CHAPTER 1

REVIEW OF SELECTED LITERATURE AND EPIPHYTE CLASSIFICATION

1.1 Review of Selected, Relevant Literature (p. 5)

Several important aspects of epiphyte biology and ecology that are not investigated as part of this work, are reviewed, particularly those published on more recently.

1.2 Epiphyte Classification and Terminology (p.11) is reviewed and the system used here is outlined and defined. A glossary of terms, as used here, is given.

1.1 Review of Selected, Relevant Literature

Since the main works of Schimper were published (1884, 1888, 1898), particularly *Die Epiphytische Vegetation Amerikas* (1888), many workers have written on many aspects of epiphyte biology and ecology. Most of these will not be reviewed here because they are not directly relevant to the present study or have been effectively reviewed by others. A few papers that are keys to the earlier literature will be mentioned but most of the review will deal with topics that have not been reviewed separately within the chapters of this project where relevant (i.e. epiphyte classification and terminology, aspects of epiphyte synecology and CAM in the epiphytes). Reviewed here are some special problems of epiphytes, particularly water and mineral availability, uptake and cycling, general nutritional strategies and matters related to these. Also, all Australian works of any substance on vascular epiphytes are briefly discussed.

Some key earlier papers include that of Pessin (1925), an autecology of an epiphytic fern, which investigated a number of factors specifically related to epiphytism; he also reviewed more than 20 papers written from the early 1880's onwards. Oliver (1930) published a thorough general study of the systematics and ecology of New Zealand vascular epiphytes. An important review of ecological life history studies of vascular epiphytes was compiled by Curtis (1952) which included more than 170 references from pre-Schimperian time onwards and covered numerous topics. Richards (1952) included a synopsis of vascular epiphyte biology in his standard textbook on the tropical rainforest. Walter (1971), and Dressler (1981) included similar epiphyte sections in their texts. A relatively brief, but to-the-point review of the ecology of tropical epiphytic orchids was presented by Holttum (1960). Two recent important papers that include large components of survey and review on general epiphyte ecology are those of Johansson (1974) and of Sanford (1974). The systematics and salient features of vascular epiphytes were discussed and reviewed by Madison (1977a).

The water relations of epiphytes is an important aspect of their biology vitally related to their ecology and evolution. Gessner (1956) investigated and reviewed water economy and related physiology and anatomy of epiphytes, particularly orchids and bromeliads. He reviewed more than 40 papers. He interpreted the role of the velamen of orchid roots as that of a sponge which absorbs water rapidly by capillary action, but entry into the cortex and stele was much slower, by osmotic processes; Walter (1951) calculated however, that internal uptake rate was still very rapid when compared with loss rates - the amount of water lost by a Vanda plant over a week could be absorbed into the stele within one hour. Such evidence supports the view that the physiological and anatomical devices most important in maintaining favourable water balance in epiphytic orchids are sited in the roots. Dycus & Knudson (1957) interpreted the velamen as an insulation against waterloss and mechanical damage and played down the role of uptake of water and minerals. Capesius & Barthlott (1975) presented evidence supporting Wallach's (1939) and Gessner's theory of the role of velamen in water (and mineral) uptake and Benzing & Ott (1981) agreed with this interpretation but rather boldly state that the passage cells of the root exodermis operate a 'one-way valve' effect (as do the foliar trichomes of the aerial bromeliads) which circumstantial evidence suggests may be the case. It has been clearly shown that this is true in the bromeliads, e.g. by Schimper (1888) and Mez (1904) but remains to be actually investigated in detail in the orchids - this is still an important need. Wallach (1939) and Dycus & Knudson presented evidence that the velamen was incapable of condensing water and gases from the atmosphere, as had been previously claimed.

Sanford & Adanlawo (1973) surveyed velamen and exodermis characters in West African orchids and found a positive correlation between thickness of velamen and aridity of environment. This perhaps supports the 'insulation against waterloss' theory but may also relate to temporary storage of water absorbed, e.g. from night mists; the reflective qualities of the velamen surface (Benzing & Ott, 1981) may then, help reduce evaporation by keeping tissue temperature lower.

Related to this is the controversy surrounding the evolution of shoot reduction in orchids and root reduction in bromeliads. Benzing & Ott (1981) argue, contrary to Rolfe (1914), that water stress is of secondary importance as a selection pressure producing aphylly in the monopodial orchids. However, they do not document the water saving potential of aphylly as has been done in relation to nutrient economy. They do not satisfactorily explain how the effect of the two different problems can be separated, especially since a) water and minerals are absorbed simultaneously, at least sometimes and b) both are limiting in epiphyte microhabitats, especially in the more exposed, outer ones. Also, the prevalence of leaf reduction among plant groups of arid terrestrial communities where nutrients are not limiting, cannot be ignored in this connection. They also argue that i. thick velamen inhibits root photosynthetic ability and, ii. this character correlates with aridity of microhabitat (Sanford & Adanlawo, 1974), and,

iii. aphyllous orchids have a thin velamen, thus, iv. aphylly is not an adaptation to water stress. However, these thickly velamen-clad orchids may simply be following a distinctly different adaptive line and thus not be comparable. An example of such a different line of adaptation to similar pressures is found in the genus *Bulbophyllum*. All species investigated by the present writer (unpublished observations), have thin roots with a *uniseriate velamen*, yet aphylly which has developed in two Australian species inhabiting outer, exposed microhabitats, i.e. *B. minutissimum* and *B. globuliforme*, has involved transfer of photosynthetic function to the pseudobulbs rather than to the roots.

Benzing's arguments favouring reduction in response to nutrient deficiency are convincing and supported by ample evidence, but the arguments against its cause by water stress are not so and the separation of the two influences remains a problem. Further evidence should be sought by researching e.g. rates of water loss and general water thrift of aphyllous orchids, the water status of their microhabitats, as well as their mineral relations. Benzing & Ott (1981) also give some useful suggestions on further research into the problem.

Another hypothesis on the origins and causes of vegetative reduction in epiphytes is put forward by Johansson (1977) supported by evidence from Ruinen (1953) on 'epiphytosis' and briefly, states that the epiphytes are partially dependent on their 'hosts' for water and nutrition and the leaves degenerated and finally became obsolete . This is not widely accepted and is certainly based on circumstantial evidence.

Related to this is the controversy surrounding the nature of the relationship between epiphytes, particularly the heliophilous, "extremely aerial", oligotrophic species, and the support tree, in regard to nutrient relations. The classical viewpoint is that typical epiphytes are quite autotrophic and have no deleterious effect on the phorophyte but the evidence of Ruinen (1953) strongly suggests that some, perhaps many epiphytes are epiparasites, using mycorrhizal connections between themselves and the cortex of the phorophyte ('epiphytosis'). Actual transfer of water and nutrients has not yet been demonstrated to confirm this and for this reason, many workers are sceptical of this theory. Radioactive tracers should be useful in clarifying this matter, though there may be such problems as leaching of salts from phorophyte foliage and their absorption by epiphytes.

Another line of (circumstantial) evidence used by Ruinen and later by Johansson (1977) is the decline of the host and frequent death of tree parts which support suspected epiparasitic species of epiphytes. Benzing (1979) offered an alternative explanation for such morbidity and mortality. He reasoned that epiphytes which colonise early in a tree's development will establish on branches and twigs that will later die as a result of the tree's growth and ontogenetic development while the epiphytes may persist on these. However, he does not explain why the epiphytes do not also decline because of microenvironmental changes brought about by tree ontogeny, e.g. increased shading and descreased throughfall.

Benzing & Seemann (1978) investigate general decline of phorophytes with heavy epiphyte loads in environments of very poor nutrient status and put forward the theory of 'nutritional piracy'. This states that oligotrophic epiphytes are very efficient at scavenging and retaining nutrients and they effectively block the cycle and deprive the phorophyte of minerals. This seems a plausible argument but needs more direct supporting evidence as yet; Benzing and co-workers have investigated various oligotrophic epiphytes, their efficiency and nutritional strategies which provide indirect support, e.g. Benzing & Renfrow (1971c), Benzing (1978a), Benzing & Davidson (1979).

In an interesting comparison with the works of Benzing and co-workers on the nutrition of epiphytes and their role in nutrient cycling within the community, Nadkarni (1981) researched the development of adventitious "canopy roots" in two different rainforests, one temperate and the other tropical montane. She found that such roots commonly invaded canopy litter accumulations associated with epiphytes thereby giving the trees access to nutrient for which surrounding terrestrial plants could not compete. This does not negate the 'nutritional piracy' hypothesis of Benzing & Seeman (1978) since, even though the soil and parent materials of all systems under discussion may be nutrient-poor, in those investigated by Nadkarni, the epiphytes are humiphilic and their subsystem eutrophic, whereas those of Benzing are humiphobic and oligotrophic and the nutrients of their subsystem is held within the epiphyte living tissues and thus is not available to the phorophytes.

Another general nutritional strategy of vascular epiphytes involves symbiotic relationships with ants, i.e. myrmecophily. Janzen (1974) investigated several such plants growing in nutrient impoverished sites in Sarawak and concluded that the gathering and dumping of insect parts in their homeepiphytes afforded the plants sufficient nutrient to survive as well as enabling the establishment of other epiphytes which do not provide shelter for the ants but exploit the accumulations (called "parasites" by Janzen). The nature of the ant/plant relationships have been disputed in the past (Janzen gives key references into the extensive earlier literature as well as constructive suggestions for research into problems) but it seems obvious that nutrition and some defence value is gained by the plant - the latter point became quite clear to the present writer when attempting to collect such plants in North Queensland (Australian antplants are briefly discussed in Chapter 2.6). Few neotropical antplant epiphytes appear to have developed cavernous organs as have many Asiatic species, but are ant-nest invaders. Perhaps this relates to the nest-building ability of the neotropical ants but the advantages to the plants seem to be similar. Madison (1979b) discusses and reviews neotropical ant-associated epiphytes and their relationships, particularly extra floral nectaries, their importance to the ants and ramifications from this. Kleinfeldt (1978) presents evidence indicating mutualism in a neotropical case, involving both nutritional and dispersal advantage for the plant.

Little comment and even fewer studies have been made on the Australian vascular epiphytes. Longman & White (1917) in a short communication detailed their observations of the plants associated with a single, felled *Litsea reticulata* (Meiss.) Benth. in STRf at Tamborine Mtn., S.E. Qld. They recorded 18 species of vascular epiphytes including one accidental, one hemi-epiphytic fig, two semi-epiphytic climbers and 14 typical epiphytes, being seven each of orchids and ferns (25 cryptogamic species were also recorded on the same tree). This compares with the epiphyte flora of a *Ficus watkinsiana* specimen in Dorrigo National Park (this individual and its epiphytes are figured on pp. 109 and 188). which, on a count in 1977, carried 24 species of vascular epiphytes, including three accidental epiphytes, four semi-epiphytic climbers and 18 typical, these being 7 ferns, 10 orchids and one dicot. The total number of individuals was ca 150 which also compares with the 200 orchids mentioned by Turner (in Longman & White, 1917) on a *Ficus macrophylla* specimen.

In their general study of the ecology of the Barrington Tops area , NSW, Fraser & Vickery (1938) included a separate treatment of the epiphytes. They mention six epiphyte-prone tree species and two cases of high fidelity in epiphyte/phorophyte relationships. The vascular epiphytes are classified into four groups, viz, 1. species of open communities, 2. obligate light species, 3. Facultative light species and 4. shade species. In all, four species of semi-epiphytic climbers were recorded and 24 typical epiphytes, i.e., nine ferns, one dicot and 14 orchids.

Herbert (1958) wrote a short paper on the natural air layering of vines and trees in epiphyte nests in Qld. He briefly discusses nest-forming epiphytes and their modes of collection and accumulation of litter and also some nest-invading species. Four tree species are detailed as growing adventitious roots into epiphytes nests they supported and two vines were found to have taken root in such situations.

Bale (1974) carried out a project on topographic effects on vegetation in the New England National Park, NSW. One part of this involved studying the effect of difference between adjacent northerly (sunny side) and southerly aspects and a section of the work was a study of the epiphytes. Several sites were chosen and one epiphyte-prone phorophyte species was used to control this effect, and vascular epiphyte species and numbers were recorded; temperature, light intensity and humidity data were also recorded over several months. He concluded that there were considerable differences and that these correlated with differences in the microclimatic factors. Two species were shown to be ecological 'wides' and six were restricted to the southerly sites. He observed that in the richer sites, epiphyte development was best in the tall shrub and small tree layer and that difference in tree growth form may be relevant to epiphyte occurrence.

Beadle (1981) briefly discussed the epiphytes in his book on the Australian vegetation. Vascular epiphytes were commonest in the tropics with species diversity decreasing with temperature and towards drier climate. They are grouped into woody species, whose roots ultimately reached the ground, including the stranglers, and herbaceous species. The lack of rigidly specific epiphyte/phorophyte relationships is noted but several cases of 'preferential' relationships are discussed.

Huxley (1982) has discussed the Australian ant-epiphytes (see further comment on p. 68).

1.2 Epiphyte classification and terminology*

At least since the time of Schimper, epiphytes have been observed and studied as a distinctive group of plants and because of their numbers (10% or more of vascular plants on the estimation of Madison, 1977) and variety of form and of ecological requirements, they have been assorted into various subgroups and categories by many authors, e.g. Grisebach (1884), Schimper (1888, 1898), Goebel (1889), Drude (1913), Warming (1925), Pessin (1925), Braun-Blanquet (1928), Oliver (1930), Went (1940), Hosokawa (1943), Pittendrigh (1948), Richards (1952), Awan (1968), and Johansson (1974). These writers used various systems which reflected their needs and degree of involvement with epiphytes specifically. Hosokawa in his 1943 paper attempted to rationalise these systems, categories and terms and present a unified and consistent approach. His system is a good one but is deficient in these ways:

a. the scope of plants included is restricted to those covered by the strict, classical meaning of the word 'epiphyte', i.e. 'a plant growing non-parasitically upon another plant'. Recent authors, such as Johansson (1974) and Madison (1977) have taken a broader view and included hemi-epiphytes (q.v.) and casual epiphytes (q.v.) though excluding accidental and parasitic epiphytes. This practice is followed here and further, true lithophytes and a new form, viz. semi-epiphytic climbers (see below) are also included; thus, extra, defined terms are needed to encompass these.

b. his terms are latinised - this is seen as an unnecessary complication and English ones are preferred here, especially since the majority of present day scientific literature is written in this language.

New Concepts and Terms (defined below):

i. concepts that the present writer has been unable to find described elsewhere in the literature and finds useful in this study : semi-epiphytic climber, pseudobulbous aphyll, root-tuft aphyll, tangle-epiphyte, fleshy cane, fan-like epiphyte

ii. terms which are in popular usage but do not appear to have been defined previously in the literature, or are previously unused synonyms : primary hemi-epiphyte, secondary hemi-epiphyte, fanplant, catchment plant, nidophil, nidophobe

iii. terms which have an established meaning, but as used widely in the literature on epiphytes, especially orchids, have a more specialised, or shifted meaning : rhizome, cane, disc

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* Glossary of terms, p. 18

Set out below is the classification system used here.* There are three basic types of classification, namely, based on mode of development, occurrence and life form, on physiognomy and on autecology. Each species can be assigned to a group in each system, i.e. the groupings are not mutually exclusive, in fact, some plants may have sufficient variability to fit more than one group in each classification type. Thus, a writer, in describing an epiphyte may elect to refer to only one type, or to two, or all three, depending on the need. Alternative terms, as used by earlier workers, are mentioned where they correspond. Many examples mentioned are figured in the Key to the Flora.

A. Classification based on occurrence, mode of development and life form.

1. **Accidental epiphytes** (ephemeral or pseudo). These are individuals of spp. that are normally terrestrial but have a dispersal method which enables disseminules to be deposited in non-terrestrial sites (usually humus accumulations) which afford at least temporary conditions suitable for germination and early growth. Such plants most often die before maturity owing to their lack of adaptation to epiphytic conditions, especially in regard to water relations. (See list p. 46)

2. **Casual epiphytes** (occasional or facultative) are similar to the above except that they are better adapted to a deficiency of water and nutrients. They therefore more effectively survive and mature and are more common as epiphytes than those in the accidental class. At the same time, most individuals of these spp., are typical terrestrials. Examples are, *Pittosporum undulatum*, which has fleshy fruits and bird transported seeds and often establishes in e.g. the nests of *Platycerium*; *Quintinia sieberi*, with small, dry, wing-transported seeds which frequently establishes on treefern trunks but usually sends roots to the ground to become a primary hemi-epiphyte (see below for definition and flora list, pp. 27-45 for more examples).

3. **Typical, True or Holoepiphytes** (eu-, proto-, epiphyta arboricola) are autotrophic spp. that normally pass their whole life cycle perched on another plant, the immediate source of all mineral nutrients being non-terrestrial. These have wind-, or animal-transported seed and are otherwise ± strongly adapted to the epiphytic way of life; they are usually incapable of terrestrial life under natural conditions. These form the largest and most typical group of epiphytes.

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* This is basically the system used by Hosokawa (1943) but has a broader scope and incorporates new terms as noted on the previous page.

4. Hemi-epiphytes (also lian-epiphytes)

   i) **Primary hemi-epiphytes** (hemiepiphyta praecoqua of Hosokawa) germinate and establish as epiphytes but send roots to the ground whence most nutrients are subsequently derived, enabling full growth and maturation as a terrestrial plant e.g. many *Ficus* spp. (strangler figs), *Schefflera* spp., *Rhaphidophora* spp. (sometimes), *Quintinia sieberi*.

   ii) **Secondary hemi-epiphytes** (hemiepiphyta postera of Hosokawa, climbing or pseudo-epiphytes) are plants that germinate and establish terrestrially, climb and presumably absorb water and nutrients via adventitious roots and eventually lose connection with the ground but continue growth epiphytically. Strict examples, i.e. that habitually lose all ground connections, are rare in the Aust. flora (e.g. *Dipodium pandanum*) and most are irregular or facultative cases such as some *Microsorium*, and occasional specimens of *Arthropteris*, *Pothos*, *Fieldia*, etc.

5. **Semi-epiphytic climbers** - vines or vine-like plants that begin life as typical terrestrials but climb by adventitious roots, some of these functioning in water and mineral uptake roles as well as anchorage. These are like secondary hemi-epiphytes but do not become detached from the ground; e.g. *Pothos*, *Rhaphidophora*, *Stenochlaena*, *Arthropteris*, *Prionotes*, *Fieldia* etc.

6. **Lithophytes** (rupicoles, saxicoles, epiliths, rupestral plants) - as for 3. but growing on a rock substrate; they are usually more tolerant of terrestrial conditions. Typical epiphytes will, under certain conditions, occasionally grow lithophytically, and rarely vice versa also. True lithophytes, i.e. those which rarely grow as terrestrials or as epiphytes are much less common than true epiphytes.

B. Classification based on physiognomy or growth form; groupings are not necessarily mutually exclusive.

Woody Plants

1. **Shrub epiphytes** (dendroepiphyta) - woody plants under 5 m tall, either branching from a single, basal, relatively short, ± erect stem, e.g. *Ficus*, *Schefflera*, *Pittosporum*, etc. or multi-stemmed from the base and often layering (rooting where stems contact

suitable substrate). The **stranglers** are a specialised group with the habit of forming a woody lattice around the phorophyte, e.g. *Ficus*, *Quintinia fawkneri*.

Herbs

2. **Creeping epiphytes** (mobiligemmi-epiphyta) have primary stems (i.e. those bearing the main perennating buds) growing appressed, or ± close and parallel to the substrate and attached to it by creeping adventitious roots. Most have erect to pendulous leaves or leafy secondary stems projecting away from the substrate. They can be subgrouped according to the degree of elongation or contraction of the primary stem which must be gauged according to the stem diameter and general size of the plant rather than measured in linear units; e.g. a small filmy fern with fronds 1 cm apart may be long-creeping while a large *Dendrobium* with stems the same distance apart will be short-creeping.
    - i. **Long-creeping epiphytes** (reptata remota) ± vine-like, travelling relatively rapidly and far re position on substrate and in the microhabitat, e.g. *Teratophyllum*, *Stenochleana*, *Arthropteris*, *Rhaphidophora*, some *Hoya* growth, juvenile *Quintinia fawkneri*.
    - ii. **Medium-creeping epiphytes** have leaves or secondary stems clearly spaced but not to the extent of being vine-like. Primary stems are sometimes ± fleshy and rhizomatous e.g. *Davallia*, *Schellolepis*, some *Rhaphidophora*, *Dendrobium agrostophyllum*, also, *Pyrrosia*, *Crypsinus*, some *Dischidia* growth, *Dendrobium carii*, *D. wassellii*, *Bulbophyllum bowkettae*.
    - iii. **Short-creeping epiphytes** (reptata densa, caespitosa?) those with primary stems contracted such that adjacent leaf stalks or secondary stem bases are in contact (very short-creeping), or separated by a distance up to equal to ca. their own thickness or so. Functionally, they are sedentary, not growing far from the point of establishment. Those which have low or appressed leaves or stems and branch regularly will become **mat-epiphytes**, e.g. *Microgonium*, *Pyrrosia rupestris*, *Dendrobium linguiforme*, *D. torresae*, *Bulbophyllum weinthalii*, some *Dischidia* growth etc.; those with longer aerial parts may be called **tuft** or **clump epiphytes**, e.g. *Lycopodium*, *Ophioglossum*, *Vittaria*,

most *Grammitis*, *Belvisia*, *Elaphoglossum*, many caulescent *Dendrobium*, *Liparis*, many *Bulbophyllum*, some *Eria*, *Podochilus* etc. A specialised group of short-creeping herbs is the **aphylls** (leafless), of two types, viz., **pseudobulbous**, e.g. *Bulbophyllum minutissimum* and *B. globuliforme* and the **root-tuft** orchids which vegetatively consist of little more than a tuft of creeping (and sometimes also aerial) roots, e.g. *Taeniophyllum* and *Chiloschista*.

3. **Sedentary epiphytes** : those which establish at a given point with the primary stem and main perennating buds growing into the air and not along the substrate and hence are of fixed position.

   i. **Fruticose herb epiphytes** have the general growth habit of shrubs but are non-woody to semi-woody and thus are usually also of smaller stature (c.f. fruticose lichens). These may be erect to pendulous and with a single main stem, e.g. *Myrmecodia* and *Hydnophytum* (both erect) or multi-stemmed, e.g. *Peperomia* (erect) *Dendrobium teretifolium* (pendulous) and allies. Some of the multi-stemmed ones may strike root on contact with suitable substrate. *Myrmecodia* and *Hydnophytum* may be further classed as **tuberous antplant** epiphytes.

   ii. **Rosette epiphytes** (fascicularis, rosulate plants) have vertical stems with very short internodes, the leaves spreading and radiating ± evenly all round, e.g. *Asplenium australasicum*, *A. nidus*, *A. simplicifrons*, *Boea*, *Didymocarpus*, (most bromeliads) etc.; very short-creeping epiphytes often appear similar to this form.

   iii. **Fanplants** also have very contracted stems but leaves are in two ranks and, in the strict sense, are conduplicately flattened at least in the basal half, ± radial and in the same plane as the stem, e.g. *Oberonia*, *Rhynchophreatia*, *Oxyanthera*. Many of the monopodial orchids have this general arrangement except that the leaves are channelled or twisted at the base, or the stem not so contracted, such that the fan effect is decreased; some short-creeping ferns e.g. *Antrophyum*, *Ctenopteris* and *Scleroglossum* are also somewhat fan-shaped : all of these can be referred to as **fan-like** herbs.

4. **Tangle epiphytes** are those which grow away from the substrate after establishing on it and thence most roots become aerial, such that the mature plant becomes a tangle of roots, stems, leaves and inflorescences.

Most are monopodial orchids with medium elongate stems, e.g. *Plectorrhiza, Thrixspermum, Micropera,* some *Sarcochilus*, etc.

5. **Catchment epiphytes** are those specialised to catch water and litter from a relatively large area and channel this to a central holding container.

   i. **Nest-forming epiphytes** (bracket epiphytes) catch leaf, twig, inflorescence etc. debris and concentrate and compact this between successive leaves which also eventually die and add to the mass. Some of the plants' roots grow into this and take up mineral nutrients released by breakdown of the debris, with water caught and channelled into the nest by the leaves. The remaining peaty mass functions as an efficient storage unit for water and mineral nutrients. The nest leaves of *Platycerium* species themselves are rather thick in the basal half and become spongy on dying; other nest formers include *Drynaria, Asplenium australasicum, A. nidus* and *A. simpliciifrons*. These epiphytes are important as their nests are often invaded by other species and form the dominants of many epiphyte micro-communities.

   A variation of the nest building theme is found in *Dendrobium speciosum* which produces bunched apogeotrophic roots, these catching litter to form a nest mass.

   ii. **Tankplant epiphytes** (cistern epiphytes)-rosettes with leaf bases forming a waterproof receptacle which holds free water, as well as debris. These are ± exclusively bromeliaceous and Neotropical - Cockayne (1928) states that some NZ *Astelia* spp. (Liliaceae) store water like bromeliads; Australia has no representatives of this life-form.

C. Classification on the basis of autecology, particularly in relation to tolerance of exposure, aridity and substrate.

1. Environmental water status preference/tolerance groupings :

   i. **Hygrophytes** (hygrophiles) - plants requiring high humidity and plentiful substrate free-water, e.g. almost all Hymenophyllaceae, *Sarcochilus australis, S. olivaceus, S. serrulatus*. Most filmy ferns, like many mosses and liverworts, are poikilohydrous, possessing a degree of "resurrection" capability i.e. ability to recover rapidly on wetting after withering and crumpling from water deficiency. Rft tree trunk bases, especially those beside streams, form typical microhabitats for such plants.

ii. **Mesophytes** (mesophiles) are plants with moderate tolerance of water deficiency. Mesophytic epiphyte microhabitats include many beneath-canopy sites in rft. Mesophytes comprise the largest group of epiphytes.

iii. **Xerophytes** (xerophiles) are strongly drought resistant and adapted to survive ± sustained intense environmental and tissue water deficit. They are usually specialised in a number of ways - many are succulent and store water in their tissues, have thick cuticles, sunken stomates, special stomatal rhythm (CAM), inherent protoplasmic tolerance of severe water deficiency, velamen-sheathed roots (orchids particularly), special water-absorbing trichomes with rapid uptake and slow loss function (many bromeliads), etc. Typical microhabitats include outer branches of rainforest emergents *(Dendrobium beckleri, D. racemosum)*, trunks, branches and rocks in open communities *(D. linguiforme, D. canaliculatum, D. johannis, Cymbidium canaliculatum, Drynaria quercifolia)* etc.

2. Light intensity preference groupings :

i. **Heliophytes** (photophytes) or sunplants are those which readily tolerate, or grow best in strong or direct sunlight. This usually correlates with xerophytism, although many epiphytes of e.g. cool, high altitude cloud rft may require strong light, relatively cool temperatures and high humidity at the same time, e.g. *Dendrobium carrii, D. fleckeri, Elaphoglossum*, etc.

ii. **Sciophytes** (skiophytes) are shade plants, i.e. intolerant of long periods of direct sunlight. Most hygrophytes will also be sciophytes as humidity correlates negatively with insolation under normal conditions.

3. Substrate preference groupings :

i. **Humiphils** (humus epiphytes, humicoles, nidophils) need substrates which roots and sometimes primary stems (rhizomes) can penetrate for protection against desiccation as well as for water and nutrient acquisition. The indications are that such plants are heavier feeders and possibly less efficient nutrient users and have roots less well adapted to resist water loss; evidence for this comes from facultative epiphyte/terrestrials or accidental epiphytes which only grow and mature in large nests or humus accumulations. Examples of other nidophilous epiphytes are : *Psilotum, Lycopodium, Davallia, Nephrolepis, Schellolepis, Asplenium polyodon, Fagraea berteriana, Cymbidium,* etc.

ii. **Humiphobes** (bark epi., nidophobes) grow roots creeping on the substrate surface and are often intolerant of root coverage. The roots are adapted to a dry rhizosphere, e.g. many orchids with velamen sheathed, arid-adapted roots; the plants often have a small-scale nutrient economy and are efficient users, e.g. most epiphytic *Sarcochilus,* many *Dendrobium* spp. from mid and upper zones, *Phalaenopsis,* etc.; aphylls and atmospheric epiphytes are all humiphobic.

iii. **Atmospheric** (aerial) **epiphytes**; many epiphytes appear to use the phorophyte for little more than anchorage since most of their absorbing-organs, i.e. roots in orchids, or, in many bromeliads, foliar trichomes - are not in contact with the substrate and apparently derive their mineral nutrients from rainwater and canopy throughfall, e.g. *Plectorrhiza, Vanda, Thrixspermum* and other tangle epiphytes and in the bromeliads, the smaller, silvery, heliophytic *Tillandsia* spp.

1.3

Glossary of important and miscellaneous terms :

These terms are defined here since, as used in some of the literature on orchids and epiphytes and in this study, they may be slightly altered from the classical meaning, or are new.

aphyll, a leafless plant

axeny, inhospitality to other forms of life; here refering to trees which bear few or no epiphytes.

cane, the narrow, elongate, scarcely fleshy, secondary stem of some sympodial orchids, which is often referred to as a pseudobulb, but this usage is misleading; c.f. fleshy cane.

catchment plant, see epiphyte classification 5, p.16.

contracted, in reference to a stem, having relatively short internodes so that leaves tend towards tufted; may also be used re the primary stem of a sympodium in which secondary stems are close-set, but in epiphytes these are mostly creeping and thus referred to as short-, or very short-creeping (c.f. these terms).

disc, the lamina, or central area of an orchid labellum.

elongate, referring to a stem, having relatively long internodes, tending towards vine-like (c.f. long-creeping).

epiphyte, an autotrophic plant which is attached to, supported by and derives its nutrition from a non-terrestrial substrate; in the strict sense does not include lithophytes.

fanplant, plant with contracted stem, leaves in two ranks, conduplicately flattened at least in the basal half, ± radially arranged (see pp. 164 and 235 of Appendix 1)

fan-like epiphyte, one with leaves so arranged as to somewhat resemble a fan.

fleshy cane, an orchid secondary stem which is succulent and shorter and thicker than a cane but not as much as a pseudobulbous stem.

frond, leaf of a fern; *basket frond,* the sterile, litter-catching frond of a nest-forming fern; *fertile frond,* one bearing sporangia; *nest frond,* litter-catching frond; *shield frond,* litter-retaining frond of a nest-forming fern, esp. *Drynaria, Platycerium*; *sterile frond,* mature frond that does not bear sporangia.

heliophyte, sun-loving plant, see p.

hemi-epiphyte, a plant that is normally epiphytic for part of its life cycle. (See p.13)

humiphil, literally humus-loving, an epiphyte which grows in humus accumulations; nest invading epiphyte (Went, 1940).

humiphobe, 'humus hater', an epiphyte which grows on a relatively hard, clean substrate, with roots ± exposed.

hygrophte, a plant requiring high humidity and plentiful substrate water. (See p.16)

lithophyte, as for epiphyte but growing on a rock substrate; see p.13.

long-creeping, in reference to a plant where the rhizome, or primary stem creeps on the substrate and has long internodes or long distances between secondary stems or leaves, relative to the stem diameter and general size of the plant; tending to be vine-like; see p. 14; c.f. medium- and short-creeping.

Malesia, a biogeographic region comprising the Malay Pen., Indonesia, the Philippine Is. and New Guinea, plus the Bismarcks (exc. Bougainville).

medium-creeping, referring to a plant with rhizome or primary stem creeping on the substrate, in which the leaves or secondary stems are well separated - by at least their own width (or petiole or stipe width) - but not to the extent of being vine-like; see p. 14.

mesophyte, a plant which requires at least moderately high humidity and substrate free-water supply for normal growth; see p. 17.

Neotropics, the tropical lands of the Americas; New World tropics.

nest, an accumulation of litter that has been caught and impounded by the leaves (or roots) of a plant; *nest-forming,* referring to a plant that forms a nest and implying special adaptation for this, see p. 16, *nest leaves,* those which impound the litter of a nest.

nidophil, literally nest-loving, implying a nest-invading plant.

nidophobe, literally nest-hating, referring to an epiphyte which grows on a relatively hard and clean substrate, i.e. preferring roots to be exposed.

non-vascular epiphyte, one from a lower taxonomic group, lacking true vascular tissue, a cryptogam, i.e. moss, liverwort, alga, fungus or lichen.

Old World, biogeographic area comprising all continents and nearby islands, except the Americas and Antarctica.

phorophyte, literally, a carrier-plant, one which acts as a substrate for an epiphyte.

pseudobulb, a short, swollen, fleshy secondary stem of a sympodial orchid.

rhizome, a creeping, primary stem which produces roots and either leaves or secondary, aerial stems; normal usage implies growing in the ground, but it is often used in reference to epiphytes and here, particularly for ferns.

rosette plant, one with a contracted, ± vertical stem, around which the leaves are evenly spaced.

root-tuft aphyll, one with a very contracted, monopodial stem, thus consisting of virtually no more than a tuft of roots.

sciophyte, (also spelled skiophyte), a shade-loving plant.

semi-epiphytic climber, a terrestrial, vine-like plant that develops a significant epiphytic root system; see p. 13.

tangle epiphyte, an orchid (usually monopodial) which grows away from the substrate and produces numerous aerial roots; see p. 15.

vascular epiphyte, one possessing true vascular tissue and thus a pteridophyte or seed plant.

wiry stem, one which is thin, fibrous, tough and somewhat flexible.

CHAPTER 2

THE AUSTRALIAN VASCULAR EPIPHYTES

2.1 Introduction - reasons for the extent and type of treatement of the flora are explained. p. 23.

2.2 Materials and Methods p. 23

2.3 Results (p. 25) are presented as a systematic list of the species against which abbreviated information in nine columns is marked. Appendix 1, the descriptive key to the flora is intended basically as a supplement to this section.

2.4 Discussion (p. 51) is organised into sections on the taxonomic groups.

2.5 Biogeography of the Australian vascular epiphytes (p. 59) with particular reference to the Orchidaceae; this discussion is based mainly on the epiphyte distributional areas i-vi and the example of the orchid genus *Sarcochilus* is detailed.

2.6 Myrmecophilous epiphytes in Australia (p. 66) - some observations and discussion are presented.

2.7 Conclusions p. 68

2.1 Introduction

Investigation and exposition of the flora has been treated as a vital and substantial part of this study, and has involved listing the species with summarised geographical, morphological and ecological information in table form within the body of the text, plus a descriptive, illustrated key to the flora in Appendix 1 (separate volume). Reasons for such a comprehensive treatment of the flora include:

a. This work is the first major one on the Australian vascular epiphytes and it is thus appropriate that the first task be to assemble, arrange and at least briefly describe them, particularly in relation to their being epiphytes and to the needs of epiphytology.

b. The epiphytes are from taxonomically disparate groups and though most have already been described in the literature, such treatments are disjunct, often in obscure publications and biassed towards pure taxonomy, etc.

c. A few species are newly described and not included yet in comprehensive or synthetic works of any type. One or two 'new' species have also been informally described.

d. Some very rare species have been included which have been left out of other synthetic works, e.g. *Lemmaphyllum*, *Monogramma* etc.

e. Ecological information is often rudimentary or absent from other flora works. This has been emphasised, particularly in relation to epiphytism.

The result has been an indispensible reference in the present study and it is hoped that it will also be useful to other students in this field.

A broad definition of 'epiphyte' has been used here, basically as defined by Madison (1977) and the subgroups used are, typical or true epiphytes, hemi-epiphytes, and semi-epiphytic climbers, as defined in the previous chapter. Included with these are the true lithophytes, a small but definite group, and accidental and casual or facultative epiphytes are listed for completeness of the survey.

2.2 Materials and Methods

1. A list of Australian vascular epiphytes, arranged systematically, was compiled from various floras and relevant botanical literature. These references are listed in the Bibliography to Appendix 1.

2. Field trips were made to numerous localities in eastern Australia[1] to investigate the flora and collect specimens, field notes and photographs of the species. Specimens were grown in glasshouses in the Botany Dept., UNE when amenable to cultivation, especially specimens that were sterile on collection so that dried or preserved specimens could be made on their becoming fertile. Others were made directly into pressed and dried or spirit-preserved herbarium specimens and retained as vouchers. These will be dispersed to the Queensland Herbarium, Brisbane, National Herbarium of NSW, Sydney and the UNE Herbarium of this Department, where appropriate; in the case of Qld, this was a request on granting of a permit to collect in that State. Living specimens were collected in the Northern Territory, particularly from the Daly R. area by Mr K. Hill and sent to the writer. Far NW Australia, Tasmania, SW WA, SA and W Victoria were not collected but covered by the literature. There are few vascular epiphytes in these areas.

3. Specimens were identified by the use of botanical keys and similar relevant literature (see Bibliography of Appendix 1) and checked where doubtful against herbarium specimens from the abovementioned herbaria and where further difficulty was involved, with the collaboration of experts such as Mr D. Blaxell, Mr P. Hind and Dr M. Tindale, all of NSW Natl. Herb. Sydney, Mr S.B. Andrews of Brisbane and Messers B. Hyland and A. Dockrill of CSIRO, Atherton.

4. Drawings and notes on morphology were made from the above specimens, sometimes using dissecting microscope where necessary, and from photographs taken in the field and glasshouse.

5. From all of the above the following were compiled: a) list of accidental epiphyte species (Results 2.3.2) and b) a list of facultative terrestrial/lithophyte/low epiphyte (Results 2.3.3), c) Table 2.1a, list of Australian epiphytes with data on geographic distribution, life form, physiognomic type, exposure preference, root cover class, disseminule type and presence or absence of CAM; these are summarised in Tables 2.1b-g; and d) descriptive, illustrated key to the Australian vascular epiphyte flora (Appendix 1).

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[1] Qld: Tozers Gap, Iron Ra, Leo Ck and Massy Ck, McIlwraith Ra; Laura, Chillagoe, Bakers Blue Mt., Mt Lewis, Mt Haig, Mt Bartle Frere, Upr N. Johnston R., Upr Tully R., Daintree R-Cape Tribulation area, Woopen Ck, Mt Spec, Eungella Ra., Rockhampton district, Noosa Hds, Bunya Mts, Yarraman, Somerset Dam area, Cunninghams Gap, Lamington Plat.; NSW: - Nightcap Ra., Wiangarie, Toonumbah, Upr Tooloom, Gibraltar Ra., Glenugie Peak, Dorrigo and Bellinger Valley, Upr Hastings R, Port Macquarie, Comboyne Plat., Gloucester, Barrington Tops, Wattagan Mts, Blue Mts., Kangaroo Valley; Vic: - Cann R.

2.3 Results

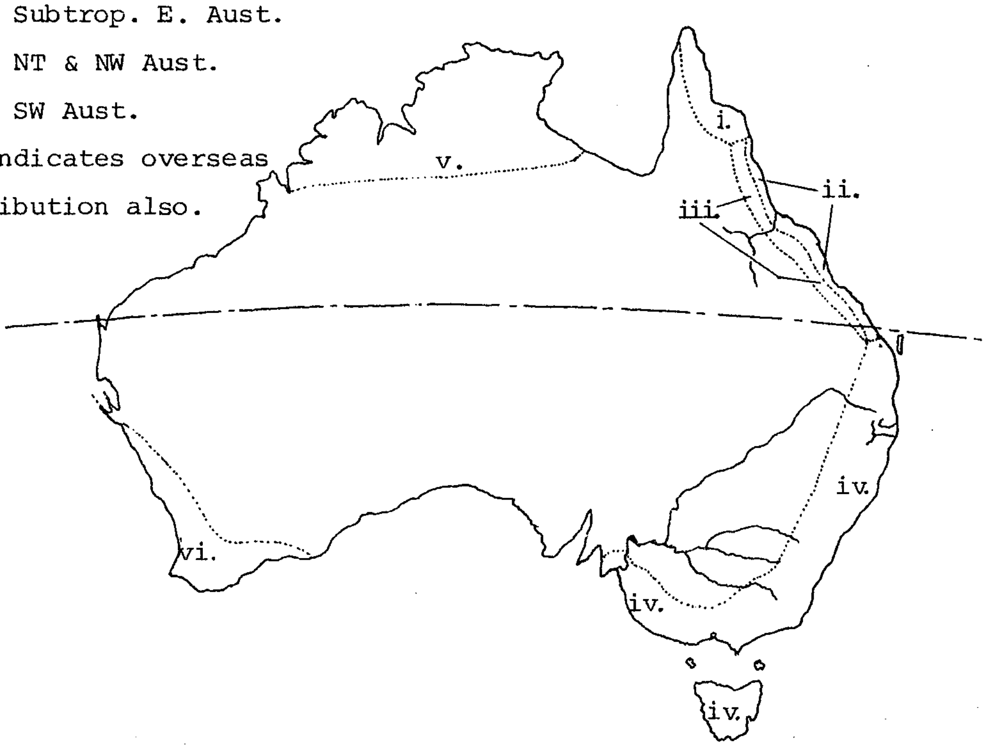
2.3.1 Vascular Epiphyte Flora List (Table 2.1a)

Data in Table 2.1a

Column 1 : Page number of sp. in key (Appendix 1).

2 : Geographic distribution of sp. :

i. C. York Pen. - S. to Cooktown.
ii. Trop. Qld lowland - Cooktown to Rockhampton below ca 600 m.
iii. Trop. Qld highland - above ca 600 m.
iv. Subtrop. E. Aust.
v. NT & NW Aust.
vi. SW Aust.
"+" indicates overseas distribution also.



3 : Life-form epiphyte type (see epiphyte classification, p.12 for details):

Acc	Accidental epiphyte
Cas	Casual, facultative epiphyte/lithophyte/terrestrial
Typ	Typical, true or holoepiphyte
HP	Primary Hemi-epiphyte
HS	Secondary Hemi-epiphyte
SEC	Semi-epiphytic climber
L	Lithophyte
T	Terrestrial

4 : Physiognomic type : (see epiphyte classification for further details)

sh	shrub	tgl	tangle epiphyte
lcr	long-creeping herb	ros	rosette plant
mcr	medium-creeping herb	fan	fanplant
scr	short-creeping herb	f-l	fan-like epiphyte
ls	leaf succulent	pb	pseudobulbous or fleshy-caned
aph	leafless herb (aphyll)	nf	nest-former
frh	fruticose herb	tf	tufted

e	erect	rtf	root tuft
		p	pendulous

5 : *Exposure preference index* : a scale of 1-5 is used, in which 1 denotes a hygrophyte which prefers microhabitats of low light intensity, cooler temperatures, higher humidity and lesser air movement, 5 indicates a xerophyte preferring the opposite extremes. These numbers mostly correlate with the phorophyte zones the plants inhabit, i.e. 1 = trunk base, 5 = outer branchlets, on exposed rocks, etc.

6 : *Root Coverage* : *a* indicates a humiphobe which prefers roots exposed, *b* indicates an intermediate preference where roots creep through or under moss or a light litter cover, *c* indicates a humiphile or nest invader, which prefers sites where roots and/or rhizomes can penetrate epiphyte nests and humus accumulations.

7 : *Plant community preference* : the terms used are those of Webb (e.g., 1978) plus a few extra for non-rft formations etc. Those given for each epiphyte sp. are the ones *most commonly* inhabited i.e. *preferred*, and are not meant to be exclusive. The abbreviations and common names of those used here are :

MVF	mesophyll vine forest .... tropical rft
SEVF	semi-evergreen mesophyll vine forest .... tall monsoon rft
DVT	deciduous vine thicket .... low, or dry monsoon rft
SEVT	semi-evergreen vine thicket .... Bottle Tree, or dry rft to rft relict scrub (trop.)
NVF	notophyll vine forest .... subtropical rft., trop. submontane rft
SNEVF	simple notophyll evergreen vine forest .... warm temperate, trop. montane rft
MFF	microphyll fern forest .... cool temperate rft
MVT	microphyll vine thicket .... dry rft (subtrop.)
MVW	microphyll vine woodland .... rft relict (subtrop.)
WSF	wet sclerophyll forest, tall open forest
Ect	rft/open community ecotone
Wdl	open woodland
Swf	swamp forest
Man	mangroves

8 : *Disseminule type* : *D*, dust seed, spores or the like; *W*, winged seed - with a membranous wing or downy 'parachute'; *F*, fleshy fruit; *A*, adherent

9 : *CAM* - presence or absence of Crassulacean Acid Metabolism as indicated by $\delta^{13}C$, a ratio less negative than -20 taken as typical of CAM plants, one more negative than -22 typical of C_3 plants. In the table, "+" indicates CAM, "-" indicates non-CAM and for those left blank, data are not available. (Data by courtesy of Klaus Winter, pers. comm.)

Table 2.1a : THE VASCULAR EPIPHYTE FLORA OF AUSTRALIA *

Pteridophytes	1 pge.in key	2 geog. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
fam. Psilotaceae									
Psilotum									
P. complanatum	7	i,ii+	Typ	p,tf,frh	2-3	c	MVF,SEVF	D	-
P. nudum	7	i-v+	",L	"	2-4	c	NVF,",", WSF	D	
Tmesipteridaceae									
Tmesipteris									
T. billardieri	8	iv+	Typ	p, scr,frh	1-2	c	SNEVF,MMF	D	
T. elongata	9	iv+	"	" " "	"	"	" "	"	
T. ovata	9	iv	"	" " "	"	"	" NVF	"	
T. parva	8	iv+	"	" " "	"	"	" "	"	
T. truncata	8	iii,iv	",L	" " "	"	"	" "	"	
T. lanceolata	9	iii+	Typ	" " "	"	"	"	"	
Lycopodiaceae									
Lycopodium									
L. carinatum	11	i+	Typ	p, scr,frh	3	b-c	SEVF	D	
L. dalhousieanum	10	i,ii+	"	" " "	3	c	" MVF	"	
L. myrtifolium	12	i-iii+	",L	p-e " "	3	c	NVF-WSF	"	
L. phlegmaria	12	i-iii+	" "	p " "	2-3	b-c	",MVF,SEVF	"	-
L. phlegmarioides	12	i,ii+	Typ	" " "	2	c	" "	"	
L. polytrichoides	11	iii+	"	" " "	3	b-c	NVF	"	
L. proliferum	11	ii,iii+	"	" " "	3	c	",MVF	"	-
L. squarrosum	10	i,ii+	",L	" " "	2	b-c	SEVF,"	"	
Ophioglossaceae									
Ophioglossum									
O. pendulum	13	i-iv+	Typ	p,scr	2-3	c	M-NVF, SEVF	D	-
Hymenophyllaceae									
Hymenophyllum									
subgenus *Hymenophyllum*									
H. cupressiforme	19	iv+	Typ,L	mcr-lcr	1-2	b	NVF-MFF	D	
H. gracilescens	20	iii	"	" "	" "	"	"	"	
H. peltatum	19	iv+	",L	" "	" "	"	MFF	"	
H. pumilum	18	iv	" "	" "	1	"	SEVF "	"	

* N.B. Appendix 1 contains key to & descr. of taxa & citation of author and publication of accepted names, plus synonymy.

Hymenophyllum (Cont.)	1 pge.in key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
subgenus *Chilodium*									
H. *bivalve*	20	iv+	Typ	mcr-lcr	1-2	b	MFF, SNEVF	D	
H. *kerianum*	21	ii	"	" "	1	"	MVF	"	
H. *lobbii*	22	iii+	"	" "	1	"	SNEVF	"	
H. *subdimidiatum*	21	iii+	"	" "	1	"	"	"	
subgenus *Mecodium*									
H. *australe*	23	iv+	Typ,L	mcr-lcr	1	b	SNEVF, MFF	D	
H. *eboracense*	24	i	" "	" "	1-2	"	SEVF	"	
H. *flabellatum*	25	iii, iv+	Typ	" "	1-2	"	SNEVF, MFF	"	
H. *rarum*	26	iv+	"	" "	1	"	" "	"	
H. *javanicum*	24	iii+	", L	" "	1	"	"	"	
H. *polyanthos*	23	i, ii+	" "	" "	1	"	SEVF, MVF	"	
H. *samoense*	23	iii+	" "	" "	1-2	"	SNEVF, NVF	"	
H. *walleri*	25	iii	Typ	" "	1	"	", NVF	"	
H. *whitei*	24	iii	"	" "	1	"	"	"	
subgenus *Craspedophyllum*									
H. *marginatum*	27	iv +	L, Typ	lcr	1	b	SNEVF, NVF	D	
subgenus *Hemicyatheon*									
H. *baileyanum*	26	iii	Typ, L	mcr-lcr	1-2	b	SNEVE, NVF	D	
Sphaerocionium									
S. *lyallii*	27	iv	L, Typ	lcr	1	b	SNEVF	D	
Apteropteris									
A. *applanata*	27	iv	Typ, L	mcr-lcr	1-2	b	MFF	D	
Microtrichomanes									
M. *vitiense*	28	iii, iv+	Typ, L	" "	1	b	NVF	D	
M. *digitatum*	28	ii +	Typ, L	" "	1	b	MVF	D	
Trichomanes									
T. *aphlebioides*	30	ii +	L, Terr	scr-mcr	1	b-c	MVF	D	
T. *johnstonense*	29	iii	" "	" "	"	" "	SNEVF	D	
Microgonium									
M. *bimarginatum*	35	i-iv+	Typ, L	lcr-mcr	1	b	SEVF, MVF, NVF	D	
M. *mindorense*	36	ii+	Typ	" "	1	b	MVF	"	
M. *motleyi*	36	i-iii+	"	" "	1	b	SEVF, M-NVF	"	
M. *tahitense*	34	ii-iv+	"	mcr-lcr	1	b	MVF, NVF	"	
Crepidomanes									
C. *barnardianum*	33	i-iii+	L	mcr-lcr	1	b	SEVF, M-NVF	D	
C. *bipunctatum*	33	" " "+	Typ, L	" "	1	b	" "	D	

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Hymenophyllaceae *Crepidomanes* (Cont.)	1 pge.in key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
C. kurzii	32	iii +	Typ	mcr-lcr	1	b	NVF,SNEVF	D	
C. majorae	34	iii	"	" "	1	b	" "	D	
C. walleri	34	iii,iv	"	" "	1	b	" "	D	
Gonocormus									
G. prolifer	31	i-iii+	Typ,L	lcr	1	b	NVF, SEVF,MVF	D	
G. saxifragoides	31	i-iv+	" "	"	1	b	" " "	D	
Reediella									
R. endlicheriana	31	iii+	Typ	lcr	1	b	NVF	D	
R. humilis	32	ii+	"	"	1	b	MVF	D	
Pleuromanes									
P. pallidum	30	iii+	L	l r-mcr	1	b	NVF	D	
Polyphlebium									
P. venosum	30	iv	Typ,L	lcr	1	b	SNEVF,MFF	D	
Macroglena									
M. brassii	37	iii	L	scr	1	b	NVF,SNEVF	D	
M. caudata	37	iii,iv	Typ	scr-mcr	1	b	" "	D	
Cephalomanes									
C. atrovirens	38	i-iii+	L,T	scr	1	b,c	MVF,NVF	D	
Didymoglossum									
D. exiguum	26	ii+	Typ	lcr	1	b	MVF	D	
Selenodesmium									
S. elongatum	38	iii-iv	L,T	scr-mcr	1	b,c	NVF	D	
S. obscurum	38	i-iii+	" "	" "	1	b,c	SEVF,MVF NVF	D	
Lindsaeaceae									
Lindsaea									
L. repens	47	i,ii+	SEC	mcr-lcr	1-2	b	SEVF,MVF	D	
L. pulchella	47	iii+	"	" "	1-2	b	NVF,SNEVF	D	
Vittariaceae									
Antrophyum									
A. reticulatum	50	i-iii+	Typ,L	p, tf	2	b	SEVF, MVF,NVF	D	-
A. subfalcatum	50	ii +	" "	" "	2	b	" "	D	
A. plantagineum	50	ii +	" "	" "	2	b	" "	D	

Vittariaceae (Cont.)	1 pge. in key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
Vittaria									
V. elongata	49	i-iv+	Typ	scr-mcr	2-3	b,c	SEVF, MVF,NVF	D	-
V. ensiformis	49	" " +	"	tf-scr	2-3	b,c	" " "	D	
Vaginularia									
V. acrocarpa	51	iii+	Typ,L	mcr	1-2	b	NVF	D	
Monogramma									
M. dareicarpa	51	" +	"	"	1-2?	b?	NVF ?	D	
Dennstaedtiaceae									
Oenotrichia									
O. tripinnata	48	iii	L	scr	1	b,c	NVF,SNEVF	D	
Davalliaceae									
Davallia									
D. denticulata	53	iii+	Typ, L	mcr	2-3	c	NVF	D	
D. pyxidata	52	iii,iv	" "	"	2-4	c	NVF,SNEVF	D	
D. solida	52	i +	" "	"	2-3	c	SEVF	D	
Humata									
H. pectinata	54	i +	Typ	mcr-lcr	3	b,c	SEVF	D	
H. repens	53	i-iii+	"	" "	3	b,c	",MVF,NVF	D	
Rumohra									
R. adiantiformis	54	iv+	Typ,L	mcr	2-3	c	NVF,SNEVF MFF	D	
Oleandraceae									
Arthropteris									
A. submarginalis	56	iii	SEC,L	mcr	1-2	b	NVF	D	
A. beckleri	57	iii,iv	" "	"	"	"	",SNEVF	D	
A. palisotii	57	" "+	" "	"	"	"	" "	D	
A. tenella	56	" "	" "	"	"	"	" "	D	
Oleandra									
O. neriiformis	55	iii+	SEC,Typ	mcr/tf	2	b,c	NVF	D	
Nephrolepis									
N. acutifolia	59	ii+	Typ,L,T	tf/mcr	3	b,c	MVF	D	
N. biserrata	60	ii+	" " "	" "	3-4	" "	"/Ect	D	
N. cordifolia	59	ii- v+	" " "	" "	3-4	" "	N,V,F," "	D	

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Nephrolepis (Cont.)	1 pge.in key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
N. hirsutula	60	i,ii,$^{V+}$	Typ,L,T	tf/mcr	3-5	b,c	MVF ect	D	
N. obliterata	61	i,iii,V+	L,T	" "	3,4	" "	" " "	D	
N. radicans	59	iii+	L,T	" "	3-4?	" "	?	D	
Grammitidaceae									
Calymmodon									
C. luerssenianus	69	iii	L,Typ	tf	2	b	NVF,SNEVF	D	
Ctenopteris									
C. contigua	67	i-iii^{+}	Typ,L	tf	1-2	b	SEVF,NVF	D	
C. fuscopilosa	68	iii	" "	"	"	b	NVF	D	
C. gordonii	69	i-iii	" "	"	"	b	"	D	
C. maidenii	67	iii	" "	"	"	b	"	D	
C. heterophylla	66	"	" "	"	1-3	b	SNEVF,MFF	D	
C. walleri	68	"	" "	"	1-2	b	NVF	D	
C. blechnoides	68	" +	L	"	1-2	b	"	D	
Grammitis									
G. poeppigiana	61	iv+	L	mcr	2-3	b	open	D	
G. billardieri	64	iv+	Typ,L	tf	1-2	"	SNEVF,MFF	D	
G. magellanica	62	iv+	" "	"	1-2	"	MFF	D	
G. meridionalis	62	iv	" "	"	1-3	"	",SNEVF,Ect	D	
G. queenslandica	65	i-iii	" "	mcr	1-2	"	MVF,NVF	D	
G. adspersa	63	iii^{+}	" "	tf	"	"	NVF,SEVF	D	
G. albosetosa	63	iii	" "	tf-scr	"	"	NVF,SNEVF	D	
G. reinwardtii	64	iii+	" "	tf	"	"	SNEVF	D	
G. stenophylla	62	iii,iv	" "	tf-scr	"	"	NVF,SNEVF	D	
G. wurunuran	64	iii	" "	tf	"	"	" "	D	
Scleroglossum									
S. wooroonooran	65	iii	Typ,L	tf	2-3	b	NVF,SNEVF	D	
Polypodiaceae									
Belvisia									
B. mucronata	81	i-iv^{+}	Typ,L	tf	2	b	SEVF,M-NVF	D	-
Colysis									
C. ampla	77	ii,iii	SEC	mcr	1-2	a-b	NVF,MVF	D	
C. sayeri	77	iii	"	"	1-2	" "	NVF,SNEVF	D	

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Polypodiaceae (Cont.)	1 pge. in key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
Crypsinus									
C. simplicissimus	79	iii	Typ,L	lcr-mcr	2-4	b	NVF,SNEVF	D	
Dictymia									
D. brownii	71	iii,iv	Typ,L	scr-mcr	2-3	b-c	NVF,SNEVF	D	
Drynaria									
D. quercifolia	79	i,iii,V+	Typ,L	mcr,nf	3-4	c	SEVF,Ect	D	
D. rigidula	78	i-iv+	" "	" "	3-4	c	" ",MVF,NVF	D	-
D. sparsisora	79	i-iv+	" "	" "	2-3	c	",NVF,Ect	D	
Schellolepis									
S. subauriculata	70	i-iii+	Typ,L	mcr	2-3	c	SEVF,M-NVF	D	
S. percussa	70	i,ii +	Typ	"	2-3	c	MVF	D	
Microsorium									
M. diversifolium	74	iv+	L Typ,SEC	mcr	2-3	b-c	NVF,SNEVF MFF,Ect	D	
M. membranifolium	76	ii	",L	"	"	"	MVF,Ect	D	
M. punctatum	73	i-iv+	" "	scr-mcr	2-4	"	",SEVF,"	D	-
M. scandens	73	iii,iv+	SEC,L	mcr	1-3	"	NVF-MFF	D	
M. grossum	74	ii,v +	Typ,L	"	2-3	"	MVF,SEVF, Ect	D	
M. superficiale	72	ii,iii+	" "	"	2-3	"	", NVF	D	
Pyrrosia									
P. lanceolata	83	i+	Typ,L	mcr-lcr	3-4	b	SEVF	D	
P. confluens	82	iii,iv+	" "	" "	2-4	b	NVE,MVT, Ect	D	+
P. dielsii	81	ii,iii	" "	" "	3-4	b	" " "	D	+
P. longifolia	83	i-iii+	" "	mcr	2-4	b	",MVF,SEVT	D	+
P. rupestris	83	iv+	" "	mcr-lcr	2-3	b	",SNEVT, Ect	D	-
Lemmaphyllum									
L. accedens	80	iii$^+$	Typ	lcr	?	?	NVF?	D	
Platycerium									
P. bifurcatum	86	iii,iv	Typ,L	tf, nf	3	c	NVF,WSF, Ect	D	-
P. hillii	87	i,ii	" "	" "	3-4	c	SEVF,MVF	D	-
P. superbum	85	ii-iv$^+$	" "	" "	2-3	c	NVF	D	±
P. veitchii	86	iii,iv	L	" "	4-5	c	Wdl	D	-

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	1 pge.in key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
Aspidiaceae									
Polystichum									
P. *fragile*	88	iii	Typ,L	tf	3	c	NVF, Ect	D	
Lastreopsis									
L. *tinarooensis*	87	iii	L	scr	1-2	b-c	NVF,SNEVF	D	
Aspleniaceae									
Asplenium									
A. *australasicum*	92	ii-iv	Typ,L	ros,nf	2-3	b-c	NVF,SNEVF	D	-
A. *nidus*	92	i,ii+	" "	" "	2-3	" "	SEVF,MVF	D	
A. *simplicifrons*	93	ii,iii	" "	" "	2	" "	M-NVF	D	-
A. *attenuatum*	92	iii,iv	L,Typ	tf	2	" "	NVF	D	
A. *flabellifolium*	94	iv,vi	L,T,Typ	"	3	c	",SNEVF, Ect	D	
A. *trichomanes*	94	" "+	L,T	"	"	"	Wdl,WSF,Ect	D	
A. *normale*	95	iii+	L,Typ	"	2-3	"	NVF	D	
A. *tenerumoides*	99	ii,iii	L	"	2	"	NVF,MVF	D	
A. *paleaceum*	95	i-iii	L	"	2-3	"	SEVF,DVT, NVF	D	
A. *pellucidum*	98	iii	Typ,L	"	2	"	NVF	D	
A. *wildii*	97	iii	" "	"	1-2	b-c	"	D	
A. *athertonense*	98	iii	" "	"	"	"	"	D	
A. *macilwraithense*	105	i,iii	" "	"	"	"	SEVF,NVF	D	
A. *tinarooense*	101	iii	" "	"	"	"	NVF	D	
A. *lewisense*	100	iii	L	"	1-2	"	NVF	D	
A. *excisum*	96	ii+	L,T	scr	1-2	c	MVF	D	
A. *polyodon*	99	i-iv +	Typ	tf	2-3	c	NVF,MVF	D	
A. *parvum*	97	iii+	Typ,L	tf	2	b-c	NVF	D	
A. *baileyanum*	105	iii	" "	scr	1-2	b-c	"	D	
A. *aethiopicum*	104	iv,vi+	L	tf	2-3	c	NVF,Ect, WSF	D	
A. *cuneatum*	103	ii,iii+	Typ,L	scr-tf	2	"	", MVF	D	
A. *laserpitifolium*	102	i,ii+	Typ,L	" "	2-3	"	SEVF,MVF	D	
A. *bulbiferum*	104	iv+	L, T	tf	2-3	"	SNEVF,MFF	D	
A. *flaccidum*	102	iv+	Typ	"	2	"	" ",NVF	D	
A. *obtusatum*	93	iv,vi+	L,T	"	3-5	"	littoral, open	D	-
A. *dimorphum*	101	ii+	L,T	"	2-3	"	Ect	D	
A. *hookerianum*	106	iv +	L,T	"	1-3	"	Wdl,Ect	D	

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Blechnaceae	1 pge.in key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
Stenochlaena									
S. *palustris*	106	i,ii,v+	SEC	lcr	3-5	b-c	MVF,Ect	D	
Lomariopsidaceae									
Lomariopsis									
L. *kingii*	89	iii+	SEC	lcr	3-5	b-c	NVF	D	
Teratophyllum									
T. *brightiae*	89	iii	SEC	m-lcr	2-4	b-c	NVF	D	
Elaphoglossum									
E. *callifolium*	90	iii+	Typ,L	scr	3	b-c	NVF	D	
E. *queenslandicum*	90	iii	" "	"	"	" "	"	D	–
Flowering Plants									
class Magnoliatae (Dicots)									
Pittosporaceae									
Pittosporum									
P. *bicolor*	112	iv	Cas	sh	3-5	c	NVF,Ect	F	
P. *undulatum*	112	"	"	"	" "	c	" "	F	
Piperaceae									
Peperomia									
P. *bellendenkerensis*	115	iii	Typ,L?	frh	?	b-c	NVF ?	A	
P. *johnsonii*	115	iii	" "	"	1-2	" "	"	A	-
P. *leptostachya*	113	i-iv	L,T	"	2	" "	",Ect	A	-
P. *tetraphylla*	114	ii-iv+	Typ,L	"	2-3	" "	"	A	-
P. sp. Massey Ck	114	i	L,Typ	"	2-3	" "	SEVF	A	-
Moraceae									
Ficus									
F. *baileyana*	117	iv	HP	sh	3-5	b-c	NVF	F	
F. *benjamina*	122	i,ii,v+	"	"	"	"	SEVF,MVF, Ect	F	
F. *crassipes*	118	ii,iii	"	"	"	"	N-MVF,Ect	F	-

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	1 pge.in Key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
Ficus (Cont.)									
F. *destruens*	118	i-iii	HP	sh	3-5	b-c	SEVF,M-NVF	F	
F. *drupacea*	120	i,ii	HP,L	"	" "	" "	" ,MVF	F	
F. *leucotricha*	119	v	" "	"	" "	" "	",DVT,Ect	F	
F. *macrophylla*	116	ii-iv	" "	"	" "	" "	M-NVF,MVT	F	
F. *obliqua*	124	i-v	" "	"	" "	" "	" ",DVT, Ect	F	
F. *pantoniana*	126	i, ii+	" "	lcr,sh	" "	" "	SEVF,MVT	F	
F. *platypoda*	125	i-v	L,HP	sh	" "	" "	DVT,Ect, Wdl	F	
F. *pleurocarpa*	119	iii	HP	"	" "	" "	NVF,Ect	F	
F. *rubiginosa*	117	iv	L,HP	"	" "	" "	",MVT,Ect Wdl	F	
F. *subpuberula*	121	i,ii,v	L,HP	"	" "	" "	DVT,Ect, Wdl	F	
F. *superba*	123	i-v+	HP,L	"	" "	" "	"M-NVF, MVT	F	
F. *triradiata*	121	iii	" "	"	" "	" "	NVF	F	
F. *virens*	124	i-v+	" "	"	" "	" "	M-NVF,SEVF, Ect	F	
F. *virgata*	122	i-iii	HP	"	" "	" "	" " " "	F	
F. *watkinsiana*	120	ii-iv	"	"	" "	" "	NVF	F	
F. *microcarpa*	123	i-ii	"	"	" "	" "	SEVF MVF	F	
Urticaceae									
Procris									
P. *cephalida*	126	ii,iii	L,Typ, T	sh	2-3	c	N-MVF	F	–
Araliaceae									
Schefflera									
S. *actinophylla*	127	i-iii iv*	HP,L	sh	3-5	c	SEVF,M-NVF	F	-
S. *versteegii*	127	i	" "	"	" "	"	"	F	
S. *elliptica*	127	i-iii	" "	"	2-4	"	", M-NVF	F	
Polyscias									
P. *wilmottii*	129	iii	HP,T	sh	2-5	c	NVF	F	
P. *elegans*	129	i-iii	Cas	"	3	c	"	F	
Motherwellia									
M. *haplosciadea*	128	iii	SEC	lcr,sh	1-3	c	NVF	F	
Escalloniaceae									
Quintinia									
Q. *sieberi*	130	iv	HP,L,T	sh	1-2	c	SNEVF,MFF	sand-like	
Q. *fawkneri*	130	iii	SEC	lcr,sh	1-3	c	NVF	"	

* introduced into iv

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	1 pge. in key	2 geog. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
Ericaceae									
Rhodondendron									
R. *lochae*	131	iii	L, Typ	sh	1-3	c	SNEVF	W	
Agapetes									
A. *meiniana*	132	iii	HP L,Typ,	sh	2-4	c	SNEVF	F	-
Epacridaceae									
Prionotes									
P. *cerinthoides*	132	iv	SEC, Typ	sh	1-2	c	MFF	sand-like	
Melastomataceae									
Medinilla									
M. *balls-headleyi*	131	i-iii	SEC, Typ, L	sh, mcr	1-2	c	SEVF, M-NVF	sand-like	
Potaliaceae									
Fagraea									
F. *berteriana*	133	i	HP, L	sh	2-4	c	SEVF	F	–
Rubiaceae									
Timonius									
T. *singularis*	134	i-iii	HP	sh	3-4	c	SEVF, M-NVF	F	-
Hydnophytum									
H. *formicarium*	135	i, ii	Typ	frh	2-4	a-b	Swf, SEVF MVF, Ect	F	±
H. sp. Leo Ck	135	i	"	"	3-4	" "		F	–
Myrmecodia									
M. *beccarii*	138	i, ii, v?	Typ	frh	3-4	a-b	Swf MVF, Ect	F	+
M. affe. *beccarii*	138	ii	"	"	2-4	" "	" " Wdl, Swf	F	
M. *antonii*	138	i+	"	"	2-4	" "	" " SEVF, Ect	F	-
M. *muelleri*	137	i	"	"	2-3	" "	" ", Swf	F	±
Asclepiadaceae									
Dischidia									
D. *nummularia*	144	i, ii+	Typ	mcr-lcr	3-4	b	SEVF, Swf MVF, Ect, Wdl	W	+
D. *ovata*	145	i+?	"	" "	2-3	b	SEVF, Ect	W	+
D. *major*	144	i+	"	" "	2-4	b	SEVF, Ect, Wdl, Swf	W	+

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	1 p. in key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
Asclepiadaceae (Cont.)									
Hoya									
H. australis	141	i-iv+	Typ,SEC L,T	m-lcr	2-5	b-c	SEVF, M-NVT,Ect	W	+
H. keysii	140	ii,iii	" " ""	" "	3-5	" "	" " "	W	+
H. macgillivrayi	141	i	" " ""	" "	2-5	" "	"	W	
H. nicholsoniae	142	i-iii	" " ""	" "	" "	" "	"	W	+
H. affe. *rubida*	140	i	" " ""	" "	" "	" "	" DVT	W	
H. poolei	143	i	L,T	" "	3-5	" "	" " Wdl	W	
H. sp. Starke Stn	140	i	L,T	" "	" "	" "	heath	W	
H. sana		i,v	L,T	" "	" "	" "	Wdl	W	
Gesneriaceae									
Boea									
B. hygroscopica	146	iii	L	ros	2-4	c	NVF,Ect	±W	-
Didymocarpus									
D. kinnearii	147	iii	L	ros	2-4	c	SNEVF,Ect	±W	
Fieldia									
F. australis	147	iv	SEC	sh,mcr	1-2	b-c	SNEVF,MFF	F	
class Liliatae (Monocots)									
Pandanaceae									
Freycinetia									
F. australiensis	151	ii	SEC,T	lcr	1-4	b	MVF	F	
F. excelsa	151	i-iii	" "	"	1-3	b	M-NVF,SEVF	F	
F. scandens	150	i-iii	" "	"	" "	b	" " "	F	
F. affe. *excelsa*	151	i,ii	" "	"	" "	b	MVF,SEVF	F	
Araceae									
Pothos									
P. longipes	152	ii-iv	SEC	m-lcr	1-2		M-NVF	F	-
Rhaphidophora									
R. australasica	153	ii,iii	SEC	lcr	1-3	b-c	M-NVF	F	
R. affe. *australasica*	153	ii	"	"	" "	" "	MVF	F	
R. pachyphylla	154	ii +	"	lcr-mcr	" "	" "	"	F	-
R. sp. Silkwood	154	ii	"	"	" "	" "	"	F?	
R. sp. Arnhem Land		v	"	"	" "	" "	SEVF?	F?	

