Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary palaeoclimates

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ABSTRACT

Greenwood, D.R., 1992. Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary paleoclimates. Rev. Palaeobot. Palynol. 71: 149–190.

Foliar physiognomic interpretations of Late Cretaceous and Tertiary palaeoclimates, such as those derived from Leaf Margin Analysis, usually rely on taxon-based observations from the forest canopy. In these analyses, Southern Hemisphere rainforests are sometimes considered analogues of North American Late Cretaceous vegetation. Past analyses have not considered taphonomic biases. Taphonomic influences on specimen-based and taxon-based approaches to foliar physiognomic analyses of palaeoclimate are assessed here using forest-floor and stream-bed leaf litter from modern Australian rainforests.

Forest floor leaf litter is markedly local in origin and is taxonomically biased towards leaves from canopy trees. Litter has smaller leaves than expected from the canopy, using either specimen- or taxon-based observations. The Leaf Size Index (LSI) is moderately robust to taphonomic bias, with a correction factor of 3:2 for canopy LSI:forest-floor LSI. Leaf margin type is highly variable using specimens or when total species numbers are low. The accuracy of palaeotemperature interpretations based on leaf margin type alone (Leaf Margin Analysis) are therefore strongly affected by taphonomic biases and local floristics. Direct comparisons between canopy and fossil leaf assemblages may therefore misrepresent the palaeoclimate of the original standing vegetation. Fluvially transported assemblages may exaggerate this bias. However, a "foliar physiognomic signature" is defined for these modern leaf beds using leaf-size, shape and margin type from specimen-, rather than taxon-based observations. Multivariate analysis (Discriminant Analysis) of the foliar physiognomic signature of these leaf beds can differentiate between leaf beds from each of the forest-types examined. Examination of modern leaf assemblages allow an a priori analysis of taphonomic influences on foliar physiognomic character, in contrast to ad hoc hypotheses used in comparisons based on canopy observations, and potentially offer more reliable reconstructions of Late Cretaceous and Tertiary palaeoclimates from leaf megafloras than have previously been shown.

Introduction

Late Cretaceous and Tertiary climates may be interpreted from leaf megafloras using foliar physiognomic analysis (Wolfe, 1971, 1985, 1990; Dilcher, 1973; MacGinitie, 1974; Dolph and Dilcher, 1980; Christophel, 1981; Christophel and Greenwood, 1989). This methodology requires uniformitarian assumptions about the relationship between the organisms and their environment (Wolfe, 1971; Dilcher, 1973; Christophel and Greenwood, 1988; Spicer, 1990). Foliar physiog-

nomic analysis considers plant communities or vegetation units (Wolfe, 1971, 1979) and generally assumes that the foliar physiognomic climatic signal can be detected in fossil leaf populations with minimal distortion (Roth and Dilcher, 1978; Wolfe, 1979; Christophel, 1981; Christophel and Greenwood, 1988; Burnham, 1989). The assumption of minimal taphonomic bias is mostly an untested assumption and can be viewed as an ad hoc hypothesis (e.g. Wolfe and Upchurch, 1987, p. 37).

Several studies of foliar physiognomy and modern climate have been equivocal, or suggested caution in its application to palaeoclimate (Dolph and Dilcher, 1979, 1980). However, Wolfe's (1971,

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1979) study of foliar physiognomy and climate in East Asian mesic forests has been widely used and cited (e.g. Parrish and Spicer, 1988; Upchurch, 1989). Wolfe's analysis represented a refinement of earlier studies (e.g. Bailey and Sinnott, 1916), but relied on regional accounts of the taxonomic composition of the forest canopy (Dolph, 1990) and only more recently has he directly sampled modern plant communities (Wolfe, 1990). Similarly, other workers (Dilcher, 1973; MacGinitie, 1974; Christophel and Blackburn, 1978; Christophel, 1981; Zastawniak et al., 1985) directly contrasted the characteristics of modern forest canopies, particularly that of Australian rainforest (e.g. Webb, 1959), to Tertiary megafloras.

Dolph and Dilcher (Dolph, 1978, 1984; Dolph and Dilcher, 1979, 1980) found that variation at the local scale will obscure correlations between foliar physiognomy and climate based on regional vegetation. Examination of modern leaf assemblages, the sedimentary behaviour of leaves and the relationship between vegetation and leaf assemblages, suggest that significant taphonomic biases may influence the taxonomic membership of plant fossil assemblages (Ferguson, 1971, 1985; Spicer, 1981, 1989; Gastaldo, 1988; Burnham, 1989; Gastaldo et al., 1989; Greenwood, 1991). Leaf assemblages are generally dominated by leaves from the immediately adjacent vegetation (Burnham, 1989; Gastaldo et al., 1989; Spicer, 1989) and so in most cases fossil leaf assemblages primarily represent local vegetation, and thus local climates. The taxonomic composition of these assemblages may also be different from the regional flora, representing a subset of the total flora.

More recently, Dolph (1990) has highlighted the problems accruing from Wolfe's (1971, 1979) original database. However Wolfe (1991) now applies a multivariate analysis using direct canopy sampling of a much wider range of plant communities. However, while vegetation sampling and analysis strategies are important, what is more urgently required is detailed analyses of the foliar physiognomy of actual sedimentary accumulations of leaves, and comparison to the forests from which the leaves came, in order to assess the degree of taphonomic bias at the scales encountered in Late

Cretaceous and Tertiary leaf megafloras (Roth and Dilcher, 1978; Christophel and Greenwood, 1988; Burnham, 1989). Christophel and Greenwood (1988) and Burnham (1989) stress that the question of greatest interest is whether a foliar physiognomic climatic signature or signal can be recognised in leaf assemblages.

Roth and Dilcher (1978) and Spicer (1981) demonstrated that lake deposits can be dominated by the smaller coriaceous sunleaves of the outer canopy. However Burnham (1989) has demonstrated that fluvial sedimentary accumulations of leaves may reflect the regional climatic signal. Christophel and Greenwood (1987, 1988, 1989) and Greenwood (1987a) reported how the original forest-type represented by Australian Tertiary leaf assemblages could be interpreted by the direct comparison of the foliar physiognomic characteristics of modern Australian rainforest leaf-litter with the Tertiary megafloras, using specimen-based observations. Using "foliar physiognomic signatures" based primarily on leaf length histograms, they demonstrated that similar leaf populations were found in both the forest-floor litter and the Tertiary leaf assemblages.

In this report, Greenwood's (1987a) initial analysis, and that of Christophel and Greenwood (1987, 1988, 1989), is taken further using both *specimen-based* and *taxon-based* observations. The specimen approach makes no assumptions about the relative accuracy of separating isolated leaves into taxa (Christophel and Greenwood, 1988). The degree of bias that exists between the original leaf populations of the forest canopy and of the forest floor is quantified here, and then forest-floor leaf beds are demonstrated to retain unique foliar physiognomic signatures using a multivariate analysis. The accuracy of foliar physiognomic analyses of palaeoclimate (e.g. Wolfe, 1979, 1990, 1991) are investigated here by examining taphonomic influences on key foliar physiognomic features and MAT, such as Wolfe's Leaf Size Index (Wolfe, 1978; Burnham, 1989) and leaf margin type (Leaf Margin Analysis). Brief accounts of the localities and methodology used for this study have been presented previously (Christophel and Greenwood, 1988, 1989); however a full account is presented here for reference in further reports.

Materials and methods

Forest-floor litter sample localities

Christophel and Greenwood (1987, 1988, 1989; Christophel, 1981, 1989; Greenwood, 1987b) demonstrated that there are taxa common in southern Australian Middle Eocene megafloras with nearest living relatives concentrated in the modern tropical rainforests of the Humid Tropical Region of northeastern Queensland (19° to 15°S, 144°30' to 146°30'E). These forests may therefore offer an analogue of Australian Eocene vegetation, and possibly for other Epochs of the Tertiary (Christophel and Greenwood, 1989). In addition, Wolfe (1979, 1985, 1990; Wolfe and Upchurch, 1987) has argued that modern Southern Hemisphere mesic-humid vegetation ("rainforest") is probably a better analogue of North American Late Cretaceous vegetation than modern Northern Hemisphere vegetation.

The northeastern Queensland rainforests are largely pristine and highly accessible and offer a substantial database (e.g. Tracey and Webb, 1975; Webb and Tracey, 1982; Brasell et al., 1980), including a number of marked study plots (Stocker and Hyland, 1981; Stocker and Unwin, CSIRO Tropical Forest Research Centre, pers. commun., 1985, 1987; Stocker et al., in press). Subtropical and temperate rainforests in New South Wales represent latitudinal and altitudinal extensions of these forests. The New South Wales forests provide an extension of the analysis of climate interactions with foliar physiognomy, incorporating microthermal forests (Microphyll Fern Forest) and latitudinal variants of the cooler tropical forests. A forest classification system, developed by Webb (1959, 1968), was applied by Tracey and Webb (1975) to map the northeastern Queensland rainforests using a combination of structural and foliar physiognomic criteria. Forest nomenclature throughout this report uses Webb's system (Webb, 1959, 1968; Tracey, 1982). The main forest types of Webb's physiognomic classification of Australian rainforests is contrasted to the equivalent forest types in Wolfe's (1979) system in Table I.

The four main forest types in the Webb classification are defined by the number of tree layers present (3 in Complex Mesophyll Vine Forest and Complex Notophyll Vine Forest, 2 in Simple Notophyll Vine Forest and 1 in Microphyll Mossy Forest), the relative contribution by species (or individuals) with entire leaf margins, microphyllous, notophyllous, or mesophyllous canopies, and the presence of characteristic life-forms (Webb, 1959, 1968; Tracey, 1982). The prevailing leaf size of the canopy leaves is indicated in the designated name of each of the forest types. In practice, each

TABLE I

Comparison of Wolfe (1979, 1985) and Webb's (1959, 1968) physiognomic forest classifications. Main mesic forest-types only

Wolfe (in part)	Webb	MAT °C*	Range*
Tropical (in part) — Paratropical Rainforest	CMVF	20–27	4–13
Paratropical Rainforest	CNVF	16–22	4–14
Notophyllous Broad-leaved Evergreen Forest	SNVF	12–20	4–15
Microphyllous Broad-leaved Evergreen Forest	MMF/MMF	10–13	8–15

Based on Wolfe (1979) and *Greenwood and Christophel (in prep.)

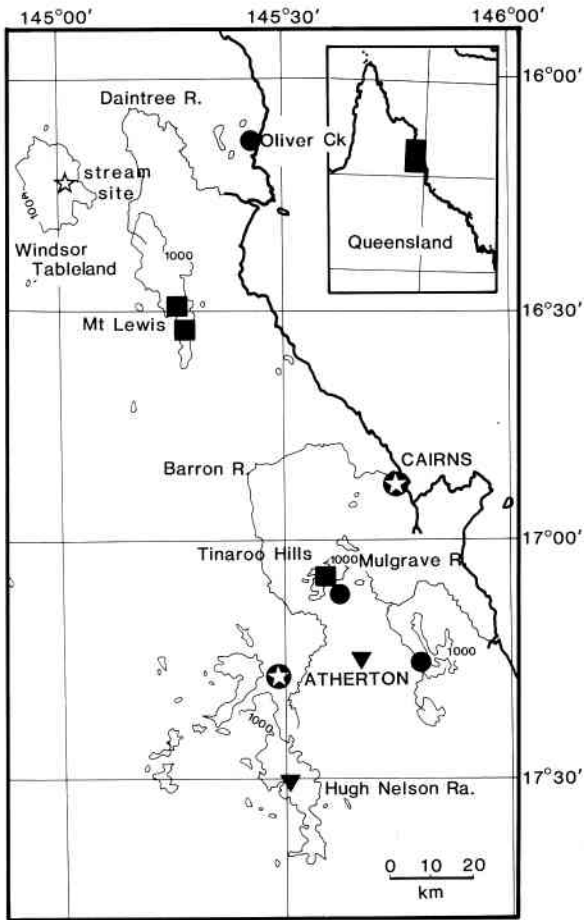| Code	Forest type	Main soil fertility class
CMVF	Complex Mesophyll Vine Forest	eutrophic
CNVF	Complex Notophyll Vine Forest	eutrophic
SNVF	Simple Notophyll Vine Forest	oligotrophic
MVFF	Simple Microphyll Vine-Fern Forest	oligotrophic
MFF/MMF	Microphyll Fern/Mossy Forest	oligotrophic–eutrophic

Fig.1. Location map showing position of Queensland forest-floor leaf-litter collections; ● CMVF sites, ▼ CNVF sites, ■ SNVF sites. A stream-bed collection site (Mt. Windsor Tableland) is indicated by a ☆. Adapted from Christophel and Greenwood, 1989.

Fig.2. Location map showing position of New South Wales (NSW) forest-floor leaf-litter collection sites.

forest type can be identified solely by the relative dominance of the *canopy* by mesophyllous, noto-phyllous (sensu Webb, 1959), or microphyllous *species* or *individual trees* (Webb, 1959; Tracey, 1982).

Sites were selected in the northeastern Queensland rainforests (Fig.1) and in New South Wales rainforests (Fig.2). A total of three sites were studied from each of three rainforest types: Complex Mesophyll Vine Forest (CMVF); Complex Notophyll Vine Forest (CNVF); and Simple Notophyll Vine Forest (SNVF). An additional Queensland site at Mt. Haig (Fig.1; Table II) was transitional between Simple Notophyll Vine Forest
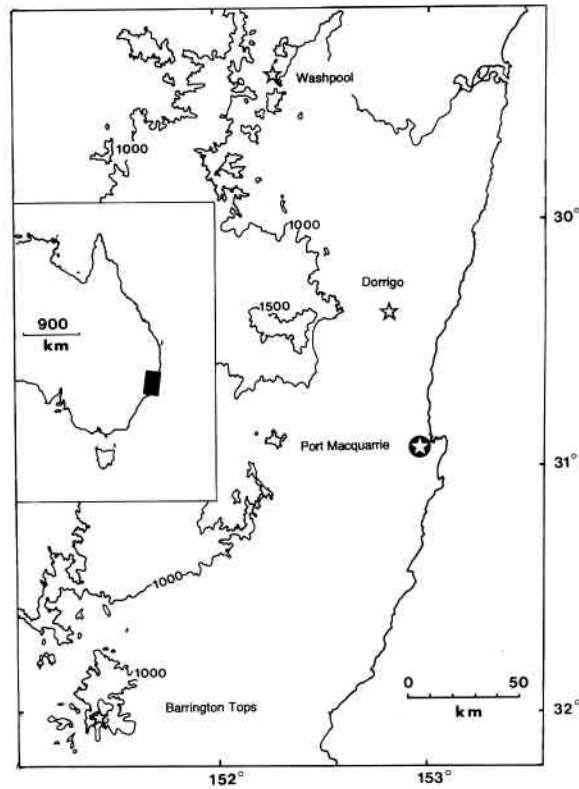
and Simple Microphyll Vine-Fern Forest (MVFF), and Microphyll Mossy/Fern Forest (MMF or MFF) was sampled at Barrington Tops in New South Wales (Fig.2; Table II). Soil types at all of the sites were derived from basaltic or granitic parent rock and thus include both eutrophic and oligotrophic soils (Webb, 1968).

Stream-bed leaf accumulations were sampled at a site in northeastern Queensland on the Mt. Windsor Tableland (Fig.1), and in New South Wales at the Washpool SNVF site (Fig.2), in Coombadjha Creek. The stream at the Mt. Windsor site flowed through forest transitional from CNVF to SNVF. The collections made there have been partially reported by Christophel and Greenwood (1988, 1989). Two sets of pools were sampled: an upstream set where leaf accumulations are believed to be from direct leaf fall from the overhanging forest canopy (autochthonous); and a downstream pool where a large leaf accumulation

TABLE II

Locations and characteristics of the forest-floor leaf litter collection sites

forest type	site	latitude	longitude	alt. (m)	MAT °C
CMVF	Mobo Creek	17°10′S,	145°39′E.	720	20.0[1]
	Mulgrave River	17°18′S,	145°48′E.	120	24.5**
	Oliver Creek	16°08′S,	145°27′E.	10	24.6[2]
CNVF	Curtain Fig	17°18′S,	145°34′E.	720	20.0[1]
	Dorrigo N.P.	30°20′S,	152°45′E.	100	19.4*
	The Crater N.P.	17°25′S,	145°29′E.	980	17.9**
SNVF	Mt. Lewis Road	16°33′S,	145°17′E.	1200	16.0**
	Mt. Lewis EP18	16°31′S,	145°16′E.	1050	17.3**
	Washpool N.P.	29°28′S,	152°22′E.	800	15.0*
(SNVF/MMF)	Mount Haig	17°05′S,	145°35′E.	1160	16.0**
MMF	Barrington Tops	32°00′S,	151°29′E.	1500	10.7*

**based on a lapse rate of 7.7°C/1000 m and a baseline datum of 25.4°C at sea level.
*based on a lapse rate of 6.2°C/1000 m 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. 714.5 m: Anonymous, 1983).
[2]T°C taken from Port Douglas (16°29′S 145°28′E; elev. 4.0 m: Anonymous, 1983).
For more detail, see Greenwood, 1987a.

is believed to be primarily transported from upstream (allochthonous). The upstream pools were temporary pondings on sand bars beyond the main channel and the leaves they contained were quite fresh, retaining their original colour with very little associated fragmentary material (suggesting little transport), whereas the downstream pool was a permanent stream feature and the leaves were mostly blackened with a significant amount of fragmentary material (suggesting transport). The total distance between the two pools was 100 m, and a significant set of rapids with boulders greater than 3 m in diameter separated the two sites.

The forest canopy at the Mt. Windsor site completely overshaded the upstream pools, but was completely clear over the downstream pool (Christophel and Greenwood, 1989). A detailed floristic examination of the surrounding forest was not made; however, *Caldcluvia paniculosa* (Cunoniaceae) and individuals of several unidentified species of Lauraceae were common at both sites. Trees of *Neorites kevesdiana* (Proteaceae) and *Geissois biagiana* (Cunoniaceae) were common at the upstream site, and a large strangler fig (*Ficus destruens*) grew on the edge of the lower pool. *Sloanea woolsii* (Elaeocarpaceae) was a common component of the canopy along the stream course

and at the lower pool. Shrubs of *Melastoma* sp. (Melastomataceae) were common along the stream banks.

The New South Wales collection at Coombadjha Creek consisted of samples from the bed of the creek in a large pool in midstream. Flow rates are not known for this stream; however, it is approximately a metre deep in the centre of the pool, but averages half a metre in the main channel. Heavy rain observed during collection (August, 1986) produced much higher flow rates within a few hours. Annual rainfall is in excess of 2000 mm and slightly seasonal. The main channel was typically 5 m wide, was not actively aggrading and has a nearly symmetric profile. The local rock is granite, producing a sandy bottom. The canopy of the surrounding forest was dominated by *Ceratopetalum apetalum* (Cunoniaceae) and *Doryphora aromatica* (Monimiaceae). Smaller trees and understory shrubs were scarce (see Table V). The stream edge was lined by understory species together with *Banksia integrifolia* (Proteaceae) and *Callicoma serratifolia* (Cunoniaceae).

Two climatic-vegetation systems have mainly been used when discussing foliar physiognomic analysis; the Holdridge Bioclimatic system (Holdridge, 1967; Dolph, 1978; Dolph and Dilcher, 1979, 1980) and Wolfe's (1971, 1979) physiognomic

classification of vegetation. The main climatic variables which affect foliar physiognomy appear to be temperature (Mean Annual Temperature or "Biotemperature") and moisture regimes — total rainfall and the effectiveness of that rainfall (Wolfe, 1971, 1979, 1990; Dilcher, 1973; Dolph and Dilcher, 1980). However, the main climatic variables of interest in palaeoclimatology appear to be MAT, the Mean Annual Range (ie. seasonal range), and only less so the amount and seasonality of rainfall (e.g. Parrish and Spicer, 1988; Upchurch, 1989; Spicer, 1990).

