

Vegetation Classification in Australia

Edited by A.N. Gillison and D.J. Anderson



Vegetation classification systems developed thus far in the Australian region are neither universally accepted nor applicable to all types of vegetation or all types of land use problems. Those suitable for classifying rainforest are not necessarily applicable to other vegetation types. In this book scientists from a variety of related disciplines discuss various developmental aspects of vegetation classification that are relevant to Australia, though the ideas and techniques are of importance internationally.

This volume brings together recent research on many aspects of vegetation classification. It is innovative, provocative and will certainly arouse controversy.

This book was published by ANU Press between 1965–1991.

This republication is part of the digitisation project being carried out by Scholarly Information Services/Library and ANU Press.

This project aims to make past scholarly works published by The Australian National University available to a global audience under its open-access policy.

Vegetation Classification in Australia

Vegetation Classification in Australia

Proceedings of a Workshop Sponsored by CSIRO Division
of Land Use Research, Canberra, October 1978

Edited by

A. N. GILLISON and D. J. ANDERSON

Commonwealth Scientific and Industrial Research Organization, Australia in
association with Australian National University Press, Canberra, Australia,
London, England and Miami, Fla., USA, 1981

First published in Australia 1981

Printed in Australia for the
Australian National University Press, Canberra

© Commonwealth Scientific and Industrial Research Organization 1981

This book is copyright. Apart from any fair dealing for the purpose of private study, research, criticism, or review, as permitted under the Copyright Act, no part may be reproduced by any process without written permission. Inquiries should be made to the publisher.

National Library of Australia
Cataloguing-in-Publication entry

Vegetation classification in Australia.

Proceedings of workshop held at Canberra,
5 and 6 October 1978.

Bibliography.

Index.

ISBN 0 7081 1309 5.

1. Vegetation classification—Australia—Congresses. I. Gillison, A. N. (Andrew Napier). II. Anderson, D. J. (Derek John). III. Commonwealth Scientific and Industrial Research Organization (Australia). Division of Land Use Research.

581'.012

Library of Congress No. 81-68097

United Kingdom, Europe, Middle East, and Africa: Books Australia, 3 Henrietta St. London WC2E 8LU, England

North America: Books Australia, Miami, Fla., USA

Southeast Asia: Angus & Robertson (S.E. Asia) Pty. Ltd. Singapore

Japan: United Publishers Services Ltd. Tokyo

Preface

The classification of Australian vegetation as we know it almost certainly began on 19 April 1770 with the English botanist Joseph Banks on H.M.S. *Endeavour*. Banks first described vegetation cover in the vicinity of what is now Point Hicks on the east coast of New South Wales, as 'sloping hills, coverd in Part with trees or bushes, but interspersd with large tracts of sand'. His impression presaged a difficult time for the earlier settlers of the next 100 years or so who had to come to grips with terminology for the 'strange and wild' vegetation of the Australian continent. In the absence of any indigenous classification, vegetation was largely described in terms of the English 'verdure' still much in the minds of the pioneers. From this period, the almost folk-oriented terms such as 'tree', 'shrub', 'woodland' and so on made their way into Australian botanical and ecological literature. The attempted equivalence with the vegetation of England and continental Europe was carried further into specific descriptions of trees such as the eucalypt 'boxes', so-named because the bark resembled the European or common box (*Buxus sempervirens*).

This early cognitive/descriptive phase has persisted in part to the present day despite such difficulties as reconciling the term 'shrub' for a 20 m tall multistemmed woody plant, with the European definition that usually refers to shrubs as plants < 2 m tall, or as Carpenter's ecological glossary of 1938 puts it, 'of smaller structure than a tree'.

From the late nineteenth century until the 1930s the physiognomic and physiologically based philosophies of Warming and Schimper set the scene for relating vegetation classification to environment, but in Australia as elsewhere, this was not developed effectively due largely to a lack of detailed knowledge of ecosystem processes or plant function. In post World War II Australia, vegetation structure and floristics proved to be the main criteria from which schemes were derived by Christian and Perry and Beadle and Costin. Wood, Williams and Ross Cochrane also used structural and floristic attributes, often within an environmental connotation.

It was not until the advent of modern computer methods in the early 1960s, that Webb, Williams and Tracey were able to develop a method of classifying complex Australian rainforests in a way that has become generally accepted by Australian ecologists. Their technique embodied the addition of life forms, and leaf size classes as well as structure and floristics but has generally remained specific for rainforest.

For vegetation in the broad sense, Specht, on the other hand developed a simple classification based on height and foliage projective cover (see this volume) that was related to plant biomass and to physiological principles.

The systems mentioned thus far are usually applied to 'natural' i.e. 'intact' vegetation, and in Webb's case, to 'climax' rainforest types. Unfortunately the systems are incompatible, e.g. most of Webbs' rainforest types fall within one structural category of Specht's system. Because they are attractively simple however, these methods have been only slightly modified by mappers of vegetation (e.g. Beard, Webb and Carnahan) for regional and continental vegetation.

Despite this, at finer scales, there has been an increasing and uncomfortable awareness among plant and animal ecologists that because most Australian vegetation is highly disturbed and often in a state of flux, classificatory systems employing largely 'static' attributes do not provide a useful basis for classifying some of the more fundamental dynamic characters of ecosystems.

This burgeoning problem led some of us to feel the time was ripe for an assessment of the status of vegetation classification in Australia, and this book is the result of a workshop that was held largely for that purpose.

The book is intended as a summary of the major lines of contemporary thought on the classification of Australian vegetation and although some time has unfortunately elapsed since the meeting in October 1978, the trends are still valid. The reader will find that some of the papers are very much set in the workshop context with the presentation of new ideas and modifications of old ones. They are not set out so much as definitive treatises but rather as stimuli to further thought. It is our hope that such a stimulus will pave the way towards a better understanding of the unique vegetation on this continent and ultimately to effective methods of classification that allow Australian vegetation to be more clearly viewed in a global context.

CANBERRA, 1981

A. N. GILLISON

Contributors

Adomeit, Mrs E. M.	CSIRO Division of Land Use Research, P.O. Box 1666, Canberra City, A.C.T. 2601
Anderson, Professor D. J.	School of Botany, University of New South Wales, P.O. Box 1, Kensington, N.S.W. 2033
Austin, Dr M. P.	CSIRO Division of Land Use Research, P.O. Box 1666, Canberra City, A.C.T. 2601
Beard, Dr J. S.	6 Fraser Road, Applecross, W.A. 6153
Boyland, Mr D. E.	Botany Branch, Department of Primary Industries, Meiers Road, Indooroopilly, Qld 4068
Bridgewater, Dr P. B.	School of Environmental and Life Sciences, Murdoch University, Murdoch, W.A. 6153
Carnahan, Dr J. A.	Botany Department, The Faculties, Australian National University, P.O. Box 4, Canberra, A.C.T. 2600
Dale, Dr M. B.	CSIRO Division of Tropical Crops and Pastures, Cnr Carmody Road and Chancellor's Place, St Lucia, Qld 4067
Fox, Dr B. J.	School of Zoology, University of New South Wales, P.O. Box 1, Kensington, N.S.W. 2033
Fox, Mrs M. D.	National Herbarium of New South Wales, Royal Botanic Gardens, Sydney, 2000
Gillison, Dr A. N.	CSIRO Division of Land Use Research, P.O. Box 1666, Canberra City, A.C.T. 2601
Graham, Mr A. W.	CSIRO Division of Land Use Research, P.O. Box 1666, Canberra City, A.C.T. 2601
Greenslade, Dr P. J. M.	CSIRO Division of Soils, Private Bag No. 2, Glen Osmond, S.A. 5064
Groves, Dr R. H.	CSIRO Division of Plant Industry, P.O. Box 1600, Canberra City, A.C.T. 2601

- Gullan, Dr P. K. National Herbarium,
Birdwood Avenue,
South Yarra, Vic. 3141
- Havel, Mr J. J. Forests Department,
Rural and Industries,
Bank Building,
54 Barrack Street,
Perth, W.A. 6000
- Hopkins, Dr M. S. CSIRO Division of Land Use Research,
P.O. Box 1666, Canberra City, A.C.T. 2601
- Johnson, Dr R. W. Queensland Herbarium,
Department of Primary Industries,
Meiers Road, Indooroopilly, Qld 4068
- Jupp, Dr D. L. B. CSIRO Division of Land Use Research,
P.O. Box 1666, Canberra City, A.C.T. 2601
- Lance, Dr G. N. Avon Universities Computer Centre,
University of Bristol,
Bristol BS8 1TW. U.K.
- Laut, Dr P. CSIRO Division of Land Use Research,
P.O. Box 1666, Canberra City, A.C.T. 2601
- Margules, Mr C. R. CSIRO Division of Land Use Research,
P.O. Box 1666, Canberra City, A.C.T. 2601
- Mayo, Mr K. K. CSIRO Division of Land Use Research,
P.O. Box 1666, Canberra City, A.C.T. 2601
- Noble, Dr I. R. Research School of Biological Sciences,
Australian National University,
P.O. Box 4, Canberra, A.C.T. 2600
- Norris, Dr K. C. CSIRO Division of Entomology,
P.O. Box 1700, Canberra City, A.C.T. 2601
- Pickard, Mr J. Antarctic Division,
Kingston, Tasmania 7150
- Specht, Professor R. L. Botany Department,
University of Queensland,
St Lucia, Qld 4067
- Thompson, Mr C. H. CSIRO Division of Soils,
Cunningham Laboratory,
Mill Road, St Lucia, Qld 4067
- Williams, Dr W. T. CSIRO Division of Tropical Crops and
Pastures,
C/- Pastoral Research Laboratory,
Private Bag, Townsville, Qld 4810

Contents

Preface

v

Contributors

vii

Introductory Notes by D. J. ANDERSON

xv

PART I ATTRIBUTES AND THEIR SELECTION

Floristic Attributes

1	Potential application of the Zürich-Montpellier system of vegetation description and classification in Australia by P. B. BRIDGEWATER	3
	<i>Structural Attributes</i>	
2	Foliage projective cover and standing biomass by R. L. SPECHT	10
	<i>Dynamic and Functional Attributes</i>	
3	The use of dynamic characteristics in vegetation classification by I. R. NOBLE	22
4	Towards a functional vegetation classification by A. N. GILLISON	30
	<i>Seral Considerations in Woody Vegetation Types</i>	
5	Disturbance and change in rainforests and the resulting problems of functional classification by M. S. HOPKINS	42
6	Structural typing of tropical rainforest using canopy characteristics in low-level aerial photographs—a case study by M. S. HOPKINS and A. W. GRAHAM	53
7	Choice of attributes to study succession in brigalow (<i>Acacia harpophylla</i>) Communities by R. W. JOHNSON	60
8	Seral considerations in heathland by R. H. GROVES and R. L. SPECHT	78
	<i>Classification Requirements in Vegetation Mapping</i>	
9	Comparison of three small-scale 1:1 000 000 vegetation mapping techniques by J. PICKARD and D. E. BOYLAND	86
10	Classification in relation to vegetation mapping by J. S. BEARD	97
11	Mapping at a continental level by J. A. CARNAHAN	107

PART II METHODOLOGY AND APPLICATION

Numerical Approaches

12	Underlying assumptions in numerical classification by W. T. WILLIAMS	117
13	Handling large data sets by G. N. LANCE	120
14	The role of certain diversity properties in the standardisation problems of numerical vegetation classification by M. P. AUSTIN	125
15	An approach to grammatical classification by M. DALE	141
	<i>The Use of Multispectral Imagery</i>	
16	The separation of traditionally mapped land cover classes by LANDSAT data by E. M. ADOMEIT, D. L. B. JUPP, C. R. MARGULES and K. K. MAYO	150

x *Contents*

<i>Vegetation and Animal Distribution</i>		
(a) <i>Vertebrates</i>		
17	A comparison of vegetation classifications as descriptors of small mammal habitat preference by B. J. FOX and M. D. FOX	166
18	Floristic classifications, small mammals and birds by P. K. GULLAN and K. C. NORRIS	181
(b) <i>Invertebrates</i>		
19	Ant distribution, vegetation and soil relationships in the Cooloola-Noosa River area, Queensland by P. J. M. GREENSLADE and C. H. THOMPSON	192
<i>Land Use Application</i>		
20	Vegetation classification and the land use geographer by P. LAUT	208
21	Vegetation classification as a basis for land use planning by J. J. HAVEL	219

Tables

1.1	Relevés collected on a grid in the Victorian whipstick between pp. 2 and 3	
1.2	27 relevés from the Karri forest of South Western Australia between pp.3 and 4	
1.3	Dominance-Structural classification	6
1.4	<i>Juncetum kraussi</i> with 2 sub-associations	6
1.5	Presence table for indicated species in salt-marsh vegetation	7
2.1	Structural formations in Australia	19
3.1	Vital attributes associated with the method of persistence	25
3.2	A comparison of the classification of Gill and the vital attributes	26
3.3	A comparison of the classifications of Gill and Noble and Slatyer	26
4.1	<i>Modal elements of the structural forma</i>	32
4.2	Soil parameters used in Fig. 4.1	37
4.3	Distribution of structural <i>modi</i> along a soil catena at Wycanna	39
6.1	Average monthly and annual rainfall for Tully, South Johnstone and Innisfail	54
10.1	Descriptive notation based on Kühler (1949) and Dansereau (1951)	98
10.2	Nomenclature of vegetation units	100
10.3	Classification of tropical grassland communities	103
14.1	An example of a stand/species table acceptable as a 'perfect group' for the two parameter model	126
16.1	Descriptions of land cover classes and sub-classes	151
16.2	Poorly separated sub-classes	157
16.3	Confusion matrix for broad classes of land cover	160
16.4	Confusion matrix for the 26 sub-classes	161
17.1	Correlation coefficients between mammal classification and vegetation classification	170
17.2	Correlation coefficients between captures for each mammal classification groups and mammal groups classified by vegetation attributes	171
17.3	Variables contributing to the first three factors in each factor analysis	171
17.4	Factor correlations	174
17.5	Contribution coefficients for independent variables	175
17.6	The proportion of variance accounted for by structural and/or floristic variables	176
17.7	Variance explained by multiple regression predictive equations for mammal factors	176
18.1	Constancy table of the floristic groups	182, 183
18.2	A brief description of the structure and environment of each floristic vegetation type	184
18.3	Mean capture success of small mammals	184

xii *Tables*

18.4	The four vegetation types compared on the basis of small mammal captures and bird species numbers	184
18.5	A list of potential food resources for birds and small mammals within a terrestrial ecosystem	185
18.6	An assessment of the abundance of plant-food resources	187
18.7	A constancy table for bird species recorded in floristic types	188
19.1	Landscape units in the Cooloola-Noosa River area	194, 195
19.2	Distribution of ant collection sites	200
20.1	Categories used in three small-scale land use classification systems	210
20.2	Structural types of vegetative cover	215

Figures

2.1	Changes in Foliage Projective Cover and Current Annual Growth Increment with age	11
2.2	The proportion of root biomass: total biomass	12
2.3	Relationship between component C and Mean Annual Temperature	14
2.4	Foliage Projection Cover of the upper stratum of Australian plant communities	16
2.5	Open communities change abruptly to closed communities	17
3.1	A summary of the 10 vital attributes associated with the method of persistence	24
4.1	Minimum spanning ordination of functional plant attributes	38
5.1	Schematic representation of reconstructive secondary succession in Complex Notophyll Vine Forest	43
5.2	Schematic representation of reconstructive secondary succession pathway and natural regeneration in rainforest	45
6.1	Location map showing the position of the Downey Creek area	55
6.2	Map of the Downey Creek area showing the distribution of the 13 forest types	58
6.3	Extended sections showing relationships between forest types and geomorphology across Downey Creek Valley	59
6.4	Diagram showing the recombination and reallocation of the 11 initial 'photograph types'	61
7.1	Ordination of 66 samples	70
7.2	Changes in cover (C), density (D), and frequency (F) with time	71
7.3	Ordination of 66 samples using unstandardised cover data showing the eleven isochronous bands	72
7.4	Ordination of 66 samples using unstandardised cover data showing successional trajectories	73
9.1	Location map showing areas mapped and test area	87
9.2	Numbers of boundaries in each state and the degree of matching	89
9.3	Sections of test area	90, 91
14.1	Relationship between stand richness and two environmental gradients	127
14.2	Stand richness in relation to pH in two grasslands in the Derbyshire dales	128
14.3	Classification of forest type data from Kolombangara with different standardisations	130
14.4	Graphic analysis of diversity properties of Kolombangara stands	132
14.5	Graphic analysis of diversity properties of Queensland rainforest stands	134
14.6	Classification of forest type stands from Kolombangara	136
14.7	Two-way table comparison of groups from floristic and diversity classifications of Kolombangara forest type data	137

xiv *Figures*

15.1	A serial shape grammar for the snowflake curve	142
15.2	The first four curves of the snowflake curve	143
15.3	A parallel shape grammar for the snowflake curve	144
16.1	Land cover sub-class boundaries superimposed on the orthophoto	153
16.2	Land cover classes coded by pixel on the geometrically corrected 'pixel grid'	155
16.3	Transformed sub-class means plotted against canonical variates	156
16.4	Pixels which were re-classified to a new sub-class	158
17.1	The study area	167
17.2	The 38 quadrats	169
17.3	A projection onto the plane of the first two principal components	172
17.4	Simple regressions of factors	173
19.1	Diagrammatic cross section across the Cooloola sandmass	193
19.2	Tree canopy area at CSIRO research sites	197
19.3	Field assessment of ground cover	198
19.4	Air and soil surface temperatures	199
19.5	Frequency of selected ant species	201
19.6	Affinity between landscape units	203
19.7	Distribution of three community elements	205
20.1	Explanation of environmental unit tables	213
20.2	An example of vegetative cover and land use mapping	214

Introductory Notes

'Map me no maps, Sir, . . .'

D. J. ANDERSON

INTRODUCTION

A keynote speaker's life is clearly not meant to be easy. Not only does the original program for this workshop suggest he is to be 'finalised'—goodness knows what one should read into that euphemism—but you will appreciate too that a keynote is the lowest note of the scale of any key. If at the end I do in fact suffer the dire fate the organisers have anticipated for me, I can only hope this will prove to be a sheltered workshop.

There is I think, a real sense in regarding this workshop as a watershed. It seems to me that academic tradition, regarding as it does abstraction and maybe even abstruseness as virtues, has turned away from conventional attempts to map variation in vegetation of the earth's surface—the familiar structural and floristic maps that owe as much to cartography as they do to botany—and now seeks to explore rather the range of methodologies that might provide us with more versatile procedures to attain ecological as well as merely geographical objectives. The watershed we have reached is the realisation that we are no longer dealing with vegetation classification as a mechanical exercise in map colouring, but rather that we are dealing with what psychologists call cognitive mapping—an abstraction covering those intellectual abilities that enable us to collect, store, manipulate and analyse data about vegetation variation in order that we may produce organised representations of that variability for a variety of practical purposes.

It is this notion that underlies the theme of this introductory address, incorporated in the words that Henry Fielding wrote more than 200 years ago: 'Map me no maps, sir, my head is a map, a map of the whole world.'

WHY CLASSIFY VEGETATION?

In attempting to provide some generalised background for our subsequent discussions at this meeting, it may not be entirely trivial or vexatious to ask ourselves why we wish to classify vegetation in the first place. As I look around the audience and think of your varied interests and expertise I realise the possible reasons are themselves pretty varied. There are certainly some who would claim an importance for recording the Australian vegetation types as a basis for both documenting an important resource base and for applied activities involving land-use planning or environmental impact studies; others among you may wish to use a classification as a first step in assessing correlations between vegetation and environment, or more specifically to generate hypotheses concerning particular ecological questions which may not be amenable to conventional

experimentation. Yet others among you may be as much concerned with the utility and maybe even the artistry of classificatory methods as such, and choose to use vegetation as your data source rather than analyse information on juvenile delinquents or other seemingly intractable multivariate problems.

Clearly our objectives in classifying will be varied, and justifiably so, depending on the context in which we choose or are constrained to operate; equally clearly our philosophical bases and associated cognitive mapping procedures may well vary in relation to these objectives. Despite these valid differences in background, however, we all face the question as to how we might best resolve three dilemmas that face any classifier, the dilemmas of

- (i) uniqueness *v.* generality
- (ii) similarity *v.* difference
- (iii) state *v.* process

in producing functional classifications.

Like most dilemmas we face in this world, there is likely no unique and probably no universally acceptable solution to any one of them, and we may have to accept therefore some compromises if we are to proceed constructively in resolving these apparent antitheses.

UNIQUENESS AND GENERALITY

Classical Aristotelean classification normally demands that entities are assigned to particular groups by reference to a comparatively small number of characters, to circumscribe or better, define what Aristotle considered the 'essence' of the group to be. Practising taxonomists have found this to be a useful basis for delimiting individual taxa, but they are not slow to realise that this procedure lacks the predictive quality of descriptions made for high order taxa such as families or phyla, in which generality rather than uniqueness is the prime objective. What is true of organismal classification is no less true of vegetation classification: the potential shortcoming of a neat physiognomic classification—while it may to some people provide the 'essence' of vegetation typification—is that it may lack flexibility and predictive value, at least in the wider sphere of potential usage I am envisaging here. The essential problem we face is to decide whether or not to seek a generally acceptable classification strategy, knowing that it will be sub-optimal for every specialist demand made of it, or rather admit the need to meld a collection of individually optimal strategies into an unwieldy global strategy when we have a paramount need for flexibility. In my view the most effective compromise might appear when we discuss attributes and scales, but I suggest we should not lose sight of this potential stumbling block in our later discussions.

SIMILARITY AND DIFFERENCE

For classification to be possible, we have to deal with entities which are simultaneously both similar and different. That this is a trivial truism makes it no less significant to our cause, but rather highlights the essential need to produce operationally useful definitions of vegetation entities before we engage the classificatory process. In practical terms

the problem is not so much in defining a similarity measure, a minimal area, an inter-stand distance or whatever, but rather to define more critically the boundaries of functionally effective entities and, in our numerical procedures, to pay closer attention to our presently empirically derived 'stopping rules'.

STATE AND PROCESS

In the context of vegetation classification, most collected data, whether they be nominal, ordinal, numeric, meristic, linked or serially dependent, are effectively parts of a state description. It has frequently been argued, and on some occasions with validity and force, that state descriptions in ecological contexts provide little real guidance to the underlying processes which generate these states. Clearly there will be situations in which we will need to use the results of a classification to predict or hypothesise changes in state—process if you like—in a vegetation matrix: successional changes and dynamic responses to varying management regimes are two such examples. Given this requirement, we will need to select our basic data for analysis with an eye not only to what is evidently present and measurable, but also to those attributes which are likely to be indicative of change—elements that we might think of as being 'process-sensitive'.

MAPS AS MATRICES

The orderly arrangement and display of a set of observations relating to a piece of vegetation can be thought of as a description of a segment of reality. In those days when men were literate and before word processors had been invented, the description of regional vegetation types had achieved a high art form in both poetry and prose, and I do not think I will be betraying other than proper British prejudice if I cite William Wordsworth, Arnold Bennett and D. H. Lawrence as examples of acute observers of regional vegetation variation: they were all cognitive map makers as well as fine wordsmiths, and maybe if we were to look at their work more closely we would see they were pretty subtle classifiers too.

In terms of academic tradition though, verbal descriptions were clearly inadequate for the reasons I have already alluded to and the map became the accepted vehicle of rigorous description, with the points, lines, areas and boundaries defining vegetation types on a sheet of paper—a *mini mappa mundi* so to speak—becoming an academically acceptable form of art nouveau.

The upsurge of interest in developing quantitative and particularly multivariate methods in the past two decades has seen the translation of states from the map to the matrix as a basic strategic device for displaying raw data; the ability to manipulate matrices has provided the vehicle for analysing such data sets with, one hopes, economy and precision and even on occasion with insight.

It is the case, I think, that any information that can be mapped can also be entered into a simple two-dimensional matrix. The essence of this exercise is that an initial ranking of our observation units, be they grid co-ordinates, quadrats or regions, can be associated with a second ranking sequence of various attributes—floristic composition, structural forms, environmental characteristics or whatever—which serve to further

describe these locations. Given that we know the nature of the problem we wish to solve, we now have a body of experience and expertise which enables us to manipulate such matrices in order to display complex bodies of multivariate and multistate data more economically as vector maps.

There are many people here better qualified than I am to discuss the appropriate strategies and tactics of matrix manipulation, but I would like to refer to two aspects of data collection that critically influence the form and eventual utility of a matrix, namely attributes and scale.

ATTRIBUTES

The first point I wish to make is that compiling data in matrix form itself involves classification; in other words, as investigators of a particular research problem we have to choose what we regard as appropriate attributes to record or measure.

Having been disrespectful, at least by implication, of physiognomic and floristically based classification, let me hasten to add that I believe they have a valid role to play still, not least because the concepts of formation and association were defined originally in terms of these attributes. Certainly structural attributes are important now not only to define formation-types, but are also important when dealing with vegetation in which floristics are not well documented (e.g. in much of the world's and especially Australian rainforest, cf. Webb *et al.* (1976)), or in those situations where structural classifications are of special value in the definition of animal habitats (e.g. for small mammals, birds and reptiles in an Australian context). (An army tank driver negotiating a forest may be justifiably immune to the floristic delights he is forced to manoeuvre through, but very properly concerned with the structural pattern exhibited by his complex obstacle.)

Similarly floristic classifications must maintain a place in vegetational schemata when our interests are primarily biogeographical, or in those situations where wildlife management may be the primary objective of an ecological investigation. It should be emphasised, however, that floristic classification may serve some purposes more economically if taxa other than species are the attributes subjected to classification, as Dale and Clifford (1976) and Walker and Guppy (1976) have illustrated recently in relation to generic and even familial assemblages. The additional point I would emphasise in this context is that made by Harper (1977): that floristic diversity in a community has ecological meaning only in so far as it is sensed by the individuals within it. This is to say that at certain scales we must be wary of imposing our anthropocentric prejudices so as to produce seemingly elegant but nonetheless ecologically irrelevant classifications.

So far I have been speaking of structural attributes in terms only of state descriptions, but it is important to appreciate that some commonly recorded structural features (or indeed absence of some structural features) may be usefully indicative of process as well as state. The vertical distribution of canopy types in a forest may have physiological implications for light attenuation and all that might imply in process terms; gaps in a canopy might have implications for regeneration pattern; evergreenness or deciduousness might well relate to litter accumulation and nutrient cycling; a spectrum of life

forms may indicate something of seasonal variation or seral change in a sample of vegetation; the analysis of dominance types might well form a basis in some vegetation types for studies in competitive processes. The possibilities, if not endless, are certainly considerable, and serve to emphasise the importance of a preliminary decision as to why we are recording particular attributes in relation to a particular classificatory objective.

Other types of attributes might be chosen deliberately to illustrate process and to predict possible change in vegetation composition; the so-called 'vital' attributes of Noble and Slatyer (1977) clearly fall into this category, as do the experimentally devised relations between such variables as seed weight and subsequent height growth of various plants reported by Grime and Jeffrey (1965). It may be that field ecologists would do well to look at some of the plant attributes studied by experimental ecologists—components of reproductive systems, leaf orientation, morphogenetic allocation of biomass, intrinsic relative growth rates, production of root exudates, for example—to see if any such attributes might either directly or in some derived way provide usable and useful additional attributes for inclusion in a data matrix. This question can only be answered by asking another: is a particular attribute correlated with or serially dependent on another already in use, and/or will it be relevant to the ecological question we are asking?

Most of the attributes I have been referring to so far can be regarded as intrinsic, in the sense that they refer to directly observable plant features or responses. In those investigations that seek to correlate vegetation variation with corresponding environmental variation, it will of course be necessary to include attributes which are in a sense external to the plants themselves. Such extrinsic attributes include not only obvious climatic, topographic and soil parameters but also encompass various forms of environmental scalar (cf. Loucks 1962), bioclimatic growth indices and data such as thermal imagery from aerial or satellite reconnaissance. A good example of vegetation classification using such indirectly acquired attributes from aerial photographs of arid rangeland in Western Australia is reported in Hacker (1979).

The list of possible attributes that could be used in vegetation classification is extensive, but I am not sure that we have always been as innovative in searching for ecologically meaningful attributes as we might have been. Innovation is not the sole criterion of good judgment and practice, however; the utility of particular attributes may well vary with different scales of investigation, and we should not neglect the documented experience that a group of qualified and experienced observers may well record differently an attribute that can take a wide range of states. Once again effective compromise should be the keynote of any initial attribute classification.

SCALE

It is again a truism to assert that natural environments are heterogeneous in both space and time, but the simplicity of this observation should not be allowed to cloud the importance of adopting appropriate scales of attribute sampling as a preface to subsequent classification. The range of possible investigatory scales, ranging as it can from continental formation types to local, small-scale vegetation mosaics, is virtually limit-

less; and a scale that is biogeographically meaningful may be several orders of magnitude too large for an ecologist who wishes to assess competitive effects between plants or the niche width of small mammals in a classificatory context. Without wishing to preach to the converted, one may justifiably ask if notions of defining 'representativeness' of vegetation units could not usefully be based on other than merely floristic criteria: I can see no inherent reason why the concept of minimal area could not be practically extended to encompass a minimal structural mosaic unit,* a minimum environmental scalar unit, or even a minimal nearest neighbour unit for some purposes. As with the consideration of attribute choice, a choice of appropriate scale or scales for a particular investigation will necessarily involve a compromise between 'intellectual' optimality and practical feasibility.

THE USER VIEWPOINT

Underlying this inchoate preamble to the substance of our later discussion in this meeting is the theme that different people will be seeking different objectives in classifying vegetation, and that in the main these varying objectives will be equally valid within their respective contexts. Even in the long run I doubt if we will all be convinced that a single classificatory approach will be optimal for all purposes; indeed to make this elementary point somewhat ruefully, I note that Mitchell (1973) in his book *Terrain Evaluation* writes 'although widely used in recognising terrain types, vegetation has not normally been regarded as definitive of units . . . the plant population of an area is an intrinsically different phenomenon from its terrain, and cannot logically be regarded as part of it . . . vegetation is an ephemeral rather than a permanent characteristic of landscape'.

While Mitchell would clearly not be everyone's choice as a defence counsel for vegetation classifiers, his comments do underline the legitimate variety of interest and objectives different practitioners of classification may have. I emphasise this point because too often debates of the kind we are about to engage in degenerate into methodological free-for-alls. Perhaps it will be more profitable if we remember at the outset that one technique is rarely better or worse or more nearly optimal than another, unless we specify particular objectives or methodological constraints that must be met.

Rather, if we accept that the major objectives of vegetation classification are subsumed under the following headings:

- (i) comparison of composition between stands of vegetation;
 - (ii) deduction of generalisations about the range of compositional variation present;
 - (iii) correlation of vegetation with environment;
 - (iv) assessment of resource potential, for management or land-use purposes;
and
 - (v) prediction of future compositional or structural changes;
- and that these objectives must be secondarily defined in terms of appropriate attributes

* The 'structural cell' of Grabau and Rushing (1968) is a case in point.

recorded at relevant scales, then we should be philosophically prepared to gain the most from the varied assortment of contributions programmed for the remaining part of this meeting.

I commend, in the face of topical political events, this liberal philosophy to you: that we attempt to shed our prejudices and follow, at the start of the meeting, the bellman who captained the ship in 'The Hunting of the Snark':

He had bought a large map representing the sea,
without the least vestige of land:
And the crew were much pleased when they
found it to be
A map they could all understand
'What's the good of Mercator's North Poles and Equators,
Tropics, Zones and Meridian Lines?'
So the Bellman would cry, and the Crew would reply
'They are merely conventional signs'.

'Other maps are such shapes, with their islands and capes!
But we've got our brave captain to thank'.
So the crew would protest 'that he's brought us the best—
A perfect and absolute blank!'

If we can thus easily shed our present philosophical positions and prejudices, or in Andy Gillison's phrase 'clear the mental register', I think we might well find that we can conveniently forget this keynote address, and rather remember this meeting not only as a watershed but also a keystone in the future development of vegetation classification in Australia.

REFERENCES

- Dale, M. B., and Clifford, H. T. (1976). On the effectiveness of higher taxonomic ranks for vegetation analysis. *Aust. J. Ecol.* **1**: 37-62.
- Grabau, W. E., and Rushing, W. N. (1968). A computer-compatible system for quantitatively describing the physiognomy of vegetation assemblages. In: *Land Evaluation* (ed. G. A. Stewart), pp. 263-75. Macmillan, Melbourne.
- Grime, J. P., and Jeffrey, D. W. (1965). Seedling establishment in vertical gradients of sunlight. *J. Ecol.* **53**: 621-42.
- Hacker, R. B. (1979). Studies of the ecology and range conditions of two arid ecosystems. Ph.D. thesis, University of New South Wales.
- Harper, J. L. (1977). *Population Biology of Plants*. Academic Press, London.
- Loucks, O. L. (1962). Ordinating forest communities by means of environmental scalars and phytosociological indices. *Ecol. Monogr.* **32**: 137-66.
- Mitchell, C. (1973). *Terrain Evaluation*. Longman, London.
- Noble I., and Slatyer, R. O. (1977). The effect of disturbance on plant succession. *Proc. Ecol. Soc. Aust.* **10**: 135-45.
- Walker, D., and Guppy, J. C. (1976). Generic plant assemblages in the highland forests of Papua New Guinea. *Aust. J. Ecol.* **1**: 203-12.
- Webb, L. J., Tracey, J. G., and Williams, W. T. (1976). The value of structural features in tropical forest typology. *Aust. J. Ecol.* **1**: 1-28.

PART I

ATTRIBUTES AND THEIR SELECTION

1

Potential application of the Zürich-Montpellier System of vegetation description and classification in Australia

P. B. BRIDGEWATER

INTRODUCTION

Traditional approaches to non-quantitative description and classification of Australian vegetation have evolved from the work of Wood (1939), through Beadle and Costin (1952) to Specht (1970) and Specht *et al.* (1973). All these approaches emphasise plant communities defined as dominance-types (term of Whittaker (1973)). Other approaches such as Beard and Webb (1974) and Muir (1977) have also emphasised structure rather than floristics. However, recent publications have examined the Zürich-Montpellier (henceforth referred to as Z-M) approach, e.g. Bridgewater (1971), Busby and Bridgewater (1977), Stuwe and Parsons (1977), Bridgewater (1978).

As in many English speaking countries, the potential application of the Z-M technique in Australia has been largely ignored, or peremptorily dismissed. Muir (1977) in discussing vegetation classification notes '[they] have produced complex classifications which are too time-consuming for large area surveys. The Zürich-Montpellier system presents similar problems'. That these attitudes persist is quite surprising because two recent accounts of the practices and procedures of the Z-M system are available in English: Westhoff and van der Maarel (1973) and Muller-Dombois and Ellenberg (1974). Although the former authors refer to the 'Braun-Blanquet approach', use of the term 'Z-M system' suggests a less pedagogical approach, and recognises that in recent years workers from many countries have made important contributions to the study of this form of phytosociology.

There seems thus a case for restating the potential value of the Z-M system within an Australian context.

PERSPECTIVE

Typical objections to the Z-M system could include: 'it is subjective', 'it requires a high input of labour', 'it requires a high taxonomic ability', and 'I don't really understand it'.

Certainly the objectivity possible with completely quantitative techniques is not available in the Z-M system. What it does offer, however, is a system of ranking vegetation samples or quadrats to indicate any groupings of such samples as may exist. Vegetation samples (often called relevés) are simply areas of landscape identified by a listing of all species present. The size of area is usually greater than the minimal area of

TABLE 1.1
Relevés collected on a grid in the Victorian whistick, and arranged into groups by tabular synthesis

Group code	A	B					C	D
		1	2	3	4	5		
Sub-group code							1	
<i>Acacia montana</i>	+ 1 2	1	+					
<i>Daucus glochidiatus</i>	+ 2 2 2							
<i>Dianella revoluta</i>	+ + 1 +							
<i>Eucalyptus sideroxylon</i>								
<i>Melaleuca decussata</i>								
<i>Londonia behrii</i>								
<i>Pulicaria pedunculata</i>								
<i>Acacia pycnantha</i>	+	+						
<i>Wahlenbergia gracilis</i>								
<i>Triozyme eatori</i>								
<i>Claudia aggregata</i>								
<i>Helichrysum obcordatum</i>								
<i>Eucalyptus microcarpa</i>	2 2 4 3 3 4 2	1 +	1	1 + 1 2	4	2 3 4 2	1 +	
<i>Eucalyptus leucoxylon</i>	3 1 1 2 2 2 2	3	3	1 2 2 4	3 2 4 1 4 3	1 +	+ + +	
<i>Grevillea alpina</i>								
<i>Dampiera lanceolata</i>								
<i>Haloragis tetragyna</i>								
<i>Baeckea ramosissima</i>								
<i>Crowea exalata</i>								
<i>Acacia williamsonii</i>	3 1	+ 4 1 + 4		1 1 4 + 2 3	2 1 3 4 4 2	3 3	1 + 4 1	5 1 + + +
<i>Danthronia pallida</i>	2 2	+ 1	1 + 1 2 + 2 + + 1	+ 1 1 + + 1	1 1 + 1 +	+ + 1	1 + 1	3 + + + +
<i>Eucalyptus viridis</i>						2 3 3 3 3 2	2 4 + 2 4	2 4 3 3 2 1 2 4 1 3 3 4
<i>Eucalyptus behriana</i>						2	1 2 1 4 4 3 4 2 3 3 3 4 3 1 4 2 2 3	4
<i>Melaleuca uncinata</i>						4	4	
<i>Acacia acuminata</i>	2	+ 3 1 + +	3	1 +	1 + 3 2 + +	1 2 +	2 1	1 2 1 2 + + 2 + 2 2 1 +
<i>Cassinia arcuata</i>	+ 3 + + 1 2 1 1 1	1		+ + 1	1 + + + +	+ + 1	+ 2 + + + +	+ + + + +
<i>Danthronia carphoides</i>	2 2 1 4 + 2	+ + 4	+ + +	1 + + 1	1 + 2 +	+ + 1	+ 3 2 1 + + 1 1	+ + + 1
<i>Pulicaria largiflorens</i>	+ + + + +	+ + + + +	+ + + + +	+ + + + +	+ + + + +	+ + 1	+ + + + 1	+ + + 1
<i>Thysanotus patersonii</i>	+	+ + + + +	+ + + + +	+ + + + +	+ + + + +	+ + 1	+ 1 1 + + +	+ + + 1 +

TABLE 1.1 *Continued*

Group code	Sub-group code	A	B	C	D	
		1	2	3	4	5
3 5 4 4 5 6 5	<i>Senecio quadridentatus</i>	++ +	++ +	++ +	1 1 1 1 1	2 3 5 3 6 4 4
0 0 0 1 1 1 1	<i>Goodenia amplexans</i>	+	+	+	+	6 3 1 5 3
7 9 9 0 1 1 0	<i>Daviesia genistifolia</i>				+	6 3 6 4 4 4 4
0 9 3 1 2 3 2 1	<i>Hibbertia exutia</i>				+	5 5 5 5 6 6 6 6
0 9 3 1 2 3 2 1	<i>Crassula macrantha</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Dichopogon strictus</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Camptopappus intricatus</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Acacia austrofaldii</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Poa australis</i> s.l.				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Bryum</i> spp.				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Briza minor</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Astroloma humifusum</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Helichrysum bracteum</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Goodenia gracilis</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Eucalyptus polyanthemos</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Olearia teretifolia</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Lepidium apelta</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Eucalyptus macrocaryncha</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Acacia diffusa</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Caladenia angustata</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Metaleuca wilsonii</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Eriostemon diffinis</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Glossodia major</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Hibbertia stricta</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Correa reflexa</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Eucalyptus polybractea</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Cassytha glabella</i>				+	0 0 0 0 0 0 0 0
0 9 3 1 2 3 2 1	<i>Goodenia varia</i>				+	0 0 0 0 0 0 0 0

2 Attributes and their Selection

the plant formation characterising the landscape (see Muller-Dombois and Ellenberg 1974). The shape of area is usually square, but can be linear or irregular in regions of narrow vegetation zones. It also acts as a one-dimensional ordination, and so embraces both the community and continuum aspects of vegetation. Without doubt the technique could require a great deal of labour by an unfamiliar operator dealing with, say, 100-200 relevés. However, there are several computer packages now available for rapid processing of large data sets using Z-M methods, and one such set is available from this author on application.

Whilst a high standard of taxonomic ability, and comprehensive taxonomic studies, are ideal prerequisites to the most beneficial operations of Z-M techniques, there is no reason not to use those techniques where taxonomic knowledge is poor. In such cases species collection numbers may be used instead of names, pending detailed taxonomic work. It should be remembered the Z-M techniques rely on detecting species interactions—and this can be achieved without knowledge of the species identity. Clearly, the success of Z-M in areas poorly known taxonomically depends on the collection of adequate voucher specimens for subsequent taxonomic work. Thus, floristic vegetation approaches, in areas poorly known taxonomically, can result in simultaneous advances in the understanding of vegetation and plant systematics.

Lack of understanding of exactly how the Zürich-Montpellier techniques work is often a major stumbling block. Many myths are still perpetuated regarding concepts such as fidelity and character species, which many authors have rightly criticised. However, these criticisms are often accompanied by references to old editions or outdated translations of Braun-Blanquet's work on phytosociology. A recent example may be found in Ratkowsky and Ratkowsky (1977). Ironically these authors are not critical of the concepts of fidelity and character species, rather they actually espouse these concepts in a way with which no practising advocate of the Z-M system could really concur!

Much of the movement away from initial dogma has occurred in the last 15 years, in response to ideas that vegetation description and classification should equate with the adoption of the ecosystem (biogeocoenose) as the basic unit of ecological study. Krajina (1960) states that 'The basic phytocoenose, an intrinsic part of the biogeocoenose, should be presented as a plant association, *sensu* Zürich-Montpellier system, liberated from the dogmatic necessity of the exclusive, selective or preferential species'. Ellenberg (1960) noted that the importance of characteristic species, or species of high fidelity, was decreasing more and more—and that such species were only of major importance in the higher vegetation units. Moore (1962), in a response to the paper of Poore (1955), further emphasised the move from *characteristic* to *differential* species.

USAGE

For a fully detailed account of the methodology of the technique, the accounts of Westhoff and van der Maarel (1973) and Müller-Dombois and Ellenberg (1974) are unsurpassed, and it is not proposed to repeat these details here. Rather, three case-studies of Australian vegetation in which the techniques have been applied will be discussed to illustrate its potential.

Case study I—The Victorian whipstick

'Whipstick' is a term used to describe the alternation of spindly mallee scrub and open-forest of *Eucalyptus sideroxylon* and *E. leucoxylon* in the central region of Victoria. A dominance-type classification of vegetation in an area of whipstick near Bendigo suggested three associations, based on the scheme of Specht (1970):

- (a) *E. sideroxylon-E. leucoxylon-E. microcarpa* Open-forest
- (b) *E. behriana-E. viridis* Low open-forest
- (c) *E. viridis* Open-scrub

To test the congruence of these associations with floristically defined associations, a sampling grid of six by eleven relevés, each 100 m apart and 10 m × 10 m, was used. Five relevés were only partially vegetated, or unvegetated, which left 61 for analysis. Species present in the relevés were allocated a value on the Braun-Blanquet (1964) cover/abundance scale.

The basic procedure of the Z-M synthetic phase, tabular sorting, was then applied to these data. Four major groups (A-D) and five sub-groups (1-5) of species and relevés emerged from this sorting process, and the results are presented in Table 1. These results show the one-dimensional ordination effect, which is particularly pronounced because of the inclusion of relevés taken in areas of transitional vegetation.

Typically, Z-M analysis involves the deliberate avoidance of heterogeneous vegetation, and aims to sample only homogeneous vegetation. Such a sampling procedure will maximise the likelihood of a clearly defined classification being produced. However, there is no *a priori* reason why tabular sorting cannot be used to analyse data collected on a grid—although such a use would not be traditional. An examination of the relevé groups defined in the table suggests there is only partial congruence of floristically defined relevé groups and the dominance-type associations. Clear congruence exists between relevé group D and *E. behriana-E. viridis* Low open-forest, but relevés referable to *E. viridis* Open-scrub and *E. sideroxylon-E. leucoxylon-E. microcarpa* Open-forest are intermingled within relevé groups A, B and C. The relevé groups appear to be controlled primarily by soil factors, including clay content (greatest in D, least in A), degree of rock outcropping (greatest in B5 and C) and degree of run-off received (least in C, B5, greatest in A). This study is reported in detail in Bridgewater (1979).

The clear correlation of the relevé groups with environmental factors is not mirrored by the dominance-type classification. At this level of investigation, a dominance-type classification is thus inappropriate. Any quantitative classification technique would doubtless reveal relevé groups which would also have a good relationship with abiotic factors. As the data are untransformed the interested reader is invited to try his favourite technique for comparison. Thus, the Z-M approach has yielded information which, although available through other techniques, usually requires a greater technological input. Moore *et al.* (1970) comment in detail on a comparison of techniques and demonstrate the greater flexibility of the Z-M system. The clear advantage of the Z-M system is that it has a low technological requirement, and these data could have been processed in the field. Such processing might have suggested other lines of investigation which could be immediately followed—an obvious advantage in locations which may be considerable distances from a research centre.

TABLE I.2
27 Relevés from the Karri Forest of South Western Australia

TABLE 1.2 *Continued*

4 Attributes and their Selection

Case study II—The Karri forest boundary

Wet sclerophyll forest in south-west Australia is dominated by Karri (*Eucalyptus diversicolor*). At the edge of the Karri forest there is a transition to Jarrah (*E. marginata*) dominated forest. Such a transition may be controlled by a combination of climatic and edaphic factors. A 5 km transect of forest adjacent to the Treen Brook road near Pemberton, Western Australia, was chosen to investigate floristic and structural changes from Jarrah forest to Karri forest.

Relevés (10 m × 10 m) from homogeneous vegetation were sampled along the length of the track. These relevés were then synthesised, using tabular sorting, into six groups (Table 1·2). For this exercise only species presence was recorded. Relevés were also classified into dominance-types (Table 1·3).

As in the previous case study, there appears to be a lack of congruence between floristically defined groups and dominance type associations. In this example, the floristic table clearly shows a gradient across the table, together with one or two clear divisions. A clearly defined boundary is not evident between sites dominated by Karri and sites dominated by Jarrah. Despite this, it would be possible to divide the table between groups A + B and groups C + D + E + F. For nomenclatural purposes, groups A and B may be called the *Acacia drummondii* community and C → F the *Eucalyptus diversicolor* community.

Both these communities have clear sub-communities. For example, the *E. diversicolor* community has an *Opercularia hispidula* sub-community, an *Acacia urophylla* sub-community, and a typical sub-community. Central to the functioning of the traditional Z-M system is the erection of a classification of vegetation units, or associations. The divisions suggested above could form the basis of such a classification. However, because the samples were collected in a confined geographical area, and in a situation where marked climatic and edaphic gradients existed, such a classification might not be widely applicable. To erect a satisfactory Z-M classification samples should be taken from a fairly wide geographical region.

Case study III—South-eastern Australian salt marsh

Data presented here are from a survey at present in progress to define plant associations for southern Australian salt marsh. Data from widely separated sites in Victoria, Tasmania and South Australia have been combined by tabular sorting, and ten associations so far defined. Table 1·4 shows one such association—the *Juncetum kraussii* ass. prov. This association table has the conventional layout of a completed association table. Species which act as differentials for this association are grouped together. In this case two sub-associations are recognisable, and one of these has two variants. Differential species of each level in the hierarchy are grouped under respective headings.

An association, *sensu* Z-M system, may be regarded as being equivalent to the species level in the taxonomic hierarchy. Although some objections exist to grouping associations in a hierarchical way, this can conveniently be accomplished, and can often provide valuable ecological insight. Where a number of association tables for a similar

plant formation exist, these may themselves be synthesised in a presence table. Each column represents an association, and the values recorded against species indicate a measure of the presence of that species in the association. All the salt marsh associations thus summarised are presented in Table 1·5. This table represents the consolidation of 206 relevés. Again the table is presented in a strictly conventional fashion. From this table, it can be demonstrated that a number of associations are linked by high presence of particular species (e.g. associations B-E by *Suaeda australis*). Linking associations in this way can indicate an alliance, which, in turn, may be grouped together in orders and eventually in classes.

Such a hierarchical grouping is of value when making comparisons over large geographical areas. All data gathered and treated by Z-M techniques can eventually be incorporated into a standard classification framework which has world wide acceptance and applicability. The need for links between Australian and other world vegetation systems may not be immediately apparent, but in this case study much insight may be gained by comparing these results with data from Mediterranean European salt marsh.

NOMENCLATURE

Nomenclature has always been a difficulty in achieving acceptance of the Z-M system, with apparently clumsy technical names often causing much anguish. Webb (1954) noted 'It makes no difference . . . if one writes for meadow *Molinio-Arrhenatheretea* . . .' However, in Australia we might write paddock for meadow! Thus the basic argument for retaining latinised associations for names is to facilitate international understanding. Few argue over Latin binomials for species, so there seems little sustainable objection to latinised names for vegetation units. In Table 1·4 I have used the standard terminology for associations, subassociations and variant. Where no clearly defined association table exists or data cover a very limited area (e.g. in case study II), then the use of 'community' is preferable to defining an association name.

CONCLUSIONS

One flexibility which clearly emerges is that Z-M techniques can be applied over a very small area or very large area, with equal ease. A further advantage of the Z-M system is that it has a low-technology requirement both in field and research centre. Contrary to often expressed opinion, associations, communities or relevé groups produced by tabular sorting are efficient mapping units—depending, of course, on the scale of the operation. Clearly the suggestion of a map of Australia based on Z-M association would be ludicrous—but maps of all Australian National Parks on this basis may well be a desirable prerequisite to adequate management. The final units in the Z-M classification are quite suitable for incorporation into dichotomous keys (an example is shown in Busby and Bridgewater (1977)). Such keys can allow untrained persons to identify units in the field to check the accuracy of maps, and monitor changes which may occur in the vegetation.

An obvious but little discussed feature of the Z-M system is that it is a polythetic process, in which all species are used to produce the classification—and remain

6 Attributes and their Selection

TABLE 1.3
Dominance-Structural classification of relevés in Table 1.2

Eucalyptus marginata-E. calophylla Open-forest = Group A + Group B

E. marginata-E. calophylla-E. diversicolor Open-forest = Group C pro parte

E. calophylla-E. diversicolor Open-forest = Group C p.p. + Group D
Group E p.p. + Group F F p.p.

E. diversicolor Open-forest = Group E p.p. + Group F p.p.

TABLE 1.4
Juncetum kraussii, with 2 sub-associations: sellierietosum and suaedetosum

Relevé number:	164	166	722	724	731	702	170	171	172	168	176	175	177	711	713
Number of species:	8	8	7	6	8	8	9	6	7	4	4	8	4	3	7
Differential species of the variants:															
<i>Stipa stipoides</i>	4	5	3	3	1	2									
<i>Gahnia filum</i>		+	3	2	+	4									
<i>Disphyma clavellatum</i>	+						1	3	2	4	1				
Differential species of the sub-association:															
<i>Selliera radicans</i>	+	+	3	4	2										
<i>Suaeda australis</i>							1	.						+	3
Differential species of the association:															
<i>Samolus repens</i>	1	+	1	+	3	1	2	1	1	1	+	+	3	3	2
<i>Sarcocornia quinqueflora</i>	+	+	+		+	+	4					+	3	3	1
<i>Juncus kraussii</i>	2	+	1	4	1	1	3	2	3	3	4	4	4	2	4
Additional species:															
<i>Distichlis distichophylla</i>	1	+				+			1	1					1
<i>Sporobolus virginicus</i>	+								3						
<i>Hemichroa pentandra</i>		+													
<i>Limonium australe</i>			+												
<i>Scirpus marginatus</i>				+	3		+						4		
<i>Parapholis incurva</i>					+										
<i>Apium prostratum</i>						3									
<i>Plantago coronopus</i>							2								
<i>Juncus revolutus</i>								2							
<i>Atriplex hastata</i>								+					1		
<i>Spergularia media</i>									+						
<i>Scirpus nodosus</i>										+					
<i>Senecio lautus</i>											+				
<i>Lythrum hyssopifolia</i>											+				
<i>Conyza canariensis</i>											+				
<i>Rhizoclonium spp.</i>												2			
<i>Agrostis billardieri</i>															
<i>Puccinellia stricta</i>														+	+

Within the sellierietosum 2 variants exists: *Stipa stipoides* variant and *Disphyma clavellatum* variant.

This association is summarised in columns I1 and I2 of Table 1.5.

TABLE 1.5

Presence table for indicator species in salt-marsh vegetation data collected from Victoria, Tasmania,
South Australia

ASSOCIATION CODE: SUB-ASSOCIATION CODE:	A	B	C	D	E	F	G	H	I	J
No. of relevés:	22	7	8	14	21	25	3	4	1	2
<i>Triglochin striata</i>		V	[V] IV	I	III	III	I		1	2
<i>Stipa stipoidea</i>	1			II	V	I	I		1	3
<i>Frankenia pauciflora</i>					V	I				
<i>Distichlis distichophylla</i>	1	II	II	[IV]	III	III	III		1	
<i>Wilsonia humilis</i>					II	II	II		V	
<i>Sarcocornia blackiana</i>					I	I	V		V	
<i>Maireana oppositifolia</i>	1		1							
<i>Agrostis billardieri</i>	1	1	II	II	II	II				
<i>Selliera radicans</i>										
<i>Atriplex hastata</i>										
<i>Spergularia media</i>										
<i>Atriplex paludososa</i>	1		V IV	I	I	II	I			
<i>Arthrocnemum arbusculum</i>	II		V	II	V	V	V			
<i>Samolus repens</i>	1		I	V	V	V	V			
<i>Hemicroca pentandra</i>										
<i>Puccinellia stricta</i>	1		I	V	I	V	V			
<i>Parapholis incurva</i>										
<i>Disphyma clavellatum</i>										
<i>Suaeda australis</i>	1		V IV	V	V	V	V	V		
<i>Sarcocornia quinqueflora</i>										
<i>Arthrocnemum halocnemoides</i>										
<i>Juncus kraussii</i>	I	II	+ III							
<i>Corolla coronopifolia</i>										
<i>Scirpus marginatus</i>	I		I	I	I	I				
<i>Sporobolus virginicus</i>										

I = species present in 1–19% of relevés

II = 20–39% species presence

III = 40–59% species presence

IV = 60–79% species presence

V = 80–100% species presence

+ = only 1 species occurrence, relevé total greater than 20.

Where the relevé total is 5 or less the actual number of occurrences is indicated by arabic numerals.

8 Attributes and their Selection

untransformed at the end. Where detailed autecological knowledge of plant species is available, the final classification at whatever level can have great predictive value. It is the possibility for applied use, as well as the strictly botanical applications, that offer so much potential for the increased use of the Z-M system in Australia.

ACKNOWLEDGMENTS

I owe a great debt to many colleagues, undergraduate and post-graduate students over the past seven years for stimulating thought and discussion on the use and potential of the Z-M system. Despite apparent inequity I must acknowledge special debt to John Busby, David Churchill, and Paul Gullan.

REFERENCES

- Beadle, N. C. W., and Costin, A. B. (1952). Ecological classification and nomenclature. *Proc. Linn. Soc. N.S.W.* **77**: 61-82.
- Beard, J. S., and Webb, M. J. (1974). *Vegetation Survey of Western Australia: Great Sandy Desert—Part I. Aims, Objectives and Methods*. University of Western Australia Press, Nedlands, W.A.
- Bridgewater, P. B. (1971). Practical application of the Zürich-Montpellier system of phytosociology. *Proc. Roy. Soc. Vict.* **84**: 255-62.
- Bridgewater, P. B. (1978). Coastal vegetation of east Gippsland, Victoria: A comparison of physiognomic and floristic classifications. *Phytocoenologia* **4**: 471-90.
- Bridgewater, P. B. (1979). Aspects of the phytosociology of Australian whipstick vegetation. *Documents phytosociologiques*, N.S. IV, 121-30.
- Braun-Blanquet, J. (1964). *Pflanzensoziologie*, pp. 865. Springer Verlag, Wien-New York.
- Busby, J. R., and Bridgewater, P. B. (1977). Studies in Victorian vegetation, II. A floristic survey of the vegetation associated with *Nothofagus cunninghamii* (Hook.) Oerst. in Victoria and Tasmania. *Proc. Roy. Soc. Vict.* **89**: 173-82.
- Ellenberg, H. (1960). Können wir eine gemeinsame Platform für die verschiedenen Schulen in der Waldtypenklassifikation finden? *Silva Fennica* **105**: 26-32.
- Krajina, V. J. (1960). Can we find a common platform for the different schools of forest-type classification? *Silva Fennica* **105**: 50-9.
- Moore, J. J. (1962). The Braun-Blanquet system—a reassessment. *J. Ecol.* **50**: 761-9.
- Moore, J. J., Fitzsimmons, S. J., Lambe, E., and White, J. (1970). A comparison and evaluation of some phytosociological techniques. *Vegetatio* **20**: 1-20.
- Muir, B. G. (1977). Biological survey of the W.A. wheatbelt. Part 2: Vegetation and habitat of Brenderup reserve. *Rec. West. Aust. Mus. Suppl.* **3**.
- Muller-Dombois, D., and Ellenberg, H. (1974). *Aims and Methods of Vegetation Ecology*, pp. 547. Wiley, New York.
- Poore, M. E. D. (1955). The use of phytosociological methods in ecological investigations. I. The Braun-Blanquet system. *J. Ecol.* **43**: 226-44.
- Ratkowsky, D. A., and Ratkowsky, A. U. (1977). Plant communities of the Mt Wellington Range, Tasmania. *Aust. J. Ecol.* **2**: 435-46.
- Specht, R. L. (1970). Vegetation. In: *The Australian Environment* 4th ed. (ed. G. W. Leeper), pp. 44-67. CSIRO-Melbourne University Press, Melbourne.
- Specht, R. L., Roe, E. M., and Boughton, V. H. (1973). Conservation of major plant communities in Australia and Papua New Guinea. *Aust. J. Bot. (Supplementary Series—Supplement 7)*.
- Stuwe, J., and Parsons, R. F. (1977). *Themeda australis* grasslands on the Basalt Plains, Victoria: floristics and management effects. *Aust. J. Ecol.* **2**: 467-76.

Potential Application of the Zürich-Montpellier System 9

- Webb, D. A. (1954). Is the classification of plant communities either possible or desirable? *Bot. Tidsskr.* **51**: 362-70.
- Westhoff, V., and Maarel, E. van der (1973). The Braun-Blanquet approach. In: *Handbook of Vegetation Science, V. Classification and Ordination* (ed. R. H. Whittaker), pp. 617-726. W. Junk, the Hague.
- Whittaker, R. H. (1973). Dominance types. In: *Handbook of Vegetation Science, V. Ordination and Classification of Communities* (ed. R. H. Whittaker), pp. 387-402. W. Junk, The Hague.
- Wood, J. G. (1939). Ecological concepts and nomenclature. *Trans. Roy. Soc. S. Aust.* **63**: 215-23.

Foliage projective cover and standing biomass

R. L. SPECHT

GROWTH OF PLANT COMMUNITIES

Plant communities must be regarded as living entities—capable of growth, maturation, senescence and regeneration. No matter what process is operating (cf. Watt 1947)—be it cyclical, primary or secondary succession, or a combination of all three—the growth of the plant community can be dissected into the following processes:

1. Net photosynthesis of the foliage canopy (which may be evergreen, semi-deciduous or seasonal).
2. Translocation of photosynthates to non-photosynthetic organs (inflorescences, stems and roots).
3. Respiration of photosynthates in non-photosynthetic organs.
4. Structural growth and/or storage of photosynthates for subsequent use.

The first stage in the growth sequence—that of net photosynthesis—is dependent firstly on the density and structure of the foliage canopy (leaf area of various layers, its geographical orientation and inclination within the canopy) capable of receiving solar energy. As leaves reflect and absorb most of the incoming solar radiation, transmitting only 10-15 per cent, multiple layering of leaves, which are oriented mostly normal to the sun's rays, appears to contribute little to net photosynthesis of the plant community. But incident solar radiation in any one locality varies in azimuth and inclination both daily and seasonally; and leaves in Australian plant communities are rarely orientated normally to the incident rays. A realistic description of the photosynthetic canopy is undoubtedly complicated; for classification, a simple measure is required. Following discussions with many plant ecologists, the concept of *Foliage Projective Cover* (FPC) (the proportion of land covered by one or more layers of photosynthetic tissue vertically above it) was proposed (Specht 1970). An assessment of the photosynthetic potential of the canopy can be obtained easily by recording the presence or absence of any photosynthetic tissues (leaves, petioles, some green twigs) which may fall within the line of vision of the intersections of two cross-wires (supported in a vertical tube, with a 45° viewing mirror) at a series of stratified observation sites throughout the plant community. For satisfactory measurements, the foliage projective cover of the canopy should be recorded on a day when wind movement is minimal. At certain sites, stems supporting the foliage canopy, or possibly a lower stratum, may obstruct a clear view of the foliage; such observations are ignored and repeated in extra stratified sampling-sites. Ideally, foliage projective cover should be recorded for each of the major strata in the plant community.

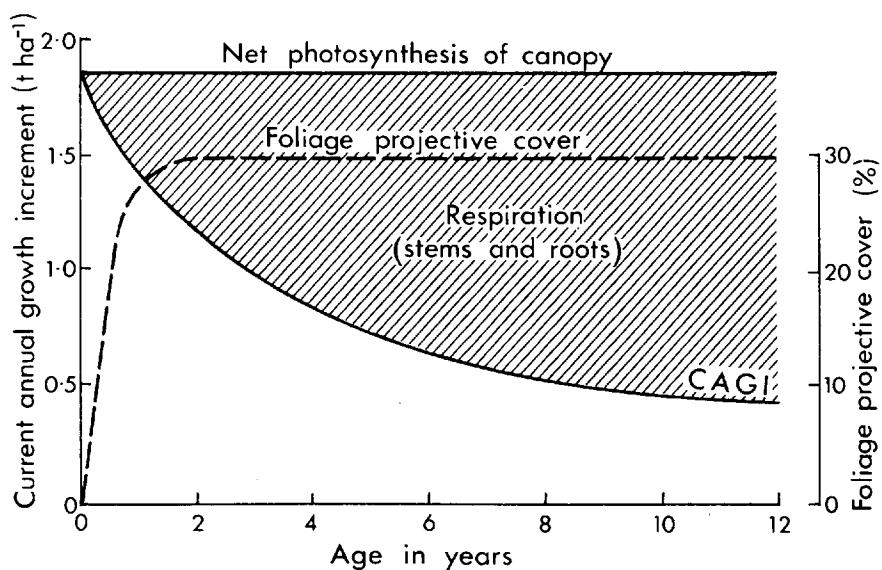
The process of photosynthesis within the leaf is, among other things, dependent on light intensity, ambient temperature, mineral nutrition, carbon dioxide supply and moisture availability. A simplistic estimate of the photosynthetic capacity of the canopy can be made as follows:

$$\text{NPI} = \text{FPC} \times \text{LI} \times \text{TI} \times \text{SFI} \times \text{MI} \quad (1)$$

where	NPI	= Net Photosynthetic Index
	FPC	= Foliage Projective Cover
	LI	= Light Index
	TI	= Thermal Index
	SFI	= Soil Fertility Index
	MI	= Moisture Index

all measured on a scale from zero to unity (Fitzpatrick and Nix 1970; Specht 1972; Specht and Brouwer 1975; Specht 1981b).

Most native Australian plant communities are dominated by trees or shrubs with evergreen canopies where defoliation and foliation tend to be synchronised so that the foliage projective cover of the canopy remains relatively constant throughout the year (Specht 1972, 1981b). (The few monsoonal Australian plant communities which contain deciduous or semi-deciduous trees and shrubs have been classified on the basis of the foliage projective cover of the community at the time of maximum leaf canopy.)

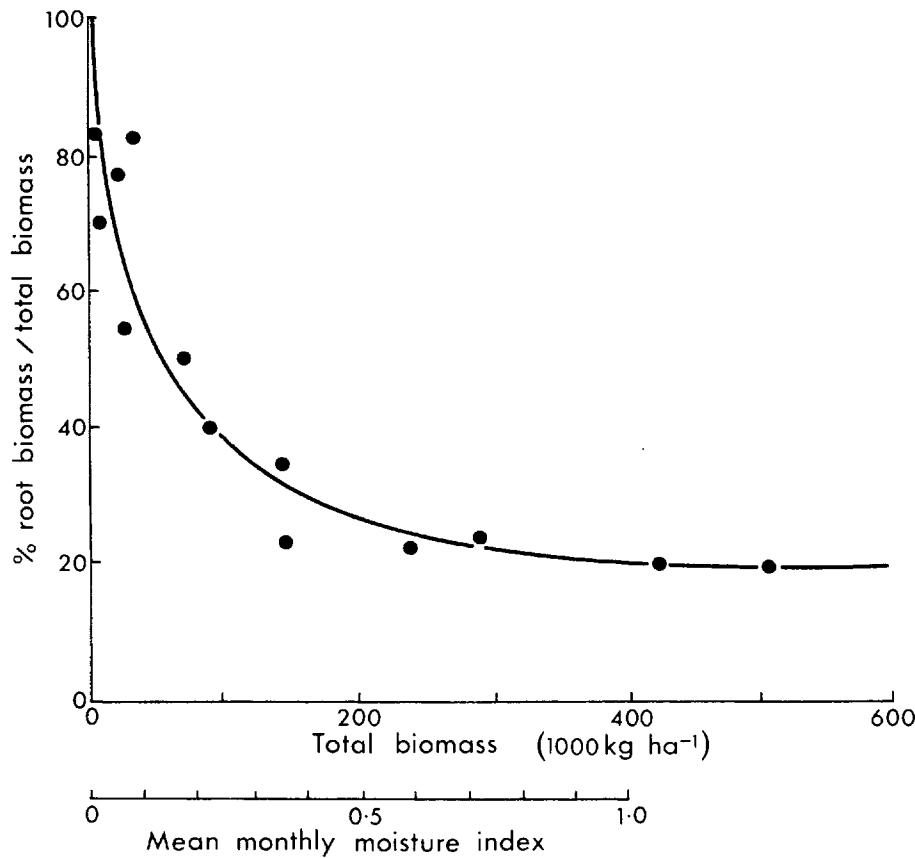


- 2.1 Changes in (1) Foliage Projective Cover (FPC) and (2) Current Annual Growth Increment (CAGI) (total tops) with age after a fire had razed a stand of mallee-broombush (*Eucalyptus incrassata-Melaleuca uncinata* association) near Keith, South Australia. Standing biomass at any point in time can be derived by integrating the values of CAGI from zero time.

12 Attributes and their Selection

Early in the developmental phase of the plant community, the foliage projective cover of the evergreen canopy approaches an optimum value in equilibrium with the evaporative power of the atmosphere in the particular locality and the water available for evapotranspiration (Fig. 2·1). If the residence time (1, 2 or possibly 3 years) of a leaf in the canopy is known, the biomass (or leaf area) of the canopy can be assessed by weighing leaves (or measuring their area) which have been collected in litter trays of standard area (Specht and Brouwer 1975).

The second major phase in the growth process is that of translocation of the photosynthate from the canopy to stems and roots. Little photosynthate is retained in the canopy except during the relatively short foliation/defoliation phase. The majority of the photosynthate appears to be distributed as shown in Fig. 2·2. In humid environments, 80 per cent of the photosynthate is retained above ground, 20 per cent is translocated to the roots. With increasing aridity, more and more of the photosynthate moves



2.2 *The proportion of root biomass: total biomass increases as the total biomass of the plant community decreases from humid to arid regions.*

to underground organs, with the driest habitats showing 80 per cent below ground, 20 per cent above.

The third major phase in the growth of the plant community is stem/root respiration. Although most of the photosynthates translocated from the leaf canopy will be immobilised as dead cells (fibres, vessels, tracheids, cork cells), the living, respiring cells (cambial, phloem, parenchyma cells) will increase in number for the most part exponentially as the plant ages. Thus, increasing amounts of photosynthates will be respired by living cells of the stems and roots as the plant community ages (Fig. 2.1). If the living, respiring tissue in roots and stems increases exponentially with time, an exponential loss, by respiration, of the relatively constant annual input of photosynthates produced in the evergreen leaf canopy may be expected. The resultant annual increment in biomass could be expressed as follows:

$$\text{CAGI} = \text{CAGI}_0 e^{-ct} \quad (2)$$

where CAGI = Current Annual Growth Increment

CAGI₀ = Current Annual Growth Increment when respiration of stems and roots is almost zero.

t = age in years

e = base of natural logarithms

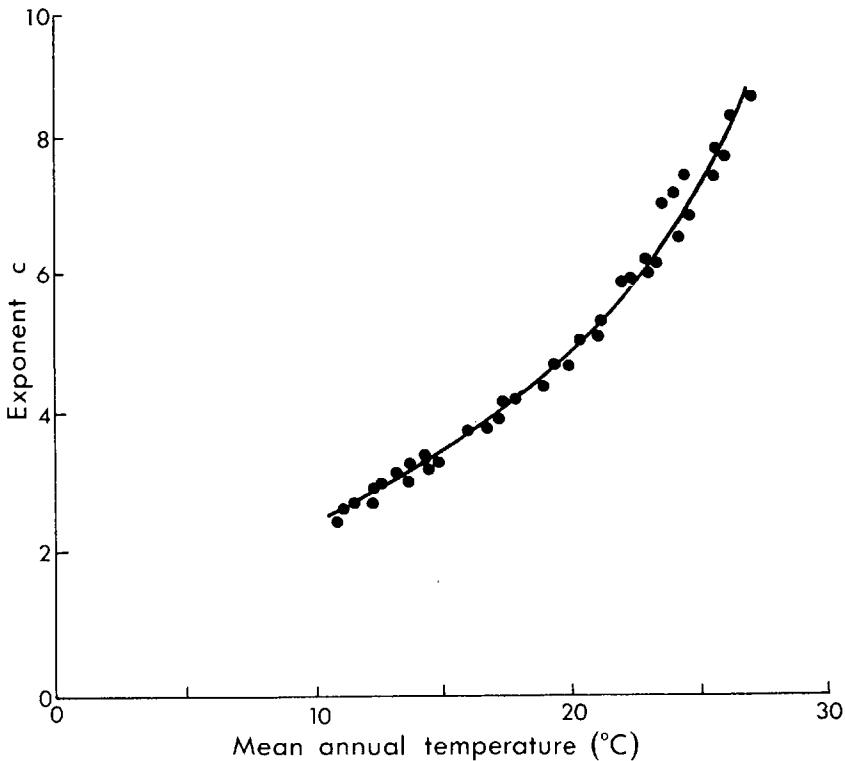
c = constant exponent

As the photosynthates translocated from the leaf canopy are largely carbohydrates, the respiratory rate of the non-photosynthetic organs will tend to show a respiratory quotient (Q_{10}) of 2.0 for each temperature increment of 10°C. The value of the exponent c in Equation (2) is thus strongly dependent on the seasonal sequence of air temperature. The value of the exponent c, estimated for plant communities along the humid eastern coast of Australia (from Cape York to southern Tasmania) is plotted against mean annual temperature (Fig. 2.3). Respiration loss increases rapidly from southern to northern Australia so that, for the same input of photosynthate, the plant community grows for a much longer period of time before maximum biomass is reached in the cooler south than in the tropical north. Thus for the same photosynthetic input, a taller community with a higher standing biomass can be expected in southern Australia.

CLASSIFICATION OF PLANT COMMUNITIES

Two-way classification (1970 version)

It should be obvious from the above discussion on the growth of plant communities, that (1) *Foliage Projective Cover* of the tallest stratum (which receives most solar energy) provides a ready assessment of the photosynthetic potential of the plant community and (2) above-ground standing biomass is an important measure of the ultimate integration of all the biological processes associated with growth. A graded series of plant communities varying in foliage projective cover (controlling the input of energy) and standing



2.3 Relationship between exponent c of the equation

$$\text{CAGI} = \text{CAGI}_0 e^{-ct}$$

and Mean Annual Temperature ($^{\circ}\text{C}$) for plant communities in humid eastern Australia (latitude 10–45°S). The exponent c on the graph is expressed as a relative value not an absolute value.

biomass (the end-product integrating all growth processes) can thus be observed throughout the continent of Australia along gradients of solar radiation, temperature, soil fertility and water balance.

Following this reasoning, Australian plant ecologists, as members of the Conservation Sub-Committee of the International Biological Programme (1967–74), agreed on a two-way classification of Australian plant communities (Specht 1970; Specht *et al.* 1974). Foliage projective cover, which varies in a continuum from humid to arid climates, was divided arbitrarily into four categories:

100-70%	dense
70-30%	mid-dense
30-10%	sparse
10-0%	very sparse

As few estimates of standing biomass had been made in Australia, volume (expressed crudely by height and density) of the tallest stratum—values readily available—was considered as the best estimate of the end-product, standing biomass. With age, however, while foliage projective cover tends to remain constant, many slender stems in the regenerating community are replaced by fewer stems of increasing girth. Hence it seemed logical that volume (as an expression of standing biomass) could be more readily expressed by height and/or life form of the uppermost stratum. The two way classification (Specht 1970) thus expressed standing biomass by Life Form/Height as follows:

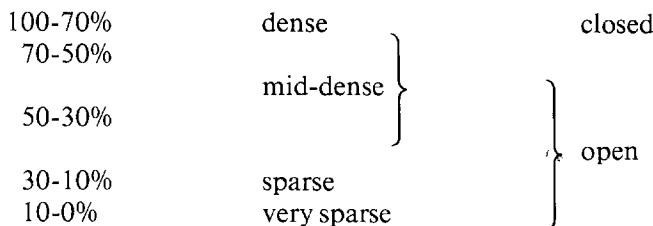
Trees	over 30 m, 30-10 m, under 10 m
Shrubs	over 2 m, under 2 m
Hummock grasses	<i>Triodia/Plectrachne</i> spp. (unique to Australia)
Herbs	graminoids, non-graminoid herbs or forbs, ferns

Subsequent field experience has shown that the two-way classification is easily understood and applicable in a wide variety of regions throughout Australia (Smith 1972-73; Specht *et al.* 1974; Beard and Webb 1974; Beard 1976; Carnahan 1976; Laut *et al.* 1977).

Two-way classification (1981 version)

The arbitrary subdivisions of foliage projective cover and Life Form/Height as expressed by Specht (1970) need minor adjustment to correct imperfections and omissions which have been noted by ecologists in various parts of Australia. Some of these improvements have already been made in a workshop organised by the Australian Biological Resources Survey (ABRS) Botanical Sub-committee (see Laut *et al.* 1977); others have arisen since that workshop. The following improvements should be made to the two-way classification of Specht (1970).

1. *Foliage Projective Cover* (FPC) is better subdivided into five rather than four categories (see Fig. 2·4, from Specht 1972).



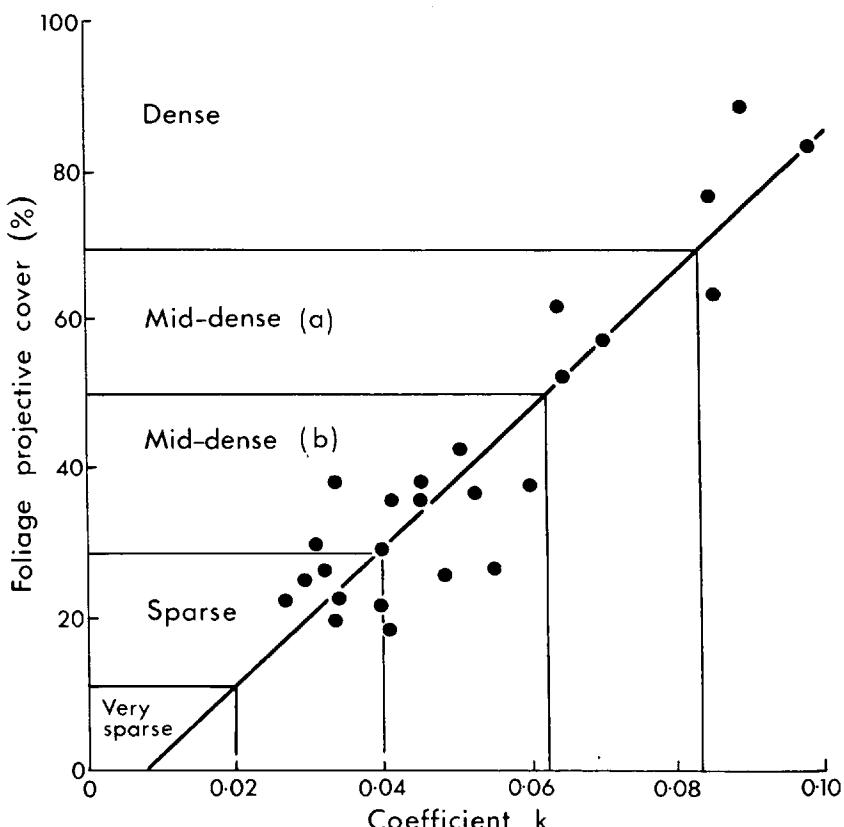
Water balance studies reveal a discontinuity between closed- and open-communities (Specht 1972, 1981; Specht *et al.* 1977; illustrated in Fig. 2·5). The few field estimates of FPC would indicate that this discontinuity occurs somewhere between 70 and 80 per cent; the lower value of 70 per cent being accepted in this chapter.

Below the disjunction of c. 70 per cent, FPC appears to decrease continuously from humid to arid regions (Fig. 2·4). Small disjunctions have been observed in south-eastern

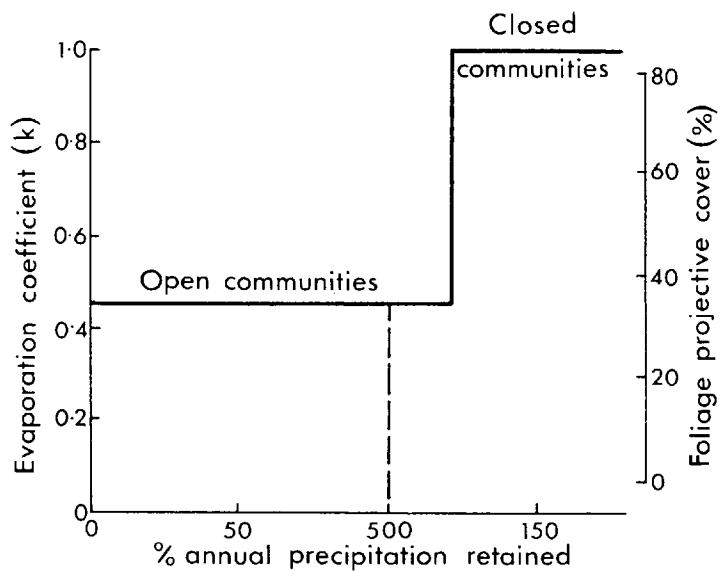
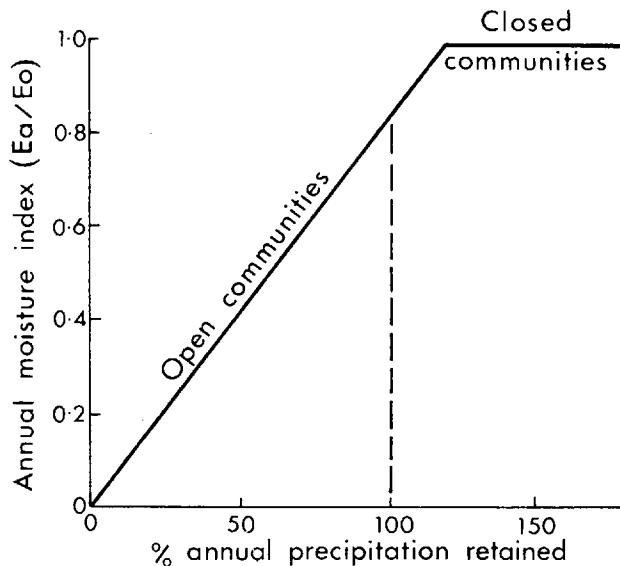
16 Attributes and their Selection

Queensland where *Acacia harpophylla* (brigalow) on heavy clay soils is found alongside *Eucalyptus populnea* (poplar box) communities on sandy soils; higher FPC is balanced by higher leaf resistances (to the loss of water vapour) in the phyllodes of the brigalow, thus equating annual evapotranspiration of the brigalow with that found in the poplar box community (with lower FPC and lower leaf resistances).

The class interval of 30 to 70 per cent FPC has been found to be too broad when describing eucalypt forests in eastern and southern Australia. A subdivision at the 50 per cent mark would enable taller and denser forests (of more commercial value) to be distinguished from less vigorous stands. Furthermore, the revised class intervals for FPC then closely parallel the Cover-Class Scale which was proposed by Braun-Blanquet (1932) and adopted by many ecologists throughout the world—namely, 100-75%, 75-50%, 50-25%, 25-5%, and 5-0%.