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	1 pge.in key	2 geog. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
Scindapsus									
S. *altissimus*	155	i +	SEC	lcr	2-5	b,c	SEVF	F	
Epipremnum									
E. *pinnatum*	155	ii +	SEC	lcr	2-4	b,c	M-NVF	F	
Orchidaceae									
subtribe Malaxidinae									
Oberonia									
O. *attenuata*	164	ii	Typ	fan	1-2	a-b?	MVF	D	
O. *palmicola*	164	i-iv	"	fan	2-4	a-b	SEVF,M-NVF	D	
O. *muelleriana*	163	i-iv +	",L	fan	3-4	a-b	" " "	D	+
O. *carnosa*	164	i	",L	fan	3-4	a-b	",Ect	D	
Liparis									
L. *reflexa*	160	iv	L	scr,pb	3-4	b-c	WSF,Ect	D	-
L. *bracteata*	161	iii	L	" "	2-3	b-c	NVF	D	-
L. *fleckeri*	161	iii	L	" "	2-3	b-c	"	D	
L. *nugentae*	162	iii	Typ,L	" "	2-3	b	"	D	-
L. *angustilabris*	162	iii	" "	" "	2-3	b	"	D	
L. *coelogynoides*	159	iv,(iii?)	" "	" "	2-4	b	",MVT	D	-
L. *persimilis*	163	i	"	" "	3	b	SEVF	D	-
subtribe Dendrobiinae									
Dendrobium									
subgenus : *Athecebium*									
§ Rhizobium									
D. *wassellii*	168	i	Typ	e,mcr,ls	4	a-b	SEVF,Ect	D	+
D. *linguiforme*	167	ii-iv	",L	mcr,ls	2-4	a-b	NVF-Wdl, Swf	D	+
D. *cucumerinum*	168	iv	"	" "	3-4	a-b	MVT,Wdl, Ect	D	+
§ 2									
D. *lichenastrum*	169	ii,iii	Typ,L	mcr,ls	2-4	b	NVF,Ect	D	+
D. *toressae*	170	ii,iii	" "	" "	2-4	b	M-NVF,WSF, Ect	D	+
§ 3									
D. *teretifolium*	170	i-iv +	Typ	p,frh,tgl	2-4	a	SEVF,M-NVF MVT,Ect,Swf	D	+
D. *racemosum*	174	iii	"	" "	3-4	a-b	NVF,Ect	D	+
D. *mortii*	173	ii-iv	"	" "	3-4	a	NVF,DVT, MVT,Ect	D	+

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§ 3 (Cont.)	1 pge.in key	2 geog distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
D. *striolatum*	171	iv	L	mcr,e,ls	3-4	b-c	WSF,Ect	D	
D. *beckleri*	173	iv	Typ	frh,ls,typ	4	a	NVF,MVT	D	+
D. *tenuissimum*	172	iv	"	p" " "	2-3	b	SNEVF,NVF	D	
D. *pugioniforme*	175	iv	"	" " " "	2-4	b	MVT," "	D	+
D. *rigidum*	175	i,ii +	"	frh,ls	3-4	a-b	Ect SEVT,MVT,	D	+
§ Monophyllaea									
D. *carrii*	177	iii	Typ	pb,mcr	4-5	a-b	NVF	D	
D. *monophyllum*	176	iii,iv	"	" "	4	" "	"	D	-
D. *schneiderae*	176	iii,iv	"	" scr	3-4	" "	"	D	
§ Dendrocoryne									
D. *speciosum*	185	(+?) ii,iv	Typ,L	pb,scr,e	3-4	b-c	MVT NVF,WSF,Ect	D	+
D. *ruppianum*	183	i-iii	" "	" " "	3-4	" "	" " "SEVF	D	-
D. *aemulum*	180	iii,iv	Typ	" " "	2-4	b	" " "	D	
D. *gracilicaule*	180	iii,iv	"	" " "	2-3	b	" MVT	D	±
D. *kingianum*	185	iv	L	" " "	3-4	c	WSF,Ect	D	
D. *falcorostrum*	183	iv	Typ	" " "	3-4	b	MFF	D	
D. *adae*	181	iii	"	" " "	3	"	NVF	D	-
D. *fleckeri*	182	iii	"	" " "	3	"	Ect "SNEVF,	D	-
D. *tetragonum*	179	i-iv	"	" " p	2	"	", Swf	D	+
§ Latourea									
D. *bairdianum*	177	iii	Typ	pb,scr,e	3-4	a-b	WSF,Ect	D	
D. *bifalce*	178	i	"	" " "	2-4	" "	SEVF	D	+
subgenus : *Eu-Dendrobium*									
§ Phalaenanthe									
D. *bigibbum*	186	i,iii +	Typ,L	pb,scr	4	a-b	DVT	D	+
D. *dicuphum*	187	v	Typ	" "	4	" "	",Swf,Wdl	D	+
§ Ceratobium									
D. *canaliculatum*	187	+ i-iii,v	"	" "	4-5	" "	Wdl,Swf	D	+
D. *carronii*	188	i+	"	" "	4	" "	Swf/Wdl	D	
D. *semifuscum*	190	i,ii +	"	" "	4-5	" "	Wdl,Swf	D	+
D. *discolor*	189	i,ii +	",L	" "	3-5	" "	Ect MVF,SEVF,	D	+
D. *johannis*	190	i+	Typ	" "	4	" "	Swf/wdl	D	
D. *antennatum*	192	i+	"	" mcr	3-4	" "	SEVF	D	+

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	1 pge.in key	2 geog. distr.	3 life form	4 physiog. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
§ Ceratobium (Cont.)									
D. *nindii*	192	i,ii+	Typ	pb,scr,e	4	a	MVF,Man., Ect	D	+
D. *mirbelianum*	191	i,ii+	"	" " "	3-4	a-b	" "	D	
§ Eugenanthe									
D. *stuartii*	194	i	Typ	pb,scr,p	2	b	SEVF	D	
§ Trachyrhizum									
D. *agrostophyllum*	193	iii	Typ,L	pb,mcr,e	3-4	b	NVF,Ect	D	-
§ Pedilonum									
D. *smilliae*	193	i,ii+	Typ,L	pb,scr,s	2-4	b-c	MVF,Ect SEVF	D	-
subgenus : *Xerobium*									
§ Grastidium									
D. *luteocilium*	195	i,ii	Typ	scr,e-s	3	b	SEVF,MVF	D	+
D. *cancroides*	195	i,ii	"	tf,s-p	2	b	" "	D	-
D. *baileyi*	196	i-iii	"	" " "	2-3	b	" M-NVF	D	-
D. *tozerensis*	197	i	",L	",e-s	3	a-b	"	D	
§ Monanthos									
D. *malbrownii*	197	i	Typ	tf,e-s	3	a-c	SEVF	D	-
Cadetia									
C. *taylori*	198	i-iii	Typ,L	pb,scr,e	3	b-c	SEVF,NVF	D	-
C. *maideniana*	199	i,ii	"	tf,ls,s	2-3	b	", MVF	D	+
C. *collinsii*	199	i	"	" " "	3	b	"	D	
C. *wariana*	199	i+	"	pb,ls,scr	3	b	"	D	+
Flickingeria									
F. *comata*	200	i+	Typ	pb,tf,e	3	b	SEVF	D	-
F. *convexa*	201	i,ii+	"	",ls,mcr	4-5	a-b	",Man	D	+
Diplocaulobium									
D. *glabrum*	201	i,ii+	Typ	pb,mcr	3-4	b	Ect SEVF,MVF	D	-
D. *masonii*	202	ii	"	" "	?	?	Man,Ect	D	
subtr. Bulbophyllinae									
Bulbophyllum									
§ Cirrhopetalum									
B. *longiflorum*	211	i+	Typ	pb,mcr	2-3	b	SEVF	D	
B. *gracillimum*	212	i+	"	" "	3	b	"	D	
B. *elisae*	210	iv	",L	"S-mcr	3-4	b	NVF,Ect	D	-

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	1 pge. in key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
§ Sestochilus									
B. *baileyi*	209	i-iii+	Typ,L	pb,ls,mcr	2-4	b	SEVF,M-NVF	D	+
§ Ephippium									
B. *masdevalliaceum*	212	i+	Typ	pb,s-mcr	3	b	Ect SEVF	D	
§ 4									
B. *nematopodum*	211	iii	"	pb,scr	3-4	b	NVF	D	-
§ Polyblepharon									
B. *macphersonii*	207	iii	"	pb,sl,scr	3	b	NVF	D	+
B. *crassulifolium*	208	iv	",L	" " "	3	b	",Ect	D	
B. *aurantiacum*	204	iii,iv	Typ	" ",mcr p	3-4	b	"	D	+
§ 6									
B. *weinthalii*	216	iv	Typ	pb,scr	4	b	NVF	D	
§ Micromonanthe									
B. *bowkettae*	213	i,iii	Typ	pb,ls,m-lcr	3-4	a-b	WSF NVF/Ect,	D	
B. *johnsonii*	214	iii	Typ	pb,mcr	3	b	",Ect	D	±
§ 8									
B. *minutissimum*	203	iv	Typ	pb,aph	4	a-b	NVF,Ect	D	+
B. *globuliforme*	204	iv	"	" "	4	b	"	D	
§ Macrouris									
B. *lageniforme*	218	iii	Typ	pb,s-mcr	2	b	NVF,SNEVF	D	
B. sp. Bellenden Ker	217	iii	"	pb,scr	4	b	"	D	
B. *newportii*	215	i,iii	",L	pb,s-mcr	3	b	"	D	
B. *bracteatum*	216	iv	"	",scr	3-4	a-b	"	D	
B. *lilianae*	214	iii	"	",mcr	3-4	b	"	D	-
B. *exiguum*	215	iv	",L	" "	3-4	b	Ect ",SNEVF,	D	
B. *tuberculatum*	219	iv+	"	", scr	3	b	"	D	
§ Globiceps									
B. *evasum*	205	iii	Typ	pb,mcr	2-3	b	NVF	D	-
§ Fruiticicola									
B. *radicans*	205	iii	Typ	ls,mcr/p	2-3	b-c	NVF	D	
§ Oxysepalum									
B. *wadsworthii*	208	iii	Typ,L	ls,mcr/e	3	b	NVF,Ect	D	
B. *gadgarrense*	206	iii	"	ls,mcr/p	3	b	"	D	
B. affe. *gadgarrense*	207	iii	"	" " "	3	b	"	D	

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subtr. Coelogyninae	1 pge. in key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
Pholidota									
P. pallida	219	i,ii	Typ,L	pb,scr	3	b-c	SEVF,MVF, Swf	D	+
subtr. Eriinae									
Eria									
E. dischorensis	222	i,ii+	Typ	pb,s-mcr	3	b	Ect SEVF,NVF,	D	
E. eriaeoides	221	iii	"	pb,mcr	3	b-c	NVF	D	-
E. fitzalani	221	i,iii	"	pb,scr	3-4	b	SEVF M-NVF/Ect	D	-
E. inornata	222	i,ii+	"	" "	3	b	" " " "	D	
E. irukandjiana	223	i,ii	"	pb,ls,scr	4	b	Ect SEVF,NVF,	D	+
E. queenslandica	220	i-iii	",L	pb,scr	3	b-c	NVF	D	
Podochilus									
P. australiensis	223	i,ii	Typ	tf,e	2-3	b	MVF,SEVF	D	-
subtr. Thelasiinae									
Oxyanthera									
O. papuana	234	i+	Typ	fan	2	b	SEVF	D	-
Rhynchophreatia									
R. micrantha	235	i,ii+	Typ	fan	2-3	b	SEVF,MVF	D	-
Phreatia									
P. crassiuscula	236	iii	Typ	ls,fan	3-4	b	WSF NVF/Ect,	D	-
P. baileyana	236	iii	"	" "	2-3	b	NVF	D	-
subtr. Cymbidiinae									
Acriopsis									
A. javanica	226	i,ii	Typ	pb,scr,nf	3	b,c	Swf SEVF,MVF,	D	
Cymbidium									
C. canaliculatum	225	i-v	Typ	pb,ls,scr	3-5	c	Wdl	D	+
C. madidum	225	i-iv	"	pb,scr	3	c	NVF,Ect	D	-
C. suave	226	iii-iv	"	scr	3-4	c	WSF	D	-
Dipodium									
D. pandanum	224	i +	HS,T	f-l,mcr	1-3	a-c	SEVF	D	-
subtr. Vandinae									
Vanda									
V. whiteana	237	i	Typ,L	f-l,tgl	3-4	a	SEVF	D	+

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<u>Vandinae</u> (Cont.)	1 pge. in key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
Luisia									
L. *teretifolia*	238	i,ii+	Typ	e,frh,ls	4	a	Ect MVF,SEVF,	D	+
Phalaenopsis									
P. *amabilis*	239	i,ii+	Typ	f-l	2,3	a	DVT NVF,SEVF,	D	+
Drymoanthus									
D. *minutus*	240	iii	Typ	f-l	3	a-b	NVF	D	
Schoenorchis									
S. *sarcophylla*	242	i+	Typ	f-l,ls	3	a	SEVF	D	
S. *densiflora*	241	i,ii+	"	fl,ls,tgl	3	a-b	MVF,SEVF	D	+
Taeniophyllum									
T. *glandulosum*	242	i-iv+	Typ	aph,rtf	3-4	a	NVF,Ect SEVF/Ect	D	
T. *flavum*	243	iii	"	" "	2	a	NVF	D	
T. *lobatum*	243	iii	"	" "		a	"	D	
T. *malianum*	244	i+	"	" "	2-3	a	SEVF	D	+
T. sp. B. Gray		iii	"	" "		a		D	
Peristeranthus									
P. *hillii*	240	iii,iv	Typ	f-l	2-3	a	NVF	D	
Robiquetia									
R. *tierneyana*	245	i,ii	Typ,L	f-l	2	a	SEVT,MVF	D	+
R. *wassellii*	245	i	"	"	2-3	a	"	D	+
Saccolabiopsis									
S. *armitii*	246	i-iii	Typ	f-l	3	a	DVT	D	+
S. *rectifolia*	247	iii	"	"	2-3	a-b	NVF	D	
Trachoma									
T. *subluteum*	249	iii	Typ	f-l,ls	3	a	NVF	D	+
T. *rhopalorrachis*	248	i+	"	" "	3-4	a	SEVF	D	+
T. aff. *rhopalorrhachis*	248	i	"	" "	" "	a	"	D	
Micropera									
M. *fasciculata*	250	i,ii+	Typ	f-l,tgl	3	a	MVT,Ect	D	+
Pomatocalpa									
P. *marsupiale*	251	i+	Typ	f-l	3	a-b	SEVT	D	
P. *macphersonii*	251	i,ii	"	"	2-3	a-b	" M-NVT	D	+

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subtribe Vandinae (Cont)	1 pge. in key	2 geogr. distr.	3 life form	4 physiogn. type	5 expos. pref.	6 root cover	7 commun. pref.	8 dissem.	9 CAM
Trichoglottis									
T. australiensis	252	i	Typ	f-l,p	2-3	a	SEVF	D	+
Thrixspermum									
T. congestum	254	i,ii	Typ	f-l,tgl	3	a	MVF,Ect	D	+
T. platystachys	253	i,ii	"	" "	3	a	"	D	
Mobilabium									
M. hamatum	254	iii	Typ	f-l,tgl	3-4	a	NVF,Ect	D	+
Plectorrhiza									
P. brevilabris	255	i-iv	Typ	f-l,tgl	2-4	a	NVF	D	
P. tridentata	255	ii-iv	"	" "	3-5	a	NVF,MVT, Ect	D	+
Papillilabium									
P. beckleri	256	iv	Typ	f-l,rgl	3	a	NVF/Ect	D	
Schistotylus									
S. purpuratus	257	iv	Typ	f-l	3	a	SNEVF, MFF/Ect	D	
Rhinerrhiza									
R. divitiflora	259	iii,iv	Typ	f-l	2-3	a-b	NVF,MVT	D	+
Sarcochilus									
S. fitzgeraldii	263	iv	L	f-l	2	b-c	NVF	D	
S. hartmannii	263	iv	L	"	3-4	b-c	Ect	D	
S. falcatus	260	iii,iv	Typ,L	"	2-4	a-b	SNEVF,MFF NVF,MVT,	D	+
S. olivaceus	262	iii,iv	" "	"	2	a	NVF	D	
S. australis	262	iv	"	"	2-3	a	SNEVF,MFF	D	
S. dilatatus	261	iv	"	"	3-4	a	NVF	D	
S. serrulatus	261	iii	"	"	2-3	a	NVF	D	
S. tricalliatus	265	ii,iii	"	"	2-4	a	DVT	D	
S. hillii	265	iv	"	"	3-5	a	MVT NVF/Ect,	D	+
S. ceciliae	266	ii-iv	L	"	3-4	b-c	Ect,Wdl	D	+
S. weinthalii	260	iv	Typ	"	3-4	a-b	NVF,MVT	D	
S. moorei	264	i	"	"	2-3	a-b	SEVF	D	+
Pteroceras									
P. hirticalcar	258	i	Typ	f-l	3	a	SEVF,DVT	D	
P. spathulatus	258	iv	"	"	2-3	a	NVT,Ect	D	
Chiloschista									
C. phyllorhiza	266	i,ii,v	Typ	aph,rtf	3	a	SEVF,MVF Man	D	+

Results 2.3.2 : Accidental epiphytes

Following is a list of a few examples of normally terrestrial species which in these instances were found growing in "low grade" epiphytic microhabitats. These were seedlings or juveniles except for the herb *Phytolacca* and small shrub *Citriobatus*, which were both fruit-bearing.

Ferns :

Lastreopsis sp. (Aspidiaceae), on mossy butt of *Schizomeria ovata*, New England National Park, NSW.

Gymnosperms :

Podocarpus amarus Bl. (Podocarpaceae), in nest of *Platycerium superbum*, Atherton Tbld, Qld.

Dicots :

Cryptocarya triplinervis R.Br. (Lauraceae), in humus in hollow limb of *Ficus obliqua*, Port Macquarie, NSW.

Phytolacca octandra L. (Phytolaccaceae), in humus in fork of *Eucalyptus viminalis* near Dorrigo, NSW.

Orites excelsa R.Br. (Proteaceae), on mossy butt of *Schizomeria ovata*, New England National Park, NSW.

Elaeocarpus holopetalus F.Muell. (Elaeocarpaceae), in humus in fork of *Nothofagus moorei*, New England NP, NSW.

Polyosma cunninghamii J.J.Benn. (Escalloniaceae), in *Dictymia brownii* nest on *Ficus watkinsiana*, Dorrigo NP, NSW.

Citriobatus pauciflorus A.Cunn. ex Ettingsh. (Pittosporaceae), in nest of *Platycerium bifurcatum*, Port Macquarie, NSW.

Dendrocnide excelsa (Wedd.)Chew, on *Sloanea woollsii*, Washpool State Forest, NSW.

Mischocarpus pyriformis (F.Muell.)Radlk., (Sapindaceae), in rotten wood of host of *Ficus obliqua*, Port Macquarie, NSW.

Kissodendron australianum F.Muell., in *Platycerium hillii* nest, McIlwraith Ra., Qld.

Brachychiton acerifolius F.Muell. (Sterculiaceae), in nest of *Platycerium superbum*, Comboyne, NSW.

Alyxia ruscifolia R.Br. (Apocynaceae), in nest of *Asplenium australasicum*, Atherton Tabld, Qld.

Parsonsia straminea (R.Br.)F.Muell., in humus in fork of *Ficus obliqua*, Port Macquarie; in humus in fork of *Ficus watkinsiana*, Dorrigo NP; in knot-hole of *Backhousia sciadophora*, Long Point, NSW.

Monocots :

Alocasia macrorhizos (L.)G.Don (Araceae) in humus pocket on *Ficus obliqua*, Port Macquarie, NSW.

Dianella caerulea Sims (Liliaceae) in humus in broken branch of *Nothofagus moorei*, NENP, NSW.

Cordyline stricta Endl. (Agavaceae), in rotten wood of host of *Ficus obliqua*, Port Macquarie, NSW.

Results 2.3.3 Facultative terrestrial/lithophyte/low epiphyte spp.

These species normally grow in well drained, moist microsites on banks or mossy rocks, e.g. in gullies or by streams and occasionally on treefern butts or mossy treetrunk bases. The list is not exhaustive; those marked * are more commonly lithophytic or epiphytic and border on casual epiphytic status.

Ferns :

Marattia salicina Sm. (Marattiaceae)
Oenotrichia tripinnata (F.Muell.) (Dennsteadtiaceae)
Pteris vittata L. (Pteridaceae)
P. cretica L. (Pteridaceae)
P. ensiformis Burm. (Pteridaceae)
Adiantum hispidulum Sw. (Adiantaceae)
Christella parasitica (L.)Lev. (Thelypteridaceae)
Cyrtomium falcatum (L.f.)Presl (Aspidiaceae)
Lastreopsis tinnarooensis Tindale (Aspidiaceae)
Cheilanthes distans (R.Br.)Mett. (Sinopteridaceae)
C. tenuifolia (Burm.f.)Sw. (Sinopteridaceae)
Pellaea falcata (R.Br.)Fée (Sinopteridaceae)
P. paradoxa (R.Br.)Hook. (Sinopteridaceae)
**Asplenium attenuatum* R.Br. (Aspleniaceae)
**A. flabellifolium* Cav. (Aspleniaceae)
**A. paleaceum* R.Br. (Aspleniaceae)
**A. wildii* F.M.Bail. (Aspleniaceae)
**A. bulbiferum* Forst.f. (Aspleniaceae)
A. obtusatum Forst.f. (Aspleniaceae)
Doodia aspera R.Br. (Blechnaceae)

Dicots :

Crassula sieberiana (Schultes)Druce (Crassulaceae)
Calandrinia eremaea Ewart (Portulaceae)
Piper spp. (Piperaceae)
Peperomia leptostachya Hook. et Arn. (Piperaceae)

**Pittosporum undulatum* Vent. (Pittosporaceae)
Epacris reclinata A.Cunn. ex Benth. (Epacridaceae)

Monocots:

Allania endlicheri Kunth (Liliaceae)
Borya serpentrionalis F.Muell. (Liliaceae)
Astelia sp. nov. (Liliaceae)
Lomandra longifolia Labill. (Xanthorrhoeaceae)
Rimacola elliptica (R.Br.)Rupp. (Orchidaceae)
Malaxis fimbriata P.S.Lavarack (Orchidaceae)
Cheirostylis ovata (F.M.Bail.)Schltr. (Orchidaceae)

Results 2.3.4 : Synopsis of the Australian Vascular Epiphyte Flora

a. Taxonomic Group Strengths

Totals : divisions 4, families 33, genera 115, spp. 378.

Breakdown :

FERN ALLIES : 2 divisions, 3 families, 3/16 (genera/spp.)

division Psilophyta : *Psilotum* 2, *Tmesipteris* 6
" Lycopodophyta : *Lycopodium* 8

FERNS : 1 division, Pterophyta : 2 classes, 13 families, 49/153
class Eusporangiatae : *Ophioglossum* 1
" Leptosporangiatae, larger families :
Hymenophyllaceae 15/46
Grammitidaceae 4/19
Polypodiaceae 10/27
Aspleniaceae 1/27

SEED PLANTS : 1 division, Anthophyta, 2 classes, 17 families 63/221
class Magnoliatae (dicots) : 14 fams, 21/61; *Ficus* 19, *Hoya* 8
" Liliatae (monocots) : 3 fams, 42/162
fam. Orchidaceae 37/152
subtribe Dendrobiinae 4/79 - *Dendrobium* 45
" Bulbophyllinae 1/26 - *Bulbophyllum*
" Vandinae 22/44

Table 2.1b Main Geographic Distribution Patterns :

	i	ii	iii	iv	v	i,ii	i,iii	i-iv	i-v	ii,iii	ii-iv	iii,iv	+
Pteridophytes	5	12	49	24	0	3	15	9	3	6	4	13	75
Orchids	29	3	34	26	1	28	0	7	1	0	6	19	37
Others	12	5	6	6	1	4	7	3	4	4	5	1	7
Totals	44	20	89	56	2	35	28	16	8	10	14	33	119

In each category is listed the number of species restricted (in Australia) to that region or combination of regions.

Table 2.1c Life Form Groupings

	Typical	Hemi	SEC	True Litho.	Cas.	Acc.
Pteridophytes	131(79)*	0	13	13	20	1
Orchids	136(20)*	1	0	5	7	3
Others	24(20)*	26	22	3	6	13
Totals	291	27	35	21	33	17

* number of species which are casually lithophytic

Table 2.1d Physiognomic Type etc

	Sedentary	lcr/mat	tgl	aph	shr	frh	nf	h'phile	h'phobe
Pteridophytes	91	78	0	0	0	0	10	40	0
Orchids	111	38	14	8	0	11	3	12	111
Others	18	26	0	0	35	11	0	18	6
Totals	120	142	14	8	35	22	13	70	117

Table 2.1e Expsoure preference index, means :

Fern allies	2.30	All pteridophytes	2.36
Hymenophyllaceae	1.10	Orchids	3.20
Polypodiaceae	2.93	Others	3.11

Table 2.1f CAM, presence or absence :

$\delta^{13}C$ ‰	(-CAM) < -23	(±CAM) -20 to -23	(+CAM) > -20	Totals
Pteridophytes	17	2	3	22
Orchids	35	2	53	90
Others	15	2	7	24
Totals	67	6	63	136

Table 2.1g Disseminule Type Groupings

	Dust	Winged	Fleshy	Adherent
Pteridophytes	159	0	0	0
Orchids	153	0	0	0
Others	4	24	39	5
Totals	316	24	39	5

2.4 Discussion

2.4.1 General considerations

About 380 species of vascular epiphytes occur in Australia, representing 33 families and 115 genera. They form 2.8% of the whole vascular flora of the continent and ca 1.4% of the estimated world vascular epiphyte flora. Since epiphytes are about 10% of the world flora (Madison, 1977*a*) and the area of Australia is very much more than 1.4% of the world land surface, the vascular epiphyte flora of Australia must be considered as very impoverished, even when compared with Africa which is also generally considered depauperate (Stewart & Campbell, 1970; Johansson, 1974; Madison, 1977*a*). Undoubtedly the reasons for this poverty relate to the scarcity of suitable environments, in turn a result of past and present aridity of climate. This is further discussed in 2.5 of this chapter. Similar reasons have been invoked to explain the African situation (Mildbraed, 1922; Richards, 1973).

Floristic poverty is compounded by low degree of endemism. No taxon higher than genus is endemic among the Australian vascular epiphytes and only eight genera, all monotypic, are truly endemic viz, *Motherwellia* (Aral.), *Prionotes* (Epacrid.), *Fieldia* (Gesner.) and the monopodial orchids *Peristeranthus*, *Mobilabium*, *Papillilabium*, *Schistotylus* and *Rhinerrhiza*. *Plectorrhiza* has two species endemic on the mainland and one on Lord Howe I.; *Sarcochilus* R. Br., in the strictest sense, has 11 species here, one extending to New Caledonia. *Dendrobium* Sections *Rhizobium* (3 spp.) and *Dendrocoryne* 10 spp.) are also largely endemic here.

2.4.2 The Groups

The <u>fern allies</u> are apparently ancient plants, both groups represented here, the Psilophyta and the Lycopodophyta, are known as fossils from as early as the mid Palaeozoic Era (Sporne, 1970). They have therefore had time to migrate to wherever conditions have been suitable in the past. Thus *Psilotum nudum* is pantropical and subtropical, though the genus *Tmesipteris*, on the other hand, is restricted to E. Australia, NZ and S.W. Pacific (1 sp. in Philippines - Jones and Clemesha, 1976) which may indicate a Gondwanaland origin. The dispersability of their dust disseminules may be countered by their ecological specialisation - they occur almost exclusively on treefern trunks in cool, moist communities.

Epiphytic *Lycopodium** species are also pantropical in occurrence and none of the eight Australian species is endemic.

The eusporangiate fern *Ophioglossum pendulum* ranges from Malagasy to Taiwan to the SW Pacific and Australia; it has ecological requirements similar to the epiphytic *Lycopodium* species. (*Ophioglossum* illus. Plate 4.3)

All the eusporangiate epiphytic pteridophytes are relatively small plants** of sedentary, tufted, pendulous habit and possibly have developed epiphytism to evade competition for light. However, their ability to develop drought tolerance seems limited, thus they are restricted to lower, more mesic microsites* (mean exposure preference index, 2.30) in wetter rainforests and are ± strongly humiphilic. Their dust disseminules facilitate dispersal to appropriate microsites within the community and also long distance to new localities.

The Hymenophyllaceae are reasonably well represented in Australia with 46 species in 15 genera; almost all are epiphytic and/or lithophytic. They appear to be strongly ecologically constrained by their almost totally unprotected leaf anatomy to growing only in the least water stressed microhabitats (mean exposure preference index, 1.10), where they can remain well drained and moderately well ventilated without rapid water loss. This is in spite of the fact that many possess considerable resurrection ability. Many, especially the smaller forms, are long-creeping and mat-forming and thus for this reason as well as the abovementioned, they are ecological equivalents of bryophytes. They are distributed ± worldwide wherever these conditions obtain, particularly in cooler areas such as tropical montane cloud forests and the like. About half of the Australian species are endemic but some of the others are widespread; several are only known from single collections in Australia but this may merely reflect their unobtrusive stature and habit and difficulty of identification.

The remaining typical leptosporangiate ferns are rather diverse both taxonomically and morphologically/physiognomically, although there is a tendency for homogeneity of life form & physiognomy within taxonomic groups.

The Vittariaceae (4 genera/7 spp. in Australia), Grammitidaceae (4/19), *Asplenium* (27), *Elaphoglossum* (2), *Belvisia* (1) and *Polystichum* (1 ep.) mostly are tufted, sedentary true epiphytes or often facultatively lithophytic. Spp. of

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* see Plate 4.1

** No extant species have secondary stem thickening though some fossil lycopods e.g., *Lepidodendron*, grew to tree size.

Antrophyum, *Vittaria* and several of *Asplenium* are pendulous whereas the rest are erect or semi-erect. Except for *Asplenium obtusatum*, a subsucculent, (non-CAM) seashore lithophyte, all typically have exposure preference indices less than 3. *Asplenium nidus* , *A. australasicum* and *A. simplicifrons* are effective nest-formers but apparently lack other drought resisting adaptations.

The Davalliaceae (3/6) are a distinctive group in being taxonomically close-knit, true epiphytes or lithophytes that have dissected leaves, medium creeping, fleshy rhizomes and are ± strongly humiphilic. While they are typical of relatively mesic microhabitats, they often occur in more xeric situations, probably owing to their nest-invading habit, some water storage capacity in the rhizome, abscisable leaves in most and deciduousness in e.g. *Davallia solida* in monsoon rainforests of the McIlwraith Ra. Both *Humata* species have resurrection ability.

Oleandra (1) and *Nephrolepis* (6) are also distinctive in morphology and habit. They are as often semi-terrestrial or lithophytic as epiphytic and are 'mobile' by means of elongated leafless stem sections, or stolons which terminate in tufts of leaves. Their leaves or leaflets are articulate and may be dropped under water stress.

The Polypodiaceae (10/27) are diverse physiognomically and ecologically but show a trend towards xerophytism using various drought-resisting adaptations. One group has medium-creeping, often somewhat fleshy rhizomes (*Drynaria*, *Schellolepis* and some *Microsorium*) and others a long-creeping, usually more wiry one (*Crypsinus*, *Pyrrosia*, *Colysis*). Leaves are usually simple, entire and articulated on the rhizome. The most effective of epiphyte nest-formers occur in the genera *Drynaria* and *Platycerium* and some old specimens may come to weigh hundreds of kilograms. *Drynaria rigidula* and *D. quercifolia* have drought-deciduous pinnae. *Platycerium* and *Pyrrosia* have a stellate indumentum best developed in *Platycerium veitchii*, the most xerophytic member of the genus. Also, these two genera are the only pteridophytes known to exhibit CAM. *Platycerium superbum* yielded a $\delta^{13}C$ value of -22.8 / indicating weak CAM while *Pyrrosia longifolia*, *P. dielsii* and *P. confluens* gave values indicative of moderate to strong CAM.

Thus this family is more advanced in characters that are, or apparently are of value in maintaining favourable water balance within the plant. This correlates with a higher mean exposure preference index of 2.93 as against 2.36 for all the epiphytic pteridophytes of Australia.

Plate 2.9

Platycerium veitchii (Underw.) C.Chr., an obligate lithophyte of open monsoonal woodland in the ranges of north and central eastern Qld. It is the sole member of the genus inhabiting dry, open communities and has a dense stellate tomentum. About one third full size.

Plate 2.10

Peperomia tetraphylla (Forst.f) Hook.& Arn., a facultative epiphyte/lithophyte with a thick, non-green watery leaf hypodermis and dense mesophyll, i.e., is non-CAM. Inhabits lower zones of moist rainforest. Pantropical. About two thirds full size.

The semi-epiphytic climber life form cuts across taxonomic lines but is well defined physiognomically and ecologically. This group includes *Lindsaea* (2 spp.), *Arthropteris* (4), *Colysis* (2), *Microsorium* (1 or 2), *Stenochlaena* (1), *Lomariopsis* (1) and *Teratophyllum* (1). The last 3 are high climbers and usually only produce fertile leaves on reaching higher zones (Holttum, 1978). SECs begin as typical terrestrial plants but climb on trees and rocks, often losing stem connection (but mostly not root connection) to the soil with age.

Pteridophytes are generally considered to be of ancient origin and slow evolving or at evolutionary dead-ends. Three features of the Australian epiphytic pteridophyte flora support such ideas. Firstly they occupy lower, less bright, less water-stressed microhabitats - only a few have been able to develop sufficient drought resistance ability to invade brighter, drier epiphyte zones. The mean exposure preference index for all pteridophytes listed is 2.36 against 3.25 for the rest of the vascular epiphytes. Second is the very low degree of endemicity, with no genera and only 61 of the 169 species endemic which indicates that speciation resulting from geographic isolation is very slow. Alternatively the high dispersibility of the disseminules may mean that isolation does not occur as often as is apparent. Thirdly, the prominence of humiphilic species in the groups further indicates a lack of ability to adapt to 'non-soil' conditions.

The dicot or magnoliate epiphytes of Australia are a smaller but diverse group with 61 species representing 21 genera and 14 families. True epiphytes are a minority group (24 spp.), hemi-epiphytes being more common (26 spp.) with semi-epiphytic climbers numbering 12 species. Woody shrubs predominate, most of which are primary hemi-epiphytes (e.g. *Ficus*, 18 spp.) but there is also a prominent contingent of sedentary fruticose herbs such as *Peperomia* (5 spp.), *Myrmecodia* (4 spp.), *Hydnophytum* (2 spp.) and some growth forms of *Hoya* and *Dischidia*. Dicots were also the most common of the accidental epiphytes recorded (12 of 17 - see Results 2.3.2).

Two special growth habits require mention, both in species of *Quintinia*. *Q. seiberi* of E. NSW is often a normal terrestrial or lithophytic shrub and tree but commonly it germinates on the trunks of treeferns and developes as a crude type of strangler or primary hemi-epiphyte. Its congener, *Q. fawkneri* of montane N. Qld develops first as a terrestrial, long-creeping, herbaceous vine, climbing up tree trunks and gradually becoming woody and thickened and thus forming a woody lattice around the phorophyte; thus it somewhat resembles in habit *Metrosideros fulgens* of NZ.

Plate 2.11

Ficus watkinsiana F.M.Bail. foliage and figs; the latter are purple with yellow spots when ripe. Terminal bud here is still covered with the stipule. Occurs in wet rainforest from N Qld to N NSW. About ½ full size.

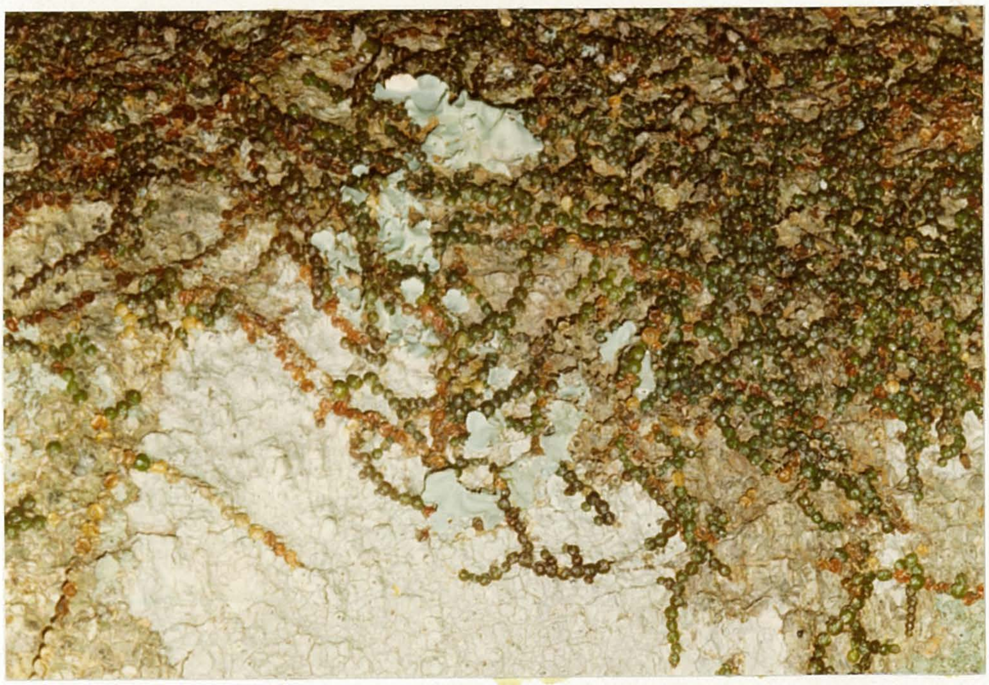

Plate 2.12 *Bulbophyllum minutissimum* (F.Muell.)F.Muell., a pseudobulbous aphyll of exposed rainforest zones or sometimes lithophytic in more open communities. It is a CAM plant and its stomates are restricted to an apical crypt in the pseudobulb. Slightly less than full size.

Disseminule type and dispersal method are biological functions that bear on epiphytism in the "other" group. Only four species have dust seed and in these is rather coarse; the rest are either fleshy and bird dispersed (27), winged and wind-blown (24) or in the case of *Peperomia* (5), adherent, presumably to passing mammals and birds. These methods of dispersal are not as effective in either covering distance or 'saturating' the surroundings to land a few seed in ideal microsites as in the dust diaspore method. This may then be one explanation for the lower numbers of dicot epiphytes and their confinement, largely to the tropics. Another is that the secondary, woody stem thickening enables most dicots to compete effectively for light as trees, shrubs or vines, hence there is not the same "need" for epiphytism as in groups where this ability is rare or absent such as monocot and pteridophyte groups.

The small group of <u>non-orchid monocots</u> likewise are not typical epiphytes but are all semi-epiphytic climbers (SEC) or hemi-epiphytes. Very often the seedlings of the araceous group (4 genera, 8 spp.) are true, low epiphytes but almost invariably send a substantial number of roots to the ground. These then are primary hemi-epiphytes but other individuals may begin as terrestrial seedlings, retain stem connection with the ground and develop epiphytic root systems thus conforming to the SEC type. *Freycinetia* (4 spp.) are ± strictly SECs and are thus "borderline" epiphytes. None of the non-orchid monocots seems to have much drought resistance as all are typical of wet rainforests and mesic microhabitats.

In species numbers, the <u>Orchidaceae</u> rival the ferns in the Australian vascular epiphyte flora (153, 152 spp. resp). Only 37 of these occur outside Australia but there are only eight wholly endemic genera and these are monotypic. The genus *Sarcochilus* R. Br. (s.s.) with 9 or 10 endemic species of a total 11 is apparently the largest "local development"; it is discussed in more detail in 2.5 of this chapter. *Dendrobium* has the largest representation with 45 species (of a world total of ca 1500; 600 in N.G.). There appears to have been some local radiation in the subgenus *Athecebium*, particularly in the sections *Rhizobium, 2, 3* and *Dendrocoryne* in the subtropics and tropical montane areas. 26 species of *Bulbophyllum* occur here and some radiation has taken place but they seem incapable of the same degree of adaptation to aridity as *Dendrobium* and are largely confined to humid, cool rainforest, especially so the smaller species. The monopodial subtribe Vandinae (Sarcanthinae) is represented in Australia

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* a) groups contributing the largest numbers (Asclepiadaceae, Rubiaceae) have their centres of origin in Malesia and are relatively recent arrivals in Aust.(c.f. Orchidaceae, p.59), thus dispersal constraints are important and, b) potential dispersal agents such as birds and mammals are commoner in the tropics.

by 44 species in 22 genera, of which *Sarcochilus* is the largest. Some speciation has occurred in others as a number of monotypic and small genera are endemic (see 2.4.1).

The life form and physiognomic groupings of the Australian epiphytic orchids reflect, in particular, their relatively high drought tolerance and consequent ability to exploit more xeric, brighter microhabitats (mean exposure pref. index. 3.20).

The great majority of orchids are sedentary forms (111 spp.), ie tufted or short-creeping but there is a significant group of medium- to long-creeping species (38) which are able to send new growth towards more suitable environmental space. Examples of the latter form include *Dendrobium carrii, D. agrostophyllum, Bulbophyllum baileyi, B. bowkettae* and *B. johnsonii* which prefer brighter microhabitats and probably the long-creeping habit enables avoidance of shading from canopy change.

Only three Australian epiphytic orchids, *Dendrobium speciosum, Acriopsis javanica* and to a lesser extent, *Cymbidium madidum*, have significant nest-building capacity. The mechanism they employ involves the massed growth of apogeotropic roots, whereas the nest-forming ferns use sterile bracket or basket fronds to catch and retain litter.

The prevalence of humiphobic orchids (111 against 12 humiphiles) which have creeping exposed or relatively exposed roots is an indication of their adaptedness in the efficient uptake and economic use of water (and minerals). Specialised root exodermis cells, apparently important in water absorption and insulating velamen (Benzing & Ott, 1981) are two relevant adaptations. CAM is another critical water-saving device that is common in the orchids. Of 93 tested, 53 yielded results indicating strong to moderate CAM and a further two showed weak CAM. CAM in the epiphyte flora is more extensively discussed in Ch. 5.

Two physiognomic forms unique to the orchids are the tangle epiphytes and the aphylls. There are at least 14 species of tangle orchids, which are defined by having numerous aerial roots. This arrangement is thought to maximise interception of mist and throughfall droplets. Aphylls of two types are known in the Australian epiphytic orchids, these being the root tuft type (*Chiloschista*, 1 sp., *Taeniophyllum*, 5 spp.) which are monopodial and have very reduced stems, and the sympodial, pseudobulbous type (*Bulbophyllum minutissimum* and *B. globuliforme*).

2.5 Biogeography of the Australian vascular epiphytes with particular reference to the Orchidaceae.

Rainforests and other relatively mesic, sheltered environments suitable for the majority of epiphytes occur in small to moderate sized, often disjunct patches, in a narrow band along the east coast of Australia from the tip of Cape York to SW Tasmania. There are a few small, isolated, depauperate refugia in northern NT and the Kimberley district of northern WA (see map, Fig 3.1a, and further discussion of this in next chapter).

The distribution of vascular epiphytes is not uniform through these areas but there are two centres of concentration, the main one in NE Qld and the other in the subtropical Tweed Shield - Bunya Mts area. The floristic richness and endemism in the various epiphyte regions (as delineated in Results 2.3.1, p. 25) are compared in the table below.

Table 2.2 Comparative floristic diversity of epiphyte distributional regions i-vi.

	total occurring	pterid.	orchids	others
montane NE Qld (iii)	198(89)*	99(49)	67(34)	30(6)
Cape York Peninsula (ii)	131(46)	35(5)	65(29)	30(12)
subtrop. SE Australia (iv)	127(56)	59(24)	59(26)	19(6)
lowland NE Qld (ii)	103(20)	37(12)	45(3)	25(5)
NW Australia (v)	10(2)	4(0)	4(1)	5(1)
SW WA (vi)	3(0)	3(0)	0	0

* numbers in parentheses are species of that group restricted to that region (in Austr.)

Thus the tropical montane area above ca 600 m is noticeably richer in total vascular epiphyte flora, in endemic species and in the pteridophytes and (less so) orchids but about equal to Cape York Pen. in "other" species, i.e. dicots and non-orchid monocots. Cape York Pen. and subtropical SE Australia are not substantially different from one another in total epiphyte flora but the latter has more pteridophytes and fewer orchids and "other" spp. NW Australia (including NT) and SW WA are both very impoverished, particularly the latter.

Considerations relevant to the regional floristic differences outlined above include :

a. the tropical montane and subtropical SE Aust. regions contain a greater diversity of habitats suitable for epiphytes than do the other regions. The more important ones are mist forests, typical rainforests, dry rainforests, rainforest relict scrubs, mesic open forests, woodland and various ecotonal communities;

b. these two regions also have both lower mean temperatures and a more evenly spread, reliable rainfall than the others, i.e. the communities and their microhabitats will generally tend to be less water-stressed;

c. according to Kershaw (1980) areas with a present MAR of 2500 mm or more would have been effective refugia in arid phases of the Tertiary and Quarternary. This means that small areas of the McIlwraith and Iron Ra. and parts of the tropical montane and subtropical SE regions, i.e. the 'core' parts of each, would have formed such refugia (Webb and Tracey, 1981; Lavarack, 1981) from which species could recolonise regenerated rainforest areas during the more mesic phases;

d. when compared with the tropical lowland region (ii), Cape York (i) is closer to, and has more ready access to the large flora pool supply of New Guinea. This is reflected in the number of N.G. species whose Australian occurrence is limited to Cape York Peninsula, e.g. *Davallia solida, Humata pectinata, Pyrrosia lanceolata, Schefflera versteegii, Fagraea beteriana, Dischidia major, Scindapsus altissimus, Liparis persimilis, Dendrobium antennatum, Cadetia wariana, Flickingeria comata, Bulbophyllum gracillimum, B. masdevalliaceium, B. longiflorum, Oxyanthera papuana, Dipodium pandanum* etc. A similar difference shows when comparing the tropical montane and SE Aust regions but the "supply line" between the former and N.G. is not so clear as that to Cape York.

e. the climates of past arid phases in NW Australia have been so severe as to exterminate all but the most arid-adaptable epiphytes;

f. SW Australia have long been isolated by vast tracts of desert and thus has not received any rainforest taxa from Malesia, direct or derived, since exchange with Australia began.

The data in Table 2.2 for SE Australia cover an area from the tropic to Tasmania but the core of this is from the vicinity of the Bunya Mts of SE Qld to the Clarence River of NE NSW (see maps, p. iv of Appendix 1). There is a marked taper off in epiphyte species numbers, most noticeable to the south, particularly in view of the fact that mesic, closed forests are not uncommon and especially in Tasmania. The following table documents this southward diminution.

Table 2.3 Decrease in vascular epiphyte spp. southwards in SE Aust.

	Fern Allies	Hymeno-phyllac.	Typ.ferns	Orchids	Others	Total
NE NSW*	6	12	27	53	15	113
Victoria	5	8	15	5	3	35
Tasmania	3	7	11	2	2	25

* north of Hunter R.

There are some rather marked barriers, e.g. the Hunter R. "dry corridor" which is only ca 50 km wide. Here, nine species of epiphytic orchids, viz, *Liparis coelogynoides, Dendrobium falcorostrum, D. beckleri, D. tenuissimum, D. kingianum, Bulbophyllum aurantiacum, Rhinerrhiza divitiflora, Sarcochilus hartmanii* and *Pteroceras spathulatus* occur in the Barrington Tops area and to the immediate north of the Hunter Valley but not in the Wattagan rainforest ca 50 km across the valley, or further south. *D. striolatum* comes as far north as the latter area but does not cross the valley.

Theory of the biogeography of epiphytic orchids in Australia (Wallace, 1974, 1975; Lavarack, 1981) basically holds that the Australian tectonic plate drifted north into contact with the SE Asian plate and biotic exchange took place, particularly towards Australia. During these times direct dry land connections between Australia and New Guinea occurred periodically and water barriers between the Sunda Is (Indonesia) and Australia would have been narrow (Nix & Kalma, 1972). Also, more mesic climates and vegetation regimes would have existed periodically in many areas across northern Australia (Kershaw, 1975, 1980). The present existence of rainforest relict scrubs ("subcoastal rainforest pockets" of Webb & Tracey, 1981) there, provide evidence of this. There was a general spread of rainforest taxa from Malesia southward as expansion and contraction of rainforest areas allowed and as the dispersal mechanisms of individual species provided. This expansion and connection of rainforest areas, alternating with contraction and isolation into refugia and relict pockets also provided conditions promoting speciation and adaptation toward drought resistance. In the process many rainforest areas would have been exterminated along with their biotas but some would have persisted and changed sufficiently slowly to enable some of the constituent species to adapt to the increasing aridity.

The radiation of the epiphytic orchid genus *Sarcochilus* R. Br. (s.s.)[2] serves as an example of a product of the above processes.

Taxonomic affinities of the distinctive subtribe Vandinae (Sarcanthinae) indicate a SE Asian origin for the *Sarcochilus* ancestor. By the above mentioned modes of migration, adaptation and speciation, the present 11 species became differentiated and spread to various environments in and near the eastern rainforests. Three morphologically distinct subgeneric groups have evolved, viz,

a) larger plants with essentially white, broad-segmented flowers with a glabrous labellum midlobe and laminate, leathery leaves (*S. fitzgeraldii, S. hartmannii, S. falcatus* and *S. weinthalii*),
b) small plants with pink, broad-segmented flowers with a hairy or papillose labellum midlobe and narrow, fleshy leaves (*S. hillii, S. tricalliatus* and *S. ceciliae*),
c) moderate sized plants with green to brown-red, narrow-segmented flowers with glabrous labellum midlobe and laminate, thinly leathery leaves (*S. olivaceus, S. australis, S. dilatatus* and *S. serrulatus*).

Some inhabit cooler, moister rainforests in shaded microsites - *S. serrulatus* and *S. olivaceus*, or more exposed situations in the same communities - *S. falcatus*, or still cooler, otherwise similar habitats - *S. australis*. Others have adapted to drier, warmer conditions and typically grow in DRf - *S. hillii, S. dilatatus, S. weinthalii, S. tricalliatus* with the latter extending to harsh, hot, dry rainforest relict scrubs in the tropics. Three are lithophytes - *S. fitzgeraldii* in moist, shaded rainforest sites, *S. hartmanii* in ecotonal and open, moderately mesic communities and *S. ceciliae* in drier, more temperature-extreme conditions.

It can be seen that the morphological groupings of *Sarcochilus* transgress the ecological ones, indicating that the former were established early in the evolution of the genus and have since radiated, coming to occupy different ecological niches.

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[2] As construed here includes only Aust. spp. (except *S. moorei*) plus 2 New Caledonian spp. Photographs of a number of species are on the next three pages.

Plate 2.1

Sarcochilus falcatus R.Br., Wrights Lookout CTRf, New England NP, NSW.

About half full size.

Group a), p. 62

Plate 2.2 *Sarcochilus ceciliae* F.Muell., lithophytic, Dangars Falls, near Armidale, NSW. Natural size. Group b), p. 62.

Plate 2.3

Sarcochilus tricalliatus (Rupp)Rupp in Forty Mile Scrub, a rainforest relict scrub on the western Atherton Tableland, N Qld. About 1½ x natural size.

Group b) , p. 62

Plate 2.4 Flower of the above. About 6 mm diam.

Plate 2.5

Sarcochilus serrulatus D.L. Jones, growing in montane mist rainforest, Baldie, Atherton Tableland, N Qld. About 1½ x natural size.

Group c), p. 62.

Plate 2.6

Sarcochilus australis (Lindl.) Reichb.f., in WTRf near Bega, S NSW. About ¾ full size.

Group c), p. 62.

2.6 Myrmecophilous epiphytes of Australia

Among the epiphytes of the Australian tropics are seven species which are adapted to host ant colonies, apparently in regular, mutualistic relationships (Janzen, 1974 and Huxley, 1978, 1980; here also for important references to literature on the morphology, taxonomy, ecology etc of the Asiatic antplants). These[3] and some examples of their insect inhabitants[4] are listed below:

Rubiaceae:

Myrmecodia antonii
" *beccarii* (Noah Ck, *Iridomyrmex cordatus*, ant)
" affe. *beccarii* (Gordonvale " " ")
" *muelleri* (Massy Ck " " ")
Hydnophytum formicarium (" ", *Crematogaster* sp., *Camponotus* sp., ants both together in the one indiv. plant)
" sp. (Leo Ck, *Iridomyrmex cordatus*, plus unident. termite, isopod, beetle and snail, all in the one specimen)

Asclepiadaceae:

Dischidia major (Massy Ck, *Iridomyrmex cordatus*)

Other epiphytes that are commonly associated with ants and their nests include *Dendrobium smilliae, D. johannis, D. antennatum* and *Dischidia nummularia* but the orchids at least, do not appear to be specially adapted as some exotic species are (see Lawler, 1979). The seeds of the *Dischidia* have an oil body which is apparently attractive to ants (Docters van Leeuwen, 1929).

The rubiaceous antplants appear to be autogamous as the flowers open little, if at all and fruit set is common. The fruits are fleshy and at least in the cases of *Myrmecodia antonii, M. muelleri* and *Hydnophytum* aff. *formicarium*, are red and eaten, and thus dispersed by, the Mistletoe-bird, *Dicaeum hirundinaceum* (personal observations from Leo Ck, Sept. 1979). However, *Myrmecodia* plants are often found growing from the underside of branches, thus ants may form a secondary dispersal method (Docters van Leeuwen, 1929). Fruit set on the *Dischidia* species is uncommon and therefore vector pollination is probable; the seeds are furnished with a downy 'parachute' as with many other asclepiads and are wind dispersed primarily and probably secondarily by ants (Docters van Leeuwen, 1929).

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[3] For details of morphology, distribution, name authorities etc., see Appendix 1; see also photographs on next page.

[4] Collected Sept./Oct. 1979; identified by R.W. Taylor, Div. Entomology, CSIRO, Canberra; specimens held there.

Plate 2.7

Microcommunity of myrmecophilous epiphytes, Massy Ck, M^c^Ilwraith Range, Cape York Peninsula, N Qld, in swamp forest. On the lower right are two *Myrmecodia* sp. specimens and on the left is *Dischidia major* (Vahl.)Merr. and behind, *Dendrobium smilliae* F.Muell. Below the *Myrmecodia* plants are several antplant seedlings.

Plate 2.8

Microcommunity of myrmecophilous epiphytes in semi-evergreen Mesophyll Vine Forest, Massy Ck, M^c^Ilwraith Range. The tuberous species on the left is *Myrmecodia muelleri* Becc. which has a young *Dendrobium teretifolium* R.Br. growing near the base of its leaf-bearing stem. Right, below, is *Hydnophytum formicarium* Jack (leaves in left lower corner) with a *D. rigidum* R.Br. plant growing on the lower left of its tuber. The large associated orchid is *D. antennatum* Lindl.

As illustrated in photographs on the previous page, myrmecophilous epiphytes tend to be gregarious and this is apparently due to the foraging, collecting and 'planting' of the seeds of these plants by the ants (Janzen, 1974; Madison 1979b; etc.).

Richards (1936) briefly discusses the importance of ants to epiphytes in Sarawak.

Huxley (1982) gives a discourse on the ant-epiphytes of Australia. She covers the taxa involved, providing a key for their identification and identifies their ant occupants as well as other organisms inhabiting the plants. Based mainly on her work in New Guinea and elsewhere (Huxley, 1978, 1980) she discusses the structure and physiology of the ant-inhabited parts, revealing important new information on absorption of nutrient material imported by the ants; the ecological implications are examined.

2.7 Conclusions

1. Australia's 380 species of vascular epiphytes constitute a very impoverished flora when compared with those of other continents. This is compounded by low endemism - only eight monotypic genera and 260 species are endemic.

2. Within the flora the pteridophytes and orchids are the largest groups with 152 and 153 species resp. Fern allies and filmy ferns are fairly well represented; almost all are restricted to mesic communities and microhabitats of low stress. The typical leptosporangiate ferns are diverse in taxonomy, physiognomy and ecology but the Polypodiaceae, the largest group, show various trends towards xerophytism. These include several adaptive lines in nest-forming ability, fleshy rhizomes, development of indumentum and of CAM. Semi-epiphytic climbers are well developed in the leptosporangiate ferns with 13 species representing seven genera; there are two ecological subgroups represented, low and high climbers.

3. The dicot epiphytes are the third largest group with 61 species. Most are not typical epiphytes but hemi-epiphytes or semi-epiphytic climbers. Further, the great majority have either fleshy, winged or adherent disseminules and this may contribute to their fewer numbers and more restricted geographic range. Secondary stem thickening allows many dicots to compete successfully for light and thus there is less need for epiphytism among them.

4. Among the dicot epiphytes are seven myrmecophytes of three genera and two families (Rubiaceae and Asclepiadaceae) plus several orchids and one other asclepiad that are often associated with ants. The rubiaceous antplants are autogamous and have fleshy fruits and bird-dispersed seeds; the asclepiads uncommonly set fruit and the seeds are 'winged' and wind-dispersed. All appear to be secondarily dispersed by ants collecting them and carrying them to their nests and this appears to account for gregariousness in these epiphytes.

5. Non-orchid monocots are few, being represented mainly by the Araceae with four genera and eight species of semi-epiphytic climbers restricted mostly to the tropics. Four species of *Freycinetia* (Pandanaceae) make up the rest of this group but are "borderline" epiphytes, apparently always having substantial connection with the soil.

6. The orchids have a considerably higher degree of endemism than the ferns, with several radiations involving up to 10 species each. Greater adaptive ability of the group is seen as the main reason for this. There is a diversity of life-forms and physiognomic types but true epiphytes of sedentary, tufted habit are commonest. There are a few humiphilic species but most have roots creeping on the substrate surface and are adapted to the poorer water relations consequent upon this; this, along with other drought resisting adaptations such as CAM, enables orchids to occupy relatively high, bright microhabitats.

7. Central in the theory of the biogeography of the Australian vascular epiphyte flora is continental drift, the collision of the Australian tectonic plate with that of Asia and subsequent biotic exchange. Climatic and consequent changes in sea level and vegetation occurred during and since this time. Rainforest areas were at times much more expansive that at present and at other times fragmented into isolated patches and refugia as at present or even more so. This fluctuation allowed more effective dispersal during mesic times and less so in the arid, but isolation gave rise to speciation during the latter which accounts for the endemic radiations e.g. as in the monopodial orchid genus *Sarcochilus*.

5. Non-orchid monocots are few, being represented mainly by the Araceae with four genera and eight species of semi-epiphytic climbers restricted mostly to the tropics. Four species of *Freycinetia* (Pandanaceae) make up the rest of this group but are "borderline" epiphytes, apparently always having substantial connection with the soil.

6. The orchids have a considerably higher degree of endemism than the ferns, with several radiations involving up to 10 species each. Greater adaptive ability of the group is seen as the main reason for this. There is a diversity of life-forms and physiognomic types but true epiphytes of sedentary, tufted habit are commonest. There are a few humiphilic species but most have roots creeping on the substrate surface and are adapted to the poorer water relations consequent upon this; this, along with other drought resisting adaptations such as CAM, enables orchids to occupy relatively high, bright microhabitats.

7. Central in the theory of the biogeography of the Australian vascular epiphyte flora is continental drift, the collision of the Australian tectonic plate with that of Asia and subsequent biotic exchange. Climatic and consequent changes in sea level and vegetation occurred during and since this time. Rainforest areas were at times much more expansive that at present and at other times fragmented into isolated patches and refugia as at present or even more so. This fluctuation allowed more effective dispersal during mesic times and less so in the arid, but isolation gave rise to speciation during the latter which accounts for the endemic radiations e.g. as in the monopodial orchid genus *Sarcochilus*.

CHAPTER 3

EPIPHYTE ENVIRONMENTS IN AUSTRALIA

3.1 Introduction (p. 71) - epiphyte environments are investigated at two different levels, i.e., macro-environmental factors affecting distribution of epiphyte-preferred habitats and microclimatic factors at two different levels in different rainforests.

3.2 Materials and Methods p. 72

3.3 Results (p. 73) are mostly presented graphically.

3.4 Discussion (p. 90) is organised into these sections:

3.4.1 Geography of epiphyte environments in Australia (p. 90)

3.4.2 The study site macroenvironments (p. 92)

3.4.3 Macrocommunity structure (p. 93)

3.4.4 Microhabitat physical factors : light intensity, maximum and minimum air temperatures, air movement, air evaporative power. (p. 95)

3.5 Conclusions p. 97

3.1 Introduction

Colonisation by, and continued survival of epiphytes in their microhabitats depends basically on the interaction of two major environmental factors. The first is *light*, an essential need of all autotrophic plants. This need is the fundamental selection pressure to which epiphytes, as plants restricted to slow growth and small stature, are responding in evolving the epiphytic habit. The second is that of *water relations* in the broad sense, i.e. availability of water to the plant. This is the ubiquitous and overriding (though not sole) environmental limitation restricting invasion of brighter microhabitats by epiphytes. Thus, the greater an epiphyte's access to light, the better it will need to be adapted to cope with water stress. Thus, also, epiphytes will tend to be more common in those situations where light intensity is maximal relative to minimal water stress.

Variation in these two factors is the product of interraction between other ecological factors such as solar input, MAR, topography, air temperature, air movement, air relative humidity and vapour pressure deficit (vpd), and macrovegetational structure. The results of some investigation of these attributes in five different subtropical rainforests particularly as related to the epiphytes, are presented and discussed below. In accordance with the above concepts, only 20% of Australian epiphytes occur either commonly or exclusively outside rainforest and other relatively closed, moist communities and thus a brief investigation of rainforest distribution and related patterns of continental climatic factors was made to illustrate the broad scale distributional situation.

Five rainforest* sites from the subtropics were chosen for investigation of macro and microhabitat factors relevant to the epiphytes. These sites, which had somewhat different epiphyte floras, were selected partly on the basis of being typical of their vegetation subformation types, and partly because a degree of constancy of some ecological variables obtained from site to site. Basic ecological details from one tropical site were compiled, as available, for comparison with the subtropical ones.

Microhabitat factors in particular were investigated to document and verify the thesis that epiphyte microenvironments become increasingly water-stressed with closeness to the forest canopy, even in the "wet" rainforests. This is not a new concept but has seldom been actually quantified.

*(sens. lat.)

3.2 Materials and Methods

1. MAR isohyets, and the distribution of rainforest and relatively closed, rainforest-related communities on the continent were drawn on Fig. 3.1a and the average annual potential evaporation on Fig. 3.1b.

2. Macrovegetation profiles were sketched from each of the subtropical sites. The transects, 50 x 25 m, were selected on the basis of being typical of the vegetation structure of each site, especially in regard to the dominant tree layer and its canopy (Figs 3.2a-e).

3. For each of the study sites, basic ecological information concerning the general habitat was compiled from various sources. This included geographic locality, altitude, topography, soil, MAR, absolute maximum and minimum temperatures, occurrence of winds and mists and macrovegetation (Results 3.3.3a-f).

4. Air movement was measured in Zones 1 and 4* at 2 hourly intervals on one essentially non-windy day each in the Dorrigo STRf and Long Pt DRf (Fig 3.4). This was done by releasing finely ground ash and timing its movement between two points separated by a known distance.

5. From within the five subtropical sites the following microhabitat factors were measured at two different levels within the forest, one at 1.5 m height against a selected tree trunk (Zone 1) and the other among the smaller branches, 2-4 m below the foliage canopy (Zone 4):

a. Irradiance during one cloudless late summer day at each site was plotted by taking quarter-hourly spot readings using a Lambda Li-185 on quantum function with one sensor in Zone 1 and another on an extension lead in Zone 4 (Figs 3.5a-e);

b. Monthly temperatures maxima and minima for 1977 at three different localities in each site. Means of the three localities of each site were graphed (Figs 3.6a-e);

c. Thermohygrographs of 6-7 days duration were taken in midsummer (Dec/Jan) and midwinter (June/July) in 1977-78 (Figs 3.7a-e). Three max./min. thermometers were set with these to check thermograph accuracy and spot checks were made with hygrometers at the beginning and end of each hygrograph.

* Zone 1 = lower trunk, Zone 2 = upr.trunk, Zone 3 = large branches, Zone 4 = small branches, Zone 5 = very small branches & twigs.

