A GEOBOTANICAL STUDY OF THE REMNANT NATURAL VEGETATION OF TEMPERATE SOUTH AUSTRALIA.

by

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LIST OF ABBREVIATIONS

BMDP	Biomedical Data Analysis Package (Dixon 1981)
b.p.	before present
CCA	canonical correspondence analysis
C.P.	Conservation Park (N.P.W.S.)
C.S.I.R.	Council for Scientific & Industrial Research, Australia (superseded)
C.S.I.R.O.	Commonwealth Scientific and Industrial Research Organization, Australia (current)
DCA	detrended correspondence analysis
GLIM	Generalised Linear Modelling (McCullagh & Nelder 1983)
hc	half-change unit
MDA	multiple discriminant analysis
NMDS	non-metric multidimensional scaling
N.P.	National Park (N.P.W.S.)
N.P.W.S.	National Parks & Wildlife Service, South Australia
NTP	Numerical Taxonomy Package (Belbin *et al.* 1984)
PCA	principal component analysis
RA	reciprocal averaging
SPSS-X	Statistical Package for the Social Sciences, Version 10 (SPSS Inc. 1986)
T.S.S.	total soluble salts
TWINSPAN	two-way indicator species analysis (Hill 1979b)
UPGMA	unweighted pair-group method using arithmetic averages (Sneath & Sokal 1973)

[SI units of mensuration are used throughout.]

SUMMARY

A floristic survey of the temperate parts ("Agricultural Districts") of South Australia was undertaken, with emphasis on the semi-arid "mallee" regions which have been relatively poorly studied in the past. Semi-quantitative data for native perennial angiosperms and gymnosperms were collected at 744 sites, each of 0.1 ha and regularly distributed over the 151 000 km^2 survey area. A total of 545 species were encountered at an average of 13.4 species per site.

A combination of multivariate clustering (Bray-Curtis/UPGMA) and ordination (DCA) methods were used to produce a two-tiered hierarchical floristic classification and to examine the patterns of intergradation between these groups. Although there were few discontinuities and a high degree of gradation at both classification levels, 164 vegetation types were defined in 38 major complexes. There is general agreement between this classification and earlier studies of more restricted scope, but the new classification is the first to have a quantified hierarchical structure and gives greater detail of mallee vegetation types and patterns than does any of the previous physiognomic/floristic classifications available for South Australia. Many vegetation types (mallee or otherwise) have geographically restricted distributions clearly reflecting the biogeographic cline spanning southern South Australia.

Relationships between vegetation and climate, geology and soils were investigated by correlation of vegetation ordinations with abiotic environmental factors, by catenation of complexes using multiple discriminant analysis, and by logistic regression of the environmental responses of individual species (selected, dominant tree and shrub species). Seasonal and tidal flooding, annual rainfall, soil texture, and soil pH, total soluble salts and calcium carbonate were the most significant correlates. The interaction of rainfall with soil texture indicated the importance of soil water relations in determining species distributions at the scale of the survey. For a number of mallee eucalypt species, the addition of longitude as an environmental variable improved response models, suggesting that these species experience some genetic cline which modifies their "environmental behaviour" east-west across their ranges.

The applications and implications of the results to vegetation management were considered. The survey provides new data on the rarity of species and vegetation types, criteria which are often used in conservation management. Continuity of floristic composition, occurrence of biogeographic variants and the mosaic nature of the landscape at all scales lead to difficulties with the concept of vegetation type rarity. This remains one of the problems of conservation management based on rarity.

DECLARATION

This thesis contains no material which has been submitted or accepted for a degree or any other award in any university. To the best of my knowledge and belief, the thesis also contains no material previously published or written by another person, except where due reference is made in the text.

I consent to the thesis being made available for copying and loan, if accepted for the award of the degree.

Ashley Sparrow.

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> I have on occasion derived much relief from the agreeable conversation and the admirable expressions of sympathy offered by friends, without which I am firmly convinced that I should have perished... Though the pain has ceased, I still preserve a clear recollection of the kindnesses I received in the past from people who, prompted by feelings of goodwill towards me, showed a concern for my sufferings. This memory will never, I think, fade for as long as I live.