Tracey (1982) provided a detailed examination of climate for the humid tropical region of northeastern Queensland where many of the study sites are located. However climatic profiles show monthly minimum and maximum temperatures and monthly rainfall for sites representative of the rainforest types examined in this study (Fig.3). The Queensland sites (Innisfail and Millaa Millaa)
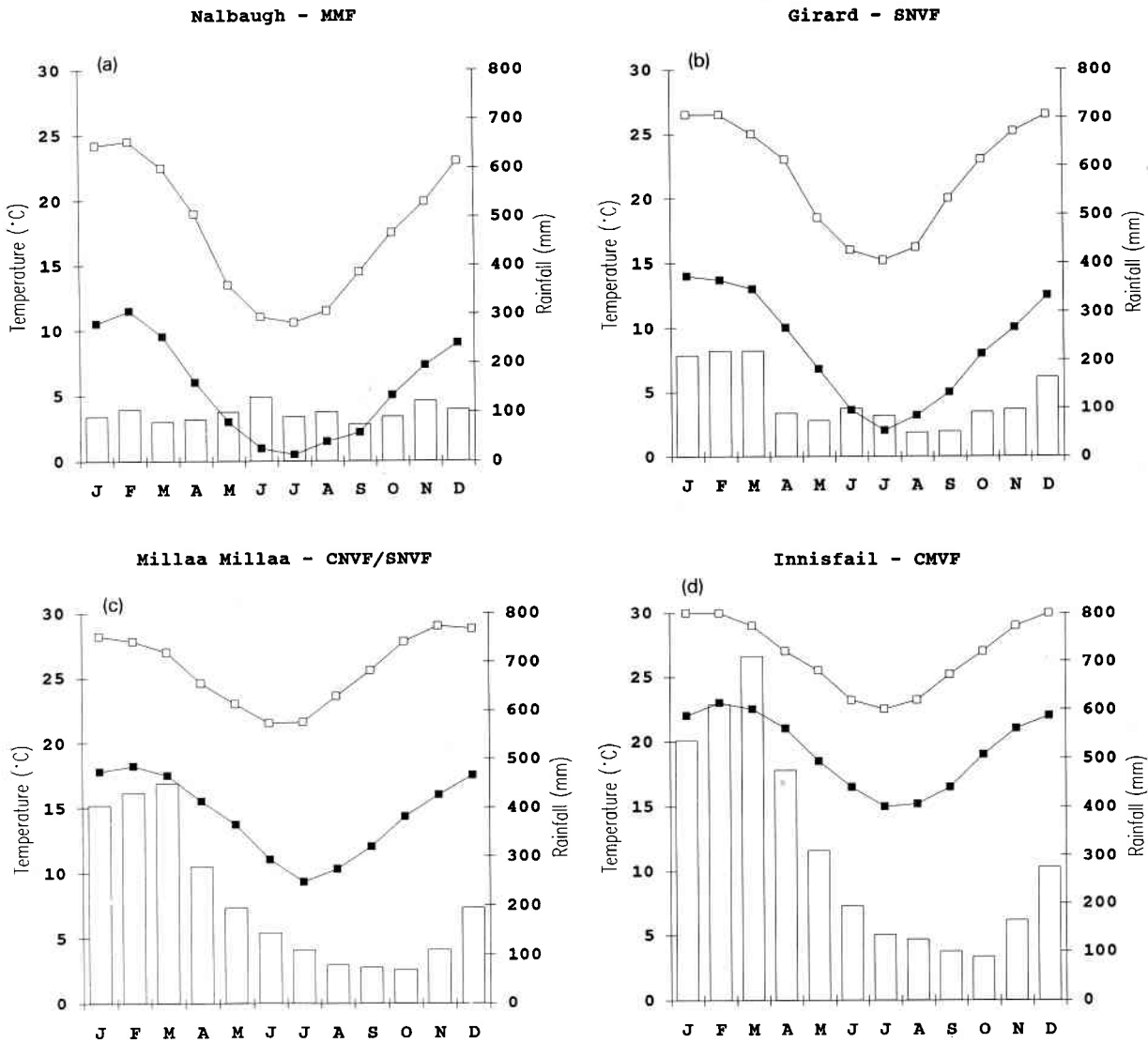

Fig.3. Climatic data for representative local areas of the Queensland and New South Wales litter collection sites. Meteorological data from Aust. Bureau of Meteorology.

have markedly higher rainfall over the period of highest temperatures; this pattern is typical for the area (Tracey, 1982). The New South Wales sites have essentially non-seasonal rainfall (Nalbaugh, MMF), or only moderately higher rainfall over the warmest months (Girard, SNVF). Some of the Queensland sites may experience a water deficit during the low rainfall months (Tracey, 1982), and this is reflected by the incidence of some facultatively deciduous trees in the canopy of CNVF at the Curtain Fig litter collection site.

Holdridge's (1967) system requires climatic detail not readily available for much of the areas in Australia where rainforest occurs. Mean annual biotemperature is calculated on the assumption that plants will be physiologically inactive when air temperature exceeds 30°C or is below 0°C, and can be approximately calculated by rescoring such days as 0°C. At no station in this study were there days where the temperatures were below 0°C, and temperatures in excess of 30°C are only experienced for short periods at the Mulgrave River and Oliver Creek CMVF sites. For the majority of sites therefore, MAT was equal to the mean annual biotemperature. A preliminary analysis of the litter collection sites is presented here (Fig.4). The biotemperature and rainfall of the sites has been estimated from records of nearby meteorological

stations (Anonymous, 1983) 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".

Collection methods

At each forest site an area approximately 20 × 20 m was arbitrarily defined. Some sites were selected within marked plots maintained by the CSIRO T.F.R.C. at Atherton. In these sites the exact position, diameter at breast height (d.b.h.), and identity of all trees over 15 cm d.b.h. were known (Stocker and Unwin, pers. commun., 1985, 1987; Stocker et al., 1989). At all forest sites, 4 sample points were selected arbitrarily within the defined area. Random selection was impractical. Within a 1 × 1 m square sample point all of the leaf litter was collected, leaving only the bare mineral soil.

Stream-bed samples were collected by hand, each sample reflecting multiple grabs sufficient to fill a typical commercially available garbage can plastic liner (i.e. plastic bag; 50 × 90 cm). A single sample was collected from each pool at the Queensland Mt. Windsor Tableland site. Two samples
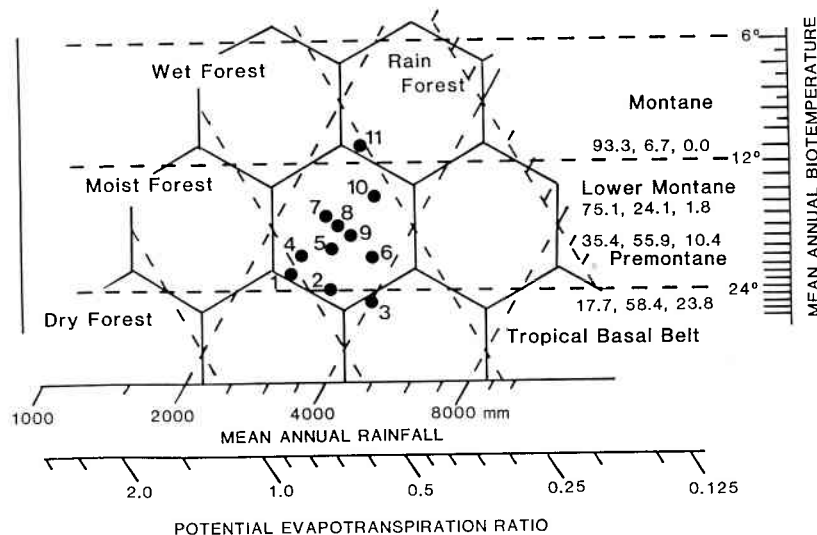

Fig.4. Portion of Holdridge's (1967) Bioclimatic vegetation classification scheme showing Bioclimatic characteristics of the Australian rainforest litter study sites.

were collected at the New South Wales Coombadjha Creek site (Washpool forest-floor litter site).

The litter from all sites was air dried and in most cases approximately 200 leaves were extracted from each sample, representing all or the majority of intact leaves present in the sample. An arbitrary cut-off was made at 224 leaves, which necessitated subsampling for the SNVF and MMF samples which typically had 300–500 leaves in each sample. The stream samples from Queensland and the CMVF and CNVF samples were not subsampled as typically single samples from these sites contained on average about 200 intact leaves.

The leaf numbers collected from each square metre of forest-floor represent the litter volume at the time of collection. Overall leaf-fall on any given area of forest-floor over a year is much greater than the number of leaves found at any single time (Webb et al., 1969; Spain, 1984). The leaf volume at any one time represents the recent leaf-fall and leaves that have persisted from a few weeks to over twelve months (Anderson and Swift, 1983). However, the majority of leaves either rot in situ or are transported laterally by local flooding (e.g. Dudgeon, 1982).

Data collection and analysis

Studies of foliar physiognomy of modern vegetation have mainly considered leaf size, usually as discrete leaf size classes (microphyll, mesophyll, etc.; Raunkiaer, 1934, as modified by Webb, 1959; Dolph and Dilcher, 1980), and leaf margin type (Webb, 1959, 1968; Dolph, 1978, 1984; Roth and Dilcher, 1978; Dolph and Dilcher, 1979, 1980; Wolfe, 1979). Leaf shape has been used less commonly (e.g. Dilcher, 1973; Dolph and Dilcher, 1979; Wolfe, 1990). However, leaf margin type (Leaf Margin Analysis) has been the most frequently used for interpreting palaeoclimate (Wolfe, 1985; Wolfe and Upchurch, 1986; Upchurch and Wolfe, 1987; Parrish and Spicer, 1988; Upchurch, 1989; Wolfe and Schorn, 1989; Spicer, 1990). Leaf size has been used less commonly (e.g. MacGinitie, 1974; Christophel and Blackburn, 1978; Wolfe, 1978, 1985; Christophel, 1981; Zastawniak et al., 1985; Wolfe and Upchurch, 1987).

Most foliar physiognomic studies have used mainly *taxon-based* observations, where the vegetation (and fossil megaflora) was characterised by the proportion of species which possessed microphylls, notophylls, mesophylls, entire or non-entire leaf margins or other leaf characteristic. These proportions may be expressed as a statistic, such as Wolfe's Leaf Size Index (LSI[1]; Wolfe, 1978; Burnham, 1989). Two versions of the LSI are in use (Wolfe, 1978; Burnham, 1989 vs. Wolfe and Upchurch, 1987) and a third has been proposed, reflecting ongoing refinements (J.A. Wolfe, pers. commun., 1991). Webb (1959, 1968) used both the proportion of individual trees and *taxon-based* observations. Some palaeobotanists (Dilcher, 1973; Christophel and Blackburn, 1978; Christophel, 1981; Zastawniak et al., 1985) have applied data from individuals in modern forests to Tertiary megafloras using the proportion of leaf *specimens* representing each foliar physiognomic character. For the purpose of this study, both *taxon-based* and *specimen-based* approaches were examined.

Specimen-based observations

The following characters were used for the specimen-based analysis of the litter samples:
(1) leaf length to the nearest mm,
(2) leaf width to the nearest mm (W_{max}),
(3) relative leaf width, expressed as:
    $RW_{max} = (\text{leaf width}/\text{leaf length}) \times 100$,
(4) leaf area, calculated from:
    leaf area = ⅔ length × width (Cain et al., 1956),
(5) position of greatest width, calculated from:

$$PW_{max} = \frac{\textit{distance from petiole along midvein to } W_{max}}{\textit{leaf length}} \times 100,$$

(6) margin type; entire or non-entire (incl. lobed).

Many foliar physiognomic analyses have used leaf area (e.g. Beard, 1944; Cain et al., 1956; Burnham, 1989), however Webb (1959) considered length a reasonable approximation of leaf size to define his modified Raunkiaer (1934) leaf size classes. Unless otherwise stated, leaf-size classes in this work are defined by length ranges (Webb, 1959[2]). The position of maximum width (PW_{max})

[1]LSI = (% microphylls + 2 × % notophylls + 3 × % mesophylls − 100 × 0.5
[2]microphyll < 75 mm; notophyll 76–125 mm; mesophyll > 125 mm

and the relative width (RW_{max}) of leaves is a measure of their departure from an ellipse. An elliptical leaf is defined as a symmetric leaf where PW_{max} is within the range 34–65% of length (i.e. width is maximal in the middle third of the lamina). A leaf is considered non-elliptic if 30% $< RW_{max} > 50\%$ (Radford et al., 1974). The position of maximum width detects ovate ($PW_{max} < 34\%$) and obovate ($PW_{max} > 65\%$) leaves, whereas relative width detects stenophyllous ($RW_{max} < 30\%$) and very wide leaves ($RW_{max} > 50\%$).

These characters were measured for every leaf from each sample (or subsample). Only complete leaves were measured. The leaflets from compound leaves were treated as simple leaves and only leaves from seed plants were considered in the analysis (i.e. no pteridophytes). Palm fronds were rare constituents of the litter and were excluded. Foliage from leptophyllous rainforest conifers (*Prumnopitys ladei* Podocarpaceae and *Araucaria cunninghamii* Araucariaceae) were encountered in some samples and were also excluded from the analysis. However, the rare leaves from broad-leaved conifers (*Agathis* spp. and *Podocarpus* s.s. spp.) were included in the analysis.

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. Leaf-size classes (e.g. Raunkiaer, 1934; Webb, 1959) are crude examples of these descriptors, but obscure much useful information.

The approach used in this study has been to use standard-sized replicated samples, and to divide the data from the characters [length, area, width (W_{max}) and position of width (PW_{max})] — into a number of arbitrary classes for individual leaves from the discrete samples. This data is presented graphically as histograms which display the relative contribution (frequency distribution) of different classes (Greenwood, 1987a; Christophel and Greenwood, 1987, 1988). These frequency distributions are used as the "foliar physiognomic signature" (Christophel and Greenwood, 1988) of discrete sets of samples. In order to refine these signatures, multivariate analysis (discriminant analysis) was employed to test the ability of particular physiognomic characters to accurately predict the correct forest type represented by a leaf assemblage.

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). Group membership of subsequent samples (e.g. fossil leaf assemblages, or fossil pollen assemblages: Kodela, 1989; Sugden and Meadows, 1989) is determined by the discriminant functions. Discriminant analysis does not assume that subsequent samples belong to the previously defined groups and so will not spuriously indicate association with the predefined groups (Sugden and Meadows, 1989).

Many Early Tertiary floras would seem to represent vegetation types without exact modern analogues (Daley, 1972; Hill, 1987). Discriminant analysis provides a means of testing whether a fossil assemblage belongs to the same group as those used in the initial analysis of modern vegetation (using leaf beds in this example) and provides a probabilistic statement on placement of the unknown samples into one or more of the groups defined by the group centroids (as defined by the discriminant functions). The results are plotted in two dimensions where the axes are rotated to maximise the separation between the predefined groups. Analysis is initially performed to maximise the variation between the predefined groups by selecting particular variables. Subsequent analyses use the discriminant functions derived from these variables to classify new samples. An explanation of the merits of Discriminant Analysis and other

multivariate analyses can be found in Sugden and Meadows (1989; and references therein).

Taxon-based observations

The taxonomic compositions of litter collected from Complex Mesophyll Vine Forest (CMVF Mulgrave R. site), Complex Notophyll Vine Forest (CNVF Dorrigo site), Simple Notophyll Vine Forest (SNVF; 2 sites — Coombadjha Ck and Mt. Lewis EP 18) and Microphyll Mossy Forest (MMF Barrington Tops) were examined to determine the potential variation between samples and in particular, potential variation due to both the arrangement of the source trees and deposition in stream beds (SNVF only). In most instances the chosen sites were experimental plots maintained by CSIRO Atherton Tropical Forest Research Centre (Stocker and Hyland, 1981; Stocker et al., in press; Stocker and Unwin, pers. commun., 1985, 1987) or study sites used by Webb and Tracey (1982).

The leaves were identified, where possible, using the CSIRO Tropical Forest Herbarium (Herbarium Australiense) at the Tropical Forest Research Centre in northeastern Queensland. New South Wales material was identified from herbarium collections at the Botany Department, University of Adelaide and foliage keys developed by Floyd (1989). In many cases identifications were not possible due to the high level of convergence seen in the leaf morphology of many tropical rainforest species and also due to the presence of undescribed species in the northeastern Queensland rainforests (B.P.M. Hyland, CSIRO, pers. commun.).

The length of every leaf was measured for all samples. Most taxa have leaves of several leaf size classes, so the modal leaf length of all the leaves of a taxon in a sample was used to derive a single characteristic leaf size class for each leaf taxon for that sample. This is in contrast to Wolfe (1978; Wolfe and Upchurch, 1987) who relegates leaves to the larger size-class where a given leaf species contains more than one leaf size class. Leaves from most species in litter exhibit a normal distribution with size, using either length or area (Greenwood, 1987a). Wolfe's argument is that by choosing the larger leaf size class present, taphonomic biases are compensated for (Wolfe and Upchurch, 1987, p. 37). This approach only provides an ad hoc

compensation for selection for smaller leaves and gives no measure of the degree of bias. By using the modal size (here), both the degree and direction of bias is directly measurable. Where both non-entire and entire leaf specimens of a single species were present in a sample, the dominant state was used as the taxon-state for that species. This situation was rare and occurred in only a few samples, usually involving a single species in a sample.

The taxon-based information is used to measure the bias in taxon-based indices of foliar physiognomy, such as Wolfe's Leaf Size Index, between leaf-beds (forest-floor and stream-bed litter) and the source canopy of the forest. This analysis assesses the accuracy of correlations between climate (such as MAT) and these foliar physiognomic indices. The Mean Annual Temperature of each forest site has been calculated from equivalent sites or from lapse rates determined from meteorological data (Anonymous, 1983) for sites within a few kilometres of each site (Table II). The proportion of species with entire leaf margins and the Leaf Size Index of each site have been plotted against the site MAT to determine how these forest-floor litter data can be used to assess Mean Annual Temperature for Tertiary megafloras. MAT is used here as this measure, rather than biotemperature (Holdridge, 1967; Dolph and Dilcher, 1979, 1980), is commonly used in actual studies of climate from Late Cretaceous and Tertiary megafloras (e.g. Dilcher, 1973; Wolfe, 1985, 1990; Parrish and Spicer, 1988).

Results

The floristic character of leaf-beds

The taxon-based foliar physiognomic approach (e.g. Wolfe, 1979, 1985, 1990) assumes that the floristic character, and hence the foliar physiognomic character of the forest, will be reflected in the leaf assemblages formed from the forest. It is important to determine how well leaf assemblages reflect the floristic character of the canopy. Several studies have used leaf litter to model fossil leaf assemblages to determine taphonomic influences on floristics (Chaney, 1924; Chaney and Sanborn,

1933; Spicer, 1981; Ferguson, 1985; Gastaldo et al., 1989; Burnham, 1989; Burnham et al., in prep.). With the exception of two studies (Chaney and Sanborn, 1933; Burnham, 1989), all of these investigations have been in deciduous Northern Hemisphere temperate broad-leaved or mixed coniferous forests. The Australian forests range from multistrata forests (3–4 tree layers) to single strata forests and so are often structurally more complex than temperate forests.

The number of species found in single samples from each site varied (Tables III–IX), with individual samples containing as few as 5 species (as leaves) in a Barrington Tops MMF litter sample (Table III), or as many as 21 species in a Mt. Lewis SNVF sample (Table IV). Typically each sample from a single site contained similar numbers of species. The total number of species found as leaves for individual sites (all samples grouped) varied from as few as 5 species (Barrington Tops MMF, Table III) to as many as 34 species (Oliver Ck CMVF, Table VIII). Of the most diverse sites (all CMVF, CNVF Crater and SNVF Mt. Lewis), the CMVF sites had the greatest variation in species present (i.e. the lowest number of species in common) between samples (Table VIII and IX; Fig.5). Membership and contribution of leaf taxa to the litter samples from the low diversity forests was constant, and the same dominants were always present in the litter (Tables III, VI; Fig.6). The Crater site is missing data for one sample (Table

VII). It would be expected that species number for the Crater site would be higher than given if data were available for the missing 4th sample (destroyed during analysis). The variation in diversity in the litter amongst the sites matches the relative diversity of the forests sampled, with Complex Mesophyll Vine Forest and the northeastern Queensland examples of the remaining forest types the most diverse (Tracey, 1982; Webb and Tracey, 1982).