3.3 Results

3.3.1 Continental distribution of rainforest, MAR & average annual potential evaporation.

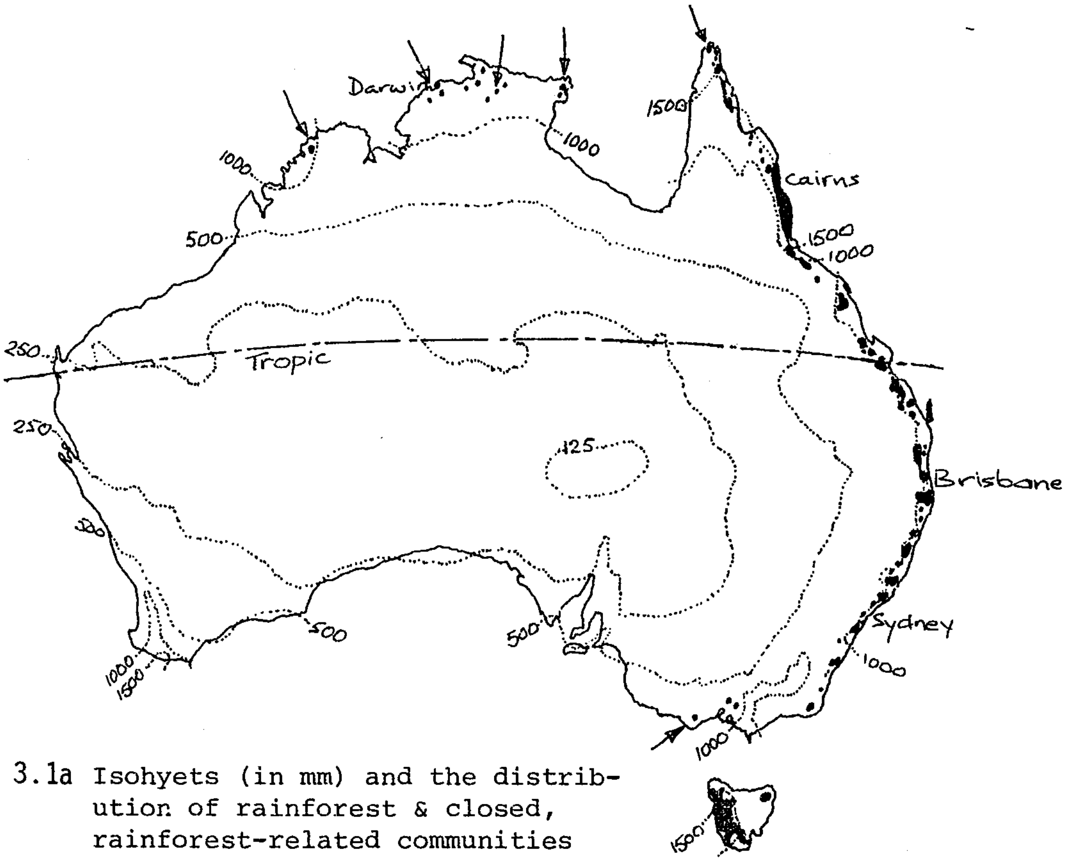


Fig. 3.1a Isohyets (in mm) and the distribution of rainforest & closed, rainforest-related communities (partly from Beadle, 1981; Stocker, in Beadle; and Webb & Tracey, 1981)

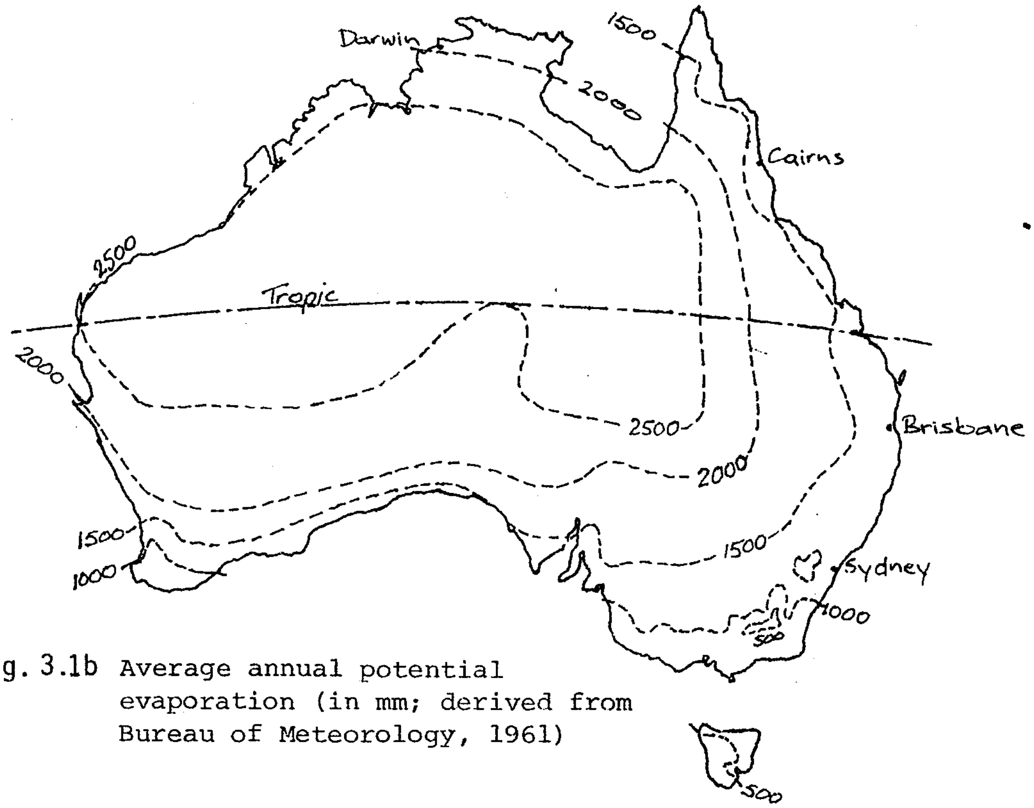


Fig. 3.1b Average annual potential evaporation (in mm; derived from Bureau of Meteorology, 1961)

3.3.2 Macrovegetation Profiles

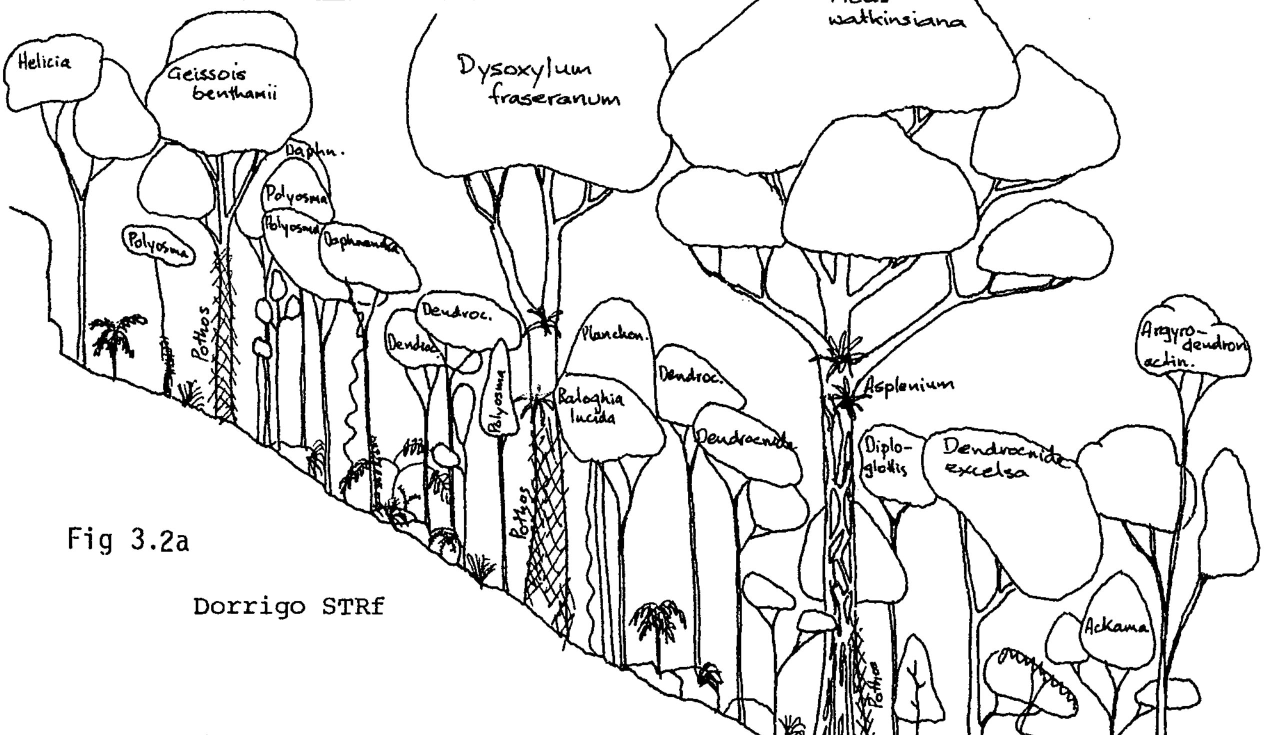


Fig 3.2a

Dorrigo STRf

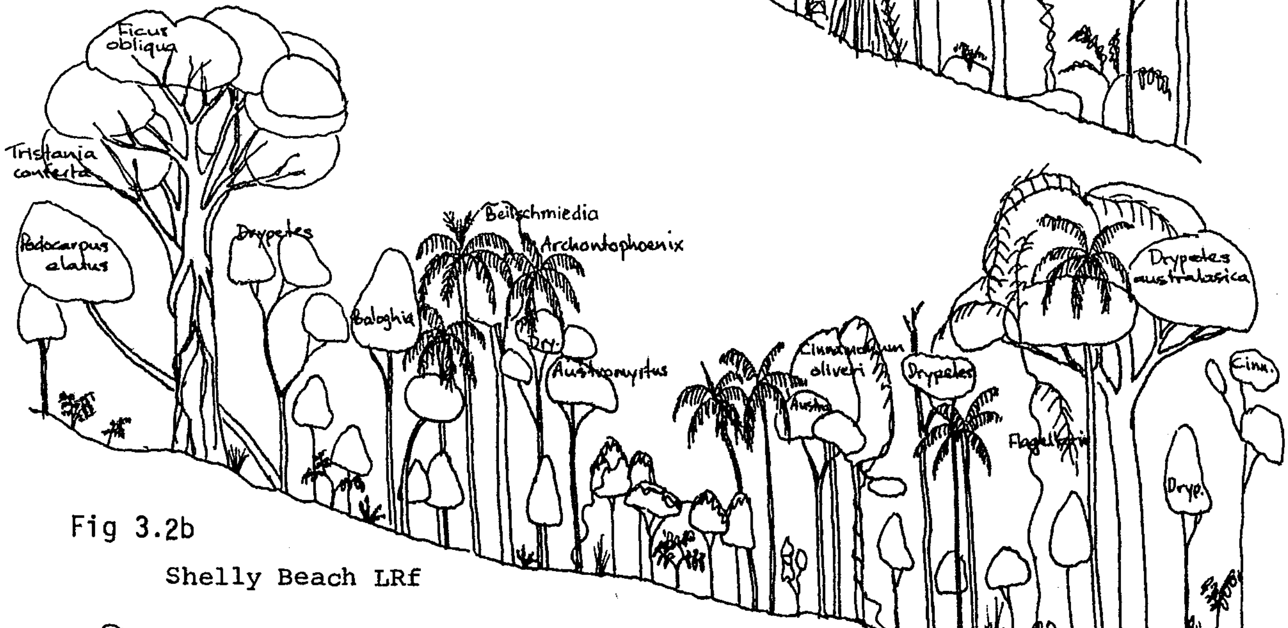


Fig 3.2b

Shelly Beach LRf

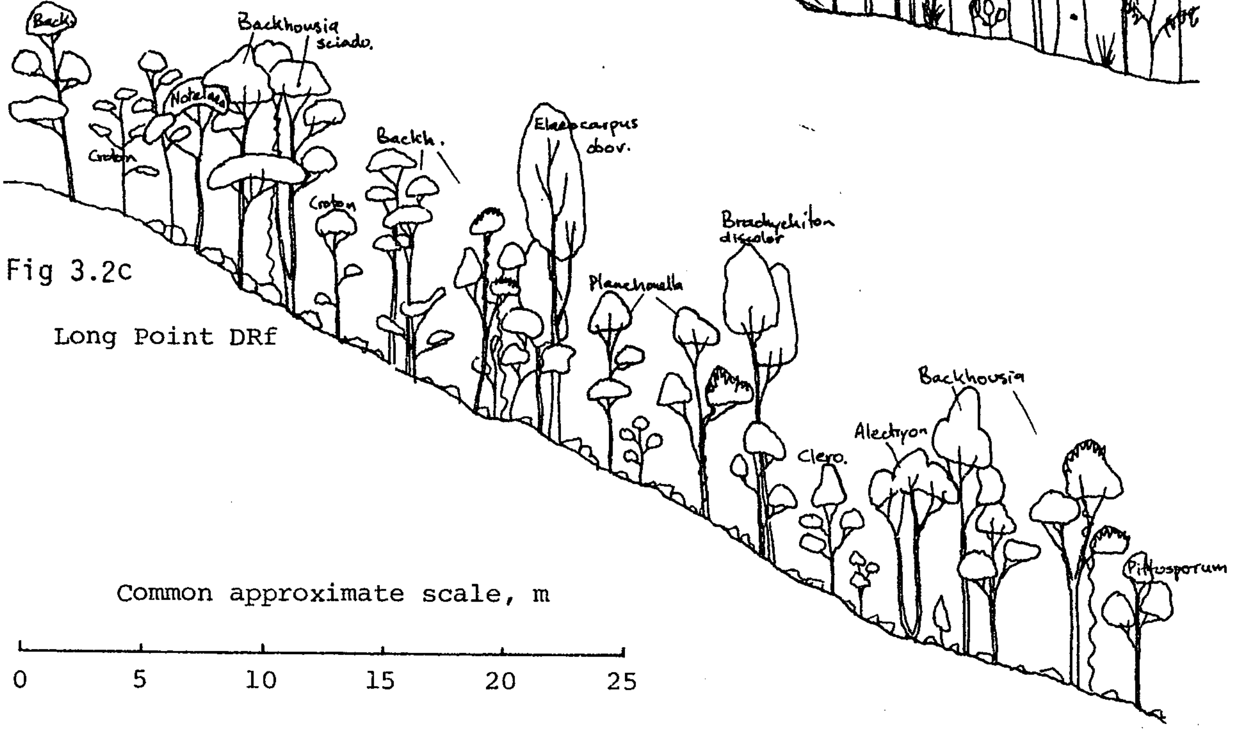


Fig 3.2c

Long Point DRf

Common approximate scale, m

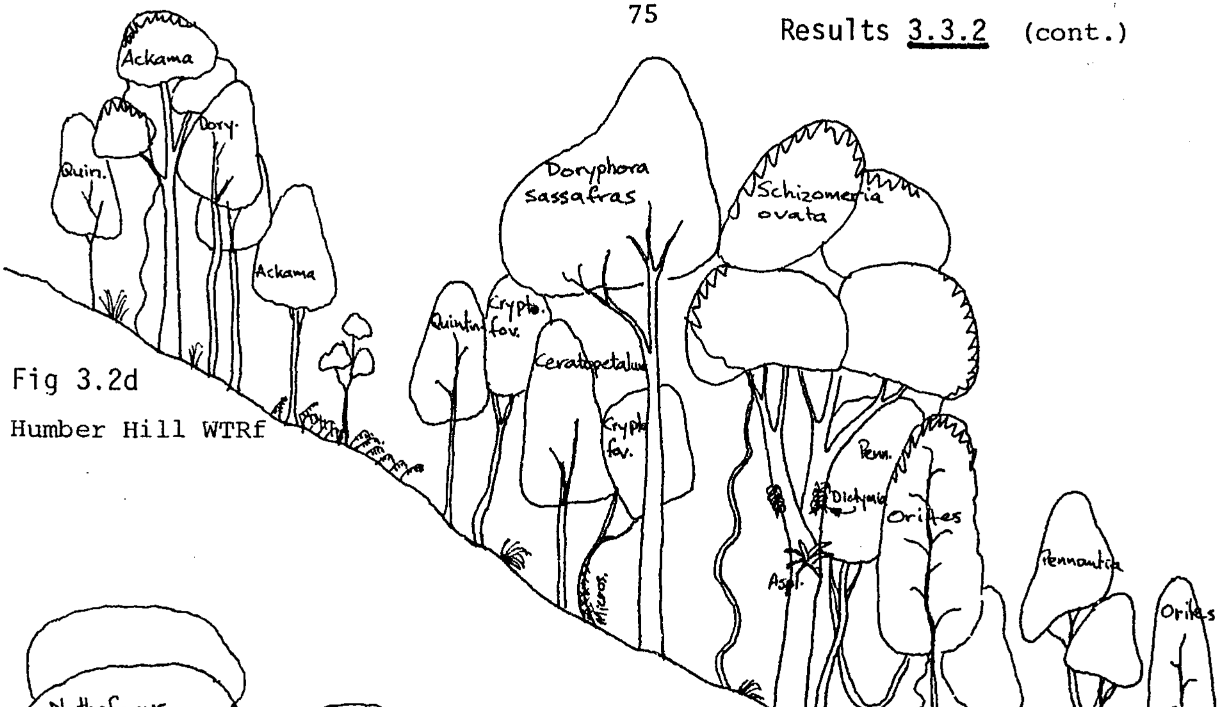


Fig 3.2d
Humber Hill WTRf

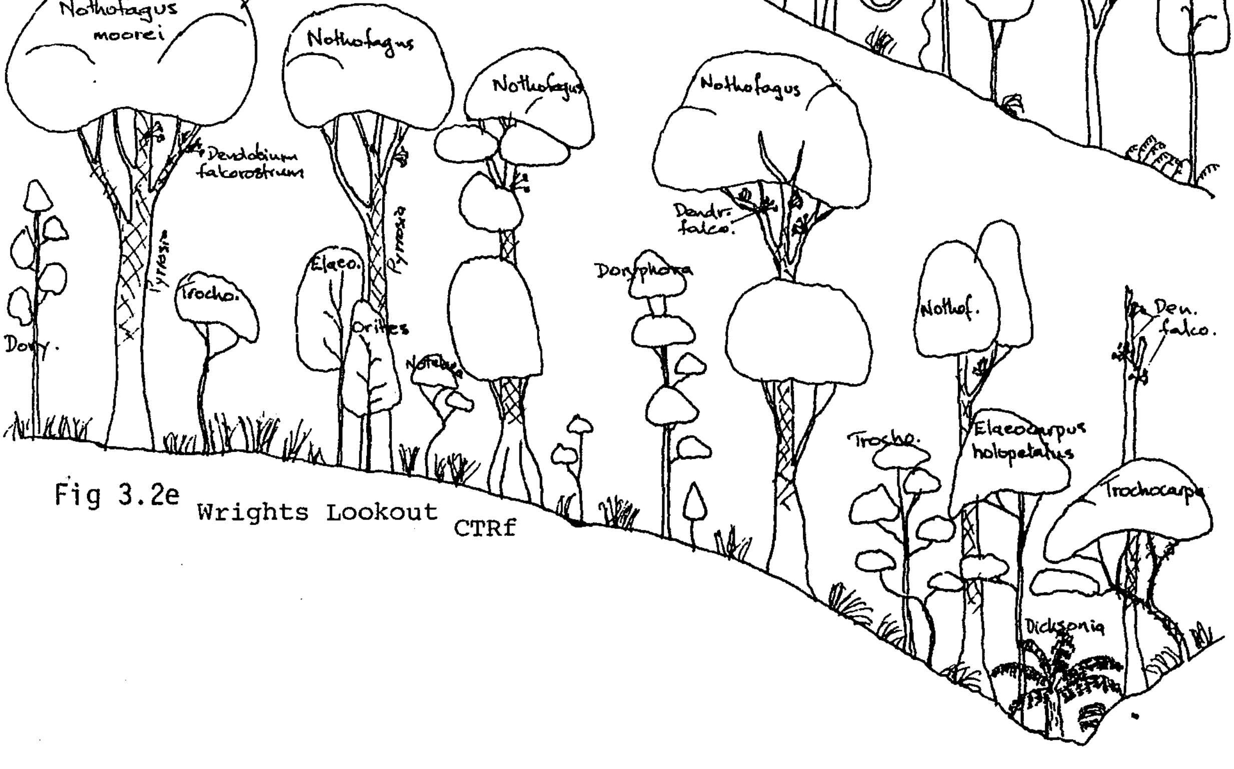


Fig 3.2e Wrights Lookout CTRf

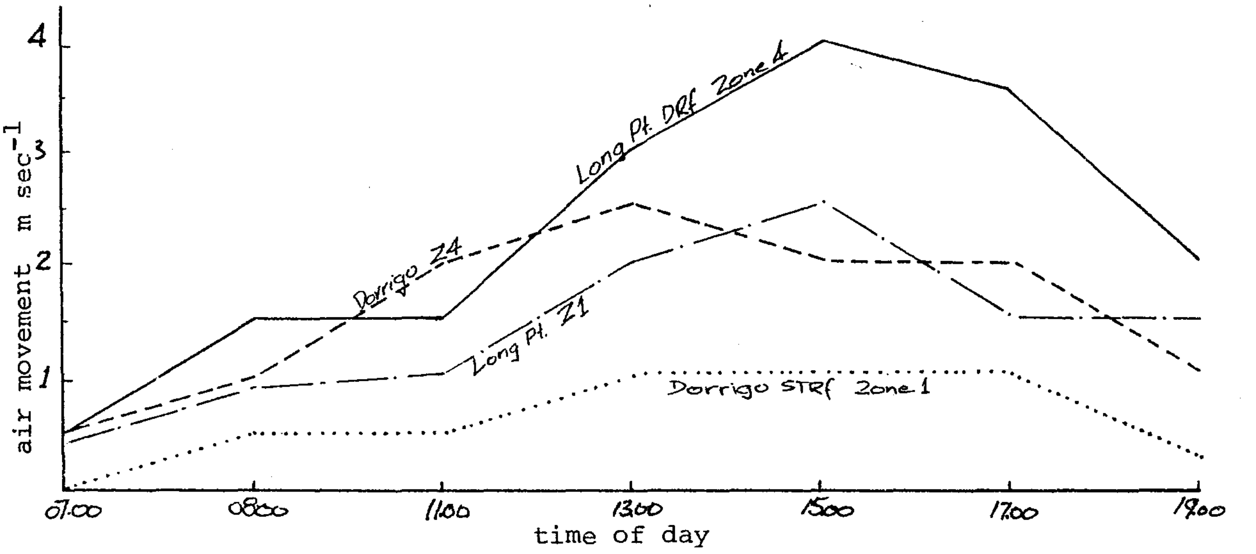


Fig 3.4 Air movement at two different levels in Dorrigo STRf on 25.2.1979 & in Long Point DRf on 20.1.1979

Results 3.3.3 The Study Sites

a) STRf Study Site, Dorrigo National Park, NSW

i) General description :

Altitude : ca. 750 m.

Topography : steep, roughly even, boulder-strewn slope of E aspect.

Soil : Krasnozem derived from basalt.

Climate : Moist subtropical/warm temperate; summer monthly maximum temperatures 31° - 35°C, summer mins. 10°-18°C, winter maxs. 15°- 18°C, winter mins. 1°- 1.5°C (1977/78 data). MAR ca 1800-2000 + mm; strong easterly orographic influence, mists common.

Vegetation : Cool subtropical rainforest (complex notophyll vine forest of Webb, 1978). Dominant tree species include *Ackama paniculata, Baloghia lucida, Argyrodendron actinophyllum, Dendrocnide excelsa, Diploglottis australis, Doryphora sassafras, Dysoxylum fraseranum, Ficus watkinsiana, Geissois benthamii, Orites excelsa, Planchonella australis* and *Sloanea woollsii.* Canopy relatively dense and even, ca 18-30 m above ground, tall shrub layer moderately prominent, low shrubs rather sparse, ground herbs sparse except for semi-terrestrial lithophytes.

(ii) Microhabitat physical factors

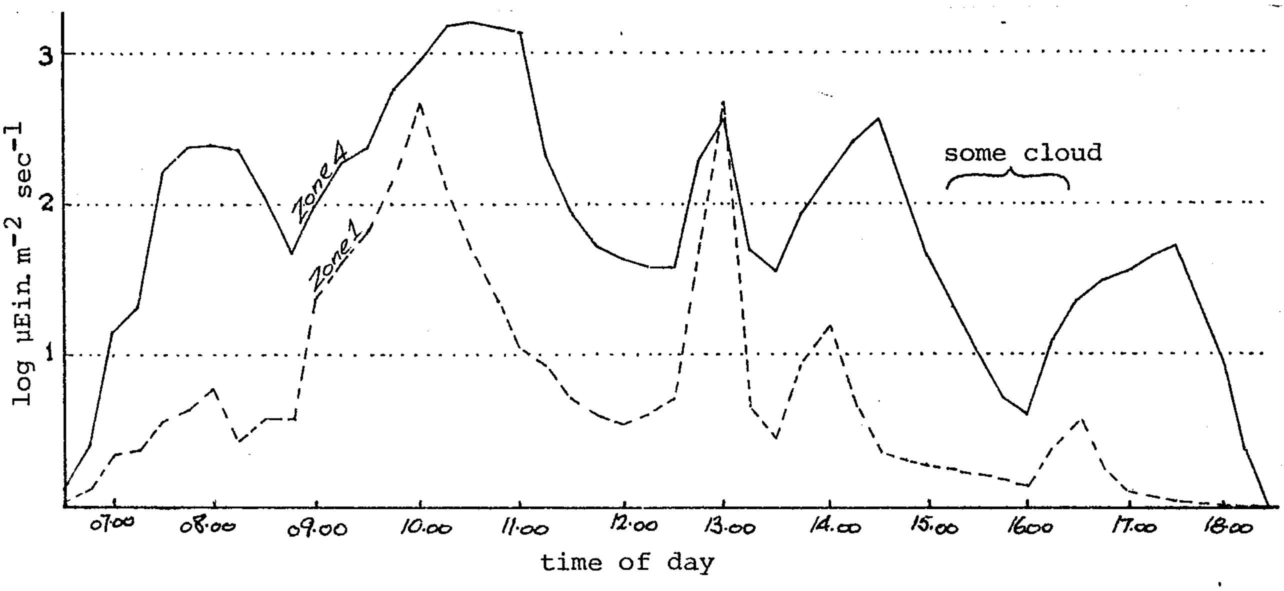


Fig 3.5a Course of light intensity at two levels in Dorrigo STRf, 24.2.1979

Plate 3.1

View over canopy of Sub-tropical Rainforest, Dorrigo NP, NSW showing its high degree of continuity and integrity, and emergents. The emergent on the right is *Dysoxylum fraseranum* and the epiphytic fern on it is *Davallia pyxidata.*

Plate 3.2

View under canopy of Dorrigo STRf. In the foreground is the 43 cm dbh *Alangium villosum* mentioned in Chapter 4.2.3 (1). Prominent on it is *Asplenium australasicum* and growing from the upper ones is nest-invading *A. polyodon.* The semi-epiphytic climber *Arthropteris tenella* can be seen near the base.

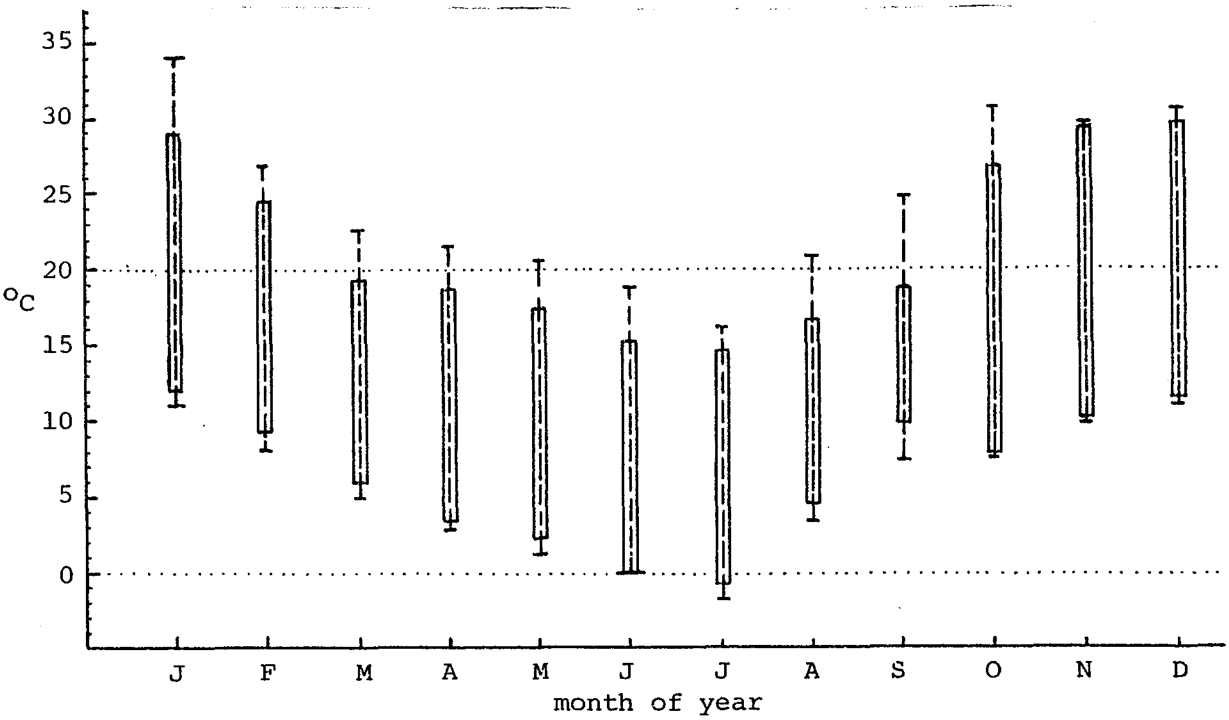


Fig 3.6a Temperature maxima & minima in Zone 1 (columns) & Zone 4 (broken lines) in Dorrigo STRf, 1977

Absolute maximum , Zone 1, 30°C; Zone 4, 34°C
" minimum, Zone 1, -1°C ;Zone 4, -2°C

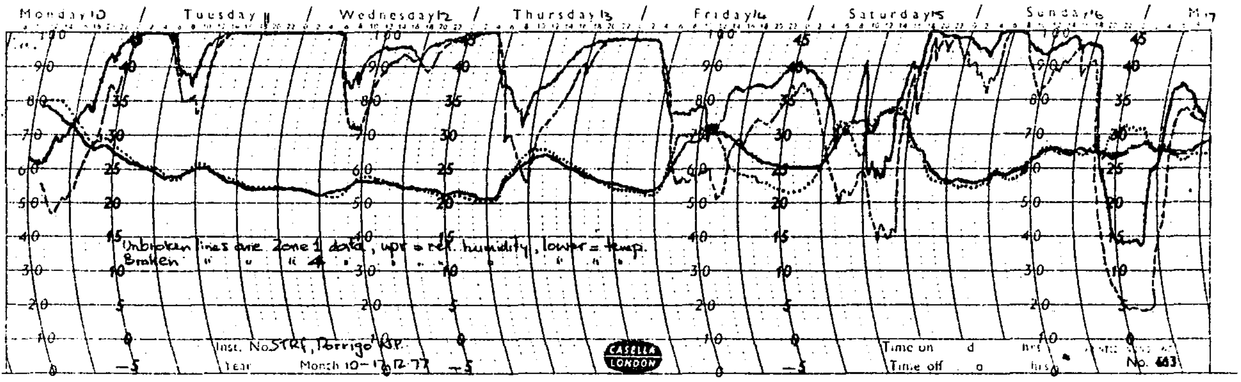


Fig 3.7a (i) Summer thermohygrographs, Dorrigo STRf, 1977 : Zone 4 graphs are superimposed onto those of Zone 1 (unbroken lines)

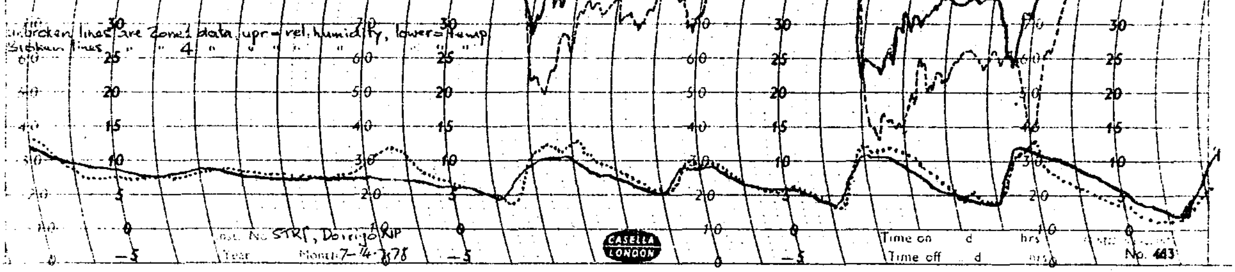


Fig 3.7a (ii) Winter thermohygrographs; details as above.

3.3.3b LRf, Shelly Beach, Port Macquarie, NSW

(i) General Description:

Altitude : ca 10 m.

Topography : gently sloping side of broad gully, ca 400 m from sea; aspect NE.

Soil : Rather fine textured red earth of moderately low fertility on ultrabasic rocks.

Climate : moist subtropical; summer max. temps. $30.5^{\circ}C-39^{\circ}C$, mins, $14^{\circ}-20^{\circ}C$, winter maxs. $15^{\circ}-18^{\circ}C$, mins. $1^{\circ}-3^{\circ}C$ (1977/78 data). M.A.R. ca 1400-1600 mm, strong maritime influence; mists uncommon. Input of salts from sea spray, blown in by prevailing NE sea breezes, often quite visible, is probably important in the mineral economy of this system.

Vegetation : Subtrop. rft (complex notophyll vine forest); dominant spp. numerous but on the plot included *Drypetes australasica, Archontophoenix cunninghamiana, Tristania conferta, Beilschmiedia obtusifolia, Planchonella australis, Mischocarpus pyriformis* and *Ficus obliqua*. Canopy with 50-80% cover, 5-12 m high, with significant light breaks; tall shrub layer not prominent, lower shrub layer moderately prominent and consisting mainly of juveniles of dominant stratum spp; ground herbs moderately common; cryptogams scarce.

(ii) Microhabitat Physical Factors:

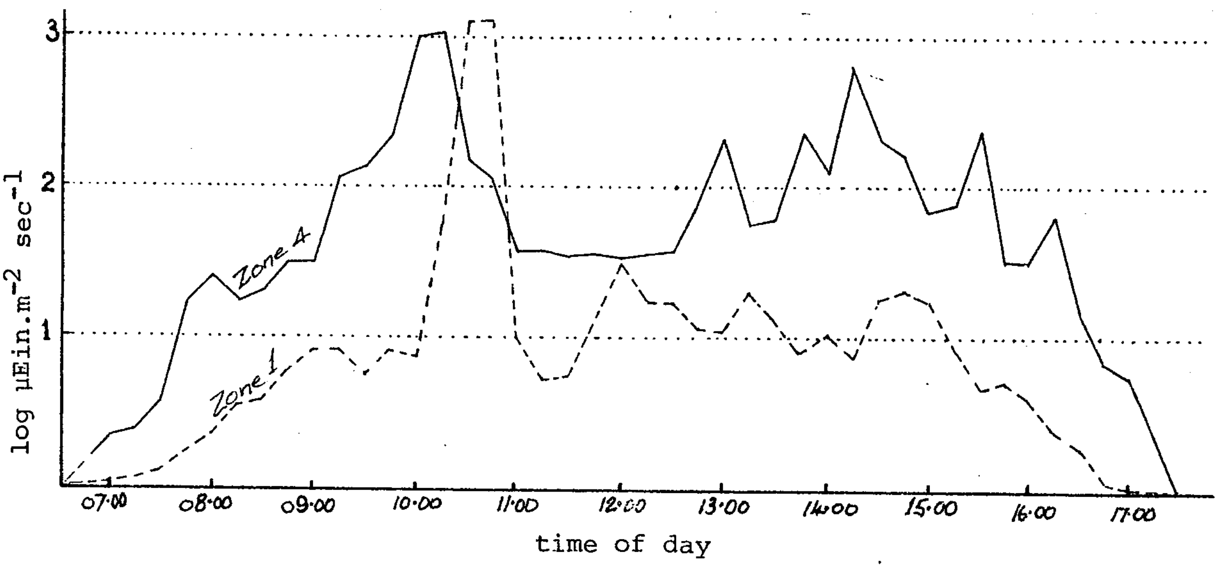


Fig 3.5b Course of light intensity at two levels in Shelly Beach LRf, 18.4.1979

Plate 3.3 Littoral Rainforest, Shelly Beach, Port Macquarie, NSW. View over canopy; some crown dieback can be seen in the middle, right, and numerous palm (*Archontophoenix cunninghamiana*) crowns.

Plate 3.4

Subcanopy view in Shelly Beach LRf. On the right is the large *Tristania conferta* bearing the strangler-fig *Ficus obliqua* mentioned in Chapter 4.2.3 (2).

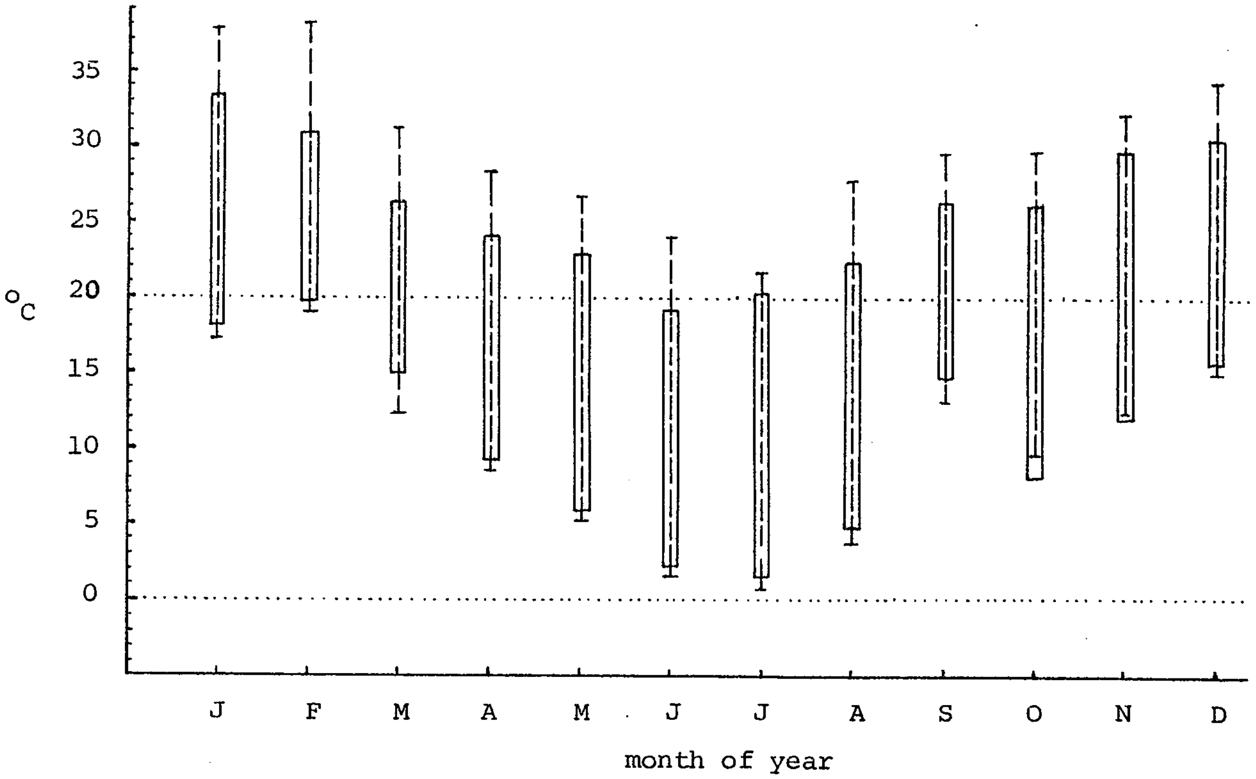


Fig 3.6b Shelly Beach LRf temperature maxima & minima, 1977
Zone 1 columns, Zone 4 broken lines
Absolute max. Zone 1, 34°C ; Zone 4, 39°C
" min. Zone 1, 1°C ; Zone 4, 0.5°C

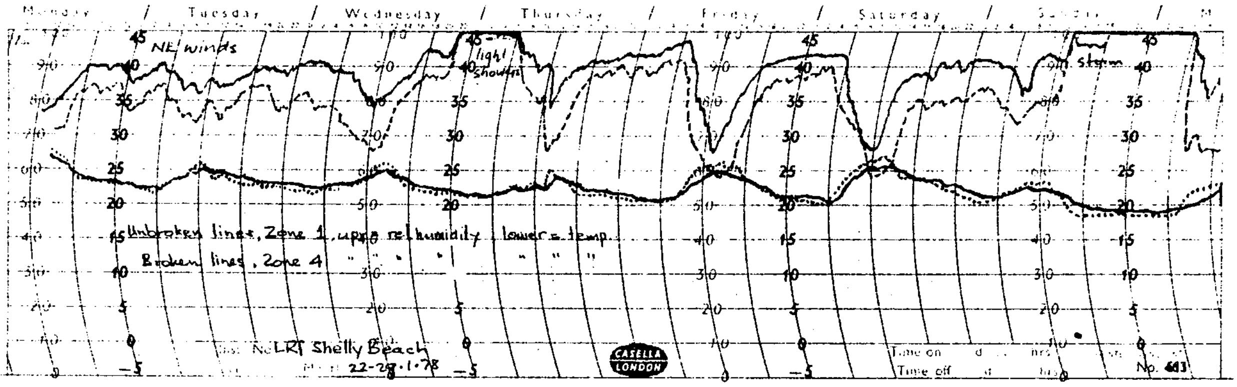


Fig 3.7b (i) Summer thermohygrographs, Shelly Beach LRf, 1977: Zone 4 graphs (broken lines) superimposed on those of Zone 1 (unbroken lines)

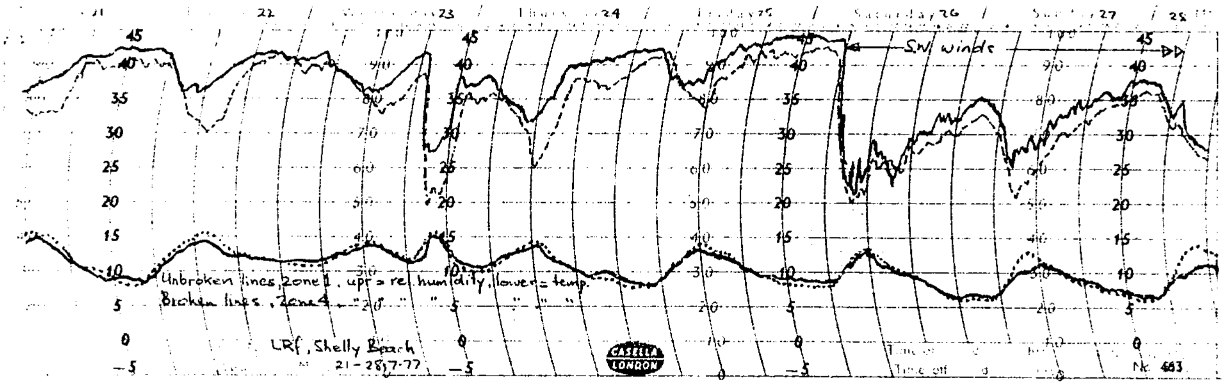


Fig. 3.7b (ii) Winter thermohygrographs ; details as above.

Results 3.3.3 Study Sites (cont.)

3.3.3c DRf, Long Point, Hillgrove, NSW

(i) General Description:

Altitude : ca 950 m.

Topography : moderately steep and roughly even, stabilized scree-slope of W aspect, just below ridge crest.

Soil : somewhat skeletal red earth of moderate fertility, derived from shales.

Climate : moderately moist subtropical/warm temperate; summer max. temps. 32°-39°C, mins. 10°-13°C, winter max. 14°-18°C, mins. 0°-3.5°C (1977/78 data). M.A.R. ca 1000-1200 mm, some orographic influence, storms prominent; night mists moderately common in autumn, winter and spring.

Vegetation*: Dry rainforest (microphyll mossy vine thicket) i.e. depauperate STRf, plus typical distinctive elements; the almost sole dominant sp. in this plot and nearby was *Backhousia sciadophora*. Canopy uneven and low (3-10 m) with numerous light breaks. Shrub layers present but dicontinuous; ground herbs sparse; cryptogams moderately common, esp. trailing mosses and foliose lichens in lower zones and crustose and "old-man's-beard" lichens above.

* Plate 5.2.1 (Chapter 5) gives an indication of the forest physiognomy.

(ii) Microhabitat Physical Factors

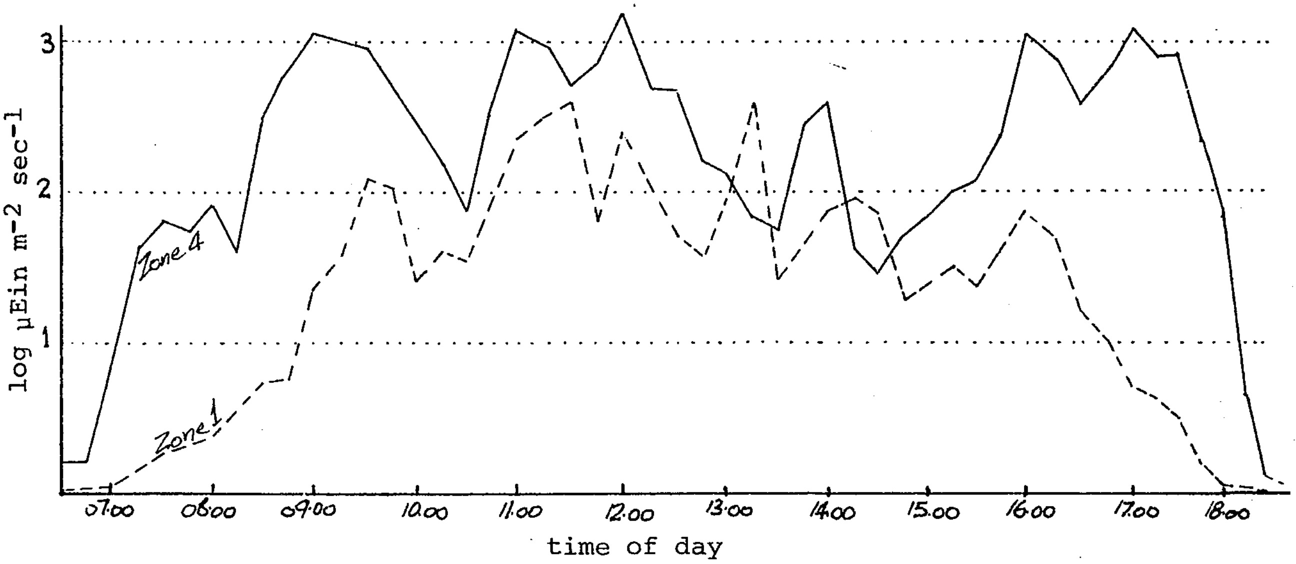


Fig 3.5c Light intensity at two levels in Long Point DRf during 20.1.1979

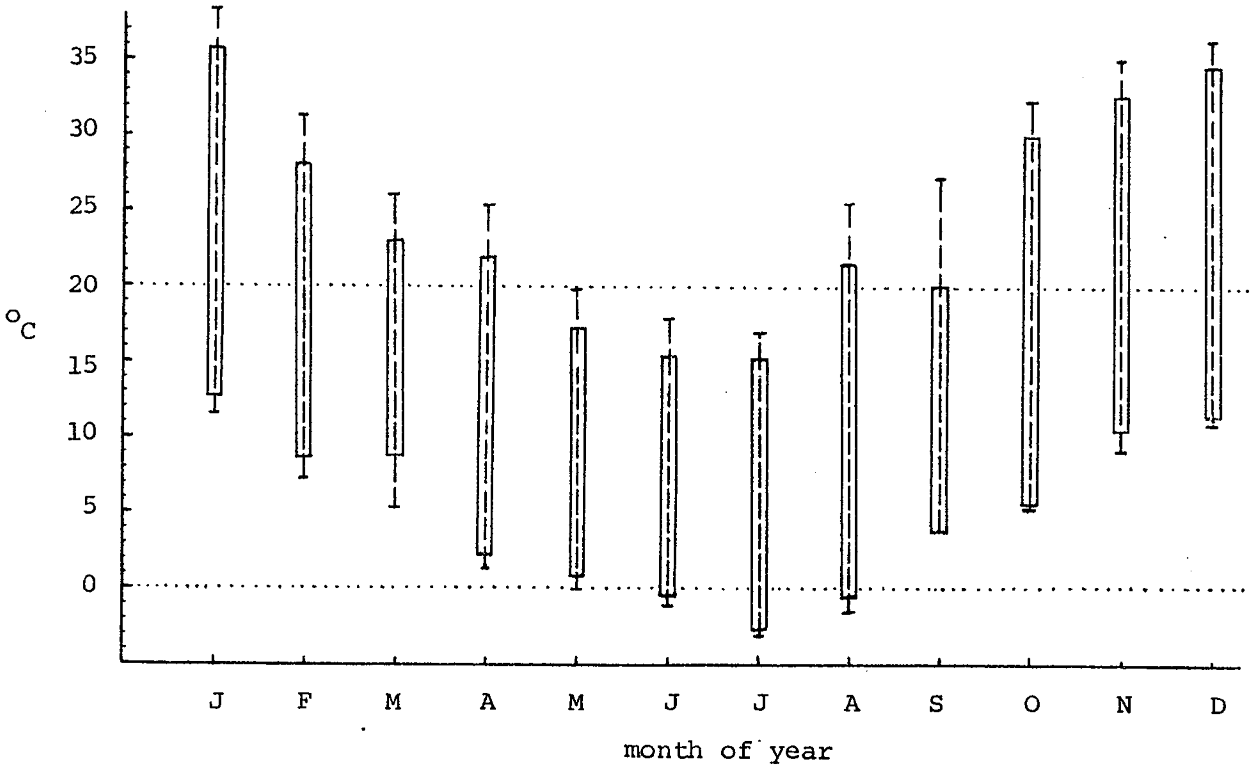


Fig 3.6c Long Point DRf temperature maxima & minima, 1977
Zone 1 columns , Zone 2 broken lines

Absolute max. Zone 1, 34°C ; Zone 4, 39°C
" min. Zone 1, -3°C ; Zone 4, -3.5°C

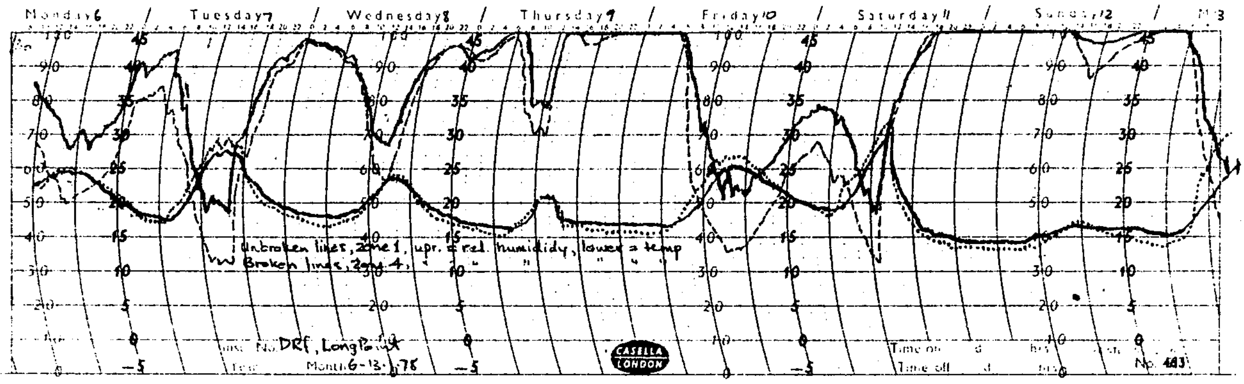


Fig 3.7c (i) Summer thermohygrographs, Long Pt. DRf, 1977 : Zone 4 graphs (broken lines) superimposed on those of Zone 1 (unbroken lines)

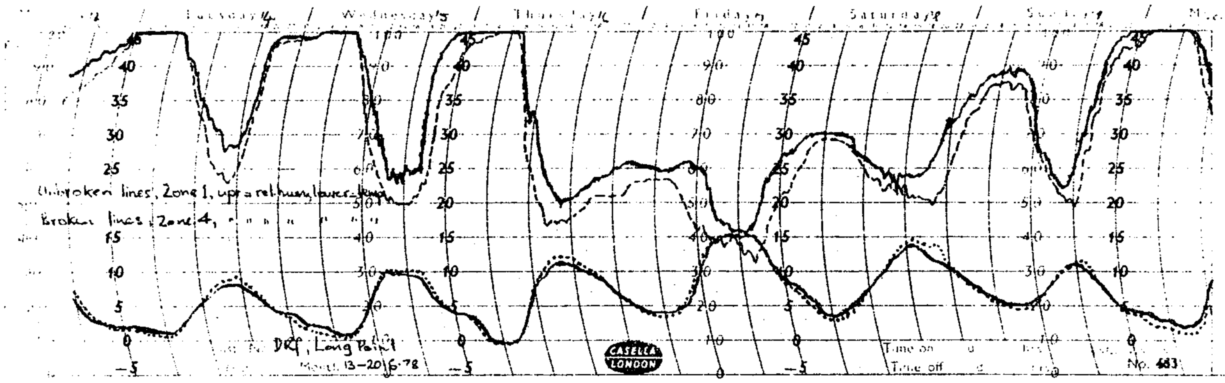


Fig. 3.7c (ii) Winter thermohygrographs ; details as above.

Results 3.3.3 Study Sites (cont.)

3.3.3d WTRf, Humber Hill, New England National Park, NSW

(i) General Description:

Altitude : ca 1000 m.

Topography : steeply sloping gully side with E aspect.

Soil : Brown earth of moderately high fertility, derived from fine sediments.

Climate : Moist warm temperate; summer max. temps. 26°-33°C, mins. 8°-12.5°C, winter maximums 10°-14°C, mins. -1 to 1.5°C (1977 data); M.A.R. ca 1400-1800 mm, relatively strong orographic influence; mists common.

Vegetation : Warm temperate rainforest (simple notophyll evergreen vine forest of Webb, 1978). Dominant tree spp. included *Ackama paniculata*, *Ceratopetalum apetalum*, *Doryphora sassafras*, *Pennantia cunninghamii* and *Schizomeria ovata*. Canopy very variable, 10-25 m high, ca 60-85% cover but large light breaks common, thus lower shrub and herb layers variable; tall shrub layer present (esp. *Quintinia verdonii* and *Pennantia cunninghamii*).

(ii) Microhabitat Physical Factors:

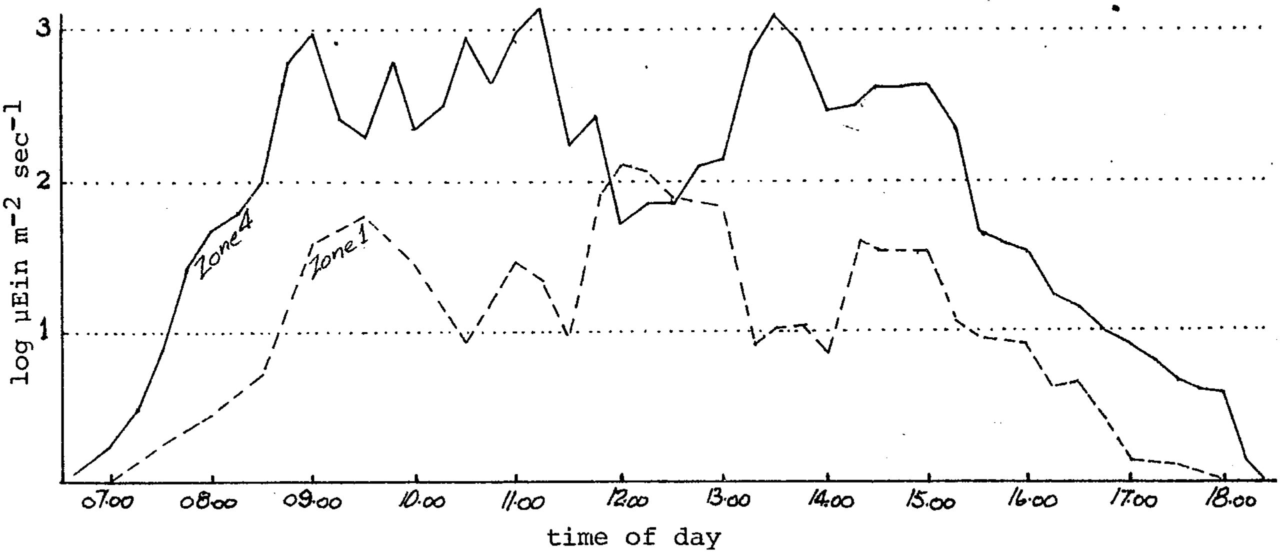
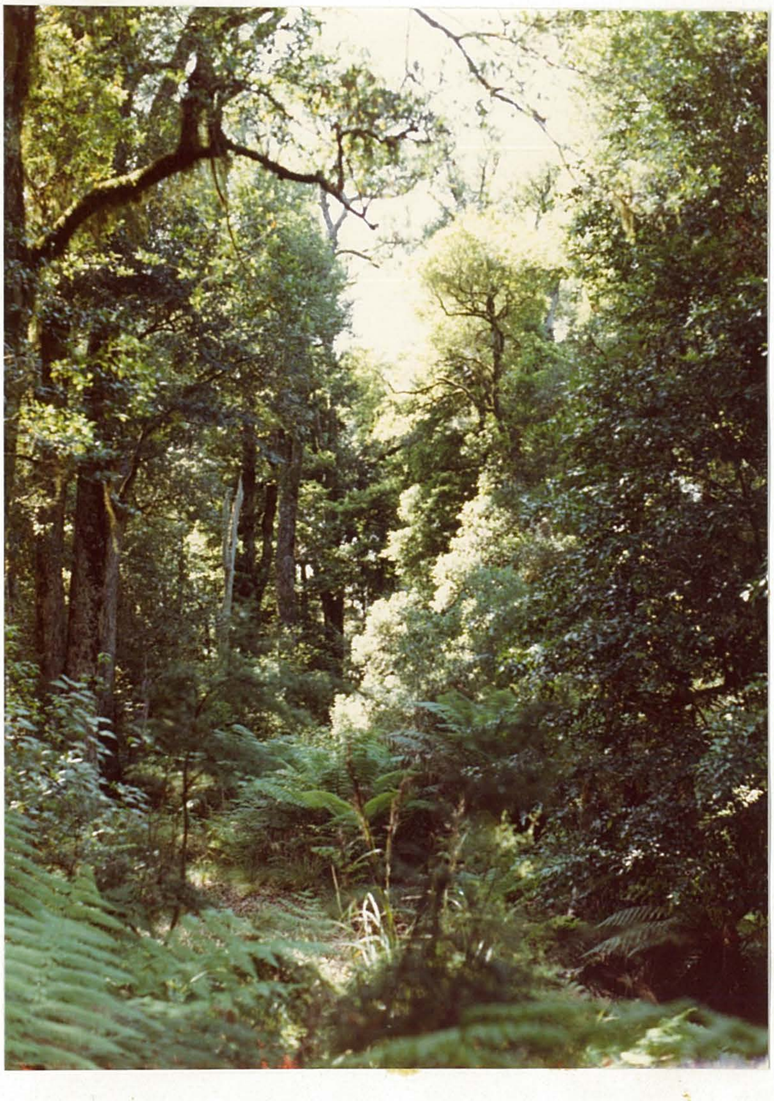


Fig. 3.5d Light intensity at two levels in Humber Hill WTRf during 3.3.1979

Plate 3.5
Sub-canopy view in Warm Temperate Rainforest, Humber Hill, New England NP, NSW showing typical structure. The pendulous, clumped epiphyte above is the fern *Dictymia brownii*.

Plate 3.6
View of Cool Temperate Rainforest, Wrights Lookout, New England NP showing typical, large lightbreak. In the foreground is the treefern *Dicksonia antarctica*.



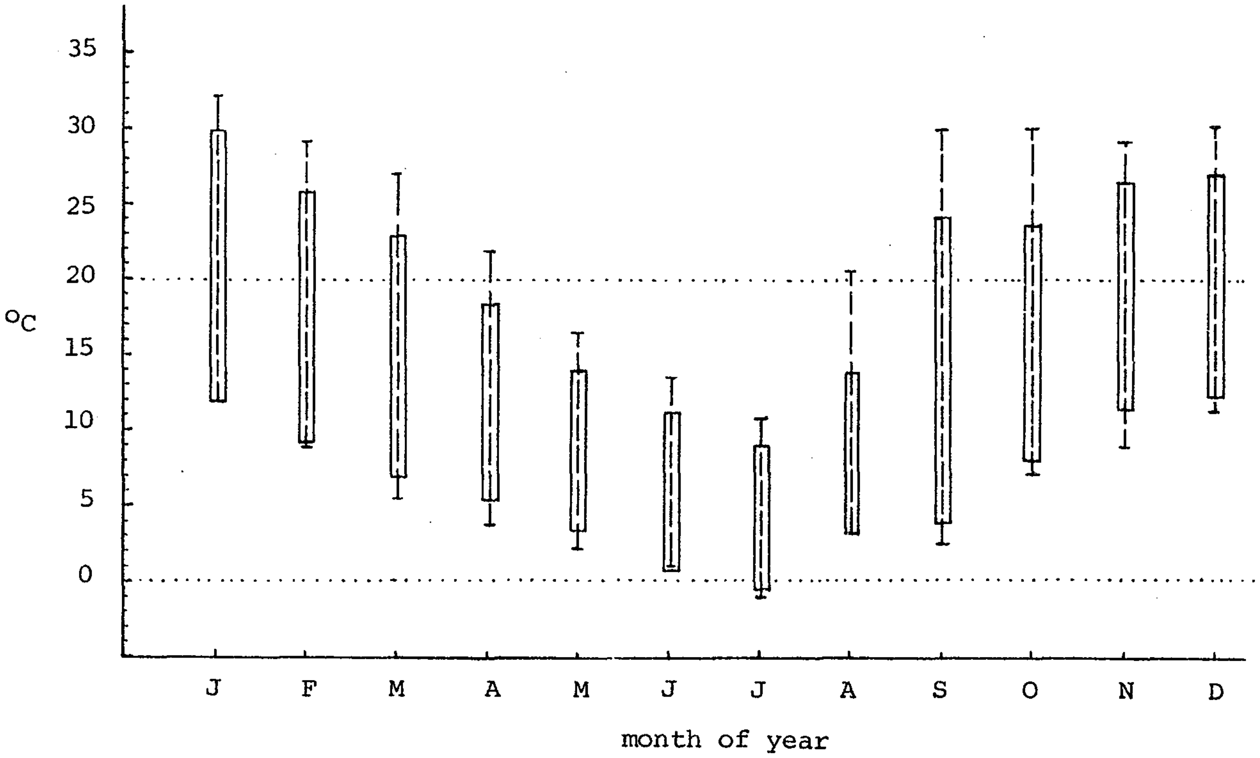


Fig 3.6d Humber Hill WTRf temperature maxima & minima, 1977
Zone 1 columns, Zone 4 broken lines

Absolute max. Zone 1, 30°C ; Zone 4, 33°C
" min. " " -1°C ; " " -1.5°C

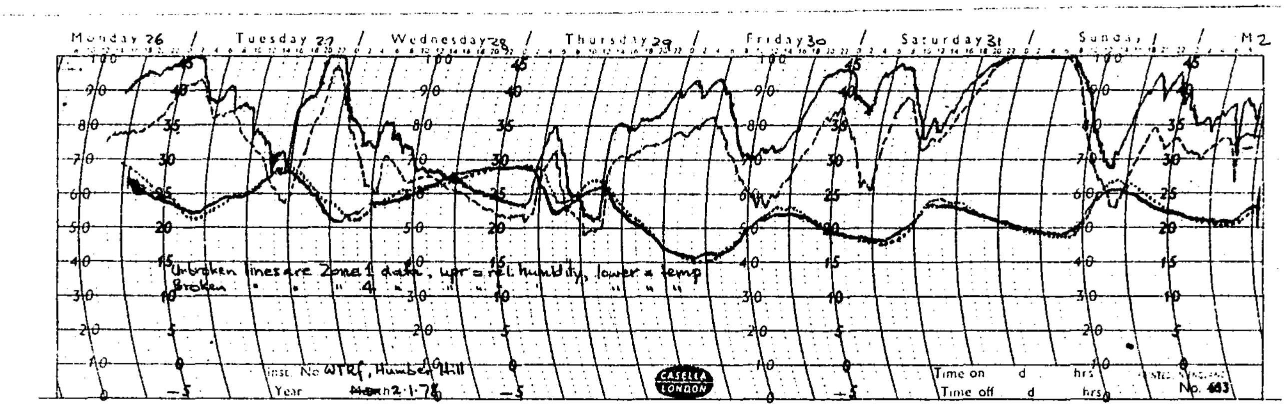


Fig. 3.7d (i) Summer thermohygrographs, Humber Hill WTRf, 1977 : Zone 4 graphs (broken lines) superimposed on those of Zone 1 (unbroken lines)

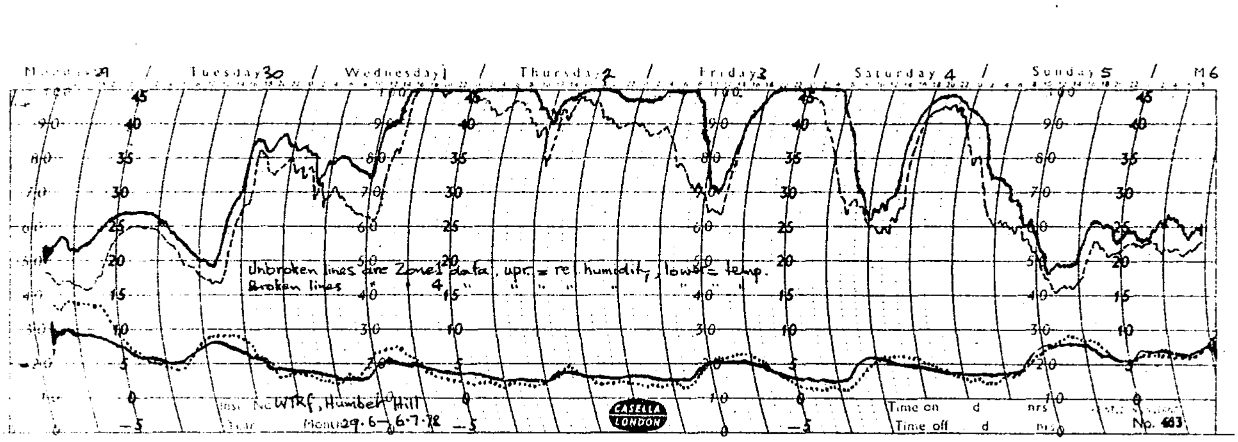


Fig 3.7d (ii) Winter thermohygrographs ; details as above.

Results 3.3.3 Study Sites (cont.)

3.3.3e CTRf, Wrights Lookout, New England National Park, NSW

(i) General Description :

Altitude : ca 1300 m.

Topography : strongly undulating with a moderate slope down towards the SE.

Soil : Brown earth derived from fine sediments; high fertility.

Climate : Moist cool temperate : summer maximum temps. 25°-30°C, mins. 8°-10°C, winter max. 9.5°-12°C, min. 12.5°-0°C (from 1977 data); M.A.R. 1500-2000 mm, ± evenly spread; strong orographic influence; mists common.

Vegetation : Cool temperate rainforest (microphyll mossy (or fern) forest of Webb), the dominant tree sp. being *Nothofagus moorei*; canopy with ca 50-80% cover, ca 15-30 m high; small tree, shrub and herb layers relatively prominent; cryptogamic epiphytes very common.

(ii) Microhabitat Physical Factors:

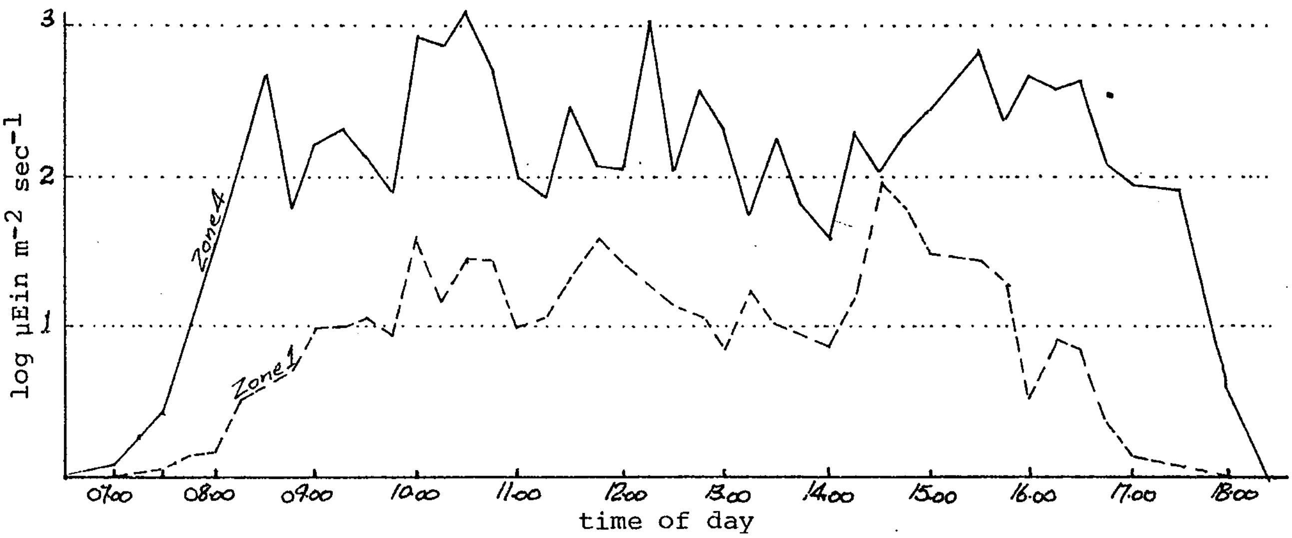


Fig 3.5e Light intensity at two levels in Wrights Lkt CTRf during 4.3.1979

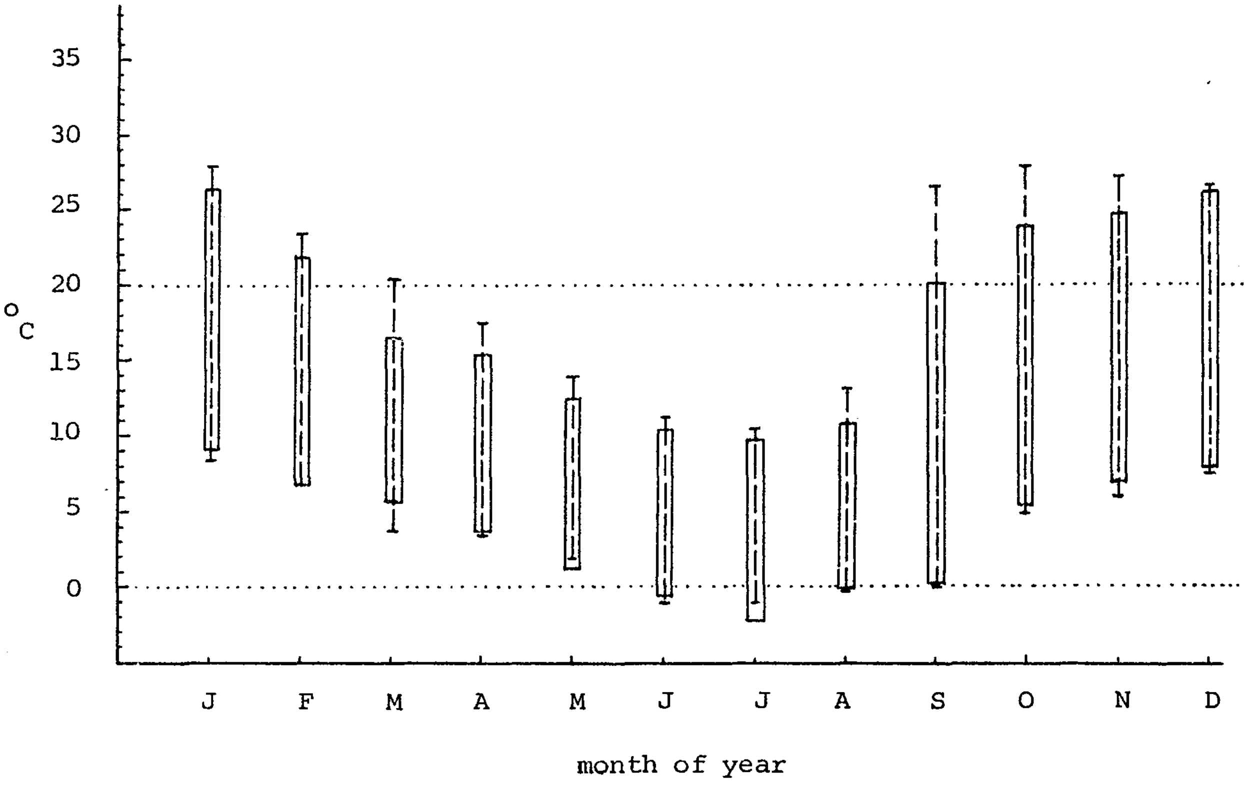


Fig 3.6e Wrights Lookout CTRf temperature maxima & minima, 1977
Zone 1 columns, Zone 4 broken lines

Absolute max. Zone 1, 27°C ; Zone 4, 29°C
" min. " " -3°C ; Zone 4, -1.5°C

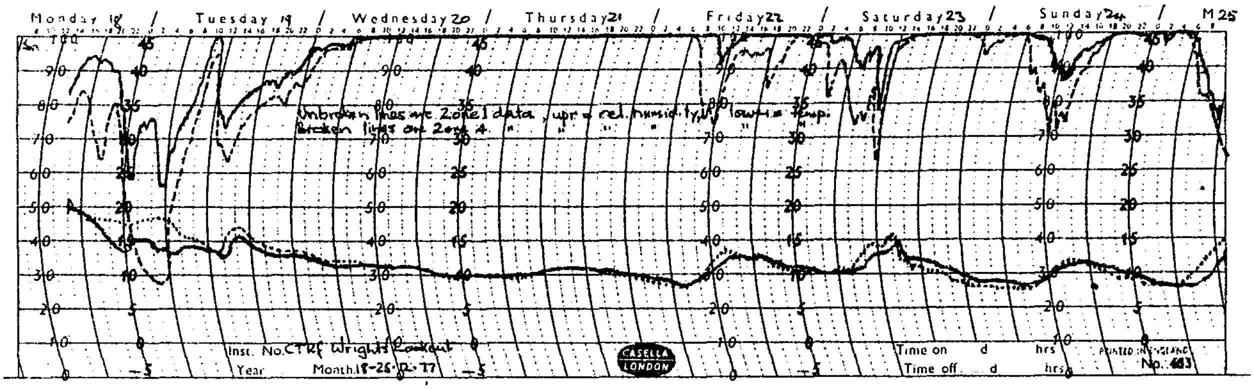


Fig. 3.7e (i) Summer thermohygrographs, Wrights Lookout CTRF, 1977 : Zone 4 graphs (broken lines) superimposed on those of Zone 1 (unbroken lines)

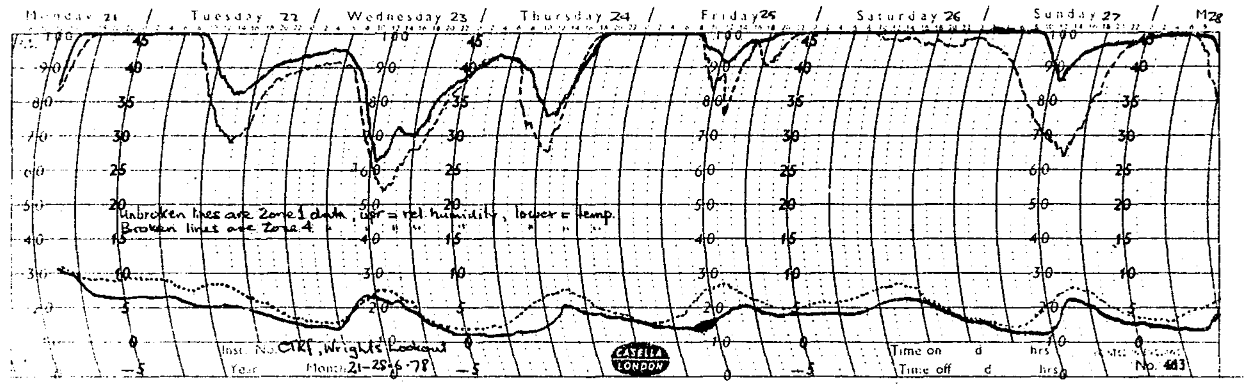


Fig 3.7e (ii) Winter thermohygrographs ; details as above.

Results 3.3.3 Study Sites (cont.)

3.3.3f SEVF, Leo Ck, McIlwraith Ra., C. York Pen., Qld. (CSIRO Experimental Plot 32)

General Description:

Latitude : 13°45' south Longitude : 143°20' east

Altitude : ca 450 m.

Topography : Plot site is near the crest of a broad SW-running ridge, the surface lightly undulating with a slight, uniform slope towards the southeast.

Soil : Sandy loam of apparent moderate fertility, derived from grantic parent material.

Climate : monsoon with wet season from Dec. to April, but also with significant rain during the dry season which also has some cloud cover much of the time, keeping temperatures down to some extent. M.A.R. is probably ca 2000 mm; temperatures mostly between 12° and 35°C (Lavarack, 1980).

Vegetation : monsoon rft (semi-evergreen mesophyll vine forest) with a moderately dense and continuous canopy at ca 10-15 m height; shrub layers present but not well developed; ground herbs moderately common; cryptogams sparse.

3.4 Discussion

3.4.1 Geography of epiphyte environments in Australia

Even though many vascular epiphytes are adapted in various ways to cope with water stress, 80% of the Australian species are more or less restricted to rainforest and similar relatively moist, closed communities. In turn, these environments are very scarce on a comparative area basis (<1% originally, now 1/3 to 1/4 of this - Webb & Tracey, 1981) and are restricted to areas of MAR > 1000 mm or so in the subtropics to ca 1400 mm in the tropics (Beadle, 1981) (See Fig. 3.1, p. 73). Soil fertility, particularly the level of phosphate, is an important determining factor in the subtropics (Beadle, 1954, 1966, 1981; Baur, 1957; Webb, 1969) but less so in the tropics (Francis, 1970) where fires and cyclones are more important (Stocker, 1981).

Another constraint on the distribution of rainforests in the tropics is the effect of higher mean temperatures resulting in stronger evaporation rates and consequent poorer plant water relations. This is reflected by the average annual potential evaporation (Fig. 3.2), the isopleths of which run roughly parallel to the isohyets, except for a disproportionate bulge to the north in evaporation rates. These factors and the seasonality of rainfall appear to be the basic reasons for the dearth of rainforest and related communities in the northwest of the continent, even where MAR is above 1000 mm. The wet season in this area is little longer than three months and all closed forests are small patches which owe their survival to the benefit of supplementary water supply from various groundwater sources such as springs, riverbeds etc. (K. Hill pers. comm.). Epiphytes gain no direct benefit from such water and thus are absent or very rare in these places.

Length and severity of the monsoonal dry season can be added to the factors limiting the occurrence of rainforest in the tropics. Even in areas of high MAR in NE Queensland, e.g. the Daintree R. district, the dry season may be quite pronounced (G. Stocker pers. comm.) and in regimes with dry seasons of increased intensity and regularity the deciduous element becomes more common in the vegetation, the structure more open and less complex, accompanied by decrease in epiphyte numbers. An illustration of this is found in the McIlwraith Ra. of Cape York Penninsula where Leo Ck, lying on the windward slopes in the path of the SE winds of the dry season, catches enough orographic rain during this time to support Semi-evergreen Mesophyll Vine Forest (SEVF), but on the drier leeward slopes and areas further inland towards Coen, the closed and semiclosed communities are reduced to Deciduous Vine Thicket (DVT). Epiphytes of the DVT are very few especially when compared with those of the SEVF (-see Table 6b, Ch.4 for the latter). The chief factor accounting for this difference is the length and intensity of the dry season (Lavarack, 1980).

As well as lower mean temperatures annually, the greater rainfall effectiveness in regard to subtropical and temperate rainforest occurrence relates to the incidence or annual spread of rain. Virtually all such rainforest, especially from the Tweed Shield Volcano area of extreme SE Qld and NE NSW and south to the Barrington Tops, occurs not only where MAR is greater than 1000 mm but also where there is no significant, regular dry season Vascular epiphytes taper off rapidly south of the Hunter R. even though rainforests continue to, and are prominent in Tasmania; reasons for this have been discussed in Ch. 2.

The 20% of Australian vascular epiphytes that normally occur only in open communities are still mostly associated with climatic factors that favour rainforest occurrence, i.e. high, even MAR and relatively low evaporation rates. A few extremely xerophytic species such as *Dendrobium canaliculatum*, *D. dicuphum* and *Cymbidium canaliculatum* extend into savannah woodland and open savannah in the tropics, sometimes to country with a MAR of only ca 600 mm and an 8-10 month dry season. In the case of the *Cymbidium* there are reports of isolated plants occurring in River Redgum trees (*Eucalyptus camaldulensis* Dehn.) on Coopers Ck in NW S. Aust. in true desert. These species are thoroughly arid-adapted with, e.g., considerable water storage capacity, strong CAM and the two *Dendrobium* species are facultatively dry-deciduous; all have thickly velamen-sheathed roots. The *Cymbidium* grows in hollow limbs and knot-holes with the roots growing into the rotten centres of the branches and trunks which remain moist for long periods after rain.