Giovanni Boccacio: "The Decameron". [Preface].
(Transl. G.H. McWilliam, Penguin, London, 1972).

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Chapter 1:
BACKGROUND AND AIMS

1.1 INTRODUCTION

Australian vegetation scientists[1] have been slower than their European and North American counterparts to examine the potential of numerical or multivariate classification and ordination analysis methods for vegetation survey, mapping and distributional studies. Indeed it is only during the last seven years that collection of data suitable for numerical analysis has become commonplace in vegetation studies in Australia. And while Australians continue to come to grips with the use of numerical approaches as descriptive tools, Austin (1987a) has challenged ecologists worldwide to use them to test major tenets of vegetation theory.

This antipodean reticence should seem surprising when one considers that in Australia, Pidgeon & Ashby (1942) and Goodall (1952, and the subsequent series of papers) produced some of the earliest important work on numerical vegetation analysis. Four factors probably account for the lack of application of these methods. Firstly, there has been a long tradition in Australia of vegetation classification primarily by broad physiognomic/structural characters, as formalised by Beadle & Costin (1952), Specht (1972) and Beard & Webb (1974). Secondly, vegetation data sets for multivariate analysis have been exclusively floristic (until recently) and comprehensive floristic data collection has been regarded as too time-consuming an undertaking for the large areas usually covered by Australian surveys in the past. Furthermore Australian vegetation is considered to be floristically diverse and complex compared with climatic equivalents in the Northern Hemisphere (Whittaker *et al.* 1979). Thirdly, the period from the late

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[1] "Vegetation science", "phytosociology" and "geobotany" are treated as roughly equivalent terms here, despite their different historical origins. "Vegetation science" has been more usually used to describe past Australian work, but "geobotany" is preferred for the thesis title because of its nuances of broad scale and environmental correlation.

1950's to the early 1970's saw turbulent debate about both theoretical and practical aspects of numerical classification in the field of taxonomy (Sneath & Sokal 1973). The implications of this debate caused plant ecologists worldwide to reappraise their approaches and, in Australia, Lange *et al.* (1965) were rather sceptical in their appraisal of numerical analysis in vegetation studies. Fourthly, multivariate methods rely heavily on access to high-speed computing facilities, which previously have not always been readily available.

Reservations about the suitability of the now-traditional Australian classification scheme, which is primarily structural and secondarily floristic, have been expressed by Johnson & Briggs (1975), Newsome & Catling (1979), Bridgewater (1978), Gillison (1981), Hopkins (1981) and Johnson & Lacey (1984), many of whom sought alternative schemes. The exact reservations and the proposed remedies largely reflect the scale and nature of their interests. For example, Hopkins favoured functional physiognomic classification for rainforests; Bridgewater espoused floristic studies for detail of temperate vegetation; and Johnson & Lacey merely proposed an expanded structural-cum-floristic approach for foresters. Amongst this selection of papers, there appears to be no consensus as to where classifiers should direct their future energies. However, if one retains the distinction between classification of rainforest and non-rainforest vegetation by Walker & Hopkins (1984), then a clear trend over the last few years towards increasing interest in floristic data for studies of arid and temperate regions can be detected (Hopkins & Griffin 1984; Myers *et al.* 1984, and the papers therein; Margules & Nichols 1987; Austin & Heyligers 1989; McKenzie *et al.*, 1989; Tiver *et al.* 1989).

The discord concerning the use of numerical methods for vegetation classification has been quelled over the last twenty years by numerous studies of the statistical theory behind multivariate analysis and comparisons of the performance of various techniques on field and simulated data sets (for review see Gauch, 1982; Greig-Smith 1983; Kershaw & Looney 1985; Orloci & Kenkel 1985). There has been critical selection and modification of particular methods suited to vegetation data sets, and demonstrations of the practical limits of both analysis and interpretation, sufficient to permit the free, but not uncritical, use of numerical methods. Australians have taken advantage of these advances in analysis in very recent years, paralleling the increased interest in floristic survey and the greater access to computing facilities.

Thus, over the last decade, vegetation science in Australia has been in a state of flux, not unlike the interparadigm stages in Kuhn's (1970) theory of scientific advancement. Further research is needed to unify and improve our ability to analyse and interpret Australian vegetation and its pattern.

