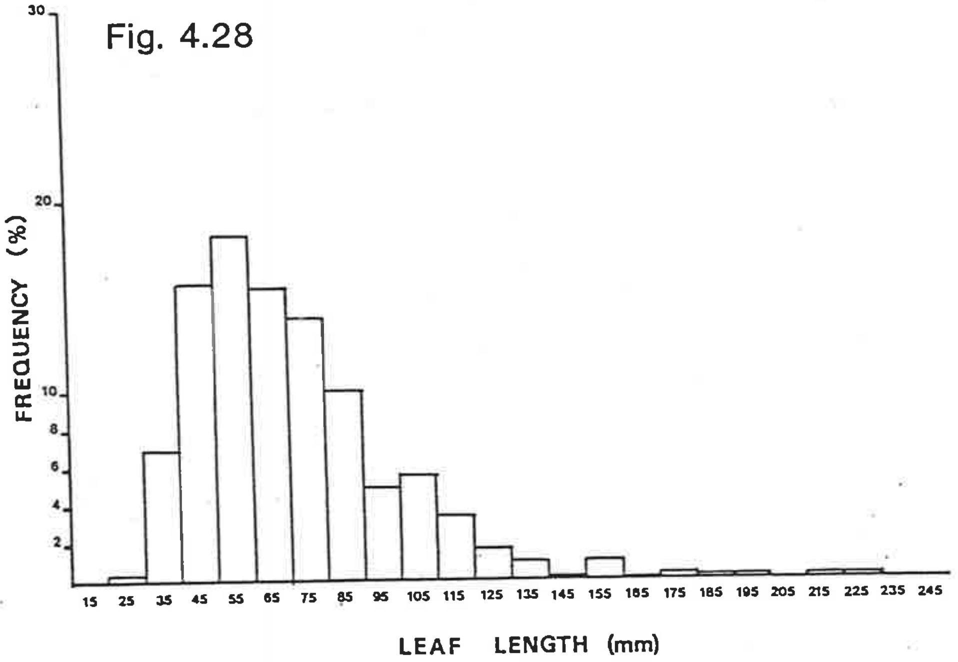


Fig. 4.29

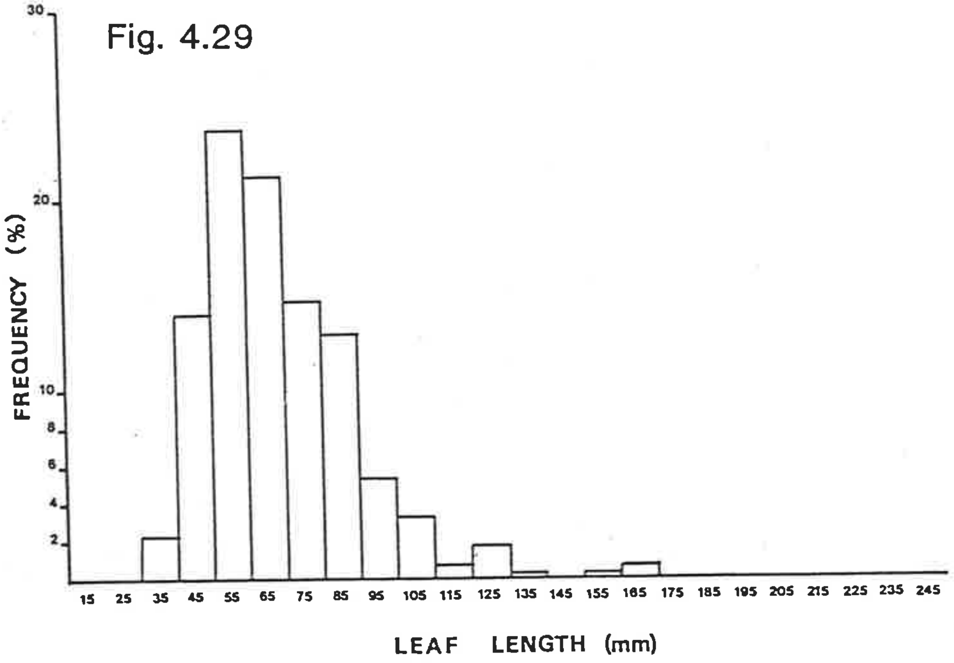


Fig. 4.30

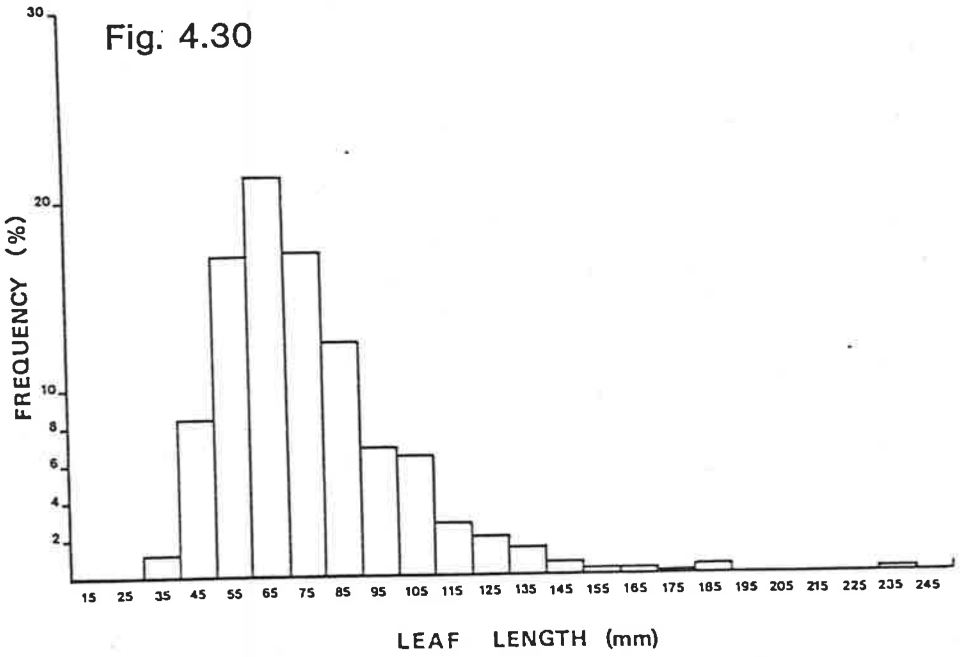
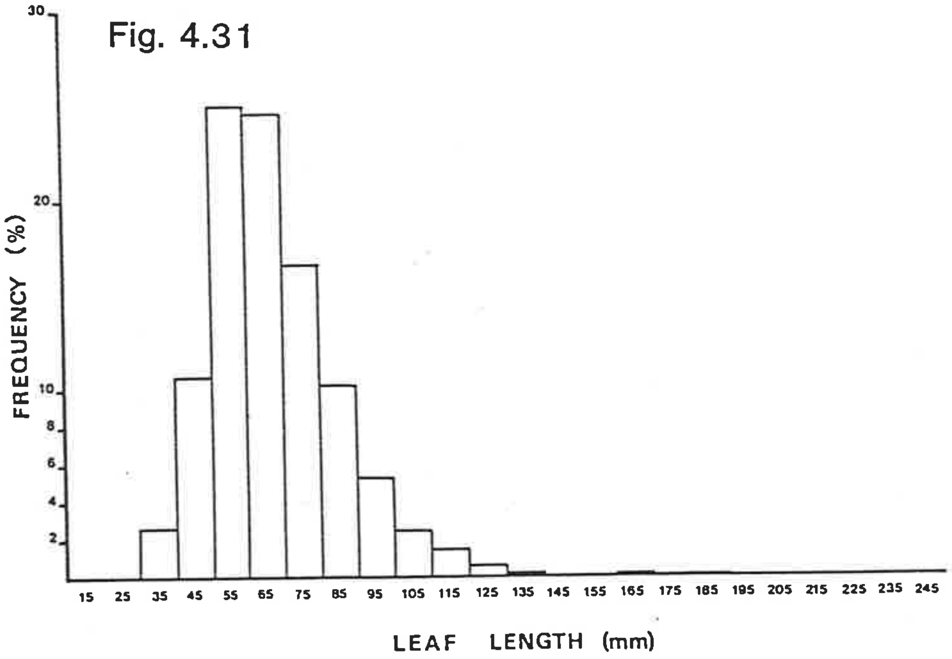


Fig. 4.31



sites	maximum		minimum		mean		percentiles				
		(range/samples)					10	20	50	80	90
Table 4.11 LEAF LENGTH											
Mt Haig	156	(110)	27	(33)	62.8	(59,67)	43	50	60	76	86
Mt Lewis Rd	270	(147)	13	(30)	66.5	(58,74)	37	44	60	85	102
Mt LewisEP18	165	(153)	27	(29)	63.5	(61,65)	42	47	60	77	88
	276	(142)	28	(34)	71.8	(68,74)	46	53	67	86	100
Table 4.12 LEAF WIDTH											
	50	(33)	6	(10)	20.1	(17,21)	13	15	20	25	28
	61	(50)	6	(9)	25.2	(21,27)	14	18	25	32	37
	65	(55)	7	(12)	26.7	(25,28)	16	20	26	32	37
	80	(53)	9	(11)	27	(--,--)	17	20	26	33	37
Table 4.13 RELATIVE LEAF WIDTH											
	55.2	(46)	17.6	(22)	32.1	(29,35)	25	27	31	36	39
	87.8	(68)	16.3	(22)	40	(36,46)	27	30	38	48	55
	78.8	(74)	11.2	(15)	44.1	(40,48)	27	33	45	55	60
	77.8	(60)	18	(19)	38.8	(37,40)	27	30	37	47	51
Table 4.14 POSITION OF MAXIMAL WIDTH (% of length)											
	70.4	(56)	31	(34)	46.6	(45,47)	41	43	46	50	51
	77.8	(62)	23.1	(25)	46.3	(44,50)	35	38	46	53	57
	74.6	(66)	18.1	(25)	45.8	(44,47)	33	40	46	52	56
	75	(59)	15.6	(24)	47.5	(42,50)	33	40	48	54	60

presence of occasional much larger leaves in the N.E. Queensland examples of SNVF (Figs 4.28, 4.29, & 4.30). In the discussion of CMVF and CNVF it was suggested that these rare larger leaves represented mainly the shade or juvenile leaves of canopy species. The absence of the larger leaves in the Coombadjha Creek samples (NSW; Fig. 4.31) suggests that perhaps this leaf dimorphism is not as pronounced in New South Wales.

The 80th and 20th percentiles of leaf length between sites are less variable than the maximum and minimum lengths (Table 4.11). If the rarer leaf sizes are excluded (i.e. the leaves in the upper and lower 10%), each site has characteristic leaf size spectra (Figs 4.28 – 4.30). The mean, median (50th percentile), 80th, and 20th percentiles, approximate this spectrum and can be used to represent the character of these sites (Table 4.11).

The frequency distributions of Leaf Width for the SNVF sites demonstrate that the leaves of the Coombadjha Creek site (NSW; Fig. 4.35) are typically narrower than the leaves of the N.E. Queensland sites (Figs 4.32, 4.33, 4.34). This can also be seen in the maximum widths for each site and both the mean and median widths (Table 4.12). As was the case for leaf length, the Mt Lewis EP 18 site (maximum width 80 mm) is at the upper end of the range exhibited for the SNVF sites (50 mm Coombadjha Ck — 65 mm Mt Lewis Rd). This reflects the presence of some very broad vine leaves in the Mt Lewis EP18 samples. An example of leaves from SNVF litter is shown in Figure 4.36.

The mean widths for the N.E. Queensland sites are however within a narrow range (25.2 mm Mt Haig – 27 mm Mt Lewis EP 18), with Coombadjha Creek markedly lower (20.1 mm). The median width values demonstrate a similar relationship (Table 4.12). Relative width (Table 4.13) confirms that the Coombadjha Creek samples contained much narrower leaves, with a much lower maximum value (55.2%; 77.8 – 87.8% for the N.E. Qld sites), and a much lower mean relative width. This variation is further discussed in Chapter 6.

Position of Maximal Width reflects the shape of the leaves. In the discussion of CNVF it was pointed out that leaves with a value greater than 33% and less than 66% of length were generally elliptic. The values given in Table 4.14 indicate

Figs 4.32 - 4.35 Frequency distributions of leaf width (mm) for SNVF - Mt Haig (4.32), Mt Lewis Rd (4.33), Mt lewis EP18 (4.34), Washpool (4.35).

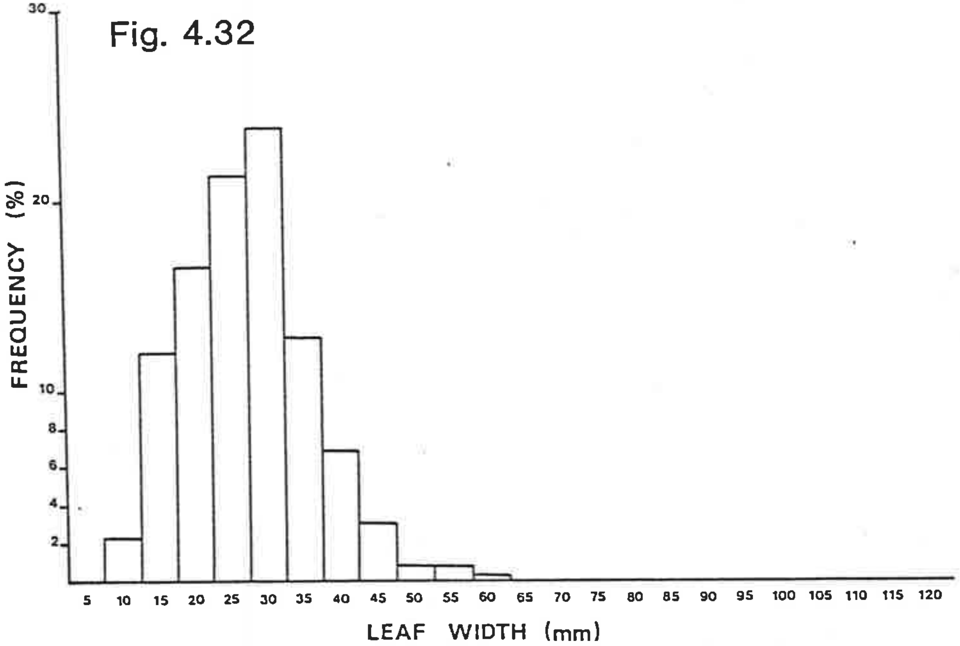


Fig. 4.32

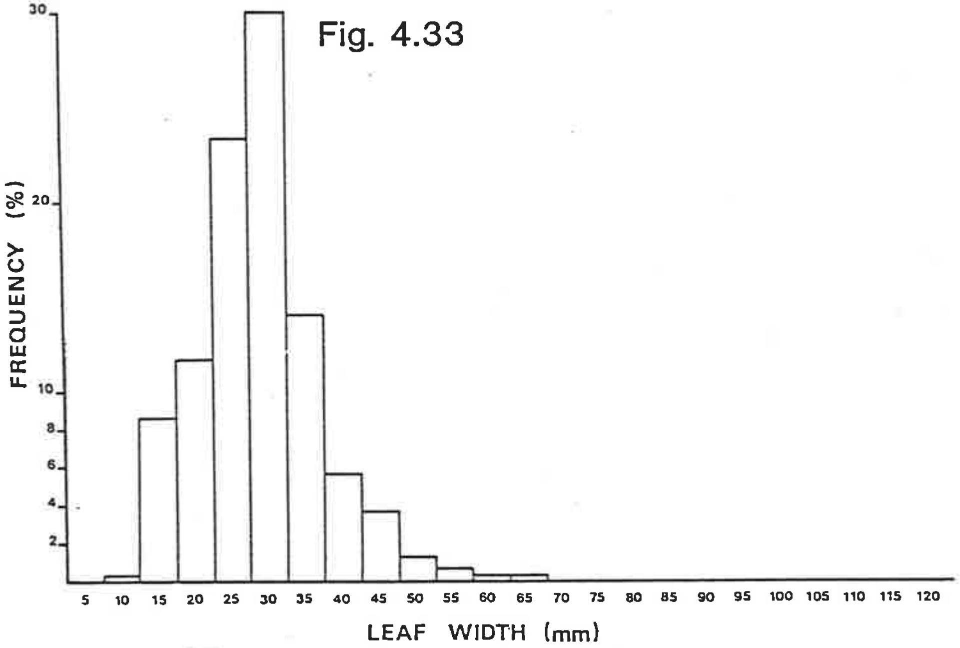


Fig. 4.33

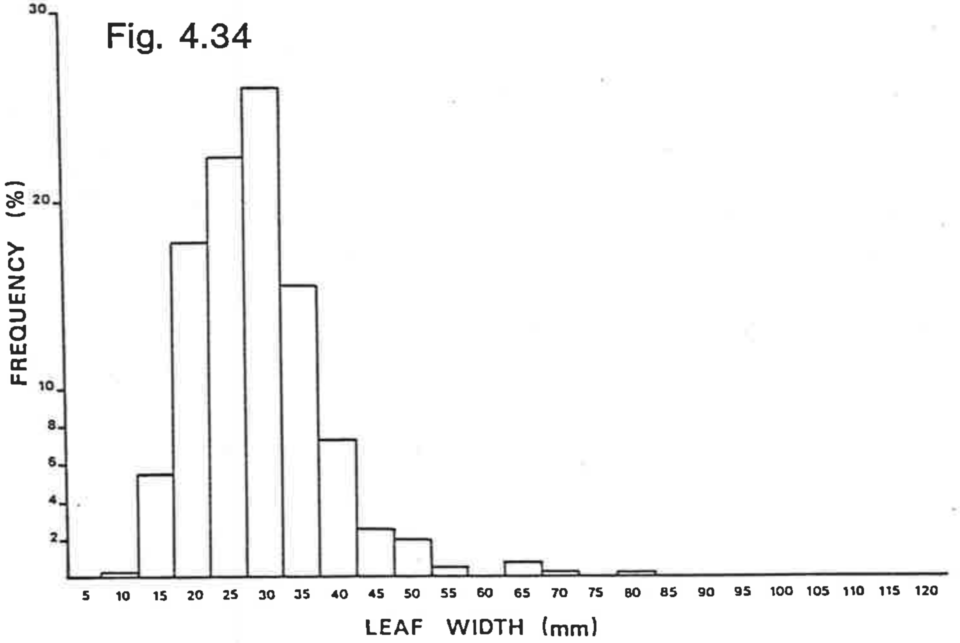


Fig. 4.34

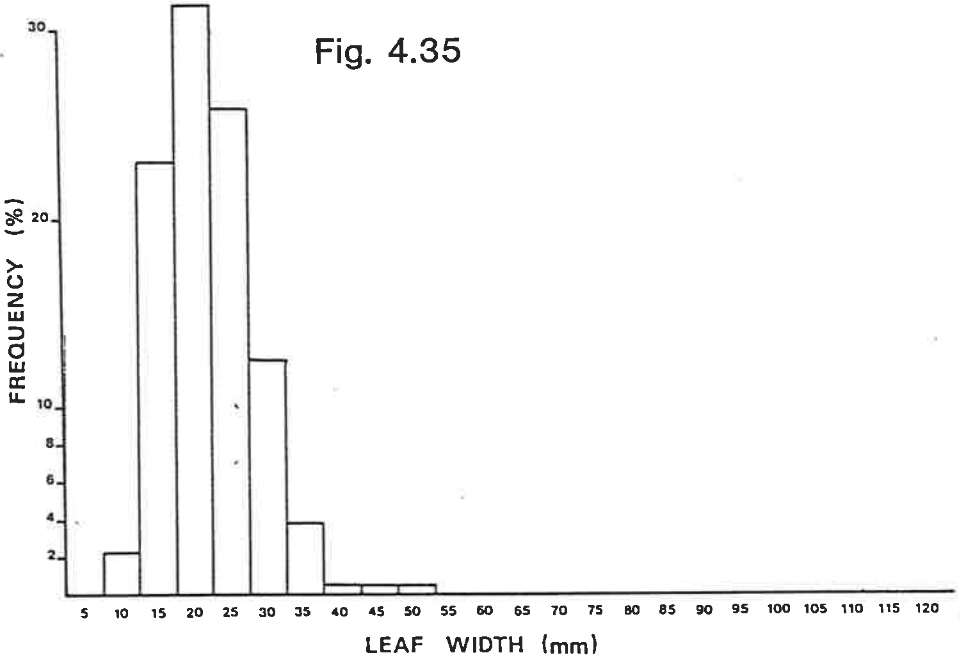
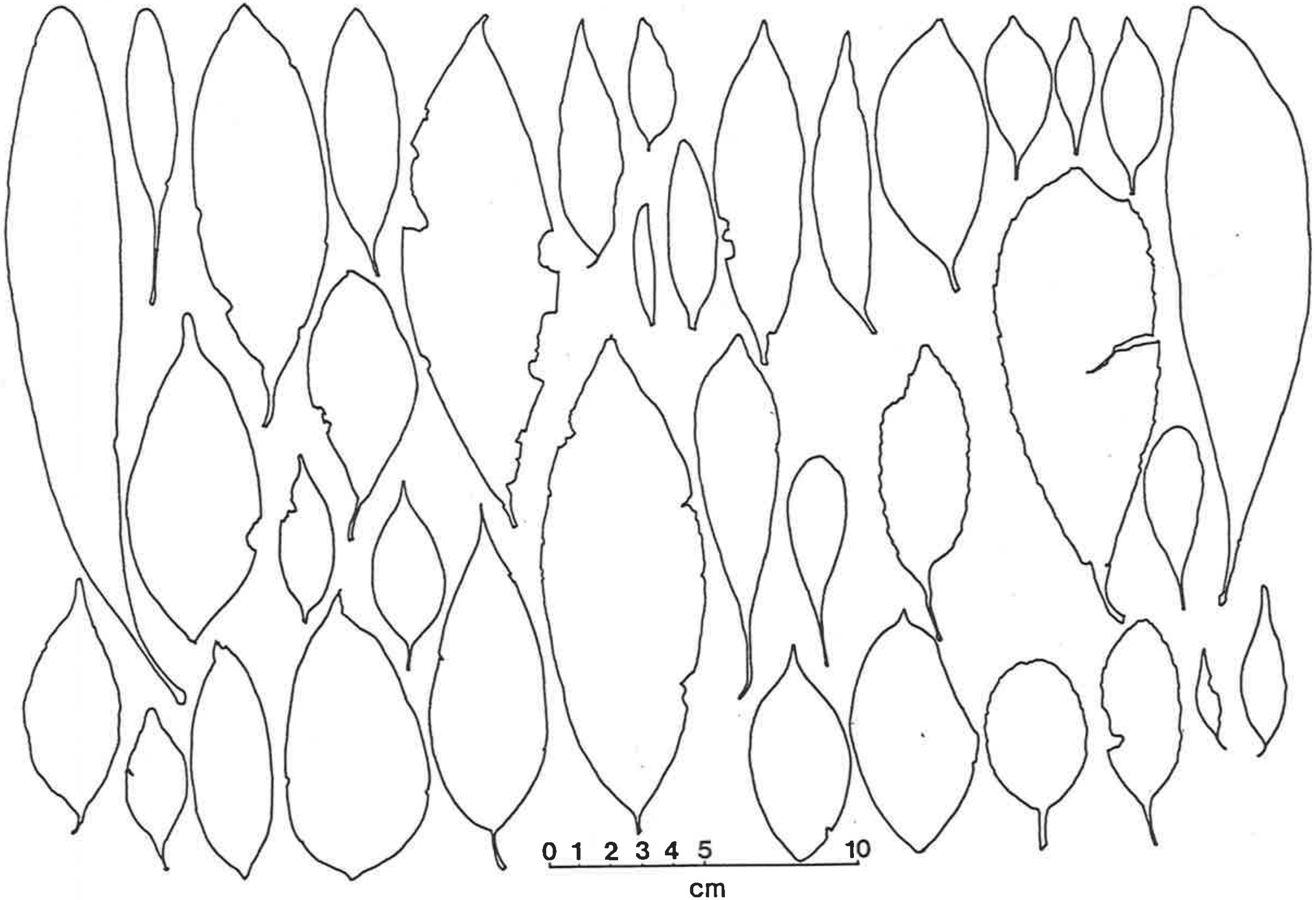


Fig. 4.35

Fig. 4.36 Silhouettes of a selection of leaves from a single sample of leaf litter from Mt Haig (SNVF, NE Qld).

Fig. 4.36



that all of the SNVF sites contained predominantly elliptic leaves, as the the 10th and 90th percentiles (33.9% – 41.1 & 51.9% – 60.9) are within these bounds.

The leaf area frequency distributions (Figs 4.37, 4.38, 4.39, 4.40) serve to emphasise the points made in the discussion on leaf length and width. The maximum leaf area for each site reflects the presence of rare very large leaves in the N.E. Queensland sites but not the N.S.W. site (Coombadjha Ck). The mean and median values fall into a small range (900 – 1400 mm^2 & 760 – 1140 mm^2), however in each case the N.S.W. site is at the lower end of the range. This is not surprising given the much narrower leaves of the Coombadjha Creek site. An important point here is that based on leaf length as a size measure (Figs 4.28 – 4.31), the Coombadjha Creek samples were comparable to the N.E. Queensland sites. However, using leaf area (Figs 4.37 – 4.40; and / or width), the size of the N.S.W. SNVF leaves are quite different. This point is discussed further in Chapter 6.

The proportion of leaves with non-entire margins for each sample for each site is given in Table 4.6. Variation between samples within the Mt Lewis EP18 and Mt Lewis Rd sites was low (4 – 17%; 4 – 11%). However the proportion of leaves with non-entire margins in samples from the Mt Haig site varied from 3 to 43%, and for Coombadjha Creek, from 63 – 93%. In the case of Mt Haig however, the much higher frequency of non-entire leaves in one sample was due to the higher frequency of leaves of a single species (*Elaeocarpus* sp, Elaeocarpaceae) in that sample.

The high variation in the N.S.W. site, Coombadjha Ck, reflected the dilution of the number of leaves with non-entire leaves by the entire leaves of a single species (*Syzygium crebinervis*, Myrtaceae; Fig. 4.41). In both these cases, it can be seen that the proportion of individual leaves with non-entire margins was substantially influenced in some samples by the proximity of source trees to the sample point. However, the general trend for each site can be determined from the site mean (Table 4.6). The N.E. Queensland sites are generally characterised by much lower proportions of non-entire leaves (7 – 16% of individuals), than the N.S.W. site at Coombadjha Creek (76%). This suggests that there is a real

Figs 4.37 – 4.39 Frequency distributions of leaf area (cm^2) for SNVF – Mt Haig (4.37), Mt Lewis (4.38), Mt Lewis EP18 (4.39), Washpool (4.40).

Fig. 4.37

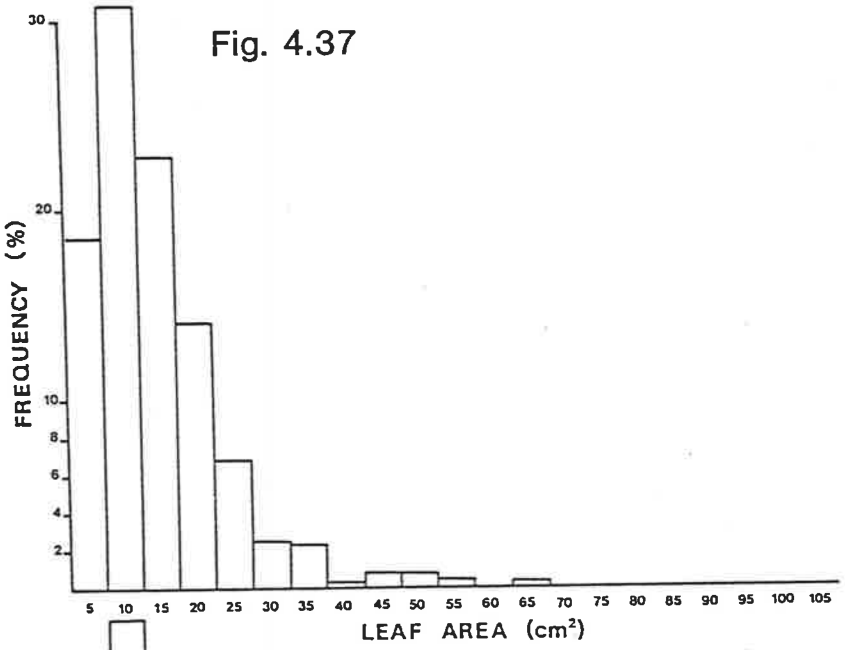


Fig. 4.38

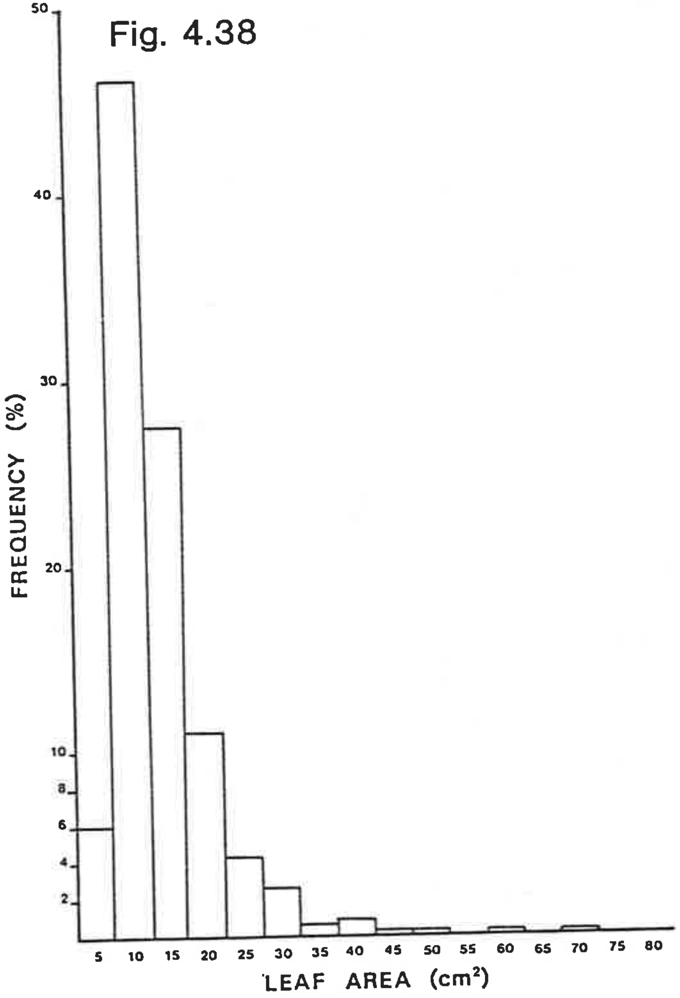


Fig. 4.40

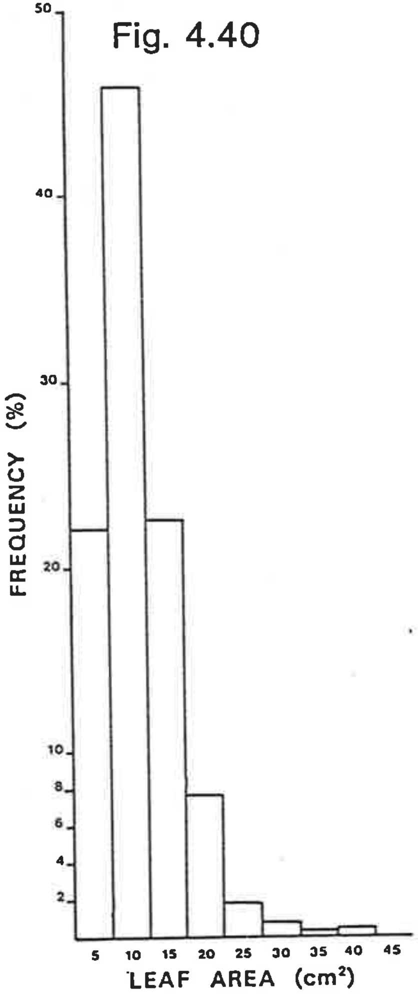
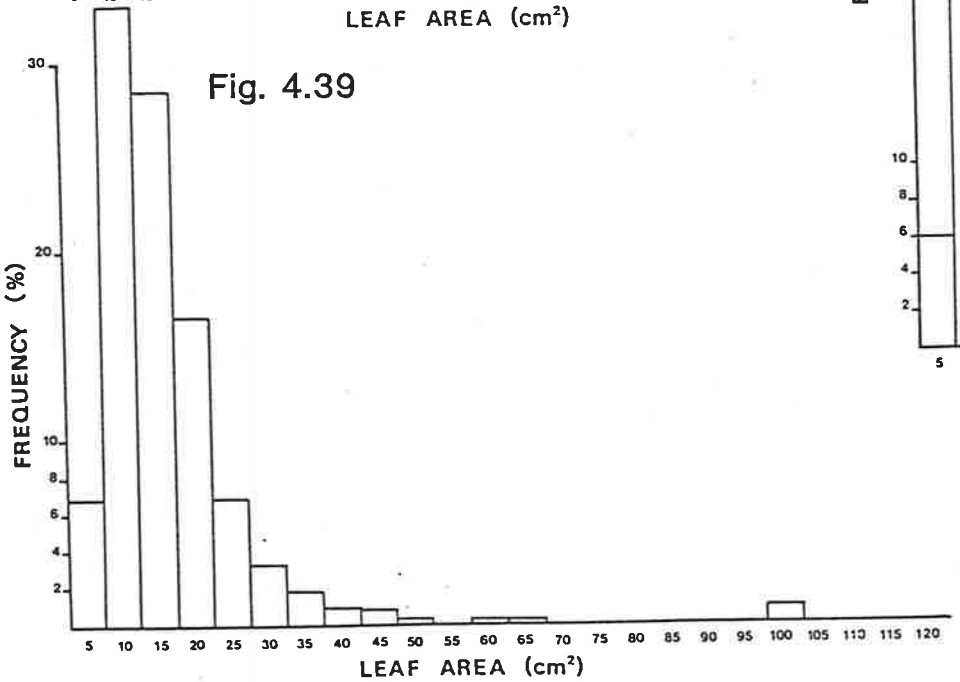


Fig. 4.39



difference in the relative proportion of non-entire leaves in leaf-beds derived from forests from the two sources.

4.4.4 Microphyll Fern Forest / Mossy Forest

The site considered in the analysis of the physiognomic signatures of litter from MFF was Barrington Tops (New South Wales). The Leaf Length Frequency Distributions are shown in Figure 4.42. Leaf length varied from a minimum of 15 mm to a maximum of 106 mm (Figs 4.42; Table 4.15), with a mean length for all of the samples of 48.6 mm. The mean length varied from 46.4 to 50.3 mm between the samples. Maximum leaf length was quite variable between samples (Table 4.15). The median length ranges from 45 mm to 49 mm length. Minimum leaf length varied from 15 mm to 19 mm. The value for the site of the 80th percentile is 61 mm, and the 20th percentile 35 mm length.

This data suggests that in contrast to the forest types with larger leaf sizes, the rarer leaf sizes (i.e. the leaves in the upper and lower 20%) are fairly consistent in their occurrence (Fig. 4.42), although the upper size limit is more variable than the lower size limit. The MFF site can be considered to have a characteristic leaf size spectrum. The mean, median (50th percentile), 80th, and 20th percentiles, approximate this spectrum and can be used to represent the character of this site, and perhaps New South Wales MFF in general.

The frequency distributions of leaf width for Barrington Tops are shown in Figure 4.43. Given the small length of the leaves from this site, the width values are quite high (Table 4.15), although the range is quite narrow (10 – 52 mm). Relative width values suggest that the leaves from the MFF site were typically fairly wide (mean = 48.7% of length; mean for CMVF = 37.2 – 40.8% of length).

The position of maximum width records the symmetry of the leaf along the short axis of the leaf i.e. it distinguishes between elliptic and both ovate and obovate leaves. Tropical rainforest trees are considered to typically have elliptic leaves (Richards, 1952). This example of cool temperate rainforest however, quite clearly is dominated by ovate leaves (position of maximal width below 34% of length) as the mean value is 37.6% (Table 4.15), and 90% of the leaves have the maximum width before the midpoint of the leaf (i.e. the value of the 90 th

Figs 4.42 – 4.44 Frequency distributions of leaf length (4.42), width (4.43), and area (4.44) for MFF – Barrington Tops.

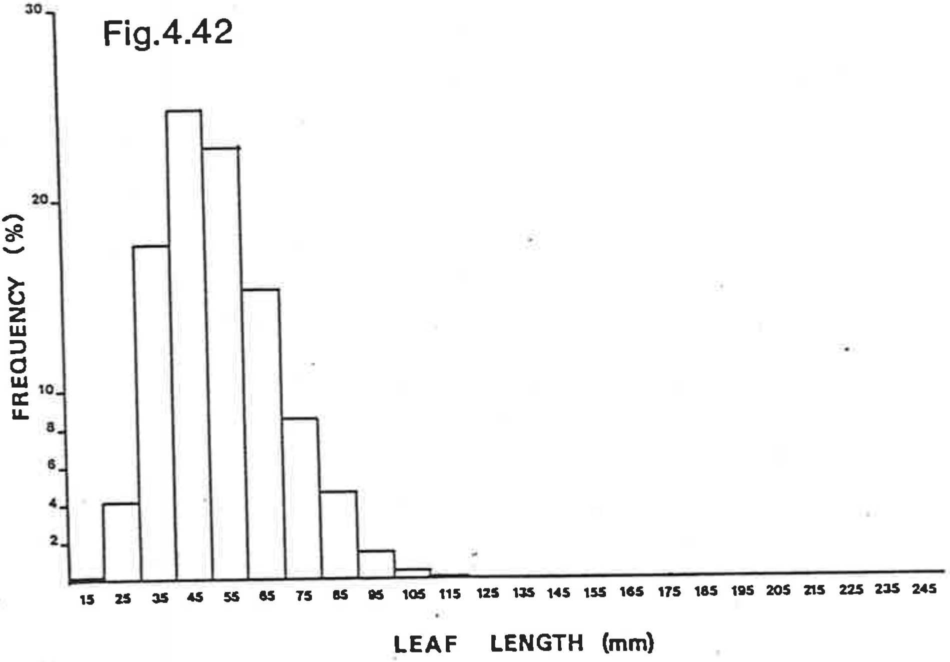


Fig.4.42

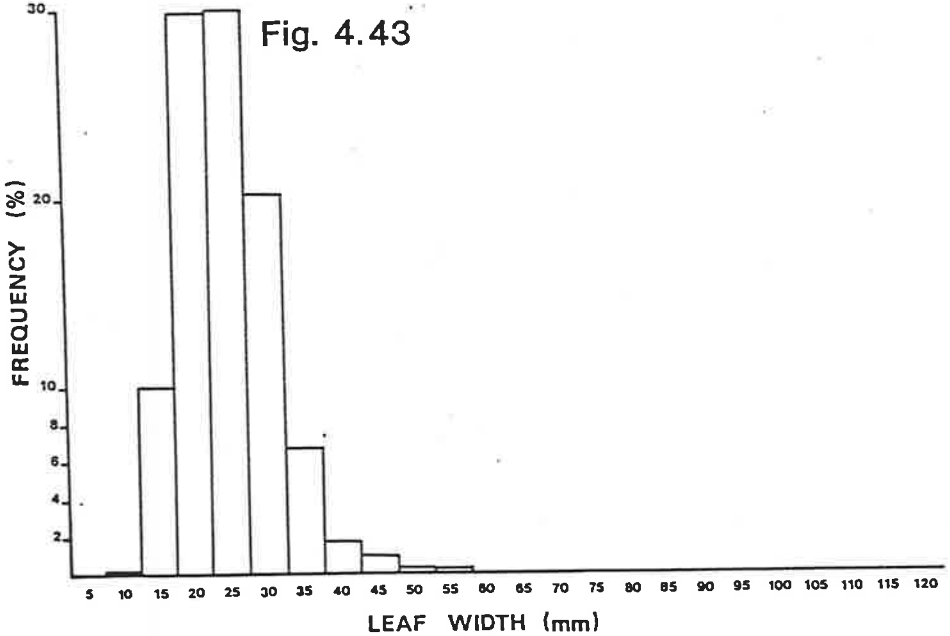


Fig. 4.43

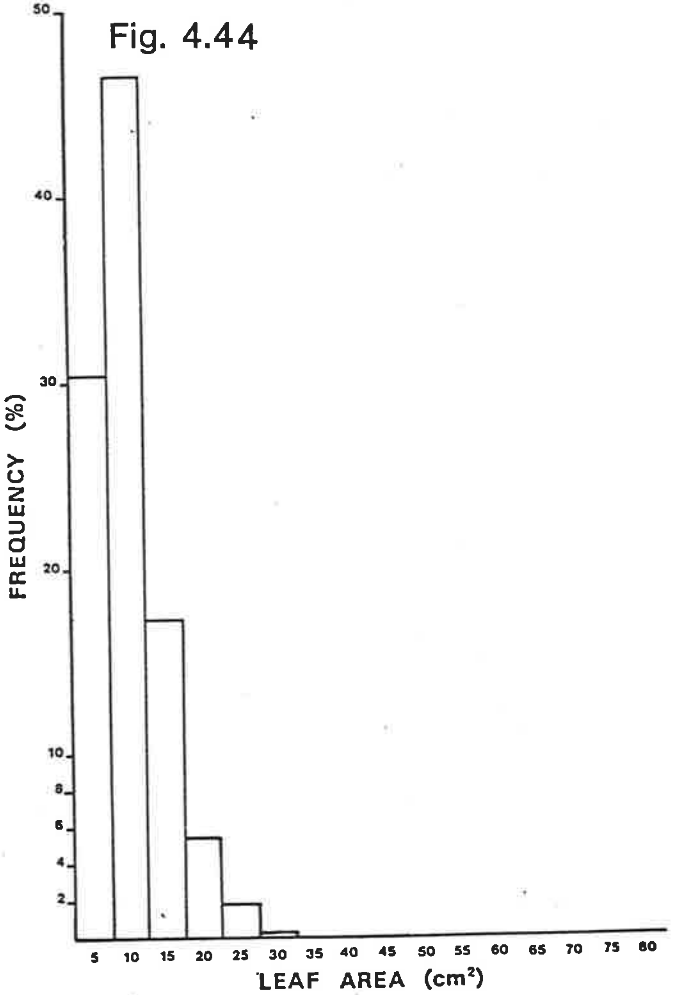


Fig. 4.44

Table 4.15 Leaf data for Barrington Tops (MFF).

	maximum		minimum		mean		percentiles				
							10	20	50	80	90
LEAF LENGTH	106	(86)	15	(19)	48.6	(50,46)	30	35	47	61	70
LEAF WIDTH	52	(37)	10	(13)	22.6	(22,24)	15	18	22	28	30
REL. WIDTH	93.3	(79)	25	(32)	48.7	(47,50)	36	39	46	59	67
POS. MAX.	60	(54)	21.7	(25)	37.6	(37,39)	29	31	38	44	46
LEAF AREA	36.6	(22)	1.4	(2)	7.8	(7,9)	3	4	7	11	14

percentile is 46.3% of length).

The frequency distribution of leaf area for Barrington Tops (Fig. 4.44) indicates a very narrow range of leaf sizes. Comparison with the frequency distribution of leaf area for the Washpool/Coombadjha Creek site (Fig. 4.40) demonstrates that the New South Wales MFF and SNVF sites have thw same leaf area physiognomic signature. The frequency distributions for leaf length for the two sites are, however, different (Figs 4.30 & 4.42).

Each of the samples from Barrington Tops recorded more than 85% of the leaves with non-entire margins (Table 4.6). Most of these are from a single species, *Nothofagus moorei*, which dominated the canopy (Fig. 4.45). These Figures are close to Webb's canopy data (100% of individuals). All of the entire margined leaves came from two species; a vine, *Smilax australis* (Smilacaceae), and a shrub, *Trochocarpa laurina* (Ericaceae; Fig. 4.45). Dolph (1984) found a similar situation in the forests of Indiana with a higher proportion of species with non-entire margins in the canopy than in the shrub layer. The influence of the two non-canopy species reinforces the point of the discrepancy between the physiognomic characteristics of leaf-beds and canopy samples.

The slight variation between samples reflects the patchy (and rare) occurrence of these species in the forest. The proportion of species with non-entire margins shows a more consistent pattern, however the low diversity of this forest type reduces the impact of the observed differences and similarities.

4.5 Discriminant Analysis.

The above discussion demonstrates that leaf litter from each of the forest types examined has a distinct physiognomic signature. However, it is necessary to demonstrate that each sample has a unique set of physiognomic characteristics which can be used to distinguish between samples of unknown origin, and predict the source forest of the unknown samples (i.e. fossil leaf samples). At a fairly crude level, it is possible to visually match the frequency distributions of leaf length, width, and position of maximal width, of the litter samples, to new samples and predict forest type (e.g. Christophel and Greenwood, 1987 1988).

Fig 4.45 Silhouettes of a selection of leaves from a single sample of litter from Barrington Tops (MFF, NSW). The leaves "A – E" represent the diversity of leaf-forms of Nothofagus moorei present. " F " is Smilax australis (Smilacaeae), a vine. "G" is the shrub, Trochocarpa laurina (Epacridaceae).

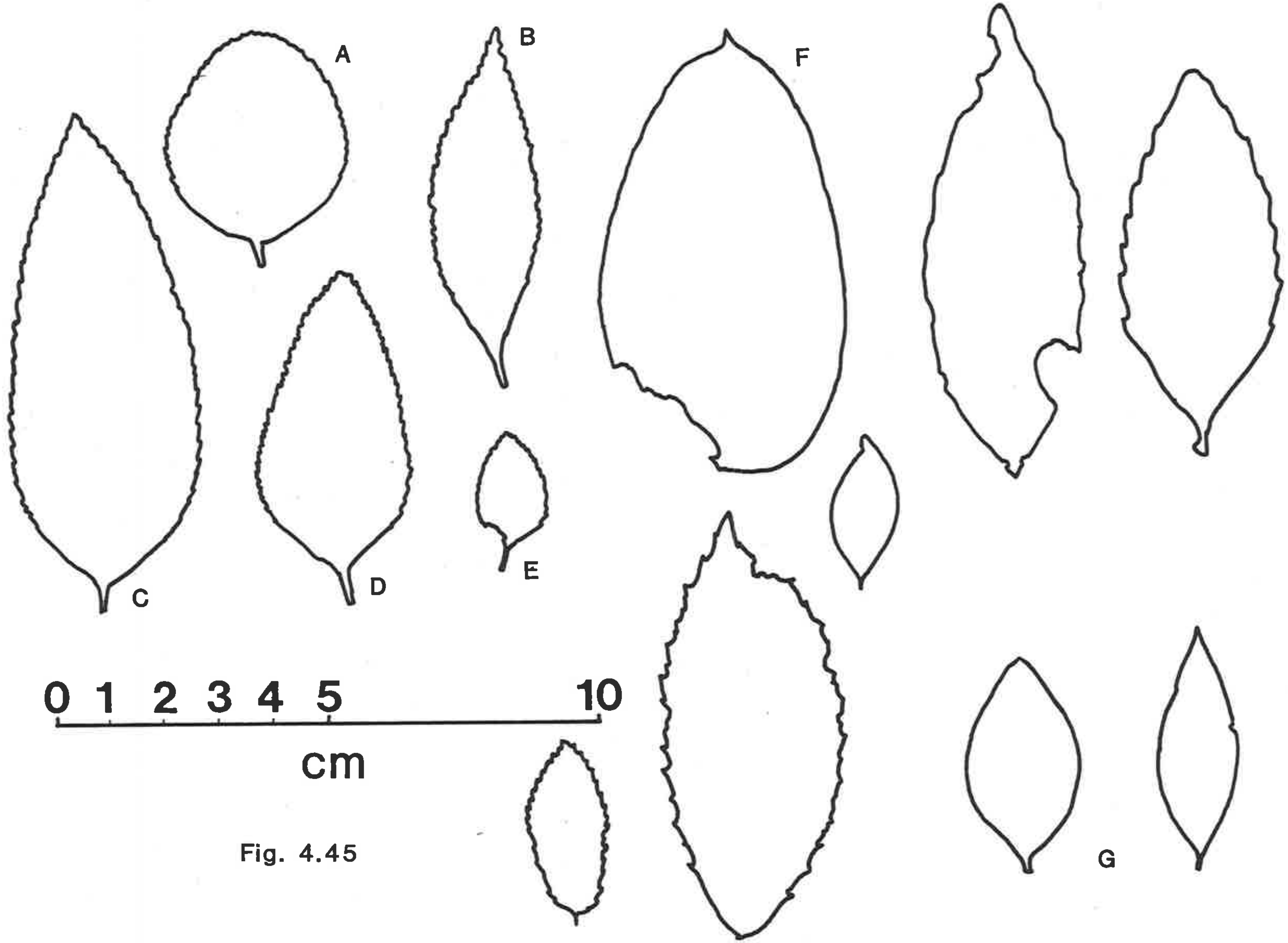


Fig. 4.45

An alternative approach is to consider all of the variables within a single statistical analysis — multivariate statistics. This procedure has the advantage of allowing a measure of the confidence of a successful match. Multivariate analyses were employed by Davis and Taylor (1980) to match foliar physiognomic classes for individual leaves based on "leaf dimension" (size) and the density of stomata on the leaves, to "microclimate regimes". Leaves collected from trees from sites in southern U.S.A. and the Panama Canal Zone were classified into a series of leaf physiognomy classes, and using a clustering routine, grouped within previously defined microclimate regimes. Discriminant analysis based on these groups was then used to produce discriminant scores to predict group membership (i.e. the microclimate regime) of new leaf samples.

Discriminant Analysis is a method of finding linear combinations of variables, known as discriminant functions, which maximise the differences (variance) between predefined groups , while minimising the variance within each group (Legendre and Legendre, 1983). The discriminant functions can be derived from any series of quantitative variables (descriptors) which describe the group, assuming that each group has a normal multivariate distribution. However, the method is quite robust to departures from normality (Legendre and Legendre, 1983).

Davis and Taylor used individual leaves in their analysis. The problem with this approach is that the microclimate regimes are based on the interaction of the individual leaves with the immediate microclimate, and not the macroclimate (Davis and Taylor, 1980). The possibility exists therefore, of co-occurrence of several microclimate regimes within a single forest site, and the presence in common of the same microclimate regimes in different forest types. An alternative approach is to consider the net characteristics of the whole leaf population.

The physiognomic character of the leaf litter samples can be defined using population descriptors — the percentiles, maximum and minimum, and mean values of the metric physiognomic characters. These population descriptors were used then as the discriminating variables in a discriminant analysis of the litter samples from the four forest types — MFF/MMF, SNVF, CNVF and CMVF. If linear discriminant functions are found which produce a clear separation of the groups (forest types), then they can be used to predict the group membership (forest type) of new leaf samples (i.e. fossil leaf bed samples). The population descriptors used are listed in Table 4.16.

The discriminant analysis calculations were made using the SPSSx (Statistics Package for the Social Sciences, SPSS Inc., 1985) program "Discriminant" on the VAX 11/785 at the University of Adelaide. This program provides the option of selecting the discriminating variables with the greatest discriminating power through the analysis (Wilks Lambda). The variables which do not contribute to the analysis can then be removed stepwise in successive analyses. The population descriptors used in the final analysis are indicated in Table 4.16 by an asterisk.

The discriminating variables based on leaf length, leaf width, and relative width, contributed most to the discriminating functions (Table 4.16). A scatterplot of the samples from each of the forest types (Fig. 4.46; Discriminant Function 1 vs Function 2) demonstrates the separation of the groups (forest types) provided by the Discriminant Functions. The classification summary of the analysis is given in Table 4.17.

It is apparent from this analysis that litter from each of the forest types examined can be separated on the basis of the population descriptors used. A re-examination of the frequency distributions of leaf length, width, and area emphasise the fact that each of the forest types have a unique "physiognomic signature" which allows them to be separated.

4.6 Discussion.

The frequency distributions of leaf length demonstrate a stepwise decrease in average leaf size from the warmest forest type (CMVF), to the coolest forest type (MFF; Fig. 4.47). It can be noted from Figure 4.47 that the maximum value for leaf length also varies stepwise, although the difference between CNVF and CMVF is minor. Width also varies stepwise between MMF and SNVF, and in turn with both CNVF and CMVF, but the latter two forest types reflect indistinguishable width signatures (Fig. 4.48).

Fig. 4.46 Scatterplot of Forest Types in Discriminant analysis (Discriminant Function 1 vs Function 2).

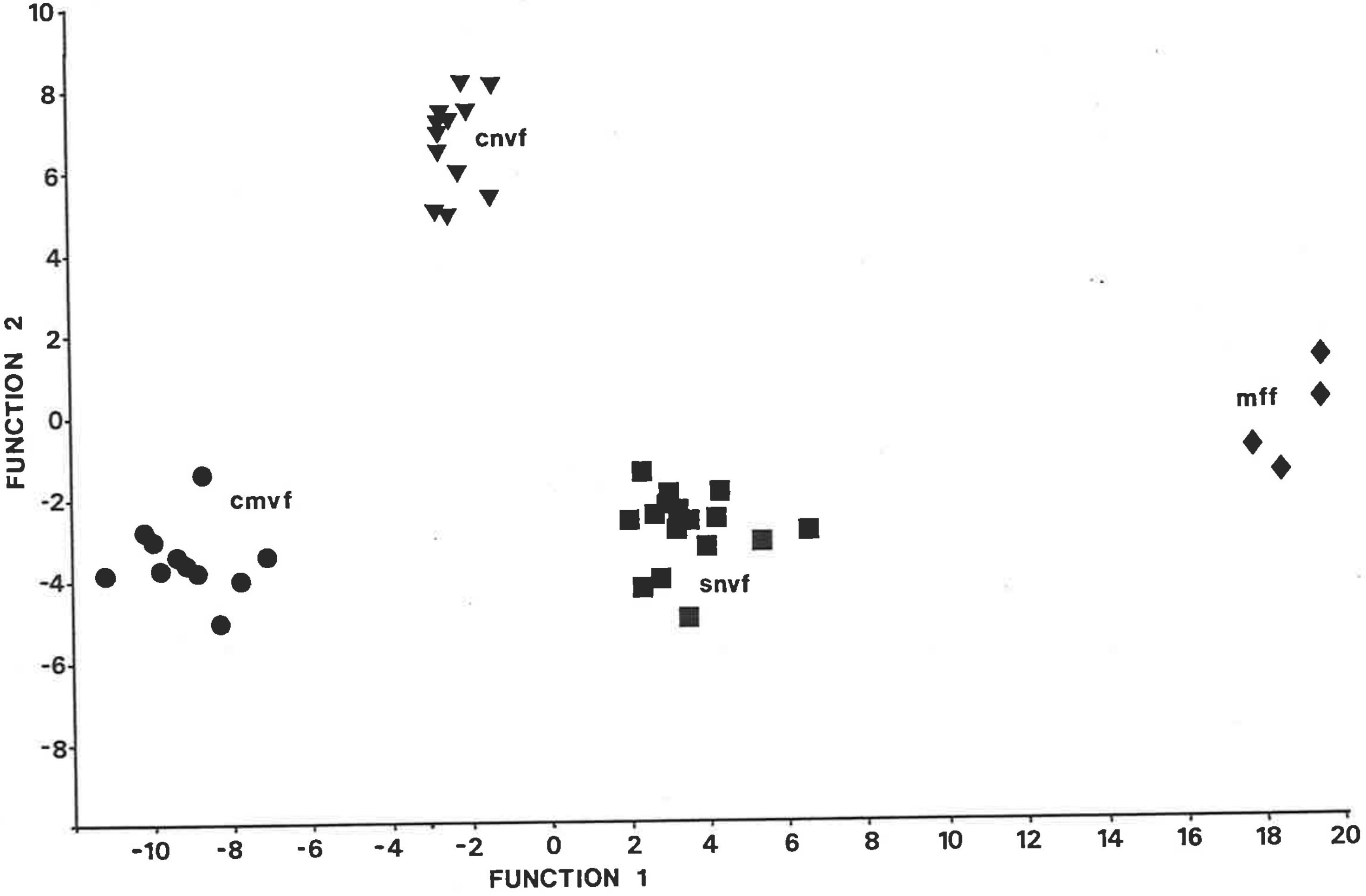


TABLE 4.16

VARIABLES USED IN THE DISCRIMINANT ANALYSIS

MEAN LEAF LENGTH	
10TH PERCENTILE	*
20	*
MEDIAN LEAF LENGTH	*
80	*
90	*
MEAN LEAF WIDTH	*
10	
20	*
MEDIAN LEAF WIDTH	*
80	*
90	
MEAN RELATIVE WIDTH	*
20	*
80	*
MEDIAN RW	
80	
90	*
MEAN POSITION OF MAX WIDTH	
10	*
20	*
MEDIAN POS MAX WIDTH	
80	*
90	*
MEAN AREA	*
10	
20	*
MEDIAN	
80	*
90	*
% LEAVES NON-ENTIRE	*

Figs 4.47 & 4.48. Composite cumulative frequency distributions of leaf length (4.47) and width (4.48) for a selected site from each of the four forest types. Light shading is MFF, crosshatching SNVF, dark shading CNVF, blank CMVF.