The general climatic inhospitality of the Australian continent then appears to be the main factor restricting the development of rainforest and similar communities. Thereby it limits the occurrence of environments suitable for vascular epiphytes and thus of the epiphytes themselves.

3.4.2 The study site macroenvironments

The five sites chosen for the recording plots in the subtropics, as mentioned in the introduction, were selected partly on the basis of being typical of their subformation types and partly because a degree of control of ecological variables obtained from site to site. These variables included:

a) available biota : the rainforest areas containing three of the plots, viz, Dorrigo STRf, Humber Hill WTRf and Wrights Lookout CTRf are directly connected and thus major barriers to migration are not present between them. Barriers of open communities between these and the other two are, or were in historical times, not greater than about 50 km wide. This, plus the fact of significant floristic overlap between sites, indicates that they all have, or at least relatively recently have had, approximately equal access to the local common flora pool;

b) time : the communities in which the plots were located all gave the appearance of being stable and mature, lacking obvious seral features;

c) soil parent material : this does vary but, with two exceptions, the important derived factors of soil texture and nutrient status do not appear to vary significantly. The Shelly Beach LRf is situated on ultrabasic rocks which are low in plant nutrient minerals but this is offset to some degree by input of cyclic salts from the adjacent ocean (J.L. Charley, pers. comm.); because of steep slope and low soil water status at Long Pt., mineral status may be somewhat limiting there (ibid);

d) topography : four of the sites were on moderate to moderately steep mid slopes of an easterly aspect and were thus free of top or bottom slope effects and were sheltered from the dry, cold westerly winds prevalent in winter and spring and exposed to the warmer, moister easterly winds. The Long Point site was exposed to the west on a steep, upper slope.

e) macroclimate : certain components of this independent ecological variable are most likely to account for the differences in vegetation between sites. These are mean temperature and MAR and to some extent the incidence of mist. Two different gradients from site to site can be delineated:

i. decreasing mean temperature from Dorrigo to Humber Hill to Wrights Lookout, while MAR and mist incidence are high (see Table 3.1, next page) and factors a) to d) above are ± constant also, and,

ii. increasing aridity from Dorrigo to Shelly Beach to Long Point, partly from decreasing MAR but also from the influence of winds - persistent, strong sea breezes (as well as low mist incidence) at Shelly Beach and the dry westerlies to which the Long Pt. plot is exposed. The latter is somewhat compensated for by higher mist incidence in the cooler months (see King, 1980).

Table 3.1 Climatic parameters of the subtropical study sites.

Site	Approx. Mean Temp. °C*		MAR, mm	Mean Diurnal Ra. °C†
	Summer	Winter		
Dorrigo STRf	25.5	7	2000	15.4 ± 2.9 19.4 ± 2.0
Shelly Beach LRf	23	10.5	1500	15.4 ± 2.8 20.26 ± 1.9
Long Point DRf	20	6.5	1100	21.6 ± 5.4 23.7 ± 3.0
Humber Hill WTRf	20.5	5	1600	14.8 ± 4.5 19.0 ± 4.4
Wrights Lookout CTRf	11.5	4	1800	14.6 ± 3.6 17.2 ± 4.8

* derived from 7 day thermohygrographs (see Figs 3.7a-e)

† mean of 12 month data given on Figs 3.6a-f, Zone 1 and Zone 4 separately.

Means of the diurnal range of monthly max./min. temperatures may give an indication of the degree of "climatic buffering" to which a site is subject. The greatest mean range of monthly max./min. temperatures was in the Long Point DRf (see Table 3.1) and least at Wrights Lookout. The high mist or cloud frequency probably explains the latter, while the dry, open, exposed nature of the DRf and its typical lack of cloud cover probably account for its greater mean diurnal ranges.

3.4.3 Macrocommunity[1] structure

Aspects of macrocommunity structure that are relevant to the epiphytes varied considerably between the different systems. Overall complexity, i.e. number of vegetational layers and different life-forms, decreased from less to more stressed systems. Thus the Dorrigo STRf had prominent emergents above the canopy, a highly integrated canopy layer and a

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[1] This term is used to refer to the overall phytocoenosium to avoid confusion with microcommunities of epiphytes.

prominent tall shrub and small tree layer, (see veg. profiles, Figs. 3.3a-e) which allow maximal epiphyte microhabitat differentiation. Contrasting with this is the situation in the CTRf and DRf where the canopy layer is rather discontinous and there are few true emergents. The DRf has an ill-formed, disparate shrub layer while the CTRf does have a distinct small tree and tall shrub layer . Thus these simpler systems offer less microhabitat variety for epiphytes. In the WTRf and LRf structural complexity is intermediate between the extremes with the former being near to the condition of the stressed systems and the LRf closer to the relatively unstressed STRf of Dorrigo.

Characteristics of the canopy are important in conditioning the microhabitats beneath. Canopy height may influence the amount of space available for ecological differentiation. Canopy density and the size and frequency of light-breaks directly regulate the intensity and depth of penetration of solar radiation as well as exercising control over air movement. As already stated and as will be argued later (and has been argued by others e.g. Pittendrigh 1948, and Richards 1952), competition for light appears to be the main evolutionary selection pressure "driving epiphytes up into the trees" and is perhaps the most powerful factors controlling the distribution of epiphytes within the macrocommunity.

The Dorrigo STRf canopy is the highest, densest and most continuous of all systems investigated yet there were still significant light-breaks as can be seen from the lumographs on Fig. 3.4a. The Shelly Beach LRf is nearest to this whilst the Humber Hill WTRf had a canopy density and height often comparable to these but with larger and more frequent light-breaks. In the most stressed systems of Long Pt DRf and Wright Lkt CTRf, patchiness becomes extreme and light penetration and consequently epiphyte 'zonation', are very irregular. Thus, in the Long Point DRf, many epiphyte species of outer zones in other systems, e.g. *Sarcochilus falcatus, Dendrobium beckleri* and *D. teretifolium*, frequently occur near the ground. Light and air movement data for this site (Figs 3.5c & 3.4, pp. 82 & 75) provide some evidence in support of this.

Two other macrocommunity structural parameters require mention - viz, tree size or dbh and number of trees per ha, especially in relation to the water- and probably nutrient-stressed systems of the DRf and the tropical SEVF. In these the number of trees per ha was higher (1167 & 824 resp.) and the basal area per ha very much lower in both (38 & 32 m^2 resp.) than in the other four systems (60-130 m^2); the nearest in trees/ha was Dorrigo

(744) and in basal area, Shelly Beach LRf with 60.5 m^2/ha. The reasons for this require some investigation, but the implication for epiphytes is the larger phorophyte stem area per ha available for colonisation is possibly one factor that contributes to the large epiphyte populations of these two systems.

3.4.4 Microhabitat Physical Factors

Irradiance

In all five sites irradiance was shown to be much stronger in Zone 4 than Zone 1 (Figs 3.5a-e). This is as expected and is simply because of the shading effect of the primary canopy and the canopy of subordinate small trees and tall shrubs. In four of the graphs, the approximate absolute difference between the average midday irradiance in the two microsites is about one order of magnitude, e.g., where Zone 1 is ca 100, Zone 4 is at ca 1000 $\mu E\ m^{-2}\ sec^{-1}$. At Long Point however, the difference was considerably less than this because of the relatively low, open structure of the DRf (see vegetation profile, Fig 3.2c). Such an effect could be expected also in the Wrights Lookout CTRf because of the openness of vegetation structure, but the lower sensor in this case was placed under a treefern (*Dicksonia antarctica* Labill.) in order to relate to the low shade-epiphyte synusia which occurs in this microhabitat.

Again, all graphs show fluctuation of approximately one order of magnitude, during the brighter hours in both zones. This is due to light breaks in the canopy and variation in canopy density. The range of fluctuation is such that the peaks of intensity in Zone 1 are higher than the low points of Zone 4; such Zone 1 peaks, however, are well above the mean level for the zone.

Thus, there is a marked zonation in irradiance within the rainforests investigated and this correlates with zonation in the epiphytic vegetation, which is discussed in the next chapter.

Maximum & minimum air temperatures

Summer maximum temperatures, being less than 40°C at the most extreme, do not appear themselves to be critical in limiting the distribution of epiphytes in the sites investigated. However, minima may be so, since at all sites except Shelley Beach LRf they went below 0° C during at least one month and did so in four months in the CTRf and DRf. This may help explain the impoverished epiphyte floras of these two sites, especially in the latter one where typical DRf orchids such as *Rhinerrhiza divitiflora*, *Dendrobium gracilicaule* and *D. beckleri*, are rare at Long Point.

Factors affecting microhabitat water status

The three main factors here are frequency of precipitation, solar heat input and air movement. Also, dependent on these are air temperature, relative humidity and atmospheric evaporative power or vapour pressure deficit.

Frequency of precipitation

This was not recorded but in the case of rainfall, was taken to correlate with MAR level, while mist frequency observations came from residents living near the study sites as well as the writers own and those of other ecologists of the Botany Dept., UNE, e.g., King (1980). From these the ranking of sites regarding precipitation frequency was as follows : Wrights Lkt Dorrigo Humber Hill Shelly Beach Long Point. Orographic influence is strongest at Wrights Lookout because of its altitude and aspect - rain and mist are very frequent; these same factors are also important at the Dorrigo and Humber Hill sites. Long Point is in the rainshadow of the coastal ranges hence it is low in both MAR and rain frequency. This is partly offset by relatively high frequency of night mists in the cooler months owing to large diurnal temperature fluctuation (see Table 3.1). Shelly Beach LRf has MAR and rain frequency both greater than Long Point, but has virtually no mists.

Precipitation frequency is important in epiphyte microhabitat water status since the substrate generally has poor water retention powers and thus the more frequent the input, even if not quantitatively large, the more readily an epiphyte can maintain supply. Rapidity of water uptake is thus important and has been demonstrated in some epiphytic species, e.g. by Walter (1951). Storage capacity will similarly be important.

Air movement

Air movement across a moist surface tends to remove the humid boundary layer, thereby increasing the potential for evaporation. This effect will still hold if the moving air is itself quite humid. Air movement was measured at two sites, Dorrigo STRf and Long DRf (Fig 3.4) and in both cases was greater in Zone 4 than Zone 1. Again, this is to be expected because of decreased obstruction to wind with increased distance above ground in the forest, and also because heating and cooling is greater and more rapid in the more exposed zones, giving rise to greater convectional air movement. Thus air movement will be important in promoting greater xericity in the more exposed zones. Heat input from solar radiation is greater in Zone 4 than in Zone 1 simply because foliage, branches, etc in the former intercept the majority of incoming radiation which is thus denied to lower zones. The light intensity data of Figs 3.5a-e show this. Heat is input with light via solar radiation as short-wave heat and is transformed to longwave form on contacting solids. Maximum temperature differences between the two microsites (see Figs 3.6a-e) further support the concept of higher daytime heat status in upper, more exposed microsites. This in turn makes for more rapid evaporation which further depletes the water status of these epiphyte microhabitats.

Comparison of hygrographs run concurrently in Zone 1 and Zone 4 provides further verification of the greater xericity of exposed epiphytic microhabitats. Almost without exception, Figs 3.7a-e show relative humidity of Zone 4 running ca 2-20% below that of Zone 1, except at saturation point. Thus vapour pressure deficit or atmospheric drying power is greater in Zone 4 than in Zone 1 and this has implications for water loss from both substrate and plant body, especially the leaves of epiphytes occupying the higher zones.

3.5 Conclusions

1. Because of continental patterns of precipitation and evaporation, and to a lesser extent soil nutrient poverty and the incidence of fires and cyclones, rainforests and similar epiphyte-favoured environments occupy only a very small proportion of the area of Australia. This directly limits the occurrence of epiphytes and their opportunity for evolution and diversification here.

2. The study sites chosen were from rainforest types STRf, LRf, DRf, WTRf & CTRf and varied in regard to macroclimate, flora and vegetation. They shared a degree of similarity in biota availability, maturity, topography and soil fertility. Climatic factors, particularly MAR,

precipitation frequency, mist incidence and mean air temperature are regarded as the main factors responsible for variations between sites in epiphyte flora and vegetation.

3. Rainforest structure varied between sites in factors that influence the occurrence and ecology of epiphytes. Such structural features include number of vegetational layers, height and density of the canopy and size and frequency of lightbreaks. These influence microclimatic factors such as intensity and depth of light penetration through the canopy, air movement, atmospheric temperature and evaporative power.

4. At all sites microclimatic factors varied markedly between Zone 1 at the tree butt and Zone 4 among the outer branches. Data collected show that Zone 4 is markedly brighter, warmer during the day and cooler at night, exposed to greater air movement and air of lower humidity and is considerably more xeric as an epiphytic environment, than Zone 1.

3.6 Recommendations for future investigation of epiphyte microclimate

With the benefit of hindsight, increased financial and technical assistance and modern electronics technology, the following recommendations could improve quantity and quality of relevant data returned:

a. the use of electronic integration units to measure mean levels of air temperature, irradiance , evaporative power of the atmosphere and air movement. This would make for sharper, more accurate differentiation between microsites.

b. continuous recording of irradiance and of temperature and humidity, particularly to clarify small-scale variation.

c. data collection over longer periods, e.g., three years, to give a better indication of annual variation.

d. monitoring of macroclimate, especially annual rainfall, precipitation frequency, mist frequency and winds.

e. the permanent or semipermanent setting up of canopy research facilities such as work platforms and access equipment to reduce time and energy spent repeatedly on temporary measures & to generally facilitate canopy research.

CHAPTER 4

SYNECOLOGY OF EPIPHYTES

4.1 Introduction

As with terminology for the life forms and physiognomy of epiphytes, ideas concerning their synecology and the related terms have varied with time and writer. There are two basic sources of variation, one from different approaches to general community classification, and the other from different opinions on whether epiphytic vegetation should be regarded as simply synusiae within communities or as microcommunities within larger communities and as such be accorded a more specialised, hierarchical classification comparable to that for the macrocommunities.

Epiphytic vegetation has been studied and classified for at least a century: Schimper (1888) and Went (1895) made observations on epiphyte synecology but these were not as developed or as systematic as those of later writers. Plant sociology in general evolved most rapidly in the first quarter of this century with the works of such authors as Clements, Braun-Blanquet, du Rietz, and others. One school of thought stressed dynamism and developed such concepts as succession and climax, while the other major one played these down, preferring to study the vegetation as it stood, in terms of present composition.

Schimper referred to the ecological groupings of epiphytes within a given community as *tiers*. Braun-Blanquet (1932), discussing plant sociology, and particularly, "dependent unions", in which he included epiphytes, stated that "... in warm moist regions ferns and seed plants also grow epiphytically and form sharply circumscribed communities (dependent communities)". Oliver (1930) maintained that the "more pronounced epiphytes form distinct ecological units in the [forest] formations"; he discussed dominance and temporal succession in them and called the units *societies*. These units were two synusiae, sun epiphytes (on branches) and shade epiphytes (on trunks), which he thus recognised as functional units of interacting components, but subordinate in, and dependent upon, vegetation units of higher order. Richards (1938) went further, emphasising the successional and subordinal aspects of epiphytic vegetation and applied Clements' (1936) *serule* (miniature, subordinate succession) concept and terminology in a study of cryptogamic epiphytes. Later however (1952), dealing with vascular epiphytes, he used a system of three synusiae (shade, sun and extreme xerophilous epiphytes) to characterise epiphytic vegetation.

Hosokawa rejected the use of phytocoenosial units, e.g., alliance, association etc., for epiphyte communities (as e.g. Ochsner, 1928, Barkman, 1958, etc., used), as the latter were subordinate *within* these units. Likewise he rejected the use of synusial units since, even though these were subordinate, they applied to terrestrial vegetation, defined by their stratification and height and as such were regarded by Hosokawa as inappropriate for use with epiphytes. Serule units, in his view, may be applicable in studies of epiphyte succession but not to epiphytic vegetation in general. He proposed (1951) a new system, parallel in concept to the overall phytocoenosial one and eventually (1954) settled on the terms, *epies* (≃ society), *epilia* (≃ association) and *epido* (≃ alliance); these were subordinate to the forest phytocoenosial units but independent of them.

In discussing epiphytic vegetation of the Nimba Range, Liberia, Johansson (1974) simply used the term *epiphyte community* (homologue of Hosokawa's epilia, in Johansson's usage) to describe any grouping of epiphytes of three or more species which were growing in close proximity to one another ("when the distance from two of them does not exceed 0.5 m to the third"). This system is simple and straightforward and does not enmesh the user in esoteric argument while providing a framework for the description of some epiphytic vegetation.

From an area containing an epiphyte flora of 153 spp and using ca 650 individual examples, he delimited 10 different community types, each named after the two most characteristic species.

Later (Johansson, 1978), discussing methods of recording epiphytes, he used a distribution chart or pseudo-graph of their spatial arrangement on the phorophyte. In this, species were listed on the left and phorophyte stem circumference graduated along the horizontal axis at the base. Against each species is marked the maximum, minimum and mean circumference of phorophyte stem on which it occurs on a particular trunk/branch system. Thus, vertical alignment of species occurrence on the chart will indicate probable presence of an epiphyte community. In 4.2.3 of this chapter a modified version of this has been used on one or two well colonised phorophytes from each of the recording plots.

Grubb et al. (1963), comparing the epiphytic flora and vegetation of a montane and a lowland forest in Ecuador, simply classified them into two synusiae, afer Barkman (1958), viz, skiophytes and photophytes. They recorded numbers of species present per family and numbers of individuals in arbitrary 15 ft. zones as bases for comparison. Sugden and Robins (1979) compared two Columbian cloud forests using the same basic approach. They recorded species present, their numbers of individuals and the % of these above half canopy height, in 14 small plots in each community.

Valdivia (1977) recorded epiphyte name, size and height above the ground in an ecological/vegetational resource study in Veracruz, Mexico. He classified them as occurring on trunks, branches, or on both. Phorophytes were also listed and bark characteristics noted.

Madison (1979) investigated the distribution patterns of epiphytes in a Sarawak rubber plantation and in a stand of dead (drowned) trees in Manaus, Brazil (in prep.). His aim was to determine objectively by statistical documentation whether distribution was random, under-dispersed, gregarious etc. and relate this to such factors as mode of seed dispersal. Part of the plantation was mapped and epiphyte species per tree marked in, giving a plan view of their distribution. In the S. American case, the trees (which at this stage were simple trunks) were intensively mapped and represented as columns divided into 30 cm segments with each epiphyte and ant garden marked in these. This study showed a high degree of gregarious distribution as also did ant-dispered epiphytes in the Sarawak study with wind and bird dispersed ones being random.

Of the epiphyte recording systems mentioned above, none appears to particularly suit the pruposes of the present study (see 4.2.1). That of Grubb et al. (1963) was part of a general vegetational study rather than of epiphytes exclusively, a point true of many earlier, uncited epiphyte accounts. This was reflected in some of his methods, e.g. the use of 15 ft hole units for comparison - such an arbitrary system may be objective but does not properly reflect ecological variation. Valdivia (1977) similarly uses simple measurement rather than relative position to record epiphyte distribution.

Johansson's (1978) distribution charts were suitable in the present study to illustrate distribution and show position and composition of epiphyte microcommunities on particular epiphyte-rich phorophytes. However, his treatment of the classification of such communities (Johansson, 1974), apt in the West African examples, do not seem to be so here owing to the apparent lack of floristic constancy in the local groupings.

The methods used by Madison (1979, and in prep.) were aimed particularly at investigating epiphyte distribution in relation to diaspore dispersal methods under somewhat controlled conditions and as such were specialised.

The aims of the Sugden and Robins (1979) study, even though they compared epiphyte diversity, abundance and general ecology in two areas, were somewhat different to those of the present one, which are stated in the beginning of the next section (4.2).

4.2 Synecology of the Australian epiphytes

4.2.1 Introduction and aims

It is not intended to present a comprehensive study of the Australian epiphytic vegetation here, or even that of the subtropics. Since virtually no previous attempt has been made to record or analyse it, a method and format was developed aimed at the general characterisation of the epiphytic vegetation of selected, initial examples from five different rainforest subformations of the subtropics and one, for comparison, from the tropics. Basically this involved the setting out of a plot in each and carrying out a detailed investigation of the occurrence and distribution of epiphytes in them. As such, the information on floristics and distribution is to some extent representative of these systems but that on density, less so, since plot sites had to be selected on the basis of *presence* of epiphytes rather than by random methods.

The term *epiphyte community* will be defined less stringently here than it has been by others (e.g. Johansson, 1974) as: *a group of individual epiphytes growing in close proximity to one another.*

Further, the names used here for epiphyte communities are intended to refer to individual stands rather than have much predictive or 'class' value regarding structure and composition. It is intended more as a reference system, using the name of the synusia qualified by the names of the most common taxa included in the group. The names of the synusiae (c.f. Richards, 1952) are:

1. Low shade-epiphytes (on trunk bases)
2. Upper shade-epiphytes (on upper trunks)

3. Mid level semishade-epiphytes (on large branches)
4. Sun-epiphytes (on small branches)
5. Extreme sun-epiphytes (on branchlets and twigs)

A variation of 1. may be usefully added, i.e., shade synusia of semi-epiphytic climbers (on trunks).

Thus, these have been defined on criteria from the environment rather than in terms of floristics.

Epiphyte microcommunities are dependent on, and subordinate in the macrocommunity vegetation and thus a full reference should also include the name of the phorophyte and of the macrocommunity in which it occurs. An example is a *Pyrrosia rupestris/Sarcochilus falcatus* sun-epiphyte community on *Acacia melanoxylon* in STRf margins.

The sites used in the present work are those described in the habitat study of Chapter 3, i.e., the Dorrigo STRf, Shelly Beach LRf, Long Point DRf, Humber Hill WTRf, Wrights Lookout CTRf and Leo Creek SEVF.

The data collected will be used firstly to comparatively analyse and characterise the epiphytic vegetation of these systems in regard to their floristic diversity and affinity, population density, and occurrence and ecological relevance of different physiognomic and life forms and relate these differences to envrionmental factors. Secondly, phorophyte/epiphyte relationships will be investigated using the local data, particularly relationships such as epiphyte proneness and axeny of tree species, specific relationships and phorophyte size/age effect.

4.2.2 Materials and Methods

In these six sites, recording plots were set up, the sizes of which were determined thus: a. a list of the epiphytes occurring in the macrovegetation stand chosen for the study site, was compiled, b. an area within the site containing most of the species listed was selected for the plot and, c. the plot was marked out at a size sufficient to include not less than 75% of the species listed.

From each plot, the following data were collected and presented thus :

i. <u>Plot location and size</u>. (For site description and discussion on altitude, topography, soil, climate and vegetation see habitat study Chapter 3).

ii. Phorophyte table - the phorophyte species were listed and against them, a) the total individuals of each species in the plot, b) the dbh (ranked with the largest first) in cm of each tree with an indication of its epiphyte load (the number of species and the total number of individuals) in brackets after each dbh. Those which carried only semi-epiphytic climbers were marked with an asterisk and those lacking any epiphytes were represented by the dbh figure only; epiphyte-bearers were underlined.

iii. Epiphyte table - all epiphyte species recorded (by climbing and the use of binoculars) in the plot were listed and against each, its phorophyte zone preference, (where 1 is the trunk base, 2, the upper trunk, 3, the large branches, 4, the small branches and 5, the twigs), the total number of individuals of the species in the plot, total number of phorophyte species colonised by it, and where applicable, the main phorophyte species and the percentage of the epiphyte carried by each. In counting individuals of a few species forming massive stands (*Pyrrosia rupestris*, *P. confluens*, *Bulbophyllum exiguum*), one individual was designated for each stand or each zone occupied in the tree bearing these. Species underlined were recorded from outside but near the plot in the same community. Species recorded from the same macrovegetation stand, but outside the plot were listed and underlined.

iv. Distribution Chart of the epiphytes on one or two major trunk/branch systems was drawn up, with species listed against the vertical axis and phorophyte stem diameter on the ordinate, similar to that used by Johansson (1978). For each species the mean phorophyte stem diameter is shown plus the range of variation in this where applicable. This is a schematised summary and facilitates the identification of microcommunities.

v. Phorophyte/epiphyte transect profiles from one or two trees in each plot were made as representative summaries of the spatial distribution of the epiphytes of each system to facilitate visualisation of the situtation within the system and comparison with other systems. These were not drawn in natural proportion or with the full number of epiphytes included but the position of each species in relation to others and to position on the tree is as occurred.

vi. A summary of the data is presented in table form (Table 4.7).

4.2.3 Results

(1) Epiphyte recording plot 1 : STRf, Dorrigo National Park, NSW

Location of plot : crest of eastern scarp of Dorrigo Plateau.

Plot Size : 50 x 25 m.

Table 1a : Phorophytes of STRf, Dorrigo N.P.

Species & total no. of each in plot		dbh & epiphyte load (spp., total indiv.) of each tree
Ackama paniculata	7	30(2,2) 21* 20* 19* 14* 14* 12* 12*
Acmena smithii	1	34*
Akania lucens	1	8*
Alangium villosum	2	43(9,31) 13(2,2) ; epiphytes (9,33)
Argyrodendron actinophylla	4	34(6,18) 38* 6* 5*
Baloghia lucida	1	23(4,4)
Capparis arborea	2	16* 13*
Claoxylon australe	1	10*
Cryptocarya foveolata	5	21* 21* 13* 8* 8*
Daphnandra tenuipes	2	18(2,3) 16*
Dendrocnide excelsa	15	82(5,12) 70(7,12) 58(3,8) 51* 49(3,5) 45 35(5,8) 28* 28* 20* 19* 17(2,5) 12, 9, 5* ; [epiphytes (9,63)
Diploglottis australis	2	35* 7*
Doryphora sassafras	2	25* 16*
Dysoxylum fraseranum	2	150(9,35) 14(2,2) ; epiphytes (10,37)
Elattostachys nervosa	3	16* 14* 11*
Endiandra crassiflora	2	19* 19*
Ficus watkinsiana	1	200(24,150)
Geissois benthamii	1	57*
Guilfoylia monostylis	2	23* 14*
Helicia glabriflora	3	20(3,5) 19* 13*
Neolitsea cassia	1	15
Neolitsea dealbata	1	9*
Orites excelsa	1	39 (3,10)
Pennantia cunninghamii	2	38* 30*
Planchonella australis	5	75(3,3) 42(11,26) 21* 10*; epiphytes (11,40)
Polyosma cunninghamii	8	25* 19* 14* 14* 13* 10* 12* 9*
Sarcopteryx stipitata	1	11*
Scolopia braunii	1	10*
Sloanea woollsii	1	150(12,67)

total tree basal area/ha = 130.8 m^2

* trees bearing only semi-epiphytic climbers

Table 1b : Epiphytes of STRf, Dorrigo plot

Species	Expos. zone	total indiv.	phoro. spp.	Main phoro.spp. & % borne
Pteridophytes				
Vittaria elongata	2-3	7	2	*Ficus* (71)
Arthropteris tenella	1-2	25	16	*Polyosma* (16)
Arthropteris beckleri	1	6	6	
Davallia pyxidata	3	13	4	*Dysoc.*, *Ficus*, *Sloanea*, all(31)
Microsorium scandens	1-2	20	17	*Planchonella* (14)
Dictymia brownii	3	11	4	*Ficus* (36), *Sloanea* (36)
Pyrrosia confluens	2-4	15	7	*Dendrocnide* (40)
Pyrrosia rupestris	2-3	5	5	
Platycerium bifurcatum	3	-	-	
Asplenium australasicum	2-4	55	11	*Ficus* (22), *Planchonella* (16)
Asplenium polyodon	1-3	11	4	*Ficus* (36), " (27), *Alang.* (27)
Dicots				
Parsonsia straminea (Acc.)	3	3	2	*Ficus* (66)
Pittosporum undulatum "	3	1	1	
Peperomia tetraphylla	2-3	62	8	*Dendrocn.* (23), *Alangium* (21)
Polyosma cunninghamii (Acc)	3	1	1	
Ficus watkinsiana	3	2	1	*Dysoxylum*
Monocots				
Pothos longipes	1-3	56	24	*Dendrocnide* (16), *Ackama* (11)
Liparis coelogynoides	2-3	14	4	*Ficus* (57)
Dendrobium speciosum	3	9	4	*Ficus* (56), *Sloanea* (33)
D. gracilicaule	3	3	3	
D. teretifolium	3-4	15	2	*Ficus* (60), *Sloanea* (40)
D. pugioniforme	2-4	25	6	" (38), " (24)
D. beckleri	4	16	2	" (63), *Dysoxylum* (37)
D. beckleri x *pugioniforme*	3-4	1	1	"
Bulbophyllum exiguum	3	12	12	" (50), " (50)
B. crassulifolium	3	21	2	" (70), *Sloanea* (30)
Sarcochilus falcatus	3-4	29	6	" (27)
S. fitzgeraldii	1-2	2	1	*Alangium*

Fig. 4.2.7

Distribution
Chart 1 : Epiphytes on trunk/branch system of *Sloanea woollsii* tree, Dorrigo N.P. STRf.

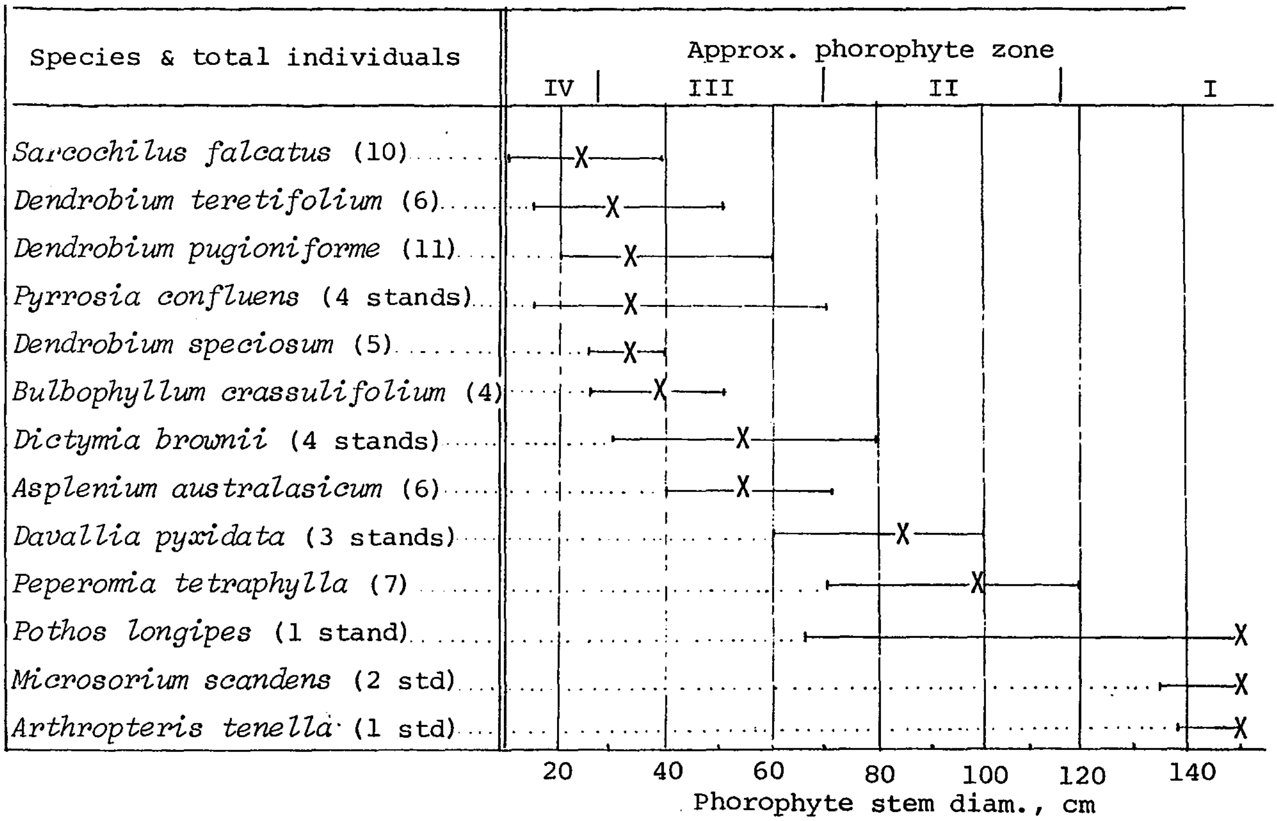
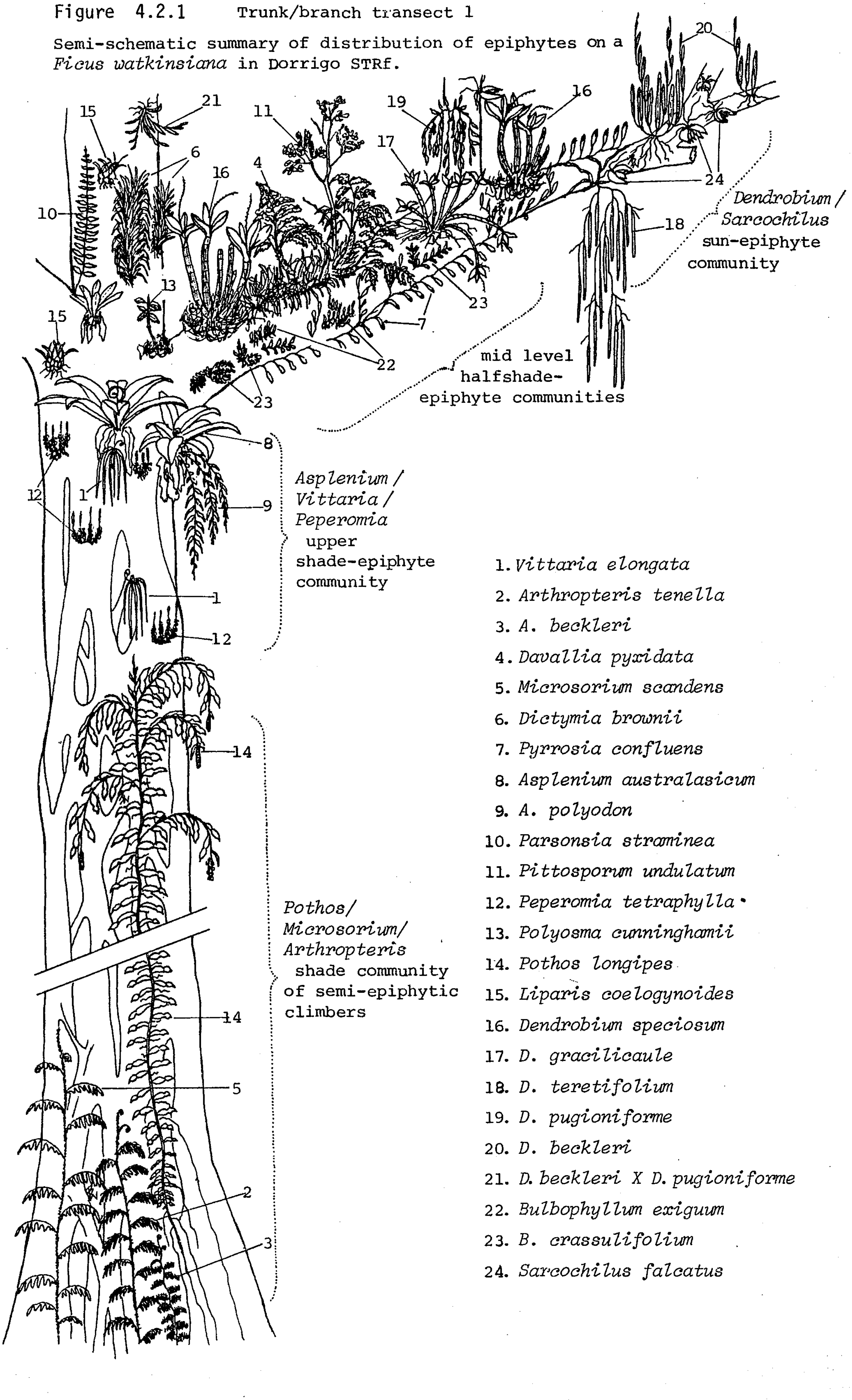


Figure 4.2.1 Trunk/branch transect 1

Semi-schematic summary of distribution of epiphytes on a *Ficus watkinsiana* in Dorrigo STRf.



1. *Vittaria elongata*
2. *Arthropteris tenella*
3. *A. beckleri*
4. *Davallia pyxidata*
5. *Microsorium scandens*
6. *Dictymia brownii*
7. *Pyrrosia confluens*
8. *Asplenium australasicum*
9. *A. polyodon*
10. *Parsonsia straminea*
11. *Pittosporum undulatum*
12. *Peperomia tetraphylla*
13. *Polyosma cunninghamii*
14. *Pothos longipes*
15. *Liparis coelogynoides*
16. *Dendrobium speciosum*
17. *D. gracilicaule*
18. *D. teretifolium*
19. *D. pugioniforme*
20. *D. beckleri*
21. *D. beckleri X D. pugioniforme*
22. *Bulbophyllum exiguum*
23. *B. crassulifolium*
24. *Sarcochilus falcatus*

(2) Epiphyte recording plot 2 : LRf, Shelly Beach

Locality of plot : Port Macquarie, NSW ; on gently sloping side of broad gully; aspect NE; ca 400 m from sea.

Plot size : 50 x 25 m.

Table 2a : Phorophytes of LRf , Shelly Beach plot

Species & total no. of each in plot		dbh & epiphyte load (spp., total indiv.) of each tree
Alangium villosum	2	15, 14
Archontophoenix cunninghamiana	31	10-16 $\overline{X}$=13.1 ± 2.2 , nil epiphytes
Austromyrtus bidwillii	3	13, 12, 11
Baloghia lucida	4	25, 25, 18, 18
Bauerella simplicifolia	3	28, 18, 13
Beilschmiedia obtusifolia	2	30(3,3) 19
Capparis arborea	1	12
Cinnamomum oliveri	3	16, 16, 14
Drypetes australasica	12	55(3,6) 45(2,4) 35, 25(1,1) 25(1,2) 22, 20(2,2) 18(1,1) 18(1,6), 18, 16, 15; total epiphytes (7,18).
Elattostachys nervosa	2	15, 10
Ficus obliqua	2	50(3,3) 30
Litsea reticulata	1	16
Mischocarpus pyriformis	3	25, 18, 12
Planchonella australis	5	19, 17, 15, 15, 14
Podocarpus elatus	1	30
Sloanea australis	2	25(1,2) 21
Tristania conferta	1	250(4,7)

Tree basal area/ha 60.5 m^2

Table 2b : Epiphytes in Shelly Beach LRf plot

Species	expos. zone	total indiv.	phoro. spp.	Main phoro.spp. & % borne
Pteridophytes				
Psilotum nudum	3	2	1	*Tristania/Ficus*
Ophioglossum pendulum	3	1	1	*Beilschmiedia/Platycerium*
Davallia pyxidata	2-4	2	1	*Tristania*
Platycerium bifurcatum	3	8	2	*Drypetes* (71), *Beilschm.* (29)
Platycerium superbum	2-3	1	1	*Drypetes*
Asplenium australasicum	2-3	-	-	
Dicots				
Pittosporum undulatum	3-4	1	1	*Ficus/Platycerium*
Ficus obliqua	3	2	2	*Tristania*
Ficus superba	3	2	1	*Beilschmiedia/Platycerium*
Ficus rubiginosa	3	-	-	(*Tristania*)
Mischocarpus pyriformis	3	2	1	*Tristania*
Polyscias elegans	3	1	1	*Ficus/Tristania*
Monocots				
Cordyline stricta	2	1	1	*Ficus/Tristania*
Orchids				
Dendrobium tetragonium	2	6	1	*Drypetes*
Bulbophyllum minutissimum	4	1	1	*Ficus obliqua*
Cymbidium sauve	3	-	-	(*Tristania*)
Peristeranthus hillii	2	6	1	*Drypetes australasica*
Rhinerrhiza divitiflora	2-3	1	1	" "
Sarcochilus falcatus	3	-	-	

Fig. 4.2.8

Distribution Chart 2 : Epiphytes on a *Tristania conferta*, Shelly Beach plot.

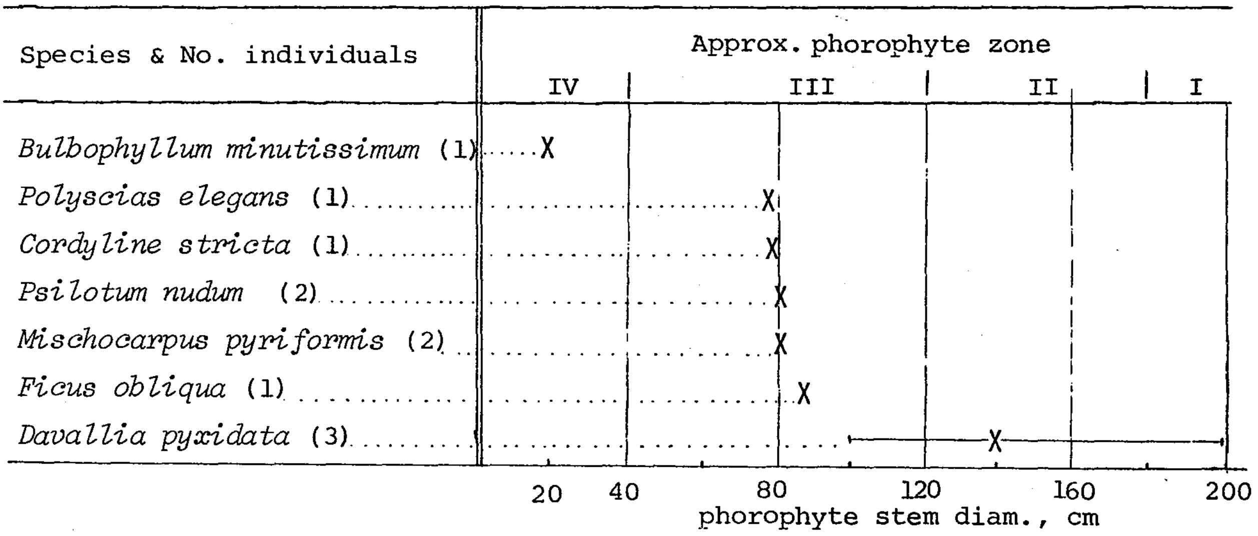
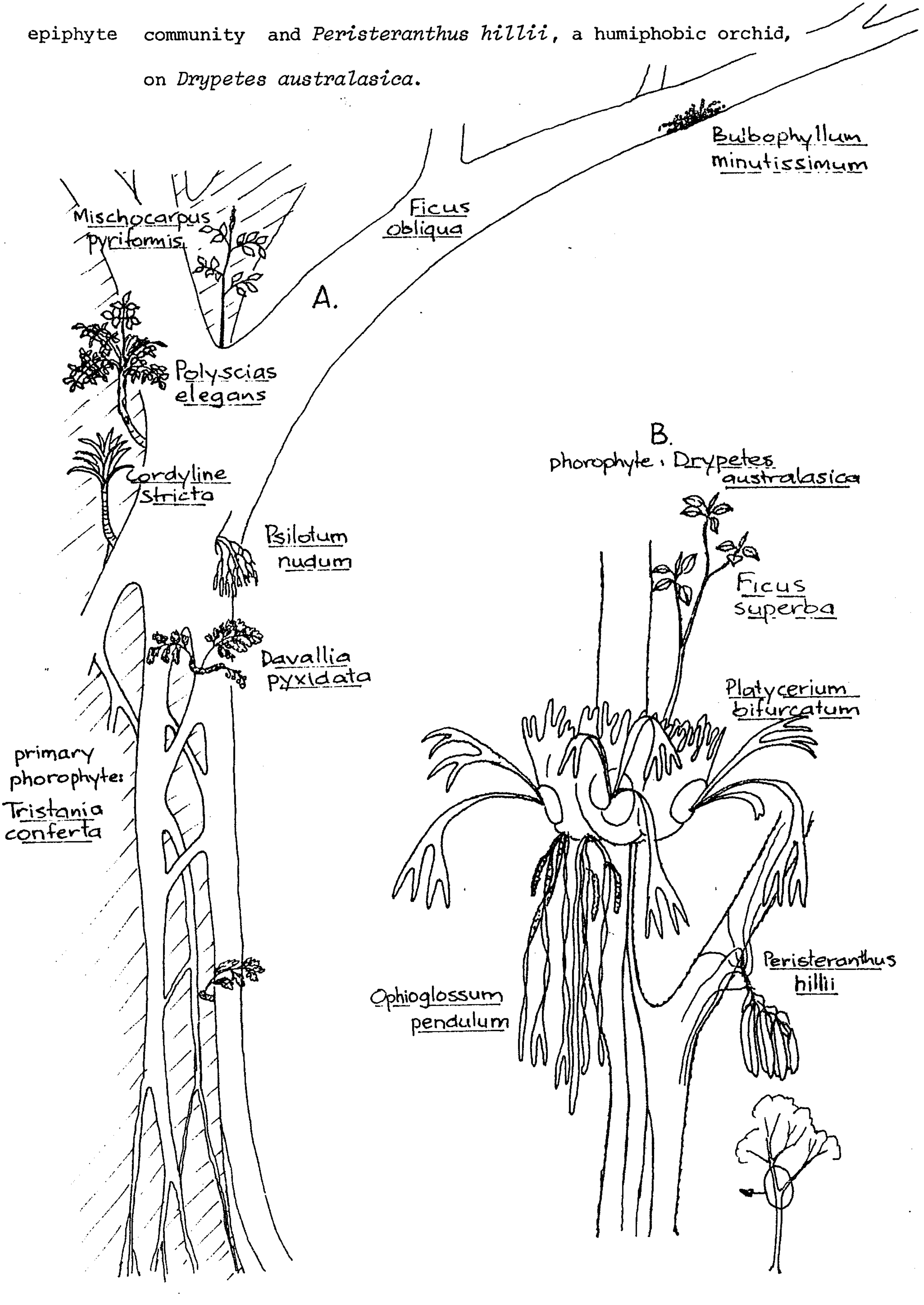


Fig. 4.2.2

Trunk/branch transect 2 : Littoral STRf, Shelley Beach, Port Macquarie

Fig. A Trunk/branch transect on *Tristania conferta* and *Ficus obliqua*

Fig. B *Platycerium bifurcatum/Ophioglossum pendulum* medium sun/shade nest-epiphyte community and *Peristeranthus hillii*, a humiphobic orchid, on *Drypetes australasica*.



(3) Epiphyte recording plot 3 : DRf, Long Point

Locality of plot : near Hillgrove,NSW ; on western side of ridgetop in gorge country, area in lee of eastern scarp of New England Tableland.

Size of plot : 20 x 30 m.

Table 3a : Phorophytes of DRf, Long Point plot

Species & total no. of each in plot		dbh & epiphyte load (spp., total indiv.) of each tree
Alectryon subdentatus	5	24(3,7) 22(3,7) 20(4,13) 18(1,2) 16(3,3); epiphytes (6,38)
Alyxia ruscifolia	1	4(2,31)
Backhousia sciadophora	31	37(1,3) 35(1,1) 33(3,9) 33(3,5) 28(2,6) 26(1,2) 24(1,1) 24(4,7) 23(2,12) 22(1,1) 22(2,5) 19(1,3) 18(2,19) 18(4,5) 17(5,20) 16(2,9) 16(1,2) 15 14(2,4) 13(4,14) 12(3,4) 12(2,6) 12(3,10) 12(3,3) 11(4,10) 10(2,5) 9(2,9) 6(3,7) 6(1,6) 6(3,31) 5(2,2); epiphytes (10,257)
Brachychiton discolor	2	24, 12
B. populneum	2	35(2,2) 22(3,3); epiphytes (3,5)
Capparis arborea	2	12(4,8) 10(2,4); epiphytes (4,12)
Clerodendrum tomentosum	2	5(4,10) 5(2,3); epiphytes (4,13)
Coelebogyne ilicifolia	1	21(3,5)
Croton insularis	3	10, 8(4,14), 5
Elaeocarpus obovatus	1	23(2,16).
Elaeodendron australe	1	10
Geijera salicifolia	1	14
Notelaea venosa	3	16(4,10) 10(3,8) 8(4,18); epiphytes (5,37)
Pittosporum undulatum	3	18(4,20) 14(3,5) 5; epiphytes (5,32)
Planchonella australis	5	10(3,22) 9(4,7) 5(2,3) 5(3,8) 5(3,4); epiphytes (8,35)
Stenocarpus salignus	2	20(1,1) 15

Total tree basal area per ha = 37.9 m^2

Table 3b : Epiphytes of Long Point DRf

Species	expos. zone	total indiv.	phoro spp.	Main phoro. spp. & % borne
Pteridophytes				
Pellaea paradoxa (Acc)	1	1	1	*Alectryon*
Pyrrosia confluens	2-4	30	9	*Backhousia* (47), *Alectryon* (13)
Asplenium australasicum	2-3	-	-	
Davallia pyxidata	2-4	-	-	
Dicots				
Parsonsia straminea (Acc)	1-2	2	2	*Backhousia, Pittosporum*
Ficus macrophylla	3	1	1	"
Orchids				
Liparis coelogynoides	2-3	2	2	*Backhousia, Alectryon*
Dendrobium speciosum	3	3	2	" (67), *Planchonella* (33)
D. gracilicaule	3	1	1	*Alectryon*
D. linguiforme	2-4	41	8	*Backhousia* (44), *Alectryon* (20)
D. teretifolium	3-4	4	4	
D. beckleri	3-4	1	1	*Planchonella*
D. pugioniforme	2-3	9	6	*Alectryon* (22), *Capparis* (22)
D. beckleri × *D. pugion.*	3	-	-	
Plectorrhiza tridentata	3-4	67	5	*Alyxia* (45), *Backhousia* (25)
Sarcochilus falcatus	3-4	153	8	*Backhousia* (42), *Planchonella* (13)
Sarcochilus hillii	4-5	123	6	" (69), *Notelaea* (15)

Fig. 4.2.9

Distribution chart 3a : Epiphytes on one *Planchonella australis*, Long Pt. DRf plot.

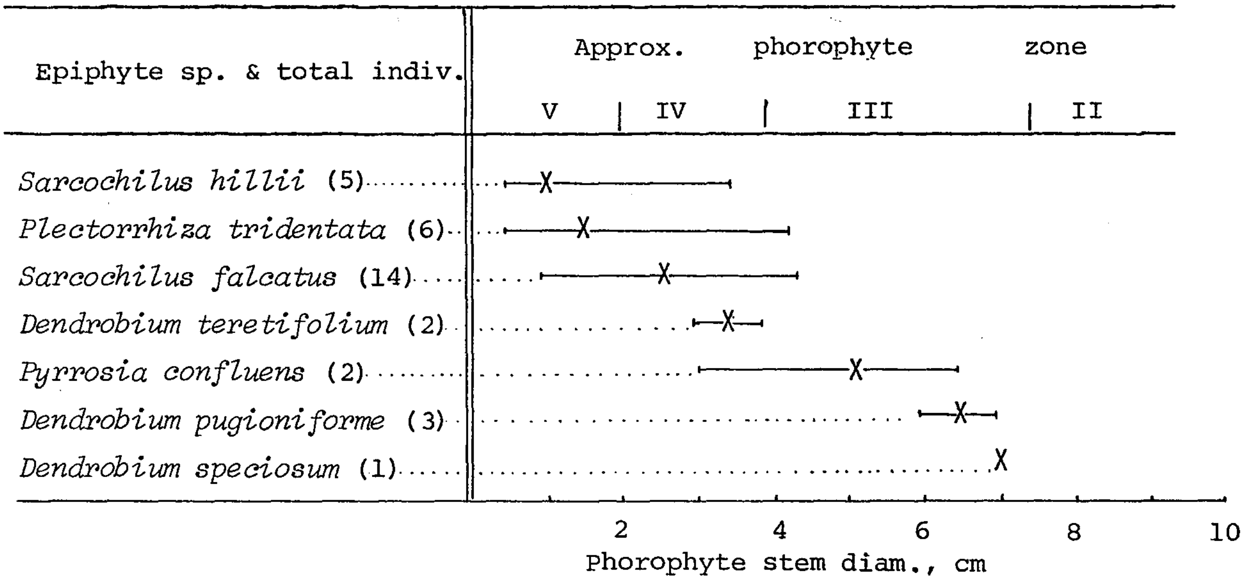
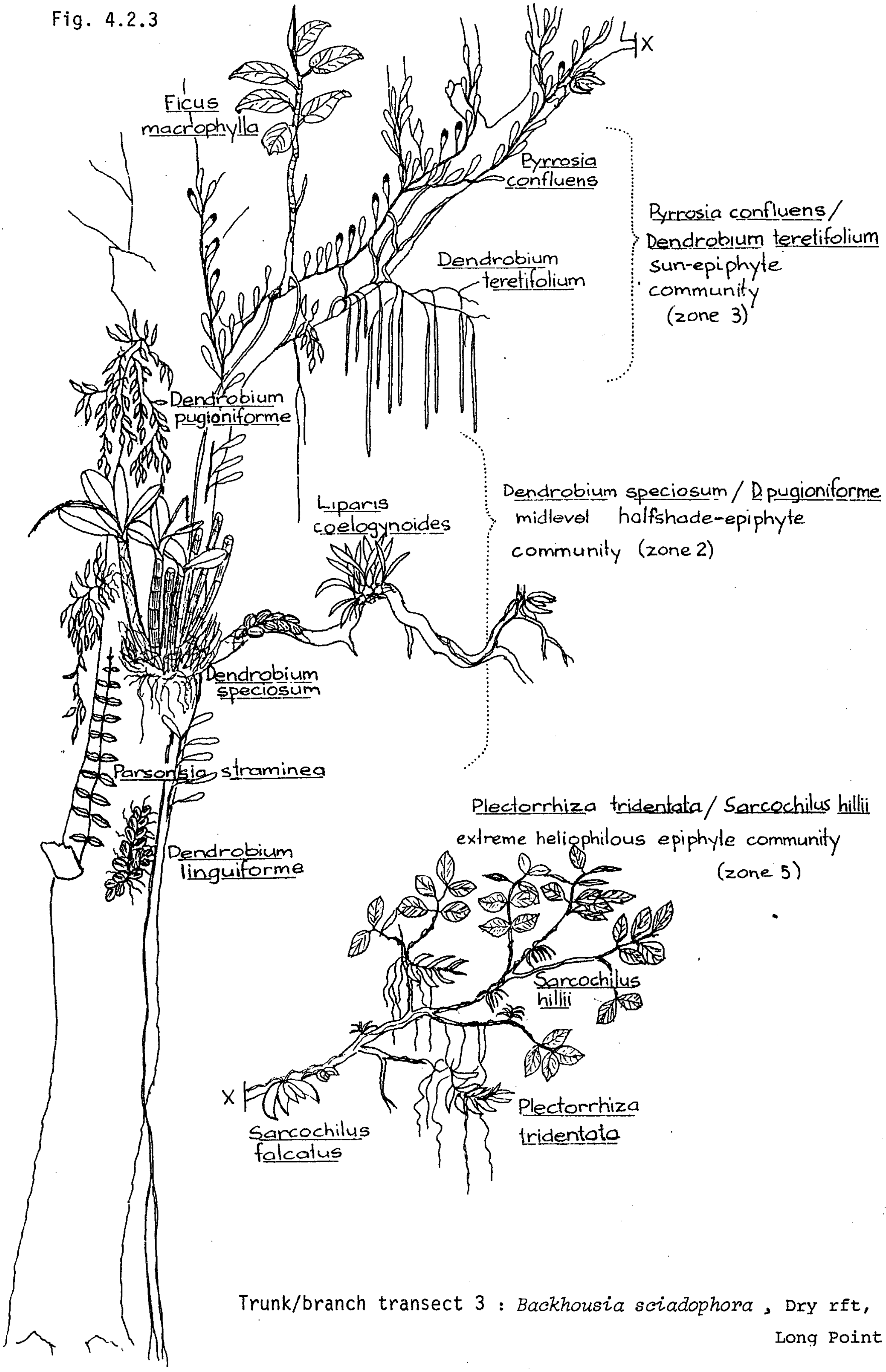


Fig. 4.2.3



Trunk/branch transect 3 : *Backhousia sciadophora* , Dry rft, Long Point.

(4) Epiphyte recording plot 4 : WTRf, Humber Hill

Location of plot : New England National Park, NSW; upper mid levels of eastern scarp of New England Tableland

Plot size ; 25 x 25 m.

Table 4a : Phorophytes of WTRf, Humber Hill, NENP

Species & total no. of each in plot		dbh & epiphyte load (spp., total indiv.) of each tree
Acacia elata	1	26
Ackama paniculata	4	100(2,2) 55(2,4) 28 18(2,2) ; epi. (4,8)
Ceratopetalum apetalum	4	24, 20, 16, 10
Cryptocarya foveolata	2	26(6,10) 20(5,8) ; epi. (7,18)
Doryphora sassafras	4	100(4,22) 50(7,18) 21(2,4) ; epi. (8,47)
Nothofagus moorei	1	74(2,3)
Orites excelsa	2	45, 35
Pennantia cunninghamii	5	35(1,1) 32(1,5) 30(4,4) 23(1,1) 18; epi. (4,11)
Quintinia verdonii	7	23, 20(1,1) 19(1,1) 17(1,1) 16, 15(1,1) 14; epi. (1,4)
Schizomeria ovata	3	120(11,42) 43(5,14) 40(2,2) ; epi. (13,58)
undetermined sp.	1	25(3,4)

Table 4b : Epiphytes in Humber Hill WTRf plot

Epiphyte sp.	expos. zone	total indiv.	phoro. spp.	Main phoro. spp. & % borne
Ferns				
Arthropteris tenella	1-2	2	2	*Cryptocarya* (50), *Pennantia* (50)
Microsorium scandens	1-2	15	7	*Quintinia* (27)
Dictymia brownii	2-3	25	4	*Pennantia* (52), *Schizomeria* (24)
Pyrrosia rupestris	3	7	5	*Doryphora* (43)
Pyrrosia confluens	3-4	13	6	*Ackama* (31)
Asplenium flaccidum	2	14	1	*Schizomeria* (100)
Asplenium australasicum	2	3	2	" (66)
Asplenium polyodon	2	1	1	*Doryphora* (100)
Lastreopsis sp. (Acc)	1	1	1	*Schizomeria* "

....cont.

Table 4 cont. Humber Hill epiphytes

Epiphyte sp.	zone	total indiv.	phoro. spp.	Main phorophyte spp. & %borne
Dicots				
Quintinia sieberi	1	-	-	
Orites excelsa (Acc)	1	1	1	*Schizomeria* (100)
Fieldia australis	1-2	2	2	" (50), *Cyathea* (50)
Orchids				
Liparis coelogynoides	3	-	-	
Bulbophyllum exiguum	2-3	1	1	*Ackama* (100)
Dendrobium speciosum	3	-	-	
D. falcorostrum	3-4	5	2	*Nothofagus* (80), *Ackama* (20)
D. pugioniforme	3	17	4	*Schizomeria* (41)
D. teretifolium	3	4	1	*Doryphora* (100)
D. tenuissimum	2-3	-	-	
Sarcochilus falcatus	3-4	19	2	*Schizomeria* (53), *Doryphora* (47)

Fig. 4.2.10

Distr. Chart 4 : Epiphytes on *Schizomeria ovata* tree, Humber Hill plot

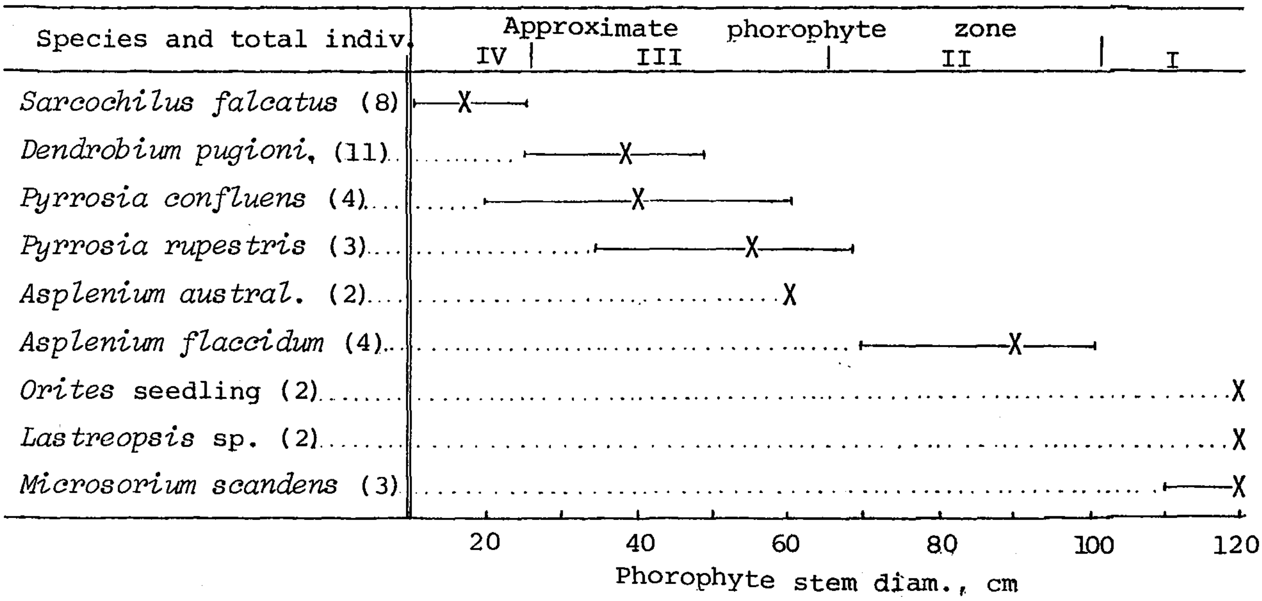
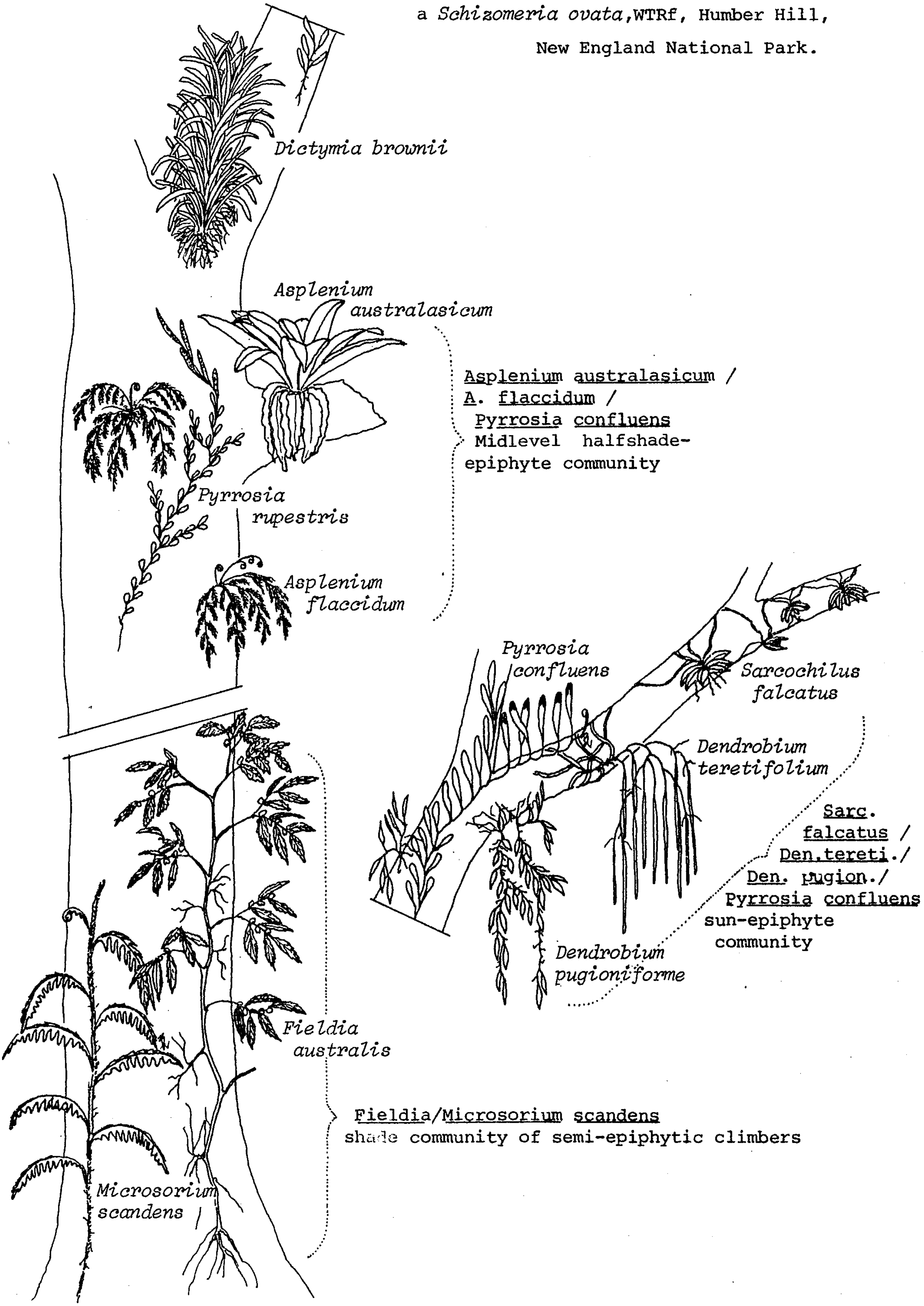


Fig. 4.2.4 Phorophyte/epiphyte transect profile 4 : a *Schizomeria ovata*,WTRf, Humber Hill, New England National Park.



(5) Epiphyte recording plot 5 : CTRf, Wrights Lookout

Location of plot : New England National Park, NSW ; top of eastern scarp of New England Tableland.

Plot size : 25 x 25 m.

Table 5a : Phorophytes of the CTRf, Wrights Lkt Plot

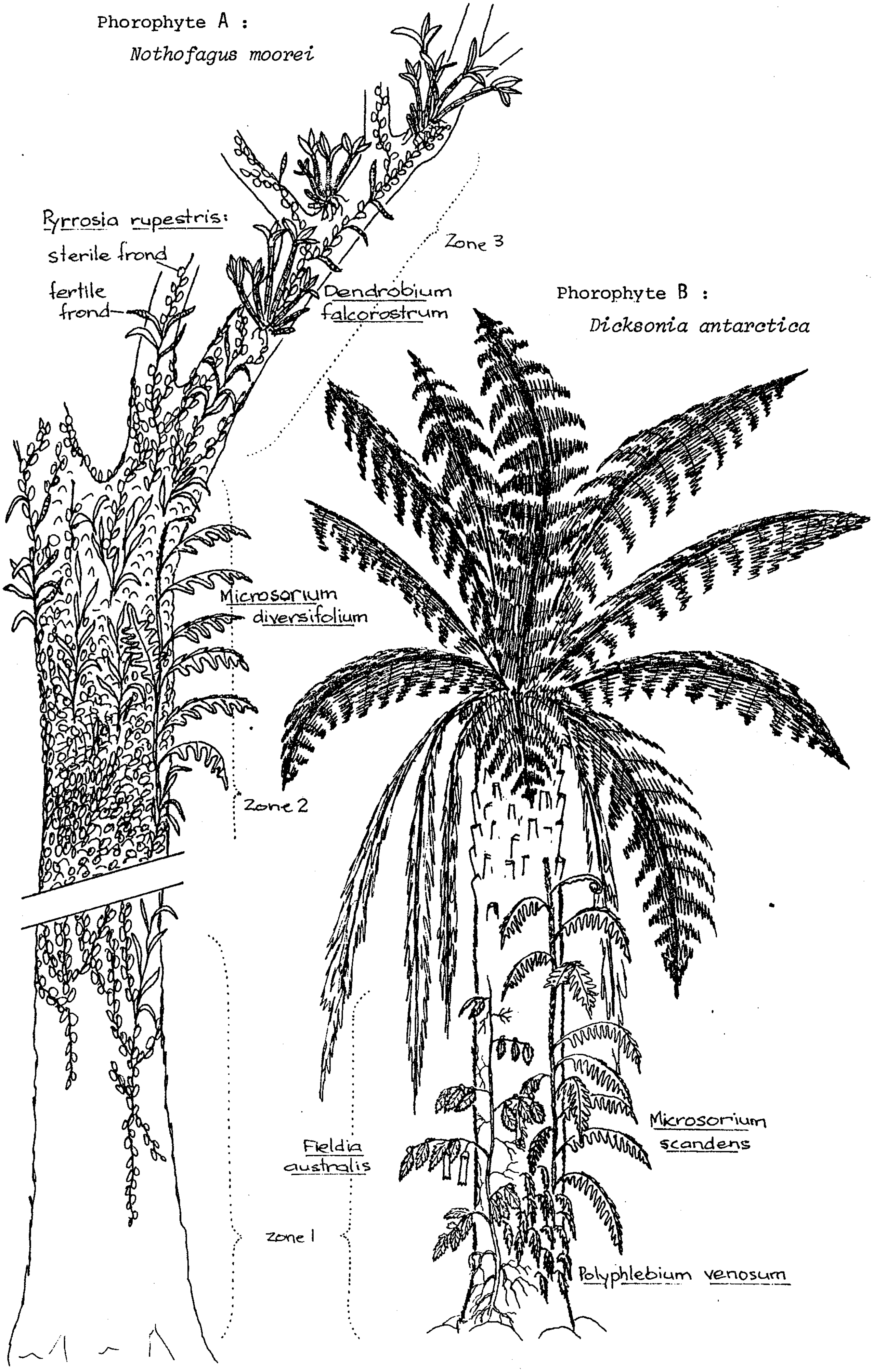
Species & total no. of each in plot		dbh & epiphyte load (spp., total indiv.) of each tree
Cryptocarya sp.	1	15
Dicksonia antarctica	1	27(3,6)
Doryphora sassafras	15	28(2,4) 27(2,4) 22, (20(1,1) 21, 20(2,4) 18(3,3) 17(1,1) 17(2,2) 17(1,1) 17, 16(1,1) 15, 15, 15; epiphytes (3,22)
Elaeocarpus holopetalus	5	34(3,8) 22(1,7) 20, 19, 12; epiphytes (3,15)
Orites excelsa	3	14, 13, 11
Nothofagus moorei	9	150(1,1) 86(2,9) 80(3,8) 67(2,4) 64, 58(1,1) 50(2,3) 51(1,1) 28(2,8); epiphytes (4,35)
Quintinia sieberi	1	32
Trochocarpa sp.	5	44(3,3) 26(3,3) 15(3,6) 13(1,1) 10(3,3); epiphytes (5,16)

Table 5b : Epiphytes of Wrights Lkt CTRf plot, NENP

Species	expos. zone	total indiv.	phora spp.	Main phoro. spp. & % borne
Pteridophytes				
Hymenophyllum cupressiforme	1	-	-	
Hymenophyllum bivalve	1-2	-	-	
Polyphlebium venosum	1	1	1	*Dicksonia*
Grammitis billardieri	1-2	-	-	
Microsorium scandens	1-2	3	2	*Trochocarpa* (67)
Microsorium diversifolium	2	2	2	" (50), *Nothofag.* (50)
Pyrrosia rupestris	2-4	22	4	*Nothofagus* (41), *Doryphora* (32)
Asplenium flaccidum	2	-	-	
Dicots				
Elaeocarpus holopetalus (Acc)	3	1	1	*Nothofagus*
Fieldia australis	1-2	5	2	*Dicksonia* (80), *Elaeocarpus* (20)
Orchids				
Dendrobium falcorostrum	3-4	23	1	*Nothofagus*
Dendrobium pugioniforme	3	4	2	*Trochocarpa* (75), *Doryphora* (25)
Sarcochilus falcatus	2-3	11	3	" (46), *Elaeocarpus* (27)

Fig. 4.2.5

Trunk/branch transects 5A,B : CTRf, Wrights Lookout, New England NP



(6) Epiphyte recording plot 6 : SEVF, Leo Creek, McIlwraith Ra., Cape York Pen.

Plot location : Lat. 13° 45' S, Long. 143° 20' E. (CSIRO Typical Site Plot E/P 32, subplots A-D).