Leaves from canopy trees within temperate deciduous forests (Spicer, 1981, 1989; Ferguson, 1985; Gastaldo et al., 1989; Burnham et al., in prep.) and evergreen tropical rainforest (Greenwood, 1987a, 1991) tend to be deposited within short distances of the source tree, with an exponential decrease in the number of leaves encountered with increasing distance from the tree. In five successively distant forest floor litter samples at the Mt. Lewis site, the leaves of the understory tree, *Acmena smithii*, were also less common in an exponential relationship (Fig.7). It is worth noting that a minor peak in leaf abundance occurs near the canopy edge of the tree. This data, together with the data presented above on relative diversity and floristic membership of forest-floor litter samples (Tables III–IX), suggests that leaf deposition is very localised within an *evergreen* closed canopy. This aspect of the taphonomy of leaf-beds will be examined in more detail below using the Mt. Lewis EP18 site.

TABLE III

Proportion of leaves of each taxon contrasted between samples from the forest floor in Microphyll Mossy Forest (Barrington Tops, N.S.W.)

Taxon		Leaf margin	Sample 1		Sample 2		Sample 3		Sample 4	
			no.	(%)	no.	(%)	no.	(%)	no.	(%)
Nothofagus moorei	c	toothed	158	70.5	188	88.3	172	76.8	192	85.7
Doryphora sassafras	c	toothed	12	5.4	22	10.3	16	7.1	25	11.2
Elaeocarpus reticulatus		toothed	22	9.8	0	0	3	1.3	0	0
Trochocarpa laurina		entire	29	12.9	3	1.4	32	14.3	7	3.1
Smilax australis		entire	2	0.9	0	0	1	0.4	0	0
Total taxa			5		3		5		3	

All leaf taxa are included.
c — canopy trees.
Smilax is a vine, all others are bushes or trees.

TABLE IV

Relative contribution of principal taxa to forest floor litter collections from SNVF (Mt. Lewis, NE Qld)

Taxon	Margin	Lifeform	1	2	3	4
Ripogonum/Smilax	entire	vine	1.5	—	1.0	—
Hypserpa laurina	entire	vine	6.0	1.5	1.5	1.0
Diospyros ferrea	entire	b tree	2.0	4.5	4.0	8.0
Planchonella euphlebia	entire	c tree	15.5	—	13.0	13.0
Pithecellobium grandiflorum	entire	c tree	2.0	17.0	8.0	4.5
Acmena smithii	entire	b tree	1.5	0.5	0.5	3.0
A. resa	entire	b tree	10.0	0.5	4.0	0.5
Argyrodendron sp.	entire	b/c tree	3.5	20.0	0.5	1.0
Ficus sp.	entire	epiphyte	1.0	—	3.5	10.0
?Buckinghamia celissima	entire	b tree	2.0	0.5	2.0	4.0
Flindersia bourjotiana	entire	b tree	0.5	2.5	0.5	1.0
Lauraceae sp. 1	entire	b tree	—	—	0.5	0.5
Lauraceae sp. 3	entire	b tree	1.5	1.0	6.5	5.0
Endiandra subtriplinervis	entire	c tree	23.5	17.0	20.5	7.0
Beilschmiedia ?obtusifolia	entire	c tree	2.5	1.5	14.0	1.0
Cryptocarya corrugata	entire	b tree	—	11.0	0.5	—
Elaeocarpus sericopetalus	non-	b tree	16.5	0.5	3.5	8.5
Corynocarpus cribbianus	non-	b tree	0.5	2.5	—	1.0
unknowns (summed)			10.0	19.5	5.5	31.0
number of taxa/sample	(27 total)		20	20	21	19

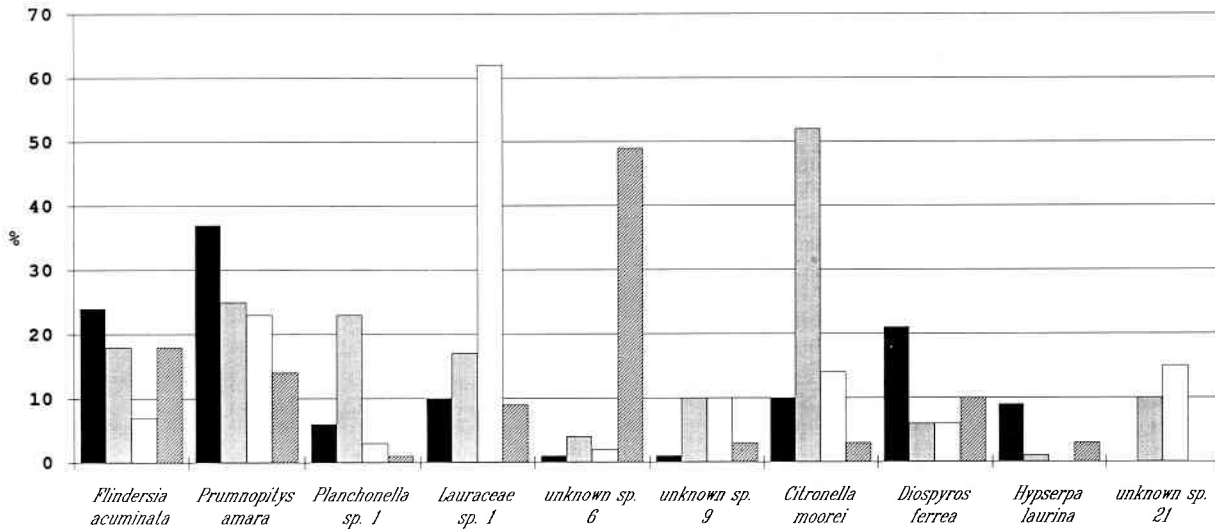c trees — canopy
b trees — subcanopy

Fig.5. Histograms demonstrating the taxonomic composition and abundance of leaf-taxa (principal taxa only) of 4 samples of forest-floor leaf-litter from CMVF.

TABLE V

Proportion of leaves of each taxon contrasted between samples from the forest floor and stream-bed in SNVF (Washpool N.P. and Coombadjha Creek, N.S.W.)

Taxon		Margin type	Forest floor samples (%)				Stream samples	
			1	2	3	4	1	2
Ceratopetalum	c	toothed	39.3	36.6	30.4	54.5	75.4	83.5
Doryphora	c	toothed	22.3	44.2	56.3	8.0	2.7	1.5
Quintinia		toothed	26.3	0	0.4	28.6	0	0
Syzygium		entire	7.1	9.4	0.9	2.7	2.7	1.0
Orites		toothed	2.2	0	2.7	2.2	1.3	3.5
Callicoma		toothed	0	0	1.8	0	8.0	8.0
Banksia		toothed	0	0	0	0	1.8	1.5
Other**		toothed	2.7	9.8	7.6	4.0	6.3	3.5
no. leaves			224	224	224	224	224	224
Total taxa			6	4	7	6	7	7
% taxa entire			16.2	25.0	14.3	16.7	14.3	14.3

c — canopy trees
***Polyscias araliafolia* and/or *Acradenia euodiiformis*
All leaf taxa are included. All are trees or bushes.

TABLE VI

Proportion of leaves of each taxon contrasted between samples from the forest floor in Complex Notophyll Vine Forest (Dorrigo, NSW)

Taxon		Sample 1		Sample 2		Sample 3		Sample 4	
		no.	(%)	no.	(%)	no.	(%)	no.	(%)
Sloanea woolsii	c	62	27.7	65	29.0	72	32.1	47	21.0
Doryphora sassafras	c	11	4.9	11	4.9	12	5.4	17	7.6
Orites excelsa		8	3.6	5	2.2	7	3.1	2	0.9
Ficus sp.		—	—	1	0.4	—	—	1	0.4
Syzygium crebinervis		—	—	—	—	1	0.4	19	8.5
Dysoxylum fraseranum	c	125	55.8	123	54.9	94	42.0	132	58.9
Smilax australis	v	—	—	—	—	—	—	1	0.4
unknowns		18	8.0	19	8.6	38	17.0	5	2.3
Total taxa (14)		224	11	224	10	224	8	224	9

c — canopy trees
v — vine

The position and identity of the main trees for part of the Mt. Lewis SNVF plot is given in Figs.8, 9 (from Stocker and Unwin, unpublished data). The placement of the litter sample points is also indicated. The relative contribution of leaves to the litter samples by selected species is shown in Fig.10 and Table IV. Common trees in the canopy and understory were *Planchonella euphlebia*, *Cryptocarya corrugata* and *Pithecellobium grandiflorum*. Common trees in the subcanopy were smaller individuals of these species, together with *Diospyros ferrea* var. *reticulata*, *Elaeocarpus* sp.,
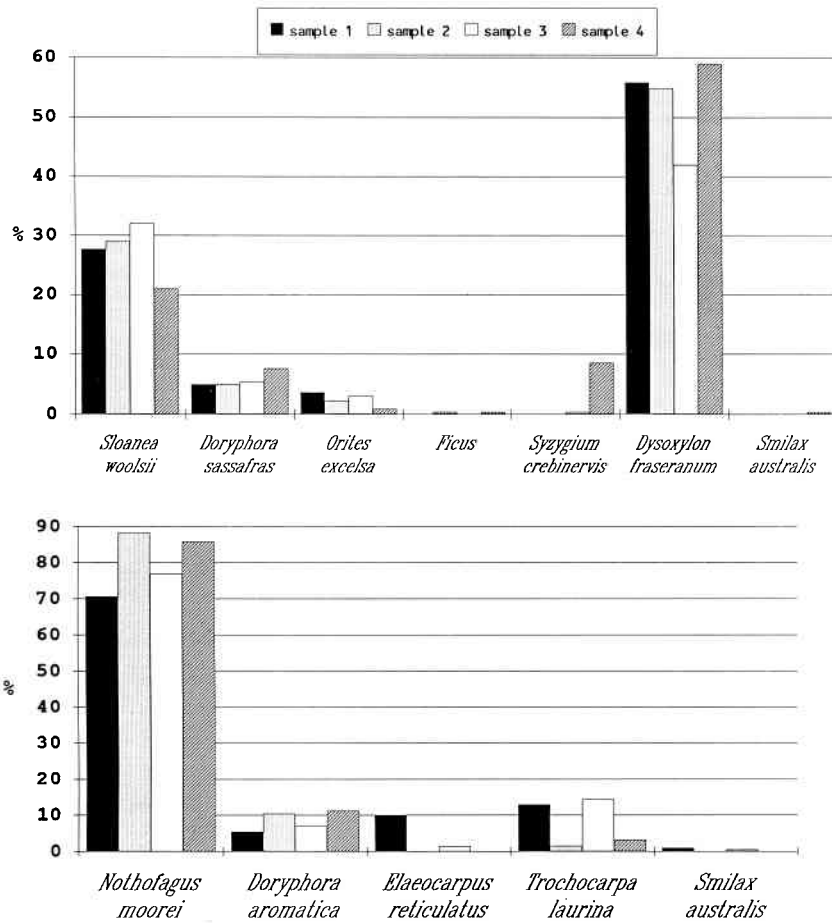
Fig.6. Histograms demonstrating the taxonomic composition and abundance of leaf-taxa (principal taxa only; proportion as percent) of 4 samples each of forest-floor leaf-litter from (a) CNVF (Dorrigo) and (b) MMF (Barrington Tops). Sample legend applies to both (a) and (b).

Flindersia spp. and individuals of several species of Proteaceae.

Different leaf taxa were dominant in each sample from the Mt. Lewis EP18 site, although leaves of Lauraceae sp. 4 and *Planchonella euphlebia* were common in 3 of the 4 samples (but not the same 3 samples). The high incidence of leaves of *P. euphlebia* did not always coincide with the close proximity of trees of this species to the sample point. Similarly, although an understory individual of *Argyrodendron* sp. was within 5 m of sample point 3, only 0.5% of the leaves were of this species. A large canopy individual of *Argryroden-dron* sp. grew close to sample points 1 and 2. This was reflected in higher leaf counts for this species

in these samples (3.5 and 20.0%), with the closest sample point recording a significant score.

The leaves of vines (e.g. *Hypserpa laurina* and *Smilax*) were rare in most samples from Mt. Lewis EP18. A significant number of leaves of *Ficus destruens*, a strangler-fig (epiphyte), were found in one sample. In general, the highest counts in a single litter sample were recorded for tree species found in the canopy. In part this may reflect the higher durability of canopy leaves, which tend to be coriaceous and thus more resistant to decay than the chartaceous and membraneous leaves of trees beneath the canopy. Overproduction of leaves by canopy trees (Stocker et al., in press; Thompson et al., in prep.) is another significant factor. What

TABLE VII

The relative contribution of taxa to forest-floor litter in CNVF (The Crater, NE Qld)

Taxon		Margin type	Sample 2*		Sample 3		Sample 4	
			no.	(%)	no.	(%)	no.	(%)
Neolitisea dealbata		entire	27	12.1	5	2.2	7	3.1
Doryphora aromatica	c	toothed	70	31.3	2	0.9	38	17.0
Geissois biagiana	c	entire	41	18.3	—	—	37	16.5
Ficus copiosa		entire	—	—	—	—	3	1.3
Ficus sp.		entire	1	0.4	6	2.7	23	10.3
Syzygium sp.		entire	—	—	1	0.4	—	—
Beilschmiedia sp.	c	entire	—	—	59	26.3	11	4.9
Prumnopitys amara		entire	—	—	18	8.0	—	—
Sloanea woolsii	c	toothed	47	21.0	—	—	—	—
Vitaceae		toothed	5	2.2	113	50.4	93	41.5
unknowns		various	33	14.7	20	8.9	12	5.4
Total taxa (21)			224	10	224	11	224	14

6 taxa were non-entire (28.6%)   [LSI: 43.0]
*one sample was destroyed before analysis was complete.
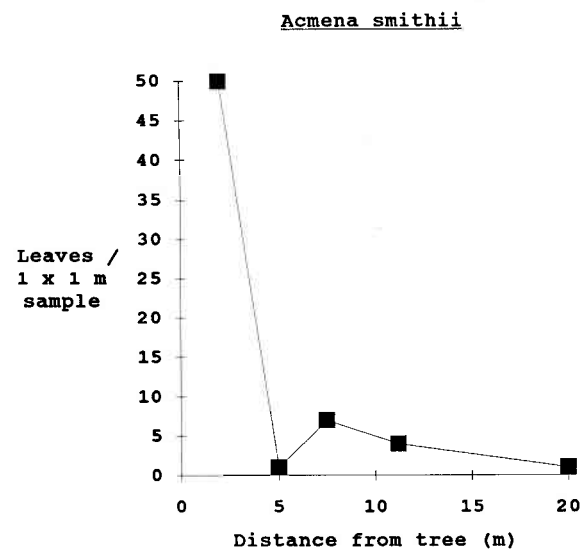c — canopy trees

Acmena smithii

Fig.7. The number of leaves of the understory tree, *Acmena smithii* (Myrtaceae), in samples successively more distant from the tree at the Mt. Lewis EP18 SNVF site. Each sample represents the proportion of leaves of this species in a sample of 224 leaves collected from a 1 × 1 m square of forest-floor litter.

is clear is that forest-floor litter reflects the closest trees (see above), with the leaves of canopy trees travelling furthest and dominating the litter. In some cases, a minor peak away from the trunk may indicate greater leaf input at the canopy edge (e.g. *A. smithii*, Fig.7; see also Greenwood, 1991, fig.3).

A comparison of the foliar physiognomy of the canopy and litter

Both Webb's (1959, 1968) and Wolfe's (1971, 1978, 1979) analyses of climate and foliar physiognomy were based on canopy tree synusiae alone and on direct *sampling of the canopy*. The relationships they detected have been applied directly to the interpretation of leaf megafloras (e.g. Christophel and Blackburn, 1978; Christophel, 1981; Wolfe, 1985; Zastawniak et al., 1985; Wolfe and Upchurch, 1986). The data presented here represent forest-floor leaf litter. Burnham (1989) found a good correspondence between the proportion of *species* (presence of individual leaves) with non-entire margins in fluvial deposits and the proportion of species with non-entire leaf margins in the standing vegetation. The data here consider leaf margin from the perspective of *individual leaves* (specimens), in addition to *species*.

The dominance of leaf fall in Australian rainforests by canopy trees (Stocker et al., in press;

TABLE VIII

Proportion of leaves of each taxon contrasted between samples from the forest floor in Complex Mesophyll Vine Forest (Oliver Creek)

Taxon	Leaf		No./sample			
	size	margin	1	2	3	4
trees						
Musgravea heterophylla	mesophyll	entire	14	3	—	—
Idiospermum australiensis	mesophyll	entire	2	25	1	—
Synima codierorum	notophyll	non-	—	9	17	—
Acmena graveolens	notophyll	entire	—	27	2	—
Lindsayomyrtus brachyandrus	mesophyll	entire	—	—	—	5
Doryphora aromatica	notophyll	non-	—	24	9	—
Medicosma sessiliflora	mesophyll	entire	4	4	—	1
Planchonella obovoidea	notophyll	entire	—	2	8	—
Beilschmiedia bancroftii	notophyll	entire	—	3	27	—
Endiandra microneura	notophyll	entire	3	5	122	26
Litsea leefeana	notophyll	entire	18	—	—	27
Storckiella australiensis	mesophyll	entire	108	—	—	107
Euodia sp.	notophyll	entire	9	—	—	13
Calophyllum sil	microphyll	entire	—	6	—	—
Cleistanthus myrianthus	mesophyll	entire	—	2	8	—
Jagera javonica	notophyll	non-	—	2	4	—
Ryparosa javonica	macrophyll	entire	4	—	2	1
?Archidendropsis xanthoxyla	microphyll	entire	—	—	—	1
Tetracera nordtiana	notophyll	entire	—	9	2	—
unknown sp. 1	notophyll	entire	—	2	—	—
unknown sp. 2	notophyll	entire	—	1	—	—
unknown sp. 3	notophyll	non-	—	—	—	1
unknown sp. 4	notophyll	entire	—	—	—	1
unknown sp. 5	notophyll	entire	3	—	—	5
unknown sp. 6	mesophyll	entire	—	—	—	1
unknown sp. 7	notophyll	entire	—	—	—	—
unknown sp. 8	notophyll	entire	2	—	—	—
unknown sp. 9	notophyll	entire	2	—	—	—
unknown sp. 10	notophyll	entire	1	—	—	—
unknown sp. 11	microphyll	entire	1	—	8	—
vines and epiphytes						
Ficus destruens	notophyll	entire	—	94	7	—
Medinillia balls-headleyi	notophyll	entire	—	1	3	—
Austroestreensis sp.	microphyll	entire	20	—	1	16
Hoya sp.	microphyll	entire	—	2	—	—
Pandorea sp.	notophyll	entire	1	—	2	1
Piper sp.	notophyll	entire	7	2	—	6
Menispermaceae	notophyll	entire	1	—	—	2
37 taxa total	LSI = 54.1	13.5%	200	224	224	213
			leaf no./sample			

TABLE IX

Proportion of leaves of each taxon contrasted between samples from the forest floor in Complex Mesophyll Vine Forest (Mulgrave River)

| Taxon		Sample 1 no.	(%)	Sample 2 no.	(%)	Sample 3 no.	(%)	Sample 4 no.	(%)
Flindersia sp.	c	24	17.0	18	9.2	7	4.6	18	12.9
unk. 2		—	—	—	—	—	—	2	1.4
unk. 3		1	0.7	4	2.0	—	—	—	—
Prumnopitys amara	c	37	26.2	25	12.8	23	15.0	14	10.1
Planchonella sp. 1		6	4.3	23	11.7	3	2.0	1	0.7
Planchonella sp. 2		—	—	2	1.0	—	—	—	—
unk. 6	?	1	0.7	4	2.0	2	1.3	49	35.3
unk. 7		3	2.1	3	1.5	1	0.7	3	2.2
Lauraceae	c	10	7.1	17	8.7	62	40.5	9	6.5
unk. 9		1	0.7	10	5.1	10	6.5	3	2.2
unk. 10		5	3.5	6	3.1	1	0.7	1	0.7
unk. 11		1	0.7	1	0.5	1	0.7	—	—
Citronella moorei	c	10	7.1	52	26.5	14	9.2	3	2.2
Diospyros ferrea		21	14.9	6	3.1	6	3.9	10	7.2
unk. 14		7	5.0	4	2.0	1	0.7	—	—
Hypserpa laurina		9	6.4	1	0.5	—	—	—	—
unk. 16		1	0.7	3	1.5	5	3.3	3	2.2
unk. 17		—	—	—	—	—	—	3	2.2
Mallotus sp.		—	—	—	—	—	—	3	2.2
unk. 19		—	—	—	—	1	0.7	1	0.7
unk. 20		—	—	—	—	1	0.7	—	—
unk. 21		—	—	10	5.1	15	9.8	—	—
unk. 22		—	—	1	0.5	—	—	—	—
unk. 23		—	—	4	2.0	—	—	—	—
unk. 25		—	—	—	—	—	—	2	1.4
unk. 26		2	1.4	—	—	—	—	—	—
unk. 27		1	0.7	2	1.0	—	—	—	—
unk. 28		1	0.7	—	—	—	—	2	1.4
unk. 29		—	—	—	—	—	—	3	2.2
unk. 30		—	—	—	—	3	2.0	—	—
Total taxa (30)		18		20		17		18	

c — canopy trees

Thompson et al., in prep.; and above) creates the expectation that a forest composed predominantly of trees with, for example, notophyllous canopies, will produce little dominated by notophylls. Based on specimens, it could be expected that canopies dominated by individual trees with entire margin leaves will produce litter dominated by entire margin leaves. These expectations are tested here. The specimen-based characteristics (leaf margin and size) and taxon-based characteristics for litter from the sites are summarised in Tables X and XI.