2.4 Foliage Projective Cover (FPC) (%) of the upper stratum of Australian plant communities plotted against the evaporative capacity (k) of the canopy (after Specht 1972). $FPC = 896.5k - 6.4$



- 2.5 Open communities change abruptly to closed communities (with FPC of 70–100%) when available water is non-limiting during any month of the year (after Specht 1981b).

18 Attributes and their Selection

2. *Life Form* (based essentially on the classificatory scheme proposed by Raunkiaer (1934)) may be subdivided as follows:

Trees (woody plants with a prominent single stem)

over 30 m*	– tall
10-30 m*	– mid-height
under 10 m	– low

Shrubs (woody plants with many stems arising at or near the base)

over 2 m	– tall
0.25-2 m†	– mid-height (1-2 m) and low (0.25-1 m)

With sclerophyllous leaves
With non-sclerophyllous leaves‡
under 25 cm†
With sclerophyllous leaves
With non-sclerophyllous leaves‡

Hummock grasses (a unique Australian life form characteristic of the grass genera *Triodia* and *Plectrachne*)

Herbs

Tussock grasses and grass-like tussock plants. Graminoid or grass-like herbs include members of the Poaceae, Cyperaceae, Restionaceae, Juncaceae and Liliales.

Grasses and grass-like plants

Sedges

Other herbs/forbs

Three height-categories may be recognised in each of these subdivisions (Perry and Lazarides 1964; Specht 1970; Laut *et al.* 1977).

over 1 m	– tall
50-100 cm	– mid-height
under 50 cm	– low (short)

* Further subdivision may be necessary in local areas. For example, in south-eastern Australia, two distinct tall forest communities dominated by tall species of *Eucalyptus* may be found—one, on richer soils, is over 40 m tall and possesses a ferny understorey; the other, on less fertile soils, is over 30 m tall, with an understorey of sclerophyllous shrubs (D. H. Ashton pers. comm. 1978; Specht 1981a). In northern Australia, most eucalypt forests are rarely more than 20 m tall; the few stands with trees over 20 m tall, are considered 'tall'. Compared with the tall eucalypt forests of south-eastern Australia, these 'tall' northern forests are mere 'dwarfs'.

† The ABRS Botanical Sub-committee recommended that shrubs be subdivided into three height categories—over 2 m, 1-2 m and under 1 m. As this decision did not cover the stunted communities found in alpine fell-fields and on windswept coastal cliffs, the original Raunkiaer subdivisions have been retained in this chapter.

‡ Non-sclerophyllous leaves include succulent, semi-succulent, and coriaceous leaf-types, characteristic of saline and semi-saline habitats where stunted mangrove, salt marsh, shrub steppe and some coastal dune communities are found.

TABLE 2.1
Structural formations in Australia (modified from Specht 1970)

Life form of tallest stratum	Foliage Projective Cover of tallest stratum				<10% (1)
	100-70% (4)†	70-50% (3+)	50-30% (3-)	30-10% (2)	
Trees* > 30 m	(T)†	Tall closed-forest	Tall forest	(Tall open-forest)‡	—
Trees 10-30 m	(M)	Closed-forest	Forest	Woodland	Open-woodland
Trees < 10 m	(L)	Low closed-forest	Low forest	Low woodland	Low open-woodland
Shrubs* > 2 m	(S)	Closed-scrub	Scrub	Tall shrubland	Tall open-shrubland
Shrubs 0.25-2 m	(Z)	Closed-heathland	Heathland	Open-heathland	Open-shrubland
Sclerophyllous	(C)	—	—	Low shrubland	Low open-shrubland
Non-sclerophyllous	(D)	—	—	—	—
Shrubs < 0.25 m	(W)	—	—	Dwarf open-heathland (fell-field)	Dwarf open-heathland (fell-field)
Sclerophyllous	(H)	—	—	Dwarf shrubland	Dwarf open-shrubland
Non-sclerophyllous	(H)	—	—	—	—
Hummock grasses	(H)	—	—	Hummock grassland	Open hummock grassland
Herbaceous layer	(G)	Closed (tussock) grassland	(Tussock) grassland	Open (tussock) grassland	Very open (tussock) grassland
Graminoids	(Y)	Closed-sedge land	Sedge land	Open-sedge land	Very open-sedge land
Sedges	(X)	Closed-herbland	Herbland	Open-herbland	Very open-herbland
Herbs	(F)	Closed-fernland	Fernland	—	—
Ferns					

* A tree is defined as a woody plant usually with a single stem; a shrub is a woody plant usually with many stems arising at or near the base.

† Symbols and numbers given in parentheses may be used to describe the formation, e.g. tall closed-forest—T4, hummock grassland = H2

‡ Senescent phases of Tall forest.

20 Attributes and their Selection

Details of these revised subdivisions are shown in Table 2·1. Although five subdivisions of FPC have been used instead of the four used in 1970, minimal changes in nomenclature of the extra categories are proposed.

Triplet notation

Classification of plant communities does not end at the tallest stratum, although this layer is logically used to distinguish major structural formations. Subformations may be recognised using lower strata. Three prefixes were proposed (Specht 1970) to cover these strata:

- | | |
|---------|-------------------------------------|
| grassy | - a well-developed herbaceous layer |
| shrubby | - a well-developed shrub layer |
| layered | - with two or more strata prominent |

Further subdivision, based on the nature of the layers—whether sclerophyllous (both shrubs and grasses), semi-succulent, succulent—was suggested.

In order to include some information on the floristic dominants of each structural formation included in Table 2·1, Beard and Webb (1974) proposed a triplet notation to express each subdivision, e.g. eM3 represents a eucalypt open-forest where e = *Eucalyptus*, M = mid-height tree, 10-30 m tall, and 3 = FPC of 30-70% (see Table 2·1). Lower strata can also be expressed in triplet notation, so that the eucalypt open-forest near Brisbane, Queensland can be expressed as eM3. aS2. tG3, where e = *Eucalyptus*, a = *Acacia* and t = *Themeda*, with other symbols as in Table 2·1. This triplet notation, introduced by Beard and Webb (1974), has been used successfully in ecological surveys by Beard (1976), Carnahan (1976) and Laut *et al.* (1977).

The triplet notation overcomes some of the nomenclatural problems involved in describing very sparse communities (with FPC less than 10%) shown in Table 2·1. The question arises as to whether the community should be called a treed- or shrubbed-grassland, heathland, low shrubland, hummock grassland or whether it is better referred to as an open-woodland or open-shrubland with a grassy, heathy, shrubby or hummock grass understorey. The problem is solved using the triplet notation—eL1. tH2 clearly refers to a hummock grassland of *Triodia* spp. with FPC 10-30%, and a scattered over-storey of low eucalypt trees.

It must be stressed that the two-way classification (Table 2·1) and the triplet notation derived from it are based on the values of the input and end point of energy flow through the plant community. They are designed to describe vegetation at any stage of its development—successional, cyclical and climax.

REFERENCES

- Beard, J. S. (1976). *Vegetation Survey of Western Australia: Murchison*. University of Western Australia Press, Nedlands, W.A.
Beard, J. S., and Webb, M. J. (1974). *Vegetation Survey of Western Australia: Great Sandy Desert*. University of Western Australia Press, Nedlands, W.A.
Braun-Blanquet, J. (1932). *Plant Sociology*. McGraw-Hill Book Co., New York.

- Carnahan, J. A. (1976). Natural vegetation. In: *Atlas of Australian Resources*. Second series. Dept National Resources, Canberra.
- Fitzpatrick, E. A., and Nix, H. A. (1970). The climatic factor in Australian grassland ecology. In: *Australian Grasslands*. (ed. R. M. Moore), pp. 3-26. A.N.U. Press, Canberra.
- Laut, P. et al. (1977). *Environments of South Australia, Provinces 1-8 and Handbook*. CSIRO Aust. Land Use Research, Canberra.
- Perry, R. A., and Lazarides, M. (1964). Vegetation of the Leichhardt-Gilbert area. In: *Lands of the Leichhardt-Gilbert Area, Queensland*. CSIRO Aust. Land Res. Ser. No. 11, pp. 152-91.
- Raunkiaer, C. (1934). *The Life Forms of Plants*. Clarendon Press, Oxford.
- Smith, F. G. (1972-73). *Vegetation Survey of Western Australia*. Vegetation Map of (1) Pember-ton and Irwin Inlet and (2) Busselton and Augusta, W. Aust. Dept. Agric., Perth.
- Specht, R. L. (1970). Vegetation. In: *The Australian Environment*. Fourth ed. (ed. G. W. Leeper), pp. 44-67. CSIRO-Melbourne University Press, Melbourne.
- Specht, R. L. (1972). Water use by perennial evergreen plant communities in Australia and Papua New Guinea. *Aust. J. Bot.* **20**: 273-99.
- Specht, R. L. (1981a). Major vegetation formations in Australia. In: *Ecological Biogeography of Australia*. (ed. A. Keast). Junk, The Hague, pp. 163-298.
- Specht, R. L. (1981b). Ecophysiological principles determining the biogeography of major vegetation formations in Australia. In: *Ecological Biogeography of Australia*. (ed. A. Keast). Junk, The Hague, pp. 299-332.
- Specht, R. L., and Brouwer, Y. M. (1975). Seasonal shoot growth of *Eucalyptus* spp. in the Brisbane area of Queensland (with notes on shoot growth and litter fall in other areas of Australia). *Aust. J. Bot.* **23**: 459-74.
- Specht, R. L., Roe, E. M., and Boughton, V. H. (eds.) (1974). Conservation of major plant communities in Australia and Papua New Guinea. *Aust. J. Bot. Suppl.* No. 7, 667 pp.
- Specht, R. L., Salt, R. B., and Reynolds, S. T. (1977). Vegetation in the vicinity of Weipa, north Queensland. *Proc. R. Soc. Qd.* **88**: 17-38.
- Watt, A. S. (1947). Pattern and process in the plant community. *J. Ecol.* **35**: 1-22.

The use of dynamic characteristics in vegetation classification

I. R. NOBLE

INTRODUCTION

In classical taxonomy there is no dispute (except in a few backward legislatures of the world) that species are phylogenetically related. Nevertheless, there is still debate about whether 'correct' phylogenetic classifications can be made. Some taxonomists (albeit a minority) argue that more emphasis should be given to phenetic classifications. Their reasons seem to be pragmatic and emphasise the need for a useful classification while not denying the underlying phylogenetic relationships. Much of the difference in approach is related to character selection and particularly to *a priori* versus 'unweighted' selection of characters.

In vegetation classification, the opportunities for debate about character selection are greatly increased. First there is no demonstrable phylogeny of community development despite many attempts to find the 'Grand Underlying Scheme'. Secondly, despite the uncertainty of the species concept, the species is still a relatively much more discrete unit than a community type.

The debate about the utility of floristic versus non-floristic characters in vegetation classification has continued for many decades. Although structural classification of vegetation has always been an integral part of our way of seeing the world—for example, in Theophrastus' classification of vegetation into trees, shrubs, subshrubs and herbs in c. 300 BC (Radford *et al.* 1974), it has been argued that floristic classification can provide a finer degree of resolution in most situations. This point has been challenged lately (Webb *et al.* 1970, 1976) with examples which show that structural classification is powerful in certain circumstances (e.g. complex rainforest systems).

However, the resolving power of the various approaches is not necessarily (or even likely to be) the main criterion in selecting a method of vegetation classification. The ease of use of structural characters by relatively untrained personnel and their geographically wide applicability is enough to justify their use in many situations.

DYNAMIC ATTRIBUTES

There are usually several purposes for a classification. For example, classical taxonomy attempts to combine within one system a method of classifying (or forming discrete groups), of naming, of indicating affinity and of indicating relationship by descent. The purpose of forming groups and attaching names should not be overlooked: 'It is curious how happy people are to have a name for something . . . even though they know nothing

about it beyond its name' (Bates 1960). Kühler (1967, p. 30) sees classification as part of the scientific method: 'The scientific method requires that observed phenomena be described, classified, and explained.' He seems to imply the classification is required before 'explanation' is possible.

A major purpose of a vegetation classification is to indicate site potential in some way. Vegetation is used as a phytometer of the environment. However, there are several sources of error implicit in this approach. For example, the vegetation may not react to the environmental parameters of particular concern to the user of the classification (under-sensitivity). Conversely the response of the vegetation may be magnified due to competitive interactions between species (over-sensitivity). In other cases, the vegetation may reflect historical information about environmental influences which may not pertain to the site at present (irrelevancy).

This last fact bears close examination. It has long been recognised that vegetation is dynamic. This dynamism can be recognised on several time scales. Climatic change usually occurs on a time scale of little direct relevance to most users of a vegetation classification. On a shorter time scale, successional changes leading to a climax vegetation have been recognised. On an even shorter, and more regular, time scale occur the seasonal changes which Raunkiaer (1934) incorporated into his system.

The validity of the classical, 'succession to climax', concepts of vegetation change has been much discussed and challenged, yet little has been done to replace these concepts with a more suitable description of vegetation development. In fact classical successional concepts have been incorporated into many vegetation classification and mapping systems (see Kühler 1967). However, the role of irregular, infrequent, but recurrent environmental events (disturbances) in shaping the vegetation at a site is important. Obvious examples are the role of blow-down in tropical forests, and fires in much of the Australian sclerophyll woodland. The vegetation at a site preserves information about the past frequency and effect of such disturbances, and it may therefore be valuable to incorporate characters reflecting this information in vegetation classification systems. These characters will convey information both about the susceptibility of the site to future disturbances, and about the possible reactions of the existing vegetation to these disturbances.

Noble and Slatyer (1977, 1980) have proposed a scheme for describing the major shifts which occur in species composition and dominance during succession in communities subject to recurrent disturbance. The scheme utilises a small number of life history characteristics pertaining to the potentially dominant species in a community. These characteristics are termed 'vital attributes', since they are vital to the role of the species in a vegetation replacement sequence. Although the scheme was not produced with a view to its application to vegetation classification, it is of interest to examine its possible application.

The emphasis on the response of species to environmental disturbances has obvious similarities with the scheme of Raunkiaer (1934), who based his classification on the position of the perennating buds which survived the most unfavourable season. The essential difference is that the vital attribute scheme is concerned with less frequent and

24 Attributes and their Selection

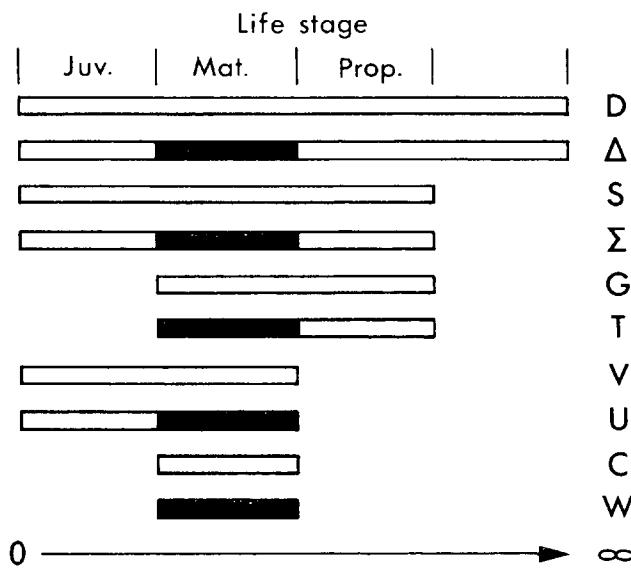
more irregular disturbances than the 'unfavourable seasons' considered by Raunkiaer, and it also emphasises the resultant behaviour of a species in a particular disturbance regime, rather than the mechanisms producing that behaviour.

The main features of the scheme are the identification of the vital attributes of the key species in a community and the categorisation of each species into a species type based on its vital attributes. Three main groups of vital attributes are recognised:

- (a) The method of arrival or persistence of the species at a site during and after a disturbance.
- (b) The ability to establish and grow to maturity in the developing community.
- (c) The time taken for the species to reach critical life stages.

Information about the species in terms of the groups of vital attributes is sufficient to derive a replacement sequence showing the variation in composition of the vegetation at a site subject to various disturbance regimes. More than one biological mechanism or phenomenon may be responsible for a particular vital attribute displayed by a species, and for a given vital attribute the biological mechanisms may differ from species to species. The vital attribute reflects the outcome of these mechanisms, i.e. the species' behaviour in response to its environment, including recurrent disturbances.

Figure 3.1 shows the vital attributes associated with the method of persistence or arrival shortly after a disturbance. The strict definitions of the vital attributes are based



3.1 A summary of the 10 vital attributes associated with the method of persistence. An open bar indicates that a method of persistence is available at a particular life stage of a species population. The method will usually result in only juvenile material being present immediately after a disturbance, but in some cases (solid bar) mature tissue will persist.

on the availability of a method of persistence in relation to critical stages in the life history of a species (see Noble and Slatyer 1980); however, here, I will describe the important vital attributes via examples.

A common example of a D species is one with well-dispersed propagules; for example, fire weeds with wind-borne seeds which become established in recently burned areas. Figure 3.1 shows that a D species is available at all stages in the life history of a species, including an indefinitely long period after the loss of reproductively mature individuals of the species from a site. In contrast Fig. 3.1 shows that an S species is similar to a D species in the pattern of availability of a mechanism of persistence, except that the mechanism remains available for only a finite period after the loss of reproductively mature individuals from a site. Examples of an S species are *Acacia* species which have long-lived seeds stored in the soil. Examples of the other vital attributes associated with the method of persistence are shown in Table 3.1. Ten vital attributes associated

TABLE 3.1

Vital attributes associated with the method of persistence after a site has been disturbed

Vital attribute	Example
D	Highly dispersed seeds
S	Long-lived seed store (often in the soil)
C	Short-lived seed store (often retained in the canopy of a species)
G	A special case of S, where all seeds germinate or perish after the first disturbance
V	A coppicing species in which the ability to coppice is established early in life
U	A species virtually unaffected by the disturbance
W	A species in which only the adults are unaffected by the disturbance, while juvenile individuals do not recover
Δ, Σ, Γ	Special cases of D, S and G in combination with V; i.e. the species has both a propagule based and a vegetative mechanism of persistence

with the mechanism of persistence are recognised. Four of these are based on propagule availability, three on vegetative resprouting mechanisms and three are a result of a combination of methods. The vital attributes are discussed in more detail in Noble and Slatyer (1980).

COMPARISON OF DYNAMIC ATTRIBUTES

As stated earlier, the vital attribute scheme was not designed specifically to be applied to vegetation classification. It is of interest to compare the categories of species defined in the vital attribute scheme with a similar classification dealing specifically with fire proposed by Gill (1980) and with the general approach of Raunkiaer (1934). Noble and Slatyer sought to find the minimum number of attributes associated with recognisably different dynamic responses to a disturbance regime. Gill's approach represents a specific analysis designed to provide useful terms to enhance communication between those interested in fire adaptations, and therefore may be taken as representing an 'ideal' set of categories for one specific application. Raunkiaer, and extensions of his scheme,

26 Attributes and their Selection

provides a set of categories specifically designed for a general vegetation classification, and represents a generalised approach.

Table 3.2 shows the classification of perennial plant species in relation to fire proposed by Gill (1980). Although it is not possible to deduce direct equivalence between Gill's classification and that of Noble and Slatyer, certain similarities are obvious. Gill's 'non-sprouters' (I to III) and the 'propagule based' mechanisms (D,S,G,C) of Noble and Slatyer are equivalent. A species with seed stored on the plant (I in Gill's classification) will usually be classified as having the C vital attribute, since such seed is unlikely to persist once the species has been lost from the site. A species with seed stored in the soil (II) will usually be classified as having the S or G vital attribute, although the Noble and Slatyer scheme is concerned not with the position of the seed pool but with its longevity. Gill's III and the D vital attribute are obviously equivalent.

TABLE 3.2
A comparison of the classification of Gill (1981) and the vital attributes related to method of persistence

A.	Plants which do not sprout, when subject to 100% leaf scorch by fire	
(a)	Seed storage on plant	I C
(b)	Seed storage in soil	II S or G
(c)	No seed storage in the burned area	III D
B.	Plants which sprout when subjected to 100% leaf scorch by fire	
(a)	Subterranean regenerative buds	
	(i) root suckers, horizontal rhizomes	IV
	(ii) basal stem sprouts	V
		{ V }
(b)	Aerial regenerative buds	
	(i) epicormic buds grow out	VI V
	(ii) continued growth of active aerial prefire buds	VII U or W
		{ U or W }

TABLE 3.3
A comparison of the classifications of Gill (1981), and Noble and Slatyer (1979). The equivalent Raunkiaer categories are also shown.

Noble and Slatyer	Gill	Raunkiaer
D	III	
S	II	
G	{ III, II }	'Therophytes'
C	I	
V	{ V, IV, VI }	Hemicryptophytes Cryptophytes (geophytes)
U	{ VII }	Phanerophytes
W		

Table 3.3 also compares the two classifications with a Raunkiaerian approach. A direct Raunkiaer classification cannot be applied since, although Raunkiaer emphasises the method by which a species survives an unfavourable period, the period considered was usually taken to be a season, or some other regularly recurring event. This shows up in the equating of therophytes with annuals. However, if the Raunkiaerian emphasis on the position of the perennating buds which survive through an unfavourable event is applied to a relatively infrequent, but recurrent event such as fire, then all of the above classes (i.e. Gill's I, II and III and Noble and Slatyer's D,S,G and C) are analogous to therophytes, i.e. their method of persistence (perennation) is via propagules (seeds).

The match between the classifications is not so close in the case of sprouting species. Gill emphasises the position of the regenerative buds and recognises hemicryptophytes (V) and geophytes (IV), but subdivides the phanerophytes into two groups depending on the type of aerial bud. This latter division is probably a useful extension to Raunkiaer's scheme which does not appear to have been suggested before.

The Noble and Slatyer approach produces a quite different result. They do not distinguish between Gill's groups IV, V and VI, or Raunkiaer's hemicryptophytes or cryptophytes and some phanerophytes, since, in dynamic terms, they have the same result. In each case regrowth is initiated from new growing points, and consequently there will be a period before the individuals regain their original vigour. However, they recognise two categories within Gill's group VII, depending on whether the juveniles can resprout, since this is important in determining the reaction of the species to frequent fires.

In summary, both Gill, and Noble and Slatyer, give more importance to propagule-based mechanisms of persistence through unfavourable events than Raunkiaer. Both schemes incorporate a finer division based on propagule mobility (D v. S,G and C), longevity (S and G v. C) and germination response to the disturbance (S v. G). These supply essential information about the species' response to irregular disturbances. Other extensions of Raunkiaer's therophyte group have emphasised finer structural or floristic divisions, quite dissimilar to these divisions (e.g. Ellenberg and Mueller-Dombois 1967).

A problem with the Gill, and Noble and Slatyer, approach is that the categories are difficult to distinguish in the field. Seed morphological characteristics are sometimes a guide to the appropriate category. However, an enormous number of different morphologies lead to dispersal methods as diverse as wind borne, borne externally on the animal, or dispersed by ingestion and eventual egestion. Therefore morphology will often not be much help even in distinguishing D species. The distinction between S, G and C are physiological, and therefore not possible to distinguish by examination of the seed in the field. A key to the recognition of the vital attributes associated with the method of persistence has been produced (Noble unpubl.); however, it requires observations of the response of a species to a disturbance regime. It will prove difficult to use in the field, especially in broad-scale surveys, since it requires that recently disturbed sites are examined. This is also true for a strict Raunkiaer classification, except that strong correlations between structure and position of the perennating buds has been observed.

28 *Attributes and their Selection*

This is relatively easy when frequent regular events such as unfavourable seasons are the basis of the classification, but it is very much more difficult to do when less regular, more disruptive disturbances are considered.

In the case of sprouting species, both Gill and Raunkiaer recognise more categories than Noble and Slatyer argue to be necessary for a description of the dynamic response of the species. This probably reflects the relative ease of observing sprouting mechanisms. The subdivisions of sprouting species used by Noble and Slatyer (i.e. U, V and W) are readily distinguished by observing the response of a species to a disturbance.

CONCLUSIONS

In summary, although I believe it is possible to prescribe a set of characters which are essential (Noble and Slatyer) and useful (Gill) in gaining information about the dynamic properties of the species composing the vegetation at a site, I believe that the recording of these characters in the field will prove difficult. However, it is necessary that suitable characters are sought. Vegetation classification and mapping often make up the first part of a management program. The management program itself often aims to manipulate or conserve the vegetation and its associated biota and other values through a sequence of natural or man-induced disturbances. Too many vegetation maps present only a description of what the vegetation composition or appearance is at a particular time. Any further information about the reactions of the vegetation to particular disturbance regimes is left to a separate, and often inadequately supported, study.

Two factors contribute to this relative neglect of dynamic characteristics of vegetation. While the importance of these studies is recognised, research aimed at investigating them is inherently long term and difficult to plan and execute. When controlled experiments are set up (e.g. prescribed burns or other artificial damage to vegetation) they are usually small scale and do not contribute information about a large enough range of species to be useful in a broad classificatory sense. The second, and in my view more important factor, is the lack of a useful theoretical base on which to develop experiments and studies of vegetation dynamics. The classical, Clementsian view of succession has dominated thinking about vegetation dynamics for most of this century. Although it is true that this approach is an adequate description of vegetation change in some parts of the world, it is inadequate in many other regions, and especially so in ecosystems subject to recurrent disturbances. Recently, alternative views of plant succession have been presented. Many of these studies have shifted the emphasis away from considering succession as a community property (and hence the interest in total community production and energy flow, species diversity etc.), to a greater emphasis on the properties of the individual species or populations involved in the vegetation changes (see Noble 1981 for a review of these developments). These developments offer the opportunity to develop a set of useful and practical characteristics which contain information about the dynamic history of a site and the reactions of the species to disturbance.

REFERENCES

- Bates, M. (1960). *The Forest and the Sea*. Museum Press, London.
- Ellenberg, H., and Mueller-Dombois, D. (1967). A key to Raunkiaer plant life forms with revised subdivisions. *Ber. geobot. Inst. ETH, Stiftg. Rübel*, Zurich 37: 56-73.
- Gill, A. M. (1981). Adaptive responses of Australian vascular plant species to fires. In: *Fire and the Australian Biota* (ed. A. M. Gill, R. H. Groves and I. R. Noble) pp. 243-71. Australian Academy of Science, Canberra.
- Küchler, A. W. (1967). *Vegetation Mapping*, pp. 472. The Roland Press Co., New York.
- Noble, I. R. (1981). Predicting successional change. In *Fire Regimes and Ecosystem Properties* (eds. H. A. Mooney, J. M. Bonnicksen, N. L. Christensen, J. E. Lordan and W. A. Reiners) U.S.D.A. Forest Service Technical Report, in press.
- Noble, I. R., and Slatyer, R. O. (1977). Post fire succession of plants in Mediterranean ecosystems. In: *Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems* (ed. H. A. Mooney and C. E. Conrad) pp. 27-36. U.S.D.A. Forest Service Gen. Tech. Rep. WO-3.
- Noble, I. R., and Slatyer, R.O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43: 5-21.
- Radford, A. E., Dickison, W. C., Massey, J. R., and Bell, C. R. (1974). *Vascular Plant Systematics*, pp. 891. Harper and Row, New York.
- Raunkiaer, C. (1934). *The Life Forms of Plants and Statistical Plant Geography*, pp. 632. Clarendon Press, Oxford.
- Webb, L. J., Tracey, J. G., Williams, W. T., and Lance, G. N. (1970). Studies in the numerical analysis of complex rain forest communities. V. A comparison of the properties of floristic and physiognomic-structural data. *J. Ecol.* 58: 203-32.
- Webb, L. J., Tracey, J. G., and Williams, W. T. (1976). The value of structural features in tropical forest typology. *Aust. J. Ecol.* 1: 3-28.

Towards a functional vegetation classification

A. N. GILLISON

INTRODUCTION

Since about the turn of the century botanists and biogeographers with an essentially European or North American botanical background have attempted to recognise major vegetation patterns around the globe and to determine causal relationships. The now somewhat traditional classifications of K  chler (1949), Fosberg (1970) and Mueller-Dombois and Ellenberg (1974) and their Australian derivatives (Beard and Webb 1974; Carnahan 1976), nevertheless provide a first generation basis for describing and mapping vegetation at scales of 1:1 000 000 and smaller. In general they attempt to provide a universal codification for major vegetation types that cuts across conflicting regional terminologies or non-equivalent units. These classifications were not designed to investigate aspects of vegetation dynamics, that is, successional changes or the effects of disturbance on vegetation which have become important aspects of ecology in recent years. This chapter investigates the possibility of developing a more dynamic-oriented attribute set for application to successional studies and to disturbed sites.

THE STATUS QUO AND SOME LIMITATIONS

Current classifications aim at describing 'typical' or 'nodal' vegetation types, preferably devoid of any 'un-natural' influence. There are good reasons why we ignore the widespread transitions between these 'typical' vegetation types or the increasing 'disturbed' types that surround them—they are exceedingly elusive of simple and comparative description. Any attempt to extend the present classificatory systems into a dynamic mode immediately plunges one into terminological conflict between 'identical' vegetation units described on an almost wholly subjective basis or else on very weak empirical grounds. Apart from Specht (see this volume) there is virtually no established classification in Australia where the diagnostic criteria are derived on a functional or even a pseudo-functional basis, i.e. there is no direct physiological basis for their selection that reflects measurable attributes of the environment. To say that 'sclerophyll' represents increasing harshness of environment versus 'mesophyll' has no application unless the statement is adequately defined, yet both attributes are still very widely and very loosely applied today. Other arbitrary criteria have crept into classifications, e.g. the 'malacophyllous' leaf of Mueller-Dombois and Ellenberg (1974) is defined thus if it collapses immediately it is placed over boiling water; a test for 'sclerophylly' sometimes used in Australian rainforest classification is positive if the leaf cracks when wrapped around a pencil.

Problems also arise where there is difficulty in matching classifications derived from faunal variables with those derived from vegetation variables or similarly between classifications of vegetation and soil variables. These difficulties arise through a lack of sufficient cross-linked functional variables between the different sets. Two-way tables (e.g. Specht this volume) cannot be applied usefully to monitor a change following the intensive logging of a rainforest, or the burning of a heathland. It is also fruitless collecting data that relate to strata or layers where these are poorly defined or show non-equivalence along a spatial or temporal continuum. From these simplistic approaches for classifying vegetation in general, more complex structural and physiognomic criteria have been used to classify rainforest (Webb 1959; Webb *et al.* 1976), for which there is only limited validation. The attributes selected for rainforest classification are mostly highly subjective, applicable only to climax types, and are often used with poor repeatability between observers. Furthermore, the system of Webb *et al.* (1976) cannot be easily applied to 'open' vegetation where they suggest floristics may be more usefully employed. Where recent environmental changes have caused 'intact' systems such as rainforests to change into open or depauperate vegetation, it is necessary to use attributes that can be applied uniformly to describe and classify vegetation change between open or closed systems. At present, classification in the Australian Region is virtually polarised between the Webb and Specht extremes with little ecological equivalence between the attributes used to describe them.

The use of floristic attributes currently provides the optimum classification at local levels where interrelationships between vegetation and other patterns are examined. It is therefore unfortunate that the most common floristic unit employed—the species—is essentially a taxonomic abstraction that was never designed to provide ecological meaning on a geographic or environmental basis. Higher-order floristic rankings can be shown to reflect some broad-scale environmental pattern but the units themselves are limited in meaning and are likely to suffer from a gross imbalance, e.g. where monotypic families are included. Floristic taxa *per se* have no easily demonstrable ecological equivalence.

To sum up, ecological problems now facing us require the development of a classificatory approach that should be relevant to the following:

- (a) the stated problem,
- (b) system dynamics,
- (c) production and conservation potential,
- (d) rapid survey,
- (e) linkage with present systems,
- (f) effective communication.

It is desirable that developments should be amenable to experimental validation as in this way the classifier can provide a working framework for the systems analyst and hence a model for informed ecological management. Recent developments such as the 'vital attributes' of Noble and Slatyer (1980), Noble (this volume) and the classification of plants via strategies (Grime 1977, 1979) are preliminary but important developments

32 Attributes and their Selection

in this regard. The stand description technique developed via gradient analysis by Kessell (1979) in which scale-flexible and variable attribute mapping is available via a computer data bank, provides an avenue for escape from standard mapping constraints where the problem requires that this be done.

A FUNCTIONAL APPROACH TO CLASSIFICATION

In this chapter a technique is described that accommodates both static and dynamic approaches in an endeavour to meet some of the requirements outlined. The method is systematised and described according to a specific nomenclature. *It is not put forward as a finite system but rather as a stimulus to develop dynamic attributes suitable for classification.*

The basic assumption is that for vascular terrestrial plants evolutionary development can be partly expressed in the response of such plants to changes in environment. Some of these responses can be described via the use of 'functional' attributes. For present purposes a plant 'functional' attribute is that which responds in a demonstrable and predictable way with a change in physical environment (see also Dansereau 1951; Fosberg 1970). For most field purposes, ecological rather than physiological response is reflected in an observed functional attribute which, depending on scale, may be described in terms of structure, morphology or anatomy. There is no implied relationship between a functional and a floristic attribute.

As an example, *leaf size, angle and type* and the *support system* or '*life-form*' (Table 4.1) can be regarded as functional variables or attributes. Evidence for the functional nature of such attributes is evident in literature (see also Raunkiaer 1934; Lewis 1972; Taylor 1975; Givnish and Vermeij 1976; Givnish 1978; Medina *et al.* 1978).

The use of individual functional attributes is limited because of the compensatory way in which certain attributes may be employed by plants, e.g. leaf size usually diminishes with increasing harshness of the environment, but in certain cases large leaves in

TABLE 4.1
Modal elements of the structural forma

Leaf size*	Leaf angle	Structural units
cm ²		
1 Pico up to 0.01	1 -vertic-	1 -phan.
2 Lepto 0.10-0.25	2 -lateric-	2 -cham.
3 Nano 0.25-2.5	3 -pendic-	3 -hemicrypt.
4 Micro 2.5-20	4 -compic-	4 -crypt.
5 Noto 20-45		5 -there.
6 Meso 45-150	<i>Leaf types</i>	6 -pter.
7 Platy 150-750	1 -ortho-	7 -bryod.
8 Macro 750-1640	2 -phyllodo-	8 -thallod.
9 Mega > 1640	3 -clado-	
	4 -gramo-	<i>Prefix types</i>
	5 -solido-	1 -epi- 4 -repto-
	6 -succulo-	2 -para- 5 -rosu-
	7 -aphyllo-	3 -sapro- 6 -lian-

* -ic- suffix indicates leaflet, e.g. picic-

extremely harsh environments (e.g. *Gunnera*, *Stilbocarpa*) may be associated with different life forms from those in 'optimum' environments and often with changes in leaf angle and leaf anatomy. Used in a combinatorial way it is therefore possible to link some of these attributes so that they form unique combinations that reflect the plant's capacity to survive in a particular range of physical environments.

It is therefore possible to construct a representative *structural forma* for a plant community from these functionally oriented structural attributes or elements. Any unique combination of states from each of these elements (Appendix 4.1) constitutes a unique descriptive unit that can be termed a *modus* (Latin (s.m. II)—manner or mode of existence, standard, way of conduct). Hence any assemblage of vascular plants can be described in terms of one or more *modi*. Although there is no implied phylogeny, each *modus* is virtually a systematic 'taxonomic' unit in its own right. But the term 'taxon' is not used here as it is likely to lead to botanical confusion.

For ecological purposes, the use of floristic taxa becomes limiting as geographic range is increased. In such circumstances I argue that the use of a conceptual unit such as the *modus* can provide a more meaningful ecological comparison between plants than can floristic taxa. As an example, two northern eucalypt 'boxes', *Eucalyptus microneura* (N.E. Australia) and *E. tectifica* (N.W. Australia), are morphologically similar and often occur in similar environments. Although floristically distinct, each collapses into the same *modus* when described in terms of the *notophyll*-sized leaves that are *pendulous*, *isobilateral* supported on a *phanerophyte*. (Hence for convenience and for numerical purposes it is possible to extract a unique combination, e.g. a *notopendic-iso-phan*.) If a *modus* forms a dominant part of a plant community it may be further qualified by adding height and foliage projective cover.

Such attributes can be linked together to provide a description of how a plant is structured in a particular environment or range of environments. This is necessarily a step further and finer than the Raunkiaer system of life-form description as it takes into account not only the position of the perennating organs at the onset of the most unfavourable annual season (Raunkiaer, 1934) but gives an indication of other functional aspects of the plant throughout its day-to-day existence.

By this means it is possible to describe any assemblage of plants in terms of its *structural forma* that is composed of the dominant *modal* types together with their height and foliage projective cover.

Leaf size

Of the nine size-classes used, two are new: *pico* is a size class that I have found to be empirically useful in the description of many Australian xeromorphic communities while *platy* is a leaf size intermediate between *meso* and *macro* that represents many of the so-called 'nomad' or mid-succession mesic rainforest species, e.g. *Macaranga*, *Mallotus*, *Aleurites* and so on (cf. van Steenis 1958). There is no other validation for adhering to these or the remaining size classes, as with the exception of the *notophyll* of Webb (1959), the remainder are those of Raunkiaer (1934) and are simple progressive points on a log scale, that are sufficiently close to be found useful in very broad classi-

fication. Although some experimental validation may show that an increase in leaf size usually corresponds with increasing water availability, there appears to be no necessity at present to depart from a scale that has been in wide use and will remain so for some time.

Leaf angle

As a crude approximation, leaves that are more-or-less laterally disposed to the stem axis ($\pm 20^\circ$) tend to be thin, broad, bilateral, and hypostomatous (stomates on the underside only) with relatively few stomates per unit area, whereas those that are vertically disposed ($< 20^\circ$) or pendulous tend to be thickened, narrow and isostomatous (stomates on both sides) with an increase in the number of stomates per unit area as well as a tendency to be isobilateral, or to have sunken stomates (and hence more able to control movement of water in times of stress). Plants with 'composite' angles on the one plant, e.g. *Acacia aulacocarpa* or *Gardenia megasperma*, are more difficult to interpret environmentally but tend to be 'mid-range' xeromorphs. At this level, no account is taken of diurnal leaf movement or nastic adaptations such as parahelionasty etc. (cf. Begg and Torsell 1974).

Leaf type

This is self-explanatory from Table 4.1. A 'leaf' is regarded as a unit capable of photosynthesis. Difficulties occur in describing aphyllous green-stemmed plants such as *Sarcostemma* but in the region these are rather few. There is often a high correlation between leaf type and leaf angle and it may be possible eventually to dispense with the latter. As with leaf size (cf. Webb 1959), leaf type may indicate physiological adaptation to environment but is likely to be more efficient in classifications when described in combination with size and angle. It is evident that because of their limited physiological relevance, present definitions of 'leaf type' will change with time.

Life form

For the present, essentially the basic life form units of Raunkiaer are used. Raunkiaer (1934) established his forms (rather tentatively) on the position of the perennating organs at the onset of the most unfavourable annual season. It is almost certain that at the time Raunkiaer was unaware of the extent or importance of other phenomena that occur, particularly in parts of the tropics where additional and often facultative life forms have developed in the face of fire, flood, predation and other periodic phenomena. Neither have some of these been taken into account by Mueller-Dombois and Ellenberg (1974) in their considerable extension of Raunkiaer's system. Conspicuous examples are the giant woody stolons (up to 25 m long) of *Hibiscus tiliaceus* in the south-west Pacific that are apparently maintained by frequent cyclones or dynamic land surfaces, as well as the lignotuberous sprouting, root-suckering and rhizomatous development of many of our fired woody plant formations. The 'underground forests' of 'geoxyllic suffrutices' in Africa that are suggested by White (1977) to have developed as a response to oligotrophic conditions are yet another example. I believe that the terms

'tree' and 'shrub' are not readily definable in the Australian context, particularly where fire occurs. Partly to circumvent such a problem, Mueller-Dombois and Ellenberg (1974) have used a 'scapose' (monopodial) or 'caespitose' (multi-stemmed) qualifier for phanerophytes, although the choice of the term 'caespitose' is less exact as *caespi* refers to tufted (Stearn 1973) rather than multi-stemmed, and is better applied to forms such as *Xanthorrhoea* and *Cycas* (otherwise rosulate phanerophytes of Mueller-Dombois and Ellenberg).

DESCRIPTION OF THE STRUCTURAL FORMA

The *structural forma* may be described by up to three dominant *modi*. If this is sufficient, or if there are no more than three easily describable strata, the *forma* can be described as *simple*. It is *complex* if there are more than three equivalent *modi* in the dominant stratum or more than three strata. A poplar box (*Eucalyptus populnea*) woodland with a mean canopy height of 12 m and 25 per cent foliage projective cover (Specht this volume) could be described as a *simple* 12/35 *noto-pendic-ortho-phan*. If strata are to be taken into account, e.g. a false sandalwood (*Eremophila mitchellii*) (sub-stratum 1) and a graminoid (*Bothriochloa decipiens*) (sub-stratum 2), then the total community is a *simple* 12/25 *noto-pendic-ortho-phan/nano-compic-ortho-phan/nano-compic-gramo-hemicrypt*. In mapping notation, numericals can be used to refer to the sequential position of each of the attribute states in Table 4.1, e.g.

S 12/35—	5311
3411	
3443	

Height/cover values can be added as continuous variables if required for substrata, but are not transcribable for numerical analysis owing to the non-equivalence that often occurs between strata of different communities. The above formula can be coded directly for numerical analysis. In most cases, however, all significantly occurring *modi* that are recorded in a sample area may be coded for numerical analysis together with height/cover of the dominant stratum as continuous variables. For mapping repetitive communities, e.g. as in the CSIRO system of land systems, each *structural forma* can be given a single alpha-numeric code and allocated a height/cover class. The poplar box woodland is a relatively simple plant community. A highly complex seasonal woody plant community with woody lianes and emergent *Callitris intratropica* (Cupressaceae) examined recently near Point Stephens in north-west Australia was described as follows:

Complex 6/70 meso-lateric-deciduo: micro-vertic-ortho-phan: nano-compic-ortho-lianophan with a *lepto-vertic-solido-phan* emergent.

(A *modus* is classified as emergent if it is the whole or part of a distinct superstructural element of < 5 per cent foliage projective cover or biomass.) The mapping notation for

36 Attributes and their Selection

this structural forma would then be:

c 2151
6/70-6211:4111:3416.1

Broadscale Australian classifications that include this specific vegetation type as well as a range of others, would be:

1. semi-deciduous microphyll vine-thicket (Webb 1959)
2. low closed forest (Specht 1970)
3. open low woodland with a dense thicket substratum (Beard and Webb 1974).

Global classifications including this type would be:

1. tropical semi-deciduous forest (IUCN 1973)
2. closed evergreen scrub with scattered trees (Fosberg 1970)
3. deciduous broadleaf and evergreen needle leaf stratified forest with tree layers of medium height with an understorey of (?) shrubs over 1 m in height with lianas present, i.e. B D ms.j (Küchler 1949)
(It is not known whether it is permissible under this scheme to combine B with D.)

I do not propose to discuss the difficulty of equating these various terminologies.

DEVELOPMENT OF A FIELD EXAMPLE

The structural pro forma method of Webb, Tracey and Williams (1976) used to describe and classify rainforest vegetation, was initially extended by me to include non-rainforest types in eastern Australia and other parts of the south-west Pacific. This resulted in an unwieldy set of about 150 attributes with large numbers of double-matching zeros in the data set, and when used via the TAXON programs produced outliers and intense clusters whose spatial relationships were difficult to interpret.

Sites chosen on a belt transect along a macro-climatic (1000 km) gradient in Queensland from Innisfail (hot wet low seasonal) to Burketown (hot dry highly seasonal) were initially classified using this system. The attribute set was then reduced via iterative classifications to a set of variables considered most likely to reflect plant function. When a classification was achieved that could be interpreted ecologically, the distribution of the 'functional' attributes was examined along the environmental gradient where there were seen to be evident relationships with edaphic and other environmental variables. Subsequent modification of this data set led to the tentative acceptance of two spatial descriptors (height and foliage cover of the dominant stratum) plus the four attributes of leaf and life-form described via non-exclusive multistates (see Williams 1976). It became clear that the use of multistates created difficulties in interpreting the diagnostic value of the attributes and necessarily restricted handling of the data set to the TAXON library instead of allowing a wider range of numerical procedures.

The next development was to combine the 'functional' attributes evident in the communities into descriptive *modi* and to standardise at unity the proportions of each

of the various elements that made up the total of the 'functional' attributes and hence *modi* within each community. (For example, in a community made up of four *modi* of which two possess the 'micro' element, one 'noto', and one 'pico', the relative proportions would be 2:1:1 or 0.5:0.25:0.25 for each of the leaf-size components.) This standardisation achieved a compromise between the two extremes of either assessing presence/absence or recording those individuals present with the attributes. The result is a useful comparator in cases where extremes of species richness are likely to be encountered, e.g. a complex mesophyll vine forest (CMVF, Webb 1959) compared with a samphire flat. The proportional estimate is also likely to provide a crude relative expression of the functional make-up of the community and the way it reflects environmental stress and resource usage.

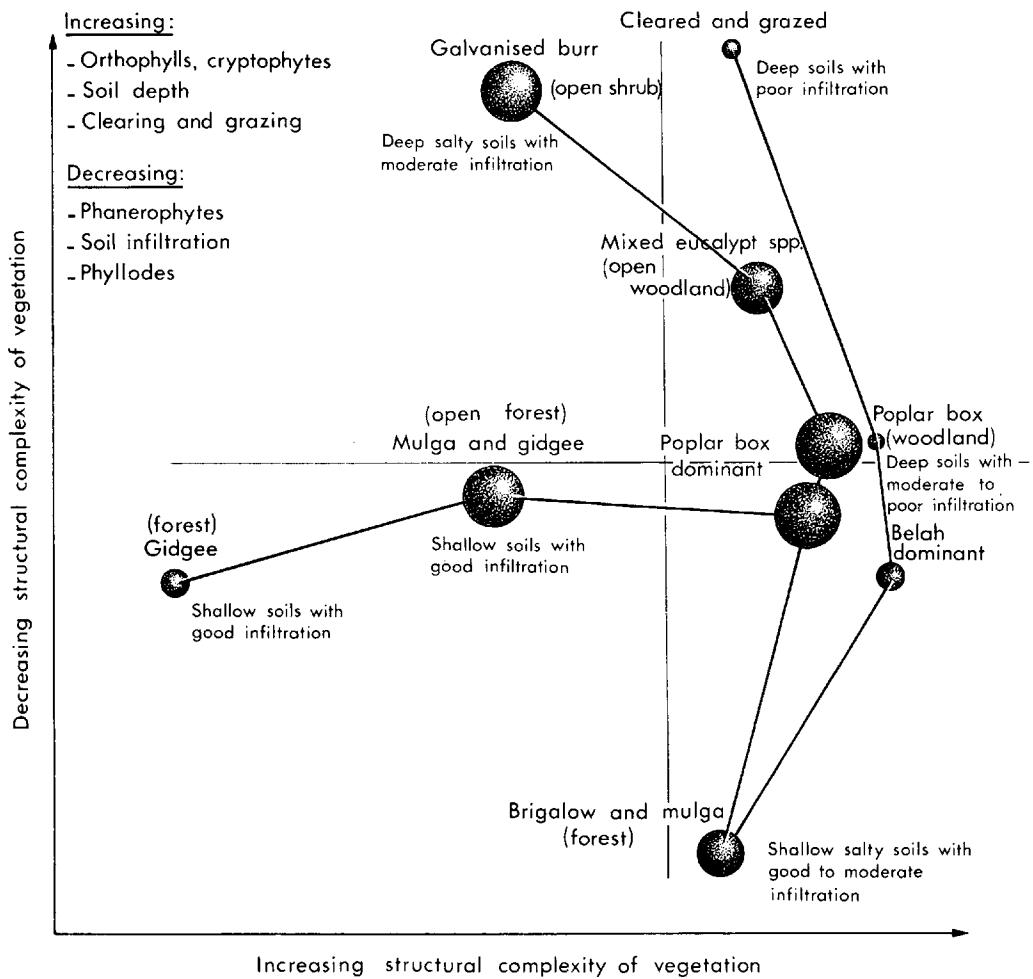
The establishment of a *modal* structure in this way allows a freedom in ecological expression that is unobtainable via the use of floristic taxa. (An alternative way of classifying *modal* data is to regard each *modus* as a unique unit that can be given a number. In this way, normal phytosociological and other numerical analyses can be carried out as for floristic taxa.) The construction of each *modus* as a unit descriptor and the association of different *modi* provide a mental picture of how the plant community is structured physiologically and physiognomically and in a way which allows a more uniform comparison between environmentally remote communities. The present attribute set has been applied recently in diverse environmental gradient situations such as in the Snowy Mountains; the highly seasonal north-west Australia; semiarid southern Queensland (Wycanna-Goondiwindi), and in a local subcoastal heath complex near the Myall Lakes in eastern N.S.W. The last two were chosen to test the resolution capacity of the attribute set and to assess its predictive potential. The first exercise related to aspects of land management and soil types and the second to a micro-scale classification of heathland based on previous extensive measurements of floristics and micro-structure by other workers, with additional data on small mammal distribution.

As the heathland exercise is described in part by Fox and Fox (this volume), where *modal* attributes were used successfully, it remains to describe the initial results of the Wycanna experiment. In doing so, I will make use of unpublished soil data kindly provided by Dr G. J. Burch of the Woodland Ecology Group in the Division of Land Use Research, CSIRO. Together with W. F. Goodwin, the survey was carried out in conjunction with a full-scale mapping exercise of an intensively managed grazing property, the land-systems of which are similar to some previously described for the Balonne-Maranoa area (Pedley 1974).

The area was sampled intensively on the ground along topo-gradients that were previously determined from aerial photo patterns. At each site, information was gathered according to the proforma in Appendix 4.1. Along the gradient, sites were also established on local soil catenas for which soil-water infiltration and soil depth data were collected (Table 4.2). Following analysis of the plant data by classificatory and ordination procedures via the CSIRO TAXON Library, the soil data were imposed on the site pattern in the ordination (Fig. 4.1, Table 4.3). From this it is evident that there is a marked relationship between site characteristics and the vegetation as described by

TABLE 4.2
Soil parameters used in Fig. 4.1

Soil depth	Infiltration (sorptivity)
Shallow = <0.3 m	Poor = <0.25
Medium = 0.3–1.0 m	Moderate = 0.25–0.5
Deep = >1.0 m	Good = >0.5



4.1 Minimum spanning ordination of functional plant attributes along an edaphic gradient in a sub-tropical semi-arid woodland ecosystem in southern Queensland. Edaphic features are superimposed on the ordination.

TABLE 4.3

Distribution of structural modi along a soil catena at Wycanna, southern Queensland

Vegetation type (after Specht)	Low open forest	Open forest	Open forest	Open forest
Floristic taxa	<i>Acacia aneura</i> (mulga)	<i>Acacia catenulata</i>	<i>Casuarina cristata</i> (belah) + <i>Acacia catenulata</i>	<i>Casuarina cristata</i> + <i>Eucalyptus populnea</i> (poplar box)
Structural modi	<i>nano vertic</i> <i>phyllodo phan</i>	<i>micro vertic</i> <i>phyllodo phan</i>	<i>noto compic</i> <i>phyllodo phan</i> + <i>micro vertic</i> <i>phyllodo phan</i>	<i>noto compic</i> <i>phyllodo phan</i> + <i>noto pendic</i> <i>ortho phan</i>
Sorptivity 'i'	0.886	0.549	0.393	0.247
Soil depth	0.3 m	(?) 0.5 m	2 + m	2 + m
Slope class	Ridge	Mid to upper slope	Foot slope	Flat

the two spatial parameters of the dominant stratum and the functionally-oriented structural attributes. It is also noteworthy that in almost every case, the 'functional' attributes or *modi* contributed most information towards group formation.

CONCLUSIONS

Results so far from both large- and small-scale surveys in widely differing environments indicate some promise in the application of functionally-oriented structural attributes for the uniform classification of diverse plant communities. This has been achieved in a way that shows some measurable relationship with the physical environment and associated biota. I believe this is a reasonable basis for proceeding with *in situ* experimentation that can determine more precisely the environmental limits to those physiognomic, morphological and anatomical attributes that best reflect the physiological capacity of the plant to optimise use of the resource. Because of the inherent complexity of plant-environment interaction, it is evident that the further development of this concept has a long way to go. As a logical extension, the association of such attributes among plants may indicate a measure of the capacity of the community as a whole to withstand 'stress' and to optimise resource use.

Provided an acceptable predictive level exists between such features and easily observed morphological characters, such data should allow further modification and validation of the *modal* attributes listed here. Attributes thus developed via an objective method are potentially more useful in describing and classifying vegetation than those selected on a parochial and subjective basis for the production of 'static' classifications.

I would emphasise that the application of the rather ponderous system of nomenclature presented here is somewhat inescapable. The major advantage of the terminology is that it allows a direct quantification of terms for numerical analysis, where unique *modal* combinations become 'taxa' in a systematic (but not phylogenetic) sense

40 Attributes and their Selection

and hence amenable to phytosociological analysis and the 'pattern analysis' of Williams (1976) as well as other numerical procedures.

With this system, field recording time is usually short—an open woodland site takes about 15 minutes to complete and a complex mesophyll vine forest site approximately 30 minutes.

Should the development of a *modal* classification prove successful, it should, by implication, ease those problems currently associated with limitations of scale and conflicting terminology. The relatively low number of attributes in the present list (<40) will also simplify data-banking. The system is open-ended so that attributes can be added to assist in specific problem areas, in which case the *modi* remain as core units. The present attribute set will undergo further modification as trials proceed. Indications are that the set for the *structural forma* is sufficiently sensitive to detect vegetation differences over a wide range of scales from a heathland mosaic to sub-continental formations. As such it provides a basis for monitoring vegetation change along spatial and environmental continua in a way that may allow a more sensitive examination of response to environmental change.

Appendix 4.1 (FIELD PROFORMA)

Site No. (28) Primary Descriptions for Structural Forma

A. N. Gillison 22.06.78

Stratum	Canopy HT (m)	FPC*		Complexity Rating	Modus				Species	Code
		Obs	Calc		Leaf Size	Leaf Angle	Leaf Type	Str Unit		
EM				5						
					NOTO	PENDIC	ORTHO	PHAN	EUC. POPULNEA	EUCPOPU
									EUC. INTERTEXTA	EUCINTE
PRIM	15	45	—	5	NANO	COMPIC	ORTHO	PHAN	EREMOPHILA MITCHELLII	EREMITC
S1	3	15	—		NANO	COMPIC	GRAMO	H'CRYPT	3 GRASS SPP.	
S2	0.10	3	—		NANO	COMPIC	GRAMO	H'CRYPT	3 GRASS SPP.	
S3										

Total Structural Modi = (3)

Floristic Taxa = (6)

Ratio $\frac{S}{F} = 0.5$

Remarks: Poplar Box Woodland with Sandalwood and Grass Sub-strata. * After Specht (this volume).

REFERENCES

- Beard, J. S., and Webb, M. J. (1974). The Vegetation Survey of Western Australia: its aims, objects and methods. *Part I of Explanatory Notes to Sheet 2, Great Sandy Desert*. Vegetation Survey of Western Australia 1:1 000 000 Vegetation Series. University of Western Australia Press, Nedlands, W.A.

- Begg, J. E., and Torssell, B. W. R. (1974). Diaphonastic and parahelionastic leaf movements in *Stylosanthes humilis* H.B.K. (Townsville stylo). In: *Mechanism of Regulation of Plant Growth*. Bulletin 12, The Royal Society of New Zealand, Wellington, N.Z., 277-83.
- Carnahan, J. A. (1976). Natural vegetation. Map (1:6 000 000) and commentary in: *Atlas of Australian Resources*, Second Series (ed. T. W. Plumb). Department of National Resources, Canberra.
- Fosberg, F. R. (1970). A classification of vegetation for general purposes in Guide to the Check Sheet for IBP Areas. In: *IBP Handbook No. 4*. (ed. C. F. Peterken) (second printing). Section IBP/CT. Blackwell Scientific Publications, London.
- Givnish, T. J. (1978). Ecological aspects of plant morphology: leaf form in relation to environment. *Acta Biotheoretica Supplement: Folia Biotheoretica* 7: 83-142.
- Givnish, T. J., and Vermeij, G. J. (1976). Sizes and shapes of liane leaves. *Amer. Nat.* 110, 743-78.
- Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Amer. Nat.* III: 1169-94.
- Grime, J. P. (1979). Plant strategies and vegetation processes. Pp. xi + 220. Wiley, Chichester.
- IUCN Secretariat (1973). A working system for classification of world vegetation. *IUCN occasional paper No. 5*. IUCN Morges, Switzerland.
- Kessell, S. R. (1979). *Gradient Modeling: Resource and Fire Management*. Springer-Verlag, N. York.
- Küchler, A. H. (1949). A physiographic classification of vegetation. *Ann. Ass. Am. Geogr.* 39: 201-10.
- Lewis, M. C. (1972). The physiological significance of variation in leaf structure. *Sci. Prog. Oxf.* 10: 25-51.
- Medina, E., Sobrado, M., and Herrera, R. (1978). Significance of leaf orientation for leaf temperature in an Amazonian sclerophyll vegetation. *Radiat. and Environ. Biophys.* 15: 131-40.
- Mueller-Dombois, D., and Ellenberg, H. (1974). *Aims and Methods of Vegetation Ecology*. Wiley, New York. 547 pp.
- Noble, I. R., and Slatyer, R. O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbance. *Vegetatio* 43: 5-21.
- Pedley, L. (1974). Vegetation of the Balonne-Maranoa area. *CSIRO Aust. Land Res. Ser.* No. 34, 180-203.
- Raunkiaer, C. (1934). *The Life Forms of Plants and Statistical Plant Geography. Being the collected papers of C. Raunkiaer*. Oxford, Clarendon.
- Simpson, G. G. (1961). *Principles of Animal Taxonomy*. Columbia University Press, New York-London.
- Specht, R. L. (1970). Vegetation. In: *The Australian Environment* 8th ed. (ed. G. W. Leeper), pp. 88-67. CSIRO/Melbourne University Press, Melbourne.
- Stearn, W. R. (1973). *Botanical Latin: History, Grammar, Syntax, Terminology and Vocabulary*. 2nd ed. David and Charles, Newton Abbot.
- Steenis, C. G. G. J. van. (1958). Rejuvenation as a factor for judging the status of vegetation types: the biological nomad theory. In: *Study of Tropical Vegetation*. Proc. Kandy Symposium. UNESCO, pp. 212-15.
- Taylor, S. E. (1975). Optimal leaf form. In: *Perspectives of Biophysical Ecology; Ecological Studies* (eds. D. M. Gates and R. B. Schmere), Springer, Berlin, 12: 73-86.
- Webb, L. J. (1959). A physiognomic classification of Australian rainforests. *J. Ecol.* 47: 551-70.
- Webb, L. J., Tracey, J. G., and Williams, W. T. (1976). The value of structural features in tropical forest typology. *Aust. J. Ecol.* 1: 3-28.
- White, F. (1970). The underground forests of Africa: a preliminary review. In: *Tropical Botany* (ed. D. J. Mabberley and Chang Kiaw Lan), pp. 51-71. *The Gardens Bulletin Singapore*, Vol. XXIX.
- Williams, W. T. (1976). The meaning of pattern. In: *Pattern Analysis in Agricultural Science* (ed. W. T. Williams), pp. 124-9. CSIRO/Elsevier Scientific Publishing Company, Amsterdam.

Disturbance and change in rainforests and the resulting problems of functional classification

M. S. HOPKINS

INTRODUCTION

There are many attributes which could be used to classify vegetation. These include:

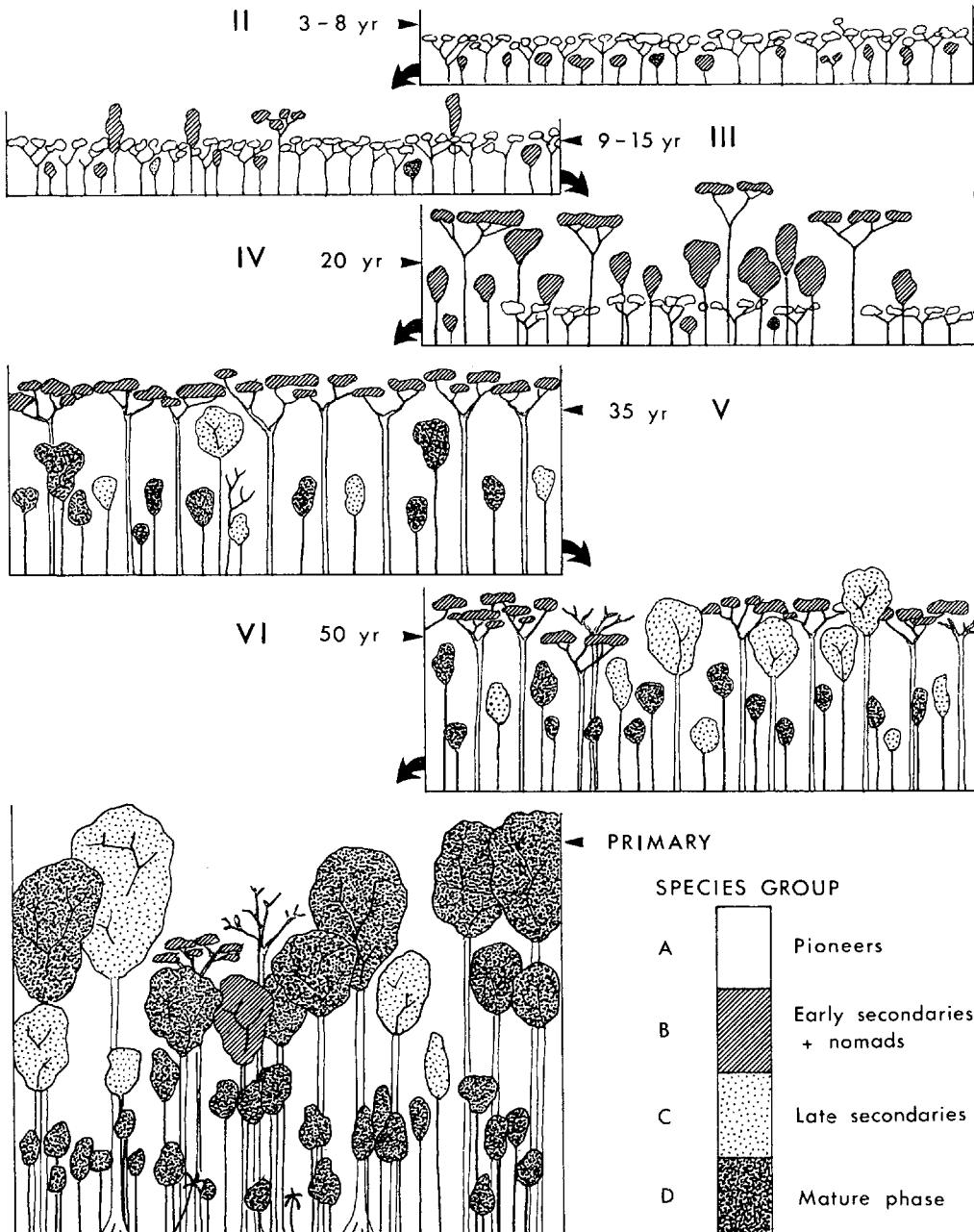
- 1 Structural/physiognomic features of the vegetation
- 2 Floristics and floristic-synthetic features (diversity, constancy)
- 3 Ecological features (e.g. vagility, stability)
- 4 Environmental features (e.g. climate, soils)
- 5 Other derived features (e.g. potential for particular land uses, wildlife characteristics, penetrability for military purposes)

Some of these characteristics are observable features of the vegetation itself (structure and floristics), some are directly or indirectly derived from the vegetation and its environment (ecological features), and the remainder are functionally or correlatively associated with the vegetation.

The value of a classification produced by an attribute set can only be judged in relation to its purpose. If the sole aim of the classification is to provide a prescribed set of 'pigeon-holes' into which the vegetation stands can be slotted for comparative and descriptive purposes, then the use of any attribute or combination of attributes may suffice. Descriptive classifications would usually incorporate observable features of the vegetation, the suitability of actual attribute sets depending on the scales of definition required, the type and scale of comparisons to be made and so forth.

Ecologists, however, usually expect a classification to provide more than just a descriptive framework. There are obvious, general relationships between structure and floristics, function and environment and there appears to be no reason why a fundamentally descriptive classification should not, by utilising correlations between these characteristics, reflect ecological features of the vegetation. Do certain floristic or structural features of the vegetation reflect plant behaviour or environmental factors which act or have acted on the stand, and how robust are the relationships? Is it possible, in fact, to construct broad ecological classifications using many attribute/factor correlations?

In the Australian context, there appear to be two broad approaches to this problem. The first, of which the Specht classification (Specht 1970, 1972; Specht *et al.* 1974) is a good example, is to examine the functional relationship between a small number of key structural features (e.g. canopy cover and height), community physiological processes (e.g. water usage) and the relevant environmental and climatic parameters. The other



5.1 Schematic representation of reconstructive secondary succession in Complex Notophyll Vine Forest. Species groups from Hopkins et al. (1977).

44 Attributes and their Selection

approach, and this is exemplified by the rainforest structural typology of Webb (Webb, 1959, 1968, 1978; Webb *et al.* 1976), is to examine the extent to which a large set of structural attributes produces groupings that reflect observed environmental and behavioural factors.

Both classifications are based on functional correlations between vegetation structure and floristics and environmental/climatic factors and depend for their successful operation and predictable extension upon the fulfilment of two interrelated conditions. First, the vegetation should be 'mature, stable, and integrated' (Beard 1944). That is, the vegetation sampled should be an accurate, integrated expression of the contemporary biological and environmental factors operating at that particular site. Second, the structure and function of vegetation should be primarily a product of interaction between the classical environmental factors, climate and soils. Are these conditions fulfilled?

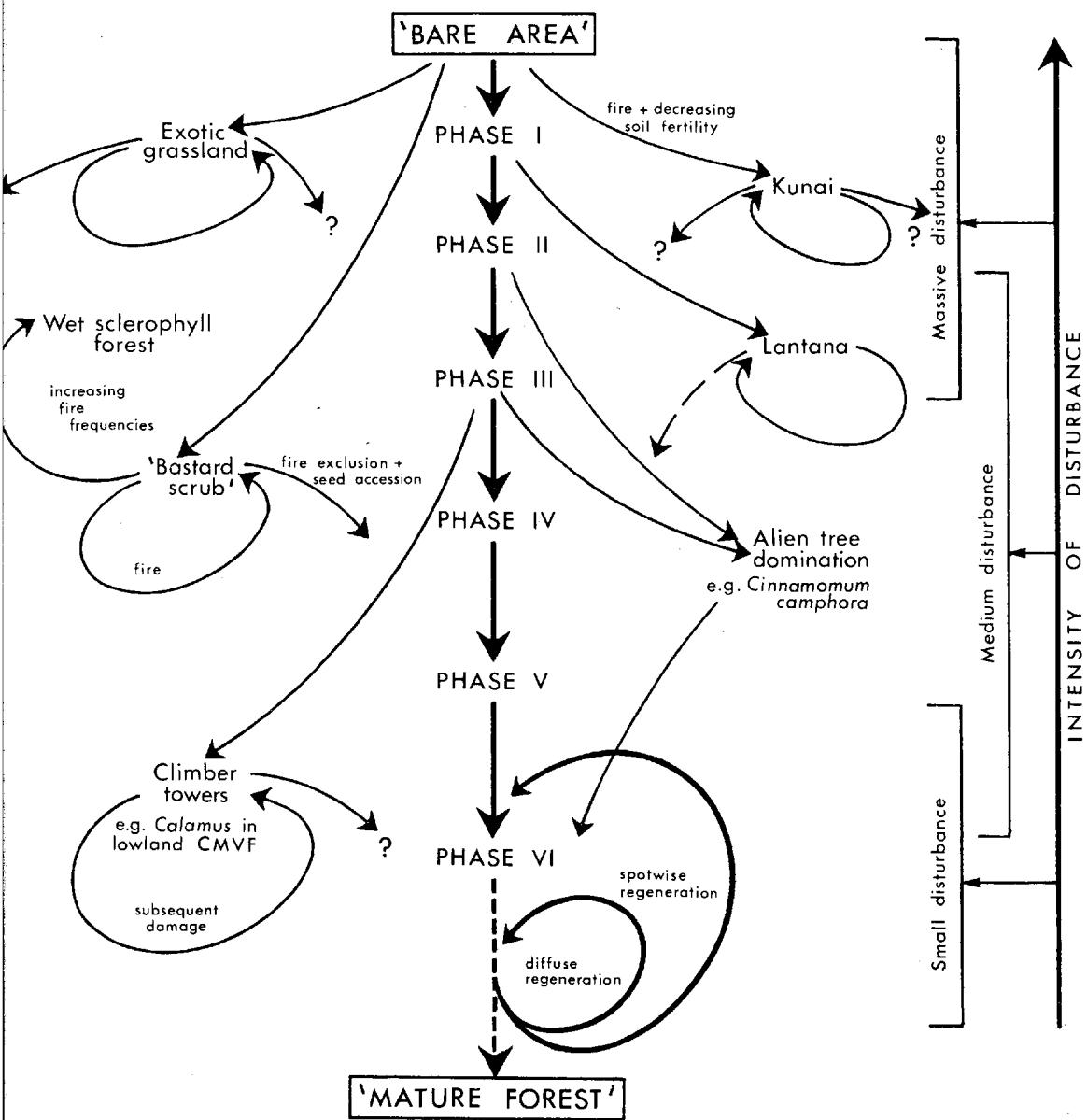
I intend to approach these questions indirectly by examining the significance of the roles of disturbance (man-made and otherwise) on the patterns of development and change that occur in vegetation and by showing that, in many cases, these are equally as important as climate and soils in dictating the type of vegetation that occupies any particular area. Although this chapter will deal almost exclusively, and very cursorily, with rainforests in the Australian region, there appears to be no reason why many of the points raised are not equally applicable to other forms of vegetation.

DISTURBANCE, SECONDARY SUCCESSION, AND CLASSIFICATION

Reconstructive or progressive successions

If one were to clear 10 ha of rainforest, it would be very unlikely that the initial regeneration would be in any way similar to the intact vegetation. In most cases, the pioneer regrowth would be constituted by species not evident in the intact forest, short-lived species which form a low, shrubby canopy a few metres high. This pioneer canopy may, under certain circumstances, represent the first phase of a species replacement sequence culminating in the re-establishment of the species and structure characteristic of the primary forest (Richards 1952; Ross 1954; Jones 1955, 1956). This process can be referred to as *reconstructive* or *progressive secondary succession* (Fig. 5.1).

During the process, the pioneer species are progressively replaced by early secondary species, late secondary species and, finally, mature phase species; there are also distinguishable trends in floristic composition (species richness, diversity, pattern diversity), structure and physiognomy, and in the regenerative strategies of the species characteristic of the various successional phases (Hopkins 1975). Schematic transect diagrams of Complex Notophyll Vine Forest (CNVF) (Webb 1959) at various stages in reconstructive species succession are shown in Fig. 5.2. However, the process would probably take 800 years or so to produce a forest which resembled the intact forest (Hopkins *et al.* 1977). In the intervening period, the site would support a sequence of vegetation 'types' which would differ in various ways (floristics, structure, physiognomy, behaviour) from the original forest.



5.2 Schematic representation of reconstructive secondary succession pathway and natural regeneration in rainforest showing some of the variations (deflections, regressions) that can occur in relation to intensity of disturbance. Phases II-IV of the progressive successional pathway correspond to those depicted in Fig. 5.1.

Secondary successions in rainforest have been extensively described in the literature (see, for example, Richards 1952, 1955; Greig-Smith 1952; Ross 1954; Kellman 1970; Webb *et al.* 1972; Gomez-Pompa and Vazquez-Yanez 1974; Whitmore 1975).

Arrested, deflected, and regressive successions

Disturbance of rainforest does not, however, necessarily initiate a constructive secondary succession. In many cases, the succession stops or is arrested at a stage prior to the establishment of the mature phase species or culminates in a forest type completely unlike the original. It suits my purpose to consider two interrelated sets of factors which can cause such variations in the secondary successional process.

Changes in physical site factors. Little is known about the resilience of rainforests, the reversibility/irreversibility of site factor changes brought about by disturbance, and of the effects these have on the pathways and results of regeneration. The extent and speed of recovery varies with the type and intensity of disturbance; it also varies between different forests. For example, nutrient losses when the vegetation is totally removed from Complex Vine Forests on kraznozem soils pose no barriers to reconstructive succession. On the other hand, similar disturbance of Mesophyll/Notophyll Vine Forests with wattles on nutrient-enriched beach sands in the Innisfail area of north Queensland almost invariably results in their conversion or transformation to *Eucalyptus intermedia-Acacia crassifolia* forests. In the latter case, regeneration of a forest similar to the original would probably require a geomorphological/vegetation sequence similar to that which produced it in the first place—a prograding beach sequence. Similar problems probably occur in predicting whether progressive, deflected or arrested successions will result from almost all disturbance-induced changes in physical site factors. For example, clearfelling of certain types of lowland rainforest in the Gogol River valley in Papua New Guinea has resulted in a substantial rise in water tables. Will the early phases of succession lower the water table and so facilitate a reconstructive secondary succession? Or will the process be deflected and culminate in the production of some form of swamp forest?

If the disturbance results in permanent, irreversible changes in key physical site conditions (e.g. drainage of a swamp forest), then the regeneration will tend to reflect the habitat change. It is doubtful, however, whether the effects such changes have on the vegetation are ever determinate since the composition of the regeneration in the 'new' site will reflect only the competitive vigour of those species that have managed to reach the site. In this way, one can imagine the same site conditions being able to support a large number of floristically-defined vegetation 'types' depending on the availability of the various potential competitors.

Changes in biological site factors. The reconstructive secondary succession can be modified by fundamentally biological factors in a number of ways. Two examples will be given to illustrate this.

First, the reconstructive secondary succession is often arrested by absence of propagules of the later phase species. The species of the earlier phases of secondary

succession characteristically have regenerative strategies or survival techniques which ensure their success after disturbance. They are 'opportunists' which produce large numbers of effectively dispersed seeds which usually have long viability. Many of the species of the mature forest, on the other hand, are not well adapted to the conditions following disturbance. If the area cleared is very large or if a geographically-isolated area of a particular forest type is cleared, then it is likely that the species of the mature phases of the typical reconstructive secondary succession will be delayed or eliminated and the succession stopped at some intermediate stage. In northern New South Wales in what was once the 'Big Scrub', for example, vast areas of lowland rainforests were cleared in the early part of this century. The forest regeneration on many of the abandoned areas now appears to be arrested at an early secondary stage. In some cases, this can be attributed to changed site conditions brought about by past land-use. In others, the re-development of the forest has been delayed apparently by a lack of mature phase species. In this latter case, will these forests cycle around a late secondary stage? Or will available species characteristic of other forest types in the area eventually enter and deflect the succession?

Second, the progressive secondary succession can be deflected or arrested if a species (or group of species) produces conditions unsuitable for later phase species. *Lantana camara*, the introduced vine-scrambler, can block reconstructive secondary succession at the pioneer phase under certain conditions (Williams *et al.* 1969; Webb *et al.* 1972). Similarly, the entry of particular species may change the disturbance regime of the site in a way which makes it unsuitable for further rainforest succession. Eucalypt regeneration tends to increase the possibility of fires as does the establishment of certain grasses. The results are disturbance-induced deflections in the succession. There are very extensive, and relatively permanent, areas of grasslands and sclerophyll-dominated forests in the Tully, Innisfail, and Cairns areas of north Queensland that appear to be a product of such past disturbance. Long periods of site occupation by such vegetation may result in physical site changes (e.g. loss of soil fertility) and so render the site unsuitable for reconstructive secondary succession. The kunai (grassland) problem in New Guinea is another prominent example of this type of mechanism.

The secondary forest classification problem

I have described briefly how disturbance of small areas of rainforest can produce secondary vegetation, of varying durability and persistence, which differs markedly from the original forest in floristic composition and structure. This has broad and far-reaching implications regarding the continuing usefulness of the present systems of structural classification. One site can support a variety of structurally and floristically defined vegetation types. If site/forest-type correlations are to be in any way useful or consistent, the forest typology must be such that secondary forests are recognised, characterised, and included meaningfully within the classification. This is not possible using the present classification systems.

Because of the vast areas of secondary forest, stagnant 'bush' and fire-degraded grasslands that exist throughout the moist tropics and subtropics, this problem of classi-

fying secondary forests can no longer be ignored. It has been estimated recently (L. J. Webb, pers. comm.), for example, that approximately three-quarters (i.e. 60 000 km²) of the original rainforest area in eastern Australia has been cleared. The area of secondary growth has not been estimated but it certainly occupies several thousand square kilometres.

DISTURBANCE AND PRIMARY FOREST CHANGE

The process of change

Primary rainforest regeneration can be viewed, albeit simplistically, in terms of the secondary sequence already described. Gaps of various sizes are continually produced by natural disturbances—wind-throws, lightning strikes, landslips, storm and cyclone damage, and individual mortality. The larger disturbances allow the establishment of species of the earlier phases of succession and usually initiate localised reconstructive successions. However, each phase of the microsere can only support a small fraction of the species that could participate; the actual participants are probabilistically determined by factors such as the spatial and temporal coincidence of gap formation with fruiting trees, viable soil seed, pre-established recruits and so forth (van Steenis 1958; Poore 1968; Webb *et al.* 1972). As the gaps become smaller, there is a tendency for the microseres to become progressively truncated since there is a continuously decreasing possibility that the species of the earlier phases of succession will be able to establish. The ultimate result of this process of decreasing size of disturbance is the 'diffuse' regeneration of van Steenis (1958).

Four features of this regeneration process are pertinent to the present discussion:

1. Disturbance is essential to the process of natural regeneration. Without disturbance there could be no change. The type of changes that occur are a product of the type, intensity, and frequency of disturbance.
2. The primary forest exists as an overlapping mosaic of regenerating units, localised reconstructive successions or microseres. The character of the forest at any particular point in time is a manifestation of the proportion of the forest area which is in particular stages of microsere development.
3. The physiognomic structure, floristic composition and structure, and dynamic ecological characteristics of the forest are as much a product of the disturbance regime to which it has been subjected as they are to the more commonly flaunted variations in climate, soils, and topography.
4. The effect of different types of disturbance on rainforest will depend on the disturbance regime within which it has evolved. Disturbance which, because of type, periodicity, or intensity, is unusual relative to a particular forest type, will have a far greater impact than that which falls within the usual disturbance regime and vice versa.

The problems that these features present for the classification of vegetation based on environmental/vegetation correlations elicited in primary forest are self evident. The

area of rainforest in Australia that has not been disturbed significantly by man is very small. By far the greater part of the remaining Australian rainforests have been logged and the degree to which the structure and composition of these forests relates to the type and intensity of disturbance has not been examined.

Development and change—the roles of history and disturbance

Disturbances and subsequent changes in rainforests are not restricted to areas of a few hectares, nor can the forests of today be explained solely in terms of changes since the advent of man. Many of the changes which are particularly significant for classification purposes have occurred at regional scales over extensive time spans. How would we expect rainforests to react to these changes? I will consider briefly three broad types of change—those induced by variations in climates, soils, and disturbance regimes—with the aim of defining general problems that these pose for vegetation classifications.

Regional climate changes and changes in disturbance regimes. It seems likely that a gradual climate change would effect a gradual change in the composition of the complex of species from which the microsere participants could be drawn; the composition and structure of the existing rainforest would change, in response to the environmental change, via the medium of microseres. Similar changes would be brought about by variations in the intensity, type and frequency of disturbance (*vide* Whitmore 1974). The relevant feature of this process of vegetation change is the speed with which the vegetation can attain a composition and structure which reflects the new conditions. Theoretically at least, one would expect rainforest composition and structure to lag behind climate changes by many hundreds, even thousands, of years. There are a number of simple and obvious reasons why this should be so. First, because of the longevity of rainforest trees, the microsere process is inherently diurnal. Even the most dramatic changes in climate, for example, would take many hundreds of years to be reflected in the vegetation. Second, and this must be a very important factor where the changes are regional in extent, the rate of change is controlled completely by the vagility and regional availability of 'suitable' species. In the Australian context, where rainforest communities occur under climatic conditions that appear to have been comparatively unstable in the past, one would expect this to result in large areas of forests which are 'relicts' of past environments, forests whose compositions and structures are out of phase with the contemporary environment.

Geomorphological/vegetative sequences and development. This section is concerned with the many ways that 'new' edaphic environments can be produced and with the vegetative/geomorphological sequences which follow.