This study is an investigation of one approach that might lead to a new way of classifying, and a better understanding of, vegetation in Australia. The approach selected for investigation is (i) fundamentally floristic, (ii) supported by multivariate analysis, and (iii) based on large area survey. Rarely have the capabilities of numerical floristic classification for broad-scale studies been examined. Indeed Noy-Meir (1970, 1971, 1974a) is the only published attempt at extending purely floristic survey to a very broad scale in Australia.

In addition, this study addresses the need for a new survey of the vegetation of South Australia. Past vegetation surveys in the State have concentrated in the high rainfall districts (see Section 1.3). Thus, in his review of the literature, Specht (1972) was consequently able to give only cursory attention to, and a tentative classification of, the vegetation in the drier-temperate and arid zones, which amount to about 90 % of the State's area. Surveying the whole of South Australia would be a task in all practical respects beyond the scope of a doctoral project. The study area was restricted to the southern, temperate portions of the State, including the areas of semi-arid mallee. The area covered is generally referred to as the "Agricultural Districts of South Australia" (see Chapter 2). This smaller area retains three points of interest from the whole-State proposition with respect to an investigative floristic study: (i) it is still relatively large in extent and contains a great diversity of vegetation types; (ii) parts of it have been intensively surveyed in the past using various non-quantitative approaches and the remainder has been only cursorily examined, thereby providing opportunities both for comparison of new approaches with previous work, and for pioneering examination of poorly-known areas; and (iii) it forms the core of the State's agricultural industry and thereby is of concern to environmental planners, managers and conservers (see Section 1.4).

It must be stressed that southern South Australia is not being used merely as a vehicle to provide a data set that permits comparisons of multivariate analysis methods or development of new techniques, as was the case with Noy-Meir (1970) and Minchin (1983). The primary interest here is in the practical aspects, the interpretation and the application of floristic classification to Australian sclerophyllic vegetation systems, and to improve understanding of the patterning within them.

1.2 REVIEW OF PHYTOSOCIOLOGY: THEORY AND METHODS

The history and development of phytosociology have been extensively reviewed many times (Becking 1957; Whittaker 1978a, 1978b; Gauch 1982; Austin 1985; amongst others), in each case with slightly different emphases dependent on the reviewer's training and interests. Noy-Meir and van der Maarel (1987) have recently provided a thoughtful account of the parallel development of plant community theory and classification methods. In view of this comprehensive literature, it would be inappropriate to give anything but a brief account of the topic here, sufficient to provide perspective for what follows.

Becking (1957) traces the origins of phytosociology back to the plant geographer Alexander von Humboldt (e.g. Humboldt 1805), who observed altitudinal and latitudinal patterns of vegetation (particularly patterns of plant physiognomy) in Central and South America. This style of plant geography has remained until modern times a valuable tool for comparisons of vegetation zoning on different continents and examinations of physiognomic and physiological vegetative convergence under equivalent climatic regimes in different parts of the world (e.g. Walter 1985).

Later during the nineteenth century, interest in Europe turned to more localised and detailed studies in vegetation, and subsequently to the use of individual species rather than physiognomic forms as indicators of vegetation and environment (e.g. Kerner 1863; Hult 1881; Drude 1890; Paczoski 1896; see Becking 1957 for a full review). This lead to the adoption of the species as the fundamental unit of the plant community and the association, "a plant community of definite floristic composition", as the fundamental unit in plant sociology at the Third International Botanical Congress (Flahault & Schroter, 1910; see Braun-Blanquet 1932). This period also saw the emergence of methods of sampling vegetation by quadrats, measures of cover/abundance and sociability, species data tabulation, and the concepts of constancy and fidelity of species to an association.

The many schools of phytosociological thought which were spread across Europe during the early twentieth century all sprang from these beginnings. Becking (1957) and the review articles in Whittaker (1978a) outline the precepts of these schools. The differences between the approaches, although at the time considered important enough to warrant the differentiation of schools, no longer appear so dramatic and reflect more the nature of the vegetation with which each dealt. For example, the vegetation in southern and central Europe, which the Zurich-Montpellier School analysed, is floristically and structurally more diverse than the Scandinavian forests and bogs with which the Uppsala School dealt, and so discriminating measures of abundance and details of physiognomic stratification are of necessity more important for studies by the latter than for the former.