Plot size : 50 x 25 m.

Table 6a : Leo Ck plot trees

Species and total no. of each in plot		dbh & epiphyte load (spp. total indiv.) of each tree
Acronychia acronychioides	5	24(10,19) 23(5,6) 12 (10(1,1) 10(1,2) epiphytes (11,26)
Alphitonia whitei	3	18, 18, 22
Antirhea tenuiflora	3	17(1,1) 14(1,2) 12 ; epiphytes(2,3)
Bubbia semecarpoides	1	11
Calophyllum sil	1	47
Canarium australasicum	3	43 27(4,8) 11
Citronella smythii	1	13
Cleistanthus sp. (RFK672)	4	13 12(2,2) 12, 12
Cryptocarya mackinnoniana	6	70(8,41) 19(2,3) 17(6,9) 16(5,8) 11(3,3) 11(1,1) ; epiphytes(13,60)
C. aff. *cinnamomifolia*	1	13
C. aff. *hypospodia* (RFK564)	15	42(7,16) 37(2,4) 35(6,18) 33(8,23) 33(5,15) 31(10,51) 30(7,31) 28(3,9) 25(6,9) 23(5,9) 23(4,6) 19(4,5) 19(1,2) 14(4,6) 12 epiphytes (25,195)
Elaeocarpus eumundi	5	17, 15, 13, 11, 10
E. aff. *ferruginiflorus*	1	12
Endiandra (?) glauca	1	16(1,1)
Endiandra aff. *glandulosa*	4	36(8,12) 29(11,21) 25(2,2) 22(2,4); epi. : (14,54)
Grevillea pinnatifida	3	38(6,17) 36, 16(1,1); epi. (7,18)
Helicia australasica	1	11
Kissodendron australianum	3	14(3,3) 13(1,1) 11; epiphytes(4,20)
Licuala muelleri	18	all 10-11 cm diam., total epi. load 5,40, *Vittaria, Schellolepis, Hoya, Cymbidium* - mostly in fibre "collar".
Pithecellobium grandiflorum	2	32(4,7) 25(1,1) ; epi. (4,9)
Podocarpus neriifolius	2	23(1,1) 11
Planchonella chartacea	2	19 11(2,2)
Rapanea porosa	3	14, 13, 12
Rhodamnia blairiana	1	37(14,32)
Sarcopteryx sp.	2	13, 12
Sloanea macbrydei	3	27(2,2) 22(3,3) 20(6,7) ; epiphytes(8,12)
Symplocus stawellii	1	15
Ternstroemia cherryi	2	12, 15
Xanthophyllum octandrum	2	12, 16
Xanthostemon chrystanthus	2	102(2,2) 58(4,13) ; epiphytes(5,16)

Total tree basal are per ha = 32.0 m^2

Table 6b : Leo Ck plot epiphytes

Species	expos. zone	total indiv.	phoro. spp.	Main phoro.& % borne
Fern Allies and Ferns				
Psilotum complanatum	2-3	3	2	*Cryptoc.aff. hypo./Platy.* (66)
Lycopodium phlegmaria	3	7	4	*Rhodamnia* (43)
Lycopodium carinatum	3-4	-	-	
Lycopodium dalhousieanum	3	-	-	
Ophioglossum pendulum	3	-	-	
Hymenophyllum sp.	1-2	2	2	*Grevillea* (50),*Rhodhamnia* (50)
Vittaria elongata	2-3	38	8	*Licuala* (50)
Davallia solida	3	9	5	*Crypt.aff.hypo.* (30)
Humata repens	2-3	7	2	*Rhodamnia* (71)
Humata pectinata	3	2	2	*Kissod.*(50),*Crypt.aff.hypo*(50)
Belvisia mucronata	2-3	1	1	" " "
Drynaria rigidula	3-4	22	4	" " " (77)
Schellolepis subauriculata	3	9	3	*Licuala* (78)
Schellolepis percussa	3	2	1	"
Platycerium hillii	3-4	28	6	*Crypt.aff.hypo.* (61)
Pyrrosia longifolia	3-4	9	3	*Acronychia* (33)
Pyrrosia lanceolata	3	-	-	
Asplenium nidus	2-3	-	-	
Dicots				
Ficus destruens	3	3	3	*Canar.*,*Rhodamnia*, *Xanthos.*
Schefflera sp.	3	-	-	
Kissodendron australianum (Acc)	2	1	1	*Endiandra/Platycerium*
Fagraea berteriana	2-3	7	3	*Crypto. aff. hyposp.* (57)
Timonius singularis	3-4	7	5	" " " (43)
Hydnophytum formicarium	2-4	33	10	" " " (33)
Hydnophytum sp.	4	4	2	" " " (75)
Myrmecodia sp.	2-4	31	5	" " " (55)
Dischidia ovata	2-3	9	4	" " " (56)
Hoya nicholsoniae	1-3	21	11	" " "(24)*Licu.* (19)
Orchids				
Dendrobium ruppianum	3	9	5	*Rhodamnia* (44)
Dendrobium tetragonum	2-3	2	2	*Crypt.aff.hypo.*,*Elaeo.eum.*
Dendrobium smilliae	3	1	1	*Crypto. mack.*
Dendrobium luteocilium	3-4	1	1	*Endiandra aff. glandulosa*
Dendrobium baileyi	2-3	27	4	*Crypt.aff.hypo.*(41), *Acron.*(44)
Dendrobium malbrownii	2-3	60	4	" " " (57)
Flickingeria comata	3-4	1	1	" " "
Bulbophyllum baileyi	2-4	53	9	" " " (28) *Rhodam.*(28)

...cont.

Table 6b cont.

Species	zone	total indiv.	phoro. spp.	main phoro. spp. & % borne
Bulbophyllum bowkettae	3	-	-	
Pholidota pallida	2-3	1	1	*Crypto.* aff. *hypospodia*
Eria fitzalani	3-4	28	3	*Kissodendron* (68)
Eria inornata	3-4	-	-	
Rhynchophreatia micrantha	2-3	1	1	*Rhodamnia*
Cymbidium madidum	2-3	4	2	*Licuala* (75)
Phalenopsis amabilis	2-3	-	-	
Totals 43		413		

Fig. 4.2.11
Distr. Chart 6a : Epiphytes on *Rhodamnia blairiana* indiv., Leo Ck. plot

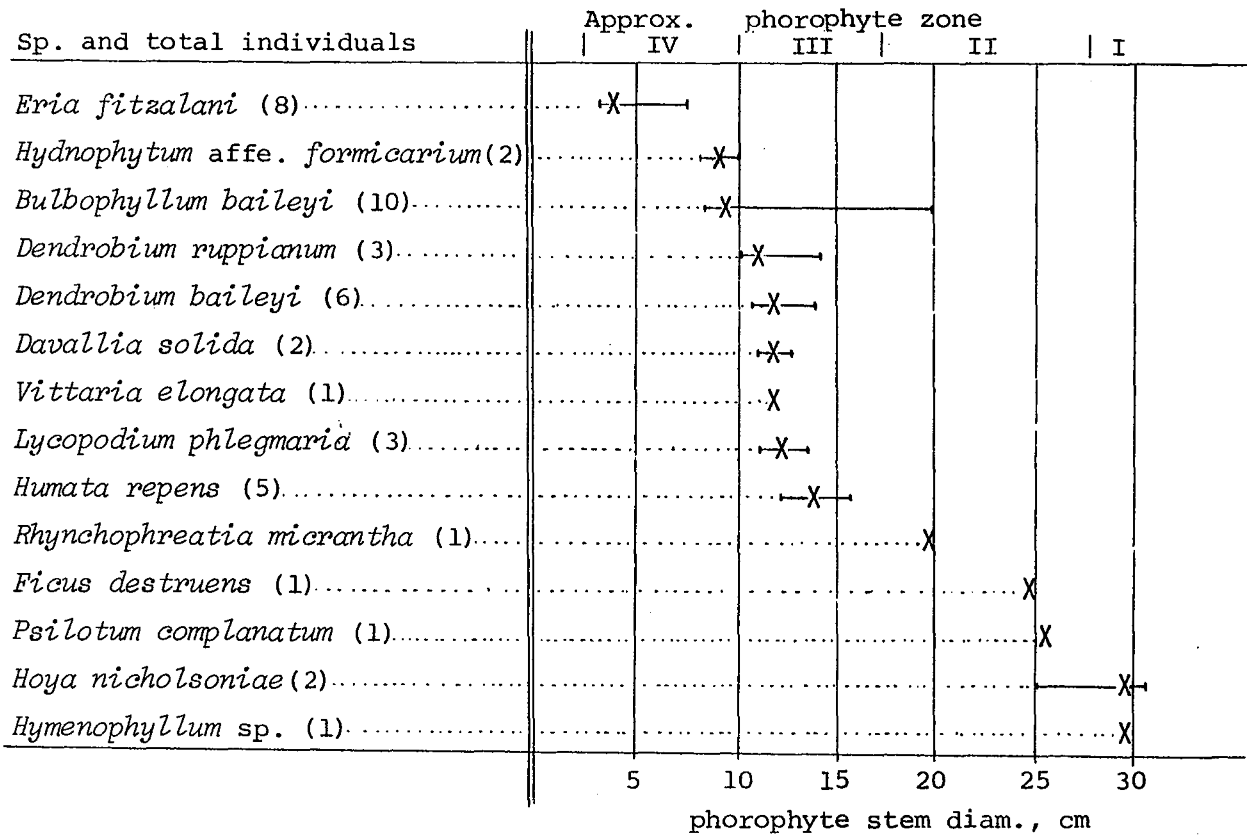


Fig. 4.2.12
Distr. Chart 6b : Epiphytes on *Cryptocarya mackinnoniana* indiv., Leo Ck.plot

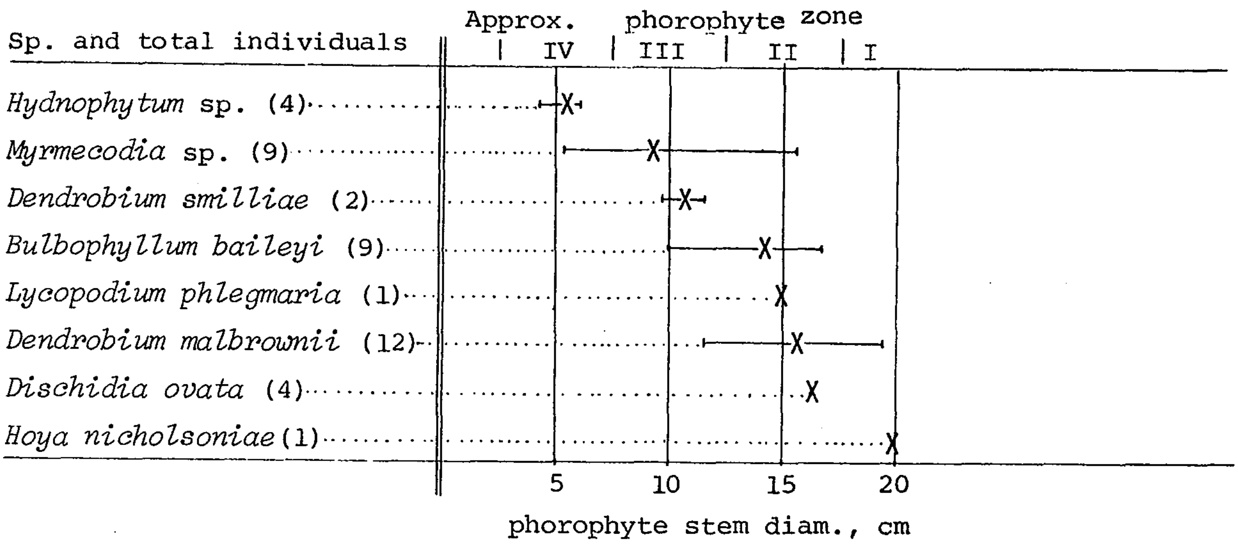
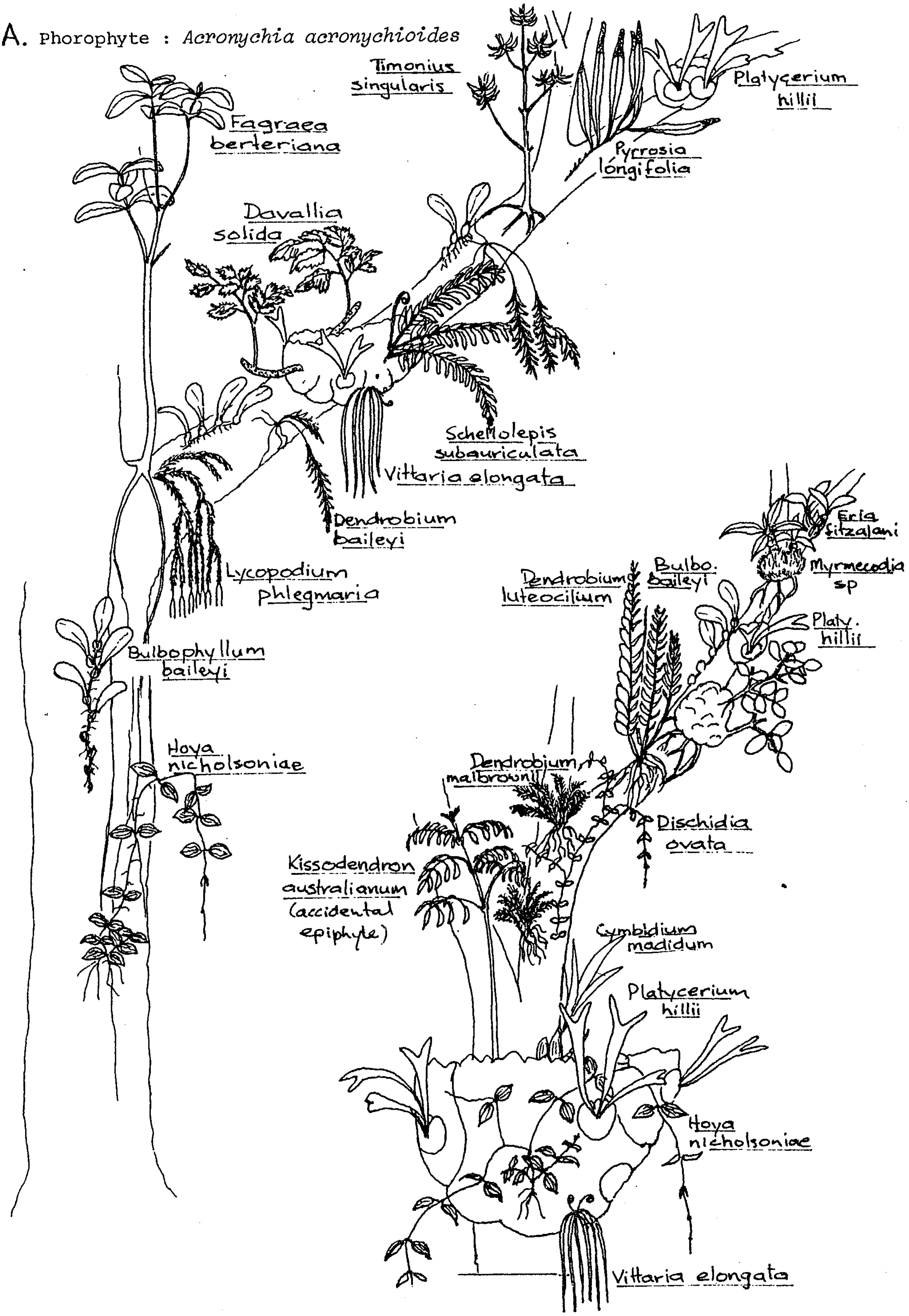


Fig. 4.2.6

Trunk/branch transects 6A,B:Leo Ck. SEVF (CSIRO plot E/P 32) McIlwraith Ra.


A. Phorophyte : *Acronychia acronychioides*

B. Phorophyte : *Endiandra* affe. *glandulosa*

Table 4.7 : Summary of phorophyte and epiphyte parameters of the six plots.

	Phorophytes					Epiphytes								
Site & plot size, m	spp	total indiv./ha	mean dbh, cm	total.basal area/ha,m^2	% trees colonised	spp	indiv./ha	orchids	ferns	others	hemi	nest-formers	SECs	Accid.
Dorrigo STRf,50x25	29	744 (93)*	38.60	130.8(16.4)*	21.5†	28	2744 (343)*	11	11	6	1	2	4	2
Shelly Bch. LRf,50x25	17	512 (75)	21.29	60.5(7.6)	14.7	19	296 (37)	6	6	7	3	3	-	3
Long Pt. DRf,30x20	16	1167 (70)	14.70	37.9(2.28)	80.0	15	8217 (495)	10	3	2	1	1	-	1
Humber Hill WTRf,25x25	11	512 (34)	34.36	77.6(4.85)	61.8	20	1776 (222)	8	9	3	-	2	3	2
Wright Lkt.CTRf,25x25	8	640 (40)	32.18	72.5(4.53)	62.5	13	1136 (142)	3	9	2	-	-	2	1
Leo Ck SEVF,50x25	30	824 (103)	20.14	32.0(4.01)	45.6	43	3304 (413)	15	18	10	4	3	-	1

* figures in brackets are actual record for the plots - per ha figures are extrapolated from these.

† not including trees bearing only semi-epiphytic climbers (such trees 59.1% of total)

4.2.4 Discussion

The following discussion is based mainly on the data derived from the six epiphyte recording plots and thus to some extent is limited by this constraint. Some other observations and papers are also discussed where relevant, particularly relating to the epiphytes.

A. The Phorophytes

From the data summarized in table 3.7, the parameters of tree species diversity, basal area per ha, total individuals per ha and mean dbh, show some significant trends. Of the subtropical systems, the Dorrigo cool STRf site was floristically richer, had more trees (except for Long Point) of larger size with a much larger biomass than any other. Floristically, the CTRf of Wrights Lookout was clearly the poorest but in tree size and biomass compared with the Humber Hill WTRf and Shelly Beach LRf. The Long Point DRf appeared anomalous in having moderate floristic diversity, very low tree basal area and much the highest number of individuals which were thus considerably smaller in size than in the other sites. The tropical SEVF of Leo Ck was comparable to the DRf system except in being floristically rich.

At two of the sites there was virtual single species dominance in the tree layer. In the DRf plot, the myrtle *Backhousia sciadophora* was present in much greater numbers (32) than any other species (*Alectryon subdentatus* 5, *Planchonella australis* 5) as well as having a greater tree basal area than of the total remainder. In the CTRf plot the beech *Nothofagus moorei*, though fewer in number than *Doryphora sassafras* (9 against 15), had a much greater basal area (9.1) against 3.9 m^2) i.e., much larger trees which were quite dominant in regard to community structure. Both of these systems are subjected to high stress levels, of cold in the case of the CTRf and water supply and cold, dry wind in the DRf and are probably near the limits for rainforest-like vegetation. Such single species dominance implies that the dominant has a clear adaptive advantage that enables it to cope with the stress (this concept will be discussed below in relation to epiphytes) and can thus favourably compete against other tree species.

B. The Epiphytes

1. Floristic Diversity

In the five subtropical sites floristic diversity of the epiphytes showed trends similar to those in the tree flora, i.e. the greatest variety was found in those systems imposing the least environmental limitation.

Thus the Dorrigo STRf site contained significantly more epiphyte species than the others. Along a gradient of increasing aridity from Dorrigo to Shelly Beach LRf to Long Point DRf, the species ratio was 28:19:15. This agrees with one of the postulates discussed by Sanford (1968) in relation to West Africa, that species diversity is greater in areas of most favourable moisture conditions. Along the other main environmental gradient obtaining in these, that of decreasing mean temperature or increasing cold, from Dorrigo STRf to Humber Hill WTRf to Wrights Lookout CTRf sites, the species count ratio is 28:20:13.

The following considerations are relevant:

i. the tree flora and vegetation is richer and more complex in systems that are less limiting and thus there will be a greater number and range of exploitable microhabitats available to epiphytes and therefore,

ii. such systems will be able to accommodate a larger number of species of the epiphyte flora pool.

iii. the epiphyte flora available in the subtropics is probably equally accessible to the sites investigated. The degree of floristic overlap, the close proximity of the sites to one another and the high dispersibility of epiphytes all support this.

iv. competition between epiphyte individuals does not appear to be as important in species selection as might be expected with the terrestrial plants. Spatial arrangement of the epiphytes suggests largely unimpeded access by individuals to light, water, minerals etc, especially in the limiting systems, i.e. space is not in high demand. Sanford (1974) reviewed some evidence of competition between epiphytes.

The Leo Ck SEVF epiphyte flora is richer than in any of the subtropical sites even though it is a somewhat water-stressed system. However, the flora poool available to it is much larger and therefore a proper comparison cannot be drawn.

2. Population Densities

The variations in epiphyte population densities do not correlate with the same factors as does floristic richness. Thus, the water-stressed Long Pt DRf site had 8217 individual epiphytes per ha which was more than double the next highest, 3304 of the Leo Ck SEVF and three times that of the next highest subtropical sites, the Dorrigo STRf with 2744. This apparent anomaly is related to a similar situation in the tree vegetation.

In the DRf plot, of the 15 species of vascular epiphytes present, 5 or 33% of these accounted for 84% (414) of the individuals. Thus, even though the flora is depauperate, a few species are sufficiently well adapted to flourish in the water-stressed conditions.

An important factor contributing to this few-species dominance (in the sense of Sanford, 1968, 1974) is the compatibility of these species with the dominant phorophyte *Backhousia sciadophora*. This species makes up about half of the tree individuals in the plot and this, combined with the much higher density of (smaller) trees when compared with the other systems and consequent larger number of sites for colonisation , creates a potential for the observed proliferation of the extreme xerophytic epiphytes. Specific illustrations of this are *Sarcochilus falcatus* with 153 individuals (31% of total epiphytes) in the plot with 42% of these growing on *Backhousia* and *S. hillii* with 123 individuals (25% of total epiphytes) 69% of which were on *Backhousia*.

It is noteworthy that these two species and the next most populous epiphyte in the DRf, *Plectorrhiza tridentata*, are small, monopodial orchids lacking much water storage capacity but which do possess CAM, a proven water-conserving mechanism (see Chapter 5); high night humidity is important to the effective operation of this process.

The relatively high incidence of mist is thus an important factor when considering the large epiphyte populations in low MAR, diurnally dry, rainforest-related communities such as the Long Pt. DRf, particularly to these small, twig epiphytes. Other workers, who have found similar correlations are Nuernbergk (1974) in E. Africa and Grubb & Whitmore (1966) and Sugden & Robins (1979) in Ecuador re differences between montane and lowland, and two mist forests, resp.

The higher degree of light penetration into the rather open DRf further improves conditions favouring these orchids since they are heliophilous epiphytes. (See Chap. 3 p. for relevant light intensity data & Vegetation Profile 3, p. for an indication of canopy condition). The volume of suitable microhabitat is thus extended - this is apparent from the vertical range these spp. occupy at Long Pt.

Large numbers of trees per ha and strong light penetration of the canopy are also relevant in explaining the epiphyte population of the tropical SEVF plot which is greater than in all others except the DRf. Few species dominance does not apply here as the most populous species, *Dendrobium malbrownii* accounts for only 15% of the total epiphytes and there are nine others accounting for more than 5% each. Floristic richness and the size of the flora pool are important but so also is the predominance of a single tree species, *Cryptocarya* aff. *hypospodia* and its wide compatibility with epiphytes. Of the 10 most populous epiphyte species, all except two had more individuals growing on this phorophyte than on any other.

3. Structural complexity of epiphytic vegetation

This involves such matters as the spatial arrangement on the phorophytes, particularly zonation or stratification, the occurrence of groupings (or communities) and the variety and incidence of physiognomic and life forms.

a. Zonation

It has been recognised by virtually all students of epiphytes that there is a distinct vertical patterning in the distribution of epiphyte within the macrocommunities in which they occur[2], i.e. a given species will mostly grow only in a given position on the phorophyte relative to the level of the foliage canopy and/or ground. Further, this is recognised as a function of

i. gradations in microclimatic factors such as light intensity, humidity (or air evaporative power), air temperature etc.,

ii. the specific needs of individual epiphyte species and their germination and establishment in microsites where these needs are met.

Such patterning then, often shows similarity from one site to another and this has lead various workers to attempt rationalisation of this and to devise a reference system of zones, strata etc. The history of such schemes has been adequately reviewed by Johansson (1974); he used a system of five zones (mentioned earlier in this chapter) and this has been basically followed here. However, owing to the degree of variation in forest physiognomy, especially in some systems such as the DRf and CTRf, predictive value of these zones is low and it must be emphasised that they are little more than a convenient, simple and subjective reference framework. Further , even in relatively well integrated forest systems such as the Dorrigo STRf, the actual situation regarding epiphyte distribution is more a continuum from tree base to outer canopy rather than a series of discrete units.

The degree of regularity of patterning or 'zonation' in epiphyte distribution within the six communities investigated was greatest in the least stressed,

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[2] Hazen (1966), attempting to apply numerical methods to epiphyte distributional analysis, concluded that the patterns investigated were random. His methods, particularly that of transformation of a branch to a straight line, failed to properly take into account microenvironmental factors and their interactions.

structurally best developed ones. In these, most so in the Dorrigo STRf, the vegetational layers are most pronounced and uniform, especially the canopy of the dominant tree layer and this in turn gives rise to a more even sorting of the environmental factors that influence epiphyte distribution. Epiphyte floristic richness also contributes to this effect because of greater 'filling in' of different microhabitats.

Examples from the three moister sites (STRf, WTRf, CTRf) include the well-defined shade community of semi-epiphytic climbers with *Microsorium* and *Arthropteris* in all three, plus *Fieldia* in the two cooler ones, WTRf and CTRf (see Phoro./Epi. transect profiles 1, 4 & 5). These are, of course, semi-terrestrial plants though occasional individuals are found growing independent of the soil. Few epiphytes have their distribution centred in the upper shade zone (2), two examples are *Peperomia tetraphylla* in the STRf and *Asplenium flaccidum* in the WTRf. In the more water-stressed DRf, LRf and SEVF, mesophytic epiphytes of this type were rare, i.e., the tree trunks, especially the bases, were mostly vacant. In all six plots, the greatest development was on the large branches, especially towards their bases, i.e. where the mid level, halfshade- epiphytes occur; reference to the Epiphyte tables, distribution charts and transect profiles will support this. The sun-epiphyte synusia has fewer and ecologically narrower species which in the subtropical systems included *Dendrobium teretifolium*, *D. beckleri* and *Sarcochilus falcatus* and in the tropical SEVF, *Eria fitzalani*, *Myrmecodia* sp., *Hydnophytum* sp., *Pyrrosia longifolia* and *Platycerium hillii*. Only one of the 6 systems had epiphytes of the extreme heliophilous synusia, i.e., on twigs in the phorophyte canopy (Zone 5). This was the Long Point DRf where *Sarcochilus hillii*, *Plectorrhiza tridentata* and sometimes *S. falcatus* thrived in this microhabitat.

The DRf plot also provides illustrations of irregularity in epiphyte zonation, e.g., one shrub of *Alyxia ruscifolia* of 4 cm dbh, less than 2 m height, carried 29 specimens of *Plectorrhiza tridentata*; the main canopy here was about 5 m above ground but thin and broken. The two *Clerodendrum tomentosum* shrubs were similar to this (see Table 3a). This effect is linked to irregularity of macrovegetational structure, particularly canopy unevenness and discontinuity,- epiphyte distribution also is less regular. Comparisons of the appropriate Vegetation Profiles, Distribution Charts and Phorophyte/epiphyte transect profiles in the Results will support this.

A further consideration here is the width of ecological tolerance of the epiphyte species of the system under consideration. Some spp. are restricted e.g the filmy fern *Polyphlebium venosum* occurs only on the bases of treefern trunks (see Phoro./epi. profile 5b) and *Dendrobium beckleri* (e.g. Phoro./ Epi. profile 1) only on the smaller branches of the upper foliage canopy; such narrow tolerances will tend to sharpen the zonation effect. Ecological wides will have the opposite effect; good examples of these are *Pyrrosia confluens* (Phoro./epi. profiles and Distr. charts from the STRf, WTRf and DRf) *P. rupestris* (in CTRf) and *Bulbophyllum baileyi* of the SEVF, Plot 6; all of these range through Zones 2, 3 and 4.

b. Physiognomic types and life forms[†]

The following table was compiled to compare the importance of the different epiphyte forms in each plot. Figures given, e.g. 12/177 represent number of species, and total number of individuals. The latter are corrected on an equal-area per plot basis.

Table 4.8: Comparison of abundance of physiognomic and life forms

	typical epiphytes							
	sedentary*	long-cr./ mat-form.	tangle	nest formers	nest invaders	hemi-epi.	semi-eip. climbers	Acc. epi.
Dorrigo STRf	12/177	3/44	1/25	3/64	4/34	1/2	4/107	3/5
Shelly Bch. LRf	5/16	1/1	-	2/9	3/5	2/4	-	3/6
Long Pt DRf	7/702	1/60	2/152	1/6	-	1/2	-	2/6
Humber WTRf	7/140	2/40	1/34	2/56	1/2	-	3/38	2/4
Wrights Lkt.CTRf	2/68	2/48	1/3	-	-	-	2/16	1/2
Leo Ck. SEVF	19/269	6/101	-	2/50	10/90	3/17	-	1/1

* tufted, fanplant, short- to medium-creeping etc. epiphytes; for explanations of any other terms, see Chapt. 1, section on terminology, pp. 18-21.

[†] meanings of these terms, as used here, are indicated in Chapter 1.2 & 1.3

The sedentary epiphytes form the largest group, partly because they are an aggregation of subgroups. However, they are ecologically alike in that they remain rooted where they germinate, i.e. they do not have the ability to grow away from the point of establishment. The great majority do hold their leaves well clear of the substrate and this presumably enables them to overcome shading by the phorophyte stem and other epiphytes. Both erect and pendulous forms exist in this group which may optimise space usage and access to light[3]. The trends in occurrence of sedentary epiphytes in the different plots run similarly to those shown in general epiphyte diversity and populations, i.e. those that are floristically richer have more species in this group and those with large totals of individuals have large numbers of individual sedentary epiphytes.

A similar general trend exists in the long-creeping and mat-forming epiphytes with regard to the variety of species but the stressed communities of particularly the CTRf and to a lesser extent the DRf have large populations of this form especially when taking into account the fact that massive stands were counted as one individual per phorophyte zone occupied. Conditions of humidity or air evaporative power and of temperature are more favourable near the substrate surface because of boundary layer effects and this is important to epiphytes in dry or cold environments. Here, a growth form in which the bulk of the plant is on or near the substrate, would be advantageous while a long-creeping, travelling habit would enable the plant to "escape" microsites that became unfavourable by shading, excessive exposure etc. Such species include *Pyrrosia rupestris*, *P. confluens*, *Bulbophyllum exiguum*, *B. minutissimum*, *Microsorium diversifolium*, etc.

Tangle epiphytes are defined as those which grow away from the substrate and produce many aerial roots. This arrangement may be interpreted as a device to trap rain throughfall and mist droplets. Only two species in the study sites conform to this type - *Dendrobium pugioniforme* and *Plectorrhiza tridentata* (see illus. p.167). The DRf epiphytes appear to rely on the occurrence of mists to some extent and the prevalence of these two tangle epiphytes and of the physiognomically similar trailing moss *Papillaria* and lichen, *Usnea* in this system correlates with this. Nuernbergk (1974) mentions a tangle epiphyte, *Angraecum erectum* and relates its physiognomy to mist prevalence in the diurnally dry, low MAR community in which it occurs in E. Africa.

Nest-forming and nest-invading (humiphilic or nidophilic) epiphytes were also less frequent in the drier and colder sites. Possible reasons for this are not obvious but may relate to their lack of drought-resisting

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[3] Another possible selection pressure bearing on the development and prevalence of the pendulous habit relates to the activity of arboreal mammals; Perry (1978) discusses mammal "paths" on branches and implications for epiphytes in Central America.

mechanisms other than litter collection and consequent difficulty in germination and successful establishment without the benefit of a nest. *Dendrobium speciosum*, the only nest-former at the Long Pt DRf site, has considerable water storage capacity in its succulent canes and ability to conserve water via CAM (see Chapter 5.2). Other common nest-formers such as *Platycerium* species and the 'birds-nest' *Asplenium* species do not have these properties. Nest-invaders possibly also fall into this category. Also, strong adaptation to cold does not seem to have evolved in species already adapted to collect litter and nor has the reverse occurred;

In the subtropics, hemi-epiphytes are *Ficus* species and the pattern of their occurrence in the study sites correlated with mean temperature, i.e. the coolest types lacked them. This may simply reflect poor development of cold tolerance in the genus or relevant section of genus (*Urostigma*).

Semi-epiphytic climbers* appear to be favoured by high MAR. They were best developed in the Dorrigo STRf (see Table 1a) and were also prominent in the Humber Hill WTRf and Wrights Lkt CTRf but quite absent from the Shelly Beach LRf and Long Pt DRf. Factors relevant to their dearth in drier rainforests include soil dryness - they are primarily terrestrially rooted, and lower humidity in phorophyte zone I and consequent lower substrate water status of the tree butts, onto which the secondary root systems of these forms grow. * Illustrated on Plate 4.2 .

Accidental epiphytes occurred at all sites, being most frequent in the STRf and LRf and less frequent in the stressed systems. This is expected as they are not adapted as epiphytes and would survive longest in less limiting conditions.

C. Epiphyte-phorophyte relationships relevant to epiphyte synecology

4. Specificity

Somewhat conflicting evidence and opinions have been given as to, i. whether particular epiphyte species occur preferentially on particular phorophyte species, ii. the degree of constancy of such relationships and iii. the reasons for their occurrence. Went (1940) collected data at Tjibodas, Java which showed a relatively high constancy in epiphyte flora for tree species; he even claimed to be able to distinguish between *Castanopsis* species on the basis of their epiphytes. His work implied that specificity was the rule rather than the exception and was thus much more common than suspected previously.

On the other hand, Johansson (1974), Sanford (1974) and Brieger (in Sanford) doubt 'special' epiphyte/phorophyte relationships, indicating that a fuller knowledge of epiphyte occurrence and of the ecological factors involved will reveal a lack of 'specialness' in them. Barkman (1958) agreed re non-vascular epiphytes but found that tree spp. had characteristic spectra of bryophytes. Table 3.10 below lists epiphyte species which were common (more than 20 indiv. per plot) in recording plots 1-6 of the present study, and which were more than 50% specific to a given tree species.

Table 4.9 : Specificity of common epiphytes in Recording plots 1-6.

Epiphyte	Plot	tot. indiv. in plot	% on phorophyte species	other phoro. spp.
Ferns				
Dictymia brownii	WTRf	25	52% on *Pennantia cunninghamii*	3
Drynaria rigidula	SEVF	22	77% on *Cryptocarya* aff. *hypospodia*	3
Platycerium hillii	SEVF	28	61% on *Cryptocarya* aff. *hypospodia*	5
Dicots				
Myrmecodia sp.	SEVF	31	55% on *Cryptocarya* aff. *hypospodia*	4
Orchids				
Dendrobium malbrownii	SEVF	57	60% on *Cryptocarya* aff. *hypospodia*	3
D. falcorostrum	CTRf	23	100% on *Nothofagus moorei*	-
Sarcochilus hillii	DRf	123	69% on *Backhousia sciadophora*	5

Although the numbers of individuals involved here are small from a statistical significance viewpoint, it can be readily seen that in the cases of all these epiphytes, except one, the degree of constancy is not great and could be readily accounted for by the abovementioned ideas of Johansson (1974) and Sanford (1974). The exception, *Dendrobium falcorostrum* with its 100% occurrence on *Nothofagus moorei* in the recording plot, was more extensively surveyed. In the New England National Park, 183 individuals were counted on beech trees and two on other phorophytes, one on a *Ceratopetalum apetalum* and the other on an *Ackama paniculata* both in the WTRf plot. These two were both small and obviously stunted in growth. Previously, the present writer has seen a single plant on a treefern, *Cyathea australis* and another on a *Schizomeria ovata* both of these were apparently healthy and occurred in the CTRf at Gloucester Tops, NSW. Occasional plants have been reported on *Casuarina torulosa* outside the CTRf by other observers. Further relevant points are i. two other epiphytic orchids occur in the CTRf, *Sarcochilus falcatus* and *Dendrobium pugioniforme* but have not been seen by the present writer on *Nothofagus* and ii. *D. falcorostrum* can be readily cultivated on treefern fibre slabs, cork slabs or potted in various media not containing beech bark or humus, given appropriate conditions of light intensity, temperature, humidity etc. It is likely that germination factors may account for this specificity; this is discussed below.

Various undocumented similar relationships have been mentioned by other workers. Perrier de la Bathie (1940), Lecoufle (1964), Kennedy (1972) and Dressler (1981) mention that the Malagasy orchid *Cymbidiella rhodochila* (*C. pardalina*) grows exclusively in the nests of *Platycerium madagascariense* and *C. humblotii* on the raphia palm (Lecoufle 1969, Kennedy 1972). *Phalaenopsis* species in the Philippines grow mainly (80%) on *Diplodiscus paniculatus* and 95% of *Vanda sanderana* plants on several dipterocarpaceous trees (Sulit 1950 , 1953). Piers (1968) notes the strong preference of *Ansellia nilotica* for the palm *Hyphaene thebaica*, *Angraecum dives* and *Polystachya adansoniae* for the baobab *Adansonia digitata*. Richards (1957) cites *Polystachya odorata* var. *trilepidis* being only known to grow on *Trilepis pilosa*. Dressler (1981) mentions that some Brazilian species of *Pseudolaelia* and *Constantia* seem to be restricted to *Vellozia*; a preferance for *V. splendens* is shown by *Polystachya johnstonii* in Malawi (Morris, 1970).

In eastern Australia, *Dendrobium aemulum* occurs in several forms, each showing high fidelity to particular trees. The so-called 'type' form is short and robust and grows in open communities on ironbark *Eucalyptus* species and as such is the only bark epiphyte to colonise any of the 400 + species of this common genus of trees. *Cymbidium suave* and *C. canaliculatum* frequently grow in hollow limbs etc. of *Eucalyptus* but not on their bark; it should be pointed out that these are not rainforest trees although they do often occur in rainforest ecotonal communities. The 'brush-box' form of *D. aemulum* is more slender and grows almost exclusively on the upper part of the rough-barked butt of *Tristania conferta*, a relative of *Eucalyptus* which inhabits rainforest ecotones; it rarely supports other epiphytes. A third, longer-caned and even more slender form (possibly an undescribed separate species as its flowers differ somewhat from those of the others) is reputed to grow exclusively in the upper crown of *Callitris macleayana* in marginal rainforest on the Atherton Tableland, Qld (B. Gray, pers. comm.); this tree does support other epiphytes. Factors relevant to such occurrences will be discussed in the next section.

5. Epiphyte-bearing ability of phorophytes

i. Phorophyte axeny & epiphyte-proneness

It has often been observed that some species of trees are epiphyte-prone while others are axenic (as used by Ruinen in her 1952 paper on epiphytosis,= inhospitable to other forms of life).

The neotropical calabash tree, *Crescentia cujete*, has been noted as a polific orchid-bearer by various writers e.g. Schimper (1888), Anon. (1906), Dressler (1981) although Sanford (1974) never observed any orchids on it in Nigeria where the tree has been introduced. Richards (1952) noted an abundance of epiphytes on *Samanea saman* planted in tropical towns. Dressler (1981) named *Acnistus* and *Paragonia* of Central America and *Elaeocarpus grandiflorus* of Thailand as good orchid 'hosts'. Johansson (1974) lists 16 tree species of the Nimba Mountains (Liberia), that bear abundant epiphytes and also numerous similar records of other writers in other parts of the world. He also lists four axenic tree species.

Palms have often been described as axenic e.g., Schimper (1888), of a common Carribean species, Sulit (1950) of palms generally in the Philippines, Sugden & Robins (1979) of palms in Columbian cloud forests; van Oye (1924) and Johansson (1974) indicated that orchids rarely colonise the oil palm *Elaeis guineensis*, although ferns do so readily. In Australia, *Dendrobium nindii* has been noted growing on palms in N. Queensland (G. Stocker, pers. comm.). Palms were common in two of the recording plots in the present study: the Shelly Beach LRf plot contained 28 Bangalow palms, *Archontophoenix cunninghamiana* which were devoid of epiphytes (see Table 2a); there were 18 fan-palms, *Licuala muelleri*, in the Leo Ck SEVF plot which bore 40 individual epiphytes of 5 species (see Table 6a) but these mostly grew in the fibre 'collar' at the top of the trunk.

Longman & White (1917) documented an epiphyte prone *Litsea reticulata* from SE Qld (see Literature Review, p.9).

Other phorophytes of the recording plots which showed prolific or axenic tendencies are listed in Table 3.10 below. Only species with five or more individuals in each plot are included except where comparisons are useful.

Table 4.10 Prolific & axenic phorophytes of recording plots 1-6.

Phorophyte sp.	plot	indiv. in plot	dbh range cm	total epi. spp., indiv.	Comments
Ackama paniculata	STRf	7	12-30	2,2	epiphytes on largest indiv. only
" "	WTRf	3	28-100	4,8	
Acronychia acronychioides	SEVF	5	10-24	11,26	small indiv. devoid
Alectryon subdentatus	DRf	5	16-24	6,38	all bearing epiphytes
Backhousia sciadophora	DRf	32	5-37	10,257	one 15 cm dbh devoid
Cryptocarya aff. *hypospodia*	SEVF	15	12-42	25,195	smallest indiv. devoid
C. mackinnoniana	SEVF	6	11-70	13,60	smallest with 1 only
C. foveolata	STRf	5	8-21	nil	all bearing semi-epi.climbers
" "	WTRf	2	20-26	7,18	both " " " "
Dendrocnide excelsa	STRf	15	5-82	9,63	7 indiv. < 30 cm dbh devoid exc. for SECs
Drypetes australasica	LRf	12	15-55	7,18	64% of all epi. bearers in plot
Elaeocarpus eumundi	SEVF	5	10-17	nil	
Polyosma cunninghamii	STRf	8	9-25	nil	all bearing SECs
Pennantia cunnginhamii	WTRf	5	18-35	4,11	
" "	STRf	2	28-30	nil	
Planchonella australis	STRf	5	10-75	11,40	smallest 2 only with SECs
" "	DRf	5	5-10	8,35	all bearing

Prolific epiphyte bearers are clearly indicated even with the limited data presented. Such species as *Acronychia acronychioides*, *Alectryon subdentatus*, *Backhousia sciadophora*, *Cryptocarya* aff. *hypospodia*, *C. mackinnoniana* and *Planchonella australis* bore a significant number and variety of epiphytes on even the smallest trees in most cases. However in the case of the apparently axenic species, caution must be exercised in predicting from the data; the cases of *Cryptocarya foveolata* and *Pennantia cunninghamii* illustrate this - in both, all individuals in the WTRf plot bore significant numbers and variety of epiphytes, whereas in a different environment, in the STRf plot, trees of the same species were not colonised (except for semi-epiphytic climbers on the lower trunks). Even so, it would appear that

Ackama paniculata has a relatively high degree of axeny as the 10 individuals from the STRf and WTRf plots bore a total of only 3 true epiphytes on the largest and presumably oldest individual and on the rest, 7 semi-epiphytic climbers of 3 species (which are not so dependent on the phorophyte). Further data collection is needed to clarify this. *Polyosma cunninghamii* is a similar case.

Questions arise, then, regarding the factors controlling specific relationships, epiphyte 'proneness' and axeny of phorophytes. Schimper (1888:92) discussed factors controlling distribution of epiphytes within the macrocommunity. In relation to the substrate, i.e. bark, he noted that its physical as well as chemical properties were probably important in selecting epiphyte species just as such properties of the soil were important to terrestrial plants.

ii. Epiphytes and allelopathy

Most workers have emphasised the importance of the various properties of the phorophyte bark in epiphyte ecology.

Bark roughness, scaliness, absorptive capacity and shedding characteristics have been seen by many observers as of prime importance, e.g., Pessin (1925), Garnett (1929), Oliver (1930), Eggeling (1947), Sulit (1950), Allen (1959), etc. Others have supposed that toxic chemicals (allelopaths) present in the bark are important in suppressing epiphytic growth, e.g. Went (1940), Piers (1968). Frei (1973a, b) demonstrated a correlation between epiphyte scarcity on *Quercus* species in Mexico and presence of specific phenolic acids (gallic, ellagic) in their barks, and also showed inhibition of orchid seed germination *in vitro* using ground bark from some axenic trees. The relevance of these results to nature has been questioned (Sanford, 1974) but indicate at least a general trend. Sanford at the same time cited unpublished data which showed a possible correlation between high bark phenolic content and axeny in rough-barked trees in optimal environments. The case of *Ackama paniculata*, mentioned above, may be similar to this as the trees in question were growing in relatively non-limiting environments and have a rough, absorbent, soft, corky bark, but bear very few epiphytes.

Another relevant case mentioned above is the ironbarks, on several of which, e.g. *Eucalyptus crebra* and *E. paniculata*, rainwater stemflow is often very frothy and where this runs onto the ground a 'scalded' perimeter develops, devoid of plant life (J.L. Charley, pers. comm.). It thus appears that the bark contains soluble, allelopathic substances which inhibit seed germination; this needs investigation. Al-Mousawi & Al-Naib (1975) observed a paucity of understory herbs in *E. microtheca* plantations in Iraq when compared with an adjacent *Casuarina cunninghamiana* stand. They later identified three volatile and five water soluble growth inhibitors from the *E. microtheca* leaves (Al-Mousawi & Al-Naib 1976; Al-Naib & Al-Mousawi, 1976).

The study of allelopathy has proliferated in the last decade or so. Rice (1979) has extensively reviewed most aspects of the work covered during this time; several areas he covered, while not actually involving epiphytes, are quite relevant here.

Firstly, he cites a number of papers on the allelopathic effects of woody seed plants on others and on understory herbs, such as the ones mentioned above dealing with *Eucalyptus microtheca*.

Secondly, he pointed out that most ecologists explain small scale vegetation patterning on the basis of competition but that there was growing evidence on the role of allelopathy here. Research along these lines may well prove fruitful in epiphyte distributional investigations.

Thirdly, a number of studies have shown allelopathic effects by trees on mycorrhiza of other plants. These include suppression of spruce (*Picea abies*) mycorrhizae by heather (*Calluna vulgaris*) and the consequent failure of spruce to establish among heather (Handley, 1963). Robinson (1972) demonstrated that runoff from heather roots and raw humus was toxic to several mycorrhizal fungi and may also protect it from pathogens. Others deal with similar interactions between *Populus* and *Boletus* (Olsen et al., 1971) and between various fungi and bacteria and other fungi associated with *Shorea robusta* (Shukla et al., 1977). Brown and Mikola (1974) demonstrated an inhibitory influence of lichens on growth of seedling mycorrhizal forest trees - the lichen *Cladonia alpestris* severely limited root tip growth and ^{32}P-uptake in *Pinus sylvestris*. Krogstad and Solbraa (1975) show depression in activity of various microbial enzymes with extracts from spruce bark.

The mycorrhizae in the above cases were apparently all ectotrophic types whereas those of orchids at least, are endotrophic. Also, although the studies dealt with effects on terrestrial plants, the allelopathic agents were mostly derived from leaves or bark, thus, implications for epiphytes are there. Studies of Went (1940) stressing bark factors, Ruinen(1953) on epiphytosis and Frei (l.c.) appear to be the only ones emphasising allelopathic axeny of trees. Thus the full import of allelopathy in epiphyte ecology has not generally been appreciated and considerable research is needed in this field, especially in relation to mycorrhizae.

Epiphyte groups known to form mycorrhizal associations include the orchids, some ferns and fern allies, the Melastomataceae and the Ericaceae at least. An aspect of phorophyte axeny and epiphyte proneness related to this, which seems to have been overlooked is the importance of substrate suitability for the mycorrhiza especially in relation to germination of the host seed. It is generally accepted that mycorrhizal infection is crucial in the germination of orchid seed and early growth at least[3]. Thus, if a given tree's bark is for any reason not suitable for the mycorrhiza of an epiphyte then the latter will not be found to colonise that tree. Conversely, if the epiphyte's symbiont is favoured by a given phorophyte bark more than by most, then the epiphyte may well preferentially colonise that tree.

A number of writers have stated that many vascular epiphytes are dependent on the presence of a bryophyte regime for successful establishment, particularly as part of seral change in epiphyte succession (Dudgeon, 1923; van Oye, 1924; Cockayne, 1928; Oliver, 1930; Curtis, 1947, etc.). Pollard (1973), Sanford (1974) and Dressler (1981) pointed out that bryophytes may not only provide ideal moisture, acidity, etc. conditions for germination of vascular epiphytes but may also insulate them from unfavourable bark factors and further, if a bark is unsuitable for such bryophytes, colonisation by any dependent vascular epiphytes will be inhibited.

A summary of considerations related to allelopathy and bark as an epiphyte substrate includes these points: a. among the chemical defences of a tree is a range of substances present in bark that inhibit the growth of fungi, bacteria etc., which would otherwise attack the tree to its detriment;

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3. Certainly some adult epiphytic orchids remain infected (see Mejstrik,1970,& Warcup ,1981) although some opinion (e.g. Nuernbergk, 1974 ; Benzing & Ott, 1981) questions whether all, or even any do.

b. such substances may also inhibit the development of non-pathogenic organisms such as epiphytes either by directly preventing germination of their diaspores, or inhibiting early growth or by suppressing growth of crucial symbionts;

c. these substances are soluble to some degree and are leached from the outer bark over time, so that in older trees with persistent bark, this becomes sufficiently free of the toxins to allow germination and establishment of epiphytes, especially bryophytes;

d. these will further alter the nature of the bark as a substrate and thus facilitate germination and establishment of more sensitive epiphytes;

e. there is variation among trees in quantity and type of such toxins produced as well as in tolerance to them among epiphytes.

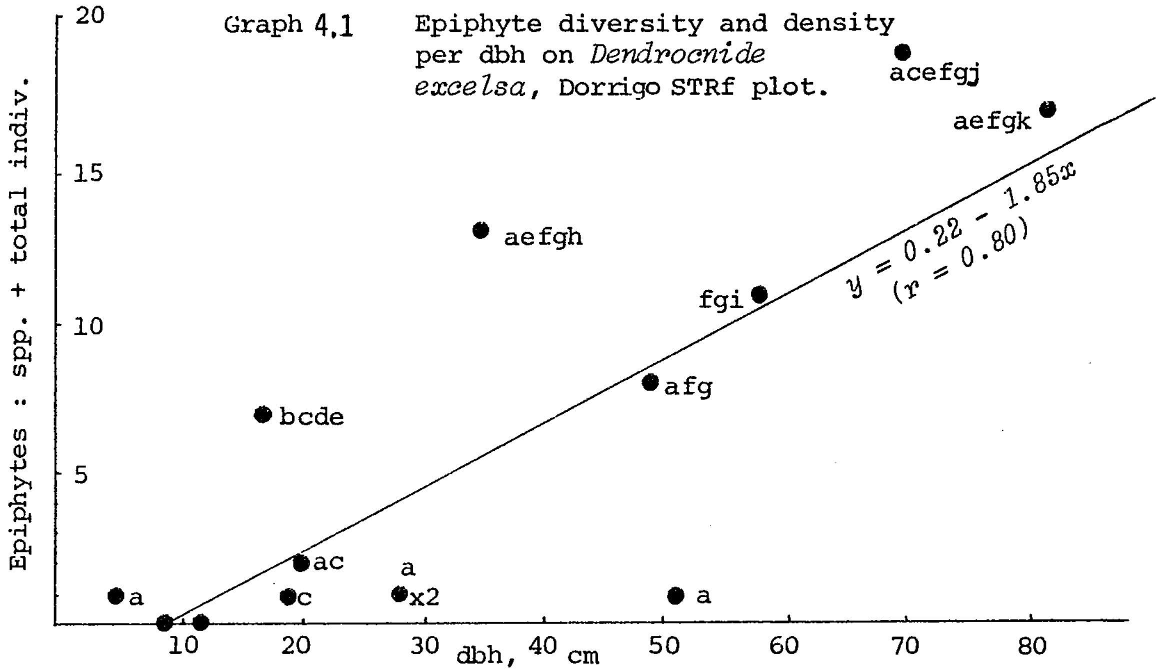
These considerations may account at least partly for phorophyte axeny and epiphyte proneness, as well as for observed specific phorophyte-epiphyte relationships.

iii. Phorophyte size/age effect

Following on the above is a phenomenon which can be called phorophyte size and age effect. Observers have noted that epiphytes are often more diverse and populous on larger, presumably older trees e.g. Went (1940), Richards (1939, 1952), Johansson (1974). Went also maintained that larger, older trees of a given species may have a qualitatively different flora from smaller, younger individuals of the same species.

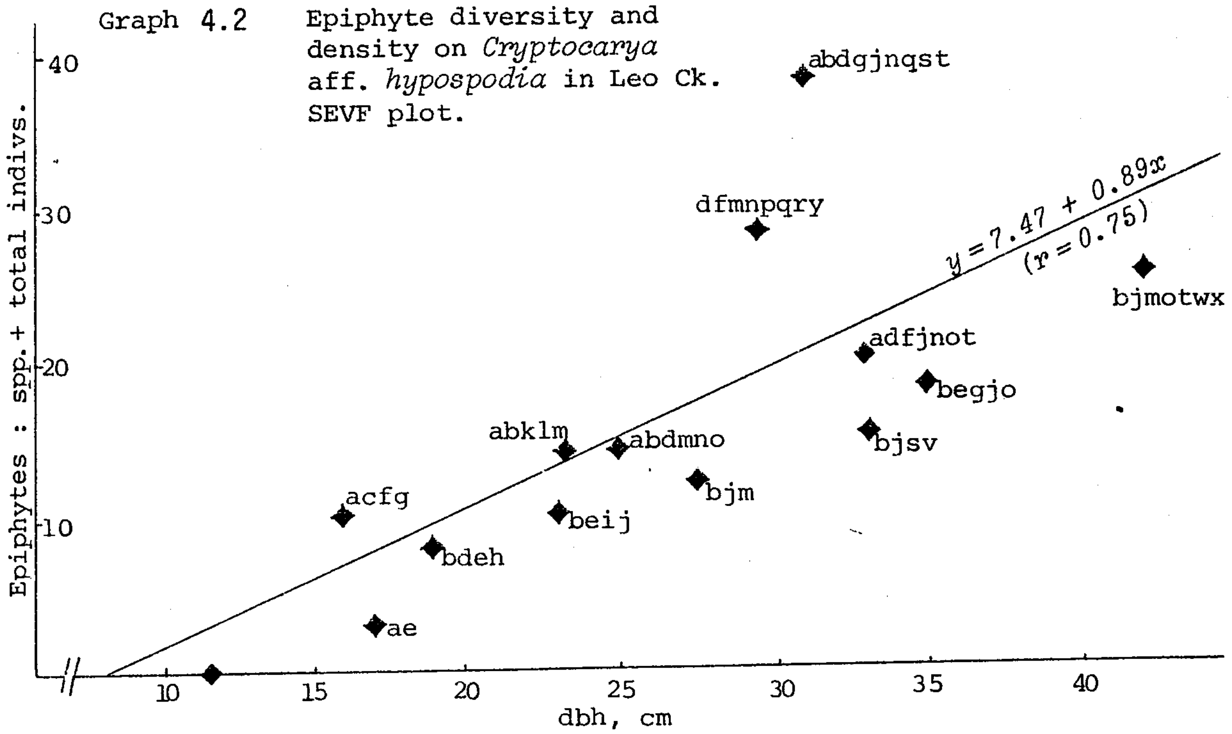
Three phorophyte species were selected from the recording plots in the present study to test these hypotheses. These were *Cryptocarya* aff. *hypospodia* of the Leo Ck SEVF, *Dendrocnide excelsa* of the Dorrigo STRf and *Backhousia sciadophora* of the Long Point DRf. They were selected as they were the most numerous (13, 14 and 30 resp.) species in their plots and were fair to good epiphyte-bearers, both of which factors enhance their suitability for statistical analysis. By using a single species in each case, from a limited area a maximum of variables was held constant, including phorophyte species differences, all macroclimatic factors plus some degree of control on microclimatic factors, topography except for minor variations, soil parent material and soil to a large degree, available flora, vegetation factors, etc. Time, i.e. age of tree was the major uncontrolled variable and this was taken as a function of tree dbh which was plotted against an epiphyte factor derived simply by adding the number of species to the number of individual epiphytes on each tree; both of these parameters were used to increase the importance of phorophyte epiphyte-acceptibility.

Results are shown on Graphs 4.1, 2 & 3, below.



Graph 4.1 Epiphyte diversity and density per dbh on *Dendrocnide excelsa*, Dorrigo STRf plot.

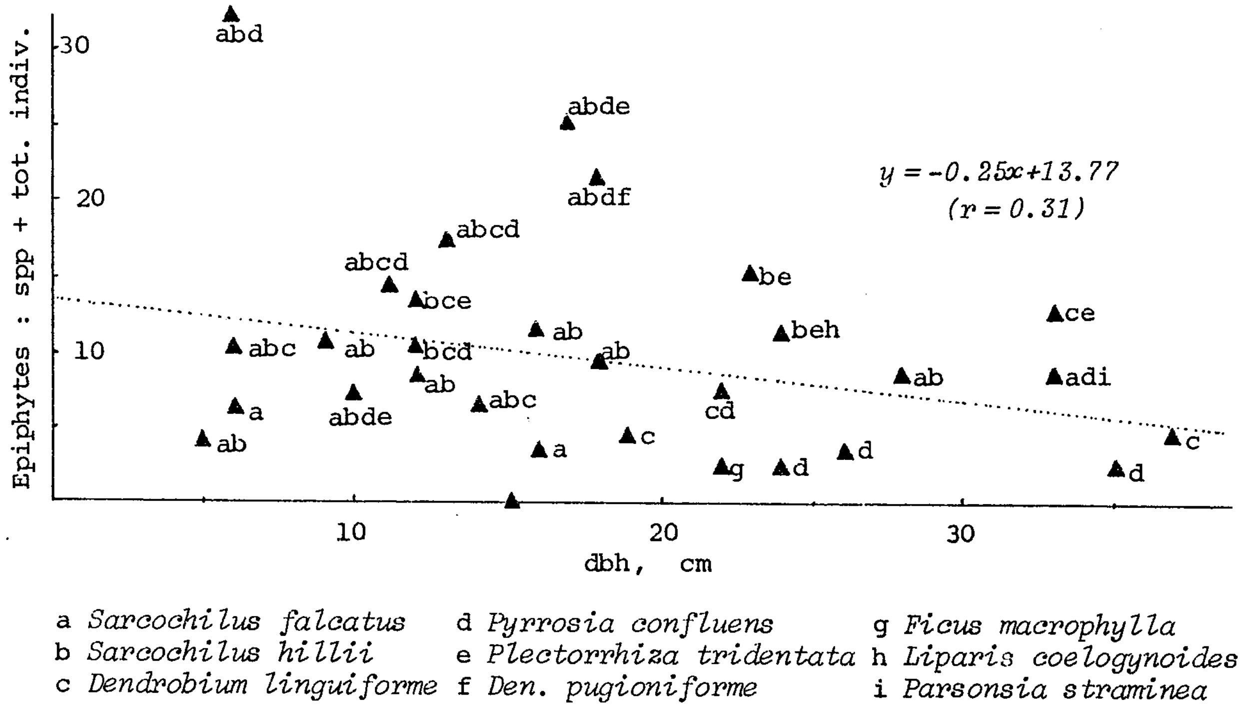
a *Pothos longipes*
b *Microsorium scandens*
c *Arthropteris tenella*
d *Arthropteris beckleri*
e *Asplenium australasicum*
f *Peperomia tetraphylla*
g *Pyrrosia confluens*
h *Asplenium polyodon*
i *Sarcochilus falcatus*
j *Dendrobium speciosum*
k *Liparis coelogynoides*



Graph 4.2 Epiphyte diversity and density on *Cryptocarya* aff. *hypospodia* in Leo Ck. SEVF plot.

a *Hoya nicholsoniae*
b *Platycerium hillii*
c *Pyrrosia longifolia*
d *Bulbophyllum baileyi*
e *Dischidia ovata*
f *Timonius singularis*
g *Dendrobium baileyi*
h *Schellolepis subaur.*
i *Belvisia mucronata*
j *Drynaria rigidula*
k *Dendrobium ruppianum*
l *Lycopodium phlegmaria*
m *Hydnophytum formicarium*
n *Myrmecodia* sp.
o *Fagraea berteriana*
p *Davallia solida*
q *Pholidota pallida*
r *Flickingeria comata*
s *Vittaria elongata*
t *Dendrobium malbrownii*
u *Humata repens*
v *Psilotum complanatum*
w *Dendrobium tetragonum*
x *Humata pectinata*
y *Hydnophytum* sp.

Graph 4.3 Epiphyte diversity and density per dbh on *Backhousia sciadophora*, Long Pt. DRf plot.



In the cases of *D. excelsa* and *C.* aff. *hypospodia* there was a strong positive correlation between dbh and epiphyte development. This was indicated by correlation coefficients ($r = 0.80, 0.75$; $P < 0.05$) which exceeded the critical levels for the 5% probability limits, i.e. there is less than a 5% probability that the observed correlated increases in dbh and epiphyte development were due to chance.

Factors contributing to this size/age effect are:

i) the older the tree, the greater the chance of epiphyte diaspores reaching it (given that dispersal is roughly even through tree life span);

ii) the larger the tree the greater the surface area for potential colonisation;

iii) in trees with persistent bark, the older the tree, the greater will be leaching and/or oxidation of the outer bark;

iv) the older the tree, the greater the accumulation of debris, dust etc., on suitable surfaces, in fissures, crotches etc. and hence improved potential for seedling establishment, particularly of humiphilic epiphytes.

v) temporal succession in the epiphytes will have had longer to develop on older trees and thus a greater variety of microhabitats will be available.

Statistical analysis of the *B. sciadophora* data indicated no significant correlation between greater epiphytic development and increased tree dbh ($r = 0.31$; $P < 0.05$). Factors which may have contributed to the differences between this case and the former two include:

1) the bark of *B. sciadophora* is flaky and slowly deciduous, i.e., there is sufficient opportunity for epiphytes to germinate and establish as the bark is obviously of suitable quality, but those which fail to develop stem encircling or penetrating root system will be sloughed off. This can be observed at times especially on larger diameter stems.

2) climatic conditions at Long Point are such that drought and/or strong westerly winds periodically cause considerable canopy defoliation and twig dieback in the DRf. This would reduce populations of the helophilous orchids of zone 5, i.e., *Sarcochilus hillii, S. falcatus* and *Plectorrhiza tridentata* (totalling 78% of all epiphytes in the recording plot). These species are commonly seen growing on dead twigs and are consequently often found fallen.

3) also because of the stressful environment, opportunity for seed germination and establishment may be spasmodic, thus interrupting the epiphyte build up.

All three phorophytes show some <u>degree of change in epiphyte flora with increase in tree dbh</u>, but in no case is this complete or even in large proportion. Rather, the changes are associated with the increase in epiphyte diversity with time (or dbh) as discussed above.

In the Dorrigo STRf plot, semi-epiphytic climbers are prominent: only three of the 14 *Dendrocnide excelsa* trees in the recording plot completely lacked these and two were the second and third smallest individuals. Among the true epiphytes, all individuals were on trees of dbh >30 cm (except one on a 17 cm tree) and *Pyrrosia confluens* and *Peperomia tetraphylla* colonised all of these but for one which completely lacked true epiphytes. The four "extra", less common epiphytes occurred on these larger trees; one was a humiphilic nest-invader, *Asplenium polyodon* requiring the prior establishment of a substantial birds-nest fern in this case and the other three only colonised the three largest *Dendrocnide* trees. Thus the qualitative changes here result from the addition of epiphyte species over time (i.e. as reflected in dbh).

A rather similar situation applies to *Cryptocarya* aff. *hypospodia* in the Leo Ck SEVF except that there are more late-colonising species which is a reflection of the larger available flora pool. Also, semi-epiphytic climbers are absent. Again, early-colonising species occurred on the full range of tree sizes in the recording plot. Another important point, even clearer here, is that seven of the late-colonising species are humiphiles, viz, *Lycopodium phlegmaria, Fagraea berteriana, Vittaria elongata, Humata repens, H. pectinata* and *Psilotum complanatum* - these were restricted to trees of over 25 cm dbh.

Backhousia sciadophora in the Long Pt. DRf plot also showed similar trends in this aspect. The less common species of epiphytes, *Dendrobium pugioniforme, Ficus macrophylla* (hemi), *Liparis coelogynoides* and *Parsonsia straminea* (Acc) only occurred on larger trees and can thus also be considered as late-colonising species. The *Ficus* and *Parsonsia* are humiphiles.

Briefly summarising epiphytic flora change on phorophytes through time as reflected in increasing phorophyte dbh in these three Australian cases, it appears that the larger and thus older the tree, the greater will be the number of follower, or late-colonising species. This is probably a result of microhabitat changes, particularly in the bark substrate environment as discussed above, certainly so in the cases of humiphilic epiphytes which require a humus accumulation or a substantial nest-forming epiphyte in which to establish. Because of a "carry through" of early-colonising species to the largest trees, a complete qualitative change in epiphyte flora does not occur in the investigated systems but rather, a build up of species occurs as environmental complexity of the substrate tree increases.

To conclude discussion on phorophyte related factors in the ecology of the epiphytic vegetation, the following points are emphasised. Epiphytes are ecologically "hyperdependent", that is to say, they are subject firstly to the independent ecological factors (cl,o,r,p,t)*, secondly to factors of the macro-vegetation and thirdly, those of the individual phorophyte. Barkman (1958) listed 13 phorophyte factors of cryptogamic epiphyte ecology and these probably apply equally to vascular species. Thus the distributional phenomena discussed here, phorophyte axeny and epiphyte proneness, phorophyte size/age effect, and specific epiphyte/phorophyte relationships are governed by a large number of variable and interrelated factors. However, some such as allelopathy and phorophyte/mycorrhizal interactions may be more important than is widely recognised at present and require considerably more research.

*climate, organisms (biota), relief (topography), parent material or substrate & time.

4.3 Summary of epiphyte synecology discussion

1. Epiphyte recording plots were set up in six different rainforest subformations, five subtropical and one tropical. Their general ecology was defined and the epiphyte synecology was discussed in relation to this particularly using data collected from the plots and elsewhere in Australia plus some exotic examples from the literature for comparison.

2. The water- and cold-stressed rainforests had a less complex and less well defined macrovegetation with fewer life forms and vegetational layers and particularly, a less dense and more interrupted canopy. This allowed greater light penetration with consequent irregularity in epiphyte 'zonation'. The water-stressed sites tended to have more numerous but smaller trees.

3. The tree flora was more diverse in less stressed rainforests with the driest and the coldest having virtual single species dominance.

4. Epiphyte floristic diversity was also greater in less stressed environments and this was related to greater variety of available microhabitats and the accommodation of a greater range of the available epiphyte flora in these.

5. Epiphyte population densities did not parallel floristic diversity - the most water-stressed system had the highest density. This was because a few species were well adapted to resist drought in particular, had high compatibility with the dominant phorophyte species and were able to proliferate, giving rise to few-species dominance.

6. Epiphytic vegetational complexity was greater in the less stressed environments and zonation was better defined because of the more regular macrovegetation and a greater variety of more narrowly adapted epiphyte species in them.

7. Epiphyte physiognomic and life forms are discussed in relation to environmental factors. Occurrence of sedentary forms and nest epiphytes tended to follow similar patterns to diversity and population but forms with their bulk close to the substrate may have an advantage in the drier and colder environments; tangle epiphytes were commoner in mist-prone environments. Hemi-epiphytes are more prevalent in warmer systems and semi-

epiphytic climbers and accidental epiphytes commoner in rainforests with a higher MAR because of their reliance on soil moisture and general lack of adaptation as epiphytes.

8. Highly specific epiphyte-phorophyte relationships are rare in Australia and require testing by rigorous data collection and analysis. Few overseas cases have been thoroughly investigated.

9. Phorophyte axeny and epiphyte proneness were investigated in the recording plots and true axeny, i.e., per species, was not established but fuller investigation is needed. However, near-axeny was found in a few tree species and a number of others were typically epiphyte prone.

10. The possible importance of allelopathy in epiphyte ecology is discussed and it is concluded that this may be more important than at present thought, especially in relation to epiphyte mycorrhiza, seed germination and seedling establishment.

11.A good correlation was found between phorophyte size (dbh) and the degree of epiphyte development in two tree species, but a poor one in another case; reasons for this are discussed.

12. Change in epiphyte flora with increasing dbh was not 100% on the three tree species investigated. Early colonising epiphyte species carried through on the larger, presumably older trees and change in epiphyte flora occurred mainly by colonisation, through time, of more dependent species.

4.4 Nest-epiphyte* communities and succession

Whereas micro-communities formed by the more humiphobic epiphytes are often ill-defined in structure and dynamics as well as floristically rather variable, those of nest-epiphytes** are easily recognised, more highly integrated in function and tend to be more constant in floristic composition.

These features relate to a basic characteristic of nest-epiphyte communities, i.e., control of the system by the nest-forming species. Also, related to this, the process of temporal succession becomes more apparent.

From numerous "side-by-side" observations#, a typical sequence might be :
i. the nest-former (mostly species of *Platycerium*, *Drynaria* or rosulate *Asplenium*) as the pioneering species, usually establishes on more or less vacant substrate and remains the sole species as it grows to maturity, accumulating litter and building the nest;
ii. the first invaders are often either accidental, casual or hemi-epiphytic dicots germinating from seed that is dropped, or falls into the top of the nest. At a similar time, pteridophytes such as *Psilotum* or *Ophioglossum* may enter. These have buried, saprophytic gametophytes that apparently develop over some time in the nest humus, after which the sporophyte emerges, usually hanging from the base of the nest (e.g., see Plate 4.3, p.150) ;
iii. over-maturity and decline of the nest-former typifies the next stage, but in regard to the micro-community as a whole, it is usually floristically the richest and structurally most complex stage, perhaps equivalent to climax. Typical invaders here include species of *Lycopodium*, *Vittaria*, *Davallia*, *Humata*, *Nephrolepis*, *Schellolepis*, *Asplenium*, *Fagraea*, *Hoya*, *Cymbidium* and various casual, accidental and hemi-epiphytic dicots (see also list below);
iv. death of the nest-former is often followed by a stage in which one or two of the invaders are favoured and become dominant, especially *Davallia*, *Nephrolepis* or *Cymbidium madidum*, sometimes to the exclusion of other species ;
v. anabrupt end comes when the nest falls by itself or with the phorophyte. At the death of the nest-former, the nest is usually large and heavy and this, combined with the lack of new root growth onto the phorophyte and the resultant loss of grip, causes the fall. This also usually results in the demise

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* N.B. "nest-epiphytes" includes both nest-formers and nest-invaders.

** Two examples are illustrated on Plates 4.3 & 4.4, p.150.

In the sense of Mueller-Dombois & Ellenberg (1974).

Plate 4.1

Upper shade-epiphyte community of *Lycopodium phlegmaria*, *Schefflera actinophylla* and *Hoya nicholsoniae* in montane rainforest, North Johnstone River, N Qld.

Plate 4.2 Shade community of semi-epiphytic climbers. The appressed species is *Rhaphidophora pachyphylla*, on the extreme left, *R. australasica*, immediate left, upper and lower on the trunk is *Pothos longipes* Schott and extreme right, *Epipremnum pinnatum*. The *R. pachyphylla* on the left carries epiphyllous bryophytes.

Plate 4.3

Asplenium australasicum nest-epiphyte community at a middle stage of development. *Ophioglossum pendulum* hangs from the lower section, *Nephrolepis cordifolia* grows from the top as well as *Hoya nicholsoniae*. N Johnstone River, N Qld, montane rainforest.