Data from only a selection of sites is presented for taxon-based observations.

Leaf margin type

Leaf margin is the main foliar physiognomic characteristic used for palaeoclimatic interpretations (e.g. Wolfe, 1979, 1985; Parrish and Spicer, 1988). Generally it was found in litter that using specimens there was a high variation between samples at some sites (Table X). There is also a poor match between the proportion of *individual*
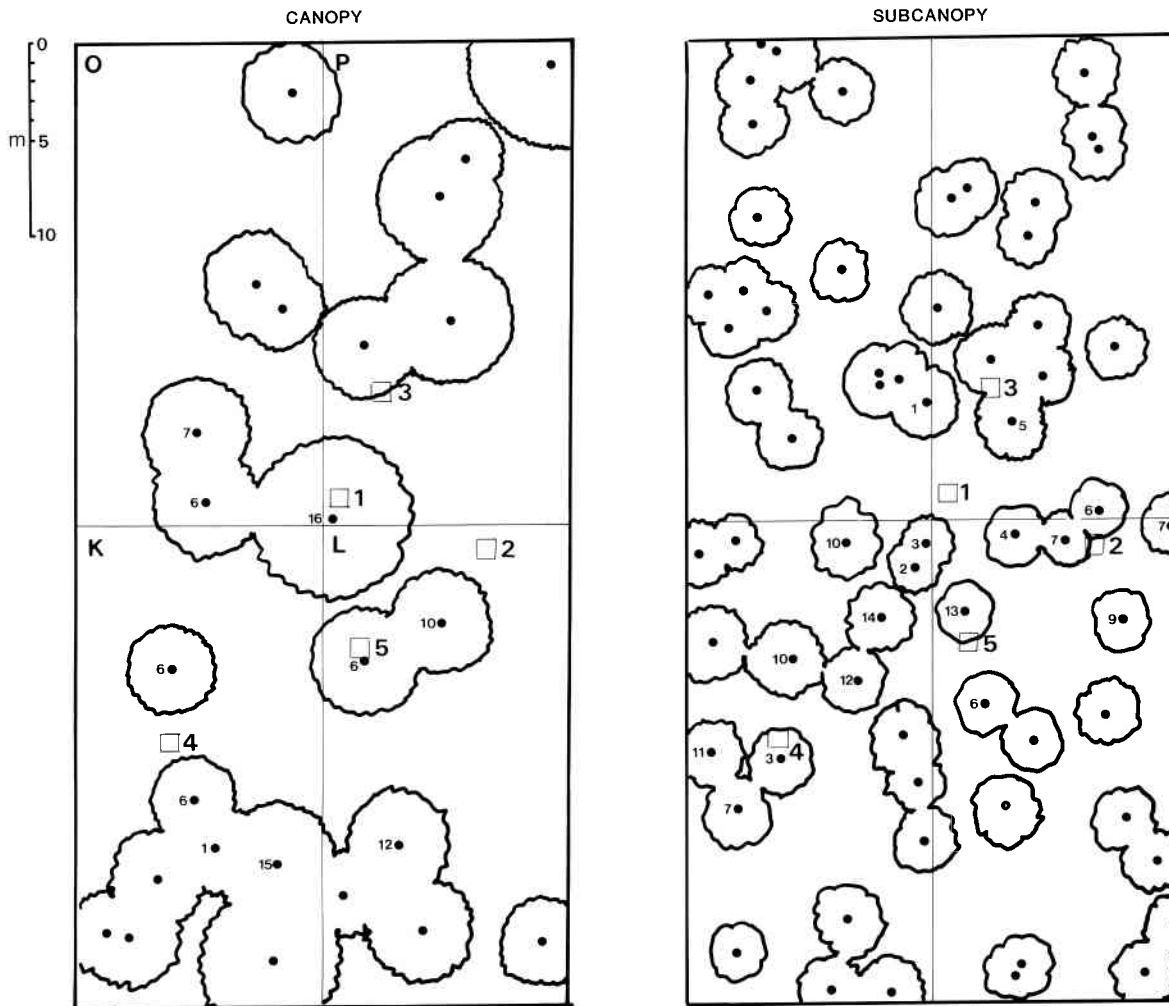
Figs.8 and 9. Map of part of the CSIRO experimental forest plot at Mt. Lewis, N.E. Queensland. Canopy (Fig.8; trees ≥20 m) and understory (Fig.9; trees 8–18 m) trees over 15 cm d.b.h. are mapped and identified (below). Forest-floor leaf-litter collection points are indicated by numbered squares. Tree canopy silhouettes are diagramatic only. Data from Stocker and Unwin, unpubl., 1985. Labelled trees as follows: (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*.

leaves with entire margins and the known ranges for the proportion of individual trees with entire margin leaves in the canopies of the forest types examined (sensu Webb, 1959, 1968; Tracey, 1982; Table XII). There is also little relationship between the proportion of leaves with entire leaf margins in the litter samples and the Mean Annual Temperature (Fig.11). This is in accord with Wolfe's (1978) expectations for *specimens*.

The *taxon-based* examination of the forest-floor litter demonstrated less variation for leaf-margin type within a single site than was indicated using specimens (Table XI). Comparison of the litter values to the expected canopy values (from Webb, 1959; Table XIII) shows a broad correspondence for most of the forest types (CMVF, CNVF and SNVF in part). The low diversity sites (Microphyll Mossy Forest and N.S.W. Simple Notophyll Vine Forest) exhibited a wider variation than the other sites and were significantly different to the expected
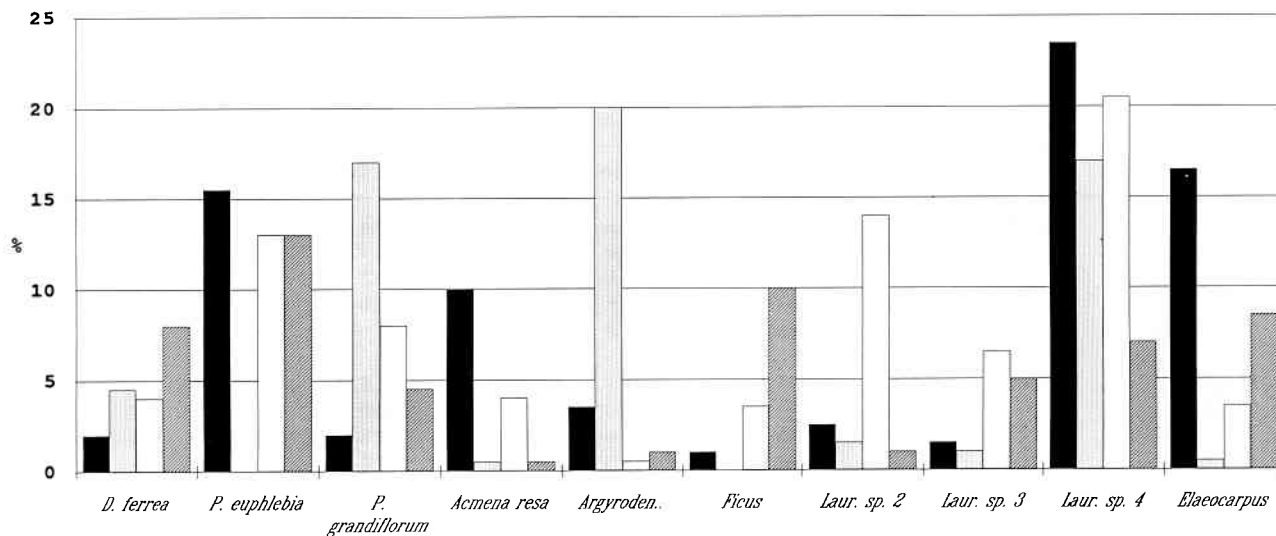
Fig.10. Histograms demonstrating the taxonomic composition and abundance of leaf-taxa (principal taxa only) of 4 samples each of forest-floor leaf-litter from SNVF at Mt. Lewis EP 18.

TABLE X

Proportion of individual specimens (leaves) with non-entire leaf margins

Forest type	Site	Samples (%)				Site mean	MAT (°C)
		1	2	3	4		
CMVF	Mobo Creek	03	01	01	02	1.7	20
	Mulgrave River	01	16	13	—	10.0	24.5
	Oliver Creek	01	26	01	01	7.3	24.6
CNVF	Curtain Fig	45	44	46	39	43.0	20
	Dorrigo N.P. (NSW)	37	38	50	50	43.1	19.4
	The Crater N.P.	61	74	51	77	65.7	17.9
CNVF-SNVF	Mt. Windsor	18	17	—	—	—	
SNVF	Mt. Lewis Road	04	06	04	—	4.7	16
	Mt. Lewis EP18	05	11	17	03	7.5	17.3
	Washpool N.P. (NSW)	63	81	93	67	76.0	15.0
	Coombadjha Ck	91	95	—	—	—	15.0
(SNVF/MVFF)	Mount Haig	03	05	43	11	13.0	16
MMF/MFF	Barrington Tops	87	99	85	93	91.0	10.7

values (Tables XI and XIII). This reflects the influence of single trees on the species composition of local leaf assemblages (see above and Wolfe, 1978), as in most cases where a single sample had much higher numbers of non-entire margin leaves than other samples from the same site, only a few, and often only a single species, were contributing the non-entire margin leaves. The higher variability of the low diversity forest-floor litter sites supports Wolfe's recommendation that leaf margin analysis should be used only for floras with high species numbers (greater than 20 species, Wolfe, 1985; Wolfe and Upchurch, 1987).

Wolfe (1979, 1985, 1990; Wolfe and Upchurch, 1987) indicates for every 4% change in the proportion of entire margin species in Southern Hemisphere mesic forests, there is a 1°C change in MAT. Evidence from Australian rainforest canopies (Webb, 1968; Greenwood and Christophel, 1990, in prep.) suggests that MAT is not the sole

TABLE XI

The foliar physiognomic characteristics using leaf-taxa of 4 forest types (1 site and 3–4 samples for each)

Site	Forest type	No. taxa	% spp. entire	% spp.			Leaf size index (LSI)
				micro-	noto-	meso-	
Oliver Ck	CMVF 1	17	94.1	11.8	58.8	29.4	58.8
(N. Qld)	2	19	84.2	15.8	57.9	26.3	55.3
	3	17	82.4	11.8	64.7	23.5	55.9
	4	16	93.7	12.5	62.5	25.0	56.3
total for site		34	88.2	13.5	64.9	21.6	54.1
Mulgrave	CMVF 1	18	94.4	11.1	77.8	11.1	50.0
(N. Qld)	2	20	95.0	10.0	70.0	20.0	55.0
	3	17	94.1	17.6	70.6	11.8	47.1
	4	18	94.4	16.7	72.2	11.1	47.2
total for site		30	90.0				49.9
Crater NP	CNVF 2	10	50.0	33.3	40.0	26.7	46.7
(Qld)	3	11	81.8	45.5	36.4	9.1	22.8
	4	14	71.4	42.9	14.3	35.7	39.3
total for site		21	71.4	42.9	28.6	28.6	43.0
Dorrigo	CNVF 1	11	63.6	36.4	54.5	9.1	36.4
(NSW)	2	10	60.0	30.0	60.0	10.0	40.0
	3	8	62.5	37.5	62.5	0.0	31.3
	4	9	77.8	44.4	44.4	11.1	33.3
total for site		14	64.3				42.9
Mt. Lewis	SNVF 1	20	85.0	40.0	45.0	15.0	37.5
(N. Qld)	2	20	85.0	45.0	35.0	20.0	37.5
	3	21	85.7	52.6	42.1	5.3	26.4
	4	19	84.2	40.0	50.0	10.0	35.0
total for site		27	85.2	37.0	37.0	18.5	33.3
Washpool	SNVF 1	6	16.2	66.7	33.3	0	16.7
(NSW)	2	4	25.0	75.0	25.0	0	12.5
	3	7	14.3	71.4	28.6	0	14.3
	4	6	16.7	66.7	33.3	0	16.7
total for site		7	14.3	71.4	28.6	0	15.0
Barr. Tops	MMF 1	5	40.0	100.0	0	0	0.0
(NSW)	2	3	33.3	100.0	0	0	0.0
	3	5	40.0	100.0	0	0	0.0
	4	3	33.3	100.0	0	0	0.0
total for site		5	40.0				0.0
Mt. Windsor	upper	26	57.7	27.0	53.8	19.2	46.1
CNVF-SNVF	lower	36	63.9	50.0	50.0	0	25.0

determining factor for leaf margin type in Australian mesic-humid forests. A linear regression of the available sites with taxon-data (Fig.12; least squares) shows a similar relationship to that detected by Wolfe (1979, 1990; Wolfe and Up-church, 1987). Burnham (1989) also found a close correspondence between the standing forest canopy and fluvial litter-beds. However the correlation from forest-floor litter is low (r sq. 0.75), with significant variation from the regression line for

TABLE XII

Comparison of the number of specimens with entire leaf margins found in the canopy and litter (% leaves/trees)

Forest type	Litter	Canopy[1]
Complex Mesophyll Vine Forest	90.0–98.3	75–95
Complex Notophyll Vine Forest	34.3–57.0	85–65
Simple Notophyll Vine Forest Qld	87.0–95.3	c. 45
NSW	7.0–37.0	
Microphyll Mossy Forest	13.0–1.0	0

[1]After Webb, 1959

some datapoints (e.g. Washpool and Mt. Lewis EP18 SNVF). Some of these values are based on low species-number sites (< 10 spp.), however the Mt. Lewis EP18 site is one of the most diverse (Table XI). The Mt. Lewis EP18 site MAT estimate may be too low as an alternative estimate of MAT for this site gave a value of 19°C (H.A. Nix, Australian Nat. Univ., pers. commun., 1991). However if this higher MAT value is accepted the Mt. Lewis datum is still significantly variant from the regression line.

TABLE XIII

Comparison of leaf sizes between leaf litter and canopy using specimens (% leaves/% individual trees)

Forest type	Litter			Canopy[1]		
	micro-	noto-	mesophylls	micro-	noto-	mesophylls
CMVF	6–25	50–70	11–39	0–5	30–40	60–70
CNVF	16–55	35–77	2–22	c. 10	c. 85	0–20
SNVF	59–85	14–36	0–11	10–70	25–95	0–20
MMF/MMF	90–96	4–10	0	95–100	0–5	0

[1]After Webb, 1959
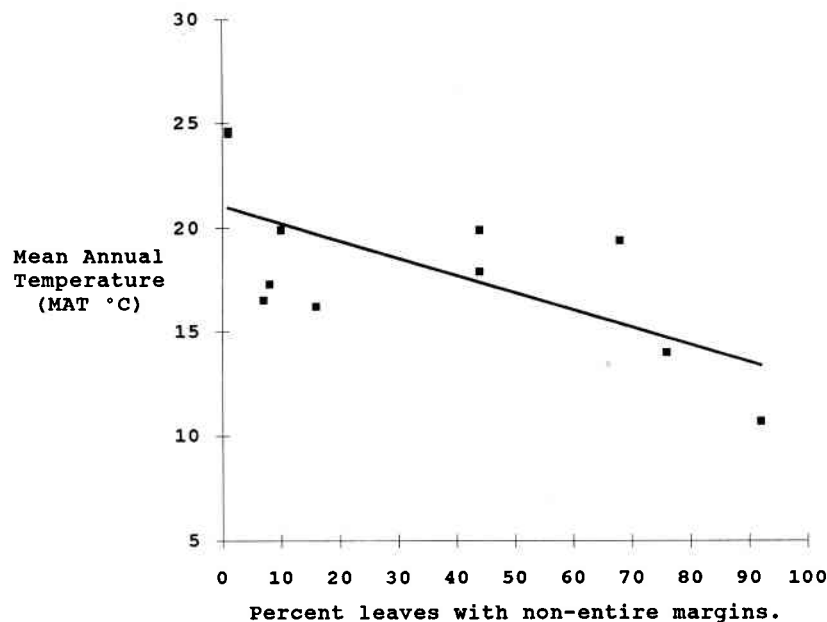
Fig.11. Plot of Mean Annual Temperature (MAT) versus the proportion of specimens with non-entire leaf margins (site means) in forest-floor leaf-litter samples from all sites.
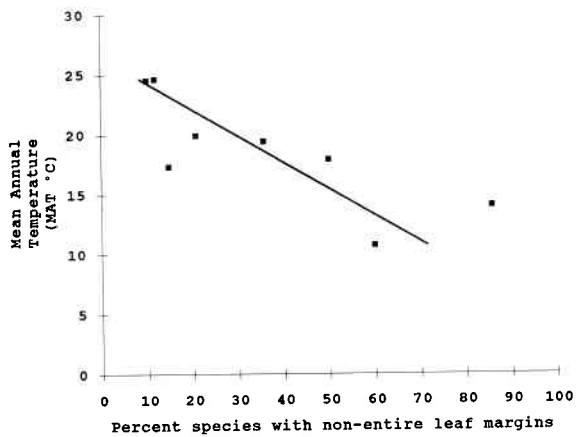
Fig.12. Plot of Mean Annual Temperature (MAT) versus the proportion of species with non-entire leaf margins in forest-floor litter samples from selected sites (data was not available for the other sites).

Leaf size

The proportion of leaves represented in the Raunkiaer-Webb leaf-size classes for litter samples from each forest type (highest and lowest values for each class) are contrasted to Webb's data for the canopy (Webb, 1959) in Table XIV. The canopy data indicate the proportion of individual trees with microphyllous, notophyllous or mesophyllous canopies. As can be seen from Table XIV, the SNVF, CNVF and CMVF leaf litters have different proportions (or values close to the upper or lower limits) of the respective Raunkiaerian leaf-size classes than recorded by Webb (1959) for the canopies of the same forest types.

The mesophyll dominated CMVF has produced notophyll-dominated litter (Table XIV) and the

TABLE XIV

Comparison of the number of species with entire leaf margins found in the canopy and litter (% taxa)

Forest type	Litter	Canopy[1]
Complex Mesophyll Vine Forest	82.4–95.0	70–90
Complex Notophyll Vine Forest	50.0–81.8	70–85
Simple Notophyll Vine Forest Qld	84.2–90	40–70
NSW	14.3–25	
Microphyll Mossy Forest	33.3–40	0

[1]After Webb, 1959

two notophyll-dominated forest types (CNVF and SNVF) have much lower numbers of notophylls than expected. Based solely on Webb's canopy data, it is likely that an unknown sample (e.g. a Tertiary leaf assemblage) of leaf litter from CMVF would be interpreted as coming from CNVF, and litter from CNVF would be interpreted as coming from SNVF (Table XIV). MFF/MMF litter has almost the same proportions of leaves in the leaf-size classes as given by Webb for the canopy and SNVF litter deviates primarily by the much greater representation of microphylls than observed in the SNVF canopy.