Fig. 4.47

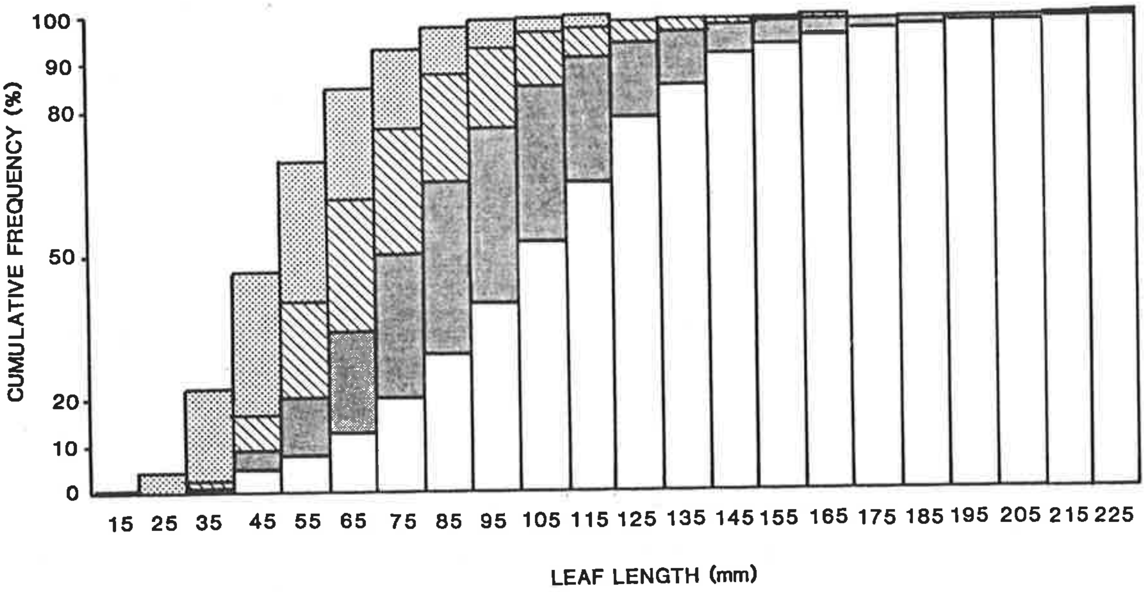


Fig. 4.48

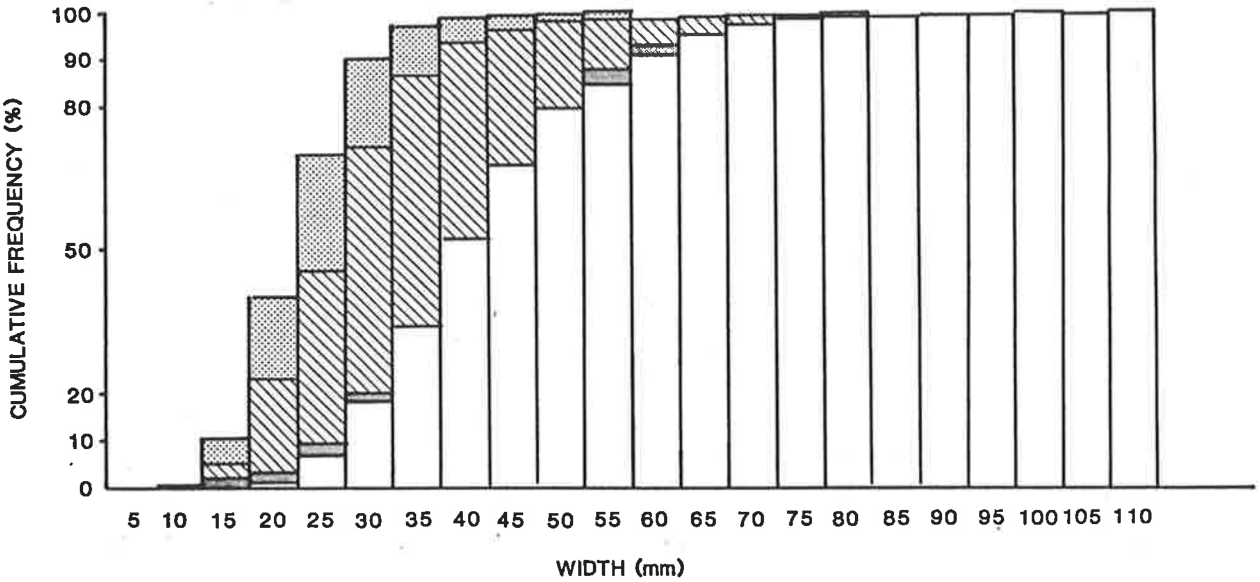


Table 4.17

DISCRIMINANT ANALYSIS OF LEAF LITTER SAMPLES:

Classification Results.

FOREST TYPE	NO. OF CASES	PREDICTED GROUP MEMBERSHIP SNVF	CMVF	CNVF	MFF
Simple Notophyll Vine Forest	15	15 100.0%	0 0.0%	0 0.0%	0 0.0%
Complex Mesophyll Vine Forest	11	0 0.0%	11 100.0%	0 0.0%	0 0.0%
Complex Notophyll Vine Forest	12	0 0.0%	0 0.0%	12 100.0%	0 0.0%
Microphyll Fern Forest	4	0 0.0%	0 0.0%	0 0.0%	4 100.0%
SNVF Streambed Litter	3	2 66.7%	0 0.0%	1 33.3%	0 0.0%

PERCENT OF "GROUPED" CASES CORRECTLY CLASSIFIED: 100.00%

Relative Width is a measure of shape (RW = Width / Length x 100) and in the CMVF samples, leaf width was found to vary only within a very narrow range (Table 4.4) suggesting that the relative width or 'wideness' of the CMVF leaves was fairly constant. The range exhibited by the other forest types suggests a greater variability in leaf shape (Tables 4.9, 4.13, & 4.15).

The position of maximum width measures the symmetry of the leaf along the short axis of the leaf. Hence, leaves with a Relative Position of Maximum Width (RMW = position of max. width / length x 100) below 35% are ovate or similar, those with a RMW between 35 – 65% are elliptic, and others are obovate or similar. The relative width data for the forest types data suggests a higher proportion of elliptic leaves in the SNVF and CMVF litter, and a higher proportion of ovate (or similar) leaves in the N.E. Queensland CNVF and the MFF litter.

Vine leaves are often much wider towards the base of the leaf, often with hastate or cordate bases. The CNVF samples have a higher proportion of vine leaves than the other forest types (determined by taxonomic identification; Chapter 7). However, a significant proportion of the non-vine leaves in the litter from this forest type were also much wider towards the base of the leaf (mostly ovate). There were very few leaves from vines in the MFF samples and the vast majority of 'ovate' leaves were from canopy trees, mainly *Nothofagus moorei* (see later).

From this analysis, it can be concluded that there are minor but consisitent differences in the proportions of non-ellliptic leaves in the litter of the MFF and CNVF from the litter of the CMVF and SNVF, and that these differences are not just due to the presence of vine leaves. Richards remarked upon the preponderance of elliptic leaves in 'Tropical Rainforest' (Richards, 1952). This difference between the 'cool temperate' MFF and the seasonal CNVF, maybe reflecting climatic differences. More importantly, this data indicates that the symmetry of leaves is a measurable component of the "physiognomic signature" of these forests. These points will be discussed further in Chapter 6.

According to Webb's canopy data (Webb, 1959; Table 2.4), the proportion of species with non-entire margins in Australian is quite variable, although a trend to higher percentages in both species and individuals with non-entire margined leaves is detectable from the warmest forest type (CMVF), to the cooler forest types (SNVF & MFF). The proportion of individual leaves with entire margins for each of the sites (by sample) for litter from the four forest types is summarised in Table 4.6.

The individual SNVF samples were quite variable within and between sites, ranging from 5 – 43% of individuals in litter from Mt Haig, and from 4 – 93% of individual leaves overall (Table 4.6). However, CMVF consistently had low numbers of non-entire margined individual leaves or species. The CNVF samples were also variable, ranging from 37 – 77%. Clearly there is no simple correlation between forest type and the proportion of entire margins represented either as individual leaves or as species in the litter. This matter is discussed further in Chapter 6.

In summary, the leaf litter from each of the four forest types — CMVF, CNVF, SNVF, and MFF — can be seen to possess distinctive foliar physiognomic signatures. The inherent variation within each forest type of the metric physiognomic characters, and the characteristic state (i.e. the mean value) of these characters, can be used to identify the source forest type of a litter sample.

Leaf length in particular, has been demonstrated to be the primary character discriminating between samples from different forest types. Leaf area, however, has been demonstrated to produce a degree of blurring at the extremes of the forest continuum, due to changes in the relative width of leaves in the seasonal forest sites.

The discriminant analysis demonstrated that it is possible to separate samples of each of the forest types using population statistics generated from the metric foliar physiognomic characters. This data suggests quite strongly that fossil leaf beds of the same taphonomic character as leaf litter can be reliably identified to their source forest type. A necessary further investigation, however, is the extent to which further taphonomic processing in actual depositional situations, such as stream beds, influence the character of these physiognomic signatures.

Chapter 5

THE TAPHONOMY OF STREAMBED ASSEMBLAGES

5.1 Sources of Taphonomic Bias in Streambed Deposits.

An understanding of the influences on the input and transportation of dead plant parts to places of deposition (Taphonomy) is important in any analysis of fossil beds to interpret the ecology of the community from which the plant parts were derived. Fossil deposits rarely preserve plant communities, rather, they preserve populations of plant organs.

Fossil leaf-beds form through the transportation of leaves from some source to a point of deposition where they may be trapped and subsequently buried by sediment. This process can be broken down into a series of discrete but related events:

1. leaf input (leaves dropped by tree)
2. leaf transport (wind and water)
3. leaf entrapment (lake etc.)
4. leaf burial

Each step in the process can be expected to alter the composition and character of the leaves carried over to the next step through progressive removal of larger, fragile leaves by mechanical and biological action (Ferguson, 1985).

Leaf-beds can be formed through the action of a variety of different physical processes which vary in duration, timing, energy (=mechanical destructive power), and setting. Thus, the importance of each step (above) in determining the character of a leaf assemblage will vary according to the nature of the processes involved (Spicer, 1980 1981; Ferguson, 1985).

For example, a leaf-bed may form in a matter of days due to storm action and resultant flooding, whereas a lake or a swamp may gradually accumulate leaves and other plant parts over thousands of years. The latter will preserve a time averaged sample of the input of leaves (Knoll, 1986) and will be structured laterally due to current action (Spicer, 1980). The storm deposit, however, will probably be unsorted and contain much larger pieces (including logs) in addition to the leaves and will reflect an instant in time of the vegetation through which the flood waters travelled (Spicer, 1980). Hence the nature of the physical processes which bring about these events will affect the attributes of the resulting leaf-bed.

Taphonomic Bias was considered by some researchers to invalidate the use of Foliar Physiognomic Analysis (eg. Hill and Gibson, 1986; Martin, 1986). Other studies however, suggested that these same processes would distort the composition and character of leaf assemblages in a measurable and predictable manner (Wolfe, 1971 1980; Spicer, 1981), and that by studying modern examples of the deposition of leaf fossils, this bias could be understood and accounted for in the analysis of Tertiary leaf beds (Roth and Dilcher, 1978; Dolph, 1984).

Most of the studies of neo-fossil leaf beds, however, have considered the taphonomic influences on species representation in a leaf assemblage and few have considered the effects on the physiognomic characteristics of the assemblage. The general conclusion of most of these studies was that leaf input into potential fossil deposits generally reflected the local vegetation only, with a pronounced bias towards the representation of the vegetation of the waters edge (McQueen, 1969; Rau, 1976; Drake and Burrows, 1980; Dudgeon, 1982; Holyoak, 1984; Hill and Gibson, 1986).

Roth and Dilcher compared the foliar physiognomy of recent leaf deposits in a small lake to the foliar physiognomy of the surrounding forest (Roth and

Dilcher, 1978). Their results indicate very strongly that the "leaf size profile" was significantly different to that determined for the surrounding forest, being biased strongly towards small, thick, sun leaves. They further found a correlation between the leaf size encountered in a sample and the distance from shore, with increasingly smaller leaves represented at greater distance.

Leaf input into water bodies is generally through direct transfer from the tree (Rau, 1976; Dudgeon, 1982; Ferguson, 1985). However, local accumulations of leaf litter may also be transported into streams during periods of high rainfall (Dudgeon, 1982). The screen of vegetation at the waters edge is usually considered to act as a filter, however, removing most of these laterally transported leaves (Spicer, 1981; Dudgeon, 1982; Ferguson, 1985). Thus, while leaf input into streams is generally going to represent essentially the riparian vegetation (Macginitie, 1969; McQueen, 1969; Drake and Burrows, 1980; Spicer, 1981; Dudgeon, 1982; Ferguson, 1985), it can be expected that some lateral transport of leaves downslope (Dudgeon, 1982) may also contribute leaves from the local area adjacent to the riparian vegetation.

There are two separate but related questions explored in this chapter. The first concerns the taphonomic bias introduced by transport processes. The leaves deposited in most fossil localities have been transported by water some distance from the source trees, and it has been suggested that larger leaves will be selectively removed by their greater susceptibility to mechanical damage and their higher loss rate due to sinking (Kaushik and Hynes, 1971; Spicer, 1981). This produces a leaf-bed dominated by much smaller leaves than the original forest (Roth and Dilcher, 1978; Spicer, 1981).

Leaf-litter from a streambed in north-east Queensland was collected to test this hypothesis by comparing the physiognomic signatures of stream transported (allochthonous) and non-transported (autochthonous) leaf litter. A series of ponds at one point along the streambed represented the direct input of leaves from the trees into the 'deposit' and was essentially forest floor litter, whereas downstream, leaves had accumulated in a trap between large boulders representing a leaf bed where the leaves had been transported to their point of deposition by the stream.

In earlier discussion it was pointed out that the streamside environment often promotes a distinctive flora which will have a higher proportion of species with non-entire margined leaves, and a higher proportion of larger leaf sizes (MacGinitie, 1969; Wolfe, 1980a). The streamside flora of some tropical forests is dominated by species with stenophylls — leaves much narrower than long (Richards, 1952; van Steen is, 1981; Whitmore, 1984). These observations suggest that where a distinctive streamside flora is present, stream-bed leaf litter will have a different physiognomic signature than litter from the forest floor.

Of the Australian rainforests examined in this study, Simple Notophyll Vine Forest has the highest sensitivity to the proportion of species (or individuals) with leaves with non-entire margins (Table 2.4). In addition, individuals in narrow gorges of the dominant canopy species, *Ceratopetalum apetalum*, of SNVF in New South Wales are known to produce stenophylls (van Steen is, 1981; Hoogland, 1960). Parallel collections of litter on the forest floor and in an adjacent large pool in a creek in SNVF in New South Wales were used to test this hypothesis for leaf size, leaf shape (presence of stenophylls), and the proportion of leaves (species and individuals) with non-entire margins.

5.2 The Effects of Stream Transport on Physiognomic Signatures.

5.2.1 Site Description: Mt Windsor NEQ

The Mt Windsor stream-bed litter site was sampled at two points along a stream flowing through SNVF on the Mt Windsor Tableland (Figs 5.1 & 5.2). Small ponds on a recently deposited bank of sand contained abundant leaves beneath a light layer of silt (Fig. 5.3). The canopy of the surrounding forest arched over the stream at this point but the canopy was not completely closed (Fig. 5.3); the leaves in these ponds were essentially direct leaf fall from the adjacent trees.

Several hundred metres downstream beyond a short patch of rapids was a moderate sized pool at the outflow of the rapid bounded by very large boulders (Fig. 5.4). The forest did not over arch this pool or the preceeding 200m of the

Fig. 5.1

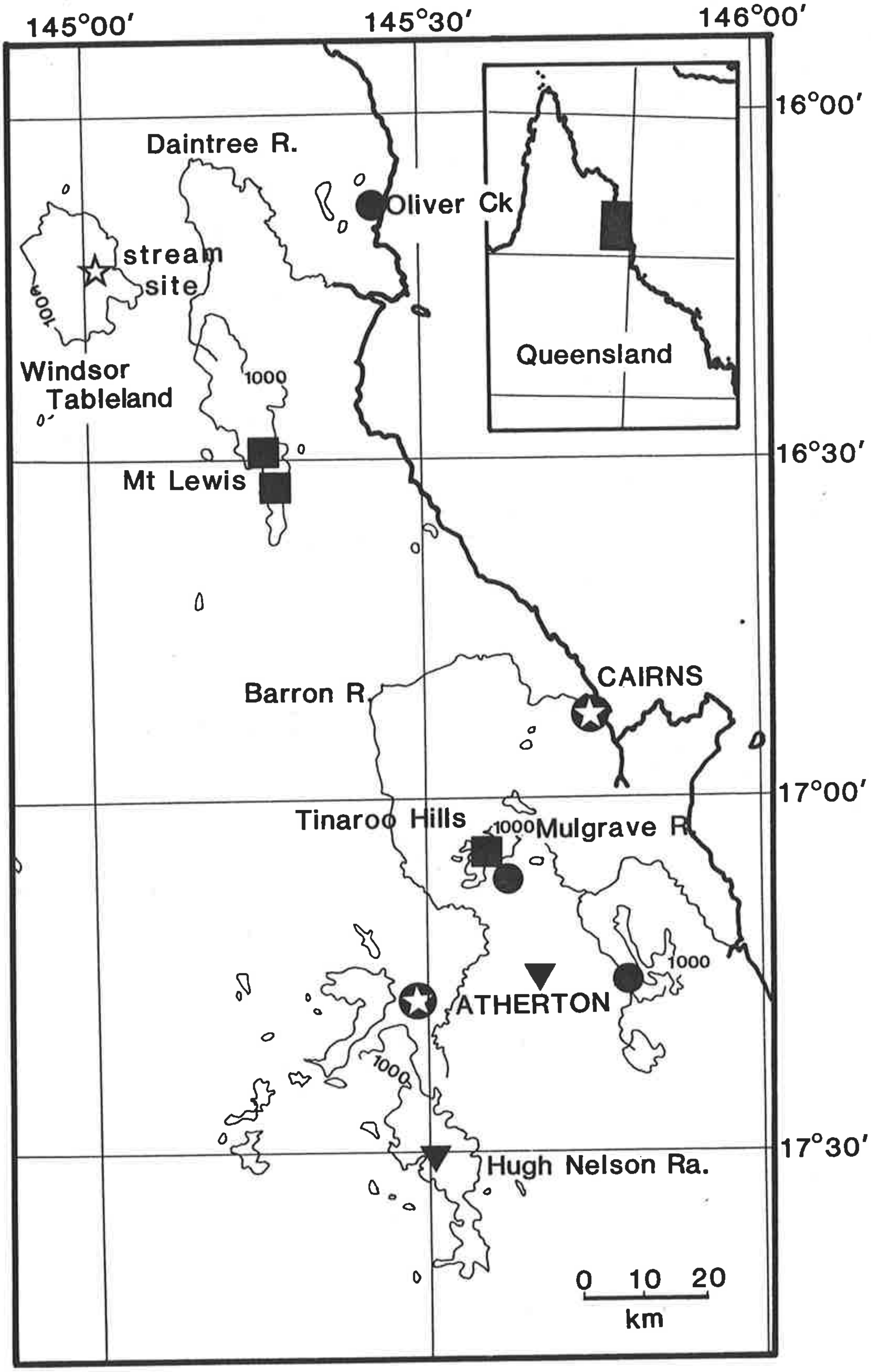
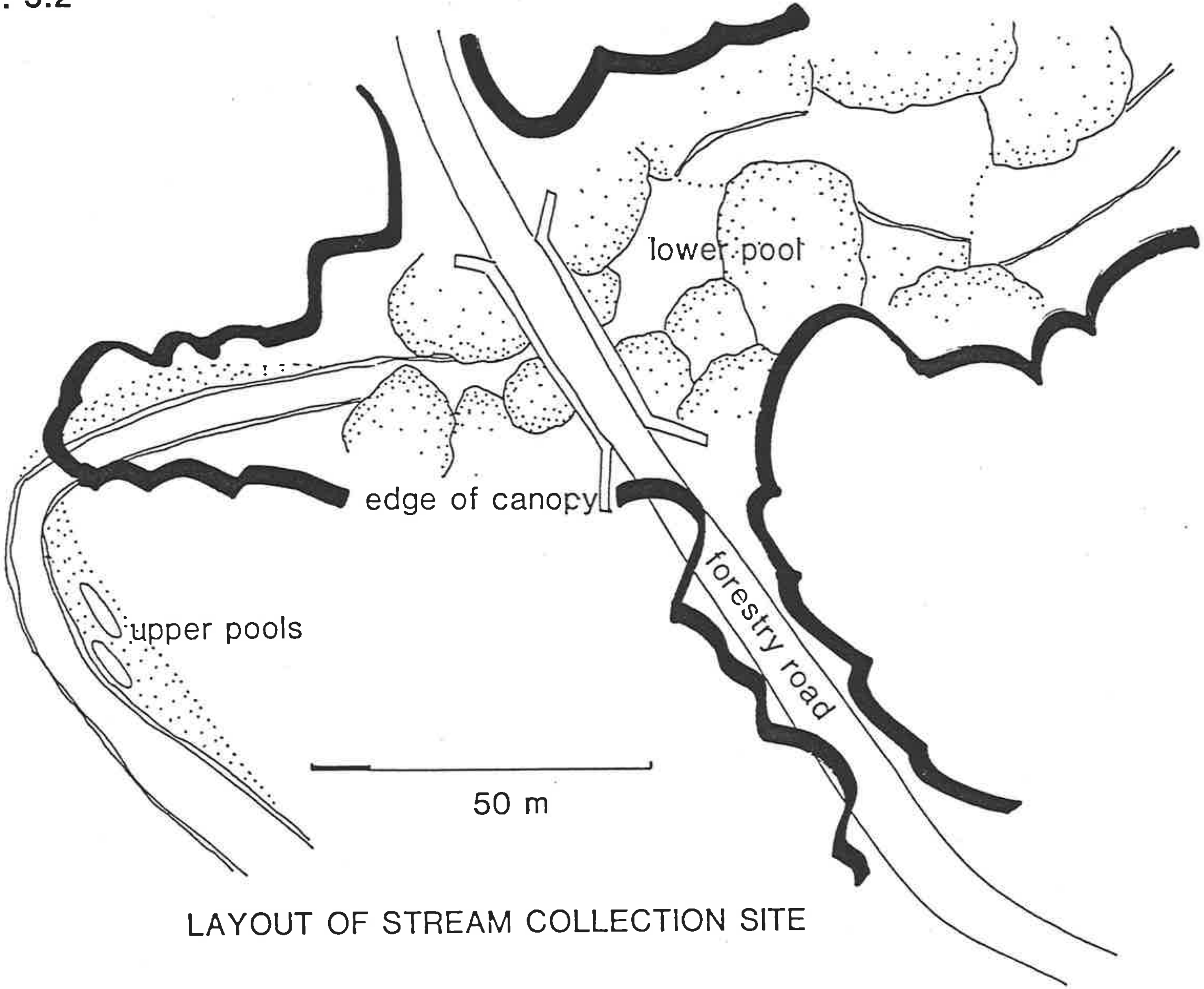

145°00′
145°30′
146°00′
16°00′
16°30′
17°00′
17°30′
Daintree R.
Oliver Ck
stream site
1000
Windsor Tableland
1000
Mt Lewis
Queensland
Barron R
CAIRNS
Tinaroo Hills
1000
Mulgrave R
1000
ATHERTON
1000
Hugh Nelson Ra.
0 10 20
km

Fig. 5.2



LAYOUT OF STREAM COLLECTION SITE

Fig. 5.3 Pools in a stream (Windsor Tableland) over-arched by forest.

Fig. 5.4 Litter accumulation in stream pool, Windsor Tableland.

stream (Figs 5.2 & 5.4), however a large fig (*Ficus* sp. Moraceae) extended a branch to the edge of the pool. Leaf input to this pool is assumed to be essentially via the stream from sources upstream, including the trees which dropped leaves into the other ponds.

The second sample point therefore might be expected to have smaller leaves due to selective destruction of larger leaves during transport (Spicer, 1980 1981; Ferguson, 1985), whereas the litter from the first sample point should have the same physiognomic signature as leaf litter from the forest floor of the streamside vegetation (Spicer, 1981).

5.2.2 Analysis.

The frequency distributions of leaf length for the upstream (i.e. autochthonous litter) and downstream (i.e. allochthonous) samples are shown in Figures 5.5 and 5.6. The frequency distributions for the two sample points is clearly different, as demonstrated by the mean leaf length values; 80.9 mm for the autochthonous litter and 68.3 mm for the allochthonous litter.

The mean value of leaf length for the upstream sample is greater than that recorded for any of the north-east Queensland SNVF sites, but is only marginally greater than the upper limit recorded for an individual sample from SNVF. The mean leaf length value for the downstream sample is however well within the range recorded for the SNVF sites (Table 4.11).

In Figure 5.7, the frequency distributions of leaf length (cumulative frequency) for the two sample points are contrasted. This Figure clearly demonstrates that the leaves from the lower pool (allochthonous leaves) are on average smaller than the leaves from the upper pools (autochthonous).

The cumulative frequency distributions of leaf width for the two sample points are shown in Figure 5.8. Again, the autochthonous litter sample contains much larger (i.e. wider) leaves than the allochthonous litter sample. The frequency distribution of leaf width for forest floor litter from Mt Lewis EP18 has been included to further analyse the differences between the two stream samples.

The frequency distribution of leaf area (cumulative) for the two stream samples emphasises the reduction of leaf size in the allochthonous sample (Fig. 5.9).

Fig. 5.5 Frequency distribution of leaf length for upstream litter sample (autochthonous).

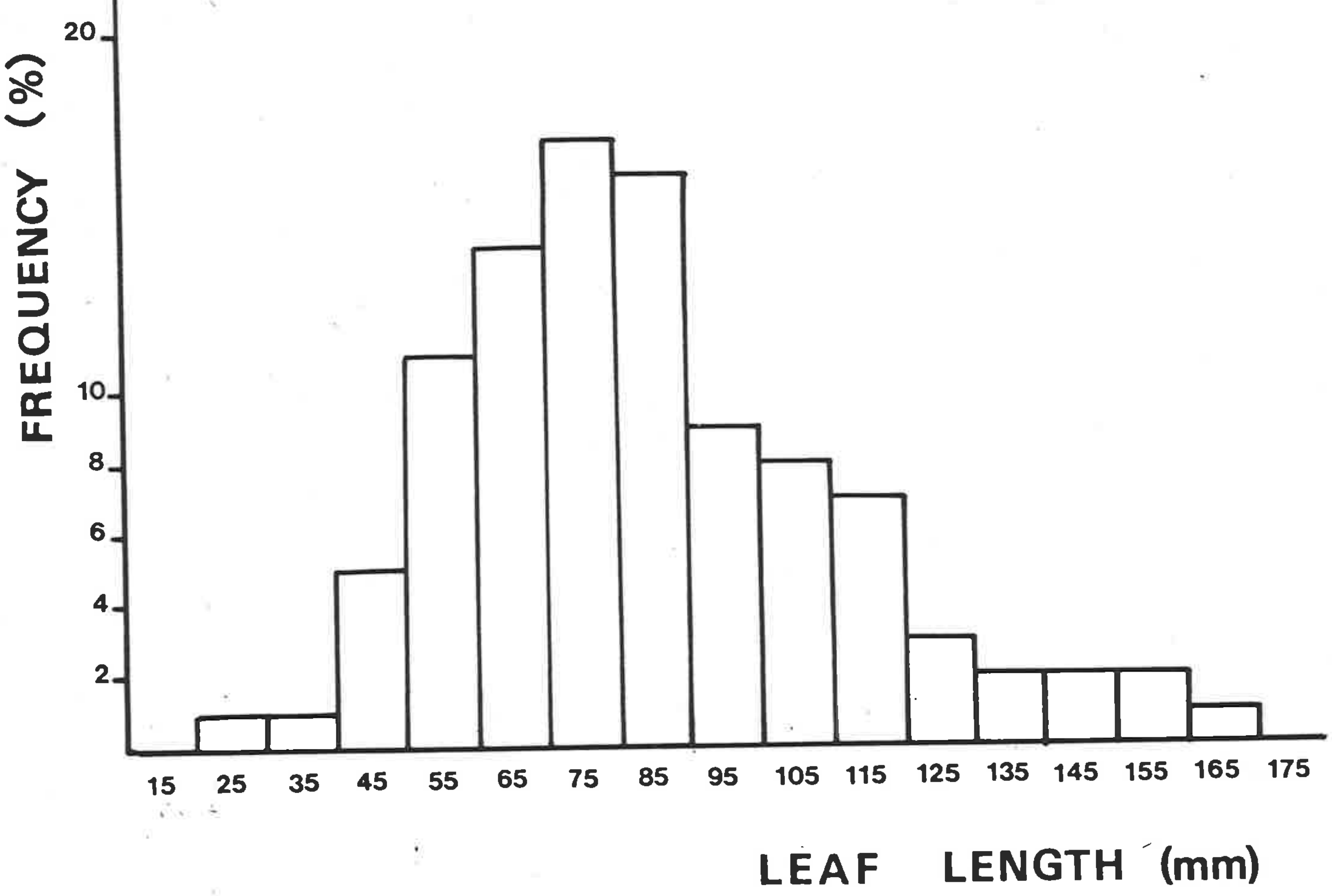


Fig. 5.6 Frequency distribution of leaf length for downstream litter sample (allochthonous).

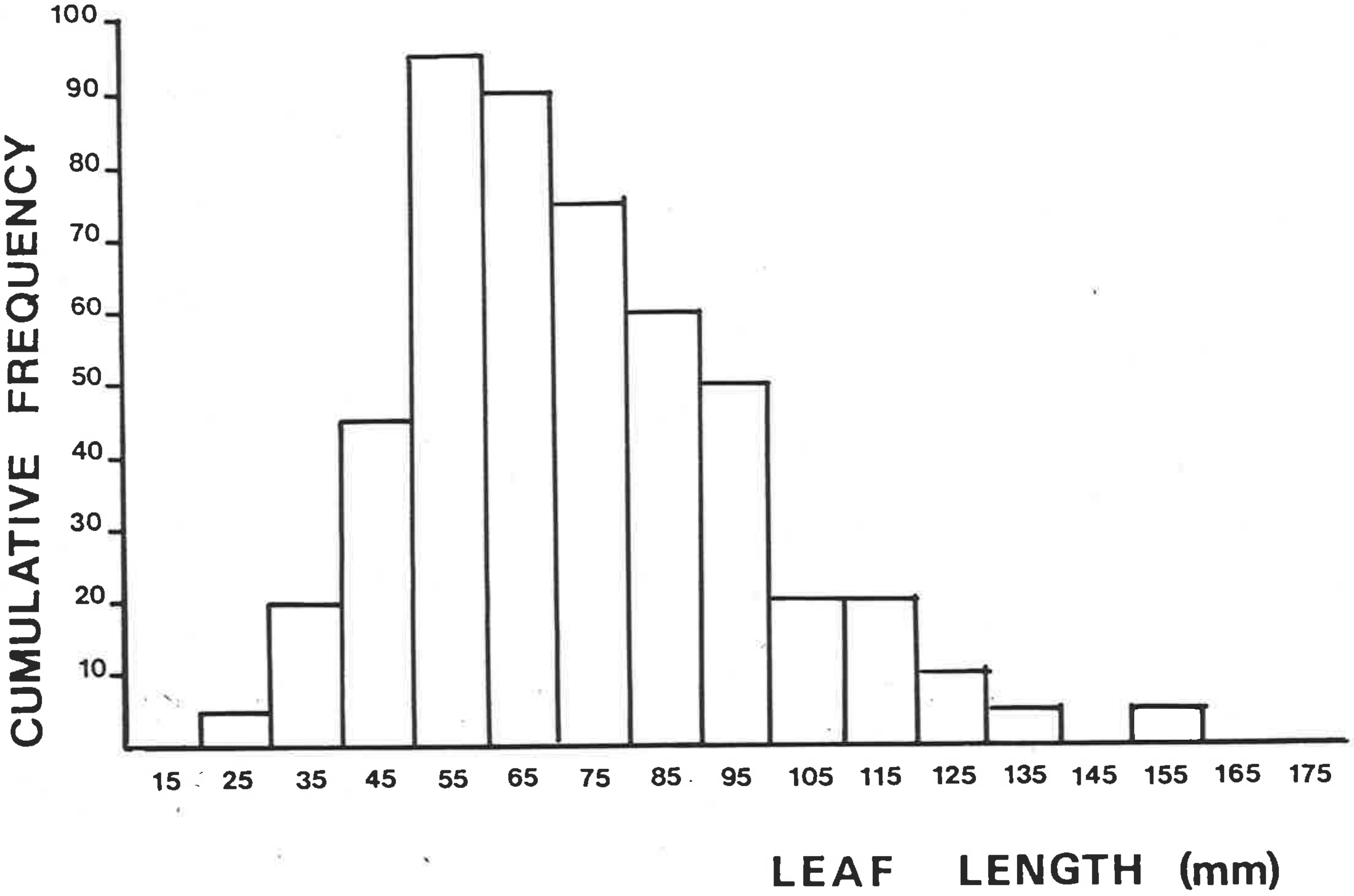


Fig. 5.7 Cumulative Frequency distributions of leaf length for upstream (autochthonous) and downstream (allochthonous) litter samples.

	mean
Autochthonous	80.9mm
Allochthonous	68.3

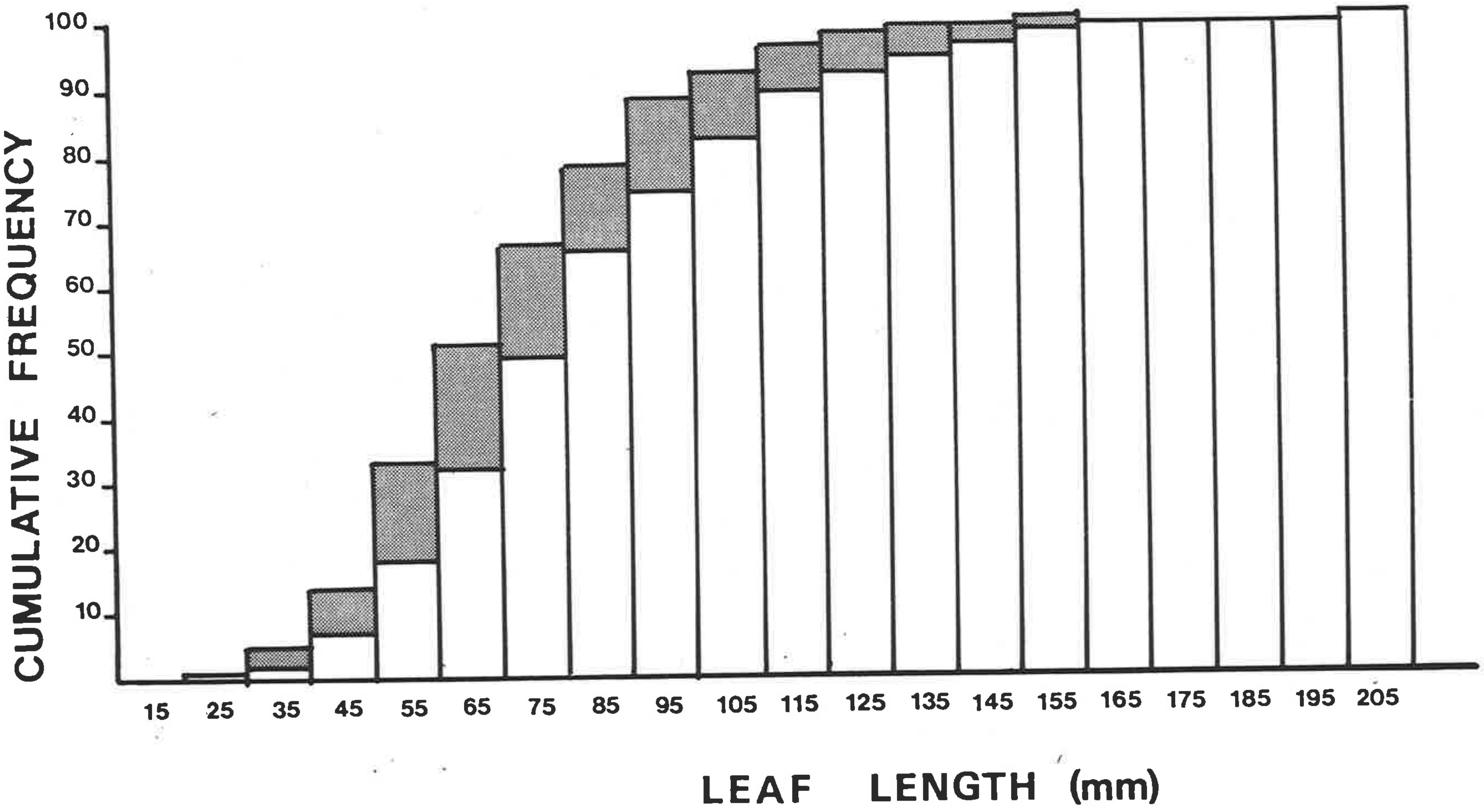


Fig. 5.8 Cumulative Frequency distributions of leaf width upstream (autochthonous) and downstream (allochthonous) litter samples compared with forest floor (SNVF Mt. Lewis EP18).

	mean	minimum	maximum
Autochthonous	33.5mm	10.0mm	72.0mm
Allochthonous	29.3	7.0	76.0
Forest floor (EP18 Mt. Lewis)	26.1	11.0	61.0

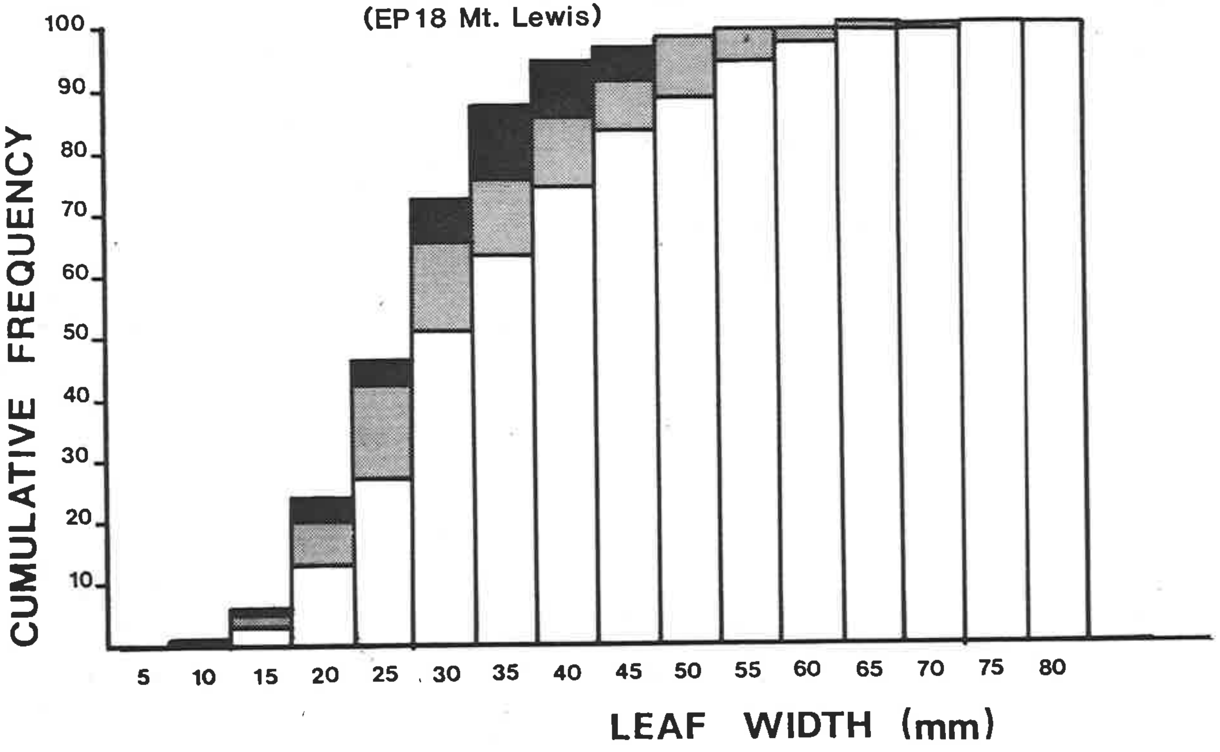
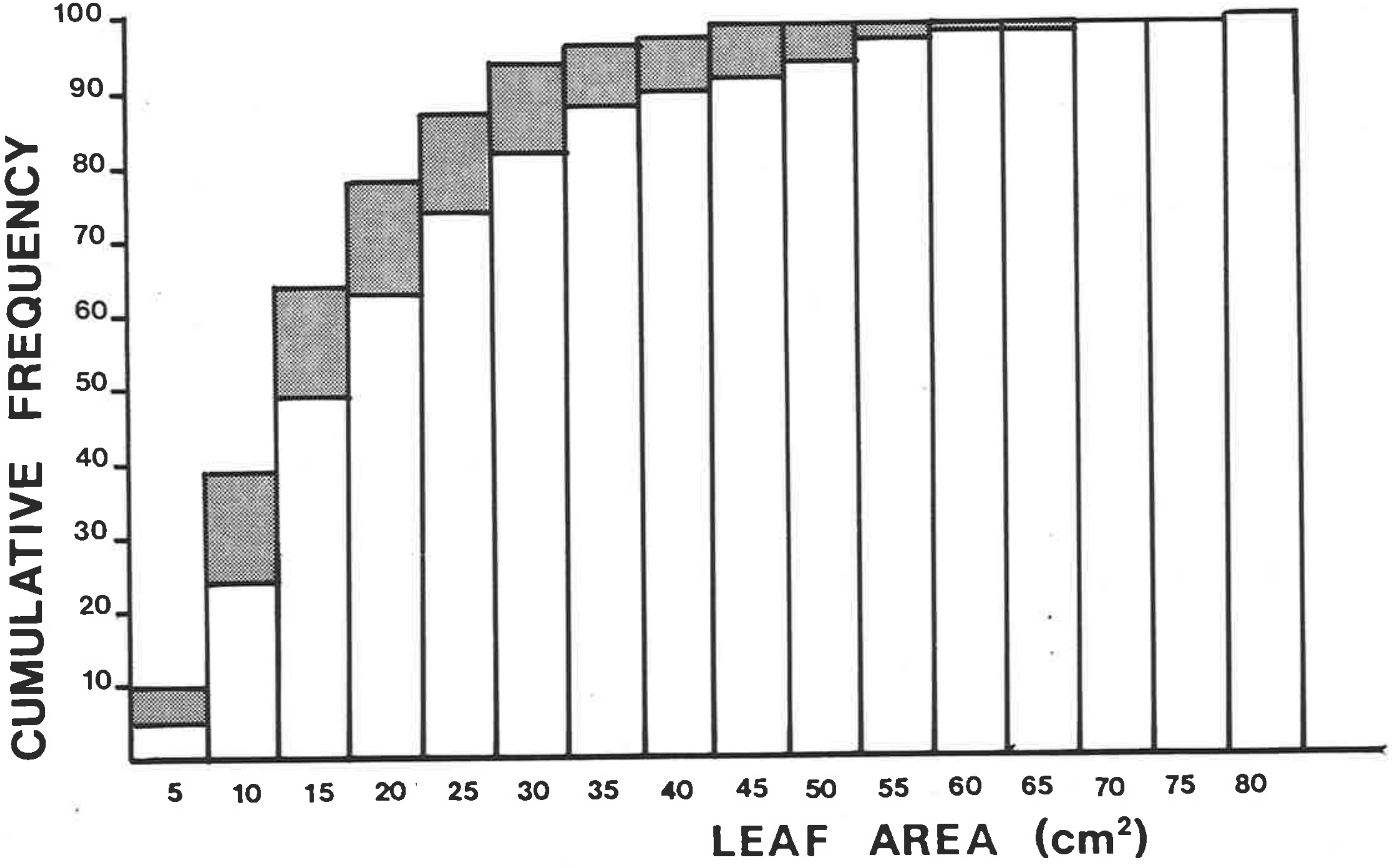


Fig. 5.9 Cumulative Frequency distributions of leaf area upstream (autochthonous) and downstream (allochthonous) litter samples.

	mean	minimum	maximum
Autochthonous	20.1mm	1.7	77.3
Allochthonous	14.6	1.2	76.0



In the leaf length distributions the maximum size for the two samples was clearly different, with the autochthonous sample including leaves up to 204 mm, whereas leaves in the allochthonous sample reached only 160 mm. The variation in maximal lengths recorded in the forest floor samples recorded similar differences (Chapter 4). This implies that the difference between the autochthonous and allochthonous samples is not significant. The maximum sizes recorded by leaf area are similar for the same samples; 77.3 cm^2 and 76.0 cm^2 respectively.

This suggests that primarily long leaves, i.e. leaves generally much longer than broad (higher L/W ratio), are breaking during transport from the upstream point to the downstream point. Leaves of equivalent area, but greater width, are better able to survive transport. The Mt Lewis EP18 site represents the upper limit of leaf size (as measured by leaf length; mean = 71.8 mm) for all of the SNVF sites considered in Chapter 4. Yet clearly, both stream samples have on average wider leaves, despite a lower value for mean leaf length for the autochthonous sample (i.e. 68.3 mm). An alternative explanation therefore, is that the streamside vegetation has on average wider leaves than the main forest.

A comparison of silhouettes from a selection of leaves from the upstream (Fig. 5.10) and downstream (Fig. 5.11) samples demonstrates the main differences in size. Each silhouette represents the largest leaf of each type encountered in the samples. No obvious differences are apparent with leaf shape, however. The overall diversity in the downstream sample is much higher than the upstream sample (upstream, 22 spp; downstream, 31 spp: see Chapter 7), with only 15 species shared in common between samples.

Litter from the surrounding forest at this site was not sampled so a comparison of the proportion of non-entire leaf margins is not as meaningful. However, the values for the two sample points are very similar and fall within the range observed for the other SNVF litter sites from N.E. Queensland (Table 4.6). This suggests that if there is a streamside bias in the proportion of species with leaves with non-entire margins, it is being masked by the input of a large proportion of leaves from the main forest. A more parsimonious explanation is that there is no streamside bias with respect to margin type in this example.

Fig. 5.10 Silhouettes of leaves from upstream litter sample.

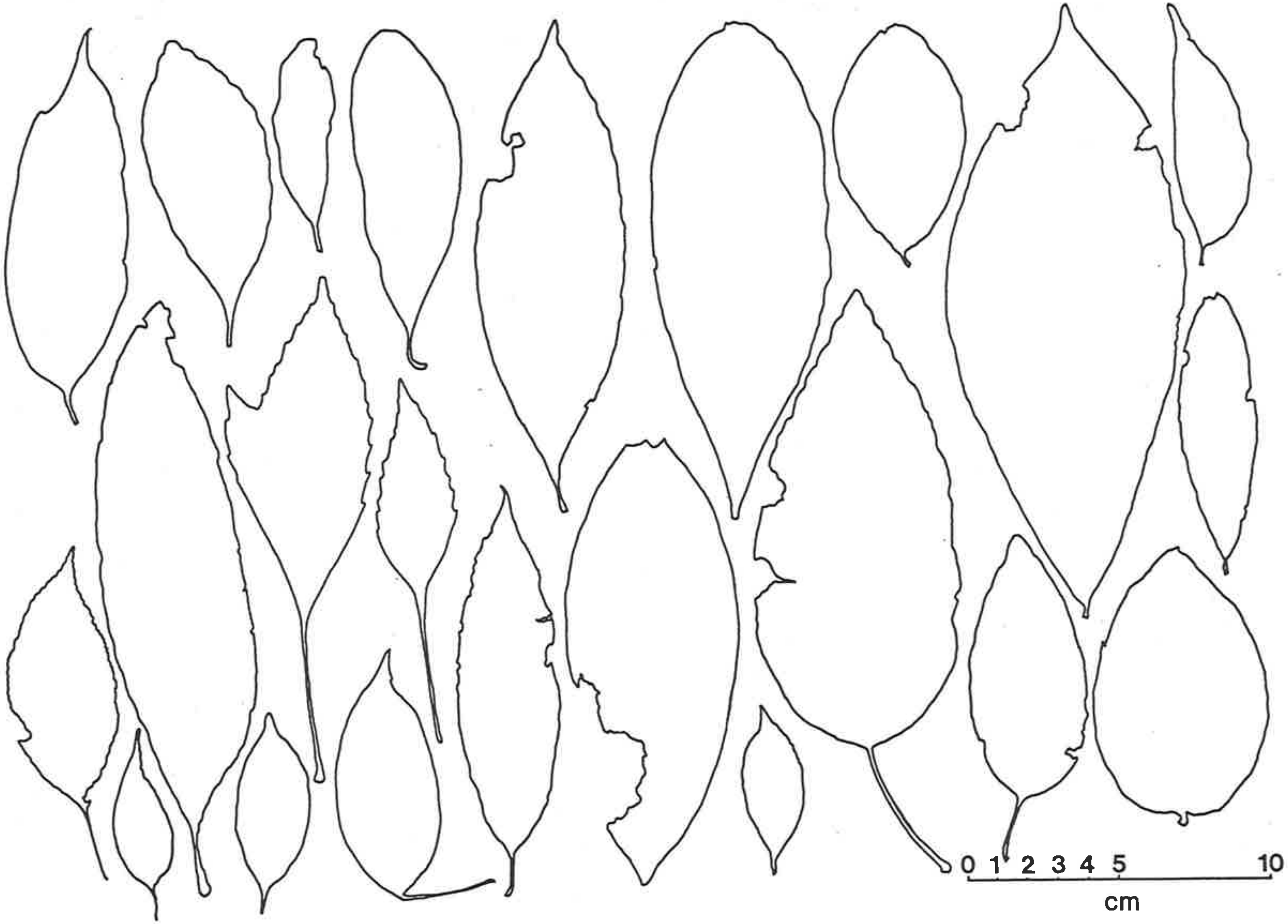
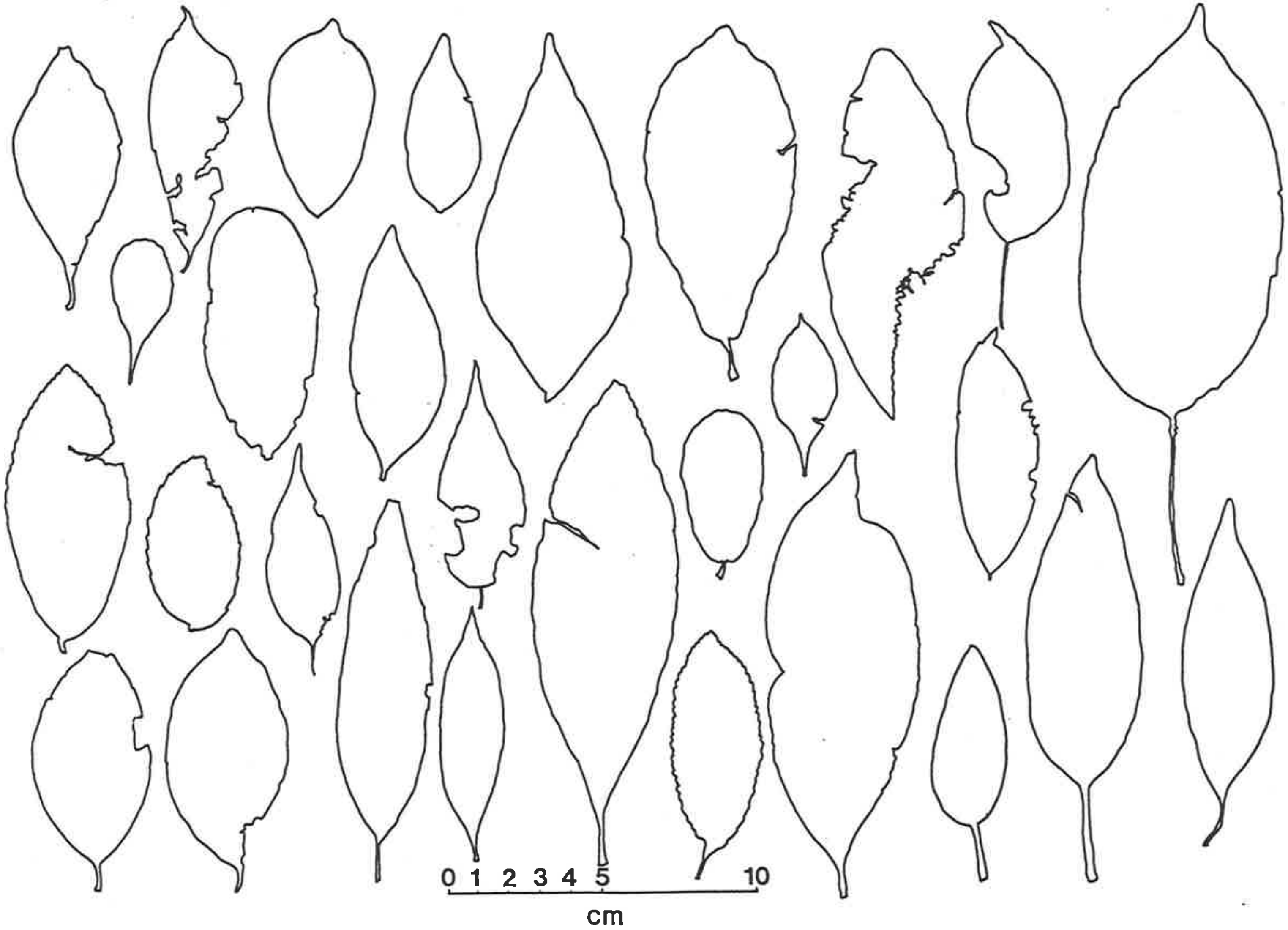


Fig. 5.11 Silhouettes of leaves from downstream litter sample.



The main conclusion that can be drawn from this evidence however, is that stream transport prior to deposition causes a significant shift in the average size of leaves in a leaf bed from the average size in forest floor litter. The leaf size distribution of a fossil leaf bed is therefore expected to be similar or slightly smaller than the leaf size distribution for leaf litter from the forest floor of the same forest type.

5.3 Streamside Bias.

5.3.1 Site Description: Washpool / Coombadjha Creek - NSW

A detailed description of the Coombadjha Creek site is given in Chapter 3, however some repetition is useful here. The Coombadjha Creek area was dominated by the canopy tree *Ceratopetalum apetalum*, with *Doryphora sassafras* as a co-dominant. A large pool on Coombadjha Creek was sampled for leaf litter (Fig. 5.12). The canopy of the forest on either side of the stream did not meet over the creek and a substantial gap existed over the pool.

The forest near the stream and the pool included some large specimens of *Callicoma serratifolia* and also *Banksia integrifolia* (Proteaceae), a species not normally associated with rainforest. The streamside vegetation consisted of an illdefined corridor of bushes and shrubs, mainly *Quintinia sieberi*, *Acradenia euodiifolia* (Rutaceae) and *Callicoma serratifolia* Andr. (Cunoniaceae). Much of the stream and pool bank was covered by a fern, *Sticherus flabellatus* (R.Br.) St.John (Gleicheniaceae).

5.3.2 Analysis.

Several bags of litter were collected from the surface of the mud at the bottom of the pool in Coombadjha Creek (Figs 5.12 & 5.13). The pool bottom was covered by leaf litter in a layer several centimetres thick. Simple hand grabs of litter were placed in plastic bags until an equivalent quantity to the forest floor collections was collected (Chapter 4) and the excess water drained off. The frequency distributions of leaf length and width for the stream sample are shown in Figures 5.14 and 5.15. The physiognomic signature of the surrounding forest is

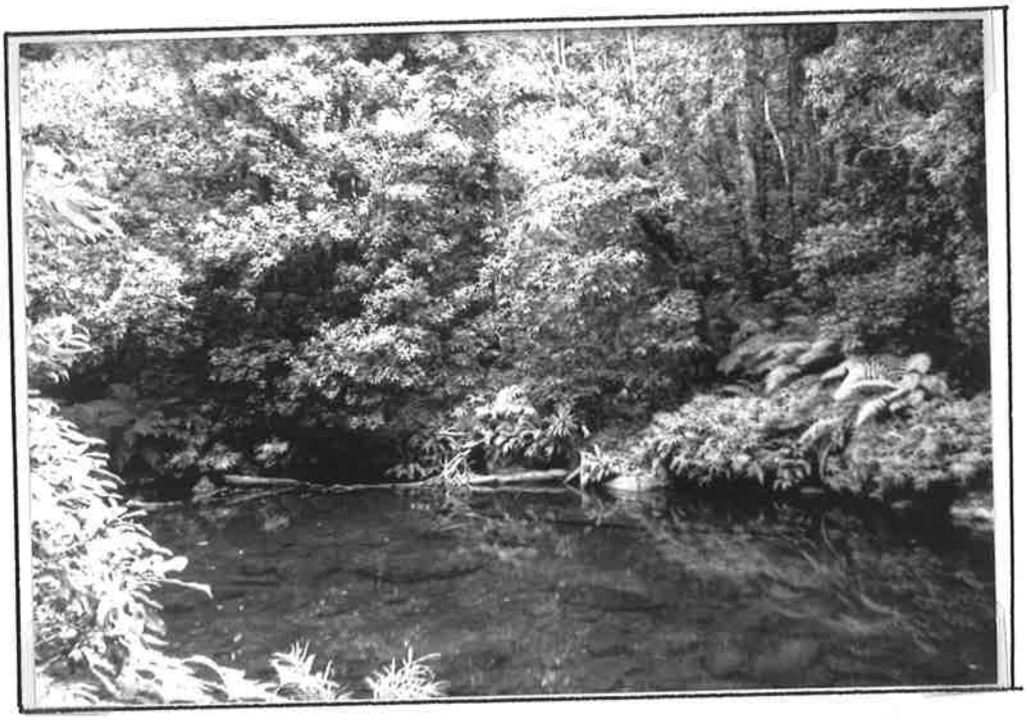


Fig. 5.12 Pool on Coombadjha Creek. Leaf collection was from a mat of leaves to the centre of the pool.