A theoretical debate in the 1920's about the nature and behaviour of plant communities had the greatest influence on the development of phytosociology over the last fifty years (Noy-Meir & van der Maarel 1987). Clements (1916, 1920) with support from Tansley (1920) propounded the theory that a plant community is a quasi-organism: its floristic composition is fixed; all species present are essential and mutually dependent upon one another, just as body organs are; and succession in the community follows a fixed path (akin to growth) to a climax type determined, in the absence of continued disturbance, only by climate. The implications of Clements' theory to phytosociologists were that communities (read, "associations") have definite bounds, and are intrinsically and uniquely classifiable. Gleason (1926) rejected this theory by claiming that plant communities are merely an aggregation of species able to tolerate the same habitat conditions and showed no organismic behaviour. Individual tolerance ranges for each species means that, as one moves between two communities, floristic composition changes gradually, corresponding to gradual habitat change. It follows that the number of possible combinations of species (associations) is almost limitless and that communities cannot be intrinsically classifiable. Cooper (1926) likewise pointed out that the climatic climax was a fallacy since succession was merely a small part of continual vegetation change at all scales of time and space.

Gleason and Cooper eventually won the day, but the effects were only gradually accepted by phytosociologists, especially by those in Europe. The methods of Braun-Blanquet and associates continued to involve sampling "typical" stands, thereby ignoring the issues of boundaries and gradation. As Ramensky (1924; see Sobolev & Utekhin 1978) in the U.S.S.R. and Cajander (1926) in Finland had independently come to the same conclusions as Gleason in the U.S.A., they alone took to displaying associations along important environmental gradients to emphasise the continual gradation of floristic composition.

With the publication of the early findings of the Wisconsin School, the full force of Gleason's "individualistic" or "continuum" theory was realised. Curtis & McIntosh (1951), Whittaker (1951), Curtis (1955) and Whittaker (1956) demonstrated that a high percentage of samples in data sets could not be assigned convincingly to associations, but were atypical or transitional as was to be expected in a vegetation continuum. Thus evolved indirect ordination, a family of methods to display the relative positions of samples (both typical *and* transitional) along preselected environmental gradients, for example polar ordination (Bray & Curtis 1957).

Also during the 1950's, numerical methods for vegetation analysis based in mathematical theory were introduced in earnest. The concepts of vegetation sampling based on sound statistical principles (Goodall 1952) were followed by classification of vegetation data by the use of indicator species pairs which show statistical non-randomness (Goodall 1953; later Williams & Lambert 1959) and detection of gradients of vegetation composition without reference to environmental variables using factor analysis (Goodall 1954b). Together with numerical clustering, these methods, with modification and improvements, are the multivariate analysis techniques used by phytosociologists today (see Section 4.2 for a review).

It is unfortunate that the development of numerical classification and indirect ordination coincided with acceptance of continuum theory by plant ecologists at large. Classification was mistakenly identified with Clements' fallacious quasi-organism theory and ordination only with continuum theory, leading to great confusion. As a result, Webb (1954) asked whether classification of plant communities was "either possible or desirable". He and Goodall (1954a) rightly concluded that, although the quasi-organismic concept of the community was unacceptable, the distribution of species fell between the extremes of complete continuity and complete discontinuity. Vegetation may have a gradational response to an environmental factor, but this was not the case in the field due to the presence of environmental discontinuities and varying degrees of ecotonal development (see also Moravec 1989). Thus classification and ordination could both be used to reveal vegetation patterns in the one data set. Ordination provides the means of observing gradation of vegetation and environment. Classification detects (environmental) discontinuities and gives a framework for interpretation of ordinations, *if* allowance is made for variation and gradation within vegetation types.

Only relatively recently has general agreement been reached that numerical classification and ordination are complementary methods to show different aspects of vegetation patterning, and that they provide reciprocal information, since they are just manipulations of the same data space (Gauch 1982). Recent phytosociological studies have made use of the two techniques in tandem.