Plate 4.4

Asplenium australasicum nest-epiphyte community - this sp. is growing behind the phorophyte trunk (leaves on left). The large fern on the right is *Schellolepis percussa*, lower left is *Asplenium laserpitifolium* and in the upper centre, *Vittaria elongata*. This community is in a senescent stage. Woopen Ck, Russell River, N Qld., lowland tropical rainforest.

of the invaders as the new environment will usually be quite different and unsuitable for their growth.

Below are listed the nest-forming and nest-invading spp. of the Australian epiphyte flora.

A. Nest formers

i. Bracket spp., habitually developing large nests :

*Drynaria rigidula**	*Platycerium bifurcatum**
D. quercifolia	*P. hillii**
D. sparsisora	*P. superbum*
	P. veitchii (lithophyte)

ii. Rosette spp., habitually forming moderate-sized nests :

*Asplenium australasicum**
*A. nidus**
A. simplicifrons

iii. Apogeotropic-root-nest formers, less effective and less commonly nest-forming than the above :

*Dendrobium speciosum**
Acriopsis javanica
Cymbidium madidum - also commonly nest-invading.

iv. Facultative nest-formers which develop a relatively large root mass. These are often nest-invaders also.

Microsorium superficiale
M. punctatum
M. grossum
Dictymia brownii

B. Nest invaders

i. Strongly humiphilic spp. which always have basal parts covered (obligate) :

Psilotum complanatum	*Tmesipteris* spp.
P. nudum	*Lycopodium dalhousieanum*
	Ophioglossum pendulum

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* Most important spp.

ii. Moderately strongly humiphilic spp. - mostly have basal parts covered (i.e. buried in nests) but sometimes growing on relatively clean surfaces where humidity levels permit :

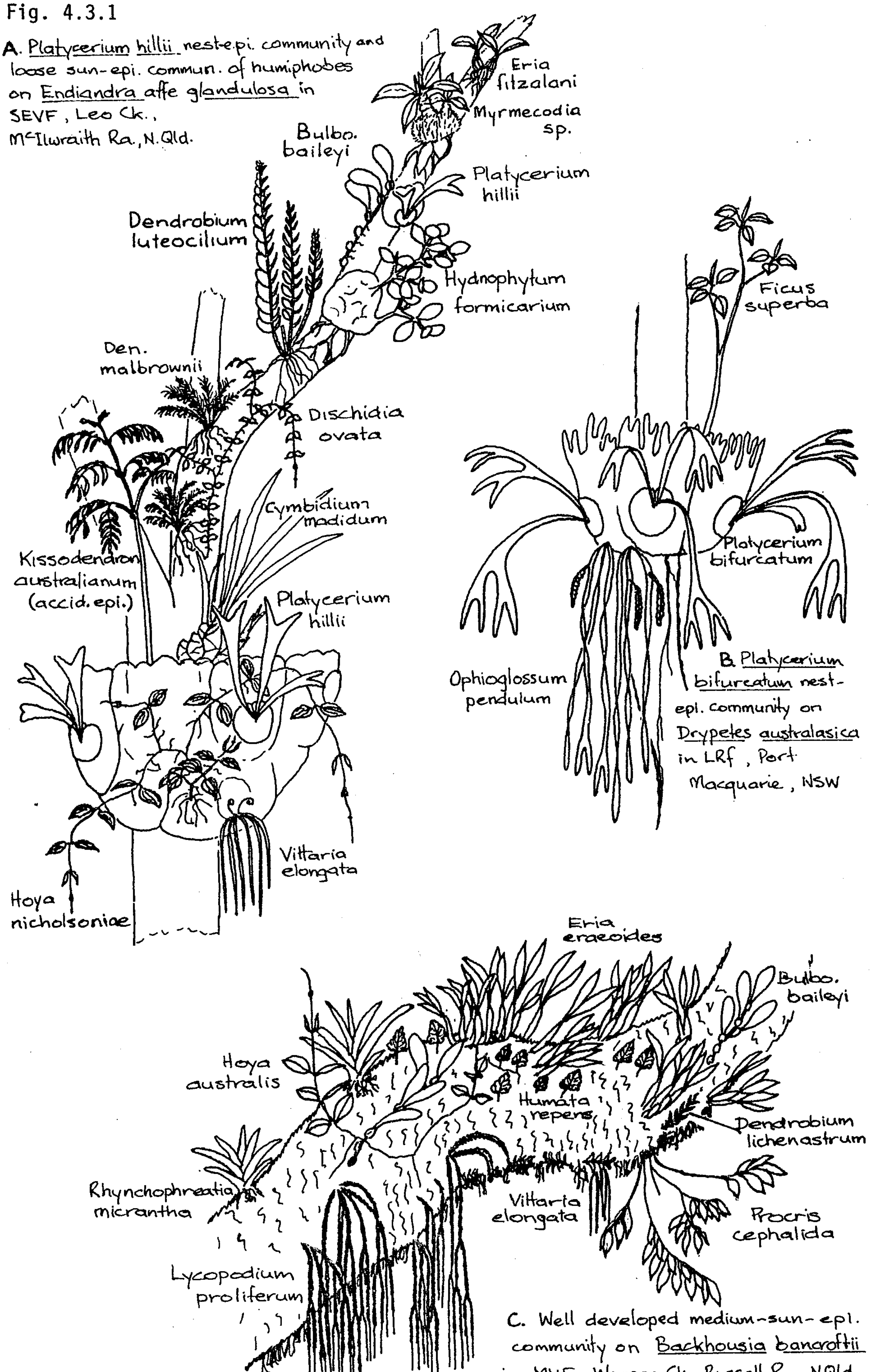
Lycopodium carinatum
L. myrtifolium
L. phlegmaria
L. phlegmarioides
L. polytrichoides
L. proliferum
L. squarrosum
Vittaria elongata
Humata repens
Humata pectinata
Rumohra adiantiformis
Davallia pyxidata
D. denticulata
D. solida
Schellolepis percussa
S. subauriculata
Asplenium polyodon
A. flaccidum
Pittosporum undulatum
P. bicolor
Procris cephalida
Polyscias elegans
P. willmottii
Ficus spp.
Timonius singularis
Fagraea berteriana
Cymbidium madidum

The trunk/branch transect diagram from Port Macquarie, Fig. 4.3.1B, depicts the early invasion stage of a *Platycerium bifurcatum* nest-epiphyte community, and that from Leo Ck, McIlwraith Ra., Fig. 4.3.1A, represents the next stage where the dominant, in this case *P. hillii*, is large and senescent. The latter example also suggests a succession above the nest community; the large *Platycerium* is in a lower zone than the younger, establishing ones and appears to have been 'left behind'. Those epiphytes established above it may represent a succession. Data from the same community on change in epiphyte flora on *Cryptocarya* aff. *hypospodia* with increased dbh (see pp. 142 & 143, esp. Graph 4.2) is at least circumstantial evidence of succession. The smallest tree in the recording plot (i.e. greater than 10 cm dbh), 12 cm dbh was vacant; the next largest (14 cm) carried one individual each of *Hoya nicholsoniae* and *Dischidia ovata* on the trunk and a *Pyrrosia longifolia* on a larger branch. Increase in species continued with increased dbh until a maximum on one tree of 31 cm dbh which carried ten species of epiphytes, three of which were in common with the two smallest trees. Only two of the first twelve colonists were humiphilic but on the other hand, five of the last seven new colonists were so.

Succession in non-nest epiphyte communities however, is not often readily apparent, but several workers have enumerated stages, presumably derived from side-by-side studies. Dudgeon (1923) listed these stages from a Himalayan *Quercus* forest :

1. crustose lichen stage, beginning on 3-4 year wood,
2. foliose and fruticose lichen, prominent 3-4 years later,
3. pioneer mosses,
4. climax moss stage at ca 20 years,
5. fern stage,
6. flowering plant stage.

Fig. 4.3.1



A. *Platycerium hillii* nest-epi. community and loose sun-epi. commun. of humiphobes on *Endiandra affe glandulosa* in SEVF, Leo Ck., McIlwraith Ra., N.Qld.

B. *Platycerium bifurcatum* nest-epi. community on *Drypetes australasica* in LRf, Port Macquarie, NSW

C. Well developed medium-sun-epi. community on *Backhousia bancroftii* in MVF, Woopen Ck., Russell R., N.Qld.

He considered this succession to be "unusually clear". Van Oye (1924) listed 3 stages from his observations on Javanese epiphytes, viz.,

1. pioneer association of Myxophyceae and *Trentepohlia* (alga),
2. invasion of mosses and small xerophytic ferns,
3. climax epiphytic association of ferns and orchids.

Oliver (1930) discussed epiphyte succession in NZ, giving the following general stages :

1. small lichens and mosses,
2. appearance of xerophytic ferns and/or orchids,
3. colonisation of fern rhizomes and orchid roots by lichens and mosses,
4. accumulation of litter and invasion by many spp., including ephemeral (accidental) epiphytes,
5. climax stage, in which typical, humiphilic spp. dominate,
6. succession ends by a) falling of community owing to loss of grip by phorophyte bark exfoliation, or, b) death of phorophyte by strangler hemi-epiphyte.

Oliver's sequence generally resembles the observations of Dudgeon and of van Oye and there are some similarities to the nest-epiphyte succession outlined above from Australia. It differs from the former two in the inclusion of the secondary moss and lichen stage (3) and in the termination resulting from bark exfoliation or by ' strangulation ' of the phorophyte by a hemi-epiphyte ; it differs from the nest-epiphyte sequence in the initial stages. The stage of litter accumulation and invasion by humiphilic spp. (climax), is a particular feature common to all , including some Australian non-nest-epiphyte communities (see branch transect from Woopen Ck, Fig. 4.3.1c, in which the litter buildup under the *Eria* is 5-10 cm deep).Such stages in Australian epiphyte communities are restricted to particularly dynamic and well developed systems.

Johansson (1974) also implies the existence of a climax when he details the siftings from 13 Liberian epiphyte communities. Four of these contained fragments of pre-existing species and in the most productive one, 10 species were represented as living specimens while the fragments of at least 6 pre-existing species were found, some of which were typical pioneers , thus an apparent complete community change had occurred. This is also a salutary, if rare, example of an archaeological method of investigating succession as it brings to bear direct observation as evidence and does not rely so much on extrapolation or theoretical estimation as do side-by-side studies.

A third, probably even more effective method of studying succession is the use of permanent phorophyte trunk/branch "plots". Such methods are rarely employed as observations should extend over at least a decade and ideally, several times this. Setting up such a study would involve the following procedures :

a) selected trunk and/or branch transects should be carefully drawn to scale and/or photographed if this is practicable; subsequent photographs should be taken from the same position, using the same lens system and scale object each time. New diagrams and/or photographs should be produced whenever sufficient change in the spatial arrangement requires this.

b) canopy height and density, and any light-breaks should be recorded in writing and diagramatically where applicable.

c) any known important unusual climatic events should be recorded, e.g. prolonged droughts or rain periods, cyclones, bushfires, etc.

d) observation frequency should be determined in the initial stages and be governed by speed of change in the epiphyte arrangement and growth.

Comparing epiphyte succession with that in major communities, certain similarities and parallels can be seen. These include the classical stages of nudation (≃ production of new surface by the phorophyte), influx of disseminules, competition in some cases and possibly a type of climax. However, there are basic differences concerning time scale and the subordinate position of epiphytes; viz., the successions will be brief as their existence is limited at a maximum, to the life span of the phorophyte; as such they can be considered as cyclic on a short term basis.

Epiphyte communities and succession must be seen in the context of their occurrence as synusial micro-communities and function as serules. Their status is one of ecological hyperdependence on firstly, the phorophyte then on the phytocoenosial community and finally, on the independent ecological factors of macroclimate, available flora, topography, parent material and time.

CHAPTER 5

EPIPHYTES AND CRASSULACEAN ACID METABOLISM (CAM)

5.1 Introduction & Review p. 157

Aspects reviewed are mainly those concerned with the ecology of CAM as it occurs in nature.

5.2 The ecology of CAM in the epiphytes *Dendrobium speciosum* Sm. and *Plectorrhiza tridentata* (Lindl.) Dockrill, (Orchidaceae). (p. 164) This is a report on a field investigation and is discussed from the viewpoint of the adaptive significance of CAM to these epiphytes in the context of their natural environment.

5.2.1 Introduction p. 164

5.2.2 Selection of site, species and individuals p. 164

5.2.3 Methods p. 168

5.2.4 Results p. 170

5.2.5 Discussion p. 179

5.2.6 Conclusions p. 183

5.3 Discussion on CAM in the Australian epiphyte flora p. 185

This covers the results of a survey of the presence of CAM in 140 epiphyte species and its relation to microhabitat xericity, synecology and evolution.

5.1 Introduction and Review

At least as long ago as the early 1890's the basic physiology of CAM was understood. Warming (1909, p.123) cites Aubert (1892) and Jost (1903) as his sources when he states "The divers structural features that obstruct transpiration at the same time constitute an obstacle to the assimilation of carbon dioxide; at night-time, during respiration, there is produced only little carbon dioxide but much malic acid, which is utilized in the manufacture of carbohydrates on the following day". He thus touched on the water economy aspect but apparently did not realise its import.

Over the last three decades or so there has been a revival of interest in CAM and it has been intensively and extensively investigated, particularly from the biochemical/metabolic pathway viewpoint (see Kluge & Ting, 1978 and reviews by Osmond, 1978 and Ranson & Thomas, 1960, as keys to the large literature). This is particularly so since the works of Thomas (1947, 1949) and coworkers, and Thurlow & Bonner (1948) established and quantified the direct causal relationship between nighttime stomatal opening and CO_2 intake, and the accompanying increase in leaf acidity. Even then CAM was largely regarded as a metabolic oddity and little comment on its ecological significance was made for some time. Ranson & Thomas (1960) apparently missed the water-saving implications - works covered by their review concentrated on investigating the metabolic pathway, particuarly the fluctuations of leaf acidity, and CO_2 and O_2 exchange. Joshi et al. (1965) and then Neales et al. (1968) appear to have been the earliest workers to fully realise the water economy implications of CAM.

CO_2 availability and carbon balance may well be the ecological problem involved for some submersed hydrophytes, e.g. *Hydrilla* (Holaday & Bowes, 1980) and *Isoetes* (J. Keely, 1981), that have been reported to have acidity rhythms typical of CAM. Water stress is obviously unimportant here, but in the case of plants of subaerial environments, this factor appears to be of central importance in the adaptive significance of CAM. It is in arid and semiarid communities that CAM plants are most prominent. As a result of brief water availability coupled with relatively high insolation rates and persistent, significant air movement, the water stress suffered by many epiphytes in otherwise moist communities is probably comparable to that experienced by terrestrial forms of semiarid climates. Thus, the preponderance of CAM plants among the Australian vascular epiphytes is not surprising; of 120 tested, $\delta^{13}C$ values indicated some degree of CAM in at least 65 (see later discussion - section 5.3).

Beginning in the early 1970s, the adaptive value and ecological significance of CAM has been brought into sharper focus in a number of autecological/ physiological studies carried out on a variety of plants in the field, under natural conditions. They have concentrated on water relations, halophytism, temperature and light relations but all of these relate more or less directly to water stress.

Among terrestrial plants, Bartholemew (1973) studied CO_2 flux and stomatal behaviour in *Dudleya farinosa* (Lindl.) Britton & Rose, (Crassulaceae), under natural conditions in coastal California, finding that as drought lengthened, CO_2 influx during the day decreased, but night influx was only affected after much longer drought. Thus stomatal opening during the day decreased with increasing drought but nocturnal opening continued much longer than this.

Opuntia basilaris Engelm. & Bigel. has been the subject of several studies in nature : Szarek, Johnson & Ting (1973) found that during prolonged drought, stomates closed completely and transpiration and CO_2 exchange ceased with internal CO_2 cycling continuing ("idling"), but typical CAM behaviour resumed within 24 hours after precipitation. They (Szarek & Ting, 1974) also demonstrated that a significant seasonal pattern of such behaviour operated and indicated how this influenced efficiency of CO_2 and water usage in relation to the environment. They established mesophyll resistence as a factor influencing CO_2 flux during the night. Later, Hanscom & Ting (1978b) investigated the effect of seasonal temperature change on CAM in this species and found acid accumulation greatest when diurnal temperature fluctuation was greatest and minimums moderate, they also found that the typical CAM behaviour pattern continued in this species during periods of minimal or nil water stress.

Nobel (1977) studied various physiology and morphological aspects of the barrel cactus *Ferocactus acanthodes* (Lem.) Britton & Rose, in its natural environment in the Colorado desert. This species was able to continue net dark CO_2

fixation 40 days after soil water became unavailable before it commenced idling, owing to its water-storing capacity; its shallow root system was seen as important in speed of response to precipitation and ability to utilize small amounts of rain. He also studied *Agave deserti* Engelm. (Nobel, 1976), which had very similar physiological characteristics to *Ferocactus*, but had a transpiration ratio indicating much more efficient water usage (25 vs 70).

Medina & Delgado (1976) investigated *Echeveria columbiana* van Poellnitz and found that CAM was most effective in the cool, dry season, even effectively accumulating malate during freezing nights - this plant was one of the few succulents successfully coping with conditions in the alpine belt (up to 4000 m) of the northern Andes. By contrast, the gymnosperm *Welwitschia mirabilis* Hook. f. grows in the Namibian desert; it is a facultative CAM plant and those specimens growing near the coast, where it is drier and has cooler nights, show more pronouced CAM as indicated by less negative $\delta^{13}C$ values[1] (Schulze, Ziegler & Stichler, 1976).

In an autecological/physiological study of *Mesembryanthemum crystallinum* L., a halophytic annual of the Aizoaceae, Winter et al. (1978) monitored the CO_2 assimilation system through the plant's life cycle, clearly demonstrating the relative adaptive values of C_3 and CAM in relation to the environment (Mediterranean coastal Israel). The seeds germinated in the cool, moist winter and with the young plants fixing CO_2 via the C_3 pathway, growth was rapid. The onset of summer drought and water stress greatly amplified malate fluctuations as the CAM pathway took over, $\delta^{13}C$ values confirming this shift. Continued growth into the dry season was seen as related to the needs of producing a large seed crop typical of an annual species.

Apparently some species are capable of such a (reversible) switch from C_3 with daylight stomatal opening and CO_2 assimilation via RuBPC, to CAM with inverted stomatal rhythm and fixation via PEPC at night, in response to

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[1] $\delta^{13}C$ values are relative ratios of carbon isotopes, comparative to that in a particular limestone standard and (expressed as ‰) are calculated thus :

$$\delta^{13}C = \left(\frac{{}^{13}C/{}^{12}C \text{ sample}}{{}^{13}C/{}^{12}C \text{ std.}} - 1 \right) \times 1000$$

In C_3, ribulose biphosphate carboxylase (RuBPC), the primary CO_2 assimilating enzyme, discriminates against the heavier isotopes much more than does phosphoenolpyruvate carboxylase (PEPC), the primary CO_2 assimilating enzyme during the dark in CAM. ^{13}C values of plants exhibiting pronounced CAM CO_2 dark fixation range from ca -10 / to -15 / while those of C_3 plants range from -25 / to -35 / . (See, e.g. Smith & Epstein, 1971, or Bender, 1971) various stresses, mostly relating to water stress in photosynthetic tissue. These have been mostly laboratory experiments on various taxa, e.g. *Mesembryanthemum crystallinum* L., subjected to salinity stress (Winter, 1973a, 1973b), low air humidity, high light intensity (Winter, 1973b) and low temperature of culture solution (Winter, 1974); the same worker (1973c) induced CAM in *Carpobrotus edulis* (L.) N.E. Brown by salt stress. Other species include *Portulacaria afra* (L.) Jacq., which is normally C_3 but can be induced to exhibit CAM under water stress, and *Peperomia obtusifolia* A. Dietr., typically C_3, under water stress changes to internal CO_2 cycling (Hanscomb and Ting, 1978a). *Frerea indica* Dalz. is a particularly interesting case - this is an asclepiad closely allied to *Caralluma* R. Br. except that it has herbaceous leaves which assimilate via the typical C_3 pathway while the succulent stem shows typical CAM behaviour. Under water stress (as in the monsoonal dry season of its native environment), the leaves are abscised but the stems continue with CAM and maintain a favourable water and carbon balance (Lange & Zuber, 1978).

Various broader overview studies have been carried out at the level of life form, community or biome, relating to the adaptive significance and ecological implications of CAM. Mooney et al. (1974) investigated the photosynthetic carbon assimilation pathways of plants along a MAR gradient in two perarid deserts, one in northern Chile, the other in Baja California. They found that the driest area, part of the Chilean desert, was quite devoid of higher plants and assumed that it was too dry (<25 mm MAR). Moving along the gradient the first vascular plants encountered were cacti (these are obligate CAM plants), further along, drought-deciduous C_3 plants appeared, mixed with more CAM species and with more moisture again, evergreen species appeared and CAM plants became much less prominent, probably because of their slow growth rates and consequent inability to compete successfully for light. C_4 plants appeared only in saline parts of these regions. They concluded from this study that CAM was the most arid-adapted of the three carbon assimilation systems. They also drew similar inferences from an investigation in southern African arid communities, as well as about the life form and ecology of facultative C_3/CAM species (Mooney et al.,1977).

Regarding this relative adaptive value of the photosynthetic systems, Winter & Troughton (1978) came to a somewhat different conclusion. They surveyed the flora of various arid to perarid, saline and non-saline communities in

Israel and the Sinai for CO_2 assimilation systems using $\delta^{13}C$ values, dawn/dusk malate levels and anatomy as criteria. Of the 105 species sampled, 79 assimilated via C_3, 22 via C_4 (mainly on saline soils) and four by CAM. In their opinion, the dearth of CAM plants indicated that it was not well suited to the high temperatures[2] and long drought that obtained in the area. Also working in this region, Lange et al. (1975) assumed that the stem-succulent asclepiad *Caralluma negevensis* performed poorly in the perarid Negev Desert because CAM was not well suited to these same conditions. In an instructive study, von Willert et al. (1978, in Kluge & Ting, 1978) investigated CAM and ecological factors of the mesembryanthemaceous flora of the Richtersveld, SW Africa, (27 species) and concluded that in these, CAM was not well adapted to cope with sudden changes in ther thermal environment caused by hot desert winds. The absence of CAM plants in the study of Philpott & Troughton (1974) on photosynthetic mechanisms of hot desert plants is further evidence that CAM is not well suited to peraridity.Thus there are two apparently opposed views on this matter.

Some taxa, particularly the Cactaceae, appear more capable of adaptation to extreme conditions than most succulents in their capacity to idle through long drought and periods of high night temperatures (Szarek, Johnson & Ting, 1973; Nobel, 1977). The implication here is that biogeographical relations and palaeoecological events may help account for the poverty of CAM plants in the desert flora of such places as Palestine and Australia, i.e.,*very* arid-adaptable taxa have not been available to such areas during the development of their present floras.

Terrestrial succulents in the Australian flora include a few species of *Salicornia*, *Suaeda*, *Carpobrotus*, *Calindrinia* and *Sarcostemma* and only the last, a single species, appears to be a ± typical CAM plant. It and *Carpobrotus* (facultative CAM - Winter, 1973c) are probably recent arrivals - they have not radiated. Of the others mentioned, only *Calindrinia* has been shown to exhibit (facultative) CAM (Winter, unpublished).

Regarding CO_2 assimilation pathways in epiphytes, a number of studies have been done, mostly with some reference to ecology and adaptation, but few, if

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[2] A number of workers have shown experimentally that high night temperatures inhibit CO_2 uptake (by forcing stomatal closure) in CAM, e.g. Neales, 1973a, 1973b; Kluge et al., 1973; Allaway et al., 1974; Troughton et al., 1974; Lange et al., 1975; etc., although the evidence is not entirely unequivocal (Osmond, 1978).

any, have been carried out under natural field conditions with a major emphasis on ecological implications. Benzing & Renfrow (1971a & b), investigated photosynthetic physiology in the bromeliad subfamily Tillandsioideae in relation to ecology and phylogeny.They monitored CO_2 uptake in two xerophytic and two mesophytic tillandsioid species and found that the former exhibited CAM and the latter, typical C_3 assimilation patterns. Uptake in the xerophytes was inhibited when the shoot surfaces were wet but not so in the mesophytes. These observations imply that the xeric species, with a dense, silvery trichome cover and succulent mesophyll, require high light intensity to photosynthesise efficiently, i.e. an exposed microhabitat where they will dry out rapidly after wetting, and where they will need the water-saving device of CAM. Such microsites will also tend to be cool enough at night for efficient CO_2 dark fixation. The reverse will apply to the mesophytes. The findings of Kluge et al. (1973) regarding *Tillandsia usneoides* L., a xerophyte, are consistent with the above.

Medina and coworkers have also done considerable research into the CAM of bromeliads, both terrestrial and epiphytic. Species of xeric environments had succulent mesophyll and exhibited net dark CO_2 fixation associated with high PEP carboxylase activity (Medina 1974); $\delta^{13}C$ values confirmed CAM in these species (Medina & Troughton, 1974). A more extensive investigation into the physiology of 80 species in 25 genera representing the three sub-families (Medina et al 1977) showed that nitrogen content of the leaf correlated positively with CAM activity and the temperature optimum for dark CO_2 assimilation was ca 15°C. One species changed from CO_2 exchange pattern typical of C_3 to one typical of CAM in response to water stress and its $\delta^{13}C$ value, -23 , also indicated this. However, another species with a typical CAM value, -13‰, subjected to the same stress, decreased its night CO_2 intake. $\delta^{13}C$ ratios for the 80 species showed a more or less continuous spectrum from extreme CAM to typical C_3. These works on CAM in the Bromeliaceae follow on earlier investigations by Coutinho (1963, 1969).

Avadhani & coworkers (Avadhani & Goh, 1974; Goh, Avadhani et al., 1977; Avadhani, Goh & Arditti, 1978) investigated stomatal behaviour and acidity and carbon assimilation patterns in various C_3 and CAM orchids and found that the former were terrestrial species while the latter were epiphytic or lithophytic. Neales & Hew (1975) tested the $\delta^{13}C$ values of six tropical orchid species and four hybrids and correlated less negative values (typical of CAM) with thicker leaves (epiphytes) and the more negative ones (C_3-like) with thin leaves (terrestrial species). Sanders (1978) in a brief review/discussion of CAM in orchids, mentions these ecological inferences and suggests implications for horticulture from them (as did Avadhani, Goh & Arditti, 1978). McWilliams (1970) compared patterns of dark CO_2 uptake, titratable acidity, percent dry weight, and leaf thickness in 30 genera of Bromeliaceae, Orchidaceae and Euphorbiaceae and found a correlation between physiology, ecology and phylogeny i.e., typically CAM species occupied the more xeric communities and sites (epiphytic, in the cases of the former two families) and were more advanced phylogenetically.

Finally, Hew & Wong (1974) discovered CAM in a fern *Drymoglossum piloselloides* Presl. and noted that this epiphyte always occupied more xeric microsites than the other epiphytic species studied - *Asplenium nidus* L., a typical C_3 plant. Further, Wong & Hew (1976) also found that another epiphytic fern inhabiting zones more xeric than most, *Pyrrosia longifolia* (Burm.f.) Morton, exhibited CAM.

5.2 The ecology of CAM in the epiphytes *Dendrobium speciosum* Sm. and *Plectorrhiza tridentata* (Lindl.) Dockrill, (Orchidaceae).*

5.2.1 : Introduction

It does not appear from the literature that any systematic, *in situ*, autecological/physiological studies have been attempted on epiphytes in relation to CAM. The present work was carried out partly in response to this need, but in particular as a contribution to the understanding of probably the most important single environmental limiting factor facing epiphytes in their evolutionary bid for greater access to light, that is, water economy. The viewpoint therefore is slanted towards clarifying matters concerned with the occurrence of epiphytes in relation to the degree of microhabitat exposure. Even though the majority are within rainforests and other mesic communities, the microsites which epiphytes inhabit impose limits on access to water and problems of dehydration which increase with the degree of exposure of such microhabitats. Some such conditions of the outer epiphyte zones and of drier epiphyte containing communities may be equal in intensity, if perhaps not in duration, to those experienced by terrestrial forms in semiarid or even perarid communities. Schimper (1903) noted that even in the wettest rainforests, xerophytic species are found in the upper zones and various other authors have commented on the xeric nature of epiphyte microhabitats (e.g.,Richards,1952, Benzing and Dahle , 1970 , Benzing and Renfrow , 1971 , Sanford, in Withner , 1974 , Goh et al., 1977 , etc.). Chapter 3 of this thesis gives details of epiphytic microclimates in five subtropical Australian rainforest systems that support this concept.

5.2.2 : Selection of Site, Species and Individuals

The site of the present study, Dry Rainforest (DRf) at Long Pt.(Plate 5.2.1) ca 70 km SE of Armidale by road, at ca 900 m altitude, was chosen because,

a) it is a relatively water stressed rainforest system, e.g., the MAR is ca 1000-1100 mm compared with 1400-2000 mm in the 4 other local systems studied - see Chapter 3 for more details.

b) it has very large populations of epiphytes - 8450 individuals per ha

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* Dr Klaus Winter suggested this project and freely gave advice on various organisational and technical matters; this is gratefully acknowledged.

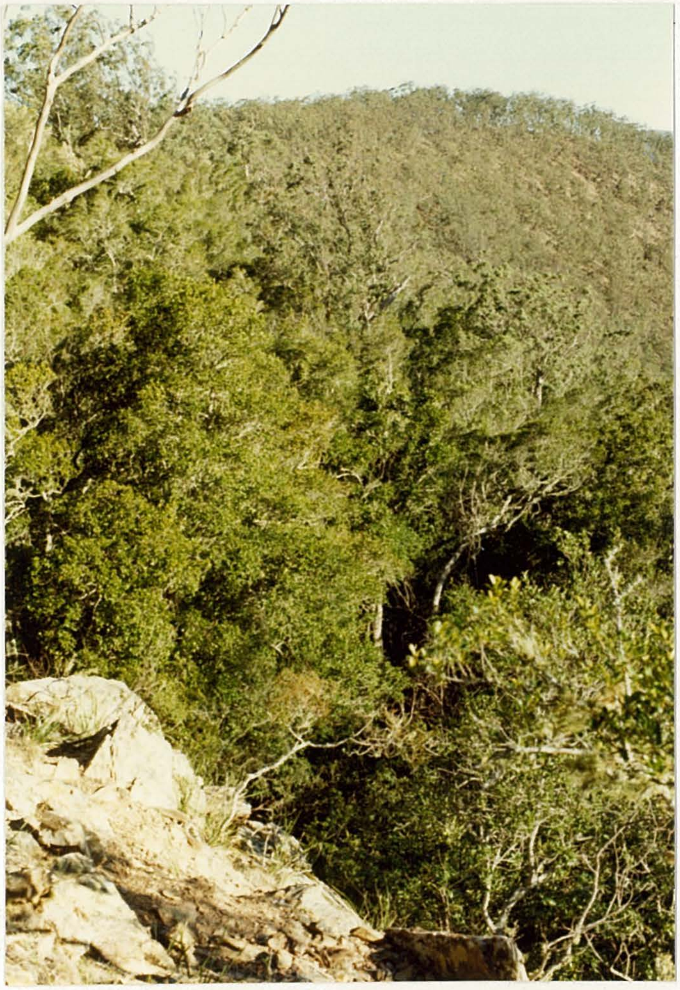


Plate 5.2.1

Dry Rainforest margin, Long Point, near Hillgrove, NSW. View looking south ; in the background is tall woodland, one of the dominant open communities of the locality. This DRf, the study area, is unusual in that it has a westerly aspect, exposing it to the cold,dry winds of winter and spring.

Plate 5.2.2

Dendrobium speciosum Sm., epiphytic on *Backhousia sciadophora* in typical sub-canopy microhabitat. These are the tree sun plant (on right) & tree shade plant. The epiphytic CAM fern *Pyrrosia confluens* is also growing on the trunk, in the middle of the picture.

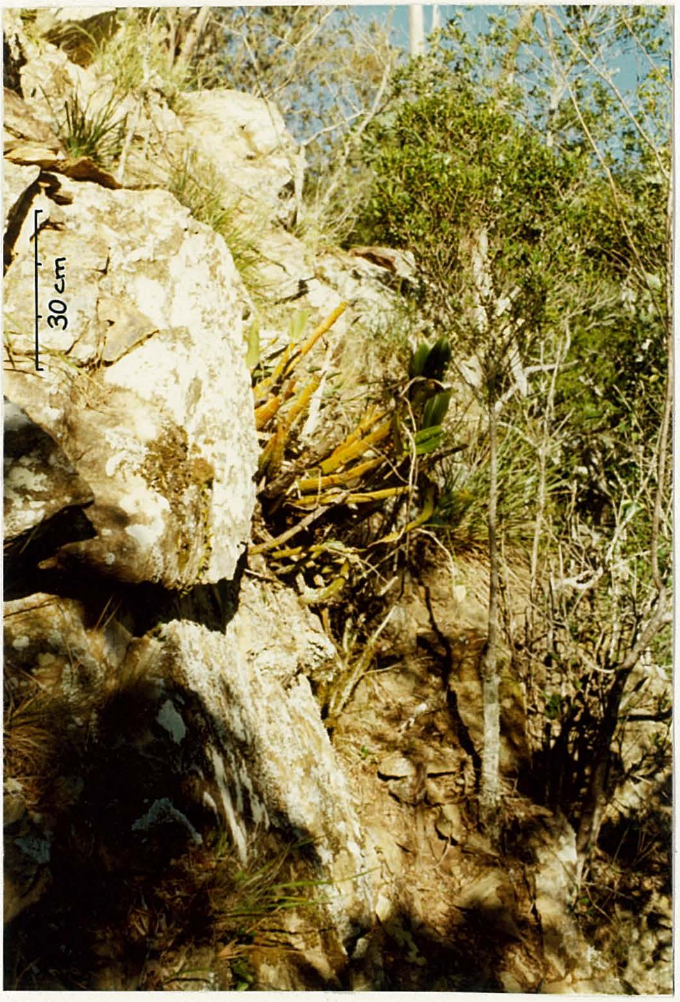


Plate 5.2.3

Dendrobium speciosum, the Long Point rock plant, on a small, shale cliff; mid afternoon, winter. NB canes on the left of the plant are mostly leafless as they are accessible to wallabies.

Plate 5.2.4

Leaf of the above plant showing sunburn patch; this surface was approximately at right angles to the sun's rays of summer, early afternoon.

Plate 5.2.5

Plectorrhiza tridentata (Lindl.) Dockrill , typical growth habit. Plant is carrying a fruit (f) of last flowering season & developing two new inflorescences (i) due for anthesis in 3-4 months (spring). To the immediate left is a small but mature plant of *Sarcochilus hillii* & a tuft of dehydrated *Papillaria* moss. The horsehair fungus, possibly *Marasmius* sp., can be seen near the twig.

Plate 5.2.6

A typical microhabitat of *Plectorrhiza tridentata* and *Sarcochilus hillii* in *Backhousia sciadophora* in DRf margin. Typical gorge country in background

against 2744 per ha in the next most populous plot, but
c) it is floristically impoverished having only 8 species with more than 50 individuals per ha, whereas mean of the other systems is 13.

The species chosen for study were selected not only because they were common, readily accessible and amenable to the techniques used, but also because they represented somewhat contrasting epiphyte forms and adaptive strategies. *Dendrobium speciosum* (Plates 5.2.2 & 3) is a large, fleshy-stemmed, sympodial, tufted epiphyte (or lithophyte) of trunks and large branches in mid zones and forms a litter-nest by means of massed apogeotropic roots which becomes spongy/peaty and acts as a water and mineral reservoir; it is moderately economical in mineral usage (see Appendix 3). *Plectorrhiza tridentata* (Pls. 5.2.5 & 6) is a small, wiry-stemmed, monopodial, aerial epiphyte growing among twigs of outer zones, usually with most roots aerial and often dangling by only one or two attached, creeping roots. It appears to be dependent on direct throughfall of rain and mist for water and mineral supply and is more stringent in its recycling of minerals.

In the case of *D. speciosum*, three specimens were monitored, each occupying variant microhabitats. The first was a lithophyte growing in an exposed microsite at the top of a low, west-facing cliff outside the DRf in open sclerophyll forest; this was designated "rock plant" and is illustrated on Plate 5.2.1. The second and third were ramets of one epiphytic clone that were organically separated by death of the older, connecting sections of the sympodium. On grew around the sunny (northern) side of the phorophyte trunk and was designated "tree sun plant" and the other, which grew around the shaded side, was called "tree shade plant"; these are illustrated in Plate 5.2.2. For *P. tridentata*, two large specimens growing in close proximity were selected, half of the leaves of one (exluding the basal pair and apical one, to reduce age effect) were used in winter and half in summer, while the other was used similarly in spring and autumn. Two plants were needed because of the small size of the species and they were used thus to allow 6 months growth and give some genotype continuity.

5.2.3 : Methods

The investigation involved measuring, every two hours for 24 hours, once each in winter (August), spring (November), summer (January) and autumn (April), the following parameters: leaf acidity, leaf undersurface diffusive resistance, leaf temperature, air temperature near the leaf, relative air humidity and solar radiation level (quanta).

Leaf acidity was measured thus:

a) with a cork borer, two 2 cm^2 leaf disks were cut in the case of *D. speciosum*, or 0.5 g (ca 4 cm^2) of *P. tridentata* leaf,

b) disks were sliced finely with a razor blade and carefully washed into a small tube of 80% EtOH for storage.

c) the samples were washed into 100 ml beakers with 20% EtOH and made up to ca 50 ml,

c) boiled gently for 15 minutes (using anti-bumping granules and hotplate), let cool and replenished to 50 ml with distilled water, then

e) titrated with 20 mM NaOH using a pH meter to show pH 7 as the end point of the reaction. The volume of NaOH used with each sample was recorded and the amount of leaf acid was calculated on the following basis:

1) 20 mM NaOH = 20 meq l^{-1}
= 20 μeq ml^{-1}

2) since one μeq of NaOH reacts with one μeq of acid, one ml of NaOH titrated repesents 20 μeq of acid in the leaf sample,

3) the mean weight per area of leaf in *D. speciosum* was calculated as 0.22 g cm^{-2} for the rock plant, 0.14 g cm^{-2} for the tree sun plant and 0.12 g cm^{-2} for the tree shade plant and thus μeq acid g^{-1} FW were calculated. For *P. tridentata*, μeq acid per sample were simply doubled to find μeq g^{-1} FW, as the leaf samples were 0.5 g.

Diffusive resistance of the leaf undersurface was taken as an indication of stomatal aperture and was measured with a Lambda LI-10S porometer in cm sec^{-1}. The leaves are hypostomatous (present writer, unpublished).

Leaf surface temperature was measured using the thermistor head of the above mentioned porometer.- 20 secs of shading was given in the day to allow some equilibration in the leaf.

Air temperature was measured using the same thermistor, allowing three minutes equilibration time and was checked against two thermometers kept at each plant.

Solar radiation was measured with a Lambda LI-185 meter on quantum function which measures photosynthetically active radiation (400-700 nm wavelength) in microeinsteins m^{-2} sec^{-1}. To moderate the differences between readings and facilitiate comparison, this data was plotted as the $\log_{10}$ of each reading. It must be pointed out that these are simply spot readings and the lines joining them on the graphs are not meant to infer intermediate readings, rather, to make them more readily visible.

Relative humidity readings were taken from a thermohygrograph and checked against a hygrometer placed at each plant.

Vapour pressure deficit was calculated from humidity and temperature data and standard vapour pressure tables, using the formula:

$$\text{v.p.d.} = \left(\frac{\text{rel.hum.\% x saturatn.vap.pr. at T, Pa}}{100}\right) - \text{sat.vap.pr.at T, Pa}$$

$$= -\text{Pa}$$

Two thermohygrographs were run, one at the rock plant and the second at the tree plants and was used for the *Plectorrhiza* microsite, which was very close to the latter. These were run for about five days to give an idea of the weather prior to the 24 hrs of measurement.

All data from the above were plotted graphically against time on a 24 hr clock.

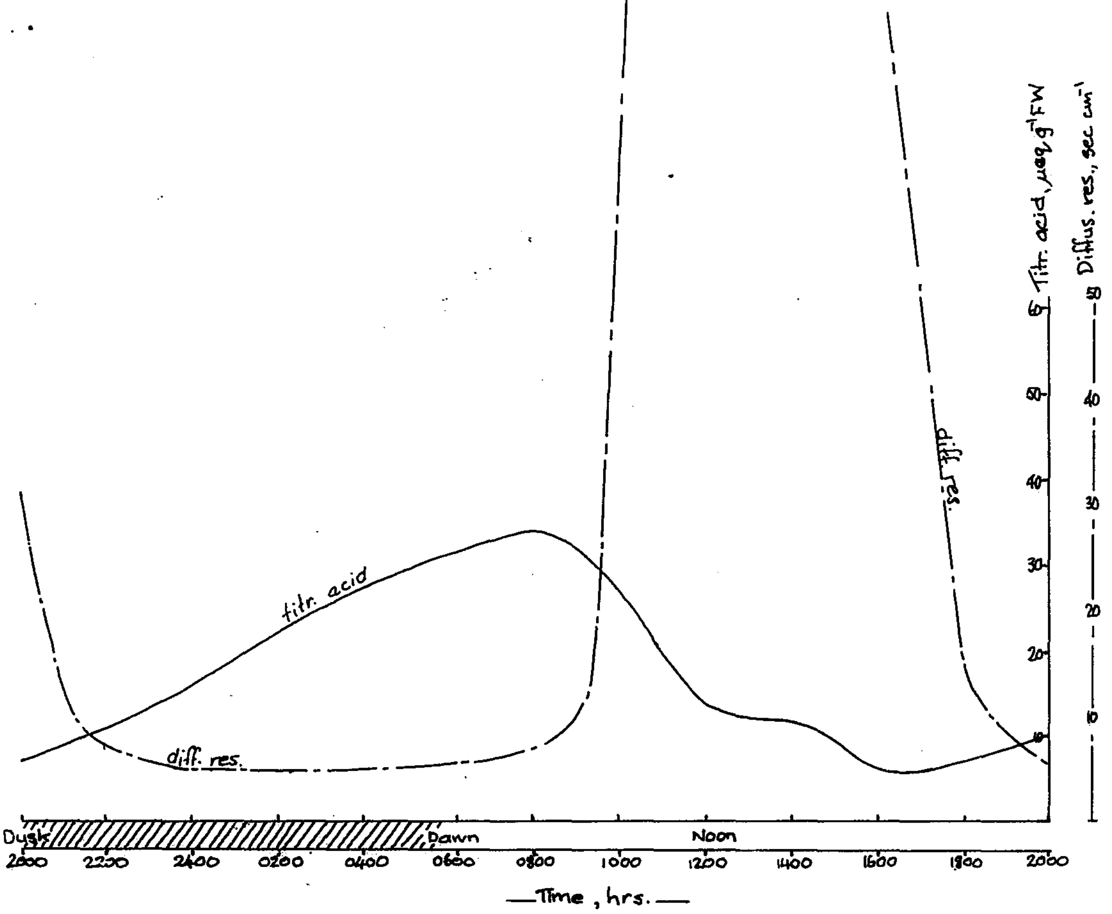
5.2.4 : Results

Graphs 5.2.1 - 10 and all data sheets and thermohygrographs are in Appendix 2 , while graphs 5.2.11 - 16 are in the text.

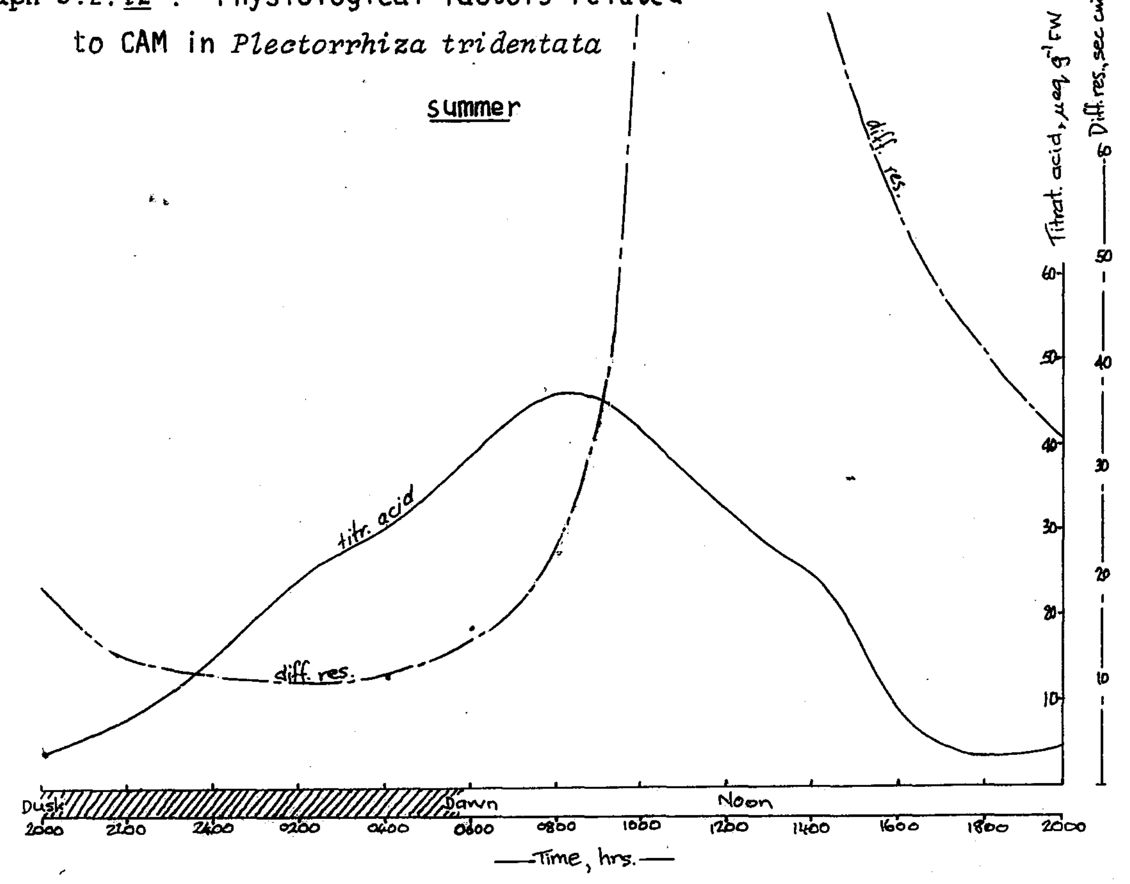
1) Environmental factors:

a) **Solar radiation.** Comparative levels of irradiance experienced by the four experimental plants ran, rock plant > *Plectorrhiza* > tree sun plant > tree shade plant. These results are mainly intended to relate to each plant's performance on the day of measuring as well as give some general indication of light intensities of the microhabitat (statistical significance and predictive value are not great). The differences are a reflection of canopy densities. The rock plant was moderately to lightly shaded during the morning by the sclerophyll forest canopy but was exposed to full sun during much of the afternoon. The tree plants were growing in microhabitats

Graph 5.2.11 Physiological factors related to CAM in *Dendrobium speciosum* rock plant, summer

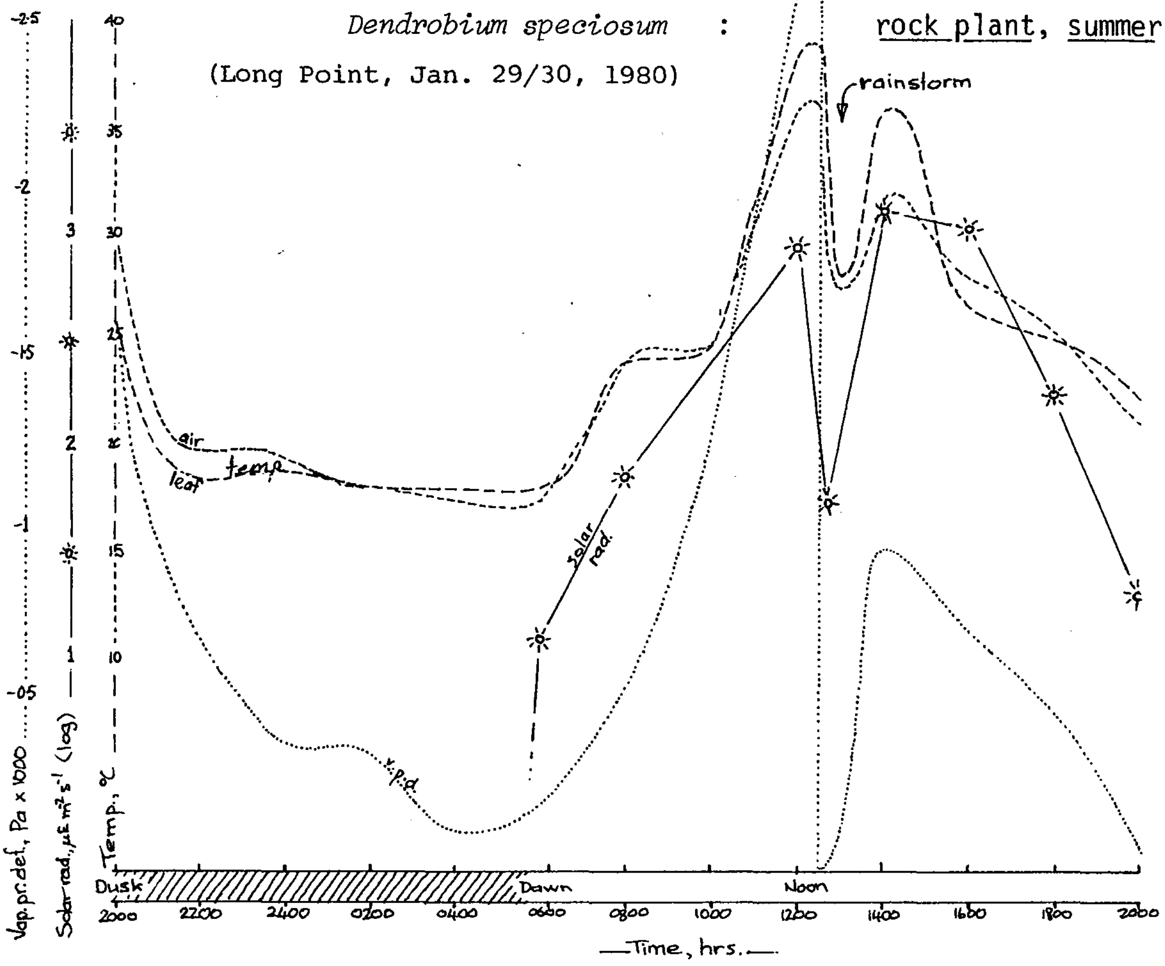


Graph 5.2.12 : Physiological factors related to CAM in *Plectorrhiza tridentata* summer



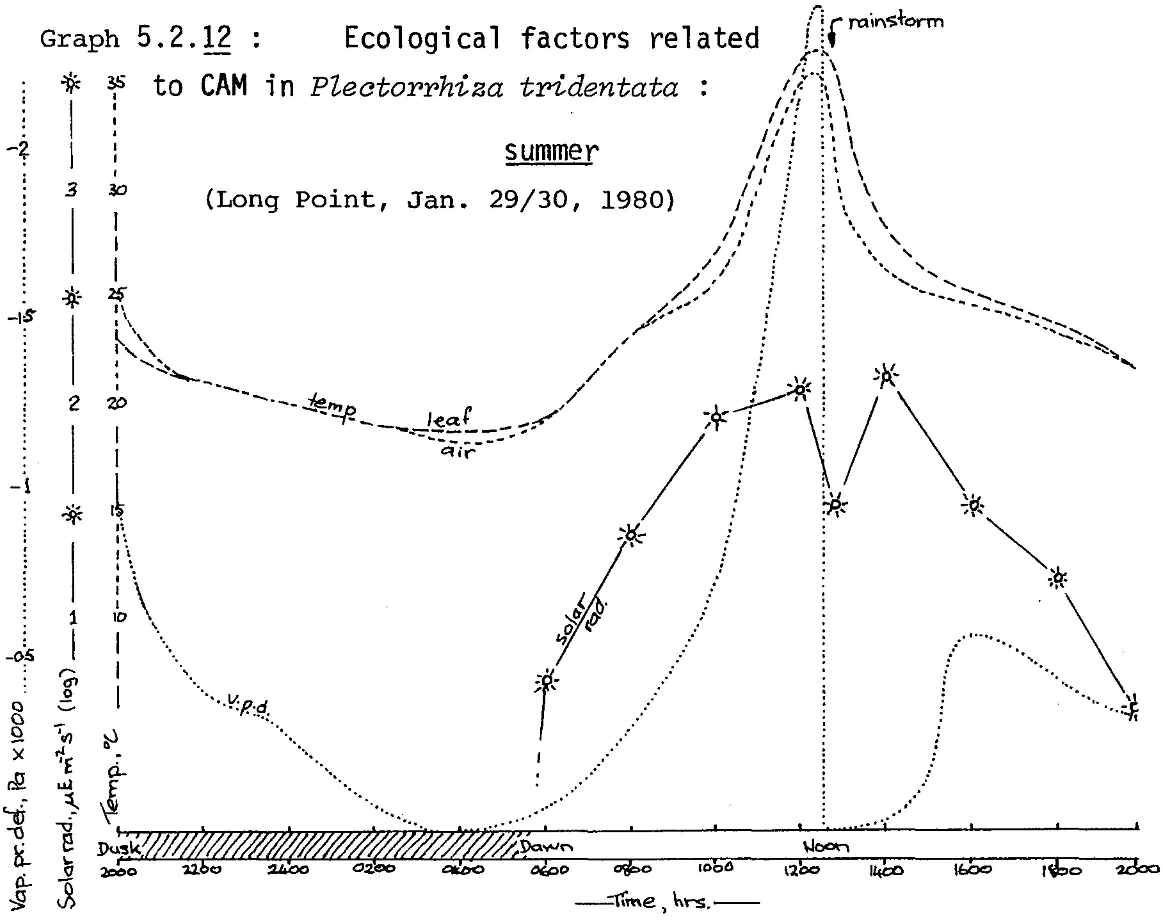
Graph 5.2.11 : Ecological factors related to CAM in *Dendrobium speciosum* : rock plant, summer

(Long Point, Jan. 29/30, 1980)



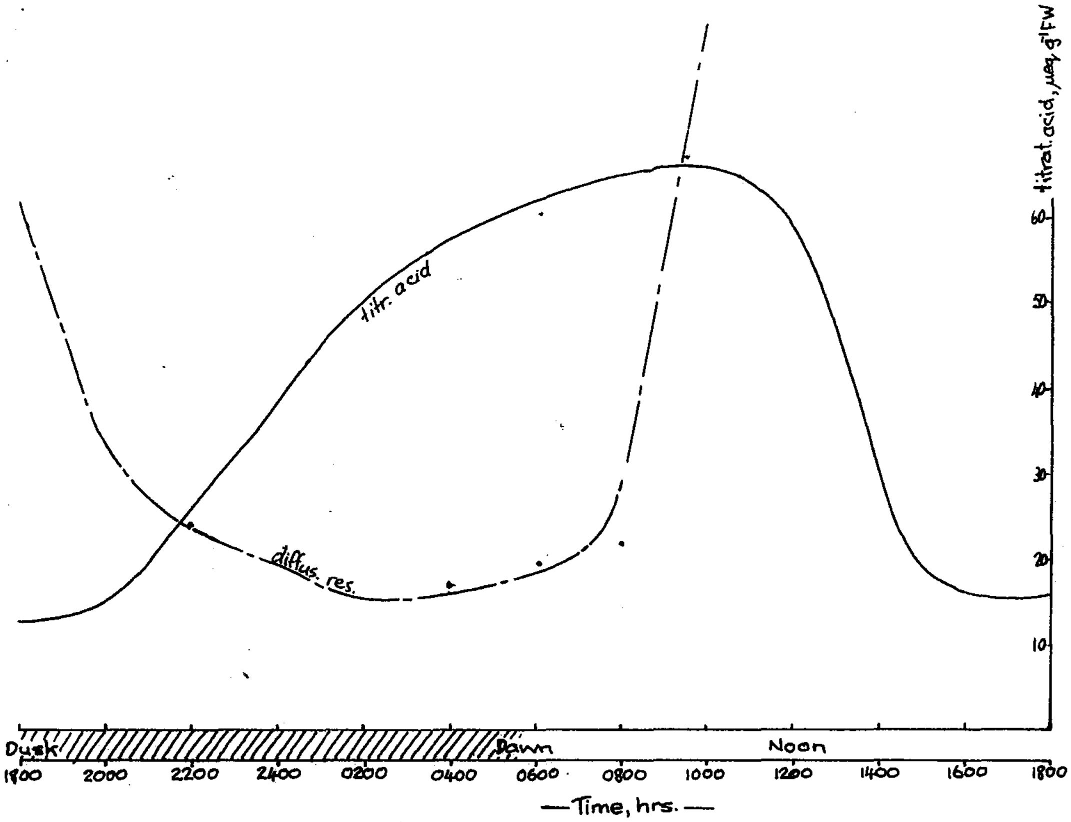
Graph 5.2.12 : Ecological factors related to CAM in *Plectorrhiza tridentata* : summer

(Long Point, Jan. 29/30, 1980)



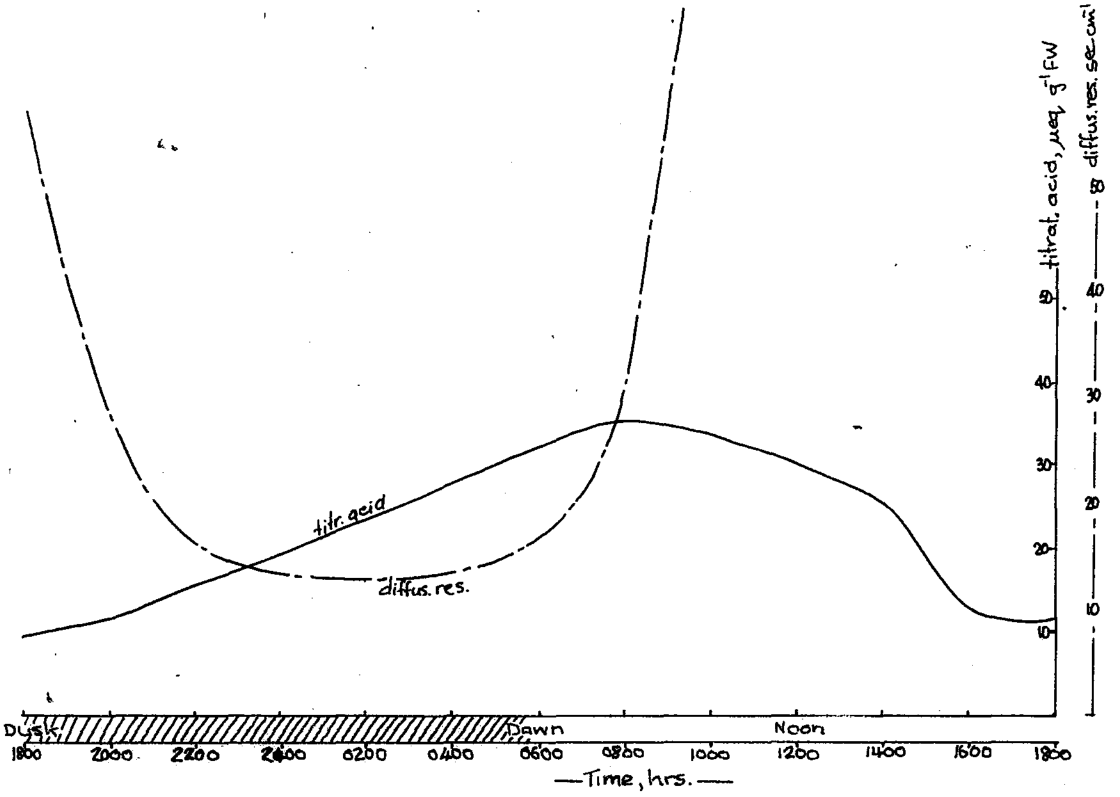
Graph 5.2.13 : Physiological factors related to CAM in

Dendrobium speciosum : tree sun plant, autumn

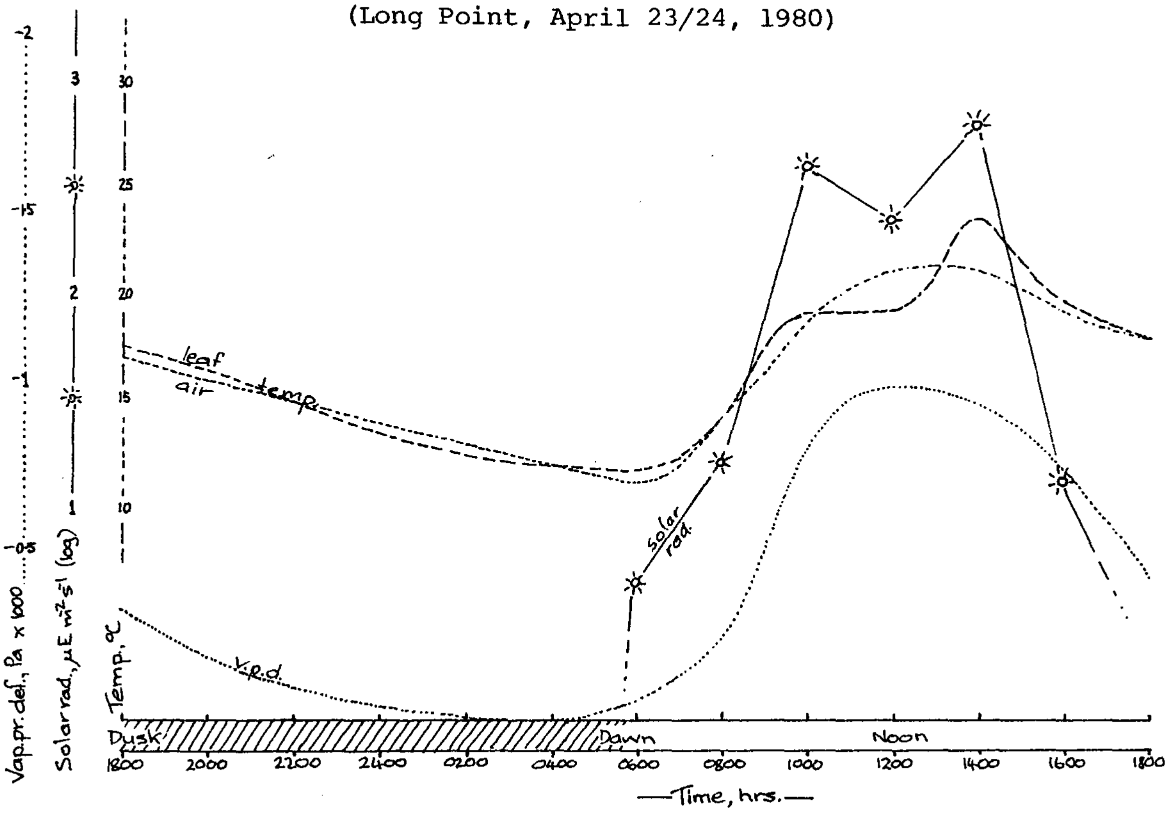


Graph 5.2.14 : Physiological factors related to CAM in

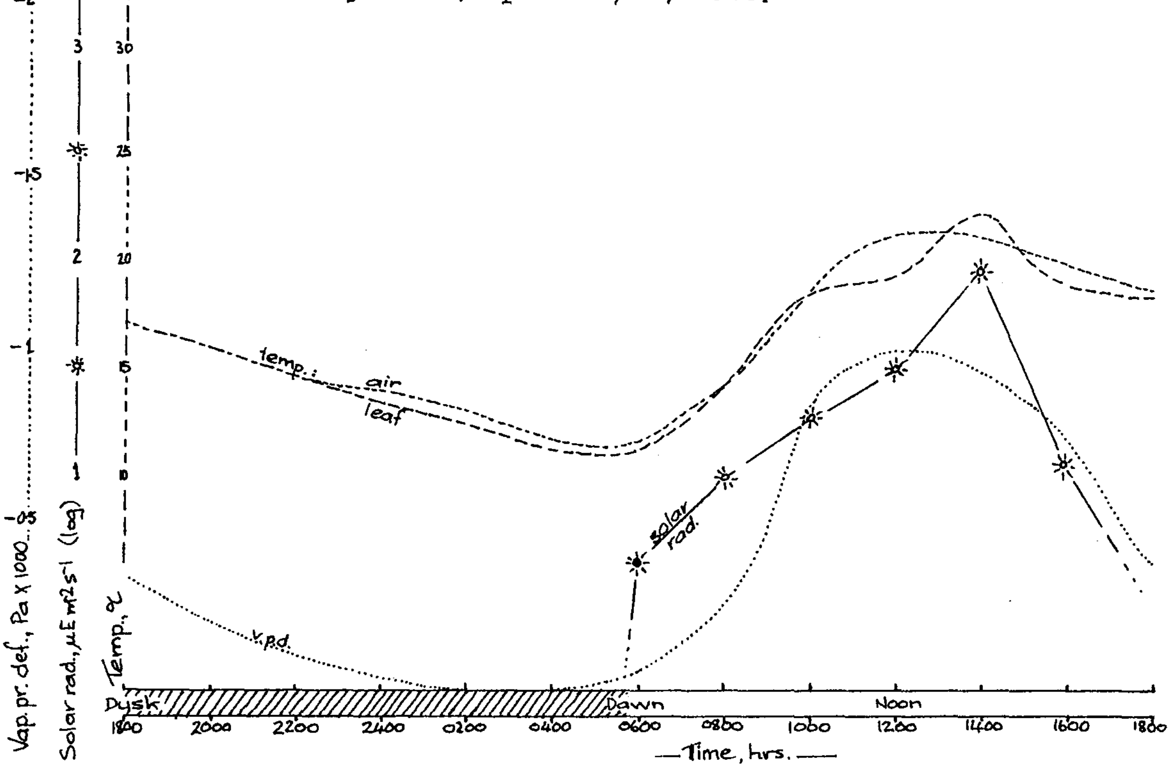
Dendrobium speciosum : tree shade plant, autumn



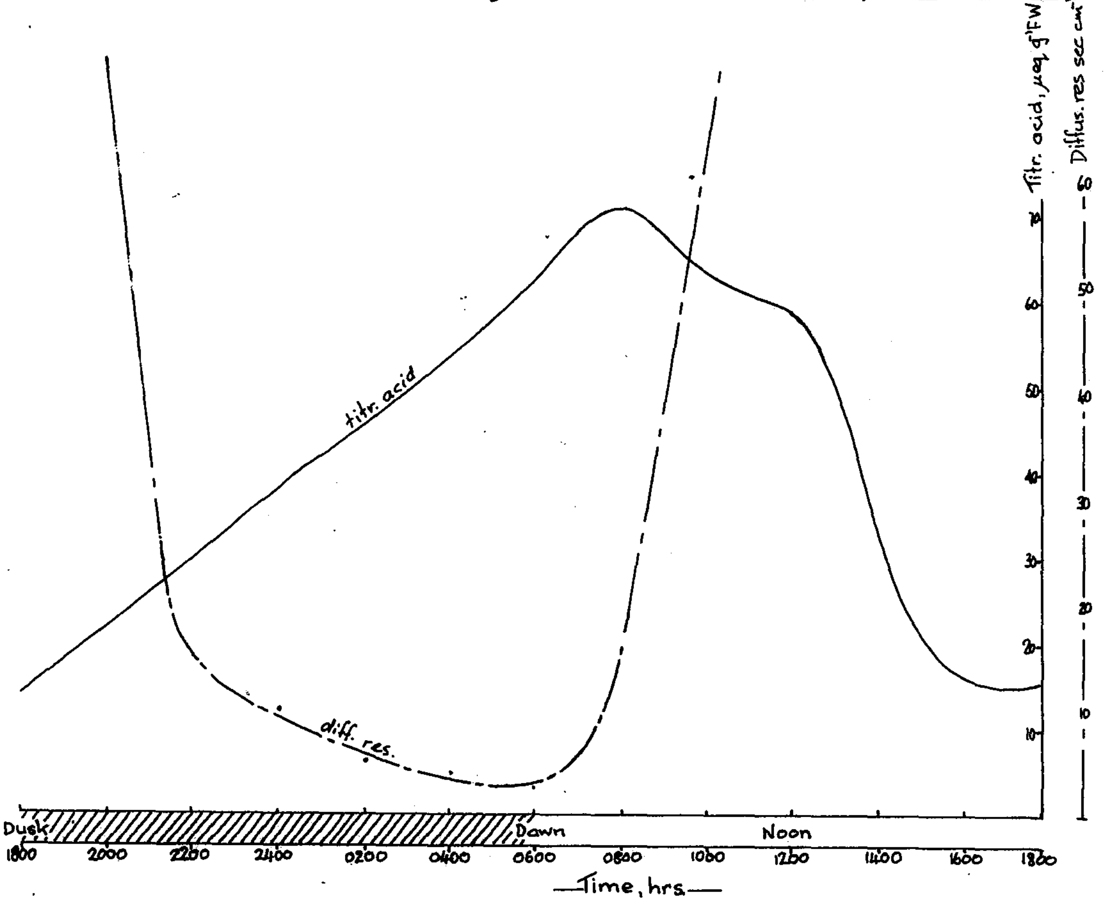
Graph 5.2.13: Ecological factors related to CAM in
Dendrobium speciosum : tree sun plant, autumn
(Long Point, April 23/24, 1980)



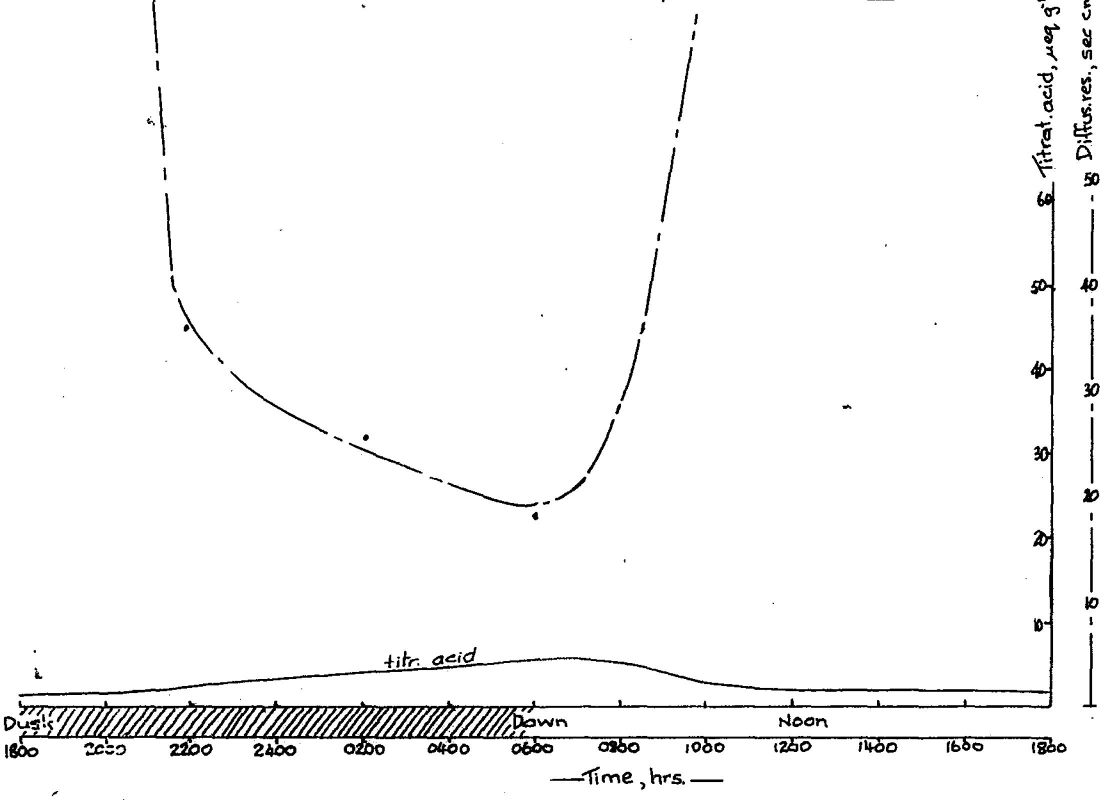
Graph 5.2.14 : Ecological factors related to CAM in
Dendrobium speciosum : tree shade plant, autumn
(Long Point, April 23/24, 1980)



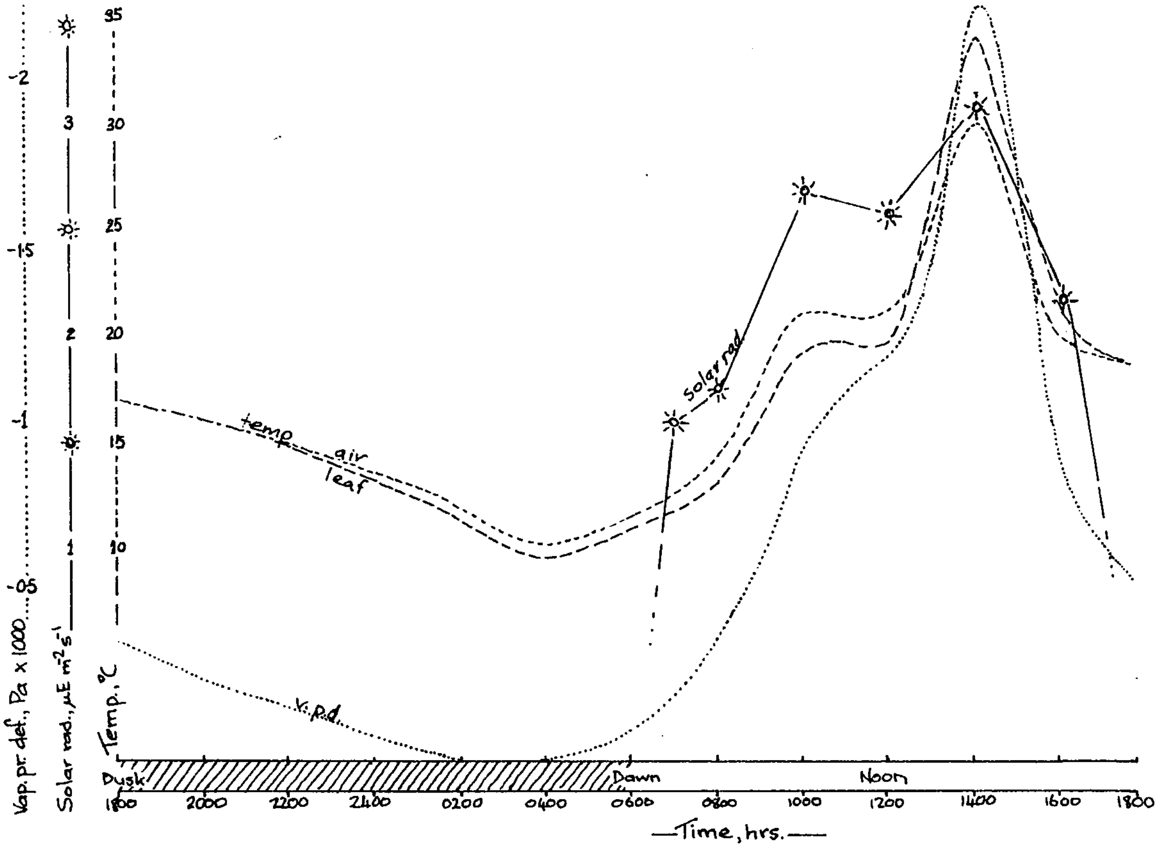
Graph 5.2.15 : Physiological factors related to CAM in *Dendrobium speciosum* : rock plant, autumn



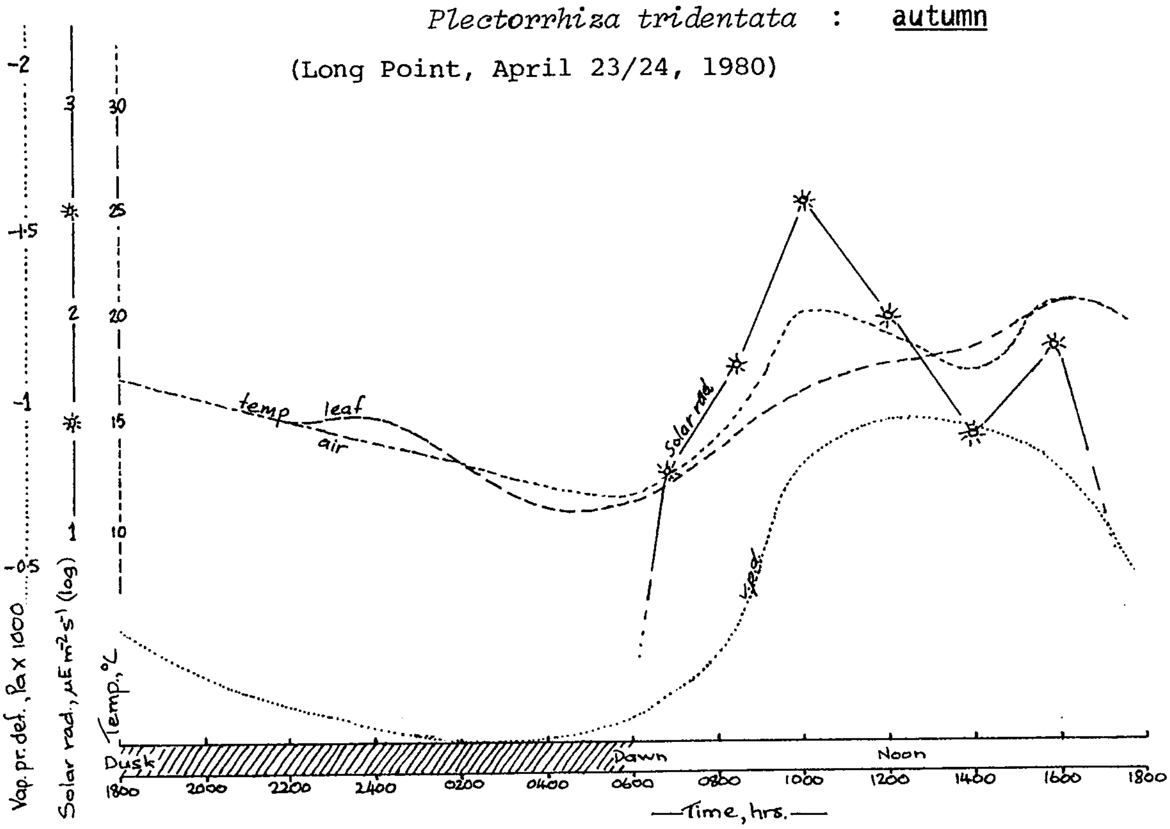
Graph 5.2.16 : Physiological factors related to CAM in *Plectorrhiza tridentata* : autumn



Graph 5.2.15 : Ecological factors related to CAM in
Dendrobium speciosum : rock plant, autumn
(Long Point, April 23/24, 1980)



Graph 5.2.16 : Ecological factors related to CAM in
Plectorrhiza tridentata : autumn
(Long Point, April 23/24, 1980)



more typical of the species in the study area, on the upper trunk of a mature tree of the dominant *Backhousia sciadophora*. They were subject to the shading of the 'normal' DRf canopy, but the shade plant side, because of the angle of the sun's rays, even in summer, was shaded by the trunk for a significant part of the day (graphs 5.2.2, 6, 10 & 14 as compared with 5.2.1, 5, 9, & 13 give an indication of this). The typical microhabitat of *P. tridentata* is among twigs of the DRf canopy or margin - here, foliage affords shade that is lighter and more irregular than for *D. speciosum* and will receive stronger sunlight generally, as indicated on graphs 5.2.4, 8, 12, & 16 as compared with the above ones.