The Complex Mesophyll Vine Forest samples showed the greatest difference between litter and canopy for both the proportion of species in each of the leaf-size classes and the Leaf Size Index (Table XV; Fig.13). Complex Mesophyll Vine Forest is in part analogous to Wolfe's "Paratropical Rainforest" (Wolfe, 1979, 1985; Greenwood and Christophel, in prep.). The samples in this instance came from forest at the upper thermal limit of

TABLE XV

Comparison of leaf sizes between leaf litter and canopy using taxon-based observations (% taxa)

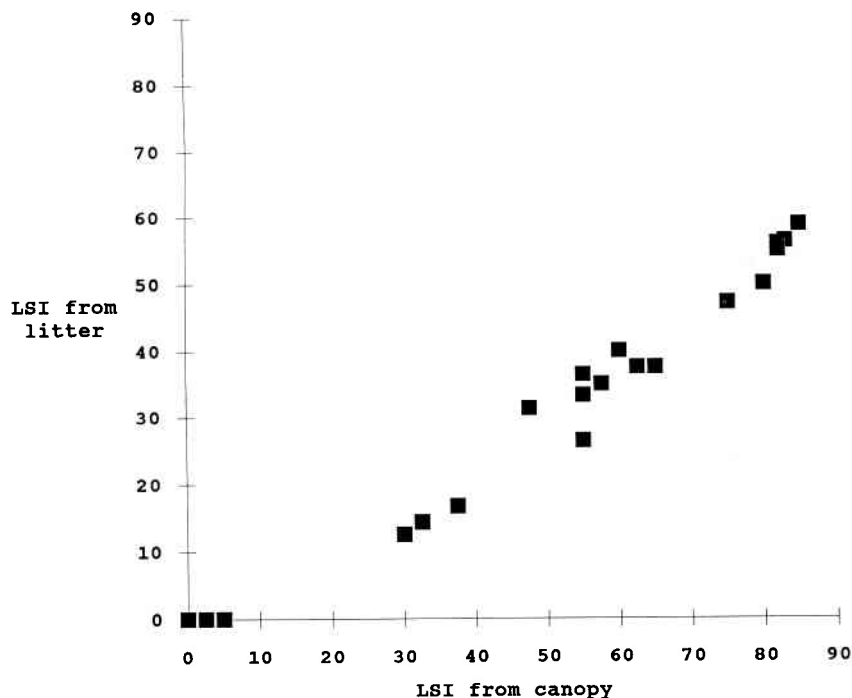| Forest type	Litter[1]			Canopy[2]		
	micro-	noto-	mesophylls	micro-	noto-	mesophylls
CMVF	11–18	58–78	11–30	0–5	30–50	50–70
CNVF	30–46	14–63	0–36	10–20	50–70	15–30
SNVF	40–75	25–50	0–20	0–40	55–75	0–30
MMF	100	0	0	90–100	0–10	0

[1]From Table XI; [2]from Webb, 1959.

Fig.13. Plot of Leaf Size Index (LSI) for canopy and forest-floor leaf-litter samples. Adapted from Greenwood, 1991.

CMVF (MAT of 26°C) and thus may be transitional to "Tropical Rainforest" as defined by Wolfe (1979).

A LSI value of 60–75 indicates a predominantly mesophyllous canopy, whereas values of 35–50 indicate a predominantly notophyllous canopy and 0–20 a predominantly microphyllous canopy (Burham, 1989). These values are based on canopy samples and Wolfe's practice (1978; Wolfe and Upchurch, 1987) of choosing the higher leaf size class for a species where leaves of two size classes are present within the same species. On this basis, the CMVF litter samples would be interpreted as having been derived from a notophyllous forest (Table VIII). The CNVF and SNVF samples in general would be correctly identified as being derived from notophyllous forest, although some of the samples are intermediate with the microphyllous values. The observed overlap for CNVF and SNVF in the ranges of all leaf-size categories and LSI may reflect the increasing bias against large leaves in litter. An increase in the average leaf size in the source canopy (Table VIII) may exacerbate this bias, producing the overlap in the leaf-size values.

The Leaf Size Index shows a gross trend for leaf size among the forest types (Tables XI and XV), decreasing from the warmest (CMVF) to the coolest forest type (MMF). Dilcher (1973) recorded a similar trend. However, the range of values for both CNVF and SNVF overlap. Wolfe groups these two forest types as "Notophyllous Broadleaved Forest" (Wolfe, 1979, 1985). There is a trend with increasing overall leaf size (i.e. from microphyll dominated canopies to mesophyll dominated canopies) for a decreasing correspondence for the ranges of species represented in the three leaf-size classes in the litter samples with the canopy values (Table XV). This matches the trend observed from the same sites for specimen-based observations (Table XIV), implying that leaf size analysis of leaf beds using taxon-based *canopy observations* will be increasingly biased with greater overall leaf size in the source forests. The Leaf Size Index employed by Wolfe (Wolfe and Upchurch, 1986; Burnham, 1989), however, would

seem to be moderately robust to these biases (below), although it would seem that the same trend is apparent, with source canopies of larger leaf size inaccurately determined.

The LSI values determined for the litter have been plotted against LSI values calculated for the canopy (Fig.13; Greenwood, 1991). The canopy values were calculated from the ranges for the number of taxa of each leaf size class given for the canopy of the respective forest types (Table XIV; Webb, 1959). Webb (1959) assigned taxa to each leaf size class on the basis of the common situation (i.e. the "mean" state) and so his values are comparable to the litter values. The midpoint was calculated from the intermediate case. The range for each canopy value represents the maximum and minimum LSI possible from the ranges and so these values are only estimates. Nevertheless, a clear trend is seen with the correspondence between litter and canopy LSI values decreasing with increasing overall canopy leaf size (Fig.13). A correction factor may be calculated from this plot (Greenwood, 1991). From the canopy estimates used here the value is about 3:2 for canopy LSI:litter LSI. This estimation suggests that leaf assemblages derived from large leaf canopies will significantly underestimate canopy values for LSI.

Foliar physiognomic signatures

The above comparison between litter and canopy suggests that a significant taphonomic bias influences the foliar physiognomic character of leaf assemblages (litter in this instance) relative to their source canopies. However, the principal issue with foliar physiognomic analysis is whether there is a decodable signal or signature in fossil leaf-beds identifying forest-types and/or climates (Christophel and Greenwood, 1988; Burnham, 1989). The leaves within each sample are treated here as a subset of the overall leaf population. The population can then be characterised population descriptors — percentiles, maximum and minimum values (and hence the range), mean and median (50th percentile) — which can be used to approximate the "foliar physiognomic signature" of discrete sets of samples in multivariate analyses.

Christophel and Greenwood (1987, 1989) used the ogives (cumulative frequency plots) of leaf length (and partly leaf width) as approximations of the "foliar physiognomic signatures" representative of leaf-beds derived from the main Webb forest types using the same sites as used here. However, the data will be discussed here in greater detail by contrasting the sites by individual foliar physiognomic characters. The relationship between each character and the MAT of each site will also be presented, using both specimen-based and taxon-based observations.

Leaf size (length and area)

The leaf length frequency histograms for litter from each of the sites (Figs.14–17) shows that this metric physiognomic character approximates a normal distribution in the litter leaf populations for each forest type. Leaf area produces almost identical distributions (Greenwood, 1987a). A feature of all of the forest types tested is that a significant but small number of leaves much larger than the general population skews the frequency distributions. This skew is more pronounced in the Complex Notophyll Vine Forest (Fig.15) and Simple Notophyll Vine Forest (Fig.16) examples from Queensland (Lat. 17°–15°S) than it is for the New South Wales (Lat. 30°–32°S) examples from the same forest types.

The position of the modal leaf size for both leaf length and area relative to the "tail" demonstrates an increasing skew to the normal distribution for the cooler forest types (SNVF and MMF; Figs.16,17). Overall, however, it is clear that there is a direct reduction in overall leaf size from the warmest forest type (and site, Oliver Ck CMVF) to the coolest forest type (Barrington Tops MMF). This is graphically illustrated by comparing the site means of leaf size (Table XVII) against the estimated Mean Annual Temperature (MAT) of each site (Table II); Figs.18,19). There is clear relationship between the mean leaf size (mean specimen length and area) and MAT. There is also a clear relationship between the Leaf Size Index (LSI) and MAT (Fig.20) for the litter sites, with a spread around the regression line of about 3°C MAT ($r^2 = 0.938$).

Webb (1968) suggested that edaphic compensation may allow particular physiognomic forest
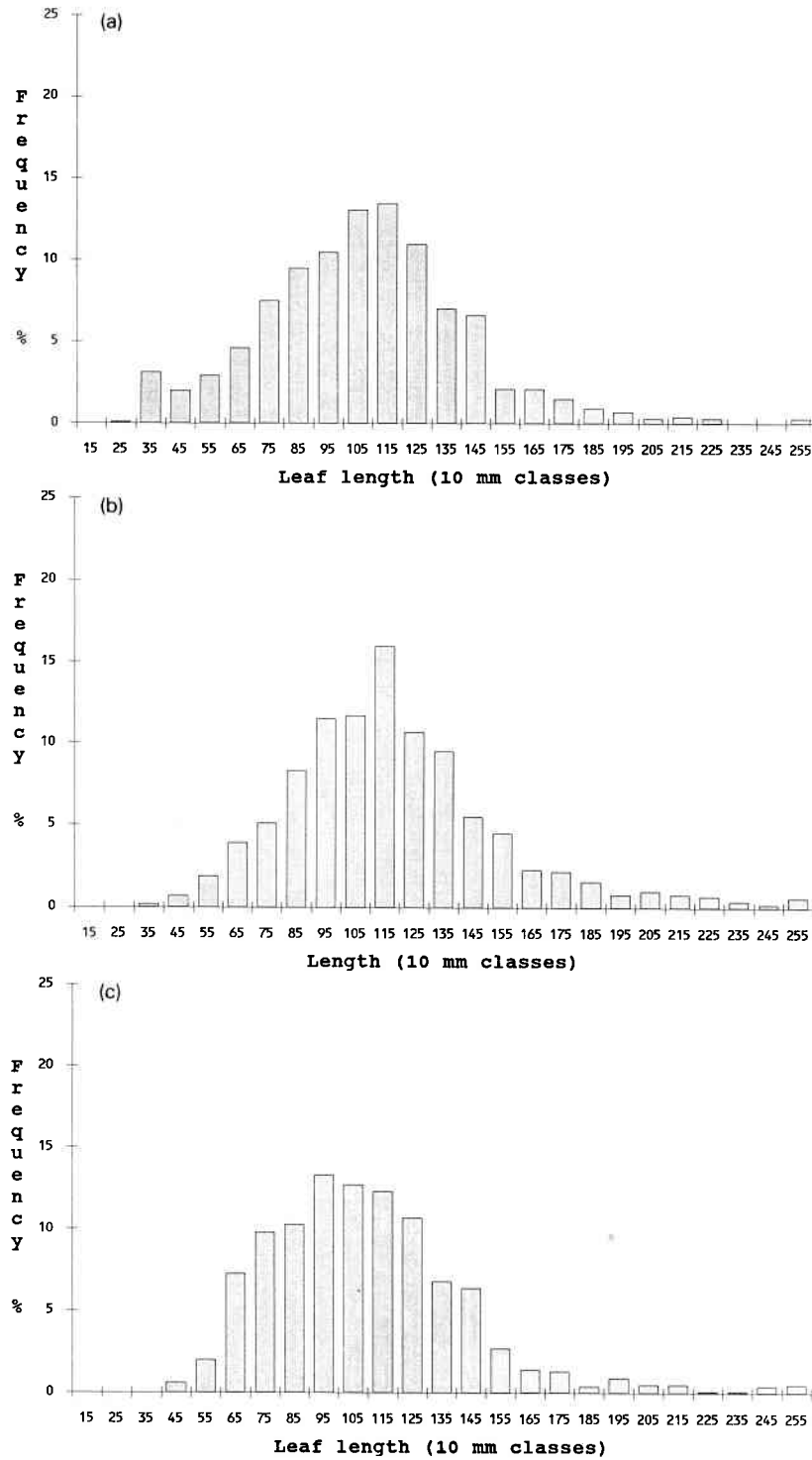
Fig.14. Histograms showing the leaf length frequency distributions (10 mm classes) of forest-floor leaf-litter for each site from Complex Mesophyll Vine Forest. Each plot represents the mean values from 4 samples of 224 leaves.
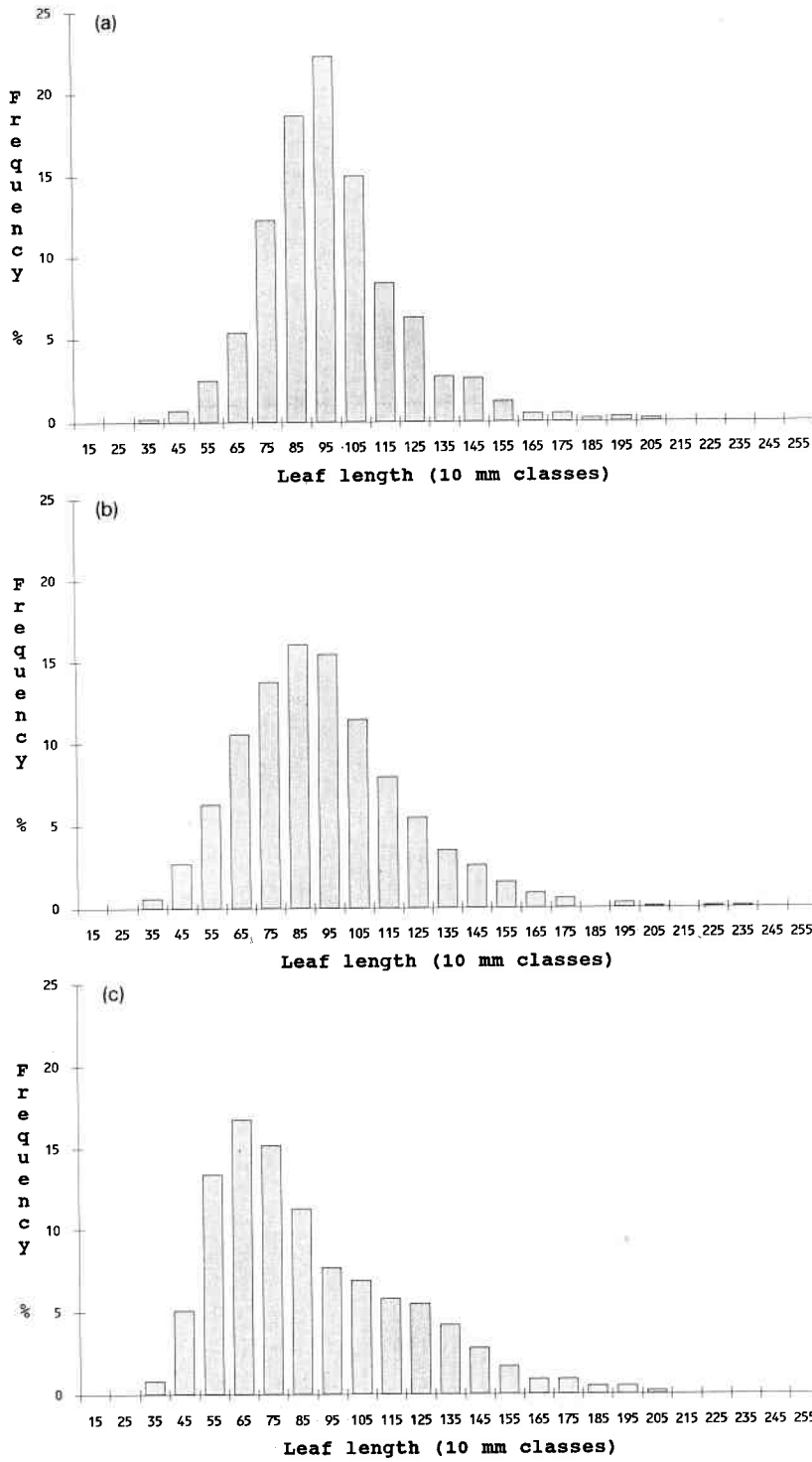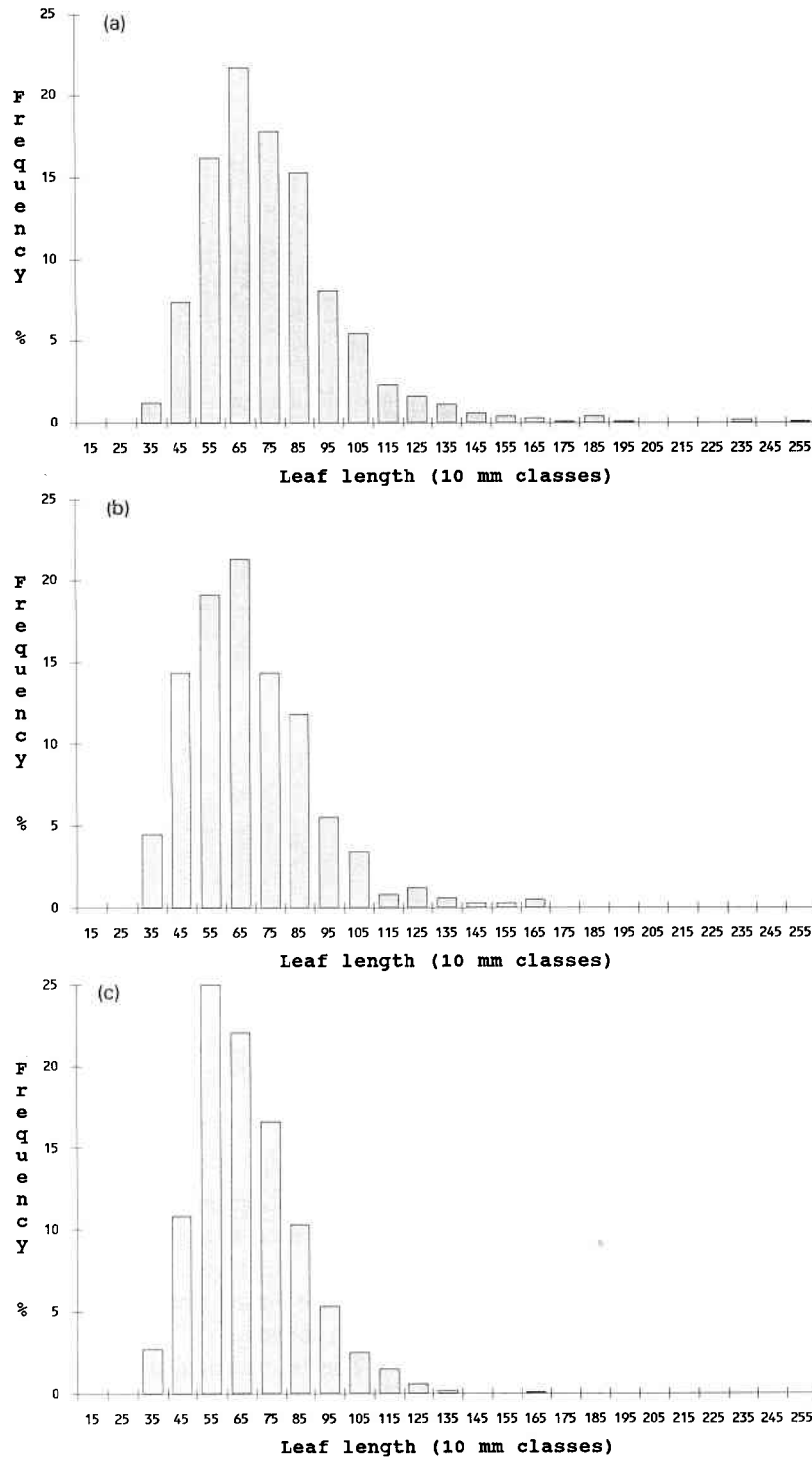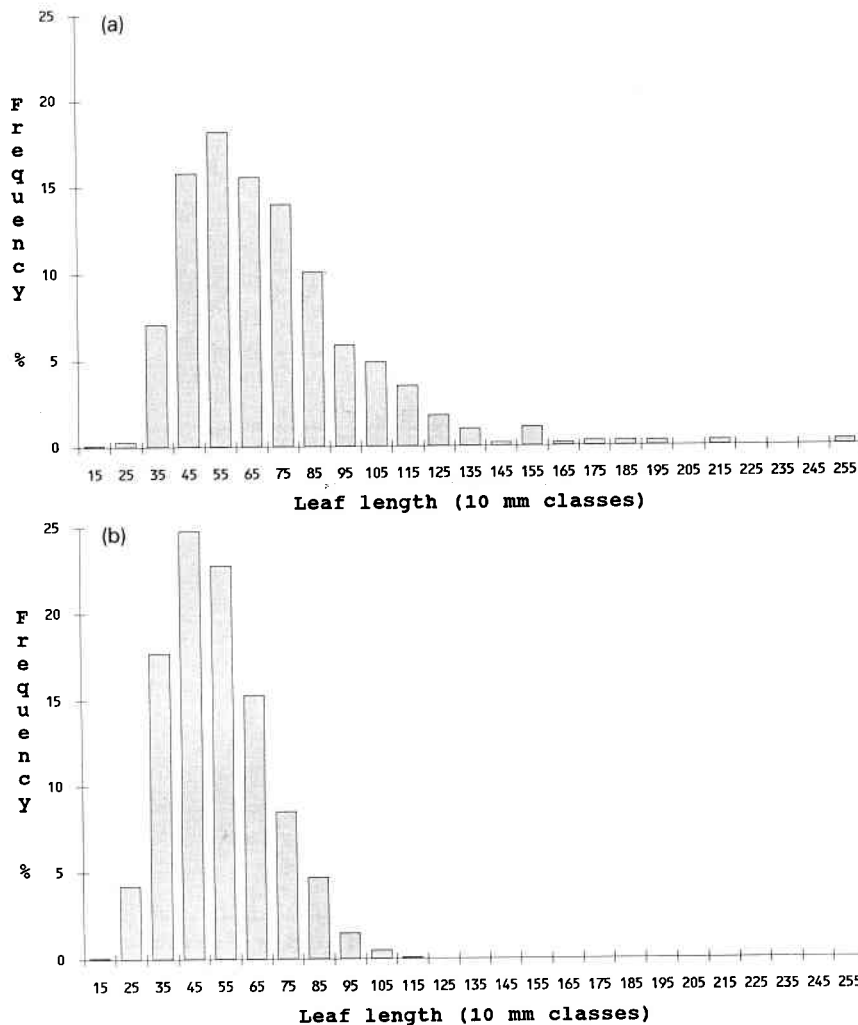
Fig.15. Histograms showing the leaf length frequency distributions (10 mm classes) of forest-floor leaf-litter for each site from Complex Notophyll Vine Forest. Each plot represents the mean values from 4 samples of 224 leaves.