1.3 VEGETATION STUDIES IN SOUTH AUSTRALIA

Early European explorers and settlers of South Australia made some observations on the vegetation (see Specht 1972), as did 19th century plant taxonomists such as Tate (1890). The first systematic account was by Diels (1906), who described and mapped eight broad vegetation "formations" over the whole of Australia. Five of these formations occur in South Australia. In increasing order of aridity, they are: sclerophyll forest; savannah forest; mallee scrub and sand heath; mulga scrub; and desert. All subsequent mapping at a continental scale, for example Cochrane (1963) and Carnahan (1976), owes a great debt to Diels' work.

More detailed studies began with a general survey of the Adelaide region by Osborn (1914) and with descriptions of the arid Nullarbor Plain – Great Victoria Desert interface at Ooldea, and the temperate eucalypt forest/woodland communities of the southern Mt Lofty Ranges by Adamson and Osborn (1922 and 1924 respectively). The latter account of the Mt Lofty Ranges included considerable discussion of the effects of climatic, geological, edaphic and disturbance factors on the association distribution patterns, suggestive of influence by the Scandinavian phytosociological schools. Most South Australian vegetation studies over the following thirty years emulated this style of approach. Other notable early phytosociological work includes studies of floristics in the mallee formation (Wood 1929), of the vegetation on Kangaroo Island and adjacent southern Yorke and Eyre Peninsulas (Wood 1930), of the chenopod steppe of the arid-zone area west of Lake Torrens (Murray 1931), and of soil-vegetation interactions in the southeastern part of the State, as part of a land-use survey for agricultural development (Taylor 1933) (see Figure 1.1).

In Wood (1937) the literature at that time was consolidated by considerable unpublished field experience to produce a major treatise on vegetation in South Australia, the first of its kind in Australia. The five "climatic formations" of Diels (1906) were retained for individual discussion. Within each formation, floristic associations (with structural qualifiers) were described, and their spatial, environmental and temporal relationships indicated by a curious, but nevertheless effective, combination of Tansleyan succession models and primitive direct ordinations along principal climatic and edaphic gradients. This method of presenting associations arose from conclusions that Northern Hemisphere concepts of associations and succession could not be applied to Australian vegetation without major modification (Wood 1939).

The major weakness of Wood (1937) was the poor coverage of areas distant from the Mt Lofty and Flinders Ranges as a result of the lack of surveys in these parts. The work did however serve to stimulate investigation of some poorly known areas during the following two decades. The dozen studies so-inspired are all indicated in Figure 1.1. They included purely phytosociological studies and more practical land-use surveys as part of a national scheme to resettle soldiers returned from the Second World War in undeveloped areas with agricultural potential. Of these surveys, Crocker (1944) in the Southeast region and Crocker (1946) on Eyre Peninsula stand out for the development of the concept of the "edaphic complex", as proposed by Wood (1939), to permit mapping of groups of associations with similar floristic and physiognomic composition, and similar edaphic requirements, and so of a highly gradational character. Crocker and Wood (1947) explained that the edaphic complex was a necessary replacement for the (climactic) formation in the sense of Tansley (1939), since South Australian plant communities are geologically very young ("<6000 years old") and have probably not reached even an approximation of a stable climax equilibrium. The edaphic complex also foreshadowed the future complementation of classification with ordination, in accordance with the theories of vegetation continuity but habitat discontinuity.

Specht's (1972) "Vegetation of South Australia" was a revised edition of Wood (1937) incorporating the results of studies from the intervening period. The important new contribution was the series of compilation vegetation distribution maps covering the State. There were two aspects on the negative side. Firstly, the primary tier of the classification had become physiognomic and was formalised. Its rigid use detracted from the impact of many floristic patterns. Some vegetation types from Diel's climatically, edaphically and floristically distinctive mulga and mallee formations were grouped together under one "structural formation" on the basis of superficial similarities of overstorey height and canopy spacing. Secondly, there was a continued relative dearth of information on the drier parts of South Australia, which must lead to concern about the true rank of vegetation types from different parts of the State which are all referred to as "associations" and "alliances". Indeed the lack of data for northern and western Eyre Peninsula and for the Murray Mallee forced Specht to admit that only a tentative classification of mallee vegetation was possible. This situation has remained unresolved as little phytosociological work has been undertaken since 1972.

