THE AUSTRALIAN VASCULAR EPIPHYTES : FLORA & ECOLOGY

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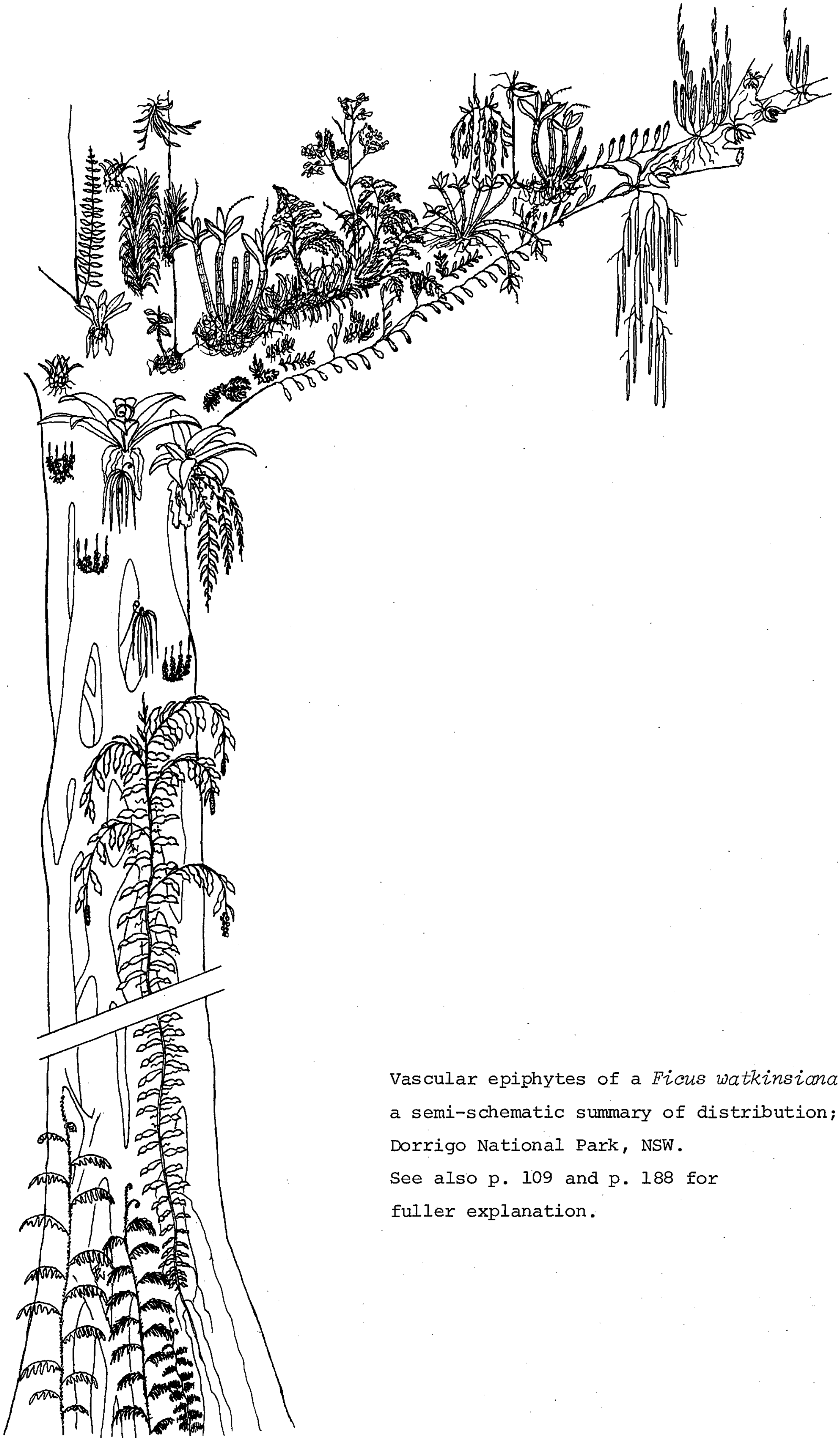
This work I dedicate to my father, Robert, who gave so much to his children and who urged me to continue my formal education as far as possible. Also, without my inheritance of his doggedness, this work would surely have foundered.



Vascular epiphytes of a *Ficus watkinsiana*:
a semi-schematic summary of distribution;
Dorrigo National Park, NSW.
See also p. 109 and p. 188 for
fuller explanation.

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Jenny Worgan typed most of the manuscript and compiled the Table of Contents, Lists of Tables, Figures and Plates. Her efficiency, cheerfulness and understanding helped considerably.

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Statement of Originality

I certify that the substance of this dissertation has not been submitted for any degree and is not being currently submitted elsewhere.

Also, all of the work recorded herein is my own except as otherwise acknowledged.