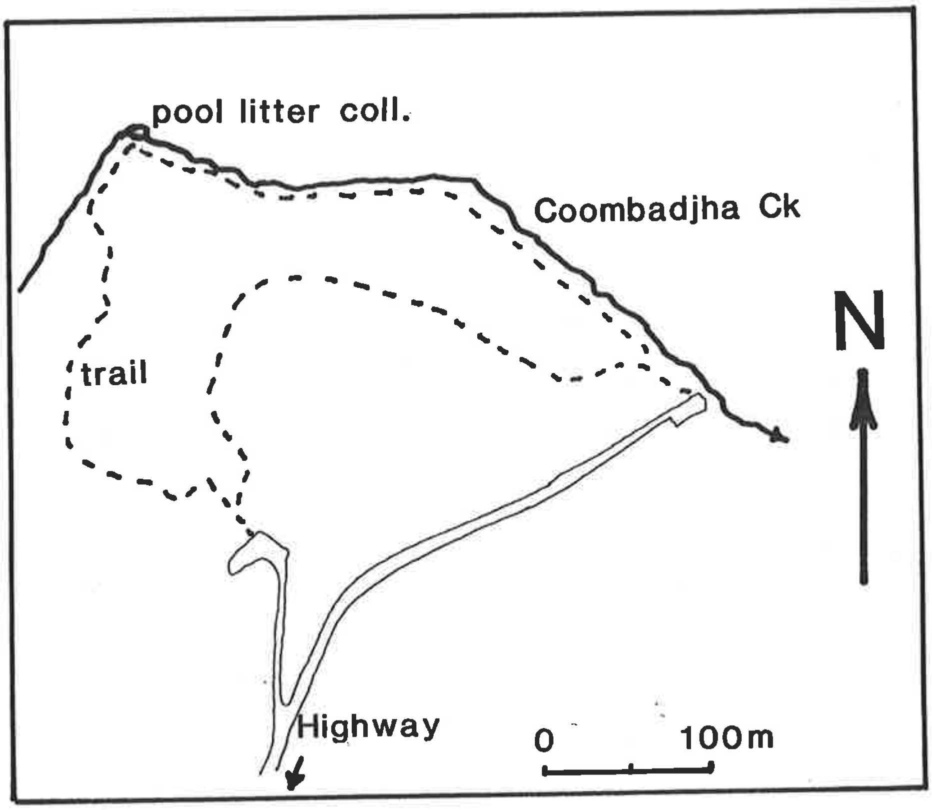


Fig. 5.13 Plan of Coombadjha Creek area (Washpool, N.S.W.).

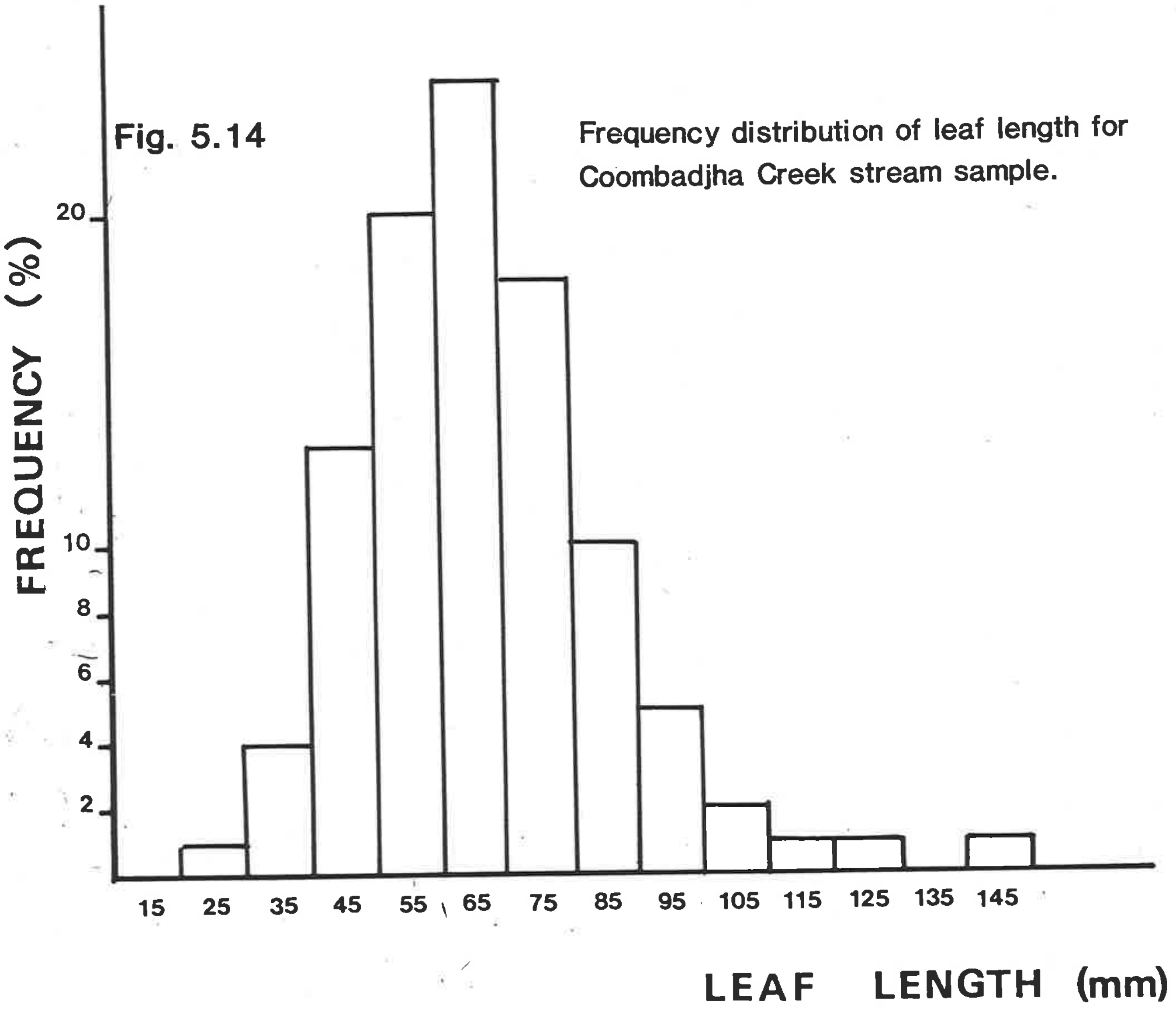
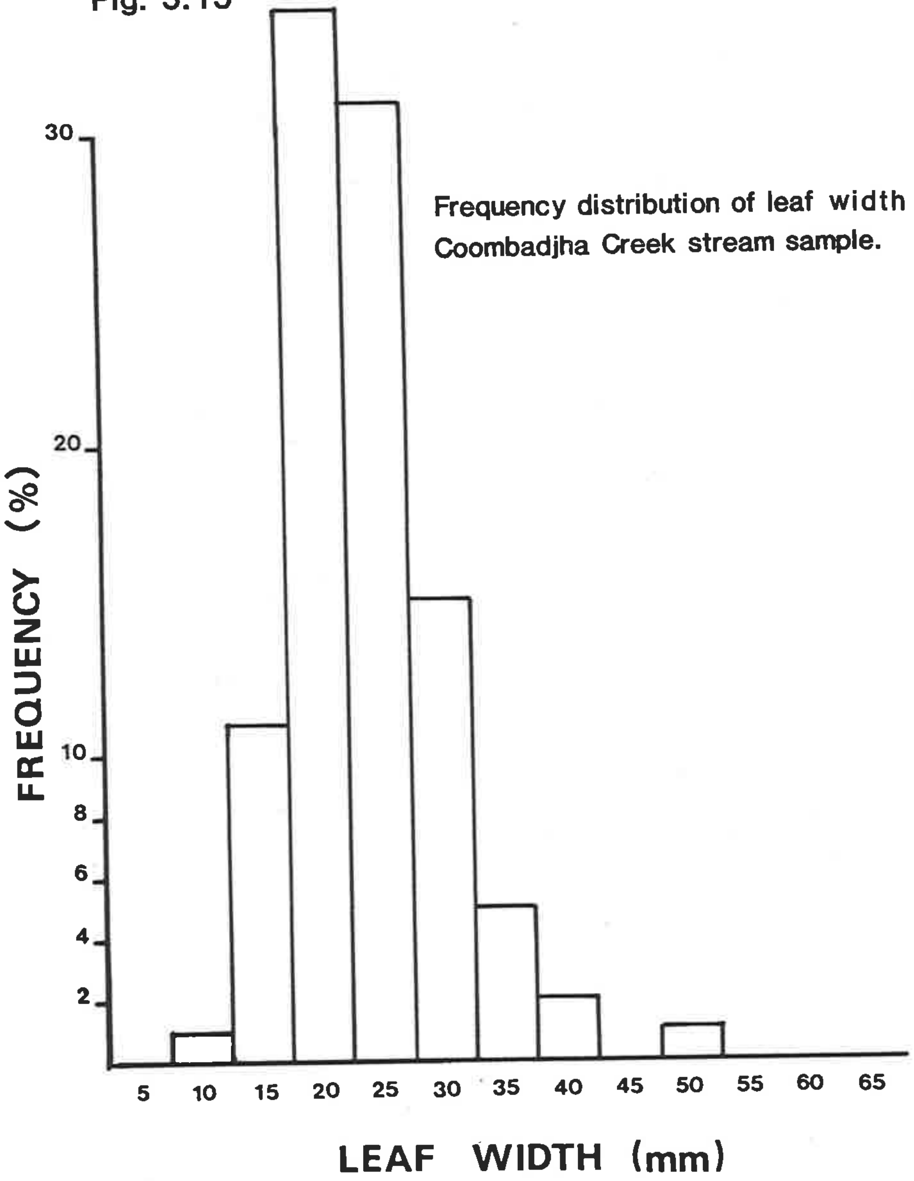


Fig. 5.14

Frequency distribution of leaf length for Coombadjha Creek stream sample.

Fig. 5.15



Frequency distribution of leaf width for Coombadjha Creek stream sample.

contrasted with the stream sample using the cumulative frequency distributions of leaf length (Fig. 5.16), leaf width (Fig. 5.17), relative width (Fig. 5.18), and leaf area (Fig. 5.19).

Overall, there are few differences between the physiognomic signatures of the Coombadjha Ck Stream and forest floor litter. The leaf width and relative width frequency distribution's for the forest floor litter and the stream samples (Figs 5.17 & 5.18), do not suggest the presence of a stenophyllous streamside vegetation. The mean leaf width of the sample is at the upper end of the range demonstrated for the forest floor samples (Table 4.12). The range of leaf shapes for the stream sample can be contrasted with leaves from a litter sample in Figures 5.20 and 5.21.

There is no difference in the proportion of non-entire leaves (individuals) between the Coombadjha Ck forest floor and stream samples (Table 4.6; Figs 5.20 & 5.21). The main difference is a greater number of leaves of *Callicoma serratifolia*, which has a serrate margin (Fig. 5.21 A). The lack of a difference in the proportion of individuals with non-entire margins is perhaps not surprising given the very high proportion of the forest flora with non-entire margins as the New South Wales SNVF litter had very low species diversity (typically 7 species in a sample; see Chapter 7). In particular, the canopy (and the litter) was dominated by *Ceratopetalum apetalum* (see Chapter 7).

The relative width frequency distributions (Fig. 5.17), however, suggests that a streamside leaf size bias maybe present at this site with the plants at the stream-edge producing on average larger (i.e. broader) leaves than in the main forest (Figs 5.20 & 5.21). However, this difference is not apparent if either leaf length (Fig. 5.16) or leaf area (Fig. 5.17) are used as the measure of leaf size.

5.4 Discriminant Analysis.

In the previous Chapter, Discriminant Analysis was used to demonstrate the unique physiognomic signatures for each of the forest types. Discriminant Analysis can also be used to test the membership of new samples to pre-existing classifications. Within the SPSSx package, the original data matrix was retained

Fig. 5.16 Cumulative leaf length frequency distributions of leaf litter from the forest floor and the bottom of a pool (stream).

	mean
Forest	62.8mm
Stream	62.4

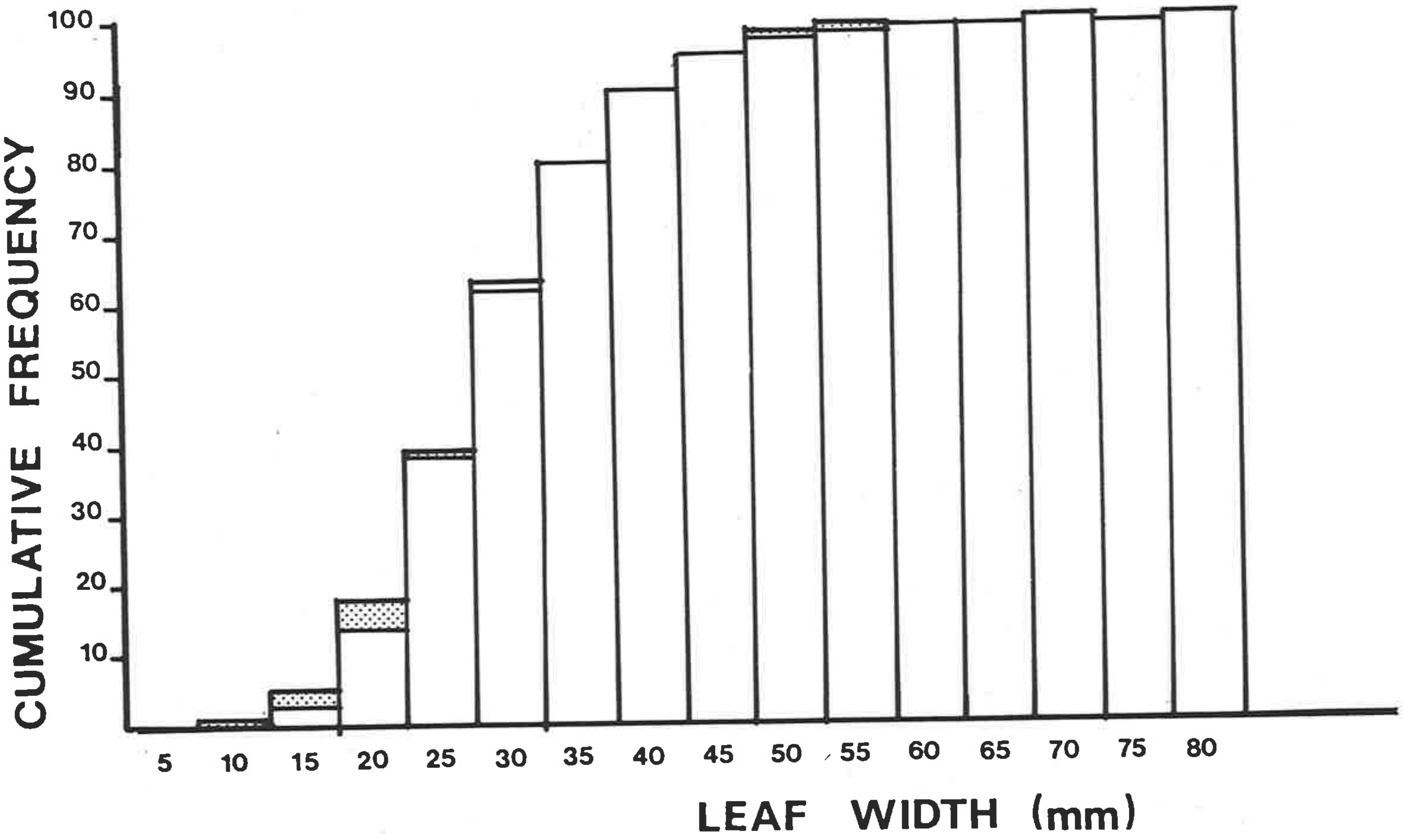


Fig. 5.17 Cumulative width frequency distributions of leaf litter from the forest floor and the bottom of a pool (stream).

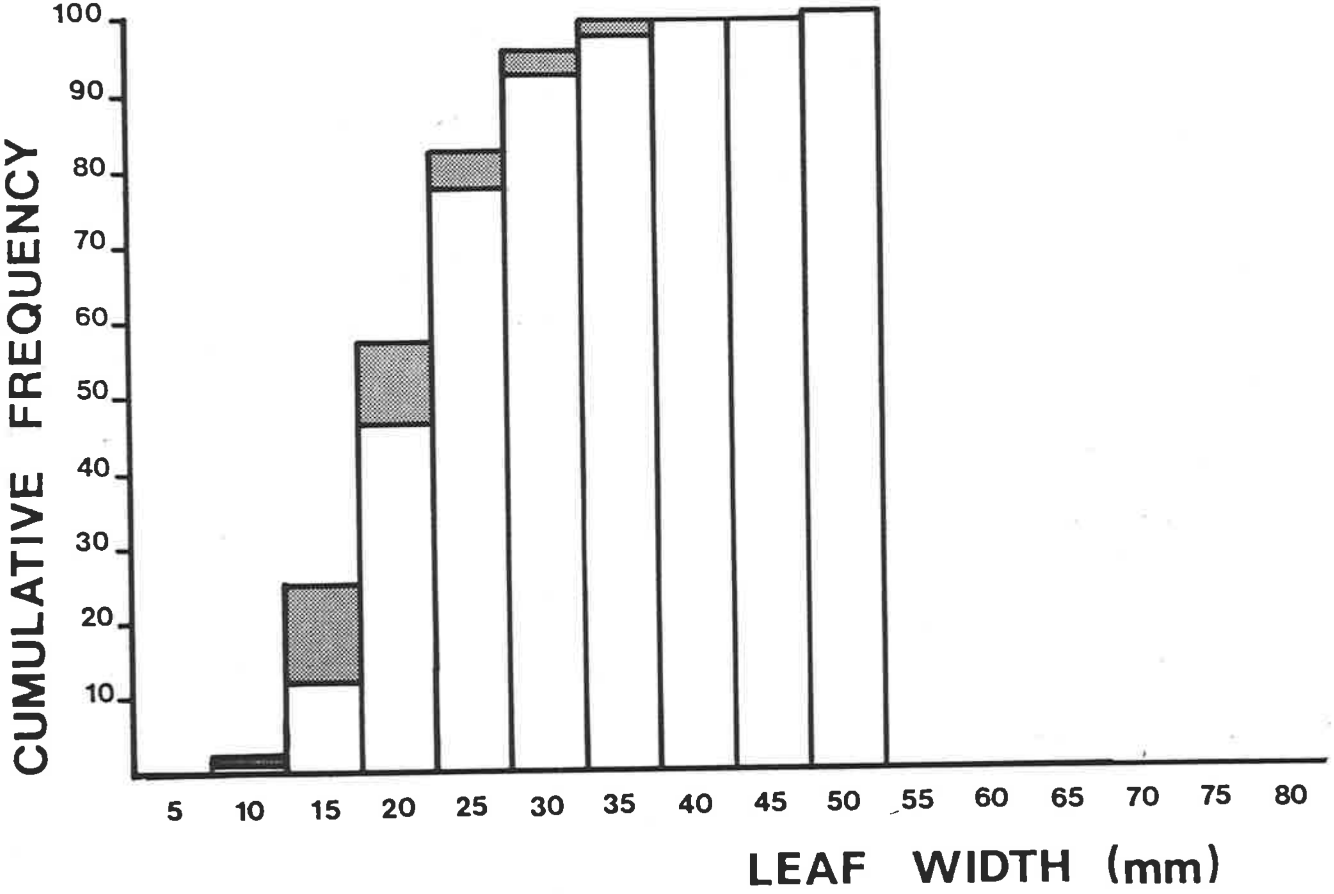


Fig. 5.18 Cumulative relative width frequency distributions of leaf litter from the forest floor and the bottom of a pool (stream).

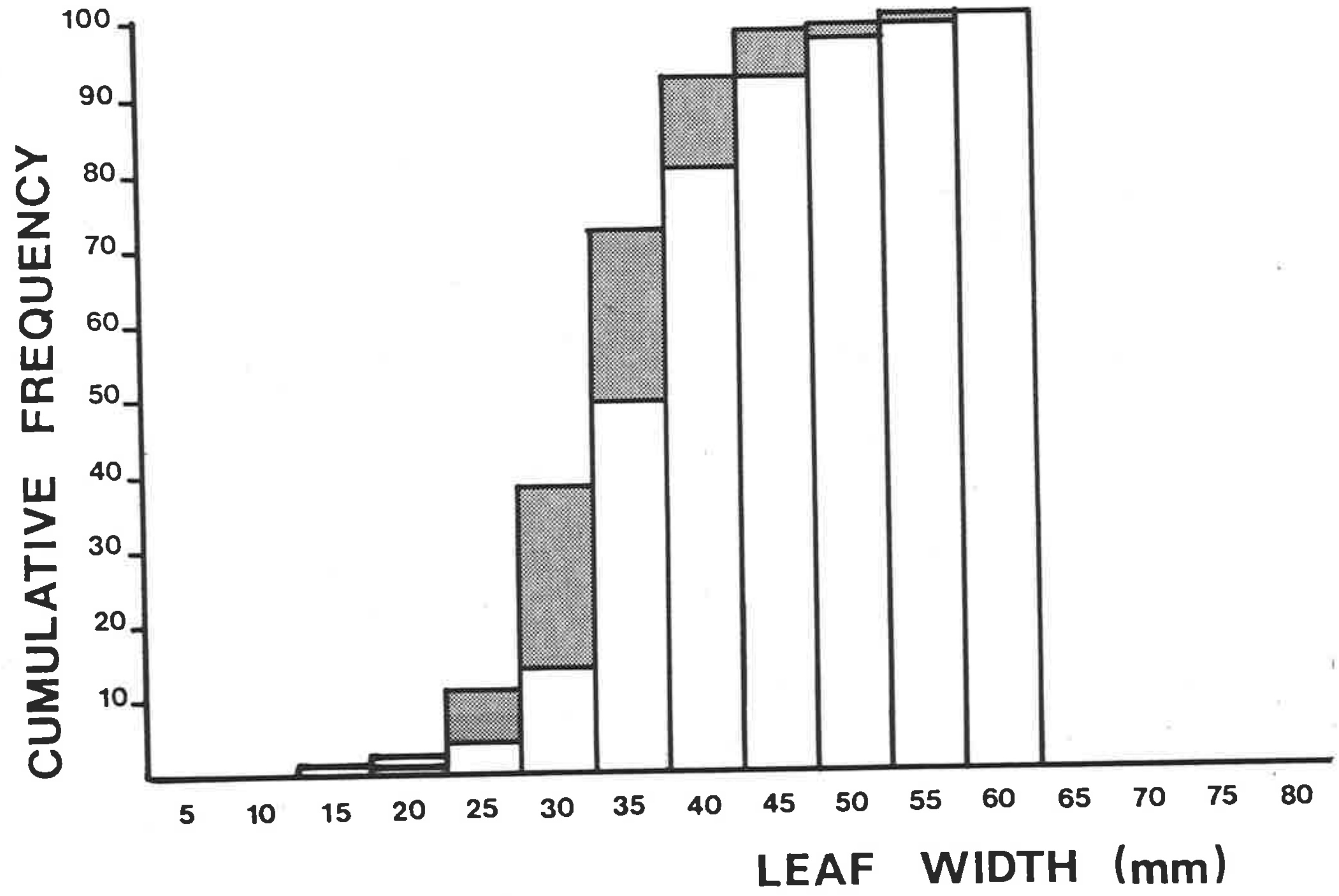


Fig. 5.19 Cumulative area frequency distributions of leaf litter from the forest floor and the bottom of a pool (stream).

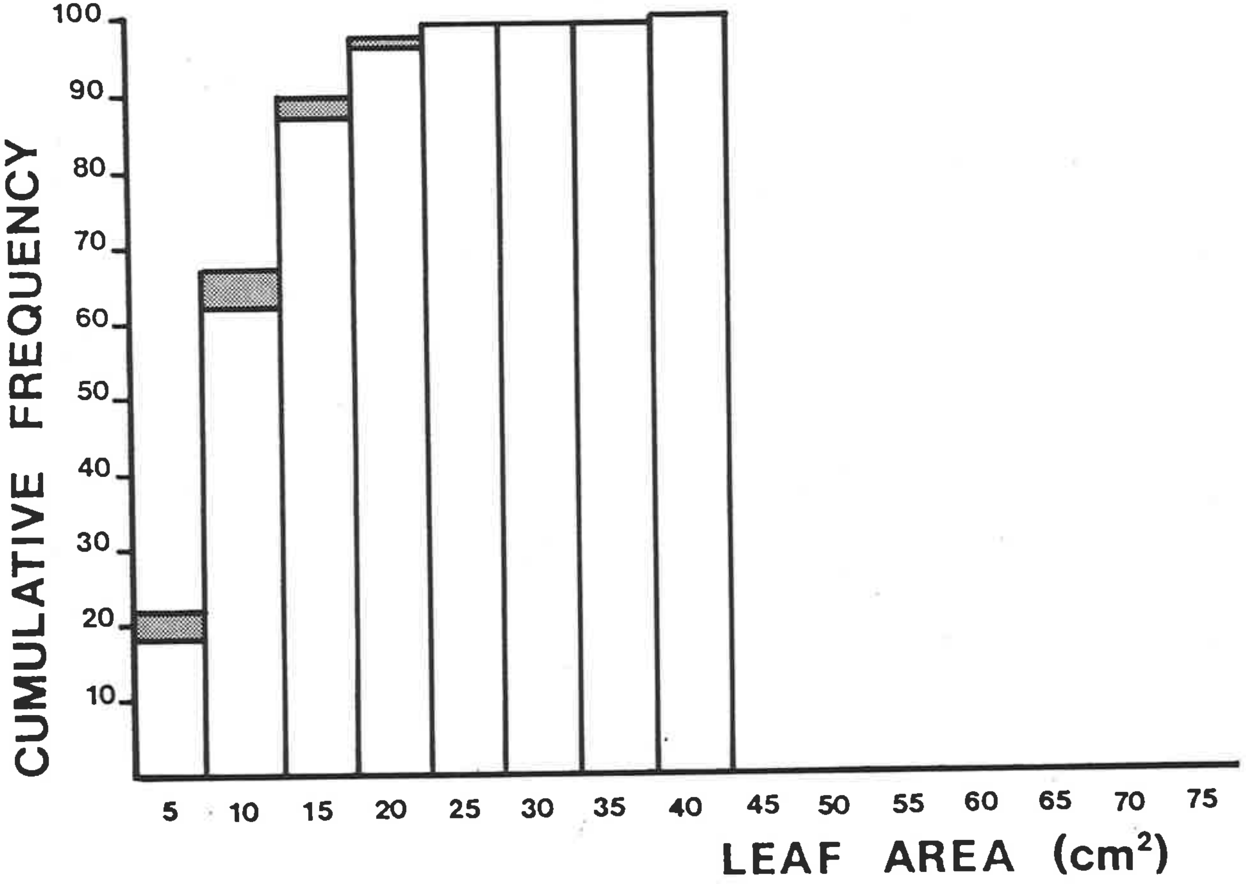


Fig. 5.20 Leaf silhouettes from litter (forest floor) Washpool/Coombadjha Ck.

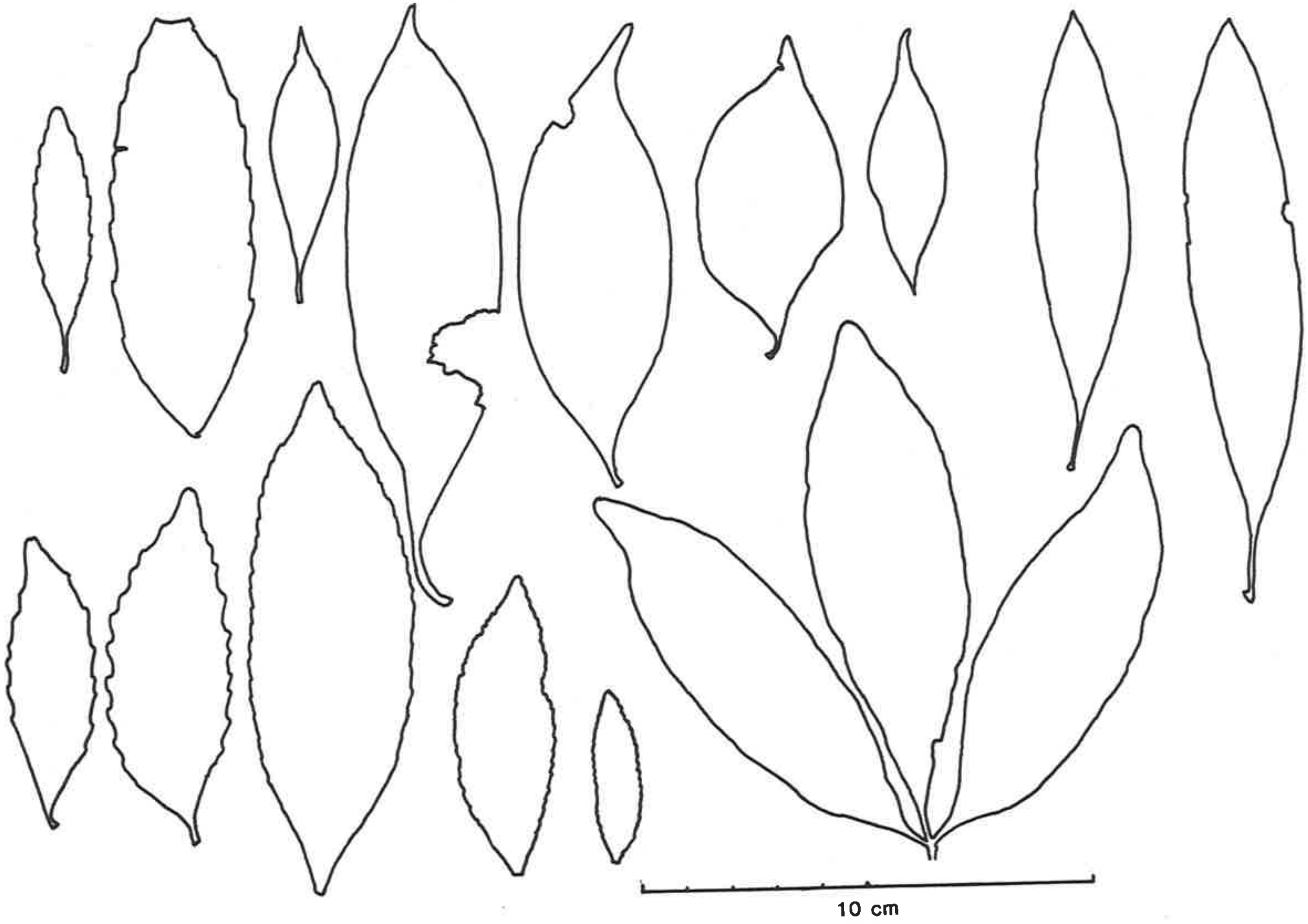
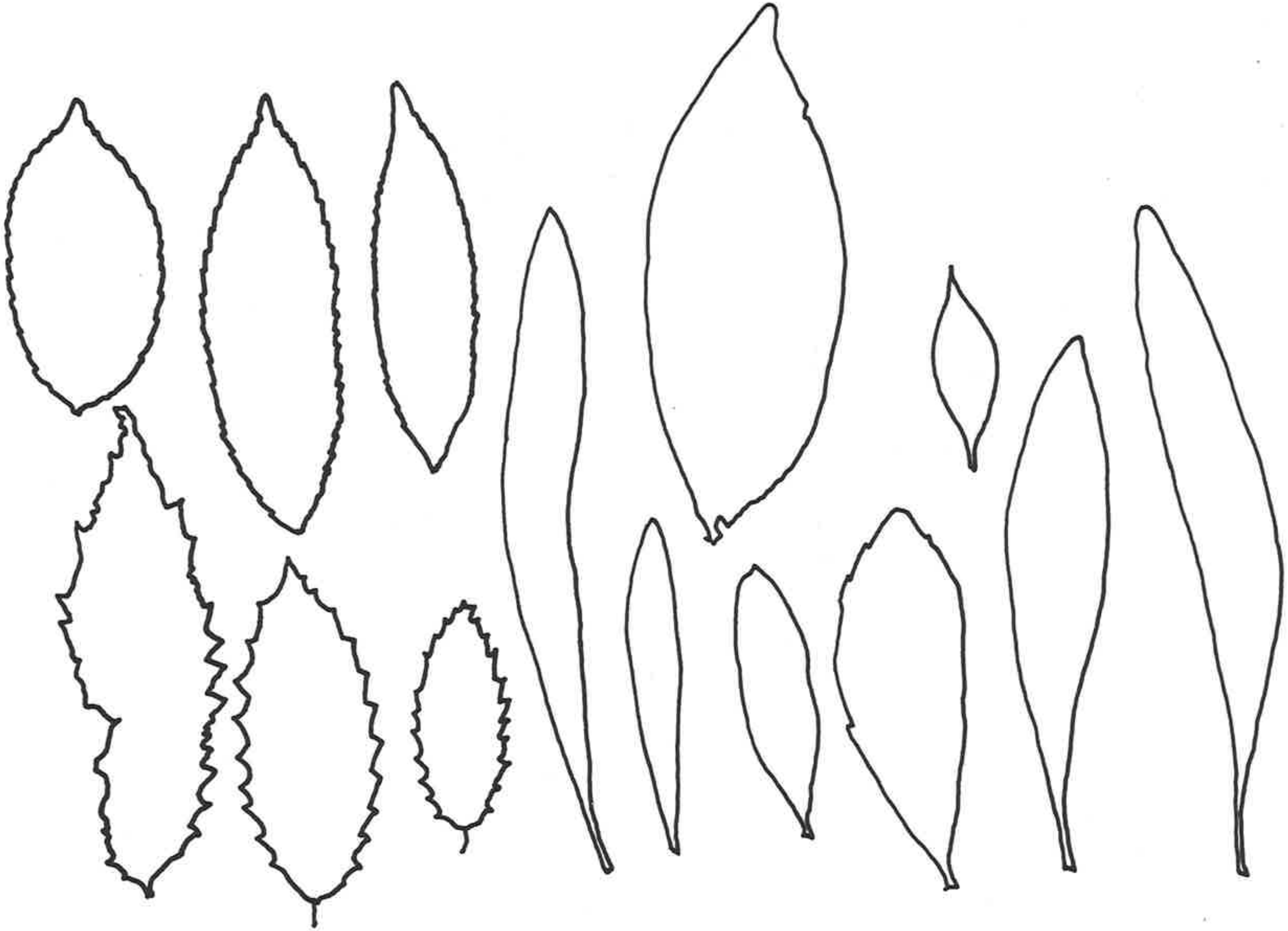


Fig. 5.21 Leaf silhouettes from streambed sample, Coombadjha Ck.



A Callicoma serratifolia.

(and thus the original Discriminant Functions), and the Stream litter samples analysed as ungrouped cases in a new Discriminant Analysis. The Scatterplot from this analysis is shown in Figure 5.22 and the classification summary in Table 5.1.

The Coombadjha Creek (SNVF New South Wales) Stream samples grouped with the other SNVF forest floor samples (Fig. 5.22), and were classified as belonging to the SNVF Group by the analysis (Table 5.1). The Mt Windsor Stream samples produced a mixed classification with one sample (the upstream sample) grouping with the CNVF forest floor samples (Fig. 5.22), and was classified as belonging to the CNVF group (Table 5.1). The downstream sample from Mt Windsor however, was grouped with the SNVF forest floor samples (Fig. 5.22), and was correctly classified as belonging to the SNVF group (Table 5.1).

5.5 Discussion.

Most fossil leaf beds are formed in water bodies, including streams. It is therefore important to understand both the taphonomic consequences of the transport of leaves on the physiognomic character of leaf beds formed in stream beds (and other water bodies), and the possible influences of physiognomically distinct streamside vegetation (MacGinitie, 1969; Wolfe, 1971 1980a). With this understanding of the inherent taphonomic bias, the physiognomic signatures of stream bed leaf deposits can be correctly related to the source forest type.

In the previous analysis, the taphonomy of two examples of recently formed or 'neofossil' leaf beds in Simple Notophyll Vine Forest were examined; one in the tropical N.E. Queensland region, the other in the essentially warm temperate New South Wales region. In general, these stream bed samples were sufficiently similar to the forest floor samples to allow direct comparison and determination of the correct forest type by Discriminant Analysis. There were however discrepancies which bear further discussion.

The Mt Windsor stream samples, and to a lesser extent, the Coombadjha Ck stream samples, demonstrate a bias towards larger leaves in the streamside vegetation reflected in the autochthonous stream litter (Figs 5.5 & 5.8). This bias

Fig. 5.22. Scatterplot of forest floor leaf litter samples and stream litter samples (Function 1 vs 2).

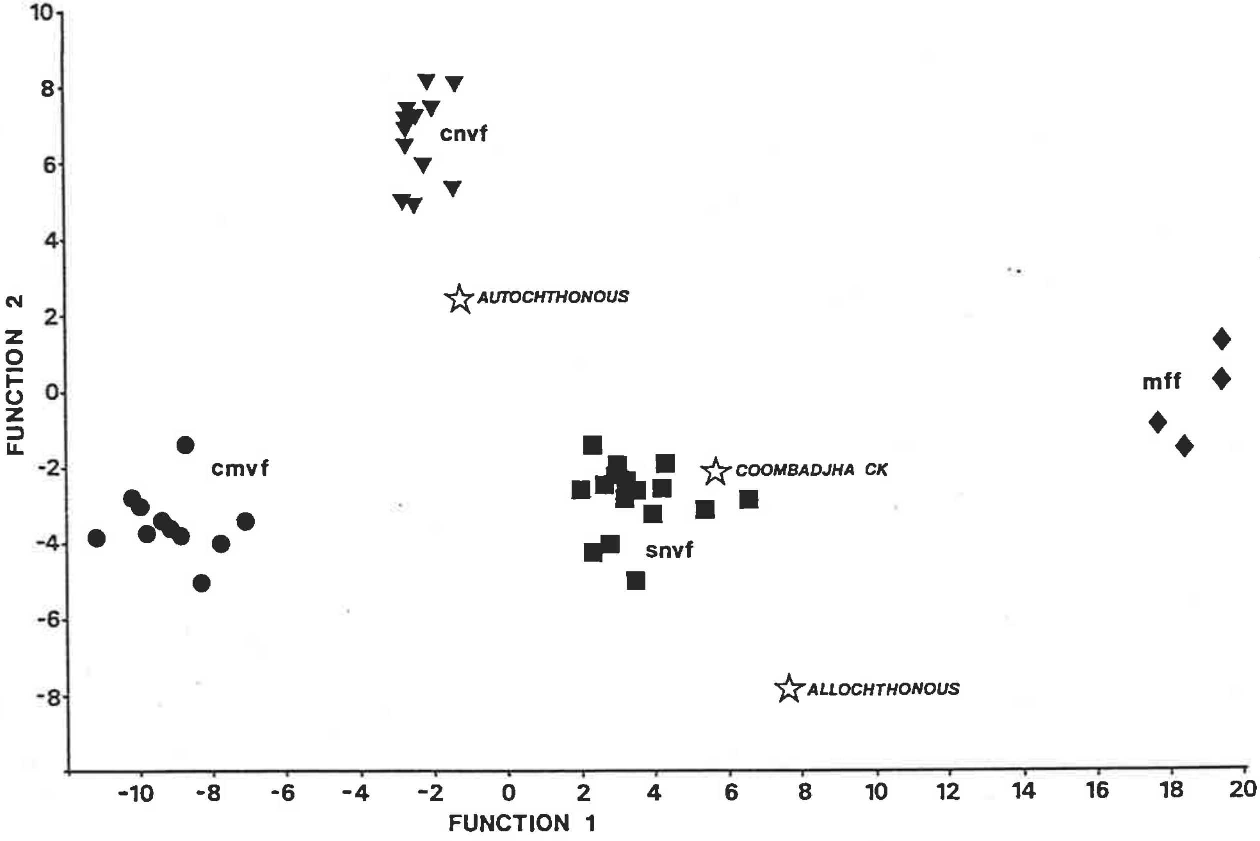


Table 5.1.

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DISCRIMINANT ANALYSIS OF LEAF LITTER SAMPLES:

                         Classification Results.

                      NO. OF          PREDICTED GROUP MEMBERSHIP

FOREST TYPE           CASES      SNVF        CMVF        CNVF        MFF
--------------------------------------------------------------------------
Simple Notophyll       15         15          0           0           0
       Vine Forest              100.0%       0.0%        0.0%        0.0%

Complex Mesophyll      11          0          11          0           0
       Vine Forest                0.0%     100.0%        0.0%        0.0%

Complex Notophyll      12          0          0           12          0
       Vine Forest                0.0%       0.0%      100.0%        0.0%

Microphyll Fern Forest  4          0          0           0           4
                                  0.0%       0.0%        0.0%      100.0%

SNVF Streambed Litter   3          2          0           1           0
                                 66.7%       0.0%       33.3%        0.0%
--------------------------------------------------------------------------