Summer/winter differences between irradiance levels are not as great as may be expected and this is partly due to the occurrence of a rainstorm on the day of the summer measurements; even so, levels are slightly higher and the "areas beneath the curves" are greater in summer.

b) **Air temperature.** These did not differ markedly between the three test plants in the DRf but were more extreme at the rock plant. Generally, changes in air temperature were gradual, but with one notable exception. This was the change brought about by the early afternoon summer rainstorm mentioned above which lowered air temperatures by about 10-15°C within a half hour (Graphs 5.2.9-12).

Summer/winter differences in air temperature were quite marked in all cases with differences in both maximums and minimums ranging between ca 10° and 15°C.

c) **Humidity** values were recorded but not graphed, rather, **vapour pressure deficit** (v.p.d.) values were derived from these and used as a better indicator of the evaporating power of the air. V.p.d. values, though negative, were graphed on the positive side of the abscissa for convenience of comparison.

Air evaporative power decreased during the night with decreasing temperature, and increasing humidity, to zero at 100% relative humidity. With increasing temperature and decreasing humidity during the day, it increased, but disproportionately so with the higher temperatures of summer. The rock plant was subjected to noticeably stronger v.p.ds. than the others in all but winter, while the *P. tridentata* microhabitat had slightly stronger v.p.d. values than that of the tree plants in summer and spring.

2) Physiological factors

d) **Leaf surface temperatures** generally were within one °C of air temperatures and the only significant deviation was during the hotter part of the day when leaf temperatures rose to 2° - 6°C above that of the air; this held in all cases. The divergence usually began within two hours after dawn and gradually increased to a maximum between noon and 1400 hrs and then gradually decreased to convergence with an hour or so of dusk.

e) **Leaf undersurface diffusive resistance** in all cases, dropped steeply around dusk and remained low until 1-2 hours after dawn, then rose steeply again and remained at levels > 80 sec cm^{-1} until dusk. Notable variations on this basic pattern include,

i. in many cases the initial steep drop changed to more gradual, with the lowest point being at, or an hour or so before dawn. This is so to a marked extent in *Plectorrhiza*, winter, spring (graphs 5.2.4, 8) and *D. speciosum* rock plant winter and autumn (graphs 5.2.4 and 15) and to a lesser extent in others.

ii. there was considerable variation in the base level to which resistance dropped; mostly it reached around 10 sec cm^{-1} but in some cases, e.g. *D. speciosum* tree plants in winter (graphs 5.2.1 & 2), did not reach 20 before climbing again.

f) **Leaf acidity.** In all cases, leaf acidity increased during the night, reaching a peak about two hours after dawn, after which it declined to a base level, usually by about 2-4 hours before dusk. Variation occurred in these ways:

i. absolute levels - in the *D. speciosum* tree plants, peak levels ranged between 57 and 66 μeq g^{-1}FW in the sun plant, excepting in summer which was 50; the shade plant ranged between 29 and 34 μeq g^{-1}FW except the winter which was up to 46; the rock plant figures fell into two groups - autumn and spring with high values - 71, 72 μeq g^{-1}FW and winter and summer with the low values of 38 and 34 resp. *Plectorrhiza* also showed two markedly different groupings, autumn and winter with 5 and 10 μeq g^{-1}FW and spring and summer of 32 and 46 resp.

ii. six of the leaf acidity curves show a steepening of rate during the two to three hours prior to reaching the maximum level: *D. speciosum* tree sun plant in winter, spring and summer, rock plant in winter and spring and tree shade plant in winter and in a minor way in spring; also less distinctly so in *Plectorrhiza* in winter, summer and spring.

5.2.5 : Discussion

From sunrise the *Dendrobium* leaf temperatures begin rising, along with that of the air but because transpiration ceases in the early morning, so does its cooling effect and the leaf will tend to heat more than the air. Coutinho (1969) noted a similar effect in *Epidendrum ellipticum*. This will be influenced by the large leaf size, its broad, laminate shape and its thickness (most leaves are at least 8 x 20 x 0.15-0.3 cm), owing to heat pickup, conductivity and loss factors and considerations of the boundary layer. Air/leaf temperature differences decrease in the late afternoon because the general radiation/reradiation balance will tip that way, and also, air movement often tend to be greater then. Differences between air and leaf temperature during the night, according to the results obtained, were minor and fluctuating; cooling via transpiration will operate but be decreased because of lower heat status of the leaf. From the results the only detectable differences in behaviour of the tree shade plant when compared with the tree sun plant was that leaf temperature tended to be slightly lower than in the sun plant in the later afternoon, probably as a result of receiving less solar input because of its greater shade.

The thermal regime of the rock plant however, was somewhat different, owing to its closeness to the ground and the paucity of shading. Thus the plant was subjected to greater and more rapid changes in heat status. During the afternoon the rock plant experienced direct irradiation so that leaf temperatures rose 4-5°C above those of the air (except in winter). Stomates apparently remained closed under these conditions (leaf surface temps. of up to 40°C), as indicated by leaf diffusive resistance results and the apparent lack of cooling. It also appears that under even greater heat stress than this, stomates may still remain closed as some leaves had rounded necrotic patches (Pl. 5.2.4) on surfaces that were at about right angles to the suns rays of early to mid afternoon. These were interpreted as 'burnt' areas where heat buildup became critical during the hottest summer weather. Thus, the thermal characteristics and cooling mechanisms of the leaves of this species do not appear to be well adapted to such a micrhabitat.

After the summer rainstorm (indicated on graph 5.2.11) diffusive resistance of the rock plant leaves dropped 2-3 hours earlier than on other days i.e., well after the storm, and the leaf temperature also dropped, from 3-5°C above that of the air (39.5°C, 36°C resp.) to 1.5°C below it. This was interpreted as a transpirational cooling effect.

Temperature regimes of air and leaf of *Plectorrhiza* showed no major variation from those of the *D. speciosum* tree plants.

Vpd was used as an indication of air evaporative power (& thus plant water loss potential) rather than RH as it more accurately takes into account the effect of heat in gas systems, especially at higher temperatures where gas thermodynamics become increasingly critical in evaporative power. Vpd's at the two *Dendrobium* tree plants were very similar because air temperatures differed little and humidity percentages were alike. Humidity values at the *Plectorrhiza* microsite were also close to these, but air temperatures , and thus vpd's , were often a little higher . Both lower relative humidities and higher temperatures at the rock plant gave rise to extreme vpd's there during the heat of the day in the three warmer seasons, but at the same time, the greater degree of exposure led to faster re-radiation of heat at night, such that night vpd's , though still stronger than in the rainforest microhabitats, were very weak in intensity.

Diffusive resistance was taken to be indicative of stomatal aperture as well as transpiration rate (see van Bavel et al., 1965, and Kanemasu et al., 1969, for discussion re the porometer and its application). The stomatal behaviour of the four study plants, as indicated by the course of diffusive resistance values obtained, was typical of the patterns of CAM plants generally, as also were the leaf acidity fluctuations.

The stomates began to open at about dusk and were moderately open by about two hours later; concomitantly acidity began to increase as, presumably, CO_2 was taken in, carboxylated into malate and stored in the mesophyll vacuoles as malic acid.[3] The steepening of the acidity curve towards the maximum can possibly be interpreted as an increased rate of malic acid accumulation from increased CO_2 intake, in turn from the continued drop in diffusive resistance, to about sunrise as shown on many of the graphs in the results. Experiments by Lange et al. (1971) on stomatal responses to humidity in epidermal strips and subsequently confirmed by Schulze et al. (1972) on intact xerophytes in the Negev Desert, showed stomates tended to open in air of high humidity and close with low humidity. Also, Conde & Kramer (1975) found that low vpd could induce a decrease in diffusive resistance in *Opuntia*. Thus, in the orchids, it appears that humidity, or vpd may exert a secondary control on stomatal behaviour and function as a 'fine-tuning' effect on

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[3] In this study CO_2 flux was not measured, nor was the acid identity determined because the evidence supporting these assumptions is considerable; in the words of Kluge & Ting (1978, p.46), "It is now generally accepted that dark fixation of CO_2 is the key reaction in CAM. Virtually all experiments conducted to date substantiate the hypothesis that malate is the first and primary stable product of CO_2 fixation in CAM."

the plants capacity to conserve water supplies.[4] This would allow maximal stomatal aperture only when v.p.d. is minimal, tissue temperatures (and water-losing cell surfaces) are coolest and air movement is at its lowest. Related to this is the early decrease in diffusive resistance shown by all test plants after the rainstorm on the summer measurement day (See Graphs 5.2.9 to 12). Such mechanisms may also help explain the higher diffusive resistance curve base levels of the winter graphs - vpd's are stronger on these than in any other season. An additional factor here may be decreased plant water status - the weather of the preceding week was particularly dry as shown on the relevant thermohygrographs.

Both *P. tridentata* and *D. speciosum* rock plant showed considerable variation in leaf acidity levels from season to season. In the latter case, spring and autumn leaf acid maxima were high at 72 and 71 μeq g^{-1}FW resp., but much lower in winter and summer (38 and 34 resp.). This effect does not correlate with water supply since

a) the summer thermohygrograph shows that rain fell 2-3 days before the test run and

b) the rock plant had root access to the soil and therefore probably to a less ephemeral water supply than the epiphytic plants.

The best explanation of this phenomenon is that *D. speciosum* is not well adapted to a microhabitat such as the rock plant grows in, in regard to the effects of the high degree of exposure and its ramifications. In the seasons when conditions of heat flux and water relations are extreme, the photosynthetic and general physiological function of the plant would be inhibited and so also, specific functions such as carbon assimilation. By comparison, the tree plants, growing in the better buffered microhabitat within the DRf, show quite constant acid production levels. Summer extremes of temperature and vpd have been discussed. In winter, temperatures within the DRf have been recorded as low as -3.5°C (see Chap. 3, p. 83) and thus in a much more exposed microsite could be expected to be one or two degrees lower than this. Medina & Delgado established that the CAM plant *Echeveria columbiana* van Poellnitz was able to effectively assimilate CO_2 on

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[4] Primary stomatal control still appears to be from mesophyll CO_2 concentration. When all useable malate has been decarboxylated and the CO_2 thus produced used up in photosynthesis, stomates open in response to low intercellular CO_2 concentration and thus stay open while CO_2 carboxylation continues. Light intitiates malate decarboxylation, building up mesophyll CO_2 concentration such that stomates close (see, e.g., Meidner & Mansfield, 1968 or Raschke, 1976).

freezing nights in the high Andes, but this species is apparently specially adapted, being one of the few succulents of these areas. *D. speciosum* does not appear to be so adapted.

Another limiting factors on the rock plant in winter is the prevalence of dry, cold, westerly winds at this time. In localities on the more sheltered eastern side of the ridge on which the present study area is sited, *D. speciosum* grows well on rocks outside the gully DRf.

A biotic factor that impinges on the lighophytic habit of the species is the depredations of macropods - any of the plants that can be reached by these browsing marsupials will inevitably suffer considerable leaf damage.

The irregular leaf acid rhythum in *P. tridentata* from season to season requires a different explanation. The plants studied were growing in a microhabitat typical for the species and seasons when leaf acid content was low were autumn and winter (graphs 5.2.4 and 16) with acidity level maximums of 5 and 10 μeq g^{-1}FW as opposed to 32 and 46 for spring and summer respectively. Low water status from poor supply and limited storage capacity appear to be the limiting factors. Water storage capacity in *Plectorrhiza* is small - the leaves are from 0.75-1.5 mm thick and roots from 1.5-2.5 mm diameter. The week preceding the days of the autumn and winter assays when leaf acid was low, were dry - no rain fell and relative humidity reached 100% only briefly on one or two nights, indicating that no mists occurred either. Further, correlated with this low nocturnal humidity was relatively high leaf diffusive resistance on these measuring nights. Depression and enhancement of CAM in response to lowered and raised water status of the plant under natural field conditions has been reported in various desert terrestrial species, e.g., *Opuntia basilaris* Szarek et al., 1973; Szarek & Ting, 1974; Hanscomb & Ting, 1978), *Agave deserti* (Nobel, 1976) and *Ferrocactus acanthodes* (Nobel, 1977). Limited stomal opening and poor leaf acid buildup in *P. tridentata* under these conditions may indicate some degree of idling in this species, though perhaps not in the full sense of the term as used in the CAM literature. Further work is needed to clarify this.

The relevance of mists to *P. tridentata* , and in explaining the large population numbers of epiphytic orchids in the gorge country DRf as at

Long Point, should be considered. According to local residents (and also King, 1980), mists are considerably more common in the gorges than on the tablelands. The propensity of this species to form tangled masses of aerial roots (as shown in Plate 5.2.5) may be an adaptation to maximise interception of mist droplets as well as rain and throughfall drops.

5.2.6 : Conclusions

The major adaptive significance of CAM in *Dendrobium speciosum* and *Plectorrhiza tridentata* as perceived in their natural circumstances, lies in the contribution it makes to water conservation while maintaining favourable carbon balance in the plant. This comes from the ability to limit stomatal opening to periods of the diurnal cycle in which the evaporative power of the air is at a minimum.

The ecological implications relate to the advantage that the adaptation confers on these orchids in successfully exploiting their xeric epiphytic niches in the water-, heat- and cold-stressed DRf of Long Point. It is probable that CAM accounts for the ability of the *D. speciosum* rock plant to survive in its poorly buffered, heavily stressed microsite. This specimen does not flourish well and the conditions the species is best adapted to are probably nearer to those obtaining at the tree plant microsites, especially on the sunny side of the phorophyte trunk.

Plectorrhiza tridentata occupies a markedly different niche. It grows in a different microhabitat to *D. speciosum* and its use of water conservation mechanisms such as CAM is even more important since it has little water storage capacity and its microhabitat may be more stressful. However, it does appear to have some ability to continue photosynthesis at a reduced level when subjected to strong water stress. *D. speciosum* was not seen to have any such faculty, but whether it does or not, it has less need of it because of the water storage capacity of firstly, its litter nest and secondly its fleshy secondary stems.

Research needs into CAM in *Dendrobium speciosum* and *Plectorrhiza tridentata* arising from this study:

a) In relation to techniques used :

i. more concentrated readings generally at the critical times of dawn and dusk to improve definition of parameter behaviour.

ii. use of integration units in measuring at least air temperature, humidity, solar radiation, to more clearly establish microhabitat differences

iii. monitoring of ecological factors over longer periods to futher clarify the environment character.

b) Experimentation on the effect of vpd on stomatal behaviour.

c) Separate studies on both species into drought effects - especially in relation to idling.

5.3 Discussion on CAM in the Australian vascular epiphyte flora

Determination of $^{12}C/^{13}C$ ratios of plant carbon by mass spectrometry has become a widely used method of detecting carbon fixing pathway type (Osmond et al., 1973). This method is based on the difference in carbon isotope discriminating powers between the primary CO_2 fixing enzymes ribulose bisphosphate carboxylase (C_3 pathway), which discriminates more against the heavier isotopes than does phosphoenol pyruvate carboxylase of the C_4 pathway (Smith & Epstein, 1971; Bender, 1971); the method of calculation of the ratio is described in 5.1, footnote 1, p.159. CAM plants may fix atmospheric CO_2 entirely via PEPC or partially by RuBPC , depending on inherited characters and/or environmental influences (Osmond et al., 1973) and thus may have carbon isotope ratios through an intermediate range. $\delta^{13}C$ ratio has also been used to infer the seasonal origin of reproductive plant tissue (Mooney et al. 1977) and even palaeoecological conditions of the late Pleistocene epoch (Troughton et al., 1974), but the main interest here is in connection with ecological implications, particulary xericity of microhabitat.

In a survey carried out in 1978-79 of CAM plants in the Australian flora[5], it was found that only a few were terrestrial species and the great majority were epiphytes. In all, 127 of the 380 species of Australian epiphytes were tested (see Flora List, Chapter 2, pp. 27-45). Of these, 61 gave $\delta^{13}C$ values ranging from -10.5‰ to -19.1 ($\bar{X}$ = -15.2 ± 1.95) indicating high to moderately high levels of CAM activity. But for one species on -20.1‰ a gap of 1.6 separates the next group of six species with values between -20.7‰ and -22.2‰ ($\bar{X}$ = 21.3 ± 0.84), which indicates a lower level of (probably facultative) CAM activity. A short gap of 0.5 separates the rest (60 species) which range up to -34.0‰ and lack conspicuous grouping. Such values are taken to indicate typical C_3 photosynthetic CO_2 fixation with perhaps the least negative of these values indicating minimal CAM.

On the basis of phylogeny, three fern allies were tested and showed C_3 values as did 20 of the 22 ferns, though *Platycerium superbum* returned

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[5] $\delta^{13}C$ determinations were made by K. Winter and the staff of the Research School of Biol. Sciences, ANU; the present writer co-operated in the provision of plant material for this and is co-author of a paper on this subject, which is in the final stages of preparation and is expected to be published during 1982 in *Oecologia*.

a -22.8‰. The other two, *Pyrrosia longifolia* and *P. dielsii* gave results indicating middle order CAM activity. *P. confluens* leaf acidity data (Winter, pers comm.) also indicates CAM in this species, which is closely allied to *P. dielsii*; on the other hand, *P. rupestris* gave a marginal -23.9‰. The result for *P. longifolia* agrees with photosynthetic and respiratory data indicating CAM, obtained for the species by Wong & Hew (1976).

Of 19 dicot epiphytes tested, eight gave values indicating significant CAM activity; all of these species are herbaceous or only slightly woody. In asclepiads of two genera, *Dischidia* (3 species) and *Hoya* (3 species) values indicated moderately strong CAM; the other two were rubiaceous antplants - one species each of *Hydnophytum* and *Myrmecodia*, which returned values indicating a lower degree of CAM. The herbs *Boea* (Gesneriaceae) and *Peperomia* (Piperaceae) gave typical C_3 results as did all of the woody dicots, i.e. *Schefflera, Ficus, Fagraea, Procris* and *Agapetes* - these are all ± hemi-epiphytic.

Two non-orchid monocots were tested - *Pothos longipes* and *Rhaphidophora pachyphylla* - both were typical C_3 plants.

Eighty seven epiphytic and lithophytic orchids were tested (as well as 5 terrestrial species - which all gave typical C_3 results): 53 gave values of pronounced to moderately strong CAM, two in the marginal category and the rest gave C_3 values, but more or less evenly graded from -23‰ to -34‰.

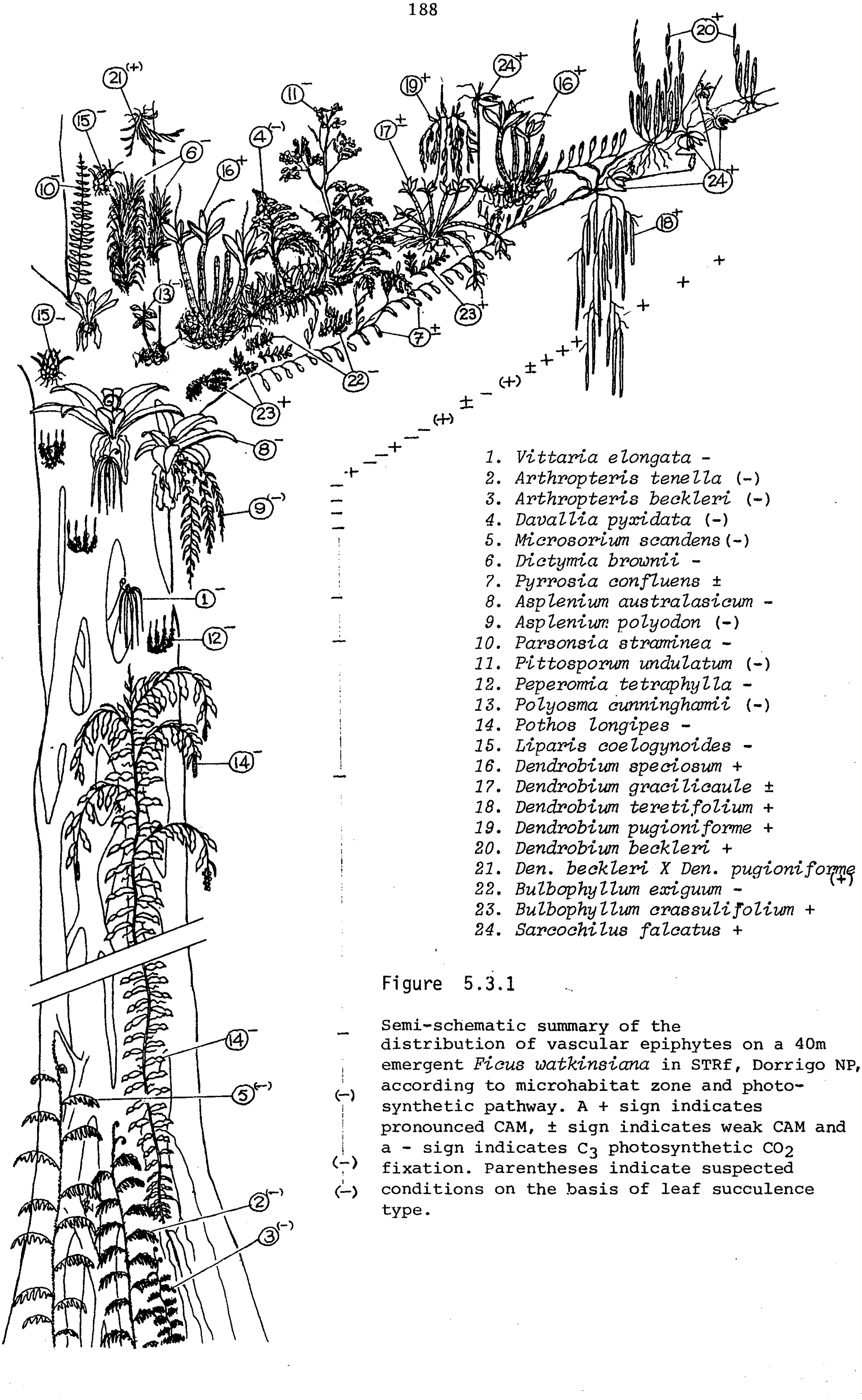
The ferns and fern allies are generally regarded as being phylogenetically and chronologically old and as not having changed greatly, at least morphologically, for a long time. Assuming that CAM is a modification from, or addition to, the typical C_3 pathway and therefore a more recent development and advancement, it is not unreasonable to suggest that in the pteridophytes, physiological evolution has also stagnated and that the above data reflect this. It is certainly true that ferns occupy lower and more sheltered epiphyte microhabitats generally (see Flora List, Ch. 2, pp. 27 - 45) and that those few that possess CAM (*Pyrrosia* species) occupy the most exposed and xeric microhabitats of all ferns. Notably, *P. rupestris*, which yielded a $\delta^{13}C$ value of -23.9‰ occupies less exposed microhabitat and flourishes best in cooler, moister communities generally than does *P. confluens*, a CAM plant.

Among the dicots, *Hoya* species are facultative terrestrial/lithophytic/epiphytic and are ecologically wide, growing in lower to upper zones of exposure; their eight readings averaged -17.6 ± 1.3. The species of the closely allied genus *Dischidia* are strictly epiphytic, inhabiting mid to upper zones of exposure and are more succulent than *Hoya*; five determinations averaged -16.6 ± 1.3. The tuberous antplants *Hydnophytum formicarium* and *Myrmecodia beccarii* both occupy mid to upper zones of moister rainforest, monsoonal and swamp forest, have good water storage capacity and thickly leathery leaves. From two values each the mean was -22.0 ± 1.1 which may indicate facultative CAM/C_3; this is consistent with their ecological syndrome. The Australian species of *Peperomia* are lithophytes and epiphytes of low, sheltered zones and have moderate to considerable water storage capacity in their colourless leaf hypodermis as is typical of this genus. Their $\delta^{13}C$ values indicate typical C_3 CO_2 assimilation - the mean of six values from three species was-29.1 ± 1.3. The gesneriad *Boea* is a lithophyte growing in moderately well sheltered positions, has herbaceous, hairy leaves and has some resurrection ability. Its $\delta^{13}C$ values of -30.4 and -34.0 are typical of C_3. The woody dicot epiphytes all have typical C_3 values and are all hemi-epiphytes, thus, the possibility of their seedlings possessing CAM ability should be investigated.

The two species of non-orchid monocots included here are semi-epiphytic climbers or hemi-epiphytes and as such usually have connection with the ground. As well as this, they are restricted to well watered, humid rainforest and grow up to ca mid zones, thus, predictably they yielded typical C_3 values. Again, the possibility of CAM in epiphytic seedlings should be investigated.

The $\delta^{13}C$ values obtained for the epiphytic orchids generally accord with the hypothesis that CAM species tend to occupy more exposed, xeric microhabitats than C_3 species. Figure 5.3.1. is a semi-schematised trunk/branch transect of an actual tree - visual perspective proportions and population numbers are not accurate but positions of the species in relation to one another and to the tree are as they occurred. The epiphytic vegetation of this phorophyte was one of the richest and most diverse encountered and the distribution shown illustrates the above point, as also, to some extent, do other transects figured in Chapter 3.

Of the 37 orchids with $\delta^{13}C$ values more negative than -22‰



1. *Vittaria elongata* -
2. *Arthropteris tenella* (-)
3. *Arthropteris beckleri* (-)
4. *Davallia pyxidata* (-)
5. *Microsorium scandens* (-)
6. *Dictymia brownii* -
7. *Pyrrosia confluens* ±
8. *Asplenium australasicum* -
9. *Asplenium polyodon* (-)
10. *Parsonsia straminea* -
11. *Pittosporum undulatum* (-)
12. *Peperomia tetraphylla* -
13. *Polyosma cunninghamii* (-)
14. *Pothos longipes* -
15. *Liparis coelogynoides* -
16. *Dendrobium speciosum* +
17. *Dendrobium gracilicaule* ±
18. *Dendrobium teretifolium* +
19. *Dendrobium pugioniforme* +
20. *Dendrobium beckleri* +
21. *Den. beckleri X Den. pugioniforme* (+)
22. *Bulbophyllum exiguum* -
23. *Bulbophyllum crassulifolium* +
24. *Sarcochilus falcatus* +

Figure 5.3.1

Semi-schematic summary of the distribution of vascular epiphytes on a 40m emergent *Ficus watkinsiana* in STRf, Dorrigo NP, according to microhabitat zone and photosynthetic pathway. A + sign indicates pronounced CAM, ± sign indicates weak CAM and a - sign indicates C_3 photosynthetic CO_2 fixation. Parentheses indicate suspected conditions on the basis of leaf succulence type.

indicating substantial C_3 assimilation, almost all inhabit middle level moderately exposed, or lower, more sheltered zones, or ameliorating factors apply.

C_3 species included in the survey that inhabit lower, sheltered microhabitats in wetter rainforest include *Dendrobium baileyi*, *D. cancroides*, *D. tetragonum*, *D. malbrownii*, *Dipodium pandanum*, *Liparis* spp., *Oxyanthera papuana* and *Rhynchophreatia micrantha*.

Another C_3 group can be differentiated inhabiting moderately sheltered to moderately exposed microhabitats of mid to mid-upper zones but have ameliorating water status related environmental factors such as inhabiting cooler, moister communities, - submontane mist forests, moist subtropical rainforests etc, e.g. *Bulbophyllum elisae*, *B. evasum*, *B. johnsonii*, *B. lilianae*, *B. nematopodum*, *Cadetia taylori*, *Dendrobium adae*, *D. agrostophyllum* *D. fleckeri*, *D. gracilicaule*, *D. monophyllum*, *D. ruppianum*, *Diplocaulobium glabrum*, *Eria eriaeoides*. Special cases include *Dendrobium smillieae* which has thin, facultatively deciduous leaves and *Cymbidium madidum* and *C. suave* which grow from hollow branches and knot holes in tree trunks and have access to greater and longer lasting water supplies in the tree's rotting core.

Of the orchids that gave $\delta^{13}C$ values indicating significant CAM, most can be shown to occupy niches that involve one or more particular difficulties related to water status.

Those with limited water storage capacity usually inhabit less exposed to moderately exposed microhabitats in more mesic communities such as the moister rainforest types - MVF, SEVF and NVF. They are mostly monopodial species of the subtribe Vandinae and include: *Phalaenopsis amabilis*, *Robequetia tierneyana*, *R. wassellii*, *Rhinerrhiza divitiflora*, *Sarcochilus moorei*, *S. falcatus*, *Thrixspermum congestum*, *Trichoglottis australiensis*, *Pomatocalpa macphersonii*, *Taeniophyllum malianum*, *Chiloschista phyllorrhiza* and *Dendrobium luteocilium*.

Another group consists of species of similar communities to the above but inhabiting outer, more exposed zones. Species tested from this group are: *Dendrobium beckleri*, *D. linguiforme*, *D. lichenastrum*, *D. racemosum*, *D. teretifolium*, *D. wassellii*, *D. discolor*, *D. nindii*, *Ephemerantha convexa*, *Luisia teretifolia, Mobilabium hamatum, Plectorrhiza tridentata, Sarcochilus hillii, S. ceciliae, Trachoma rhopalorrhachis, Micropera fasciculata, Vanda whiteana.*

A third, smaller group of truly xerophilous species that grow in exposed microhabitats in open communities and are subjected to some of the most oppressive water regimes of any Australian epiphytes, includes: *Dendrobium canaliculatum, D. bigibbum, D. semifuscum, D. dicuphum, D. linguiforme* and *Cymbidium canaliculatum.*

The ranges of $\delta^{13}C$ values for these three groups suggest that the harsher the water regime as a result of all relevant factors, the more pronounced is CAM in the species. The mean and standard deviation of each was 15.2 ± 1.3 ("mesophytes"), 14.4 ± 1.1 (xerophytes), 13.8 ± 1.4 (extreme xerophytes, exc. *C. canaliculatum*). These results do not have a great deal of statistical significance or predictive value because of sample sizes, subjectivity in designating species to type of microhabitat, etc., but do indicate that a more extensive sampling and rigorous statistical treatment may produce significant support for such a hypothesis.

The consistent differences in $\delta^{13}C$ values between leaf and stem tissue in epiphytic orchids, deserve comment. Winter et al. tested separately both leaf and succulent stem tissue of 17 species and in 15, leaf values were more negative than those of the stems, the mean % difference being 8.6 ± 4.9. Thus it appears that carbon assimilated by the stem is fixed via CAM proportionately more than it is in the leaf. Considering that there may well be net movement of carbohydrate from leaf to stem, especially since the latter are succulent storage organs, such differences may not reflect their photosynthetic ability either quantitative or qualitative. However, that some orchid pseudobulbs effect significant photosynthesis, and this via CAM, is shown by the leafless *Bulbophyllum minutissimum* which yielded a $\delta^{13}C$ value of -17.0‰.

Several workers when studying photosynthetic and related physiology in specific taxonomic groups have found that type of CO_2 fixing pathway and degree of CAM activity correlated with both phylogeny within the group and with the ecology of the species concerned. McWilliams (1970), investigating rates of dark CO_2 uptake and acidification in the Bromeliaceae, Orchidaceae and Euphorbiaceae, first came to this conclusion and showed that the successful radiation of these families into xeric environments depended on CAM as well as a complex of other xeromorphic characters. The findings of Neales and Hew (1975) regarding orchids they investigated, are in general agreement with these. Medina and coworkers (Medina, 1974; Medina & Troughton, 1974; Medina et al., 1977) found an association between CAM, leaf anatomy, ecology and phylogeny of bromeliad species and suggested evolutionary trends within the group on the basis, that the species of more stressful environments had less negative $\delta^{13}C$ values and greater CAM involvement, thicker leaves etc and belonged to more advanced groups taxonomically.

The results of this survey support the above findings when considering the epiphytes as a group - regarding, a) the more "primitive" vascular plants lacking CAM and being ecologically restricted to more mesic environments and , b) CAM species being in phylogenetically more advanced groups and being able to exploit the better illuminated, though more xeric, epiphytic microhabitats. The $\delta^{13}C$ values obtained in the survey also indicate that more strongly xerophilous species have a greater CAM involvement in CO_2 fixation than relatively mesophilous species (Winter et al. in prep.).

CAM is thus an important character in the drought resistance syndrome of xerophytes, functioning as a control mechanism on water loss by transpiration. The more extreme the xerophytism , the greater the likelihood that CAM will be associated with other adaptations that effect improvement of plant water status. Perhaps the toughest, most xerophilous epiphyte in the Australian flora, *Dendrobium canaliculatum* R. Br., is a fine example here. This orchid grows on the branches of open-crowned *Melaleuca* species in open tropical monsoon savannah woodland, where the annual dry season may be as long as eight months, during which time precipitation may be negligible and maximum air temperatures of 40°C common. It has the least negative $\delta^{13}C$ values for the survey, -13.1‰ for leaf tissue and -10.5‰ for pseudobulb, indicating pronouced CAM; the leaves are semi-terete and succulent and deciduous under extreme conditions; the pseudobulbs are very thick and succulent and thus store considerable water.

Ecological factors under which CAM functions most effectively and where its conferred advantages will be of maximum benefit, are presumably those which will predispose plants to the evolution of CAM ability. These factors include,

a) the most influential, that of limiting environmental water status, which in epiphyte ecology, in spite of relatively high water input per time, occurs as a result of poor substrate retentive powers coupled with ± strongly evaporative atmospheric conditions. This gives rise to persistently recurring, at least moderately intense substrate deficits which impose evolutionary selection pressure for rapid uptake ability and storage capacity as well as for economical usage as provided by CAM,

b) at least moderately strong light intensities are required to effect the CAM mechanism and drive the photosynthetic systems of epiphytes with leaves specially adapted to water stress - e.g. in the aerial Tillandsioideae with a dense covering of absorptive trichomes and many orchids with succulent, centric leaves,

c) lack of strong competition for light is important since growth rates associated with CAM are slow,

d) Relatively large fluctuation in diurnal temperature range heightens CAM action - data presented in Chapter 4 show that this effect increases with microhabitat exposure,

e) nights of moderately low temperatures appear necessary for the efficient action of CAM enzymes; increased exposure will tend to provide this condition as well as,

f) higher humidity and lower v.p.d. at night, which is crucial in the water saving effect of CAM,

These factors all obtain in epiphyte microhabitats and more so in those towards the outer, more exposed zones. Therefore many epiphytes have evolved CAM and these increase in diversity and their degree of CAM involvement with increased microhabitat exposure.

A fundamental implication then, from the works of others as reviewed in 5.1, from the experimental work outlined and discussed in 5.2 and from the results of Winter's survey, as well as evidence from Chapter 3 on epiphyte synecology, and Chapter 4 on epiphytic microhabitats is that the epiphytic life-form/biotope is a major area of CAM development and evolution. Further, acceptance of CAM as an important drought-resisting adaptation gives strong implicit support for the concept of xericity of epiphyte microhabitat and of its intensification with increased exposure and, in turn, for the importance of light as a selection pressure in the evolution of epiphytes.

GENERAL CONCLUSIONS

The vascular epiphyte flora of Australia is diverse and comprises 380 species, yet is impoverished when compared with those of other continents of comparable latitude. This appears to be the result of past and present widespread aridity in Australia.

The orchids and pteridophytes have approximately equal representation and together make up ca 80% of the total. The others, mainly dicotyledons, are diverse taxonomically as well as in their physiognomic types and life forms, disseminule types and dispersal methods. This group includes seven species of antplants from three genera and two different families.

The pteridophytes show a very low degree of endemism which may be connected with their apparent low capacity to adapt and speciate. This slowness to change is reflected in their ecology - the number of species that have been able to adapt to the higher, drier, lower fertility microhabitats is very small, especially when compared with the orchids. In this latter group much more rapid speciation is evident with consequent higher endemism including local radiations of up to 10 species, such as in the genus *Sarcochilus* R. Br. (s.s.). They also display adaptiveness towards coping with the higher, more water- and nutrient stressed microhabitats, e.g. the fleshy-leaved *Dendrobium* species.

Judging from phyletic relations and centres of diversity of taxonomic groups, the majority of Australian vascular epiphytes are derived from Malesia or have diversified from such taxa. This migration has taken place relatively recently in geological time, subsequent to the northward drift of the Australian tectonic plate and its collision with that of SE Asia. Palaeoecological conditions, sea levels and dry land connections with New Guinea and Indonesia have fluctuated since the collision. This has given rise to periods of more widespread mesic climates and vegetation, allowing for movement of taxa, alternating with drier climates and contraction of rainforests into disjunct patches and relicts which have served as refugia for dependent constituents. These same conditions probably promoted adaptation to harshness of environment as well as differentiation and speciation among epiphytes, particularly the orchids.

The selected vegetation study sites differed in floristics and synecology of both macrovegetation and the epiphytes. These differences are related to between-site variation in environmental factors, particularly mean annual rainfall, precipitation frequency, mist incidence and mean air temperature.

Light penetration, air movement, evaporative power and temperatures were important in producing the measured differences in light intensity, maximum and minimum air temperatures and air movement between Zone 1 at the tree butt and Zone 4 among the small branches of the canopy. The rainforest structural features which most influenced the occurrence and ecology of epiphytes in the study sites were number of vegetational layers, canopy height and density, and size and frequency of lightbreaks.

Epiphyte flora was richer in less stressed rainforests i.e., the wettest, most fertile, least temperature-extreme sites had the greatest diversity and number of vascular epiphyte species. This is probably because their greater macrovegetational complexity gives rise to a greater variety of microhabitats, as well as being climatically more equable. The complexity of the epiphytic vegetation in these systems was thus greater also, with stronger tendency to form microcommunities and greater diversity of life forms and physiognomic types.

Epiphyte population numbers in the study sites showed a different trend to that for floristic diversity - epiphyte numbers were greater in more stressed environments. One of the most water-, temperature- and nutrient-stressed sites had much greater numbers of epiphytes even though from much fewer species and this was related to extreme specialisation to these conditions, leading to a few-species dominance and a great proliferation of these species.

Interpretation of the occurrence and adaptive value of physiognomic types and life forms is difficult but correlations observed indicate that long-creeping or travelling, typical epiphytes may be better able to cope with water- and temperature-stressed situations, perhaps because their bulk is close to the substrate and they are able to grow into new microhabitat space, e.g., toward, or away from shading from canopy change. Tangle epiphytes were more common in mist-prone environments and their physiognomy is interpreted as a throughfall- and mist-trapping adaptation. Semi-epiphytic climbers are more common in forests with high MAR, probably because of their dependence on soil moisture.

Specific epiphyte-phorophyte relationships of high constancy appear to be rare in Australia. If any exist then much more extensive and detailed surveying will be required in order to demonstrate them decisively. This is also largely the case with true axeny of tree species; in some cases, e.g. *Eucalyptus* species, allelopathy does appear to be involved. This factor may be more important generally in epiphyte ecology, particularly in connection with mycorrhiza and germination, than has been realised.

On tree species that are favourable to epiphyte colonisation, pioneer species tend to be either humiphobic, 'independent' types or nest-formers. With increasing phorophyte age and consequent development of a greater range of microhabitats, later colonists tend to be more dependent, many being humiphilic and nest-invading types.

The greater the requirement of an epiphyte species for strong light,the more rigorously it will need to control its water economy as a result of the stronger atmospheric evaporative power which occurs in more exposed microsites. Perhaps the most severe water loss suffered by many plants is via transpiration through open stomates during the warmer, drier parts of the day. Thus, the physiological mechanism known as CAM which not only restricts stomatal opening to the dark hours of the daily cycle but also exerts a secondary control governed by air evaporative power, is a very effective and important device in the water economy of such epiphytes. This is demonstrated in the investigation of CAM in *Dendrobium speciosum* and *Plectorrhiza tridentata* in Chapter 5. CAM is common among the Australian epiphytes, particularly the heliophilous, xerophytic species and among these it shows a tendency for strongest activity in the ones inhabiting the most exposed microhabitats.

Epiphytes generally also have considerable problems in their nutrient economy and especially in the exposed, outer canopy microhabitats, nutrient availability is meagre owing to less opportunity for humus accumulation and for rainwater to pick up soluble minerals in throughfall and stemflow. One economising device found in *D. speciosum* and *P. tridentata* is a high rate of mineral withdrawal from old leaves, particularly N, P and K (see Appendix 3). The withdrawal rate is not as high in *Dendrobium speciosum* as in *Plectorrhiza tridentata* but the former also employs a second adaptation, i.e., a litter-collecting habit which enables a larger-scale interception of the mineral cycle. Mutually beneficial relationships with scavenging ants are used by some epiphytes - the ants have been likened to "extra roots" (Janzen, 1974) in scavenging nutrient rich detritus and returning it to the antplant.

Finally, evidence presented in this dissertation from surveys and investigations in Australian forest/epiphyte systems, supports the thesis that,

a) there is a gradation in environmental factors, particularly water availability and atmospheric evaporative power, from low level forest microsites which are cooler, moister and more humid and shaded, to the upper canopy, brighter, warmer, drier ones, and,

b) there is a range of epiphytic plant species that are adapted to tolerate a range of stress levels such as those imposed by environmental water (and nutrient) status and,

c) these plants characteristically occupy microhabitats appropriate to their stress tolerances and are photosynthetically adapted to light intensities which apply in these microhabitats;

d) the nearer to the upper canopy where stronger light is available, that an epiphyte grows, the better it will need to be adapted towards efficient uptake and usage of water and minerals and to tolerance of high stress levels related to these;

e) CAM is a very important adaptation in this connection and is particularly so to the heliophilous, xerophytic epiphytes;

f) epiphytism has been developed by small, slow growing plants as a means of evading competition for light by larger, more vigorous plants.

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APPENDIX 1 :

THE VASCULAR EPIPHYTE FLORA OF AUSTRALIA

- a descriptive, illustrated key : See separate volume.

APPENDIX 2 : pp. 211-220

a. Figs. (Graphs) 5.2.1 to 5.2.9 - graphs from CAM chapter.

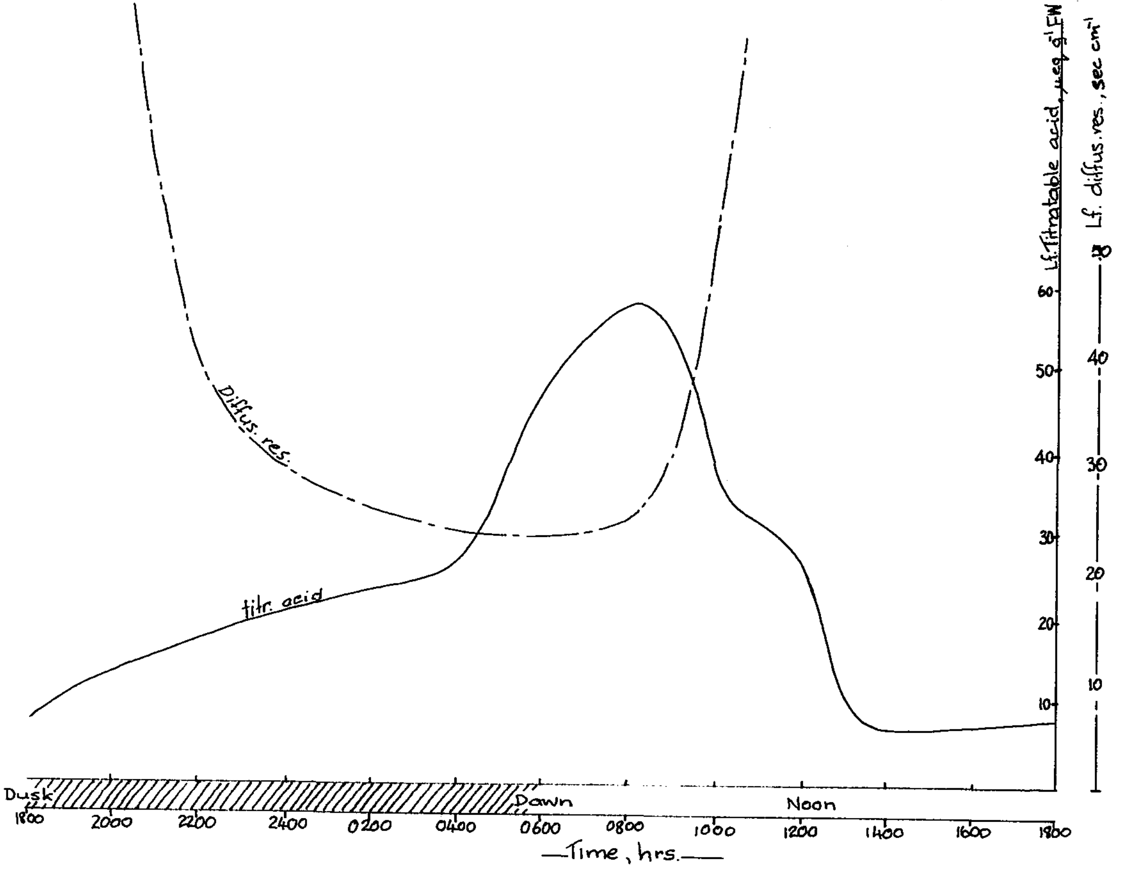
b. Tables 5.1 to 5.4 - data from which the graphs of the CAM chapter were derived.

c. Figs. (Thermohygrographs) 5.2.17 to 5.2.20 - thermohygrographs from Long Point from microsites of *Dendrobium speciosum* and *Plectorrhiza tridentata* specimens studied in CAM Chapter, 5.2.

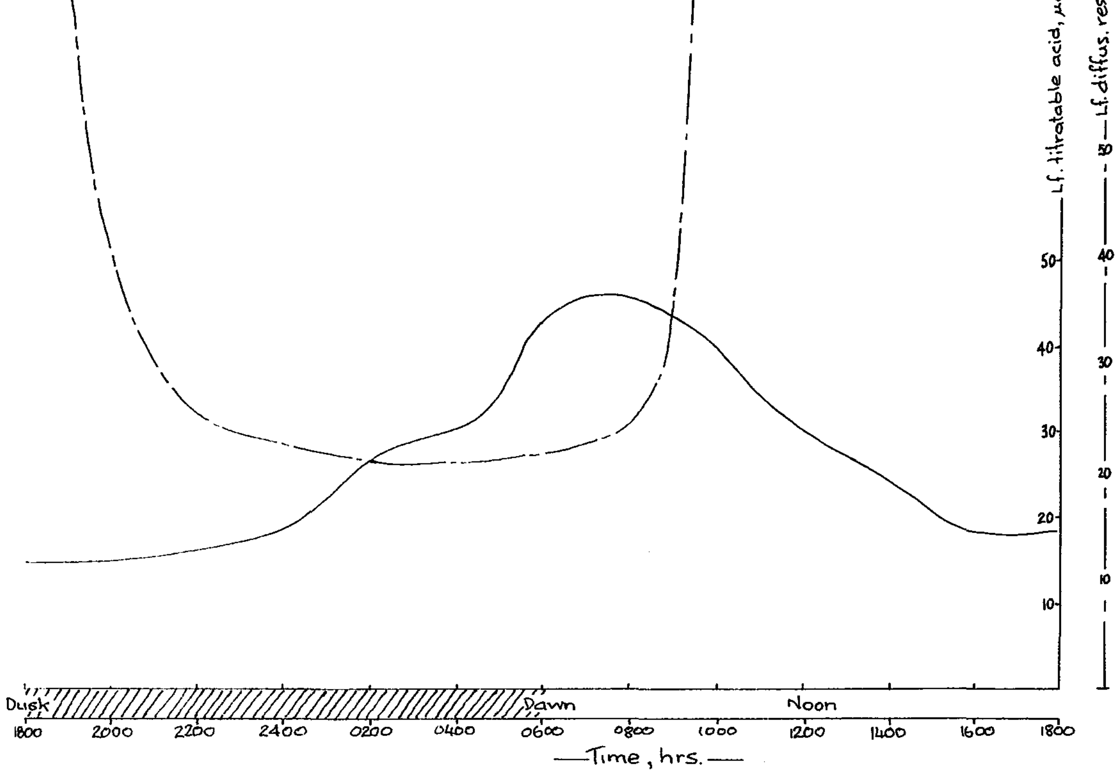
APPENDIX 3 : p. 225

Table 6.1 Some mineral analyses of *Dendrobium speciosum* and *Plectorrhiza tridentata*.

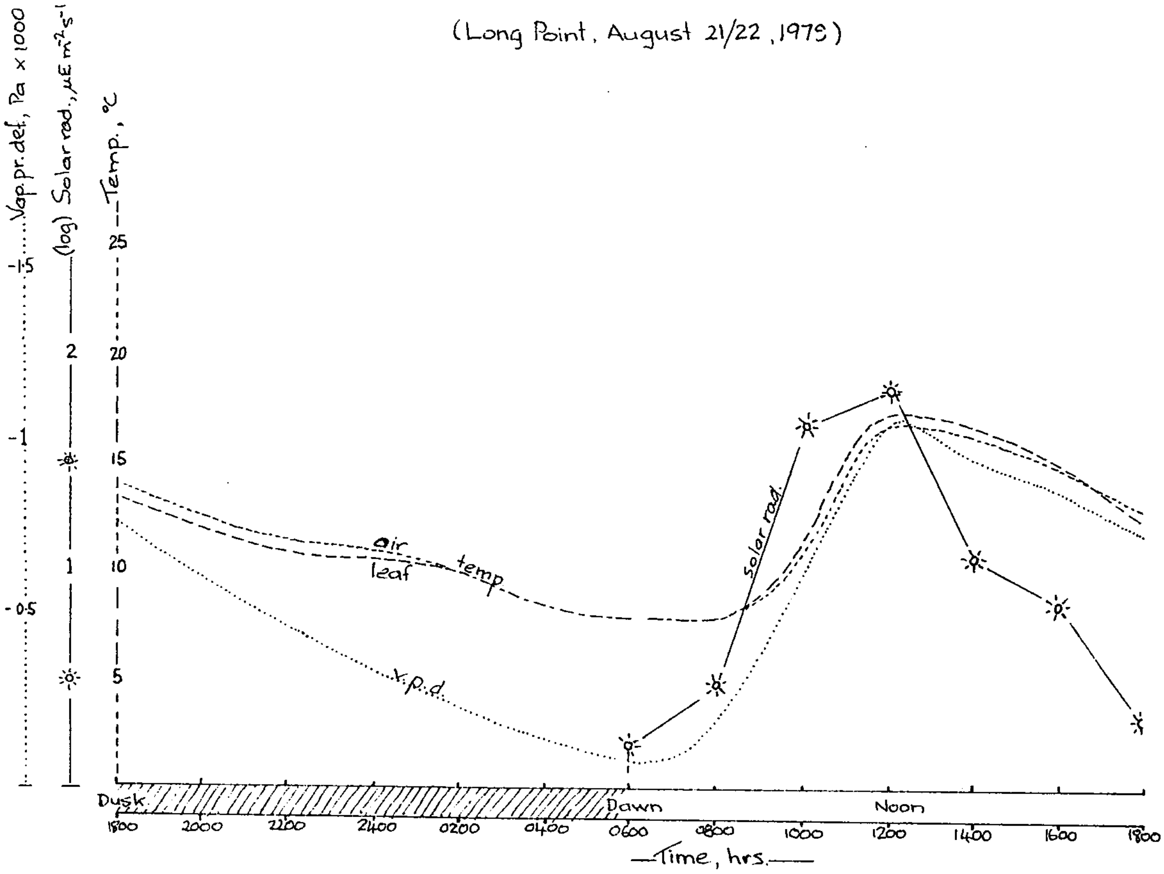
Graph 5.2.1 : Physiological factors related to CAM in *Dendrobium speciosum* : tree sun plant, winter



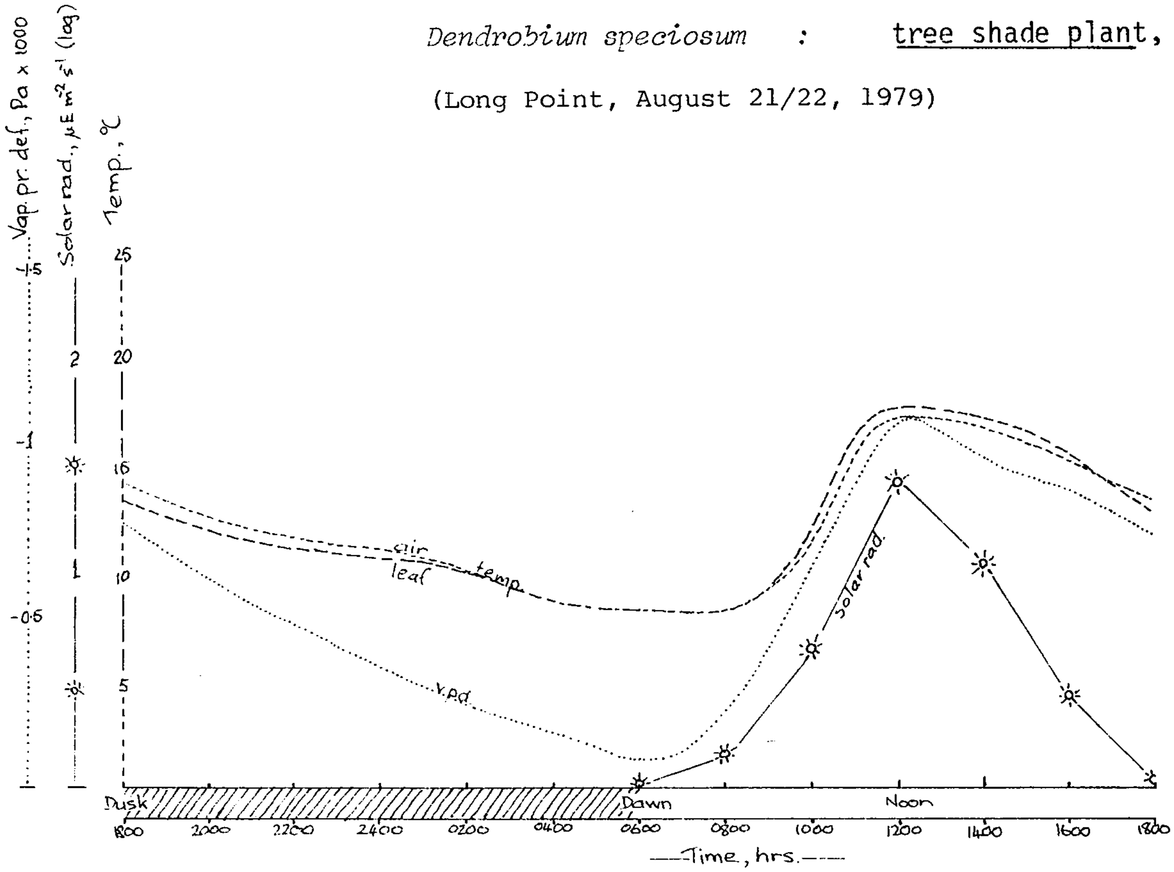
Graph 5.2.2 : Physiological factors related to CAM in *Dendrobium speciosum* tree shade plant, winter



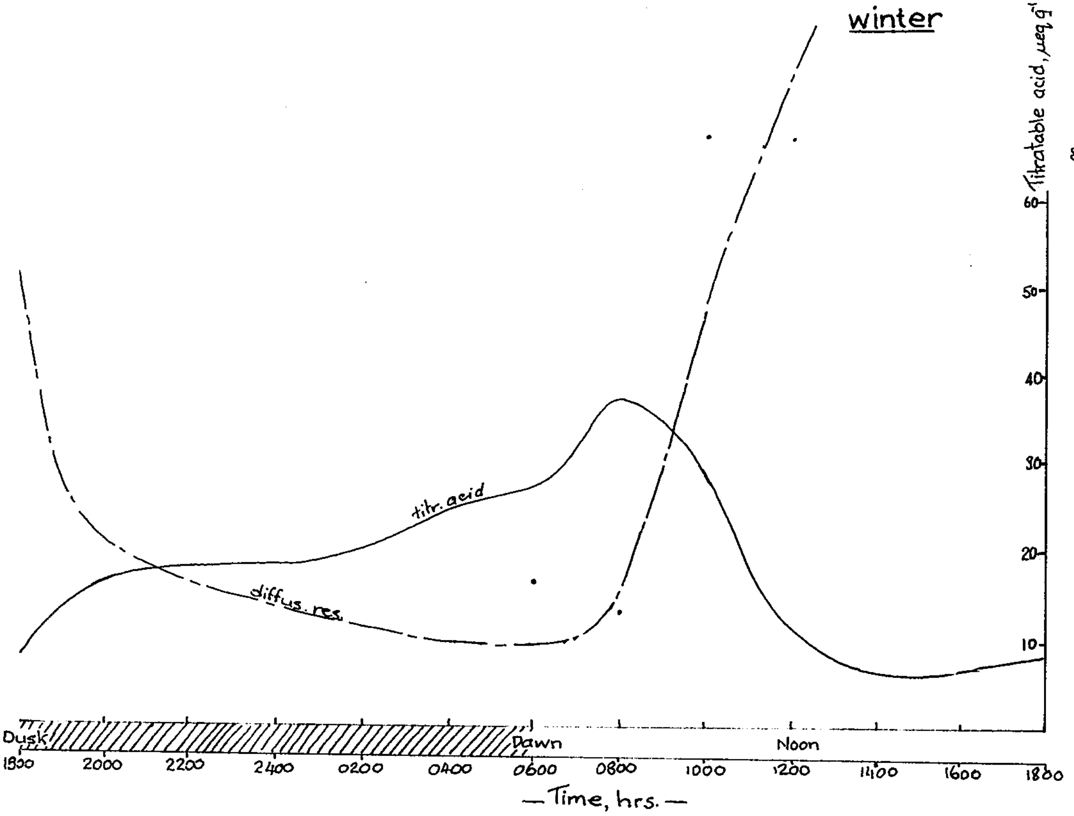
Graph 5.2.1 : Ecological factors related to CAM in
Dendrobium speciosum : tree sun plant, winter
(Long Point, August 21/22, 1979)



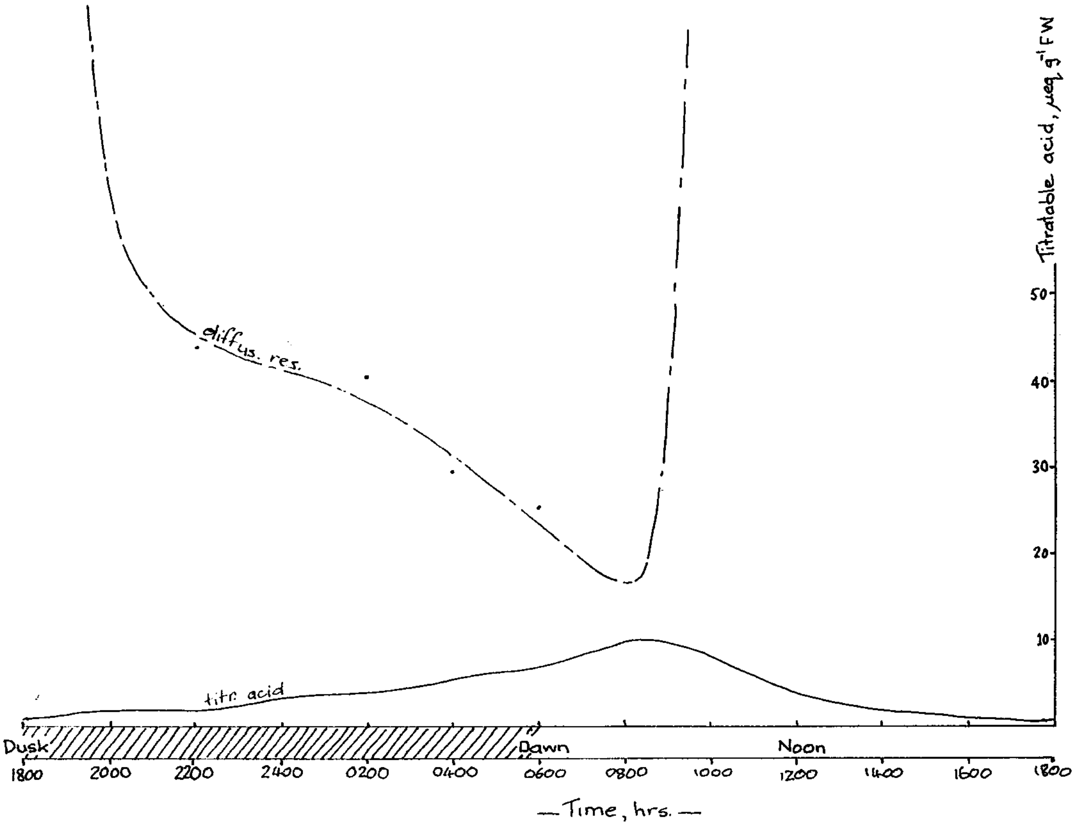
Graph 5.2.2 : Ecological factors related to CAM in
Dendrobium speciosum : tree shade plant, winter
(Long Point, August 21/22, 1979)



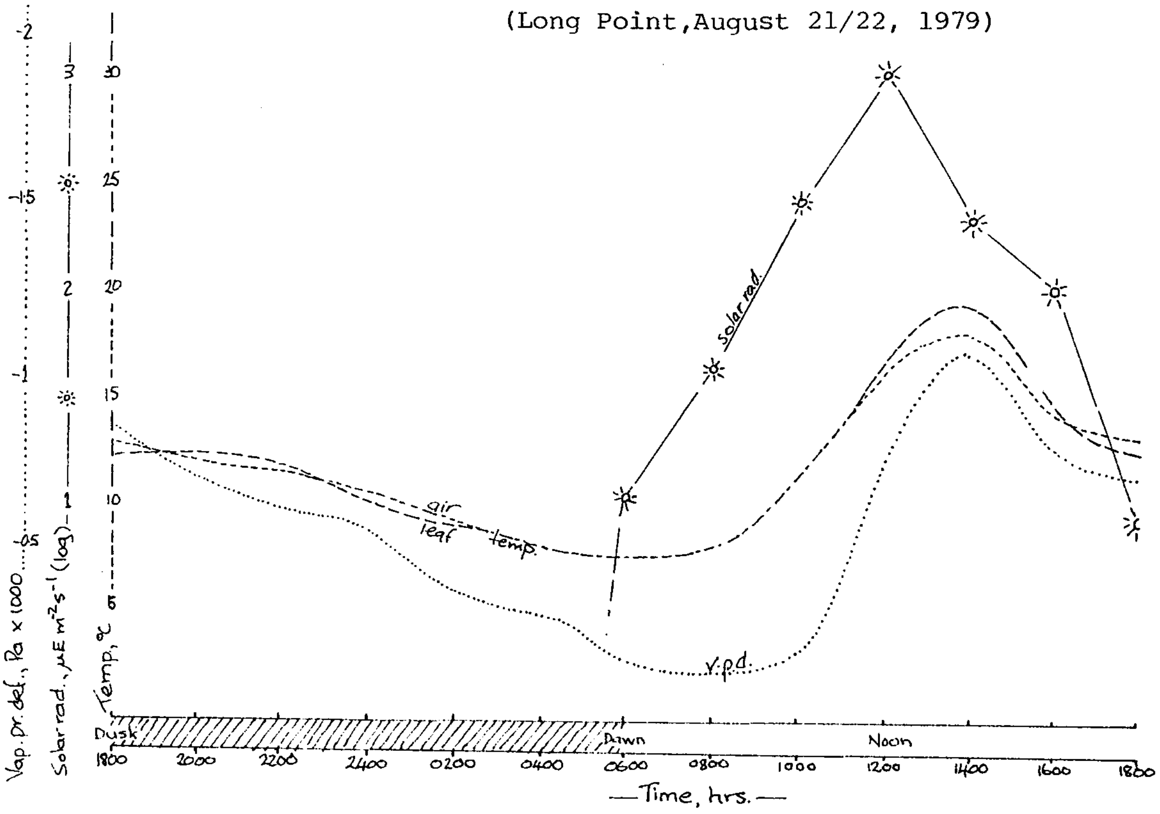
Graph 5.2.3 : Physiological factors related to CAM in *Dendrobium speciosum* : rock plant, winter