If one looks at a prograding beach dune sequence (e.g. the Kurrimine and Cowley Beach areas near Innisfail, north Queensland) one finds that it has resulted in a whole range of vegetation 'types'—*Eucalyptus intermedia* open forests and open woodlands, *Acacia aulococarpa/E. intermedia* open and closed forests, *Melaleuca quinquenervia* closed forests, *M. leucadendron* closed forests, *M. viridiiflora* open woodlands, sedge swamps, pandan swamps, mangroves, and at least three types of rainforest (Hopkins,

50 *Attributes and their Selection*

Graham and Murtha 1979). It is possible in most cases to give a plausible explanation for the existence of most 'types' in edaphic terms. Even here, we are never sure whether the postulated environmental correlations reflect 'causal' or 'conditional' relationships (see van Steenis 1961, for examples). Similarly, one has to accept that quite a substantial part of the area is occupied by intermediate forms of vegetation which may or may not be explicable in terms of variations in soils. Assuming these problems can be recognised and circumvented, it is often possible to postulate a series of geomorphological/vegetation sequences which lead to the existence of the various 'types'. Are these developmental pathways primary successions? And, if so, are the vegetation 'types' along the pathways 'seral' vegetation types? The answers to these questions depend on the primary source of impetus for the vegetation change; the age-old dilemma—'Is it allogenic or autogenic change?' If the pathway is basically a vegetation relay pathway with the vegetation having an overriding influence, at each stage, on the future directions of change, then the pathway can be considered to be a primary succession and the intermediate vegetation types to be seral. If, however, the pathways were primarily edaphic relay systems, then the vegetation types merely reflect temporal edaphic differentiation. The attachment of descriptive epithets such as 'edaphic climaxes' and 'seral' to vegetation types under these circumstances would appear to be pointless; virtually all vegetation types could be, simultaneously, considered as 'seral' and 'edaphic climaxes'.

The present state of knowledge does not allow the differentiation of the alternate pathways of development. In the meantime, the usefulness of terms such as 'seral' and 'edaphic climaxes' in the context of rainforest/edaphic development is doubtful.

ATTRIBUTES OF CHANGING FORESTS

Two points were raised at the beginning of this chapter:

1. To what extent are rainforests mature, stable, and integrated?
2. To what extent are the rainforests of today a reliable and reproducible expression of contemporary patterns of climate and soils?

The answer to both these questions is 'very little'. Although the present distributions of rainforests are within a broad framework of climate and soils, they are prevented from being a full, integrated, predictable and correlatable expression of the physical environment in a number of ways.

1. Disturbance can produce a wide range of variations in vegetation, floristically and structurally, some of which is not causally or conditionally related to changes in site physical environmental factors.
2. The diurnal nature of the mechanisms of change in rainforests results in many areas of rainforest being out of phase with contemporary environmental factors.
3. Because of their generally poor vagility and the ease with which geographical barriers to their 'movement' can be produced, many rainforest types are enmeshed within a spatial framework laid down in the past. Many areas are

unlikely to support the types of forest which, considering climate and soils only, could be supported. This is because suitable framework species and structural forms necessary to effect the change are no longer present in the region.

4. The character of autochthonous rainforest developmental sequences is shadowy. As Walker (1972) reflected, 'The occurrence of floristic groups in a variety of mixtures, qualitatively and quantitatively, their environmental tolerances being in part dependent on their fellow groups, makes it difficult, if not impossible, to specify environment from the vegetation alone'.

The result is contemporary vegetation/site correlations which are blurred and in flux.

The question now is whether there are any attributes of the vegetation which could be expected to overcome these problems of meaningfully classifying these changing forests. There is no easy solution; floristic attributes are of limited use for regional comparisons because of the difficulties of comparing different floras. They are also of limited use at local levels because of difficulties in extracting precise species/site correlations. Time and skilled-user constraints limit their use in survey methodologies. Floristics are, however, one of the only links we have with the palaeoecological record and, as such, will always be indispensable.

Structural attributes are not so limited, but structural classifications suffer from the present disadvantage in that they do not deal satisfactorily with the now widespread areas of secondary and disturbed forests. It should be possible to overcome this problem by incorporating additional structural and derived ecological features of vegetation into existing classifications. In this regard there are a host of possibilities that warrant investigation. In particular, there are many 'behavioural' and ecological characteristics of species and vegetation stands that possibly could be inferred from structural and biological characteristics of the stands and which would relate to successional status and to the dynamic behaviour of communities (see, for example, Budowski 1965; Grubb 1977; and papers by Gillison and Noble in this volume).

REFERENCES

- Beard, J. S. (1944). Climax vegetation in tropical America. *Ecology* **25**: 127-58.
 Budowski, G. (1965). Distribution of tropical American rainforest species in the light of successional processes. *Turrialba* **15**: 40-2.
 Gomez-Pompa, A., and Vazquez-Yanes, C. (1974). Studies on the secondary succession of tropical lowlands: the life cycle of secondary species. In: *Proc. First Intern. Congr. of Ecology* (The Hague). 336-42.
 Greig-Smith, P. (1952). Ecological observations on degraded and secondary forest in Trinidad, British West Indies. II. Structure of the communities. *J. Ecol.* **40**: 316-30.
 Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* **52**: 107-45.
 Hopkins, M. S. (1975). Species patterns and diversity in the subtropical rainforest. Ph.D. Thesis, University of Queensland.
 Hopkins, M. S., Graham, A. W., and Murtha, G. (1979). The vegetation of the Cowley Beach area, Joint Tropical Research Establishment, North Queensland. CSIRO Div. Land Use Res. Tech. Memo 79/13.

52 Attributes and their Selection

- Hopkins, M. S., Kikkawa, J., Graham, A. W., Tracey, J. G., and Webb, L. J. (1977). An ecological basis for the management of rainforest. In: *The Border Ranges: A Land Use Conflict in Regional Perspective* (ed. R. Monroe and N. C. Stevens), pp. 57-66. Royal Society of Queensland, Brisbane.
- Jones, E. W. (1955). Ecological studies on the rainforest of southern Nigeria. IV. The plateau forest of the Okomu forest reserve. Part I. The environment, the vegetation types of the forest, and the horizontal distribution of species. *J. Ecol.* **43**: 564-94.
- Jones, E. W. (1956). Ecological studies on the rainforest of southern Nigeria. IV (continued). The plateau forest of the Okomu forest reserve. Part II. The reproduction and history of the forest. *J. Ecol.* **44**: 83-117.
- Kellman, M. C. (1970). *Secondary Plant Succession in Tropical Montane Mindanao*. pp. 174. Austr. Nat. Univ., Canberra. Publication BG/2.
- Poore, M. E. D. (1968). Studies in Malaysian rainforest. I. The forest on Triassic sediments in Jengka forest reserve. *J. Ecol.* **56**: 143-96.
- Richards, P. W. (1952). *The Tropical Rainforest*. pp. 450. Cambridge University Press.
- Richards, P. W. (1955). The secondary succession in the tropical rain forest. *Sci. Prog., Lond.* **43**: 45-57.
- Ross, R. (1954). Ecological studies on the rainforest of southern Nigeria. III. Secondary succession in the Shasha Forest Reserve. *J. Ecol.* **42**: 259-82.
- Specht, R. L. (1970). Vegetation. In: *The Australian Environment* (ed. G. W. Leeper), pp. 44-67, 4th ed. (CSIRO—Melbourne University Press, Melbourne).
- Specht, R. L. (1972). Water use by perennial evergreen plant communities in Australia and Papua New Guinea. *Aust. J. Bot.* **20**: 273-99.
- Specht, R. L., Roe, E. M., and Boughton, V. H. (eds.) (1974). Conservation of major plant communities in Australia and Papua New Guinea. *Aust. J. Bot. Suppl. Ser.* **7**: 1-667.
- Steenis, C. G. G. J. van (1958). Basic principles of rainforest sociology. *Proc. Kandy Symposium on Study of Tropical Vegetation*. pp. 212-15. UNESCO, Paris.
- Steenis, C. G. G. J. van (1961). Axiomas and criteria for vegetatiology with special reference to the tropics. *Trop. Ecol.* **2**: 33-47.
- Walker, D. (1972). Vegetation of the Lake Ipea Region, New Guinea highlands. II. Kayamanda swamp. *J. Ecol.* **60**: 479-504.
- Webb, L. J. (1959). A physiognomic classification of Australian rainforests. *J. Ecol.* **47**: 551-70.
- Webb, L. J. (1968). Environmental relationships of the structural types of Australian rainforest vegetation. *Ecology* **49**: 296-311.
- Webb, L. J. (1978). A general classification of Australian rainforests. *Australian Plants* **9**: 349-63.
- Webb, L. J., Tracey, J. G., and Williams, W. T. (1972). Regeneration and pattern in the subtropical rainforest. *J. Ecol.* **60**: 675-95.
- Webb, L. J., Tracey, J. G., and Williams, W. T. (1976). The value of structural features in tropical forest typology. *Aust. J. Ecol.* **1**: 3-28.
- Whitmore, T. C. (1974). Change with time and the role of cyclones in tropical rainforest on Kolombangara, Solomon Islands. Oxford, Comm. Forestry Institute, paper no. 46, 92 pp.
- Whitmore, T. C. (1975). *Tropical Rainforests of the Far East*. pp. 278. Oxford, Clarendon Press.
- Williams, W. T., Lance, G. N., Webb, L. J., Tracey, J. G., and Dale, M. B. (1969). Studies in the numerical analysis of complex rainforest communities. III. The analysis of successional data. *J. Ecol.* **57**: 515, 535.

Structural typing of tropical rainforest using canopy characteristics in low-level aerial photographs—a case study

M. S. HOPKINS and A. W. GRAHAM

INTRODUCTION

Rainforest in Australia now exists on a small fraction of the area that it covered at the time of white settlement. Of the remaining area, quite a significant, although as yet undetermined, portion is secondary forest at various stages of development or regression. The land use pressures exerted on these remaining forests are many—protective reservation (e.g. catchment protection), forest exploitation (e.g. woodchipping, selective logging), conversion and management (e.g. agricultural, silvicultural, and pastoral conversion), and recreational, scenic, and scientific conservation. In view of the intensity of these pressures and the variable success rate of land use in these rainforest areas (see, for example, Monroe and Stevens 1977), it is surprising that there have been so few regional inventories of rainforest to guide both land use and forest management decisions and provide a baseline against which future resource changes can be monitored.

At least part of the problem is typology. What sort of information could and should be collected in the inventory, and how should rainforests be classified and mapped? Two primary constraints apply to the methodology. First, if the technique is to be of any use in rapid inventories, the information necessary to facilitate the basic classification and mapping must be discernible by some form of remote sensing. A large range of potentially useful remote sensing techniques has been developed, from the conventional infra-red, panchromatic, and colour aerial photographic techniques to the satellite-borne multispectral scanners (as in the ERTS, LANDSAT and SKYLAB programs) and radar photography (e.g. SLAR, Side Looking Airborne Radar). Each of the techniques has specific advantages. Radar, for example, can penetrate cloud and, because of this, radar photography has distinct advantages in many rainforest areas where continuous cloud and mist cover is a problem. Since the longer wavelengths can penetrate the closed rainforest canopies, their use would facilitate the study of the soil surface and mineral features. Similarly, the possibilities of automated interpretation and classification of multispectral images and the continuous monitoring capabilities of the ERTS and LANDSAT type systems make these techniques very attractive. Despite the rapid advances in the use of these techniques, their application in typing at a scale suitable for land planning is limited by the general lack of ground-based information in rainforest, particularly in the tropical areas, against which the images can be calibrated. At this

stage it appears that a critical examination of the commonly-used methods of pattern recognition (conventional aerial photograph interpretation) and typology and classification of rainforest is a necessary prerequisite to the more sophisticated methods of remote sensing and monitoring.

The second constraint concerns the usefulness of the typology. As only canopy characteristics of the forest and general topographic/terrain features can be utilised, the typology will be unavoidably vegetative. To be of any use as a resource inventory typology, it must also be an ecological classification—it must reflect basic features of the physical environment (e.g. topography, climate, soil parent materials, drainage) as well as descriptive and biological forest features.

The question then, is: will interpretation of the canopy characteristics of rainforest produce a rainforest typology of any ecological significance at a scale pertinent to land management? We will address this question by examining the significance of forest types recognised solely from canopy characteristics in a small area (64 km^2) of tropical rainforest near Innisfail, north Queensland.

THE AREA

The small area of rainforest we have used to illustrate the capabilities of aerial photograph 'typing' is situated in the rugged coastal ranges which constitute the Atherton Tablelands scarp (Fig. 6.1). The area was ideal for our purpose since, at the beginning of the exercise, little detailed information on the geomorphology, soils, or forests of the area was available. The geology had been mapped at a 1:250 000 scale (de Keyser 1964) and the vegetation at a 1:100 000 scale (Tracey and Webb 1975). A Queensland Forestry Department topographic map at 2 inches to the mile scale (approx. 1:31 500) was also available.

Access is difficult so that the area has not been disturbed substantially by man. Although roading reached the area in 1967 and a small section (approx. 3 km^2) was logged in 1969, the road remains impassable for much of the year.

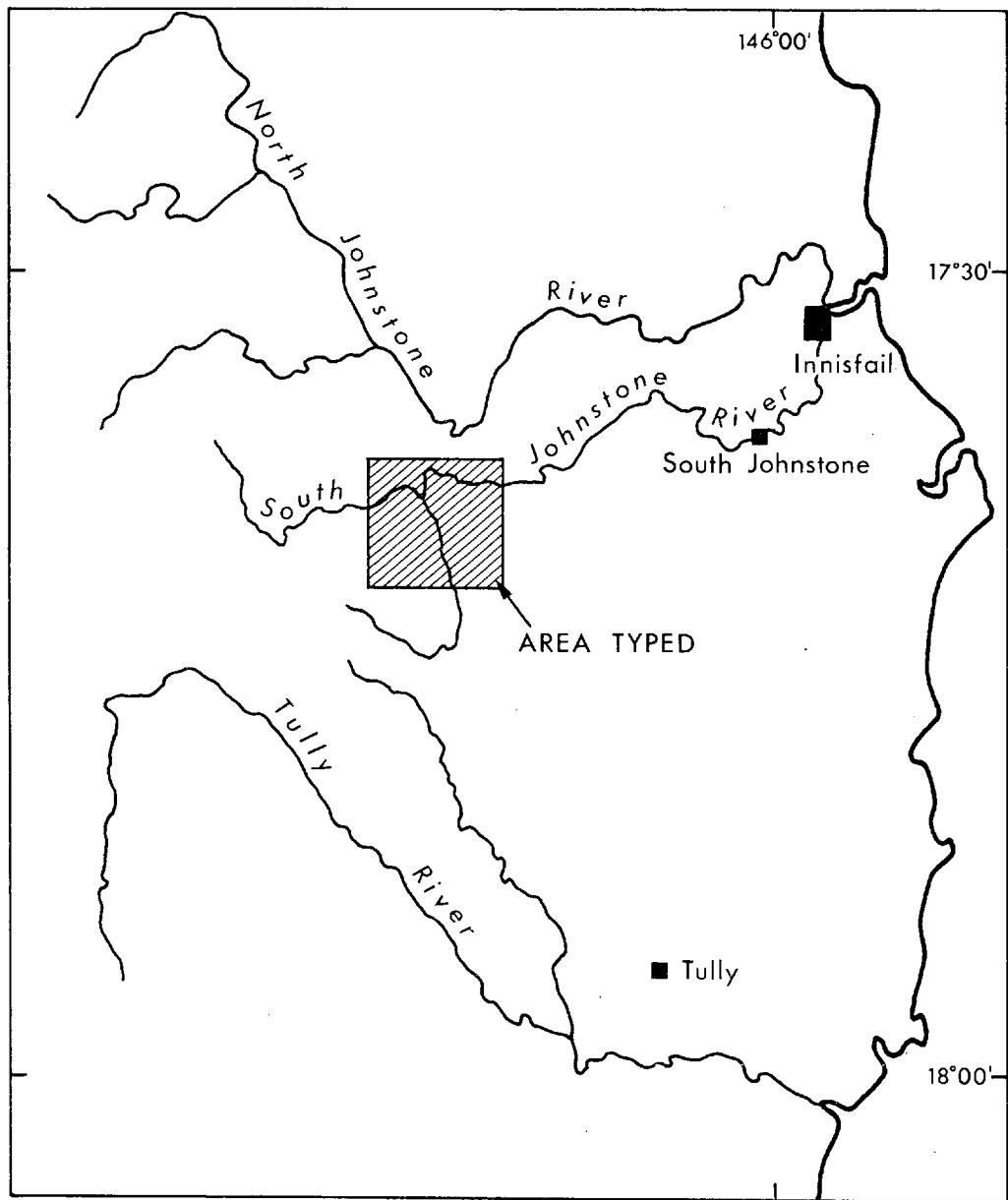
CLIMATE

Long-term climatic information is available for the nearby towns of Tully, South Johnstone, and Innisfail. Average monthly and annual rainfall figures for these three

TABLE 6.1
Average monthly and annual rainfall, in millimetres, for Tully, South Johnstone and Innisfail. Data from Bureau of Meteorology (1971)

	Years of records	J	F	M	A	M	J	J	A	S	O	N	D	Total
Innisfail	84	538	597	680	482	294	185	125	117	91	82	152	264	3609
South Johnstone	29	538	627	664	412	210	163	98	87	87	74	121	179	3259
Tully	37	736	794	813	525	333	227	165	143	125	109	168	244	4382

centres are given in Table 6·1. Average annual rainfall in the region varies from 3250 to 3600 mm with estimates exceeding 5000 mm in the more mountainous areas. As indicated in Table 6·1, summer rainfall accounts for 75–90 per cent of the annual total



6.1 Location map showing the position of the Downey Creek area

and cyclonic rains produce significant seasonal and regional variations. Rainfall intensity can be high with falls of 500–800 mm over a 24-hour period.

Average summer (December to February) maximum temperatures range from 28°C at higher elevations to 30°–32°C towards sea level. Average winter maxima are 5°–7°C lower. Frosts are rare. Relative humidities are highest from February to April (90–100 per cent) but are generally above 65 per cent throughout the year. The greatest diurnal variations occur in the cooler months.

GEOMORPHOLOGY

The Downey Creek catchment is located between Permian granites to the west and Silurian-Devonian Barron River Metamorphics (low-grade metamorphic flysch equivalents) to the east. From the valley floor (about 400 m a.s.l.) steep slopes rise to the remnants of an elevated peneplain at about 580 m a.s.l. with peaks rising to 920 m. The lower valley floor is mostly Pliocene-Pleistocene olivine basalt derived from the infilling of the Tertiary Johnstone River valley to the north. The lower reaches of Downey Creek are deeply incised in a steep-walled gorge.

GENERAL SOILS DESCRIPTIONS

The soils of the region have been described broadly by Isbell, Webb and Murtha (1968).

The most common soils on the granites are red or yellow deep friable earths (Gn 3.14 and Gn 3.74—Northcote 1971). Soil depth is very variable. Weathering depths may exceed 40 m (de Keyser and Lucas 1968). Some of the deeper upland granite soils have not been described.

The soils developed on the metamorphic rocks are generally shallower than the granite soils. The most extensive soils are friable loams (Um 4.41 and Um 4.43) with associated friable earths (Gn 3.14 and Gn 3.11). The friable earths are developed on amphibolites and basic schists (Isbell, Stephenson and Murtha 1976).

On basalt plateaux, soils are deep, red friable earths—kraznozems (Stace *et al.* 1968), Gn 3.11 (Northcote 1971). The morphologies and chemical properties of these basalt soils have been described in detail by Isbell, Stephenson and Murtha (1976) and Gillman (1976). Associated soils include red porous earths, Gn 4.11, and deep mottled brown friable earths Gn 3.51.

METHODS

The vegetation of the area was mapped from colour and black and white aerial photographs (altitude 442 m; 152.02 mm lens; 230 mm × 230 mm colour prints produced with optimum density filter). Since few conspicuous species could be recognised easily in the photographs (e.g. *Acacia aulacocarpa* A. Cunn. ex Benth.), the vegetation was typed primarily on structural canopy features. These were:

- crown diameters; average width and abundance of conspicuously small and large crowns.
- crown colour and colour density.

- canopy evenness; number, size, and distribution of emergents where present.
- canopy uniformity; colour; vertical uniformity and tree crown size.
- degree of disturbance; number, size, and distribution of canopy gaps.
- presence and abundance of key life forms and recognisable structural forms (e.g. palms, climber-towers)
- discreteness of adjacent tree crowns.

The forest 'photograph types' so produced were then assessed by ground survey. A series of line transects was designed to traverse most forest types. At regular (200 m) intervals along these transects, the following information necessary to describe both the vegetation and gross features of the environment was collected:

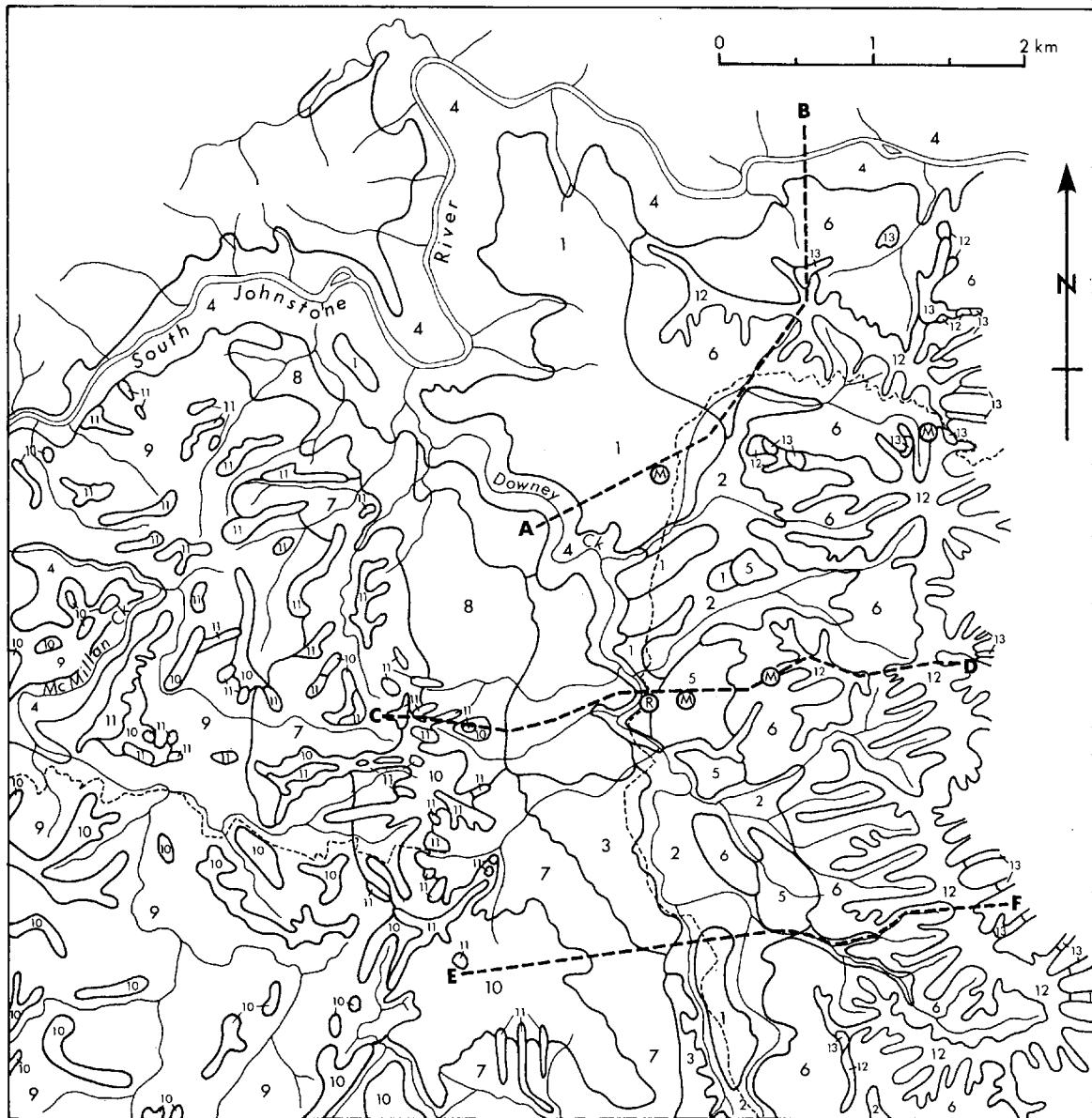
- structural features of the vegetation were recorded using the structural proforma of Webb, Tracey and Williams (1976).
- spot lists of trees, understorey plants and seedlings were made. All species that could not be identified in the field were collected. These were later identified by B. Hyland (CSIRO Division of Forest Research, Atherton).
- prominent environmental features of the site were recorded (including slope, drainage, soil parent materials, soil type and brief profile descriptions, percentage soil surface covered with undecomposed plant debris).
- nomenclature of the forest/environment types followed that of Webb (1959, 1968) where possible.

RESULTS

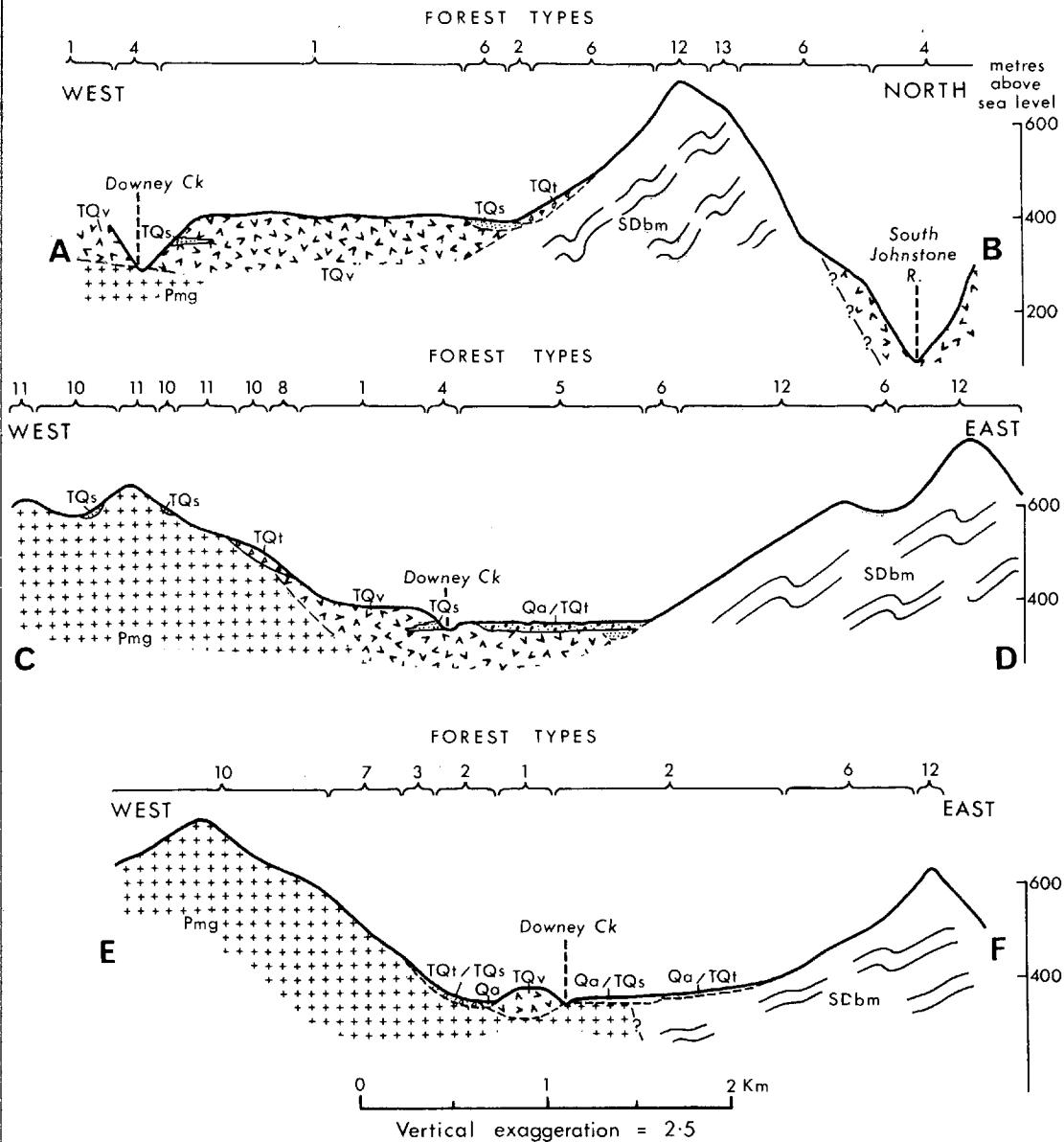
The forest structural/environmental types

Thirteen structural/environmental forest types were recognised following the ground survey. These are:

1. *Complex Mesophyll Vine Forest* on basalt.
2. *Complex Mesophyll Vine Forest* on mixed colluvium/alluvium, seasonally inundated and swampy.
3. *Complex to Mixed Mesophyll/Notophyll Vine Forests* on granite lower slopes and colluvial shelves.
4. *Complex Mesophyll Vine Forest* on steep slopes and shallow soils.
5. *Mixed Mesophyll Vine Forest* on metamorphic colluvial/alluvial plateaux.
6. *Mixed Mesophyll/Notophyll Vine Forest* on metamorphic knolls and lower slopes.
7. *Mixed Notophyll/Mesophyll Vine Forest* on granite midslopes.
8. *Mixed Notophyll/Mesophyll Vine Forest* with emergents on granite.
9. *Complex Mesophyll/Notophyll Vine Forest* on upland granite.
10. *Simple Notophyll Vine Forest* on upland granite ridges.
11. *Simple Notophyll Vine Forest* dominated by *Acacia aulacocarpa* on granite ridges.
12. *Simple Mesophyll/Notophyll Vine Forest* on metamorphic ridges.
13. *Simple Notophyll Vine Forest* with *Acacia aulacocarpa* on metamorphic ridges.



6.2 Map of the Downey Creek area showing the distribution of the 13 forest types. Positions of the rain gauge and thermo-hydrograph sites are indicated. Profiles along AB, CD, and EF are shown in Fig. 6.3. See text and Appendix 6.1 for description of forest types.



6.3 Extended sections showing relationships between forest types and geomorphology across Downey Creek Valley: AB ridge profile; CD ridge profile; EF gully profile. Geological units: Qa Quarter alluvium, sand and gravel; TQ_s Pliocene-Pleistocene sediments, clay, silt, sand, gravel, including charcoal deposits; deposits marginal to upper basalt flows; TQ_v Pliocene-Pleistocene basalt; Pmg Permian Mareeba Granite; SDbm Silurian-Devonian Barron River Metamorphics. Forest Types as listed in text.

The distribution of the thirteen types across the area is shown in Fig. 6.2 and is closely associated with changes in geology and topography; the most important relationships are shown in cross-sectional diagrams in Fig. 6.3. The main structural features, the photogrammetric characteristics, the landform and soils of each of the types, and below-canopy temperature and humidity data from four of these forest types are given in Hopkins *et al.* (in prep.). These data suggest that the microclimates under the various forest 'types' are substantially different but we do not know whether these differences are related primarily to vegetation or to topographic/environmental features.

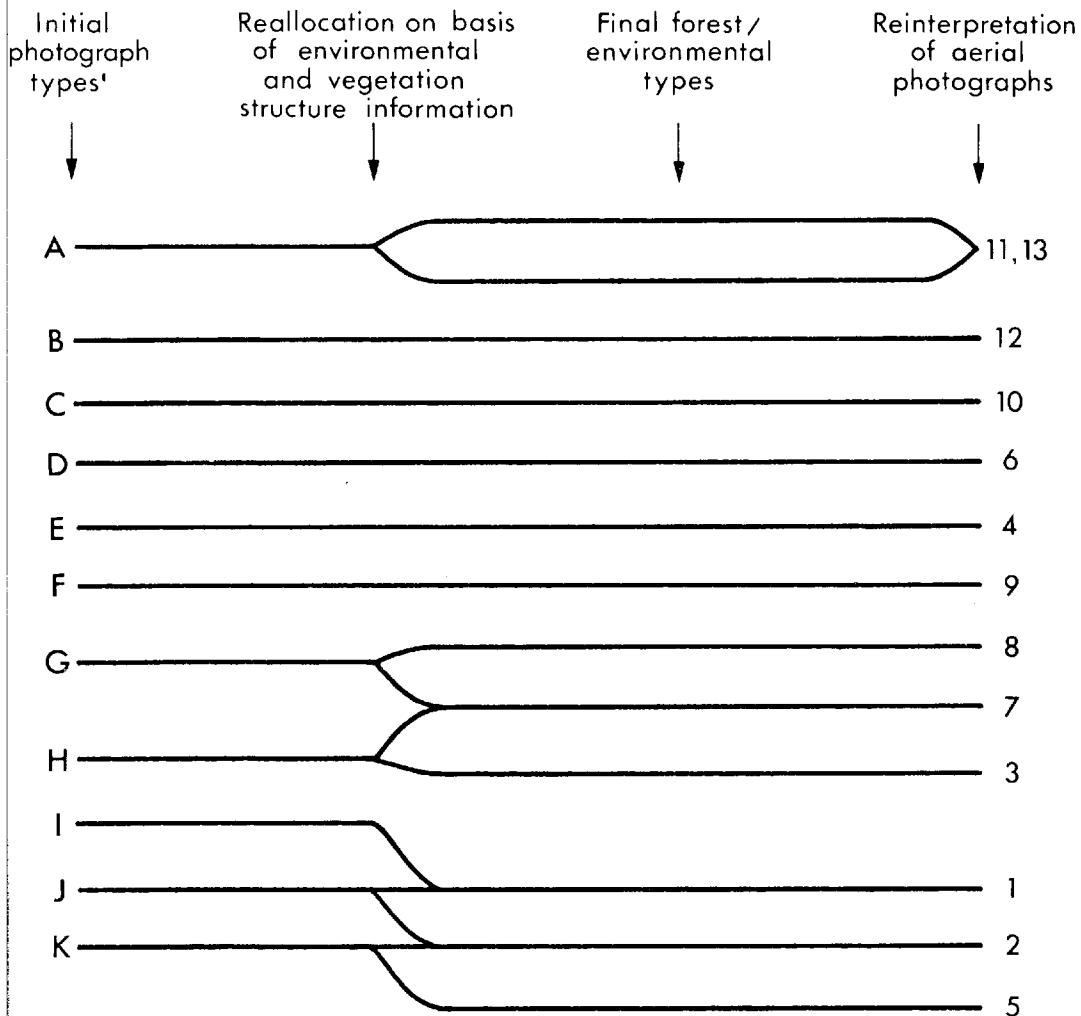
Assessment of the interpretation/typology process

As with most aerial photograph/vegetation mapping exercises, our final forest types and map units are a product of:

1. Photographic interpretation and initial mapping of photograph types.
2. Ground truthing of the 'photograph types'.
3. A re-allocation, re-interpretation, and re-mapping procedure during which 'photograph types' are recombined or subdivided according to environmental and vegetation data collected during the ground inspections. (Re-interpretation of the photographs is required where newly created types require mapping.)

The amount of re-allocation and re-interpretation gives some measure of the efficiency and dependability of the technique and the discreteness of the recognised patterns. Figure 6.4 depicts the process of re-allocation and re-interpretation which led to the production of the thirteen final vegetation/environmental types in the present case. Of these, five (4, 6, 9, 10 and 12) required no re-allocation or re-interpretation. The remaining eight types required varying amounts of re-allocation. Types 3, 7 and 8 were produced by a redivision of photograph types G and H. These types represent a topographic/altitudinal catena on granite soils. In the initial interpretation, this continuum was subdivided into two forest types (G and H); inspection on the ground subsequently indicated that three types based on vegetation structure and topography/soil features could be distinguished profitably. Types 1, 2 and 5 represent the complex forests on the flat valley floor of Downey Creek and, as seen in Fig. 6.4, required considerable re-allocation and re-interpretation following ground truthing. The original photograph types I and J were identical but were distinguished by wrongly assumed substrate differentiation. Similarly, on-ground information on forest structure and surface drainage substantiated a sub-division of photograph type K into types 2 and 5.

Two factors, therefore, contributed to the comparatively large degree of re-allocation required to produce the final forest types. First, we misinterpreted the photographs in some cases; it seems likely this error would be minimised with experience. Second, there is always some doubt about the scaling of map units, the number of forest units that should be recognised, and so on. In most cases, the vegetation structure



6.4 Diagram showing the recombination and reallocation of the 11 initial 'photograph types'

and canopy features are continuously variable, and one is left to ascertain subjectively the most profitable number of units in the continuum or catena. This judgment varies as the ground information accumulates and often leads to re-allocation and re-interpretation. In this regard, it is interesting to note that only two of the final thirteen forest types could not be satisfactorily re-interpreted on the photographs. Types 13 and 11, both Notophyll Vine Forests but on different soils, can not be differentiated. There is some reason to believe that both these forest types are secondary forests produced by gross past (?cyclonic) damage.

DISCUSSION

The typing of tropical rainforest using canopy features on low-level aerial photographs could, in general, be interpreted in terms of soil parent materials, drainage, topography, and past disturbance. On the ground, these could be classified by the structural features outlined by Webb (1959, 1968) and Webb *et al.* (1976). Assessment of the suitability of the technique for carrying out rainforest resources inventories, however, requires the following consideration.

Vegetation classification and description

The use of structural/physiognomic classifications for the mapping and typing of tropical rainforest is usually supported on three grounds: First, the classifications can be used rapidly by a wide range of untrained observers. Unlike floristic classifications, for example, their use is not limited to a select group of tropical botanists who are familiar with the incredibly large numbers of species in the field. Second, since the stand structure and physiognomy are functionally related to environment, it is often possible to use these to predict environmental features to some degree (Webb 1968). Third, in contrast to floristics, structural/physiognomic attributes can be used to compare forest types on a regional and continental basis. This paper highlights a fourth advantage of structural/physiognomic classifications; they are directly and easily adaptable to aerial photographic interpretation at small scales. There are, however, a number of problems associated with their use in their present state of development. The rainforest typology of Webb (1959, 1960, 1968) and Webb *et al.* (1976) requires further refinement if it is to be useful in classifying rainforest at a fine scale. The range of types described by Webb (1959, 1968) appears to be inadequate at the 1:25 000 to 1:100 000 scales. Similarly, basic dichotomies in the Webb classification are based on non-structural forest features and require a taxonomic or behavioural knowledge of forests (e.g. the distinction between 'raingreen' and 'strictly evergreen' in Webb (1968)). The use of these characteristics would have to be avoided if the typology were to be useful in rapid surveys. On the other hand, if the open-ended approach to classification recommended by Webb *et al.* (1976) were to be adopted, it would be necessary to standardise some form of nomenclature for types and compile a hierarchy of attributes.

Classification of other forest values

The question arises as to whether the descriptive vegetation/environmental typology would provide a suitable framework within which other forest values (e.g. timber volumes, estimated extraction costs; aesthetic, scientific, silvicultural, agricultural, and pastoral potentials) and forest behavioural values (e.g. regrowth behaviour) could be scaled in an inventory-type coverage. Many of the other forest values are directly related to various aspects of forest physiognomy, structure, and environment and, provided specific information for each value is collected as well as the descriptive vegetation information, there appears to be no reason why specialised typologies cannot be produced within, or scaled to, the vegetation/environment framework. Prediction, typing,

and mapping of bird habitats, for example, require additional structural information on vegetation and ground surface cover related to avian use of habitat and information on the availability of types of flowers and fruit (Kikkawa 1968). Similarly, the prediction of pastoral potential requires the calibration of certain specific features (e.g. fertiliser requirements) relevant to agrarian uses (see, for example, Teitzel and Bruce 1971a, 1971b, 1972a, 1972b, 1973a, 1973b). The feasibility of scaling various forestry values (e.g. standing and extractable volumes of particular grades of timber) to the structural vegetation typology, is, however, doubtful. Because the grading of timbers is fundamentally a taxonomic exercise and there is little reason to believe that species distributions are strongly correlated with structural types, it is questionable whether the structural typology could effectively predict exploitable timber volumes and values even if scaled at 'representative' sites. It seems likely that some features of forest inventory (e.g. predicted extraction costs) could be scaled more usefully and easily.

Secondary forests and the typology

In this chapter we have been concerned only with primary rainforest. However, large areas of the rainforests which exist today are in various stages of recovery following selective logging, or exist as secondary forest of different ages after cyclones or clearfelling and abandonment. Can these disturbed forests be recognised in aerial photographs using vegetation canopy features and can they be usefully incorporated into rainforest classifications? At this stage (and our assertion is based on our own attempts to type disturbed rainforests in north and south Queensland from aerial photographs), we do not believe that they can. In the case of partially disturbed (e.g. selectively logged) forests, the distinguishing canopy characteristics of the various forest types are altered and the type differences become blurred. The canopy structure after logging relates primarily to the type and intensity of logging (e.g. removal of emergents) and the degree and age of recovery (e.g. crown size, canopy evenness) rather than environmental features and original forest patterns. For example, the substrates on the uplands to the west of the mapped area consist variously of basalts, granites which have been re-exposed after the basalts have been eroded back (i.e. very substantially enriched by basalt), and granites. On the ground, the soils and forest types developed on these substrates are distinct. The forests, however, have been logged and it is no longer possible to interpret their pattern from aerial photographs with any degree of confidence. Areas of logged Mesophyll Vine Forests on basalt exist at elevations around 800 m in this area. The problems associated with classifying and mapping small areas of disturbed forests at a broad scale from aerial photographs have been highlighted by Tracey and Webb (1975), who grouped them variously with Mesophyll Vine Forests on lowland granites, Simple Notophyll Vine Forests on upland and highland granites, and Simple Microphyll Vine-Fern Forests on highland granites.

Similar difficulties in aerial typing and structural classification occur where large areas of forest have been extensively disturbed (e.g. felled and/or burned) and replaced by secondary regrowth of various types. Although it has been suggested that the spatial patterns of forest types are robust and remain so after gross disturbance (Webb *et al.*

1977), it is firstly questionable whether the various forms of forest regrowth can be recognised in aerial photographs and secondly, whether the secondary forests can be described and classified in terms of structural and physiognomic features in a manner which retains both information on the original forest patterns and reflects the present environment of the secondary forest. We are not aware of any evidence which correlates the structure or floristic composition of secondary forests with patterns of original forest types and/or the types or intensities of disturbances which produced them; nor are we aware of any attempts to determine the degree to which the physical site factors of secondary forests can be predicted from the structure of the secondary forest itself or from the structure of the parent vegetation. In their present state rainforest structural classifications do not satisfactorily deal with secondary forests at even a purely descriptive level.

EXTRAPOLATION FROM REPRESENTATIVE GROUND-TRUTHED AREAS

In this study, aerial photographic interpretation only distinguished different types of forest within the defined study area, and most information on the environment and the structural classification of these 'types' was achieved by ground-truthing of 'key' areas. Having examined such representative areas, we question whether these final forest/environmental types can be effectively recognised outside the study area, from aerial photographs alone. Our own experience suggests that, in general, this is not possible. Some forest types such as Complex Mesophyll Vine Forest on basalt appear to be very distinct and are usually recognisable. The structural characteristics of most of the other forests appear to be reproduced on different soil parent materials and in different topographical situations at different altitudes and rainfall conditions. It seems likely that photographic types can only be extrapolated with safety to comparable and usually adjacent areas.

We conclude that the present usefulness of aerial photographic interpretation and structural typing in providing a framework for resource inventory at 1:25 000 to 1:100 000 scales in rainforest areas is limited primarily by its lack of capability in areas of partially disturbed or secondary forest. Under these conditions, pattern interpretation is unreliable and the present typology unsuitable. These drawbacks could be partially overcome if suitable seral characteristics could be found and included in the typology.

REFERENCES

- Bureau of Meteorology (1971). *Climatic Survey. Northern Region 16—Queensland*. 64 pp.
Gillman, G. P. (1976). Red Basaltic Soils in North Queensland II. Chemistry. *CSIRO Aust. Div. Soils. Tech. Pap.* **28**: 23-49.
Hopkins, M. S., Graham, A. W., O'Brien, J. B., and Meier, L. E. (1981). The tropical rainforests of Downey Creek with notes on landform, climate, and meteorological conditions under forest canopies. *CSIRO Division of Land Use Research* (in prep).
Isbell, R. F., Webb, A. A., and Murtha, G. G. (1968). *Atlas of Australian Soils*, Sheet 7. North Queensland. With explanatory data. *CSIRO Aust. Melbourne University Press*.

- Isbell, R. F., Stephenson, P. J., and Murtha, G. G. (1976). Red Basaltic Soils in North Queensland I. Environment, morphology, particle size characteristics and clay mineralogy. *CSIRO Aust. Div. Soils Tech. Pap.* **28**: 1-22.
- Keyser, F. de (1964). Innisfail, Qld—1:250 000 Geological Series. Bur. Miner. Resour. Aust. Explan. Notes SE/55-6.
- Keyser, F. de., and Lucas, J. G. (1968). Geology and mineral deposits of the Hodgkinson and Laura Basins, north Queensland. *Bur. Miner. Resour. Aust. Bull.* **84**.
- Kikkawa, J. (1968). Ecological association of bird species and habitats in eastern Australia: similarity analysis. *J. Anim. Ecol.* **37**: 143-65.
- Monroe, R., and Stevens, N. C. (eds.) (1977). *The Border Ranges—A Land Use Conflict in Regional Perspective*. Proceedings of a symposium sponsored by the Royal Society of Queensland and ANZAAS, Queensland Division. 81 pp.
- Northcote, K. H. (1971). *A Factual Key for the Recognition of Australian Soils*. 3rd edn. Rellim Tech. Pubs., Glenside, S.A. 123 pp.
- Stace, H. C. T., Hubble, G. D., Brewer, R., Northcote, K. H., Sleeman, J. R., Mulcahy, M. J., and Hallsworth, E. G. (1968). *A Handbook of Australian Soils*. Rellim Tech. Pubs., Glenside, S.A. 435 pp.
- Teitzel, J. K., and Bruce, R. C. (1971a). Fertility studies of pasture soils in the wet tropical coast of Queensland. 1. Soil-vegetation classification units. *Aust. J. Exp. Agric. Anim. Husb.* **11**: 71-6.
- Teitzel, J. K., and Bruce, R. C. (1971b). Fertility studies of pasture soils in the wet tropical coast of Queensland. 2. Granitic soils. *Aust. J. Exper. Agric. Anim. Husb.* **11**: 77-84.
- Teitzel, J. K., and Bruce, R. C. (1972a). Fertility studies of pasture soils in the wet tropical coast of Queensland. 3. Basaltic soils. *Aust. J. Exper. Agric. Anim. Husb.* **12**: 49-54.
- Teitzel, J. K., and Bruce, R. C. (1972b). Fertility studies of pasture soils in the wet tropical coast of Queensland. 4. Soils derived from metamorphic rocks. *Aust. J. Exper. Agric. Anim. Husb.* **12**: 281-7.
- Teitzel, J. K., and Bruce, R. C. (1973a). Fertility studies of pasture soils in the wet tropical coast of Queensland. 5. Mixed alluvial soils. *Aust. J. Exper. Agric. Anim. Husb.* **13**: 306-11.
- Teitzel, J. K., and Bruce, R. C. (1973b). Fertility studies of pasture soils in the wet tropical coast of Queensland. 6. Soils derived from beach sand. *Aust. J. Exper. Agric. Anim. Husb.* **13**: 312-18.
- Tracey, J. G., and Webb, L. J. (1975). Vegetation of the humid tropical region of north Queensland. Rain Forest Ecology Unit, CSIRO Division of Plant Industry, Long Pocket Laboratories, Indooroopilly, Queensland. (Key to accompany maps, Dept National Mapping, Canberra.)
- Webb, L. J. (1959). A physiognomic classification of Australian rain forests. *J. Ecol.* **47**: 551-70.
- Webb, L. J. (1960). A new attempt to classify Australian rain forests. *Silva fenn.* **105**: 98-104.
- Webb, L. J. (1968). Environmental relationships of the structural types of Australian rain forest vegetation. *Ecology* **49**: 296-311.
- Webb, L. J., Dale, M. B., Tracey, J. G., and Kikkawa, J. (1977). Structural classification as a method to predict site potential in the development and conservation of tropical humid forest lands. Transactions of the International MAB-IUFRO Workshop on Tropical Rainforest Ecosystems Research. Hamburg-Reinbek 12, 17.5. 1977.
- Webb, L. J., Tracey, J. G., and Williams, W. T. (1976). The value of structural features in tropical forest typology. *Aust. J. Ecol.* **1**: 3-28.

*Choice of attributes to study succession in brigalow (*Acacia harpophylla*) communities*

R. W. JOHNSON

INTRODUCTION

Brigalow (*Acacia harpophylla*) characterises the canopy layer of open-forest and woodland communities which occupied 6 million hectares of semi-arid north-eastern Australia in the 500-750 mm rainfall belt. Because the soils supporting *A. harpophylla* communities are relatively fertile, extensive areas have been cleared and replaced by sown pastures. *A. harpophylla* has the capacity to sprout freely from roots when damaged and an important aspect of management for continued animal production is the prevention of retrogressive succession towards an *A. harpophylla* dominant community.

The types of attributes that can be used to study successional changes are infinite, though their individual usefulness in particular situations may vary from highly informative to insignificant.

They are basically of two types: non-biological and biological

Non-biological attributes

Changes in the environment may parallel changes in the biological composition of any area over time. Successional changes from *Dichanthium sericeum* open grassland with scattered clones of *Acacia harpophylla*, commonly called brigalow patchy plain, to low grassy *A. harpophylla* woodland have occurred in historical time. Total nitrogen content and available phosphorus in the surface soil under the *A. harpophylla* clones are considerably higher than under the surrounding grasslands, suggesting that the occurrence of *A. harpophylla* may induce changes in soil fertility. Similar differences were noted by Isbell (1962). Based on observations one could also speculate that on heavy cracking clays an increase in gilgai microrelief accompanies successional change from grassy *A. harpophylla* woodlands to *A. harpophylla-Geijera parviflora* open forests. Support for the influence of *A. harpophylla* in gilgai formation was presented by Russell *et al.* (1967).

Little research has been undertaken in Australia to study changes in non-biological attributes during succession. Selection of attributes is difficult because the choice is infinite and one has to assume before undertaking a study that any selected attributes do undergo change and, as well, play an important role in the system. While monitoring soil and environmental processes might be fruitful, in general the biotic component is the most convenient to study. Vegetation on a particular site best integrates and reflects

the effective sum of both physical and biological factors of the environment and I have confined my discussion in this chapter to attributes concerned with the vegetation.

Biological attributes

Each species grows within its special range of environmental tolerances and its presence provides information about the habitat in which it is found. Assessment of its importance, whether it be a measure of cover, density, biomass etc. can help to narrow down this range of environmental tolerance. Two species, growing together, further sharpen our knowledge of the environmental complex. Combinations of species with their overlapping indicator values can therefore indicate ever more specific information about the environment. Therefore whether we are studying plants in a relatively stable situation or in a dynamic situation like succession, the presence of particular species and their importance are the most useful attributes for documenting changes in the ecosystem.

Morphological attributes can be used in studying succession but their value seems greatest where the flora is not well known or identification is difficult. Various morphological features such as leaf size and bark type have been regarded as adaptations by species for particular environments and the usefulness of physiognomic data as attributes has been demonstrated in other plant communities (Webb *et al.* 1970).

Biological attributes are of two basic types

- (a) *Floristic attributes*. These are dependent on the identification of taxa usually to the level of species, though as shown by Dale and Clifford (1976) coarser subdivisions may be used. The attributes may be simply presence or a measure of importance such as density of cover or they may be synthetic attributes such as frequency or diversity.
- (b) *Vegetation attributes*. These are taxonomically independent attributes though they are sometimes mistakenly regarded as by-products of the floristic attributes. Attributes of this type can be life form, type of regeneration or leaf size and do not require identification of taxa. In some cases the presence of a vegetation attribute can be assessed from a floristic list and its importance estimated from a measure of the importance of the various species in the community. Where this can be done, e.g. woodiness, the use of such attributes reduces the discriminatory power of the data though it may be useful in summarising changes. In many cases, however, extrapolation from species lists can only be regarded as an exercise in formulating a hypothesis and testing the hypothesis must involve the direct measurement of the attribute itself. Changes in the amount of succulent fruit produced or in the structure of the community with time can only be determined by direct measurement.

Austin (1977) pointed out the potential of multivariate analysis as an aid to greater understanding of succession while commenting on the great lack of studies of this type. Attributes selected from multivariate studies have been presence (van der Maarel 1969;

Williams *et al.* 1969) and frequency (Austin 1977) and both ordination and classification have been used to examine successional trends.

METHODS

Data from two study sites, both on the Brigalow Research Station near Theodore, Queensland, were used to assess the usefulness of various attributes.

Site 1

This area, which supported an *Acacia harpophylla*-*Geijera parviflora* open forest, was cleared by pulling in September 1963. The trash was burnt in December 1963 and six 20 m × 20 m plots were permanently marked on the burnt surface. Since burning, data have been recorded from each plot at eleven points in time. The first recording was made in September 1964, nine months after burning and the last in March 1975, approximately 11 years after burning. Forty quadrats were systematically placed to provide a uniform coverage of the vegetation in each plot though the precise location of each quadrat varied slightly from time to time. Data recorded were presence, density and canopy cover of each species using the technique of Daubenmire (1959). This study site provided an opportunity to study secondary succession following a severe disturbance.

Site 2

This area, 2.7 km by 0.4 km, contains a range of plant communities, most dominated by *A. harpophylla*. In a central belt 2.7 km by 20 m, 182 contiguous plots each 20 m × 20 m were permanently marked and data recorded of various attributes including heights of trees, shrubs and lianas, diameter-breast-height of trees and canopy cover and density of all species. From a preliminary ordination analysis of the data the distribution of plots along the major axis of variation appeared to parallel the successional change from *Dichanthium affine* grassland with *A. harpophylla* through *A. harpophylla*-*Geijera parviflora* open forest to *A. harpophylla* semi-evergreen vine thicket.

It is difficult to differentiate between zonal and mosaic patterns and a successional pattern and it is perhaps dangerous to attempt to explain existing patterns in terms of succession. However, personal observations and observations of other workers (Blake 1938; Isbell 1962) indicate the *A. harpophylla* communities are undergoing change and have expanded their range in recent times at the expense of grassland. With the above reservation, this study site provided an opportunity to speculate about primary succession from grassland.

Because of problems in sampling vegetation containing a variety of growth forms from small ephemeral herbs to tall trees, the latter were sampled in the whole plot but nested subsets of the plots were used to record attributes from the understorey shrub and ground layers. For comparative studies in this chapter sixteen plots were selected, the criteria used in selection being that the soil should be a uniform cracking clay and that the plots should be spread along the whole of the successional gradient.

RESULTS AND DISCUSSION

Site 1

(a) *Floristic attributes*

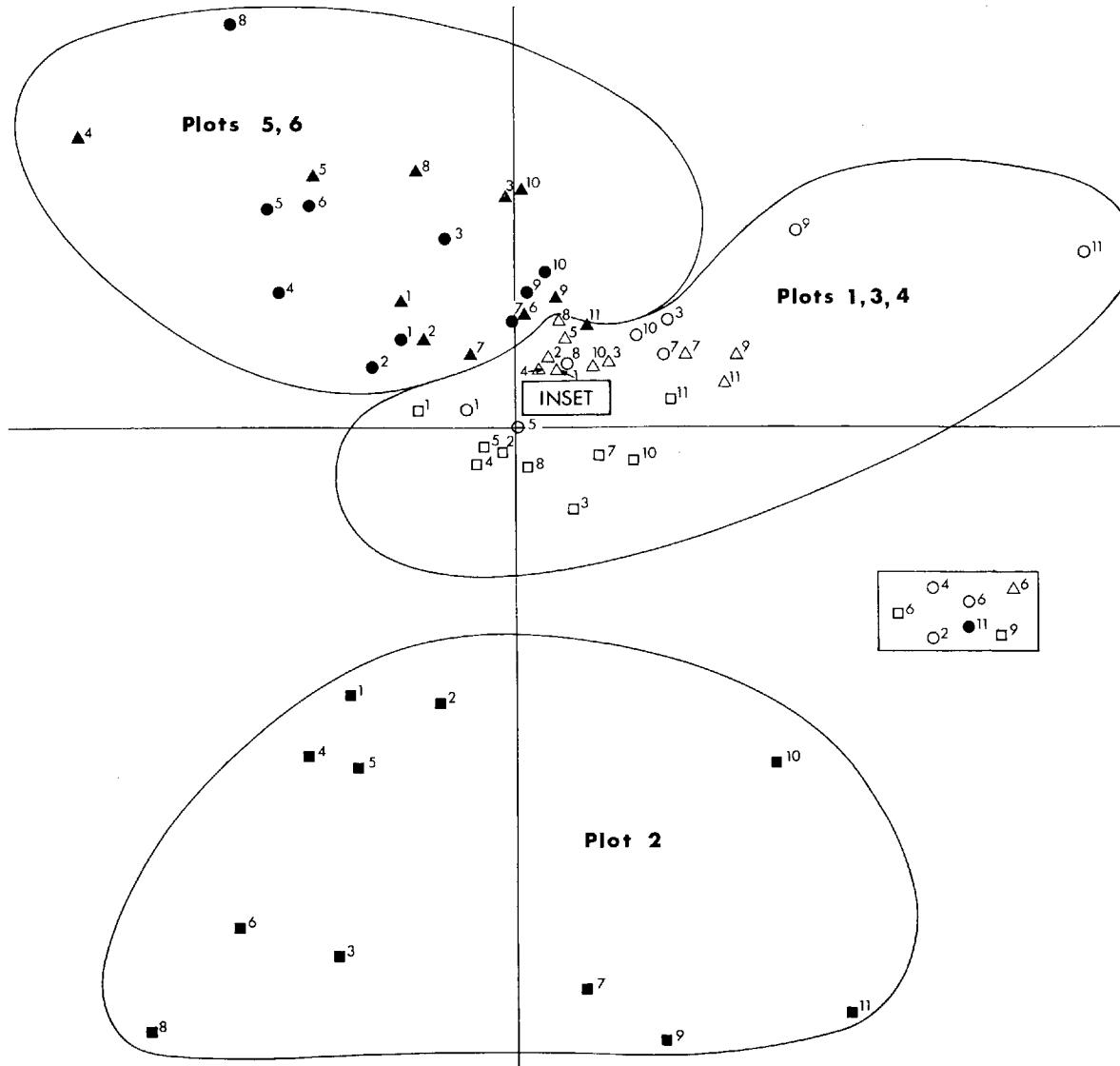
Presence. This is the simplest of these attributes to record. A total of 142 species were recorded during the 11-year period. Of these 13.5 per cent occurred at only one recording date and provided little information, while 25 per cent were always present. In fact 52 per cent could be regarded as persisting throughout the sampling period while 13 per cent behaved as decreasers and 16 per cent as increasers. The remaining species were found only at the intermediate sampling periods. For classification and ordination this attribute proved very effective in space discrimination but was much less effective in time discrimination. Plot 2 was clearly shown to be different from the rest while Plots 5 and 6 and Plots 1, 3 and 4 remained relatively discrete groups throughout the sampling period (Fig. 7.1). However, in analyses of individual plots over time and of the combined plot data over the whole period, while a general successional pattern was detectable, relationships from one period to the next were obscured. They did indicate that changes with time were strongly preconditioned by the initial floristic composition and chance appeared to play a lesser role in determining the outcome of successions.

Density, frequency and canopy cover. These provided additional information and their use in understanding successional change varied with species. In the root suckering perennial *Acacia harpophylla* little change in density or frequency was recorded after the first sampling, 9 months after the burn, while canopy cover increased greatly from 10 per cent to 49 per cent. In contrast, the annual pioneers such as *Abutilon oxycarpum* and *Sesbania cannabina* reached their maximum density and frequency in the second summer after burning, though their cover peaked in the first summer (Fig. 7.2). In general any decline in the population of a species was indicated first by a decline in cover and often much later by a decline in density and frequency.

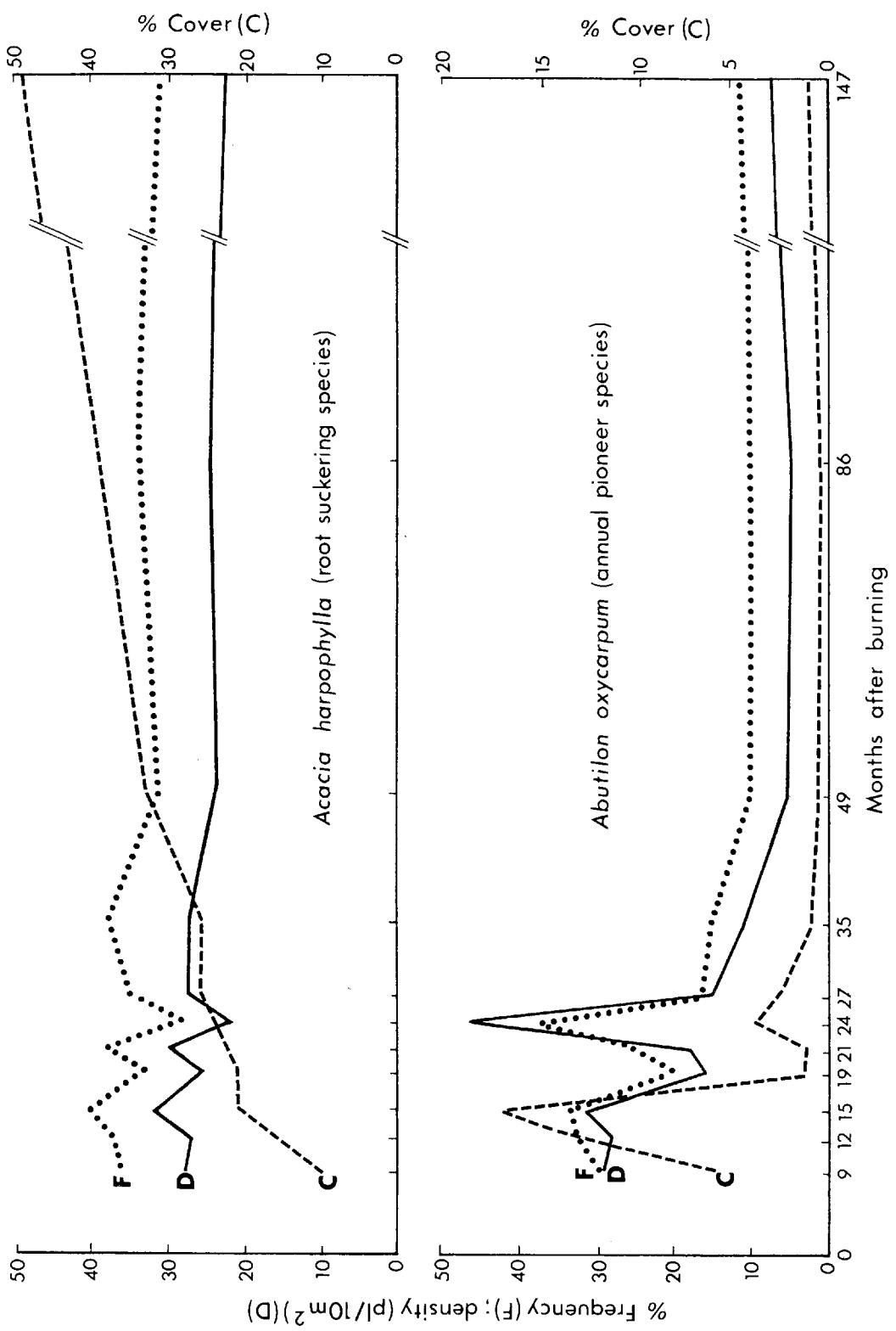
All three attributes were used in classification and ordination programs to study the plots in time and in space and in combined time and space. Using standardised data, cover was far more useful than density or rooted frequency in studying the relationships among plots at individual sampling periods and was marginally better than using presence but none gave a clear understanding of the successional change over time. In contrast, analyses using unstandardised cover data gave a very clear portrayal of the changes occurring over time (Fig. 7.3). On the basis of this ordination successional trajectories for each plot over time were constructed and from these it would be possible to crudely predict trends at least in the short term (Fig. 7.4). Because of the possible ingress of species new to the existing data set, extrapolation over longer periods is much more uncertain.

The close association between change in canopy cover and succession emphasises the importance of the role of *Acacia harpophylla* itself in controlling the outcome of the change. Restricting the analysis to sampling dates during summer-autumn periods the contribution of *A. harpophylla* to the total community canopy cover rose from 26 per cent to 37 per cent.

Synthetic attributes. Attributes such as diversity and maturity were calculated using, where appropriate, density, frequency and cover as importance values. Species richness, based on the absolute number of species, increased until the summer, 12 months after the burn, but for the next 10 years there was little change though numbers fluctuated

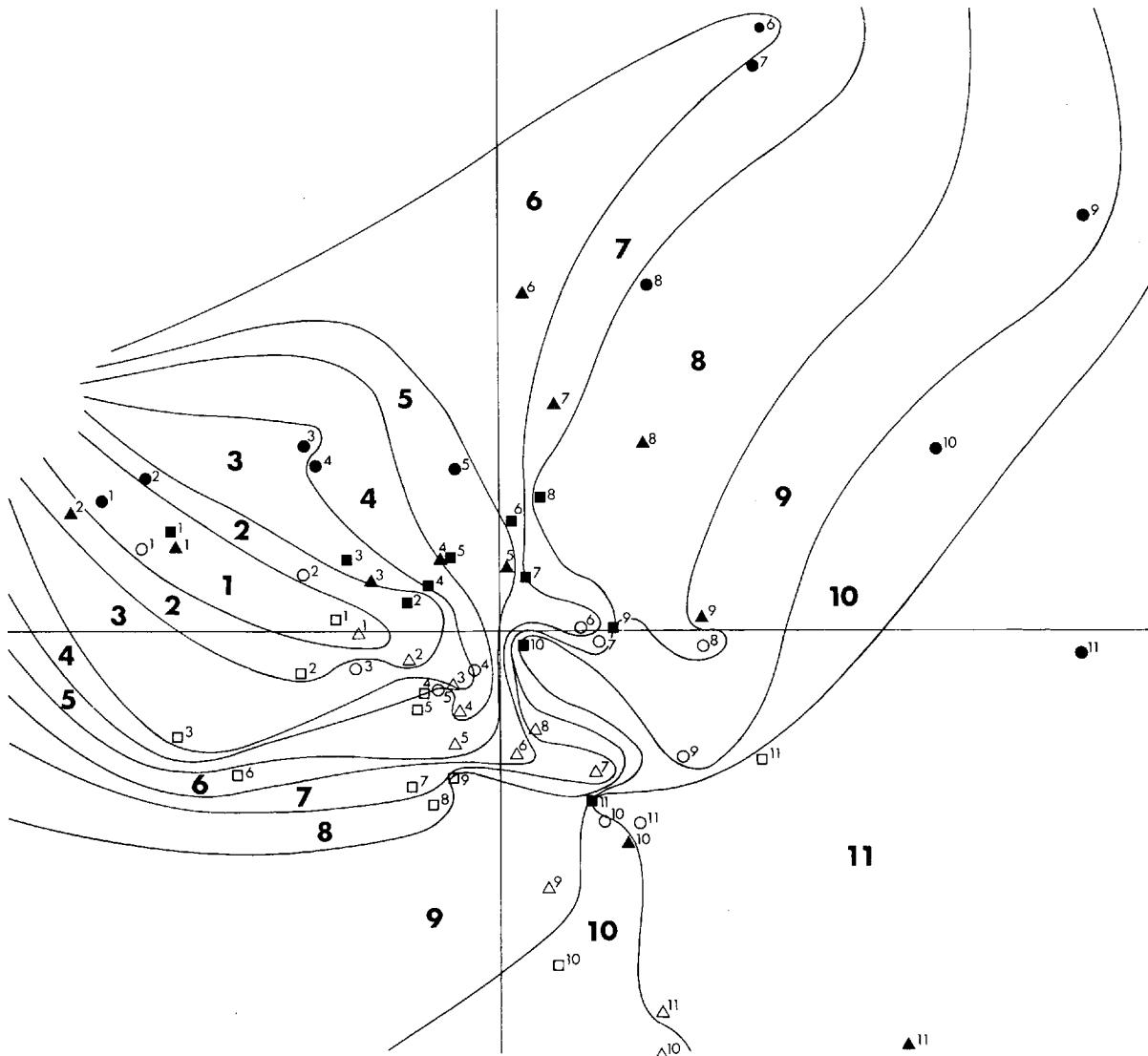


7.1 *Ordination of 66 samples (6 plots × 11 times) using principal co-ordinate and analysis based on presence/absence data. Open triangle, plot 1; closed square, plot 2; open circle, plot 3; open square, plot 4; closed triangle, plot 5; closed circle, plot 6.*



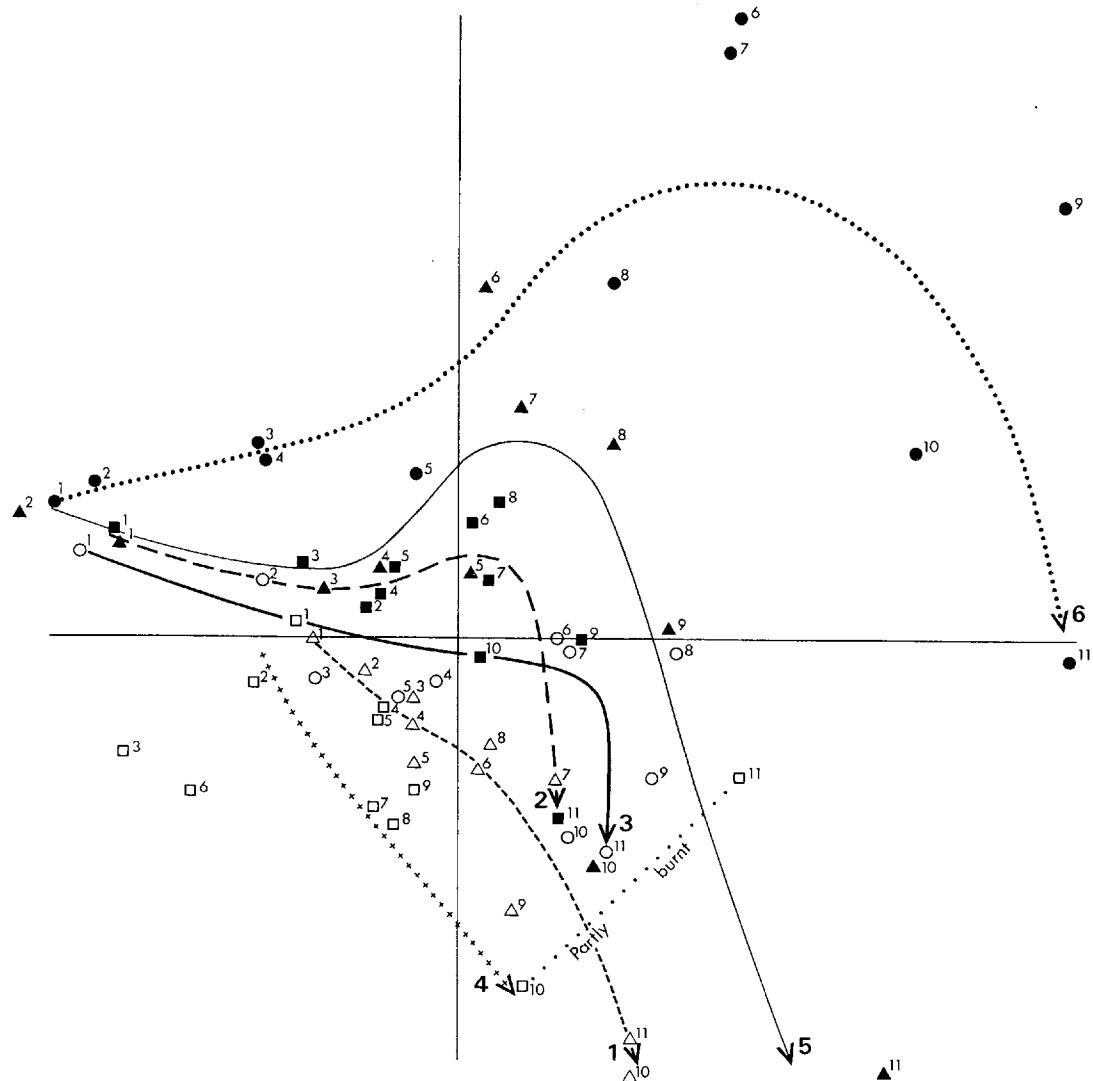
7.2 Change in cover (C), density (D), and frequency (F) with time.

depending on seasonal conditions. However, as species richness generally increases with increasing density it is often useful to compare species richness in samples reduced to a common density or possibly, amount of biomass (Hurlbert 1971). As density and biomass increase greatly during the early stages of succession in plots of fixed size, this aspect of diversity was investigated using density, frequency and cover as measures of



7.3 *Ordination of 66 samples using unstandardised cover data showing the eleven isochronous bands. Bands 1 to 11 represent successive sampling periods from 9 to 147 months after burning (see Figs. 7-1 and 7-2).*

importance. Each of the various published indices (Odum 1971) for standardising species richness was calculated but for any single attribute they gave varying patterns of diversity and variation increased further with the use of different attributes. Expressing the number of species in terms of log importance (Margalef 1958) provided the most stable index and with all three attributes there was an initial increase in this aspect of diversity after which it remained fairly constant or declined slightly.



7.4 Ordination of 66 samples using unstandardised cover data showing successional trajectories of the vegetation on the six plots (see Fig. 7.1 for explanation of symbols).

Species evenness (Shannon-Weaver Index of Diversity/log number of species) also showed an initial increase followed by a decline, with the decline being recorded first at 2 years using cover, then frequency and finally density at 7 years after the fire. The Shannon-Weaver Index of Diversity showed an almost parallel trend while the pattern of dominance indicated by the Simpson Index was similar but opposite in trend.

A number of Indexes of Maturity, based on that of Pichi-Sermolli (1948), was calculated using density, frequency and cover as importance values. These express the ratio of total importance to the number of species present.

The most useful index was given by Total Cumulative Plot Cover/Number of Species and this showed a consistent upward trend when summer-autumn sampling dates only were considered.

(b) *Vegetation attributes*

A general increase in the woodiness of the vegetation was recorded, which was reflected both in the number of woody species present at each sampling date and in the total cumulative cover of woody individuals. While the number of species capable of forming trees increased from four, 12 months after burning, to eleven at the final sampling the total cover of woody individuals increased from 27 per cent to 45 per cent of the total community cover. This was largely due to the presence of *Acacia harpophylla*.

No direct measurement of vegetation attributes was made but it is possible to speculate on changes in these attributes on the basis of species-backed data. The abundance of succulent fruit is one attribute that appeared to follow a consistent successional pattern. The number of species possessing succulent fruit increased from eleven to seventeen over the study period while the total cover of the succulent fruited species as a percentage of the total cover of the community increased steadily from 3 per cent to 23 per cent up until the second last sampling 6 years after the burn then fell to 13 per cent at the last sampling. If we eliminate the cover contribution of *Acacia harpophylla*, a species without succulent fruit, from the total cover of the community, the cover of succulent fruited species increased from 2.5 per cent to 34 per cent, falling to 21.5 per cent at the final sampling. Whether the speculation that the abundance of succulent fruit increased markedly during the first 6 years of succession is correct was not proven and, in fact, would be difficult to prove. Because a species has the capacity to produce succulent fruits, an estimate of its importance does not measure the capacity of individuals at any point along the successional gradient to produce fruit. The reproductive tolerance of a species is much narrower than its vegetative tolerance and there is not necessarily any direct relationship between cover and the quantity of fruit produced. Because species have varying fruiting times direct measurement of this attribute would be very time consuming.

Site 2

Because attributes recorded in different strata were obtained from nested plots of different sizes and the type of attribute varied according to the stratum it is not strictly possible to combine them for direct comparison with other plots. Canopy cover was the

most convenient quantitative community attribute for overall comparison but sampling by the line intercept method to obtain data for the woody strata proved insufficiently intense for cover to be used as a highly reliable individual plot measure.

(a) *Floristic attributes*

Presence. A total of 101 species was recorded in the sixteen selected plots but because of the great ecological distance between the end plots only two species, *Acacia harpophylla* and *Cyperus gracilis*, were recorded from all plots; 29 per cent of the species occurred in only one plot while 12 per cent could be regarded as relatively constant species. About 24 per cent could be classified as increasers and 16 per cent as decreasers while the sporadic distribution of the remaining species made it impossible to categorise them. Because of the great turn-over in species, presence was very useful in providing a meaningful ordination which revealed a plausible successional pattern in both stands and species along the major axis of variation. Indicators of early stages in succession are the tree *Lysiphyllo caronii* and the shrub *Myoporum deserti* while in the latter stages *Croton insulare* and the *Macropteranthes leichhardtii* enter the community.

(b) *Quantitative attributes.* An ordination of stands based on standardised canopy coverage data was no clearer and more distorted than that using presence, while the species ordination was markedly inferior. Where unstandardised cover data were used the stands were placed along the major axes in ascending order of the canopy cover of the most common species so that no obvious successional pattern was revealed.

The number of species recorded in each plot varied from twenty to thirty-five but because sample size varied with stratum an assessment of the overall change in species richness was not possible. There was a marked decrease in species richness in the ground vegetation which paralleled an increase in species richness in the shrub and tree layers. In the latter strata, species richness, whether expressed by the total number of species or standardised on the basis of equal importance values such as height or diameter-breast-height, tended to remain constant or even fall slightly with the introduction of semi-evergreen vine thicket elements even though there were changes in species composition.

In the tree stratum there was a general increase in the cumulative totals of diameter-breast-height, height and canopy cover but the trend became less clear-cut towards the semi-evergreen vine thicket. There was a similar increase in the cumulative total of height of shrubs and lianas. In contrast, in the ground vegetation there was a marked decline in canopy cover with maximum values for cover of individual species occurring in the same or earlier successional plots than those for density.

An index expressing cumulative height of lianas per unit species provided a relatively stable indication of maturity while similar trends were obtained using total canopy cover per unit species, indicating that with more reliable canopy cover data this might again prove a useful index.

CONCLUSIONS

Succession involves a directional change in the specific composition of a plant community (Moravec 1969). Species replace one another with time and therefore in studying succession over a long time period the recording of presence of species alone

76 Attributes and their Selection

enables the isolation of indicator species which can be used to place vegetation stands in successional time.

In the study of primary succession this attribute was sufficient to order both species and plots in a sequence which resembled a successional pattern. Standardised canopy cover data added nothing to the stand ordination, which showed more distortion than when presence was used, while the species ordination was unsatisfactory. While cover data contain information in addition to presence, the relative lack of success of ordinations based on this attribute is a reflection of the inadequacies of standard non-linear ordination techniques rather than the attribute itself.

By contrast in the study of secondary succession the time span appeared too short for presence to express adequately the obvious changes that had occurred. Where combined site \times time presence data were analysed the spatial pattern dominated the ordination and only when data from individual plots over time were analysed separately was the successional pattern revealed. Under these circumstances subtle changes in vigour became more important and analyses using standardised cover data were superior to those based on presence. However, the ordination using unstandardised cover data gave the clearest presentation of succession in combined space and time.

Very dynamic situations, such as the early stages of secondary succession once ecesis has begun, involve changes in dominance in a highly competitive situation. With time, homeostatic controls lead to a more stable and balanced system. Populations of species exert temporary control over the system and are in turn replaced so that measures of dominance are perhaps more useful in describing dynamic events than where conditions are more stable. *Acacia harpophylla* assumed dominance at a very early stage and its relative importance increased with time. Its overriding dominance and the fact that it was still increasing in canopy cover at the last sampling, so that the study involved only one arm of its non-linear response curve, contributed to the success of this particular ordination in displaying successional change. Frequency and density were much less satisfactory attributes.

The initial differences among plots appeared to result from slight differences in the habitat and the original vegetation and the persistence of these differences indicates that chance appeared to play only a minor role in determining the direction of change. The decreasing importance of a species along the successional gradient was first indicated by a reduction in canopy cover and loss of vigour followed by reductions in frequency and density.

Except in the early stages of secondary succession, little change in overall species richness, expressed by number of species present, was recorded in both studies. During secondary succession various measures of diversity showed an increase in the initial stages but as *A. harpophylla* increased its dominance a trend towards reduced diversity appeared. Because maturity involved increases in structural complexity, indices expressing a measure of dominance, such as canopy cover, relative to the number of species were very informative.