Fig.16. Histograms showing the leaf length frequency distributions (10 mm classes) of forest-floor leaf-litter for each site from Simple Notophyll Vine Forest. Each plot represents the mean values from 4 samples of 224 leaves.

Fig.17. Histograms showing the leaf length frequency distributions (10 mm classes) of forest-floor leaf-litter for each site from (a) Microphyll Vine Fern Forest and (b) Microphyll Fern Forest. Each plot represents the mean values from 4 samples of 224 leaves.

types to occur outside of their normal climatic limits. Dilcher (1973) also stressed the influence of moisture regimes on leaf size in foliar physiognomic studies. Greenwood and Christophel (in prep.; Greenwood, 1987a) similarly demonstrated that Complex Notophyll Vine Forest substantially overlaps the range of temperatures (MAT and MART) of both Complex Mesophyll and Simple Notophyll Vine Forest in northeastern Queensland. All of the samples used in this analysis occurred outside of this temperature range and were mostly from within areas of high rainfall lacking seasonal drought (Greenwood, 1987a; N.B.

Curtain Fig is mildly seasonally dry). The leaf length histograms reproduced here should therefore be used as a guide for assessing the classification of the forest type for a leaf assemblage as they are biased towards mesic, non-seasonal evergreen forests.

The forest correlation between leaf length and MAT (Fig.18), however, demonstrates that the highest probability thermal match will be a forest type sample with the same size leaves or smaller, and correspondingly, with the same MAT or less. Upper and lower limits to the predicted MAT of a fossil leaf assemblage's source forest can thus be

TABLE XVI

Number of leaves of all Taxa present in Stream-bed Litter Collections from CNVF-SNVF (Mt. Windsor, NE Qld)

Taxon	Margin	Leaf size			Upper (1)		Lower (2)	
		m-	n-	me-	no.	%	no.	%
Sloanea woolsii	non-	—	1	—	2	0.5	20	8.0
Caldcluvia paniculosa	non-	—	1	—	22	5.1	33	13.3
Geissois biagiana	non-	—	—	1	5	1.2	—	—
Neorites kevesdiana	non-	—	—	1	42	9.8	—	—
Doryphora aromatica	non-	2	1*	—	1	0.2	9	3.6
Ficus sp.	entire	—	1	—	—	—	6	2.4
Myristica sp.	non-	1	—	—	8	1.9	4	1.6
Syzygium sp.	entire	1	—	—	7	1.6	1	0.4
Ceratopetalum sp. 1	non-	1	—	—	2	0.5	4	1.6
Rhodamnia sp. 1	entire	1	—	—	—	—	1	0.4
Melastoma sp. 1	entire	1	—	—	—	—	1	0.4
Lauraceae sp. 1	entire	—	2	1	36	8.4	3	1.2
Lauraceae sp. 2	entire	2	1	—	61	14.3	11	4.4
Lauraceae sp. 3	entire	1	2	—	1	0.2	48	19.3
Lauraceae sp. 4	entire	1	—	—	—	—	6	2.4
Lauraceae sp. 5	entire	—	2	1	1	0.2	5	2.0
?*Loranthaceae* 1	entire	1	—	—	—	—	1	0.2
unk. 1	entire	—	1	—	6	1.4	1	0.4
unk. 2	entire	—	1	—	—	—	16	6.4
unk. 3	entire	—	1	—	—	—	1	0.4
unk. 12	non-	1	—	—	—	—	5	2.0
unk. 15	non-	—	1	—	14	3.3	8	3.2
unk. 16	entire	—	1	—	—	—	2	0.8
unk. 18	entire	—	1	—	—	—	2	0.8
unk. 19	non-	—	1	—	—	—	4	1.6
unk. 20	entire	—	1	—	4	0.9	1	0.2
unk. 22	non-	1	—	—	—	—	3	1.2
unk. 25	non-	2	1	—	26	6.1	2	0.8
unk. 27	entire	—	1	—	—	—	6	2.4
unk. 29	entire	1	—	—	—	—	2	0.8
unk. 30	entire	2	1	—	22	5.1	6	2.4
unk. 31	non-	—	1	—	—	—	1	0.2
unk. 32	entire	1	—	—	4	0.9	5	2.0
unk. 33	entire	1	—	—	—	—	3	1.2
unk. 36	entire	—	1	—	60	14.0	4	1.6
unk. 37	non-	2	1	—	6	1.4	3	1.2
unk. 38	non-	1	—	—	—	—	4	1.6
unk. 40	entire	—	1	—	17	4.0	12	4.8
unk. 43	entire	1	—	—	1	0.2	—	—
unk. 44	entire	—	1	—	32	7.5	—	—
unk. 45	entire	1	—	—	8	1.9	—	—
unk. 46	non-	—	1	—	54	12.6	—	—
unk. 47	entire	—	—	1	25	5.8	—	—

% entire (upper) 57.7   total no. of species 26 (7) 37 (18)
      (lower) 63.9   leaves 428 249   [LSI: 46.1]   [25.0]

*size in each pool was different

TABLE XVII

Leaf shape of leaf populations from forest-floor litter from 4 forest types

Forest-type and Site	Mean length	RW_{max} (% of length)			PW_{max} (% of length)		
		max.	min.	mean	max.	min.	mean
CMVF Oliver Ck	103 mm			37.8	65.8	16.3	47.8
Mulgrave R	112	missing data		40.7	75.6	22.7	47.1
Mobo Ck	101			37.0	84.8	12.7	47.4
CNVF Curtain Fig	93	105.0	22.6	45.5	69.0	15.0	35.2
Crater NP	83	100.0	5.2	49.6	72.4	11.6	42.7
Dorrigo NP	88	96.7	18.5	32.5	71.0	23.9	50.0
SNVF Mt. Lewis EP18	72	78.8	11.2	44.1	74.6	18.1	45.8
Mt. Lewis Rd	64	87.8	16.3	40.0	77.8	23.1	46.3
Washpool	63	77.8	18.0	38.8	75.0	15.6	47.5
SNVF MMF Mt. Haig	67	55.2	17.6	32.1	70.4	31.0	46.6
MMF Barrington	49	93.3	25.0	48.7	60.0	21.7	37.6

elliptic — RW_{max} 30–50% and PW_{max} — 34–65%
stenophyllous — $RW_{max} < 30\%$ ovate — $PW_{max} < 34\%$
other — $RW_{max} > 50\%$ obovate — $PW_{max} > 65\%$
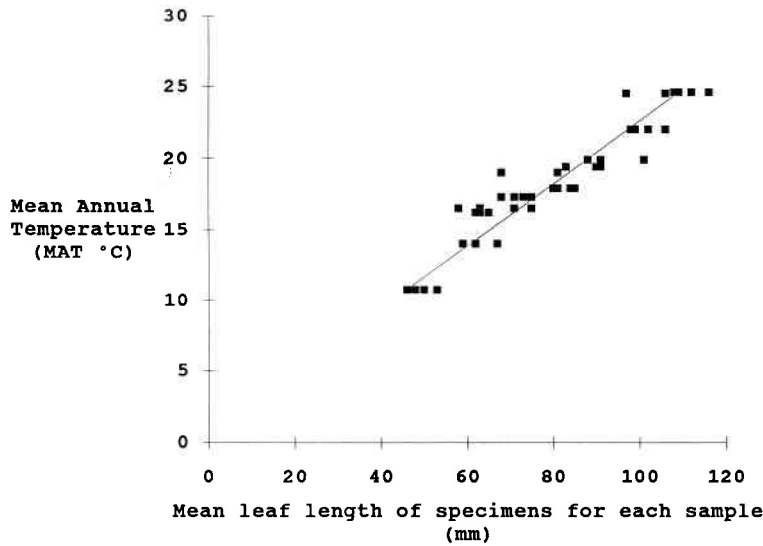
Fig.18. Plot of the mean leaf length of all specimens encountered at each forest-litter site versus the MAT of the site.

set by assessing the potential shift from the original depositional foliar physiognomic signature (in particular the leaf size bias) to that observed in the collected assemblage. This methodology potentially offers an accurate means of assessing MAT, taking into account taphonomic influences on the leaf assemblage (including collection effects). However, depositional sorting in sedimentary environments (e.g. lake or stream) may increase the size bias (Roth and Dilcher, 1978; Spicer, 1981), further affecting MAT assessments based on leaf size.

Leaf shape; relative width and the position of greatest width

Most palaeobotanists concerned with foliar physiognomic indices of palaeoclimate have paid little attention to leaf dimensional characters other than size. Dolph (1976) found that most dimen-
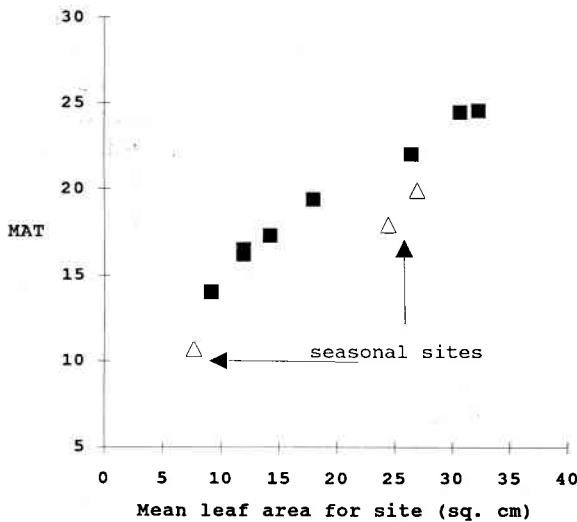
Fig.19. Plot of the mean leaf area of all specimens encountered at each forest-litter site versus the MAT of the site.

sional characters of leaf shape were too closely correlated to be of any use as separate data. Leaf shape, however, in some cases is strongly under the control of the local environment (Taylor, 1975; Givnish, 1978, 1984; Rood et al., 1986; Sokal et al., 1986). Streamside trees, for example, are often stenopyllous (Richards, 1952; van Steensis, 1981; Whitmore, 1984), that is, much narrower than long, and modern "tropical rainforests" are often characterised by woody plants with elliptic leaves

with an extended acumen or "drip-tip" (Richards, 1952; Webb, 1968; Givnish, 1984). Similarly, rainforest lianas are characterised by leaves with hastate or peltate bases, and heart-shaped lamina. Leaf width is also sensitive to annual rainfall, with trees in tropical forests producing leaves with decreasing relative width along decreasing rainfall gradients (Webb, 1968; Givnish, 1984). Leaf shape therefore reflects aspects of climate and significant biases in leaf shape (and size) may be present in megafloras dominated by riparian vegetation (MacGinitie, 1974; Roth and Dilcher, 1978).

The majority of leaves from the litter sites were elliptic (Table XVII). Leaf width decreases proportionally from the warmest sites (CMVF) to the coolest site (MMF). If leaf width (W_{max}) is plotted against the estimated mean annual temperature (MAT) of each site (linear regression/least squares: Fig.21), the relationship is seen to be less significant than for leaf length or area (Figs.18,19). Two of the CNVF sites (Curtain Fig and The Crater) and the MMF site (Barrington Tops, NSW) are more climatically seasonal (rainfall and/or the mean annual range of temperature) than the other sites. The correlation between MAT and leaf width is higher ($r = 0.9521$) if these sites are omitted from the linear regression.

Relative leaf width (RW_{max}) and the position of maximum width (PW_{max}) measure aspects of leaf
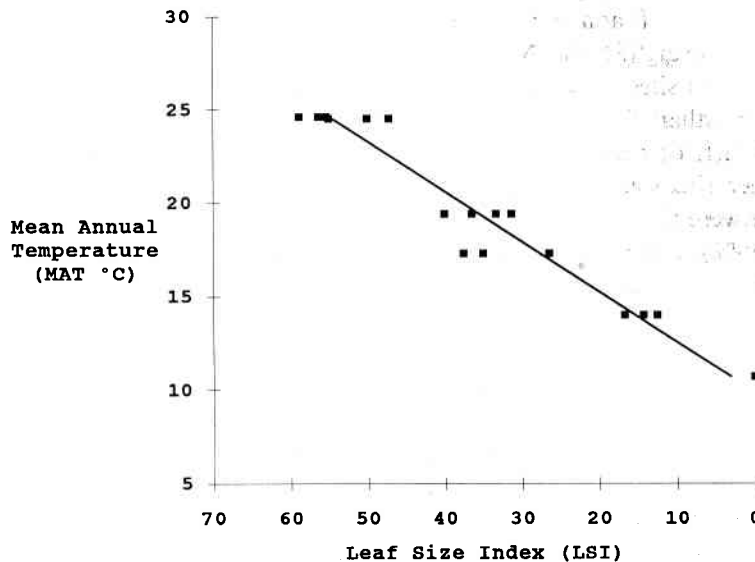
Fig.20. Plot of Leaf Size Index (LSI) of each sample versus the MAT of each forest-litter site.
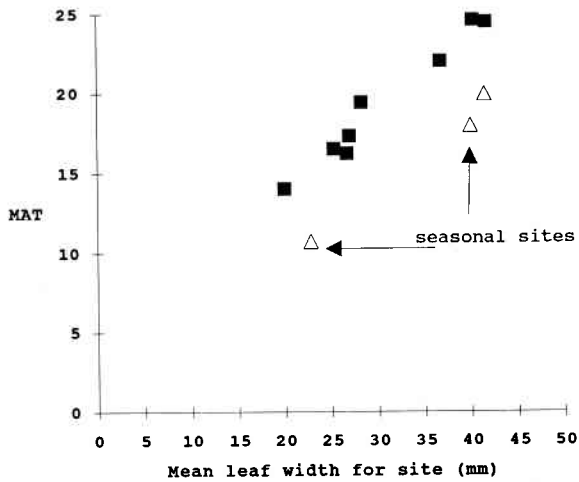
Fig.21. Plot of the mean leaf width (W_{max}) of all specimens encountered at each forest-litter site versus the site MAT.

shape (Table XVII). Leaf populations which deviate from an elliptical leaf (i.e. stenophylls, obovate and ovate leaves) can be identified by these measures. The leaf-litter in most cases were dominated by elliptical leaves (CMVF, CNVF in part, SNVF in part; Table XVII). The leaf litter from some sites were noticeably more ovate (CNVF Curtain Fig, MMF). In both cases where non-elliptic leaves are dominant (or significant) a small number of species were responsible, with for example leaves of *Nothofagus moorei* in MMF litter and vine leaves (Vitacaeae) in Curtain Fig CNVF litter, contributing the majority of non-elliptic leaves. The litter from the Mt. Haig (SNVF–MMF) and Dorrigo (CNVF N.S.W.) sites were composed of leaves much narrower than for most other leaf litter (RW_{max} 32.5, 32.1, compared to 40.0–48.7; Table XVII). Neither site was close to a water course, yet the leaves were close to being stenophyllous (i.e. $RW_{max} < 30\%$), a leaf shape commonly associated with riparian vegetation (Whitmore, 1984).

The effect of stream deposition on foliar physiognomic signatures

A stream on the Mt. Windsor Tableland in northeastern Queensland (Fig.1) was used to test the hypothesis that leaves transported by a stream would demonstrate a proportionate decrease in the average leaf size from that observed for the leaf size frequency in leaf litter of the forest floor. The Mt. Windsor Tableland experiment has been reported by Christophel and Greenwood (1988, 1989), however, additional data is presented here. The Mt. Windsor study demonstrated that the transported (allochthonous) leaf assemblage in the lower pool contained leaves that were on average smaller (mean leaf length, all specimens, 65.7 mm) than the leaves in the non-transported (autochthonous) upstream pools (mean leaf length 80.9 mm) (Christophel and Greenwood, 1989). These values range between the middle range of SNVF litter and just less than the lowest value recorded for CNVF litter (Table XVII).

The relative proportion of each leaf size class varied significantly between the Mt. Windsor stream-collected litter samples (Table XI). This can be illustrated by the LSI values; 46.1 (upper pools) and 25.0 (lower pool) respectively. The upper pools value exceeds the range expected from CNVF litter (31.3–40.0), however the LSI value for the lower pool is almost within the range seen in the SNVF litter (Table XI: 26.4–37.5). The upper pools value is within the range expected from a predominantly notophyllous canopy. This result may indicate that the streamside vegetation is introducing a proportionately greater number of mesophyllous leaves than was detected in forest-floor litter from comparable forest. The much lower value for the lower pool suggests that transported leaf assemblages are selectively losing the larger leaf class within each taxon.

The Mt. Windsor samples were from forest transitional between CNVF and SNVF (given as SNVF by Christophel and Greenwood, 1988, 1989). The proportion of species with entire leaf margins (57.7 and 63.9%) for the two samples are within the range of canopy values (taxon-based) for Queensland SNVF, but outside the range for CNVF. The Mt. Windsor stream values are within the range expected for litter from CNVF. This suggests that the stream samples at Mt. Windsor may be enriched with leaves from the canopy compared to equivalent forest-floor litter samples or perhaps that at this site the stream-edge forest had a high proportion of species with non-entire leaf margins. There would appear to be no effect on the proportion of species with non-entire mar-

gins due to stream transport (cf. leaf size using taxa, above and leaf size by specimens; Christophel and Greenwood, 1988, 1989) as the values for the upper (autochthonous) sample and the lower (allochthonous) sample are not significantly different. However, as the discussion below will show, the taxonomic character of the upper and lower pool leaf samples was different.

The upper pool sample was much larger with 428 leaves, compared to 249 leaves in the lower pool sample. A total of 44 leaf taxa were identified from the two samples (Table XVII) of which 7 leaf taxa were found only in the upper pool sample and 18 in the lower pool sample. About half of the leaf taxa found in the upper pool sample (19 of 26) were also found in the lower pool sample (with 37 taxa). The upper pool sample has 6 leaf taxa with greater than 7% of the specimens each, whereas the lower pool sample has only 3 leaf taxa with greater than 7% of the specimens each. The most abundant leaf taxa in each sample are quite different (Table XVI).