PERCENT OF "GROUPED" CASES CORRECTLY CLASSIFIED: 100.00%

--------------------------------------------------------------------------
```

towards larger leaves is seemingly compensated however, by a shift to smaller leaf sizes following stream transport of the litter over small distances (100 metres), presumably by the selective survival of the smaller leaves (Mt Windsor downstream; Figs 5.7 & 5.8). A further important point is that the upper and lower limits of average leaf length for the streambed litter was within the range observed for the forest floor SNVF samples, and outside the range observed for the forest floor samples from the forest types with the next largest (CNVF, Table 4.7) and next smallest leaves (MFF, Table 4.15; Fig. 4.47).

These results suggest a number of points. In Chapter 4 it was demonstrated that each of the four forest types examined — CMVF, CNVF, SNVF, and MFF — had a unique and identifying physiognomic signature. The results discussed above suggest that the taphonomic bias associated with stream deposition is measurable, and in the case of SNVF (above), is of a scale which (in most cases) still permits a correct determination of the source forest type.

The direction of this bias is generally towards smaller leaf sizes in a fossil deposit than in the original input of leaves from the (streamside?) vegetation. However, the generally larger leaves of the streamside vegetation may produce a bias (compared to the forest interior) towards the upper end of the range of leaf sizes for the forest type. As a general rule then, leaf beds with a leaf size physiognomic signature at the lower end of the range observed for SNVF forest floor litter should be considered to have originated in that forest type. The situation with the other forest types needs further clarification, however.

In Chapter 3 the difference between the leaf size characteristics of the rainforest canopy (from Webb, 1959) were contrasted with the size characteristics of the forest floor for the four forest types (Fig. 4.1). The degree to which the leaf size 'spectrum' of litter represented by the proportion of leaves in each of the Raunkiaer/Webb leaf size classes deviated from the canopy decreased with decreasing average leaf size.

Leaf litter is a deposited leaf assemblage, and so in the same manner as a fossil leaf assemblage, it experiences changes in representation through taphonomic processes. To reverse the analogy, given the decreasing taphonomic bias demonstrated for the four forest types in the transition from canopy characteristics to litter, it is plausible that the degree of taphonomic bias in the average leaf size of a stream bed leaf deposit will vary for each of the forest types. Based on the canopy → litter example, it is reasonable therefore, to suggest that the direction of the change in the taphonomic bias will also be to produce an increasing bias with an increase in the average leaf size of the source forest of the leaf input.

This last point has several important implications. It has been demonstrated above that streambed leaf beds derived from SNVF can be demonstrated to have originated in that forest type. If the direction of the taphonomic bias of leaf size is the same as the canopy → litter, then MFF can be similarly related to fossil beds derived from this forest type. Fossil leaf beds derived from CNVF and CMVF, however, may not be distinguishable without first determining the degree of taphonomic bias and streamside bias for these forest types. It would seem however, that fossil leaf beds derived from CNVF and CMVF can be reliably distinguished from SNVF and MFF derived fossil leaf beds.

Chapter 6

FOLIAR PHYSIOGNOMY AND CLIMATE

6.1 Forest Classification and Climate.

Many systems of climatic classification have been used to explain the modern world distribution of vegetation types. Two in particular — Holdridge's Bioclimatic system, and that used by Wolfe in his physiognomic classification — have been used to link the foliar physiognomy of vegetation to climate (Holdridge, 1967; Dolph, 1979; Dolph and Dilcher, 1979 1980; Wolfe, 1980a). Both of these systems concentrated on some aspects of temperature. An essential difference between these systems is Holdridge's use of "Biotemperature" as opposed to the annual average and the annual range of temperature used by Wolfe.

Biotemperature is determined by calculating the mean annual temperature (the mean of the maximum and minimum) for all days where the temperature is above 0°C or below 30°C (Holdridge, 1967). All days where the mean temperature is below 0°C are counted as 0°C, and days where the minimum temperature is less than 0°C are calculated using 0°C as the minimum. On days where the temperature exceeds 30°C, the daily mean temperature is ideally calculated from hourly readings, with each reading above 30°C counted as 0°C. Each vegetation unit is defined by a combination of the annual mean rainfall, and the Biotemperature (Fig. 6.1).

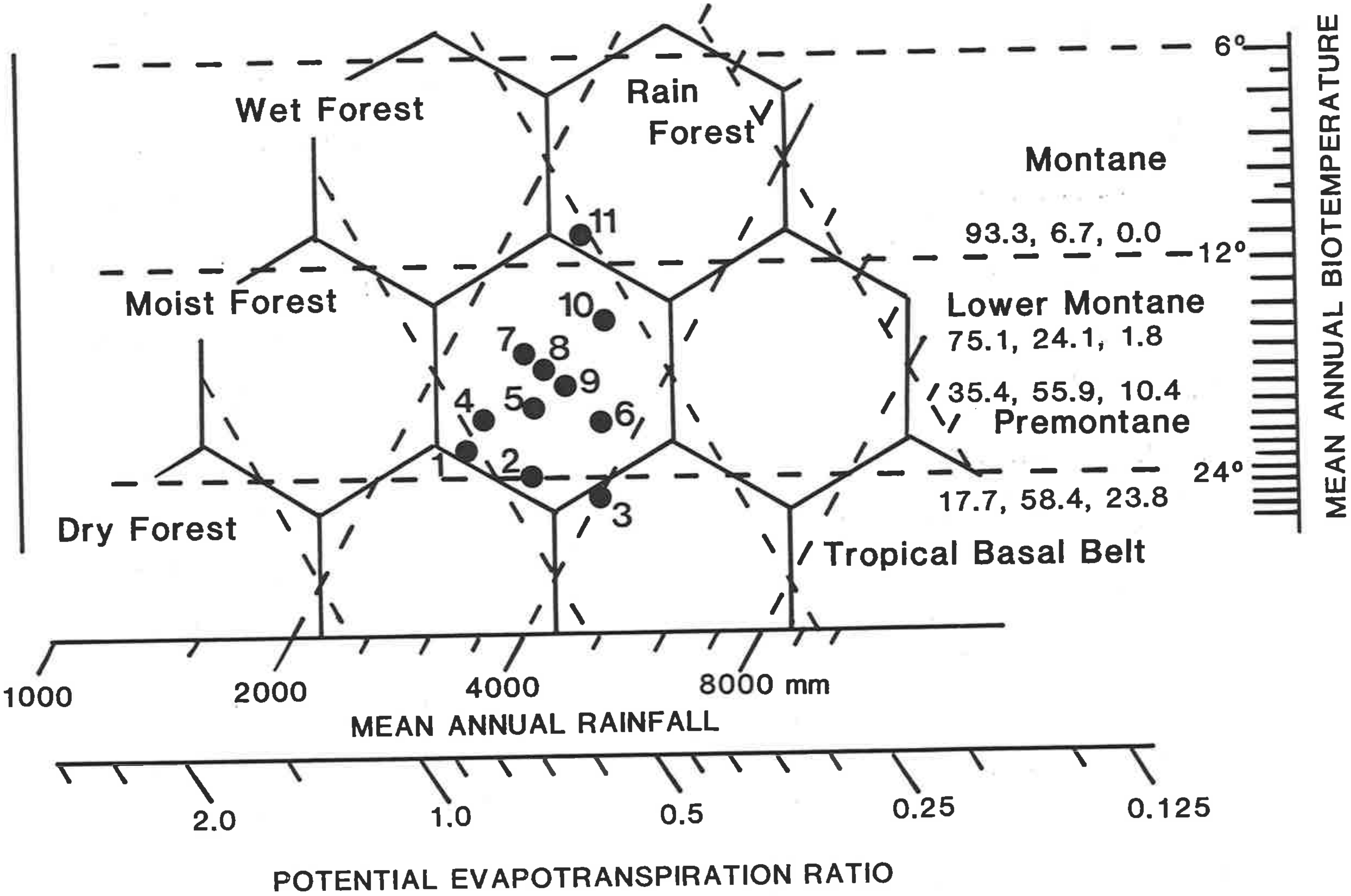
This latter criterion makes Holdridge's system difficult to apply in areas where daily temperature exceeds 30°C for small parts of the day and for discontinuous

Fig. 6.1 Holdridge Diagram with litter collection sites.

CMVF 1 - 3, CNVF 4 - 6, SNVF 7 - 10, MFF 11.

The mean percentages of Webb's leaf size classes
for litter for each forest type is listed
on the right of the diagram.

Fig. 6.1


Wet Forest
Rain Forest
Montane
93.3, 6.7, 0.0
Moist Forest
Lower Montane
75.1, 24.1, 1.8
35.4, 55.9, 10.4
Premontane
17.7, 58.4, 23.8
Dry Forest
Tropical Basal Belt
1
2
3
4
5
6
7
8
9
10
11
6°
12°
24°
MEAN ANNUAL BIOTEMPERATURE
1000
2000
4000
8000 mm
MEAN ANNUAL RAINFALL
2.0
1.0
0.5
0.25
0.125
POTENTIAL EVAPOTRANSPIRATION RATIO

periods over the year as most meteorological data is only recorded perhaps four times a day (eg. Anon., 1983). Holdridge's rationale is that plant growth does not occur above 30°C or below 0°C so that the temperature characteristics of the remainder of the year are the main determinant of vegetation character (Holdridge, 1967).

Dolph and Dilcher used the Holdridge climate classification to find correlations between the foliar physiognomic characteristics of the vegetation and climate of Costa Rica and the U.S. states of North and South Carolina (Dolph, 1979; Dolph and Dilcher, 1979 1980). In the first study Dolph found no correlation between the percentage of species having leaves with entire margins with either mean annual average biotemperature, mean annual precipitation, the potential evapotranspiration ratio, or a combination of these variables (Dolph, 1979). Dolph found a very high level of variation between adjacent sites due to changes in the local species composition. These results are in marked contrast to the correlations presented for regionally defined vegetation types (eg. Wolfe, 1971 1980a).

The analysis of the vegetation of the Carolinas examined a greater variety of foliar physiognomic characteristics, including leaf size and margin type (Dolph and Dilcher, 1979). Dolph and Dilcher found variation at the local level obscured the relationship between climate and the prevailing foliar physiognomy. However, a study of leaf-size variation (the proportion of species with 'large leaves') found that three foliar belts could be recognised for the vegetation of Costa Rica (Dolph and Dilcher, 1980). Again however, they found very high levels of variation between adjacent sites.

Dolph and Dilcher suggested on the basis of the high observed variation between local sites that correlations based on regional vegetation oversimplify complex interactions at the local scale between species composition, foliar physiognomy, and the environment (Dolph, 1979; Dolph and Dilcher, 1979 1980). Deposition of leaf material is generally considered to be local (Dolph, 1979 1984; Ferguson, 1985), and so leaf beds are likely to represent the foliar physiognomic characteristics of local vegetation (Dolph, 1979 1984; Dolph and Dilcher, 1979

1980: Roth and Dilcher, 1978).

It is therefore important to understand correlations between the foliar physiognomic characteristics of local vegetation and the local climate. More particularly, it is necessary to understand the correlations between the foliar physiognomic characteristics of leaf beds and the local climate, and hence the climatic signal contained in the leaf-beds formed from the local vegetation.

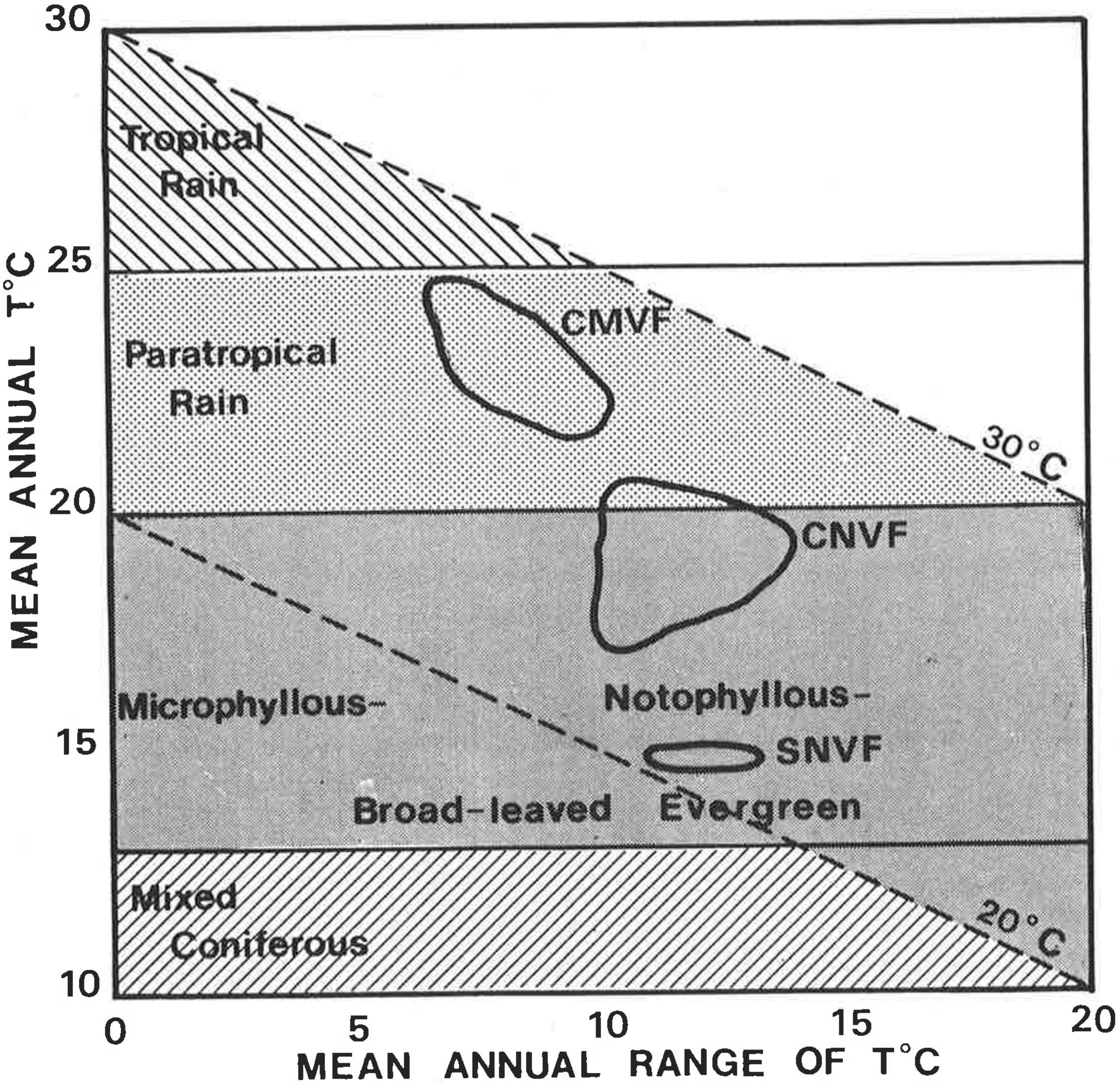
Wolfe's physiognomic classification of the S.E. Asian forests is based on correlations of forest structure and foliar physiognomy (mainly the proportion of canopy species with non-entire margin leaves) with annual average temperature and the annual range of temperature (Wolfe, 1980a; Fig. 6.2). Webb's forest classification however, is based on correlations of forest structure and physiognomy (including both leaf size and margin type) with a combination of edaphic and climatic attributes (Webb, 1959 1968). Leaf size, however, was more strongly under the influence of annual average temperature than other factors (Webb, 1968).

Wolfe compared his classification to Webb's forest types using data from a small number of meteorological stations within Australia to provide the climatic characteristics for each of the main forest types — MFF, SNVF, CNVF, and CMVF (Fig. 6.2), and the structural and physiognomic characteristics listed by Webb (1958).

Webb's Complex Mesophyll Vine Forest was considered by Wolfe to be analogous to his Paratropical Rainforest. Wolfe's Paratropical Rainforest is distinguished from Tropical Rainforest on the basis of the presence of only three tree layers in the Paratropical Rainforest (compared to four in Tropical), and the correlation of this forest type to the climatic limit of an annual average temperature below 25°C, and above 20°C (i.e. Megathermal Vegetation), and a mean warm month temperature below 30°C (Fig. 6.2).

The Complex Notophyll and Simple Notophyll Vine Forest of Webb's classification were regarded by Wolfe as representing the upper and lower climatic limits of his Notophyllous Broadleaved Evergreen Forest (Fig. 6.2). The climatic limits of this forest type are defined by a annual mean temperature below 20°C, and

Fig. 6.2 Wolfe's forest classification contrasted to Webb's forest types (from Wolfe, 1980).



above 13°C (i.e. Mesothermal vegetation), and a mean warmest month above 20°C.

As discussed above, Wolfe's forest classification is based on correlations between regional vegetation and climate, and in particular, the foliar physiognomic characteristics of the canopy species. The correlations noted by Webb were also of a regional nature and gave little detail. It is necessary therefore, to examine the climatic limits of Webb's forest types in more detail, and from this basis examine the correlations between the foliar physiognomic characteristics of leaf beds formed from local vegetation and the local climate.

6.2 The Climatic Characteristics of Australian Rainforest.

Holdridge's system requires a detail of information not readily available for much of the areas in Australia where rainforest occurs, however a preliminary analysis of the litter collection sites is presented here. Figure 6.1 also shows the Holdridge classification of the litter collection sites. The biotemperature of the sites has been estimated from records of nearby meteorological stations (Anon., 1983; Table 6.1) at equivalent elevation within a 50 km radius of the sites. As can be seen from this Figure, most of the sites are not 'rainforest' as defined by Holdridge's system, with much of what is considered 'rainforest' under other classifications, classified as 'wet forest'.

Wolfe criticised Holdridge's system for applying unrealistically high lower limits to the rainfall criteria for the boundary between 'wet forest' and 'rainforest' (Wolfe, 1980a). Certainly under Holdridge's classification there is almost no rainforest in Australia's tropical region (see Fig. 2.10). The sites included on the Holdridge Diagram cover most of the climatic range of Webb's main forest types (CMVF, CNVF, SNVF, MFF). It is clear from this diagram that Webb's forest types do not correspond to Holdridge's forest types. The climatic characteristics of CMVF however, overlap across the 'Wet Forest' and 'Rainforest' of Holdridge's climatic classification (Holdridge, 1967).

The mean proportion of leaves for each forest type (all samples for all sites

Table 6.1 Climatic data for selected stations, Anon., 1983.

QUEENSLAND

	LATITUDE	ALTITUDE	MIN T C	MAX T C	RANGE	MEAN	LOCATION
1	13 57	192.6	20.5	30.3	9.8	25.4	Coen P.O.
2	10 35	67.9	24.0	29.2	5.2	26.6	Thursday Is. Aero
3	12 47	18.6	21.3	29.5	8.2	25.4	Iron Ra. Aero
4	16 53	3.0	20.7	28.9	8.2	24.8	Cairns Aero
5	15 28	1.5	22.4	28.7	6.3	25.5	Cooktown
6	17 23	899.2	14.4	25.6	1.2	20.0	Herberton
7	17 12	714.5	15.5	25.0	9.5	19.8	Kairi Exp. Stn.
8	16 23	3.4	23.1	29.1	6.0	26.1	Low Isles
9	16 29	4.0	20.4	28.8	8.4	24.6	Port Douglas
10	17 00	335.3	16.4	28.9	12.5	22.7	Mareeba
11	16 06	106.7	21.9	27.4	5.5	24.7	Fitzroy Is.
12	18 16	5.5	19.0	29.1	10.1	24.1	Cardwell
15	19 11	57.6	21.5	27.7	6.2	24.6	Cape Cleveland
13	17 51	6.7	19.5	27.5	8.0	23.5	InniS.F.ail
14	17 36	18.3	18.3	28.2	9.9	23.3	Sth Johnstone
16	19 15	3.4	19.5	28.7	9.2	24.1	Townsville
17	18 40	13.7	17.6	29.6	12.0	23.6	Ingham
18	20 03	2.4	21.2	27.7	6.5	24.5	Hayman Is.
19	21 09	3.7	17.7	26.6	8.9	22.2	MacKay AERadio
20	21 06	13.7	16.6	27.4	10.8	22.0	MacKay Suger Mill
21	21 39	57.9	21.2	26.0	4.8	23.6	Pine Islet
22	20 24	12.5	17.9	28.8	9.9	22.9	Proserpine
23	23 06	10.4	17.7	25.8	8.1	21.8	Yeppoon
24	24 32	602.0	13.7	23.1	9.4	18.4	Bulburin For.
25	24 52	13.7	16.6	26.4	9.8	21.5	Bundaberg P.O.
26	24 02	85.3	18.2	25.1	6.9	22.7	Bustard Hd.
27	23 30	77.7	19.7	24.5	5.8	22.6	Cape Capricon
28	25 14	108.5	16.0	26.8	10.8	21.4	Childers P.O.
29	24 44	99.1	18.7	25.3	6.6	22.0	Sandy Cape
30	24 54	30.5	15.8	26.0	11.2	21.4	Bundaberg Aero.
31	26 48	46.0	16.5	24.4	7.9	20.5	Caloundra
32	28 10	6.1	17.8	25.7	7.9	21.6	Coolangata
33	26 12	76.2	14.8	25.2	10.4	20.0	Pomong (OMO)
34	26 49	180.4	12.9	25.1	12.2	19.0	Croamhurst
37	26 11	94.2	14.0	26.8	12.8	20.4	Gympie
38	26 28	105.2	13.7	26.8	13.1	20.3	Imbil Forest
40	25 33	1.8	14.9	26.3	11.4	20.6	Maryborough
41	27 57	19.8	15.1	25.0	9.9	20.1	Southport
42	27 58	525.8	13.0	22.1	9.1	17.6	Mt. Tambonhe
43	27 26	2.1	15.7	25.6	9.9	20.7	Brisbane Airport
44	27 22	52.7	12.8	25.2	12.4	19.0	Samford CSIRO
45	27 19	1.5	14.9	25.0	10.1	20.0	Sandgate
46	26 24	9.1	16.2	25.3	9.1	20.8	Tewantin P.O.
47	27 35	24.4	14.5	24.8	10.3	14.7	Ormiston-Redlands
48	26 38	30.5	13.1	25.5	12.4	19.3	Nambour
49	28 10	5.5	15.1	24.3	9.2	19.7	Coolangata Aero.

Table 6.1 continued.

NEW SOUTH WALES

	LATITUDE	ALTITUDE	MIN T C	MAX T C	RANGE	MEAN	LOCATION
50	27 20	640.1	13.6	20.7	7.1	17.2	Mt. Glorious
51	33 52	92.0	14.0	22.0	8.0	18.0	Sydney RO
52	34 25	18.3	13.3	21.6	8.3	17.5	Nth Wollongong
53	31 19	225.0	12.8	22.6	9.8	17.7	Bellangry S.F. 1
54	---	1200.0	--	--	9.8	10.5	Bellangry S.F. 2
55	36 40	13.4	8.2	22.1	13.9	15.2	Bega
56	37 09	914.0	2.3	17.1	14.8	9.7	Bondi S.F.
57	33 42	900.0	7.4	17.2	9.8	12.3	Wentworth Falls
58	33 43	1030.0	8.0	16.7	8.7	12.4	Katoomba
59	33 27	975.0	5.5	16.6	11.1	11.1	Lidsdale S.F.
60	34 01	1188.7	4.2	15.7	11.5	10.0	Gurang S.F.
61	31 28	9.1	12.0	24.0	12.0	18.0	Wauchope S.F.
62	31 23	146.0	11.2	24.0	12.8	17.6	Yarras/Mt. Seaview
63	29 41	9.0	13.3	25.5	12.2	19.4	Grafton
64	28 51	152.0	14.6	23.6	9.0	19.1	Alstonville
65	28 21	18.0	14.0	25.8	11.8	19.9	Murwillumbah
66	30 27	22.9	12.0	25.6	13.6	18.8	Bellingen
67	30 55	128.0	15.5	23.0	7.5	19.3	Smoky Cape LH
68	30 19	5.0	13.7	23.1	9.4	18.4	Coffs Harbour
69	31 52	6.0	12.9	23.1	10.2	18.0	Harington P.O.
70	29 26	2.0	13.0	24.7	11.7	18.9	Harwood Sugar Mill
71	28 49	9.0	13.4	22.5	11.9	19.5	Lismore P.O.
72	28 38	91.0	16.4	23.5	7.1	20.0	Cape Byron LH
73	29 26	29.0	15.3	23.0	7.7	19.2	Yamba Pilot Stn.
74	29 39	999.7	6.7	19.4	12.7	13.1	Mt. Mitchell
75	28 45	520.0	12.3	21.9	9.6	17.1	Tabulam
76	30 59	1032.0	5.3	19.0	13.7	12.2	Walcha P.O.
77	28 28	365.8	10.3	23.6	13.3	17.0	Urberville
78	29 42	1060.0	7.4	18.8	11.4	13.3	Glen Innes
79	30 14	1350.0	5.8	16.9	11.1	11.4	Guyra
80	30 31	980.0	7.3	20.3	13.0	13.8	Armidale
81	30 36	1016.5	6.3	20.1	13.8	13.2	Uralla
82	28 54	670.6	8.6	21.5	12.9	15.1	Girard S.F.
83	30 37	1036.3	8.4	17.8	9.4	13.1	Styx River
84	28 45	701.0	12.2	21.8	9.6	17.0	Muirne
85	28 19	4.9	13.3	25.3	12.0	19.3	Condong Sugar Mill
86	28 36	381.0	11.8	21.5	9.7	16.7	Whian Whion
87	29 01	15.2	14.0	24.5	10.5	19.3	Broadwater Sugar Mill
88	30 06	500.0	8.2	22.5	14.3	15.4	Clouds Creek
89	30 07	30.5	14.3	23.7	9.4	19.0	Woolgoola S.F.
90	31 26	16.5	13.1	21.9	8.8	17.5	Port Macquarie
91	37 04	731.5	5.5	17.4	11.9	11.5	Nalbaugh S.F.

VICTORIA

	LATITUDE	ALTITUDE	MIN T C	MAX T C	RANGE	MEAN	LOCATION
92	39 08	88.7	11.1	16.2	5.2	13.7	Wilsons Prom.
93	37 42	45.4	8.8	20.1	11.3	14.5	Orbost
94	37 49	14.0	8.7	19.9	11.2	14.3	Bairnsdale
95	38 06	4.6	8.2	19.4	11.2	13.8	Sale
96	37 32	88.4	7.7	20.6	12.9	14.2	Cann River

pooled) represented in three of Webb's leaf size classes — Microphyll, Notophyll, and Mesophyll — has been included on the Holdridge Diagram (Fig. 6.1). A gradation in the proportional representation in each size class can be seen from the Montane to the top of the Tropical Basal Belt. The CNVF sites (4, 5, & 6) differ from the CMVF sites (1, 2, & 3) by the relative proportions of Microphylls and Mesophylls. The MFF site (11) and the SNVF sites (7, 8, 9, & 10) differ by the relative proportions of Microphylls and Notophylls. This suggests that two main foliar belts can be recognised on the basis of the dominant leaf size class (i.e. Microphyll in MFF and SNVF, Notophyll in both CNVF and CMVF), and that these foliar belts can be divided into secondary belts on the basis of the relative proportions of the lesser leaf size classes.

Wolfe considered Webb's CMVF to represent his Paratropical Rainforest and both CNVF and SNVF to represent his Notophyllous Broadleaved Forest (Wolfe, 1980a). However, a more detailed examination of the climatic characteristics of the total range of these forest types in N.E. Queensland (Fig. 6.3), suggests that the climatic limits of the Australian rainforests overlap the boundaries of Wolfe's forest types.

The Figure represents a series of sites selected from meteorological records (Anon., 1983) for stations on the east coast of Australia known to be at a similar altitude and within 20km of a mapped occurrence (Webb and Tracey, 1982) of one of the four rainforest types considered. An additional criterion was that the station had to have an annual average rainfall in excess of 1000mm, as this seems to be the general cut-off for rainforest in Australia. Some additional sites were added from literature sources (Tracey, 1982; Brasel, et al., 1985). The data for each of the stations are given in Table 6.1. The annual mean temperature for each litter site was calculated from lapse rates determined from these stations (Figs 6.4 & 6.5). The annual range of temperature was estimated from the nearest station.

The climatic distribution of CMVF in the lowlands is defined by a minimum annual average temperature of 22°C, with a few sites with an annual average temp. in excess of 25°C (eg. Cooktown and Low Isles). Complex Mesophyll

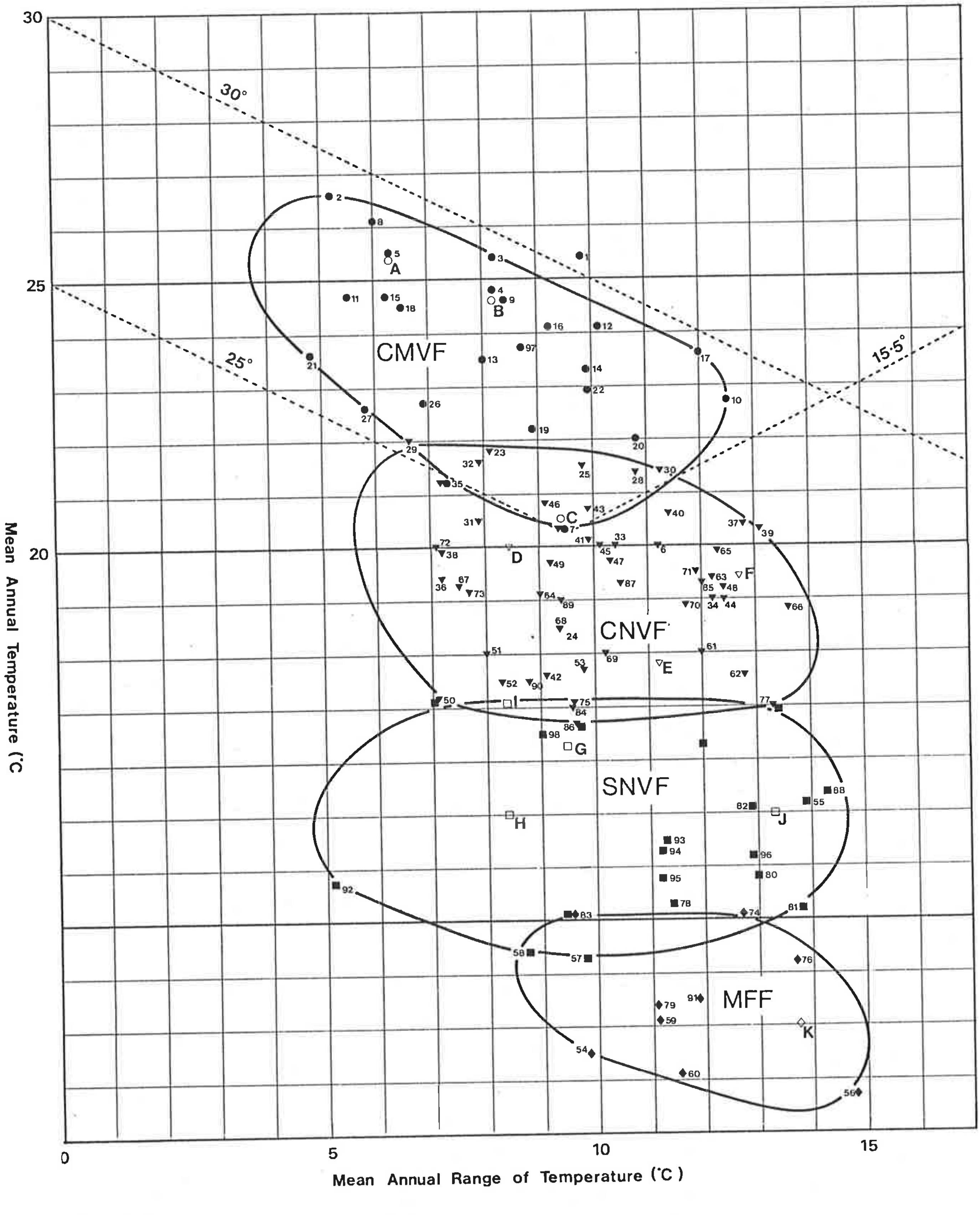


Fig. 6.3 The climatic characteristics of Australian rainforest.

Base diagram from Wolfe, 1980. Climatic data from Anon., 1983.

A Oliver Ck

B Mulgrave R.

C Mobo Ck

D Curtain Fig

E The Crater

F Dorrigo

G Mt Haig

H Mt Lewis Rd

I Mt Lewis EP18

J Washpool

K Barrington Tops

Fig. 6.4

Temperature change with altitude between latitude 17°00'S -- 18°40'S

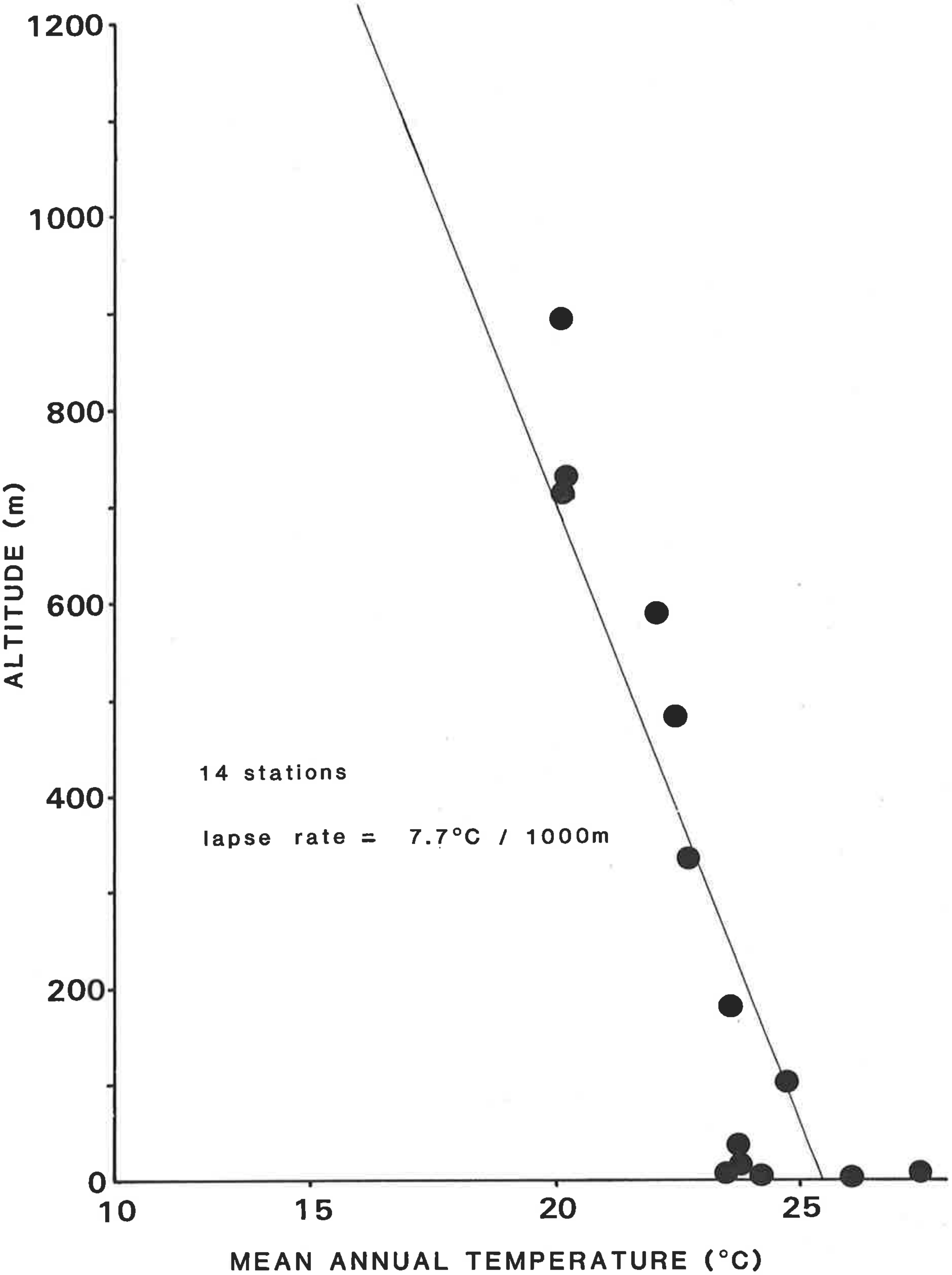
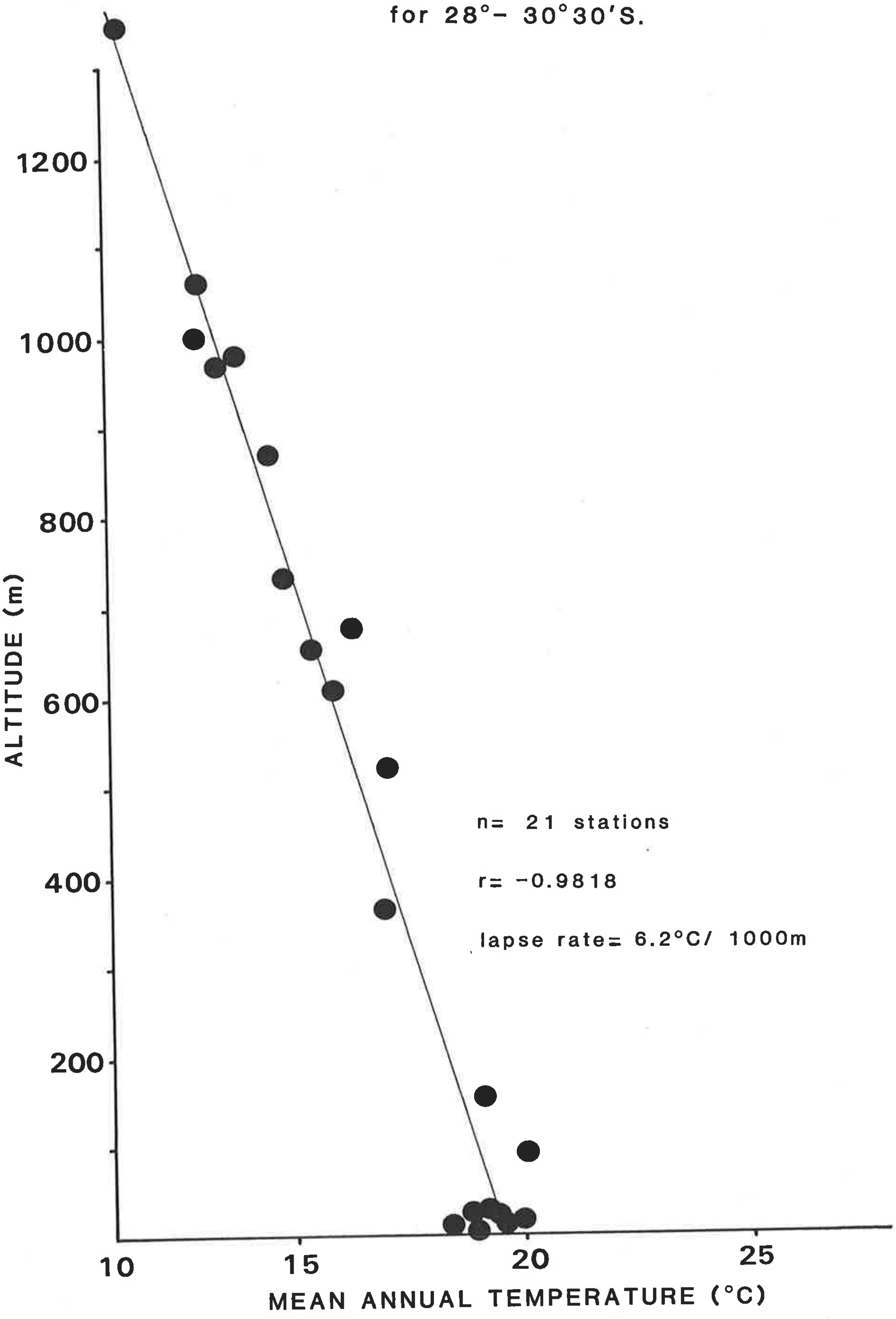


Fig. 6.5 Temperature change with altitude for 28°- 30°30'S.



n= 21 stations

r= -0.9818

lapse rate= 6.2°C/ 1000m

Vine Forest occurs within 10 km of Cooktown and further to the north, and also on the Low Isles (Tracey and Webb, 1975; Tracey, 1982; Webb and Tracey, 1984). It would seem therefore, that CMVF (in part) is intermediate between Wolfe's Tropical Rainforest and his Paratropical Rainforest.

A zone of overlap in the climatic characteristics of CMVF and CNVF is indicated for the Atherton Tableland area of N.E. Queensland (sites Gadgarra, Kairi, and Mobo Creek). Complex Mesophyll Vine Forest (type 1b of Tracey, 1982) and Simple Mesophyll Vine Forest (type 2a) occurs on the basalt soils of the eastern edges of the Atherton Tablelands. Complex Notophyll Vine Forest (type 5a of Tracey, 1982) occurs at similar altitudes on the more seasonally dry western half of the Tablelands on the same soils.

In this area CMVF and MVF occurs at an annual average temperature of around 21°C, but seems restricted to areas where the warmest month is greater than 25°C, and the coldest month greater than around 15°C (Fig. 6.4; eg. Gadgarra and Mobo Creek). Webb and Tracey emphasised the role of soil type (and hence fertility) in controlling structural type in this region (Webb, 1968; Tracey, 1982). The overlap in the climatic boundaries of CMVF and CNVF on the Atherton Tableland reflects this edaphic interaction.

The climatic data for the CNVF and SNVF sites indicate a zone of overlap at about 18 – 20°C annual average temperature (Fig. 6.3). CNVF seems to be limited by the 17°C and 12°C mean coldest months, and a lower limit of 22°C for the mean of the warmest month. The SNVF sites, however, suggest that the climatic limits of this forest type are defined by an upper limit of about 13°C for the mean of the coldest month, a lower limit of the mean warmest month of 18°C, and an upper limit of around 23°C; indicating a small overlap in the thermal requirements of SNVF and CNVF.

From this analysis it is clear that Webb's forest types are not strictly analogous to Wolfe's forest types. Complex Mesophyll Vine Forest overlaps across the upper limit of Paratropical Rainforest into Tropical Rainforest, and Complex Notophyll Vine Forest similarly overlaps the climatic boundary between the "warm temperate" Notophyllous Broadleaved Evergreen Forest, and Paratropical Rainforest. Simple Notophyll Vine Forest however, is well within the climatic limits of Wolfe's Notophyllous Broadleaved Evergreen Forest.

Webb makes no direct connection between climatic classification and his forest classification (Webb, 1959), however he does suggest causal links with annual average temperature and annual rainfall (including seasonality; Webb, 1968). The influence of edaphic factors (soil fertility) is considered by Webb to be a major determinant of forest type in conjunction with the climate (Webb, 1959 1968).

The overlap between CNVF and SNVF shown on Wolfe's climatic classification (Fig. 6.3) illustrates the capacity of CNVF to supplant SNVF and CMVF on less favourable sites on soils of high fertility at the climatic limits of the latter two forest types, and for CMVF to occur beyond the thermal limits detected in the lowlands on highly fertile soils under very high rainfalls (Webb, 1968; Tracey, 1982). However Webb's classification is based on the correlation of both structural and foliar physiognomic features with environmental factors.

In the introduction to the thesis the point was made that the presence of structural features can only be inferred from the fossil record. Foliar physiognomy however, can be directly observed. In the following section the relationship between foliar physiognomy and climate is examined independant of structural criteria i.e. the correlation between leaf size and margin type to climate independant of forest type.

6.3 Leaf Size and Climate.

6.3.1 Leaf Length and Temperature.

Some studies have found that the mean leaf length for particular taxa (Potts and Jackson 1986; Conran 1987; Hu Chia 1986) is strongly correlated with the source of the material and by inference, is refecting the average response of the population to environmental factors.

According to Webb (1968), the prevailing leaf length class in the canopy of Australian rainforests is controlled primarily by temperature. Wolfe (1980a) suggested that the annual average temperature (the mean of the mean annual maximum and minimum temperatures) of an area is an important determinant of foliar physiognomy, mainly the proportion of species with entire margins, but also leaf size.

The extent to which this relationship was reflected in the litter samples was tested by a linear regression of the estimated annual average temperature of the litter collection sites and the mean length recorded for each site (Fig. 6.6). The average annual temperature for most sites was estimated by calculating the lapse rate for the local area of each collection site (**Table 6.1**). The known elevation of each site then gave an estimate of the annual average temperature (Figs 6.4 & 6.5; Table 6.2).

Figure 6.6 shows a clear relationship between the mean leaf length for the litter collection sites and the estimated annual average temperatures of the sites. The small variation present possibly reflects interaction with edaphic factors or seasonal variation in rainfall between sites as these factors are also known to affect leaf size (Webb, 1968).

6.3.2 Leaf Width and Temperature.

Width does not decrease stepwise along a linear gradient from the warmest to the coolest forest type (Fig. 4.47). There are however apparent differences in the signatures of the four forest types. The leaves in CMVF differ from the leaves in the CNVF litter by a general increase in length. This relationship is reflected by the high similarity in the cumulative frequency distributions of leaf area for CNVF and CMVF.

A linear regression of the mean leaf width for each site with the estimated annual average temperature of each site (Fig. 6.7) also suggests that there is no simple relationship between leaf width and the temperature characteristics of the forest types. With all of the sites included the correlation is not as good as demonstrated for leaf length (r= 0.9482 for length; r= 0.8024 for width). However, if the strongly seasonal sites are excluded from the regression i.e. Curtain Fig (CNVF type 5a of Tracey, 1982 — seasonal rainfall), The Crater (CNVF type 5b of Tracey, 1982 — seasonal temperature), and Barrington Tops (MFF — seasonal temperature and rainfall?) — a much more significant correlation is

Fig. 6.6 Mean leaf length for each site plotted against the mean annual temperature of the site.

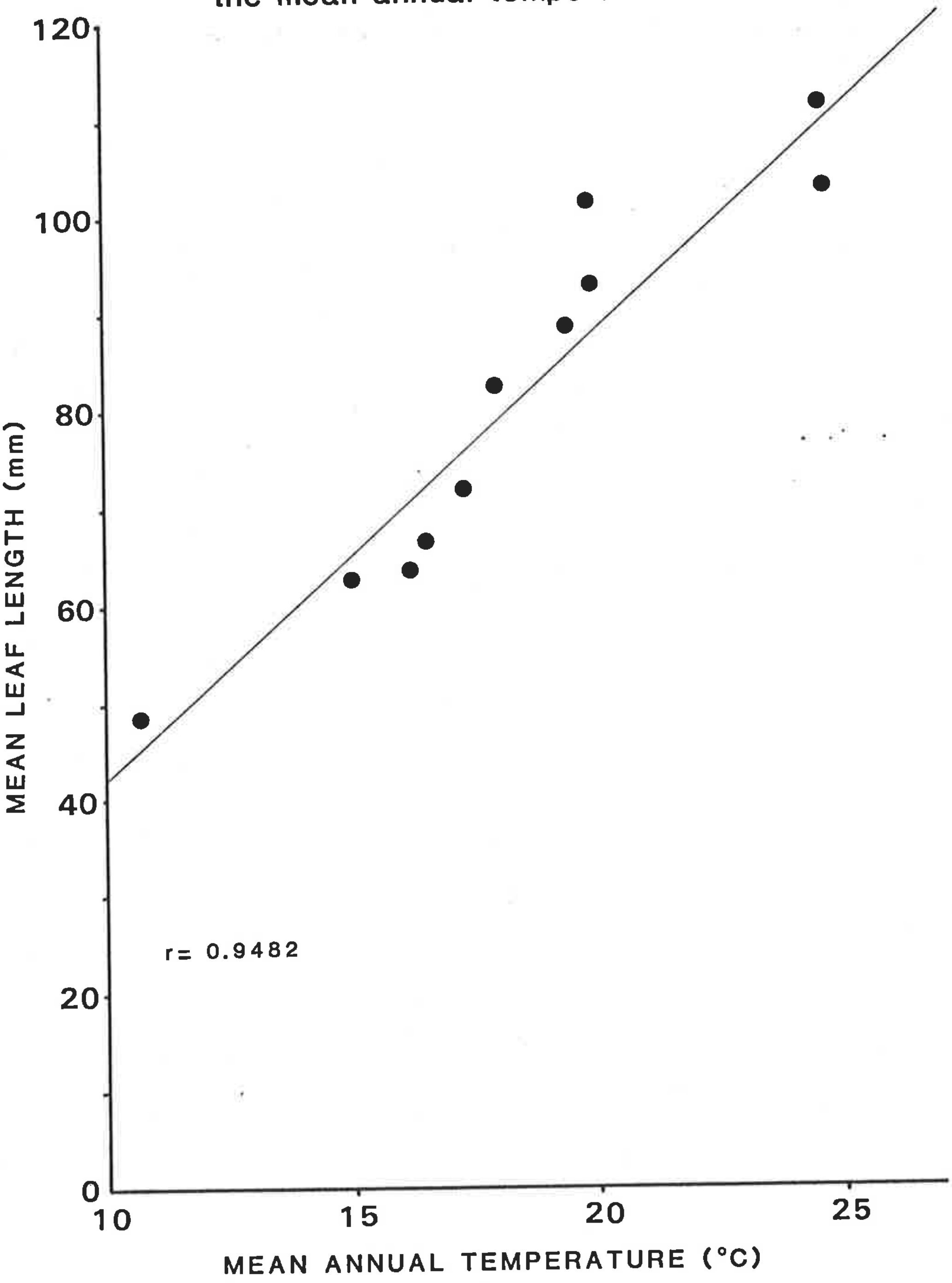
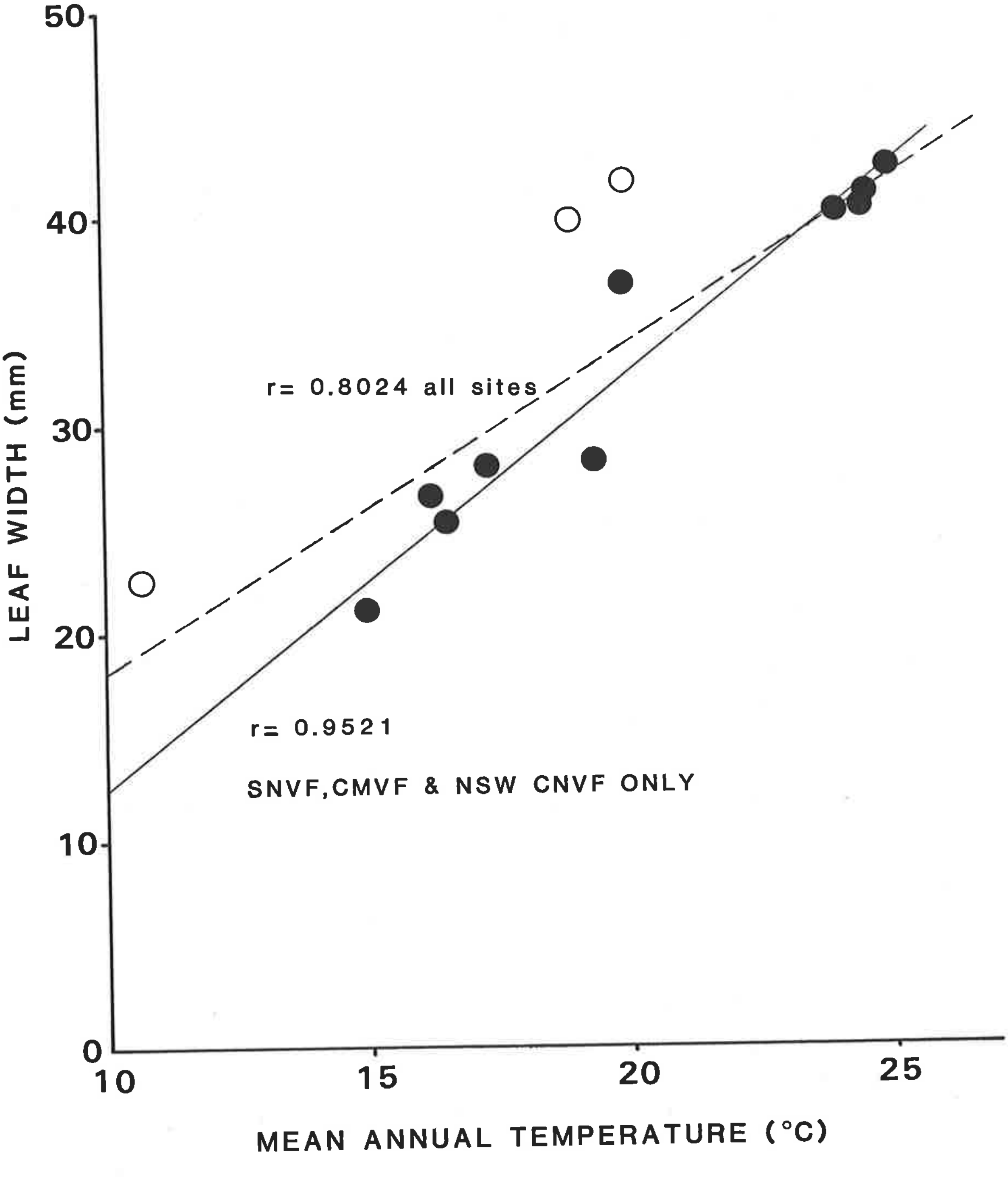


Fig. 6.7



LEAF WIDTH (mm)
50
40
30
20
10
0
10
15
20
25
MEAN ANNUAL TEMPERATURE (°C)
r= 0.8024 all sites
r= 0.9521
SNVF,CMVF & NSW CNVF ONLY

Table 6.2

Mean Leaf length and Estimated Mean Annual Temperatures for the Leaf-litter Collection Sites.

Forest / Site		Elevation	Mean Leaf Length	Estimated Temperature
MFF	Barrington Tops	1500m	48.6mm	10.7 *
SNVF	Mt Haig	1160	66.5	16.5 **
	Mt Lewis Rd	1200	63.5	16.2 **
	Mt Lewis EP18	1050	71.8	17.3 **
	Washpool Ck	800	62.8	15.0 *
CNVF	Curtain Fig S.F.	720	92.9	19.9 (1)
	The Crater N.P.	980	82.6	17.9 **
	Dorrigo N.P.	100	88.4	19.4 *
CMVF	Mobo Ck	720	101.3	19.9 (1)
	Oliver Ck	10	103.0	24.6 (2)
	Mulgrave River	120	111.7	24.5 **

* based on a lapse rate of 7.7°C / 1000m and a baseline datum of 25.4 C at sea level.

** based on a lapse rate of 6.2°C / 1000m and a baseline datum of 20 C at sea level.

(1) T°C taken from Kairi Experimental Station (17°12′S, 145°34′E; elev. 714.5m; Aust. Bur. Met., 1983).

(2) T°C taken from Port Douglas (16°29′S, 145°28′E; elev. 4.0m; Aust. Bur. Met., 1983)

acheived (r= 0.9521).

These results suggest that whereas leaf size as measured by leaf length is increasing proportionally with increases in the annual average temperature, leaf width is also influenced by rainfall and temperature variation. This variablity can also be expected to influence the relationship of the mean leaf area to the climate.

6.3.3 Leaf Area and Temperature.

The foliar physiognomic signatures of the four forest types demonstrated that leaf area did not discriminate effectively between MFF and SNVF, and between the two N.E. Queensland examples of CNVF, and CMVF (Fig. 4.48). A linear regression of leaf area and the estimated annual average temperature of the leaf litter collection sites (Fig. 6.8) demonstrates a lesser correlation (r= 0.9056) than demonstrated for leaf length and annual average temperature (r= 0.9482). If the more seasonal sites are excluded (see discussion above), a more significant correlation is demonstrated (r= 0.9678).

This data emphasises the point made above that the Curtain Fig, Crater, and Barrington Tops sites appear to be responding to their more seasonal climates by producing on average wider leaves than would be produced at the same annual average temperature under a non-seasonal regime (eg. Dorrigo CNVF). This evidence suggests that leaf length is a better indicator of the prevailing temperature characteristics of a forest than leaf area (or width). Leaf area and width may therefore act as indicators of the seasonality of the climate.

A linear regression of the position of maximal width and annual average temperature (Fig. 6.9) demonstrates no relationship between these two variables, however serves to illustrate the preponderance of leaves with the widest part in the lower third of the leaf in the seasonal sites. This effect could be due to the high proportion of vine leaves in the Curtain Fig site (28.1 – 40.6 % of leaves), however in the Crater and Barrington Tops litter samples the proportions were no greater (or in the case of Barrington Tops, significantly less; 0 – 1.3 %) than for the other sites.

The higher proportion of leaves with a position of maximal width in the lower

Fig. 6.8

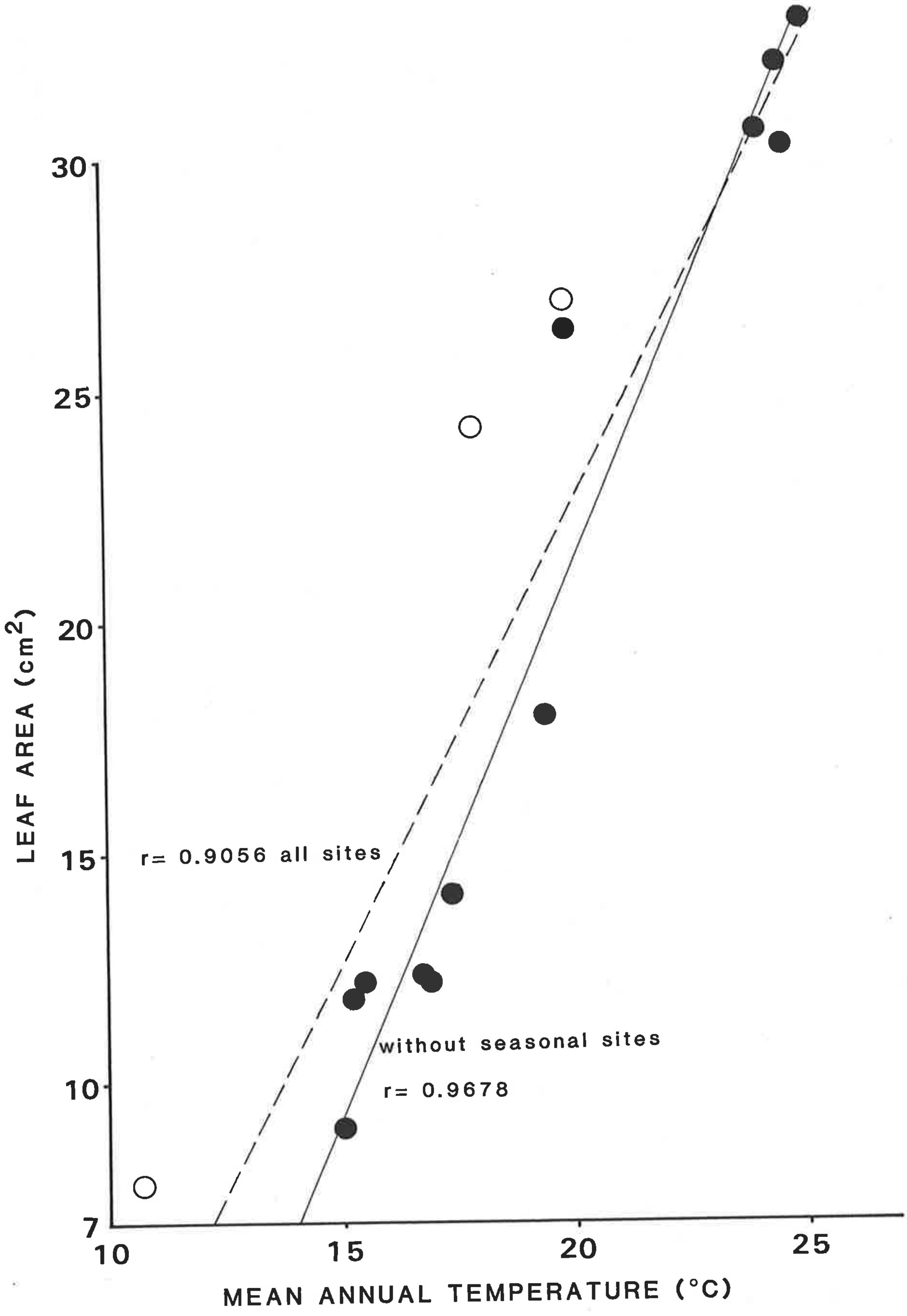
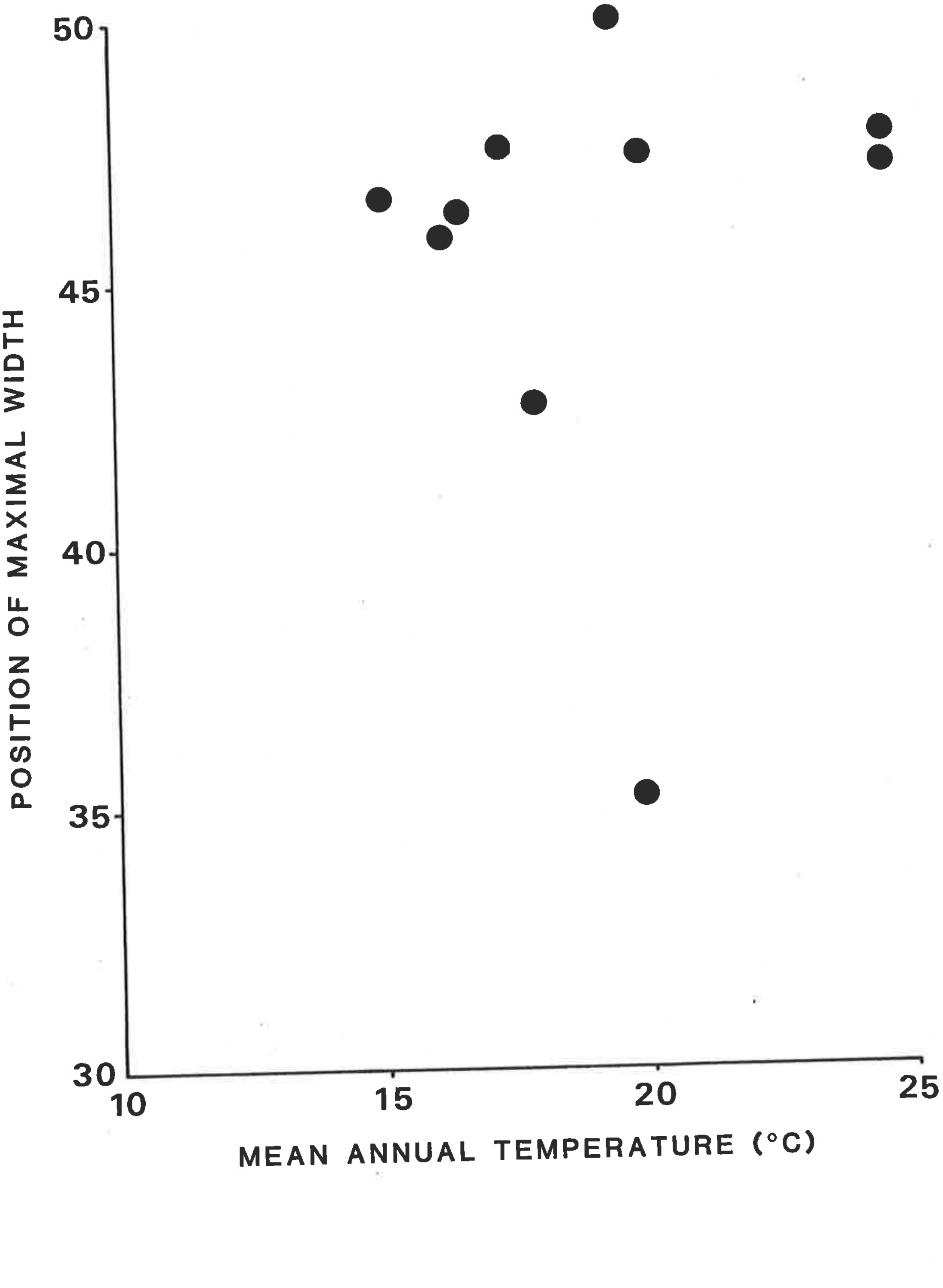

LEAF AREA (cm2)
30
25
20
15
10
7
10
15
20
25
MEAN ANNUAL TEMPERATURE (°C)
r= 0.9056 all sites
without seasonal sites
r= 0.9678

Fig. 6.9


50
45
40
35
30
10
15
20
25
POSITION OF MAXIMAL WIDTH
MEAN ANNUAL TEMPERATURE (°C)

third of the leaf (i.e. non-elliptic) in the Curtain Fig, Crater and Barrington Tops sites suggests a causal linkage between seasonality and leaf shape. The lack of more detailed data on climate for the litter collection sites prevents further analysis at this stage. The general uniformity and narrow range of the annual average range of temperature for rainforest sites in Australia (Fig. 6.3) suggests that perhaps other factors are important in producing these differences in leaf width and position of width, perhaps the incidence of extreme weather conditions such as frost or occasional short droughts.

6.4 Leaf Margin Analysis.

Bailey and Sinnott observed that the floras of particular regions showed a correlation between the proportion of species with non-entire margins and the temperature characteristics of that region (Bailey and Sinnott, 1916). Wolfe's physiognomic and climatic classification of the moist forests of SE Asia took this observation further, and demonstrated strong relationships between the proportion of canopy species in these forests with non-entire margins and both the annual average temperature and the annual average range of temperature (Wolfe, 1971, 1980a).

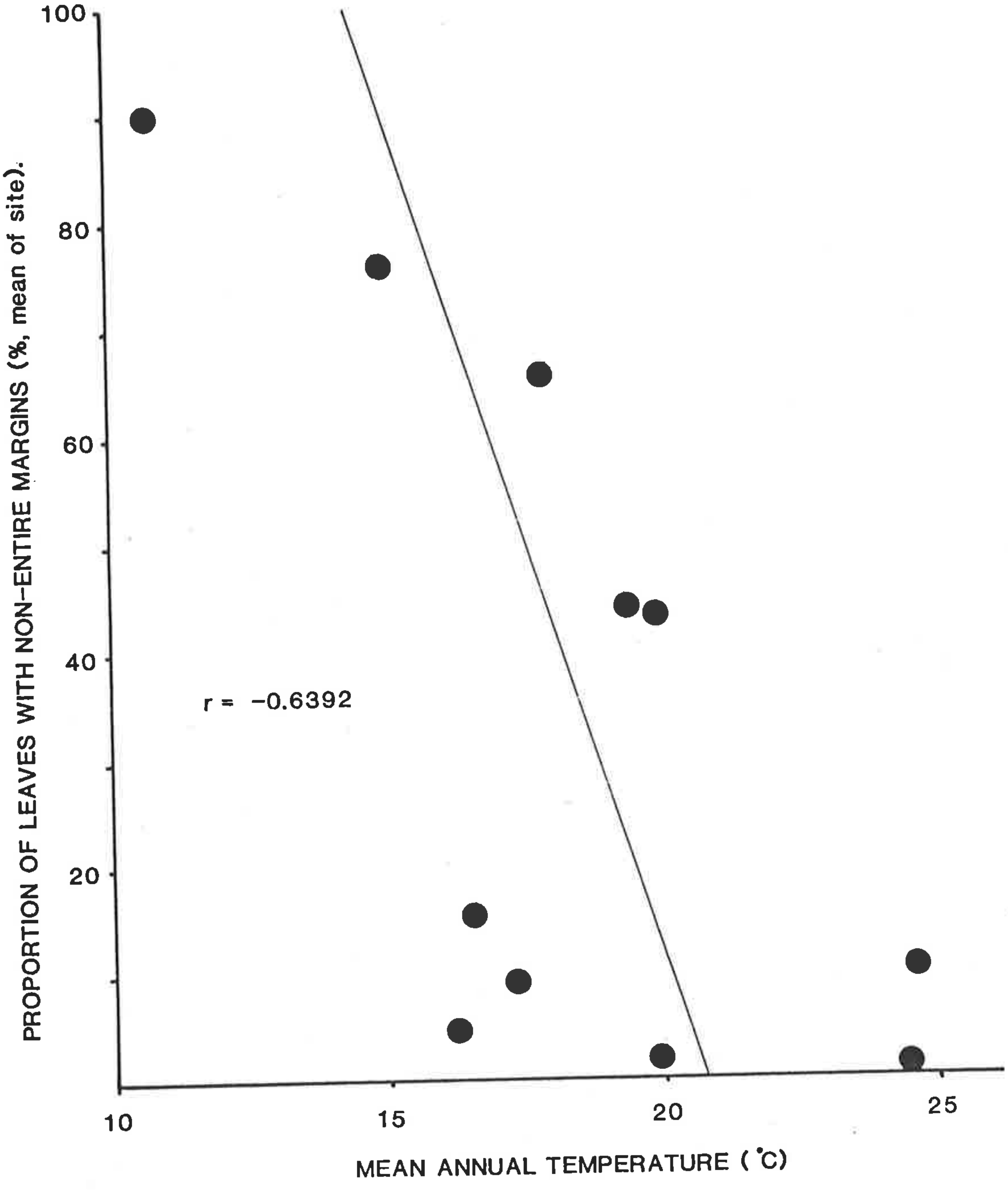
Dolph criticised Wolfe for only considering canopy species as he found that the subordinate species in the forests of Indiana showed no correlation with annual average or annual average range of temperature (Dolph, 1984). Fossil leaf beds are likely to contain leaves from all of the synusiae of the forest, and not just those of the canopy (Ferguson, 1985).

The greatly differing species diversity between sites, however, (eg. Barrington Tops, total 5 spp; Mt Lewis EP18, total 27 spp), suggests caution with a comparison based on the proportion of species with non-entire margins. A linear regression of the mean proportion of leaves with non-entire margins for each site, and the estimated annual average temperature of each site, shows no clear relationship between these factors (Fig. 6.10).

There is a general trend toward higher proportions of individual leaves with non-entire margins for each site with increasing latitude (Table 6.3) and to a lesser

Fig. 6.10

RELATIONSHIP OF LEAF MARGIN TO MEAN ANNUAL TEMPERATURE.



extent in the tropics, with increasing altitude. Seasonal range of temperature [ie the annual range of temperature of Wolfe (1971 1980a)] also generally increases with latitude. The change along the east coast of Australia, however, is slight, and the local variation is often greater than the variation between distant regions (Fig. 6.11). The incidence of frost, and hence the incidence of extremes in the daily minimum temperature, increase with latitude, particularly further inland (Anon., 1983).

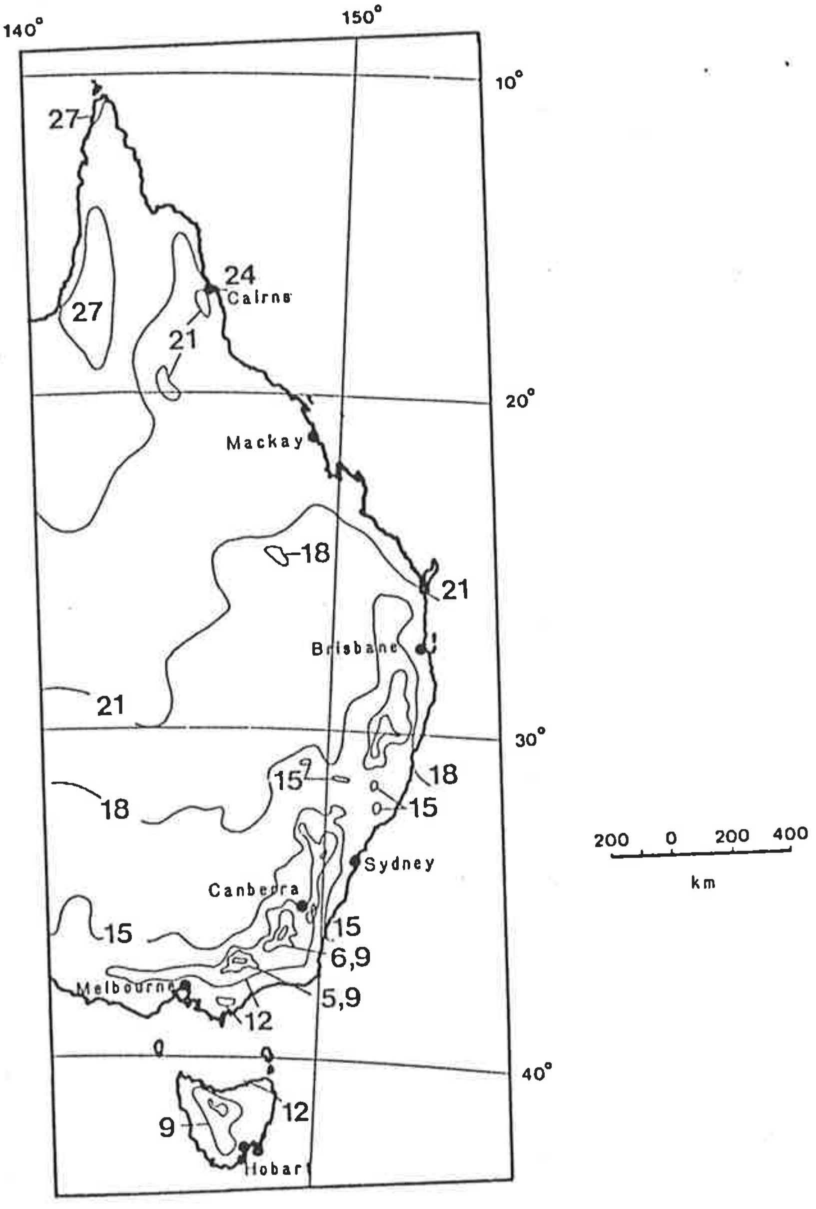
The incidence of these temperature extremes is seemingly masked in the annual range of temperature used by Wolfe (1971 1980a). For example, despite similar annual average temperature and annual average ranges of temperature, the number of frost days experienced by Kairi and Grafton is quite different (c.10 to c.30 days/year). This may reflect an averaging effect from much milder days over the same measuring period for Grafton. This is perhaps an area which should be further examined.

6.5 Discussion.

The discussion of the climatic characteristics of the forest types (above) illustrated the interaction of edaphic — soil type — and climatic factors — temperature and rainfall — in determining forest type in N.E. Queensland (Fig. 2.1). The strong correlation between the mean leaf length of the leaf litter from the sites and the estimated annual average temperature of these sites suggests that leaf length is primarily controlled by temperature, whereas the structural complexity of the forest is determined by an interaction of edaphic and climatic factors (eg. Webb, 1968; Tracey, 1982).

At the extreme climatic limits of a forest type — eg. lower temperatures or more seasonal rainfall — higher soil fertility may allow that forest type to persist beyond the normal climatic limits. That is, the structural characteristics persist (Webb, 1968; Tracey. 1982). The foliar physiognomy however, more strongly reflects the climatic conditions. This implies that the dominant signal preserved in the foliar physiognomic characteristics of leaf beds derived from the rainforests types examined in this study will be climatic.

Fig. 6.11



MEAN ANNUAL TEMPERATURE, EASTERN AUSTRALIA. (Anon., 1983)

Dolph dismissed leaf width as a separate character in foliar physiognomic studies (Dolph, 1975). The data presented in Chapter 4 indicated that perhaps leaf width was reflecting different determinants to those influencing leaf length. The analysis of correlations with temperature found that the seasonal sites (mainly rainfall) departed from the expected width values for the estimated annual average temperatures of the sites. This in turn was reflected in a reduced correlation for leaf area and the annual average temperature.