Numerical analysis methods have been used only sparingly in vegetation research in South Australia. Rayson (1957), Lange (1968) and Barker & Lange (1969) made use of association analysis (Goodall 1953) to examine patterning in small areas of intense interest. Noy-Meir's (1970, 1971, 1974a) survey of the Murray River Basin took in some 50 000 km^2 of eastern South Australia. Due to the large scale and methodological thrust of the project, the results permit little detail below the formation level. Recent studies by McKenzie & Robinson (1987) on the Nullarbor Plain, and Margules & Nichols (1987) and Tiver *et al.* (1989) on Eyre Peninsula have employed multivariate methods. There is a tendency in the first two to simplify data and analysis such that the full potential of numerical floristics is not explored. None of the above provide an adequate test of floristic survey and numerical analysis for understanding temperate or arid-zone vegetation patterns in South Australia, nor appreciation of their relationships to environmental patterns.

1.4 BUT WHY CLASSIFY VEGETATION ?

Classification is a "fundamental, ubiquitous mental activity" (Gauch 1982) and "with vegetation, as with other natural objects, Man early felt the need to classify" (Goodall 1953). Classification is essential for two key components of human knowledge: memory and communication (Russell 1948). Communication of knowledge by language is only possible through classification, since every noun is the name of a class. In this sense, vegetation classification provides a vocabulary for communication of botanical ecological information.

To a biologist, a classificatory vocabulary has no innate merit. Its value lies solely in the use to which it can be put, in the information that it is able to convey. The descriptive power of a classification (here "classification" is used in a very general sense that does not preclude ordination) can be applied in three ways which are neither entirely distinct nor independent.

The phytosociologist typically correlates a classification with habitat variables such as climate, soils and disturbance history. In this way, theories of vegetation distribution are challenged and hypotheses are generated in fields as diverse as plant physiology, interspecific competition and mutualism, evolution and genetics, which might be tested by intensive experimental methods.

The second application of a classification concerns non-phytosociologists and is as a predictive tool. Classification units are the result of integration of many characteristics of plant communities. Correlation of a variable of interest with a classification in a small locale can permit extrapolation over a much larger area without individual reference to multitudinous community characters. Thus might an agriculturalist readily map cropping potential, a forester timber yield or a zoologist the distribution of a species of animal.

The third application can best be illustrated by an example from South Australia. Over 150 years, the southern part of the State has been extensively cleared of vegetation for agricultural development (see Section 2.6). With the rise of the conservation ethic (Whitelock 1985), there is governmental interest in protection and preservation of examples of natural ecosystems, using selection criteria such as diversity, representativeness and rareness. Surveys for these purposes (Barritt & Mowling 1978; Mowling 1979; Moore 1985) have made improvised and unsubstantiated modifications where Specht's (1972) classification was found to be inadequate, particularly with respect to semi-arid mallee. Confusion has ensued owing to the lack of adequate description of the vegetation. The other frequently-consulted source of guidance for conservation assessment is Laut *et al.* (1977) in which "environmental associations" were defined, described and mapped on a statewide basis by LANDSAT satellite imagery supported by ground-truthing. These environmental associations are broad landscape units of uniform topography, geology, soils, vegetation and land-use, or at least mosaics of them of uniform density. The scale of these landscape units provides the greatest difficulty for their application to conservation, which, with few exceptions, now deals with vegetation at a scale an order of magnitude more detailed.

Thus, aside from the theoretical aspects of vegetation classification associated with phytosociology, the need to address the confusion surrounding approaches to remnant vegetation conservation in South Australia's agricultural districts is a strong incentive for a phytosociological survey and analysis of this area. To this end, this study will consider implications of floristic survey to management for conservation purposes.

1.5 SPECIFIC AIMS

In the light of the preceding general discussion, it is possible to formulate specific aims for a phytosociological study of southern South Australia:

1. To undertake a floristic survey with constant sampling density such that all parts of the study area are equally and well represented.