A few very large trees of *Geissois biagiana* and *Neorites kevesdiana* occurred near the upper pools, but were not seen further downstream. The leaves of these species are generally notophylls to mesophylls and coriaceous. Leaves of *Caldcluvia paniculosa* were twice as common in the lower pool than in the upper pool sample (13.3 and 5.1% respectively). No leaves of *Geissois biagiana* and *Neorites kevesdiana* were found in the lower pool sample implying that the large leaves of these species were not transported downstream in this instance. The leaves of a large strangler fig (*Ficus destruens*) present in the stream-bank canopy surrounding the lower pool accounted for only 2.4% of the leaves in the lower pool sample. Other canopy trees common in the forest adjacent to the lower pool were well represented but did not dominate the lower pool sample (*Sloanea woolsii*, Lauraceae sp. 3 and taxon 40). The steam-bank vegetation was dominated by *Melastoma* and numerous ferns (primarily *Sticherus flabellatus*). However only 1 *Melastoma* leaf (0.4% of specimens) was found in the lower pool sample. Fern leaves were encountered in the lower pool sample but not included in the tally. No vine leaves were found in either sample, although a single leaf from a stem (canopy)

parasite (Loranthaceae) was found in the lower pool sample.

The differences in leaf taxon abundance observed between the upper pool sample and the lower pool sample (Table XVI) are equivalent to those observed between samples from forest-floor leaf litter samples from a single site (e.g. Table VI), although the difference in overall species number is significant (discussion above). The particular species present or absent in each stream sample suggest that while a significant input from the local canopy was present in the lower (?allochthonous) pool sample, an equally significant proportion of leaves were likely to have been transported from upstream. In both instances the leaves of canopy and subcanopy trees were dominant. In some instances where leaves of a species were present in both samples (Table XVI), the leaves in the lower pool were smaller than the leaves of the same species in the upper pool sample.

A physiognomically distinct Streamside flora

Fluvially deposited leaf assemblages are common in the Tertiary fossil record (Greenwood, 1991). Commonly a riparian vegetation may have different foliar physiognomic characteristics to the interfluvial forest (Richards, 1952; MacGinitie, 1974; Whitmore, 1984). A second series of collections from a stream at the Washpool forest-floor litter site in New South Wales (Coombadjha Creek; Fig.2) tested the hypotheses that stream-bed leaf assemblages would (a) have a high proportion of leaves from stream-side plants (±stenophylls; Wolfe, 1978; Wolfe and Upchurch, 1987) and (b) that the leaves of the canopy trees would dominate. The samples of forest-floor litter collected at Washpool SNVF site for the primary analysis of rainforest litter foliar physiognomy were used as a baseline for comparison with leaf mats collected from the bed of Coombadjha Creek. Stream-bed leaf mats were collected from Coombadjha Creek at the same time as the forest-floor samples, about 100 m from the forest floor collection point, in a large pool in a slow moving part of the creek.

There is no significant difference between forest-floor and stream-litter for either leaf length or width (Fig.22). This suggests that leaves of significantly similar size (length, area and width) were
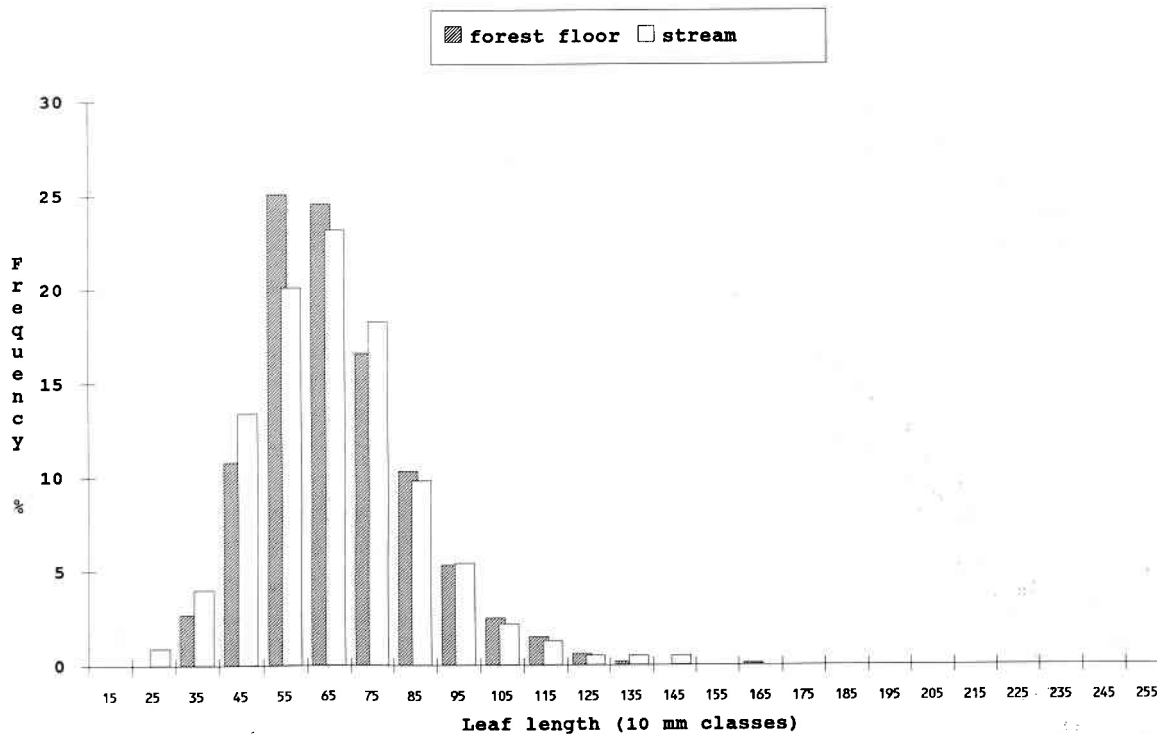
Fig.22. Histograms showing the leaf length distributions (10 mm classes) of forest-floor leaf-litter for the Washpool and Coombadjha Ck SNVF leaf populations.

contributing to the forest-floor and stream-bed litter. This result is in marked contrast to the significantly smaller leaves found in lake sediments by Roth and Dilcher (1978). The broad correspondence between samples in the Mt. Windsor samples demonstrates also that the leaves entering the stream were not significantly stenophyllous, as no markedly narrow leaves were detected.

The Coombadjha Creek SNVF stream litter and forest floor litter collections had similar proportions of leaf taxa with entire margins (Table V). The Coombadjha Creek samples are outside the range for the canopy (New South Wales SNVF; Table XIV), however total species number is low at this site.

The canopy dominants in the SNVF at Coombadjha Creek are *Ceratopetalum apetalum* and *Doryphora sassafras*, both of which have serrate leaf margins. These two taxa were the most common leaves in the forest-floor litter samples (Table V; Fig.23). Leaves of *C. apetalum* dominated the stream sample, but leaves of *D. sassafras* were

"scarce", with between only 1.5 and 2.7% of leaves representing this species, compared to 8.0, 22.3, 44.2 and 56.3 (mean 32.7%) in the forest-floor samples (Fig.23). Highly fragmented leaves of *D. sassafras* were common in the stream sample (only whole leaves were counted). Leaves of the streamside plants, *Banksia integrifolia*, *Callicoma serratifolia*, *Quintinia sieberi* and *Polyscias araliafolia* were present, but not strongly represented (<8.1% in all samples).

Multivariate analysis of foliar physiognomic signatures

Dilcher (1973, figs.5,6) demonstrated a sequential decrease in mean leaf length for major world vegetation types along broad thermal and moisture gradients. Similarly the histograms from the Australian rainforest litter of the frequency of leaf length (Figs.14–17) demonstrate a stepwise decrease in leaf size with a decrease in MAT (e.g. Figs.19,20). Christophel and Greenwood used these histograms (including the cumulative fre-
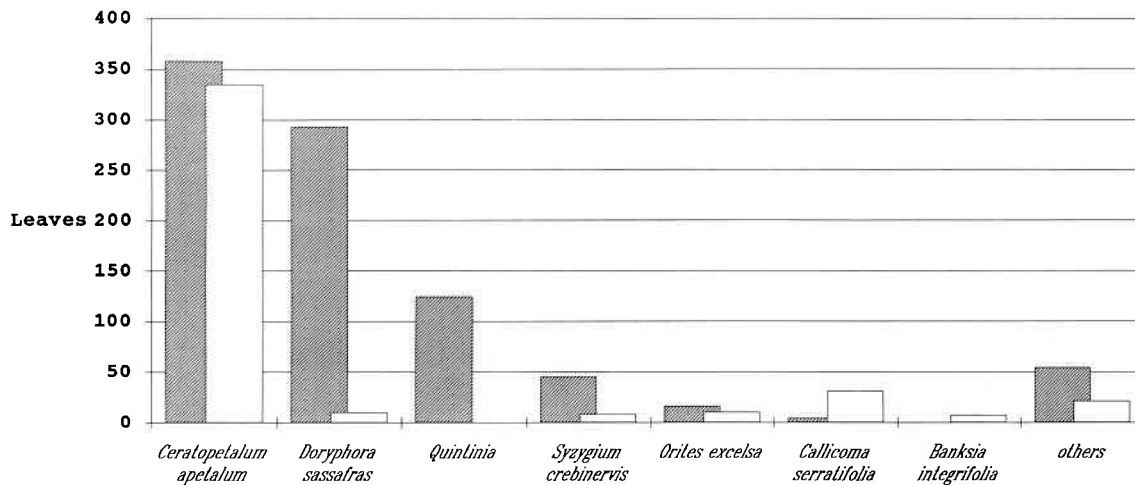
Fig.23. Histograms demonstrating the taxonomic composition and abundance of leaf-taxa of 4 samples of forest-floor leaf-litter from SNVF at Washpool and 2 samples from a stream-bed in nearby Coombadjha Ck.

quency Ogives) to define a series of "physiognomic signatures" (Christophel and Greenwood, 1987, 1988) or "foliar physiognomic signatures" (1989) that identify leaf assemblages derived from one of the rainforest types examined. In the broader sense used here, the *Foliar Physiognomic Signatures* are defined as being composed of a number of separate elements, represented by these histograms, but also including the data from the non-metric physiognomic characters. These data are combined for the multivariate analysis discussed below.

Each sample was characterised by population statistics of the foliar physiognomic characters. The "Discriminant" program on the SPSSx statistical package (Statistics Package for the Social Sciences, SPSSx Inc., 1985) was used. The variables with the greatest discriminating power were selected and the variables which did not contribute to the analysis (low variance) were removed stepwise in successive analyses. Most of the variance of these population descriptors was contained in the mean, median, 10th, 20th, 80th, 90th and the difference between the 80th and the 20th percentiles. The length values have a greater variance than the width or position of width. This altered set of population descriptors correctly classified 100% of all the samples (Fig.24; Table XVIII) where they had been previously designated to their forest type. This result strongly demonstrates a unique "foliar physiognomic signature" which

discriminates between leaf-litter from each forest type.

The basal axis (discriminant Function 1) of the scatterplot of the discriminant analysis (Fig.24) represents primarily leaf length. The vertical axis (discriminant Function 2) represents the leaf shape characters (position of greatest width PW_{max} and relative width RW_{max}). The four forest types are closely clustered and arrayed horizontally from coolest to warmest site, reflecting the very strong correlation between leaf length and MAT (Fig.18). The slight horizontal separation of the MMF and CNVF litter samples from the other samples (CMVF and SNVF) reflects the greater proportion of non-elliptic leaves in the litter from the more seasonal sites. This variation hides the fact that the forest types do not so much represent discrete entities (using leaf length), but rather a continuum.

To assess the influence of post depositional taphonomic biases, the stream-bed collected litter samples (Mt. Windsor and Coombadjha Creek) were included in the discriminant analysis. The sample from the stream-bed in Simple Notophyll Vine Forest at Coombadjha Creek was clearly classified with the SNVF samples (Fig.24). The two samples from SNVF–CNVF at Mt. Windsor gave mixed outcomes. The autochthonous sample (non-transported) was placed closer to the CNVF samples than SNVF in the discriminant plot and was correctly classified as CNVF (Table XVIII).
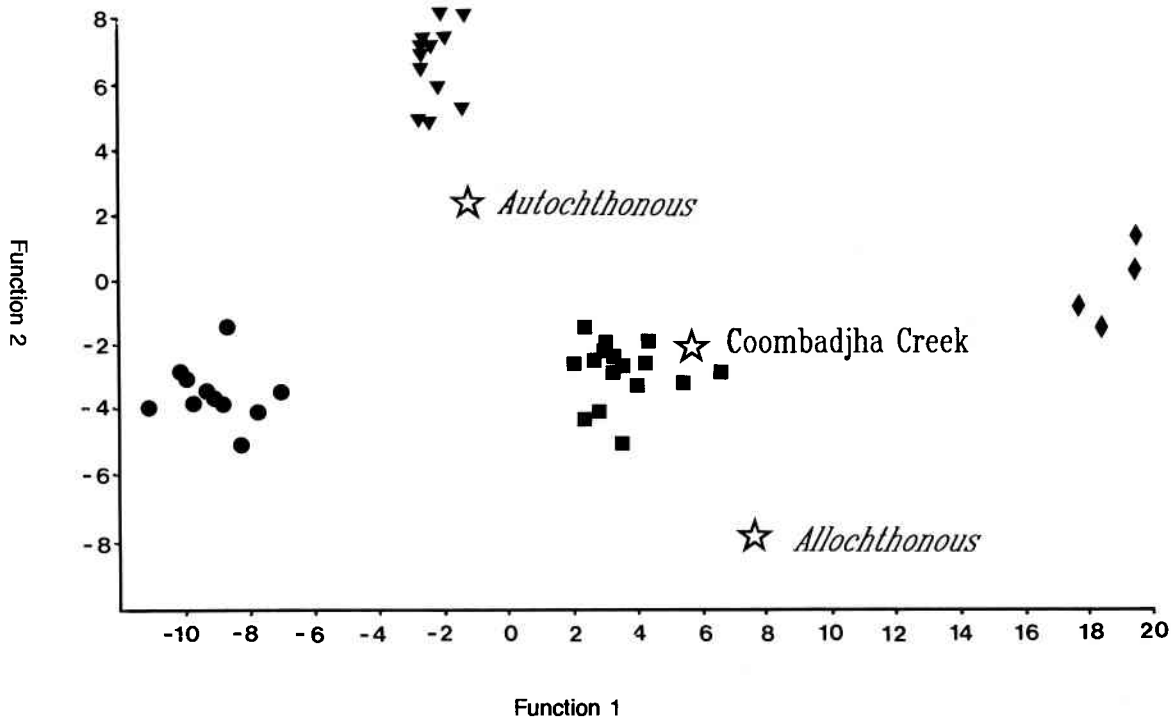
Fig.24. Scatter plot from the Discriminant Analysis of the forest-floor leaf-litter populations using foliar physiognomic population descriptors. Stream-bed leaf populations are indicated by ☆; allochthonous and autochthonous from Mt. Windsor.

TABLE XVIII

Classification table from Discriminant Analysis (SPSSx Inc., 1985) of forest-floor litter using foliar physiognomic population descriptors. See text

Forest-type	No. of Cases	Predicted Group Membership			
		MMF	SNVF	CNVF	CMVF
Microphyll Mossy Forest	4	4 100.0%	0 0.0%	0 0.0%	0 0.0%
Simple Notophyll Vine Forest	15	0 0.0%	15 100.0%	0 0.0%	0 0.0%
Complex Notophyll Vine Forest	12	0 0.0%	0 0.0%	12 100.0%	0 0.0%
Complex Mesophyll Vine Forest	11	0 0.0%	0 0.0%	0 0.0%	11 100.0%
Stream-bed litter (ungrouped)	3	0 0.0%	2 66.7%	1 33.3%	0 0.0%

100% of "grouped" cases correctly classified.

The allochthonous sample (transported) was classified with the SNVF samples, but was outside the group.

The results with the Mt. Windsor samples indicate that (as a consequence of the importance of leaf size) transport and (?)subsequent loss of larger leaves may bias a leaf assemblage to incorrect classification based on foliar physiognomic criteria.

The evidence from the taxon-based analysis (Table XVI) suggests that this occurs partly through the selective loss of large leaf-size classes from individual leaf taxa. The Coombadjha Creek sample, however, indicates that where transport is minimal, assemblages retain the same foliar physiognomic signature as forest-floor litter.

Discussion

Most foliar physiognomic studies of North American Late Cretaceous and Tertiary palaeoclimates (e.g. Wolfe, 1985; Wolfe and Upchurch, 1986, 1987; Parrish and Spicer, 1988; Wolfe and Schorn, 1989; Upchurch, 1989) are based primarily on Leaf Margin Analysis (Wolfe, 1971, 1979). Dolph (1984, 1990) has questioned the methodology and theoretical basis of Leaf Margin Analysis, primarily focussing on the regional character of Wolfe's (1971, 1979) data set and the applicability of East Asian mesic forests. Some other studies have made more general foliar physiognomic comparisons between modern forest canopies and megafloras (e.g. Dilcher, 1973; MacGinitie, 1974; Christophel, 1981; Zastawniak et al., 1985). Dolph and Dilcher (Dolph, 1978, 1984; Dolph and Dilcher, 1979, 1980) stressed that local relationships may override regional patterns. As most fossil leaf assemblages are likely to represent local vegetation (Spicer, 1981, 1989; Ferguson, 1985; Gastaldo et al., 1989; Greenwood, 1991), local and not regional relationships between climate and foliar physiognomy are likely to be detected in megafloras (Roth and Dilcher, 1978; Burnham, 1989). Wolfe (1990, 1991) has sought to counter some of these criticisms using a multivariate analysis of modern vegetation, however this new analysis and Wolfe's (1971, 1979) earlier analyses do not consider potential taphonomic biases a priori.

Burnham (1989) examined fluvial accumulations of leaf litter and found a good correspondence between the foliar physiognomy and the regional climate. In this study, leaf-litter from the forest-floor and from stream-beds were contrasted to the canopy to test the ad hoc assumption that canopy correlations between foliar physiognomy and climate are preserved with minimal taphonomic bias in leaf assemblages. However, forest-floor litter is not a fossil deposit and stream-bed litter collections only indicate one type of sedimentary facies and with the limited sampling used, only partly address the potential variation within this sedimentary environment. Nevertheless, a number of important observations can be made about the taphonomic biases inherent in foliar physiognomic analyses of palaeoclimate based on canopy observations.

Taxon- and specimen-based observations

The main purported strength of foliar physiognomic analysis over nearest living relative (floristic) analogies is its independence from accurate taxonomic sorting of the megafloras, thus avoiding misinterpretations stemming from erroneous identifications of plant megafossils (Wolfe, 1971, 1979, 1985, 1990; Christophel and Greenwood, 1988, 1989). Therein lies a contradiction. With taxon-based observations and indices (e.g. Leaf Margin Analysis and Leaf Size Index), accurate separation of the leaf specimens in a megaflora becomes critical for foliar physiognomic analysis, as does the number of taxa. A specimen-based approach avoids this potential problem (Christophel and Greenwood, 1988, 1989).

Australian rainforest litter reflects the taxonomic composition of the local forest canopy, with the same dominants in the canopy as the litter in most cases. However, individual samples often do not reflect the nearest trees, but the largest close sources of leaves. Of note was the clear numerical dominance of the litter by leaves of the canopy trees. This is due in part to overproduction and the greater biomass of the canopy trees, compared to the subcanopy and other forest synusiae (Stocker et al., in press; Thompson et al., in prep.), but also the non-dehiscent behaviour of the leaves of ground herbs and some epiphytes (Gastaldo, 1988; Greenwood, 1991). The greater durability of canopy leaves, versus non-canopy leaves, is also important.

Fluvially transported assemblages (e.g. Mt. Windsor) may also exhibit substantial mixing resulting in higher species number and a lack of dominants compared to comparable forest-floor litter. This result suggests that where fossil assemblages have clear dominants in successive samples

that either the canopy of the local vegetation is uniformly dominated by those species, or that the leaf assemblage has experienced minimal transport and consequent mixing.

The foliar physiognomy of canopy and litter

Litterfall is dominated by leaves from the canopy trees, however, the foliar physiognomic characteristics of the litter is quantifiably different from that expected for the canopy (Tables XII–XV). Using either specimens (mean length) or taxa (LSI), smaller leaves were recorded in litter than in the whole canopy. The degree of bias for LSI between the expected canopy values and those observed for litter was 3:2 (Fig.13), suggesting a correction factor for this leaf size index. Fluvial transport may strongly select against the large leaf size class within taxa, increasing this bias (see Table XVI).

The number of leaves with entire margins was highly variable between samples from the same site, particularly where overall diversity was low (Tables X,XI). The number of leaves with entire margins in litter was often outside of the range expected of individual trees with entire leaf margins in the same forest-type (Table XII). In some cases the proportion of leaf species with entire margins was highly variable between samples (Table XI), indicating the strong influence of the local species composition of the vegetation (Figs.11). Low species-number in some litter samples was found to strongly influence the correlation between species with entire margins and MAT (Fig.11). The litter and Australian canopy data (Webb, 1968; Greenwood and Christophel, 1990, in prep.) therefore suggest caution in the application of Leaf Margin Analysis.