Why the more seasonal sites should produce on average wider leaves is not clear. However, it can be suggested that the foliar physiognomic signatures discussed in Chapter 4 may be sensitive to the seasonality of the original climate of an area, in addition to the primary temperature characteristics. Similar comments apply to the incidence of species and individuals with non- entire margins, however the exact relationship here is even less understood (Wolfe, 1980a).

Chapter 7

LEAF LITTER AS A SPECIES ASSEMBLAGE

7.1 Introduction.

The previous chapter(s) outlined the physiognomic character of leaf litter from four types of Australian rainforest. The central aim was to determine the taphonomic bias from canopy to forest floor and thus determine the physiognomic signature of leaf beds derived from the four forest types. This was done independant of the taxonomic identity of the leaves and pooled the physiognomy of all the component taxa.

Some foliar physiognomic methods are based on the proportion of species in a flora represented in discrete classes e.g. the proportion of species with non-entire margins (Wolfe, 1980a 1987). There remain however, a number of questions relating to the taphonomic influences on the species composition of fossil leaf beds, and the recognition of species in diverse sets of leaves from leaf assemblages.

Rainforest communities are generally species rich with a high level of heterogeneity in species composition over small distances (Ashton, 1984; Connell, et al., 1984; Lieberman, et al., 1985). However, while Tertiary leaf beds in Australia are often fairly diverse, the diversity recorded for individual sedimentary units within these fossil localities is quite low (e.g. the Eocene Anglesea flora, whole flora c. 100 species; individual clay lenses 20 – 30 leaf-taxa: Christophel, et al., 1987).

The leaf-bed represented in a clay lens would be expected to represent a local area of the original forest (Dolph, 1979; Dolph and Dilcher, 1979a; Ferguson, 1985). The diversity recorded by Christophel, et al. (1987) for the lenses at Anglesea is much lower than that recorded within quite small areas of most types of rainforest (e.g. Ashton, 1984; Connell, et al., 1984; Liebermann, et al., 1986). The question remains, therefore, to what extent does the diversity in fossil leaf beds reflect the diversity in the original communities?

The composition of fossil floras has often been interpreted as representing most of the species which grew in the local area, and often the abundances of the fossil leaf taxa are taken as an indicator of the relative importance of that species in the local vegetation.

In addition, many foliar physiognomic studies have used the proportion of species represented in particular physiognomic categories. Most commonly, the characteristic leaf size of each species has been used to assess the leaf size distribution of a vegetation (e.g. Chaney and Sanborn, 1933; Beard, 1944 1955; Webb 1959; Grubb, et al., 1966; MacGinitie, 1969; Dilcher, 1973; Dolph and Dilcher, 1979a). Bailey and Sinnott (1915 1916), and more recently, Wolfe (1971 1980 1987), used the proportion of species with non-entire margins.

This procedure makes a number of assumptions which are perhaps flawed. Bailey and Sinnott's and Wolfe's observations are based on regional floras (Bailey and Sinnott, 1915 1916; Wolfe, 1971 1980a) and so may be argued to be unrepresentative of the local leaf fall found in most fossil deposits (Dolph, 1984; Ferguson, 1985). However, the leaf size and leaf margin studies relied on the assumption that species relationships observed in the local vegetation (i.e. the proportion of species in each physiognomic class and the actual class of a species (e.g. Dolph and Dilcher, 1980), will be the same for both the vegetation and the leaf beds.

Several studies on recently deposited leaf litter in lake beds however, have found that these leaf beds gave a very biased account of the species composition of the vegetation of the surrounding catchment, and the abundance of individuals of those species in that vegetation (e.g. McQueen, 1969; Rau, 1976; Drake and

Burrows, 1979; Hill and Gibson, 1986).

There are several factors which will determine the foliar representation of taxa by in a fossil deposit and in turn the recorded diversity for a fossil flora. It is generally assumed that plant material is deposited within a small distance (100's of metres) of the life position of the source plant (Chaney, 1924; Chaney and Sanborn, 1933; Ferguson, 1985), although 'catastrophic' deposition such as during volcanic eruptions or floods suggests that material may occassionally be transported great distances (10's to 100's of kms; Spicer, 1980).

In the more general cases however, such as cut-off stream meanders and lakebeds, leaf input is essentially going to represent the local or at best, extra-local vegetation (Ferguson, 1985; Spicer and Wolfe, 1987). Leaf input by particular taxa to these depositional basins is therefore going to be determined by leaf availability and influences on leaf transport from the tree to the water body (Chaney, 1924; Rau, 1976; Ferguson, 1985). The taxonomic diversity of a deposit is going to reflect the diversity of the immediate area contributing leaves to the deposit (Ferguson, 1985), and the probability that leaves from particular species will actually enter the deposit.

This probability will be governed by a number of factors (Chaney, 1924; Rau, 1976; Ferguson, 1985):

1. the distance of the tree(s) from the depositional basin,
2. the abundance of the trees in the local vegetation and the abundance of the leaves on the trees (which is assumed to be proportional to the size of the tree),
3. obstructions between the trees and the depositional basin such as screening vegetation.

Work in Temperate forests (Ferguson, 1985) has demonstrated that leaves are transported horizontally not much further than the height of the source tree and that the majority of the leaves land within a few metres of the trunk. The complex stratification of tropical forests adds additional complexity to the fall-path of leaves (Bourgeron, 1983; Golley, 1983; Ferguson, 1985) as the canopy of trees at lower levels will potentially deflect or prevent passage of leaves from the canopy to the forest floor. Similarly, the often well developed screen of vegetation along streams and lakes potentially will filter the flow of leaves from the forest interior to a depositional site (Spicer, 1981; Ferguson, 1985).

A further issue is the morphological variation of the species contained in a deposit. Several studies using leaf morphology in taxonomic analyses have commented on the often high level of variability in leaf size and shape within plant populations (e.g. Hu Chia et al., 1986; Burnham, 1986). Eckenwalder (1986) stressed the need for palaeobotanists to be aware of the natural variability in leaf form within a species at one locality when making decisions about species boundaries.

The convergence in leaf form in rainforest leaves from quite unrelated species has attracted considerable comment by numerous researchers, as has the distinctive leaf form of the various synusiae in rainforest and the differences between leaves of various stages in the growth of large trees (Richards, 1952). This last point is of particular importance as it has often been commented that there are often quite extreme differences between the size and general morphology of 'sun' and 'shade' leaves from rainforest leaves (Richards, 1952; Roth, 1984; Fig. 4.11).

It is reasonable to expect that leaves of both types from a single species or individual may occur together in a fossil leaf bed. Similar heterophylly in *Populus* (Salicaeae) prompted Eckenwalder to caution against the setting of very strict morphological boundaries when describing Tertiary fossil species from leaves (Eckenwalder, 1986).

Leaf litter to a large extent preserves a level of morphological variation within individual species similar to that expected in a fossil leaf bed. Therefore, analysis of the level of variation within taxa within litter samples will suggest a level of variation to be expected in a fossil leaf bed. Such an analysis will allow better appreciation of taxonomic boundaries in fossil taxa defined from leaf morphological data.

As a result, this chapter explores three issues:

1. the variation in species diversity and representation between leaf bed samples from a single forest type, and between forest types, and the causes of

this variation;

2. the controls on representation in fossil leaf beds;
3. the level of variation in leaf morphology within individual species from litter samples to assess, a) the representation of individual species in leaf size classes, and b) to determine the boundaries of leaf taxa in leaf beds.

The leaves in each sample from the litter collections have either been identified to a species, or assigned to an artificial grouping (or parataxon). The number of leaves in each taxon for each sample has been tallied, and the number of species in common between samples from the same site determined to measure the overall diversity of the site. A comparison of the frequency of each taxon in each sample for one site from each of the forest types is used to illustrate the local nature of the leaf fall.

A sample from a single site from each of the forest types has been selected where the synusial origin of the leaves is previously known. The physiognomic characteristics of a selected group of species from each of these samples is discussed individually and the level of variation within each species is then assessed.

7.2 Measuring Taxonomic Diversity in Leaf Beds.

The number of species (and parataxa) identified for each sample is given in Table 7.1. There is a clear trend for the N.E. Queensland SNVF sites to have the highest diversity. The CMVF and CNVF litter samples have comparable diversity. The New South Wales SNVF has a very low diversity, comparable to the MFF from New South Wales, however this reflects the very low diversity of these forests.

The autochthonous stream samples (sample no. 1 site 4, and site 5) from SNVF have a very similar number of species to individual forest floor samples from equivalent sites of SNVF. The allochthonous sample from N.E. Queensland (sample no. 2 site 4), however, has a diversity similar to the site totals for the N.E. Queensland SNVF.

Complex mesophyll Vine Forest is generally more species rich than SNVF (Webb, et al., 1970 1984). The lower diversity of CMVF litter compared to

Table 7.1

Number of Species Recorded for Each Site.

Forest-Type	Site	Sample no. 1	2	3	4	Site Total
SNVF/NEQ	Mt Haig	19	23	21	20	28
	Mt Lewis Rd	20	18	22	20	26
	Mt Lewis EP18	21	19	20	20	27
	stream	22	31	--	--	38
/NSW	Washpool	7	4	7	7	7
	Stream	7	--	--	--	7
CNVF/NEQ	Curtain Fig	16	12	13	14	24
	The Crater	14	16	--	15	23
/NSW	Dorrigo	10	10	10	10	15
CMVF/NEQ	Oliver Ck	--	17	16	19	32
	Mulgrave R	18	20	17	18	30
	Mobo Ck	17	18	15	19	33
MFF	Barrington Tops	5	3	5	3	5

SNVF litter (Table 7.1) is at first sight contradictory but is explainable in terms of the spatial distribution and relative size of trees in each of the forest types.

The Complex Mesophyll Vine Forest's typically have three tree layers, and the largest trees may reach 45 metres (Tracey, 1982). These massive trees dominate the local canopy with large spreading crowns (pers. observ.) and it is not uncommon to have the understory near such individuals dominated by saplings of these trees. However, the spatial heterogeneity of these forests is such that within a distance of 200 metres the canopy will be composed of very different species (Ashton, 1984; Connell, et al., 1984; Lieberman, et al., 1985).

In contrast Simple Notophyll Vine Forest often has only two tree layers with the tallest trees at 30 – 35 metres with a much narrower crown than the canopy and emergent trees in CMVF. The smaller size of the canopy trees in SNVF ensures that a smaller area of the canopy is dominated by a single species than is the case in CMVF. With each litter sample only 10 – 20 metres from the other samples, the physical size and spread of the canopies of the trees in CMVF ensures that fewer species were contributing leaves to the collection points than in the SNVF.

The representation of the principal species of one site from each forest type is contrasted between samples in Figures 7.1 – 7.8, where the length of each bar represents the frequency of leaves belonging to a taxon from that sample.

As can be seen from the histograms, the frequency of occurrence of the taxa selected varies considerably between samples in some cases, and only by a small amount in other cases. The dominant leaf taxon varies quite markedly between each of the samples from the CMVF example, Mulgrave River (Fig. 7.1). Taxon 4 is co-dominant with taxon 1 in sample 1, whereas taxon 12 (sample 2), taxon 8 (sample 4), and taxon 6 (sample 5) are clearly dominant in the other samples. Taxon 6 is only represented by a single leaf in sample 1, yet represents over 35% of the leaves from sample 5.

Both of the CNVF examples, Curtain Fig (N.E. Queensland, Fig. 7.2) and Dorrigo (New South Wales, Fig. 7.3; Table 7.4), reflect a slightly different situation to the CMVF with two species dominating all but one sample. Taxon

Fig. 7.1 Relative contribution of 5 taxa to four litter samples from CMVF (Mulgrave River)

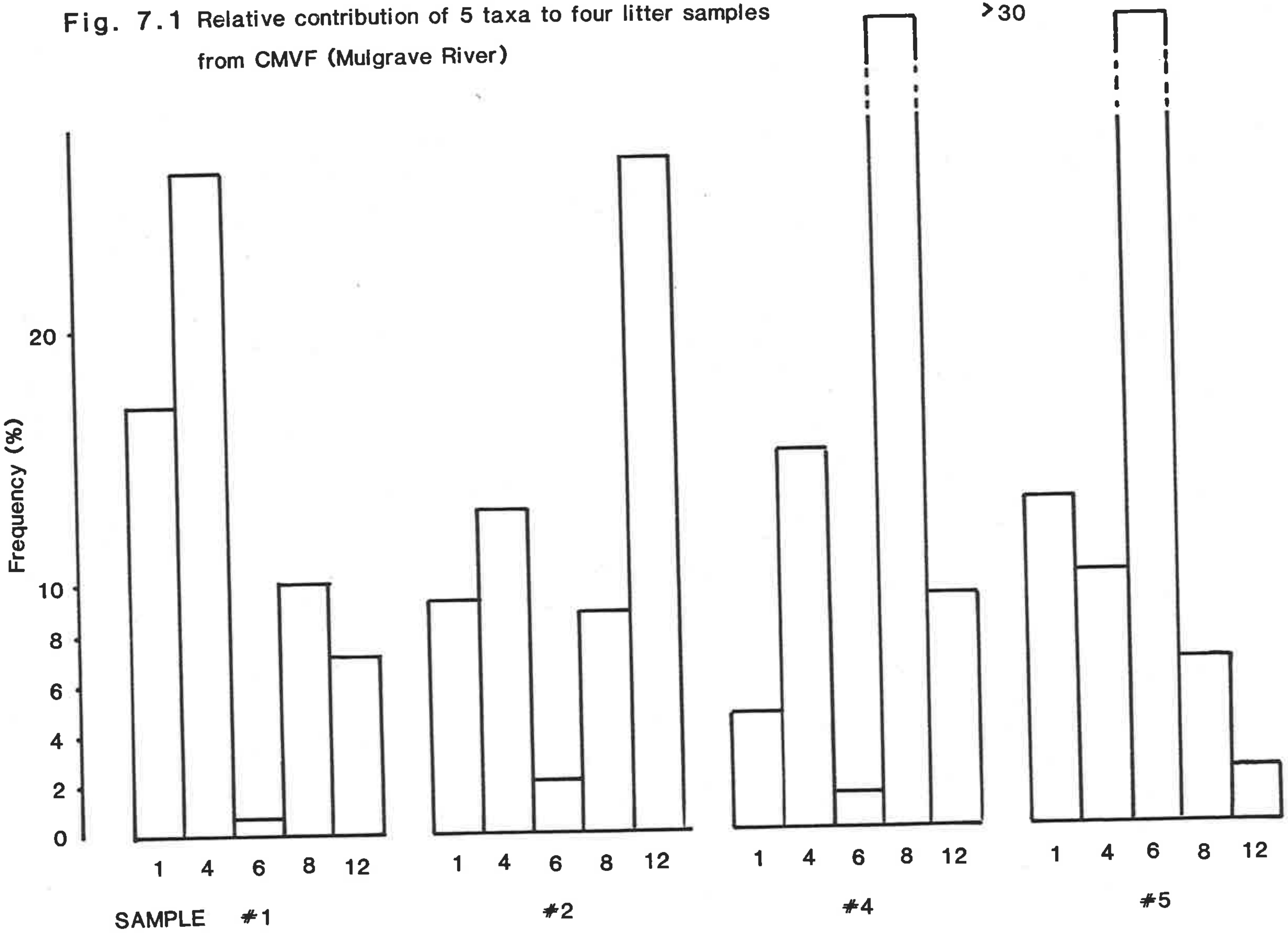


Fig. 7.2 Relative contribution of 5 taxa in four litter samples from CNVF (Curtain Fig.)

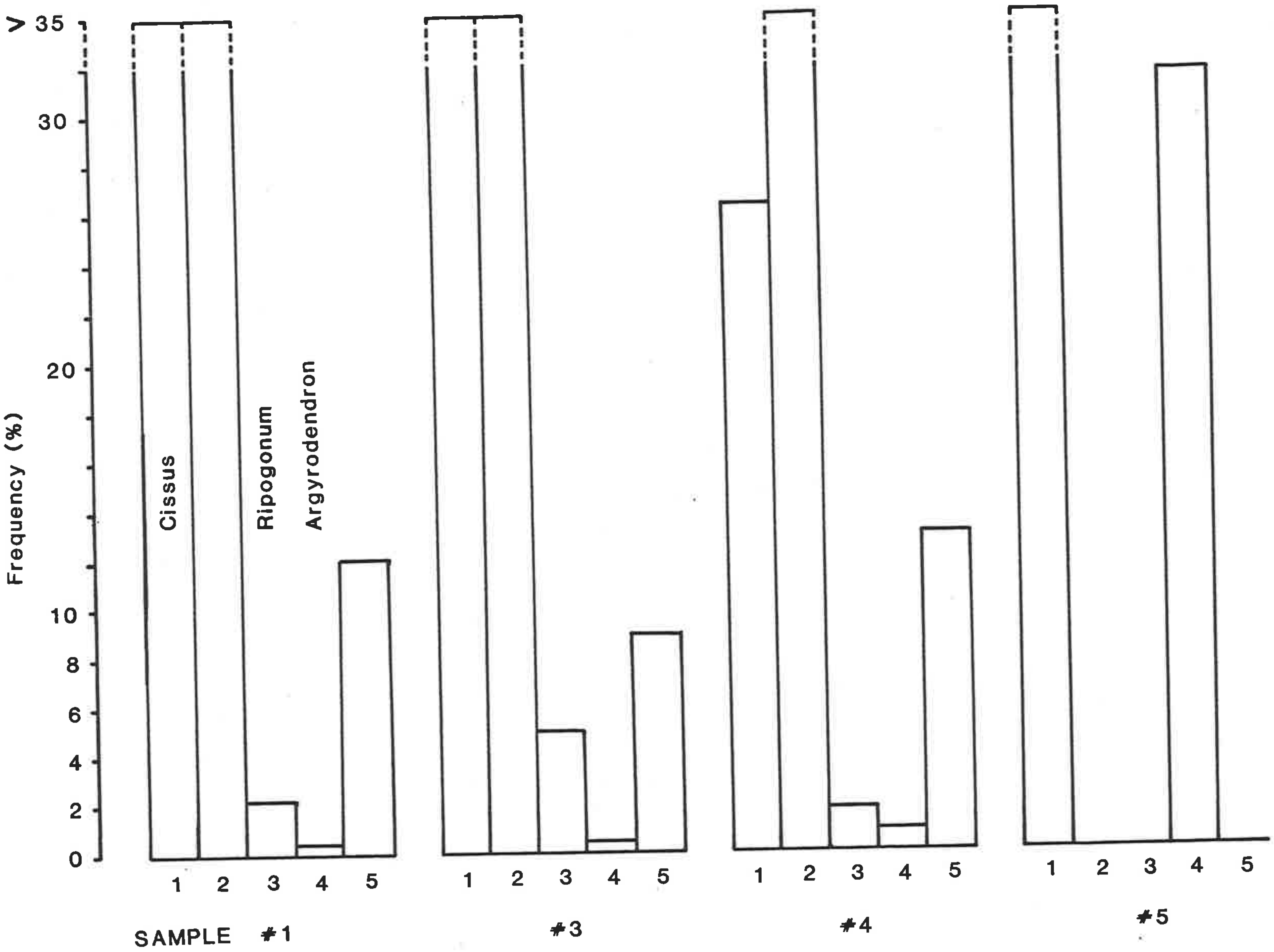
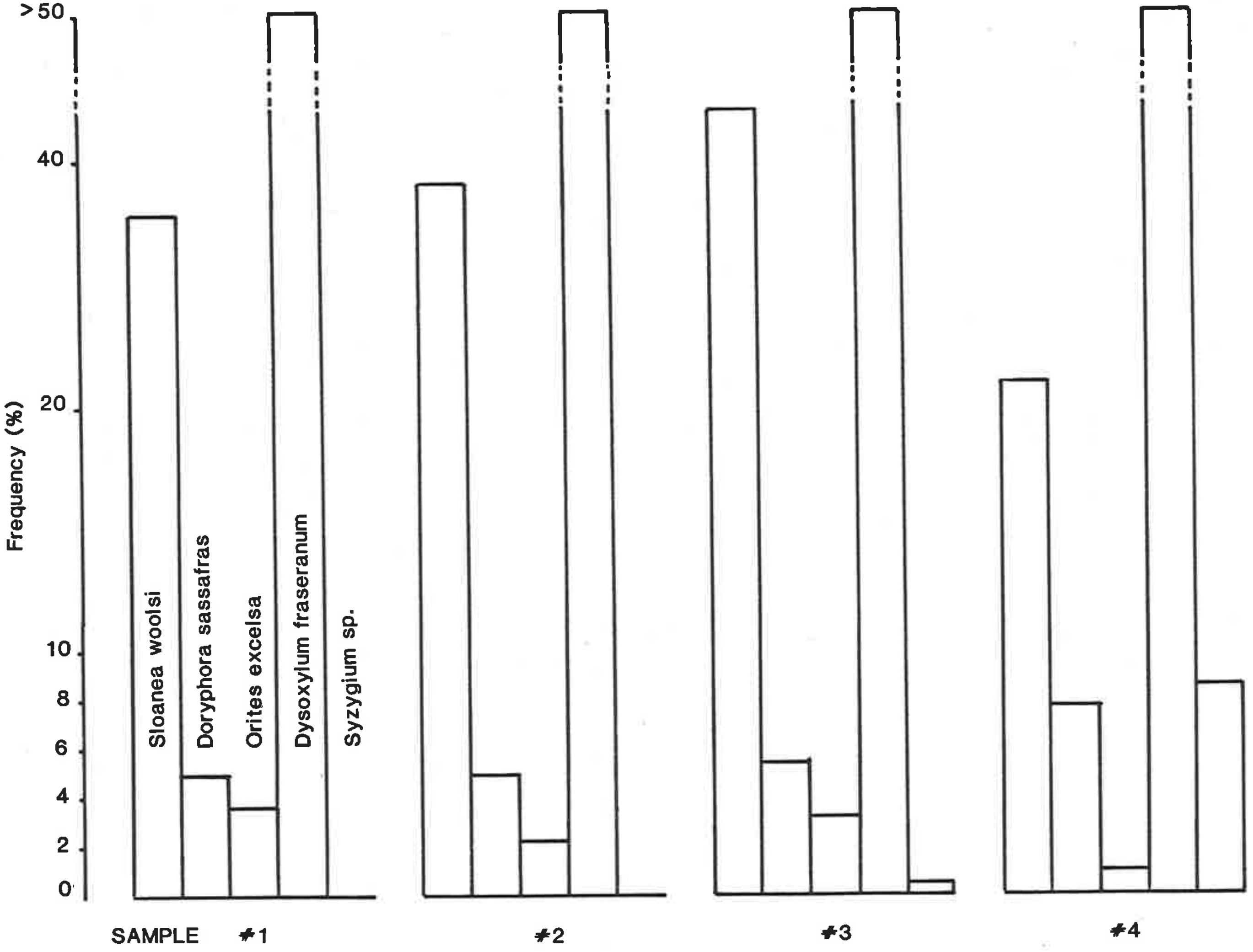


Fig. 7.3 Relative contribution of 5 taxa to four litter samples from CNVF (Dorrigo, NSW).



1 of Curtain Fig represents a vine, *Cissus antarctica* (Vitaceae), and taxon 2 a canopy tree, *Toona australis* (Meliaceae). Both of the dominant taxa in the Dorrigo example are canopy trees, *Sloanea woolsii* (Elaeocarpaceae), and *Dysoxylum fraseranum* (Meliaceae). The other taxa present at these sites vary greatly in frequency between samples.

The SNVF examples represent a site from the diverse N.E. Queensland forests (Mt Lewis EP18, Figs 7.4 – 7.7) and the species poor New South Wales SNVF (Coombadjha Ck, Fig. 7.8). The Mt Lewis data will be discussed in detail later, however a brief comparison with the other site and the other forest types is presented here.

Three of the samples from the Coombadjha Ck SNVF site were dominated by two species, *Ceratopetalum apetalum* and *Doryphora sassafras*, however, all had high frequencies of *C. apetalum*. The subcanopy tree and shrub species varied greatly in frequency between samples, with some totally absent in one sample and very abundant in another (e.g. *Quintinia sieberi*).

The Mt Lewis EP18 SNVF site demonstrated a pattern of representation and abundance between samples similar to the Mulgrave River CMVF example. With the possible exception of taxon 15 (Lauraceae), no taxon occurred in all samples at a similar frequency. In particular, in contrast to the CNVF examples and the Coombadjha Ck SNVF example, no species was or were dominant in all of the samples.

The Barrington Tops MFF example (Fig. 7.9) demonstrates a similar pattern to the CNVF and Coombadjha Ck SNVF examples with one species dominating each sample (*Nothofagus moorei*), and the other species varying greatly in frequency between samples. In each of these cases, the main canopy tree species of the site has dominated the leaf litter samples.

These observations have implications to the interpretation of fossil leaf beds. Often a particular horizon in a fossil leaf bed will reveal localised concentrations of the leaves of particular taxa. In situations of quiet water and direct fall of leaves into the point of deposition, it is plausible that these concentrations reflect the presence of a nearby large tree (and prolific source of leaves). The relationship

Figs 7.4 – 7.7. Relative contribution of all taxa to four litter collections from Mt Lewis EP18.

Fig. 7.4

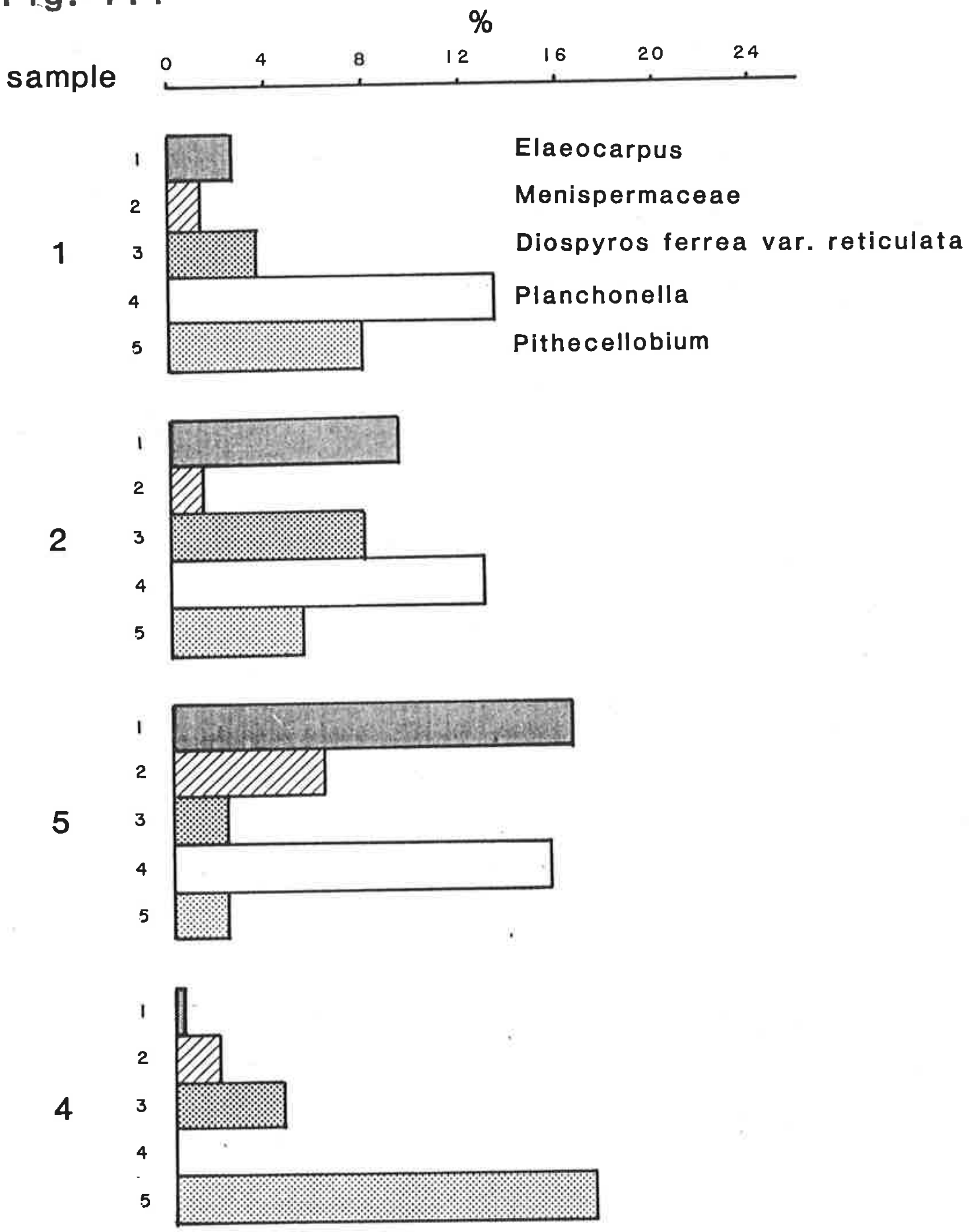


Fig. 7.5

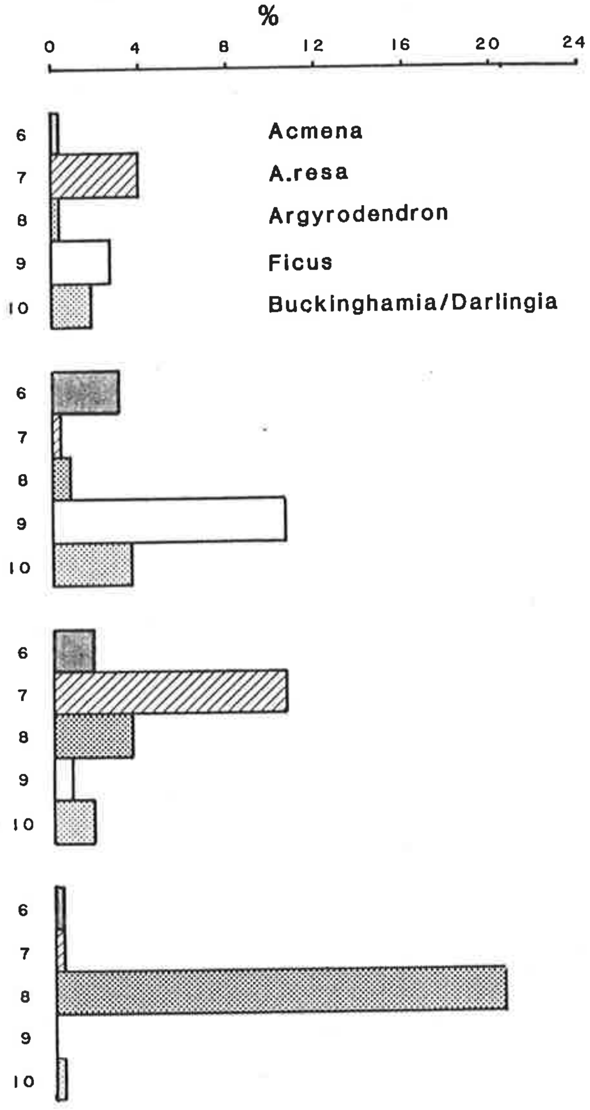
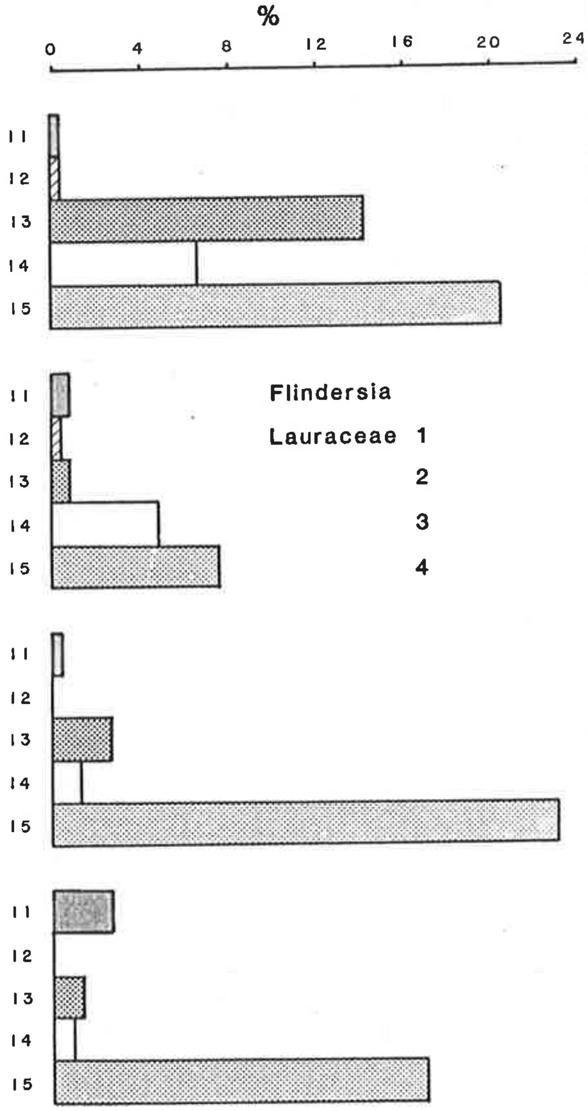

%
0
4
8
12
16
20
24
6
7
8
9
10
Acmena
A.resa
Argyrodendron
Ficus
Buckinghamia/Darlingia

Fig. 7.6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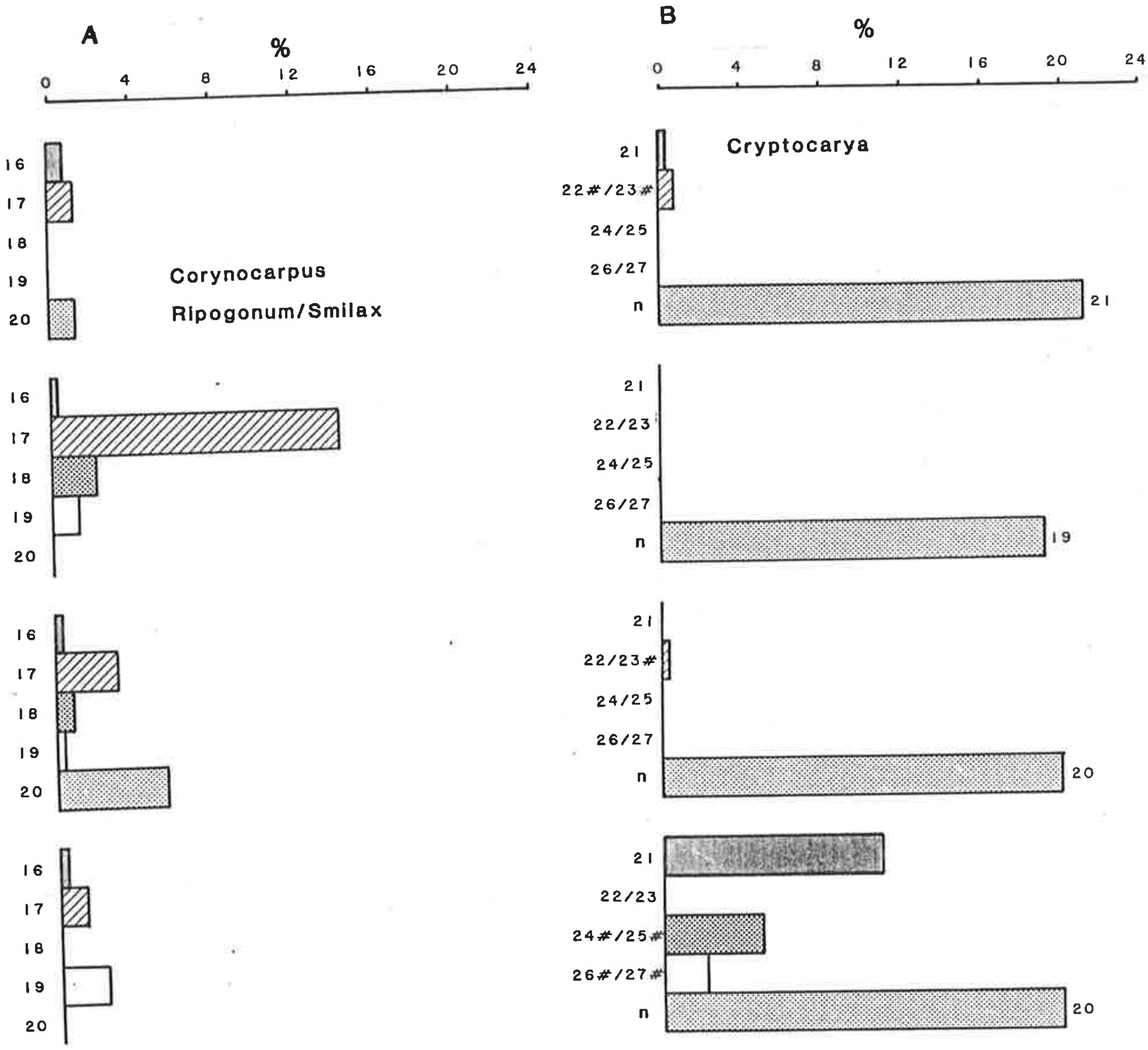
Flindersia
Lauraceae 1
2
3
4

Fig. 7.7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18
19
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Corynocarpus
Ripogonum/Smilax
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B
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0
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8
12
16
20
24
Cryptocarya
21
22#/23#
24/25
26/27
n
21
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22/23
24/25
26/27
n
19
21
22/23#
24/25
26/27
n
20
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22/23
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26#/27#
n
20

Fig. 7.8 Relative contribution of 6 taxa in four litter samples from SNVF (Washpool, NSW).

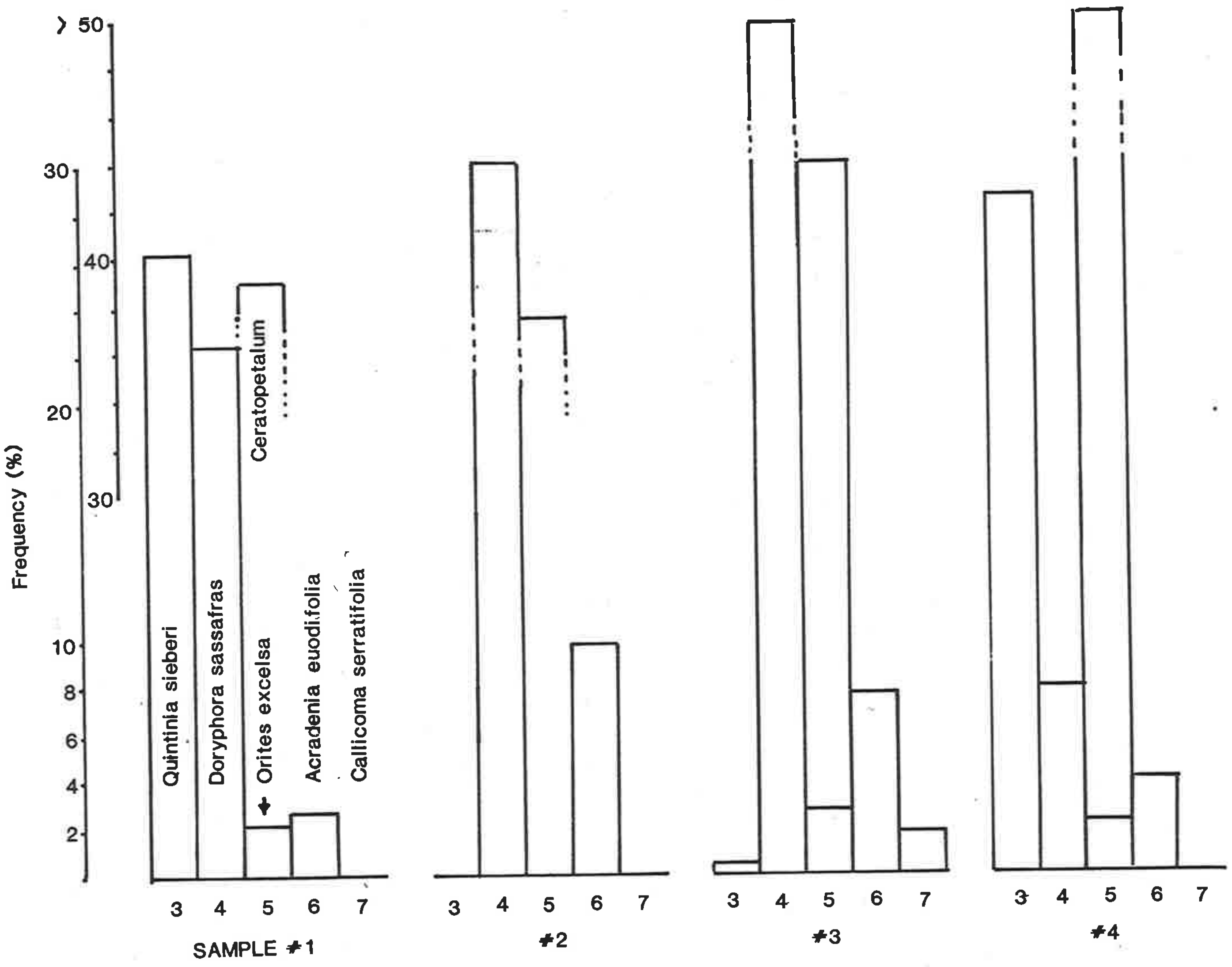
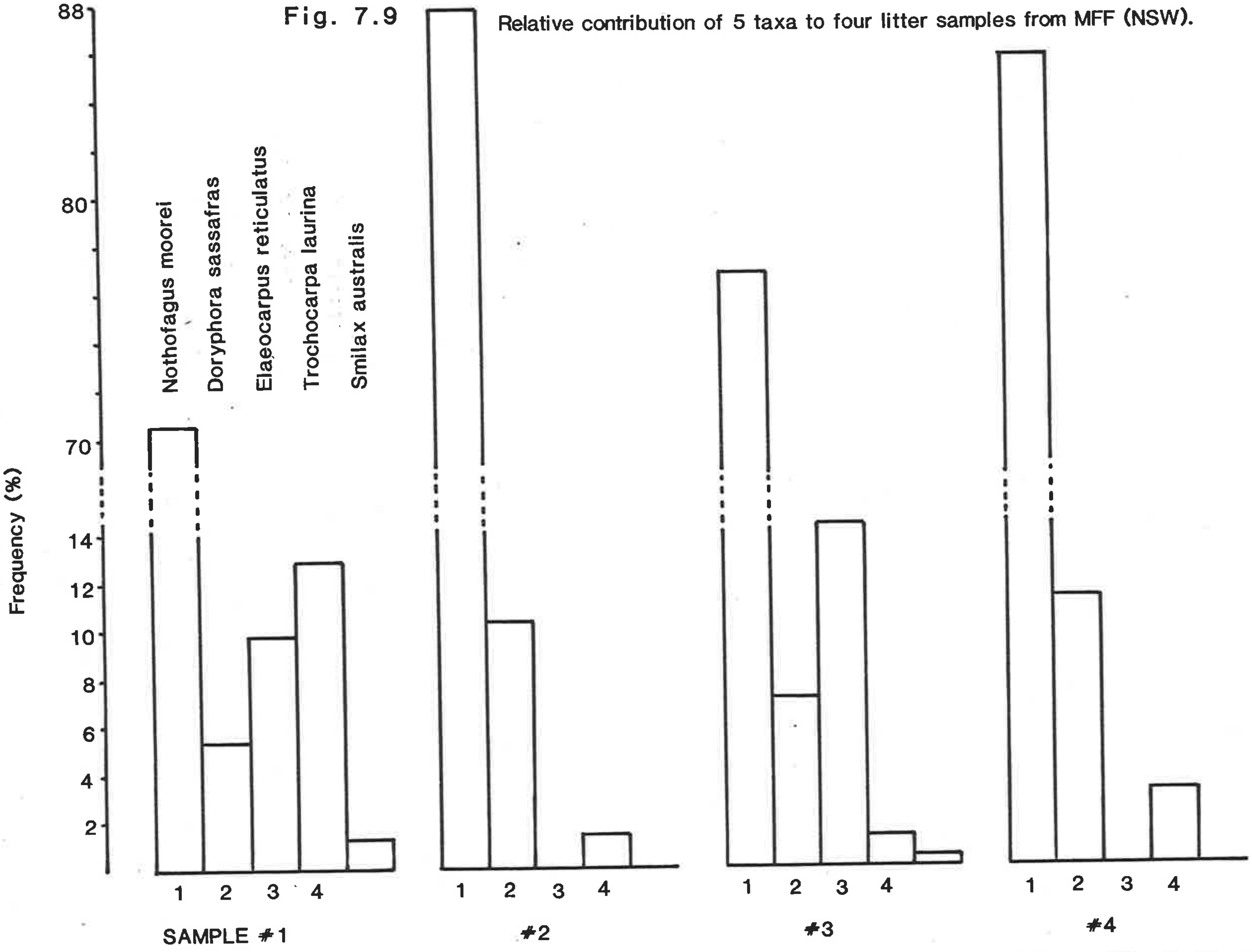


Fig. 7.9 Relative contribution of 5 taxa to four litter samples from MFF (NSW).



between the size (and by inference, size of its leaf input) and position of a tree in the forest, to its representation in leaf beds, is examined in the next section.

7.3 Leaf Movement in a Rainforest.

Two studies were made to assess the movement of leaves in a tropical rainforest environment. In an initial study, two transects were run out from the trunk of an isolated individual of the rainforest conifer, *Prumnopitys amara* (Podocarpaceae) in a patch of Complex Notophyll Vine Forest on a hill near Atherton (Fig. 7.10).

Access to a CSIRO permanent plot (Experimental Plot 18) in the Mt Lewis area (Fig. 3.13) provided an opportunity to examine leaf movement in more detail in Simple Notophyll Vine Forest. All of the trees in an area 500 x 250 m were previously identified and numbered and their positions mapped by CSIRO researchers (G. Stocker and G. Unwin, CSIRO Centre for Tropical Forest Research, Atherton N.E. Queensland, pers. com, 1985).

This data allowed both the identification of many of the leaves in the litter samples, and the source of these leaves. The presence of a diverse, but largely unidentified shrub layer, however, ensured the input of a significant number of leaves of unknown origin.

7.3.1 Site description.

The first study was sited in a small patch of Complex Notophyll Vine Forest on a small volcanic hill behind the town of Atherton, Queensland (Fig. 7.10). The north slope was chosen as the forest was less disturbed here. The site characteristics of the nearby Curtain Fig site apply to this area, although Atherton probably experiences greater seasonal dryness then the Curtain Fig area (Gordon, 1971; Tracey, 1982; Fig. 2.10).

A number of individuals of *Prumnopitys amara* (Podocarpaceae) were found growing through the forest and an isolated individual upslope from a small stream was selected. The first transect ran upslope from the tree, whereas the second ran downslope to a small stream. The number of leaves of *P. amara* in a square metre were recorded at 2 metre intervals along each transect (Fig. 7.11).

Fig. 7.10 Location of study site, P. amara leaf movement.

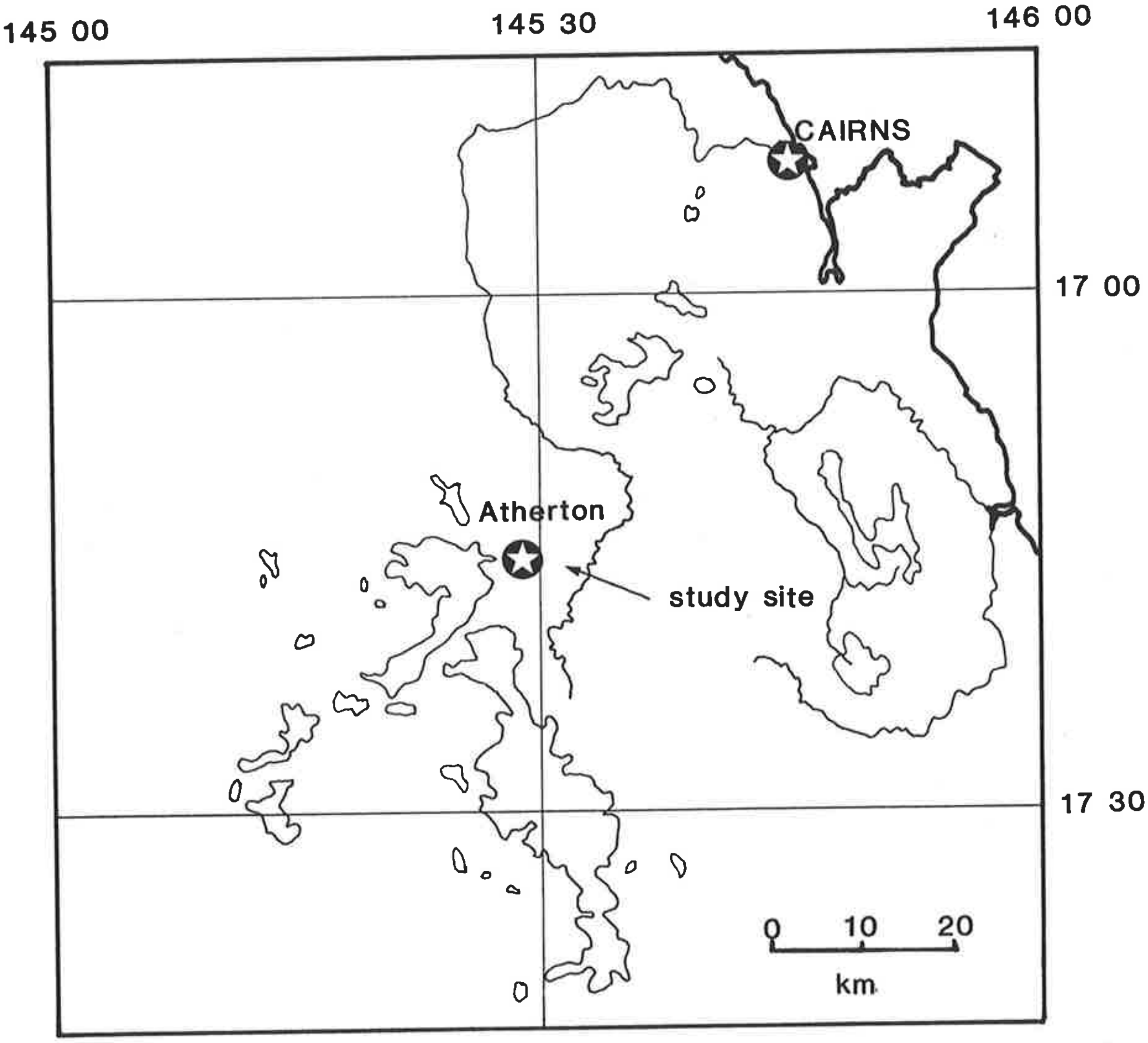
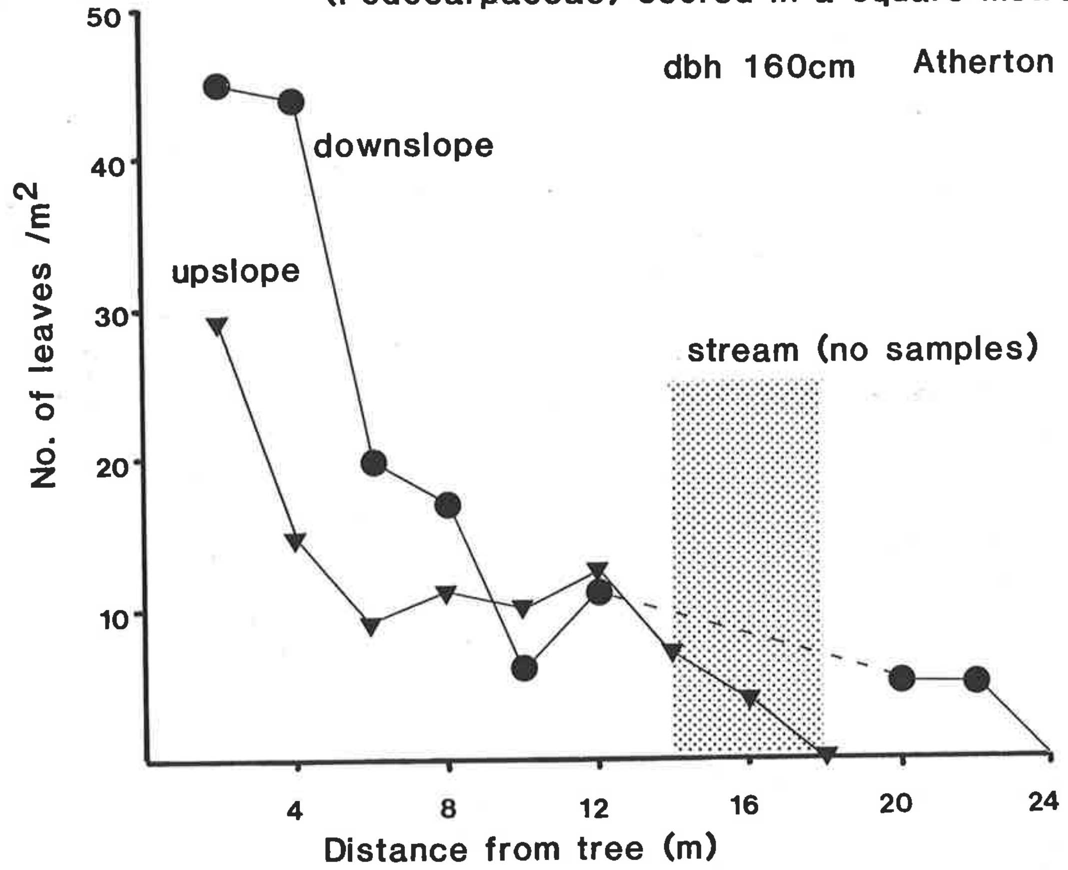


Fig. 7.11 Number of leaves of *Prumnopitys amara* (Podocarpaceae) scored in a square metre.

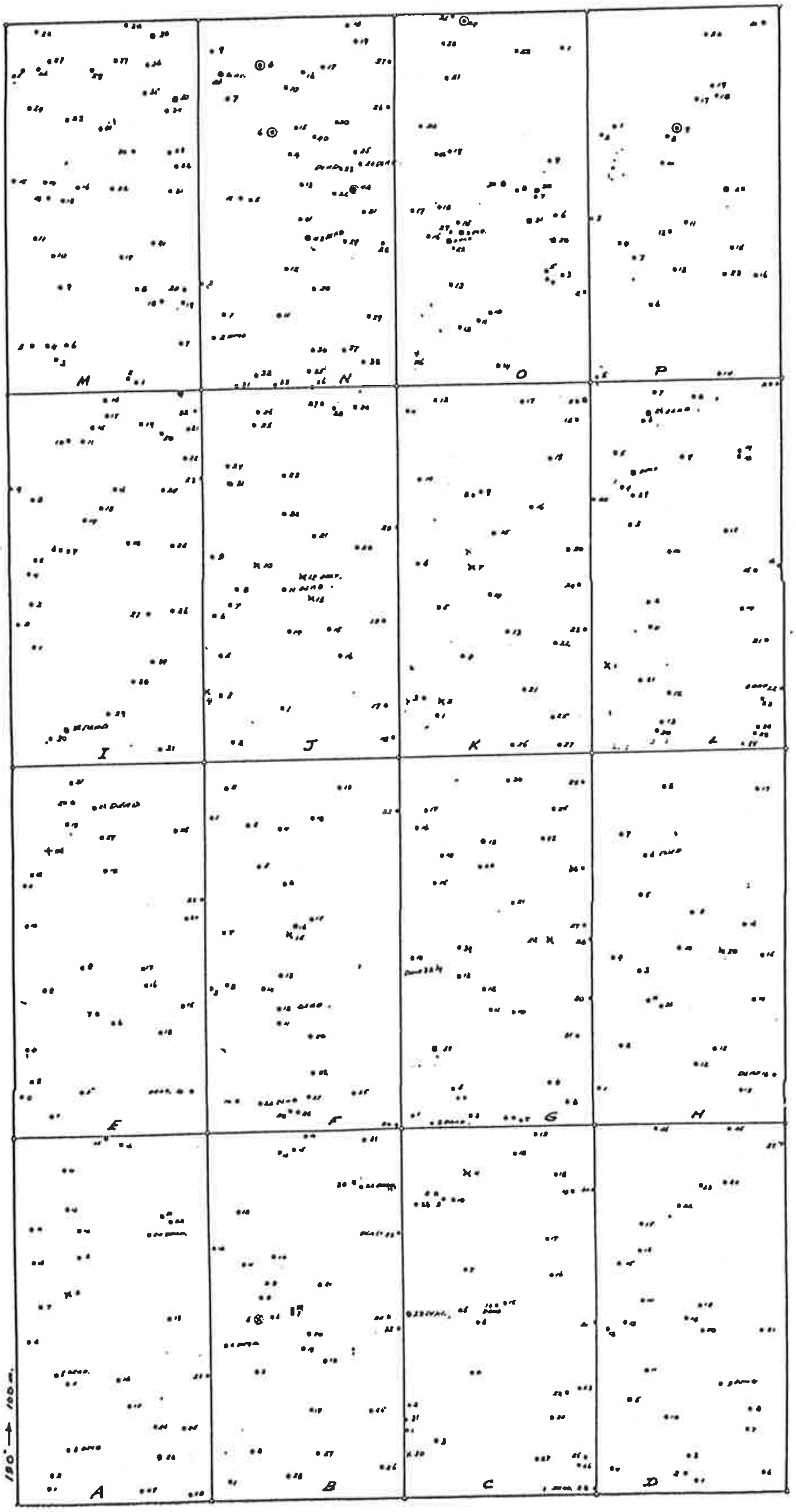


Ferguson (1985) found that leaves from an isolated individual lime tree (*Tilia x vulgaris*, Tiliaceae) in a European deciduous forest were not disseminated far from the source tree. The distribution of leaves around the tree approximated a negative exponential function, with a very sharp reduction in leaf numbers over a short distance. The frequency of leaves counted for the two transects from *Prumnopitys amara* (Fig. 7.11) shows a similar relationship. It is worth noting that the number of leaves in equivalent positions were greater for the downslope transect than for the upslope. This data implies that there is a tendency for leaves to preferentially move downslope.

The second study sought to study leaf movement in greater detail on the CSIRO permanent plot, EP 18. Five litter samples were collected within one section of the plot (subplots k, l, o, and p; Fig. 7.12) using the routine outlined for the determination of physiognomic signatures in chapter 3. A plan of the outline of the canopy of the trees in the main canopy and the sub-canopy of the forest of the area adjacent to the litter collection points was prepared using the known heights of the trees on the site to allow a visual understanding of the relative sizes of the trees potentially contributing leaves to the litter (Figs 7.13 & 7.14). The litter collection points are also indicated. All of the trees within a radius of 5 metres (sub-canopy) or 10 metres (canopy) of the four litter collection sites used are indicated.

Several large trees dominated the canopy over the local area of the litter collection points: *Prumnopitys ladei* (Podocarpaceae) - a nanophyllous conifer; *Stenocarpus* sp nov. (Proteaceae) - with finely divided bipinnatifid leaves; *Argyrodendron* sp. (Sterculiaceae); *Pithecellobium grandiflorum* Benth. (Mimosaceae); and several medium to large individuals of *Planchonella euphlebia* (Sapotaceae). Several species were also common in the understory; *Cryptocarya corrugata* C.White and Francis (Lauraceae), *Flindersia bourjotiana* F.Muell. (Rutaceae), *Synima cordieri* (F.Muell.) Radlk. (Sapindaceae), *Diospypros ferrea* (Willd.) Bakh. var *reticulata* (R.Br.) Bakh. (Ebenaceae), and saplings of some of the canopy trees. Isolated individuals of *Beilschmiedia* aff. *B. obtusifolia* (F.Muell. ex Meissner) F.Muell. (Lauraceae), *Corynocarpus cribbianus* (F.M.Bailey) L.S.Smith

Fig. 7.12 Plan of Experimental plot 18, Mt Lewis NQ.



Species of tree within a radius of 5 metres (subcanopy) or 10 metres (canopy) of the litter collection points.

---

1. Argyrodendron sp
2. Diospyros ferrea var reticulata
3. Flindersia bourjotiana
4. Buckinghamia celissima
5. Acmena smithii
6. Planchonella euphlebia
7. Cryptocarya corrugata
8. Synima cordieri
9. Randia sp.
10. Pithecellobium grandiflorum
11. Xylopia sp.
12. Elaeocarpus sp.
13. Endiandra sp..
14. Darlingia darlingiana
15. Cardwellia sublimis
16. Prumnopitys ladei

Figs 7.13 & 7.14. Outline of tree canopies in the subcanopy (trees 8 - 18m: Fig. 7.13) and canopy (trees over 20m: Fig. 7.14). Numbers on maps refer to list above.

Fig. 7.13

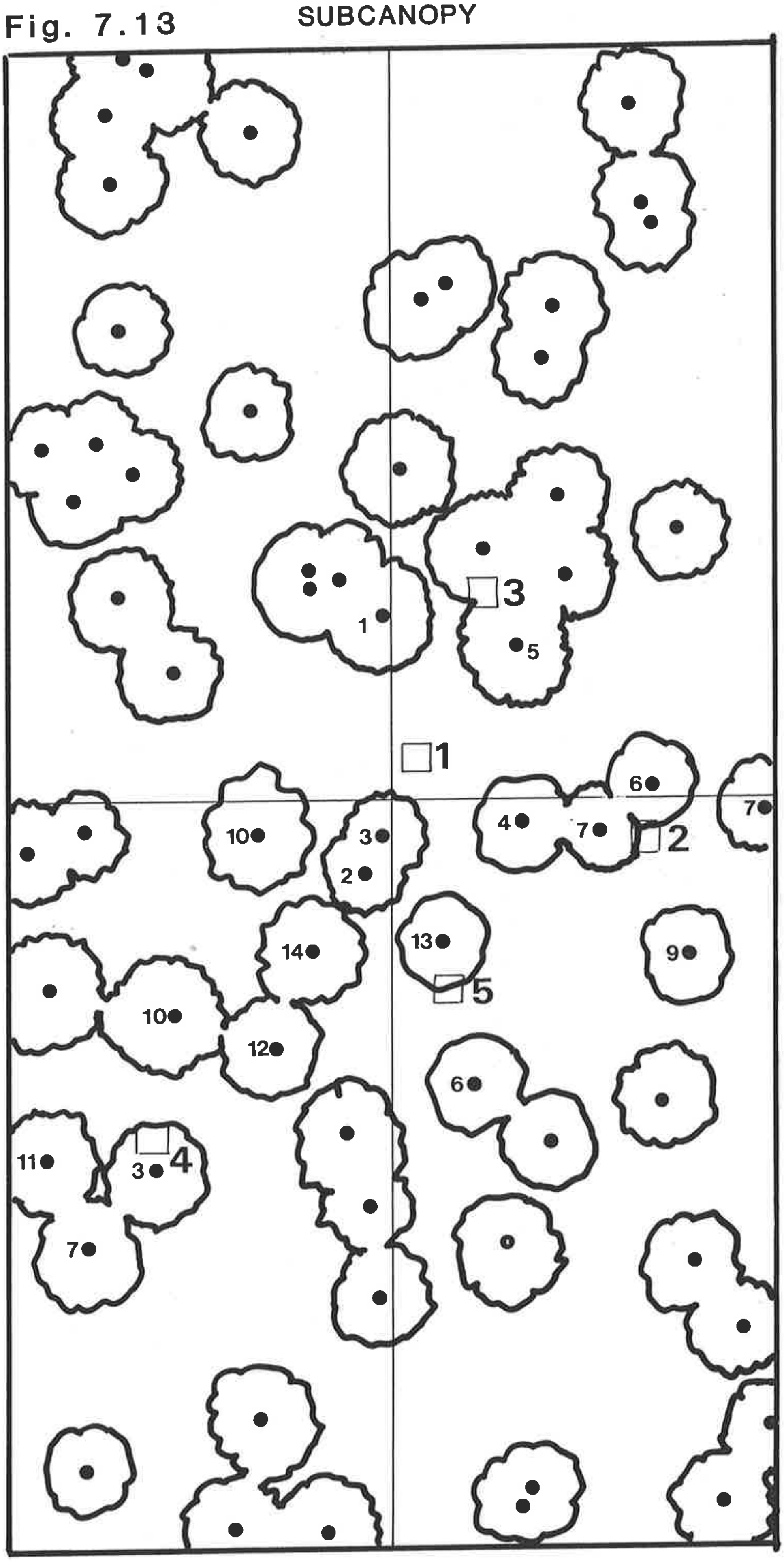
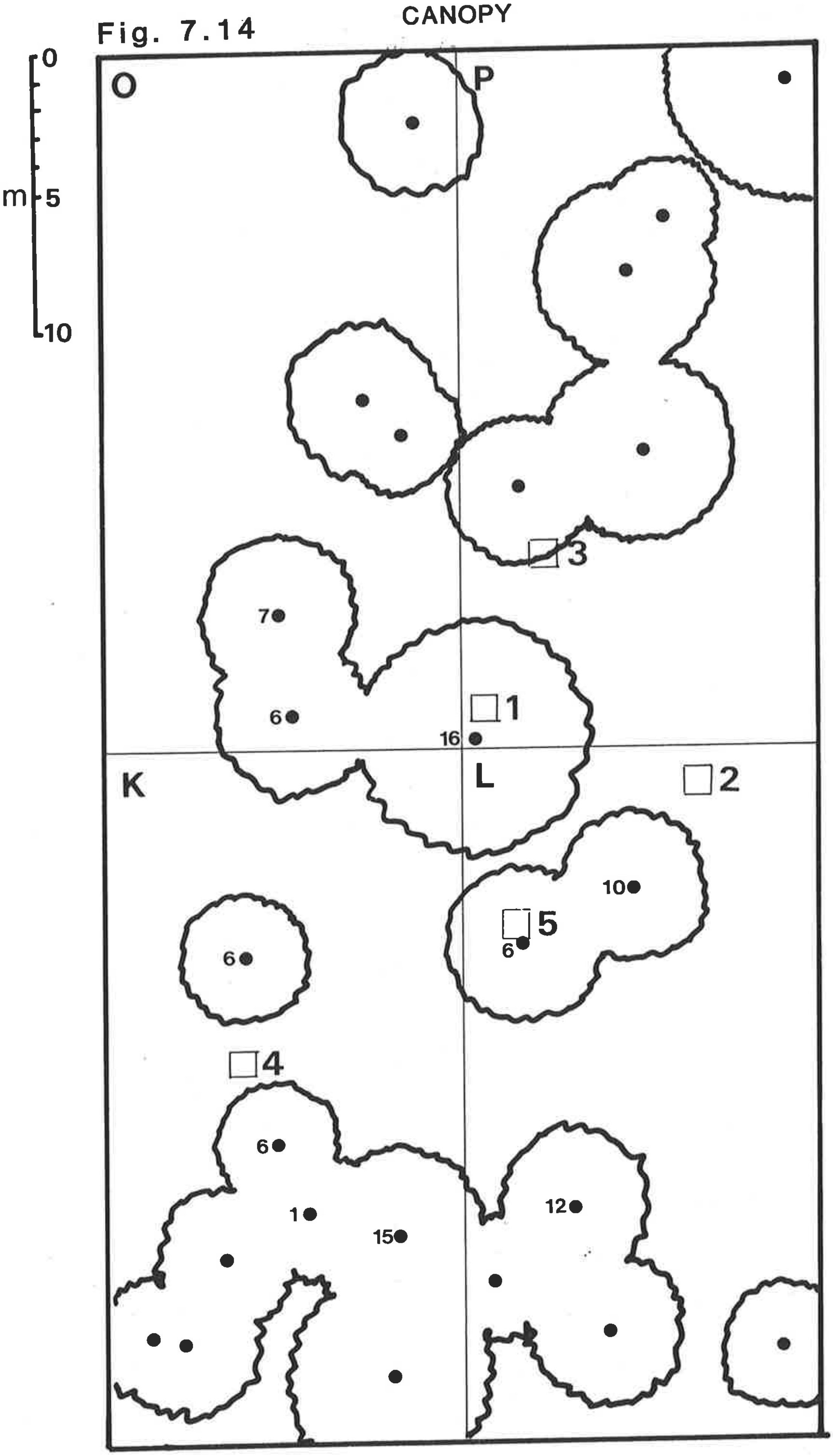


Fig. 7.14



(Corynocarpaceae), *Acmena smithii* (Myrtaceae), *Darlingia darlingiana* (F.Muell.) L.A.S.Johnson, *Buckinghamia celsissima* F.Muell., and *Cardwellia sublimis* F.Muell. (Proteaeceae) were also potential contributers of leaves to the litter samples.

The foliage of *Prumnopitys ladei* is shed as small to large branchlets containing 10 - 100 individual leaves 0.5 - 1.5 cm long (i.e. Nanophylls sensu Webb, 1959) while the bipinnatifid leaves of *Stenocarpus* sp. nov. were usually fragmented in the litter samples. These factors make comparison between the frequency of leaves of these species with the other species difficult to interpret and so they have been omitted from the analysis.

The transect study was not repeated for EP 18, although the samples collected occur at differing distances from an isolated individual of *Acmena smithii* (Fig. 7.15). Only one individual of this species occurred in the study area and so it is reasonable to assume that all of the leaves of *A. smithii* encountered in the samples came from that tree.

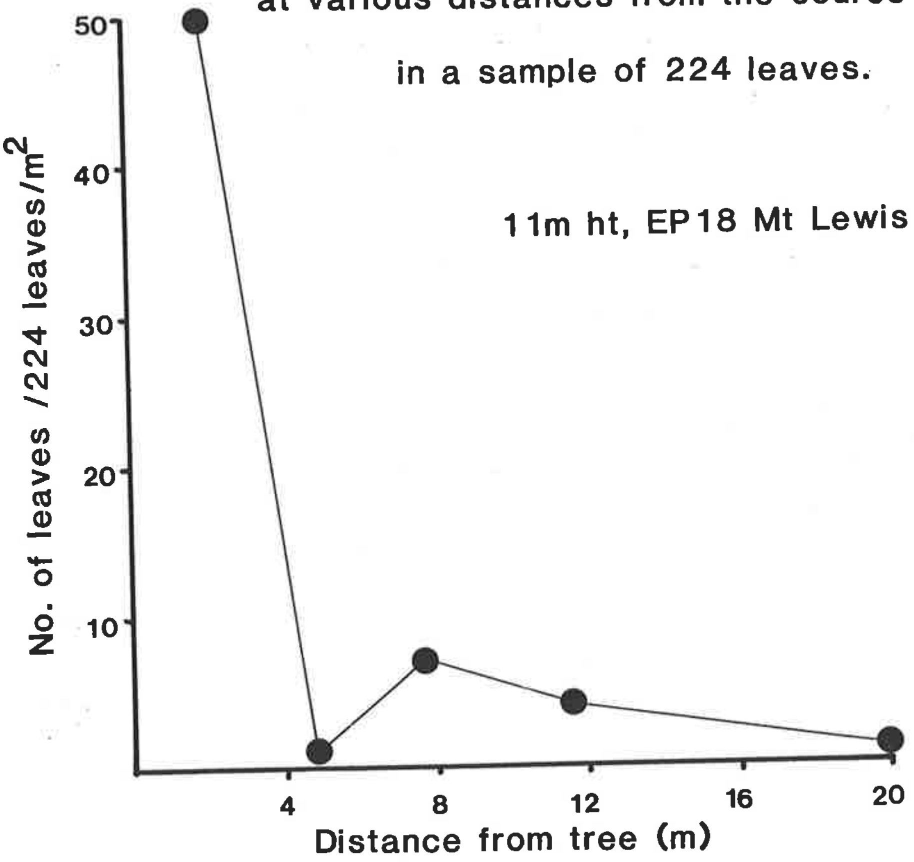
The frequency scores represent the proportion of leaves of Acmena smithii in a sample of 224 leaves from a square metre of ground. The frequency distribution approximates a negative exponential distribution (Ferguson, 1985) with leaf presence sharply dropping with increasing distance. The two sets of data are not strictly comparable, however, as the EP 18 data represents the number of leaves in subsamples of 224 leaves at varying distances and positions, whereas the *Prumnopitys amara* example is based on total counts of leaves along transects. Even so, the trends in both cases are consistent and demonstrate the local nature of the leaf rain.

7.3.2 Analysis of Litter Composition.

Ferguson found that litter in a European deciduous forest was heterogeneous (Ferguson, 1985). The leaves from particular taxa were concentrated near the source trees and leaves of these species were scarce or absent a short distance from the source tree. Similar results were found in this rainforest example.

The relative contribution of each taxon in the total litter collections to each sample are displayed as frequency histograms in Figures 7.4 – 7.7. The contribution of each taxon varies greatly between samples, giving each sample a distinctive

Fig. 7.15 Number of leaves of _Acmena smithii_ at various distances from the source tree in a sample of 224 leaves.



11m ht, EP18 Mt Lewis

taxonomic character, to the extent that the dominant leaf taxon is different in each case. For example, taxa 1 (*Elaeocarpus* sp.) and 15 (Lauraceae?) have the highest frequencies in sample 1, whereas in sample 2, the highest frequency taxa are 17 (unknown) and 4 (*Planchonella euphlebia*), with taxon 15 in particular almost absent from sample 2. This pattern is repeated for most of the taxa for the four samples (Figs 7.4 – 7.7).

The trees nearest and/or numerically greatest within a small radius (10 metres) of each sample generally dominate the litter sample (Figs 7.12 & 7.13). This suggests that litterfall from nearest (and greatest) leaf sources swamps leaf input from more distant sources. The contribution of leaves from more distant sources would in addition, have been initially diluted by the distance effect discussed above. Similar results were obtained by Chaney (1924) and Ferguson (1985) in coniferous and deciduous forests respectively.

A few taxa seem to reverse this observation, however, e.g. *Planchonella euphlebia* being absent from sample 4 (Fig. 7.4), despite a nearby individual of that species (Fig. 7.13). A likely explanation is the screening effect of smaller trees and shrubs, and possibly swamping of the local leaf rain by leaves of the shrub species.

The main conclusion that can be drawn from this data is that the local input into leaf beds will only represent trees within a small distance of the site of deposition. Fossil leaf beds will therefore only reflect the species composition and foliar physiognomic character of the local vegetation. This data supports the conclusions of the various studies on the input of leaves into lakes (McQueen, 1969; Rau, 1976; Hill and Gibson, 1986; Wolfe and Spicer, 1987) and Arctic streams (Holyoak, 1984) that leaf deposits generally are biased towards the local vegetation e.g. that of the waters edge.

7.4 Morphological Variation within Taxa in Litter Samples.

Each of the forest types have been shown to be physiognomically distinct (Chapter 4). The discussion above in (this chapter) made the point that leaf fall is essentially local, and that leaf deposits derived from local leaf fall will be dominated by the leaves from individual trees over short distances within the leaf bed. This implies that the variation in leaf morphology observed within a species will be largely represented in the leaf litter, and by inference, a fossil leaf bed.

Each of the four forest types differs stucturally by the number of layers or strata present (Webb, 1959 1968; Tracey, 1982; Lowman, 1986). Each of these strata has a different microclimate (Richards, 1952 1983; Aoki, et al., 1975; Whitmore, 1984; Roth, 1984). This heterogeneity can be expected to produce morphological differences between individual leaves of the same species from different positions on the one tree (Roth, 1984).

Representatives of all of these leaf types can be expected to enter the litter, although their probability of entry will vary according to the distance from the ground, and the presence of obstructing foliage. The degree of variation for two species from a sample from a single site from each of the four forest types has been assessed below. A pair of species from SNVF and CNVF from New South Wales has been included in addition to a site from N.E. Queensland of these forest types as the former has been demonstrated to be physiognomically distinct to the N.E. Queensland examples.

The method used is purely descriptive, with the basic physiognomic data from Chapter 4 used to characterise the morphology of the set of leaves of the two selected species from each example. The leaf length and width frequency distributions serve to illustrate the level of variation to be expected in these characters in samples of leaves from leaf beds derived from the four forest types. In addition, they highlight the transition in leaf form from the 'shade' to the 'sun' leaf.

7.4.1 Variation Within Species from CMVF.

The Oliver Creek collection site represents an example of the "optimal development of rainforest in Australia" (Tracey, 1982) i.e. Type 1a of CMVF. The canopy at this site was partially dominated by several individuals of *Idiospermum australiense* and so this species is used to examine variation in the morphology of the leaves of the canopy trees. Leaves of the sub-canopy species, *Citronella* *moorei*, were also common in some samples.

The cumulative frequency distributions of leaf length for leaves from these species from one litter sample are contrasted in Figure 7.16. The leaves of the canopy species are clearly on average much larger than the leaves of the sub-canopy species (Fig. 7.16). In each case, the distribution of leaf lengths approximated a normal distribution (i.e. the cumulative frequency distribution was sigmoidal), and not a bimodal distribution as might be expected from the extreme shade and sun leaves. However, the expectation was for the canopy species to be represented by on average smaller leaves than the sub-canopy species. Figure 7.17 shows the full range of leaf size observed for *Idiospermum* in the litter sample, with a few quite small and very large leaves present.

7.4.2 Variation Within Species from CNVF.

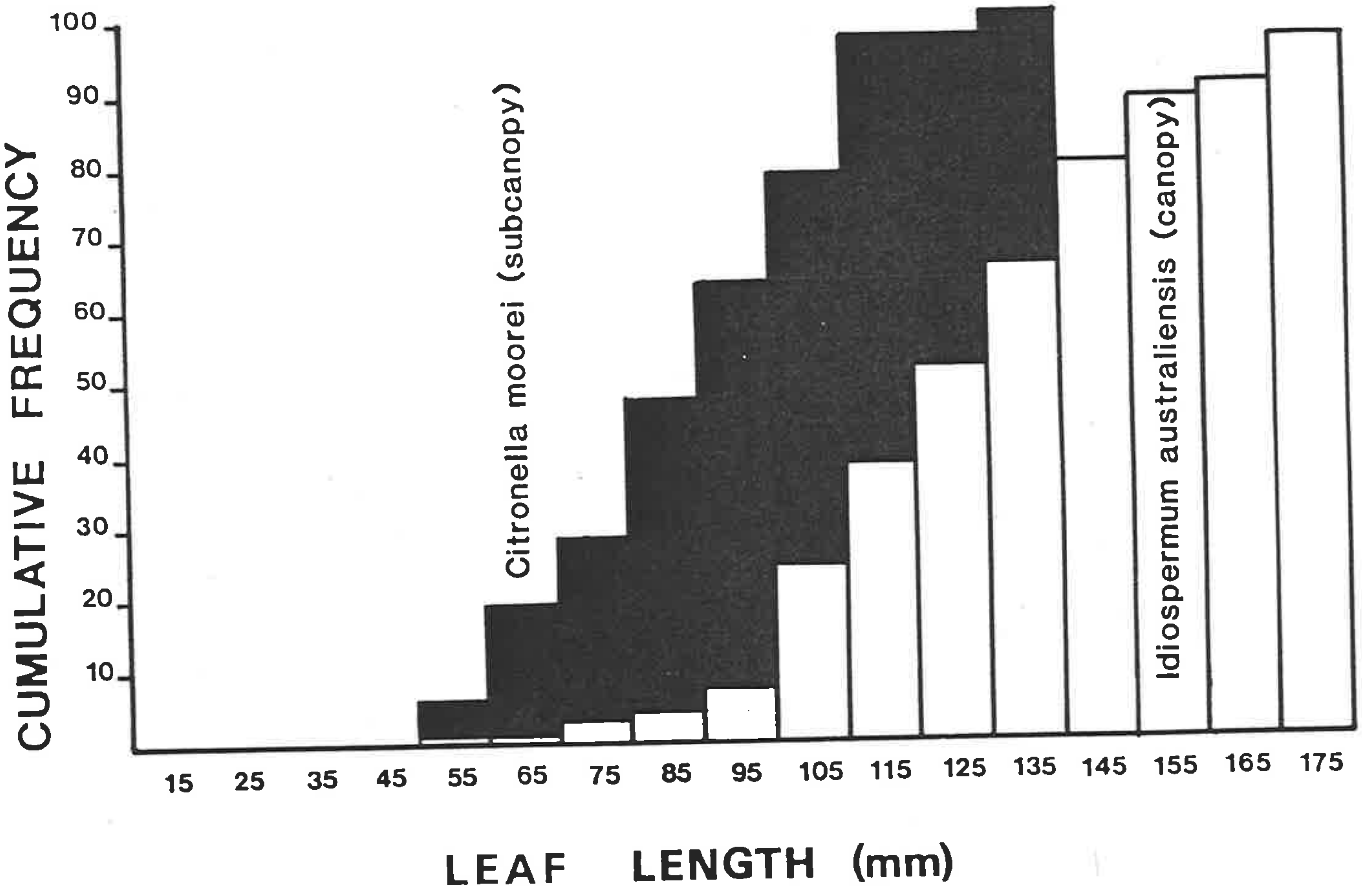
The forest canopy at the Dorrigo litter collection site was dominated by two species; *Sloanea woolsii* (Elaeocarpaceae) and *Dysoxylum fraseranum* (Meliaceae). The leaves of these two species were common in most of the samples from Dorrigo (see above), and represent the morphological variation of leaves from canopy species. The cumulative frequency distributions of length for *S. woolsii* and a sub-canopy species, *Doryphora sassafras*, are shown in Figure 7.18.

The cumulative frequency distribution demonstrates that the leaves of the canopy species, *Sloanea woolsii*, are generally much larger than the leaves of the sub-canopy species, *Doryphora sassafras*. The *Sloanea* leaves also have a wide range of size, with some quite small leaves also present (Fig. 7.19). This pattern matches that demonstrated for the CMVF example, with the canopy species represented in the litter by a wider range, and on average larger leaves, than the sub-canopy species.

7.4.3 Variation Within Species from SNVF.

The Mt Lewis Road site is of interest because of the common occurrence of the conifer, *Podocarpus smithii* Laubenf. (Podocarpaceae) in the canopy. *Podocarpus leaves* are common in some recently described Tertiary leaf beds (Greenwood, 1987; Christophel and Greenwood, 1987). Two size-morphotypes were sometimes

Fig. 7.16 Cumulative frequency distribution of leaf length



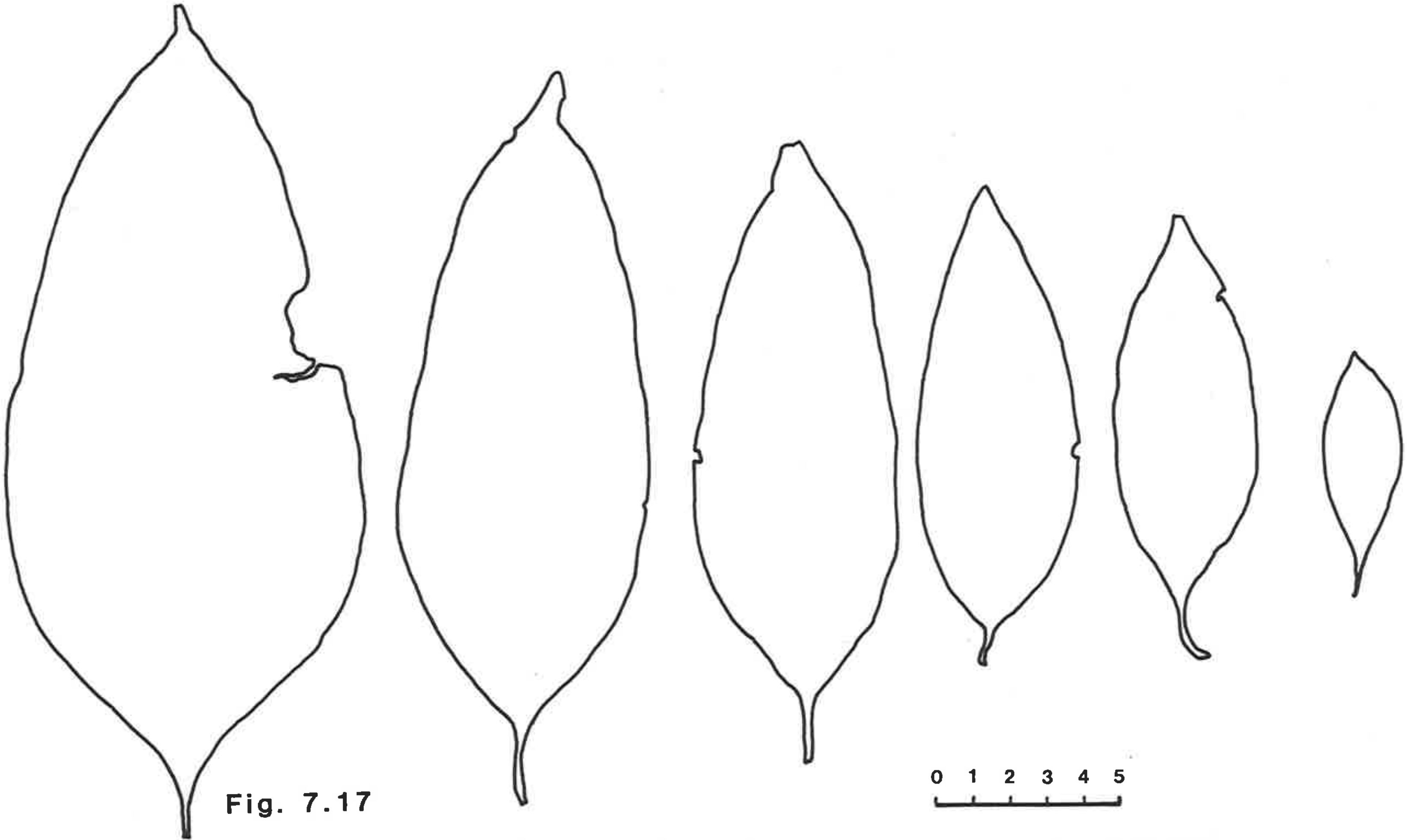
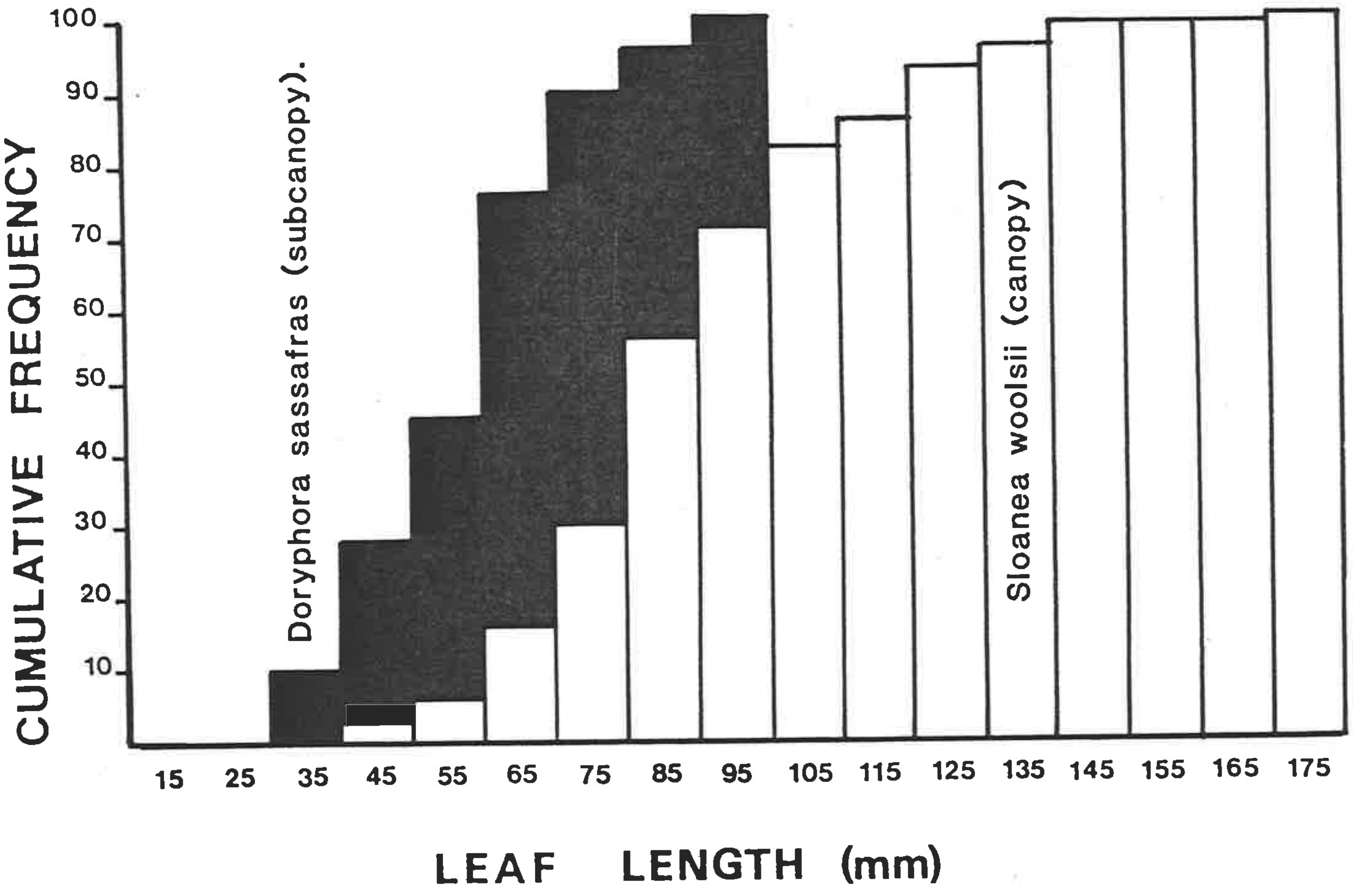


Fig. 7.17

Silhouettes of Idiospermum leaves to show the size range present in litter.

Fig. 7.18 Cumulative frequency distribution of leaf length



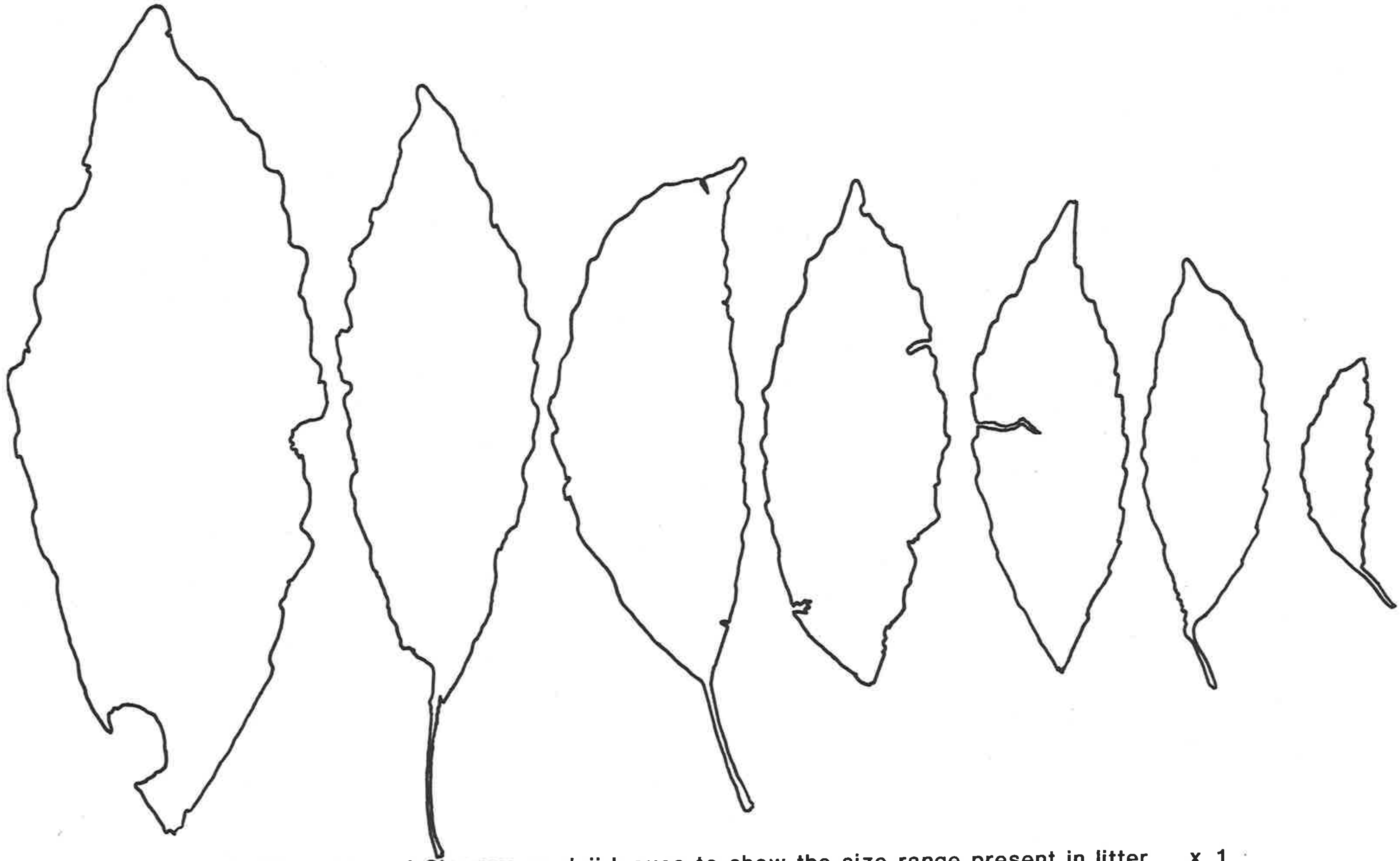


Fig. 7.19 Silhouettes of Sloanea woolsii leaves to show the size range present in litter. x 1

present in these deposits and therefore it was of interest to the author to determine the level of variation in leaf size (length and width) in a leaf bed to clarify species boundaries in the fossils.

Some modern species of *Podocarpus* exhibit large variation in leaf size between juvenile and adult foliage (Greenwood, 1987), and it was necessary to discover whether this represented a 'cutoff' continuum, or whether leaf size in *Podocarpus* had a bimodal frequency distribution. The length frequency distribution of *Podocarpus smithii* is shown in Figure 7.20. Clearly leaf length is normally distributed (i.e. the cumulative frequency distribution is sigmoidal) between a minimum value of 65 mm and a maximum length of 115 mm.

The leaf length frequency distributions of the canopy species, *Cryptocarya corrugata* (Lauraceae), and the subcanopy tree, *Elaeocarpus* sp. (Elaeocarpaceae), demonstrate a clear difference in the sizes of leaves of these two species (Fig. 7.20), with the canopy species in this case with the smaller leaves. The *Cryptocarya* was the most common leaf taxon in this sample (94 /224 leaves), and it demonstrates the dominance of the litter by the smaller leaves of the canopy.

The leaf length cumulative frequency distributions for *Ceratopetalum apetalum* (canopy species) and *Quintinia sieberi* (understory species) from Coombadjha Ck are shown in Figure 7.21. The Figure show that there is a slight tendency for the understory species, *Quintinia sieberi*, to have smaller leaves than the canopy species *Ceratopetalum apetalum*. These results are in contrast to those obtained for SNVF in N.E. Queensland where the canopy species had much smaller leaves than the subcanopy species.

7.4.4 Variation Within Species from MFF.

The canopy at the Barrington Tops MFF site was dominated by *Nothofagus moorei* (Fagaceae), and this is reflected in the domination of the litter samples by this species. However, a second species in addition to N. moorei, *Doryphora sassafras*, can also be used to represent the morphological variation in leaves from tree species. The shrub species, *Elaeocarpus reticulatus*, was sufficiently common in the litter samples to allow meaningful discussion of the level of morphological variation in the leaves of that synusiae.

Fig. 7.20 Cumulative frequency distribution of leaf length

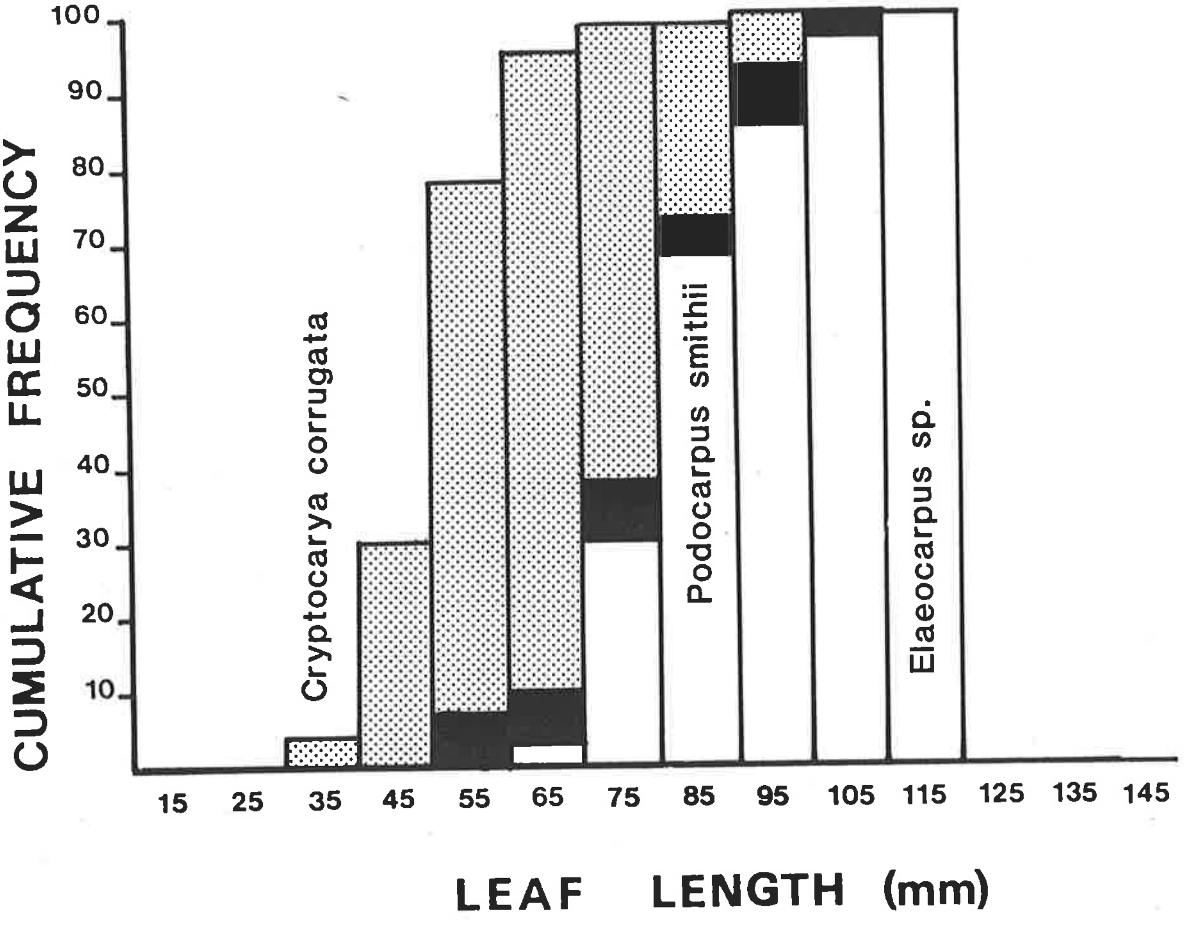
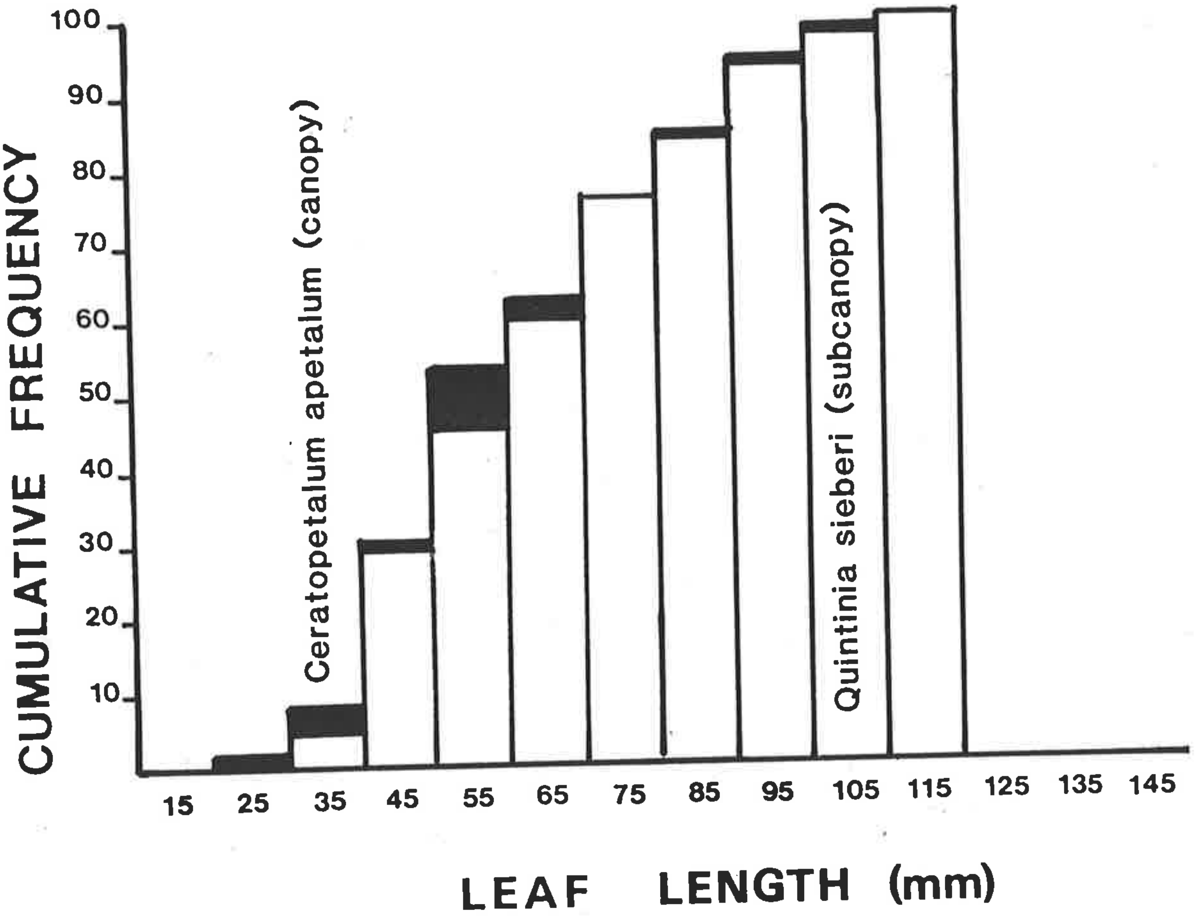


Fig. 7.21 Cumulative frequency distribution of leaf length



The variation in leaf length for these species is shown in a cumulative frequency distribution plot in Figure 7.22. The leaves of the canopy species, *Nothofagus moorei*, are on average smaller than the leaves of the shrub species, *Elaeocarpus reticulatus*, and the other canopy species, *Doryphora sassafras*. The range of sizes observed for the *Elaeocarpus* leaves is also wide (Fig. 7.23).

The difference in average leaf size between *Nothofagus moorei* and *Elaeocarpus reticulatus* matches the pattern seen in the N.E. Queensland SNVF example discussed above. The leaf size frequency distributions reflect the input of the smaller sun leaves of the canopy. However, the wide range of size observed for *N. moorei* illustrates the point that leaves from many parts of an individual tree (or several trees) will reflect the variety of microclimates acting on them, and thus will represent a variety of physiognomic types (e.g. Davis and Taylor, 1980).