Signed [redacted]

Date 25. 1. 82

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List of Abbreviations

Afr.	Africa
Amer.	America
Austr.	Australia
C.	Cape
ca.	about
CAM	Crassulacean Acid Metabolism
cm	centimetre(s)
cosmopol.	cosmopolitan
CTRf	cool temperate rainforest (MFF*)
diam.	diameter
DRf	dry rainforest (MVT* or SEVT*)
DVT*	deciduous vine thicket
E	east
Ect	rft/open community (ecotone)
esp.	especially
Fig.	Figure
Fl.	flowering (period)
fls.	flowers
incl.	including
infl.	inflorescence
Is.	Islands
lvs.	leaves
LRF	littoral subtropical rainforest (NVF*)
m	metres
MAR	Mean Annual Rainfall
MFF*	microphyll fern forest (CTRf)
mm	millimetres
Mt.	Mount, Mountain
MVF*	mesophyll vine forest (trop. rft)
MVT	microphyll vine thicket (DRf)
MVW*	microphyll vine woodland (rft relict scrub)
N	north
N. Cal.	New Caledonia
NG	New Guinea
NT	Northern Territory
NVF	complex notophyll vine forest (STRf)
NZ	New Zealand
NSW	New South Wales
occas.	occasional(ly)
Pac	Pacific
PAR	Photosynthetically Active Radiatn.
Pen.	Peninsula
Qld	Queensland
R.	River
Ra	Range
rft	rainforest
SEC	Semi-epiphytic climber
SEVF*	semi-evergreen mesophyll vine forest (tall monsoon rft)
SEVT*	semi-evergreen vine thicket (Bottle Tree scrub to relict rft scrub or DRf)
SNEVF*	simple notophyll evergreen vine forest (WTRf)
S	south
sp.	species (singular)
spp.	species (plural)
ssp.	subspecies
STRf	subtropical rainforest (NVF*)
Tas.	Tasmania
tblds	tablelands
temp.	temperature
trop.	tropical
usu.	usually
var.	variety
Vic.	Victoria
W	west
Wdl	woodland
WSF	wet sclerophyll forest or tall open forest
WTRf	warm temperate rainforest (SNEVT*)
±	more or less
μE, μEin	microeinstein, unit of irradiance (quantum)

* Following Webb, 1978

Abstract

Firstly, recent literature dealing with the systematics and ecology of vascular epiphytes is reviewed, as are a selection of older key papers. The classification and terminology of vascular epiphytes is briefly reviewed and discussed and the system used here is delineated; terms are defined, including a number of new and previously ill-defined ones.

The Australian vascular epiphyte flora is then described in a tabulated list and in a more detailed, illustrated descriptive key (Appendix 1). The flora is next discussed in relation to its taxonomic composition, diversity and affinities biogeography, life forms and physiognomic forms, and diaspore dispersal methods; these are also briefly related to basic ecology of the groups.

Next, physical ecological factors of epiphyte environments in Australia are investigated. This includes discussion of continental macroclimate and its bearing on the distribution of epiphyte-favoured vegetation types, particularly rainforests, and investigation of microclimate components at different levels within selected sites in five different rainforest subformations of the subtropics. The results of this show that microsites near the canopy are considerably brighter, drier and more temperature-extreme than are those near the tree trunk bases.

Beginning with a review of relevant works, the synecology of epiphytes is next discussed and the system of study for use here is outlined. The epiphytic vegetation of five subtropical sites (those mentioned above) and a tropical one, are investigated using this system which involves marked plots and the recording of all trees and epiphytes within them. The data derived from these are used in conjunction with that mentioned above and other observations for comparison and discussion of such topics as epiphyte floristic diversity, population density, vegetational complexity, occurrence of different epiphyte forms, specificity of epiphyte/phorophyte relationships, phorophyte axeny and epiphyte-proneness, allelopathy and phorophyte age effect. Observations and review on nest-epiphytes and succession are discussed.

Some basic functions of CAM in two epiphytic orchids were investigated under field conditions and the results are discussed in relation to its adaptive significance; the results of a survey of CAM in the Australian epiphytes are discussed and from this and the former, it is concluded that CAM is a very important water-conserving mechanism particularly to the heliophilous epiphytes. Relevant literature is reviewed.

It is generally concluded from all of the above that epiphytism has been developed by small, slow-growing plants to avoid competition for light and in doing so, they have had to concomitantly adapt to water-stress and nutrient deficiency.

General Introduction

According to the Oxford English Dictionary, the word *epiphyte*, in botanical usage[1], means *a plant which grows on another plant; usually restricted to those which derive only support (not nutrition) from the plants on which they grow*. From the same authority, it was first used in the literature by John Lindley in 1830 (in *Nat. Syst. Bot.* 264, as the derived adjective *epiphytic*). Its etymological origin is from the Greek *epi*, upon + *phyton*, plant (Flood, 1960). Thus, other reference texts give the meaning of *epiphyte* as, e.g., *a plant which grows on other plants but not parasitically; an air plant* (Jackson, 1928); *a plant growing on another plant but not deriving food from it* (Usher, 1966); *plant attached to another plant, not growing parasitically upon it but merely using it for support* (Abercrombie et al., 1966); ... and so on.