Foliar physiognomy and climate: forest signatures

Despite the variation between the foliar physiognomic characteristics of forest-floor litter and the canopy of each forest-type, a clear foliar physiognomic signal can be recognised. Leaf-litter from each forest-type examined can be characterised by a combination of population descriptors and foliar physiognomic indices. Discriminant Analysis using specimen-based population descriptors sorts leaf populations into their most likely matching foliar physiognomic forest-type (Fig.24). Mean Leaf Length/Area and the Leaf Size Index, are strongly correlated with Mean Annual Temperature (Figs.18–20). However, there is an error of about 3°C MAT for the LSI/MAT correlation. Leaf margin type (% species entire) in leaf litter is less strongly correlated with MAT than demonstrated from canopy observations, although there is broad agreement with Wolfe's (1979, 1985, 1990; Wolfe and Upchurch, 1987) analysis of Southern Hemisphere mesic-humid forests.

Fluvial leaf assemblages may preserve the foliar physiognomic characteristics of the forest-floor litter unchanged (e.g. Coombadjha Creek; see also Burnham, 1989), or fluvial transport may cause further reduction in mean leaf size (Mt. Windsor). On this basis, MAT estimates based on leaf size, such as mean leaf length (Fig.18) or LSI (Fig.20), represent *minimum* MAT estimates, as significant bias towards smaller leaves in fluvial megafloras will bias MAT estimates to cooler values than actually prevailed (Wolfe, 1971, 1978). However, separate sedimentary facies (e.g. channel vs. lake) may require individual taphonomic correction factors (Roth and Dilcher, 1978; Greenwood, 1991).

The foliar physiognomic interpretation of megafloras

The following conclusions can be made from this study:

(1) Fossil leaf assemblages are likely to be dominated by the leaves of the dominant (most common) species of the local forest canopy. However, some locally common canopy tree species may be absent, or rare, as leaves in a fossil assemblage due to selective preservational bias.

(2) Taphonomic factors preferentially enrich litter with small leaves relative to the whole canopy, and local spatial heterogeneity will strongly control the contribution of entire margin leaves. In consequence of (1) and (2), canopy correlations between climate and foliar physiognomy (e.g. Leaf Margin Analysis) are not preserved unbiased in fossil leaf assemblages and local relationships are more important than regional relationships. Tapho-

nomic biases and local-scale floristics have a significant affect on the accuracy of MAT estimates using Leaf Margin Analysis.

(3) However, forest litter preserves a characteristic foliar physiognomic signature which includes a strong climatic signal, with for example leaf size (mean length and LSI) in litter from mesic evergreen forests strongly correlated with MAT. However, fluvial transport increases the bias between litter and canopy, influencing this correlation.

Modelling leaf megafloras with forest-floor leaf litter incorporates taphonomic biases a priori, in contrast to the ad hoc assumptions of canopy comparisons. Leaf assemblages retain a foliar physiognomic climatic signal (Burnham, 1989) or signature (Christophel and Greenwood, 1987, 1989). The foliar physiognomic characteristics of leaf assemblages can be used to predict both vegetation-type and particular aspects of the palaeoclimate (mainly MAT). Specimen- versus taxon-based approaches offer alternative methodologies, although it is unclear from this study whether one is superior to the other. Multivariate approaches to foliar physiognomic analyses of palaeoclimate (e.g. Wolfe, 1990; this study) offer a greater potential for reliable reconstructions, but must include corrections for taphonomically sensitive characters, such as leaf size, and must not rely on characters sensitive to local variation, such as leaf margin type.

This study was limited to more-or-less continually wet, high-rainfall forest-types — rainforest — and so the existing data set can only be applied to megafloras that are believed to have been formed within analogous vegetation. Within Australia, Early Tertiary megafloras often represent this type of vegetation (Christophel and Greenwood, 1989). Wolfe (1985, 1990) has argued that modern mesic Southern Hemisphere vegetation is the best analogue of North American Late Cretaceous vegetation. However, some Australian Early Tertiary megafloras represent non-rainforest vegetation, or combinations of several physiognomically distinct vegetation-types (e.g. Greenwood et al., 1990). Further work is under way by the author and co-workers to quantify the foliar physiognomic characteristics of leaf-beds formed from a greater variety of modern vegetation types and

sedimentary settings (Greenwood, unpubl.; Christophel and Johnson, 1990, unpubl.; Greenwood and Christophel, 1990, in prep.).

References

Anderson, J.M. and Swift, M.J., 1983. Decomposition in tropical forests. In: S.L. Sutton, T.C. Whitmore, and A.C. Chadwick (Editors), Tropical Rainforest: Ecology and Management. British Ecological Society Special Publication No. 2. Blackwell, Oxford, pp.287–309.

Anonymous, 1983. Climatic Averages. (Microfiche) Australian Bureau of Meteorology, Melbourne.

Bailey, I.W. and Sinnott, E.W., 1916. The Climatic Distribution of Certain Kinds of Angiosperm Leaves. Am. J. Bot., 3: 24–39.

Beard, J.S., 1944. Climax vegetation in tropical America. Ecology, 25: 127–158.

Brasell, H.M., Unwin, G.L. and Stocker, G.C., 1980. The quantity, temporal distribution and mineral-element content of litterfall in two forest types at two sites in tropical Australia. J. Ecol., 68: 123–139.

Burnham, R.J., 1989. Relationships between standing vegetation and leaf litter in a paratropical forest: implications for paleobotany. Rev. Palaeobot. Palynol., 58: 5–32.

Burnham, R.J., Wing, S.L. and Parker, G.G. (in press). The reflection of deciduous forest communities in leaf litter: implications for autochthonous litter assemblages from the fossil record. Paleobiology 18(1):

Cain, S.A., de Oliveira Castro, G.M., Murca Peres, J. and da Silva, N.T., 1956. Application of some phytosociological techniques to the Brazilian rain forest. Am. J. Bot., 43: 911–941.

Chaney, R.W., 1924. Quantitative studies of the Bridge Creek flora. Am. J. Sci., 8: 127–144.

Chaney, R.W. and Sanborn, E.I., 1933. The Goshen Flora of West-Central Oregon. Contr. Paleontol., Carnegie Inst. Publ. 439, 103 pp.

Christophel, D.C., 1981. Tertiary Megafossil Floras as Indicators of Floristic Associations and Palaeoclimate. In: A. Keast (Editor), Ecological Biogeography of Australia. Junk, The Hague, pp.379–390.

Christophel, D.C., 1989. Evolution of the Australian flora through the Tertiary. Plant Syst. Evol., 162: 63–78.

Christophel, D.C. and Blackburn, D.T., 1978. The Tertiary megafossil flora of Maslin Bay, South Australia: a preliminary report. Alcheringa, 2: 311–319.

Christophel, D.C. and Greenwood, D.R., 1987. A megafossil flora from the Eocene of Golden Grove, South Australia. Trans. R. Soc. South Aust., 111(3): 155–162.

Christophel, D.C. and Greenwood, D.R., 1988. A comparison of Australian tropical rainforest and Tertiary fossil leaf-beds. In: R. Kitching (Editor), The Ecology of Australia's Wet Tropics. Proceedings of the Ecological Society of Australia, 15. Surrey Beatty, Chipping Norton, NSW, pp.139–148.

Christophel, D.C. and Greenwood, D.R., 1989. Changes in climate and vegetation in Australia during the Tertiary. Rev. Palaeobot. Palynol., 58: 95–109.

Christophel, D.C. and Johnson, K.R., 1990. The effect of mosaic rainforest distribution and taphonomy on the physiognomy of modern leaf deposits: implications for Cretaceous and Paleogene paleoclimatic reconstructions. Abstracts with programs. Geol. Soc. Am., Ann. Meet., Dallas, 1990, p.A35.

Daley, B., 1972. Some problems concerning the Early Tertiary climate of southern Britain. Palaeogeogr., Palaeoclimatol., Palaeoecol., 11: 177–190.

Dilcher, D.L., 1973. A Paleoclimatic Interpretation of the Eocene Floras of Southeastern North America. In: A. Graham, (Editor) Vegetation and Vegetational History of Northern Latin America. Elsevier, Amsterdam, pp.39–59.

Dolph, G.E., 1976. Inter-relationships among the gross morphological features of Angiosperm leaves. Bull. Torrey Bot. Club, 103: 29–34.

Dolph, G.E., 1978. Variation in leaf size and margin type with respect to climate. Cour. Forschungs inst. Senckenberg, 30: 153–158.

Dolph, G.E., 1984. Leaf form of the woody plants of Indiana as related to environment. In: N.S. Margaris, M. Arianoustou-Farragitaki and W.C. Oechel (Editors), Being Alive on Land. Tasks for Vegetation Science 13. Junk, The Hague, pp.51–61.

Dolph, G.E., 1990. A critique of the theoretical basis of leaf margin analysis. Proc. Indiana Acad. Sci., 99(1): 1–10.

Dolph, G.E. and Dilcher, D.L., 1979. Foliar Physiognomic Analysis as in aid in determining paleoclimate. Palaeontographica Abt. B, 170: 151–172.

Dolph, G.E. and Dilcher, D.L., 1980. Variation in leaf size with respect to climate in the Tropics of the Western Hemisphere. Bull. Torrey Bot. Club, 107: 29–34.

Dudgeon, D., 1982. Spatial and seasonal variations in the standing crop of periphyton and allochthonous detritus in a forest stream in Hong Kong, with notes on the magnitude and fate of riparian leaf fall. Arch. Hydrobiol. Suppl., 64(2): 189–220.

Ferguson, D.K., 1971. The Miocene Flora of Kreuzau, Western Germany: 1. The leaf remains. North Holland, Amsterdam, 297 pp.

Ferguson, D.K., 1985. The origin of leaf-assemblages — new light on an old problem. Rev. Palaeobot. Palynol., 46: 117–188.

Floyd, A.G., 1989. Rainforest Trees of Mainland South-eastern Australia. Forestry Commission of New South Wales. Inkata, Melbourne, 420 pp.

Gastaldo, R.A., 1988. Conspectus of phytotaphonomy. In: W.A. DiMichelle and S.L. Wing (Editors), Methods and Applications of Plant Paleoecology. The Paleontological Society Special Publication No. 3. Univ. Tennessee, pp.14–28.

Gastaldo, R.A., Bearce, S.C., Degges, C.W., Hunt, R.J., Peebles, M.W. and Violette, D.L., 1989. Biostratinomy of a Holocene oxbow lake: a backswamp to mid-channel transect. Rev. Palaeobot. Palynol., 58: 47–59.

Givnish, T.J., 1978. Ecological aspects of plant morphology: Leaf form in relation to environment. In: R. Sattler (Editor), Theoretical Plant Morphology. Acta Biotheor., 27. Suppl.: Folia Biotheoretica, 7, pp.83–142.

Givnish, T.J., 1984. Leaf and Canopy Adaptations in Tropical Forests. In: E. Medina and C. Vazquez-Yanes (Editors), Physiological Ecology of Plants of the West Tropics. Tasks for Vegetation Science, 12. Junk, The Hague, Ch. 5, pp.5–84.

Greenwood, D.R., 1987a. The Foliar Physiognomic Analysis and Taphonomy of Leaf-beds derived from Modern Australian Rainforest. Thesis. Univ. Adelaide (unpubl.).

Greenwood, D.R., 1987b. Early Tertiary Podocarpaceae: Megafossils from the Eocene Anglesea locality, Victoria, Australia. Aust. J. Bot., 35(2): 111–133.

Greenwood, D.R., 1991. The taphonomy of plant macrofossils. In: S.K. Donovan (Editor), Fossilization: The Processes of Taphonomy. Belhaven Press, London, Ch. 7, pp.145–169.

Greenwood, D.R. and Christophel, D.C., 1990. Leaf Margin Analysis of Late Cretaceous and Tertiary climates. Modern Southern Hemisphere rainforests as analogues. Abstracts with programs. Geol. Soc. Am., Annu. Meet., Dallas, 1990, p.A306.

Greenwood, D.R., Callen, R.A. and Alley, N.F., 1990. Tertiary macrofloras and Tertiary stratigraphy of Poole Creek Palaeo-

channel, Lake Eyre Basin. (Abstracts) 10th Australian Geological Convention. Hobart, Tasmania, February 4–9, 1990.

Hill, R.S., 1987. Discovery of *Nothofagus* fruits corresponding to an important Tertiary pollen type. Nature, 327: 56–58.

Holdridge, L.R., 1967. Life Zone Ecology. Tropical Science Center, San Jose, Costa Rica, 206 pp.

Kodela, P.G., 1989. Modern pollen rain from forest communities on the Robertson Plateau, New South Wales. Aust. J. Bot., 38: 1–24.

Legendre, L. and Legendre, P., 1983. Numerical Ecology. Elsevier, Amsterdam, 419 pp.

MacGinitie, H.D., 1974. An Early Middle Eocene flora from the Yellowstone-Absaroka Volcanic Province, Northwestern Wind River Basin, Wyoming. University of California Publ. Geol. Sci., 108, 103 pp.

Parrish, J.T. and Spicer, R.A., 1988. Late Cretaceous terrestrial vegetation: a near-polar temperature curve. Geology, 16(1): 22–25.

Radford, A.E., Dickison, W.C., Massey, J.R. and Bell, C.R., 1974. Vascular Plant Systematics. Harper and Row, New York, 891 pp.

Raunkiaer, C., 1934. The Life Forms of Plants and Statistical Geography. Oxford University Press.

Richards, P.W., 1952. The Tropical Rainforest; An Ecological Study. Cambridge University Press, 450 pp.

Rood, S.B., Campbell, J.S. and Despins, T., 1986. Natural poplar hybrids from southern Alberta I. Continuous variation for foliar characters. Can. J. Bot., 64: 1382–1388.

Roth, J.L. and Dilcher, D.L., 1978. Some considerations in leaf size and margin analysis of fossil leaves. Cour. Forschungs inst. Senckenberg, 30: 165–171.

Sokal, R.R., Crovello, T.J. and Unnasch, R.S., 1986. Geographic variation of vegetative characters of *Populus deltoides*. Syst. Bot., 11: 419–432.

Spain, A.V., 1984. Litterfall and the standing crop of litter in three tropical Australian Rainforests. J. Ecol., 72: 947–961.

Spicer, R.A., 1980. The importance of depositional sorting to the biostratigraphy of plant megafossils. In: D.L. Dilcher and T.N. Taylor (Editors), Biostratigraphy of Fossil Plants. Successional and Paleoecological Analyses. Dowden, Hutchinson and Ross, Pennsylvania, pp.171–183.

Spicer, R.A., 1981. The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England. U.S. Geol. Surv. Prof. Paper, 1143, 77 pp.

Spicer, R.A., 1989. The formation and interpretation of plant fossil assemblages. Adv. Bot. Res., 16: 96–191.

Spicer, R.A., 1990. Fossils as environmental indicators: Climate from plants. In: D.E.G. Briggs and P.R. Crowther (Editors), Palaeobiology: A Synthesis. Blackwell, Oxford, pp.401–403.

Stocker, G.C. and Hyland, B.P.M., 1981. Rainforests of tropical northeastern Australia. In: N.C.W. Beadle (Editor), The Vegetation of Australia. Gustav Fischer, Stuttgart, pp.167–170.

Stocker, G.C., Thompson, W.A., Irvine, A.K., Fitzsimon, J.D. and Thomas, P.R., (in press). Rainforest litterfall in tropical Australia. 1. Annual and site patterns. J. Ecol.

Sugden, J.M. and Meadows, M.E., 1989. The use of Discriminant Analysis in reconstructing recent vegetation changes on the Nuweldberg, South Africa. Rev. Palaeobot. Palynol., 60: 131–147.

Taylor, S.E., 1975. Optimal leaf form. In: D.M. Gates and R.B. Scmerl (Editors), Perspectives in Biophysical Ecology. Ecol. Studies 12. Springer, Berlin, pp.73–86.

Thompson, W.A., Irvine, A.K., Stocker, G.C., Thomas, P.R. and Fitzsimon, J.D. (in prep.). Rainforest litterfall at a lowland and a tableland site in tropical Australia. 2. Species attributes.

Tracey, J.G., 1982. The Vegetation of the Humid Tropics of North Queensland. CSIRO, Melbourne, 124 pp.

Tracey, J.G. and Webb, L.J., 1975. Vegetation of the Humid Tropical Region of North Queensland. (15 maps at 1:100,000 scale + key.) Rainforest Ecology Unit, Div. Plant Industry, CSIRO Long Pocket Laboratories, Indooroopilly, Queensland.

Upchurch, G.R. Jr., 1989. Terrestrial environmental changes and extinction patterns at the Cretaceous-Tertiary boundary, North America. In: S.K. Donovan (Editor), Mass Extinctions: Process and Evidence. Belhaven Press, London, Ch. 10, pp.195–216.

Upchurch, G.R. Jr. and Wolfe, J.A., 1987. Mid-Cretaceous to early Tertiary vegetation and climate: evidence from fossil leaves and woods. In: E.M. Friis, W.G. Chaloner and P.R. Crane (Editors), The Origin of Angiosperms and their Biological Consequences. Cambridge University Press, Ch. 4.

Van Steensis, C.G.G.J., 1981. Rheophytes of the World. Sijthoff and Noordhoff, Alphen aan den Rijn, The Netherlands.

Webb, L.J., 1959. A physiognomic classification of Australian rainforests. J. Ecol., 47: 551–570.

Webb, L.J., 1968. Environmental determinants of the structural types of Australian Rain Forest Vegetation. Ecology, 49: 296–311.

Webb, L.J. and Tracey, J.G., 1982. Rainforests: data on floristics and site characteristics. Biogeographic Information System, Bureau of Flora and Fauna, Canberra.

Webb, L.J., Tracey, J.G., Williams, W.T. and Lance, G.N., 1969. The pattern of mineral return in leaf litter of three subtropical Australian forests. Aust. Forestry, 33(2): 99–110.

Whitmore, T.C., 1984. Tropical Rainforests of the Far East. (2nd ed.) Clarendon Press, Oxford.

Wolfe, J.A., 1971. Tertiary climatic fluctuations and methods of analysis of Tertiary floras. Palaeogeogr., Palaeoclimatol., Palaeoecol., 9: 27–57.

Wolfe, J.A., 1978. A paleobotanical interpretation of Tertiary climates in the Northern hemisphere. Am. Sci., 66: 694–703.

Wolfe, J.A., 1979. Temperature parameters of Humid to Mesic Forests of Eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. U.S. Geol. Surv. Prof. Pap., 1106: 1–37.

Wolfe, J.A., 1985. The distribution of major vegetational types during the Tertiary. In: E.T. Sundquist and W.S. Broecker (Editors), The Carbon Cycle and Atmospheric CO_2. Natural Variations Archean to Present. Am. Geophys. Union, Geophys. Monogr. 32, pp.357–375.

Wolfe, J.A., 1990. Palaeobotanical evidence for a marked temperature increase following the Cretaceous/Tertiary boundary. Nature, 343: 153–156.

Wolfe, J.A., 1991. CLAMP: A method of accurately estimating paleoclimatic parameters from leaf assemblages. Abstracts

with Programs, Vol. 23, No. 5, Geol. Soc. Am., Annu. Meet., p.A179.

Wolfe, J.A. and Schorn, H.E., 1989. Paleoecologic, paleoclimatic, and evolutionary significance of the Oligocene Creede flora, Colorado. Paleobiology, 15(2): 180–198.

Wolfe, J.A. and Upchurch, G.R. Jr., 1986. Vegetation, climatic and floral changes at the Cretaceous–Tertiary boundary. Nature, 324: 148–152.

Wolfe, J.A. and Upchurch, G.R. Jr., 1987. North American nonmarine climates and vegetation during the Late Cretaceous. Palaeogeogr., Palaeoclimatol., Palaeoecol., 61: 33–77.

Zastawniak, E., Wrona, R., Gozdzicki, A. and Birkenmajer, K., 1985. Plant remains from the top part of the Point Hennequin Group (Upper Oligocene), King George Island (South Shetland Islands), Antarctica. Stud. Geol. Pol., 81: 143–164.