7.5 Discussion.

This chapter sought to explore two related areas; the level of variation observed in the membership of samples by contributing taxa due to the spatial pattern of the source trees, and the morphological variation observed in natural populations of leaves. These areas are important in understanding the variation in species membership and contribution to fossil leaf beds, and in defining species boundaries in fossil leaves.

In earlier discussion it was suggested that fossil leaf beds are not fossilised communities, but rather, fossilised assemblages of plant parts. The proposition was then put that the abundance of taxa and representation of taxa within fossil leaf beds will therefore be modified by taphonomic influences on the leaves after they are lost from their source tree(s) and will not so much reflect the abundance of the individual trees in the local forest, but rather will reflect the probability of leaves from particular taxa and individual trees entering the deposit (Chaney, 1924; Rau, 1976; Ferguson, 1985). The data presented above would tend to add considerable weight to these propositions, and support the use of careful consideration of the implications of the relative abundances of taxa within fossil leaf beds and the inferred abundances of these taxa in the reconstructed source

Fig. 7.22 Cumulative frequency distribution of leaf length

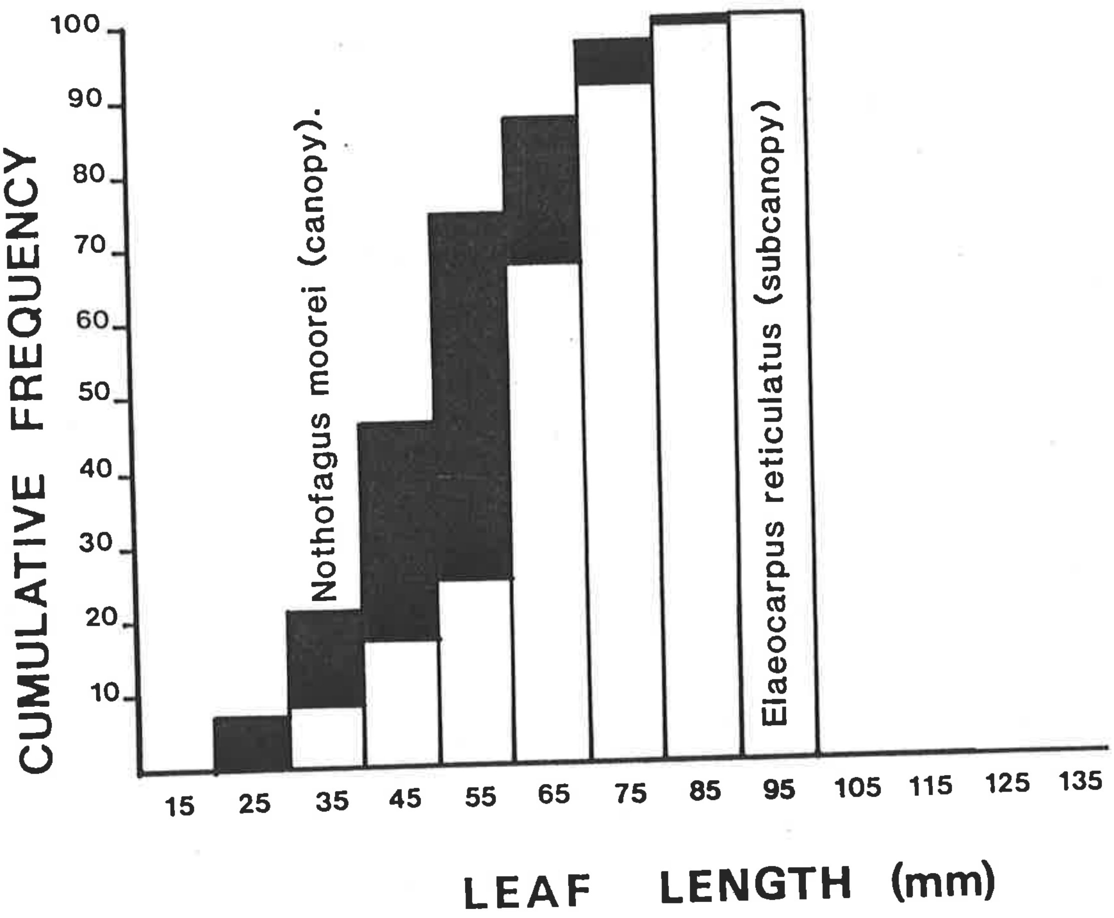
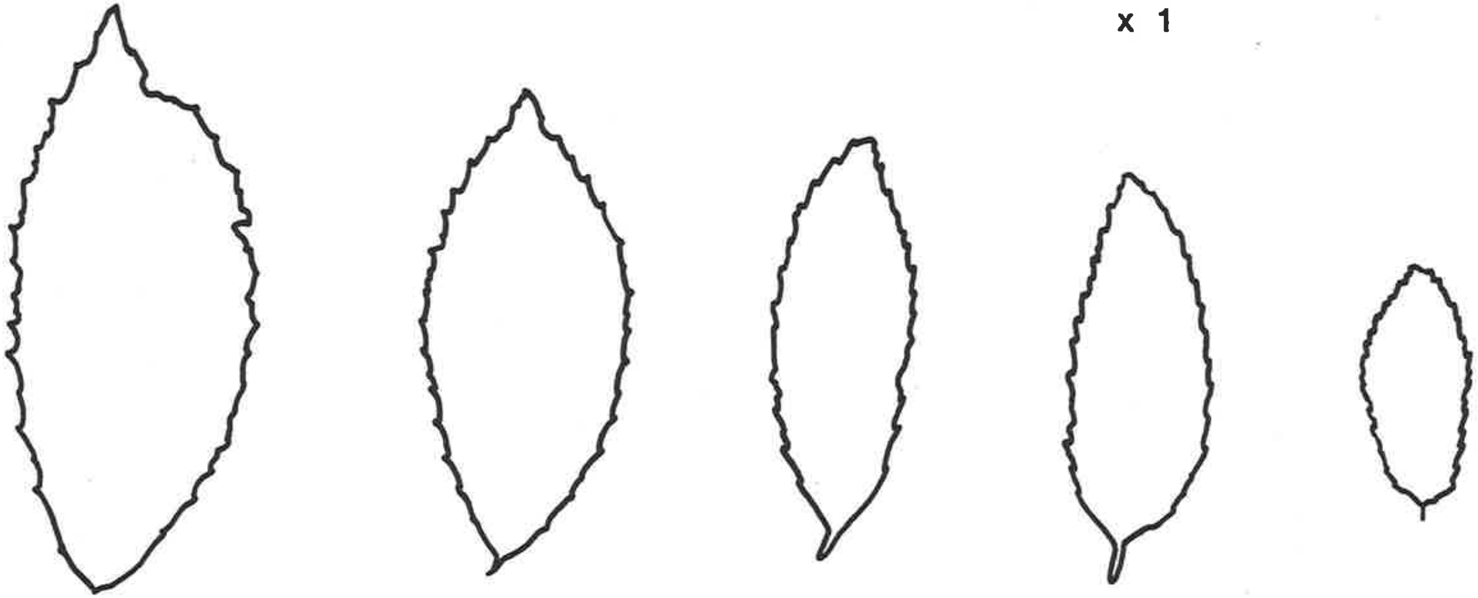


Fig. 7.23

Silhouettes of *Elaeocarpus* *reticulatus* leaves to show the size range present in litter.

x 1



vegetation.

Many foliar physiognomic analyses are based on the proportion of species represented in particular physiognomic classes, such as leaf size or margin type (e.g. Dolph and Dilcher, 1980; Wolfe, 1980a). On the basis of the information presented above, leaf beds are predicted to contain a biased species assemblage. Predictions based on the foliar physiognomic character of individual species must therefore be used with caution.

The analysis of the range of sizes of individual taxa illustrated the often wide range in leaf beds. Often occassional very large or very small leaves are present. In some cases, the extreme sized leaves also represent extreme morphotypes (e.g. *Darlingia darlingiana*; Figs 3.1 & 4.11). It is plausible that such extreme size and morphotypes will be recognised as distinct entities. Such a result will bias observations based on the proportion of species represented in particular classes. There is not only the possibility of erroneously assigning extreme size morphotypes to separate species, but also the possibility of wrongly determining the characteristic size class of a species due to biased leaf samples of individual species i.e. species represented by only a few individual leaves may reflect only the upper or lower end of a wide size range.

According to Richards (1952) and Roth (1984) the leaves of plants in the successive layers of 'Tropical Rainforest' have a distinctive morphology. The leaves of these different synusiae might therefore be expected to exhibit their own physiognomic signatures. The results presented here suggest that in some cases the leaf length frequency distribution of the canopy and understory species is different (e.g. *Nothofagus moorei* and *Elaeocarpus reticulatus* in MFF). In other cases, however, either the leaf length frequency distributions of leaves from species from the two synusiae were similar (e.g. *Ceratopetalum apetalum* and *Quintinia sieberi* SNVF Coombadjha Ck), or in contrast to the expected, the leaves of the canopy species were much larger than the leaves of the understory species (e.g. *Sloanea woolsii* and *Doryphora sassafras* CNVF Dorrigo).

These results suggest that in the anomalous examples either a significant input of leaves from within the canopy of the canopy trees was influencing the result, or other unknown factors were biasing the leaves of the understory species to smaller sizes. However, the canopy of CNVF and CMVF is more stucturally complex and of a greater vertical extent than in SNVF and MFF (Lowman, 1984).

The greater variety of potential microclimates in the canopy of CMVF and CNVF therefore suggests that leaves from the canopy trees of these forests will vary greatly in size. The greater lignification of these leaves will also ensure their over-representation compared to the understory species. Nevertheless, the above results suggest caution in the assignment of synusial character to fossil leaf species on the basis of leaf size alone. Further analysis, however, may alter this assessment.

Chapter 8

THE ROLE OF FOLIAR PHYSIOGNOMY IN THE PALAEOECOLOGICAL ANALYSIS OF TERTIARY LEAF BEDS.

8.1 The Analysis of Tertiary Leaf beds.

In the introduction it was suggested that the purpose of palaeobotanical analyses of fossil leaf beds was to determine the character and composition of palaeovegetation. Palaeoecology was defined as the science concerned with the analysis of the pattern of interaction between components of the original vegetation that gave rise to a fossil bed. In this sense, palaeoecology can be considered to be a synthesis, and largely interpretative. Foliar physiognomic analysis was introduced as a method whereby climate and the character (type) of vegetation could be predicted, allowing the placement of the identified components (the fossil taxa) into an ecological context.

The valid use of palaeoecological analyses requires an understanding of the taphonomic processes which have brought the plant parts together in the fossil assemblage, and how the pattern present in the taphocoenosis can be interpreted to reveal the original pattern of the plants in their life positions. Previous studies which used foliar physiognomic analysis had largely ignored the taphonomy of the leaf beds, and compared the physiognomic characteristics of whole vegetation to what is essentially a collection of isolated plant parts, or in the case of theoretical studies, considered the whole vegetation alone (Dolph and Dilcher, 1979a; others) or the response of individual leaves (Davis and Taylor, 1980), and not the leaf beds formed from the vegetation. The outcome of some of these studies was to condemn foliar physiognomic analysis as yielding uninterpretable data (Dolph and Dilcher, 1979a).

This study used leaf litter as an analogue of fossil leaf beds, and it must be stressed that ultimately the characteristics of leaf beds formed in a variety of sedimentary environments, from a wider spectrum of forest types, must be studied to fully understand the relationship between the physiognomic characteristics of these beds and the source forests (e.g. Roth and Dilcher, 1978). Nevertheless, leaf litter provides a valuable tool to further examining the relationship between the characteristic foliar physiognomy of leaf beds formed from particular vegetation types and the environment.

A number of specific conclusions can be made about the taphonomy of leaf beds and the effects on the foliar physiognomic characteristics of the leaf beds. Clearly, leaf litter (forest floor and stream bed) has different physiognomic characteristics to the forest canopy, primarily through a greater representation of smaller leaf-size classes (Fig. 4.1) and the inclusion of leaves from all synusiae. It is also apparent that leaf beds, such as leaf litter, formed in the absence of major resorting or the mixing of leaves from discrete sources, maintain a distinctive physiognomic signature which can be used to identify the source of a leaf assemblage.

8.2 Foliar Physiognomic Analysis of Tertiary Leaf Bed Based on Leaf Margin Type.

The earliest attempts to use foliar physiognomy to predict palaeoclimate were based on Bailey and Sinnott's observations on the correlations between the proportion of species with leaves with non-entire margins in a "flora" and the climate of the region (Bailey and Sinnott, 1915 1916). This method, later refined by Wolfe (1971, 1980, 1985, 1987), uses a direct comparison of the percentages of species present in a fossil asssemblage with non-entire margins, and the percentages in modern vegetation. A crude measure of the relative sizes of leaves is used also, but not in the formal manner used by MacGinitie (1965), Christophel (1981), or Zastawniak et al. (1985) based on Webb's data for Australian rainforests.

It is often remarked that the Australian flora has a much lower proportion of species with non-entire margin leaves than comparable regions (Bailey and Sinnott, 1916; Wolfe, 1980a, 1985, 1987), and this is certainly the case if the whole non-arid flora is considered. However, if only rainforest vegetation is considered, a slightly different picture emerges.

Webb found that the proportion of species with non-entire margins was higher in the cooler Australian rainforests (MFF and SNVF) than in subtropical and tropical rainforests (Webb, 1959; Table 2.4). However the variability in the proportion of non-entire species in the canopy was very high, reflecting differences between the southern Australian MMF and SNVF, and the N.E. Queensland MMF and SNVF, and possibly also local differences.

The exact physiological basis for non-entire margins is not understood (Wolfe, 1980a), however in Australia it would seem not to be a simple relationship with annual average temperature such as reported for the mesic forests of S.E. Asia by Wolfe (1980a). Results based on an analysis of the proportion of individual leaves with non-entire margins in litter samples (Chapter 6) suggest that it may be linked to the temperature extremes experienced by the forests and perhaps also edaphic factors.

The annual average temperatures experienced by SNVF in N.E. Queensland and New South Wales are comparable (Figs 2.8 & 2.9), however the New South Wales forests experience greater temperature extremes between summer and winter whereas the sub-montane climate of N.E. Queensland experiences fairly uniform temperatures with a greater diurnal range than a seasonal range.

Wolfe's correlations between the proportion of species with non-entire margins and temperature is based on regional species lists for the forest types he recognised (Wolfe, 1980a). Dolph criticised Wolfe for restricting his analysis to canopy trees, and used his analysis of the flora of Indiana to illustrate the different foliar physiognomy of the sub-canopy trees and bushes (Dolph, 1984). He further added that there was no correlation with the proportion of species with non-entire margin leaves in this stratum and the annual average temperature.

In the study reported in this thesis, two of the sites examined had high numbers of individuals and species (as a proportion of the total flora) with leaves with non-entire margins — MFF at Barrington Tops and SNVF at Washpool/Coombadjha Creek. A consideration of the foliar physiognomy of individual species at these sites suggests that the sub-canopy trees and bushes (*Trochocarpa laurina* in MFF, and several species including *Quintinia sieberi* and *Syzygium crebinervis* in SNVF) were the sole species present with entire margined leaves.

This data therefore supports Dolph's findings (Dolph, 1984), but perhaps more importantly, emphasise the point that leaf litter, and hence fossil leaf beds, will contain leaves from all synusiae (Ferguson, 1985), and therefore a greater diversity of foliar physiognomies than the canopy alone (Davis and Taylor, 1981; Roth, 1984).

It is also important to consider the possible influences of streamside trees. Streamside vegetation is often predicted to have a higher proportion of species and individuals with entire margins (Wolfe, 1980a) and their leaves are generally considered to be larger than those of the local forest (MacGinitie, 1969) due to the milder conditions experienced. It is assumed these differences will bias foliar physiognomic analysis of stream deposited leaf-beds (Macginitie,1969; Wolfe, 1971 1980a). By contrasting the proportions of leaves and species with non-entire margins between forest floor and stream deposited leaf-beds, this hypothesis was tested for Australian rainforest.

In the examples studied, Simple Notophyll Vine Forest in N.E. Queensland and New South Wales, no significant change in the proportion of non-entire margined leaves, either as individual leaves or the proportion of species, was found between the stream-deposited leaf litter (and thus originating mainly from streamside vegetation) and the typical values for SNVF in N.E. Queensland, in the first example, or the values for the forest floor samples collected in the nearby SNVF, in the case of the New South Wales example.

While these results can not be considered conclusive, it is nevertheless possible to suggest that in the case of SNVF in Australia, the streamside flora has only a minimal influence on the proportion of species and individuals with leaves with non-entire margins detected in a stream-bed leaf deposit. However, the generally low proportion of species and individuals with non-entire margined leaves in Australian rainforests restricts the utility of palaeoclimate indices based on correlations between annual average temperature or the annual range of temperature and leaf margin percentages (e.g. Wolfe, 1980a).

Wolfe (1980a) found a correlation between annual average temperature and the proportion of (canopy) species in the moist forests of SE Asia. This study however, found no correlation between annual average temperature and the number of individual leaves with non-entire margins in the whole flora. According to Dolph's study on the forests of Indiana (Dolph, 1984), the restriction of the correlation to canopy species by taxonomic sorting could detect a correlation. I have demonstrated a major flaw with this argument.

The early enthusiasm for palaeoclimate analysis based on foliar physiognomic comparisons stemmed from a dissatisfaction with floristic analysis. The main sources of concern related to erroneous identifications (Dilcher, 1971 1973; Roth and Dilcher, 1978), and concerns over the extrapolation of the thermal requirements of modern species to putative Early Tertiary close relatives (MacGinitie, 1969; Wolfe, 1971 1980a).

Reliance on the identification of Early Tertiary species as "canopy species" on the basis of the preference of the modern closest relative, reintroduces the potential sources of error outlined for floristic analysis. In addition, such a method introduces the assumption of the maintainance of common ecological niche through the Tertiary (MacGinitie, 1969; Dolph. 1984).

This is a tenuous hypothesis at best as many examples of closely related species adopting different roles can be found in rainforests, and perhaps in other forest types (e.g. *Clusia flava* (Clusiaceae) adopting different life-forms under different circumstances in Jamaican rainforests; Kelly, 1985). A further complication is the basis of comparison on the proportion of canopy species with non-entire margined leaves. Clearly if a large group of species in a deposit can not be identified to a close modern relative, then the exact proportions can not be determined.

8.3 Foliar Physiognomic Analysis of Tertiary Leaf Beds Based on Leaf Size.

The use of leaf size as an index of palaeotemperature relates to Raunkiaer's observations on the relationship between the prevailing leaf size of species, as represented by a series of leaf size classes based on leaf area (Raunkiaer, 1934), and climate. These observations were incorporated into "physiognomic forest classifications" (e.g. Beard, 1944 1955; Cain et al., 1956; Richards, 1952; Webb, 1959 1968), based on the proportion of species (and individuals; Webb, 1959) represented in each leaf size class (modified in Webb, 1959).

In most cases, a positive correlation was noted for leaf size and temperature in addition to precipitation (e.g. Beard, 1944, Webb, 1959 1968). These correlations were then used by palaeobotanists in conjunction with leaf margin analysis as an alternative to floristic analysis (Roth and Dilcher, 1978).

In most instances, the method was based on a direct comparison of the proportions (as a percentage of the total flora) of species or individual leaves in the fossil flora in Raunkiaer's leaf size classes (as modified by Webb, 1959) to the values for modern forest classifications (e.g. MacGinitie, 1969; Christophel, 1981; Zastawniak, et al., 1985). Alternative schemes based on the proportion of the flora with 'large leaves' (Dilcher, 1973; Dolph and Dilcher, 1979a & b 1980) continued with the use of the proportion of species in each size class.

In each of these examples the primary flaw was the treatment of the fossil leaf bed as fossilised vegetation, and the failure to appreciate that the foliar physiognomic characteristics of the modern forest types referred to the canopy alone (Roth and Dilcher, 1978; Dolph, 1984). Leaf beds, however, consist of leaves derived from all of the synusiae of the forest (Ferguson, 1985) and will therefore reflect a diversity of potential foliar physiognomies, including leaf size (Davis and Taylor, 1980; Roth, 1984).

This point is well illustrated by Roth and Dilcher's study of a modern lake leaf deposit (1978) and by Spicer's study on leaf transport (1981). In both instances, they found that their leaf beds were dominated by the small coriaceous 'sun leaves' of the canopy. Results from a comparison between the proportions of leaves from forest floor leaf litter and the canopy data of Webb (1959) for four types of Australian rainforest (Fig. 4.1) clearly emphasise the same point.

The distribution of leaf sizes in leaf beds is clearly different from that of the forest canopy. Comparisons between the relative proportions of canopy species or individuals within the leaf size classes, and the proportions in fossil leaf beds is therefore clearly invalid. The cause of this change in proportions would seem to be a combination of the input of leaves from all synusiae and the selective survival of the tougher small coriaceous sun leaves of the topmost part of the canopy.

8.4 Foliar Physiognomic Analysis of Tertiary Leaf Beds Based on Foliar Physiognomic Signatures.

In Chapter 4 it was argued that leaf beds derived from forest types with different foliar physiognomic characteristics would retain unique foliar physiognomic signatures (Figs 4.46 & 4.47). These signatures represented a combination of the different levels of variation in leaf size (length, width and area), shape (relative width, position of maximal width), and the proportion of species and individuals with non-entire margins, for each forest type.

Tertiary leaf beds in Australia are often stratified, with leaves often occurring in discrete beds (e.g. Christophel, et al., 1987). These beds can be considered analogous to leaf beds on the forest floor (i.e. leaf litter), although in many instances the leaves may have experienced resorting in the water body. Generally though, the foliar physiognomic characteristics of leaf beds match those of leaf litter from the same forest type. Fossil leaves collected from discrete stratigraphic horizons can be compared directly to the litter physiognomic signatures.

However, fossil deposits are generally treated as a total unit, and the foliar physiognomic characteristics determined from the sum of all the fossil leaves (e.g. MacGinitie, 1969 1974; Christophel, 1981; Zastawniak, et al., 1985). This procedure makes the assumption that each stratigraphic unit within the deposit is ecologically equivalent i.e. represents the same vegetation type. Work on modern depositional environments (e.g. Spicer, 1981; Scheihing and Pfefferkorn, 1984) and some plant fossil beds (e.g. Spicer and Hill, 1979; Christophel, et al., 1987) has demonstrated that different plant communities can be represented in locally associated leaf beds. It is necessary, therefore, to restrict the comparison of foliar physiognomic signatures to samples of common stratigraphic origin.

8.5 Summary and Conclusions.

Ferguson commented that leafbeds give a distorted impression of past vegetation (Ferguson, 1985). He attributed this to the influences of taphonomic processes and the selective nature of leaf input and the restricted area from a local vegetation likely to contribute to a leaf bed (Ferguson, 1985). Roth and Dilcher (1978) and Dolph (1984) also drew attention to the potential differences between the character of vegetation, and leaf beds formed from that vegetation.

Because of the apparent and predicted discrepancies between the foliar physiognomic characteristics of vegetation and leaf beds formed from that vegetation, numerous researchers have cautioned the use of foliar physiognomic analysis on fossil leafbeds (e.g. Roth and Dilcher, 1978; Dolph and Dilcher, 1979a & b; Dolph, 1984; Martin, 1986).

In this study, leafbeds were demonstrated to retain a physiognomic signature which could be used to predict the forest type and climatic characteristics of the vegetation which produced fossil leaf beds. The use of comparisons based on the proportional representation of individual taxa in physiognomic classes, however, was demonstrated to introduce added sources of error.

Species based methods (e.g. Wolfe, 1980 1985 1987) are dependant on the reliable sorting of the whole flora into discrete taxonomic entities, and the assumption that the leaf bed was taxonomically representative of the local vegetation. This study suggests that taxonomic sorting requires an appreciation of the natural level of variation within taxa in leaf-beds. The wide variability observed between leaves from the same individual at different stages and levels within the tree will promote erroneous identification of extreme morphotypes, biasing foliar physiognomic analyses based on species.

The very local nature of leaf fall and input into depositional sites also suggests caution. Most leaf-beds will only reflect the individual trees within a small distance of the site. The high spatial heterogeneity in local species composition in modern rainforests (e.g. Ashton, 1984; Connell, et al., 1984) suggests that the local leaf fall will be distinctly biased between adjacent samples. The analysis of the taxonomic content of the litter at several sites suggests that this heterogeneity will be strongly reflected in leaf-beds (e.g. Figs 7.4 – 7.7). The species composition may therefore be distinctly biased towards particular species sets. These may bias foliar physiognomic analyses based on species attributes.

8.6 Future Research.

Roth and Dilcher (1978) suggested that leafbeds formed in a variety of depositional circumstances and a variety of plant communities needed to be studied to fully determine the relationship between the foliar physiognomic characteristics of vegetation and the leafbeds formed from them. This study considered four rainforest types over a range of climatic conditions, and examined two streambed depositional sites.

The data from these sites allowed a better appreciation of the problems associated with applying the foliar physiognomic characteristics of vegetation (e.g. the canopy characteristics of Webb, 1959) to leafbeds. The major point, however, was the existence of unique foliar physiognomic signatures in each of the forest types.

Several areas, however, remain to be explored. The comparison between the three CNVF sites — two essentially seasonal sites in N.E. Queensland and a non-seasonal site in New South Wales — indicated that leaf shape may be responsive to seasonality in rainfall and possibly temperature. Also, only one forest type, SNVF, was considered in an actual depositional circumstance.

This study could be continued to cover a greater number of seasonal sites to further understand the interactiuon between leaf shape and climate. Also, a greater range of forest types could be included to increase the understanding of the relationship. Ideally, it would be useful to include a range of sites covering a wide range of climatic extremes within each of the forest types to allow the definition of the foliar physiognomic field within the thermal field defined in the climatic analysis.

A final, and perhaps most important extension to this study, would be a survey of further examples of modern depositional sites covering several examples of each of the forest types. This further work is, however, limited by the availability of such sites.

A recent trip to N.E. Queensland (July, 1987) has demonstrated that several examples of leafbeds formed in old meander loops exist in the lowland area near Cairns (A. Graham and N. Hopkins, CSIRO Tropical Forest Research Centre, Atherton, Queensland, pers. com., 1987). These leaf beds would allow an extension to CMVF. No examples of the other forest types are presently known to exist, but a further survey of the area may yield such sites.

An increasing number of Early Tertiary leafbeds are being studied in Australia (e.g. Christophel and Greenwood, 1987 1988; Hill, 1987a). Preliminary comparisons between the foliar physiognomic characteristics of these leafbeds and the physiognomic signatures discussed here, were presented by Christophel and Greenwood (1987, 1988). Further work based on a finer resolution (as discussed here) of the physiognomic signatures of the modern leaf beds will result in a clearer understanding of the character of vegetation and climate in Australia during the Early Tertiary.

Chapter 9

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APPENDIX 1. Leaf data for all sites

Leaf Data for Oliver Creek (CMVF)

A = FOREST TYPE
C = SITE NUMBER
E = LEAF WIDTH (mm)

B = SAMPLE NUMBER
D = LEAF LENGTH (mm)
F = POSITION OF MAXIMAL WIDTH (mm)

Site Location:
16 08 S 145 27 E

Elevation:
20 metres

No. of Leaves with
Non-entire margins;

sample	%
3	1
4	16
5	13

A	B	C	D	E	F
2	5	3	100	30	42
2	5	3	126	50	60
2	5	3	96	40	47
2	5	3	96	45	46
2	5	3	66	22	34
2	5	3	96	40	40
2	5	3	126	46	62
2	5	3	110	50	48
2	5	3	124	40	70
2	5	3	126	52	62
2	5	3	120	50	60
2	5	3	116	58	58
2	5	3	120	42	52
2	5	3	106	59	58
2	5	3	74	33	35
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2	5	3	150	60	60
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2	5	3	100	40	50
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2	5	3	126	60	70
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2	5	3	122	55	61
2	5	3	115	44	60
2	5	3	107	54	52
2	5	3	110	47	56
2	5	3	120	67	60
2	5	3	114	48	58
2	5	3	103	40	40
2	5	3	100	40	52
2	5	3	130	52	60
2	5	3	315	49	160
2	5	3	236	56	120
2	5	3	216	100	115
2	5	3	230	105	125
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2	5	3	130	36	55
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2	5	3	152	40	80
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2	5	3	140	44	70
2	5	3	154	52	70
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2	5	3	90	19	34
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2	5	3	140	44	60
2	5	3	100	28	40
2	5	3	86	31	40
2	5	3	130	44	60
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2	5	3	112	84	30
2	5	3	115	10	45
2	5	3	122	09	55
2	5	3	102	12	40
2	5	3	138	13	50
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2	5	3	120	09	50
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2	5	3	60	28	25
2	5	3	60	25	30
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Leaf Data for Mulgrave River (CMVF)

A = FOREST TYPE
B = SAMPLE NUMBER
C = SITE NUMBER
D = LEAF LENGTH (mm)
E = LEAF WIDTH (mm)
F = POSITION OF MAXIMAL WIDTH (mm)

Site Location:
17 18 S 145 48 E

Elevation:
120 metres

No. of Leaves with
Non-entire Margins;

sample	%
2	1
3	26
4	1
5	1

A	B	C	D	E	F
2	4	2	112	37	52
2	4	2	112	37	50
2	4	2	125	42	56
2	4	2	111	38	52
2	4	2	101	29	46
2	4	2	121	38	54
2	4	2	122	72	61
2	4	2	86	40	48
2	4	2	70	27	38
2	4	2	86	44	45
2	4	2	56	22	26
2	4	2	60	22	22
2	4	2	105	32	45
2	4	2	94	31	43
2	4	2	126	38	57
2	4	2	89	27	38
2	4	2	115	39	50
2	4	2	122	39	55
2	4	2	140	50	51
2	4	2	125	53	41
2	4	2	130	50	70
2	4	2	100	37	40
2	4	2	56	28	32
2	4	2	72	32	40
2	4	2	129	47	61
2	4	2	101	40	51
2	4	2	115	38	50
2	4	2	112	40	51
2	4	2	114	36	51
2	4	2	117	35	50
2	4	2	110	32	46
2	4	2	71	24	35
2	4	2	165	57	91
2	4	2	166	62	65
2	4	2	140	54	50
2	4	2	130	61	41
2	4	2	160	56	70
2	4	2	110	30	45
2	4	2	94	28	40
2	4	2	118	39	50
2	4	2	118	39	54
2	4	2	126	44	51
2	4	2	80	43	38
2	4	2	120	40	60
2	4	2	65	29	33
2	4	2	96	35	52
2	4	2	85	32	41
2	4	2	82	44	41
2	4	2	118	44	46
2	4	2	152	56	52
2	4	2	102	42	32
2	4	2	142	50	60
2	4	2	100	31	55
2	4	2	92	43	48
2	4	2	48	23	30
2	4	2	52	20	28
2	4	2	81	25	32
2	4	2	70	22	30
2	4	2	77	42	41
2	4	2	56	22	30
2	4	2	55	30	28
2	4	2	73	36	35
2	4	2	84	26	40
2	4	2	110	43	70
2	4	2	106	27	50
2	4	2	107	33	49
2	4	2	120	38	53
2	4	2	127	43	55
2	4	2	88	32	40
2	4	2	111	37	46
2	4	2	95	32	45
2	4	2	110	35	50
2	4	2	100	36	46
2	4	2	111	35	46
2	4	2	105	37	35
2	4	2	140	42	62
2	4	2	110	57	50
2	4	2	170	58	75
2	4	2	106	39	42
2	4	2	130	38	55
2	4	2	80	25	30
2	4	2	110	35	44
2	4	2	110	31	45
2	4	2	119	45	57
2	4	2	65	29	35
2	4	2	56	23	20
2	4	2	97	28	46
2	4	2	140	47	63
2	4	2	85	30	40
2	4	2	121	36	55
2	4	2	84	50	39
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2	4	2	78	44	36
2	4	2	88	46	34
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2	4	2	132	47	61
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2	4	2	138	42	58
2	4	2	106	32	46
2	4	2	200	56	106
2	4	2	113	47	51
2	4	2	140	61	62
2	4	2	83	38	35
2	4	2	127	43	60
2	4	2	124	42	50
2	4	2	111	37	49
2	4	2	100	32	43
2	4	2	83	23	39
2	4	2	91	63	34
2	4	2	60	38	25
2	4	2	75	35	35
2	4	2	60	34	32
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2	4	2	106	30	50
2	4	2	97	37	47
2	4	2	112	46	55
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2	4	2	123	38	56
2	4	2	109	29	50
2	4	2	125	38	52
2	4	2	110	35	40
2	4	2	84	30	40

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2 4 2  82  48  31
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2 4 2 104  33  45
2 4 2 136  42  64
2 4 2 131  43  60
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2 4 2  63  38  32
2 4 2 105  36  45
2 4 2  86  29  42
2 4 2  76  27  32
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2 4 2 110  31  47
2 4 2  88  28  38
2 4 2  93  31  44
2 4 2 125  40  55
2 4 2 101  33  46
2 4 2 115  33  50
2 4 2  73  24  30
2 4 2 110  45  65
2 4 2  96  44  53
2 4 2  62  40  35
2 4 2 104  39  39
2 4 2  86  38  50
2 4 2  83  26  34
2 4 2 210  98  70
2 4 2 156  53  60
2 4 2 136  55  50
2 4 2 105  35  46
2 4 2  83  30  40
2 4 2  68  40  26
2 4 2 195  53  93
2 4 2 114  40  47
2 4 2 106  38  50
2 4 2 126  42  60
2 4 2 133  44  62
2 4 2 126  39  60
2 4 2 143  45  65
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2 4 2 100  30  45
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2 4 2 190  60  70
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2 4 2 136  45  60
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2 4 2 115  36  55
2 4 2 140  41  70
2 4 2 120  41  55
2 4 2 126  56  48
2 4 2 110  36  45
2 4 2 100  38  49
2 4 2  74  31  40
2 4 2  88  37  46
2 4 2  74  39  44
2 4 2  78  40  30
2 4 2  94  28  42
2 4 2 100  28  47
2 4 2 100  28  45

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2 4 2  82  27  35
2 4 2 112  41  53
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2 4 2  96  33  42
2 4 2  81  37  32
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2 4 2 109  39  50
2 4 2 121  38  55
2 4 2 125  43  57
2 4 2 110  34  50
2 4 2 104  28  50
2 4 2  98  29  46
2 4 2 114  40  57
2 4 2  76  27  36
2 4 2  87  50  45
2 4 2 103  45  36
2 4 2 120  43  47
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2 4 2  80  23  37
2 4 2  87  33  40
2 4 2  98  36  45
2 4 2 103  34  46
2 4 2 123  38  56
2 4 2 108  50  60
2 4 2  60  19  30
2 4 2  62  24  30
2 4 2 148  37  60
2 4 2 102  36  42
2 4 2 110  41  50
2 4 2  96  50  40
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2 5 2  83  37  37
2 5 2  86  41  40
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2 5 2  70  37  35
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2 5 2  68  38  30
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2 5 2  98  53  55
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2 5 2  50  23  26

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2 5 2  70   34   42
2 5 2 112   32   62
2 5 2 106   33   60
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2 5 2 109   26   46
2 5 2  70   24   42
2 5 2  71   28   33
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2 5 2  75   41   40
2 5 2  67   24   33
2 5 2  97   43   47
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2 5 2  70   26   32
2 5 2 115   44   67
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2 5 2  76   28   37
2 5 2 106   28   45
2 5 2 100   43   50
2 5 2  62   33   32
2 5 2 112   47   53
2 5 2 107   31   46
2 5 2 122   42   48
2 5 2 113   61   56
2 5 2 102   54   47
2 5 2 115   65   51
2 5 2 123   48   52
2 5 2 103   45   47
2 5 2 101   61   26
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2 5 2 120   35   52
2 5 2  71   26   35
2 5 2 123   34   36
2 5 2  99   39   50
2 5 2 142   52   80
2 5 2 108   51   52
2 5 2 115   41   46
2 5 2 104   38   47
2 5 2  90   43   45
2 5 2 106   62   53
2 5 2 122   53   63
2 5 2 180   49  106
2 5 2  81   31   42
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2 5 2 120   58   63
2 5 2 102   35   46
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2 5 2  85   34   40
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2 5 2  66   23   30
2 5 2  51   31   23
2 5 2  34   10   22
2 5 2 117   47   55
2 5 2  96   31   46
2 5 2 103   49   56
2 5 2  87   32   41
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2 5 2  92   33   40
2 5 2  97   56   52
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2 5 2  77   46   40
2 5 2 122   42   60
2 5 2 126   55   50
2 5 2  73   35   33
2 5 2 106   39   45
2 5 2  80   26   30
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2 3 2 162   67   88
2 3 2  76   31   38
2 3 2  96   37   45
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2 3 2  35   10   18
2 3 2  27   11   12
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2 3 2 107   52   56
2 3 2  97   36   47
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2 3 2  72   37   42
2 3 2 135   64   70
2 3 2  41   21   16
2 3 2  34   19   16
2 3 2 128   63   80
2 3 2 140   58   66
2 3 2 112   43   67
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2 3 2 116   65   65
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2 3 2  47   16   22
2 3 2  66   29   36
2 3 2  91   42   50
2 3 2 107   40   52
2 3 2 120   47   60
2 3 2  93   39   50
2 3 2 150   56   70
2 3 2 126   44   63
2 3 2 116   52   60
2 3 2  92   43   48
2 3 2 144   58   80
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2 3 2 121   50   60
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2 3 2 127  50  66
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2 3 2 100  42  45
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2 3 2 142  67  75

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2 3 2 104  43  50
2 3 2 106  47  50
2 3 2 100  47  57
2 3 2  85  40  42
2 3 2 116  47  60

2 3 2 115  62  52
2 3 2  50  28  30
2 3 2  98  44  44
2 3 2 170  75  86
2 3 2 142  58  76
2 3 2 100  47  48
2 3 2 106  44  45
2 3 2  98  52  43
2 3 2  98  45  42
```