A knowledge of variation in species composition with time can help to make informed statements about the position of stands in successional space. This, in itself,

does not help in explaining the processes involved but a knowledge of the biological characteristics of the individual species would assist in understanding the associated environmental changes and interactions in the ecosystem. In general this information is lacking and to overcome these shortcomings vegetation attributes which may have adaptive significance may be selected for study. Erection of hypotheses based on floristic attributes can be useful in deciding which attributes should be selected. In this study the increasing importance of succulent fruit in the early stages of secondary succession is suggested.

REFERENCES

- Austin, M. P. (1977). Use of ordination and other multivariate descriptive methods to study succession. *Vegetatio* **35**: 165-75.
- Blake, S. T. (1938). The plant communities of western Queensland and their relationships, with special reference to the grazing industry. *Proc. Roy. Soc. Qld* **49**: 156-204.
- Dale, M. B., and Clifford, H. T. (1976). On the effectiveness of higher taxonomic ranks for vegetation analysis. *Aust. J. Ecol.* **1**: 37-62.
- Daubenmire, R. (1959). A canopy-coverage method of vegetational analysis. *Northw. Sci.* **33**: 43-64.
- Hurlbert, S. G. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**: 577-86.
- Isbell, R. F. (1962). Soils and vegetation of the brigalow lands, eastern Australia. CSIRO Aust. Soils and Land Use Series 43.
- Maarel, E. van der (1969). On the use of ordination models in phytosociology. *Vegetatio* **19**: 21-46.
- Margalef, R. (1958). Information theory in ecology. *Gen. Syst.* **3**: 36-71.
- Moravec, J. (1969). Succession of plant communities and soil development. *Folia geobot. phytotax.*, Praha **4**, 133-64.
- Odum, E. P. (1971). *Fundamentals of Ecology*. 2nd edn., pp. 546. W. B. Saunders Company, Philadelphia.
- Pichi-Sermolli, R. E. (1948). An index for establishing the degree of maturity in plant communities. *J. Ecol.* **36**: 85-90.
- Russell, J. S., Moore, A. W., and Coaldrake, J. E. (1967). Relationships between subtropical, semi-arid forest of *Acacia harpophylla* (brigalow), microrelief and chemical properties of associated gilgai soil. *Aust. J. Bot.* **15**: 481-9.
- Webb, L. J., Tracey, J. G., Williams, W. T., and Lance, G. N. (1970). Studies in the numerical analysis of complex rain-forest communities V. A comparison of the properties of floristic and physiognomic-structural data. *J. Ecol.* **58**: 203-32.
- Williams, W. T., Lance, G. N., Webb, L. J., Tracey, J. G., and Dale, M. B. (1969). Studies in the numerical analysis of complex rainforest communities. III. The analysis of successional data. *J. Ecol.* **57**: 515-35,

Seral considerations in heathland

R. H. GROVES and R. L. SPECHT

INTRODUCTION

The term 'heath' or 'heathland' was originally applied by northern European botanists to some southern Australian vegetation which was structurally similar to the heaths of north-western Europe dominated by *Calluna vulgaris* and described by Gimingham (1972). As well as the obvious structural similarities, there were certain similarities in floristics (e.g. genera of the southern family Epacridaceae were similar to the ericaceous genera familiar to European botanists) and in the inability of the land to sustain anything other than extensive sheep or cattle grazing and then only with regular burning.

Heathland vegetation usually consists of evergreen, sclerophyllous shrubs less than 2 m high (Specht 1970). The foliage projective cover of the shrub layer may vary from dense (70–100 per cent) to mid-dense (30–70 per cent) and these two variants have been termed closed- and open-heath respectively (Specht 1970 and this volume). Under the tall shrub layer, there is often a layer of shorter shrubs less than 1 m high (sub-shrubs). The third or ground layer comprises, to varying degrees, an assemblage of grass-like monocotyledons which in this chapter are referred to as 'graminoids'.

Many plant communities in which shrubs predominate may be termed 'heaths' or 'heathlands'. Some of the confusion in use of the terms has been clarified by Specht (1979a) for both lowland and upland heaths with an array of different life forms and foliage projective covers in the upper stratum. In general in this paper we shall use the term 'heathland' in the sense of Specht (1970) referred to above.

Three generalisations may be made about heathland vegetation despite the diversity in terminology and fine structure. There is a wide climatic diversity in the distribution of heathlands around the southern and eastern coasts and in montane areas of Australia. Heathlands occur as islands of structurally similar vegetation over this extensive region. Climate varies from strictly Mediterranean (south-west Western Australia) to a mixture of winter and summer rainfall (South Australia to northern New South Wales) to sub-tropical (southern Queensland) to strictly tropical (Cape York Peninsula). Invariably, however, heathlands occur on acid soils poor in most plant nutrients (Specht and Rayson 1957a; Groves 1981a).

Heathlands are invariably subject to periodic fires and there is an array of responses of heathland species to fire. Most species are able to regenerate from underground organs such as lignotubers (synonymous with rootstocks or burls), rhizomes or tubers and a few from epicormic buds following fire. Some species can regenerate after fire only from seeds, while other species may reproduce both vegetatively and sexually. Gill and Groves (1981) reviewed the literature on these different types of responses of heathlands

to fire in terms of fire type, frequency, intensity and seasonality (the so-called 'fire regime' of Gill 1975).

A third generalisation which may be made for most Australian heathlands is that floristic diversity is high. Specht (1979b) presented information on this characteristic and showed that it could be as high as that in tropical rainforest. Up to 36 species were recorded from an area as small as 8 m² in south-east South Australia. Up to 20 species were recorded from 1 m² in the Myall Lakes region (B. J. Fox pers. comm.). Time from the last fire, the density of the strata and the complexity of the microtopographic pattern may all affect floristic diversity. For example, Specht *et al.* (1958) showed that of a total of 36 species recorded soon after a fire only 20 had survived at 25 years and it was suggested that only half of these would persist after 50 years from fire. Rayson (1957) showed how species composition of a heathland may change considerably over small distances on a re-sorted sand dune because of microtopographic features influencing both the amount of rainfall and the depth of sand over clay.

In this chapter we wish to develop the idea of heathlands as a continuum of a range of sclerophyll shrublands in which various factors influence their structure and thus their classification. Initially we shall consider soil moisture levels and discuss two distinctive nodes on the continuum. We shall then discuss the role of a number of interacting factors in maintaining heathlands as low shrublands. Finally we shall return to the over-riding influence of fire frequency in affecting heathland dynamics and consider, briefly, its successional status.

SOIL MOISTURE

In areas of heathlands, such as south-east South Australia, Wilsons Promontory in Victoria, in northern Tasmania and at various places on the east coast, two distinct types of heathland may be recognised readily. They have been termed 'wet' and 'dry' heathlands because the former are seasonally waterlogged, although they may also be droughted for part of the year. These two terms reflect differences in the soil profiles on which these two heathland types occur and parallels with the Australian situation are to be found in north-western Europe and in the western Cape region of South Africa. Wet heathlands occur on some different podzolic soils (the groundwater podzols of Stephens 1956) in which a relatively shallow horizon of sand (usually less than 25 cm) overlies a relatively impermeable horizon of cemented clayey sand, or even bedrock, as at Jervis Bay (F. Ingwersen pers. comm.). Dry or 'sand' heathlands, on the other hand, occur on more freely draining soils (often sandy) in which the sand profile may be 150 cm deep or more. Some typical examples of these different soil profiles were described by Groves and Specht (1965).

As a result of the different depths of the relatively impermeable B horizon, or to the parent rock itself, soil moisture relations differ markedly between sites on which these two heathland types occur, although the sites themselves may be quite close and receive similar amounts of rain. Other differences occur—shoot biomass of wet heathlands is lower (Groves and Specht 1965) and graminoids in the ground layer are more conspicuous. The two communities may sometimes even be distinguished on the floristics of

the graminoid component. For example, at Wilsons Promontory, Victoria, the dominant shrubs (*Casuarina pusilla* and *Leptospermum myrsinoides*) are the same in the two heathlands but in the wet heathland the graminoid *Lepidosperma neesii* is dominant in the ground layer and in the dry heathland *Hypolaena fastigiata* is the main graminoid (Groves and Specht 1965).

The two subassociations of wet and dry heathlands may best be considered as two nodes in a continuum of floristic changes induced by a gradation in soil moisture characteristics. Regrettably, the root system and soil moisture relationships of wet heathlands have still to be described in the detail provided by Specht and Rayson (1957b) and Specht (1957) for a typical dry heathland in south-eastern South Australia. Gullan (1976) found all the species of wet heathland at Cranbourne, Victoria, to have specialised aerating tissues in their roots if they were waterlogged. Anatomically, the specialisation in monocotyledons, such as the graminoids, is different from that in dicotyledons, such as *Melaleuca*. Further research on root systems, at the levels of both the community and of individual species, seems warranted, especially in relation to periodic changes in water status of the heathland community.

At other sites in coastal Australia, some of the dominant shrub species, rather than those of the ground layer, may change and thereby reflect the differences in moisture regimes between the two soil types. In Victoria, shrubs of *Leptospermum myrsinoides* typical of the dry heathland may give way to those of *L. juniperinum* on seasonally wetter sites. On the central coast of New South Wales, Siddiqi and Carolin (1976) reported differences in the tolerances of three *Banksia* species (*B. serratifolia*, *B. aspleniifolia* and *B. ericifolia*) according to the degree of waterlogging they could tolerate. Similar results are available for a suite of *Banksia* species at a southern Queensland site (M. P. Bolton pers. comm., as in Specht 1981a). Established plants of *Banksia collina* from a sandy ridge were able to withstand only 27 days of waterlogging, compared with 50 days for dune ecotypes of *B. aemula* (syn. *B. serratifolia*) and *B. oblongifolia*, and 80 days for a swamp ecotype of *B. oblongifolia* before succumbing, whilst plants of *B. robur*, a shrub confined to the wettest and most poorly drained sites, were still alive after 98 days of waterlogging.

As well as the differences in shoot biomass and floristics arising in response to different soil moisture characteristics, structural differences may also occur. The height of the mature community increases in wet heathland with decreasing duration of waterlogging and, conversely, in dry heathlands height may increase with decreasing duration of droughting. At the two ends of the continuum in soil moisture, which probably represent different depths of the water table, taller shrubs or small trees may become emergent with time. *Melaleuca* spp. (e.g. *M. squarrosa* in south-eastern Victoria and *M. quinquenervia* sens. lat. in southern Queensland) are the main emergent shrubs at the wetter end of the continuum and at the other end *Eucalyptus*, *Leptospermum* and *Banksia* are the main genera which may become emergent on deep sands with decreasing incidence of droughting. The implications of these changes for community productivity were discussed by Jones, Groves and Specht (1969) but their implications for community structure and classification remain relatively unexplored.

NUTRIENTS AND MICRO-ORGANISMS

Apart from the effects of different periods of waterlogging and/or droughting of the upper soil horizons discussed above, what other factors determine whether some faster growing shrubs become emergent and eventually dominate the shrub stratum? We suggest there are several other factors, of which nutrient status and mycorrhizal infection may be significant, but especially as they interact.

Heathlands invariably occur on soils deficient in most plant nutrients, especially phosphorus and nitrogen. The parent materials are inherently low in minerals (Beadle 1962) and the soils formed from them have, over geologic time, been leached (Wild 1961). Heathland species have a range of ecophysiological mechanisms which enable them to grow under these low-nutrient conditions (Specht and Groves 1966; Groves 1981a, b). Soil nutrient level may be further depleted by regular fire to the point where lack of nutrients, especially phosphorus, may limit growth of the heathland shrubs. Particularly in regions such as around Sydney, heavy summer rains often follow fire and thus are capable of eroding the less nutrient-poor layer of the surface soil (Groves 1977). If artificial fertilisers are added to the nutrient-depleted heathland some species may respond preferentially, e.g. *Leptospermum laevigatum* in the dry heathland at Wilsons Promontory, Victoria (Burrell 1968 and pers. comm.) and soon emerge above the shrub canopy. A further example is that of *Angophora woodsiana* which Connor and Wilson (1968) showed to emerge above the heathland in response to additions of complete fertiliser and regular fires.

If the emergent shrubs are myrtaceous, as in the case of *Leptospermum*, *Melaleuca* and *Eucalyptus*, there seems to be a need not just for added phosphorus, but also for mycorrhizal infection to occur. Other genera of heathland shrubs may also need the presence of different types of mycorrhizae to enhance their establishment and growth (Gullan 1976). Burrell (1968 and pers. comm.) showed that both phosphorus and mycorrhizal infection were necessary for successful establishment of seedlings of the typical calcareous dune shrub *Leptospermum laevigatum* in acid heathland soils. Once established, its higher growth rate enabled it to emerge above the heathland canopy in about five years. Depending on the subsequent fire regime, and especially fire frequency, community structure may thus be changed. Man's activities—conscious or unconscious—in adding nutrients, in creating conditions for soil particle movement or in depleting scarce nutrients still further by regularly burning and/or grazing shrublands have increased the diversity of heathland types over recent time.

FIRE FREQUENCY

No discussion of heathland dynamics can ignore the over-riding importance of fire in affecting floristic composition and community structure. We have already made passing reference to it throughout this chapter and there are several recent reviews of the subject, both for heathlands of Australia (Specht 1981b) and of the world (Gill and Groves 1979). We wish to make several points.

Specht (1981b) showed for heathlands from a wide geographic area in southern and eastern Australia that after a fire a large percentage of the regenerating shoot biomass

came from lignotubers, rhizomes, tubers etc. He showed seedling regeneration to be generally poor in wetter sites but it became increasingly important in drier sites. There is a linear relationship between the proportion of the community regenerating after a fire from rootstocks and the foliage projective cover of the shrub layer of the heathland (Fig. 1 of Specht 1981b).

The generalised pattern of regeneration after fire in Australian heathlands was described by Gill and Groves (1981). The early post-fire successional stage, lasting two to three years, is dominated by sedges or restioids or *Xanthorrhoea* spp. and some geophytes. Annual species, especially grasses and herbs, are rare and are found only in the first year or two after fire. Up to five to six years from fire, shrub species able to regenerate from rootstocks, such as *Casuarina* and *Leptospermum*, become dominant and species in the subshrub layer are prominent. After six years or so, shrubs, many of which are proteaceous, and which regenerate from seed become more important. Specht *et al.* (1958) recorded a senescent stage about 40 to 50 years after fire in south-eastern South Australia, but such mature communities are rarely found in Australia.

Fires induced by man have probably been more frequent in Australia than in most other regions of shrubland, and especially in regions such as the coastal lowlands of southern Queensland. Only relatively recently over the last 10 years or so have older stands of heathland existed, mainly as a result of preservation of some areas in nature reserves, e.g. near Tidal River, Wilsons Promontory National Park. To retain the present structure and floristics of heathlands a program of burning every 12 to 15 years may be the most favourable (Gill and Groves 1981). More frequent burning, and especially as often as every three years, leads to an increase in the proportion of vegetatively regenerating graminoids in the ground layer. Fire frequencies of 5 to 10 years may favour the development of the subshrub layer. A regime of two fires two to three years apart may eliminate the seed-regenerating shrubs which if protected from fire for long enough would otherwise dominate the heathland (Burrell 1968; Gill and Groves 1981).

Whilst these simple recommendations for management of heathland areas may be used to promote floristic and structural diversity, management of heathlands by fire is also, and increasingly, directed towards maintaining or enhancing faunal diversity, especially of small mammals. For example the New Holland mouse (*Pseudomys novaehollandiae*) and the short nosed bandicoot (*Isoodon obesulus*) seem to prefer early stages of succession after fire in dry heathlands (Braithwaite and Gullan 1978; Fox and Fox 1978). The heath-rat (*Pseudomys shortridgei*) is most prevalent in southern Victorian heathlands 5 to 6 years after fire when floristic diversity is also high (Cockburn 1978). In the Myall Lakes area of New South Wales some small mammals (e.g. *Rattus lutreolus*) seem to require a dense graminoid layer, whilst others seem to require a less dense cover of sub-shrubs (e.g. *Pseudomys novaehollandiae*). The distribution of other small mammals is positively correlated with taller shrub cover (e.g. *Rattus fuscipes*) (B. J. Fox pers. comm. and this volume). Together, these examples imply that both the structure and floristics of heathlands are significant for creating small mammal habitat. This seems an aspect of heathland ecology where animal and plant ecologists may collaborate most fruitfully in the near future.

In the short term, changes in the relative proportions and in the flora of the three layers which constitute Australian heathlands are strongly influenced by the previous fire regime and especially fire frequency. An understanding of the ecological effects of past and present regimes gives man a powerful tool to manage heathlands for a variety of purposes in the future.

CONCLUSIONS

We see the different stages of heathlands in Australia in two ways. First, they represent edaphic climaxes (and not climatic ones) and at any one time they represent various stages of pyric succession, the generalised pattern of which we have described. In classical Clementsian terms pyric succession is secondary, in that in most cases some propagules survive fire—usually as seeds or underground shoots or roots. Individual post-fire patterns may not necessarily be repeated, even in the same region, because no two fire regimes will ever be identical. Pyric succession in heathlands is more a gradual elimination of individuals present from the outset than a replacement of initial species by new species, as Hanes (1971) pointed out for Californian chaparral. It is best represented by the initial floristic composition model of Egler and not the relay floristic model implicit in the Clementsian concept (Noble, this volume).

By applying the concepts of Watt (1947) to a mature *Calluna* heath in north-eastern Scotland, Barclay-Estrup and Gimingham (1969) showed that the life cycle of the community comprised four phases—the pioneer, building, mature and degenerate phases. Different phases of the pyric succession shown by Australian heathlands may be recognised in a similar way, though the degenerate phase in Australian heathlands is rarely seen. While the stages of heathland in the short term may be thought of as being linear, in the longer term the cyclical nature of heathlands may need to be stressed provided they can be protected from fires for long enough. Gimingham (1978) discussed the vulnerability of the degenerate phase of *Calluna* heathland to invasion by tree species, such as *Betula* and *Pinus sylvestris*, and it may be that in the future Australian heathlands will be similarly susceptible to long-term change.

For the present, we conclude that the range of heathlands in Australia are edaphic climaxes which show various stages of secondary pyric succession. We suggest that none of the communities can be considered seral stages in a primary autogenic succession.

ACKNOWLEDGMENTS

We wish to thank Barry Fox, Paul Gullan and Frank Ingwersen for comments on an earlier draft of this chapter and Matt Bolton for allowing us to cite his unpublished results.

REFERENCES

- Barclay-Estrup, P., and Gimingham, C. H. (1969). The description and interpretation of cyclical processes in a heath community. I. Vegetational change in relation to the *Calluna* cycle. *J. Ecol.* **57**: 737-58.
- Beadle, N. C. W. (1962). An alternative hypothesis to account for the generally low phosphate content of Australian soils. *Aust. J. Agric. Res.* **13**: 434-42.

- Braithwaite, R. W., and Gullan, P. (1978). Habitat selection by small mammals in a Victorian heathland. *Aust. J. Ecol.* **3**: 109-27.
- Burrell, J. (1968). The invasion of Victorian heathlands by *Leptospermum laevigatum*. *Proc. Ecol. Soc. Aust.* **3**: 39.
- Cockburn, A. (1978). The distribution of *Pseudomys shortridgei* (Muridae: Rodentia) and its relevance to that of other heathland *Pseudomys*. *Aust. Wildl. Res.* **5**: 213-20.
- Connor, D. J., and Wilson, G. L. (1968). Response of a coastal Queensland heath community to fertilizer application. *Aust. J. Bot.* **16**: 117-23.
- Fox, B. J., and Fox, M. D. (1978). Recolonization of coastal heath by *Pseudomys novaehollandiae* (Muridae) following sand mining. *Aust. J. Ecol.* **3**: 447-65.
- Gill, A. M. (1975). Fire and the Australian flora: a review. *Aust. For.* **38**: 4-25.
- Gill, A. M., and Groves, R. H. (1981). Fire regimes in heathlands and their plant ecological effects. In: *Heathlands and Related Shrublands* (ed. R. L. Specht). *Ecosystems of the World*. Vol. 9b, pp. 61-84. Elsevier Scientific Publishing Company, Amsterdam.
- Gimingham, C. H. (1972). *Ecology of Heathlands*: pp. 266. Chapman and Hall, London.
- Gimingham, C. H. (1978). *Calluna* and its associated species: some aspects of co-existence in communities. *Vegetatio* **36**: 179-86.
- Groves, R. H. (1977) Fire and nutrients in the management of Australian vegetation. In: *Proc. Symp. Environ. Consequences of Fire and Fuel Management in Mediterranean Ecosystems* (Tech. Coord. H. A. Mooney and C. E. Conrad), pp. 220-9. USDA For. Serv. Gen. Tech. Rpt WO-3, Washington.
- Groves, R. H. (1981a). Heathland soils and their fertility status. In: *Heathlands and Related Shrublands* (ed. R. L. Specht) *Ecosystems of the World*. Vol. 9b, pp. 143-50. Elsevier Scientific Publishing Company, Amsterdam.
- Groves, R. H. (1981b). Nutrient cycling in heathlands. In: *Heathlands and Related Shrublands* (ed. R. L. Specht) *Ecosystems of the World*. Vol. 9b, pp. 151-63. Elsevier Scientific Publishing Company, Amsterdam.
- Groves, R. H., and Specht, R. L. (1965). Growth of heath vegetation. I. Annual growth curves of two heath ecosystems in Australia. *Aust. J. Bot.* **13**: 261-80.
- Gullan, P. K. (1976). Vegetation of the Royal Melbourne Botanic Gardens annexe at Cranbourne. Ph.D. Thesis, Monash University.
- Hanes, T. L. (1971). Succession after fire in the chaparral of southern California. *Ecol. Monogr.* **41**: 27-52.
- Jones, R., Groves, R. H., and Specht, R. L. (1969). Growth of heath vegetation. III. Growth curves for heaths in southern Australia: a reassessment. *Aust. J. Bot.* **17**: 309-14.
- Rayson, P. (1957). Dark Island heath (Ninety-Mile Plain, South Australia). II. The effects of microtopography on climate, soils and vegetation. *Aust. J. Bot.* **5**: 86-102.
- Siddiqi, M. Y., and Carolin R. C. (1976). Studies in the ecology of coastal heath in New South Wales. II. The effects of water supply and phosphorus uptake on the growth of *Banksia serratifolia*, *B. asplenifolia* and *B. ericifolia*. *Proc. Linn. Soc. N.S.W.* **101**: 38-52.
- Specht, R. L. (1957). Dark Island heath (Ninety-Mile Plain, South Australia). IV. Soil moisture patterns produced by rainfall interception and stem-flow. *Aust. J. Bot.* **5**: 137-50.
- Specht, R. L. (1970). Vegetation. In: *The Australian Environment* (ed. G. W. Leeper), 4th edn (rev.), pp. 44-67. CSIRO (Aust.) and Melbourne University Press, Melbourne.
- Specht, R. L. (1979a). Introduction. In: *Heathlands and Related Shrublands* (ed. R. L. Specht) *Ecosystems of the World*. Vol. 9a, pp. 1, 18. Elsevier Scientific Publishing Company, Amsterdam.
- Specht, R. L. (1979b). The sclerophyllous (heath) vegetation of Australia: the eastern and central States. In: *Heathlands and Related Shrublands* (ed. R. L. Specht) *Ecosystems of the World*. Vol. 9a, pp. 125-210. Elsevier Scientific Publishing Company, Amsterdam.

- Specht, R. L. (1981a). The water relations of heathlands: seasonal waterlogging. In: *Heathlands and Related Shrublands* (ed. R. L. Specht) *Ecosystems of the World*. Vol. 9b, pp. 99-106. Elsevier Scientific Publishing Company, Amsterdam.
- Specht, R. L. (1981b). Responses of selected ecosystems: heathlands and related shrublands. In: *Fire and the Australian Biota* (ed. A. M. Gill, R. H. Groves, and I. R. Noble). pp. 395-415. Aust. Acad. Sci., Canberra.
- Specht, R. L., and Groves, R. H. (1966). A comparison of the phosphorus nutrition of Australian heath plants and introduced economic plants. *Aust. J. Bot.* **14**: 201-21.
- Specht, R. L., and Rayson, P. (1957a). Dark Island heath (Ninety-Mile Plain, South Australia). I. Definition of the ecosystem. *Aust. J. Bot.* **5**: 52-85.
- Specht, R. L. and Rayson, P. (1957b). Dark Island heath (Ninety-Mile Plain, South Australia). III. The root systems. *Aust. J. Bot.* **5**: 103-14.
- Specht, R. L., Rayson, P., and Jackman, M. E. (1958). Dark Island heath (Ninety-Mile Plain, South Australia). VI. Pyric succession: changes in composition, coverage, dry weight, and mineral nutrient status. *Aust. J. Bot.* **6**: 59-88.
- Stephens, C. G. (1956). *A Manual of Australian Soils*: 2nd edn, pp. 54. CSIRO (Aust.), Melbourne.
- Watt, A. S. (1947). Pattern and process in the plant community. *J. Ecol.* **35**: 1-22.
- Wild, A. (1961). A pedological study of phosphorus in 12 soils derived from granite. *Aust. J. Agric. Res.* **12**: 286-99.

Comparison of three small-scale (1:1 million) vegetation mapping techniques

JOHN PICKARD and D. E. BOYLAND

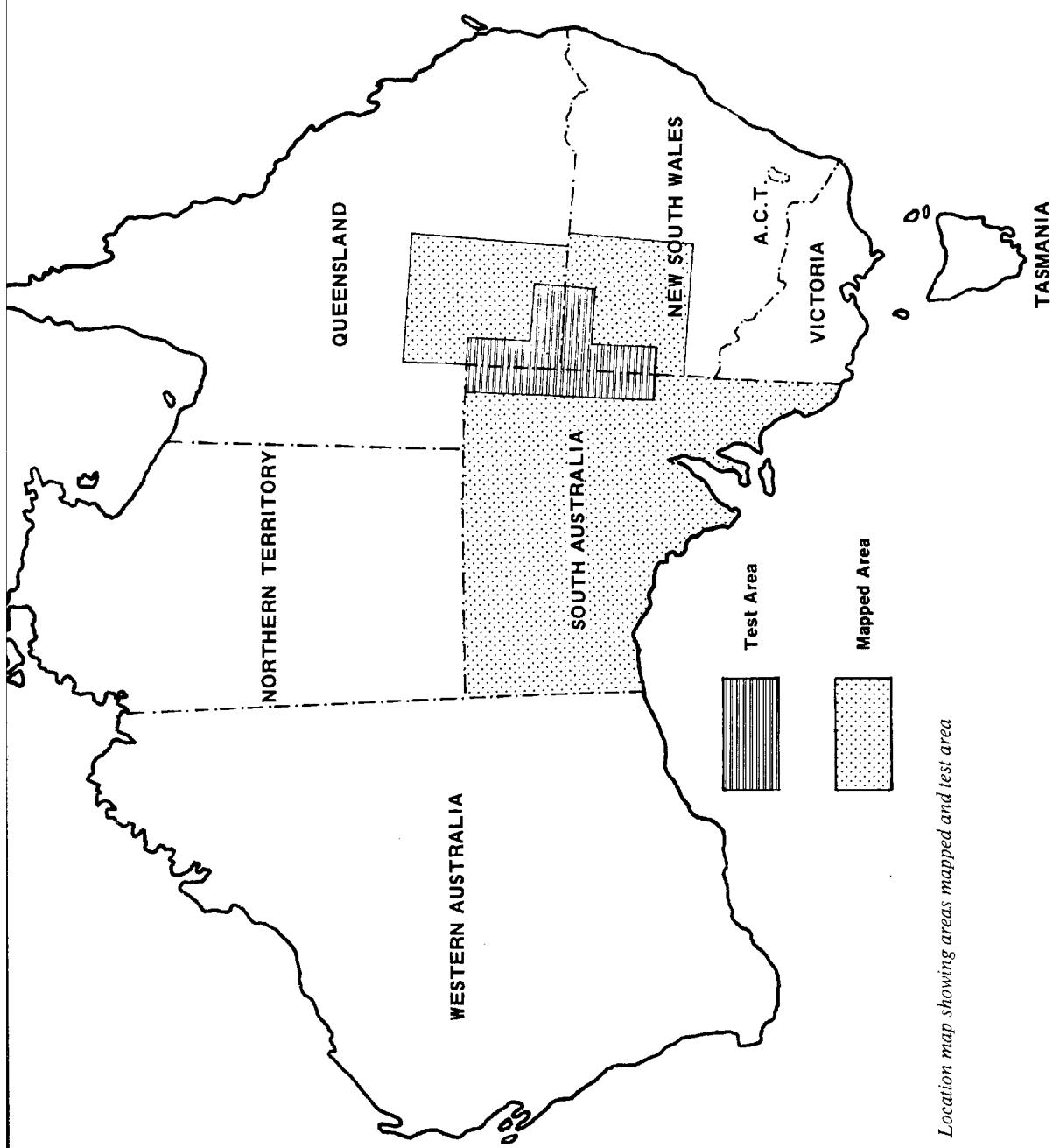
INTRODUCTION

After many years of little activity, vegetation mapping is once again an active science in Australia. Although a range of scales is being used, the Australian continental standard is 1:1 000 000. At least three mapping groups are preparing maps at this scale: Western Australia (Beard 1974, 1975a, 1975b, 1976; Beard and Webb 1974), Queensland (Dawson and Boyland 1973; Boyland 1977; Boyland unpub.) and New South Wales (Pickard unpub.). However, at the time of writing, each group is using different techniques although there is general agreement on standardisation of scales and principles.

Aerial photographs form the basis for all modern vegetation mapping and terrain evaluation in general. Indeed, vegetation mapping is only one facet of terrain evaluation which includes mapping of geology, geomorphology, land use, water resources etc. (Mitchell 1973). All are mapped following the traditional stereo examination of vertical black and white airphotos, delineation of photo-appearance types using tone, texture, location, pattern, size and shadow (Colwell 1960). These boundaries are transferred to a topographic base map and then field checked. After further interpretation, the map is compiled, drawn and published. The method is rapid, accurate, relatively inexpensive and has been tested throughout the world (Colwell 1960; Beckett 1968).

The introduction of satellites has allowed photography from much higher altitudes. The imagery from LANDSAT is widely used for terrain evaluation (e.g. Laut *et al.* 1977a, 1977b; Story *et al.* 1976; Adomeit *et al.* this volume). This imagery allows broad views but like traditional airphotos suffers from problems of resolution and scale. At 1:85 000 (the standard scale of Australian airphotos) the vegetation *per se* is difficult to interpret and on LANDSAT photographic imagery it is virtually impossible. There are cartographic limitations as well. The smallest unit which can be shown is approximately 2 or 3 mm across i.e. 2 or 3 km at 1:1 million.

In arid and semi-arid areas it is bare ground rather than vegetation which is seen on airphotos at a scale of 1:85 000. Indeed at this scale, the mapping units may approach land systems rather than vegetation associations. This is not surprising because a land system is defined as 'an area, or group of areas throughout which there is a recurring pattern of topography, soils and vegetation' (Christian and Stewart 1953). This definition is similar to Grant's (1968, 1975) terrain pattern: 'an area containing a recurring topography, soil associations and natural vegetation formations'. Other definitions in the terrain evaluation literature echo these and it follows that one can use a vegetation,



9.1 Location map showing areas mapped and test area

topography, soils or landsystem map to predict any one of the others with equivalent accuracy although some amalgamation or splitting of units may be necessary within boundaries. This has been done in the CSIRO Land Research series where vegetation and soils maps are abstracted from land systems maps. In Western Australia, Beard (1974) has reinterpreted 1:250 000 geological maps to prepare 1:1 000 000 vegetation maps.

In south-western Queensland Dawson and Boyland (1973) reinterpreted a 1:500 000 land system map to prepare a 1:1 000 000 vegetation map. Immediately south of this area in New South Wales, Pickard (unpub.) reinterpreted 1:250 000 geological maps to prepare a 1:1 000 000 vegetation map. West of both these areas Laut *et al.* (1977b) prepared land system maps using LANDSAT imagery. This triple junction (Fig. 9.1) provides a unique opportunity to compare the maps along 10.5 degrees of the shared borders.

MAPPING METHODS

Queensland

The vegetation map was produced by abstraction from the 1:500 000 land system map. The aim of the multidisciplinary project was 'to produce a physical inventory in the area' (Dawson and Boyland 1974). Land systems were mapped on stereopairs of vertical airphotos at 1:80 000 scale. The land system map was compiled at 1:250 000 and published at 1:500 000. The vegetation map was published at 1:1 000 000.

Boyland has since revised the map of major vegetation groups prepared by the amalgamation of the land systems. The original interpretation of the 1969 black and white 1:85 000 airphotos was re-examined and boundaries modified accordingly for vegetation mapping. This was supplemented by additional ground traverses. The maps were then compiled at 1:250 000 for publication at 1:1 000 000. Vegetation was classified on structural formations with further subdivision based on floristics. In this unpublished map 23 vegetation associations are distinguished.

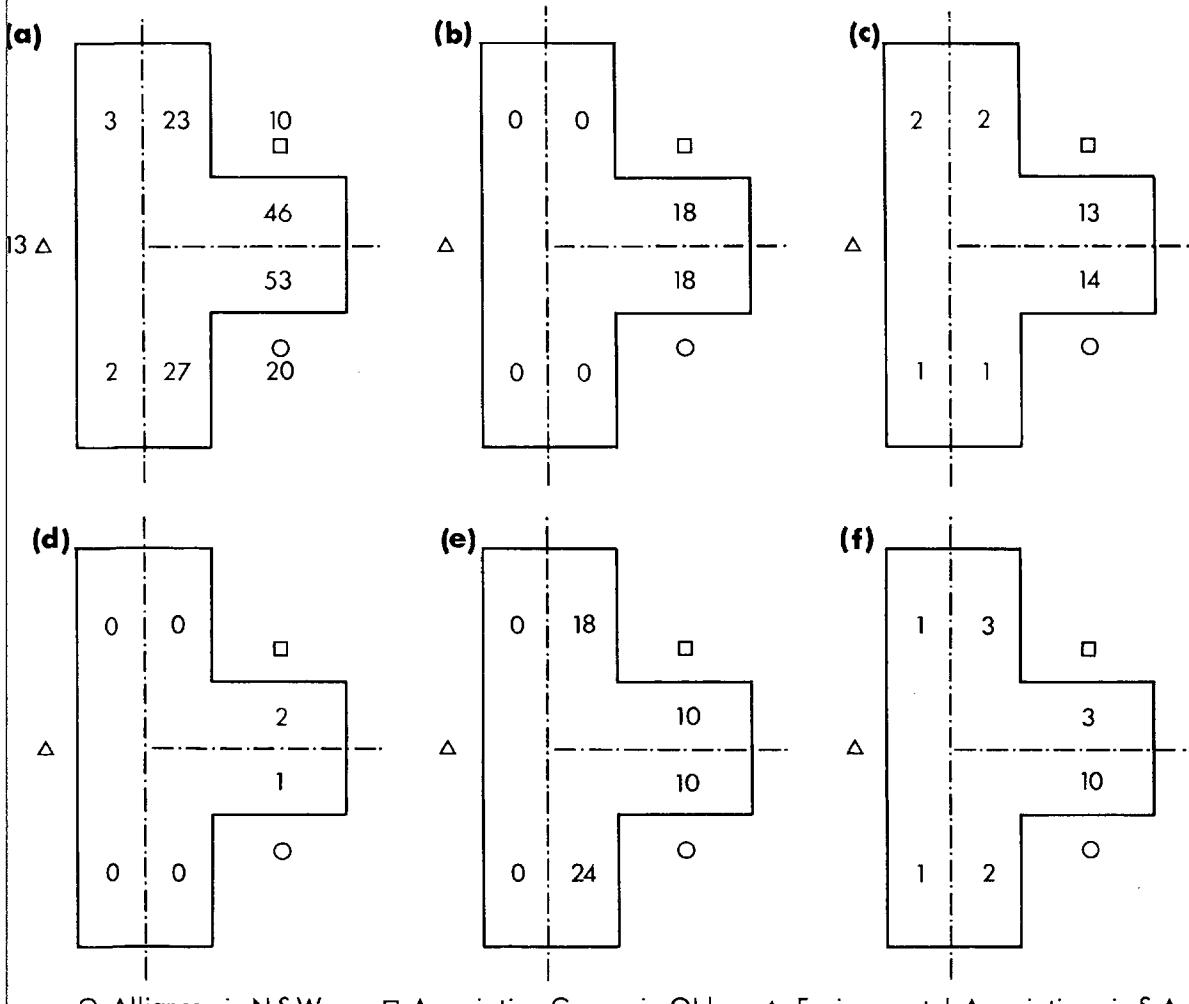
New South Wales

The aim of the N.S.W. project was to prepare a 1:1 000 000 vegetation map and accompanying notes. Extensive ground traverses on most public roads and station tracks provided ground truth for the concurrent and subsequent reinterpretation of 1:250 000 geological maps. These maps were originally prepared using airphotos. The vegetation maps were compiled at 1:250 000 for publication at 1:1 000 000 after several stages of field checking.

South Australia

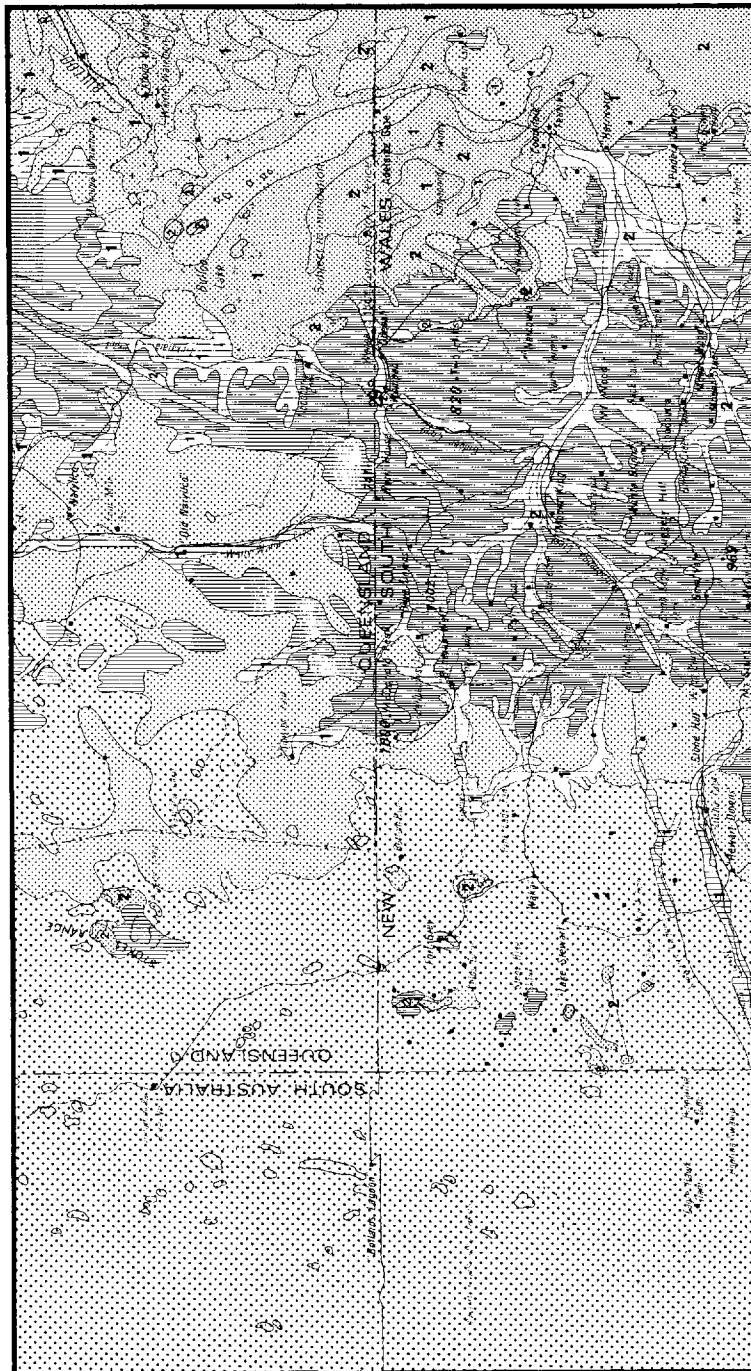
Although the South Australian study was primarily methodological (Laut *et al.* 1977b), another purpose was to map land attributes of all South Australia and to evaluate LANDSAT imagery for interpretation of vegetation cover. First generation black and white negatives of Bands 4 and 7 were used to prepare imagery at 1:1 000 000 scale.

These were interpreted visually and the environmental regions mapped. Limited ground and aerial checking provided ground truth. The maps were initially published as composite LANDSAT images (Laut *et al.* 1977b) and later on topographic bases (Laut 1978).



9.2 Numbers of boundaries in each State and the degree of matching

- (a) Boundaries hitting border and number of units mapped in test area
- (b) Perfect matches i.e. agreement within 1 km across the border
- (c) Mismatches i.e. agreement > 1 km < 5 km
- (d) Bad mismatches i.e. agreement > 5 km < 10 km
- (e) Number of apparently irreconcilable boundaries which can be absorbed in unit(s) across border
- (f) Irreconcilable boundaries



SOUTH AUSTRALIA
ENVIRONMENTAL ASSOCIATIONS

- 1 Sirzelecki Desert
- 2 Chenopod shrubland, hummock grassland, tussock grassland

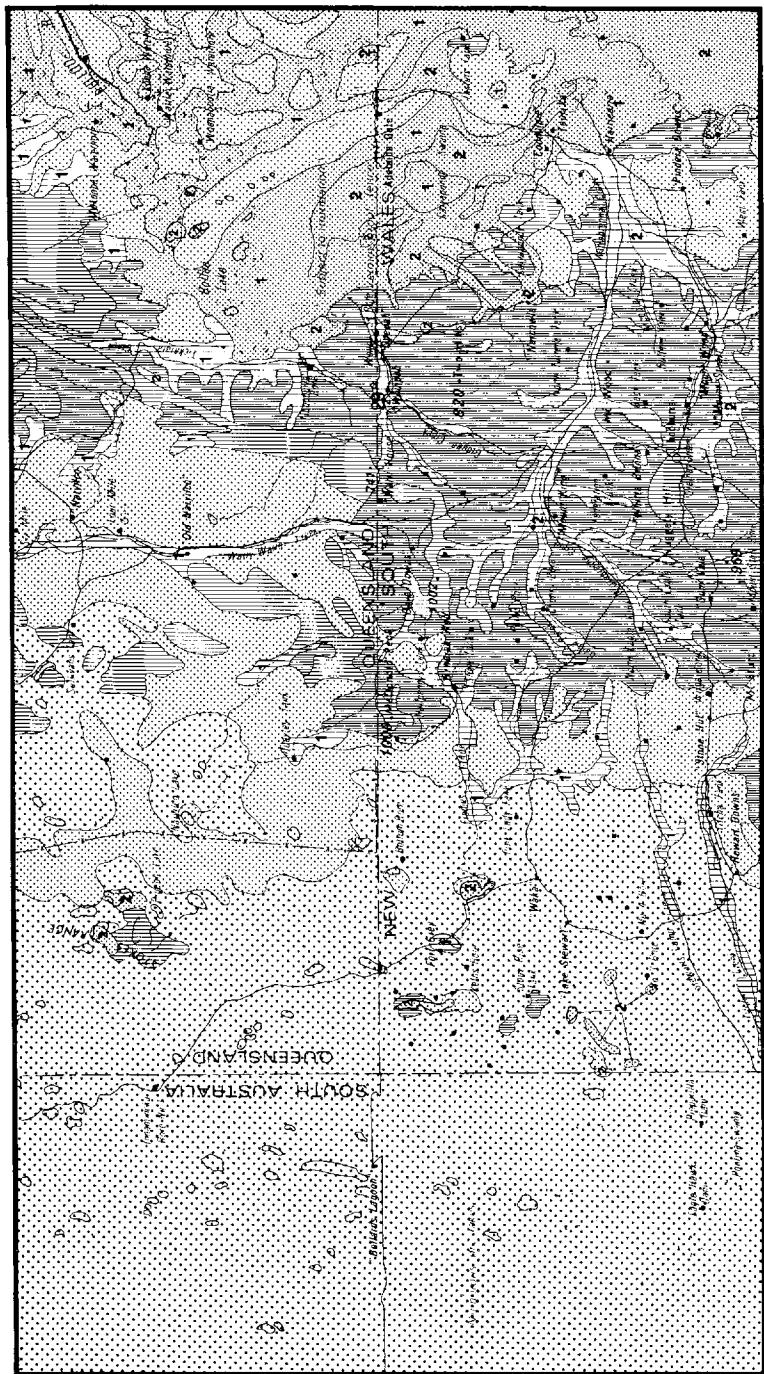
QUEENSLAND
FLORISTIC ASSOCIATIONS

- 1 Spinifex, shrub
- 2 Acacias, whitewood
- 3 Mitchell grass, short grass, forb
- 4 Short grass, forb (alluvia)
- 5 Gidgee
- 6 Bluebush, lignum/herbland complex
- 7 Sparse hermland (dry lakes)

NEW SOUTH WALES
ALLIANCES

- 1 *Acacia aneura*, *A. ligulata*
- 2 *Acacia aneura*
- 3 *Astrebla* spp.
- 4 *Eucalyptus microtheca*
- 5 *Acacia cambagei* - *Eucalyptus camaldulensis*
- 6 *Atriplex nummularia*
- 7 *Eragrostis australasica*, *Muehlenbeckia cunnighamii*
- 8 *Miscellaneous* communities

(a)



PLANT COMMUNITIES

- Desert complex
- Acacia aneura
- Chenopod/Eragrostis australasica complex
- Astrebla spp.
- Miscellaneous communities

(b)

9.3 Sections of test area (a) showing original mapping and (b) showing reconciliation

COMPARISONS

We make a three-way comparison of three different teams with different aims and different methods. We compare the maps along the borders and for 1° depth on each side (Fig. 9.1) giving a total test length of 10.5° or 1100 km and a test area of 190 000 km². The degree of matching or mismatching of boundaries across each border is assessed in five classes (Fig. 9.2). Boundaries form a perfect match if they are <1 km (i.e. <1 mm) apart as this is the limit of map resolution. We present reduced maps showing the units as originally mapped (Fig. 9.3a) and as rationalised (Fig. 9.3b). We have chosen Queensland as the standard for rationalisation because the basis of the vegetation mapping is likely to be more accurate.

RESULTS

Relevant statistics are given in Fig. 9.2. The number of mapping units recognised in the three states varies considerably as does the detail of mapping. However, examination of original maps indicates that the mapping in both Queensland and New South Wales is similar in detail. The South Australian mapping units are considerably larger than those in the other States.

Queensland/New South Wales

Overall the agreement is good; some 67 per cent of Queensland boundaries and 60 per cent of N.S.W. boundaries match within 5 km; and 39 per cent and 33 per cent within 1 km respectively. There are very few bad mismatches, i.e. >5 km or >10 km. A number (22 per cent and 19 per cent respectively) of boundaries can only be reconciled by absorbing them in the unit across the border. Thus, in the Bulloo Overflow region, the Queensland blue bush (*Chenopodium auricomum*) / lignum (*Muehlenbeckia cunninghamii*) / hermland is equivalent to three N.S.W. communities: *Maireana sedifolia*, *Eragrostis australasica* and *Atriplex nummularia*.

However, there remain three boundaries in Queensland and ten in N.S.W. which cannot be reconciled. The three in Queensland appear to be due to differences in air-photo interpretation and two in N.S.W. have the same difficulty. The remaining eight in N.S.W. arise from a major difference in community erection and definition. In Queensland, Boyland erected two major mulga (*Acacia aneura*) communities: in the west *Acacia aneura/Atalaya hemiglaucha* on the sand plain, which changes at 143°50'E to *Acacia aneura*. In New South Wales, Pickard did not make the same distinction and mapped silcrete-capped hills as *Acacia aneura-Acacia tetragonophylla*. The silcrete-capped hills in Queensland support a complex of bastard mulga (*Acacia clivicola*), *Acacia aneura*, lancewood (*A. petraea*) and in places bendee (*A. catenulata*).

Definitions of some other communities vary but these are easily reconcilable e.g.

Queensland
Eucalypt

New South Wales
Eucalyptus microtheca or
E. ochrophloia

Alluvial country (Short grass, forb associations with <i>Eucalyptus</i> woodlands fringing channels)	included in various communities: <i>E. largiflorens</i> <i>E. camaldulensis</i> , <i>Acacia cambagei</i>
Dry lakes	Included in <i>Eragrostis australasica</i>

The comparison did reveal a previously unknown community in N.S.W. *Acacia calcicola* forms extensive communities in Queensland and reaches the New South Wales border at 141°45'E and 142°00'E, but was not mapped in New South Wales by Pickard. On rechecking field books, Pickard found the stands had been recognised but because of their limited area, they were regarded as within the range of the *Acacia aneura* community which was mapped here.

Several communities in New South Wales do not cross into the Queensland test area: *Eucalyptus terminalis*, *Acacia excelsa*, *Eucalyptus populnea*, *Casuarina cristata*-*Heterodendrum oleifolium*. All but the last occur in Queensland but further east.

Queensland/South Australia

The great disparity in unit size is clearly indicated by reference to original maps. Obviously most of the Queensland boundaries will not have matches. There were two mismatches ($> 1 \text{ km} < 5 \text{ km}$) but no perfect matches or bad mismatches. One of the South Australian boundaries remains irreconcilable although close inspection reveals that a change in interpretation of the boundary of the Cooper Creek floodplain would remove the problem. The three irreconcilable boundaries in Queensland could be treated similarly. The large number (18, or 79 per cent) of Queensland boundaries which can be absorbed into South Australian units is due to the very broad definition of the latter.

New South Wales/South Australia

The results here are similar to the Queensland/South Australia comparison i.e. large discrepancy in number (27 v. 2) but 89 per cent capable of absorption in South Australia.

There are two irreconcilable boundaries in New South Wales (one in South Australia) in the Mundi Mundi Plain area (lat. 31°35'S). The broad regions in South Australia apparently do not always follow vegetation boundaries.

The fair agreement ($> 1 \text{ km} < 5 \text{ km}$) of the sand dune/sand plain boundaries on both sides of the border, is a consequence of the methods used. In New South Wales, Pickard separated the two (i.e. *Acacia aneura*-*Acacia ligulata* v. *Acacia aneura*) on a line surrounding most of the dunes on the topographic map base. This is a tacit acceptance of the land system concept and the agreement across the border is to be expected.

DISCUSSION

The results show quite clearly that the methods form a gradient in several respects:

	S.A.	N.S.W.	Qld
Accuracy	↔	increasing	↔
Time/cost	↔	increasing	↔
No. of units	↔	increasing	↔
Usefulness in arid areas	↔	decreasing	↔
Usefulness in humid areas	↔	very sharply decreasing	↔

All the maps achieve their stated aims although their usefulness as vegetation maps in the field varies. No users have submitted adverse reports on any of the maps in the test area. This is a poor test of merit and probably reflects the communicative inertia of most users. The results here support the conclusion of Laut *et al.* (1977b) 'that structural formations of vegetation cannot be identified on black and white prints of LANDSAT imagery by visual interpretation without extensive ground truthing'. We have both made many field traverses to verify our mapping and this, together with the higher resolution of our methods, accounts for greater accuracy. Graetz *et al.* (1976) reached similar conclusions on LANDSAT on the Mundi Mundi Plain. In a comparison of a traditional CSIRO land systems map and LANDSAT, Story *et al.* (1976) found that the 'imagery could play a worthwhile part in surveys of arid regions at approximately 1:1 000 000 scale ...'. However, they warned that comprehensive field sampling is necessary. The value of the methods will alter drastically towards the eastern or southern coasts of Australia. The increasingly complex topography, geology and climate will very quickly eliminate both Pickard's and Laut's methods for any but the most preliminary surveys.

Standardisation

Our results raise practical questions about standardising surveys. As pointed out by Beard and Webb (1974) 'for practical reasons there is a need for some consistent and logical system of classification, some consistent terminology and a mapping notation'. We agree with the further comments of Beard and Webb that it would be unwise to adopt a rigid classification and terminology in advance. It would be better to consider this towards the end of the survey and to adopt in the meantime a flexible system.

When all the 1:1 000 000 maps have been published they might be incorporated into a second edition. One team from one institution can resolve discrepancies between the original mappers as indicated here. We have both attempted in our respective maps to use a consistent terminology, notation, etc. which is a minor variant of the overall Australian standard. Even so, we are unable to reconcile all the differences because some are due to differences in ecologists rather than in methods. An example is Boyland's concept of *Acacia aneura* and *Acacia aneura/Atalaya hemiglaucha* versus Pickard's concept of *Acacia aneura*, *Acacia aneura-Acacia tetragonophylla* and *Acacia aneura-Acacia ligulata*.

Story *et al.* (1976) summarise this problem when they say 'since the process is highly subjective, identical mapping would be very unlikely if two teams surveyed the same area independently. The [CSIRO Land Research Series] survey reports do not stress this point and some indeed tacitly present the land systems as distinct and definite units by stating that they were *recognized* during the interpretation, when in fact they were erected'.

Clearly the problem is one of subjectivity. In principle, objective methods with clearly defined and unambiguous rules for class definition should provide more agreement between adjoining surveys. However, the methods available are still in a state of flux and there is no agreement on methodology. Results of various objective studies over very large areas indicate that further investigation is warranted (Noy-Meir 1971; Boyland 1974; Laut *et al.* 1975).

Regardless of the system adopted—objective or subjective—site data must be collected. Ideally, as advocated by Walker *et al.* (1973), these data should be collected in a standardised format but again, agreement on one standard is virtually unattainable. However, standardisation is a secondary issue provided data are compatible for verification of mapping, checking of units and comparison between surveys.

REFERENCES

- Adomeit, E. M., Jupp, D. L. B., Margules, C., and Mayo, K. K. (this volume). The separation of traditionally mapped land cover classes by LANDSAT data.
- Beard, J. S. (1974). Great Victoria Desert. *Vegetation Survey of Western Australia. 1:1 000 000 Vegetation Series*. University of Western Australia Press, Nedlands, W.A.
- Beard, J. S. (1975a). Nullarbor. *Vegetation Survey of Western Australia. 1:1 000 000 Vegetation Series*. University of Western Australia Press, Nedlands, W.A.
- Beard, J. S. (1975b). Pilbara. *Vegetation Survey of Western Australia. 1:1 000 000 Vegetation Series*. University of Western Australia Press, Nedlands, W.A.
- Beard, J. S. (1976). Murchison. *Vegetation Survey of Western Australia. 1:1 000 000 Vegetation Series*. University of Western Australia Press, Nedlands, W.A.
- Beard, J. S., and Webb, M. J. (1974). Great Sandy Desert. *Vegetation Survey of Western Australia. 1:1 000 000 Vegetation Series*. University of Western Australia Press, Nedlands, W.A.
- Beckett, P. H. T. (1968). Method and scale of land resource surveys, in relation to precision and cost. In: *Land Evaluation* (ed. G. A. Stewart), Macmillan, Melbourne. pp. 53-63.
- Boyland, D. E. (1974). 'Vegetation' in Western arid region land use study—Part 1. *Div. Land Util. Tech. Bull.* No. 12. Qld Dep. Prim. Indus.
- Boyland, D. E. (1977). Vegetation map. *Western Arid Region Land Use Study—Part 2*. Govt Printer, Brisbane.
- Christian, C. S., and Stewart, G. A. (1953). General report on survey of Katherine-Darwin region, 1946. CSIRO Land Res. Ser. 1.
- Colwell, R. N. (ed.) (1960). *Manual of Photographic Interpretation*. American Society of Photogrammetry, Washington D.C.
- Dawson, N. M., and Boyland, D. E. (1974). Western Arid Region Land Use Study Part 1. *Div. Land Util. Tech. Bull.* No. 12. Qld Dep. Prim. Indus.
- Dawson, N. M., and Boyland, D. E. (1973). Map of Major Vegetation Groups. *Western Arid Region Land Use Study. Part 1*. Govt Printer, Brisbane.
- Graetz, R. D., Carnegie, D. M., Jacker, R., Lendon, C., and Wilcox, D. G. (1976). A qualitative evaluation of LANDSAT imagery of Australian rangelands. *Aust. Rangeland J.* 1, 52-9.

96 *Attributes and their Selection*

- Grant, K. (1968). A terrain evaluation system for engineering. *CSIRO Division of Soil Mechanics. Technical Paper No. 2.* CSIRO Melbourne.
- Grant, K. (1975). The PUCE Programme for terrain evaluation for engineering purposes. 7. Principle. *CSIRO Div. Applied Geomechanics Technical Paper 15.*
- Laut, P. (1978). Supplementary maps for 'Environment of South Australia'. *CSIRO Division of Land Use Research Technical Memorandum 78/8.*
- Laut, P., Heyligers, P. C., Keig, G., Löffler, E., Margules, C., Scott, R. M., and Sullivan, M. E. (1977a). *Final Report of a Feasibility Study for an Ecological Survey of Australia.* CSIRO Aust. Division of Land Use Research, Canberra.
- Laut, P., Heyligers, P. C., Keig, G., Löffler, E., Margules, C., Scott, R. M., and Sullivan, M. E. (1977b). *Environments of South Australia, Provinces 1-8.* CSIRO Aust. Division of Land Use Research, Canberra.
- Laut, P., Margules, C., and Nix, H. A. (1975). *Australian Biophysical Regions.* Dept Urban and Regional Development, Aust. Govt Publ. Services, Canberra.
- Mitchell, C. W. (1973). *Terrain Evaluation.* pp. 221. Longman, London.
- Noy-Meir, I. (1971). Multivariate analysis of the semi-arid vegetation in south-eastern Australia: nodal ordination by component analysis. *Proc. Ecol. Soc. Aust.* **6**: 159-93.
- Story, R., Yapp, G. A., and Dunn, A. T. (1976). Landsat patterns considered in relation to Australian resources surveys. *Remote Sensing of Environment* **4**: 281-303.
- Walker, J., Ross, D. R., and Beeston, G. R. (1973). The collection and retrieval of plant ecological data. *CSIRO Woodland Ecol. Unit Pub. 1.* Division of Land Use Research, Canberra.

Classification in relation to vegetation mapping

J. S. BEARD

INTRODUCTION

It is no coincidence that the great names in Australian vegetation classification have been mappers, notably Beadle and Costin (1952), Williams (1955), Perry (1956, 1960). This is because it is more meaningful to arrange the vegetation units which are mapped, and relate them to one another, in some logical system. It is possible to map an array of unrelated units and this has been done, e.g. Acocks (1951) in South Africa, but the result is less than satisfactory. A mapper can normally be expected to be interested in classification in both its theoretical and practical aspects because it is a useful tool, a means to an end; the end here being a fuller and more comprehensive understanding of our Australian plant cover. On the other hand there are also non-mappers who are interested in classification and while we must not underestimate the contribution of such people we must be wary of the pitfalls. The mapper starts off with a series of actual known vegetation units and classifies them. The non-mapper too frequently—especially in these days of increasing isolation of urban academics from the real world of nature—tends to treat classification as a mental exercise and to dream up a system into which vegetation units may theoretically fit. The world scene is dominated by such systems, classically those of Rübel (1930) and Schimper and von Faber (1935), more recently Fosberg (1961), Ellenberg and Mueller-Dombois (1967) and Schmithüsen (1968). It is very tempting to do this, and I have myself perhaps been addicted to it in the past, when I produced a physiognomic classification for the plant formations of tropical America (Beard 1944, 1955). Being a mapper, however, I can at least claim that it was framed on the basis of accurately known factual data, which was recognised by Cain and Oliveira (1959) in their *Manual of Vegetation Analysis* who wrote ‘it seems to us that Beard’s classification of tropical American climax vegetation has the great virtue of not slavishly following a preconceived hierarchy. It is an attempt to deal with the actualities of the vegetation on a tripartite basis’.

It is because of this attitude that when the Vegetation Survey of Western Australia was started by Martyn Webb and myself in 1964 we argued as follows (Beard 1969, p. 254; Beard and Webb 1974, p. 9):

For practical reasons there will be a need for some consistent and logical system of classification, some consistent terminology and a mapping notation, for use in the description of vegetation and in the cartography. On the other hand it is not possible to predict accurately in advance of the survey what vegetation units are going to be found and how they need to be treated. In a general way, of course the vegetation types of Western Australia are known, but it would be unwise to adopt a rigid classification and terminology in advance. It would be better to consider this towards the end of the survey and to adopt in the meantime a flexible system.

It would have been tempting to propose at the outset a classificatory system expressed in a two-way table such as Specht's 'Structural Forms of Vegetation in Australia' (Specht 1970). Instead we adopted a Descriptive System. An entirely different line of development in the physiognomic treatment of vegetation had been opened by Küchler (1947). Classification in its usual sense (here involving grouping entities around abstract type concepts) was rejected. Küchler proposed instead a system of descriptive notation using four series of symbols—predominant growth-form, height, density and special features—which can be combined so as to show the important features of plant cover. This represented essentially a geographer's approach to the characterisation of plant cover for mapping purposes and is most useful for over-all description of regional vegetation rather than for detailed work on plant communities. Küchler has applied this system, amplified in 1949, in vegetation mapping. The simplicity of the system has commended itself to later workers, and despite criticisms which can be levelled at it, Ross Cochrane (1963) has shown that it could be adapted for use in Australia. In point of fact, as Dansereau has shown (1951), Küchler's system, for all its practical value to a geographer, is open to considerable criticism by ecologists. Major divisions in the system are of unequal significance and tend to ignore features not found in the North Temperate Zone. Dansereau set out to reform the system, making it more logical and comprehensive and appropriate to the needs of descriptive ecologists. He did so successfully but in the process transformed it from its original role as a mapping notation into an elegant ecological characterisation which is too elaborate for use in mapping.

It was decided to develop a simpler descriptive notation based on Küchler and Dansereau, shown in Table 10.1. Each vegetation unit as it comes up is allotted a capital letter and two small letters, written as a triplet with the floristic category first

TABLE 10.1
Descriptive notation based on Küchler (1949) and Dansereau (1951)

(1) <i>Physiognomy of dominant stratum</i> (capital letters)	
T Tall trees > 25 m tall	G Bunch grasses
M Medium trees 10—25 m tall	H Hummock grass (spinifex)
L Low trees < 10 m tall	F Forbs
S Shrubs > 1 m tall	X Lichens and mosses
Z Dwarf shrubs < 1 m tall	C Succulents
(2) <i>Floristic</i> (small letters)	
e <i>Eucalyptus</i>	
a <i>Acacia</i>	
t <i>Triodia</i>	
x Heterogeneous (mixed or other)	
(3) <i>Density</i> (small letter)	
d Dense canopy. Projective foliage cover > 70%	
c Mid-dense canopy. Projective foliage cover 30-70%	
i Incomplete canopy—open, not touching. Projective foliage cover 10-30%	
r Rare but conspicuous. Projective foliage cover < 10%	
h Barren, vegetation largely absent. Projective foliage cover negligible	
p Scattered groups. No definite foliage cover	

then the capital and finally the small letter for density. These triplets are printed on the map and have come to be known as Beard-Webb formulae. The concept of projective foliage cover has been brought in from Specht (1970) as it is a valuable means of quantification of density. The height-life form classes (Physiognomy) are very similar to Specht's except for our use of the letter C for chenopodiaceous succulent and semi-succulent shrubs, which we consider desirable to separate in mapping from sclerophyll shrublands.

With the approach to completion of the Vegetation Survey of Western Australia it has become possible to compile a two-way table to embrace the mapped units (Table 10.2).

In the course of the many years' work on this vegetation survey numerous problems have been encountered and many interesting things have come to light. One of these, in relation to classification, is the important part played by scale. For the mapping of a given area, the larger the scale the larger the map and vice versa. Alternatively, with a given size of map, the larger the scale the smaller the area the map portrays, and vice versa. A vegetation map of the largest possible conceivable scale would be a diagram of a quadrat on which all the individual plants and their coverage were marked. Such a map inevitably represents a relatively tiny area. For the mapping of more extensive areas, the scale has to be reduced. It then becomes impossible to represent individual plants, and they have to be grouped into communities whose boundaries are mapped. At progressively smaller scales fewer communities can be represented and there has to be progressive generalisation of the map.

It therefore follows that for the vegetation mapper there can be no absolute concept of the plant community. The concept is dictated by the scale he is using and the ability to represent units on the map. To give concrete examples, the vegetation maps of Lord Howe Island (Pickard 1974) which covers 13 km², of Tasmania (Jackson 1965) covering 42 450 km², and of the Murchison Region of Western Australia (Beard 1976) about 385 000 km², represent units of quite a different order from one another, because of the progressive generalisation which is obligatory with increasing scale.

It follows also that there can never be any absolute standard for an inventory of plant communities of Australia since the number of communities is dependent upon the scale at which they are being considered. To my mind it is meaningless to attempt to draft a list of plant communities of Australia and to inquire whether they are adequately represented in conservation reserves unless this is accompanied by stringent specifications of scale and scope, and that is hardly possible in the present state of our knowledge of Australian vegetation.

To give another practical example, in 1967 I published a paper on an intensive study of an area of approximately 585 ha in the Western Australian mallee near Ravensthorpe. Using an aerial photograph specially enlarged to a scale of 1:16 000 seven plant communities could be recognised by their photo-patterns and were mapped at this scale. When the local map sheet at 1:250 000 came to be published (Beard 1972) the seven communities could no longer be separately represented and they were shown as a single unit described as 'mosaic of mallee and mallee-heath'. As the area covered by this

TABLE 10.2
Nomenclature of vegetation units as used in the vegetation survey of Western Australia
I. Communities with a single significant layer

Life form/height class	Canopy			Cover		
	Dense 70–100%	Mid-dense 30–70%	Incomplete 10–30%	i	Sparse <10%	b negligible
T Tall trees	>30 m	Dense Tall Forest	Tall Forest	Tall Woodland	Open Tall Woodland	
M Medium trees	10–30 m	Dense Forest	Forest	Woodland	Open Woodland	
L Low trees	<10 m	Dense Low Forest	Low Forest	Low Woodland	Open Low Woodland	
S Shrubs	>1 m	Dense Thicket	Thicket	Scrub	Sparse Scrub	
Z Dwarf shrubs	<1 m	Dense Heath	Heath	Dwarf Scrub	Sparse Dwarf Scrub	
G Bunch grasses		Dense Grassland	Mid-dense Grassland	Open Grassland	Sparse Grassland	
H Hummock grasses			Grassland	Open Hummock Grassland	Sparse Hummock Grassland	
F Forbs		Dense Herbfield	Mid-dense Herbfield	Grassland	Sparse Herbfield	
X Lichens and mosses			Herbfield	Open Herbfeld	Sparse Mat Plants	
C Succulents			Mat Plants	Open Mat Plants	Succulent Steppe	Succulent Steppe

2. Communities with more than one significant layer						
Description	Cover of tree/shrub layer			Cover		
	Incomplete 10–30%	i	Sparse <10%	r	Very sparse Negligible	b Absent
Wooded Bunch Grassland	Savanna Woodland	Tree Savanna	Tree Savanna	Sparse Tree Savanna	Grass Savanna	
Wooded Hummock Grassland	Steppe Woodland	Shrub Savanna	Shrub Savanna	Sparse Shrub Savanna	Grass Steppe	
Wooded Succulent Steppe	Thickly Wooded	Tree Steppe	Tree Steppe	Sparse Tree Steppe	Succulent Steppe	
	Succulent Steppe	Shrub Steppe	Shrub Steppe	Sparingly Wooded		
Heath with Trees		Lightly Wooded	Lightly Wooded	Succulent Steppe		
Heath with Shrubs		Succulent Steppe	Succulent Steppe	Tree Heath		
Heath with Mallee		Scrub Heath	Scrub Heath	Scrub Heath		
		Mallee Heath	Mallee Heath	Mallee Heath		

mosaic is relatively large, extending over a distance of 120 km, it can also be represented in this way at the 1:1 000 000 scale but has had to be amalgamated under the general title of mallee-heath at 1:10 000 000 (Beard, 1979).

Mapping in Western Australia has been proceeding at the 1:250 000 and 1:1 000 000 scales. The Beard-Webb formulae and the nomenclature in Table 10.2 were devised to suit these scales. They are not necessarily applicable at other scales. Carnahan's (1976) map of Australia at 1:6 000 000 employed a modification of the Beard-Webb approach, essentially a simplification to suit his smaller scale. At the opposite extreme for physiognomic vegetation studies at a very large scale, Muir (1976, 1977a,b, 1978) has intensified our classification, expanding it with several new Life Form/Height classes for a more intensive definition of stratification. Thus Low Trees have been divided into two, LA 5 to 15 m tall and LB < 5 m; a class for the mallee life-form has been introduced and given the letter K, divided into both tree and shrub forms; shrubs are divided into five height classes, bunch grasses into two, while additional classes have been introduced for mat plants (M), herbaceous species (J), sedges (V) and cryptogams (X). This serves to emphasise the point that scale dictates procedure.

I myself have found it necessary to modify my own approach to classification in the course of the survey to suit requirements of particular situations, which it was quite possible to do as we had avoided any preconceived rigid system at the outset. Last year the 1:1 000 000 map sheet was prepared covering the Kimberley District, the northern-most portion of Western Australia, and I encountered for the first time some special problems in the mapping of wooded tropical grasslands. These had already been well documented in CSIRO Land Research work in the Kimberley District and the Northern Territory but any mapping had been on a Land System basis. These communities have two significant layers, a tree layer and a predominantly grassy ground layer. Both layers vary physiognomically and floristically and do so independently of one another. Mapping should therefore endeavour to represent both layers. As the grass layer was considered to be dominant it was the basic element in the classification and is to be represented by the map colour. The tree layer as a secondary element is to be represented by an overprinted symbol for trees varying in size and density. The Beard-Webb formula is readily accommodated to a two-layered community by writing a triplet for each layer separated by a full stop, e.g. e₃¹Mi.cGc. In the Kimberley District there are both bunch grasslands and hummock grasslands, and in addition an intermediate type known to the pastoralists as 'curly spinifex', formed by *Plectrachne pungens*, a perennial coarse wiry grass belonging to a genus in which many species but not all are hummock grasses, and which itself may adopt a hummock grass form under adverse conditions but does not normally do so. It was considered desirable to map curly spinifex grasslands separately. Furthermore it was desirable to divide the bunch grasslands into three types, so that the full classification became as follows:

- Grassland 1. *Savanna* (i) Grass layer closed and of bunch-grass form.
 - a. *High-grass Savanna*. Grasses > 100 cm tall, drought-evading.
 - b. *Tall bunch-grass Savanna*. Grasses 50-100 cm tall, drought-evading.

- c. *Short bunch-grass Savanna.* Grasses <50 cm tall, annuals or short-lived perennials.
 - Savanna* (ii) Grass layer closed and of 'curly spinifex' form.
 - d. *Curly spinifex communities.* Grasses 50-100 cm tall, perennial, drought-resisting.
- Grassland 2. *Steppe* Grass layer open and of hummock-grass form. Grasses perennial, evergreen.

This treatment follows Beard's (1966) discussion of the subject and is closely similar to Perry's in Stewart *et al.* (1970). Table 10·3 combines the variation of the tree and grass layers.

In the Beard-Webb system savanna is represented by the letter G and the colour olive, while steppe is represented by the letter H and the colour red. In working on the Kimberley map it was found necessary as in Muir's work to intensify the classification in the case of the savannas. It was easy enough to create four different shades of olive, but the mapping notation required four different forms of the letter G, which was solved as follows:

- G** High-grass savanna
- G** Tall bunch-grass savanna
- g** Short bunch-grass savanna
- G** Curly spinifex.

My point therefore is that classification should be flexible and adaptable, and devised not as an abstract exercise but to suit a particular set of vegetation units which one is mapping or describing.

Hitherto I have spoken entirely about physiognomic forms of classification and this was not because I feel there are no others worth discussing, merely because classification must be suited to scale. I have been dealing with mapping mainly at 1:250 000 and 1:1 000 000 scales, and for Australia at these scales and in the present state of our knowledge, the physiognomic approach appears the most rewarding. Floristic approaches including mathematical ordination techniques may be very valuable especially for intensive study of relatively small areas and can be employed in mapping provided the floristic communities have recognisable photo-patterns. As I have been using Western Australian examples through this chapter I will allude to the work of Havel (1968, 1975) which was undertaken with the object of determining plant associations in a forest and woodland understorey, first on the Swan Coastal Plain and later in the jarrah forest of the Darling Range, and the value of these associations for predicting site quality for forestry purposes. On the Swan Coastal Plain no plant communities associated with particular sites were readily apparent to the observer within a matrix of Banksia low woodlands. Principal component analysis was employed as a basis for ordination and association analysis as a basis for classification after recording of 67 'pilot plots'. Continuous variation in both soil and vegetation was observed but 11 types or noda were recognised as indicated by the presence of certain species. These ground vegetation types were found to be mappable by photo-patterns, and maps of four sample

TABLE 10.3
Classification of tropical grassland communities

Tree and shrub layer	Bunch grasslands	Curly spinifex*	Hummock grassland
High > 100 cm Drought-evasive	Tall, 50–100 cm Drought-evasive	Short < 50 cm Annual or short-lived perennial	50–100 cm Drought-resisting
Trees and shrubs forming a canopy, which is generally light	Tall bunch-grass savanna woodland	Short bunch-grass savanna woodland*	Curly spinifex savanna woodland
Trees scattered	Tall bunch-grass tree savanna	Short bunch-grass tree savanna	Curly spinifex tree savanna
Trees very scattered or sparse	Tall bunch-grass sparse tree savanna	Short bunch-grass sparse tree savanna	Curly spinifex sparse tree savanna
Shrubs only	Tall bunch-grass shrub savanna*	Short bunch-grass shrub savanna*	Curly spinifex shrub savanna*
Trees and shrubs absent or virtually so	Tall bunch-grass savanna	Short bunch-grass savanna	Curly spinifex savanna*

* Indicates no actual occurrences found in the Kimberley District.

Note: If trees < 10 m tall, insert the word 'low' appropriately.

areas were published in the paper (Havel 1968) without any indicated scale. The four areas totalled 6014 acres (2434 ha).

In the subsequent study of the Darling Range northern jarrah forest 320 plots were recorded representing a total enumeration of all trees on 51.8 ha and cover assessment of all species of 5120 one-metre square quadrats. The data were analysed mathematically by computer as before and according to the author's summary (Havel 1975):

The feasibility of using plant indicators to define sites in northern jarrah region has been demonstrated. The task has not been without problems, in that the vegetation and the associated environmental factors form a complex continuum which does not lend itself to easy manipulation. It is difficult to delineate any clearly defined groups or types, with the result that typing and mapping of vegetation cannot be reduced to a simple mechanical process. On the positive side, the nature of the continuum ensures that the effect of any misallocation is minimal.

Nineteen continuum segments or 'site-vegetation types' were defined in terms of composition, structure and environmental features but in this case only a few of them could be recognised by photo-patterns. Type A consists of *Melaleuca-Banksia* communities in swampy bottomlands and types M, L and Y of *Eucalyptus wandoo* woodlands. These could be distinguished from the fifteen others all of which are understorey types in forest of *E. marginata-E. calophylla* but these had no distinctive photo-patterns and could not be mapped separately from one another except laboriously by ground survey. Thus when a vegetation map of the northern jarrah forest was required for an environmental survey the best that could be done was to present a map of landforms listing those site-vegetation types which occur within each landform.

In conclusion may I say that I feel that our greatest need today is for more mapping. If we are to have a more thorough understanding of Australian vegetation it must be mapped. I feel it would not be too strong a statement to say that descriptive ecology today does not achieve its full potential unless it involves mapping. Aerial photography has now been available to us for a generation and has brought mapping within easy reach of all. We need mapping programs, working down from initial small-scale overall surveys to more intensive work at larger and larger scales. We have already a good new map of all Australia at 1:6 000 000 (Carnahan 1976) based as far as possible on published sources so as to reduce the uncertain sketch-map component. The western third of the continent has been recently mapped at the 1:1 000 000 scale and nearly all of it has been published (Beard 1974, 1978). We need now to complete mapping of the continent at this scale; this is the first and most urgent priority. I am glad to have been assured that the Australian Biological Resources Study is keenly interested in this objective and that mapping programs are underway in both N.S.W. and Queensland. It is to be hoped that other States will follow suit.

REFERENCES

- Acocks, J. P. H. (1951). *Veld Types of South Africa* (with map 1:1 500 000). Government Printer, Pretoria.
 Beadle, N. C. W., and Costin, A. B. (1952). Ecological classification and nomenclature. *Proc. Linn. Soc. N.S.W.* 77: 61-82.

- Beard, J. S. (1944). Climax vegetation in tropical America. *Ecology* **25**: 127-58.
- Beard, J. S. (1955). The classification of tropical American vegetation types. *Ecology* **36**: 89-100.
- Beard, J. S. (1966). Grassland nomenclature in Australia. *Ecol. Soc. Aust. Broadsheet No. 1*, 17-20.
- Beard, J. S. (1967). A study of patterns in some West Australian heath and mallee communities. *Aust. J. Bot.* **15**: 131-9.
- Beard, J. S. (1969). The vegetation of the Boorabbin and Lake Johnston areas, Western Australia. *Proc. Linn. Soc. N.S.W.* **93**: 239-69.
- Beard, J. S. (1972). *The Vegetation of the Newdegate and Bremer Bay Areas, Western Australia*, pp. 32. Vegmap Publications, Perth.
- Beard, J. S. (1974). *Great Victoria Desert*. Vegetation Survey of Western Australia, 1:1 000 000 series. Explanatory Notes to Sheet 3. University of Western Australia Press, Nedlands, W.A.
- Beard, J. S. (1975a). *Nullarbor*. Vegetation Survey of Western Australia, 1:1 000 000 series. Explanatory Notes to Sheet 4. University of Western Australia Press, Nedlands, W.A.
- Beard, J. S. (1975b). *Pilbara*. Vegetation Survey of Western Australia, 1:1 000 000 series. Explanatory Notes to Sheet 5. University of Western Australia Press, Nedlands, W.A.
- Beard, J. S. (1976). *Murchison*. Vegetation Survey of Western Australia, 1:1 000 000 series. Explanatory Notes to Sheet 6. University of Western Australia Press, Nedlands, W.A.
- Beard, J. S. (1978) *Kimberley*. Vegetation Survey of Western Australia, 1:1 000 000 series. Explanatory Notes to Sheet 1. University of Western Australia Press, Nedlands, W.A.
- Beard, J. S. (1979) Vegetation (map. 1:10 000 000). In *Western Australia 1828-1979, an Atlas of Human Endeavour*, ed. N. Jarvis. Education Dept, W.A., Perth.
- Beard, J. S., and Webb M. J. (1974). *Great Sandy Desert*. Vegetation Survey of Western Australia, 1:1 000 000 series. Explanatory Notes to Sheet 2. University of Western Australia Press, Nedlands, W.A.
- Cain, S. A., and de Oliveira, Castro G. M. (1959). *Manual of Vegetation Analysis*. Harper, New York.
- Carnahan, J. A. (1976). *Natural Vegetation*. Atlas of Australian Resources, 2nd Series. Dept Natural Resources, Canberra.
- Dansereau, P. (1951). Description and recording of vegetation upon a structural basis. *Ecology* **32**: 172-229.
- Ellenberg, H., and Mueller-Dombois, D. (1967). *Ber. geobot. Inst. ETH*, Stiftung Rübel, Zurich.
- Fosberg, F. R. (1961). A classification of vegetation for general purposes. *Trop. Ecol.* **2**: 1-28. Also in 'Guide to the check sheet for ecological IBP areas' by G. F. Peterkin, *IBP Handbook 4*: 73-120. Blackwell, Oxford and Edinburgh.
- Havel, J. J. (1968). The potential of the northern Swan Coastal Plain for *Pinus pinaster* plantations. *Forests Dept Bull.* **76**. Perth.
- Havel, J. J. (1975). Site-vegetation mapping in the northern Jarrah forest (Darling Range). I. Definition of site-vegetation types. *Forests Dept Bull.* **86**. Perth.
- Jackson, W. D. (1965). Vegetation. In *Atlas of Tasmania* (ed. J. L. Davies). Lands and Surveys Dept, Hobart.
- Küchler, A. W. (1947). A geographic system of vegetation. *Geogrl Rev. N.Y.* **37**: 233-40.
- Küchler, A. W. (1949). A physiognomic classification of vegetation. *Ann. Ass. Am. Geogr.* **39**: 201-10.
- Muir, B. G. (1976). Biological Survey of the Western Australian Wheatbelt. Part 1. Tarin Rock and North Tarin Rock Reserves. *Rec. W. Aust. Mus. Suppl.* No. 2.
- Muir, B. G. (1977a). Biological Survey of the Western Australian Wheatbelt. Part 2. Vegetation and habitat of Brenderup Reserve, *Rec. W. Aust. Mus. Suppl.* No. 3.
- Muir, B. G. (1977b). Biological Survey of the Western Australian Wheatbelt. Part 4. Vegetation—West Brenderup Reserve, *Rec. W. Aust. Mus. Suppl.* No. 5.
- Muir, B. G. (1978). Biological Survey of the Western Australian Wheatbelt. Part 5. Dongolocking Nature Reserve, *Rec. W. Aust. Mus. Suppl.* No. 6.