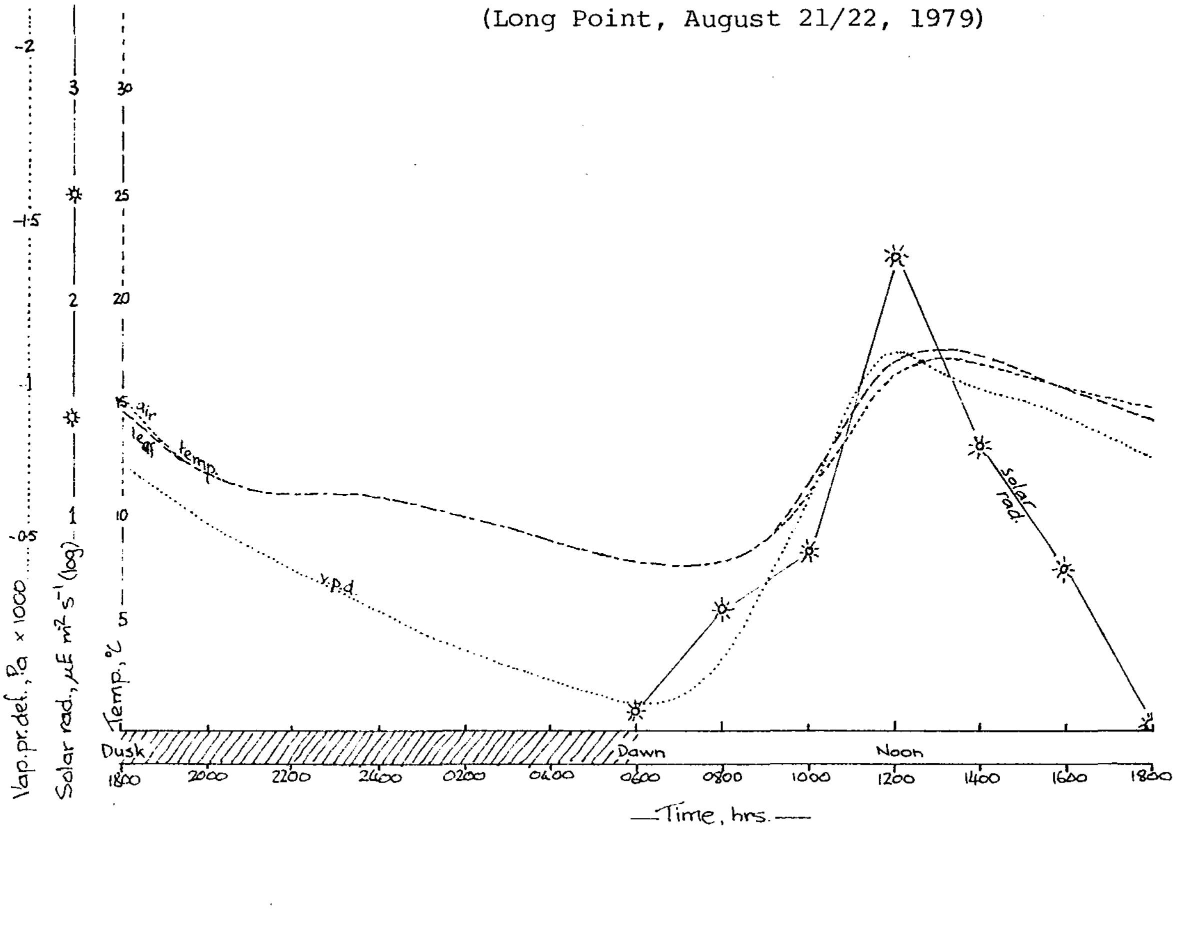
Graph 5.2.4 : Physiological factors related to CAM in *Plectorrhiza tridentata* : winter



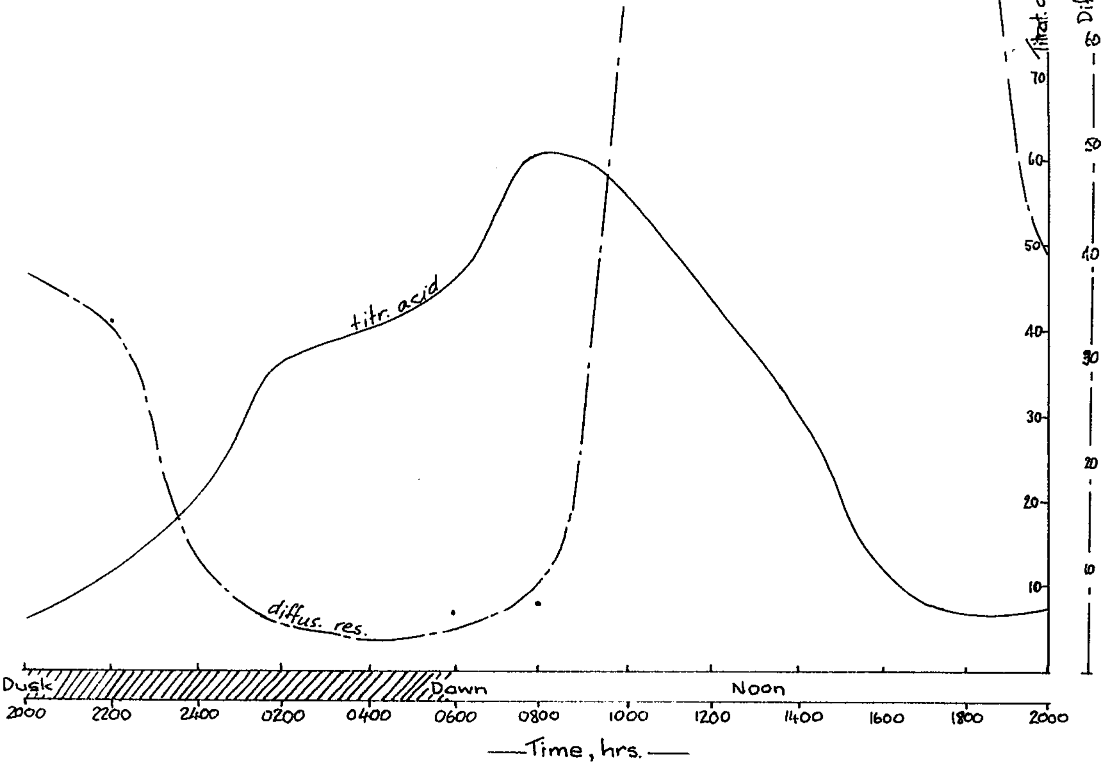
Graph 5.2.3 : Ecological factors related to CAM in *Dendrobium speciosum* : rock plant, winter
(Long Point, August 21/22, 1979)



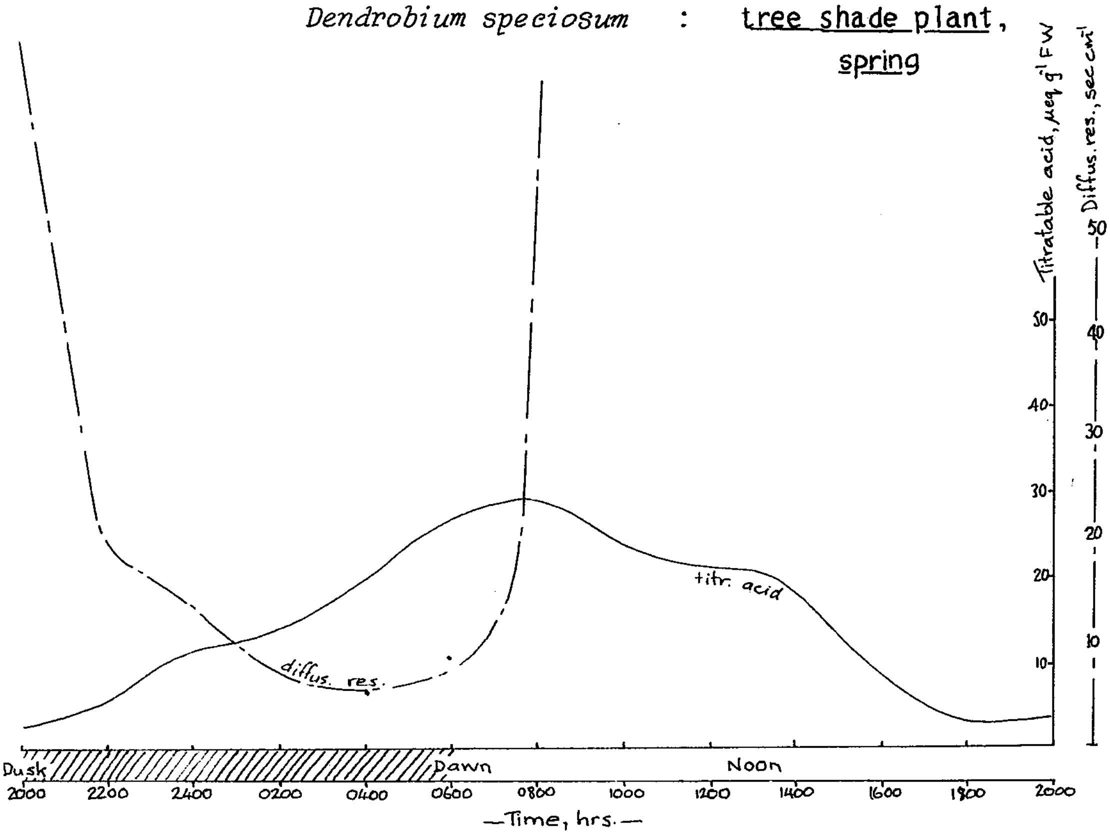
Graph 5.2.4 : Ecological factors related to CAM in *Plectorrhiza tridentata* : winter
(Long Point, August 21/22, 1979)



Graph 5.2.5 : Physiological factors related to CAM in *Dendrobium speciosum* : tree sun plant, spring

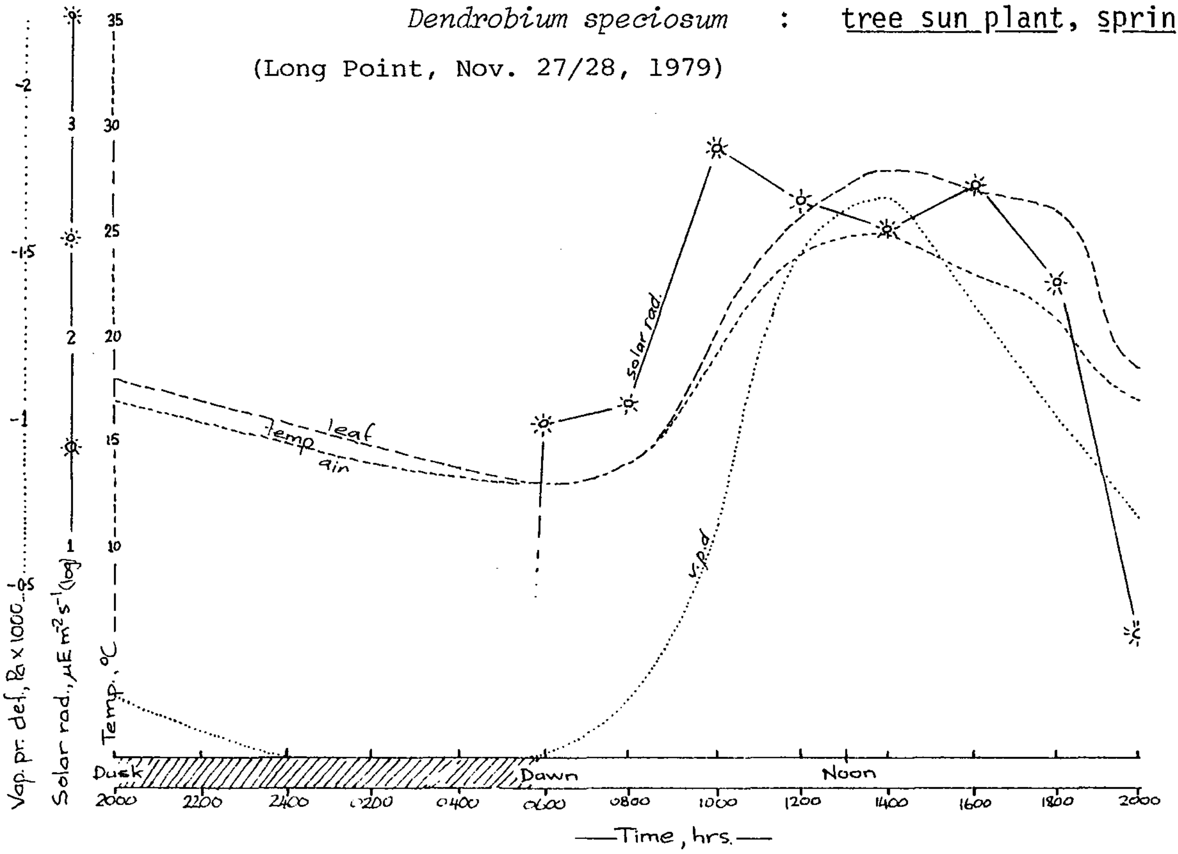


5.2.6 : Physiological factors related to CAM in *Dendrobium speciosum* : tree shade plant, spring



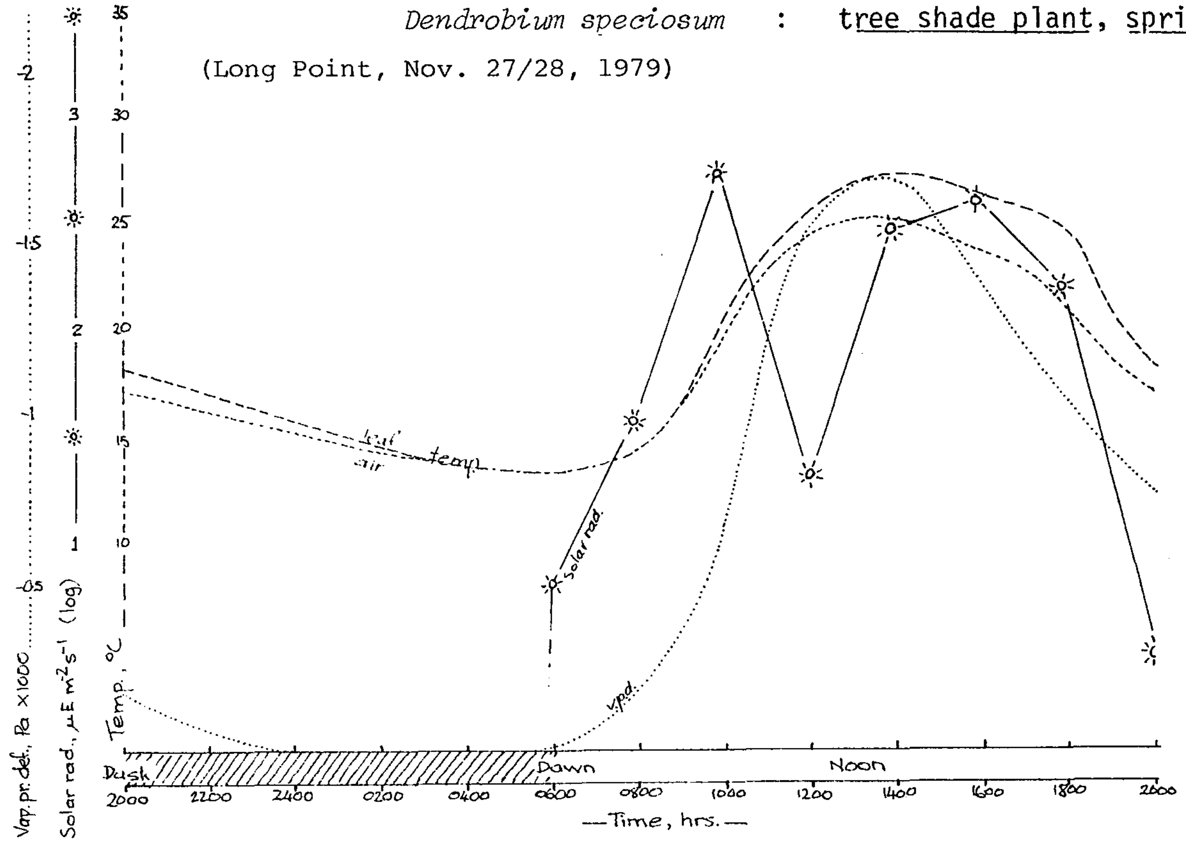
Graph 5.2.5 : Ecological factors related to CAM in *Dendrobium speciosum* : tree sun plant, spring

(Long Point, Nov. 27/28, 1979)

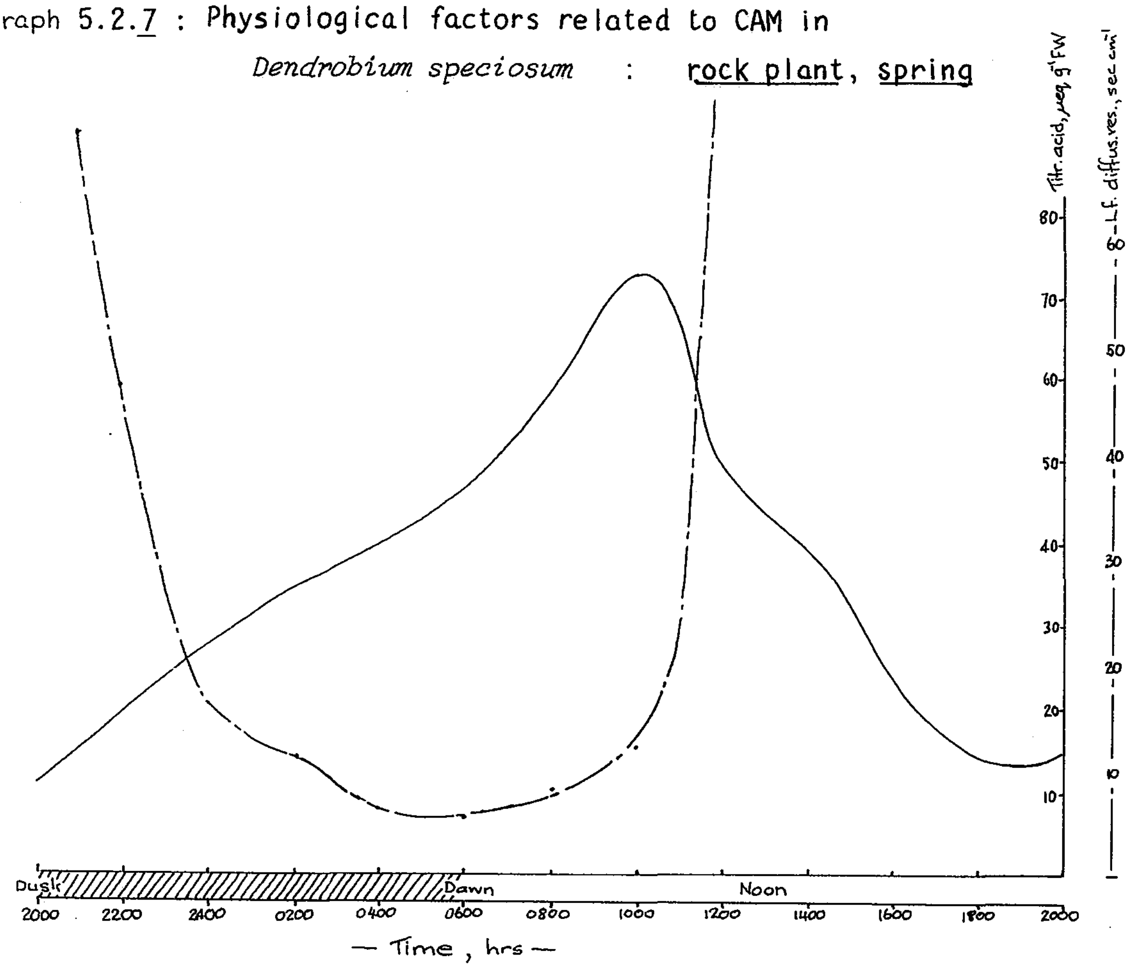


Graph 5.2.6 : Ecological factors related to CAM in *Dendrobium speciosum* : tree shade plant, spring

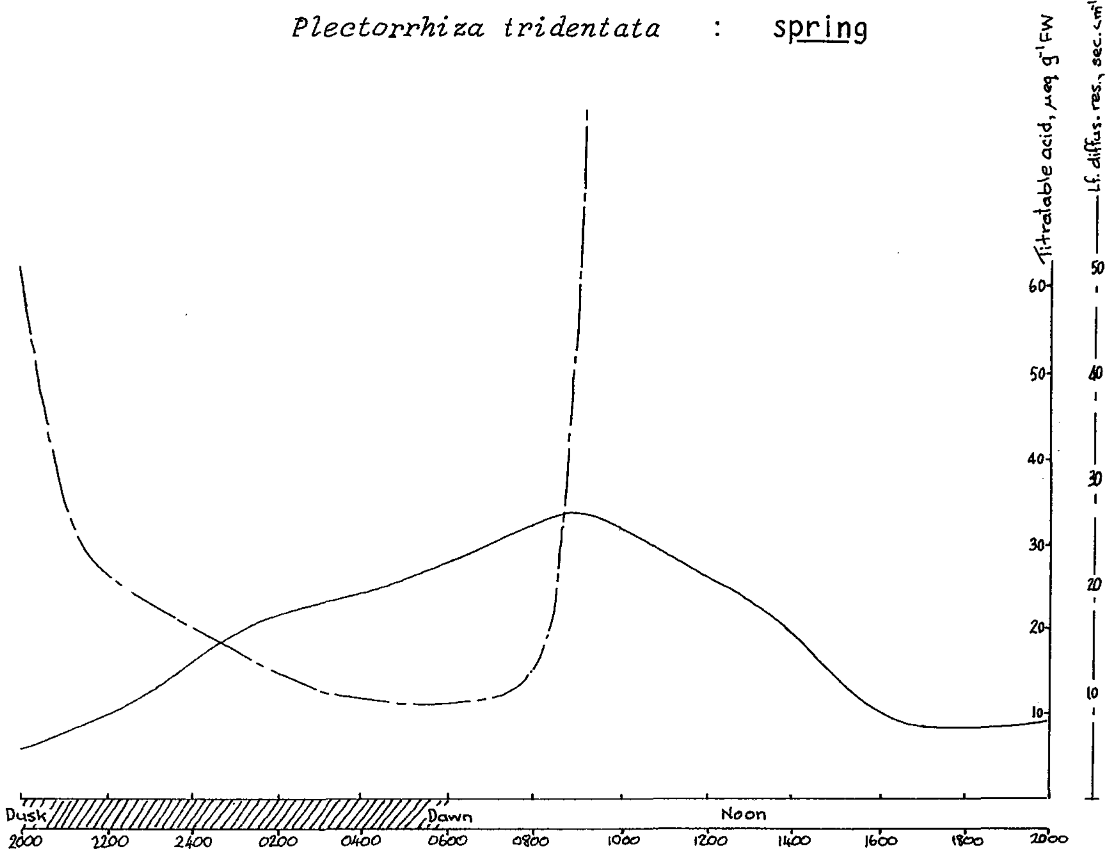
(Long Point, Nov. 27/28, 1979)



Graph 5.2.7 : Physiological factors related to CAM in *Dendrobium speciosum* : rock plant, spring

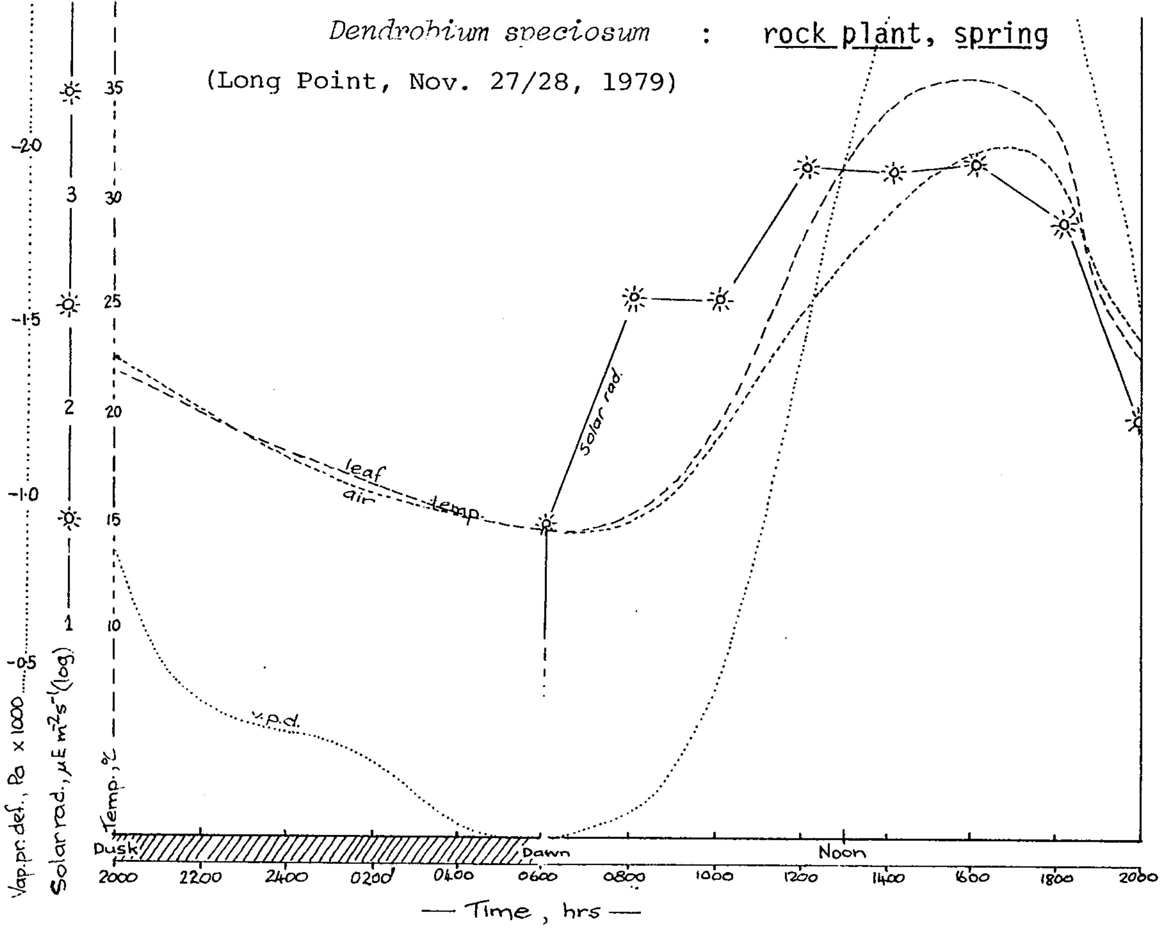


Graph 5.2.8 : Ecological factors related to CAM in *Plectorrhiza tridentata* : spring



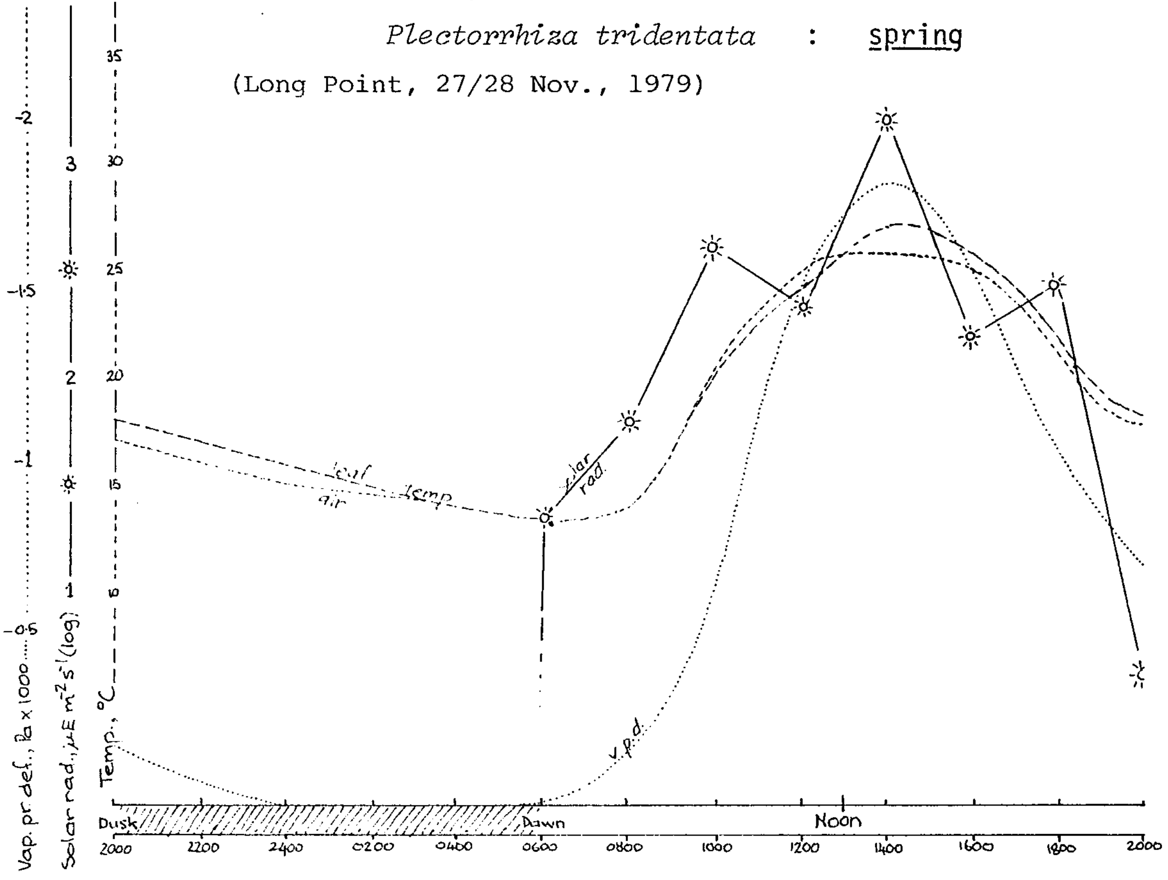
Graph 5.2.7 : Ecological factors related to CAM in *Dendrobium speciosum* : rock plant, spring

(Long Point, Nov. 27/28, 1979)

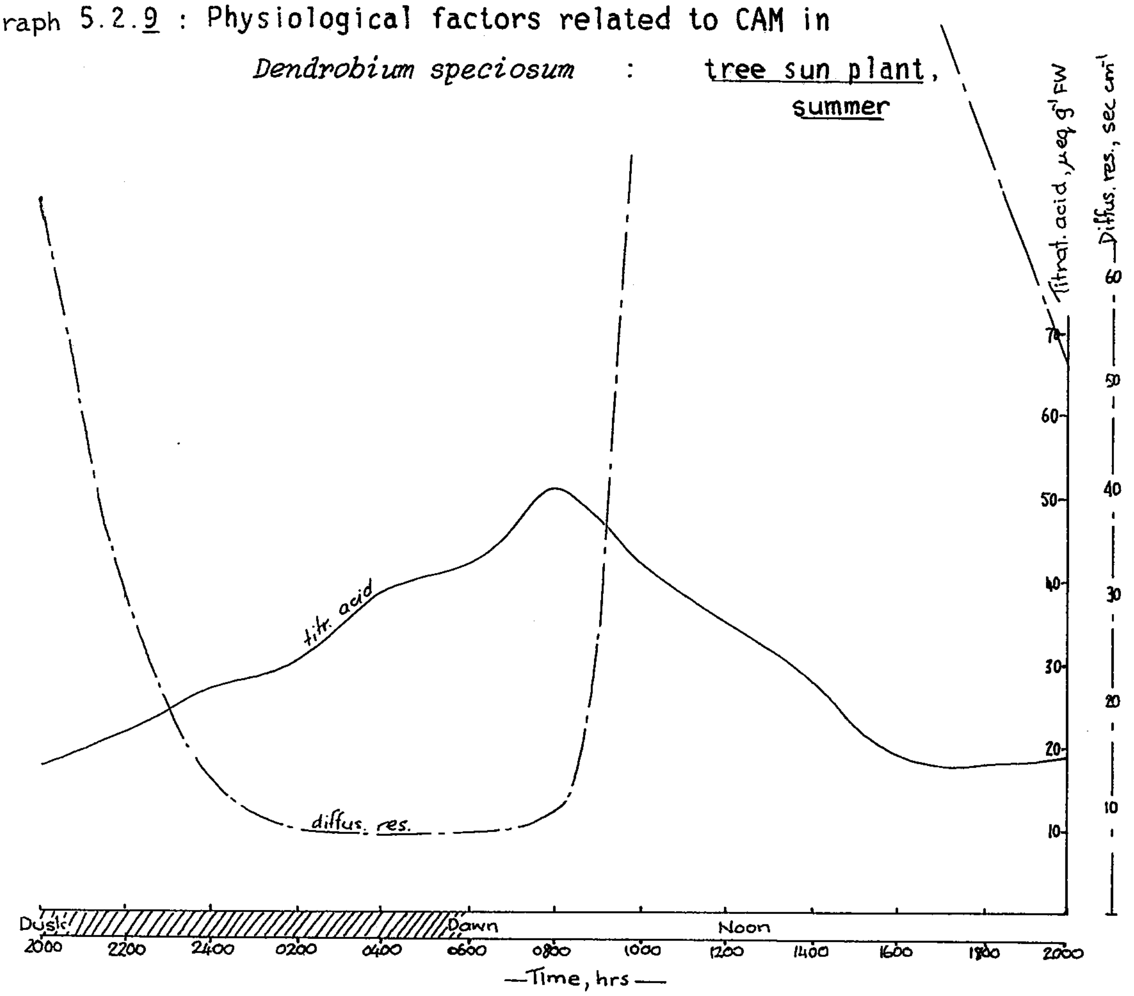


Graph 5.2.8 : Ecological factors related to CAM in *Plectorrhiza tridentata* : spring

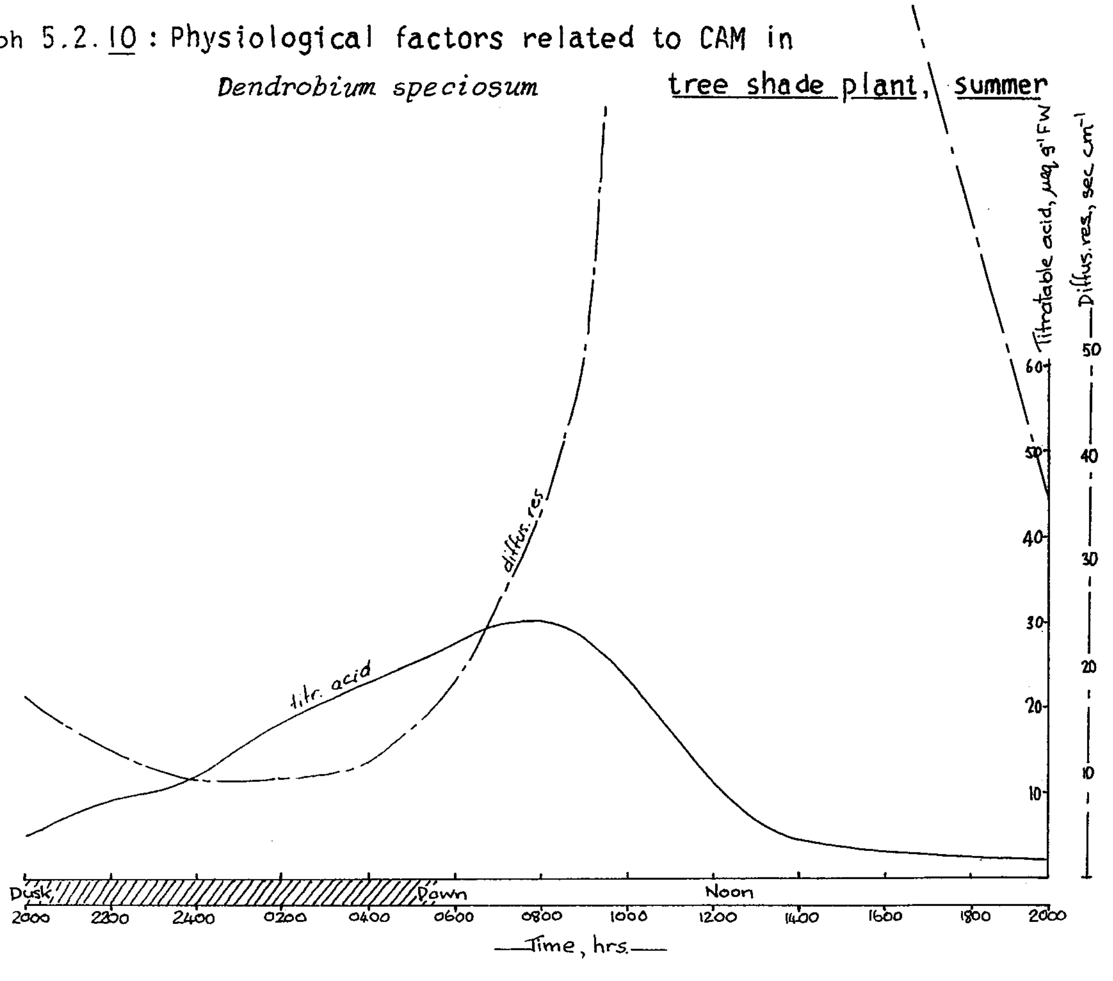
(Long Point, 27/28 Nov., 1979)



Graph 5.2.9 : Physiological factors related to CAM in *Dendrobium speciosum* : tree sun plant, summer

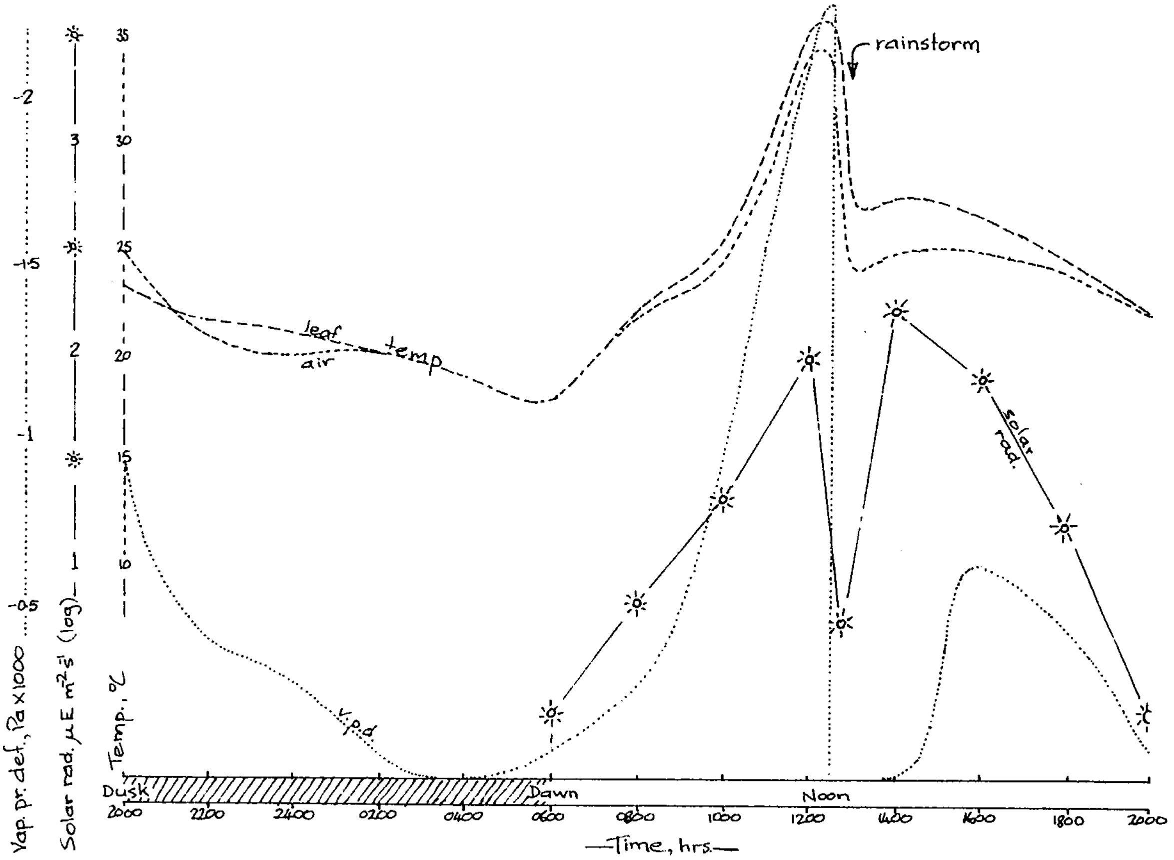


Graph 5.2.10 : Physiological factors related to CAM in *Dendrobium speciosum* tree shade plant, summer



Graph 5.2.9 : Ecological factors related to CAM in *Dendrobium speciosum* : tree sun plant, summer

(Long Point, Jan. 29/30, 1980)



Graph 5.2.10 : Ecological factors related to CAM in *Dendrobium speciosum* : tree shade plant, summer

(Long Point, Jan. 29/30, 1980)

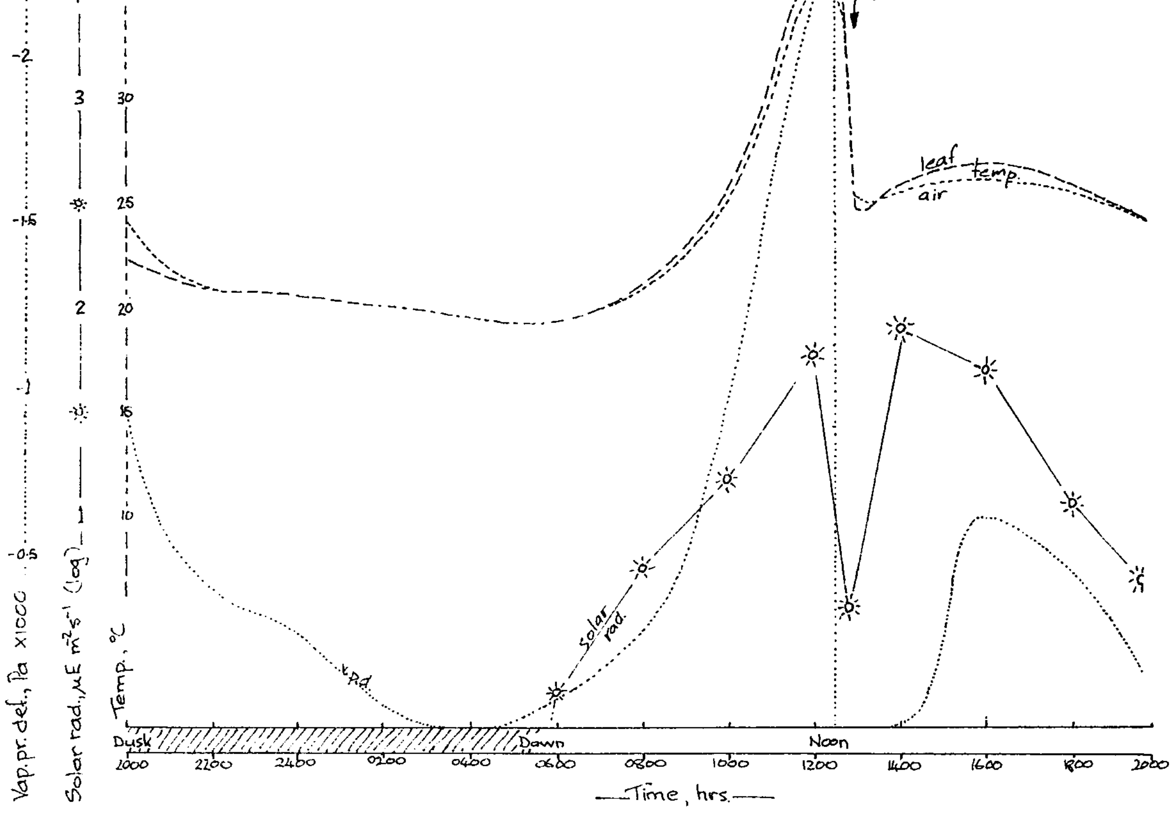


Table 5.1

Winler

August 21/22·8·79	Dendrobium speciosum (rock)								Den. spec. (tree, sun)								Den. spec. (tree, shade)						Plectorrhiza						
Time	Quanta μE m⁻² sec⁻¹	Leaf temp. °C	Air Temp. °C	Rel. Humidity %	Vap. press. deficit Pa	Diffusive resist. cm sec⁻¹	ml NaOH/4cm² sample	Titr. acid μeq/g FW	Quanta	Leaf temp	Air temp	Rel. humid %	Vap. press deficit	Diffus. res.	ml NaOH/4cm² sample	titr. acid μeq/g FW	Quanta	leaf temp	air temp	Diff res	ml NaOH/4cm² sample	titr. acid μeq/g FW	Quanta	leaf temp	air temp	diff res.	ml NaOH/.5g sample	titr. acid μeq/g FW	μeq/2cm²
1800 hrs (6 pm)	3·5	12·5	13	46	-508	42	0·35	8	0	13·5	14	56	-735	>100	0·25	9	0	13·5	14	>100	0·5	15	·05	15	15·5	>100	0·025	1	0·2
2000 hrs		12·5	12	50	-701	17	0·8	17		12	12·5	58	-606	83	0·45	13		12	12·5	41	0·5	15		12	12	47	0·05	2	0·4
2200 hrs		12	11·5	54	-622	13	0·7	18		11	11·5	65	-417	39	0·6	17		11	11·5	26	0·55	17		11	11	36	0·05	2	0·4
2400 hrs		10	10·5	57	-546	11	0·8	18		11	11	73	-341	35	0·7	20		10·5	11	22	0·6	18		11	11	34	0·075	3	0·6
0200 hrs		9	9	65	-401	10	0·9	20		10	10	82	-220	35	0·8	23		10	10	22	0·9	27		10	10	33	0·1	4	0·8
0400 hrs		8	8	71	-311	8	1·1	25		8·5	8·5	87	-144	24	0·9	26		8·5	8·5	21	1·0	30		9	9	24	0·15	6	0·6
0600 hrs	11·4	7·5	7·5	82	-187	13	1·2	27	1·5	8	8	91	-97	24	1·65	47	0·9	8	8	23	1·4	43	1·2	8	8	21	0·175	7	0·7
0800 hrs	45	8	8	86	-160	13	1·7	38	3	8	8	80	-214	31	2·0	51	1·4	8	8	25	1·5	46	3·7	8	8	14	0·25	10	1·0
1000 hrs	270	11·5	11·5	85	-203	55	1·3	29	50	11·5	11	50	-656	55	1·3	37	4·5	11·5	11	>100	1·3	40	7	11·5	11	>100	0·2	8	0·8
1200 hrs	1080	17	16·5	60	-751	55	0·5	11	75	17·5	17	45	-1065	>100	0·4	21	25	17·5	17	>100	1·0	30	16·5	17	16·5	>100	0·1	4	0·4
1400 hrs	125	19·5	18	48	-1077	78	0·3	7	12	17	17	50	-969	>100	0·25	7	10·5	17	16·5	>100	0·8	24	21	17·5	17	>100	0·05	2	0·2
1600 hrs	165	14·5	14	50	-749	>100	0·3	4	7·4	16	15·5	52	-874	>100	0·25	9	2·6	15·5	15	>100	0·6	18	5·8	16	16	>100	0·025	1	0·1
1500 hrs	9	13	13	52	-719	96	0·35	8	2·1	14	13·5	54	-680	>100	0·3	9·5	1·2	14	13·5	>100	0·6	18	1·7	15·5	15	>100	0·025	1	0·1

Fig. 5.2.17a

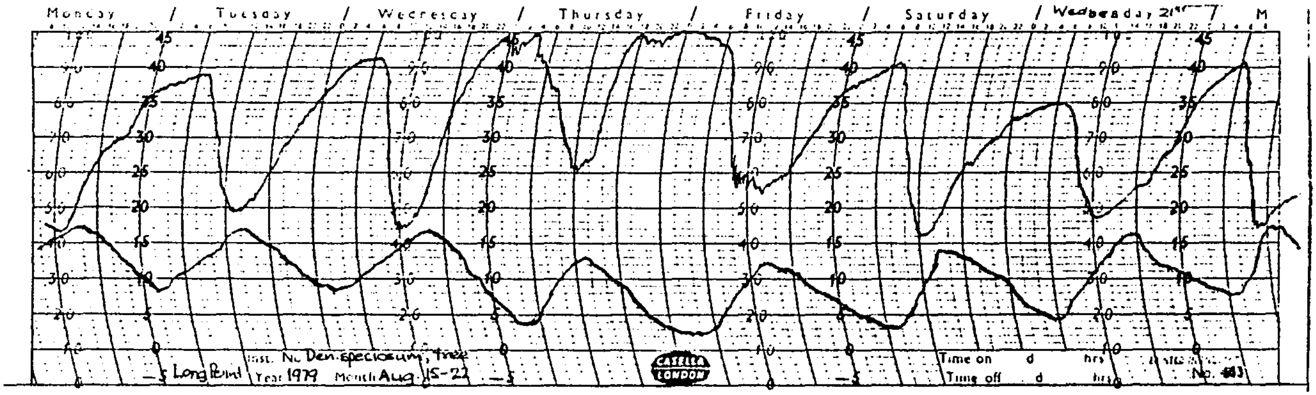


Fig. 5.2.17b

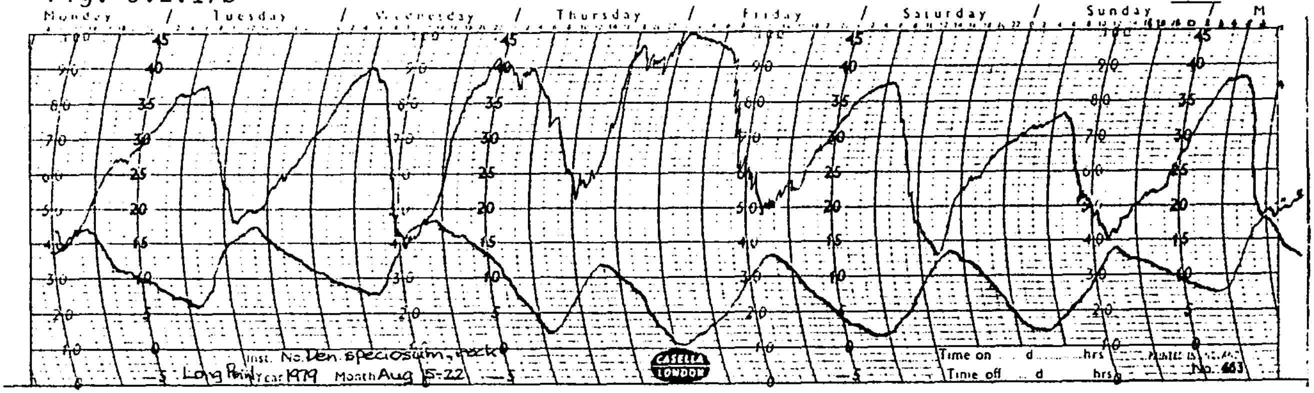


Table 5.2

Spring

November 27/28.11.79	Dendrobium speciosum (rock)								Den. spec. (tree, sun)								Den. spec. (tree, shade)						Plectorrhiza						
Time	Quanta μE m⁻² sec⁻¹	Leaf temp °C	Air Temp. °C	Rel. Humidity %	Vap. press. deficit Pa	Diffusive resist. cm sec⁻¹	ml NaOH/4cm² sample	titr. acid μeq/g FW	Quanta	Leaf temp	Air temp	Rel. humid %	Vap. press deficit	Diffus. res.	ml NaOH/4cm² sample	titr. acid μeq/g FW	Quanta	leaf temp	air temp	Diff. res.	ml NaOH/4cm² sample	titr. acid μeq/g FW	Quanta	leaf temp	air temp	diff res.	ml NaOH/0.5g sample	titr. acid μeq/g FW	μeq/2cm²
2000 hrs Dusk 7.30		22.5	23	70	-844	>100	0.5	11		18	17	93	-136	38	0.25	7		18	17	68	0.1	3		18	17	50	0.5	6	2.7
2200 hrs		20	20.5	82	-340	46	0.8	19		17	16	96	-73	34	0.4	12		17	16	20	0.2	6		17	16	21	0.25	10	4.5
2400 hrs		18.5	18	88	-149	16	1.2	27		16	15	100	0	11	0.85	21		15.5	15	14	0.4	12		16	15	17	0.4	16	7.2
0200 hrs		17	16.5	90	-187	11	1.0	34		15	14	100	0	4.4	1.1	37		16.5	14	73	0.45	14		15	14.5	12	0.55	22	9.9
0400 hrs		15.5	15.5	98	-35	6.3	1.8	39		14	13.5	100	0	3.2	1.4	41		14	13.5	5.9	0.65	20		14	14	9.2	0.6	24	10.8
0600 hrs Dawn 5.30	30	14.5	14.5	100	0	56	2.1	46	41	13	13	99	-15	5.9	1.65	47	6	13	13	9.2	0.9	27	21	13.5	13.5	9.0	0.7	28	12.6
0800 hrs	40	15.5	15	75	-55	8	2.6	58	50	14	14	90	-160	6.5	2.1	62	35	14	14	>100	0.95	29	60	14	14	12	0.8	37	14.4
1000 hrs	550	17.5	17	80	-400	12	3.2	72	600	20	19	70	-659	6.8	2.0	57	500	20	19	>100	0.8	24	400	20.5	20	>100	0.5	32	14.4
1200 hrs	1500	28	25	54	-1457	>100	2.1	48	450	25.5	24	50	-1493	>100	1.5	44	150	25	24	>100	0.7	21	200	24.5	24	>100	0.7	26	11.7
1400 hrs	1440	34	29	39	-2446	>100	1.7	39	330	28	25	49	-1447	>100	1.05	31	264	27	25	>100	0.6	18	1500	25.5	27	>100	0.5	20	9.0
1600 hrs	1560	35.5	32	38	-1140	>100	0.4	20	500	27	23	55	1448	>100	0.4	12	400	26	23	>100	0.25	8	150	25	25.5	>100	0.25	10	4.5
1800 hrs	810	33	31	43	-1563	>100	0.55	12	180	26	21	58	-1045	71	0.5	7	132	24.5	21	>100	0.1	3	246	21	22	>100	0.2	8	3.6
2000 hrs	79	26	25	54	-1437	>100	0.35	14	3.7	24	19.5	68	-725	3.7	0.3	7.5	3.4	21	20	93	0.1	3	4.2	19	20	90	0.2	8	3.6

Fig. 5.2.18a

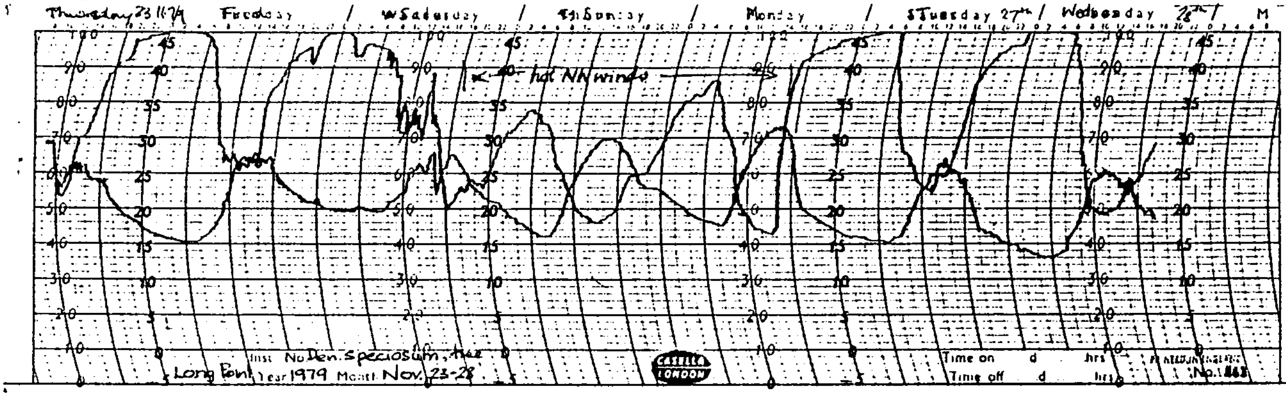


Fig. 5.2.18b

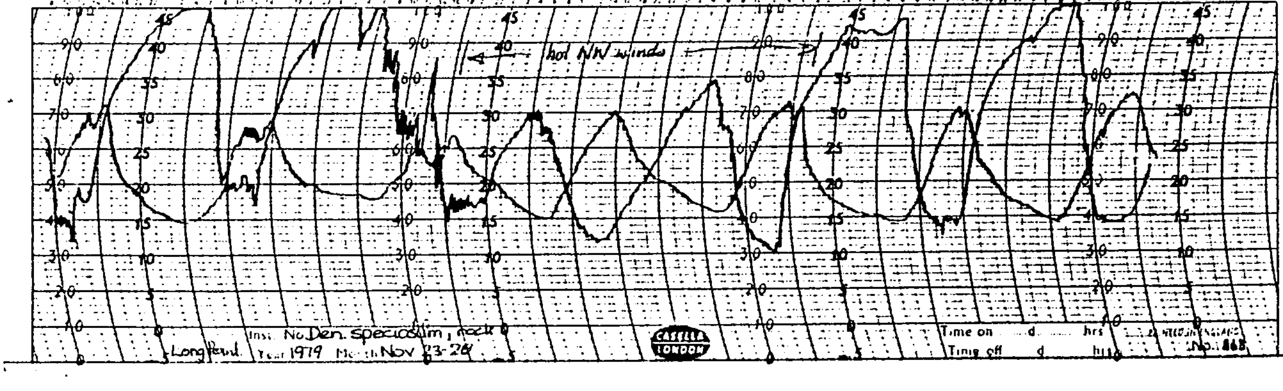


Table 5.3

Summer

January 29/30·1·80	Dendrobium speciosum (rock)								Den. spec. (tree, sun)								Den. spec. (tree, shade)						Plectorrhiza						
Time	Quanta µE m⁻² sec⁻¹	Leaf temp. °C	Air Temp. °C	Rel. Humidity %	Vap. press. deficit Pa	Diffusive resist. cm sec⁻¹	ml NaOH/4cm² sample	titr. acid µeq/g FW	Quanta	Leaf temp	Air temp	Rel. humid %	Vap. press deficit	Diffus. res.	ml NaOH/4cm² sample	titr. acid µeq/g FW	Quanta	leaf temp	air temp	Diff. res	ml NaOH/4cm² sample	titr. acid µeq/g FW	Quanta	leaf temp	air temp	diff. res.	ml NaOH/0.5g sample	titr. acid µeq/g FW	µeq/2cm²
2000 hrs Dusk 7.30		25.5	31	65	-574	31	0.3	7		23	25	70	950	67	0.6	17		23	24.5	17	0.13	4		23	25	19	0.1	4	1.8
2200 hrs		18.5	20	71	-678	7	0.5	11		21	21.5	84	-390	51	0.75	21		21	21.5	12	0.25	8		21	21.5	12	0.2	8	3.6
2400 hrs		19	20	83	-396	5	0.7	16		20	21	88	-230	12.5	0.1	26		20	21	9	0.4	12		20	20	9	0.30	14	6.3
0200 hrs		18	18	90	-207	4	0.15	22		20	20	97	-70	8	1.0	29		20	20	5	0.6	18		14	19	8	0.6	24	10.8
0400 hrs		18	18	94	-120	6	1.2	27		19	18.5	100	0	7.5	1.3	38		19	19	11	0.75	23		19	18	8.5	0.75	30	13.5
0600 hrs Dawn 5.5	12.4	18	[illegible]	90	-200	6.5	1.4	31	2	18	18	97	-62	9	1.45	41	15	18	15	18	0.9	27	4	19	14	18	0.55	38	17.1
0800 hrs	75	24	24	57	-557	6.3	1.5	34	6.7	22	22	51	-240	9.8	1.1	50	5.5	22	21.5	33.2	1.1	30	24	23	23	22	1.2	46	20.7
1000 hrs	100	26	26	60	-842	73	1.7	27	21	25.5	24.5	50	-454	>100	1.4	41	15	25.5	24.5	>100	0.6	24	85	25.5	27	>100	1.1	42	18.9
1200 hrs	900	35	32	54	-2830	>100	0.65	15	98	35.5	34.5	63	-2141	>100	1.2	54	57	35.5	34.5	>100	0.35	11	111	34.5	36	>100	0.8	52	14.4
rain storm →	40		28	100	0				36		24	100	0				35		24				32						
1400 hrs	1100	39	36.5	80	-951	>100	0.55	12	165	27.5	25	100	0	>100	0.55	27	75	27.5	26	>100	0.15	4.5	127	26	28	>100	0.6	24	10.8
1600 hrs	1140	26.5	28	80	-1193	71	0.2	5	71	26.5	25	82	-624	>100	0.65	19	48	26.5	24.5	>100	0.1	3	52	24.5	25	54	0.2	8	3.6
1800 hrs	177	25	25.5	84	-522	15.5	0.25	6	15	24.5	24	55	-661	72	0.55	16	10.5	24.5	23.5	64	0.08	2.25	15	23	23.5	41.5	0.07	3	1.4
2000 hrs	21	21	21	96	-99	7	0.45	10	2.1	22	21	78	-53	51	0.6	17	3.8	23.5	23	34	0.1	3	3	21	22	31	0.1	4	1.8

Fig. 5.2.19a

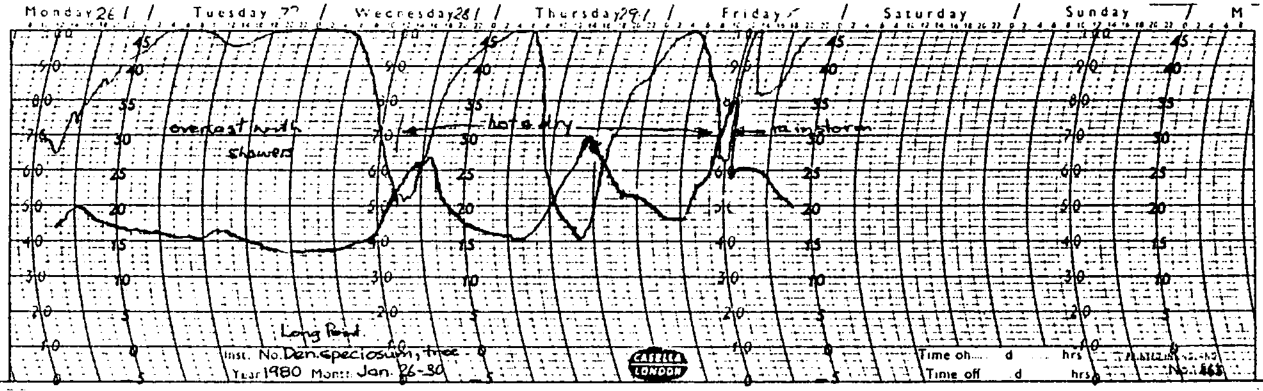


Fig. 5.2.19b

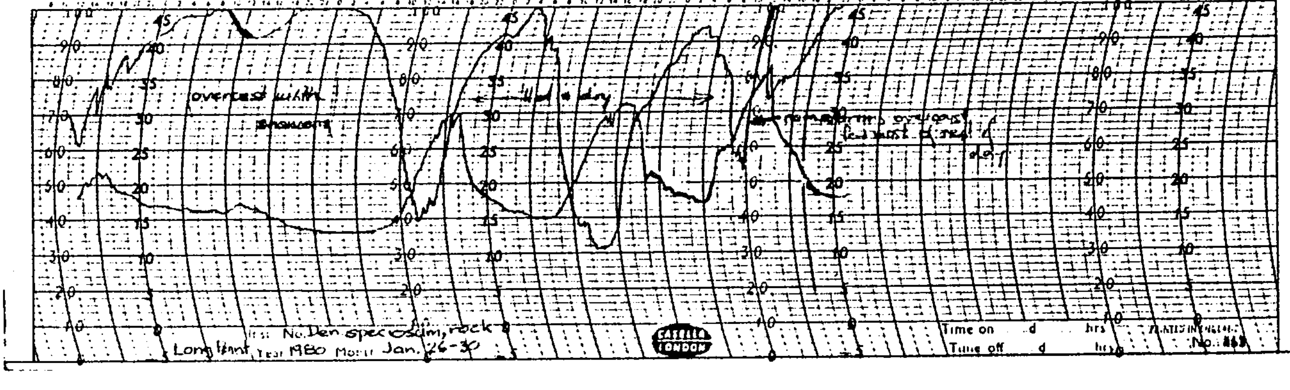


Table 5.4

Autumn

April 23/24·4·80

Time	Dendrobium speciosum (rock)							
	Quanta µE m⁻² sec⁻¹	Leaf temp °C	Air Temp °C	Rel. Humidity %	Vap. press. deficit Pa	Diffusive resist. cm sec⁻¹	ml NaOH/4cc sample	Titr. acid µeq/g FW
1800 hrs (dusk 6.30)		17	17	83	-324	56	0.15	14
2000 hrs		16	16	86	-254	146	0.15	22
2200 hrs		15	15	90	-171	10	1.3	30
2400 hrs		13	13.5	95	-73	7	1.7	38
0200 hrs		11.5	12	100	0	5	2.0	40
0400 hrs		9.5	10	100	0	4	2.3	54
0600 hrs (Dawn 6.16)	38	11	11.5	94	-52	2.5	2.7	63
0800 hrs	58	14	15	80	-341	17	3.1	71
1000 hrs	400	17.5	21	63	-920	67	2.8	64
1200 hrs	350	17.5	21	51	-1217	>100	2.5	59
1400 hrs	1200	34	30	48	-2206	>100	1.5	31
1600 hrs	135	21	20	64	-841	81	0.7	16
1800 hrs	~1	18.5	18	78	-455	67	0.15	15

Time	Den. spec. (tree, sun)							
	Quanta	Leaf temp	Air temp	Rel. humid %	Vap. press deficit	Diffus. res.	ml NaOH/4g sample	titr. acid µeq/g FW
1800 hrs		17.5	17	88	-232	51	0.45	13
2000 hrs		16.5	16	91	-164	27	0.5	15
2200 hrs		15	15	94	-102	12	0.9	26
2400 hrs		13.5	14	98	-32	15	1.3	38
0200 hrs		12.5	13	100	0	12	1.7	50
0400 hrs		12	12	100	0	14	2.0	57
0600 hrs	1.44	11.5	11	96	-52	15	2.1	62
0800 hrs	15.9	14	14	55	-254	17	2.2	65
1000 hrs	400	19	18.5	68	-688	66	4.5	61
1200 hrs	210	19	21	56	-1074	>100	2.2	60
1400 hrs	600	23.5	21	52	-1194	>100	1.0	31
1600 hrs	13.5	17	19.5	70	-680	>100	0.5	16
1800 hrs	-	18	18	83	-352	76	0.5	16

Time	Den. spec. (tree, shade)					
	Quanta	leaf temp	air temp	Diff res	ml NaOH/4cc sample	titr acid µeq/g FW
1800 hrs		17	17	59	0.3	9
2000 hrs		16	16	29	0.4	11
2200 hrs		16.5	14.5	16	0.5	15
2400 hrs		13.5	14	14	0.6	18
0200 hrs		12.5	13	12	0.75	23
0400 hrs		11	11.5	15	0.9	27
0600 hrs	3.8	11	11	16	spilled	
0800 hrs	9.6	14	14	21	1.15	34
1000 hrs	18	18.5	18.5	>100	1.65	32
1200 hrs	30	19	21	>100	0.95	29
1400 hrs	90	22	21	>100	0.8	26
1600 hrs	10.5	18.5	19.5	>100	0.4	12
1800 hrs	-	18	18.5	59	0.4	11

Time	Plectorrhiza						
	Quanta	leaf temp	air temp	diff res.	ml NaOH/0.5g sample	titr. acid µeq/g FW	µeq/2cm²
1800 hrs		17	17	>100	0.15	1.2	2.4
2000 hrs		16	16	>100	0.13	1.0	2.0
2200 hrs		15	15	36	0.26	2.0	4.0
2400 hrs		16	14	28	0.4	3.0	6.0
0200 hrs		13	13	25	0.22	3.6	7.2
0400 hrs		12	12	20	0.55	4.4	8.8
0600 hrs	15	11	11.5	18	0.7	5.0	10
0800 hrs	15	13.5	14	28	0.6	4.8	9.6
1000 hrs	600	16	20	70	0.3	2.4	4.8
1200 hrs	120	17.5	19	>100	0.73	1.8	3.6
1400 hrs	18	18.5	17	>100	0.2	1.6	3.2
1600 hrs	90	20.5	20.5	>100	0.18	1.4	2.8
1800 hrs	-	19	19.5	>100	0.15	1.2	2.4

Fig. 5.2.20a

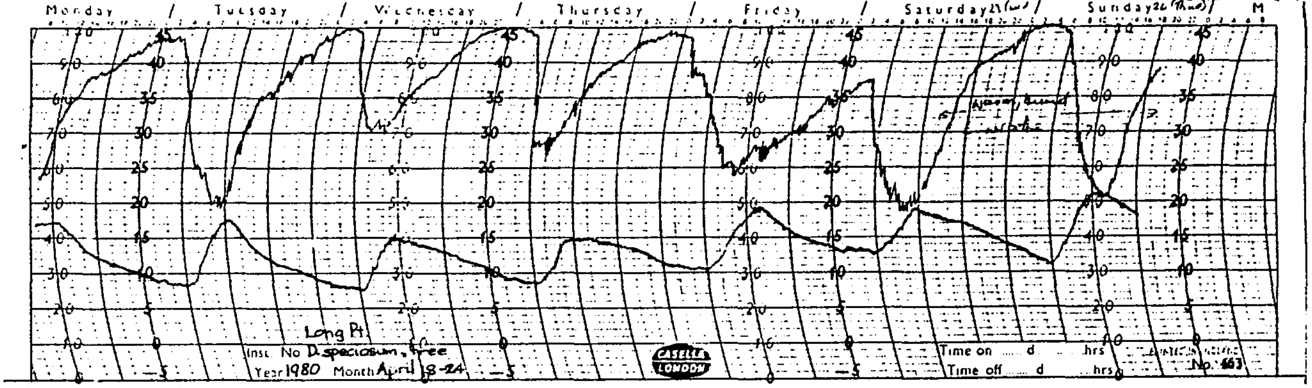
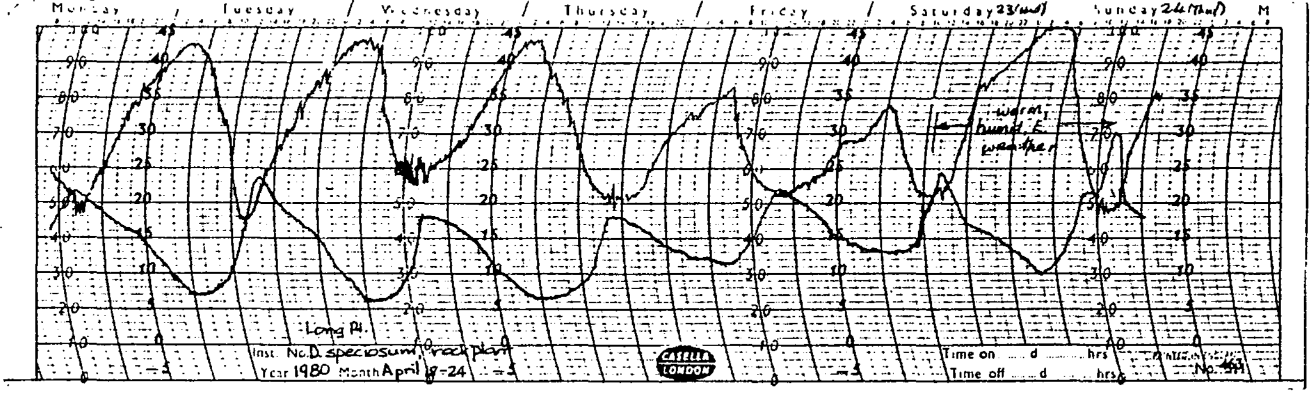


Fig. 5.2.20b



Appendix 3

Results of some analyses of total nitrogen, phosphorus and potassium in leaves and flowers of *Dendrobium speciosum* and *Plectorhiza tridentata*; material collected from Long Point during 1980.

	ug/g dry weight		
	N	P	K
a. *Dendrobium speciosum*			
Leaves: means of single leaves from five plants:			
young mature leaf	9651	1417	193
senescent leaf	6472(33) *	638(55)	80(58)
abscised leaf	3344(65)	313(78)	53(73)
Flowers: means of one lot each from two plants:			
freshly opened flowers	13780	1860	358
abscised flowers	6030(56)	997(46)	160(55)
b. *Plectorrhiza tridentata*			
Leaves: means from leaf pairs from 5 plants:			
young, mature leaves	11785	2226	183
senescent leaves	6515(45)	1105(50)	90(51)
abscised leaves	2565(78)	639(76)	74(77)
Flowers: means of one lot each from two plants:			
freshly opened flowers	29166	2683	318
abscised flowers	7114(76)	639(76)	74(77)

* Figures in brackets are percent reductions from levels in a) young mature leaves or, b) fresh flowers.