Leaf Data for Mobo Creek (CMVF)

A = FOREST TYPE
C = SITE NUMBER
E = LEAF WIDTH (mm)
B = SAMPLE NUMBER
D = LEAF LENGTH (mm)
F = POSITION OF MAXIMAL WIDTH (mm)

Site Location:
17 10 S 145 39 E

Elevation:
720 metres

No. of Leaves with
Non-entire Margins;

sample	%
1	3
2	1
3	1
4	2

A	B	C	D	E	F
2	1	1	143	47	55
2	1	1	151	52	69
2	1	1	97	33	43
2	1	1	93	34	37
2	1	1	107	36	46
2	1	1	54	33	26
2	1	1	96	41	42
2	1	1	117	46	61
2	1	1	95	39	50
2	1	1	70	36	40
2	1	1	107	34	56
2	1	1	131	45	61
2	1	1	69	29	33
2	1	1	74	26	30
2	1	1	68	33	19
2	1	1	43	17	17
2	1	1	126	34	60
2	1	1	72	26	35
2	1	1	92	54	38
2	1	1	93	41	50
2	1	1	97	40	51
2	1	1	93	46	37
2	1	1	104	43	50
2	1	1	92	42	48
2	1	1	115	42	56
2	1	1	115	28	65
2	1	1	120	38	60
2	1	1	65	27	30
2	1	1	61	22	27
2	1	1	66	28	35
2	1	1	82	36	40
2	1	1	91	29	42
2	1	1	100	37	44
2	1	1	75	38	42
2	1	1	81	37	45
2	1	1	76	24	35
2	1	1	91	34	44
2	1	1	112	42	50
2	1	1	105	42	50
2	1	1	120	46	65
2	1	1	115	45	58
2	1	1	105	44	56
2	1	1	145	53	74
2	1	1	55	25	30
2	1	1	125	55	60
2	1	1	106	41	55
2	1	1	91	41	41
2	1	1	56	24	27
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```

Leaf Data for Curtain Fig (CNVF)

A = FOREST TYPE
C - SITE NUMBER
E = LEAF WIDTH (mm)
B = SAMPLE NUMBER
D = LEAF LENGTH (mm)
F = POSITION OF MAXIMAL WIDTH (mm)

Site Location:

Elevation:
c. 750 metres

No. of Leaves with Non-entire Margins;

sample	%
1	45
2	44
3	46
4	39

A	B	C	D	E	F
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3	1	1	103	54	39
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3	1	1	86	48	18
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3	1	1	78	36	19
3	1	1	62	40	14
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Leaf Data for The Crater (CNVF)

A = FOREST TYPE
C = SITE NUMBER
E = LEAF WIDTH (mm)

B = SAMPLE NUMBER
D = LEAF LENGTH (mm)
F = POSITION OF MAXIMAL WIDTH (mm)

Site Location:
17 25 S 145 29 E

Elevation:
c. 1000 metres

No. of Leaves with
Non-entire Margins;

sample	%
1	61
2	74
3	51
4	77

A	B	C	D	E	F
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3	1	2	121	56	58
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Leaf Data for Dorrigo (CNVF)

A = FOREST TYPE
B = SAMPLE NUMBER
C = SITE NUMBER
D = LEAF LENGTH (mm)
E = LEAF WIDTH (mm)
F = POSITION OF MAXIMAL WIDTH (mm)

Location of Site:
30 20 S 152 45 E

Elevation:
c. 200 metres

No. of Leaves with Non-entire Margins;

sample	%
1	37
2	38
3	50
4	50

A	B	C	D	E	F
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3 4 3  36  10  20
3 4 3 106  31  52
3 4 3  70  23  35
3 4 3  63  26  35
```

Leaf Data for Mt Haig (SNVF)

A = FOREST TYPE
C = SITE NUMBER
E = LEAF WIDTH (mm)

B = SAMPLE NUMBER
D = LEAF LENGTH (mm)
F = POSITION OF MAXIMAL WIDTH (mm)

Site Location:
17 05 S 145 35 E

Elevation:
1160 metres

No. of Leaves with
Non-entire Margins;

sample	%
1	3
2	5
3	43
4	11

A	B	C	D	E	F
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1	5	1	85	36	55
1	5	1	58	33	28
1	5	1	85	39	42
1	5	1	83	35	41
1	5	1	68	37	36
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1	5	1	49	20	20
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1	5	1	59	24	25
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1	5	1	54	18	20
1	5	1	45	19	16
1	5	1	45	17	21
1	5	1	116	37	53
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1	5	1	75	29	34
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Leaf Data for Mt Lewis Road (SNVF)

A = FOREST TYPE
C = SITE NUMBER
E = LEAF WIDTH (mm)

B = SAMPLE NUMBER
D = LEAF LENGTH (mm)
F = POSITION OF MAXIMAL WIDTH (mm)

Site Location:
16 33 S 145 17 E

Elevation:
c. 1200 metres

No. of Leaves with
Non-entire Margins;

sample	%
1	4
2	6
3	4

A	B	C	D	E	F
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1	1	2	88	36	26
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1	1	2	46	15	20
1	1	2	60	20	30
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1	1	2	83	13	35
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1	1	2	76	13	22
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Leaf Data for Washpool / Coombadjha Creek (SNVF New South Wales)

A = FOREST TYPE
C = SITE NUMBER
E = LEAF WIDTH (mm)

B = SAMPLE NUMBER
D = LEAF LENGTH (mm)
F = POSITION OF MAXIMAL WIDTH (mm)

Site Location:
29 28 S 152 22 E

Elevation:
C. 800 metres

No. of Leaves with Non-entire Margins;

sample	%
1	63
2	81
3	93
4	67

A	B	C	D	E	F
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1	1	5	55	20	25
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Leaf Data for Mt Lewis EP18 (SNVF)

A = FOREST TYPE
C = SITE NUMBER
E = LEAF WIDTH (mm)

B = SAMPLE NUMBER
D = LEAF LENGTH (mm)
F = POSITION OF MAXIMAL WIDTH (mm)

Site Location:
16 31 S 145 16 E

Elevation:
1050 metres

No. of Leaves with
Non-entire Margins;

sample	%
1	5
2	11
3	17
4	3

A	B	C	D	E	F
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1	1	3	120	35	57
1	1	3	85	35	47
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Leaf Data for Barrington Tops (MFF)

A = FOREST TYPE
C = SITE NUMBER
E = LEAF WIDTH (mm)

B = SAMPLE NUMBER
D = LEAF LENGTH (mm)
F = POSITION OF MAXIMAL WIDTH (mm)

Site Location:
32 00 S 151 29 E

Elevation:
c. 1500 metres

No. of Leaves with
Non-entire Margins;

sample	%
1	87
2	99
3	85
4	93

A	B	C	D	E	F
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4	1	1	49	24	15
4	1	1	52	23	20
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4 4 1  41  13  19
4 4 1  39  12  16
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4 4 1  48  28  14
4 4 1  38  20  15
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4 4 1  45  18  18
4 4 1  75  31  30
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4 4 1  40  24  13
4 4 1  52  25  14
4 4 1  35  20  12
4 4 1  49  24  17
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4 4 1  44  20  23
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4 4 1  61  24  28
4 4 1  60  20  26
4 4 1  46  18  20
4 4 1  52  27  17
4 4 1  92  35  41
4 4 1  80  32  33
4 4 1  77  36  30
4 4 1  66  30  27
4 4 1  25  21  10
4 4 1  51  20  21
4 4 1  51  23  21
4 4 1  52  16  17
4 4 1  68  33  17
4 4 1  68  28  30
4 4 1  66  26  23
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4 4 1  70  33  20
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4 4 1  58  22  23
4 4 1  51  15  23
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4 4 1  47  19  21
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4 4 1  32  17  13
4 4 1  55  21  25
4 4 1  68  34  30
4 4 1  45  22  16
4 4 1  50  25  20
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4 4 1  68  27  29
4 4 1  60  24  25
4 4 1  49  21  22
4 4 1  64  22  31
4 4 1  82  30  39
4 4 1  54  25  25
4 4 1  50  22  26
4 4 1  47  21  23
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4 4 1  60  25  25
4 4 1  56  23  25
4 4 1  28  17  09
4 4 1  30  19  09
4 4 1  35  25  11
4 4 1  43  23  13

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4 4 1  41  21  12
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4 4 1  39  15  16
4 4 1  39  22  16
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4 4 1  34  18  13
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4 4 1  68  24  30
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4 4 1  66  23  31
4 4 1  73  23  30
4 4 1  77  30  38
4 4 1  73  34  34
4 4 1  87  37  38
4 4 1  83  33  37
4 4 1  42  21  14
4 4 1  40  18  12
4 4 1  27  19  08
4 4 1  42  23  17
4 4 1  44  18  18
4 4 1  48  18  20

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4 4 1  51  30  20
4 4 1  45  18  20
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4 4 1  32  23  09
4 4 1  29  20  10
4 4 1  78  29  32
4 4 1  67  26  30
4 4 1  76  19  22
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4 4 1  34  27  10
4 4 1  47  17  19
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4 4 1  42  19  12
4 4 1  47  23  16
4 4 1  40  20  12
4 4 1  60  23  23
4 4 1  48  27  16
4 4 1  46  27  15
4 4 1  61  30  25
4 4 1  49  24  16
4 4 1  25  20  14
4 4 1  58  29  19
4 4 1  47  22  13
4 4 1  50  21  18
4 4 1  53  21  20
4 4 1  62  25  23
4 4 1  55  24  22
4 4 1  38  17  18
```

Leaf Data for Mt Windsor Stream Site (SNVF)

A = FOREST TYPE
C = SITE NUMBER
D = LEAF WIDTH (mm)

B = SAMPLE NUMBER
D = LEAF LENGTH (mm)
E = POSITION OF MAXIMAL WIDTH (mm)

Site Location:
16 13 S 145 04 E

Elevation:
c. 880 metres

No. of Leaves with
Non-entire Margins;

sample	%
1	18
2	17

A	B	C	D	E	F
9	1	1	83	29	37
9	1	1	75	28	26
9	1	1	49	25	20
9	1	1	56	21	19
9	1	1	100	48	52
9	1	1	70	19	37
9	1	1	51	25	18
9	1	1	50	24	23
9	1	1	52	26	32
9	1	1	58	28	40
9	1	1	41	24	20
9	1	1	50	35	27
9	1	1	66	29	35
9	1	1	46	15	15
9	1	1	52	24	36
9	1	1	45	31	20
9	1	1	55	26	22
9	1	1	85	29	32
9	1	1	33	24	20
9	1	1	58	18	24
9	1	1	75	38	36
9	1	1	80	23	32
9	1	1	44	15	20
9	1	1	52	26	34
9	1	1	60	25	30
9	1	1	56	23	30
9	1	1	90	38	46
9	1	1	60	32	30
9	1	1	70	26	36
9	1	1	110	30	50
9	1	1	87	30	60
9	1	1	54	22	30
9	1	1	75	44	40
9	1	1	54	17	23
9	1	1	32	16	14
9	1	1	35	12	16
9	1	1	68	25	43
9	1	1	63	25	30
9	1	1	74	28	50
9	1	1	65	19	30
9	1	1	40	16	14
9	1	1	42	17	17
9	1	1	25	07	10
9	1	1	48	19	20
9	1	1	47	23	20
9	1	1	42	18	17
9	1	1	72	30	36
9	1	1	90	30	40
9	1	1	46	12	22
9	1	1	77	25	28
9	1	1	46	24	22
9	1	1	68	32	40
9	1	1	86	21	38
9	1	1	55	20	24
9	1	1	40	12	20
9	1	1	120	34	55
9	1	1	46	28	35
9	1	1	70	40	40
9	1	1	70	36	36
9	1	1	85	34	50
9	1	1	55	16	25
9	1	1	45	25	25
9	1	1	136	47	70
9	1	1	83	43	45
9	1	1	89	42	42
9	1	1	70	25	50
9	1	1	50	22	25
9	1	1	56	27	18
9	1	1	60	29	22
9	1	1	87	46	55
9	1	1	55	19	22
9	1	1	57	25	22
9	1	1	34	11	20
9	1	1	62	25	40
9	1	1	107	44	52
9	1	1	87	38	47
9	1	1	46	32	22
9	1	1	56	31	38
9	1	1	72	38	50
9	1	1	102	44	60
9	1	1	70	24	27
9	1	1	55	29	25
9	1	1	100	35	56
9	1	1	60	32	40
9	1	1	40	20	25
9	1	1	90	34	40
9	1	1	90	25	40
9	1	1	70	32	35
9	1	1	45	24	22
9	1	1	66	25	28
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9	1	1	53	18	30
9	1	1	48	34	30
9	1	1	72	38	40
9	1	1	76	40	40
9	1	1	50	22	27
9	1	1	110	52	60
9	1	1	80	32	42
9	1	1	120	36	60
9	1	1	105	37	40
9	1	1	47	25	28
9	1	1	91	44	50
9	1	1	76	29	32
9	1	1	92	46	50
9	1	1	78	40	53
9	1	1	80	47	42
9	1	1	80	31	47
9	1	1	47	22	25
9	1	1	60	35	40
9	1	1	68	24	40
9	1	1	47	17	30
9	1	1	76	40	37
9	1	1	35	17	22
9	1	1	41	16	26
9	1	1	60	28	22
9	1	1	39	21	17
9	1	1	24	12	12
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9	1	1	45	20	18
9	1	1	56	27	27
9	1	1	65	38	27
9	1	1	55	30	25
9	1	1	60	25	28

9	1	1	87	40	42
9	1	1	80	27	43
9	1	1	90	43	60
9	1	1	86	31	54
9	1	1	70	38	25
9	1	1	60	30	22
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9	1	1	58	18	15
9	1	1	45	20	30
9	1	1	56	24	38
9	1	1	57	28	43
9	1	1	66	28	20
9	1	1	36	13	20
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9	1	1	130	50	60
9	1	1	78	36	48
9	1	1	60	18	34
9	1	1	125	62	70
9	1	1	110	49	66
9	1	1	65	24	38
9	1	1	80	33	23
9	1	1	63	23	17
9	1	1	92	28	40
9	1	1	77	26	38
9	1	1	74	46	29
9	1	1	100	44	48
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9	1	1	60	20	40
9	1	1	50	20	23
9	1	1	76	22	30
9	1	1	52	26	26
9	1	1	97	30	40
9	1	1	95	29	37
9	1	1	64	26	30
9	1	1	87	40	50
9	1	1	96	46	60
9	1	1	113	50	63
9	1	1	55	20	21
9	1	1	110	48	50
9	1	1	86	24	45
9	1	1	61	16	30
9	1	1	90	36	40
9	1	1	31	16	15
9	1	1	54	28	33
9	1	1	70	18	40
9	1	1	47	21	12
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9	1	1	56	30	22
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9	1	1	109	41	50
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9	1	1	76	30	31
9	1	1	55	32	20
9	1	1	73	32	30
9	1	1	75	27	30
9	1	1	95	49	42
9	1	1	46	16	23
9	1	1	57	27	31
9	1	1	71	26	24
9	1	1	76	30	43
9	1	1	74	43	50
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9	1	1	72	28	23
9	1	1	150	76	65
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9	1	1	80	50	29
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9	1	1	71	31	23
9	1	1	56	24	27
9	1	1	62	30	23
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9	1	1	63	24	32
9	1	1	43	18	20
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9	1	1	61	28	38
9	1	1	47	25	27
9	1	1	56	21	40
9	1	1	94	36	38
9	1	1	67	42	29
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9	1	1	92	30	42
9	1	1	80	32	50
9	1	1	55	22	21
9	1	1	46	14	22
9	1	1	40	22	20
9	1	1	88	39	46
9	1	1	130	50	65
9	1	1	70	23	36
9	1	1	60	21	23
9	1	1	77	41	35
9	1	1	63	26	35
9	1	1	45	20	21
9	1	1	110	30	44
9	2	1	107	29	35
9	2	1	62	25	23
9	2	1	80	27	30
9	2	1	70	21	30
9	2	1	122	42	65
9	2	1	131	66	60
9	2	1	53	24	26
9	2	1	68	27	35
9	2	1	71	24	40
9	2	1	56	29	33
9	2	1	55	26	23
9	2	1	71	30	26
9	2	1	70	24	37
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9	2	1	98	36	50
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9	2	1	60	30	26
9	2	1	118	42	40
9	2	1	117	63	45
9	2	1	105	35	36
9	2	1	78	42	30
9	2	1	75	31	41
9	2	1	107	29	40
9	2	1	110	30	43
9	2	1	80	28	25
9	2	1	89	47	40
9	2	1	57	18	30
9	2	1	80	34	40
9	2	1	76	34	38
9	2	1	114	39	42
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9	2	1	73	29	35
9	2	1	61	21	40
9	2	1	146	43	60
9	2	1	120	60	40
9	2	1	84	30	50
9	2	1	100	34	42
9	2	1	76	30	40
9	2	1	112	52	50
9	2	1	66	20	30
9	2	1	66	40	24
9	2	1	63	17	40
9	2	1	80	32	42
9	2	1	93	44	30
9	2	1	58	21	20
9	2	1	49	22	30
9	2	1	65	27	43
9	2	1	59	24	27
9	2	1	69	30	42
9	2	1	77	27	33
9	2	1	50	18	32
9	2	1	68	30	28
9	2	1	67	38	28
9	2	1	70	25	31
9	2	1	40	15	25
9	2	1	51	19	21
9	2	1	47	23	20
9	2	1	37	18	22
9	2	1	55	29	31
9	2	1	150	52	58
9	2	1	94	43	35
9	2	1	66	32	20
9	2	1	67	27	42
9	2	1	107	40	60
9	2	1	78	28	37
9	2	1	106	55	50
9	2	1	100	42	41
9	2	1	161	72	74
9	2	1	88	39	41
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9	2	1	94	36	42
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9	2	1	74	36	38
9	2	1	92	38	43
9	2	1	65	34	28
9	2	1	116	54	48
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9	2	1	60	24	25
9	2	1	88	42	33
9	2	1	100	32	40
9	2	1	90	53	35
9	2	1	150	51	70
9	2	1	80	26	33
9	2	1	106	68	52
9	2	1	157	60	70
9	2	1	66	25	38
9	2	1	53	20	31
9	2	1	83	46	40
9	2	1	146	56	76
9	2	1	56	18	30
9	2	1	74	29	30
9	2	1	93	40	60
9	2	1	111	41	45
9	2	1	71	22	43
9	2	1	112	49	42
9	2	1	102	32	36