106 *Attributes and their Selection*

- Perry, R. A. (1956). The plant ecology of the Ord-Victoria area, north-western Australia. M.Sc. Thesis, University of Adelaide.
- Perry, R. A. (1960). Pasture lands of the Northern Territory, Australia. *CSIRO Aust. Land Res. Ser. No. 5.*
- Pickard, J. (1974). Vegetation map and notes. In *Environmental Survey of Lord Howe Island* (ed. H. F. Recher and S. S. Clark) Aust. Museum, Sydney.
- Ross Cochrane, G. (1963). A physiognomic vegetation map of Australia. *J. Ecol.* **51**: 639-56.
- Rübel, E. (1930). *Pflanzengesellschaften der Erde*. Huber, Bern and Berlin.
- Schimper, A. F.W., and von Fabér F. C. (1935). *Pflanzengeographie auf physiologischer Grundlage*, 3rd ed. Fischer, Jena, 2 vols.
- Schmithüsen, J. (1968). *Allgemeine Vegetationsgeographie*, 3rd ed. de Gruyter, Berlin.
- Specht, R. L. (1970). Vegetation. In *The Australian Environment* (ed. G. W. Leeper). CSIRO and Melbourne University Press.
- Stewart, G. A., Perry, R. A., Paterson, S. J., Traves, D. M., Slatyer, R. O., Dunn, P. R., Jones, P. J., and Sleeman, J. R. (1970). Lands of the Ord-Victoria area, W.A. and N.T. *CSIRO Aust. Land Res. Ser. No. 28.*
- Williams, R. F. (1955). Vegetation Regions. *Atlas of Aust. Resources*. Dept Nat. Development, Canberra.

11

Mapping at a continental level

J. A. CARNAHAN

INTRODUCTION

I have selected as my examples of mapping at a continental level the vegetation maps of the Soviet Union by Sochava and Lukicheva (1964); of the conterminous United States by Küchler (1964); and of Australia by Carnahan (1976). The compilers of these maps had the advantage of being able to cover very large areas while still working within national boundaries. Each map portrays natural vegetation, either actual, reconstructed, or potential. The maps are also comparable in that each shows the distribution of slightly more than 100 vegetation types.

The earlier map of the vegetation of the Soviet Union by Lavrenko and Sochava (1954) would have provided a better comparison in terms of scale. However, the selected map is more widely accessible, and also reflects a new approach to classification by Sochava (1964). The legend of the map by Sochava and Lukicheva (1964), and the explanatory text, have been published in English (American Geographical Society 1965).

The map by Küchler (1964) was reprinted with very slight modifications as a 'second edition' in 1975. However, the accompanying manual has not been reprinted. The map and text have also been published in a condensed form (Küchler 1970).

In each case, I have considered how the mapped vegetation types are defined, and how these defined types are classified. The three examples are arranged in the order of increasing emphasis on classification.

UNITED STATES

Küchler (1964) defined each of his mapped vegetation types in terms of its physiognomy and of its floristic characters, including both dominants and other components. However, the legend of the map is limited to a nomenclature of convenience, and it is necessary to refer to the manual to understand more clearly how each type is defined. This can be demonstrated by a few examples.

65. Grama-buffalo grass (*Bouteloua-Buchloë*).

Physiognomy: Fairly dense grassland of short grass with somewhat taller grasses in the eastern sections.

Dominants: *Bouteloua gracilis*, *Buchloë dactyloides*.

69. Bluestem-grama prairie. (*Andropogon-Bouteloua*).

Physiognomy: Dense, medium tall grassland with many forbs.

Dominants: *Andropogon scoparius*, *Bouteloua curtipendula*, *B. gracilis*.

81. Oak savanna (*Quercus-Andropogon*).

Physiognomy: Tall grass prairie with broadleaf deciduous trees scattered singly or in groves.

Dominants: *Andropogon gerardii*, *A. scoparius*, *Quercus macrocarpa*.

84. Cross timbers (*Quercus-Andropogon*).

Physiognomy: Medium tall grass with broadleaf deciduous trees scattered singly or in extensive groves.

Dominants: *Andropogon scoparius*, *Quercus marilandica*, *Q. stellata*.

100. Oak-hickory forest (*Quercus-Carya*).

Physiognomy: Medium tall to tall broadleaf deciduous forests.

Dominants: *Carya cordiformis*, *C. ovata*, *Quercus alba*, *Q. rubra*, *Q. velutina*.

106. Northern hardwoods (*Acer-Betula-Fagus-Tsuga*).

Physiognomy: Tall broadleaf deciduous forest with an admixture of needleleaf evergreen trees.

Dominants: *Acer saccharum*, *Betula allegheniensis*, *Fagus grandifolia*, *Tsuga canadensis*.

In the legend, the vegetation types are grouped into broad categories. Thus, types 65 and 69 are listed under 'Grasslands' and types 81 and 84 under 'Grassland and Forest combinations', within the broader heading of 'Central and Eastern Grasslands'. Type 100 is listed under 'Broadleaf Forests' and type 106 under 'Broadleaf and Needleleaf Forests', within the broader heading of 'Eastern Forests'. However, Kückler clearly specified in the manual that these groupings are for convenient reference only. He emphasised that his vegetation types are characterised solely by life forms and taxa, and that they are not meant to be units of some hierachic classification. This approach, called 'classless' by Kückler, is reflected in the individualistic characterisation and nomenclature of his vegetation types.

At the same time, some of Kückler's names for types do include terms suggesting some sort of classification, as do the descriptions of the physiognomy of some types. Further, he did allow that his groups in the legend might serve as the nuclei for a classification, even though he intended them only for convenient reference.

AUSTRALIA

Carnahan (1976) defined each of his mapped vegetation types according to a structural-floristic system. This incorporates features of the systems devised by Specht and his associates for their survey of Australian plant communities (Specht 1970; Specht, Roe and Boughton 1974) and by Beard and Webb for their vegetation survey of Western Australia (Beard 1969; Beard and Webb 1974). The system defines each vegetation type in terms of three characters of the tallest stratum, namely typical genus or family, growth form, and projective foliage cover, together with the growth form of the most significant lower stratum. If the foliage cover of the tallest stratum is less than 10 per cent, the definition also includes the typical genus or family of the most significant lower stratum.

Only these characters are shown in the legend of the map. The classification is developed in the commentary. The principal structural forms are defined in terms of the growth form and the foliage cover of the tallest stratum, according to the nomenclature of Specht (1970). These structural forms are divided into subforms according to the growth form of the most significant lower stratum, and the vegetation types are finally separated out on floristic characters.

For example, vegetation with a tallest stratum of medium trees (10-30 m), having foliage cover in the range 30-70 per cent, is classed as 'open-forest'. Forests of this form with a lower stratum of low shrubs (under 2 m) are classed as 'open-forest with low shrubs'. Finally, such a subform dominated by species of *Eucalyptus* is classed as '*Eucalyptus* open-forest with low shrubs'. This is the type that is coded as eM3Z on the map.

Again, vegetation with a tallest stratum of low trees (under 10 m), having foliage cover in the range 10-30 per cent, is classed as 'low woodland'. One subform of this structural form is 'low woodland with tussock grasses'. One type of this subform is '*Melaleuca* low woodland with tussock grasses'. This is the type that is coded as mL2G on the map.

As a further example, vegetation with a tallest stratum of low trees, having foliage cover less than 10 per cent, is classed as 'low open-woodland'. One subform of this structural form is 'low open-woodland with low shrubs'. Finally, such a subform, with the tallest stratum dominated by species of *Acacia* and the lower stratum by members of the Chenopodiaceae, is classed as '*Acacia* low open-woodland with chenopodiaceous low shrubs'. This is the type that is coded as wL1kZ on the map.

This system was not intended to be consistent with any proposed universal system. It reflects the apparent need to use an indigenous scheme of classification to accommodate the distinctive vegetation of Australia.

SOVIET UNION

The basic mapping units of Sochava and Lukicheva (1964) represent formations or groups of formations. These are not formations in the traditional Western sense. The concept is nearer to that of the association.

However, these formations are not defined simply in terms of floristic composition and community structure. Ecology and geography are also taken into consideration, especially where a species is dominant over an extensive and heterogeneous territory (Gribova and Isachenko 1972). Thus, among the larch forests and sparse forests of *Larix dahurica* (*L. gmelini*), Sochava distinguished as a special formation the northern taiga larch sparse forests. (These correspond to legend item 32 of the map.) On the other hand, he treated the oak forests of *Quercus mongolica* as a single formation (corresponding to legend item 66), since these have a clear ecological and geographical area.

Some of the mapping units of necessity involve a complex of intrinsic and environmental characters. An example is the distinctive forest-steppe of central European Russia. This is legend item 69: Meadow steppes (*Stipa joannis*, *S. stenophylla*, *Festuca sulcata*, *Bromus riparius* and meadow-steppe forbs) and steppified meadows—forest-

steppe with oak forests (specific names are given as in the legend). This corresponds to the kind of vegetation described by Lavrenko and Sochava (1954) as 'European meso-xerophytic steppes and xeromesophytic meadows, combined with *Quercus robur* forests (forest-steppe)'.

The classification used by Sochava and Lukicheva is consistent with the classification of world vegetation developed by Sochava (1964). This universal classification reflects a concept of the vegetative cover of the world as a hierarchy of dynamic systems. There is considerable emphasis on historical relationships. It is evident, for example, that historical factors could be relevant in the classification of such a unit as the European forest-steppe. In the broader sense, all existing vegetation is seen as the present expression of an ongoing evolutionary process.

The formations or groups of formations are combined into phratries of formations. The significance of these for mapping has been discussed also by Gribova and Isachenko (1972). Phratries of formations are regional-typological units, established on the basis both of structural-floristic and of ecological-geographical relationships. The nomenclature reflects the geographical relationship. Thus legend item 32 is a component of the Angaride phratry, which occupies a large part of eastern Siberia, and embraces a wide range of communities, mostly dominated or co-dominated by *Larix dahurica*. Legend item 66 is a component of the Manchurian phratry, which consists of a range of forests, mostly dominated or co-dominated by species of *Quercus*. Item 69 is a component of the Black Sea phratry, which consists of a range of steppe communities with considerable floristic overlap among the grassy elements.

In the dynamic context, the widespread development of the Angaride phratry is related to the extension of the dominance of *Larix dahurica* during the general deterioration of the climate in the late Pleistocene. On the other hand, the forests of the Manchurian phratry are little changed derivatives of Pliocene forests (Belov and Lavrenko 1977).

Phratries of formations are combined into types of vegetation. (I use the literal translation to emphasise that these are quite different from the basic mapping units that were called 'vegetation types' by Kühler and Carnahan.) These categories are again established on the basis of a complex of criteria, and this is perhaps reflected in the rather eclectic nomenclature. For example, the Angaride phratry is a component of the Boreal type of vegetation; the Manchurian phratry, of the Nemoral type of vegetation; and the Black Sea phratry, of the Steppe type of vegetation.

The largest category in the world classification is the system of types of vegetation. The delimitation of these categories is related both to floristic regions and to geographical zones. All the types of vegetation in the Soviet Union are components of the Northern Extratropical system.

This treatment differs considerably from that of Lavrenko and Sochava (1954). The authors of the earlier map grouped their mapping units in the legend into broad categories such as '*Larix* Forests' and 'Hardwood Forests', against a background of 'zonal vegetation types'.

The idea of classifying vegetation as a complex of dynamic systems is being developed further (Sochava 1972). This continuing activity is reflected in the treatment

of the vegetation of the Soviet Union in the more recent but smaller-scale map by Isachenko and Gribova (1977).

DISCUSSION

I have confined my attention to some classificatory approaches that have actually been used in recent mapping of vegetation at continental scales. They provide some interesting contrasts.

Küchler (1964) and Carnahan (1976) both defined their vegetation types in terms solely of physiognomy and floristics. Any classificatory elements in Küchler's approach are essentially informal. He emphasised that his vegetation types are not meant to be components of a hierarchic classification. Carnahan used an organised classificatory system, in which each vegetation type is defined by characters that assign it to a floristic subdivision of a structural subform of a principal structural form.

The basic mapping units of Sochava and Lukicheva (1964), namely the formations or groups of formations, are not defined solely in terms of physiognomy and floristics, but also take ecology and geography into consideration. In view also of the smaller scale of their map, their units may not be very readily comparable with those of Küchler or Carnahan. Further, these mapping units are components of a complex system of classification, which reflects a concept of the vegetative cover of the world as a hierarchy of dynamic systems.

Küchler (1973) has reviewed many of the problems involved in applying various types of classification to the compilation of maps of vegetation. In particular, he has cited the argument that vegetation is itself a tangible integrated expression of all environmental features. On this basis, some vegetation mappers have argued that vegetation is sufficiently complex to be considered to the exclusion of all other aspects of the ecosystem, at least at small scales, as in his own map (Küchler 1964). However, a Soviet reviewer has criticised Küchler's map on the grounds of insufficient geographical differentiation (Semenova-Tyan-Shanskaya 1967). A similar criticism could probably be levelled at Carnahan's map. For example, *Eucalyptus* woodland with tussock grasses (eM2G) is mapped over a very wide geographical range. It is true that the commentary specifies the regional floristic differences within this type, in terms both of the dominant species of *Eucalyptus* and of the principal grasses; but these differences are not reflected in the map.

In the light of this problem, it is interesting to consider the system proposed by UNESCO (1973) for international use in classifying and mapping vegetation at scales of 1:1 000 000 or smaller. This system is the result of many years of work and discussion by numerous distinguished specialists, including Küchler and Sochava. The compilers adopted a primarily physiognomic approach. Their initial division of vegetation is into five formation classes, namely closed forest, woodland, scrub, dwarf-scrub, and herbaceous vegetation; and the next subdivision, except in the last class, is into mainly evergreen, mainly deciduous, and extremely xeromorphic subclasses. However, they also thought it necessary to use some features of the environment rather than of the vegetation itself, on the grounds that physiognomic characters are not always clearly identifiable with important ecological habitats.

For example, legend item I.A.6c(2), 'Broad-leaved temperate evergreen ombrophilous swamp forest', is the broad-leaved subformation, of the temperate swamp formation, of the temperate and subpolar ombrophilous formation group, of the mainly evergreen subclass, of the closed forest formation class. The example given for this vegetation type is '*Eucalyptus ovata* forests of Victoria'. These forests exhibit some structural variation, but they are represented in particular within the areas of Victoria mapped as eM3Z by Carnahan (1976).

On the whole, the UNESCO system does not appear to be very appropriate for the vegetation of Australia. In particular, it is difficult to map Australian vegetation effectively, even at small scales, without taking account of the distinctive nature of the native flora. As Beard and Webb (1974) have pointed out, a few distinctively Australian genera, notably *Eucalyptus*, *Acacia*, and *Triodia*, dominate and give a characteristic appearance to much of the vegetation.

POSTSCRIPT

I am now compiling a map of the actual present vegetation of Australia, which will provide a sequel to the map of natural vegetation (Carnahan 1976) by reflecting the changes that have been brought about by European settlement. A necessary prerequisite for this work is to give further thought to the most appropriate system of classification for Australian vegetation.

I adhere to the view that the reader of the map will be assisted by an organised classification. It appears to me that the greater part of the present vegetation of Australia can be effectively defined and classified in terms of the system that I used for the map of natural vegetation. It is true that this system has some arbitrary features, which are pointed up in other contributions to this volume. Various elaborations are possible, but it is necessary to strike a balance between precision and practicality; some non-botanical users have expressed appreciation of an approach that they can understand.

However, there are other issues to be considered. One already referred to is the question of some kind of geographical differentiation. This might be achieved, for example, by expanding the floristic component of the map code to the species level, but this would present cartographic difficulties, given the necessarily small scale of a continental map.

Again, the compilation of a small-scale map involves considerable enough problems of generalisation when the object is to represent natural vegetation. The greater complexity of the disturbed vegetation of the present day presents greater problems of generalisation. When the dynamic nature of disturbed vegetation is also taken into account, the question inevitably arises whether such vegetation should be mapped in terms of dynamic complexes.

For example, Sochava (1972) has based a dynamic concept of classification on the 'epiassocation', being the aggregate of all the variable conditions of vegetation related to a particular basic association (the 'maternal nucleus'). Epiassociations are generalised into higher epitaxa, such as epiformations. Belov and Lavrenko (1977), in applying Sochava's dynamic approach to the compilation of a vegetation map at the scale of 1:2 500 000, found it possible to make cartographic distinctions between the major

components of the epitaxa, namely basic communities, regenerating series, stable-derivative communities, and agricultural lands. If such distinctions within the epitaxa could not be portrayed at the smaller scale of a continental map, they would have to be indicated and explained through the elaboration of the legend.

REFERENCES

- American Geographical Society (1965). Physical-geographic Atlas of the World, Moscow, 1964. *Sov. Geogr.* 6: (5-6): 1-403.
- Beard, J. S. (1969). The vegetation of the Boorabbin and Lake Johnston areas, Western Australia. *Proc. Linn. Soc. N.S.W.* 93: 239-69.
- Beard, J. S., and Webb, M. J. (1974). The Vegetation Survey of Western Australia: its aims, objects and methods. *Great Sandy Desert*. Part I of Explanatory Notes to Sheet 2. Vegetation Survey of Western Australia, 1:1 000 000 Vegetation Series. University of Western Australia Press, Nedlands.
- Belov, A. V., and Lavrenko, N. N. (1977). [Problems of geobotanical mapping of the Baikal-Amur railway region]. In: *Geobotanicheskoye Kartografirovaniye 1977*, pp. 3-19. Academy of Sciences of the U.S.S.R., Leningrad.
- Carnahan, J. A. (1976). Natural vegetation. Map (1:6 000 000) and commentary. In: *Atlas of Australian Resources Second Series* (ed. T. W. Plumb). Department of National Resources, Canberra.
- Gribova, S. A., and Isachenko, T. I. (1972). [Vegetation mapping at survey scales]. In: *Polevaya Geobotanika IV*, pp. 137-330. Academy of Sciences of the U.S.S.R., Leningrad.
- Isachenko, T. I., and Gribova, S. A. (1977). [Vegetation (U.S.S.R.)]. Map (1:25 000 000). In: *Bol'shaya Sovetskaya Entsiklopediya* 3rd edn (ed. A. M. Prokhorov), Vol. 24(II), facing p. 57. 'Soviet Encyclopedia', Moscow.
- Küchler, A. W. (1964). *Potential Natural Vegetation of the Conterminous United States*. Map (1:3 168 000) and manual. Special Publication No. 36, American Geographical Society, New York.
- Küchler, A. W. (1970). Potential natural vegetation. Map (1:7 500 000) and text. In: *The National Atlas of the United States of America*, pp. 89-92. United States Geological Survey, Washington.
- Küchler, A. W. (1973). Problems in classifying and mapping vegetation for ecological regionalization. *Ecology* 54: 512-23.
- Lavrenko, E. M., and Sochava, V. B. (1954). *Geobotanicheskaya Karta SSSR*. Map (1:4 000 000). Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad.
- Semenova-Tyan-Shanskaya, A. M. (1967). [On the new vegetation map of the U.S.A. at scale 1:3 168 000]. In: *Geobotanicheskoye Kartografirovaniye 1967*, pp. 72-5. Academy of Sciences of the U.S.S.R., Leningrad.
- Sochava, V. B. (1964). [A new world vegetation map]. In: *Geobotanicheskoye Kartografirovaniye 1964*, pp. 3-16. Academy of Sciences of the U.S.S.R., Moscow-Leningrad.
- Sochava, V. B. (1972). [Classification of vegetation as a hierarchy of dynamic systems]. In: *Geobotanicheskoye Kartografirovaniye 1972*, pp. 3-18. Academy of Sciences of the U.S.S.R., Leningrad.
- Sochava, V. B., and Lukicheva, A. N. (1964). [Vegetation (U.S.S.R.)]. Map (1:15 000 000) and text. In: *Fiziko-geograficheskii Atlas Mira*. (ed. I. P. Gerasimov *et al.*), plates 240-1 and pp. 280-3. Academy of Sciences of the U.S.S.R., Moscow.
- Specht, R. L. (1970). Vegetation. In: *The Australian Environment*. 4th edn (ed. G. W. Leeper), pp. 44-67. CSIRO and Melbourne University Press, Melbourne.
- Specht, R. L., Roe, E. M., and Boughton, V. H. (1974). Conservation of major plant communities in Australia and Papua New Guinea. *Aust. J. Bot.* Supplementary Series No. 7.
- UNESCO (1973). *International Classification and Mapping of Vegetation*. Ecology and Conservation Publication No. 6. UNESCO, Paris.

PART II

METHODOLOGY AND APPLICATION

Underlying assumptions in numerical classification

W. T. WILLIAMS

The title of this volume, and indeed a perusal of ecological literature, suggests that the natural instinct of an ecologist faced with an unwieldy mass of data is to classify it; but it is not always clear that the implications of this decision receive the attention they deserve. Classification is primarily a means of finding a level of information which can be easily summarised and communicated. To say that an area is largely covered by vascular plants provides too little information; to give a detailed account of every plant in the area provides too much. But classification is not the only solution; ordination techniques, such as principal co-ordinate analysis and its more esoteric counterparts, or the computation of a minimum spanning tree, fulfil a similar function, but are less often used. The use of a classificatory strategy is equivalent to postulating that the population under study is discontinuous; and the great majority of existing classificatory computer programs are forced to find or invent discontinuities, even if the data are continuous or even random. It is therefore reasonable to inquire why the assumption of discontinuity is so common.

I believe that there are two main reasons, the first of which is a matter of historical convention. Much of the early work on numerical classification of ecological data was carried out in Europe, and particularly in England. In that country centuries of cultivation have imposed a mosaic structure on the land; moreover its geological history of faulting and folding is such that it is possible in a day's drive to encounter exposures of a high proportion of horizons from the Precambrian to the Recent. In Australia, on the other hand, once one leaves the eastern seaboard, cultivation is minimal or non-existent; and it is possible to drive for a week and never leave the Cretaceous. It may therefore well be, as Goodall (1961) once suggested, that the vegetation might more accurately be assumed to be continuous. However, even if this assumption were correct, there may still be a second, more compelling, reason for resorting to classification: its versatility and computational convenience. If the number of sites is very large, both principal co-ordinate analysis and the minimum spanning tree become intolerably cumbersome or even computationally impracticable; in such cases there is no realistic alternative to using classificatory programs, such as DIVINF or REMUL, which are capable of handling large data-sets.

Problems may be encountered even with small data-sets. The use of P.Co.A. implies that relationships are linear, and the unreality of this assumption in ecology has frequently been pointed out (see, e.g., Austin and Noy-Meir 1971; Austin 1976). Both

non-linearity and discontinuity (which may be regarded as an extreme form of non-linearity) are apt to result in a P.Co.A. in which the proportion of information extracted by the first two vectors is uncomfortably low—often as low as 20 per cent. A number of ‘catenation’ techniques for the ordination of non-linear data have been suggested (Noy-Meir and Whittaker 1977), but are still in an early stage of development. The minimum spanning tree is insensitive to non-linearity and discontinuity, but may not be unique if all inter-site distances are not different. Inter-site distance ambiguities are particularly common with presence-and-absence data; the tree actually obtained is then likely to be a function more of the computational algorithm used than of the structure of the data, and its use in such cases is unwise.

It follows that there will be many occasions when classification, though not the ideal solution, is the only practicable one; and a new problem then arises. A decade ago an ecologist was fortunate if he had access to a single classificatory program; there are now so many that the main problem is that of choice. For an ecologist who uses a computer only rarely, it is tempting to use the program which is nearest to hand, or with which he is most familiar; but this is to abrogate his ecological responsibilities. A classification is never unique, and the choice of a particular classification always implies a particular purpose. Even though numerical classifications are usually regarded as ‘general-purpose’ classifications, there remain three areas in which the user’s prior choice is vital.

The first is the set of attributes recorded. Given a collection of plants, a taxonomist may be primarily interested in details of embryogeny or floral structure; an ecologist in those aspects of morphology or physiology which fit a plant to its environment; an agronomist in dry-matter yield, or in palatability or digestibility for cattle. A classification based on any one such set of attributes may be quite useless for either of the others. The second choice concerns the inter-site distance to be used, and here it is essential for the user, or his numerical adviser, to be familiar with the algorithms actually used by existing programs and with their algebraic properties. He must decide, for example, whether he wishes double-zero matches to count towards likeness or not; whether outlying values are to be exaggerated in importance or largely neglected; whether his primary interest is in shape or size. In agglomerative programs all such alternatives are available by the use of different distance-measures; a general account is given in Williams (1971) and in the standard text-books (e.g. Sneath and Sokal 1973; Clifford and Stephenson 1975). If, on the other hand, an ecologist proposes to use one of the Canberra divisive programs, he needs to know that DIVINF uses the Shannon information measure, is symmetric (i.e. counts double-zero matches), and is very sensitive to group size; that ASYM (not yet available on the TAXON library) uses the Jaccard measure, is asymmetric (i.e. ignores double-zero matches), is completely insensitive to group size but sensitive to species richness; and that REMUL is based on the Canberra metric, whose very distinctive properties need to be fully understood before it is used.

The third choice is only for those who are able to use an agglomerative classification. It is essential for them to decide whether the data are to be handled without distortion, so that if there are no sharp discontinuities in the data, none will be found; or whether

the pattern is to be 'sharpened' by the use of an intensely-clustering 'space-dilating' strategy. The choice here is one of the fusion strategy to be used, since every such strategy is associated with some aspect of space-manipulation (for details, see Williams *et al.* 1971).

The fact that so wide a variety of programs is available does not mean that all problems have been solved, for they have not. The classification of frequency data is a case in point. Such data can be classified by any one of a number of options in the information-statistic program CENPERC or the metric program MULCLAS; and it is natural to inquire whether any one of the options is likely to be the most profitable. Several workers have essayed comparisons of this type, with wildly discrepant results. The algorithms are evidently sensitive to some aspect of the configuration of the data, but what this is, is quite unknown. Another difficult area is that of 'stopping-rules', algorithms for determining how many classificatory groups should be extracted. The recent proposal by Ratkowsky and Lance (1978) has proved effective for a limited number of attributes of mixed type; whether it will be equally effective for a species-rich presence-and-absence matrix remains to be tested. A method recently proposed by Sandland and Young (1979), which will prevent random data from being subdivided, has proved powerful in those cases in which the data are replicated.

Nevertheless, in most areas of numerical classification the day of intuitive comparison of a large number of strategies is over; enough is known to make possible, in most cases, a rational choice of a particular strategy for a particular problem, and to provide reasons for such a choice. This should be the aim of any worker in this field.

REFERENCES

- Austin, M. P. (1976). On non-linear species response models in ordination. *Vegetatio* **33**: 33-41.
 Austin, M. P., and Noy-Meir, I. (1971). The problem of non-linearity in ordination; experiments with two-gradient models. *J. Ecol.* **59**: 763-73.
 Clifford, H. T., and Stephenson, W. (1975). *An Introduction to Numerical Classification*. Academic Press, New York, pp. xii + 229.
 Goodall, D. W. (1961). Objective methods for the classification of vegetation. IV. Pattern and minimal area. *Aust. J. Bot.* **9**: 162-96.
 Noy-Meir, I., and Whittaker, R. H. (1977). Continuous multivariate methods in community analysis: some problems and developments. *Vegetatio* **33**: 79-98.
 Ratkowsky, D. A., and Lance, G. N. (1978). A criterion for determining the number of groups in a classification. *Aust. Comput. J.* **10**: 115-17.
 Sandland, R. L., and Young, P. C. (1979). Probabalistic tests and stopping rules associated with hierarchical classificatory techniques. *Aust. J. Ecology* **4**: 399-406.
 Sneath, P. H. A., and Sokal, R. R. (1973). *Numerical Taxonomy*, W. H. Freeman & Co., San Francisco, pp. 573.
 Williams, W. T. (1971). Principles of clustering. *Ann. Rev. Ecol. and Syst.* **2**: 303-26.
 Williams, W. T., Clifford, H. T., and Lance, G. N. (1971). Group-size dependence: a rationale for choice between numerical classification. *Comput. J.* **14**: 157-62.

Handling large data sets

G. N. LANCE

GENERAL

There are several examples of problems which require the classification of large data sets. Probably the most obvious one is the analysis of LANDSAT imagery. In this case there are thousands of pixels on each image and these must be classified; however, the problem is relatively straightforward because each pixel is defined by only four numerical attributes. Hence the overall task is not too time consuming on a high-speed computer.

The other class of problems which involves large data sets is different because each individual is defined by *many* attributes of various mixed types. Thus the computer programs required for classification need to be quite sophisticated and thus tend to be time consuming. It was the need to tackle problems of this type which led to the development of REMUL (Lance and Williams 1975) and it is the purpose of this chapter to draw attention to how this program can be used to handle several thousand individuals described by mixed attributes without excessive use of computer time. A specific example will be quoted which illustrates how REMUL has been used to classify nearly 8000 landform elements each described by eleven attributes—comprising seven numericals, one qualitative and three disordered multistates.

THE BASIC FEATURES OF REMUL

REMUL has been fully documented elsewhere (Lance and Williams 1975). Briefly, it is a divisive polythetic classificatory program. The inter-attribute correlation matrix is computed (Lance and Williams 1968) and used to determine the attribute on which to divide the population so as to obtain the optimum split (monothetic) into two groups A and B. Having performed this split each individual member of both groups is examined to determine whether it is really best located in the group where the split has placed it. If not it is tagged to indicate that it should move. After all individuals have been examined in this way all the changes indicated are made and two new groups A' and B' are created. (This tagging method means that the *order* in which the individuals are examined does not affect the result.) Even now the groups may not be perfect but no more reallocation is attempted at this stage.

Since *all* attributes have now been allowed to influence the location of the individuals the process has become polythetic.

The classification proceeds by now splitting the least homogeneous of A' and B'. This sequence continues until the required number of groups (N) have been formed. At

this stage further reallocation is allowed but *all* individuals are examined in *all* groups, furthermore several passes through the reallocation cycle are allowed until convergence is complete; this usually occurs in less than ten cycles.

The computer time needed for this procedure is clearly proportional to the square of the number of attributes (to determine the splitting attributes) and to the square of the number of individuals (because of the reallocation phase). In practice it has been found that up to 250 individuals described by up to 100 attributes can be classified at reasonable cost.

THE ADDITIONAL FACILITIES AVAILABLE IN REMUL

One of the most useful extensions to REMUL is that once a set of groups has been obtained further individuals may be examined and the group which they are most like can be determined. Thus these individuals can be 'classified' but the original groups are not allowed to alter. The important point to realise is that this process is very quick because it is only necessary to compute N 'distances' for each individual, i.e. the distance d_N of the individual from the 'centres' of the N groups, and to select the value of N for which d_N is a minimum.

One difficulty is, however, apparent. Suppose that with each group there is associated a group radius r_N , then the distance d_N of the new individual from the group centre may be $<$ or $>$ r_N . If $d_N < r_N$ then the individual can be considered to really belong to that group. However, if $d_N > r_N$, this means that, although the individual is 'most like' this group, it is still further from the group centre than any existing member of the group. Hence it is considered to be the start of a *new group* and further individuals may prefer to be associated with *it* rather than to any of the original N groups.

When new groups form in this way their centres are adjusted as new members appear until a group of ten has accumulated after which the group is 'frozen'. This technique is a compromise attempt to get reasonable accuracy without increasing computing time unduly. In practice it is found that if this procedure is followed exactly the number of new groups formed is unacceptably large when thousands of individuals are to be allocated to a small number of groups. Thus we allow a factor p to be applied to r_N before the test on d_N is made. If, for example $p = 2$, then we allow an individual to belong to the group provided it is within *two* radii of the centre. We have found that in most cases a p value of about 1.25 is a suitable value.

When all new individuals have been treated in this way the number of groups will have increased from N to N' . The technique is now to repeat the original classification procedures but to ask for N' groups and to include, with the individuals originally used to obtain the N groups, those individuals which define the extra groups. Having done this the other individuals which remain to be classified are compared with the N' groups. This time very few, if any, new groups will appear and the classification of the total population can be considered to be complete.

Another feature of REMUL which has sometimes proved to be useful is that the first classification can be by-passed altogether. In this case a set of individuals is provided and the group to which each belongs is specified. Then the allocation of further indivi-

duals to these groups proceeds as above. This method has been found useful in a few medical applications when the diseases of some patients were 'known' and those of others were to be determined.

As mentioned above, LANDSAT imagery produces data with large numbers of pixels. Furthermore certain sections of the data about an image are considered to be known and the remainder of the data has to be allocated to the specified defined groups. From what has been said this is the type of problem for which REMUL has been designed. However, to date, REMUL has not been used on LANDSAT data and no comparison has yet been made with the other techniques designed for this purpose. This is an interesting research project which it is hoped will be tackled shortly.

EXAMPLES OF THE USE OF THESE FEATURES

Landform elements

The largest data set to which the method has so far been applied arose in the classification of landform elements (Speight 1976). This problem involved 7963 landform elements and in the first instance a type set of 300 was selected as being representative of the total population and twenty groups were obtained from these by classification. On allocation of the remaining 7663 elements new groups appeared. The final outcome was that the type set grew to 508 elements which then defined 34 groups.

In this particular problem it was necessary to clarify the relationships between these 34 groups using numerical techniques. So the centres of each were thought of as defining typical individuals and these were grouped to form 7 major groups. Hence it was possible to describe each of these in terms of *their* constituents and they were named as

1. Hillcrests and plateaux
2. Upper hill slopes
3. Simple hill slopes
4. Middle and lower hill slopes
5. Footslopes
6. Terraces, valley flats and dolines
7. Riverine plains

The 34 groups were constituent parts of these seven and, for example (7) contained small riverine plains, floodplains and large riverine plains.

In his conclusions Speight makes the following remarks which seem to indicate that REMUL was very satisfactory for his purpose.

The fact that the classification so plausibly reflects morphogenetic concepts as well as more deeply intuitive generalized concepts of terrain is a first, subjective confirmation of its value. The usefulness of the technique in geomorphic research lies principally in the explicit enumeration of landform attributes, each of which may be individually studied for its morphogenetic significance in various terrains.

Australian Aboriginal bark paintings

In this study (A. F. Collings, pers. comm.) there were 371 bark paintings and of these 83 had been placed in 7 groups by an Aboriginal informant and a further 166 were placed in 7 other groups by another informant. The criteria (attributes) used by these people for their groupings is unknown because they would not divulge the criteria on religious grounds.

An anthropologist from Sydney University described all the paintings by 12 numerical and 30 multistate attributes (some with as many as 16 states). REMUL was then used to allocate the remaining 122 paintings; 51 went into the defined 14 groups but the rest formed 9 new groups. Among these new groups there were three which were quite substantial, indicating that they were composed of paintings which were *not* represented in the original 14 groups.

This example is not directly relevant to the classification of vegetation but it has been included because it is an example of how REMUL has been used in fairly complicated ways. In commenting on REMUL Dr Collings has stated that 'in terms of classification, it has been neither better nor worse to any detectable degree than MULCLAS or MULTBET in *this* study with these attributes. Using the informants' groups as a basis, the identification process appears to have been very successful.'

INVERSE ANALYSIS

It is possible to consider the classification of vegetation as an inverse problem. This occurs when quadrats are described by the plant species growing in them. Clearly large data sets arise if there are many quadrats and/or species. Recently, a program has been written (INVER) which is able to provide a classification of the attributes even when they are mixed (Lance and Williams 1979). Preliminary studies of its use indicate it to be a powerful method.

In brief INVER calculates a matrix of similarity measures relating the attributes. These measures may then be used by any of the standard TAXON programs, which perform classification from measure matrices, e.g. MULCLAS (Lance and Williams 1967a, 1976b) or MINSPAN (Gower and Ross 1969).

AVAILABILITY OF REMUL AND INVER

Both these programs have been developed sufficiently so that they have been made available on the TAXON library. However, no undertaking can be given that they will never be altered but if changes are made they will be by way of improvements (we hope!). Specifications of both programs are available from the author.

With programs such as REMUL it is impossible to give any information as to their limitations. It is, however, fair to say that core storage space is less limiting than computer time—and hence cost which depends significantly on CPU time. All the quite large runs given above as examples of the use of REMUL cost less than \$100. There is a limit on the number of states in multistate attributes, namely, twenty. However, there are other good reasons why multistates should not have too many states.

At the time of writing a TAXON Users Manual is in the course of preparation. It is an authoritative guide to *all* programs on the TAXON library. Anyone interested should send their names to the author.

CONCLUSIONS

REMUL has been and is being used to study large data sets. Since the classification of vegetation often involves many species and attributes it is probable that REMUL is the only way of handling such data because the attributes are usually mixed.

REFERENCES

- Gower, J. C., and Ross, G. J. S. (1969). Minimum spanning trees and single linkage cluster analysis. *Appl. Statist.* **18**: 54-64.
- Lance, G. N., and Williams, W. T. (1967a). Mixed-data classificatory programs I. Agglomerative systems. *Aust. Comput. J.* **1**: 15-20.
- Lance, G. N., and Williams, W. T. (1967b). A general theory of classificatory sorting strategies I. Hierarchical systems. *Comput. J.* **9**: 373-80.
- Lance, G. N., and Williams, W. T. (1968). Mixed-data classificatory programs. II. Divisive systems. *Aust. Comput. J.* **1**: 82-5.
- Lance, G. N., and Williams, W. T. (1975). REMUL: A new divisive polythetic classificatory program. *Aust. Comput. J.* **7**: 109-12.
- Lance, G. N., and Williams, W. T. (1979). INVER: A program for the computation of distance-measures between attributes of mixed types. *Aust. Comput. J.* **11**: 27-8.
- Speight, J. G. (1976). Numerical classification of landform elements from air photo data. *Z. Geomorph.* **25**: 154-68.

The role of certain diversity properties in vegetation classification

M. P. AUSTIN

INTRODUCTION

Dale and Webb (1975) have argued strongly that a satisfactory method of vegetation classification requires a clear statement of the properties to be possessed by members of a group defined by such a classification. They support this argument by presenting a numerical classification method based on an explicit two-parameter model for a phytosociological 'association' (MacNaughton-Smith 1965; Dale and Anderson 1973; Dale and Webb 1975; Dale 1976 and also Austin 1972 for development of the model). These authors indicate that their paper will have 'served its purpose if it encourages phytosociologists to examine their own methods for it is only from an explicit account of these that a good numerical simulation method can be developed' (Dale and Webb 1975).

The present chapter is intended as a preliminary response to this challenge. It will be argued that their model is incomplete, in that certain vegetation properties need to be taken into account. The literature on these properties is reviewed and their role in data standardisation discussed to indicate their importance. Examples are presented to show that use of these diversity properties alone can provide significant ecological information from a simple graphic vegetation analysis.

Two difficulties complicate the discussion of numerical classification of vegetation, 1. the failure of ecologists to state their purpose and 2. the absence of any developed theory regarding vegetation composition. In this chapter, the purpose of vegetation classification is the definition of vegetation groups such that the ecological differences between groups are maximised assuming that the best indicator of ecological differences is the quantitative floristic composition of the vegetation. The expression 'ecological differences' is used to indicate differences in seral status, disturbance or historical factors as well as current differences in environmental factors. 'Quantitative floristic composition' refers to quantitative measures of performance for individual species present at a site. The possible role of community structure theories (Whittaker 1975) in relation to numerical classification methods has not been examined (Whittaker 1973a; Goodall 1973) though the significance of theoretical considerations of non-linearity has been profound for ordination (Austin 1976; van Groenewoud 1976; Noy-Meir and Whittaker 1977).

TWO-PARAMETER MODEL

The vegetation model of Dale (Dale and Anderson 1973; Dale and Webb 1975) states:

$$P_{ij} = a_i b_j / (1 + a_i b_j)$$

TABLE 14.1

An example of a stand/species table acceptable as a 'perfect group' for the two-parameter model (from Fig. 1 of Dale and Webb 1975)

Species	Stands									
	1	2	3	4	5	6	7	8	9	10
a	8	1	1	1	1	1	1	1	1	1
b	1	0	0	0	0	0	0	0	0	0
c	1	0	0	0	0	0	0	0	0	0
d	1	0	0	0	0	0	0	0	0	0
e	1	0	0	0	0	0	0	0	0	0
f	1	0	0	0	0	0	0	0	0	0

where P_{ij} is the probability of finding species j in stand i for presence/absence data and the relative amount of species j for certain types of quantitative data. a_i is a stand richness coefficient, i.e. related to the number of species per stand, and reflects the 'difficulty' of the stand for plant growth; b_j is a species constancy/dominance coefficient reflecting the species 'ability' to occupy stands. The vegetation data matrix of stands and species is divided in such a way that members of the resulting groups have a maximal fit to the model.

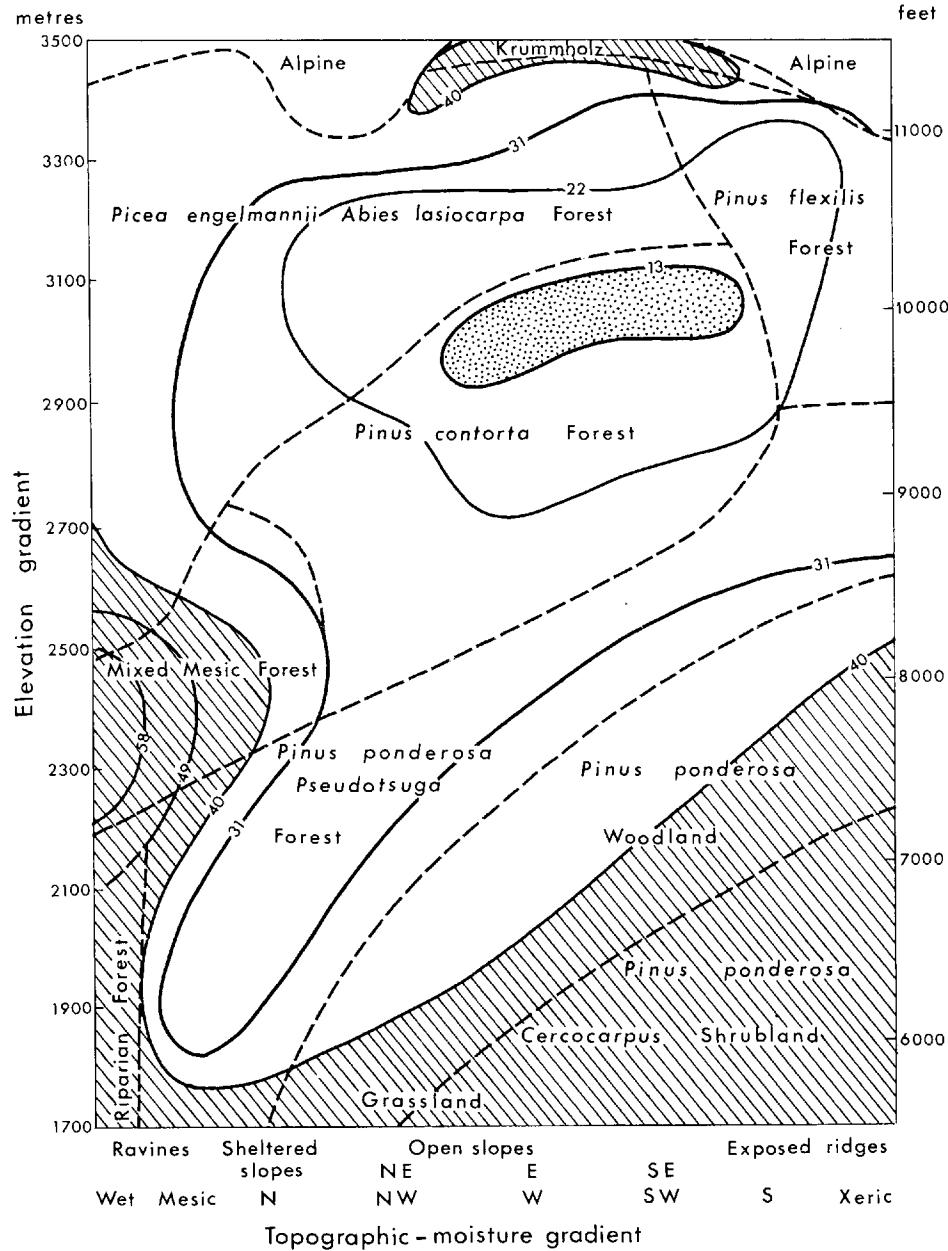
Table 14.1 shows an example of a 'perfect' group as defined by the model. Many ecologists would reject such a group on the grounds that stand one is different from stands two to ten. Stand one differs in species richness, total vegetation per stand and has a different dominance structure. The implication of this is that the model is incomplete relative to *some* ecologists' concepts of what the homogeneity properties of a vegetation group should be. Species richness and dominance are components of species diversity as usually considered. Do these properties of a stand have a special ecological relevance of their own such as to justify their inclusion in any definition of a vegetation group?

DIVERSITY PROPERTIES

One aspect of community theory which has been extensively examined recently is the behaviour of measures of species diversity. One link between this work and problems discussed here are the observations of Austin and Greig-Smith (1968) on certain vegetation properties which influence classification results. They recognised three such properties.

1. Stand richness (species richness): number of species per stand.
2. Stand abundance (standing crop): amount of vegetation (in some absolute unit of measure) per stand, or sum of the quantitative species measurements for the stand.
3. Stand dominance (species predominance): the largest proportion of the stand abundance contributed by a single species.

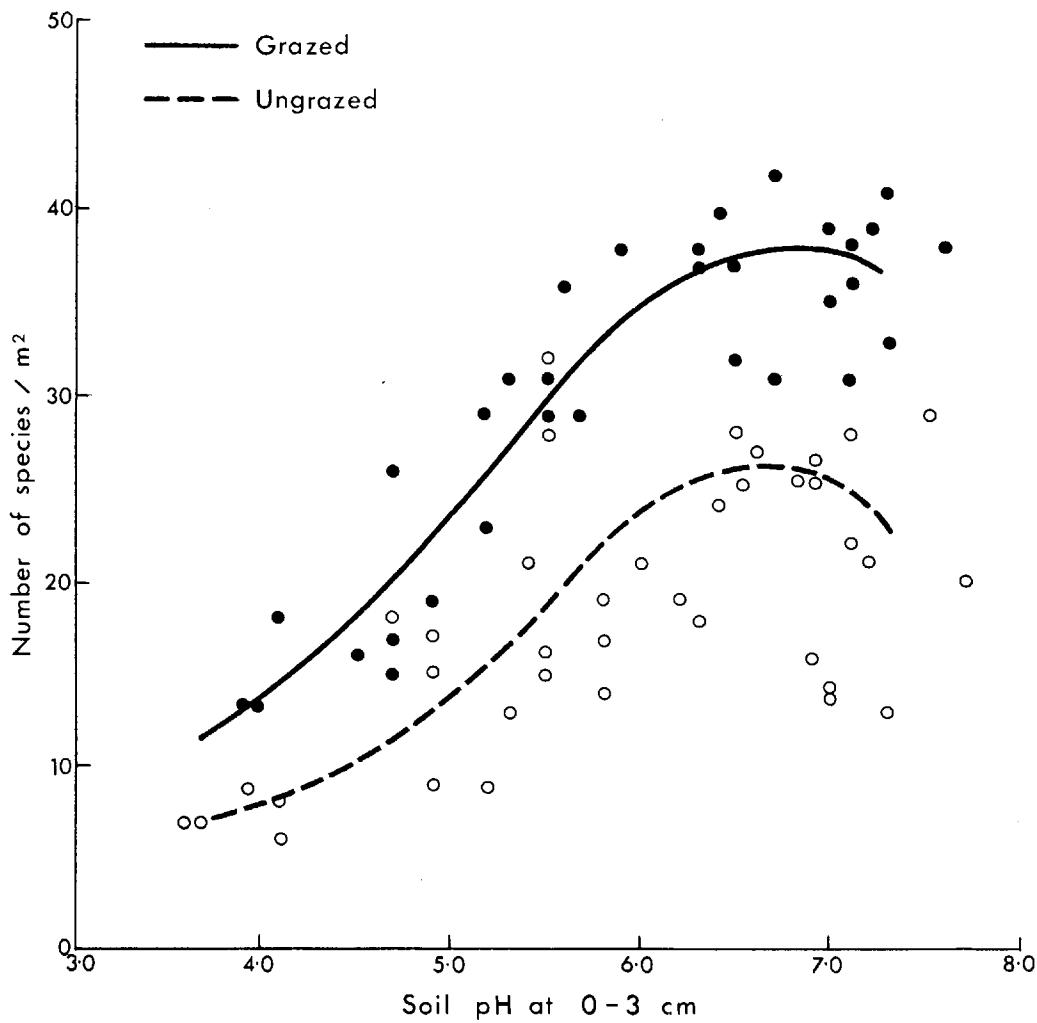
The terms and definitions used here differ slightly from the original publication (original terms shown in brackets). Austin and Greig-Smith tentatively suggested that if



- 14.1 Relationship between stand richness and two environmental gradients, elevation and the topographic moisture index (redrawn from Peet 1978). Solid line: stand richness isopleths. Broken line: forest type boundaries. Hatched areas: stand richness > 40 species per 0.1 ha. Stippled areas: stand richness < 13 species per 0.1 ha.

gross differences in these properties existed between stands, an ecological or environmental explanation of these vegetation differences might be possible.

There now exists an extensive literature dealing with these properties and their correlation with environment (see for example Whittaker 1965, 1972; various authors in Brookhaven Symposium 1969; Peet 1974, 1978; Grime 1973, 1974). Detailed examples of the correlation are given by a number of workers (McNaughton 1967;



14.2 Stand richness (species density) in relation to pH in two grasslands in the Derbyshire dales (redrawn from Grime 1973). ●—Cressbrookdale; grazed by sheep and cattle.○—Lathkilldale; ungrazed, burnt sporadically. The samples used are one square metre quadrats located at random. The curves are freehand interpretations by the present author.

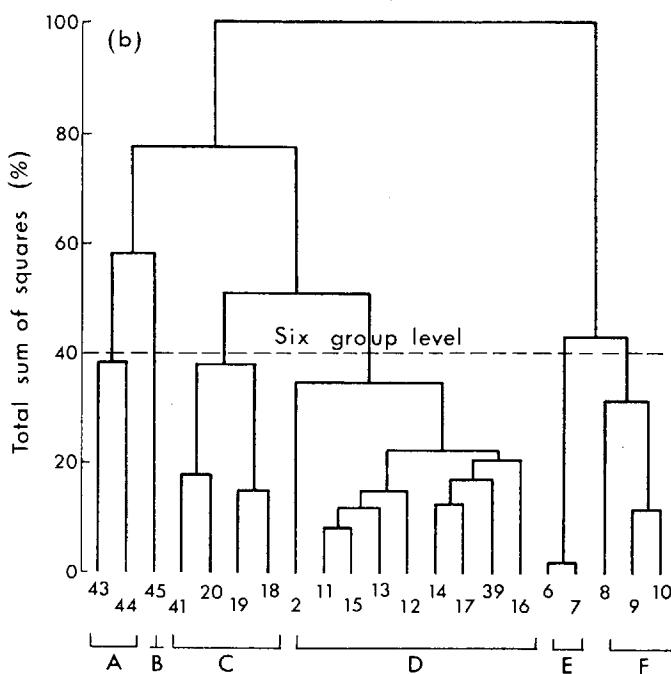
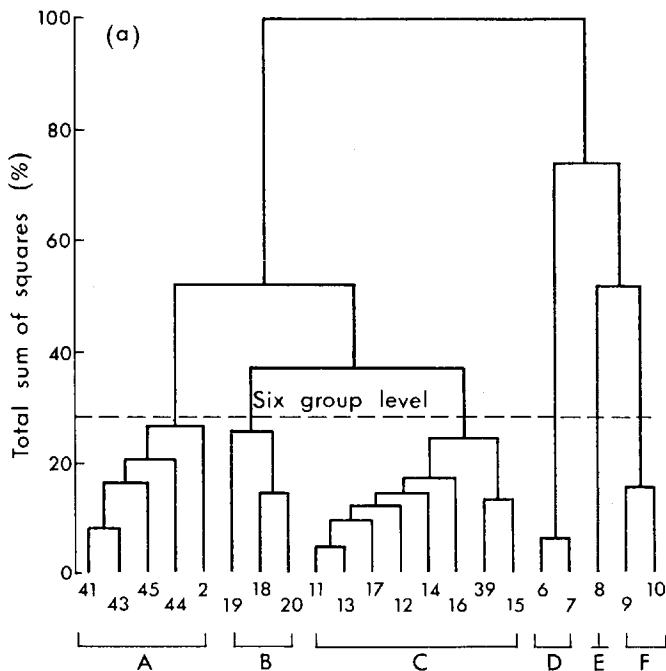
Grime 1973; Peet 1978; Glenn-Lewin 1977). Peet (1978) shows how species richness (= stand richness) is related to two environmental factors by means of a direct gradient analysis (Fig. 14.1). He also shows that 'dominance' as measured by Simpson's index (Simpson 1949), which closely correlates with stand dominance (Whittaker 1972), has a distinct but similar pattern of response to the environmental factors. Seral changes in stand richness and abundance (biomass) are also described. Grime (1973) shows variation in species richness with pH and in addition, the influence of grazing on the relationship (Fig. 14.2). A number of theoretical studies based on diversity/environment correlations have been made. McNaughton (1967) has shown relationships between richness, dominance and biomass for Californian grasslands (though see Austin 1968) and related these and other correlations with environmental gradients to niche theory (McNaughton and Wolf 1970). Grime (1973, 1974) has developed a complex hypothesis regarding the behaviour of dominance and species richness in relation to gradients of environmental stress and disturbance. He suggests high dominance occurs under minimal environmental stress and high stand richness under intermediate stress levels. Peet (1978), however, indicates that although the correlation between diversity measures and environmental gradients may be clear, the type and pattern of correlation appears to be different in different regions.

Current evidence indicates that there is a close (causal?) relationship between diversity measures and environment. In the absence of an explicit model of vegetation variation incorporating diversity properties, reliance on floristic differences appears to be ignoring an important source of ecological information without justification.

ROLE OF DIVERSITY PROPERTIES IN STANDARDISATION

Austin and Greig-Smith (1968) examined a number of standardisations with a single set of tropical rainforest data using a single classificatory technique. Their results using euclidean distance with and without stand normalisation are shown in Fig. 14.3. Stands with high diversity, group A in Fig. 14.3 (high values of McIntosh's index (McIntosh 1967)), appear to form a homogeneous group while stands with higher total density and high dominance, groups D-F in Fig. 14.3 (low index values), appear heterogeneous with absolute euclidean distance. After stand normalisation, the diverse stands appear relatively more heterogeneous (groups A-C in Fig. 14.3b) than the stands with high stand abundance in the data matrix. The conclusion drawn from this study was that for any real stand/species matrix which contained substantial heterogeneity, a standardisation might be appropriate for one subset of the data matrix but be distorting for another subset. No single standardisation may be acceptable over the whole of a data set. A second conclusion the authors reached was that the diversity properties previously mentioned were important in determining the effect of different standardisations, though no theoretical analysis was attempted.

Noy-Meir and his colleagues have clarified the mathematical implications of data standardisations (Noy-Meir 1973; Noy-Meir *et al.* 1975; see also Dale 1964). For euclidean measures of similarity, Noy-Meir *et al.* (1975) show that the similarity coefficient depends on the abundance of species and the richness of stands, and various



14.3 Classification of forest type data from Kolombangara with different standardisations (redrawn from Austin and Greig-Smith 1968). (a) Euclidean distance unstandardised, (b) Euclidean distance, stand normalised. Broken line and letters indicate six-group level of classification.

standardisations will alter the relative contributions of particular species depending on their abundance and whether they occur in 'poor' stands (i.e. stands with few species and low amounts of vegetation). They conclude that standardisation could profoundly alter results and lead to qualitatively different interpretations of the data, the magnitude of such effects varying between data sets. These authors offer no ecological criterion or rationale for choosing a particular standardisation, suggesting that it depends 'on the nature of the problem, or the purpose of the study as defined by the ecologist' (Noy-Meir *et al.* 1975). Clifford and Stephenson (1975) also provide a discussion of data standardisation and suggest that the choice depends on 'customer-satisfaction'.

Standardisations are often *designed (chosen)* to remove differences in diversity properties between stands, e.g. stand normalisation to remove differences in stand abundance. Alternatively by choosing to give equal weight to all species, differences in stand abundance may be markedly changed. An ecological rationale for data standardisation appears to require recognition of the role of diversity properties.

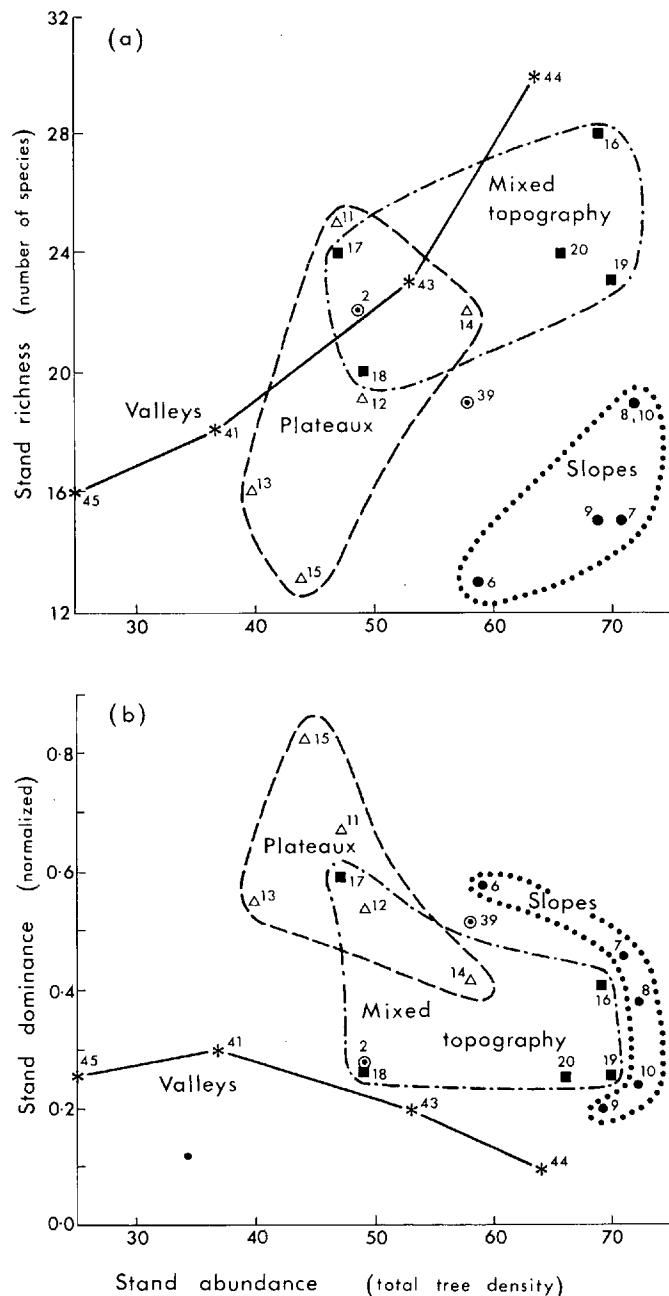
STAND ANALYSIS OF DIVERSITY PROPERTIES

The importance of these diversity properties can be examined by studying their use in vegetation analysis. Can they provide ecological information independently of other floristic attributes? Two examples are presented to illustrate this approach using previously analysed and published data sets.

Forest type data of Austin and Greig-Smith (1968)

The data set is taken from a larger set obtained during a survey of Kolombangara Island in the Solomon Islands. The data consist of a number of tree stems greater than 12 inches (30 cm) girth for all species for 21 stands each of 0.3 acres (0.12 ha). Greig-Smith, Austin and Whitmore (1967) can be consulted for further details. This subset of the stands was chosen for further analysis by Austin and Greig-Smith (1968) as the results obtained from an association-analysis were judged to be unsatisfactory when compared with available environmental information. The stands consist of four groups from geographically distinct areas with markedly different topography, plus two stands from other areas. Table 2 of Austin and Greig-Smith (1968) gives details. The data were used to test various forms of standardisation but no entirely satisfactory result was obtained (Fig. 14.3).

The diversity properties defined earlier were calculated for each stand, stand abundance being determined as total number of stems ≥ 12 inch (30 cm) girth per stand. Stand dominance is logically dependent on species number and when used with an integer measure such as density, the possible maximum and minimum dominance is a function of stand abundance and stand richness (Austin 1968). The measure of stand dominance was therefore expressed as a proportion of the range between the maximum and the minimum possible values using the formulation $Z_{ij} = (X_{ij} - X_{i,min}) / (X_{i,max} - X_{i,min})$ where X_{ij} is the dominance values j in stand i and $X_{i,max}$ and $X_{i,min}$ are the theoretical maximum and minimum values respectively. (A similar standardisation was



14.4 Graphic analysis of diversity properties of Kolombangara stands (Austin and Greig-Smith 1968). Different property combinations are characteristic of different topographic positions. —*: Merusu valley stands; —Δ: Sandfly plateau stands; - - - : Sandfly stands with heterogeneous topography; —: Sandfly stands with steep slopes; ●: other stands. Stand numbers as in Fig. 14.3.

used to remove scale effects between the diversity properties when classifying stands using the properties as attributes, see Fig. 14.5.)

Consideration of the scatter diagrams obtained from graphing the diversity properties (Fig. 14.4) indicates that in the *three*-dimensional space defined, there is no overlap between the stands from the four geographical areas. The valley stands have low stand dominance and varied levels of stand richness and abundance. The topographically heterogeneous stands from 257 m on the Sandfly transect are intermediate with respect to dominance and total density (abundance). The Sandfly plateau stands tend to have intermediate values but with higher stand dominance, particularly stand fifteen which is marked by extreme dominance of a particular species (*Teysmanniodendron aherneanum*) and low stand richness.

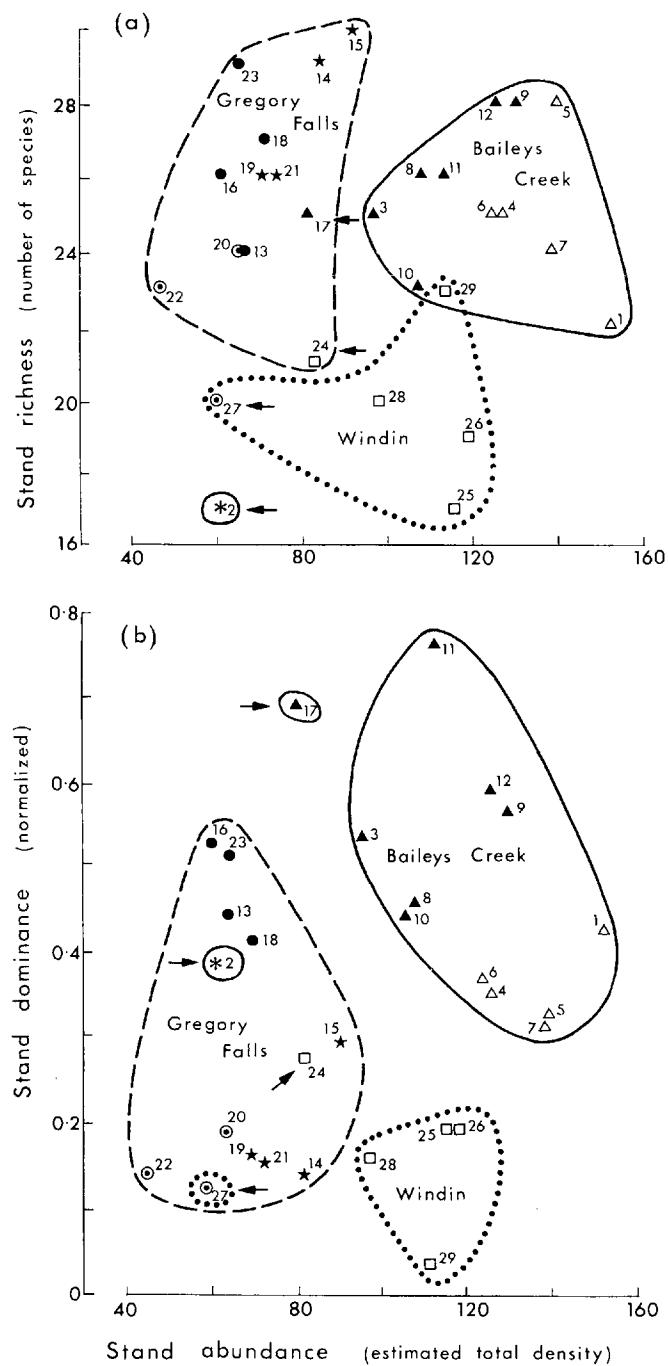
The analysis of the diversity properties clearly reveals the geographical (environmental?) relationships of the stands without elaborate computation (compare with the ordination (Fig. 9) of Greig-Smith *et al.* 1967). Further new information is provided by the observation that distinct vegetation differences exist between stand fifteen and other stands.

Queensland rainforest data of Dale and Webb (1975)

The floristic data set is taken from three geographically distinct tropical rainforest plots in north Queensland. Each plot was subdivided into a number of stands (see Dale and Webb 1975; Webb *et al.* 1967 for further details). The original density data were categorised to simulate the use of a cover/abundance scale in the 1975 paper. For the purposes of this preliminary study, the density values were reconstituted by substituting the mid-class density value for each category, e.g. class five (density range 7-12) is given a density value 9.5. In addition the Windin stands were adjusted for difference in area (cf. Dale and Webb 1975).

Graphic analysis of diversity properties reveals that with the exception of four stands, the three geographical areas occupy distinct volumes in the property-space (Fig. 14.5). A numerical classification of the diversity properties using the incremental sum of squares (Ward's method, Ward 1963) from the CLUSTAN package (a commercially available software package for numerical classification) confirms the behaviour of the four 'odd' stands but at a seven-group level reflects some interesting substructure within the geographical plots (Fig. 14.5) not mentioned in the original paper. An atypical or 'odd' stand is defined as one in which the diversity group to which it belongs does not otherwise occur in that geographical area (as shown in Fig. 14.5). Examination of the atypical stands shows that stand two has low stand richness and low stand abundance suggesting disturbance. The other stands have respectively low stand abundance (27), low stand richness (24) and high stand dominance (17), relative to other stands from their areas.

Dale and Webb (1975) were concerned that no numerical methods other than their two-parameter model indicated the special (geographical) significance to be attached to the three groups of stands. The graphic analysis of diversity properties shows this but the four 'odd' stands distort an agglomerative classification of the diversity properties.



14.5 Graphic analysis of diversity properties of Queensland rainforest stands (Dale and Webb 1975). The three geographical areas are distinct with four stands (\leftrightarrow) showing unusual property combinations for their locality. Symbols show seven group classification using diversity properties, see text for details. Stand numbers as in Table 1 of Dale and Webb (1975).

Whether these same four stands contributed to the failure of the other numerical methods tried is not known. The two most extreme of the odd stands (2 and 27) have the lowest a_i values for their group using the two-parameter model. The a_i values are 'in a sense the degree of expression of the Association (group)' (Dale and Webb 1975). The diversity properties therefore suggest that for the purpose of defining an association these stands might be better excluded as extreme, possibly disturbed, variants.

The graphic analysis reveals that the diversity properties may be used to produce a computationally parsimonious ordination and may provide previously unsuspected interpretations.

DISCUSSION

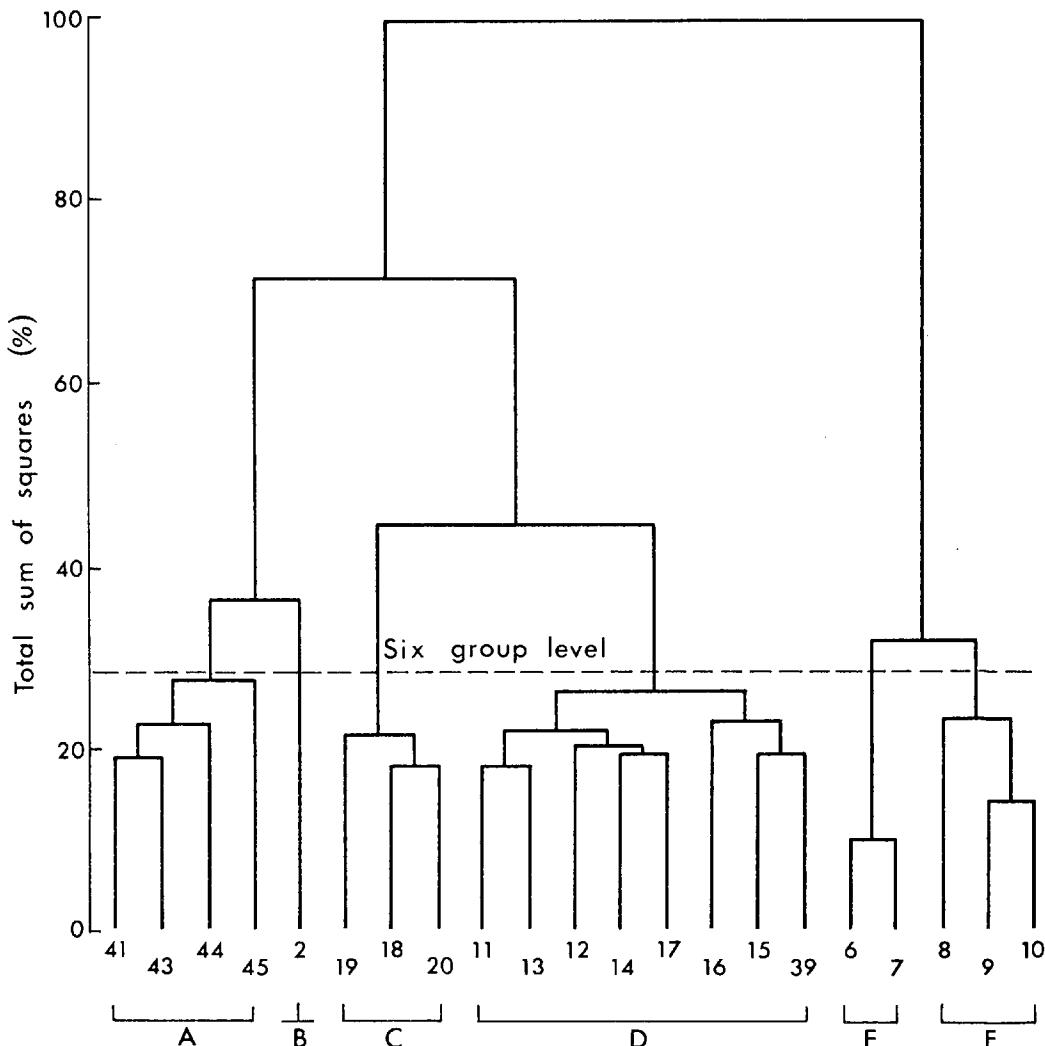
The explicit two-parameter model for vegetation classification has close relationships with the diversity properties discussed here. The stand coefficient a_i values for a vegetation group are monotonically related to stand abundance, which may explain the similarity in results between the two-parameter model and the diversity-properties graphic analysis. The evidence from Table 14.1 and the graphic analysis suggests that the model (Dale and Webb 1975) may be insufficiently sensitive. The discussion of diversity properties indicates that it may also be incomplete.

Although no universally acceptable vegetation model is apparent, there is a consensus among many ecologists that diversity properties are important. The suggestion that there are three distinguishable properties may contribute some new understanding to the old controversies between different schools of vegetation classification. The Braun-Blanquet School requires that relevés from the same association should have similar species numbers (stand richness), see Westhoff and van der Maarel (1973) for a discussion of this. The Scandinavian school of dominance classification reflects emphasis on a second of the diversity properties (Whittaker 1973a), stand dominance. The third property, stand abundance, does not seem to have been directly utilised in classification approaches previously (Whittaker 1973b). A requirement that groups should show uniformity in all three properties as well as floristic composition would appear to merit further study, though this is defining further minimal variance properties for vegetation groups (cf. Dale and Webb 1975).

The need to consider the information to be obtained from diversity properties before standardisation is clear from Figs. 14.4 and 14.5. The influence of these properties on similarity measures must also be considered. The recent empirical study of Booth (1978a, b) with qualitative data shows the dangers of using symmetric measures of similarity which include double-zero matches; stand richness can then dominate the classification, giving groups with similar species numbers but no species in common.

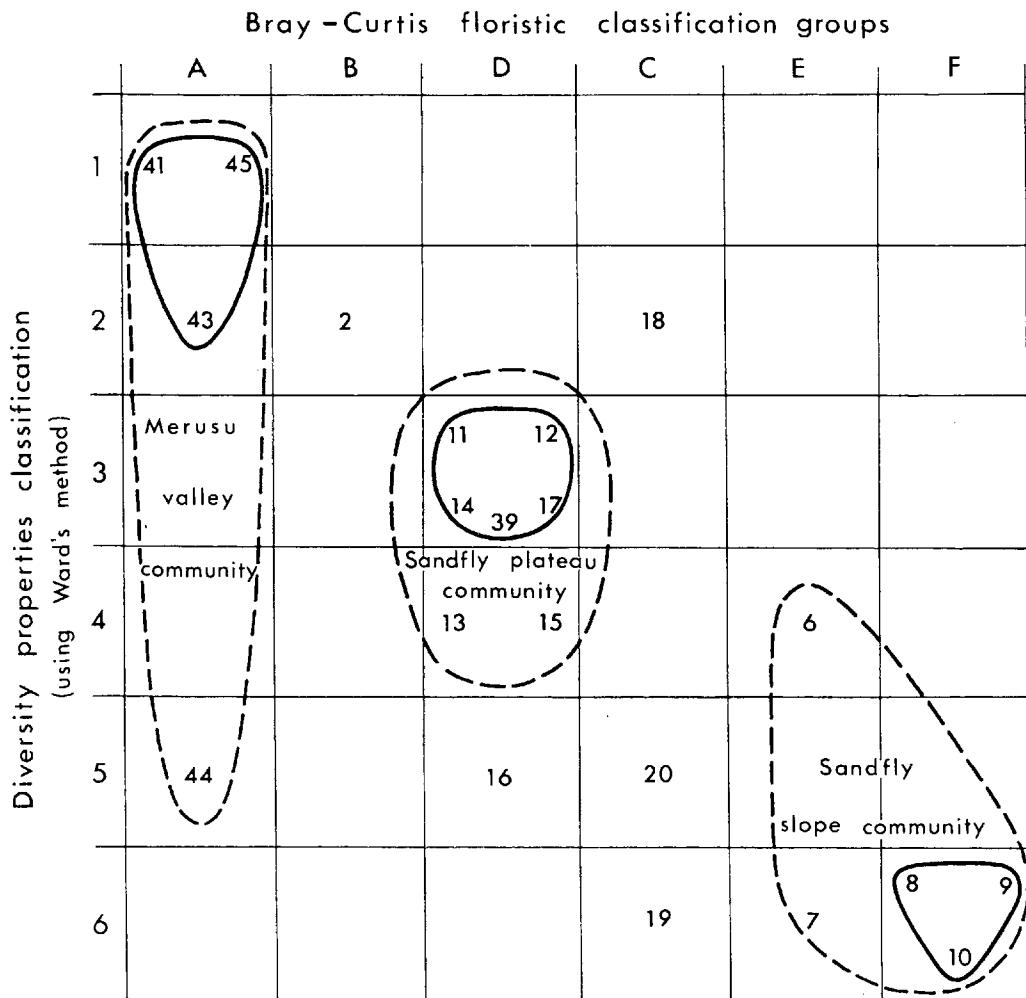
An interim solution for vegetation classification may be to use an asymmetric coefficient for floristic classification based on quantitative data and compare the resulting groups with those from a classification based on diversity properties. A two-way table of the classification results could be examined for ecological meaning and decisions on suitable grouping taken subjectively. Booth (1978b) has recently used this approach where no definite criterion, except maximising the number of occurrences on the principal diagonal, could be used to determine the best classification for this purpose.

An example analysis can be provided for the Kolombangara data set. Figure 14.6 shows the floristic classification obtained using the Bray-Curtis coefficient (Bray and Curtis 1957) with Ward's method (Ward 1963). The grouping obtained constitutes the best classification so far obtained for distinguishing the geographical groupings of stands though the sorting strategy used is not strictly appropriate. The dendrogram structure does not suggest any gross differences due to stand richness, abundance or dominance



14.6 Classification of forest type stands from Kolombangara (Austin and Greig-Smith 1968) using unstandardised density data with Bray-Curtis coefficient and the combinatorial strategy for Ward's method.

(cf. Fig. 14.3). The two-way table (Fig. 14.7) using the Bray-Curtis classification and a similar Ward's method classification of the diversity properties summarises the complex relationships present in the stand-species matrix. The ecologist must then decide which grouping satisfies his purpose. In this case, groups with clear relationships with environment which may have validity beyond the sample analysed have been recognised.



14.7 Two-way table comparison of groups from floristic and diversity classifications of Kolombangara forest type data of Austin and Greig-Smith (1968). An interpretation of the co-incidence groups is given in terms of noda: typical stands only (solid lines), and groups: broad community types (broken lines) with greater importance attached to floristic similarity.

The role of diversity properties in any future vegetation model is still uncertain. Peet (1978), in discussing species richness (stand richness), shows that the patterns of relationship with environment depend on the physiognomic structure of the vegetation. Patterns of stand richness for different growth forms reflect the presence or absence of other vegetation strata: shrub stand richness depends on the presence of trees. Glenn-Lewin (1977) showed similar correlations in a regression study with the percentage cover of coniferous trees providing the best predictor of total species (stand) richness. The examples used here were restricted to trees to avoid this problem of interactions between strata. The dependence on structure does suggest that an explicit model may require the incorporation of growth form, along with floristics and vegetation properties.

A number of conclusions can be drawn from this examination of diversity properties in relation to vegetation classification. The most explicit model for classification to date, the two-parameter model of Dale and Webb (1975), is incomplete in the sense that it does not incorporate these properties. Current methods of data standardisation and choice of similarity measures should take more account of their effect on diversity properties before making a decision on which to use. The suggested diversity properties, stand richness, abundance and dominance can yield ecological information without detailed knowledge of the species concerned. We cannot as yet develop a better model than the two-parameter one but it is clear that diversity properties deserve more attention from plant ecologists and methodologists interested in vegetation classification than they have received previously.

ACKNOWLEDGMENTS

I should like to thank Professor dr. V. Westhoff for kindly providing facilities in his department, E. van der Maarel and M. J. A. Werger for discussions and J. Louppen for assistance with computing. D. Wishart's CLUSTAN package was used for the classifications.

REFERENCES

- Austin, M. P. (1968). Relationships among functional properties of Californian grassland. *Nature, London* **217**: 1163.
- Austin, M. P. (1972). Models and analysis of descriptive vegetation data. In: *Mathematical Models in Ecology* (ed. J. N. R. Jeffers) pp. 61-86. Blackwell Scientific Publications, Oxford.
- Austin, M. P. (1976). On non-linear species response models in ordination. *Vegetatio* **33**: 33-41.
- Austin, M. P., and Greig-Smith, P. (1968). The application of quantitative methods to vegetation survey. II. Some methodological problems of data from rain forest. *J. Ecol.* **56**: 827-44.
- Bray, J. R., and Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* **27**: 325-49.
- Booth, T. H. (1978a). Numerical classification techniques applied to forest tree distribution data. I. A comparison of methods. *Aust. J. Ecol.* **3**: 297-306.
- Booth, T. H. (1978b). Numerical classification techniques applied to forest tree distribution data. II. Phytogeography. *Aust. J. Ecol.* **3**: 307-14.
- Brookhaven Symposium in Biology 22. (1969). *Diversity and Stability in Ecology*. pp. 264. Brookhaven National Laboratory BNL 50175 (C-56). New York.