From these the meaning appears to be clear but still certain ambiguities remain. For instance, most definitions refer to the epiphyte not deriving nutrients from its substrate plant but many studies show that some, even most of the minerals absorbed by many epiphytes, come from stemflow much of which mineral content is leached from the phorophyte (bearer-plant). Most writers have interpreted the word to mean *non-parasitic* i.e., such nutrient sources used by the epiphyte are not available to the phorophyte (but see, however, Herbert, 1958, and Nadkarni, 1981, reviewed in Ch. 1). Even so, *epiphyte* is sometimes used in a broad sense to include parasites such as mistletoes.

Another problem, less easily disposed of, centres on the *growing upon* part of the definition. Lianas *growing upon* trees could perhaps, in the broadest sense, be called epiphytes but these are usually classified separately as most do not attach themselves to their support by actually growing *onto* it. There are some however, that do attach by growing adventitious roots onto the support and sometimes these roots may ramify and produce substantial root systems. As such, they probably derive nutrients from the outer, dead tissues of the support plant and from stemflow

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1. N.B. the same word is used in pathology in reference to a plant, e.g. fungus, growing on the skin of an animal.

etc. Such vine /epiphytes are a problem as the classical definition does not exclude plants that grow upon a bearer-plant *as well as in the soil at the same time*[1]. A further clarification of the definition, involving major source of nutrients would appear to be useful (see Ch. 1.2).

Epiphytes have fascinated botanists ever since Europeans first ventured to the tropics where vascular epiphytes are common, varied and prominent in many different plant communities. Columbus is credited with the first recorded comment on vascular epiphytes when he wrote in his log in 1492 that many of the tropical trees "have a great variety of branches and leaves, all of them growing from a single root" (from Gessner, 1956). Perhaps most of the plants transported from the tropics to Europe for the horticultural trade from the 17th century to the present, have been epiphytic species of orchids, bromeliads, aroids, ferns and others. Not only are they attractive, with highly ornamental foliage, inflorescences and flowers but they are a small and manageable size at maturity. Also they are often ± strongly drought tolerant with minimal nutrient needs and thus may thrive on neglect, an important necessity of indoor plants for people who appreciate their beauty without appreciating cultural requirements, or are forgetful or neglectful.

Probably the most intriguing attribute of epiphytes is that they grow *independent of the ground* and that this is their normal, 'chosen' way of life. From this arise the questions of how they manage to survive and indeed, thrive in such apparently arid and nutrient-poor situations, especially since other plants have their roots in the ground where they are protected and water and minerals are not severely limited. Also the environmental forces that gave rise to the development of the epiphytic way of life, the mode of development and evolutionary steps and the phyletic origins of epiphytes all pose questions of great interest. Though basically of a survey/review type, this dissertation attemps to clarify some of these problems.

More specifically, the Australian vascular epiphytes have not been the subject of a comprehensive study previously and the present one is an attempt at laying some groundwork and initiating some specific lines of

1. A separate group, viz, semi-epiphytic climbers, has been instituted here to accommodate these (see Ch. 1.2).

investigation. Accordingly, the epiphytic *flora* has received considerable attention in this report and more specific reasons for this are detailed in the introduction to the flora chapter (Ch. 2).

Similarly, the synecology of the epiphytes has been little studied and this has been approached here by developing a system of recording of data from plots in different rainforests as a basis for comparison and discussion. Five such epiphyte recording plots were in the subtropics but only one tropical representative was investigated, owing partly to the great distances involved and the associated expense and partly also to the writer's experience with the tropical disease Leptospirosis while there.

Defining and characterising epiphyte microhabitats present great problems relating to the number of ecological variables, their fluctuation over even very short distances, and their interactions with one another. The patchiness of substrate and the importance of the vertical dimension in epiphyte ecology multiply these problems. Even so, some attempt is made in this study to coarsely characterise macro-microhabitat physical factors to relate to the flora and vegetation work. A full attempt at such an investigation will require a major project with the emphasis on this aspect and will involve considerable equipment (and expense), extensive data collection and appropriate analyses.

The ecology and adaptive significance of the physiological mechanism known as Crassulacean Acid Metabolism (CAM) has been investigated in two epiphytic orchids under natural field conditions and a survey of CAM in the Australian epiphytes was carried out in co-operation with others in an attempt to assess its importance in the ecology of epiphytes.

For several reasons, non vascular epiphytes are not investigated in this study. The state of taxonomy and naming of the Australian flora requires a great deal more work to bring it to a state where it can be readily worked with by non-experts in that field. Also, their physiology, especially water relations and poikilohydry set them clearly apart from most vascular epiphytes and give rise to ecological relations that are also quite different. For these reasons particularly, they require specialisation of study.

Thus, N.B. in the present work, where the word epiphyte is used without qualification, it is to be taken as referring to *vascular* epiphytes.