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9 2 1  96  54  62
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9 2 1 140  59  55
9 2 1 105  46  45
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9 2 1  56  22  30
9 2 1  71  25  48
9 2 1  95  43  40
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9 2 1  83  33  30
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9 2 1  96  44  45
9 2 1  80  40  31
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9 2 1 138  59  62
9 2 1  93  48  40
9 2 1 106  49  45
9 2 1 130  62  50
9 2 1  85  24  43
9 2 1  72  26  24
9 2 1  79  30  50
9 2 1  57  28  36
9 2 1  72  32  45
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9 2 1  87  45  50
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9 2 1  80  41  38
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9 2 1 103  43  42
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9 2 1  82  34  40
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9 2 1 110  48  53
9 2 1 106  44  50
9 2 1  80  30  31
9 2 1 120  53  76
9 2 1  77  27  35
9 2 1  55  16  27
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9 2 1  50  19  25
9 2 1  94  37  40
9 2 1 135  52  65
9 2 1  70  37  30
9 2 1  67  30  25
9 2 1  78  24  28
9 2 1  54  29  25
9 2 1  60  20  35
9 2 1  96  39  40
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9 2 1  99  39  60
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9 2 1  50  19  22
9 2 1  52  23  20
9 2 1  55  20  25
9 2 1  76  26  30
9 2 1  66  27  30
9 2 1  98  40  35
9 2 1  90  48  50
9 2 1  50  22  17
9 2 1  36  14  14
9 2 1  42  24  16
9 2 1  37  15  16
9 2 1  58  19  25
9 2 1  68  21  40
9 2 1  53  20  34
9 2 1 104  44  42
9 2 1  87  32  35
9 2 1  81  36  47
9 2 1  57  29  24
9 2 1  64  21  26
9 2 1  45  22  26
9 2 1  25  10  12
9 2 1  91  42  35
9 2 1  51  28  24
9 2 1  72  31  30
9 2 1  62  29  28
9 2 1  80  35  30
9 2 1  56  24  26
9 2 1  93  50  41
9 2 1  72  38  33
9 2 1  55  26  25
9 2 1  75  44  30
9 2 1  63  25  30
9 2 1  96  33  40
9 2 1  74  30  35
9 2 1  61  26  28
9 2 1  74  26  30
9 2 1  77  31  36
9 2 1  57  29  20
9 2 1  63  28  36
9 2 1  25  18  13
9 2 1  43  21  24
9 2 1  67  23  32
9 2 1  61  34  36
9 2 1  72  28  34
9 2 1  57  28  27
9 2 1  76  39  32
9 2 1  63  30  26
9 2 1  53  34  23
9 2 1  46  28  20
9 2 1  47  17  20
9 2 1  64  26  36
9 2 1  80  31  38
9 2 1  41  16  25
9 2 1  44  13  16
```

Leaf Data for Coombadjha Ck Stream Site (SNVF)

A = FOREST TYPE
C = SITE NUMBER
E = LEAF WIDTH (mm)

B = SAMPLE NUMBER
D = LEAF LENGTH (mm)
F = POSITION OF MAXIMAL WIDTH (mm)

Site Location:
29 28 S 152 22 E

Elevation:
c. 800 metres

No. of Leaves with
Non-entire Margins;

sample	%
1	91

A	B	C	D	E	F
9	1	2	38	16	20
9	1	2	91	30	39
9	1	2	85	28	38
9	1	2	74	23	21
9	1	2	58	17	24
9	1	2	67	26	33
9	1	2	52	18	25
9	1	2	55	21	21
9	1	2	67	24	28
9	1	2	45	26	22
9	1	2	30	12	14
9	1	2	86	22	46
9	1	2	74	25	40
9	1	2	60	19	30
9	1	2	36	13	17
9	1	2	40	18	17
9	1	2	63	27	32
9	1	2	50	24	25
9	1	2	81	31	37
9	1	2	101	31	50
9	1	2	69	24	34
9	1	2	53	18	22
9	1	2	61	19	19
9	1	2	57	25	32
9	1	2	71	24	25
9	1	2	63	22	28
9	1	2	43	16	18
9	1	2	60	25	28
9	1	2	52	18	17
9	1	2	65	22	30
9	1	2	80	26	37
9	1	2	68	25	24
9	1	2	42	17	17
9	1	2	53	19	20
9	1	2	85	26	37
9	1	2	71	21	32
9	1	2	55	19	23
9	1	2	74	25	30
9	1	2	62	18	28
9	1	2	64	25	31
9	1	2	67	22	30
9	1	2	53	19	24
9	1	2	53	21	27
9	1	2	46	19	25
9	1	2	69	23	30
9	1	2	80	28	36
9	1	2	66	27	31
9	1	2	52	24	26
9	1	2	60	22	30
9	1	2	107	24	57
9	1	2	92	30	42
9	1	2	110	30	47
9	1	2	68	27	29
9	1	2	49	19	22
9	1	2	40	13	20
9	1	2	68	17	31
9	1	2	36	15	14
9	1	2	65	19	25
9	1	2	82	32	42
9	1	2	68	24	30
9	1	2	76	27	35
9	1	2	69	31	30
9	1	2	64	21	26
9	1	2	50	19	22
9	1	2	67	28	34
9	1	2	62	20	26
9	1	2	78	29	32
9	1	2	65	29	35
9	1	2	62	21	26
9	1	2	81	30	40
9	1	2	44	22	20
9	1	2	32	15	16
9	1	2	97	30	45
9	1	2	80	24	40
9	1	2	40	19	18
9	1	2	41	18	19
9	1	2	39	16	18
9	1	2	122	48	58
9	1	2	87	27	37
9	1	2	75	23	30
9	1	2	58	19	27
9	1	2	68	18	34
9	1	2	72	28	36
9	1	2	75	26	34
9	1	2	86	32	41
9	1	2	75	25	32
9	1	2	60	20	30
9	1	2	55	18	28
9	1	2	62	20	35
9	1	2	98	38	48
9	1	2	62	20	30
9	1	2	71	19	27
9	1	2	70	23	30
9	1	2	102	17	60
9	1	2	137	18	80
9	1	2	50	12	25
9	1	2	48	15	22
9	1	2	59	24	27
9	1	2	58	33	31
9	1	2	81	26	33
9	1	2	90	24	40
9	1	2	85	26	37
9	1	2	76	23	36
9	1	2	40	16	18
9	1	2	42	16	20
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9	1	2	76	24	33
9	1	2	88	27	34
9	1	2	71	36	30
9	1	2	100	32	46
9	1	2	69	22	33
9	1	2	69	26	25
9	1	2	93	38	40
9	1	2	91	27	46
9	1	2	52	16	23
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9	1	2	55	21	24
9	1	2	71	25	30
9	1	2	54	20	25
9	1	2	52	21	24
9	1	2	41	17	20
9	1	2	22	09	09
9	1	2	48	17	23
9	1	2	45	16	20
9	1	2	40	14	14

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9 1 2  54  18  25
9 1 2  62  17  28
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9 1 2  70  12  40
9 1 2 132  23  68
9 1 2  60  09  28
9 1 2  57  20  26
9 1 2  45  13  21
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9 1 2  37  13  16
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9 1 2  59  20  28
9 1 2  24  12  12
9 1 2  31  07  15
9 1 2  57  22  26
9 1 2  34  14  17
9 1 2  68  27  32
9 1 2  62  19  25
9 1 2  70  24  33
9 1 2  58  20  28
9 1 2  81  24  37
9 1 2  50  19  18
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APPENDIX 2. Leaf data for Discriminant Analysis.

	LEAF LENGTH						LEAF WIDTH						RELATIVE WIDTH						% POSITION						LEAF AREA						non-entire
	m	10	20	50	80	90	m	10	20	50	80	90	m	10	20	50	80	90	m	10	20	50	80	90	m	10	20	50	80	90	%
121	075	42	53	071	088	115	26	14	19	25	33	39	37	23	29	39	43	48	50	38	44	51	57	61	14	04	06	12	20	29	03
131	058	35	40	052	072	092	22	12	14	21	28	32	38	29	32	37	43	50	45	33	38	45	52	58	09	03	04	07	15	19	05
141	063	38	46	055	077	099	27	15	20	28	33	37	46	29	36	44	58	64	45	36	40	46	50	53	12	04	06	11	17	22	43
151	071	41	53	064	082	101	26	16	19	26	32	37	39	28	33	39	45	50	44	36	39	44	49	53	13	05	06	11	18	23	11
112	063	43	50	060	072	086	25	15	17	24	33	37	41	27	34	41	48	55	47	32	43	48	53	58	11	05	06	09	16	20	04
122	065	44	50	063	078	088	26	14	20	26	31	35	43	17	31	46	53	60	44	27	41	46	50	56	12	06	07	10	13	17	06
142	062	41	46	056	074	092	29	21	23	28	33	38	49	36	42	49	56	63	46	37	42	46	50	55	13	06	07	10	17	23	04
113	075	46	56	070	086	107	28	18	20	27	34	39	39	28	31	37	46	55	48	35	44	48	54	62	16	06	08	11	20	28	05
123	073	47	55	066	082	105	28	18	21	27	34	38	40	30	33	40	46	50	49	37	44	49	55	63	15	06	08	12	18	24	11
143	071	51	56	070	083	092	26	17	20	26	31	35	37	27	29	35	46	50	50	37	43	50	59	66	13	06	08	12	17	20	17
153	068	44	53	064	083	099	26	16	18	25	33	37	40	26	32	38	46	53	42	32	37	44	49	51	13	05	06	10	18	24	03
115	067	47	54	066	078	090	21	13	16	21	27	29	32	26	29	32	35	38	46	41	43	46	49	52	10	04	06	09	14	17	63
125	062	42	50	058	072	086	22	15	17	21	26	31	36	29	32	36	39	42	47	41	45	48	50	52	10	05	05	80	13	17	81
135	059	41	50	056	066	084	17	11	12	16	22	27	29	23	25	28	33	37	46	40	43	46	48	51	08	03	04	06	10	14	93
145	062	45	51	061	072	081	20	14	15	19	24	26	32	27	29	32	35	37	47	41	44	48	50	53	09	04	05	08	12	14	67
211	102	65	79	100	119	136	38	26	29	38	45	49	38	30	33	37	42	49	46	40	43	46	49	53	27	12	14	26	37	44	03
221	098	65	76	092	111	130	35	24	27	34	43	48	37	29	32	36	41	46	47	40	44	46	50	55	25	10	14	21	33	42	01
231	106	71	84	103	123	144	38	24	28	35	46	54	36	28	30	34	40	50	48	39	44	47	52	56	29	11	15	24	37	54	01
241	099	64	80	097	116	129	36	23	28	36	42	48	37	30	32	35	39	47	50	42	46	50	53	58	25	10	15	23	33	38	02
232	106	52	88	107	131	150	46	23	33	46	58	67	43	35	39	42	47	53	50	44	47	50	53	58	36	08	17	32	54	62	01
242	106	71	85	106	122	140	39	27	30	38	45	53	37	29	31	34	40	52	46	38	42	46	48	54	29	13	18	26	37	46	16
252	097	67	76	093	112	128	40	26	31	38	47	56	42	31	35	40	49	56	48	40	44	48	52	56	27	12	16	24	36	43	13
223	116	79	92	112	130	160	41	13	30	40	54	60	36	10	31	38	44	50	49	41	44	48	52	56	32	10	13	29	43	54	01
233	112	76	92	110	130	150	41	12	27	40	52	63	35	10	30	37	44	51	47	37	41	46	50	58	34	10	16	28	42	61	26
243	108	70	82	102	125	160	38	12	21	39	50	57	40	10	34	42	49	56	46	37	42	46	50	54	31	09	12	26	40	51	01
253	109	65	86	110	126	140	41	12	27	40	52	63	40	12	33	42	47	56	47	39	43	48	51	56	32	09	13	24	41	64	01
311	091	70	79	089	101	114	41	29	33	40	48	56	46	32	37	46	53	61	33	23	27	35	38	42	26	15	18	23	32	39	45
321	091	63	75	087	103	120	42	26	31	41	52	57	47	33	38	48	55	61	34	26	30	34	38	43	27	12	15	24	36	43	44
331	101	66	77	094	120	145	43	27	31	40	52	62	44	27	30	44	53	59	37	23	27	40	46	49	31	14	17	26	39	54	46
341	088	66	77	090	097	112	40	26	30	38	50	55	45	32	36	43	53	62	36	28	33	37	40	43	24	12	15	22	32	38	39
312	081	56	63	074	090	123	44	32	35	42	52	57	56	40	50	58	62	65	43	32	37	43	47	53	25	13	15	21	31	45	61
322	084	53	63	075	105	130	38	22	24	35	49	57	45	34	38	45	50	57	49	42	44	48	54	61	24	08	10	17	37	50	74
332	080	48	56	070	102	126	38	21	26	35	50	58	49	35	45	53	58	61	38	24	28	37	47	51	23	07	09	16	35	47	51
342	085	49	57	078	104	136	40	25	28	37	51	61	49	35	42	51	57	62	41	26	33	44	48	50	26	09	11	20	36	52	77
313	090	52	70	088	105	130	29	18	21	28	36	40	33	26	29	32	36	40	51	43	46	50	55	60	19	06	09	16	26	33	37
323	090	52	72	087	105	125	28	18	21	27	35	39	32	26	28	31	34	37	49	42	46	49	54	58	18	07	09	16	26	31	38
333	091	56	71	088	106	130	29	19	22	28	36	39	32	26	29	32	35	38	51	41	46	51	57	63	19	07	09	16	27	34	50
343	083	56	67	080	095	116	27	18	20	26	33	37	33	26	29	33	36	39	49	43	45	48	52	56	16	07	09	14	21	29	50
411	046	28	35	045	056	069	22	14	16	21	27	29	49	35	40	46	54	65	39	30	34	39	43	48	07	03	04	06	10	12	87
421	050	31	38	047	060	075	24	16	19	23	29	32	50	38	42	46	57	66	37	29	31	35	42	47	09	04	05	07	12	15	99
431	048	30	37	046	057	068	22	15	16	21	27	30	47	35	39	43	53	66	37	28	32	38	42	46	07	03	04	07	10	13	85
441	053	30	38	049	061	073	23	17	18	23	28	30	49	35	39	47	57	71	38	28	32	38	43	46	08	04	05	07	12	15	93
911	068	42	47	065	087	100	29	17	21	28	38	44	44	31	35	43	52	56	49	37	40	48	59	64	15	05	07	11	22	28	18
921	081	50	57	076	103	119	34	19	23	30	44	52	42	32	35	41	49	53	47	37	40	45	55	61	20	07	09	15	29	40	17
912	062	40	47	061	076	086	22	15	17	21	26	30	36	29	31	35	40	44	47	40	43	46	50	53	10	04	05	08	13	16	91

A MEGAFOSSIL FLORA FROM THE EOCENE OF GOLDEN GROVE, SOUTH AUSTRALIA

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Running head: Golden Grove fossil flora

ABSTRACT

A new Eocene plant megafossil locality is reported from near Golden Grove, South Australia. Well preserved mummified leaves, fruits and flowers and impressions are abundant in a lens structure within the East Yatala sand pit operated by Monier. Preliminary analysis has identified a rainforest flora containing Elaeocarpaceae (*Sloanea*/*Elaeocarpus*), Lauraceae, Myrtaceae (*Myrtaciphyllum*), Proteaceae (*Banksieaephyllum*, aff. *Neorites*), Sterculiaceae (*Brachychiton*), Podocarpaceae (*Decussocarpus*, *Podocarpus*), and the fern *Lygodium*. Physiognomic analysis of the leaves suggests that the closest analogue is with Complex Notophyll Vine Forest. The Monier Golden Grove Eocene flora has some taxonomic similarity in common with other southern Australian Eocene floras, but has a distinctive character which supports the idea of a regionally diversified rainforest vegetation in southern Australia in the Eocene.

Introduction

In January, 1986, a fossiliferous clay lens was uncovered during sand quarrying operations at the Monier East Yatala Sand Pit in Golden Grove, South Australia (138°43'30" Long, 34°47'10" Lat). Golden Grove is located approximately 25 km north-east of Adelaide city centre (Fig. 1). The lens was found amidst cross bedded, fresh water sands and the entire depositional sequence suggests a meandering stream system with possible lacustrine elements.

While this is the first megafossil flora described from the Golden Grove area, other plant fossils have been reported from the region. Indeed, Eocene clays containing dispersed plant fossils have been described in several papers (e.g. Lange 1978a, Lange 1978b, Lange 1980), but a precise description of the location of the deposit is not given in any of them. As a recent drilling program by the S.A. Mines and Energy Department has indicated that the lateral extent of the new lens is extensive (Neville Alley, S.A. Mines and Energy Department, pers. comm.), it is possible that these earlier reports were based on material from the same system. However, it is known that the earlier material did not come from the Monier quarry, and hence precise geological comparison between the earlier reported material and the Monier Golden Grove Locality may never be possible. They may be palynologically correlated, however.

A preliminary palynological analysis (W.K. Harris, Western Mining Co., pers. comm.) placed the lens at the base of the *Proteacidites pachypolis* Zone of the Eocene. A second palynological analysis (Neville Alley, S.A. Mines and Energy Department, pers. comm.) supports placement in this zone. The deposit is therefore either just younger than the Maslin's Bay deposit located 30 km south of Adelaide or equivalent to it. The Monier Golden Grove deposit is slightly older than the Anglesea deposit in Victoria (Christophel, Harris & Syber 1987) (Fig. 1).

Materials and Methods

Portions of the lens are highly oxidised and plant remains are preserved as brown impressions in beige matrix with no organic remains present. The majority of the lens contains carbonized remains within a grey matrix, and mummified leaves are floated from this material by placing blocks of the clay in a 2-3% hot aqueous solution of H_2O_2 to disaggregate the matrix. Many of these leaves are naturally translucent and can be photographed directly with transmitted light (Figs 2-6). The rest are black, opaque, and were observed and photographed with UV light to study the venation detail using the technique of Christophel, Harris & Syber (1987). This type of preservation is shown in Figs 7-9.

A sample cuticle is then prepared using the method discussed in Christophel, Harris & Syber (1987) and the leaf is mounted between glass slides in Phenol Glycerin Jelly.

All leaves illustrated in this paper are housed in the Adelaide University Palaeobotany collection. Fruits and flowers obtained from the macerate are stored in 1% phenol in 50% ethanol in sealed vials, in the same collection.

Components of the Megafossil Flora

The commonest leaf taxon from the mummified horizons at Golden Grove is a serrate-margined notophyll (Fig. 2). This taxon has superficial similarities to Sloanea/Elaeocarpus (Elaeocarpaceae). A recent study of extant species of this family found that leaves of Elaeocarpus L. and Sloanea L. could not be separated, but that they consistently clustered distinctly from other genera in the family and from other architecturally similar families (Moira Turnbull, Adelaide University, pers. comm.) The Golden Grove fossils similar to Figure 2 consistently clustered with the extant Elaeocarpus/Sloanea complex.

Another common taxon in the Monier Golden Grove flora is *Banksieaephyllum* Cookson & Duigan (Fig. 9). As the name suggests, the leaf is very similar to those found in the tribe Banksieae (Proteaceae), but as Christophel and Greenwood (1987) suggested, this could also represent the foliar organ of *Musgraveinanthus* Christophel (1984). This is supported by the occurrence of *Musgraveinanthus* in the Monier Golden Grove deposit, which is the only locality other than the type locality (Anglesea) from which it has been reported. *Banksieaeidites arcuatus* Stover, the pollen type found in *Musgraveinanthus* inflorescences, is also found as a dispersed grain at Golden Grove.

The Lauraceae has been suggested as an important family in Australian Early Tertiary floras. Based on the characters discussed by Hill (1986) as diagnostic of the family, we have confirmed at least two common leaf taxa at Golden Grove (Figs 3,4) which may be assigned to that family. The importance of the family in the Monier Golden Grove flora is therefore confirmed.

Leaves of *Myrtaciphyllum* Christophel & Lys are also frequently encountered in the Golden Grove flora (Fig. 7). However, a preliminary investigation indicates that the Golden Grove Myrtaceae leaves belong to different species than the two described by Christophel & Lys (1986).

Two leaf types collected at the Monier Golden Grove locality are known only rarely from other Early Tertiary deposits. These are leaves of *Brachychiton* (Sterculiaceae) and the fern *Lygodium* (Schizeaeaceae). *Brachychiton* Scott & Endl. is very common as impressions in the leached portion of the lens, where it is recovered in both a three and five lobed form. Less common in the mummified portions of the lens, it has thus far only been collected in a three-lobed form from that material (Fig. 8). *Lygodium* is not only recovered as sterile pinnules (Fig. 6) but has also been collected as numerous fertile fronds. These can be seen to contain spores, which have yet to be studied and compared to their extant counterparts.

The gymnosperms are thus far represented at Golden Grove by two genera of the Podocarpaceae, *Decussocarpus* Laubenf. and *Podocarpus* L'Herit. ex Pers. sens. strict. *Decussocarpus* twigs are common, and appear morphologically intermediate between *D. maslinensis* Blackburn, described from Maslins Bay, South Australia, and *D. brownii* (Selling) Greenwood, from Anglesea (Greenwood 1987). It is quite likely that the three therefore represent a range of forms in one highly variable taxon. Similar variation can be seen in modern examples of the genus [e.g. *D. vitiensis* (Seeman) Laubenf., Greenwood, 1987]. Golden Grove material of this species has been illustrated earlier by Christophel and Greenwood (1987).

Podocarpus leaves are less common, and while much longer, have epidermal features identical to *Podocarpus platyphyllum* Greenwood described from Anglesea (Greenwood, 1987).

One further leaf type is worth describing, in that it is reasonably common and also has not been previously reported. These leaves are pinnately compound (Fig. 5) and on the basis of their stomatal arrangement and epidermal hair bases can be ascribed to the Proteaceae. They bear a superficial similarity to immature leaves of *Neorites* L.S.Sm.

While the identity of no other leaf taxa have been confirmed at this time, a preliminary estimate of approximately 30-35 leaf types for the deposit is made. However, the present collection contains only approximately 400 leaves, and so the preliminary nature of the estimate must be emphasized. Four fruit/flower types have been thus far recovered, but only specimens of *Musgraveinanthus* have been identified.

Physiognomic Analysis

The general elliptic shape, broad lamina, and the presence of well developed 'drip tips' on many leaves (e.g. Fig. 4), strongly suggest that the Golden Grove flora was derived predominantly from rainforest vegetation. These features are often cited as being characteristic of rainforest leaves, particularly lowland tropical rainforest (Richards, 1957). The presence of typical rainforest taxa e.g. Elaeocarpaceae (*Sloanea*/*Elaeocarpus*), Proteaceae (Musgraveinae, *Neorites*), Myrtaceae (*Syzygium* type), Lauraceae, Podocarpaceae (*Decussocarpus*, *Podocarpus*) strengthens this impression, although representatives of some of these families are also found in more open forest types. It is appropriate therefore to compare the foliar physiognomy of the Golden Grove flora to that of modern rainforest.

The use of foliar physiognomic analysis for the interpretation of fossil leaf-beds based on forest canopy data has been criticized for ignoring the effect of transportation and the differential input and preservation of leaves prior to sedimentation (Martin 1986; Christophel & Greenwood 1987). Recent research, however, suggests strongly that leaf-litter from each of the main rainforest types recognized by Webb (1959, 1968) and Tracey (1982) has a unique physiognomic "signature" and that this signature is often retained in stream-deposited leaf-litter (Christophel & Greenwood 1987). Work in progress by the second author supports this. The physiognomic features of primary importance are length, width, shape and margin type. Leaf length only will be considered in this paper, as it is sufficient to illustrate the physiognomic signature.

Figure 11 shows the frequency distribution of leaf-length for the four main rainforest types recognised by Webb and the frequency distribution for the Golden Grove flora using mummified leaves. As can be seen from the figure, the extant rainforest types can be clearly separated on leaf-length alone. Figure 12 shows the same data plotted as a cumulative percentage for each length class. The CNVF forest type has been presented as two separate sites to better illustrate the intrinsic physiognomic variability of litter from NE Queensland (The Crater) and

N.S.W. (Dorrigo) from this type. Standard errors for the data from these sites are presented in Table 1. These results indicate that the Golden Grove Eocene vegetation was physiognomically closest to CNVF (Complex Notophyll Vine Forest) from The Crater N.P. and less so to CNVF from Dorrigo in northern N.S.W. Dorrigo and The Crater fall within the Mesotherm seasonal Torresian zone of Nix's bioclimatic classification of Australia (Nix 1982).

Comparison With Other Eocene Floras

As mentioned above, the Monier Golden Grove flora is similar in age to the Maslin's Bay flora and is somewhat older than the Eocene Anglesea flora. It is younger than the Nerriga flora (Hill 1982) but can still be usefully compared with it, as all are Eocene. Figure 10 is a table comparing the major (as well as some of the unique minor) taxa from the four deposits.

Perhaps the strongest similarities to the Golden Grove megafossil flora may be seen in the Anglesea locality. While the diversity of the Anglesea flora is shown as much higher (100+), this represents a composite of 6 separate fossiliferous lenses. Taken separately, the lenses at Anglesea have a diversity much more similar to Golden Grove (Christophel, Harris & Syber 1987). The strongest links between the two are the very similar Elaeocarpaceae leaves, *Musgraveinanthus*, *Myrtaciphyllum* and *Brachychiton*. They also have in common *Decussocarpus*, *Podocarpus*, Lauraceae, *Banksieaephyllum* and *Lygodium*, but these are not restricted to those localities. Physiognomically, however, Golden Grove is interpreted as CNVF, whereas the New Site lenses at Anglesea were interpreted by Christophel (1981) and Christophel & Greenwood (in press) as being closest to SNVF (Simple Notophyll Vine Forest) from N.E. Queensland (Fig. 12).

The diversity of Golden Grove is similar to Nerriga, but there are very few shared taxa, and the only feature in common is really the shared importance of the Lauraceae. Maslin Bay has a few taxa in common with Golden Grove, but in general Maslin Bay has a high diversity with no truly common taxa, while Golden Grove has fewer, well represented taxa and hence suggests a quite different floristic association. Preliminary physiognomic analysis of the Maslin Bay flora by the second author has detected minor differences which suggest that the Maslin Bay flora was sourced from a warmer vegetation type (Greenwood, unpublished data).

The absence of both the Zamiaceae and Gymnostoma Johnson at the Golden Grove locality is somewhat surprising considering the commonness of both at Anglesea and their presence in the other deposits. While further collecting may reveal either or both of these taxa, their absence to date may be taken as evidence that they are not major components of the Monier Golden Grove flora.

The preliminary investigation of the Golden Grove flora has revealed a vegetation typical of the southern Australian Eocene floras studied to date, in that it appears to have been sourced from a rainforest vegetation (Complex Notophyll Vine Forest sensu Webb, 1959, 1968) of reasonable diversity in a mesotherm environment (sensu Nix 1982). There are differences between it and the other documented floras of similar age, as is expected based on the temporal and spatial differences in the localities. While numerous similarities in taxa present have been highlighted in Figure 10, it must be emphasized that these are similarities in natural and form genera, and there is no evidence yet (possibly excluding Podocarpaceae) to suggest that the same species are occurring in the different localities.

The Monier Golden Grove flora represents South Australia's only known mummified leaf flora still available for collection and study (a collection of several thousand Maslin's Bay specimens exists in the

Botany Department of Adelaide University, but the locality is no longer collectable), and it is hoped that further work will provide us with deeper insights into the evolution of South Australia's flora. Much of South Australia's coal reserve which is currently being considered for development is Eocene in age, and hence Golden Grove will hopefully provide a benchmark for studies of these floras when they are eventually developed.

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Figure 10. Megafossil taxa at Australian Localities.

Locality Taxa	Golden Grove	Maslin Bay	Anglesea	Nerriga
Austrodiospyros	?	R	C	
Musgraveinanthus	X		X	
Elaeocarpaceae	C	?	C	?
Myrtaciphyllum	C		X	
Brachychiton	C		R	
Decussocarpus	C	X	C	
Podocarpus	X		X	
Gymnostoma		R	C	R
Zamiaceae			C	R
Lauraceae	C	X	C	C
Lygodium	C	R	X	
Banksieaephyllum	C	X	X	
Total Diversity	30-35	100+	100+	25-30

C = common (> 10%)

X = present (1 - 10% - possibly more common, but not assessed)

R = rare (< 1% of flora)

? = similar but unconfirmed

FIGURE CAPTIONS

Figure 1. Map of eastern Australia giving the location of the Golden Grove locality relative to the Eocene localities of Maslin Bay, Anglesea and Nerriga, and two of the sites from which litter was collected for the physiognomic comparison.

Figures 2-4. Transparent mummified leaves from Golden Grove. Scale bars = 1 cm. Fig. 2. Elaeocarpaceae aff. *Sloanea*/*Elaeocarpus*; Figs 3,4. Lauraceae.

Figures 5,6. Transparent mummified leaves from Golden Grove. Scale bars = 1 cm. Fig. 5. Proteaceae aff. *Neorites*; Fig. 6. Fern pinnule, *Lygodium*.

Figures 7-9. Opaque mummified leaves photographed using UV light source. Scale bars = 1 cm. Fig. 7. *Myrtaciphyllum*; Fig. 8. *Brachychiton*; Fig. 9. *Banksieaephyllum*.

Figure 11. Frequency histograms of leaf length (10 mm classes) for Microphyll Mossy Forest (MMF), Simple Notophyll Vine Forest (SNVF), Complex Notophyll Vine Forest (CNVF), Complex Mesophyll Vine Forest (CMVF), Golden Grove, and Anglesea. Forest nomenclature follows Webb (1959, 1968) and Tracey (1982). Each of the data sets for the modern forests is based on four samples of 200 leaves collected from litter (Christophel and Greenwood, 1987). Golden Grove data is based on 156 complete leaves from the initial 1986 collections. Standard Errors are plotted.

Figure 12. Cumulative frequency histograms for the data presented in Fig. 11. Two separate localities for CNVF are given: the Crater National Park (open triangles) and Dorrigo (solid triangles). These two localities reflect the extremes of the range seen in litter samples from N.E. Queensland and N.S.W.

A COMPARISON OF AUSTRALIAN TROPICAL RAINFOREST AND TERTIARY FOSSIL LEAF-BEDS

by

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ABSTRACT

The fossil record is revealing the nature of Australian vegetation prior to the Miocene contact between Australia and Asia. There are divergent views on whether fossil leaf beds always give an accurate picture of past vegetation. Leaf litter from sites in modern Australian tropical rainforests, however, reflect the physiognomic character of the surrounding forest. Complex Mesophyll (CMVF), Complex Notophyll (CNVF), and Simple Notophyll Vine Forests (SNVF) have characteristic foliar physiognomic signatures. The physiognomic signature of stream bed deposits of SNVF leaf litter was within the range of variation observed for forest floor leaf litter from SNVF.

These results suggest that Tertiary fossil leaf-beds can be used in some instances to reconstruct past vegetation based on the physiognomic characteristics of the fossil leaves and the overall representation of taxa where modern affinities can be determined. The physiognomic character of the Eocene leaf assemblages from Anglesea in Victoria appears to match tropical montane and sub-tropical rainforest (Simple Notophyll Vine Forest) from Australia in both physiognomic character and the presence of some taxa.

The Anglesea flora has many elements in common with the modern wet tropical flora of northern Queensland. The Podocarpaceae is represented by at least six species from five modern genera at Anglesea (*Dacrycarpus*, *Decussocarpus*, *Falcatifolium*, *Podocarpus* and *Prumnopitys*), whereas only two genera are present in the modern wet tropical forests of Australia (*Podocarpus* and *Prumnopitys*).

Many angiosperm taxa characteristic of the modern Australian wet tropical forests are also found as significant components of the Anglesea fossil flora, including *Gymnostoma* (Casuarinaceae), *Musgravinaeanthus* and *Orites* (Proteaceae), *Austrodiospyros* (Ebenaceae), *Brachychiton* (Sterculiaceae) and *Quintinia* (Escalloniaceae). In the case of

Gymnostoma, and species of the Musgraveinae, the modern taxa are restricted to a small region in northern Queensland. The close match to the Anglesea Orites species is also restricted to the same region.

At Noah Creek in N.E. Queensland, the streamside vegetation is dominated by the only extant Australian species of Gymnostoma and an undescribed species of Orites which is highly similar to the Anglesea fossil species. Podocarpus and Prumnopitys are also present.

These facts, along with the rarity of some of the plant associations found at Anglesea and Noah Creek (e.g. the Gymnostoma/Orites Musgraveinae association) suggest that Noah Creek may provide as good a comparative model as possible for the Anglesea flora.

The demonstration of the correlation between rainforest type and physiognomic analyses of leaf litter from modern Australian rainforests, coupled with the evidence that similar types of plant associations can be noted from the modern forests and the Eocene floras, suggests that a more accurate interpretation than previously expected of Australian vegetation prior to the Miocene may be possible. The existing evidence predicts that forests very similar to those found in the modern wet tropics of Australia were present in southern Australia in the Eocene, prior to Australia's contact with Asia.

INTRODUCTION

The widespread acceptance of the plate tectonics theory of continental drift has promoted the idea that much of the Australian flora has either been inherited from the pan-Gondwanan flora, or is autochthonous, evolving from the more labile members of the ancient Gondwanan flora. There is however debate as to the extent to which the composition of Australia's tropical rainforests reflect immigration by northern taxa into Australia (mainly from the extensive rainforest flora of the Malesian region), or the persistence of Gondwanan taxa (Barlow, 1981; Whiffin & Hyland, 1986).

The post-Miocene northern invasive flora corresponds largely to the "Indo-Malayan" element espoused by Burbidge (1960) and her predecessors, and is based on the observation that for many taxa found in the tropical rainforests of Australia, a much higher diversity is present in Malesia, often with only a single species present in Australia (Martin, 1982; Whiffin & Hyland, 1986).

There are contradictory views however. Webb *et al*. (1986) suggest that the integrated nature of tropical rainforest with its highly interdependent synusiae, makes the idea of individual rainforest taxa colonising the Australian tropics en masse, implausible.

An ever-growing catalogue of Early Tertiary pollen records of taxa with affinities to modern genera in the Australian tropical rainforests is demonstrating that some so-called Indo-Malayan or Malesian taxa were present in Australia well before the establishment of the link between Asia and Australia (Martin, 1978, 1982). Similar finds of plant megafossils [*Parafatsia*, (Blackburn, 1982) and *Austrodiospyros*, (Basinger & Christophel, 1986)] have reinforced the expectation amongst some botanists that analysis of Early Tertiary vegetation may now be able to provide insight into the origins of the Australian tropical rainforest flora.

METHODS OF COMPARING FOSSIL AND MODERN VEGETATION

There are two main methods used to reconstruct past vegetation. The more traditional approach has been to identify the modern affinities of most of the fossil taxa from a deposit and infer from the ecological preferences of the closest modern relatives the nature of the palaeoenvironment. This method has given contrasting interpretations of the Early Tertiary vegetation of southern Australia, with palynologists initially predicting a cool to warm temperate vegetation dominated by Nothofagus and Podocarpaceae (Kemp, 1982), whereas the megafossil record suggests a vegetation of sub-tropical to tropical character (Christophel, 1981). This is explained by the fact that fossil pollen often reflects the regional flora with prolific producers such as Nothofagus swamping the samples, whereas fossil leaf beds generally reflect the local flora (Martin, 1982).

Numerous studies on modern plant communities have demonstrated a link between leaf form and size, or physiognomy, and the environment (Dolph, 1978; Davis & Taylor, 1980; Givnish, 1984). In Australia, Webb (1959, 1968) classified Australian rainforest on physiognomic criteria, primarily leaf size and margin type, using canopy leaves. These studies have given rise to the idea that the physiognomic characteristics of fossil leaf beds may yield significant palaeoecological information (Dolph & Dilcher, 1979). This constitutes the second main method of reconstructing past vegetation and is usually referred to as leaf or foliar physiognomic analysis.

FOLIAR PHYSIOGNOMIC ANALYSIS OF FOSSIL AND MODERN TROPICAL RAINFOREST LEAF BEDS

Previous attempts to apply leaf physiognomic analysis to Tertiary floras assumed a direct correspondence between the physiognomic characteristics of the forest community and the leaves found in a fossil deposit (Dolph & Dilcher, 1979; Christophel, 1981). This assumption has been questioned on the grounds that most of the studies on modern forest communities have dealt with regional floras (Roth & Dilcher, 1978) or have been based exclusively on canopy leaves (Martin, 1982). The physiognomic analysis of three Eocene floras by Christophel (1981) was further questioned by Nix (1982) who suggested that as southern Australia lay in high southern latitudes in the Eocene, a tropical (Megathermal) or subtropical (Mesothermal) climate was not possible for Anglesea, Nerriga, or Maslin Bay.

In order to further refine the foliar analysis of Australian Tertiary floras, a study of the physiognomic characteristics of leaf litter from the types of tropical rainforest recognised by Webb (1968) was initiated. Leaf litter on the forest floor represents the leaves of all the members of the plant community in the immediate vicinity, and not just a single stratum (Ferguson, 1985), whereas most foliar physiognomic studies are based on either herbarium specimens or field collections of living leaves. The leaves in leaf litter better reflect a fossil leaf bed than herbarium collections, as recent studies (Ferguson, 1985) have found that leaves do not travel in air much further than the height of the parent tree, and that larger leaves tend to be screened out by intervening vegetation, producing a different physiognomic character than the original forest (Drake & Burrows, 1980).

A fossil leaf bed is usually formed in a stream or lake where water flow was reduced to allow settling of both the leaves and a layer of sediment. Several studies have suggested that where the point of leaf deposition is some distance from the source of the leaves, such as in a lake where the leaves have been brought in by a stream, the resultant leaf bed will be dominated by the lakeside and streamside flora with the smaller, more coriaceous canopy leaves distorting the physiognomic interpretation (Roth & Dilcher, 1978; Drake & Burrows, 1980). These changes are the net result of the preferential destruction of larger, more fragile leaves from the interior of the forest due to hydrodynamic forces in the stream, and the low input of leaves from the interior of the forest due to the screening effect of the streamside and lakeside vegetation (Ferguson, 1985). These same studies have also found that these effects become more pronounced with increasing distance from shore, and hence source.

When leaves are deposited directly into a potential fossil deposit, such as by forest on a flood plain with numerous ox-bow lakes or ephemeral channels in a braided stream system, the resultant leaf bed will closely resemble the leaf litter from the same forest. The study on modern leaf litter from Australian tropical rainforest has found that each of the three forest types examined has leaf litter with a characteristic physiognomic signature. The implication is that where fossil leaf beds come from situations like that described above, it is possible to make a direct comparison between the forest types and the fossil vegetation.

Three rainforest types were examined ranging from the tropical lowland (Complex Mesophyll Vine Forest or CMVF), to the montane tropical rainforest (Simple Notophyll Vine Forest or SNVF), and the forest physiognomically intermediate between these two (Complex Notophyll Vine Forest or CNVF). Samples were taken from several localities in N.E. Queensland in the region of Cairns and Atherton (Fig. 1), with each sample representing all of the litter scraped from a square metre of ground. Approximately 200 leaves from each sample were measured for length, width (as a fraction of length), and the position maximum width (as a fraction of length). The type of margin and the taxonomic identity of each leaf was also recorded but will not be considered here. A frequency histogram of leaf length for the three forest types indicates the clear partitioning of the leaf litter from different forest types (Fig. 2). The mean value for each character for each sample has been plotted on a box diagram (Fig. 3) to illustrate the characteristic physiognomic signature of the three forest types from the region studied.

The SNVF leaf litter was characterised by microphylls (< 75 mm length) with an average width of 30-40% of length (narrow elliptic), and were generally symmetric about the midpoint of the leaf. The CNVF leaf litter was composed of a mixture of microphylls and notophylls (75-125 mm length) with an average width of 40-45% of length and distinctly ovate (position of maximum width < 35% of length). The CMVF leaf litter was characterised by much larger leaves than the SNVF, mainly notophylls but with a significant component of mesophylls (> 125 mm length) with an average width of 30-35% of length, and symmetric about the midpoint of the leaf. A small proportion of leaves in the CMVF litter were distinctly ovate, often with hastate bases, representing vine leaves.

In addition to the forest floor samples, two collections were made from two successive pools in a stream flowing through Simple Notophyll Vine Forest on the Windsor Tableland. The results suggest that these two samples have similar physiognomic characteristics to leaf litter from the surrounding forest type. This data suggests that where leaves have been deposited with little transport after leaf fall, the physiognomic characteristics (the physiognomic signature) can be used to compare leaf populations from unknown forest type to leaf populations from known forest types. On this premise, collections of fossil leaves from two Eocene localities from southern Australia, Anglesea in Victoria, and a newly discovered deposit near Golden Grove in South Australia (Fig. 4A), were measured in the same manner as the leaf litter. These results are also plotted on the box diagram (Fig. 3).

The Anglesea samples were characterised by microphylls with an average width of 30-35% of length (narrow elliptic), and the position of maximum width was on average 40-45% of length, reflecting a small group of ovate leaves in some samples. This situation is to a lesser extent found in some SNVF litter samples. Overall, the Anglesea and SNVF samples appear to have the same physiognomic signature (Fig. 3). The Golden Grove sample has a physiognomic signature at the upper limit of the length character for SNVF (Fig. 3). Field observation of oxidised material on fresh clay blocks from Golden Grove suggest that further collections may give a much greater average length, increasing the similarity with the physiognomic signature of CMVF litter.

In the original study of the physiognomic characteristics of the Anglesea flora, Christophel (1981) suggested a similarity to either Simple Notophyll Vine Forest or Complex Notophyll Vine Forest. This present study supports a similarity to SNVF, although the fossil leaves are generally narrower than the SNVF litter. The variation between the individual samples of fossil leaves is similar to that seen for the SNVF litter, which represents two distinct sites. The Golden Grove sample appears quite distinct from the Anglesea samples and is intermediate between CMVF and SNVF.

It is clear that same fossil samples are not close matches to the suggested analogous modern forest types; however, given the high southern latitude of Australia in the Eocene, some differences must be expected. What is apparent though, is that there were forests very like SNVF and perhaps CNVF growing in southern Australia in the Eocene.

TAXONOMIC AFFINITIES OF THE ANGLESEA FLORA

The Anglesea flora, while incompletely known, is nevertheless revealing a wealth of detail about the past vegetation and suggesting that many taxa now restricted to N.E. Queensland formerly grew in the

Eocene forests of southern Australia. For example, the conifer family Podocarpaceae is often considered an indicator of cool temperate conditions due to their conspicuous presence in Tasmanian and New Zealand rainforests. The megafossils attributed to the Podocarpaceae from Anglesea represent modern genera associated with tropical montane or less commonly, tropical lowland rainforest (*Dacrycarpus*, *Falcatifolium*, *Podocarpus* and *Prumnopitys*; Greenwood, 1986). A total of six species have been described to date, including a species of *Podocarpus* which is closely related to *P. smithii*, a species of restricted occurrence in N.E. Queensland which grows in Simple Notophyll Vine Forest. *Prumnopitys* in Australia is also restricted to the same area (Fig. 4B). The *Decussocarpus* species described has also been found at a New Eocene deposit at Golden Grove, South Australia.

Several angiosperm taxa described from Anglesea also have their closest extant relatives growing in the North Queensland rainforests. *Musgraveinanthus* (Christophel, 1984) has affinities with the Musgraveinae (Proteaceae), all of which have a distribution restricted to northeastern Queensland (Fig. 4B). Remains of *Gymnostoma* (Casuarinaceae) have also been described from Anglesea (Christophel, 1980). Only one species of *Gymnostoma* occurs in Australia, and it is also restricted to this same region (Fig. 4B). A lobed Proteaceae leaf type is frequently encountered in some lenses of the Anglesea locality, and this fossil has been found to be most similar to an extant species of *Orites* from northeastern Queensland which is as yet undescribed (Figs 4C, 5D). This extant species has an auriculate, clasping leaf base which is also found in the fossil and is unique within the tribe.

Hill (1978) described two species of fossil *Bowenia*. One species from Anglesea has since been collected as a complete pinnule (Fig. 5A). The restricted distribution of extant *Bowenia* is shown in Fig. 4C.

Using the positive identification of five of the taxa described above from Anglesea - Podocarpus, Bowenia, Gymnostoma, Musgraveinanthus and Orites - and considering the restricted distributions of their extant counterparts, a very small region remains within which to look for a modern analogue of the Anglesea vegetation. In so doing, however, it must be stressed that the basic realities of shifting continents, changing climates and natural selection over 40 million years guarantee that exact equivalent floras would not exist. None-the-less, modern communities which demonstrate strong taxonomic and physiognomic similarities to the Anglesea fossil flora might well be helpful in further interpreting the as yet unknown elements of that and other fossil floras.

One such possible direct comparison for the Anglesea flora was found in an area of rainforest near Noah Creek (16°07'S, 145°26'E), a small river north of the Daintree River, draining Thornton Peak on the northeastern coast of Queensland (Fig. 4A). This locality and its similarity to Anglesea have been described in detail by Christophel et al. (1987). It is worth noting, however, that at one point along Noah Creek the streamside vegetation is dominated by one of the rare populations of Gymnostoma in the region, and by the undescribed species of Orites. Several hundred metres downstream from this spot, the vegetation is a typical lowland tropical forest (CNVF)whose component taxa include two of the three described species of the Musgraveinae, and Bowenia.

If the rest of the taxa thus far identified from the Anglesea locality are compared with the known flora from the Noah Creek area, it may be seen that virtually all the modern equivalents are present in the Noah Creek flora (Fig. 6). The strong presence of Myrtaceae, Lauraceae, Proteaceae and Elaeocarpaceae in the Anglesea flora is reflected in the Noah Creek vegetation. The rarer occurrences at Anglesea of Quintinia, Brachychiton, Lygodium and possibly Linospadix also have their equivalents at Noah Creek. In general, Noah Creek appears to provide as good a comparison as is likely to be found in the extant Australian vegetation for the part of the Anglesea vegetation thus far identified. In addition, all of the floristic and physiognomic variation recorded for Anglesea can be found in an area at Noah Creek no larger than the fossil locality. The utility of the area as a comparative model may be tested by attempting to determine the affinities of some of the as yet unidentified elements of the Anglesea flora using the rest of the plant taxa present at Noah Creek as starting points.

The new mummified Eocene flora from Golden Grove, South Australia, was discovered in January, 1986 (Fig. 4A). While slightly older than the Anglesea deposit, it contains a number of the key taxa found at Anglesea, and hence provides a possibility of studying the evolution of some of the taxa over reasonably short periods of time. As may be seen in Fig. 6, *Musgraveinanthus*, *Banksieaephyllum*, *Podocarpus* and *Lygodium* are found in both Eocene deposits. It is particularly interesting to note that both *Musgraveinanthus* and *Banksieaephyllum* are present in both floras, but neither leaves of the Musgraveinae nor reproductive structures of the Banksineae have been recovered at either locality. As these two are sub-tribes of the Banksieae, it is not beyond possibility that we could be dealing with an Eocene plant which combined features of the two sub-tribes. The Golden Grove *Musgraveinanthus* is shown in Fig. 5C.

DISCUSSION

By examining the physiognomic and taxonomic data presented above it is possible to discuss several points.

(1) By graphically presenting the physiognomic data collected from the leaf litter from different sites in northern Queensland (Figs 2, 3) it is clearly evident that the differences in canopy physiognomy which

allowed Webb (1959) to define his Complex Notophyll Vine Forest, Simple Notophyll Vine Forest and Complex Mesophyll Vine Forest are reflected in litter samples from those forest types. This litter data can then be compared directly to physiognomic data collected from fossil leaf deposits, which are interpreted as being litter from fossil vegetation. This was done with the result that strong physiognomic similarities were shown between three Eocene deposits from southern Australia and Webb's three forest types mentioned above. This then provided one piece of evidence for the hypothesis that the Eocene floras of southern Australia were most similar to the wet tropical vegetation of northern Australia.

(2) Examination of the taxa thus far identified from the Eocene Anglesea Locality showed that their nearest living relatives in Australia are found in these same wet tropical forests. Not only are specific (and rare) taxa such as members of the Musgraveinae, Podocarpus smithii, Bowenia and Gymnostoma found there, but the general floristic composition when examined at the family level is similar. A preliminary examination of the Golden Grove Eocene Flora suggests similar comparisons.

(3) By closely examining one locality in northeastern Queensland (Noah Creek) where the rarer extant relatives of the Anglesea flora are found, it can be seen that both floristically and physiognomically all tested elements of the Anglesea flora can be accounted for within a small area similar in size to the fossil deposit. This demonstrates the viability of direct comparisons between the southern Australian Eocene Floras and the Wet Tropical Forests of northern Australia.

This paper began with the question of the origin of the Australian Tropical Rainforests. We believe that the fossil evidence clearly shows that the ancient relatives of a growing number of extant Australian rainforest taxa are to be found in the Eocene forests of southern

Australia. Not only were these taxa present, but they were in similar associations, were in forests of similar general composition, and represented vegetations with similar physiognomic signatures to those of modern day northern Australia. While some extant rainforest taxa (e.g. Ficus, Saurauia) as yet have no Australian fossil record and may possibly be Malesian in origin, the majority of northern Australian rainforest taxa, and perhaps their associations, appear to be autochthanous.

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CAPTIONS

Figure 1. Location of leaf-litter collection sites (black squares). 1000 metre contour indicated.

Figure 2. Frequency histograms of leaf length for Simple Notophyll Vine Forest, Complex Notophyll Vine Forest, Complex Mesophyll Vine Forest, and the Anglesea fossil deposit. Based on four samples of 224 leaves, Standard Errors indicated.

Figure 3. 'Box Diagram' displaying the physiognomic signatures of SNVF (open), CNVF (open), CMVF (open) the Anglesea flora (open) and the Golden Grove flora ( ). The stream samples of SNVF are indicated by the inverted solid 's. Means of each are indicated by solid symbols.

Figure 4. Maps showing location of fossil localities, Noah Creek and distribution of selected taxa.

4A. Fossil localities and Noah Creek.

4B. Distribution of extant *Gymnostoma* and Musgraveinae.

4C. Distribution of extant *Orites* sp. nov. and *Bowenia*.

4D. Distribution of *Prumnopitys ladei* and *Podocarpus smithii*.

Figure 5. Fossil and extant rainforest taxa.

5A. Fossil *Decussocarpus* - Specimen GG124 from Golden Grove, South Australia. Scale bar = 1 cm.

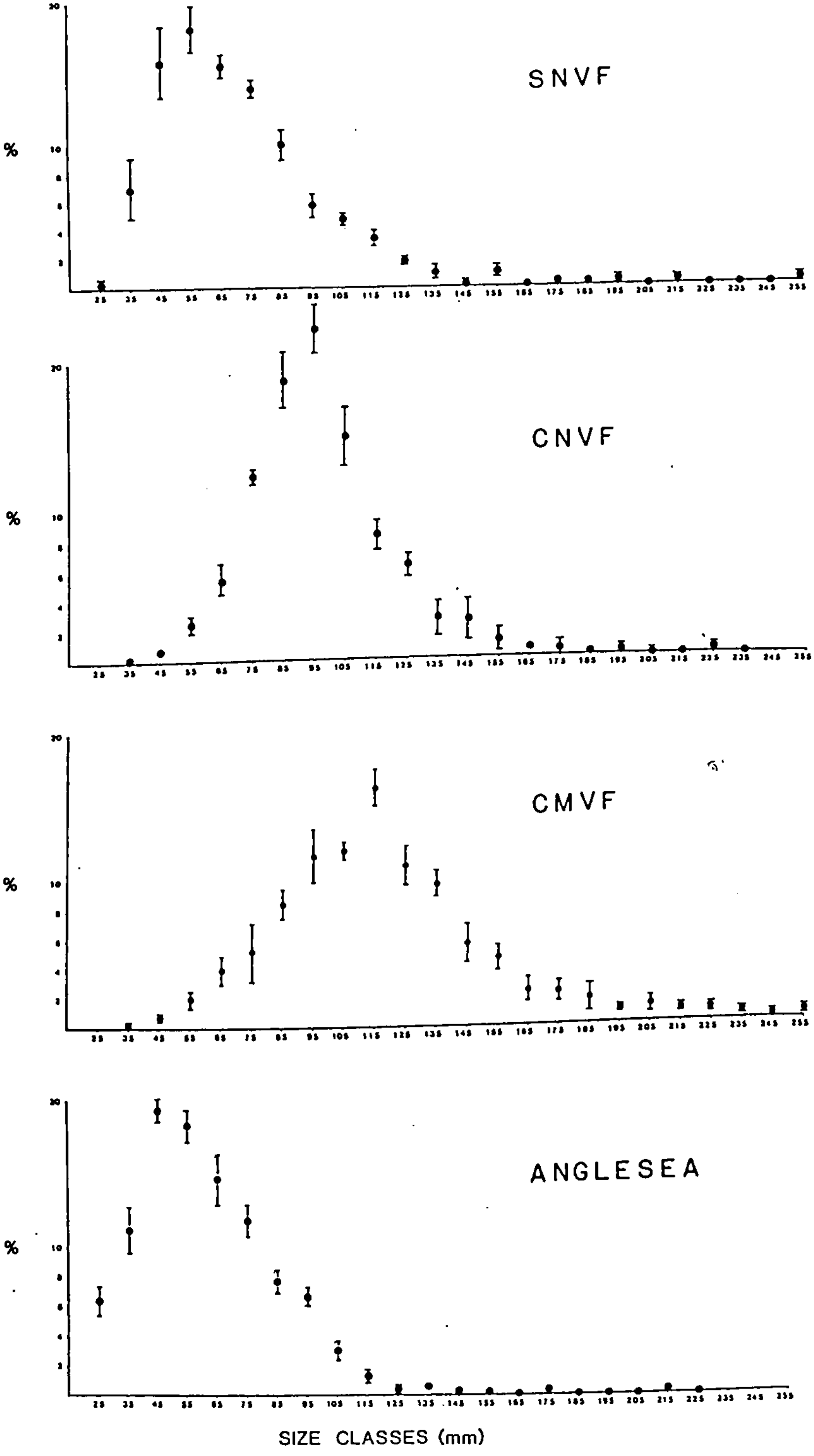
5B. *Bowenia eocenica* Hill 1978 from Anglesea, Victoria - Specimen A2249. Scale bar = 1 cm.

5C. *Musgraveinanthus* - Specimen GG144 from Golden Grove, South Australia. Scale bar = 1 cm.

5D. *Orites* sp - Juvenile leaf of undescribed species from Noah Creek, Queensland. Scale bar = 2 cm.

Figure 6. Comparison of identified megafossil taxa from Anglesea, Victoria, and Golden Grove, South Australia with the vegetation at Noah Creek, Queensland.

FIGURE 2


SNVF
CNVF
CMVF
ANGLESEA
%
20
10
8
6
4
2
25
35
45
55
65
75
85
95
105
115
125
135
145
155
165
175
185
195
205
215
225
235
245
255
SIZE CLASSES (mm)

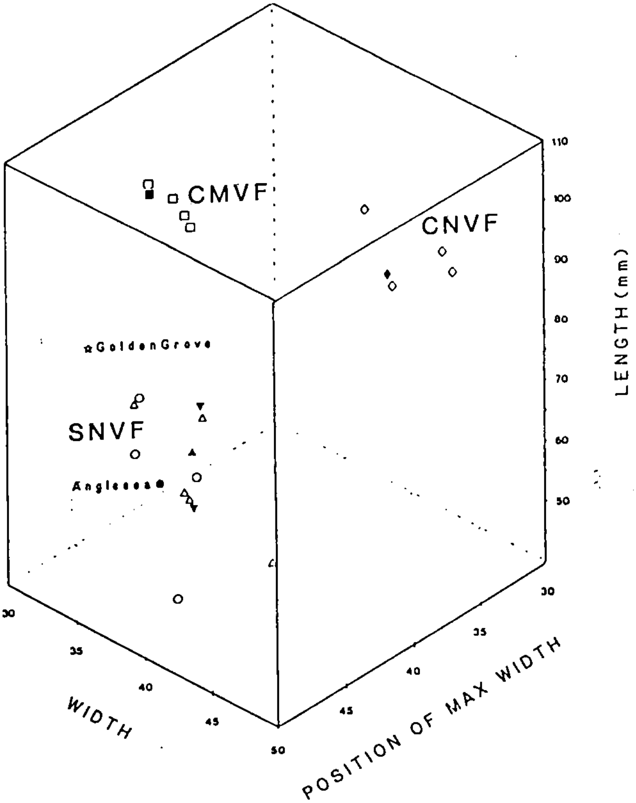

CMVF
CNVF
SNVF
Golden Grove
Anglesea
LENGTH (mm)
110
100
90
80
70
60
50
30
35
40
45
50
WIDTH
30
35
40
45
POSITION OF MAX WIDTH

FIGURE 3

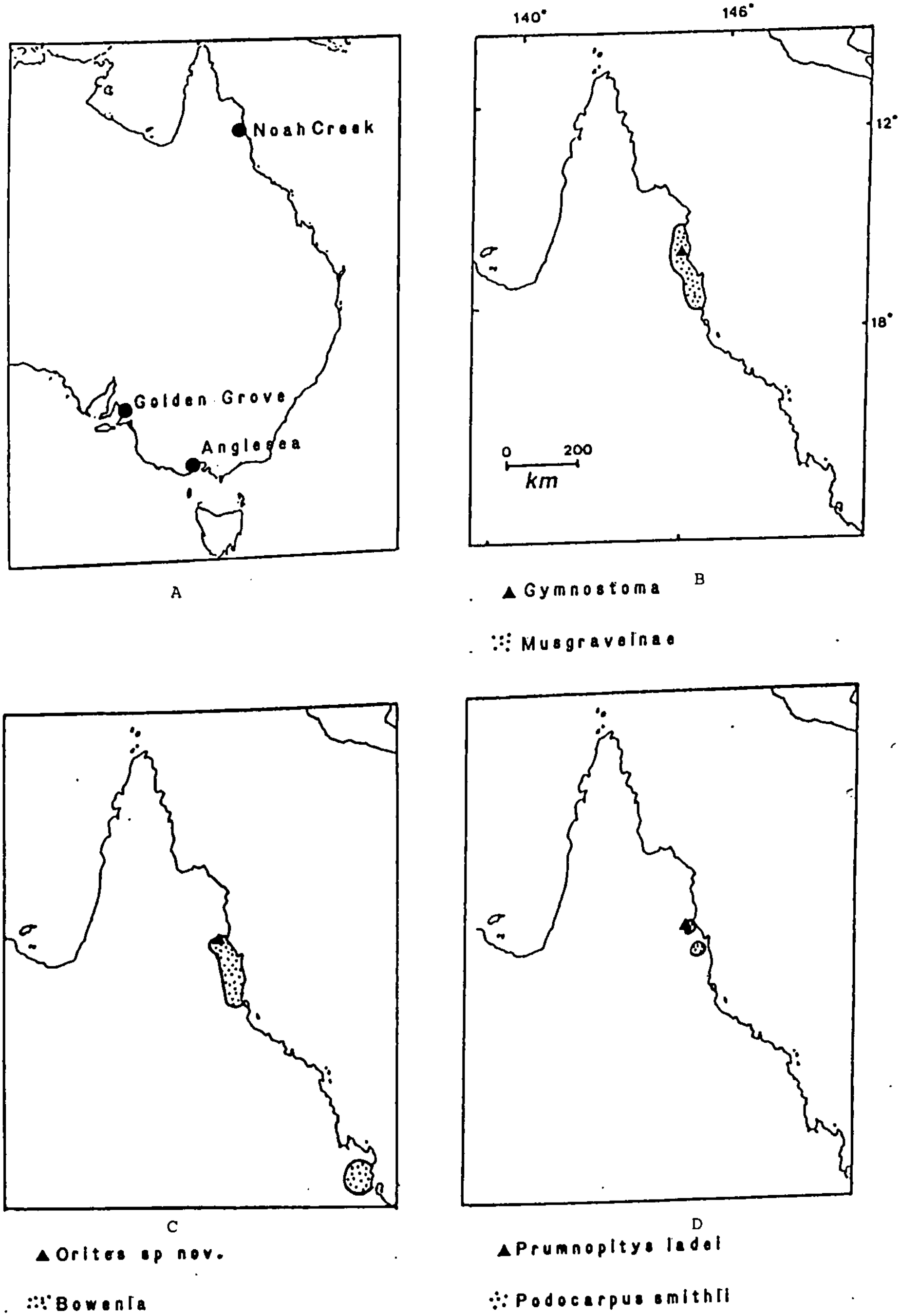

Noah Creek
Golden Grove
Anglesea
A
140°
146°
12°
18°
0
200
km
B
▲ Gymnostoma
∵ Musgraveinae
C
▲ Orites sp nov.
∵ Bowenia
D
▲ Prumnopitys ladei
∵ Podocarpus smithii

FIGURE 4

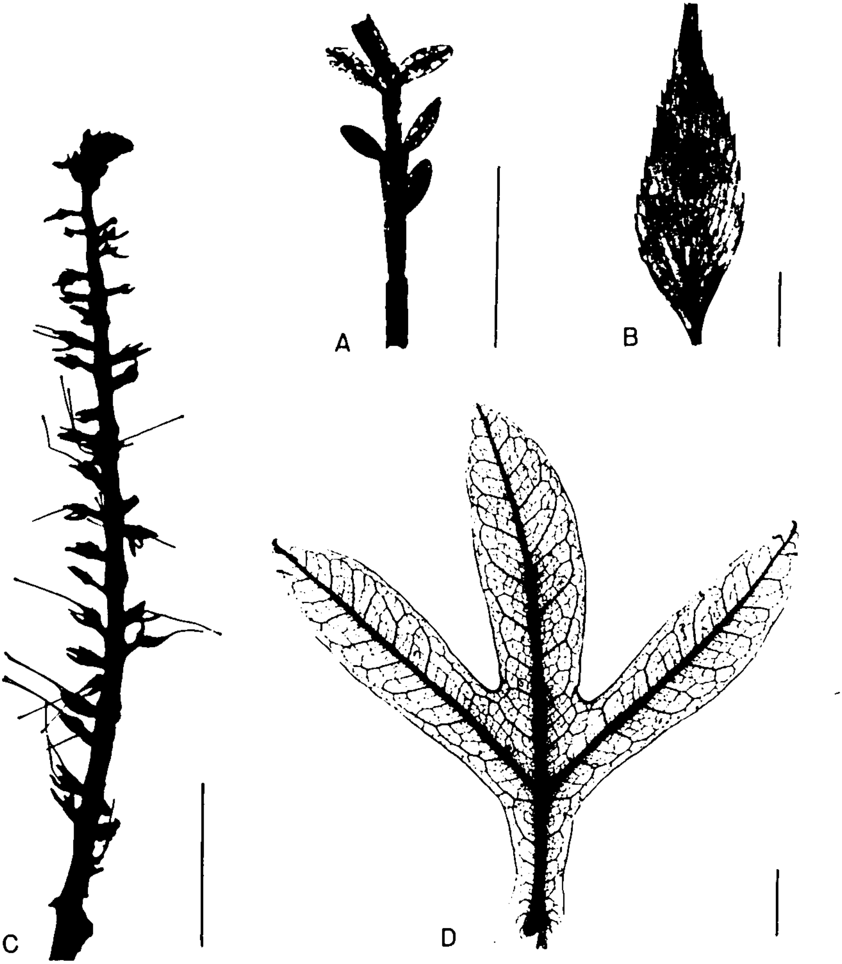

A
B
C
D

FIGURE 6

FOSSIL AND EXTANT RAINFOREST SITES
(Species Numbers in Parentheses)

TAXA	Anglesea	Golden Grove	Noah Creek
Gymnostoma	(1)	-	(1)
Musgravineae	(1)	(1)	(3)
Orites sp.nov.	(1)	-	(1)
Bowenia	(2)	-	(1)
Lygodium	(1)	(1)	(1)
Podocarpus	(1)	(1)	(2)
Decussocarpus	(1)	(1)	-
Prumnopitys	(2)	-	(1)
Dacrycarpus	(1)	-	-
Falcatifolium	(1)	-	-
Brachychiton	(1)	(1)	(1)
Quintinia	(1)	-	(1)
Linospadix?	(1)	-	(2)
Other Cycads	(1)	-	(1)
Ebenaceae	(1)	(1)	(2)
Elaeocarpaceae	(1)	(2)	(2)
Myrtaceae	(2)	(2)	(7)
Other Proteaceae	(2)	(3+)	(5)
Lauraceae	(5+)	(3+)	(9)
Banksieaephyllum	(1)	(1)	?
TOTAL DIVERSITY	(80+)	(40+)	(110+)