- Clifford, H. T., and Stephenson, W. (1975). *An Introduction to Numerical Classification*. Academic Press, New York.
- Dale, M. B. (1964). The application of multivariate methods to heterogeneous data. Ph.D. Thesis, University of Southampton.
- Dale, M. B. (1976). Classification: recent advances and future possibilities. In: *Pattern Analysis in Agricultural Science*. (ed. W. T. Williams) pp. 102-9. CSIRO Melbourne-Elsevier Scientific Publishing Company, Amsterdam.
- Dale, M. B., and Anderson, D. J. (1973). Inosculate analysis of vegetation data. *Aust. J. Bot.* **21**: 253-76.
- Dale, M. B., and Webb, L. J. (1975). Numerical methods for the establishment of associations. *Vegetatio* **30**: 77-87.
- Glenn-Lewin, D. C. (1977). Species diversity in North American temperate forests. *Vegetatio* **33**: 153-62.
- Goodall, D. W. (1973). Numerical classification. In: *Handbook of Vegetation Science Part V: Ordination and Classification of Communities* (ed. R. H. Whittaker) pp. 575-616. Junk, The Hague.
- Greig-Smith, P., Austin, M. P., and Whitmore, T. C. (1967). The application of quantitative methods to vegetation survey. I. Association-analysis and principal component ordination of rain forest. *J. Ecol.* **55**: 483-503.
- Grime, J. P. (1973). Control of species density in herbaceous vegetation. *J. Env. Managt* **1**: 151-67.
- Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature, London* **250**: 26-31.
- Groenewoud, H. van (1976). Theoretical considerations on the covariation of plant species along ecological gradients with regard to multivariate analysis. *J. Ecol.* **64**: 837-78.
- McIntosh, R. P. (1967). An index of diversity and the relation of certain concepts to diversity. *Ecology* **48**: 392-404.
- McNaughton, S. J. (1967). Relationships among functional properties of Californian grassland. *Nature, London* **216**: 168-9.
- McNaughton, S. J., and Wolf, L. L. (1970). Dominance and the niche in ecological systems. *Science* **167**: 131-9.
- MacNaughton-Smith, P. (1965). Some statistical and other numerical methods for classifying individuals. Home Office Research Unit Report No. 6, H.M.S.O. London.
- Noy-Meir, I. (1973). Data transformations in ecological ordination. I. Some advantages of non-centering. *J. Ecol.* **61**: 329-41.
- Noy-Meir, I., Walker, D., and Williams, W. T. (1975). Data transformations in ecological ordination. II. On the meaning of data standardisation. *J. Ecol.* **63**: 779-800.
- Noy-Meir, I., and Whittaker, R. H. (1977). Continuous multivariate methods in community analysis: some problems and developments. *Vegetatio* **33**: 79-98.
- Peet, R. K. (1974). The measurement of species diversity. *Ann. Rev. Ecol. Syst.* **5**: 285-307.
- Peet, R. K. (1978). Forest vegetation of the Colorado Front Range: patterns of species diversity. *Vegetatio* **37**: 65-78.
- Simpson, E. H. (1949). Measurement of diversity. *Nature, London* **163**: 688.
- Ward, J. H. Jr (1963). Hierarchical grouping to optimize an objective function. *J. Amer. Stat. Ass.* **58**: 236-44.
- Webb, L. J., Tracey, J. G., Williams, W. T., and Lance, G. N. (1967). Studies in the numerical analysis of complex rain forest communities. I. A comparison of methods applicable to site/species data. *J. Ecol.* **55**: 171-91.
- Westhoff, V., and van der Maarel, E. (1973). The Braun-Blanquet approach. In: *Ordination and Classification of Communities* (ed. R. H. Whittaker), Handbk. Veg. Sci. 5, 617-726. Junk, The Hague.

140 *Methodology and Application*

- Whittaker, R. H. (1965). Dominance and diversity in land plant communities. *Science* **147**: 250-60.
- Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon* **21**: 213-51.
- Whittaker, R. H. (1973a). Approaches to classifying vegetation. In: *Ordination and Classification of Communities* (ed. R. H. Whittaker), Handbk. Veg. Sci. 5, 323-54. Junk, The Hague.
- Whittaker, R. H. (ed.) (1973b). *Ordination and Classification of Communities*. Handbk. Veg. Sci. 5, Junk, The Hague.
- Whittaker, R. H. (1975). *Communities and Ecosystems*. 2nd edn Macmillan, New York.

A grammatical approach to vegetation classification

M. B. DALE

INTRODUCTION

There is nothing so difficult as a beginning in poesy unless perhaps the end; I will therefore avoid both and start in the middle. The classification of vegetation has been, like England, the paradise of individuality, eccentricity, heresy, anomalies, hobbies and humour. In the 27 years since the debut of numerical classification in Australia (Goodall 1952), we have learned something, but we must still admit the monstruosity, like love, that the will is infinite and the execution confined.

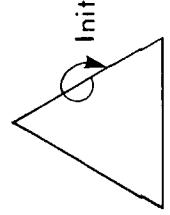
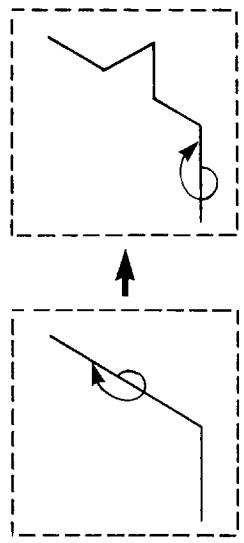
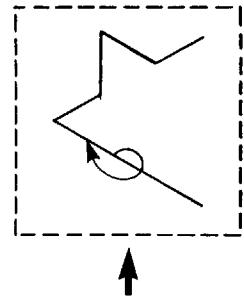
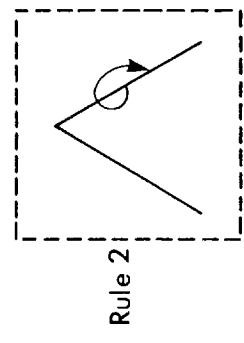
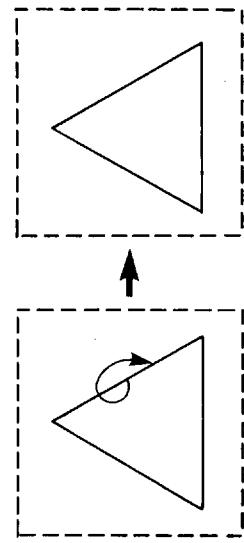
Before you accuse me of being a sophisticated rhetorician inebriated with the exuberance of my own verbosity, let me suggest that the illumination of the darker corners of numerical classification demands a stronger theoretical basis; certainly one stronger than the present statistical approaches have provided. These latter do not address the major premise that pattern is for an agent, and concentrate instead on the internal characteristics of the data. In contrast, I think grammar theory does address the major premise, and hence does provide a better basis for classification. And if you find this exposition somewhat untidy then remember a sweet disorder in the dress kindles in clothes a wantonness, and that a little rebellion now and then is a good thing.

GRAMMARS AND NATURAL CLASSIFICATION

Formally a grammar has four parts—a set of terminal symbols, a set of nonterminal symbols, a special initial symbol and a set of production rules specifying the conditions under which a string of symbols may be written as another set of symbols. As a simple example I shall use a shape grammar (Fig. 15.1) redrawn from Gips (1974), which draws snowflakes (Fig. 15.2). In the first grammar each rule is applied serially, i.e. one rule at a time. In contrast a much simpler grammar is possible (Fig. 15.3) if all rules which can be applied are applied in parallel. I should also note that where lines are replaced by other lines, the endpoints of both sets of lines are assumed to have fixed position.

What branches then grow out of this stony ground. The beginnings lie in the work of Lindenmayer (1968) who became interested in grammars as a means of formalising the processes of morphological development. He introduced a parallel grammar with an empty terminal set of symbols, and followed the developments produced for a fixed number of rule applications. These grammars were unlike any traditional linguistic grammars and are now called L-systems. Using such grammars it proved possible to examine development in certain kinds of organisms and organs, which were essentially

Production rules



— Terminal symbol

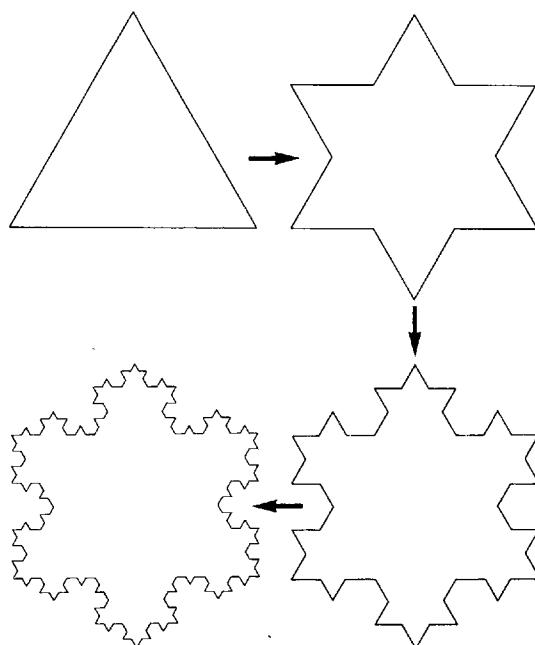
Initial symbol

Non-terminal symbol

15.1 A serial shape grammar for the snowflake curve

1- or 2-dimensional. Recent work by Reusch (1976) and Mayoh (1974) allows 3-dimensional development and certain other modifications, though these have as yet been little used. As an aside, Herman (1969) showed that even quite simple organisms were equivalent to Turing machines, and hence were universal computers. Herman (1970) also discussed the role of environment although his discussion is not ecologically orientated.

All this may not seem of great importance to ecologists, but the key points here are that grammars are concerned less with the kinds of end products produced than with the rules or processes governing these productions, and that mathematical techniques can

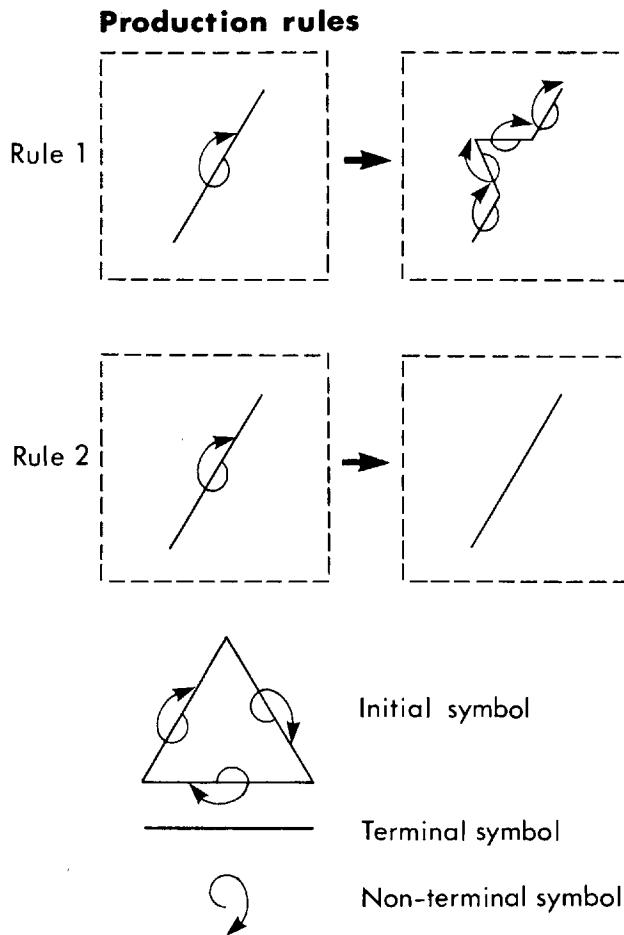


15.2 *The first four curves of the snowflake curve*

be used to prove interesting theorems about classes of grammars, leaving the way open to a replacement of simulation with analysis.

An important development was the work of Hogeweg (Hogeweg and Hesper 1974). Using a specified Lindenmayer grammar (a bracketed propagating deterministic two sided grammar to be precise), she generated examples of tree structures. She then examined, using standard polythetic agglomerative methods, the patterns of trees produced. However, the description of the trees was made using global properties whereas the grammar uses only local operations. The results show that the classes obtained correspond in large measure with the rules of generation, except in certain cases of convergence.

This is, I feel, important; it means that in classifying we may expect to recover at least some of the rules generating the variation. I would argue that where such rules are precisely recovered and can be seen to conform to mechanisms in the underlying biology, then we have a natural classification.



15.3 *A parallel shape grammar for the snowflake curve*

INFERENCE AND DESCRIPTION

While Hogeweg's work is an important demonstration, in general we shall not know the grammar, and our problem becomes one of inference of grammars.

Coulon and Kayser (1978) pointed out that this is not a standard statistical problem. If we examine certain games of chess using statistics we shall discover certain probable sequences of moves, for example, standard opening. However, we shall not discover the

rules (or grammar) of chess. There are, however, procedures for inferring grammars (Biermann and Feldman 1972; Fu and Booth 1975) and it is important to know under what conditions such inference is possible. I shall return to this a little later. Of course we must have examples of sentences in the language generated by the grammar, and hopefully some which are not, for the problem is to generate all and only grammatical sentences. Clearly we must know the terminal symbols, that is the descriptors, for any inference is predicated on the set of descriptions and on the relationships admitted between them. Remember in the snowflakes we had to fix the endpoints of lines and choose lines as primitives.

Relationships are, then, perfectly proper constituents of grammar rules. Unfortunately the surveyors of numerical classifications have been at a great feast of languages and stolen the scraps, for apart from a few preliminary studies (Dale 1968; Williams *et al.* 1969), relationships in the form of logical dependency have always been regarded as a misfortune to be avoided or tolerated. The grammatical basis suggests that the existence of such dependencies is not only acceptable but advantageous, for it limits the selection of further rules for application. It can be argued that the taxonomic hierarchy reflects just such constraints; the genetic productions which resulted in the initial members of high level taxonomic groups also prohibited future application of whole suites of alternative rules.

ERROR AND SIMILARITY

Given that we have decided on our descriptors for vegetation, and can infer grammars from examples, how does this help us in defining an appropriate classification technique? Now the critical point in a classification is the selection of a similarity measure, for the various heuristics for sorting are of no particular fundamental significance. Clearly for any two types of vegetation, A and B, we can take examples and generate a grammar for each type. What we need is a means of comparing them. Fu and Lu (1977) first suggested a means of doing this, which has considerable attractions. By adjoining extra rules to a grammar we can provide means of correcting certain kinds of error. Fu and Lu suggested that for a specified set of permitted errors we could take the type A grammar, expand it for error correction, and generate examples in type B. We must make errors to do this but we can determine the minimum number, and kind, of errors (for probabilistic grammars maximum likelihood estimation if possible). The similarity of type A and type B is then measured by a possibly weighted sum of errors, which in simple cases is a Levenshtein metric (Tanaka and Kasai 1976). Fu and Lu (1977) actually applied this technique to the problem of classifying hand written letters with some success. It clearly is applicable to all our standard coefficients of similarity.

The definition of similarity in terms of minimal numbers of errors is very attractive, because it focuses attention on mechanisms by which one type can be 'converted' to another. Such conversion should of course be a biologically acceptable sequence of processes. For example, the genetic process of mutation is simply a means of producing substitution errors. We may be mistaken in our estimate of similarity since this depends on what errors actually did occur, but our concept of similarity is tied to the allowable

set of errors. To be precise we should also include weighting of different kinds of error, for some errors may be more far reaching than others, but it seems unlikely we shall find any simple means of assigning other than equal weights at least initially.

APPROXIMATE INFERENCE

Grammar theory has now led us to a concept of natural classification, to the notion of similarity as a function of error, and to the importance of determining the descriptors. So far I have assumed that it was necessary to infer the correct grammar for some set of patterns. However, Wharton (1974) has considered the possibility of approximate inference, where the grammar is in some sense close to the correct one. I mentioned earlier the conditions under which inference is known to be impossible for any finite sample if the examples are arbitrarily presented. Wharton showed that it was possible to define a metric between languages so that the degree of approximation of one language by another could be quantified. He then showed that approximation is possible in more cases than exact inference. To be precise any recursively enumerable grammar can be approximated but not all can be exactly inferred. He also showed that if the examples are presented in a particular manner then approximate inference can be obtained in a finite number of samples whereas precise inference is obtained only in the limit.

I have introduced Wharton's work here partly because it is interesting intrinsically, and partly to show that proofs in grammar theory can have practical importance. However, I must now turn to the specifics of vegetation analysis lest you reject my moonwashed apples of wonder.

THE LIQUID MODEL—RING GRAMMAR AND NICHES

Analogy, while often misleading, is the least misleading thing we have, so I shall start from an analogy. I want to suggest that vegetation is not the solid repetitive structure implied by Tansley and Braun-Blanquet, nor the gaseous effluvium of Gleason and Ramensky. Instead I shall suggest that it is analogous to a supercooled liquid, for it has local structure but not global structure. The fundamental ecological principle is not selection but interaction and it is with interaction, its pattern and processes that ecology is concerned. However, this is a microscale phenomenon, and we need other sorts of models for macro variation, just as a liquid theory has two sorts of model. The macro models deal with flow and viscosity, the micro with establishment and competition. Neither is better, 'he does it with better grace, but I do it more natural'.

It is perfectly possible to provide grammatical models for both scales of investigation. The macroscale is equivalent to examining texture in pictures, and there are various proposals in the literature for doing that which I will not discuss here. The microscale is less well served, and I shall start with some work of Mayoh (1974) on the partitioning of France. The idea was to make the partition on religious grounds so that the neighbouring countries each adjoined a part of France of their own creed. This is in fact demonstrably impossible, but Mayoh introduced rings of symbols to represent the surrounding countries, which is very like the point clump sampling of Williams *et al.* (1969). Indeed Cormack (pers. comm.) reports that under any point in a barley field

there are roots of 33 different plants, and this is roughly equivalent to saying that interactions involve neighbours of neighbours of neighbours but no more. Indeed we would expect many fewer important interactions in fixed communities. I propose therefore to describe a plant by a ring of neighbours and use these rings as strings in the grammar inference processing. The rings record the state of neighbouring plants which is not necessarily the species. We must establish some equivalence classes, for otherwise all plants are unique, but the actual choice will reflect our interests. Since writing grammar inference programs is a tedious occupation most unsuited to FORTRAN, progress is somewhat slow, and I have no results to show you as yet of this detailed approach.

A more traditional approach has been adopted by Haeffner (1975) who has attempted to develop an ecological grammar using the niche concept. In effect he establishes an environmental framework, then slots in species until no more can be entered. However, each species can modify the environment and the relationship of the other species already present. Haeffner uses a transformational grammar of some complexity to do this. As a simple example

both

Man's might is exceeded by wisdom and loving
and

To be wise and loved exceeds man's might

are transformations of the same basic structure although they no longer convey the same sense. It is this mapping from underlying structure to surface structure which made transformational grammars useful to linguists. However, the approach is encyclopaedic since we have to record vast amounts of information about each species. As an exercise demonstrating the flexibility of grammars, it is appealing but its major role is, I think, to demonstrate the essential barrenness of the niche concept itself. Just as in succession there is no cure for birth and death except to enjoy the interval, niche theory rather likes asking if you are a beer teetotaller or a champagne teetotaller.

SEMANTICS AND SEX

There remain some intractable problems in vegetation study which will complicate any modelling, and of these sex is by far the most prominent. (Lechery, lechery, still wars and lechery, nothing else holds fashion.) The difficulty is that sexual reproduction, in plants at least, is not necessarily a local affair. We must arrange that our models permit such activity only when appropriate partners are present. We might opt for scattered context grammars where the symbols surrounding other symbols can have arbitrary relationships but we still need what are really semantic constraints to establish that the reproductive operator is only applied in acceptable situations. We can, however, use more complex grammars such as affix grammars (Watt 1977) where such constraints can be established in a formal framework. These grammars are relatively recent introductions and problems of inference have still to be faced (but see Klein 1973). They were originally designed in computer science to establish formal type correspondence across assignment operators, a role very reminiscent of their suggested use in sexual reproduction.

The complexities of grammar theory have their own insidious attractions, and we should always remember that what's done we may partly compute but know not what's resisted. Omar Khayyam talked of the

grape that can by logic absolute
the two and seventy jarring sects confute

and he may be right in more ways than one. One very simple grammatical approach has been adopted by Bradbury and Loya (1978). Using a very simple grammatical inference method, they examined the patterns of coral distribution on a reef with some interesting results. The method certainly requires some increased sophistication, but as much in presenting and interpreting the results as in fundamentals of the inference algorithm. We must always be careful to relate our theoretical exercises to the realities of vegetation. Wherefore I will finish and be wise with speed; a fool at forty is a fool indeed.

REFERENCES

- Biermann, A., and Feldman, J. (1972). A survey of grammatical inference. In: *Frontiers of Pattern Recognition* (ed. S. Watanake), pp. 31-54. Academic Press, New York.
- Bradbury, R. H., and Loya, Y. (1978). A heuristic analysis of spatial pattern of hermatypic corals at Eilat Red Sea. *Amer. Midl. Nat.* **112**: 493-507.
- Coulon, D., and Kayser, D. (1978). Learning criterion and inductive behaviour. *Pattern Recognition* **10**: 19-25.
- Dale, M. B. (1968). On property, structure, numerical taxonomy and data handling. In: *Modern Methods in Plant Taxonomy* (ed. V. H. Heywood), pp. 185-97. Academic Press, New York.
- Fu, K. S., and Booth, T. L. (1975). Grammatical inference introduction and survey Parts I & II. *IEEE Transactions Systems, Man & Cybernetics SMC* **5**: 95-111, 409-23.
- Fu, K. S., and Lu, S. Y. (1977). A clustering procedure for syntactic patterns. *IEEE Trans. Systems, Man & Cybernetics SMC* **7**: 734-42.
- Gips, J. (1974). Shape grammars and their uses. Ph.D. Thesis, Dept of Computer Science, Stanford University.
- Goodall, D. W. (1952). Objective methods for the classification of vegetation. 1. The use of positive interspecific correlation. *Aust. J. Bot.* **1**: 40-63.
- Haeffner, J. W. (1975). Generative grammars that simulate ecological systems. *Simulation Council Proceedings Series* **5**: 189-211.
- Herman, G. T. (1969). The computing ability of a development model for filamentous organisms. *J. Theoret. Biol.* **25**: 421-35.
- Herman, G. T. (1970). Role of environment in development models. *J. Theoret. Biol.* **29**: 329-41.
- Hogeweg, P., and Hesper, B. (1974). A model study on biomorphological description. *Pattern Recognition* **6**: 165-79.
- Klein, S. (1973). Automatic inference of semantic deep structure rules in generative semantic grammars. *Proc. Internat. Conf. on Computational Linguistics, Pisa*, 27/VIII-1/IX Vol. 2, 557-74.
- Lindenmayer, A. (1968). Mathematical models for cellular interaction in development, 1. Filaments with one sided inputs. *J. Theoret. Biol.* **18**: 280-99.
- Lu, S. Y., and Fu, K. S. (1977). Stochastic error correction syntax analysis for recognition of noisy pattern. *IEEE Trans. Computing CT* **25**: 1268-77.
- Mayoh, B. H. (1974). Multidimensional Lindenmayer organisms. In: *Lecture Notes in Computer Science* No. 15 (ed. G. Goos and E. Hartmanis), 302-26.

- Reusch, P. J. A. (1976). A common approach to retrieval concepts and multidimensional developmental systems based on lattice-like structures Pt III. In: *Gesellschaft für Mathematik und Dataverarbeitung mbH*. Bonn Bericht Nr. 90, 1-70.
- Tanaka, E., and Kasai T. (1976). Synchronization and substitution error correcting codes for Levenshtein metrics. *IEEE Trans. Information Theory IT 22*: 156-62.
- Watt, D. A. (1977). The parsing problem for affix grammars. *Acta Informatica 8*: 1-20.
- Wharton, R. M. (1974). Approximate language identification. *Information and Control 26*: 369-74.
- Williams, W. T., Lance, G. N., Webb, L. G. J., Tracey, J. G., and Connell, J. H. (1969). Studies in the numerical analysis of complex rain forest communities. IV. A method for the elucidation of small scale pattern. *J. Ecol. 57*: 635-54.

The separation of traditionally mapped land cover classes by LANDSAT data

E. M. ADOMEIT, D. L. B. JUPP, C. MARGULES and
K. K. MAYO*

INTRODUCTION

Traditional techniques for mapping land resources, used in the Division of Land Use Research, CSIRO (Christian and Stewart 1968; Austin and Basinski 1978), appear to be reasonably cost effective in terms of time and money. However, effective mapping of the changeable features of the landscape, such as vegetation and surface hydrology, is handicapped by the lack of up-to-date aerial photography. Often land resource maps are compiled using relatively old photography, in which case the changeable features must be mapped by ground survey, or else photography must be commissioned—both fairly expensive procedures.

LANDSAT provides a possible additional (or alternative) source of up-to-date and relatively inexpensive data for mapping, and there is great interest in the opportunity it may provide for monitoring general land cover, and land use changes. At present, the delay in receiving the data may be six months or more but (we hope) when Australia's planned receiving station becomes operational the delays will be considerably less.

The aim of current research is to determine whether LANDSAT data are 'discriminating' enough to provide the same, or similar, divisions of land as traditional mapping techniques, in which an interpreter uses aerial photography to identify land patterns which assist in the mapping and description of land attributes. The work reported here is an initial investigation using a statistical comparison between the results of such a traditional mapping exercise, and the distributions of LANDSAT reflectances covering the same area.

LAND COVER MAPPING FROM AERIAL PHOTOGRAPHS

The study area comprises approximately 30 km² on the south coast of New South Wales, surrounding and including the township of Batemans Bay, and lies within the larger area covered by the South Coast Project (Austin and Cocks 1978), a study of methods for collecting and analysing data for regional land use planning carried out by the CSIRO Division of Land Use Research.

* Contact author.

Aerial photograph interpretation and mapping by members of the study team with field experience in this region resulted in a map and summary description of the surface land resources and current land use.

A scale of 1:25 000 was chosen for this map because:

- (a) it was the scale chosen for the South Coast Project, and therefore permitted direct comparison with its data base;
- (b) topographic maps at that scale were readily available; and
- (c) 1977 colour aerial photographs, nominally at that scale, were available in stereo pairs.

The initial mapping and description were made from the 1977 colour aerial photographs and the South Coast Project data. The boundaries and descriptions were then checked during a brief field visit. Some subsequent changes were made, mainly to the descriptions.

The description was developed as a two-level hierarchical classification, consisting of five geographically discrete classes which were further subdivided into a total of 26 sub-classes. Table 16.1 lists these classes, and gives the sub-class descriptions together

TABLE 16.1
Descriptions of land cover classes and sub-classes

Class	Sub-class description
(1) Urban	1 - built-up 2 - developed open space (e.g. playing fields) 5 - undeveloped open space (with some tree cover) S - unfinished development T - hind dunes and swales within urban areas
(2) Forests	E - very dense forest F - very sparse forest G - intermediate forest D - forest regeneration H - partly cleared forest Q - roads and road verges within forest areas 4 - areas of impeded drainage with forest cover (mixed eucalypts and casuarinas)
(3) Swamps	C - mangrove woodlands B - samphire shrub (herb) lands A - mixed (samphire, scattered mangroves, reedlands and minor channels) P - low, tree-covered rises
(4) Cleared and regrowing land	3 - pastures J - bare ground 6 - degenerating pasture (woody regeneration) I - recent clearing with scattered trees remaining O - cleared alluvial flats (known to be subject to inundation)
(5) Open water and water's edge	R - open water M - channels (with scattered mangroves) U - mud banks (usually with oyster racks) 9 - sand banks 8 - beaches

with the symbols used later in the graphs and maps. The 'contextual' (in the sense that adjacent classes influence the classification of an area) nature and land use character of the classes is clear from Table 16.1. For example, subclass Q (roads in forests) is included in the 'Forests' class, and subclass 8 (beaches) is included in the 'Water and waters' edge' class, while subclass 5 (undeveloped open space) contains grassland and forested areas associated with urban areas and hence is in the 'Urban' class.

Some subclasses within the Forests class reflect the effect of aspect to the sun. Slopes facing south to south-east are, on average, cooler and moister than slopes facing north to north-west. The two ends of the associated forest cover gradient associated with this effect are easily recognised by the denser growth on the southern slopes (subclass E) relative to the sparser growth on the northern slopes (subclass F). In the northern part of the study area, relief is lower, reducing this aspect effect, and forest cover there which does not seem to fit either description has been classified as 'intermediate'.

The boundaries were then transferred onto a black-and-white orthophotomap of scale 1:25 000 (Fig. 16.1) which had been compiled from black-and-white aerial photographs (of scale 1:40 000) taken in September 1975, one month before the LANDSAT image was recorded. During this process, adjustments, based on the 1975 black-and-white photographs, were made to the map to match it as closely as possible with the conditions prevailing during the LANDSAT overpass. For example, some of the extensive clearing visible on the 1977 colour photographs had not occurred in 1975.

Because of the time differences, the map does not exactly represent land cover as it was in September 1975; however, it is as accurate as available information (other than the LANDSAT data) allows.

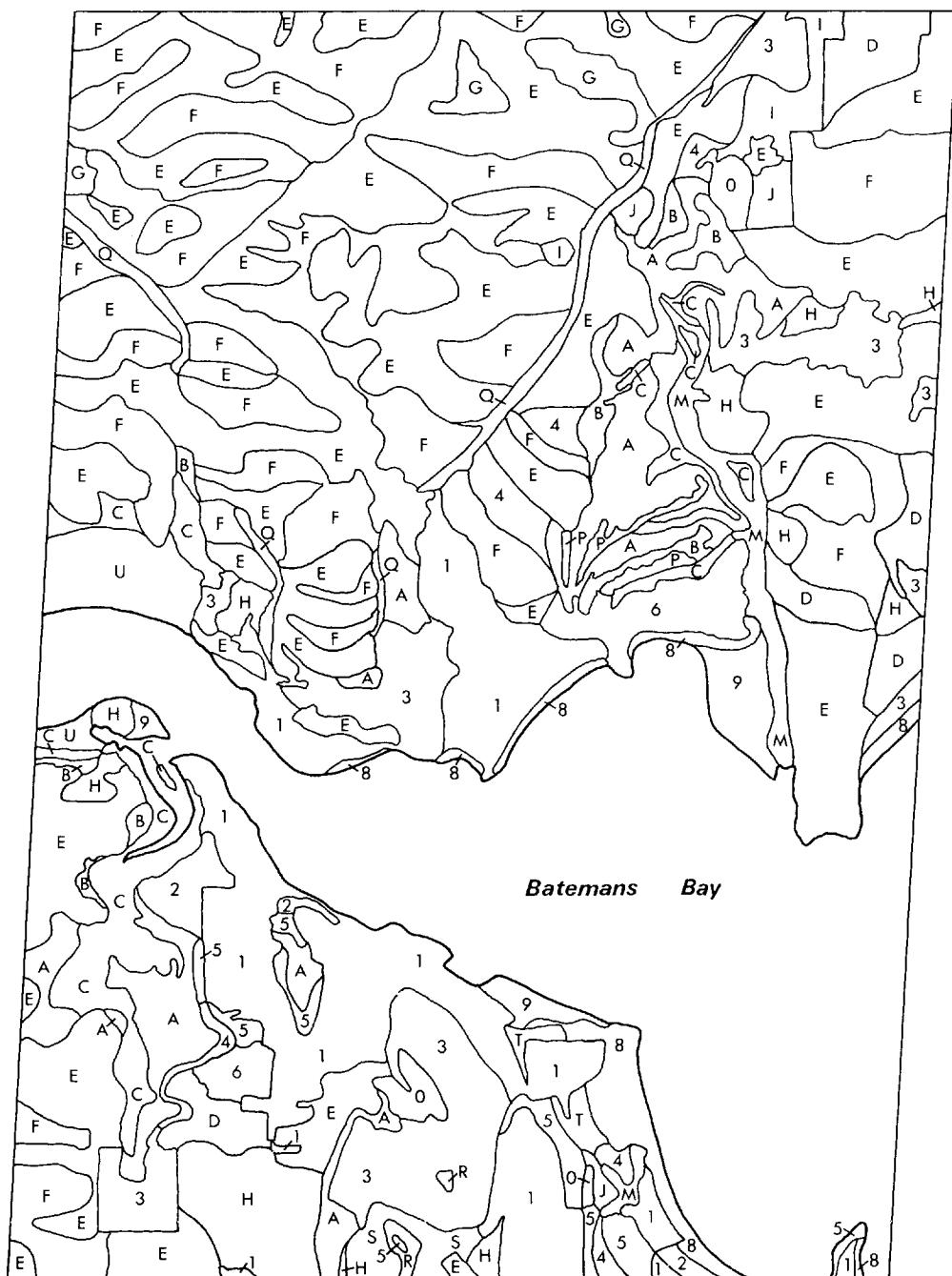
LOCATING THE LANDSAT DATA IN THE STUDY AREA

The study area is covered by 6640 pixels, each of which represents an area on the ground of approximately 80×80 m (or 3×3 mm on a 1:25 000 map), and forms the basic spatial unit of LANDSAT data. Each pixel is characterised by four reflectance values representing the intensity of light received by the satellite in each of a green, red, and two infra-red frequency bands.

It was crucial for this exercise that the pixels be located as accurately as possible on the land cover map so that a class, or subclass, could be coded for each one. LANDSAT data, however, do not provide individual pixels with geographical co-ordinates, and registration of the scene requires some prior analysis of the data.

This analysis usually involves both correcting for geographic distortions in the LANDSAT data, as described in Appendix 16.1, and identification of some pixels as 'recognisable' ground features with known geographic co-ordinates. For example, visual matching using false colour composite images has been used, as have colour displays equipped with a cursor to record the pixels matched with ground features (MacDonnell 1978).

For this exercise, a different approach was developed. The pixels were simultaneously located by aligning the map with a 'pixel grid'. This consisted of a geometrically



16.1 Land cover sub-class boundaries which can be superimposed on the orthophoto. Refer Table 16.1 for coding

corrected (see Appendix 16.1) and finely drawn mesh outlining pixel boundaries, produced by a CALCOMP plotter at the scale of 1:25 000.

An initial classification of the pixels in this grid, which appeared to define some very well-separated and identifiable classes, was available. The classification method is described briefly in Austin and Mayo (1978). This prior classification was attached to the pixel grid, and aligned using the easily recognisable ground features such as open water, beaches, channels, sand banks, swamp areas, pastures and linear features such as roads, so that similarly designated units agreed. Although using the prior classification in this way must introduce some loading in favour of the above classes into the later analysis, their spectral properties (or 'signatures') are *so* distinctive in the coastal situation (cf. the canonical variates plot (Fig. 16.3), and its discussion) that its effect on the conclusions concerning land cover is unlikely to be significant. It is important, however, to notice that this method of alignment depends on the presence of such distinctive classes.

Following the careful matching of the LANDSAT data and the orthophotomap, the land cover class and sub-class derived from the mapping was coded for each pixel using the aligned pixel grid as reference (Fig. 16.2). The only significant problem was to decide into which class to code a pixel covering more than one mapped class. In such cases, a decision was made logically on the basis of dominant area.

ANALYSIS OF SPECTRAL SEPARATION BETWEEN CLASSES

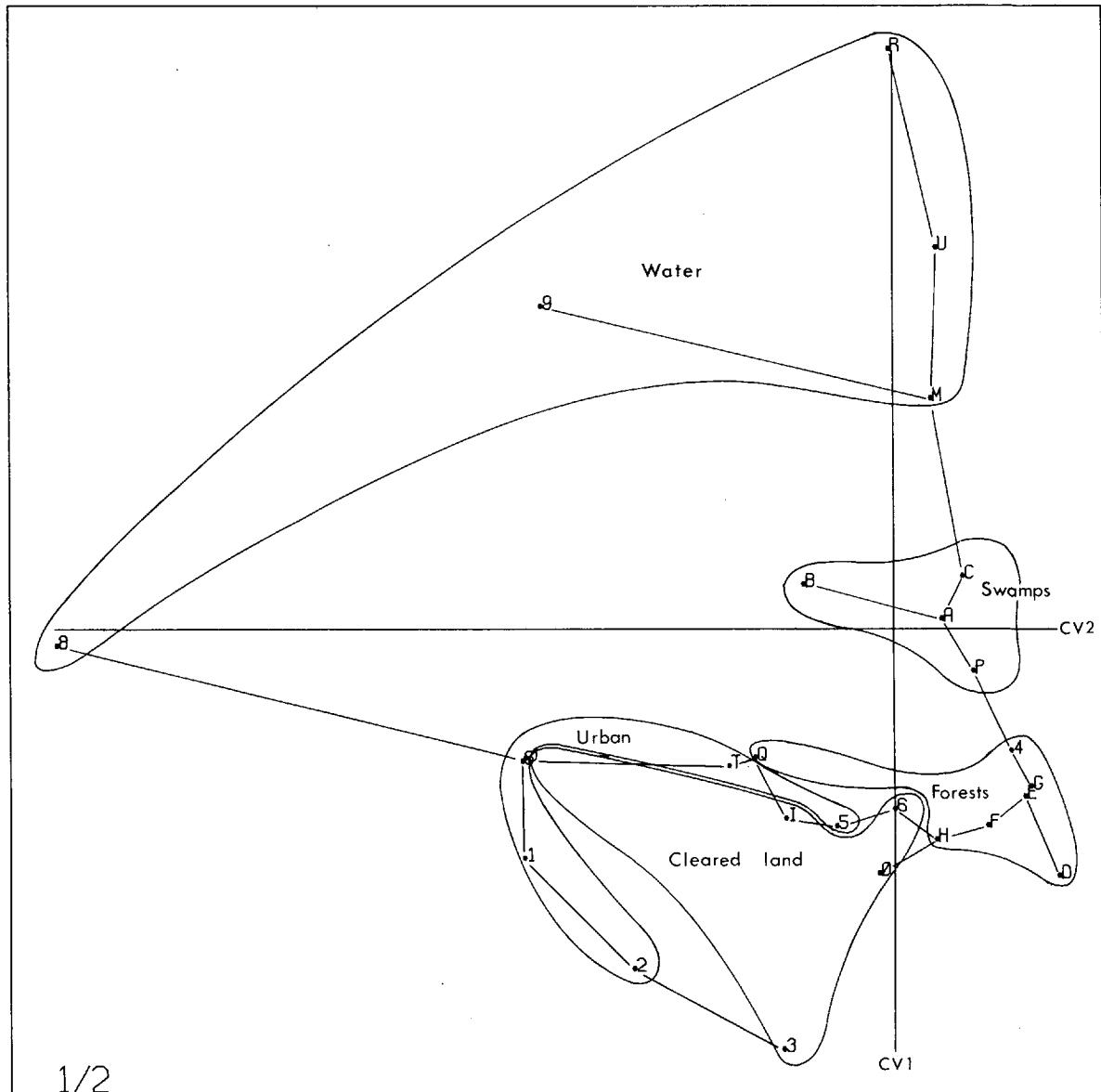
The spectral 'signature' of a class of pixels is defined here by the means, and variances and covariances (or dispersion) of the reflectances. Land classes are said to be well-separated spectrally if their 'signatures' are distinct in that the class means are well-separated relative to the dispersion of reflectance values within the classes.

The separation between the mapped classes was therefore measured by the Mahalanobis distance statistic, (e.g. as described in Rao 1952; or Hope 1968), and examined graphically by canonical variates analysis. A computer program (CANAL), written by D. Ratcliff of CSIRO Division of Mathematics and Statistics, was available for the analysis which provided additional information to the standard ORSER program of the same name (O'Callaghan and Turner 1977). The mathematics are summarised, in more detail, in Appendix 16.2.

The Mahalanobis distance (see Appendix 16.2) is a useful measure of 'similarity' between the reflectances of a given pixel and the 'signature' of a mapped class. The distance may also be used to measure the spectral separation between the classes, as described in Appendix 16.2, and a statistical F-test of the significance of the separation, which concentrates attention on the poorly separated subclasses, is available (cf. Rao 1952).

Transformation of the LANDSAT data to canonical variates provides a graphical display of the between sub-class separation, and the Mahalanobis distance. In Fig. 16.3, the transformed means of the 26 sub-classes are graphed in terms of the first two canonical co-ordinates. These first two transformed variables are constructed from the two highly correlated pairs of channels—4 and 5 ($r=0.919$), and 6 and 7 ($r=0.904$)—

which account for 96 per cent of the discriminating power in the data. While the third canonical variate is important for classification accuracy for some groups, its small contribution to the *total* discriminating power is apparent from the open nature of the



16.3 Transformed sub-class means plotted against canonical variates 1 and 2, with superimposed 'minimum spanning tree'

'minimum spanning tree' (Gower and Ross 1969) which is drawn linking close neighbours among the subclass means.

The transformation to canonical variates means that the euclidean distance between transformed points is the Mahalanobis distance. Moreover, a circle of radius one about any of the transformed means represents one 'standard deviation' of the pooled within sub-classes dispersion. That is, if plotted means are 'close' in both Figs. 16.3 and 16.4, the Mahalanobis distance is 'small', and if they are within radius one, then considerable overlap exists between the classes, even when the Mahalanobis distance is judged 'significant'.

The broad classes are also indicated on Fig. 16.2, and an obvious result is the clear separation of the Water and Swamp classes from Forests, Cleared Land, and Urban. This discrimination between water and land, as well as the within-class separation between beaches (8), sand banks (9), open water (12), and channels and mud banks (M and U) was an important factor in the accurate alignment of the grid. It is interesting, however, that the minimum spanning tree linked beaches (8) with bare ground (J) rather than sand banks (9).

The sub-classes of the Forests, Cleared Land, and Urban classes are much less distinct, and in particular, the various Forest sub-classes are very poorly separated in terms of Mahalanobis distance. In Table 16.2 pairs of sub-classes are listed in order of increasing Mahalanobis distance (D^2), together with the number of pixels in each sub-class (n_1 and n_2) and the F-ratio associated with them. The significance of the F-ratio is indicated

TABLE 16.2
Poorly separated sub-classes

Sub-class 1	Sub-class 2	n_1	n_2	D^2	F	Sig.
E	G	1655	64	0.0562	0.8652	
G	4	64	66	0.1420	1.1532	
A	C	313	190	0.1701	5.0253	**
H	6	187	88	0.1754	2.6231	*
E	F	1655	941	0.1969	29.5705	**
E	4	1655	66	0.1990	3.1556	*
F	G	941	64	0.2116	3.1689	*
F	H	941	187	0.2302	8.9748	**
S	6	63	88	0.2476	2.2713	*
H	O	187	35	0.3299	2.4501	*
O	5	35	63	0.3202	1.8005	
I	Q	45	49	0.3731	2.1867	*
J	S	26	34	0.3817	1.4052	
A	P	313	19	0.4975	2.2267	*
F	4	941	66	0.4980	7.6755	**
F	6	941	88	0.5056	10.17	**
O	6	35	88	0.5099	3.19	*
H	5	187	63	0.5126	6.036	**
Q	T	49	16	0.5653	1.704	
E	H	1655	187	0.5757	24.17	**

** p = <0.01

* p = <0.05

PEEEEEEGGG0DDD E EEPAPR4P4 PGPPPGCPFFFF EE4G4GGGD P G E4GG DEGF00 21QJQF EGD
 4GEE G FD FEDD E4APE FGPPPAAPGEGF GPFP GP DDEPG44FDE DD00 520155QF FE GG
 D 444 4CG4GC4 H 44 4GPIB4A4 C 40P4P4 E444C4G 444 4D GD00 0I IGGPE E DD4
 P44PPP0PPP GGGCCP DD E66 TACP44 DDD P4PPGE4EE44 PG4P4445120 0TPPP44EGE GP
 P4G444GP44PG44PP4 C 01 GAP DD4DGF 4PP44 GDDDF4EE4 G GF11D06 2 0ITEC 4 DDD
 4PPP G P4PPPPP0PPP0DD EEF DD 4PP EPP444F FFE444 D60 G01JS 0 Q4FEC4 4DD4 4
 PGGE GGGPGCE44EDEGGEGCPCP DD DFDDDDDEDEDD44GPGG GDGF 4164 GCGSSS PGGGC4G GG4 4
 PGP 4PPGP0DED6I1H PPPP44 GG DD DD0FD04COP FF 4 F1BPPG405TS Q504 4D4 DDD
 44444FPE44P GG GFIFFH 444F4DE444C DD PFG D 444F4 P111 6P4 4D0DEDDDD
 E PGPF4PP4 P PG4PFDE4 4DDEEEGEPF 4DDEG4PDDDP G4PPA DDTTPGPEDDDDD
 4E 4PPPG4GG 4G4P4P4 GFDPFGDDD D DDD DD D 4P DDF4 G H F02T1 DDDDDDD
 4PP G4PPPG44G4P4P4 4G PG FFP4GGDDDGDDG G4G4G1 SQSP C P4PSBB00ED4D030EGG40
 4PPGGGG F44E4EGGP4 4G PG FFP4GGDDDGDDG G4G4G1 SQSP C P4PSBB00ED4D030EGG40
 644GGH5F E4E4PG44 F 4EGGP FGPP44H4D4 E 444D66 SSSQA BAAAJ B FDDDE DDDDE E5
 TS644EEPP 44P46 4FDDG4P E444E4E44 FDD D0PFB OF BB PFII10FEEDEDDDD FDD
 CQJJAP444PPPEFFP 4P4P4 DE 4P4CF P DDEFE60 6T4PACCBCCC P4DF D4P4GDDDD DDD
 4PTST PPGF4DGDGDD4P4FDFG4 E 444DDE F0 I6D GBC BSSSSB 4DDBB DDDDD
 P4FQ1JQ EP GP46 CPPP444GP4 0DGPFPFD0D00 GG BMBBBC MCPGCG PDD GD 4D
 EP444GPATFQ DDD 0 H0GE EG44 DD GPPRA4PG6F D DDCGCG MBBB AMBFPF GD0 P4 CGD
 PPPPPPPPTP PFF D64H06EFF P444D0D0DD TBBP4F4GG 4M CMWBBT T 04PPD3 DPF4CFP
 G44 4P44F10PGP4 4 FF 444GGGD 61111156444 CPP M C1B2 0C44DE40 P4P4
 GC E 444FFII 0PPPPG4D G4G4G4F4G0C4 41111156444 CPP M C1B2 0C44DE40 P4P4
 444G64 0 H 0 CPP 4GFD4E CPPP4K 41111156444 CPP M C1B2 0C44DE40 P4P4
 D FPPF II4PGGFF 4P 4GFD4E CPPP4K 41111156444 CPP M C1B2 0C44DE40 P4P4
 GD FPPG IDE F E 4E4P GDD444ERF0M1J0JSSQF DDDDBBAM CUUHRG0D4 DDDDD
 4GFF EP44PG4TH PE4EEEPPG46444 JSSSB5J81414GPDG4B CCCMC 4DDDD DGDFDDDD 0000
 DG4EE H GCCCP111 HDE4C4 6 4 1111111101 E DF CC AUVC4DD4 4D4GDDDD
 E4EEE 0DDECCCAPI 4D4 4DD4 PP 111601P11TPDE4DGB CCCMC MUC4DDD D F4 DDDDD 4 G
 FGGDDF DH PACCA16444CPGDGG4P 0 6 6 DD D DDF C CM UUCCFGDDDD DDDDD
 4 GGGP D0 PMCPPI6 DD PDF4P4 44650D 4GDD D08C CCCM M U M PGDDDDDDDDDD
 4 G GGGHHA CGPAISH0DH E4FH P4G 1STDDDD ECDDDD PCP CC PMUU MEDDDDD
 FD APG4 A CPPPPF444 446 P4PTST DD P4 4FPCPCPCCCCCMUUMV4D0DDDDDDDDDD3D
 G D04 CE C44PFP4 4 H H644FPP6 6DDDDG 4GDFCCC ACC C UUUC4DDD 4DD3
 A PP M 4EP CCP H6DEPP6E P444HT066 DE G PC4C BP P CC MUU444DE4E4 DDD
 MHHHHH MAA APPG1 0G 0 D FG4FQT05 DDDDFP 44 C C C A CPAU GD0DDDD
 M CPP1TPP60DFGF64F4109TQDDDDGDP 44 C C C A CPAU GD0DDDD
 M 4GPGPFDDG4G 0TPPPIFT116 HDDDPFP PPP A P APPTCUC4EGDDDGDD3 DE
 R R P0E4P DF4DF 61CP4P1TS1ST DDD B G PPPPCPFD4ABK 4 FG 4D03330A
 R MQ F4FF1JP4DE EDTTM4ET6P4T7D DDFBF IF44DH D0F00FARRA 4G 33330
 UR PIIPPT PPP4P4P445PMCP46T640TFDDDDP10 HQOSI H000J9UCP444 EE 330DD
 RCIFFJ 6FPP 0 PH52 300F10TSOSF05FHH0DFO00050H0001 UPFDDDDDD3D 3
 MCPI1 6P4 6ST 22 0F6T1S1J I J 6 T99 UU9B8J18 U 4 DDDDD 333
 UARPH0T100PGG11000 2 004F60T102 88J50UUUU UP GDDDD 333
 U C JT01QTPCMPT T ISJII 9U MMU AGGGFDDD 331
 UBJ 1 212 D 0 JSJ 9U RU U 4G44DDD3 1J
 M4D6B9U MT20T 00T S 9 R R BPGP GD3 31S
 U U4A4B 9 U0B20 DDD0 DDD0D0T S8 U UPD4D33218 9
 UU RU U UJ2332 SPTT05505T 8 9URRC4 GD38 9
 B B ABTAMUUMT99UUU UT2 88 8999J88 8J RUP44 3399
 D IIQD3H MCT S89 M J8 999999 999999
 D0 DDD04DDP M C0 89 U UU M4GCD319
 DDDDDDDDDF BA U 2 899 U U UGDDDD0
 DDD DDD 9 M MP 8889 U U C MMMCU
 DDDDD GCP C 45 32 89 U U UU VV
 DDD44BB MMHP42 3338889 U U UU
 DDDDBBB 46 3 1 3 8889 U U UU
 DDFBB F 3331 2 885 999 9
 D44GGDUF F 1122 2 8 301619 U
 DD BBCCP BBA 3 J23 2301T53 B999
 FBBBBB ABB 61T22 SDH001 2 J 19U
 F BBBB BBBBPRABT1032321BC622232 289 U
 F BBB4AABBBBBBBA F 32 2PC6322322 2 S9U
 0 BPPP BBD 432 22230F532 22 22 89
 IPAPPPP AP PD332 10D22 2222 33222 18 UUU
 P BBBBPF4 HEFD02 23 222 3 88 89 9U
 R A DDEP BBMCPED03 237 2 2 2 TJ158 S 9
 644444 D4DAB BUUM P E02 222 3 18888888
 0F44DDDDDE B AGPF32 222 2 2D 3 J1J988888 9
 H0 44DD4 CP4 FFFF552 J0 23300 6 308 8888 8
 FDFDDDDDPDPRACAG FFFT5SJ8 S0DDDHDF 8 B 10J
 4F0GGDDDDGE CCAPG4GP185 2 S5DD 4DDFF66 0632 T66FJ 9
 E0166DGP F PFFEET 4EC D08S0DD03 0PE23330 0F123THFFI 8
 P055H64DPMAPAE 4P4461FH0DD0 TT 220T1511 9
 FF4EDDOF C60056 FF4F1020DDF 21 J2221JJ1JJ 9
 4G FF4 GF0H4P52TF1J20 0I10DHD0 2T 2 11TQ 220IBCPB 9
 4P D0D0FD03H204CP101T01030D0 B2 1J1TPF220DTSTMJ 9
 G4 551600H2 54EPPPT10303DFP0 TIPS ITTS233TSSBB88
 DG 000HDF055120F0FFFF6F00000DPCA1JJJ2 1TJITFTS 1I AQ 8B 9
 00FD004D6F00BHEFF100F4 EPMP51199Q1SSSJ10S111T1H622 9 9 UUUAB99
 D HH 0E44 DDD P4TSIF0EDG4CC J9991 1FFF1 TT 1IFCBFD022 9 AII9
 P4D00D01 H HF 4PP4G1T0F20D0EPP J 991 P1PPFIJSSJ J1HPCPE2 1 9 U UM09
 PP DDD11 FDDD 44P4P1J1J2051FFP 1BB JAP4402 TQJIS0DPMAT 11 2 9 VU UVA299

16.4 Pixels which were re-classified to a new sub-class, shown plotted on the geometrically corrected 'pixel grid'

by * and ** for significance at the 10 per cent and 1 per cent levels respectively. However, given the small D^2 values, all of the sub-classes shown overlap considerably.

THE POORLY SEPARATED SUBCLASSES

The analysis focuses attention on two groups of poorly separated subclasses, essentially from the Forest and Cleared Land classes, which need discussion in biophysical terms.

Group 1

Densest forest (E), sparsest forest (F), intermediate forest (G) and areas of impeded drainage with forest cover (4) form the tightest group, with E and G being unresolvable by LANDSAT spectral data. However, Fig. 16.3 suggests that there is a gradient between sub-class 4, which is closest to the swamp class, through overlapping forest types to sub-class F and further to H, which is partly cleared forest. The well-separated forest sub-class D represents forest regeneration, and consists of green, highly reflective acacias and immature eucalypts.

The lack of any spectral separation between sub-classes E and G was not entirely unexpected, since the original distinction was made on the basis of tone, colour and (importantly) texture, as perceived by the mapper using the colour photographs in stereo.

Group 2

Partly cleared forest (H), cleared alluvial flats (subject to inundation) (O), degenerating pasture (woody regeneration) (6), and undeveloped open space (5) are from three contextually different classes (Forest, Cleared Land, and Urban). Inspection of the areas mapped as 6 and O show, however, that they both have a sparse tree cover, and, together with H and 5, represent areas disturbed in some way by man. These areas have a similar regenerating tree cover, and were mapped using local knowledge as well as differences in photographic pattern. The position of this group in Fig. 16.3 between the main forest and urban sub-classes suggests an interesting gradient of disturbance and regeneration.

REALLOCATION OF PIXELS

The Mahalanobis distance provided a decision rule, or discriminant function, for allocating a pixel to a sub-class on the basis of its reflectance values. The rule is simply to assign it to the sub-class with *smallest* distance, or in terms of the canonical variate plot (Fig. 16.3), to the *nearest* mean.

A useful means of testing the discriminant function is to apply it to each pixel and record the class, or sub-class, to which it is allocated. The resulting contingency table, or 'confusion matrix', showing the number of pixels reallocated by the rule to each of the originally defined classes, measures, to some degree, the effectiveness of the discriminant function as a trained classifier.

Table 16.3 shows the confusion matrix for the five classes, and except for the Cleared Land class shows reasonably successful classification. The overall percentage of correctly reallocated pixels (sum of diagonal as a percentage of the total) is 79 per cent

TABLE 16.3
Confusion matrix for broad classes of land cover

	Urban	Forests	Swamps	Cleared	Water	% of original cover
Urban	416	73	50	121	7	62.4
Forests	95	2488	295	223	6	80.1
Swamps	3	66	493	8	5	85.7
Cleared	76	125	51	296	0	54.0
Water	77	3	107	1	1555	89.2

which, given the geographic definition of the classes, and particularly the contextual nature of the cleared class, is acceptable.

In Table 16.4, however, the confusion matrix for the 26 sub-classes shows considerable reallocation. The densest forest sub-class (E), for example, has been reallocated to every other sub-class except open water, and the overall percentage of correctly allocated pixels is only 39.8 per cent.

There is no doubt that some of these problems may be attributed to

1. differences between the land cover map and the true situation during the LANDSAT overpass (including tidal differences, extra clearing of land, and the effects of recent rainfall);
2. boundary decisions based on dominant land cover within an area being overruled by dominant reflectances, and poor representation of small patches by pixels;
3. remaining errors in the LANDSAT data, such as the striping effect in channel 6 and lack of radiometric resolution (Merembeck *et al.* 1974), and
4. the simplicity of the discriminant function, which takes no account, for example, of the different dispersions within each sub-class.

However, the confusion matrix listed is likely to be optimistic as a measure of the predictive ability of the rule (Lachenbruch and Mickey 1968), since the test set is the same as the training set and much more attention to the problems it displays is needed.

At this stage, one likely reason for the reallocation problems among the forest and cleared land classes is the use of different scales of pattern in the mapping and discriminant function classifications. The human interpreter, faced with similar spectral overlap between the classes as the LANDSAT discriminant, intuitively takes into account spatial pattern, or texture, in a neighbourhood of the point of attention in his decision, whereas the discriminant function reduces the focus to a single pixel.

The breaking down of a single class, mapped in terms of spatial patterns, such as densest forest (E), to a mosaic of diverse classes is illustrated in Fig. 16.4. This plots the pixels which were reallocated and the class to which they were assigned. Figure 16.4 also shows how well the discriminant function works for sub-classes such as open water and pasture. In addition the hatched area on Fig. 16.4 shows a cleared area, 'found' by LANDSAT, which was cleared in the month between the black-and-white photography and the LANDSAT overpass.

TABLE 16.4

Confusion matrix for the 26 sub-classes

	1	2	5	S	T	E	F	G	D	H	4	Q	A	B	C	P	3	J	6	I	O	R	M	8	9	U	% correctly classified
Urban	1	156	83	3	27	40	1	6	1	1	3	15	1	2	3	4	25	29	7	37	14	2	54	2	30.2		
	2	7	15	1			1						1	2	2	7	1	2	1	1						39.5	
	5	7	3	5	4	4	1	4	1	2	2	1	2	2	2	8	1	2	6	4	1	2			4.8		
	S	4			1							1	1					6	3			3				41.2	
	T	3	1	1	2		2		1			1		1			1	1	2							12.5	
Forests	E	3	3	6	8	13	257	121	209	371	10244	4	15	13	21228	18	7	15	28	51	5	2	1	2	15.5		
	F	11	6	7	112	185	64203	23	101	5	7	2	8	93	8	18	24	27	31	1	5					19.7	
	G	1	16	5	11	11	14						5						1							17.2	
	D		14	5	16	68							2						2	1	2					46.9	
	H	1	3	3	1	7	7	22	7	39	5	19	3	1	1	14	12	3	3	11	23	1	1	1	2.7		
	4		5	4	6	14	2	17			2	2	3	9				1								25.8	
	Q	1	1	3	5	3	1	1	1	9			3				5	7	6	2		2			18.4		
Swamps	A	1	3	2	9	2	1	2	12	1	81	47	73	45	3		2	7		20		2				25.9	
	B	3	1	3	3	2	1	8			27	21	71	27			1			2		1			58.5		
	C	1				1															17		7		37.4		
	P										2	1	2	11											57.9		
Cleared	3	4	19	8	5	9	2	5	12	3	1	2	4	1	6	201	5	3	17	43	4				56.8		
	J	1	7	2		1							4				5	1			5				19.2		
	6	1	7	3	1	14	5	6	3	6	2	2	3	8	1	1	6	4	13	1	1			6.8			
	1	2	1	2	5	3	1	1	7				3	3	2	14	2								31.1		
	O	1	1	3	1	4	3	1	1	2			2	3	3	1	4	7							20.0		
Walter	R	1		1			2	1			3	4	2	1			1	1	1	1290	5	9	61	64	89.4		
	M	8	3	1	1							6	4	11	2			4	22	1	25				27.5		
	9	1										1	2							58	7				70.7		
	U																		7	5	41	3	68.3				
	N.I.																		5	8	64		82.1				

CONCLUSIONS

The 'broad' classes consisting of Urban, Forest, Swamp, Cleared Land, and Water categories were found, despite their contextual definition, to be well-separated in the LANDSAT spectral data.

Among the sub-classes, open water (R), beaches (8), sand banks (9), and channels and mud banks (M and U) separate well, confirming the demonstrated value of LANDSAT in coastal and estuarine studies (cf. Carter and Schubert 1974; Bukata *et al.* 1977). Although pastures (3), forest regeneration (D), and developed urban sub-classes (1 and 2) separate well, the implication of the poor separation of the forest, cleared land and some urban sub-classes might be that aerial photograph interpretation currently remains the best means of traditional land cover mapping at the scale considered here. This conclusion is in accord with the findings of Thie (1976) in Canada.

There remains, however, the possibility that more refined methods which account for spatial pattern and texture might considerably improve classifications based on LANDSAT data. Tubbs and Coberly (1978), for example, have shown how spatial auto-correlation between pixel reflectances can disturb a discriminant function like the one used in this paper. More positively, since the human eye can perceive, in false colour composite images of the study area, patterns based on aspects such as those used by the mapper to differentiate forest sub-classes, there is reason to suppose that a more appropriate classification method might do the same. While there has been considerable work on texture analysis (cf. Haralick and Shanmugam 1974) there remain difficult problems of relating patterns in LANDSAT data with these patterns relevant to the objectives and scale of air-photograph based land cover maps.

APPENDIX 16.1

ERRORS IN THE LANDSAT DATA AFFECTING PIXEL LOCATION

In this type of exercise, several types of distortion inherent in any LANDSAT scene must be considered.

1. *Earth-related errors*

The most important is due to the rotation of the earth during the time taken for the scanner to scan one line. As there are six scanners operating in parallel, this results in a systematic latitude dependent shift every 6 scanlines,

$$\text{shift} = 34 \cos(\text{latitude})$$

The two other earth related errors, earth curvature and earth oblateness, should be insignificant over such a small area, and were ignored.

2. *Platform errors*

These only occur between scenes, and do not affect a single scene.

3. Sensor errors

These include scan angle error, scan non-linearity and mirror speed error, and also the very important aspect ratio distortion. Scan angle error should have been negligible, as the study area is located near the centre of the scene. Scan non-linearity and non-constant mirror speed were also assumed zero, as the scanline length of the study area (80 pixels) is so small that errors should be constant. The aspect ratio was corrected by showing only the non-overlapping part of each pixel, so that each pixel became effectively 57.10×79.06 metres, instead of 80×80 metres.

APPENDIX 16.2 MEASURING CLASS 'SEPARATION'

1. Mahalanobis distance

Let x_{ij} be the j 'th of n_i individuals making up the i 'th class of a total of q classes of p -variate samples and let $N = \sum_{i=1}^q n_i$ be the total number of such individuals.

For example, for LANDSAT data, $p = 4$ and \underline{x}_{ij} is the vector of the four reflectances for the j 'th pixel out of n_i which were coded to (sub) class i . If the pixels are assumed to be independent samples from the classes (an assumption questioned in the conclusions to this study) and each class is $N(\mu_i, \Sigma)$ for constant covariance matrix Σ then the Mahalanobis distance between a pixel \underline{z} and the i 'th class is defined to be

$$D_i^2 = (\underline{z} - \mu_i)^T \Sigma^{-1} (\underline{z} - \mu_i).$$

The Mahalanobis distance between the i 'th and j 'th classes is similarly defined to be

$$D_{ij}^2 = (\mu_i - \mu_j)^T \Sigma^{-1} (\mu_i - \mu_j)$$

and provides an 'optimally' weighted measure of separation between the classes.

Under the assumption of multivariate normality (Hawkins and Rasmussen 1973) if \underline{z} is a pixel from group i , then D_i^2 and D_j^2 respectively follow central and non-central chi-squared distributions with p degrees of freedom and non centrality D_{ij}^2 . That is,

$$E(D_i^2) = p,$$

$$\text{and } E(D_j^2) = p + D_{ij}^2.$$

The probability, therefore, that \underline{z} would be correctly classified to group i depends on the size of D_{ij}^2 . If D_{ij}^2 is large the probability of this classification is large.

In practice, sample estimates are used instead of μ_i , and Σ is estimated by the pooled within-class dispersion matrix (Hope 1968). Since in this study, some of the classes contain relatively few pixels, and the dispersion differs considerably between groups, the use of D_{ij}^2 is more to calibrate decisions than to make strict inferences.

Morrison's (1967) version of Rao's (1952) F-test for the significance of D_{ij}^2 given the sizes of the samples from the classes has been used as a means of taking the differing

sample sizes into account along with D_{ij}^2 itself. That is, given the above (ideal) assumptions, the statistic

$$F = \frac{n_i n_j (N - p - q + 1)}{p(n_i + n_j)(N - q)} D_{ij}^2$$

would be distributed as F with p and $(N - p - q + 1)$ degrees of freedom under the hypothesis that there is no difference between the means of the classes. It should be emphasised, however, that the test is used in the text only to focus attention on those classes between which both D_{ij}^2 and F are small, relative to arbitrary cut-off levels such as $p = 0.1$ and $p = 0.01$.

2. Canonical variates

The total sum of squares and cross products matrix

$$\begin{aligned} T &= \sum_{i=1}^q \sum_{j=1}^{n_i} (x_{ij} - \bar{x}_{..}) (x_{ij} - \bar{x}_{..})^T \\ &= \sum_{i=1}^q n_i (\bar{x}_{ii} - \bar{x}_{..})(\bar{x}_{ii} - \bar{x}_{..})^T + \sum_{i=1}^q \sum_{j=1}^{n_i} (x_{ij} - \bar{x}_{ii})(x_{ij} - \bar{x}_{ii})^T \\ &= B + W \end{aligned}$$

can be analysed into 'between' and 'within' class variance covariance matrices. This analysis of variance and covariance is valid whatever assumptions are made about x_{ij} , although when x_{ij} is $N(\mu_i, \Sigma)$ the pooled within class dispersion matrix

$$V = \frac{1}{(N - q)} W$$

is an efficient estimate for Σ , and may replace it in the expression for Mahalanobis distance.

The canonical variates are the coefficients (y) of the linear combinations of the original variables which maximise the ratio of between to within class variance

$$\lambda = \frac{y^T B y}{y^T W y}$$

subject to various constraints, such as $y^T T y = 1$. It is easily shown that they are eigenvectors for the generalised eigen-problem

$$B y = \lambda W y.$$

The eigenvalues, λ , are ratios of between to within group variance attained by the canonical variates, and measure the discriminating power provided by that (transformed) variable.

For the present exercise, canonical variates provide an optimal display of class separation, since Rao (1952) showed how the first t ($\leq p$) canonical variates maximise the total D^2 in t dimensions. That is, Fig. 16.3 is a display of the data in two dimensions which maximally presents the separation between groups in the sense of maximum total D^2 . For the 26 sub-class analysis, these first two canonical variates, in fact, account for 96 per cent of the total discriminating power.

Separation of Traditionally Mapped Land Cover Classes 165
REFERENCES

- Austin, M. P., and Cocks, K. D. (eds.) (1978). *Land Use on the South Coast of New South Wales. A Study in Methods of Acquiring and Using Information to Analyse Regional Land Use Options*. CSIRO, Australia.
- Austin, M. P., and Basinski, J. J. (1978). Biophysical survey techniques. In: *Land Use on the South Coast of New South Wales*, Vol. I, Ch. 4 (ed. M. P. Austin and K. D. Cocks). CSIRO, Australia.
- Austin, M. P., and Mayo, K. K. (1978). Some results from principal component analysis on LANDSAT imagery. *Proceedings US-Australia Workshop on Image Processing Techniques for Remote Sensing*, Canberra, May 1978.
- Bukata, R. P., Bruton, J. E., and Jerome, J. H. (1977). Determination of water quality by means of remotely-sensed and locally-acquired optical data. In: *Environmental Analysis* (ed. G. W. Ewing), pp. 13-28. Academic Press, New York.
- Carter, V. C. and Schubert, J. (1974). Coastal wetlands analysis from ERTS MSS digital data and field spectral measurements. In: *Proc. 9th Int. Symp. on Remote Sensing of the Environment*, Vol. I, 15-19, pp. 1241-60.
- Christian, C. S., and Stewart, G. A. (1968). Methodology of integrated surveys. In: *Aerial Surveys and Integrated Studies*, pp. 233-80. Proc. Toulouse Conf. 1964., UNESCO, Paris.
- Gower, J. C., and Ross, G. J. S. (1969). Minimum spanning trees and single linkage cluster analysis. *Appl. Statist.* **18**: 54-64.
- Haralick, R. M., and Shanmugam, K. S. (1974). Combined spectral and spatial processing of ERTS imagery data. *Remote Sensing of Environment* **3**: 3-13.
- Hawkins, D. M., and Rasmussen, S. E. (1973). Use of discriminant analysis for classification of strata in sedimentary successions. *Mathematical Geology* **5**: 163-77.
- Hope, K. (1968). *Methods of Multivariate Analysis*. University of London Press, London, 288 pp.
- Lachenbruch, P., and Mickey, R. M. (1968). Estimation of error rates in discriminant analysis. *Technometrics* **10**: 1-11.
- McDonnell, M. J. (1978). Digital image rectification and enhancement on a mini computer: analysis and results. In: *Proc. 12th Int. Symp. on Remote Sensing of the Environment*, Vol. III, pp. 1687-95.
- Merembeck, B. F., Borden, F. Y., and Applegate, D. N. (1974) Transference of ERTS-1 spectral signatures in time and space. In: *Proc. 9th Int. Symp. on Remote Sensing of the Environment*, Vol. I, 15-19, pp. 153-61.
- Morrison, D. F. (1967). *Multivariate Statistical Methods*. McGraw-Hill, New York.
- O'Callaghan, J. F., and Turner, B. J. (1977) CSIRO-ORSER user's manual. Working paper PPG-77-4. Picture processing and Graphics Section, CSIRO, Division of Computing Research, Canberra.
- Rao, C. R. (1952). *Advanced Statistical Methods in Biometric Research*. Wiley, New York.
- Thie, J. (1976). An evaluation of remote sensing techniques for ecological (biophysical) land classifications in northern Canada. *Proc. 1st meeting Can. Comm. on Ecological (biophysical) Land Classification*. Petawawa, Ontario, pp. 129-47.
- Tubbs, J. D., and Coberly, W. A. (1978). Spatial correlation and its effect upon classification results in LANDSAT. *Proc. 12th Int. Symp. on Remote Sensing of the Environment* Vol. III, pp. 775-81.

A comparison of vegetation classifications as descriptors of small mammal habitat preference

BARRY J. FOX and MARILYN D. FOX

INTRODUCTION

The field study of small mammals, especially survey work, is always hampered by the secretive and mostly nocturnal habits of the animals. Vegetation can be used as a visible and immobile indication of small mammal communities to predict either which small mammals might be found in a given habitat or, the converse, in which habitats one might expect to locate a given mammal species. A variety of methods has been used to study habitat requirements of mammals, such as direct measurement (McCloskey 1975) and experimental manipulation (Rosenzweig 1973). Habitat requirements of species relevant to this study have been investigated by Posamentier (1976), Fox and Fox (1978) and Braithwaite and Gullan (1978).

The primary purpose of this chapter is to examine some vegetation classifications in the terms of their usefulness as small mammal habitat descriptors. Five different methods of vegetation classification have been chosen for investigation, ranging from purely structural to purely floristic methods. In addition it is intended to identify those habitat attributes which are important to small mammals and hence should be incorporated in future vegetation classifications to maximise their value in describing small mammal habitats.

THE STUDY AREA

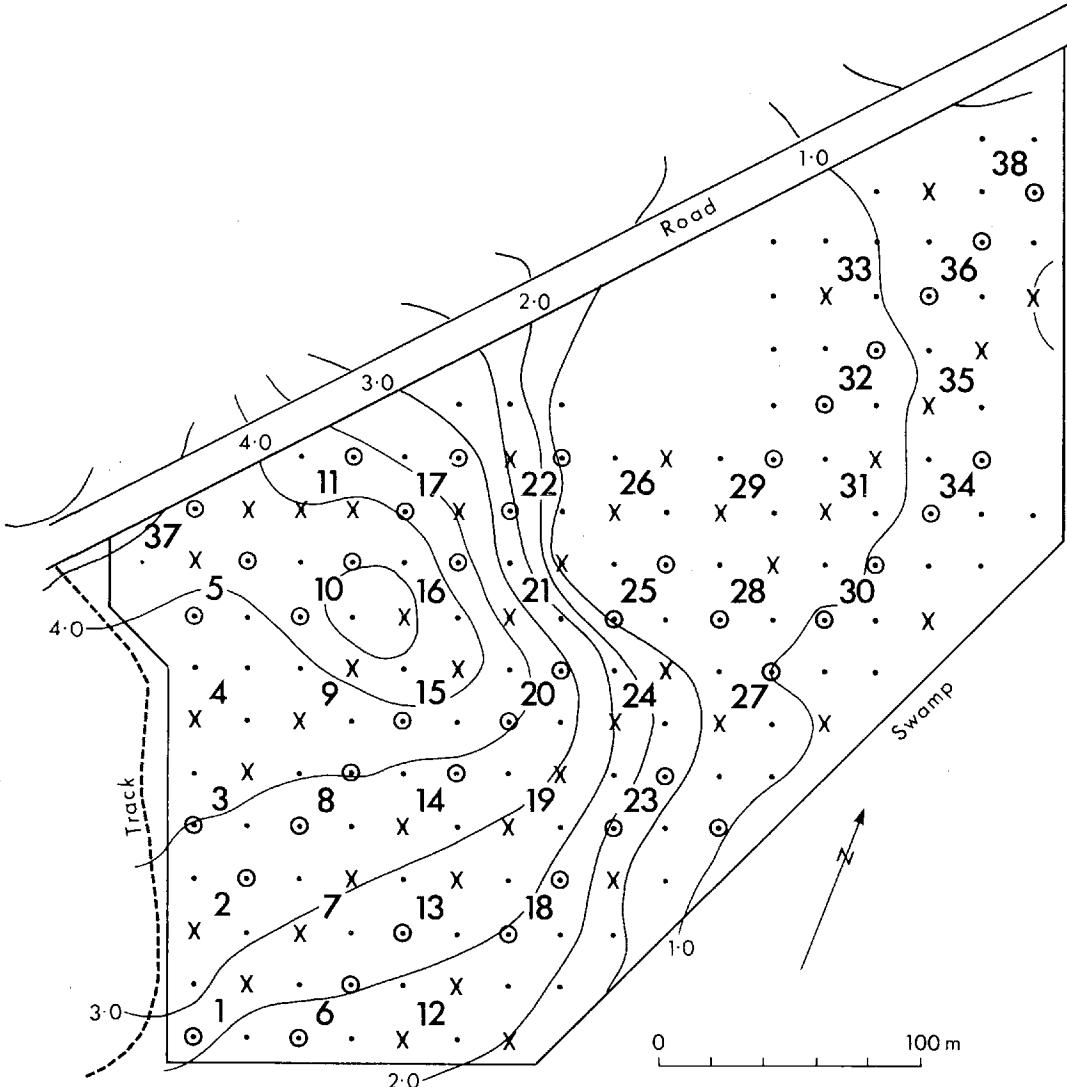
The study site was located in coastal heathland in Myall Lakes National Park ($32^{\circ}28'S$, $152^{\circ}24'E$) 200 km north of Sydney, N.S.W. The area selected occupies part of a former inter-barrier lagoon on Pleistocene sand inland of forested high dunes, which form the outer barrier of the Eurunderee embayment (Thom 1965). The terrain on the plot rises 4 m from a swamp to a low transverse ridge with scattered eucalypts and tall dry heath.

As well as including the full range of swamp and heath communities, the plot supports a rich small mammal fauna (nine species) compared to other areas in the park and to heathland elsewhere (cf. Posamentier 1976).

A survey of the small mammal community was begun in February 1974. Most of the area was burnt in a wildfire in August 1974 and the monitoring of small mammal response to post-fire vegetation changes continued to May 1978. By August 1977, when the vegetation survey was carried out, most of the vegetation had apparently returned to its early 1974 state. There were indications that parts of the plot had also burnt in 1971 and 1968.

METHODS

Trap stations (176) were permanently marked on a 20 m grid covering 7 ha (Fig. 17.1). Small mammals were trapped, identified, marked and released at one or two month intervals using standard techniques.



17.1 The study area showing contour lines with a spacing of 0.5 m. Trapping stations 20 m apart are shown as points while the numbers represent the position of the 38 four-station quadrats around each number. Structural modi data were collected on a transect along the long diagonal (Q1-38). Odd-numbered data set stations are shown with a circle and even-numbered stations with a cross.

Five methods of vegetation classification were examined and compared to the small mammal classification and species' distributions.

- (a) A structural classification was attempted using light intensity measurements at six levels from ground level to 2 m and the incident intensity above the canopy. From these an index of the amount of vegetation between each level was calculated. Details of the method and its application to the measurement of small mammal habitats is given in Fox and Fox (1978) with its relation to other methods in Fox (1979). The amount of vegetation present in each of the six layers and the total of these were used as attributes to characterise the vertical distribution at a station. The coefficient of variation for each of these attributes (calculated from four points at each station) was taken as a measure of the horizontal patchiness at that level and these were also included as attributes.
- (b) A map of the structural formations of Specht (1970) was prepared from visual examination of each station.
- (c) Using additional attributes, mainly the dominant plant species present and a subjective estimate of soil moisture, it was possible to produce eight vegetation units that provided finer resolution of the structural formations in (b).
- (d) A classification using structural *modi* developed by Gillison (see this volume) was tested on a transect of 16 contiguous 20 m × 20 m quadrats along the long diagonal of the study area (Fig. 17·1, Q1 to 38). Five additional quadrats were included in vegetation types not adequately represented by the transect.
- (e) A systematic floristic survey was made by sampling within a 1 m² quadrat at alternate trap stations. Each species was scored on a 0–4 scale representing the number of quadrat quarters over which its foliage projected.

Data from groups of four adjacent stations were pooled to form 38 quadrats as shown in Fig. 17·1.

ANALYSIS AND RESULTS

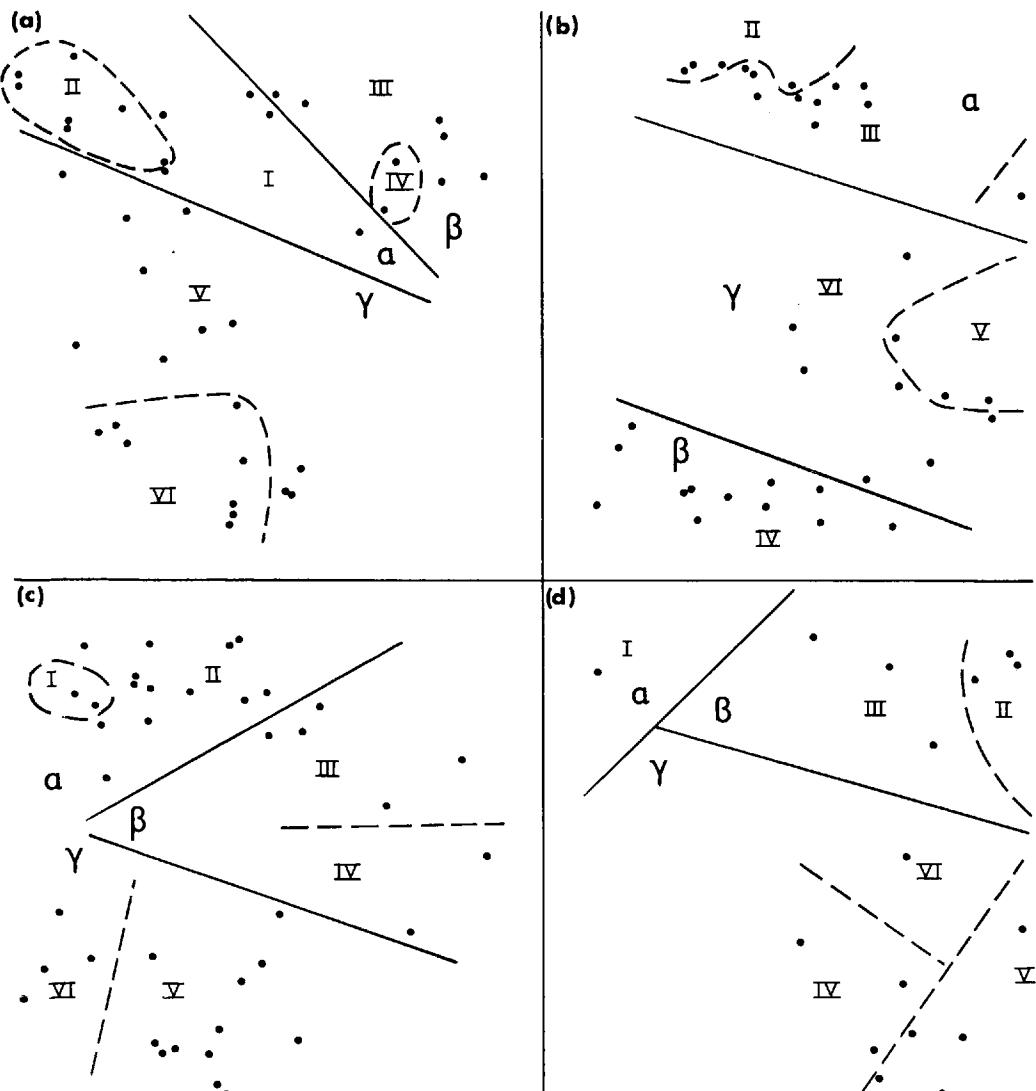
Classification comparisons

Each of the 38 four-station quadrats shown in Fig. 17·1 was allocated to a formation recognised in the Specht classification; five categories were used in this case. A three-group classification was also produced by pooling the most similar categories. Eight vegetation units were recognised, so that the quadrats were allocated into an eight-group classification which was reduced to a five and then a three-group classification by amalgamating the most similar units complementary to those in the Specht classification. Each of the other methods produced a number of attributes for each quadrat: structural (14), structural-modal (26) and floristic (59); and were amenable to pattern analysis.

Six species of small mammals were captured in sufficient numbers, during the three years 1975–7 (Fox 1980) to warrant analysis. Using these six species as attributes, the mammal classification thus formed served as the basis for comparing the ability of the

vegetation classifications to describe and distinguish small mammal habitats. The similarity measure used in all cases was the Canberra metric with double-zero comparisons suppressed and a small positive value substituted in zero-non-zero comparisons.

Ten groups were formed using the flexible strategy of the CSIRO TAXON program MULCLAS (Williams 1976). Six and three-group classifications were derived from the



17.2 The 38 quadrats displayed on the first two principal co-ordinate axes with the six-group (I to VI), and three-group (α to γ) classifications overlain: (a) mammals; (b) structure; (c) floristics; (d) structural modi.

dendograms produced for each data set. Principal co-ordinate analysis (Gower 1966) was carried out for each data set as well and the ordinations displayed on the first two Gower vectors with the classification groups overlain in Fig. 17.2. The Gower vectors for each of the classifications were then used for pairwise canonical co-ordinate analyses comparing the six-group mammal classification in turn with each of the six-group vegetation classifications. Canonical correlation for each of the first three vectors was greater than 0.999 for the structural, floristic and structural-modal classifications analysed, so that it was not possible to use this to distinguish between methods.

The groups already determined during each vegetation classification were used to obtain group means for each of the six mammal species. In this way groups formed on the basis of floristic or structural information could be directly compared on the basis of mammal data for those groups. The problem of matching groups is the main obstacle to such comparisons. Matching was determined from matrices of Canberra metric distance measures to decide which vegetation group was closest to each mammal group in the six-dimensional species space. A two-dimensional representation of this for six-group comparisons is shown in Fig. 17.3.

Once matched, each classification was then correlated with the mammal classification using group means for the six species and all groups. The resulting correlations (and sample sizes) are shown in Table 17.1. It was also possible to correlate classifications over groups for each species separately; an example is shown in Table 17.2 for five and six-group comparisons. The markedly different correlations for some species with different classifications led to a closer examination of the factors relating small mammals and their habitats.

Factor analysis and species comparisons

The two extreme methods of classification (structural and floristic) were selected for closer examination. A factor analysis (Dixon 1975) was carried out on the mammal, structural and floristic data sets using principal component analysis to extract three,

TABLE 17.1

Correlation coefficients between the mammal classification and vegetation classification in turn, based on the mean number of mammal captures for each species ($n = 6$) in the number of groups shown. Groups were independently determined from attribute sets as described in the text. All correlations shown are significant at $p < 0.001$

Number of groups	Specht	Vegetation units	Classification method		
			Structural	Structural -modal	Floristic
3 ($n = 18$)	0.82	0.80	0.90	0.83	0.98
5 ($n = 30$)	0.90	0.93	—	—	—
6 ($n = 36$)	—	—	0.78	0.83	0.87
8 ($n = 48$)	—	0.90	—	—	—
10 ($n = 60$)	—	—	0.71	0.94	0.81

TABLE 17.2

*Correlation coefficients between mean number of mammal captures (for each species separately) for each mammal classification group and mean number of mammal captures (for each species separately) for groups formed by each vegetation classification method in turn. Correlations for each species are shown over the five or six groups used. Significance levels for all tables are shown as: * p < 0.05, ** p < 0.01, *** p < 0.001*

Species	Classification method and number of groups				
	Specht (n = 5)	Vegetation units (n = 5)	Structural (n = 6)	Structural -modal (n = 6)	Floristic (n = 6)
<i>Antechinus stuartii</i>	0.66	0.71	**	*	*
<i>Sminthopsis murina</i>	0.84	0.13	0.61	0.91	0.54
<i>Mus musculus</i>	0.53	0.81	0.89	-0.06	0.77
<i>Pseudomys novaehollandiae</i>	0.30	0.99	0.86	-0.10	0.64
<i>Pseudomys gracilicaudatus</i>	***	*	*	**	*
	0.98	0.94	0.71	0.96	0.91
<i>Rattus fuscipes</i>	0.44	0.41	0.94	0.97	0.17

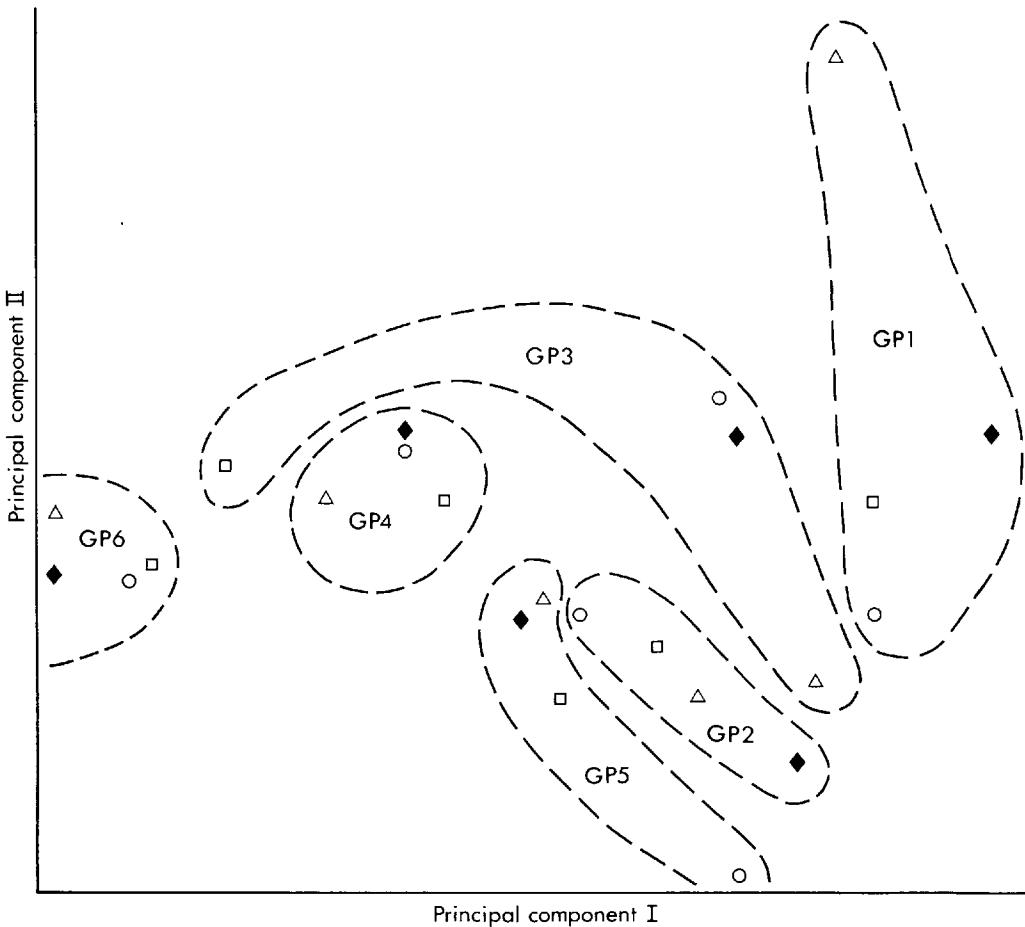
TABLE 17.3

Variables contributing to the first three factors in each factor analysis together with their factor loadings. Abbreviations in structural factors refer to the vegetation index calculated for the layer mentioned (see text) or the coefficient of variation for the layer

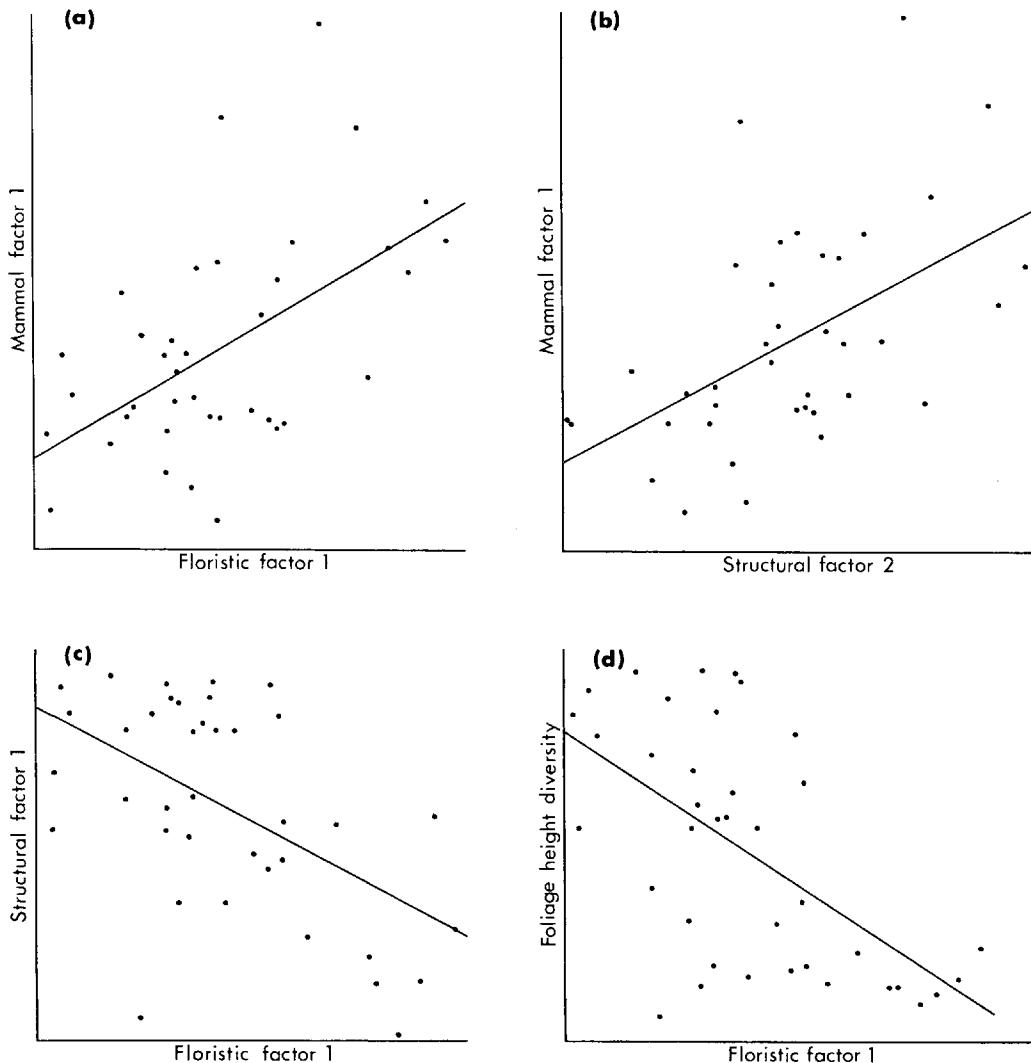
Mammal Factors		
	MF1	MF2
+0.84 <i>P. gracilicaudatus</i>		+0.94 <i>P. novaehollandiae</i>
+0.80 <i>M. musculus</i>		+0.40 <i>S. murina</i>
-0.56 <i>S. murina</i>		
Floristic Factors		
	FF1	FF2
+0.81 <i>Banksia asplenifolia</i>	+0.90 <i>Caustis pentandra</i>	+0.89 <i>Pteridium esculentum</i>
+0.77 <i>Kunzea capitata</i>	+0.74 <i>Boronia pinnata</i>	+0.83 <i>Leucopogon lanceolatus</i>
+0.69 <i>Phyllota phylloides</i>	+0.68 <i>Hibbertia fasciculata</i>	+0.78 <i>Restio tetraphyllus</i>
+0.60 <i>Leptocarpus tenax</i>	+0.68 <i>Trachymene incisa</i>	+0.69 <i>Caustis flexuosa</i>
+0.60 <i>Darwinia leptantha</i>	+0.54 <i>Melaleuca nodosa</i>	
-0.53 <i>Banksia serratifolia</i>		
Structural Factors		
	SF1	SF2
-0.82 Vegetation 0 to 0.2 m		+0.91 Vegetation 0.5 to 1.0
+0.78 Vegetation 1.5 to 2.0 m		-0.76 Coefficient var. 0.5
+0.78 Vegetation 1.0 to 1.5 m		to 1.0
+0.66 Coefficient var. 0 to 0.2 m		+0.65 Total vegetation
	SF3	
		+0.82 Coefficient var. total
		-0.66 Total vegetation

four and six factors respectively. The principal component axes were then orthogonally rotated using a vari-max rotation to produce factor axes that either maximised or minimised the contribution of each attribute. These are shown, together with their factor loadings, for the first three factors in Table 17.3. From this factor scores were calculated for each quadrat.

It was proposed to examine the relationship between mammal, structural and floristic factors using multiple regression of factor scores. Cooley and Lohnes (1962 p. 116) indicate that 'linear functions of variates are more likely to be normal than are the component variates'. The factors were not found to depart markedly from normality and the relationships between those examined approximated linearity (e.g. Fig. 17.4).



17.3 A projection onto the plane of the first two principal components representing the position of the group means for each classification in the 6-dimensional species space. The six-group classifications are shown with the mammal groups as the solid symbols, the structural groups as open squares, floristic groups as open circles and structural taxa groups as open triangles.



17.4 Simple regressions of factors ($n = 38$ in all cases):

	Ordinate	Abscissa	Equation
A	Mammal factor 1	Floristic factor 1	$y = 0.01 + 0.57x, r = 0.538, p < 0.001$
B	Mammal factor 1	Structural factor 2	$y = 0.01 + 0.55x, r = 0.538, p < 0.001$
C	Structural factor 1	Floristic factor 1	$y = 0.07 - 0.55x, r = 0.541, p < 0.001$
D	Foliage height diversity	Floristic factor 1	$y = 4.1 - 0.69x, r = 0.591, p < 0.001$

TABLE 17.4

Factor correlations (n = 38). Upper triangle, correlation coefficients; lower triangle, partial correlation coefficients with the effects of other variables removed. FHD = foliage height diversity; MSD = mammal species diversity; PSD = plant species diversity; Topog = topography. (MSD is a linear function of mammal factors and was removed from the partial correlation analysis to avoid a singular matrix.)

	FHD	SF1	SF2	SF3	MF1	MF2	MF3	Mammal	Floristic	FF1	FF2	FF3	PSD
FHD	1.000	0.859	-0.294	-0.234	-0.512	0.385	0.220	* **	0.363	-0.591	0.088	0.199	0.035 FHD
SF1	0.803	1.000	0.022	-0.044	-0.351	0.260	0.221	*	0.397	-0.541	0.024	0.254	0.110 SF1
SF2	-0.341	0.565	1.000	-0.052	0.538	-0.372	0.242	-0.309	0.162	-0.504	0.153	0.013 SF2	
SF3	-0.472	0.230	0.189	1.000	-0.029	0.027	-0.496	0.343	0.107	0.262	-0.328	0.350 SF3	
MF1	-0.184	0.159	0.246	-0.118	1.000	-0.114	0.002	*	0.394	0.538	-0.366	-0.184	-0.055 MF1
MF2	0.110	-0.047	-0.208	0.008	0.344	1.000	0.072	0.239	*	-0.382	0.078	*	-0.108 MF2
MF3	0.008	-0.026	0.185	-0.208	-0.006	0.254	1.000	0.005	-0.219	-0.285	0.427	-0.238	MF3
FF1	-0.046	-0.120	-0.164	0.025	0.500	-0.271	-0.069	*	1.000	-0.000	0.000	0.196 FF1	
FF2	-0.128	0.155	-0.345	0.118	-0.150	0.009	-0.088	*	0.085	1.000	-0.000	0.217 FF2	
FF3	-0.140	0.152	0.076	-0.374	-0.192	-0.334	0.410	*	0.125	0.085	1.000	0.282 FF3	
PSD	0.168	0.064	-0.134	0.476	-0.035	0.147	-0.205	*	0.167	0.033	0.463	1.000 PSD	
Topog.	0.070	0.334	-0.521	0.435	-0.173	0.179	0.046	*	-0.006	-0.075	0.149	-0.378 *	

The additional variables of plant species diversity, mammal species diversity and foliage height diversity were included as measures that reflected the total community rather than factors in that community. The diversity measure used was the inverse of Simpson's (1949) measure of concentration (see Hurlbert 1971; $\Delta_3 = [\sum_i (n_i/N)^2]^{-1}$, n_i is the value in each of i classes and N is the total). Table 17.4 shows the correlation matrix for the variables to be used in the analysis.

The most significant regressions are shown for mammal factors with floristic (Fig. 17.4a) and structural (Fig. 17.4b) factors. The relationship between the first structural and floristic factors is shown in Fig. 17.4c, while the relationship between foliage height diversity and that of the floristic factor is shown in Fig. 17.4d.

Using this data matrix (Table 17.4) stepwise multiple regression analyses (Dixon 1975) were performed with each of the mammal factors and mammal species diversity in turn as the dependent variable. A similar analysis was conducted using captures for each species in turn as the dependent variable. The results of both analyses are presented in Table 17.5. The direction of correlation is indicated, together with the contribution coefficients and an indication of their significance for the variables used. Contribution coefficients are the product of the standard partial regression coefficient for a variable and its correlation coefficient with the dependent variable (see Power 1972; Fox and Fox 1978). The value of the contribution coefficient may be taken as the

TABLE 17.5

Contribution coefficients (see text) for independent variables, determined from multiple regressions for species and factor dependent variables. Significance levels are shown for each variable included and the total equation

Dependent variable Mammal	Independent variables							Total R ²	Equation F
	FF1	Floristic FF2	FF3	PSD	SF1	Structural SF2	SF3		
<i>R. fuscipes</i>	-0.05		*** +0.35					0.40	11.5 ***
<i>A. stuartii</i>				*	** -0.11	* +0.14	-0.15	0.40	7.2 ***
<i>S. murina</i>					** +0.13	*** -0.26	*	0.47	9.8 ***
<i>P. novaehollandiae</i>				** -0.10	-0.07			+0.19	0.36 **
<i>M. musculus</i>				-0.07		** -0.16		0.23	5.2 *
<i>P. gracilicaudatus</i>	*** +0.46		*	-0.04		** +0.15		0.65	21.3 ***
MF1	*** +0.25			*** +0.25				0.50	17.4 ***
MF2			** -0.14				** +0.18	0.32	8.1 **
MF3			** +0.13			*	-0.20	0.33	8.4 **
MSD			** -0.03			*** +0.20	** +0.24	0.47	9.8 ***

proportion of the variance attributable to that variable. The sum of contribution coefficients is the multiple coefficient of determination (R^2) shown in Table 17.4, together with the significance level of the whole equation. Non-significant variables have only been included where they increased R^2 by more than 5 per cent without markedly reducing the significance of the total equation.

To investigate the different relationships exhibited by mammal species to each of the classification methods (see Table 17.2) it was decided to run the same multiple regressions with (a) only floristic and (b) only structural variables. These results and their relation to the combined regressions are shown in Table 17.6.

As a test of the multiple regression analysis it was repeated using half of the data base to make the predictions and the other half to test those predictions. An adequate sample

TABLE 17.6

*The proportion of variance accounted for (R^2) by structural and/or floristic variables.
(MF = mammal factor, MSD = mammal species diversity)*

Requirements category	Dependent variable	Structure	Independent variables Floristics	Both = Structure + floristics
ONE ONLY	<i>R. fuscipes</i>	0.06	0.40	$0.40 = 0 + 0.40$
	<i>A. stuartii</i>	0.39	0.19	$0.40 = 0.29 + 0.11$
	<i>S. murina</i>	0.46	0.34	$0.47 = 0.47 + 0$
	<i>P. novaehollandiae</i>	0.23	0.26	$0.36 = 0.19 + 0.17$
BOTH	<i>M. musculus</i>	0.14	0.07	$0.23 = 0.16 + 0.07$
	<i>P. gracilicaudatus</i>	0.42	0.55	$0.65 = 0.15 + 0.50$
	MF1	0.43	0.47	$0.50 = 0.25 + 0.25$
	MF2	0.22	0.25	$0.32 = 0.18 + 0.14$
EITHER	MF3	0.29	0.32	$0.33 = 0.20 + 0.13$
	MSD	0.33	0.28	$0.47 = 0.44 + 0.03$

TABLE 17.7

Variance explained by multiple regression predictive equations for mammal factors derived from the odd-numbered data set. Correlation coefficients between observed mammal factor values for the even-numbered data set and those predicted for it from the odd-numbered data set

Mammal factors	Odd data set variance explained (n = 42)	Correlation with even data set (n = 42)	Significance
MF1	47%	0.43	p < 0.005
MF2	36%	0.63	p < 0.001
MF3	30%	0.15	N.S.

size was obtained by analysing single trapping stations rather than pooling four adjacent stations into quadrats. Floristic and structural information was available for 84 single stations. As the stations had been systematically located, the two sub-samples were taken as the odd- and even-numbered stations (see Fig. 17·1). The odd-numbered stations were then subjected to the same procedures of factor analysis and multiple regression used for the four-station quadrats. The predictive equations from the odd-numbered data set were used to calculate predicted values for each dependent variable using the values for the independent variables obtained from the even-numbered data set. The predicted values were then correlated with the observed values for the mammal factors in the even-numbered data set (Table 17·7). The first two factors show highly significant correlations.

DISCUSSION

Three plant communities are recognised by each classification. These are illustrated by the groups overlain on the principal co-ordinate ordinations (Fig. 17·2), and correspond to swamp-wet heath, dry heath and forest.

The six-group classifications are close to the limit of interpretation, and although useful information can be derived from a 10-group level of classification, it is not justified when compared to the mammal classification. The degree of misclassification (when compared to the mammal classification) increases with the number of groups but this is largely due to the problem of matching groups (see group 1 and particularly group 3 in Fig. 17·3). The correlation of group means (Table 17·1) illustrates this point.

The most obvious point to emerge from the comparison of classifications is that they are all highly correlated with the mammal classification, and with each other as well. This is supported by the high canonical correlations and the correlations with the mammal classification shown in Table 17·1.

However, if one examines the between-group correlations for each species (Table 17·2) it is apparent that there are substantial differences between classification methods. Modifying the Specht classification by the addition of floristic information (vegetation units) does improve the correlation with the mammal groups. This is probably due to the distinction that can be made between wet and dry heath in the 'closed heath' category, a distinction recognised by mammals. At the six-group level (Table 17·2) both structural and structural-modal classifications appear to relate more closely to a greater number of species than does the floristic classification.

The three mammal factors extracted dissociate the mammal community into three pairs of species. These are: *Pseudomys gracilicaudatus* and *Mus musculus* (MF1), most often captured in the wet heath habitat, *Rattus fuscipes* and *Anthechinus stuartii* (MF3), with most captures in forest or woodland areas of the plot, and the group (MF2) formed by *P. novaehollandiae*, with a lesser contribution from *Sminthopsis murina*, which is captured mainly in dry heath.

Structural factor one (SF1) represents a vegetation profile with a sparse and patchy distribution of foliage below 20 cm but with substantial vegetation between 1 m and 2 m. Minor contributions came from foliage above 2 m and homogeneity of vegetation

from 1 m to 1.5 m. This is a description of a tall dry heath profile. SF2 represents the amount and constancy of vegetation below 1 m and the total amount of vegetation present, and describes a short wet heath. SF3 represents reduced total vegetation and a patchy horizontal distribution of what is present, and is not readily interpreted.

The pattern of factor correlations (Table 17.4) shows the correspondence between mammal and structural factors. Less correspondence is seen in the pattern for mammal-floristic factor correlations. However, the structural and floristic factors show high diagonal correlations (1:1, 2:2, 3:3) and low correlations between other pairs. The linkage between structural and floristic factors is reinforced by the highly significant correlation ($p < 0.001$) between foliage height diversity (FHD) and floristic factor one, and the significant correlation ($p < 0.05$) between plant species diversity (PSD) and structural factor three, both of which are maintained in partial correlations.

Partial correlation coefficients between pairs of variables with the effects of other variables removed (Table 17.4) indicate underlying relationships that can provide a better indication of likely causality. This offers a very different picture, with no significant correlations between mammal and structural factors, although significant correlations remain between mammal and floristic factors. This is probably explained by the floristic factors (FF2 and FF3) acting through the structural factors (SF2 and SF3) to produce the correlations between mammal and structural factors. The significant partial correlations between SF2-FF2 and SF3-FF3 support this. All structural factors are significantly partially correlated with changes in topography and also with foliage height diversity.

The contribution coefficients for multiple regression equations with the coefficient of determination (R^2) maximised (Table 17.5) show that species are highly correlated with, if not dependent upon, markedly different sets of factors. This had already been indicated by the species correlations for each classification shown in Table 17.2. Some indication of the mechanisms operating can be obtained from Table 17.6. The first three species show that a regression incorporating both structural and floristic factors makes no improvement in R^2 and so are placed in the 'one only' category. The last three species, on the other hand, show a marked increase in R^2 when both sets of factors are included rather than just one and have been included in the 'both' category.

The species pairs corresponding to each mammal factor have been placed together and this illustrates a most interesting point; in each pair, one species is better predicted by structural factors while the other is better predicted by floristic factors. This is clearly shown in the last column of Table 17.6.

This would appear to indicate a partitioning of resources along an axis of structural-floristic attributes. There is some evidence that this ecological separation may be facilitating the partitioning of food resources in that the two marsupial insectivores (*A. stuartii* and *S. murina*) are predicted by structural variables. The herbivore *P. gracilicaudatus* is predicted very largely by floristic factors as is *R. fuscipes* which, although an omnivore, does have a significant amount of plant material in its diet. The other two rodents have a large proportion of seeds in their diet and their habitat preferences include both structural and floristic components.

Species contributions are clearly not strictly additive, as is indicated when mammal factors are the dependent variables (Tables 17.5 and 17.6). In all three cases there is no improvement using both sets of factors and the variance accounted for by each set is about the same. This probably results from the partitioning within each species pair (or factor); these have been placed in the 'either' category.

Mammal species diversity as an indicator of the total community requires both sets of factors to maximise R^2 , although when both are used the proportion of variance attributable to floristics is only 3 per cent even though a 14 per cent increase over structural factors alone have been achieved.

Although pattern analysis and multiple regression analysis, as we have used it, are largely for generating hypotheses, we have made an effort to test the predictive power of the multiple regression equations. The 38 quadrats (each of four trapping stations) were insufficient to subdivide but it was possible to obtain two equal data sets by halving the data available on single trapping stations. Predicted and observed values were highly correlated (Table 17.7) for the first two factors but there was no significant correlation for the third factor (only 30 per cent of the variance was accounted for in the predictive equation). There was a marked similarity in the equations derived from single stations and those already examined for the four-station quadrats. We feel that this test, although limited, does support the validity and usefulness of the factors and multiple regression equations obtained by this method of analysis.

The use of both floristic and structural variables in predicting *P. novaehollandiae* habitat usage agrees with the results previously found for this species in N.S.W. heath (Posamentier 1976), on a rehabilitated sand mining path (Fox and Fox 1978) and in Victorian heathland (Braithwaite and Gullan 1978). Braithwaite and Gullan (1978) found both floristic and structural variables to be important for all species except *R. lutreolus*. They make the observation that the range of structural variation at Cranbourne may have been insufficient to detect structural differences for *R. lutreolus*.

Structural and floristic variables and classifications based on them are highly correlated and contain much of the same information. Consequently at a coarse scale (three factors in this study) mammal habitat classification can probably be adequately served by either type of analysis. However, if finer resolution is required, especially for reference to species' distributions, it is imperative that both types of data be used in the classification. This is particularly so for the 'both' category in Table 17.6 and also for the 'one only' category, unless prior information is available on which factors are important. Distinction between floristic and structural variables may be an important component of small mammal habitat selection. We have attempted to investigate not only the importance of floristic and structural vegetation variables but also to identify the contribution that various attributes can make to describing and predicting small mammal habitats.

ACKNOWLEDGMENTS

We would like to thank A. N. Gillison and R. Bennett for collecting the structural-modal field data. A. N. Gillison made these data available to us and R. Bennett was of

great assistance with some of the computing using the CSIRO TAXON Library. M. Westoby kindly read and commented on an earlier draft. Both authors acknowledge support from Commonwealth Postgraduate Research Awards and we thank the Zoology Department, University of N.S.W., for permission to use their Smith Lake Field Station. This work was carried out while both authors were postgraduate students at the School of Biological Sciences, Macquarie University, Sydney.

REFERENCES

- Braithwaite, R. W., and Gullan, P. K. (1978). Habitat selection by small mammals in a Victorian heathland. *Aust. J. Ecol.* **3**: 109-27.
- Cooley, W. W., and Lohnes, P. R. (1962). *Multivariate Analysis for Behavioural Sciences*. Wiley, New York.
- Dixon, W. J. (ed.) (1975). *Biomedical Computer Programs*. University of California Press, Berkeley.
- Fox, B. J. (1979). An objective method of measuring the vegetation structure of animal habitats. *Aust. Wildl. Res.* **6**: 297-303.
- Fox, B. J. (1980). The ecology of a small mammal community: secondary succession, niche dynamics, habitat partitioning, community structure and species diversity. Ph.D. Thesis, Macquarie University, Sydney.
- Fox, B. J., and Fox, M. D. (1978). Recolonization of coastal heath by *Pseudomys novaehollandiae* (Muridae) following sand mining. *Aust. J. Ecol.* **3**: 447-65.
- Gower, J. C. (1966). A Q-technique for the calculation of canonical variates. *Biometrika* **53**: 582-5.
- Hurlbert, S. H. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**: 577-86.
- McCloskey, R. T. (1975). Habitat dimensions of white-footed mice *Peromyscus leucopus*. *Am. Midl. Nat.* **93**: 158-67.
- Posamentier, H. G. (1976). Habitat requirements of small mammals in coastal heathlands of New South Wales. M.Sc. Thesis, University of Sydney.
- Power, D. M. (1972). Numbers of bird species on the Californian Islands. *Evolution* **26**: 451-63.
- Rosenzweig, M. L. (1973). Habitat selection experiments with a pair of co-existing Heteromyid rodent species. *Ecology* **54**: 111-17.
- Simpson, E. H. (1949). Measurement of diversity. *Nature, London* **163**: 688.
- Specht, R. L. (1970). Vegetation. Chapter 5 in, *The Australian Environment* ((ed.) G. W. Leeper). 4th edn. CSIRO and Melbourne University Press.
- Thom, B. G. (1965). Late Quaternary coastal morphology of the Port Stephens-Myall Lakes Area, N.S.W. *J. and Proc. R. Soc. N.S.W.* **98**: 23-36.
- Williams, W. T. (1976). Techniques and principles of pattern analysis. In: *Pattern Analysis in Agricultural Science*. (ed. W. T. Williams) CSIRO Melbourne, Elsevier, Amsterdam.

Floristic classifications, small mammals and birds

P. K. GULLAN and K. C. NORRIS

INTRODUCTION

Recent work on small mammal populations has reported considerable success in the use of floristic classifications as indicators of preferred habitats (Braithwaite and Gullan 1978; Cockburn 1978; Braithwaite *et al.* 1979; Stoddart and Braithwaite 1979). These authors attribute the usefulness of floristic classifications to the close relationship between floristics and edaphic conditions, seral stages and the availability of food. Relationships between floristics and food are particularly useful for predicting the preferred habitats of herbivores such as *Rattus lutreolus* (Braithwaite and Gullan 1978; Watts and Braithwaite 1978) but as invertebrate populations vary with soil type, leaf litter and plant species (Mathews 1976), floristic classifications may also reflect food resources for omnivores and insectivores (Cockburn 1978; Stoddart and Braithwaite 1979).

Most of the above work is based on intensive sampling for mammals on a fine grid (25 m intervals) over a long period (one or more years). The floristic variation described in these studies is therefore often subtle and the time taken to gather and analyse the floristic data is small compared with the time taken to gather the mammal data. Consequently the collection of detailed floristic data and the use of complex numerical sorting techniques are a reasonable investment.

In primary surveys such as those undertaken by the Land Conservation Council in Victoria, large areas are covered in a short time so that sampling for animals is much less intensive. As a consequence, compared with fine scale work, any floristic sampling and analysis will form a proportionately larger amount of the study time and vegetation variation will be much greater.

This chapter outlines such a broad scale survey and the success of the resultant floristic classification in determining preferred habitats for small mammals and birds.

METHODS

The data presented are from part of the catchment of the Gippsland Lakes, Victoria, an area of approximately 21 000 km². They were collected from 118 sites within an approximate 10 km radius from Ensay during October and November 1977. The catchment area was divided into 5 minute × 5 minute (lat. long.) rectangles, within which four sample sites were selected so that each differed markedly from the others in gross habitat features (e.g. creek, hilltop, hillside, swamp, etc.). At each site 20 large (20 × 20 × 40 cm)

TABLE 18.1

Constancy table of the floristic groups, showing those species with a 50 per cent or greater frequency within a group. The cover/abundance is the average value for all occurrences within the group. Numbers in italics are the frequency, times a numerical equivalent of the cover/abundance symbol, + = 1, 1 = 2, 2 = 4, 3 = 6, 4 = 8, 5 = 10. The numbers on the right of the species names represent a food category which each species provides (see Table 18.5).

Species	1	2	3	4
<i>Drimys lanceolata</i> (1, 3)	50 1 100			
<i>Coprosma hirtella</i> (1)	72 1 144			
<i>Olearia phlogopappa</i>	50 + 50			
<i>Eucalyptus delegatensis</i> (2, 3)	50 2 200			
<i>Asperula scoparia</i>	61 1 122			
<i>Eucalyptus rubida</i> (2, 3)	78 1 156			
<i>Ranunculus graniticola</i> (3, 4)	67 + 67			
<i>Leucopogon suaveolens</i> (1)	88 2 352			
<i>Platylobium formosum</i> (2, 3)	50 1 100			
<i>Eucalyptus pauciflora</i> (2, 3)	61 2 244			
<i>Tieghemopanax sambucifolius</i> (1)	61 2 244			
<i>Stellaria pungens</i>	67 1 134	53 + 53		50 + 50
<i>Polystichum proliferum</i>	61 1 122		84 2 336	
<i>Acacia dealbata</i> (2)	63 2 332	85 1 170	90 2 360	53 1 106
<i>Acaena anserinifolia</i>	94 1 188	65 1 130	72 1 144	54 1 106
<i>Hydrocotyle</i> spp. (4)	83 1 166	78 1 156	84 1 168	85 1 170
<i>Luzula campestris</i> (4)	72 + 72	53 + 53		64 + 64
<i>Poa australis</i> spp. agg. (2)	94 3 564	71 1 142		90 2 360
<i>Geranium</i> spp. (4)	72 + 72	85 1 170		64 + 64
<i>Poranthera microphylla</i> (4)	61 + 61	91 + 91		85 + 85
<i>Pteridium esculentum</i> (4, 5)	56 1 112	85 1 170	84 2 336	69 + 69
<i>Cassinia aculeata</i>	50 1 100	71 1 142	60 1 120	74 1 148
<i>Clematis aristata</i> (3)	77 + 77	85 + 85	72 + 72	
<i>Lomandra longifolia</i> (2)	61 1 122	85 1 170		90 1 180
<i>Dianella tasmanica</i> (1, 3)	83 1 166	65 + 65		50 1 100
<i>Viola hederacea</i> (3, 4)	89 1 178	100 1 200	78 1 156	58 1 116
<i>Lomatia myricoides</i> (2, 3)	56 1 112	50 1 100		
<i>Lagenophora stipitata</i> (3, 4)		53 + 53	50 + 50	
<i>Eucalyptus dives</i> (2, 3)		65 1 130	50 1 100	
<i>Hypochaeris radicata</i> (3, 4)		78 + 78		
<i>Oxalis corniculata</i> (3, 4)		85 + 85	78 + 78	58 + 58
<i>Senecio quadridentata</i> (4, 5)		50 + 50		79 + 79
<i>Cassinia longifolia</i>		78 1 156		53 2 212
<i>Pomaderris aspera</i>	91 2 364		78 2 312	
<i>Blechnum nudum</i>	72 1 144		50 1 100	
<i>Acacia melanoxylon</i> (2)	72 1 144			
<i>Adiantum aethiopicum</i>	91 1 182			
<i>Dichondra repens</i> (4)	85 1 170			
<i>Eucalyptus bridgesiana</i> (2, 3)	59 2 236			
<i>Gratiola peruviana</i> , (3, 4)	59 1 118			
<i>Leptospermum phyllicoides</i> (3, 4)	78 3 468			
<i>Plantago varia</i> (4, 5)	72 + 72			
<i>Prostanthera lasianthos</i> (3)	65 1 130			
<i>Prunella vulgaris</i> (3, 4)	65 + 65			
<i>Rubus fruticosus</i> (1, 5)	72 + 72			

TABLE 18.1 (Continued)

Species	1	2	3	4
<i>Veronica plebeia</i> (3)		59 + 59		
<i>Hakea eriantha</i> (2, 3)	59 + 59			
<i>Pimelea axiflora</i> (3)	53 + 53			
<i>Stellaria flaccida</i> (3, 4)	59 1 118			
<i>Carex appressa</i> (2, 5)	59 1 118	72 1 144		
<i>Lepidosperma laterale</i> (2)	93 1 106			
<i>Lepidospermum grandifolium</i> (2, 3)	50 1 100			
<i>Senecio linearifolius</i> (3, 4)		78 1 156		
<i>Tetrastrhena juncea</i> (2)		50 1 100		
<i>Eucalyptus obliqua</i> (2, 3)		72 1 144		
<i>Olearia lirata</i> (3)		66 2 264		
<i>Bedfordia salicina</i> (3)		78 2 312		
<i>Billardiera scandens</i> (3)		60 + 60		
<i>Cyathea australis</i>		60 1 120		
<i>Dicksonia antarctica</i>		78 2 312		
<i>Histiopteris incisa</i> (4, 5)		60 1 120		
<i>Olearia argophylla</i> (3)		66 1 132		
<i>Australina muelleri</i> (4)		54 1 108		
<i>Coprosma quadrifida</i> (1)		54 1 108		
<i>Drymophila cyanocarpa</i> (1, 3)		54 1 108		
<i>Asperula scoparia</i>			53 1 106	
<i>Haloragis tetragyna</i>			79 1 158	

cage traps were laid in a line (approx. 5 m intervals) within a uniform vegetation (visually assessed), baited with a mixture of peanut butter and rolled oats and left for two nights. Every bird species seen or heard at each site over the two days was recorded. Vegetation descriptions were a visual estimate of cover/abundance (Braun-Blanquet scale—Table 18.1) of each vascular plant species within or projecting over a quadrat running the length of the trap-line and 5 m to each side.

The floristic data were analysed using a normal/inverse polythetic, agglomerative classification (MAGIC, see Gullan 1978) and the results reviewed on a two-way table. For each floristic group defined, mean small mammal capture rates were determined and compared using a Student t-test. The same was done for numbers of bird species recorded within each floristic group.

RESULTS

From the 118 sites, 12 floristic groups were distinguished. These groups fell into four main relatively even floristic communities at similar altitudes. For brevity, the largest representative group from each community has been chosen for discussion. These four groups constitute 60 per cent of the classified quadrats. The constancy table (Table 18.1) shows the frequency of occurrence of each species (above 50 per cent) within each floristic vegetation type (along with its average cover/abundance). There are clear qualitative and quantitative floristic distinctions between each vegetation type, which in turn represent very different environments (Table 18.2). These environments differ significantly in the abundance of small mammals (mostly *Rattus fuscipes*) and in the number of bird species they support (Tables 18.3 and 18.4).

TABLE 18.2

A brief description of the structure and environment of each floristic vegetation type. Soil information and nomenclature is based on Stace et al. (1972), structural vegetation types are after Specht (1970)

Vegetation type 1

Alpine Open Forest: Mean altitude (m): 1250 ± 100 .
 Soil type: Alpine Humus Soil. Coarse grained, friable organic soil. High N, low P.
 Climate: Reliable high rainfall, snow for 2 months of the year.
 Structure: Trees to 25 m—20% cover, shrub layer 1 to 4 m—30%, ground layer to 0.5 m—100%.

Vegetation type 2

Riparian Open Forest: Mean altitude (m): 330 ± 200 .
 Soil type: Alluvial Soil. Friable, sandy soils. Low N,P.
 Climate: Moderate winter rainfall. Subject to flooding in late spring and winter.
 Structure: Trees to 25 m—15%, shrub layer 1–4 m—80%, ground layer to 0.5 m—60%.

Vegetation type 3

Wet Tall Open Forest: Mean altitude (m): 770 ± 250 .
 Soil type: Kraznozem. Friable, loam to clay-loam soil. Highly organic surface horizons. High N and P.
 Climate: Reliable high rainfall. High humidity, no frosts or snow.
 Structure: Trees 15–50 m—40%, shrub layer 2–10 m—60%, ground layer to 0.5 m—30%.

Vegetation type 4

Dry Open Forest: Mean altitude (m): 700 ± 250 .
 Soil type: Solodic Soil (duplex soils). Hard, clayey and coarse granular soil. Very low in N and P.
 Climate: Moderate rainfall. Very hot summers, frost in winter.
 Structure: Trees to 20 m—40%, shrub layer 2–3 m—40%, ground layer 0.3 m—60%. (Although Table 18.1 does not show it several species of *Eucalyptus* always occurred in this vegetation, but no single species had a frequency of 50% or more).

TABLE 18.3

Mean capture success of small mammals (%) and mean number of bird species recorded for all sites in each floristic vegetation type

Vegetation type	1	2	3	4
Mean mammal captures (%)	8 ± 5	13 ± 6	24 ± 7	3 ± 1
Mean bird spp. no.	10 ± 3	18 ± 4	17 ± 5	6 ± 3

TABLE 18.4

The four vegetation types compared on the basis of small mammal captures and bird species numbers, with a Student t-test. An asterisk () means a significant difference at $p = 0.05$*

Mammal captures				Bird spp. no.			
	1	2	3		1	2	3
2	*					*	
3	*	*				*	NS
4	*	*	*			*	*

DISCUSSION

These results clearly demonstrate the following:

1. That large quadrats, sampled at low intensity, produce a floristic classification in which differences between groups are large. Subtle variation, such as that shown in Braithwaite and Gullan (1978), is largely obscured.
2. These groups reflect major climatic, edaphic and geographic differences and represent structurally different vegetations.
3. Mammal and bird populations differ in type and density between these different environments.

This means that floristic classifications used within a frame-work of large-area primary survey are useful in demonstrating different density mammal and bird habitats. However, this is of limited use to the zoologist if the environments delineated by floristics are so different that they can be more easily identified in another way, and from our data this may appear to be the case. In order to justify the floristic approach to habitat description in zoological primary surveys, the floristic classification must provide greater insight into animal ecology. In short, it must improve the primary survey from being an animal inventory to that of a preliminary ecological investigation.

Food resource availability

As mentioned earlier, in fine scale work with mammals, the value of a floristic classification in reflecting animal densities is usually related to a close association between floristics and available food resources. Table 18.5 lists small mammal and bird food resources, in which the first five categories relate directly to floristics. Using the floristic information in Table 18.1, a very crude abundance measure of food categories 1-5 has been calculated for each vegetation type. This was done by assigning a quantitative value to each cover/abundance symbol, multiplying this by the frequency of each plant species within each vegetation group, and summing these values for all species which

TABLE 18.5

A list of potential food resources for birds and small mammals within a terrestrial ecosystem

Category 1	Berries and drupes
Category 2	Seeds (dry fruits)
Category 3	Nectar and/or pollen
Category 4	Soft leaf and stem material
Category 5	Edible roots, rhizomes and tubers
Category 6	Large fungi (ascomycetes, basidiomycetes)
Category 7	Flying insects
Category 8	Leaf and twig surface invertebrates
Category 9	Bark invertebrates
Category 10	Leaf litter invertebrates
Category 11	Invertebrates in plant body
Category 12	Vertebrates

qualified for these five categories (Tables 18·1 and 18·6). Although the values are crude they represent a means by which vegetation types can be compared, provided qualifications about the plants involved are included in the comparison.

The remaining six categories cannot be quantified but (as will be seen in later discussion) their likely abundance within each vegetation type can be inferred, particularly if climatic and edaphic information are taken into account.

In order to decide whether this information is useful in determining 'good' and 'bad' animal habitats, some knowledge of the animals' biology is necessary. For the mammals, this must include *Rattus fuscipes*, as this species formed > 95 per cent of the captures.

Mammals

R. fuscipes (Waterhouse) is a largely ground-dwelling omnivore. In a forest situation its diet will consist of seeds, berries, drupes, roots, soft leaf and stem material (not mature ferns or coarse grasses), fungi (ascomycetes and basidiomycetes) and a variety of invertebrates (Warneke 1971). The critical seasons for this animal are:

1. Summer: when young born in early summer have entered the population and the previous season's adults are still alive (most animals survive only one breeding season). At this time there is high competition for food resources. If there is a food shortage then the smaller and less experienced young (next season's breeding stock) will suffer.
2. Winter: when seeds, berries and invertebrates are in shortest supply.

The four vegetation types described in Table 18·1 will now be examined in the light of this information on *R. fuscipes*. The types are listed in decreasing order of resource importance.

Vegetation type 3: This is the best vegetation resource for *R. fuscipes*. It is the most productive and supports the largest trees and shrubs. Eucalypt leaves, broad-leaved trees, shrubs and fern fronds, form a deep, moist leaf litter of the type that produces a rich invertebrate fauna. In addition, in this forest, the invertebrates which graze the dense canopies at all levels produce frass which is in turn utilised by coprophagous litter invertebrates (Mathews 1976). Thus the litter and its invertebrate fauna appear to be the most important food source for *R. fuscipes* throughout most of the year (Warneke 1971; Robinson 1976). In spring and summer, the availability of protein and fat-rich invertebrates and seeds assumes prominence (the main seed source in this vegetation is *Acacia dealbata*, Table 18·1). In winter, when invertebrates are scarce, the availability of high quality vegetable food is important for *R. fuscipes*. In this vegetation, both above and below-ground edible plant material is in good supply (Table 18·6) mostly through herbaceous composites and the deltoid ferns *Histiopteris incisa* and *Pteridium esculentum* (both of these ferns have tender, edible fronds in the juvenile stage as well as carbohydrate-rich rhizomes). At this time *R. fuscipes* will eat bark (Warneke 1971), possibly that of *A. dealbata*, which releases a thick, sugary sap when wounded. Another

TABLE 18.6

An assessment of the abundance of plant-food resources (categories 1-5 Table 18.5) within each floristic vegetation type. These values, taken from Table 18.1, are the sums of all the figures in italics for each vegetation type for each food category

Food category	Vegetation type			
	1	2	3	4
1	1000	150	200	100
2	1800	1950	800	600
3	1100	2200	1600	300
4	600	1500	800	650
5	100	500	700	150

obvious winter food source consists of the macro-fungi which are common in type 3 vegetation.

Vegetation type 2. The second highest capture frequency of *R. fuscipes* occurred in this vegetation which is floristically richer than vegetation type 3 but this richness is largely in ground and shrub layer plants. The vegetation is comparatively open above 4 m. Below 4 m the predominant shrub species are small-leaved, sclerophyllous, *Leptospermum* spp. Increased sclerophyll of shrub layer plants and decreased canopy density of plants over 4 m, along with periodic (often yearly) flooding, results in less leaf litter and associated invertebrates. This is partially offset by a variety of plant species which supply seeds over much of spring and summer (e.g. *Acacia* spp. in spring; *Rubus parvifolius* and *Leptospermum phyllicoides* in summer; *Carex appressa*, *Lepidosperma laterale* and various grasses in late summer). In winter, an abundance of above and below ground plant material in friable soil provides the main potential food source.

Vegetation type 1. In the summer, seeds, berries and drupes of monocotyledons and dicotyledons are in great abundance in this vegetation type. However, here two important factors operate against a consistently high mammal capture rate. The first is climatic (snow and freezing winters), which presumably severely limits food resources for 3 to 4 months. The second is the presence of *Eucalyptus pauciflora* in much of the vegetation, the leaf litter of which supports a poor invertebrate population (Wood 1971). When sites in this vegetation with and without *E. pauciflora* were compared (those with *E. pauciflora* were also low in drupaceous plants), the former showed a 2 per cent trap success while the latter showed a 17 per cent success. This patchiness of good and bad food sites makes vegetation type 1 a poor overall habitat for *R. fuscipes*.

Vegetation type 4. This is the worst of the four types for *R. fuscipes* because of the climatic extremes (hot dry summers and below-zero temperatures in winter) and poor food resources. Leaf litter is shallow due to low shrub and tree biomass (these soils have the lowest N and P of the study, Stace *et al.* 1972). The range of seed, berry and drupe producing plants is also very small and there are relatively few herbaceous plants for winter food. The soil is rocky and hard so digging for tubers etc. is difficult, a situation *R. fuscipes* usually avoids (Taylor 1961).

Birds

Birds are generally much more mobile than small mammals. Because resources available in a future or previous season are largely irrelevant, interpretation of seed, berry or nectar production will be related to the period of this study (October-November).

Vegetation type 3. The abundance of invertebrates in the dense and varied canopy of this vegetation as well as the productive leaf litter, make vegetation type 3 suitable for a range of bird species (Table 18.7). As well as leaf feeding and leaf litter invertebrates, pollen and nectar seeking insects are in good supply because of the prolific flowering of the large tree composites *Bedfordia salicina*, *Olearia argophylla* and *O. lirata*, and a range of lesser flowering species which are all insect pollinated. Two eucalypts, *E. radiata* and *E. dives* were in flower and provided nectar and pollen to honeyeaters as well as insects. The humid atmosphere associated with vegetation type 3 indicates a suitable habitat for a variety of flying insects, particularly hemipterans and dipterans (mosquitoes) which are preyed upon by fantails and other flycatchers.

TABLE 18.7

A constancy table for bird species recorded in floristic types. It contains species all with a within-group frequency of 50% or more, or species which are virtually exclusive to one vegetation type

	1	2	3	4
<i>Brown thornbill</i>			70	
<i>Striated thornbill</i>			50	
<i>Striated pardalote</i>	66		70	
<i>Grey fantail</i>	58	71	88	
<i>Golden whistler</i>	50	57	70	
<i>Grey shrike-thrush</i>	58	86	65	50
<i>White-throated tree creeper</i>	50	64	82	
<i>Yellow-faced honeyeater</i>	58	78	65	
<i>Fantail cuckoo</i>		71	53	
<i>Spotted pardalote</i>		50	53	
<i>White-naped honeyeater</i>		78		
<i>Crimson rosella</i>	50			
<i>Yellow robin</i>		64	50	
<i>Rufous whistler</i>		64	65	
<i>Kookaburra</i>		64	50	
<i>Eastern whipbird</i>		50	53	
<i>White-browed scrub wren</i>		64	82	
<i>Yellow-tufted honeyeater</i>		64		
<i>Oriole</i>		64		
<i>Welcome swallow</i>		57		
<i>Satin bower-bird</i>		43		
<i>Sacred kingfisher</i>	36			
<i>Silvereye</i>			50	
<i>Lyrebird</i>			35	
<i>Rufous fantail</i>			30	
<i>Shining bronze cuckoo</i>			99	
<i>Crescent honeyeater</i>			53	

Note: Common names after the *Reader's Digest complete book of Australian birds*. Sydney, Reader's Digest, 1976.

Vegetation type 2. This vegetation, although equal in range of bird species to vegetation type 3, supports a slightly different species complement (Table 18·7). Noticeably uncommon are the upper and medium canopy leaf feeders such as striated and brown thornbills, silvereyes and striated pardalotes. This is related to a lower density and diversity of plants in these strata. Vegetation type 2 also lacks the specialist leaf litter feeder, the lyrebird. Obvious water-oriented birds such as swallows and kingfishers are present in this vegetation. Nevertheless vegetation types 2 and 3 share a large number of their commoner birds, most of which are insectivorous and/or nectivorous. Vegetation type 2 had a variety of insect pollinated plants in full flower during the months of the study. These plants, although usually less than 4 m high are densely packed and common at all levels below 4 m. (*E. dives* and *E. radiata* and two species of Proteaceae were also flowering at the time and are a resource for honeyeaters.)

Vegetation type 1. Although this type has the greatest potential for attracting seed, berry and drupe feeding birds, none of the plant species providing these foods was in fruit during the study. Similarly, because of lower temperatures at 1200 m, few plants were in flower at this time. Of the common birds, it was noticeable that each had a markedly different feeding niche. Five of these birds were the most common on the whole study area. In contrast, vegetation types 2 and 3 often contained birds of restricted distribution with usually two or more species for each vegetation stratum or food type (e.g. 3 spp. of honeyeaters, 2 spp. of thornbill, 2 spp. of whistler etc.).

Vegetation type 4. Each of the two tree layers and the shrub layer of this type is represented by a single plant genus. In these strata this low diversity associated with low canopy density suggests a correspondingly low invertebrate diversity and abundance. This is compounded by the low abundance of insect pollinated flowers (a few ground cover species and *E. polyanthemos* in flower during Oct.-Nov.) and a shallow leaf litter. Consequently, vegetation type 4 had low bird numbers at all times, with no bird species of frequency > 50 per cent. All birds described in this habitat were common in vegetation types 1, 2 and 3.

CONCLUSION

These vegetation types, defined by floristic means alone, obviously differ in the type, amount and period of availability of food resources for mammals and birds. Vegetation type 3 is the best overall food reserve because of its high productivity, its wide range of niches for invertebrates, its range of edible plant tissue for mammals and its consistently cool-temperate climate, so that many of these resources are available for most of the year.

Vegetation type 2 is more seasonal; flowering time is important since flowers produce and attract the food resources—nectar, pollen and insects. The environment is less stable because of seasonal flooding and drying. Finally, there is no deep leaf litter, probably as a result of flooding and the type of leaves on the main canopy species, and this will reduce the number of litter invertebrates in spring and summer.

Part of vegetation type 1 is potentially the best habitat during summer. At this time birds and mammals will be abundant where berry, drupe and seed producing plants are in good supply and where *E. pauciflora* leaf litter is minimal. All alpine eucalypts of this study flower in summer and so provide an added food source. Nevertheless the severe winters and patchiness of this productive vegetation suggest vegetation type 1 is a relatively poor food resource for vertebrates during spring.

Vegetation type 4 is the least productive resource for the whole year. Its cold winters and hot, dry summers stress plants, particularly in the low nutrient soils. The vegetation is floristically poor with few food plants and there are always few invertebrates.

This floristic classification, although providing minimal evidence for truly definable animal-plant relationships, does provide a basis for erecting hypotheses. It is clear that a knowledge of flowering and fruiting times and types as well as the quality of leaf, root, rhizome and tuber tissue of plants can add valuable insight into the reasons for variation in animal types and numbers in a natural environment.

The period that these resources are available is of particular relevance to the prediction of bird diversity and abundance at times other than that of the study. For example it is likely that in late summer vegetation type 1 will have a much greater bird diversity. We therefore suggest that for the return provided, the floristic information collected and analysed for this chapter was a reasonable investment.

ACKNOWLEDGMENTS

The authors express their thanks to all members of the Fisheries and Wildlife, and National Herbarium survey teams, for assistance in the collection and collation of these data. Thanks are also due to Professor A. K. Lee, Mr A. Cockburn and Mr W. B. Emison for reading and commenting on early drafts.

REFERENCES

- Braithwaite, R. W., and Gullan, P. K. (1978). Habitat selection by small mammals in a Victorian Heathland. *Aust. J. Ecol.* 3: 109-27.
- Braithwaite, R. W., Cockburn, A., and Lee, A. K. (1978). Resource partitioning by small mammals in lowland heath communities of South-Eastern Australia. *Aust. J. Ecol.* 3: 423-45.
- Cockburn, A. (1978). The distribution of *Pseudomys shortridgei* (Muridae: Rodentia) and its relevance to that of other heathland *Pseudomys*. *Aust. Wildl. Res.* 5: 213-19.
- Gullan, P. K. (1978). Vegetation of the Royal Botanic Gardens Annex at Cranbourne, Victoria. *Proc. Roy. Soc. Vict.* 90: 225-40.
- Mathews, E. G. (1976). *Insect Ecology*. University of Queensland Press, St Lucia, Queensland.
- Robinson, A. C. (1976). Population ecology of *Rattus fuscipes*. Ph.D. Thesis, Monash University, Clayton, Victoria.
- Stace, H. C. T., Hubble, G. D., Brewer, R., Northcote, K. H., Sleeman, J. R., Mulcahy, M. J., and Hallsworth, E. G. (1972). *A Handbook of Australian Soils*. Rellim Technical Publications, Glenside, South Australia.
- Stoddart, D. M., and Braithwaite, R. W. (1979). A strategy for colonization and utilization of a fire-adapted habitat in the brown bandicoot (*Isoodon obesulus*; Marsupialia, Peramelidae). *J. Anim. Ecol.* 48: 165-79.

- Taylor, J. Mary (1961). Reproductive biology of the Australian bush rat, *Rattus assimilis*. *Univ. Calif. Publ. Zool.* **60**: 1-66.
- Warneke, R. M. (1971). A field study of the Australian bush rat, *Rattus fuscipes* Waterhouse (Rodentia: Muridae). *Wildl. Contr. Vict.* **14**: 1-115.
- Watts, C. H. S., and Braithwaite, R. W. (1978). The diet of *Rattus lutreolus* and five other rodents in Victoria. *Aust. Wildl. Res.* **5**: 47-57.
- Wood, T. G. (1971). The effects of soil fauna on the decomposition of *Eucalyptus* leaf litter in the Snowy Mountains, Australia. In *Colloquium Pedobiologiae*, 4th Dijon, 1970 (UNRA publ. 71-7), Paris.

*Ant distribution, vegetation, and soil
relationships in the Cooloola-Noosa River area,
Queensland*

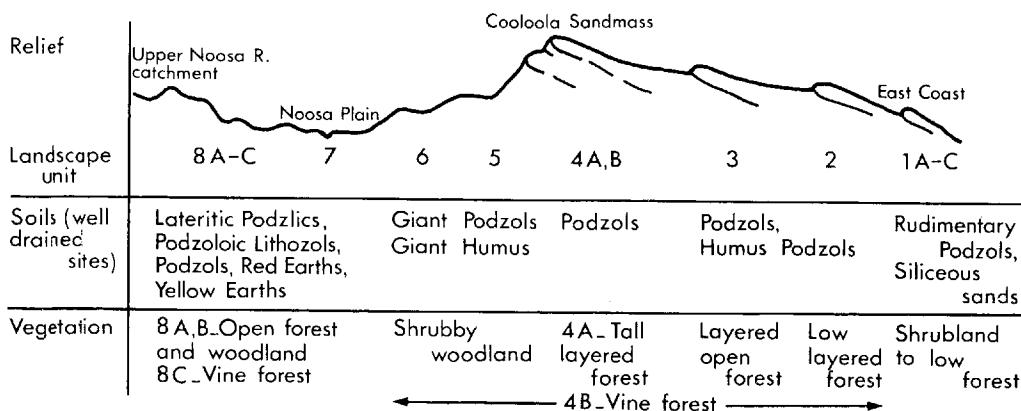
P. J. M. GREENSLADE and C. H. THOMPSON

INTRODUCTION

A survey of the ants (Hymenoptera: Formicidae) of the Cooloola-Noosa River area has been carried out as a zoological contribution to a multi-disciplinary study of the region by CSIRO Division of Soils, Brisbane. We are concerned primarily with soil-soil fauna relationships, but to a large extent soil exerts its influence on the fauna indirectly through effects on vegetation. We are therefore users of vegetation classifications and look for a system that can be applied consistently and fairly rapidly with little prior knowledge of floristics or seral status of a vegetation type. A structural classification meets these requirements. Vegetation structure is also of direct significance in ecological studies of soil and soil surface invertebrates such as ants. The mass and dispersion of vegetation determine both the physical framework within which above-ground activity takes place and the availability of food and hence carrying capacity. Some ant species depend on prey and exudates from woody plants; others feed in the ground layer on invertebrates belonging to the complex of decomposer organisms whose abundance tends to vary with the supply of dead plant material. Vegetation structure also influences ground layer invertebrates through its effects on the climate near the surface of the soil (Brian and Brian 1951). Many ants require high temperatures to achieve full activity but at the same time are liable to be adversely affected by accompanying high saturation deficits (Greenslade 1972; Nel 1965, 1967).

The Cooloola-Noosa River area considered consists of coastal sand dunes, coastal plains and low sandstone hills (Fig. 19.1). It has a range of habitats with different soils, vegetation, drainage and microclimates within the same general climatic region and so provides an opportunity for relating the responses of the ant fauna to local changes in environmental factors. For example, all of the soils on the sand dunes have essentially the same grain size and loose surface consistence; consequently it is possible to relate ant distribution patterns to vegetation and its structure since the physical properties of the surface soil remain relatively constant. By including some sites on the sandstones of the upper Noosa River we can also examine effects of variation in soil surface properties. In this chapter we consider results from well-drained sites in a single period, February 1977. This helps to reduce two other factors: seasonal effects and variation due to soil drainage.

There are no previous reports of the ecology or biogeography of ant faunas of eastern Australia apart from an account of the penetration of New Guinea based taxa into Australian vine forests by Taylor (1972).



19.1 Diagrammatic cross section across the Cooloola sandmass and Upper Noosa River Catchment. After Thompson and Moore (in press).

THE COOLOOLA-NOOSA RIVER ENVIRONMENT

Regional climate

The area has a humid and subtropical climate with a mean annual rainfall of 1400 to 1700 mm (Thompson and Moore, in press), which has a strong summer incidence. On average, precipitation exceeds evaporation from January to July inclusive, although sufficient rain to recharge the soil profile and initiate leaching can occur in any month. Maritime influences are responsible for a low amplitude of fluctuations in air temperature. The average daily and seasonal range of temperature at Double Island Point on the coast is only about half that experienced at Gympie, 50 km inland. This coast-inland gradient may well be of significance within the area with which we are concerned because it extends some 20 km from the coast.

Geomorphology and soils

The Cooloola sandmass is one of the large accumulations of wind-blown sands which occur as islands and mainland deposits along the Queensland coast (Coaldrae 1962; Thompson 1975). It is made up of successive overlays of silica sands which have been blown in from the coast during the Quaternary to form overlapping systems of large compound dunes reaching elevations of 200 m and extending some 10 km inland. A low coastal sandplain 1-4 km wide—the Noosa Plain—lies along the western margin of the dunes, separating them from the low sandstone hills of the upper Noosa River catchment.

TABLE 19.1
Landscape units in the Cooloola-Noosa River area

Landscape unit	Landform	Soil ¹ and solum depth	Vegetation
1 A	Seacliffs and exposed adjacent slopes	Siliceous Sands Uc1.21 on truncated Podzol remnants	Shrubby woodlands: <i>Banksia integrifolia</i> , over dwarf shrubs < 1 m high
	Active sandblows	Siliceous Sands Uc1.21	Colonising shrubland patches of limited species diversity: <i>Banksia</i> , <i>Acacia</i> , <i>Casuarina</i> , <i>Callitris</i> spp.
	V-shaped young dunes	Minimal Podzols Uc3.21 (< 1 m)	Dwarf to low forests: <i>Eucalyptus</i> , <i>Tristania</i> , <i>Angophora</i> spp. The most heterogeneous unit. The shrubby woodlands of Unit 1A and the seaward edges of Unit 1C are severely deformed by wind
2	V-shaped dunes, slight erosion	Young Podzols, Uc2.21 (< 2 m)	Low layered forests 12-19 m high: <i>Eucalyptus signata</i> , <i>Angophora woodsiana</i> over open <i>Acacia</i> , <i>Leptospermum</i> , <i>Xylomelum</i> understorey. Other tree species are <i>Eucalyptus intermedia</i> , <i>Tristania conferta</i> , <i>Banksia serrata</i> , <i>Casuarina torulosa</i> . Three years' fire protection gives 90% grass or grass- <i>Pteridium</i> ground cover. Tree canopies are open so that effective cover is only c. 60% (Fig. 19.2)
3	Lobate U-shaped dunes, moderate erosion	Podzols, Uc2.21, Uc2.22 (2-6 m)	Layered grassy open forests: emergent <i>Eucalyptus pilularis</i> 20-30 m tall; <i>Angophora woodsiana</i> , <i>Casuarina torulosa</i> 18-20 m tall over open <i>Banksia</i> , <i>Acacia</i> , <i>Leptospermum</i> , <i>Casuarina</i> lower storey. More variation in vegetation with geomorphic components than in Unit 2. <i>Casuarina torulosa</i> becomes prominent on the trailing arms of dunes. Ground cover (grasses, <i>Pteridium</i>), up to 80%
4	Broad U-shaped dune remnants, strongly eroded	Giant Podzols, Uc2.21, Uc2.22 (6-10 m)	Tall layered woodland and forest: <i>E. pilularis</i> 30-40 m tall, <i>E. intermedia</i> , <i>A. woodsiana</i> , <i>Syncarpia hillii</i> , <i>C. torulosa</i> , <i>T. conferta</i> , <i>Banksia serrata</i> . <i>Acacia</i> , <i>Leptospermum</i> , and <i>Casuarina</i> , species form a scattered to dense understorey according to fire frequency. Ground cover (grasses, <i>Pteridium</i>), up to 80-90%
	Ridges		
B	Interdune corridors	Giant Humus Podzols, Uc2.20 (6-10 m)	Simple and complex notophyll vine forests and microphyll vine forests, 20-40 m tall. Vine forest occurs in sheltered situations from Units 2-5 but is most frequent between the high dunes of Unit 4. Included here are minor occurrences of secondary low mesophyll vine forest with sclerophyll emergents

Notes: ¹ Great soil group (Stace *et al.* 1968) and Northcote Factual Key notation (Northcote 1971).

² Ant faunas of the poorly drained areas are not considered in this chapter.

Source: After Thompson and Moore (in press).

TABLE 19.1 (Continued)

Landscape unit	Landform	Soil ¹ and solum depth	Vegetation
5	Large U-shaped dune remnants, severely eroded	Giant Podzols, Uc2.22, Giant Humus Podzols, Uc2.33 (10-15 m)	Shrubby woodlands: <i>E. signata</i> , <i>Angophora costata</i> 12-15 m tall above <i>Banksia serrata</i> 3-8 m tall with <i>Acacia flavescens</i> , <i>Leptospermum stellatum</i> over <i>Epacris</i> , <i>Xanthorrhoea</i> and other heath genera
6	Old, broad whaleback sandhills	Giant Humus Podzols, Uc2.20, Uc2.33 (12-20 m)	Shrubby woodlands: <i>E. signata</i> etc; floristically very similar to Unit 5 but with emergents generally less robust
7	Noosa Plain ²	Humus Podzols, Uc2.20, Uc2.33, Acid Peats, o, Peaty Podzols Uc2.33	Sedgelands and wet heath; shrubland and shrubby woodland in some better drained situations
8	Sandstone hills and plateaux		
A	Stony rises	Podzolic Lithosols, Uc2.12 (<1 m)	Shrubby, grassy woodlands: <i>E. signata</i> , <i>A. costata</i> , over <i>Casuarina littoralis</i> , and <i>Acacia</i> spp.
B	Crests, upper slopes	Lateritic Podzolics, Gn2.74, Gn3.84 (<2 m)	Open grassy forests: <i>E. signata</i> , <i>E. intermedia</i> , <i>A. costata</i> , 20-30 m tall
C	Alluvial platforms	Podzols, Uc5.31, Uc2.31, Yellow Earths and Red Earths, Gn2.14, Gn2.24 (2 m)	Vine forests including small areas of tall layered forests with sclerophyll emergents over a mesophyll understorey
D	Middle and lower ² slopes, drainage lines	Gleyed Podzolics and Soloths, Dy3.41, Dy3.81 (<2 m), Humic Gleys, Dy2.81 (<2 m), Acid Peats, o	Woodlands to open woodlands, sedgelands

Notes: ¹ Great soil group (Stace *et al.* 1968) and Northcote Factual Key notation (Northcote 1971).

² Ant faunas of the poorly drained areas are not considered in this chapter.

Source: After Thompson and Moore (in press).

Eight periods of dune-building have been recognised in the sand-mass, interspersed with more stable periods in which soil formation and water erosion were the dominant processes (Thompson and Moore, in press). Dunes formed during six of these periods occupy most of the present ground surface forming a parent material-age sequence in which depth of soil-weathering and leaching increase with dune age. The soils and vegetation of the different dune systems are briefly summarised in Table 19.1. With the exception of sea cliffs, bare sandblows and newly vegetated areas, all the soils of the freely-drained dunes are Podzols with solum depths ranging from <1 m on the youngest dunes to >20 m on the oldest. Water-tables within 12 m of the surface are fairly common in interdune corridors and have led to the development of Humus Podzols. All the dune soils have very low plant nutrient levels and both depth and intensity of soil development determine nutrient content in any given metre depth of soil.

Shallow water-tables and seasonal water-logging prevail on the Noosa Plain and on poorly drained lower slopes in the upper Noosa River catchment. Humus Podzols and Acid Peats occupy most of the Noosa Plain but Gleyed Podzolic soils and Humic Gleys are the common soils of poorly drained sandstone areas. Lateritic Podzolic soils commonly occur on broad crests and upper slopes of the low sandstone hills with some areas of Podzolic Lithosols on outcrops of quartzose sandstones. There are also limited occurrences of Podzols, Red Earths and Yellow Earths. Most of these soils have sandy loam A horizons which set hard when dry.

Vegetation

On well-drained sites both structure and floristics of the vegetation vary with landform, degree and depth of soil weathering and exposure to wind, and have been further modified by management practices. A range of vegetation types from shrubland, shrubby woodlands, and open forests to tall layered forests, and vine forests can be placed in a series of eight major landscape units which relate vegetation, soils and landforms (Fig. 19.1; Table 19.1), against which the distribution of the fauna can be viewed.

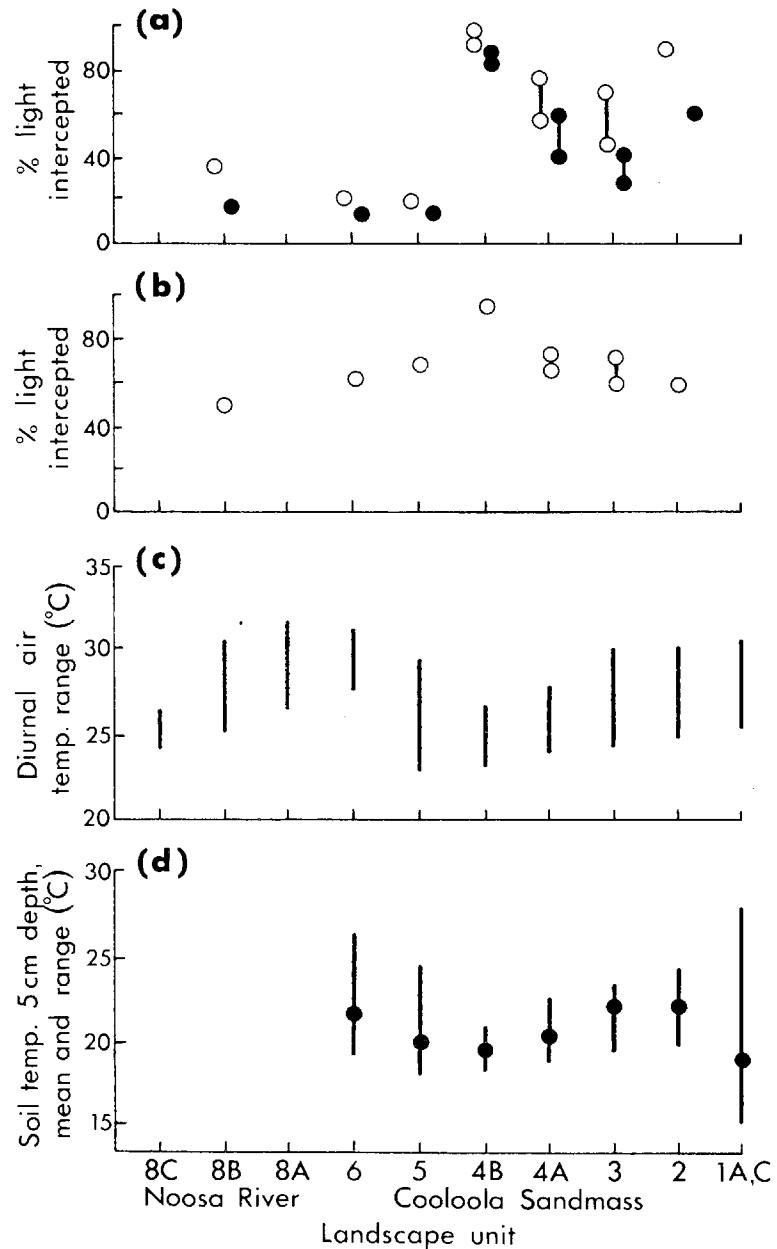
Selective logging over many years has altered the tree canopy cover over much of the area and controlled burning at about three-year intervals has affected both density and species composition of understorey and ground cover. Fire appears to have been responsible for a mosaic of shrub and grass dominated areas in the layered forests. In shrubby woodlands, about 50 per cent of the soil surface is exposed immediately after burning. On one site, a six-year protection from fire allowed a heathy ground layer to reach 90 per cent cover. Management has therefore increased variability in vegetation so that more than one structural type now occurs in what was previously regarded as a single natural unit.

The vegetation of the area has been previously described by Coaldrake (1961), Harrold (1971) and Webb and Tracey (1975). The broad summaries of Table 19.1, however, are based on detailed descriptions of the vegetation at ten CSIRO research sites (Walker and Hopkins pers. comm.), with some modification according to our overall impression of each unit as a whole.

At Cooloola, Unit 1 represents the youngest dune-soil association and Unit 6 the oldest. As soil weathering proceeds in the young sands the accumulation and organisation of plant nutrients in the soil, litter layer and vegetation exceeds the rate of loss from leaching and erosion. With time there is an accompanying rise in the mass and height of vegetation from Unit 1 to Unit 4A (Fig. 19.1). The greatest biomass, in the vine forests of Unit 4B, is a rather special case in which the controlling factors are shelter from wind and access to deep water tables. Plant biomass declines on the older, strongly leached sands of Units 5 and 6, resulting in more open vegetation. On the sandstone hills vegetation height and cover increase again as one passes from Unit 8A to 8C.

Microclimates

The main features of the regional climate that are likely to be significant to the ant fauna are high humidities, relatively small daily and seasonal range of fluctuation in temperature and low maximum temperatures. These climatic influences are accentuated in the

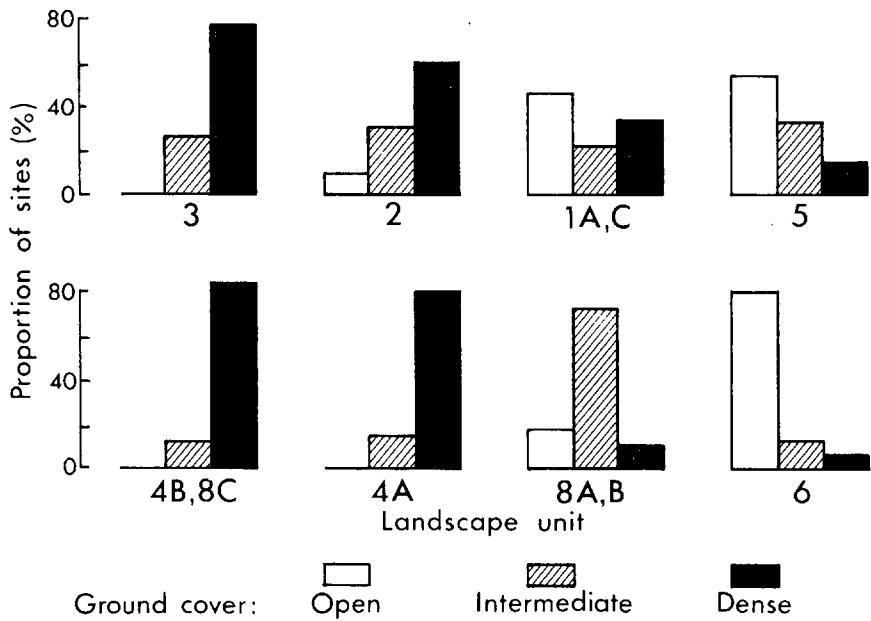


- 19.2 Tree canopy area at CSIRO research sites, light interception and temperatures in landscape units:
- Total canopy area (%) of trees and shrubs > 2 m tall measured off air-photographs (open circles) and effective canopy cover (ratio of total canopy area % to (c)) (solid circles).
 - Proportion of incoming light intercepted at half canopy position as measured by photometer against that recorded at canopy windows.
 - Range of air temperatures in shade recorded during daytime sampling for ants, February 1972.
 - Mean soil temperature and range at 5 cm depth at CSIRO research sites over 24 hours on 7 May 1977.

taller, denser forests and moderated in more open vegetation with a less complete ground cover.

Figure 19.2 attempts to relate canopy structure, interception of sunlight, and temperature regimes in landscape units. (In addition to these data it should be mentioned that in the region, frosts do occur and air temperatures may exceed 35°C.) There is great variation in temperature within units and the soil temperatures at 5 cm depth (Fig. 19.2d) have been selected because they show less spatial variability than temperatures at or above the soil surface. According to Fig. 19.2, maximum temperatures and the range of fluctuation tend to vary inversely with effective canopy cover and interception of sunlight, declining from Unit 1 to 4B, increasing from Units 5 to 6 and declining again from 8A to 8B.

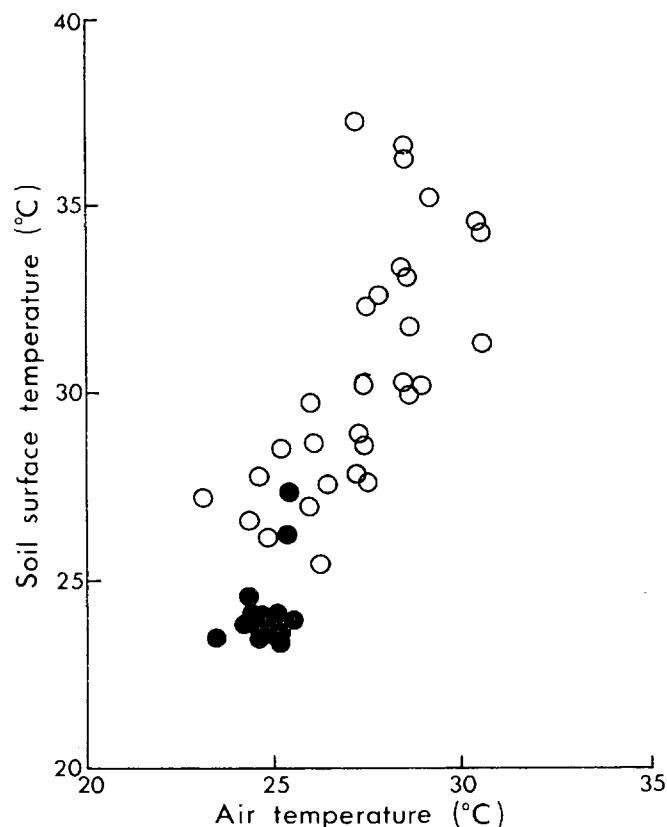
At the soil surface, however, these overall unit differences are modified by the nature and extent of ground cover. At all sites at which ants were sampled, the density of total ground cover (i.e. ground layer vegetation plus leaf litter), was subjectively assessed (Fig. 19.3). When ants were sampled, records were made of air temperatures in shade c. 1 m



19.3 Field assessment of ground cover (ground layer vegetation plus leaf litter) at ant collection sites: open 33% or more bare soil exposed; dense, virtually no soil exposed

above the ground, and of soil temperatures 1 mm below the surface in sun and shade. Fig. 19.4 compares the two extremes of ground cover, vine forest (Units 4B, 8C) with a dense litter layer, and shrubby woodland (Units 5 and 6) with considerable exposures of bare soil. In vine forest, air temperatures were lower, showed a smaller diurnal range

and the soil surface was generally cooler than the air above it. In Units 5 and 6, soil surface temperatures showed a much wider amplitude and commonly exceeded air temperatures.



19.4 Air and soil surface temperatures in vine forests (solid circles), and shrubby woodlands (open circles)
February 1977

ANT DISTRIBUTIONS

Sampling was based on standardised hand collections, each taking 30-60 minutes over an area of about 1 ha within a landscape unit and usually centred on a soil profile site. These collections were supplemented at a few sites by pitfall trapping and extraction of litter samples in Tullgren funnels. The method is intended for reconnaissance survey, relating ant distribution to broad patterns of landscape. It yields a habitat \times species frequency matrix akin to plant quadrat data but differing in that each individual sample is incomplete. Although most hand collections were made in the day, a few nocturnal samples were also obtained. Over much of Australia there is a succession of groups of ant species that are active at different times of the day and night and collections need to be spread over the 24-hour period. But in this mild coastal climate periodicity is not strongly expressed and even the most exclusively nocturnal species can be found during

TABLE 19.2
Distribution of ant collection sites in landscape units, February 1977

Landscape unit	Upper Noosa River catchment				Cooloola sandmass					
	8C	8B	8A	6	5	4B	4A	3	2	1
Hand samples	5	9.5 ¹	5	6	13	9	11	9	12	8
Pitfall traps ²	—	—	—	1	1	1	1	1	1	1
Litter samples	—	—	—	0.5	1	1.5	1	2	0.5	—
Total samples	5	9.5	5	7.5	15	11.5	13	12	13.5	9
Total species	33	62	38	56	69	55	82	62	69	45
Relative diversity (species per 5 samples ³)	33	42	38	44	40	35	47	38	39	33

Notes: ¹. Fractional entries are due to incomplete samples obtained over a brief period or under unfavourable conditions.
². 20 trap-days are equated with one hand sample.
³. Obtained by plotting cumulative species against cumulative samples.

the day in nests under logs and in soil close to the surface. Nevertheless, not all the ant species present on a site are represented in any one collection since there is some variability in timing and conditions of maximum surface activity and hence in the likelihood of a species being recorded. Distribution patterns are also blurred by movement of foraging ants between structural and geomorphic elements within landscape units and occasionally between units.

Results for February 1977 are summarised in Table 19.2. Altogether, more than 280 ant species have been recorded from a total of 21 different habitats in the Cooloola-Noosa River area. Reduction, selection and detailed analysis of these data are the next stages of this project. Here we describe some of the more important types of ant distribution patterns and changes in the structure of ant communities in relation to soil and vegetation.

Distribution of species

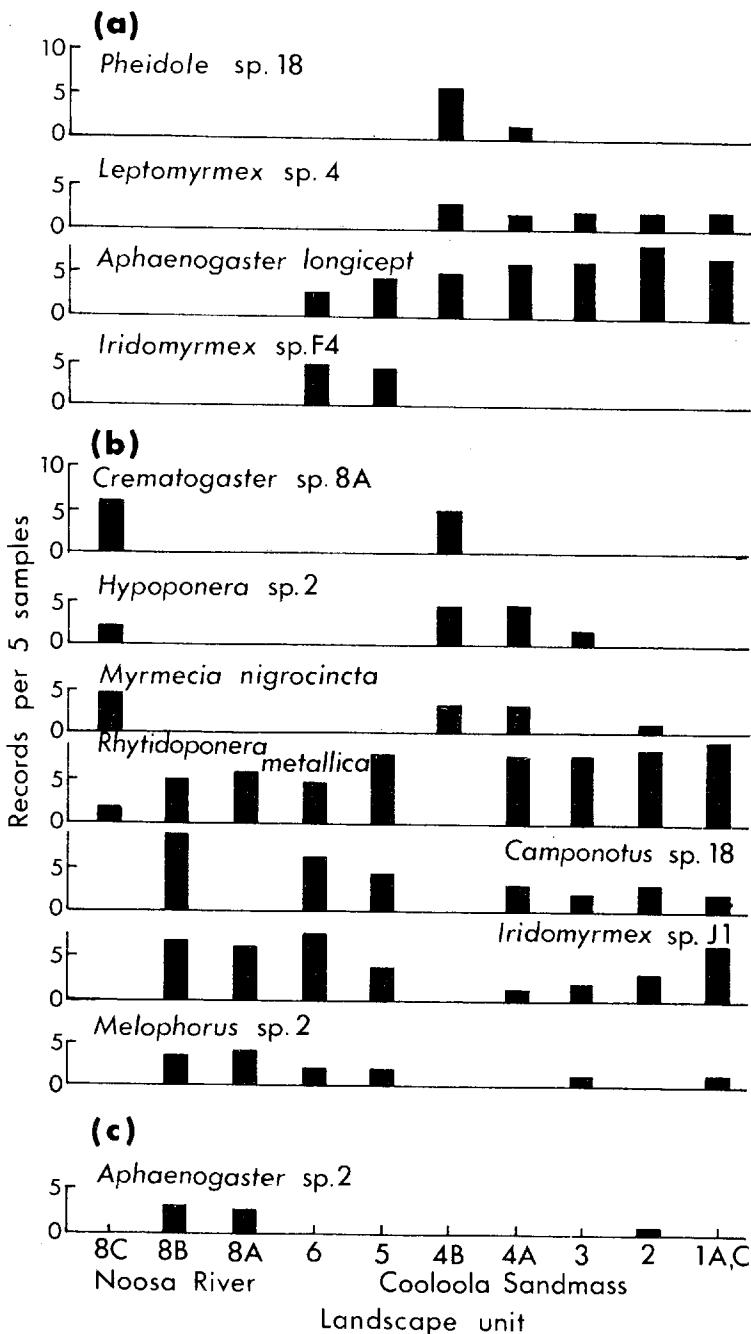
There are three basic distribution patterns related to soil (Fig. 19.5):

- (a) Restricted to the Cooloola sands.
- (b) Widely distributed in respect to soil.
- (c) Occurring only on soils derived from Noosa River sandstones.

Within these patterns species can be ranked according to their preference for shaded or well insolated situations:

1. Restricted to or centred on the coolest most shaded habitat, vine forest (e.g. *Pheidole* sp. 35, **Crematogaster* sp. 5) (Fig. 19.5).
2. Extending from the vine forests into layered forests (e.g. *Leptomyrmex varians* Emery, *Hypoponera* sp. 3, *Myrmecia nigrocincta* F. Smith).
3. Widely distributed in relation to vegetation (e.g. *Aphaenogaster longiceps* (F. Smith), *Rhytidoponera metallica* (F. Smith), *Camponotus* sp., *nigroaeneus* group).

* Numbered species are represented by voucher specimens in the Australian National Insect Collection, CSIRO Division of Entomology, Canberra.



19.5 Frequency of selected ant species in landscape units: (a) only on Cooloola sands; (b) widely distributed in respect to soil; (c) mainly on Noosa River sandstone derived soils

4. Restricted to or centred on well-insolated shrubland, woodland and open forest, never or rarely occurring in undisturbed vine or layered forests (e.g. *Iridomyrmex* spp., *Melophorus* sp.).

Few of the ant species in vine forest are restricted to one soil type, suggesting that adaptation is primarily to the micro-climatic environment. Conversely some of the commonest and most widely distributed species, such as *Rhytidoponera metallica* are scarce in vine forests. *Aphaenogaster longiceps* is exceptional, being very closely tied to soil properties, and its distribution appears to be correspondingly independent of vegetation and associated microclimates. It nests in loose, unstable sands where there are few competitors; locally it becomes very abundant on eroding slopes of dunes in Units 1-4. The importance of the soil factor is also demonstrated by the replacement of *A. longiceps* by *Aphaenogaster* sp. I on the harder sandstone derived soils (Fig. 19.5). One record of this second species from Cooloola at the base of a Unit 2 dune leads us to consider that a lens or stratum of more coherent material (e.g. Teewah Sand), may approach the surface at this point. The distribution of species such as *Iridomyrmex* sp. *agilis* group and *Melophorus* sp. emphasise climatic similarities in the open vegetation of Units 1, 5, 6, 8A and 8B.

Physical disturbance caused by establishment of access tracks and logging operations that change the tree canopy and ground cover favours the extension of certain species beyond their normal range. Tracks provide well isolated habitats that allow *Iridomyrmex* sp. *agilis* group and *Melophorus* sp. to penetrate Units 3 and 4A. In Units 5 and 6 tracks provide unstable, disturbed nest sites for *Aphaenogaster longiceps*.

The selected ant species in Fig. 19.5 are common ones with clear cut distribution patterns, but many other species are either much scarcer or else occur sporadically and so carry little information individually. In Fig. 19.6a species lists for landscape units are compared by calculating a coefficient of faunal similarity: number of species shared by any two units as a percentage of total species in both units together. Taking 25 per cent and 50 per cent as significant levels of similarity gives four sets of positive associations:

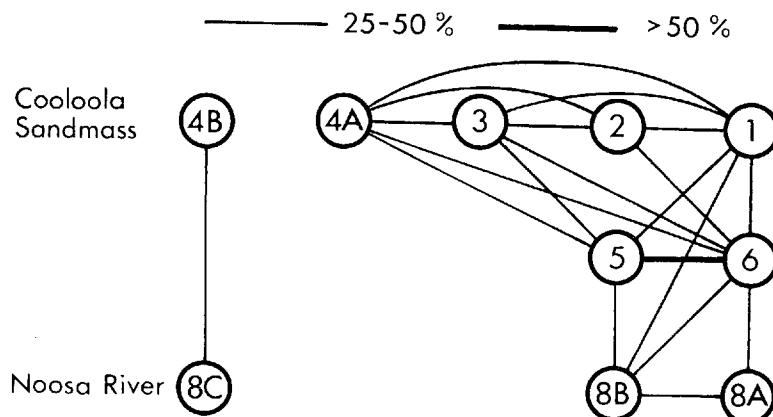
1. Between the two climatically similar groups of vine forests (4b and 8c) which are isolated from all other faunas.
2. Between all the Cooloola sandmass units (1-6), indicating the importance of soil type here.
3. A close similarity between the shrubby woodlands of Units 5 and 6 which parallels their floristic similarity (Table 19.1).
4. The faunas of the Noosa River open forests and woodlands (Units 8A, 8B) linked to each other and the faunas of the more open Cooloola units.

Community structure

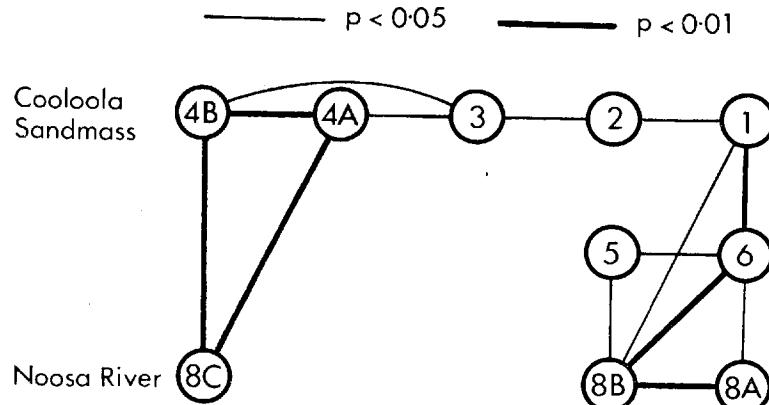
The ant faunas of landscape units can also be compared in terms of community organisation. We use the expression 'community' with reservations as the nearest zoological equivalent of vegetation (i.e. all the plants in an area) to refer to all the animals in an

area (Tweney and Hughes 1956). These ant communities are structured primarily by the presence of dominant species: abundant and influential, affecting the occurrence of other species (Greenslade 1976). Nine community elements (made up of five elements plus two sets each with two sub-groups) are recognised, distinguished by species' role

(a) Faunistic similarity (% shared species)



(b) Similarity in community structure (r)



Temperature increasing →

Vegetation cover and shade increasing ←

- 19.6 Affinity between landscape units in terms of: (a) faunistic similarity; (b) similarity of community structure. Landscape units are arranged in three series in which ground layer insolation and temperatures increase from left to right

and status, and particularly by the means with which they avoid interaction with dominants. Examples of each of these elements, included in Fig. 19.5, are listed below.

1. Dominant epigaeic* dolichoderinae

(a) *Iridomyrmex* spp.

(b) Epigaeic members of other Dolichoderine genera (e.g. *Iridomyrmex* spp. *Leptomyrmex varians* Fig. 19.5).

Over the greater part of Australia competing colonies of dominant *Iridomyrmex* set up a mosaic pattern with which the rest of the ant community must conform. Dominance is achieved through efficient social organisation, rapid communication, success in competition, and abundance. In humid climates *Iridomyrmex* tends to be replaced by other, related dolichoderine genera such as *Leptomyrmex*.

2. Subordinate camponotine Formicinae

Members of genera such as *Camponotus* and *Polyrachis* (e.g. *Camponotus* sp., Fig. 19.5) commonly coexist with *Iridomyrmex* through differences in size of worker and time of foraging and by their submissive or evasive behaviour.

3. Taxa whose occurrence depends on physical properties of the environment such as climate and soils (e.g. *Melophorus* sp., *Aphaenogaster* spp., Fig. 19.5)

Competition is avoided by special adaptation to extreme climates or soil types, for example the association of *A. longiceps* with unstable sands. The genus *Melophorus* has radiated in central Australia where it becomes active at high temperatures when most other ants cease foraging.

4. Cryptic and/or involved as predators and scavengers in the decomposer complex. Many species both nest and forage within decaying logs (e.g. *Hypoponera* sp. 3, Fig. 19.5), or soil or litter. They are often small in size and are at the periphery of the adaptive zone occupied by ants and must compete with other small predators such as Acari and Coleoptera which are closely adapted to life under bark and in the upper layers of the soil (Greenslade 1979).

5. Opportunists

These species (e.g. *Rhytidoponera metallica*, Fig. 19.5) have wide physical tolerances and are effective colonisers of disturbed or temporary habitats but rarely achieve high population densities in the face of competition from other species.

6. Generalised Myrmecines

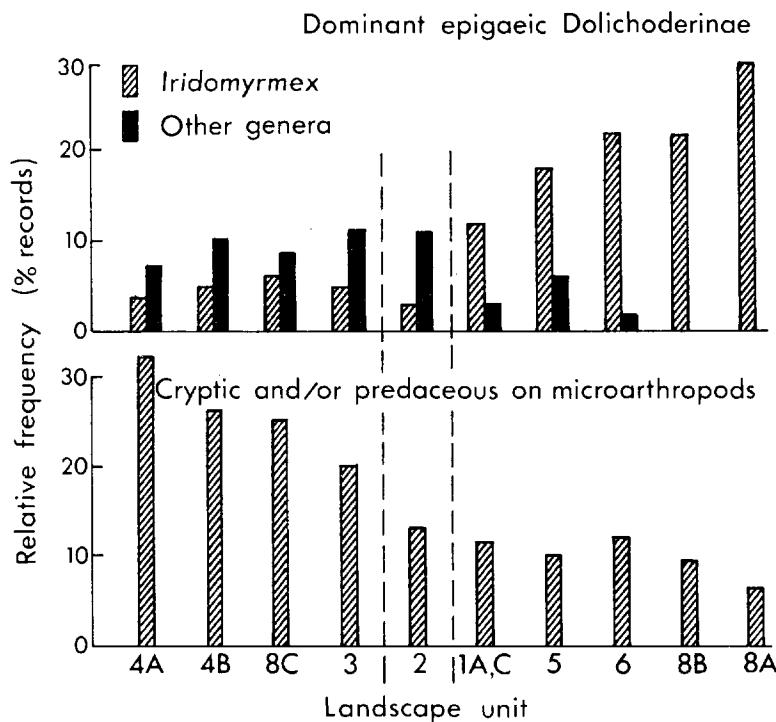
Members of genera *Crematogaster*, *Pheidole* and *Monomorium* (e.g. *Pheidole* sp. 35, Fig. 19.5), are recent additions to the Australian ant fauna on an evolutionary time scale (Brown 1973), and show little coadaptation to the rest of the community.

7. Large, solitary foragers (e.g. *Myrmecia nigrocincta*, Fig. 19.5)

Although large size insulates this group from interaction with many other ants it places them in direct competition with non-social predators and scavengers such as large Coleoptera and arachnids (Greenslade 1979).

* Epigaeic: active on and above the surface of the soil.

Correlation coefficients (r) have been calculated for the frequency of these nine community elements taking each pair of landscape units in turn (Fig. 19.6b). In this case two groups are obtained, the vine forests and taller layered forests (Units 3, 4A, 4B, 8C), and the lower, more open shrublands, woodlands and forests in Units 1, 5, 6, 8A and 8B, linked by Unit 2. In the first group, ant communities of quite different species composition (Fig. 19.6a), have a similar community structure. On the other hand, despite faunistic similarity, Units 1 to 6 on the Cooloola sandmass show significant structural differences when the relative frequency of different kinds of species is taken into account.



19.7 Distribution of three community elements by relative frequency in landscape units

Fig. 19.7 contrasts the distribution by landscape unit of two of these community elements. Dominant *Iridomyrmex* are frequent in the open vegetation of the second group of units, and are partly replaced by other Dolichoderinae in the forests of the first group. This reflects their dependence on high rates of activity requiring relatively high temperatures, and rapid, unimpeded movement across the soil surface. Cryptic species and predators on microarthropods in litter and logs show the reverse distribution and their importance increases in cool, moist forests. Here the production of dead plant material is greater and, since the forest floor is unlikely to dry out, decomposition is uninterrupted assuring the supply of invertebrate prey.

DISCUSSION AND CONCLUSIONS

The composition of ant faunas is strongly influenced by soil type, which determines the pool of species from which communities develop. They do so under the influence of vegetation structure which affects both microclimate and carrying capacity. On the eastern coast of Australia where low maximum temperatures tend to be limiting for ants, the two influences of vegetation act in opposition to each other. Any increase in primary production, canopy height and cover favours greater carrying capacity but at the same time insolation at the soil surface is reduced. The relative diversity (species richness) of the ant faunas of landscape units in Table 19.2 can be interpreted as the result of these two processes. Diversity is low amongst the low, relatively unproductive vegetation of the youngest dunes in Unit 1 where, in addition, some soils are physically very unstable and both drainage and insolation may be excessive. With the increase in height and mass of vegetation, ant diversity increases with dune age through Unit 2 to Unit 4A, to a large extent as the result of the increasing frequency of cryptic species (Fig. 19.7). Greater carrying capacity apparently outweighs the adverse effects of increasing canopy and ground cover. The trend is not continued to vine forests; in Units 4B and 8C shade and low temperatures become critical and diversity falls.

We have virtually no information on the actual temperature preferences and tolerances of Australian ants but the importance of temperature in vine forests can be inferred from the biogeographical affinities of their ant faunas. More than 30 per cent of records from vine forests are of species belonging to genera and species groups adapted to cool climates and with Bassian distributions centred on the wet forests of south-eastern Australia. These species make up 25 per cent of records in the tall forests of Unit 4A but less than 20 per cent in the remaining landscape units. In the woodlands and open forests of Units 5, 6 and 8B diversity rises again as the effects of increasing insolation compensate for lower carrying capacity. Rather low diversity on the Podzolic Lithosols of Unit 8A is probably due to high insolation, the influence of shallow, stony soils and scarcity of nest sites.

In order to fully understand Australian landscapes as ecosystems, studies must include the zoological component. Our work in the Cooloola-Noosa River area demonstrates strong relationships between ant populations and vegetation. At Cooloola, vegetation type is closely related to depth and intensity of soil weathering and dune age. Similar relationships are likely to emerge for other animal groups and in other areas, provided landforms, soils and vegetation are factually described. Simple, readily applicable systems for classifying vegetation and other elements of the landscape are therefore essential in describing and understanding its ecology.

ACKNOWLEDGMENTS

We are grateful to D. J. Ross for technical assistance with both pedological and ant studies, to J. Walker and M. S. Hopkins for information on the vegetation of research sites, and to G. Blackburn for comments on an earlier version of this paper.

REFERENCES

- Brian, M. V., and Brian, M. D. (1951). Insolation and ant population in the west of Scotland. *Trans. R. Ent. Soc. Lond.* **102**: 303-30.
- Brown, W. L. (1973). A comparison of the Hylean and Congo-West African rain forest ant faunas. In *Tropical Forest Ecosystems In Africa and South America: A Comparative Review* (ed. B. J. Meggers, E. S. Ayensu and W. D. Duckworth) Smithsonian Institution Press, Washington, D.C. pp. 161-85.
- Coaldrake, J. E. (1961). Ecosystems of the coastal lowlands, southern Queensland. *CSIRO Aust. Bull.* 283. Melbourne.
- Coaldrake, J. E. (1962). The coastal sand dunes of southern Queensland. *Proc. R. Soc. Qld* **72**: 101-15.
- Greenslade, P. J. M. (1972). Comparative ecology of four tropical ant species. *Insectes Sociaux* **19**: 195-212.
- Greenslade, P. J. M. (1976). The meat ant *Iridomyrmex purpureus* (Hymenoptera: Formicidae) as a dominant member of ant communities. *J. Aust. Ent. Soc.* **15**: 237-40.
- Greenslade, P. J. M. (in press). A guide to ants of South Australia. South Australian Museum, Adelaide.
- Harrold, A. G. (1971). Cooloola—an ecological mosaic. *Queensland Naturalist* **20**: 7-14.
- Nel, J. C. (1965). Influence of temperature and relative humidity on water loss in workers of the meat ant *Iridomyrmex detectus* (Smith) (Dolichoderinae: Hymenoptera). *Aust. J. Zool.* **13**: 301-15.
- Nel, J. C. (1967). Reactions of workers of the meat ant *Iridomyrmex detectus* (Smith) (Dolichoderinae: Hymenoptera) to light and atmospheric humidity. *J. Ent. Soc. S. Afr.* **30**: 111-15.
- Northcote, K. H. (1971). *A Factual Key for the Recognition of Australian Soils*. Rellim Tech. Pubs., Adelaide.
- Stace, H. C. T., Hubble, G. D., Brewer, R., Northcote, K. H., Sleeman, J. R., Mulcahy, M. J., and Hallsworth, E. G. (1968). *A Handbook of Australian Soils*. Rellim Tech. Pubs., Adelaide.
- Taylor, R. W. (1972). Biogeography of insects of New Guinea and Cape York Peninsula. In *Bridge and Barrier: the Natural and Cultural History of Torres Strait* (ed. D. Walker), Dept of Biogeography and Geomorphology, Research School of Pacific Studies, Publication No. BG/3, A.N.U., Canberra, pp. 213-30.
- Thompson, C. H. (1975). Coastal areas of southern Queensland: some land use conflicts. *Proc. R. Soc. Qld* **86**: 109-20.
- Thompson, C. H., and Moore, A. W. (1981). Studies in landscape dynamics in the Cooloola-Noosa River area, Queensland. I. Introduction, soil landscapes and research objectives. *CSIRO Aust. Div. Soils Divl. Rep.* (in press).
- Tweney, C. F., and Hughes, L. E. C. (eds.) (1956). *Chambers's Technical Dictionary*. W. & R. Chambers Ltd, Edinburgh & London.
- Webb, L. G., and Tracey, J. G. (1975). The Cooloola rain forests. *Proc. Ecol. Soc. Aust.* **9**: 317-21.

Vegetation classification and the land use geographer

P. LAUT

INTRODUCTION

To the layman or the casual observer, vegetative cover, i.e. present-day vegetation of a particular area, may appear to be an obvious and readily observed surrogate for many forms of non-urban and industrial land use, and may be regarded as an important factor in assessing land use potential for some purposes. In a very general way vegetative cover is important for land use mapping and most present day land use studies depend heavily on the distribution of particular forms of vegetative cover to map land use, but to be relevant this must be done with the fore-knowledge of what these forms of vegetative cover actually represent. Such classifications are commonly preliminary exercises which are later modified by the inclusion of additional information such as tenure and rural agricultural statistics.

There is a long tradition of using vegetative cover as a first level 'indicator' of land use. In England, it extends back to the Domesday Book compiled by the Normans. It was also used for some of the more significant modern examples of rural land use mapping studies such as Stamp's land use survey of Great Britain (Stamp 1931) and the Tennessee Valley Authority's land use maps (Kristjanson 1953), both begun in the 1930s.

In the post World War II period, vegetative cover has played a considerably greater role in land use mapping because of the increasing availability of aerial photographs and more recently, of satellite imagery. In these, the distributions of certain forms of vegetative cover are obvious and may be mapped rapidly with relatively little ground checking. This is much less expensive than field by field observation, but precludes the possibility of gathering more specific land use information such as the presence of certain types of animals.

Where vegetative cover has been used as a surrogate for land use mapping, the classification must be limited to those forms of vegetation that are both distinctive on the imagery and are closely tied to a specific form of use. Thus classes are usually limited to broad structural classifications such as forest, woodland, grassland, perhaps with natural or cultural notation where there is sufficient evidence.

PURPOSE OF LAND USE STUDIES

The purpose of contemporary land use studies is to provide those who make decisions about land use or land use policies with information about type and intensity of land

use, production or potential production of particular activities, about the relationships between land use and land resources and between land use and the socio-economic conditions of the population dependent on those land resources. In areas where land use change is imminent, land use maps may be particularly significant since they allow comparisons of present and proposed uses with subsequent evaluation of the proposed changes. Until recently, such evaluations used very simple criteria since the intent was usually to evaluate one of the possible alternatives rather than compare a number of alternatives at the same time. Such changes were usually associated with urban and industrial expansion but more recently they have involved the assessment of a range of proposed uses, from mining activities to conservation, with increasingly more complex forms of evaluation and the need to examine land use patterns and options over much larger areas. For example, questions such as: 'What will be the impact of expanding urban settlement at the expense of horticultural activities in near metropolitan areas?', may not be answered satisfactorily simply by examining contemporary land use of those areas. Frequently such questions involve a search for lands capable of replacing those lost to the new use, and involve questions which can only be answered adequately by detailed land resource information of which vegetative cover is but one element.

As noted above, land use information and land resource information have not been used in an objective and explicit fashion in the past. However, there is a growing awareness of the need to adopt new methodologies in land use planning which are objective, and to use information explicitly (McHarg 1969; Austin and Cocks 1978). It could be assumed that with increasing government involvement in land use planning and policy development (Laut 1977) more detailed and accurate land resource and land use information and consequently more detailed and accurate land use classifications may be required. At present, it seems doubtful whether this can be provided simply by improving vegetative cover classification alone, since much of the information required is at the level of the operational or household unit and consists of measures of productivity and economic and social well-being.

It may be that a hierarchy of land use classifications at varying scales is the requirement, with broad classifications of all the land resources and more detailed classification at larger scales for particular areas. In such an approach it is likely that distributions of land use classes will still be mapped on remotely sensed images using vegetative cover as a surrogate. It is important that the classes of vegetative cover recognised should signify important changes in land use rather than being used simply because they are recognisable on the imagery.

LAND USE CLASSIFICATIONS

Land use classifications vary according to the purpose and scale of the study. For the purposes of this chapter I intend to devote most comment to the broader general purpose type land use surveys at scales of from 1:1 000 000 to 1:250 000.

Three typical classification systems within this range are the Canada Land Inventory Land Use Classification (McClellan, Jensak and Hutton 1968), the USGS Land Use Classification System for Use with Remote Sensor data (Anderson, Handy and Roach

TABLE 20.1
Categories used in three small-scale land use classification systems

C.L.I.*	U.S.G.S.†	Australia 1:1 million land use series
2. Horticulture, poultry and fun operations	02. Agricultural land 01 Crop land and pasture 02 Orchards, groves, bush fruits, vineyards and horticultural areas	2. Cropping with or without grazing 21 Cropping and grazing 211 Cereals for grain and grazing
3. Orchards and vineyards	03 Feeding operations 04 Other	212 Fodder and grazing 213 Irrigated fodder and grazing
4. Cropland	03. Rangeland 01 Grass 02 Savannas (Palmetto Prairies) 03 Mixed	214 Other crops and grazing
5. Improved pasture and forage crops	04. Forest land 01 Deciduous 02 Evergreen (Coniferous and other) 03 Mixed	22 Cropping 221 Orchards, plantations and vineyards 222 Horticulture 223 Rice 224 Sugar cane 225 Cotton 226 Linseed 227 Other cereals 228 Other crops
6. Rough grazing and rangeland (a) Natural grasslands (b) Woodland grazing	05. Water 01 Streams and waterways 02 Lakes 03 Reservoir 04 Bays and estuaries 05 Other	3. Grazing 31 Natural or improved pasture 32 Limited grazing
7. Woodland (a) Productive woodland (trees > 25% canopy and > 20 m in height) (b) Non-productive woodland	06. Non-forested wetland 01 Vegetated 02 Bare	4. Forestry 41 State forest or equivalent 42 Timber reserve 43 Privately managed forest
8. Swamp, marsh, bog	07. Barren land 01 Salt flats 02 Beaches 03 Sand other than beaches 04 Bare exposed rock 05 Other	5. Recreation and/or environmental protection 51 National park or similar reserve 52 Other nature scenic or recreation reserve 53 Water supply
9. Unproductive land (a) Sand (b) Rock		6. Institutional use 61 Defence reserve 62 Aboriginal reserve 63 Other
10. Water		7. Mining 71 Open cut 72 Reserve
		8. Unused for above purposes 81 Crown land 82 Freehold or crown leasehold
		9. Water feature Land cover within land use classes 3-8 (a) Forest land (native species) (b) Forest plantation (c) Woodland (d) Shrubland (e) Grassland (f) Wetland, forested (g) Wetland, non-forested (h) Barren land

* Canada Land Inventory

† United States Government Survey

1972) and the Australia 1:1 000 000 Land Use Series (NATMAP AUSTRALIA). The first was completed for the settled areas of Canada basically at a scale of 1:250 000, but included some special areas of intensive rural land use at 1:50 000. The second and third schemes are dependent upon the use of high level remote sensors, especially satellite imagery. The classes for non-urban uses in each of these classification systems are presented in Table 20.1

Of the three, the USGS classification is obviously the most dependent on interpretation of vegetative cover from imagery, with the Australian scheme being the most heavily modified by other information. Each is based on a simple structural classification for initial mapping of geographical distributions of vegetation classes. There is also a common requirement for subdivision of structural classes according to origin, i.e. whether the vegetative cover occurs naturally or is cultivated. There is a more limited information requirement about individual crops or species as in the Australian example or about groups of species as in the horticultural and orchards categories, or to indicate forestry potential.

In terms of actual and potential land use, the most unsatisfactory categories are those associated with woodlands (CLI) and forests (USGS and Australian) since they imply capacity for forest production and conservation yet do not indicate whether this is current or potential. (In the case of the Australian system this is only partly offset by the overlay of tenure information.) Further, only in the CLI classification is there any attempt to define the class in terms of structure.

ENVIRONMENTS OF SOUTH AUSTRALIA

In 1975 the Division of Land Use Research, CSIRO, was commissioned by the Commonwealth Department of Environment and Conservation to undertake a feasibility study for an ecological survey of Australia (Laut *et al.* 1977). The keynote of this study was the development of a methodology for rapid mapping and description of environments using LANDSAT imagery, which could be used throughout Australia. The study was intended to cover a test area of 410 000 km² of southern South Australia in two years but in 1977 the mapping program was extended to include all of South Australia.

The task of mapping and describing the land resources of South Australia was seen as a possible first step in providing land information for the whole continent. Consequently the methodology adopted for the feasibility study had to be readily adaptable for the remainder of the continent survey by small groups of biophysical scientists within a decade (Anon. 1976).

A modified form of integrated reconnaissance survey was adopted. This approach offers flexibility in the size of area for which information is recorded and provides an observed spatial association among attributes, desirable both for regionalising land resources and for storing environmental data. In 'Environments of South Australia' (Laut *et al.* 1977a) a simple hierarchy of areal units is used to provide the necessary scales to describe environmental conditions. These range from *environmental units*, the smallest areal unit, through *environmental associations* and *environmental regions* to

environmental provinces (Laut *et al.* 1977b). At each of these levels there are standardised tabular descriptions of appropriate attributes of the environment. The environmental unit is used to describe landforms, surface water, soils, vegetative cover, native vegetation and land use. Environmental associations are the smallest areal units used to describe mean annual rainfall and evaporation, groundwater resources, landform descriptions for groups of environmental units and conservation areas. Environmental regions are used to tabulate regional climate, including climatic classifications (Köppen and Thornthwaite) monthly distributions of minimum, maximum and mean temperatures, monthly rainfall probabilities and monthly evaporation.

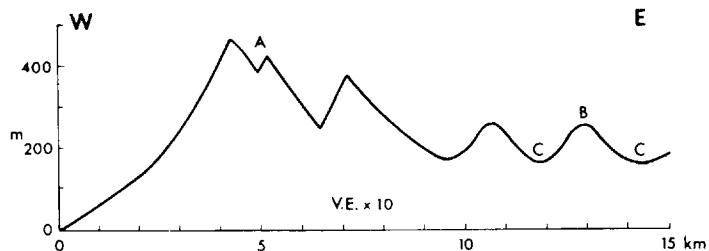
Environmental unit tables (see Fig. 20.1) which are arranged by environmental associations form the greater part of province reports. The relative area of each unit in the association is recorded as dominant (67 per cent or more of the association), co-dominant (34-66 per cent), subdominant (5-33 per cent) or minor (less than 5 per cent of the association). The tables are then arranged so that each group of land attributes can include a maximum of two sets of data per unit thus allowing dominant/subdominant, dominant/minor and co-dominant combinations of surface water, soils, vegetative cover, native vegetation and land use.

The environmental association, which corresponds to an individual occurrence of a land system, was the basic mapping unit. For each province, team members compiled previous research data, undertook reconnaissance field studies and interpreted LANDSAT imagery (black and white, bands 5 and 7 at a scale of 1:250 000) to prepare a map for each discipline (geomorphology, soils, vegetation and land use). Boundaries were examined, modified, or rejected by common agreement until a set of environmental association boundaries proved satisfactory to all disciplines.

VEGETATION AND LAND USE MAPPING

As present-day vegetative cover and land use in South Australia are closely related and involve joint interpretation of LANDSAT imagery patterns, a common map of vegetative cover and land use was prepared as an input for the mapping of environmental associations and the preparation of environmental unit tables. An open-ended fractional notation system was used to code the vegetative cover and land use of each mapped area (see Fig. 20.2) in which the numerator describes vegetative cover and the denominator, the land use. In this way the vegetative cover classification has been maintained, rather than obliterated in the land use classification. The maps were not included in the province reports but were published separately (Heyligers, Laut and Margules 1978).

The vegetative cover classification consists of two elements, 'state' and 'type' which, in the environmental unit tables, are supplemented by 'overhead flora' and 'ground flora' and by three descriptors of 'native vegetation' (formation, relative area and alliance) where it occurs. The land use classification, which consists of four elements (utilisation, products/purpose, average size of holdings and special features), both interprets vegetative cover in terms of land use and adds information derived from other sources.

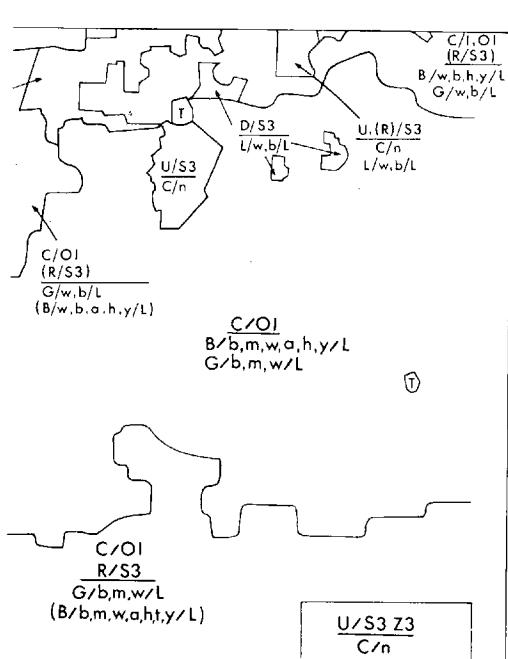


Typical land section

	Environmental unit A	Environmental unit B	Environmental unit C
Relative area	Co-dominant	Co-dominant	Subdominant
Landform			
Type	Hogback ridge	Ridge	Valley floor
Slope class (%)	30-56	30-56	1-3
Maximum slope (%)	100	56	5
Dimension	Long	Long	Long
Frequency	Frequent	Frequent	Common
Rock type	Quartzite	Shale	Alluvium/shale
Surface water			
Form	Channelled	Channelled	Channelled
Area/width	1-5 m	1-5 m	10 m
Depth	Shallow	Shallow	Medium
Origin/purpose	Streams	Streams	Streams
Permanence	Intermittent	Intermittent	Intermittent
Quality	General suitability	General suitability	General suitability
Liability to flood	-	-	-
Soil			
Symbol and name	Um5.41 : reddish dense loams	Um5.11 : reddish powdery calcareous loams	Dr2.23 : hard pedal red duplex soils
Relative area	Dominant	Dominant	Dominant
Surface roughness	Rock outcrop	Rock outcrop	None
Depth	Shallow	Shallow	Deep
Drainage	Well drained	Well drained	Well drained
Reaction trend	Neutral	Alkaline	Alkaline
Stoniness	None	None	None
Vegetative cover			
State	Disturbed natural	Degraded natural	Degraded natural
Relative area	Dominant	Subdominant	Dominant
Type	Low open woodland	Tall shrubland	Open woodland
Overhead flora	Native pine, gilja, black oak	Elegant wattle, birdseye, native fuchsia	River red gum, coolibah box
Ground flora	Grasses and ephemeral forbs	Grasses and ephemeral forbs	Grasses and ephemeral forbs
Native vegetation			
Formation	L1 : low open woodland	L2 : low woodland	M2 : woodland
Relative area	Dominant	Dominant	Dominant
Alliance	<i>Callitris columellaris</i> ; <i>E. socialis</i> - <i>E. brachycalyx</i> ; <i>Casuarina cristata</i>	<i>Callitris columellaris</i> ; <i>Casuarina cristata</i>	<i>E. camaldulensis</i> ; <i>E. intertexta</i>
Land use			
Utilization	Extensive grazing	Extensive grazing	Pastoral
Relative area	Dominant	Minor	Dominant
Product	Wool, beef	-	Wool, beef
Special features	-	-	-
Land limitations	Sheet erosion	Sheet erosion	Gullyling locally

20.1 Explanation of environmental unit tables

VEGETATIVE COVER



20.2 An example of vegetative cover and land use mapping

The 'state' of vegetative cover is indicative of the degree of disturbance or alteration of the original vegetation by man's use of the land resource. Four categories were recognised.

- (a) *Undisturbed natural*: vegetation, by and large, is in its natural state or if it has been disturbed by man there has been substantial recovery.
- (b) *Disturbed natural*: vegetation has been utilised but the original composition and structure remain and vegetation will recover in a relatively short period.
- (c) *Degraded natural*: vegetation has been intensively utilised and its original composition and structure has been changed significantly, but there has been no deliberate attempt by man to replace naturally occurring species or to use fertilisers. Vegetation in this category will require long time periods and protective management to recover.
- (d) *Cultural*: natural species largely or completely replaced by introduced species, frequently with management practices involving additional inputs such as fertilisers, irrigation water, cultivation and weedicides.

'Type' of vegetation refers to the kind and density of the characteristic plants, i.e. structural formations, and is a modified form of Specht's (1972) classification (see Table 20.2) which is extended to include cultural vegetation. Overhead and ground flora (the

TABLE 20.2
Structural types of vegetative cover

Visually dominating plant forms	Approximate foliage cover as projected on the ground*		
	> 30%	10-30%	< 10%
NATURAL VEGETATIVE COVER			
<i>Trees</i>			
Trees > c.10 m	Forest	Woodland	Open woodland
Trees < 10 m	Low forest	Low woodland	Low open woodland
<i>Shrubs</i>			
Mallees	Mallee	Open mallee	Open mallee
Other shrubs > c.2 m	Scrub	Tall shrubland	Tall open shrubland
Shrubs < 2 m	Heath	Shrubland	Open shrubland
		Low shrubland	Low open shrubland
<i>Herbs</i>			
	Herbaceous vegetation	Herbaceous vegetation	Herbaceous vegetation
CULTURAL VEGETATIVE COVER			
Trees, mallees	Forest plantation	Parkland	Open parkland
Shrubs; pruned trees and trained vines	Horticultural plantation	Shrub parkland	Open shrub parkland
Herbaceous plants	Grassland	Grassland	Grassland
	Cropland	Cropland	Cropland

* After Specht (1972).

additional attributes of vegetative cover in environmental unit tables) provide information about plants dominant in, or characteristic of, the unit. Common names of plants are used to aid the non-botanically minded user and in many cases floristic information is not at species but at a more general level, e.g. exotic conifers, sedges or crops. The terms *overhead* and *ground* are used in a general sense: overhead overtops ground, thus ground flora may be a shrubby vegetation in a woodland, or annual grasses in a saltbush shrubland. The maps produced in this study, to the best of the author's knowledge provide the first small scale maps of present day vegetative cover of South Australia using Specht's (1972) classification.

DISCUSSION

The vegetative cover classification adopted in *Environments of South Australia* was intended to be of particular use to the land use geographer, and more indirectly, to the land use planner, especially at the regional and state levels. The two ecologists and the land use geographer in the team combined to develop both classifications so it was expected that the vegetative cover classification would be highly relevant to the land use classification. In general, it meets the land use geographer's requirements of:

- (a) recording what actually exists at a specific point in space and time,
- (b) attempting to define the medium-term state of vegetation relative to assumed common management practices for the land use involved,
- (c) allowing (relative to the scale of the exercise) monitoring changes in vegetative cover which are indicative of land use change, i.e. radical changes in state, structure and dominant flora, and
- (d) indicating in varying degrees potential land use opportunities.

However, there are a number of obvious problems with both the schema and its implementation and perhaps even with the underlying philosophy, regarding prediction of other land use parameters from which land use potential is derived.

It is extremely difficult to establish 'hard' criteria for classifying vegetation into *undisturbed*, *disturbed* and *degraded* natural classes. In practice, because the study was dealing with relatively large mapped areas of individual classes at a scale of 1:250 000, it was relatively easy to use the classification. Those of the team involved in classifying vegetative cover and land use acknowledged that the implementation of these classes had to be highly subjective and depended heavily on consensus for the classification of areas considered marginal. However, from this experience, it is apparent that without more rigorous definition and establishment of criteria, the classification would be difficult to apply to small areas, and would remain subject to the personal perceptions of the surveyor with consequent loss of repeatability, and comparison through time. On the other hand, apart from conservation, this is not a particularly important characteristic for land use studies, since in most forms of land use it is the continued presence of certain species either for grazing or for forestry which is important.

'Type' of vegetation is a common descriptive indicator of the nature of the landscape as a whole, of man's imprint on that landscape, and of both potential for land use change and of difficulties associated with land use change such as clearing changes. At the scale

at which the classification was applied it presented no particular problems to team members and the extension of the system to include *cultural* vegetation was both sensible and convenient. (It would be difficult to over-emphasise the importance of including *cultural* vegetation in the classification of vegetative cover for the land use geographer as opposed to simply mapping *natural* vegetation, especially as the former may not have existed for some time.)

Again, the inclusion of information on overhead and ground flora offered no particular problems but provided the specific advantages of naming the most common species for assessment of land use potential where applicable, especially for conservation. The greatest difficulty in using this element was deciding how much information should be included. The scale of the exercise precluded the inclusion of such information as the presence of rare plants, or plants which host particular fauna, yet such information could be of paramount importance to the conservationist.

Since this classification was developed and used only in South Australia, it has not been adequately tested in forest environments. This could be of particular importance to the land use geographer since there is no particular place to record potential forest productivity either for all or for particular (e.g. commercial) species, and even at a scale of 1:250 000 such information is of considerable importance for land use studies. This is somewhat analogous to recording edible species for livestock in semi-arid areas, although the species preferences of foresters are much better known.

Finally, there is the matter of compatibility between the schema used to classify vegetative cover in *Environments of South Australia* and other schemas of vegetation classification. At the level of broad scale survey, vegetation surveys of historical vegetation have limited utility for land use studies except: (a) where a relationship is known to exist between a native species and an introduced species which may be important in a rural development program; or (b) to assess the relative loss of particular species, alliances or associations for conservation purposes. But it should be stressed that such studies are usually conducted at scales much larger than 1:250 000.

A more important question is whether the classification adopted in the South Australian study, including vegetative cover and land use, can form part of a hierarchy of vegetation classification which is useful to biological as well as land use studies, or conversely, whether there is an alternative, widely accepted vegetation classification system which is more useful than that used in the vegetation cover section of the South Australian system for land use studies. Perhaps it should be pointed out that there was no other vegetation classificatory system considered to be sufficiently well developed for South Australia at the commencement of the study to effectively replace the Specht system.

As a non-taxonomist I often find it difficult to appreciate the particular advantages of vegetation classificatory systems, especially when many of the attributes used may be of limited consequence to the land resource user. I can only comment adversely on the lack of a widely accepted vegetation classification system suitable for Australian land use studies, whereas in Canada the soils classification is used by all soils scientists and is relevant to land users.

REFERENCES

- Anon. (1976). Report on a feasibility study for an ecological survey of Australia. CSIRO Aust. Div. of Land Use Res. Tech. Memo. 76/10.
- Anderson, J. R., Handy, E. E., and Roach, J. T. (1972). A land use classification scheme for use with remote sensor data, United States Geological Survey Circular 671. United States Department of the Interior, Washington, D. C., U.S.A.
- Austin, M. P., and Cocks, K. D. (1978). Land use on the South Coast of New South Wales. Volume 1. *General Report* (ed. J. J. Basinski) CSIRO, 130 pp.
- Heyligers, P. C., Laut, P., and Margules, C. (1978). Vegetative cover and land use maps for the agricultural districts of South Australia. CSIRO Aust. Div. Land Use Res. Tech. Memo. 78/1.
- Kristjanson, K. (1953). T.V.A. land acquisition experience applied to dams in the Missouri Basin. South Dakota State College. Brookings.
- Laut, P. (1977). The South Australia Ecological Survey—a base for a state-wide land information system? URPIS FIVE. Proceedings of the Fifth Australian Conference on Urban and Regional Planning Information Systems. Canberra.
- Laut, P., et al. (1977a). *Environments of South Australia*. Vols. 1-7. CSIRO Division of Land Use Research. Canberra.
- Laut, P., Heyligers, P. C., Keig, G., Löfller, E., Margules, C., and Scott, R. M. (1977b). *Environments of South Australia*. CSIRO Division of Land Use Research, Canberra.
- McClellan, J., Jensak, L., and Hutton, C. (1968). A guide to the classification of land use for the Canada Land Inventory. Policy and Planning Branch, Department of Energy, Mines and Resources, Ottawa.
- McHarg, I. L. (1969). *Design with Nature*. Natural History Press, pp. 197. Garden City, N.Y.
- NATMAP AUSTRALIA 1:1 000 000 Land Use Series.
- Specht, R. L. (1972) *The Vegetation of South Australia*, 2nd ed. Government Printer, Adelaide.
- Stamp, L. (1931). The history and early development of the Land Utilization Survey of Great Britain. *Geogr. J.* 78: 46-53.

Vegetation classification as a basis for land use planning

J. J. HAVEL

INTRODUCTION

Land use planning can be loosely defined as the art of allocating various uses of land to different parts of a region in a way that maximises their utility and minimises conflict between uses, without degrading the land resource. Cocks (1978) defines it as the exclusion of undesirable, impractical or unacceptable uses and the selection of preferred uses. Recognition of what constitutes undesirable or preferred uses depends on policies which may or may not involve social and economic criteria. This type of approach could be, and in the past has been interpreted as matching land use with landscape. This may then reduce the information needs for land use planning simply to a study of biophysical attributes of the land. On the other hand, if socio-economic considerations are allowed to over-ride biophysical constraints, the resulting poor management may lead to over-exploitation and degradation of the land resource.

Most of the earlier studies by the CSIRO Division of Land Research were of this type (Gunn and Nix 1977). They were mostly carried out at the broad scale reconnaissance level, at scales of 1:250 000 or smaller, and were based on the interpretation of aerial photographs in which changes in vegetation and landforms are principal features causing differences in patterns. The studies covered remote, undeveloped regions, where land use policies were generally as yet not formulated. Although in some comparable overseas studies of multiple uses of land, as for instance the Canada Land Inventory (1965), greater attention was given to the human aspect of the planning, the accent has generally been on the biophysical aspect. Only recently has adequate recognition been given to the fact that the use of land involves people—it is used by people, for people, within the limits that other people allow. The socio-economic factors are therefore just as important as biophysical factors, if not more so (Kennedy and Lodge 1976). Injection of finance and labour, in such forms as fertiliser on poor soils and irrigation in dry climates, can compensate for limitations of the original physical environment. Biological components are, even more than physical factors such as soil fertility, subject to change: the vegetation and fauna of the more densely populated parts of Australia are, to a large degree, exotic rather than indigenous.

Cocks (1978) considers that biophysical inventory should be undertaken only when basic policies on land use have been formulated and expressed as quantitative exclusions and preference rules; in other words, when it is clearly known what should be measured. This leads to an important conclusion concerning the use of vegetation

classification in planning the use of land: it can rarely be the sole basis of land planning, but can generally be used in conjunction with other bases.

Within this limitation, the usefulness of vegetation classification depends on its relevance to the set of land uses under consideration in a given region. Vegetation can be a factor in its own right, or it can serve as an indicator and integrator of other factors which in themselves are more relevant, but also more difficult to assess and to map (Havel 1975a; Austin 1978). In addition, Austin (1978) considers that the description of the vegetation of a region provides a context for informed discussion of that region in relation to other areas.

VEGETATION AS A DIRECT FACTOR IN LAND USE

The uses of land in which vegetation features directly as the object of management or source of productivity are conservation of indigenous flora, grazing on indigenous pastures and silviculture and utilisation of indigenous forests. In all these cases the object of land management is to retain the vegetation in its original condition, or, at most, to raise its productivity without greatly altering its composition. All these land uses are practised extensively, with limited input of capital and labour per unit area. Closely related to them are the conservation of fauna and dispersed low-density recreation, in which vegetation still plays a key, though less direct role. In those forms of land use in which the object of management is the replacement of the original vegetation by a more productive or more saleable crop, the significance of vegetation classification is lower. It can still serve as indicator and integrator of environmental factors, such as climate and soils, which are more directly relevant to the new form of land use. It may also have some direct relevance at the point of transition, reflected in the cost of removing the original vegetation. The prime examples of this type of land use are arable agriculture, horticulture, grazing on improved pastures and exotic tree plantations. A significant feature of these land uses is a greater injection of finance and labour. The greater the injection, the lesser the dependence on the original condition of land. On the negative side, the new system is generally less stable. Cessation of the injection of capital and labour generally leads to decline in productivity.

At the other extreme of the range are those land uses in which the original vegetation is of little significance. Urbanisation, mining and construction of communication lines (roads, railways, pipelines, powerlines, air fields) fit into this category. Vegetation may be of some use as an indicator of potential: it has been used to define broad limits of superficial ore bodies in the case of mining, and to define the physical characteristics of soils as they affect civil engineering, but generally this lacks precision. The cost of removing the vegetation before construction may also be significant, though in these days of heavy clearing and earth-moving machinery even the tallest and most dense forest is no longer a major obstacle. A new situation is created by demands either that the mining and engineering techniques disturb the vegetation as little as possible, or that rehabilitation of the vegetation be undertaken afterwards. In both cases, knowledge of the original vegetation is important.

There are numerous examples of successful correlation of the potential for various types of land use with vegetation types. They include conservation of flora (Specht *et al.* 1974; Webb 1966; Heddle *et al.* 1979; Bibelriether 1972; Pišta 1972), primary and economic productivity of forests (Rodin *et al.* 1974; Becker 1972; Iwaki 1974; Havel 1968), utilisation of forests (L'vov 1970; Bludovský 1973), silvicultural potential, in particular regeneration (Aubréville 1965; Havel 1971; Peřina and Kantor 1973; Timbal 1971; Smologonov *et al.* 1973; Mayer 1976) and range grazing (Forest Range Task Force 1972). In all of these, vegetation is the primary object of management.

There are also a number of studies dealing with fauna conservation (Dziezciolowski 1970; El'skij 1975; Pattemore and Kikkawa 1975; Christensen 1980), recreation (Gal'perin 1973; Tichý 1972) and catchment management (Dimitrovský 1973; Wicht 1971; Michal 1973; Branson 1975; Havel 1975c; Heddle 1981; Batini *et al.* 1976). In all these land uses, vegetation still plays a very important role, though one which is perhaps less direct.

USE OF VEGETATION AS INDICATOR AND INTEGRATOR OF ENVIRONMENTAL FACTORS

There is an even greater number of studies dealing with correlation of vegetation with the physical factors of the environment. This subject represents a substantial portion of ecological literature, and it would be futile to attempt to review it here. The difficulties involved in relating vegetation to environment have been enumerated by Goodall (1970). The need for attempting such correlation so that vegetation classification can be applied to planning the use of land has been stressed by Schlenker and Kreutzer (1976) and Havel (1968, 1975a and b). Of particular importance are Korchagin's (1968) conclusions that plant communities are better indicators of the environment than individual species, that the relationship between plants and environment may vary from region to region, and that it is readily distorted by human interference.

It is important to remember that the quantitative correlation between vegetation and other environmental features such as climate, topography and soils, is never one hundred per cent. Similarly, in the many studies which attempt to define the productivity of an economic crop in terms of climatic and edaphic parameters (Nix 1968; Czarnowski *et al.* 1967; Austin *et al.* 1977) the correlation is again never one hundred per cent. If the prediction of the performance of an exotic crop on the basis of the original vegetation were simply a three step sequence (original vegetation indicates that climate and soil are such and such, and the productivity of the exotic crop under such conditions will be ...) it could be expected to be very imprecise. However, both the original vegetation, and the exotic crop replacing it, often respond to the sum total of environmental factors in a similar way. The prediction can therefore be quite sound, particularly if there is a set of pilot plots on which the performance of the exotic crops can be compared with surrounding original vegetation (Havel 1968).

The usefulness of vegetation as indicator and integrator of environmental conditions is affected by several factors, such as time, scale and the choice of attributes for classi-

fication. Climate operates on a broad scale and tends to be reflected in the structure of the vegetation, whereas edaphic differences operate on a finer scale and are more likely to be reflected in the floristic composition of the vegetation. The degree to which vegetation reflects the environmental conditions is determined by its stability: undisturbed vegetation, or vegetation which has had sufficient time to recover from a disturbance, reflects environmental conditions more accurately than recently disturbed vegetation which is undergoing seral changes. It is therefore not surprising that difficulties are sometimes experienced in relating vegetation to the underlying climatic, topographic and edaphic conditions (Pedley 1974; Carnahan 1976). This in turn limits the usefulness of vegetation as the basis for land use planning.

USE OF VEGETATION CLASSIFICATION IN LAND USE PLANNING

To consider the above discussion with relation to socio-economic factors leads to the conclusion that vegetation classification is most useful as a planning tool in the early stages of the development of a region, when the disturbance of the original vegetation is minimal, and when there are few socio-economic constraints on planning. This is also the stage at which climatic and edaphic maps are generally unavailable, and vegetation maps are more easily compiled. Even under these conditions, some knowledge of climate, topography and soils is desirable for planning the more intensive forms of land use, such as arable agriculture, hence the value of integrated surveys such as those of CSIRO or Canada Land Inventory. With increased development and disturbance, vegetation classification becomes progressively less useful and less feasible. By historical accident, the least disturbed regions in temperate countries tend to be those in which environmental factors are most limiting, for example cold or dry climates, and infertile soils. In such regions there are generally clear, strong relationships between vegetation and the environmental features. It is no accident that the use of vegetation in land use planning has been more successful in Finland and Siberia, Canada, and Western Australia than in southern Europe, southern U.S.A., and Victoria respectively (Ilvessalo 1970; Smologonov *et al.* 1973). An interesting feature of the literature on the use of vegetation classification in planning the use of land is the rapid decrease of published information as one progresses from theoretical to applied studies and ultimately to routine application (Havel 1980). The last can virtually be counted on the fingers of one hand because of the difficulty that planners and managers experience in keeping up with classification theory (Dyrenkov and Chertov 1975), the bewildering profusion of alternative schemes of classification, and the excessive number and over-definition of categories which leads to hopeless fragmentation (Pobedinskij 1976). Description of routine application also lacks the prestige of theoretical studies.

HOW TO MAXIMISE THE USEFULNESS OF VEGETATION CLASSIFICATION TO LAND USE PLANNING

As a basic premise I assume that the classification of vegetation is like any other technological innovation: in order to be used, it must fulfil a need (Twiss 1974). The

potential users of the classifications must be already aware of the need, or the need must be brought to their attention. Until the need is recognised, there can be no sale. It is a simple yet often overlooked fact. A second fact also often overlooked is that a classification system, no matter how sophisticated conceptually and technically, is still a raw product when viewed as a saleable technological innovation. It must be tested in the field and its weaknesses identified and corrected: it must be attractively packaged and actively promoted, and the sale supported by adequate servicing.

It is not enough for the creator of a classification scheme to sit back and let the world discover its excellence. As a first step, he would do well to consider his clientele. In the case of land use planning, his nearest link, his most readily identifiable customers, are the administrators in federal, state or local government. Beyond them are the ministers or councillors, to whom the administrators are responsible. The administrators must be persuaded that the classification scheme is workable, and that it will do the job reliably and at a reasonable cost, so that they in turn can persuade their minister or councillor that the proposed planning of the use of land means a justifiable expenditure of public monies. It is here that the scale of mapping enters into consideration. The scheme must be suitable for presentation as a broad concept, yet must also work in detail. It is unlikely that any single classification or any single criterion can do this, and a combination of classifications, for example structural and floristic or vegetation and geomorphological, may be needed to cover the full range. The broad concept is needed to persuade the decision maker who controls the resources. The details are needed by the man in the field who carries out the detailed planning. In either case, the clearer and more attractive the presentation, the greater the chance of acceptance. A series of coloured maps of a known area, which relate vegetation classification to a number of land uses, is preferable to a listing of complex computer programs (Kaiser *et al.* 1972). People tend to mistrust that which they cannot comprehend.

Public servants tend to be, both by nature and by training, conservative. Persuading them that a classification scheme is useful will, almost certainly, involve a sample application. This can be time-consuming, but can also be useful as a means of discovering and eliminating weak spots in the scheme. The latter point is important because the researcher's involvement does not end with the acceptance of the classification scheme. No scheme is so perfect that it fits all and every situation. It is applied in the field by people who are fallible, and there is always scope for reducing expenditure. To adjust, to correct, and to help improve efficiency and reduce costs, are essential parts of the after-sales service.

It is my belief that whenever vegetation classification has been used successfully in planning the use of land, most of the above requirements have been met (Canada Land Inventory 1975; Forest Range Task Force 1972; Garrison *et al.* 1977; Havel 1968; Forests Department of Western Australia 1976; Jurdant *et al.* 1974; Walker and Angus 1978). That the classification and mapping of vegetation rarely form a sole basis for planning land use is irrelevant. What is more important is that they do not remain merely academic exercises, when so much needs to be done in planning the rational use of land.

REFERENCES

- Aubréville, A. (1965). Les forêts tropicales denses australiennes et leurs conifères. *Bois For. Trop.* **104**: 3-16.
- Austin, M. P. (1978). Vegetation. In: Biophysical background studies. *Land Use on the South Coast of New South Wales* (ed. R. H. Gunn), Vol. 2. CSIRO Australia.
- Austin, M. P., Basinski, J. J., Cocks, K. D., and Ive, J. R. (1977). South Coast Project: pre-print of chapters describing land use planning methodology. CSIRO Division of Land Use Research, Tech. Memo. 77/19. Canberra, Australia.
- Batini, F., Selkirk, A. B., and Hatch, A. B. (1976). Salt content of soil profiles in the Helena Catchment, Western Australia. *Res. Pap., For. Dep. West. Aust.* No. 23.
- Becker, M. (1972). Etude des liaisons station-production dans une forêt sur sols hydromorphes. *Rev. For. Fr.* **24**: 269-87.
- Bibelriether, H. (1972). Zur Entwicklung im Nationalpark Bayerischer Wald zwischen 1850 und 1970. *Forstwiss. Centralbl.* **91**: 296-307.
- Bludovský, Z. (1973). Relation of forest typological and economic regionalization of state forest farms in Czechoslovakia. *Lesn.* **19**: 949-64.
- Branson, F. A. (1975). Natural and modified plant communities as related to runoff and sediment yields. In: *Coupling of Land and Water Systems* (ed. A. D. Hasler), pp. 157-72. Springer Verlag, Berlin.
- Canada Land Inventory (1965) Report No. 1 *Objectives, Scope and Organization*. Dep. Regional Econ. Expans., Canada.
- Carnahan, J. A. (1976). Natural vegetation. In: *Atlas of Australian Resources* (ed. T. W. Plumb). Australian Dept of National Resources, Canberra.
- Christensen, P. E. (1980) The biology of *Bettongia penicillata* Gray, 1837 and *Macropus eugenii* Desmarest 1804 in relation to fire. *Bull. For. Dep. West. Aust.* No. 91.
- Cocks, K. D. (1978). Rural planning: marshalling the data. *Roy. Aust. Planning Inst. J.* **16**(3).
- Czarnowski, M. S., Humphreys, F. R., and Gentle, S. W. (1967). Site-index as a function of soil and climatic characteristics. Repr. from *Ekol. Polska* **15A**(23): 495-504.
- Dimitrovski, K. (1973). Infiltration capacity of forest soils in the Jizera Mts as measure of the hydrological role of the forests. *Lesn.* **19**: 1015-28.
- Dyrenkov, S. A., and Chertov, O. G. (1975). Lesnaia tipologija v SSSR i za rubezhom. (In Russian). [Forest typology in USSR and abroad.] *Itogi Nauk. Tech., Lesovedenie i Lesovedstvo* **1**: 190-253.
- Dzieciolowski, R. (1970). Variation in red deer (*Cervus elaphus* L.) food selection in relation to environment. *Ekol. Polska* **18A**: 635-45.
- El'skij, G. M. (1975). Kachestvennaya ocenka lesnykh mestoobitanii kopytnykh zhivotnykh. (In Russian). [Quantitative evaluation of the habitat of ungulates.] *Lesnoe Khoz.* **1**: 66-9.
- Forest Range Task Force (1972). The Nation's Range Resources—A Forest-Range Environmental Study. *USDA For. Serv., For. Res. Rep.* No. 19.
- Forests Department of Western Australia (1976). A perspective for multiple use planning in the northern jarrah forest.
- Gal'perin, M. I. (1973). The use of forest typology in the landscape management of suburban forests. *Ekol.* **5**: 46-51. English translation, Consultants Bureau, Plenum Publishing Corporation, New York.
- Garrison, G. A., Blugstad, A. J., Duncan, D. A., Lewis, M. E., and Smith, D. R. (1977). Vegetation and environmental features of forest and range ecosystems. *Agriculture Handbook No. 475*, USDA Forest Service.
- Goodall, D. W. (1970). Studying the effects of environmental factors on ecosystems. In: *Analysis of Temperate Forest Ecosystems* (ed. D. E. Reichle), pp. 19-28. Chapman and Hall, London.
- Gunn, R. H., and Nix, H. A. (1977) Land units of the Fitzroy Region, Queensland. *CSIRO Aust. Land. Res. Ser.* No. 39.

- Havel, J. J. (1968). The potential of the northern Swan Coastal Plain for *Pinus pinaster* Ait. plantations. *Bull. For. Dep. West. Aust.* No. 76.
- Havel, J. J. (1971). The Araucaria forests of New Guinea and their regenerative capacity. *J. Ecol.* **59**, 203-14.
- Havel, J. J. (1975a) Site-vegetation mapping in the northern jarrah forest (Darling Range). I. Definition of site-vegetation types. *Bull. For. Dep. West. Aust.* No. 86.
- Havel, J. J. (1975b) Site-vegetation mapping in the northern jarrah forest (Darling Range). 2. Location and mapping of site-vegetation types. *Bull. For. Dep. West. Aust.* No. 87.
- Havel, J. J. (1975c). The effects of water supply for the city of Perth, Western Australia, on other forms of land use. *Landscape Planning* **2**: 75-132.
- Havel, J. J. (1980).
- Heddle, E. M. (1980). Effects of changes in soil moisture on the native vegetation of the northern Swan Coastal Plain, Western Australia. *Bull. For. Dept. West. Aust.* No. 92.
- Heddle, E. M., Loneragan, O. W., and Havel, J. J. (1979). Vegetation complexes of the Darling System. In: *Natural Resources Atlas of the Darling System*. Department of Conservation and Environment, Western Australia.
- Ilvessalo, Y. (1970). Metsiköiden luontainen kehitys-ja puuntuottokyky pohjois-lapin kivennaismailta. [Natural development and yield capacity of forest stands on mineral soils in northern Lapland.] *Acta For. Penn.* **108**: 4-43.
- Iwaki, H. (1974). Comparative productivity of terrestrial ecosystems in Japan, with emphasis on the comparison between natural and agricultural systems. In: *Proc. First International Congress of Ecology*, The Hague 1974, pp. 355-60. Pudoc, Wageningen, Netherlands.
- Jurdant, M., Gérardin, V., and Bélair, J. L. (1974). Ecological land survey, the bio-physical basis of land-use planning. The Saguenay-Lac-Saint-Jean Region, Quebec. In: *Proc. First International Congress of Ecology*, The Hague, 1974. pp. 140-3. Pudoc, Wageningen, Netherlands.
- Kaiser, H. F., DeBower, K., Lockard, R., and Putman, J. W. (1972). Forest-Range Environmental Production Analytical System: *FREPAS*. *Agriculture Handbook* No. 430, USDA Forest Service.
- Kennedy, J. R., and Lodge, J. J. (1976). *Gembrook State Forest: A Case Study in Multiple Use*. Forest Commission, Victoria, Australia.
- Korchagin, A. A. (1968). Nekotorye voprosy ispol'zovaniya rastitel'nogo pokrova kak indikatora sredy. (In Russian). [Some questions regarding the use of vegetative cover as an indicator of the environment.] *Bot. Zh.* **53**: 203-13.
- L'vov, P. N. (1970). Nekotorye kachestvennye pokazateli drevesiny eli, sosny i listvenicy pritundrovoi podzony. (In Russian). [Some quantitative indices of the wood of spruce, pine and larch in the tundra-forest transition zone.] *Lesn. Zh.* **13**: 18-21.
- Mayer, H. (1976). Waldbauliche Behandlung von Schutzwäldern. In: *Proc. XVI IUFRO World Congress*, Norway 1976, *Proc. Div. I.* pp. 24-35.
- Michal, I. (1973). Potenciální vodní eroze půdy a lesní typy. [Potential water-caused erosion and forest types.] *Lesn.* **19**: 323-40.
- Nix, H. A. (1968). The assessment of biological productivity. In: *Land Evaluation*. (ed. G. A. Stewart), pp. 77-87. Macmillan, Melbourne.
- Pattemore, V., and Kikkawa, J. (1975). Comparison of bird populations in logged and unlogged rain forest at Wiangarie State Forest, N.S.W. *Aust. For.* **37**: 188-98.
- Pedley, L. (1974). Vegetation of the Balonne-Maranoa area. In: *Lands of The Balonne-Maranoa. CSIRO Aust. Land Res. Ser.* No. 34: 180-203.
- Peřina, V., and Kantor, P. (1973). Možnosti differenciacie obnovnich způsobů v lesích ČSR. [Possibility of differentiating regeneration methods in the forests of the Czechoslovak republic.] *Lesn.* **19**: 1069-94.
- Pišta, F. (1972). Lesní společenstva Šumavského pralesa. [Forest communities of the Šumava virgin forest.] *Lesn.* **18**: 415-37.

- Podebinskiya, A. V. (1976). Lesnaya typologiya i primenenie ee v lesnom khozyaistve. (In Russian.) [Forest typology and its application in forest management.] *Lesnoe Khoz.* **10**: 25-31.
- Rodin, L. E., Bazilevich, N. I., and Rozov, N. N. (1974). Primary productivity of main world ecosystems. In: *Proc. First International Congress of Ecology*, The Hague 1974. pp. 176-81. Pudoc, Wageningen, Netherlands.
- Schlenker, G., and Kreutzer, K. (1976). Vergleich von Klassifikationssystemen für forstliche Standortskartierungen. In: *XVI IUFRO World Congress*, Norway, 1976, *Proc. Div. 1*: pp. 219-38.
- Smolonogov, E. P., Kirsanov, V. A., Makhonin, A. S., and Kostyuchenko, I. S. (1973). Principles of the compilation and use of forest typological classifications in forest organization in mountainous countries. *Soviet J. Ecol.* **4**: 486-92. English translation by Consultants Bureau, Plenum Publishing Corporation, New York.
- Specht, R. L., Roe, E. M., and Boughton, V. H. (1974). Conservation of major plant communities in Australia and Papua New Guinea. *Aust. J. Bot. Suppl.* **7**.
- Tichý, J. (1972). O hodnocení vegetace, zejména lesův krajině. [On the evaluation of vegetation, with a special reference to forests in the landscape.] *Lesn.* **18**: 881-900.
- Timbal, J. (1971). Application des techniques écologiques aux reboisements en Tunisie. *Rev. For. Fr.* **23**: 25-37.
- Twiss, B. C. (1974). *Managing Technological Innovations*. Longmans, London.
- Walker, P. A., and Angus, J. F. (eds.) (1978). In: Socio-economic background studies. *Land Use on the South Coast of New South Wales. A Study in Methods of Acquiring and Using Information to Analyse Regional Land Use Options*. Vol. 3. CSIRO Australia.
- Webb, L. J. (1966). The identification and conservation of habitat types in the wet tropical lowlands of north Queensland. *Proc. R. Soc. Qld* **78**: 59-86.
- Wicht, C. L. (1971). The influence of vegetation in South African mountain catchments on water supplies. *South African J. Sci.* **67**: 201-9.

Index

- Aerial photographs, use of, 53-65, 86, 99, 150
Agglomerative classification, 118, 183; *see also* Classification, types of
Air temperatures, 198
Alliance (Z-M), 5
Ant distribution, vegetation and soil relationships, 192-207
Aristotelian classification, xvi
Association (Z-M), 4
Association tables, 4
Asymmetric coefficient, 118, 135; *see also* Jaccard measure
Attributes, xviii; biological, 66-7; non-biological, 67; derived, 42; dynamic, 22; ecological, 42; environmental, 42; floristic, 3-9, 31-2, 33, 51, 67, 69, 75; floristic-synthetic, 42; functional, 30-40; morphological, 67; structural/physiognomic, 42, 51; vegetation, 67, 74; vital, 23-8
- Bassian distributions, 206
Beach dune sequence, 49-50, 195
Big scrub, 47
Bird habitats, prediction, typing, mapping, 62-3
Biogeocoenose, 2
Biogeographical affinities, ants, 206
Biomass, 12, 72, 80
Bray-Curtis coefficient, 136-7; Ward's method, 136-7
- Canada Land Inventory, (CLI) classifications, 210-11
Canberra metric, 170; *see also* Similarity measures
Canonical correlation, 170; variates, 165
Canopy cover, 69-70; *see also* Cover
Characters, *a priori* versus 'unweighted', 22
Character species, 2; *see also* Species
Characteristic species, 2; *see also* Species
Classes (Z-M), 5
Classification, types of: agglomerative, 118, 183; Aristotelian, xvi; dominance, 135; floristic, 22; functional, 30-40; global vegetation, 36; irrelevancy of, 23; modal, 35; normal/inverse polythetic agglomerative, 183; over sensitivity; phenetic, 22; physiognomic, 31; Specht, 42; status quo and limitations, 30-1; structural, 44-192; *Theophrastus'*, 22; tropical grasslands, 103; undersensitivity, 23; strategy, 117; vegetation classification as a complex of dynamic systems, 110-12
CLUSTAN, 133; *see also* Computer programs
Complex Mesophyll Vine Forest, 37
Complex Notophyll Vine Forest, 44
- Computer programs: CANAL, 154; CLUSTAN, 133; MAGIC, 183; ORSER, 154; *see also* TAXON computer programs
Confusion matrix, 159-61
Congruence, 3
Constancy table, 188
Contribution coefficients, 175
Continuum segments, 104
Cooloola-Noosa River area, 192-207
Correlation coefficients, 205
Cover: cover/abundance scale, 3; class scale, 16; foliage projective, 10-21, (definition of) 10, 99
Cryptic species, 205; *see also* Species
Current annual growth increment, CAGI, 13
Cyclone damage, 61
- Deciduousness, 11
Density, 69-70
Dichotomous keys, 5
Differential species, 2; *see also* Species
Direct gradient analysis, 129
Disturbances, 23, 28; in rainforests, 42-51; affecting ant distribution, 202
Diurnal mechanisms, 50
Dominance, 129
Diversity: plant species, mammal species and foliage height, 175; properties, 126-39; role of in standardisation, 129; Shannon-Weaver index of, 72; Simpson index, 72; Simpson's measure of concentration, 175
Dominance classification, Scandinavian school of, 135; *see also* Classification
Dominance coefficient, 126
Dominance-type associations, 3
Dune-building, 195; *see also* Beach dune sequence, 49-50
Dynamic attributes, 23-9; comparison of, 25; *see also* Attributes
- Edaphic gradient, *see* Gradients
Edaphic relay systems, 50
Environmental associations, 211
Environmental regions, 211
Environmental units, 211
Epiassociation, 112
Epiformations, 112
Epigaeic, 204-5
Epitaxa, 112
- Factor analysis, 170
Fire, 26, 81
Foliage Projective Cover (FPC), 10-21; definition of, 10, 99; *see also* Cover

- Fidelity, 2
- Floristics: 'quantitative floristic composition', 125; survey, 168; classifications, small mammals and birds, 181-91; *see also* Attributes
- Food resource availability, 185
- Forest-steppe, 109
- Formation classes, 111
- Frequency, 69-70
- Functional attributes, 30-40; definition, 32
- Gower vectors, 170
- Gradients: edaphic, 38-9, 59-60, 127, 193; elevational, 127
- Graphic analysis, 133
- Grammars, 141-9; approximate inference, 146; error and similarity, 145; grammar and niches, 146; inference and description, 144; liquid modelling, natural classification, 141; production rules, 142; semantics and sex, 147
- Growth of plant community, 10
- Habitat \times species matrix, 199
- Heathland, 78-85; fire frequency, 81; floristic diversity, 79; noda, 79; nutrients and micro-organisms, 81; soil moisture, 79; regeneration response, 78
- Height/cover values, 35; *see also* Cover
- Height-life form classes, 99
- Importance values, 70
- Initial floristic composition, 83
- Integrated reconnaissance survey, 211
- Inter-site characteristics, 118
- Inverse analysis, 123
- Jaccard measure, 118
- Kolombangara Island, 131
- Land cover classes, 151
- Land use classification, 209-10
- Land use studies, purpose of, 208-9
- LANDSAT, 86, 122; separation of classes, 150-65, 211-12
- Landscape units, 194-5, 205
- Layers, 10, 205
- Leaf properties: angle, 34; area, 10; as biomass, 12; form, 18, 34-5; size, 33; type, 34
- Life form, 18, 34-5
- Life history characteristics, 23
- Light index, 11
- Light intensity measurements, 168
- Lindenmayer grammar, 143; *see also* Grammars
- MAGIC, 183; *see also* Computer programs
- Mahalanobis distance, 154-7, 163
- Malacophyllous leaf, 30
- Mallee, 99
- Mallee-heath, 99-100
- Mapping: Beard-Webb formula, 99-101; types of Kuchler, 107-8; comparison of methods of vegetation mapping, 86-96; descriptive notation, 98; descriptive system, 98; of Australian vegetation—Carnahan, 108-9; of Soviet Union—Sochava and Lukicheva, 109; standardisation, 94-5; units, 5
- Maps as matrices, xvii
- Maturity Index, Pichi-Sermanni, 72
- Microclimates, 196-7
- Minimum spanning tree, 38, 118, 157; ordination, 38
- Modus, 33; *modal* elements, 32-40
- Moisture index, 11
- Multiple regression of factor scores, 172
- Nastic adaptations, 34
- Nomad, 33
- Nomenclature (Z-M), 5
- Non-linearity, 125
- Non-sprouting species, 26; *see also* Species
- Normal/inverse polythetic agglomerative classification, 183
- Opportunists, 47
- Orders (Z-M), 5
- Ordination, 2, 118; *see also* Graphic analysis; Minimum Spanning Ordination
- Partial correlation coefficients, 178
- Partitioning of resources, 178
- Pattern, zonal and mosaic, 68; successional, 68
- Persistence, 25-6
- Photosynthates, translocation of, 10
- Photosynthesis, net, 10; index, 11
- Phytocoenose, 2
- Phratries, 110
- Phytometer, 23
- Pioneer species, 44; *see also* Species
- Pitfall trapping, 199
- Pixels, 152; errors in LANDSAT data affecting pixel location, 162; reallocation of, 159
- Polythetic process, 5; *see also* Classification, types of
- Principal co-ordinate analysis, 118, 170
- Pro forma, structural, 36
- Propagule-based mechanisms, 26
- Rainforests, 42-65; secondary forest classification problem, 47; disturbance and primary forest process of change, 48-50; attributes of changing forests, 50-1
- Raingreen, 62
- Raunkiaerean approach, 26-8, 33-5
- Regeneration response, 78

- Rélay floristic model, 83
 Relevés, 1, 3, 4
 Relevé groups, 5
 Remote sensing, 53; *see also* LANDSAT
 Respiration, 10; stem/root, 13
 Sandfly plateau, 133
 Scale, xix, 99, 104, 151, 217
 Scaling, forestry values, 63
 Scandinavian school of dominance classification, 135; *see also* Classification
 Sclerophyll, 30
 Seral vegetation, 50; in brigalow (*Acacia harpophylla*), 66-77
 Similarity and difference, xvi
 Similarity measures: Canberra metric, 170; Jaccard coefficient, 118, 135
 Simpson's index, 129
 Soil catenas, 37
 Soil fertility index, 11
 Soil parameters: infiltration and depth, gradient, 37-9; in heathlands, 79-81; moisture, 168; importance of, 202; temperatures, 198
 Soil types, 195-6
 Solar radiation, 10
 Space-dilating strategy, 119
 Species: character, 2; characteristic, 2; constancy, 126; cryptic, 205; differential, 2; diversity, 126, 175; dominance, 168; non-sprouting, 26; pioneer, 44; predominance, 126; richness, 70, 72, 126, 129; sprouting, 27-8
 Spectral separation, 154; signature, 154
 Stability, 42
 Stand attributes, richness, abundance, dominance, 126, 135
 Standardisation (of data), 37
 Standing crop, 126
 State and process, xvii
 Stopping-rules, 119
 Strata, 20, 75, 138; *see also* Layers
 Strategies, 31
 Strictly evergreen, 62
 Structural forma, 33-40
 Structural formations in Australia (Specht), 19, 168, 215
 Structural modi, 168, 177; *see also* Modus
 Structural typing of rainforests, 53-65; interpretation, 60-1; geomorphology, 56; methods, 56; pro forma, 36; secondary forests and typology, 63; soils 56
 Succession: arrested, 46-7; Clementsian, 28; concepts, 25; cyclical, 10; deflected, 46-7; directional, 75; pattern, 68; primary, 10; progressive, 44-5; pyric, 83; reconstructive, 44-5; regressive, 46-7; site factors, 46-7; secondary, 10, 44, 76
 Sun and shade effects, 198
 Swan Coastal Plain, 102
 Tabular sorting, 3, 5
 Taiga, 109
 TAXON computer programs, 36, 118, 123-4, 168; ASYM, 118; CENTPERC, 119; DIVINF, 117-18; INVER, 123; MINSPAN, 123; MULCLAS, 119, 123, 169; REMUL, 117-18, 120-4; *see also* Computer programs
 Thermal index, 11
 Tolerance, reproductive vs. vegetative, 74
 Topogradients, 37, 59, 143
 Triplet notation (Specht), 20
 Tullgren funnels, 199
 Turing machines, 143
 Two-parameter model, 125, 135, 138
 Two way classification (Specht), 15
 UNESCO system of classifying and mapping vegetation, 111
 Uniqueness and generality, xvi
 United States Geological Survey (USGS) classification, 210-11
 Unstandardised density data, 136
 User viewpoint, xx
 Vagility, 42, 50
 Vari-max rotation, 172
 Vegetation and land use mapping, 212-16
 Vegetation classification and land use geography, 208-18
 Vegetation classifications as descriptors of small mammal habitats, 166-80
 Vegetation classification, basis for land use planning, 219-226; as direct factor in land use, 220-1; as indicator and integrator of environmental factors, 221; in land use planning, 222; maximise usefulness of, 222-3
 Vegetation cover: as a surrogate, 208; classification, 216; 'state', 215
 Vegetation, cultural, 217
 Vegetation units, nomenclature of Beard, 100
 Vital attributes, 23-8, 31
 Whipstick, 3
 Xeromorphs, 34
 Zürich-Montpellier (Z-M) system, 1-9

Contributors

Mrs E.M. Adomeit
Professor D.J. Anderson
Dr M.P. Austin
Dr J.S. Beard
Mr D.E. Boyland
Dr P.B. Bridgewater
Dr J.A. Carnaham
Dr M. Dale
Dr B.J. Fox
Mrs M.D. Fox
Dr A.N. Gillison
Mr A.W. Graham
Dr P.J.M. Greenslade
Dr R.H. Groves
Dr P.K. Gullan
Mr J.J. Havel
Dr M.S. Hopkins
Dr R.W. Johnson
Dr D.L.B. Jupp
Dr G.N. Lance
Dr P. Laut
Mr C.R. Margules
Mr K.K. Mayo
Dr I.R. Noble
Dr K.C. Norris
Mr J. Pickard
Professor R.L. Specht
Mr C.H. Thompson
Dr W.T. Williams

Jacket design by ANU Graphic Design
Printed in Australia