2. To appraise the use of recently-developed techniques for floristic analysis to Australian temperate / semi-arid sclerophyllous vegetation.

3. To produce a framework floristic classification for the study area, with emphasis on mallee vegetation.
4. To examine the patterns of vegetation types and the distribution of dominant species in relation to important environmental gradients as possible causal factors.
5. To assess the value of floristic survey and numerical analysis for development and implementation of vegetation conservation strategies.

The structure and logic of the approach used, and of this thesis, are outlined in Figure 1.2.

Chapter 2:
STUDY AREA

2.1 INTRODUCTION

In this chapter, the study area will be described in terms of its topography, geology, soils and climate. Broad features of the vegetation will also be discussed with particular reference to land-use and clearance for the purposes of agricultural development.

The development of the vegetation sampling strategy (Chapter 3) and the analyses of vegetation-environment relationships (Chapters 5, 6 & 7) rely substantially on the background material provided here.

2.2 LOCATION

The study area is the Agricultural Districts of South Australia (Figure 2.1). This area has an east-west span of 780 km, a maximum north-south span of 720 km and covers 156 000 km^2 (S.A. Department of Environment and Planning figure). The State's coastline forms the southern boundary of the area. The northern boundary of the Agricultural Districts corresponds approximately with the northern limit of mallee vegetation (see Section 2.5) and with the 225 mm isohyet of mean annual rainfall (see Section 2.4). In two regions, these ecological delimiters do not correspond with the bounds of the study area. A large expanse of mallee vegetation on the Great Victoria Desert dunefield to the west of the Gawler Ranges and Lake Gardiner was excluded on practical grounds since adequate vehicular access was impossible. The northern Flinders Ranges were not included as they were regarded as outside the aims and interests of the project. The Flinders Ranges flora contains many arid, relict and endemic species which make the vegetation distinctive (viz. the "Flinders Complex" of Specht 1972), and mallee is restricted to scattered relict patches.

Eight of the State Herbarium of South Australia's floristic regions (Jessop & Toelken 1986) occur wholly or partially in the survey area: Southeast, Murraylands, Southern Mt Lofty Ranges, Northern Mt Lofty Ranges, Flinders Ranges, Kangaroo Island, Yorke Peninsula and Eyre Peninsula (Figure 2.2). These floristic regions are used as convenient subdivisions of the study area, with the exception of the Flinders Ranges, whose southern reaches are united with the Northern Mt Lofty Ranges for the purposes of this project.

2.3 GEOLOGY, TOPOGRAPHY AND SOILS

Geology, topography and soils are closely related features of any environmental system and are in many ways interdependent. In South Australia, topography is largely an expression of structural and tectonic geology, and soils are derived from surface geological features[2] with lesser influence from topography, climate and vegetation (Ward 1966; Maud 1972). For this reason these three factors will be discussed together in this section.

The geological features of southern South Australia are well reviewed by Alderman (1973), Ludbrook (1980) and the Geological Survey of South Australia (1982). Most of the discussion presented below is derived from these sources.

The study area can be divided into nine provinces on the basis of structural geology (Geological Survey of South Australia 1982) as illustrated in Figure 2.3. The oldest of these provinces is the Gawler Craton which consists of Archaean and Early to Middle Proterozoic rock, and which extends over Eyre

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[2] This view of soil genesis does not correspond with the views of, for example, Walter (1985), who maintained that the nature of vegetation and soils are both primarily determined by climate and that soil is only dependent to a lesser degree on parent rock. This difference in interpretation of soils is due to a difference in scale of the concept. Walter considered world-wide vegetation patterns to define nine "zonobiomes" based on climatic criteria. At this scale, the suite of *possible* soil types is significantly determined by climate e.g. podzolic soils do not form in desert areas. However, southern South Australia falls into only one zonobiome and one zonoecotone. Consequently, at this finer scale (within a zonobiome), differences between soil types (within the suite of possible types) become important for vegetation, and, as Ward (1966) showed, these soil types *are* most strongly influenced by parent material.

Peninsula and southern Yorke Peninsula. Extensive weathering has reduced much of the craton to a gently undulating plain which gradually slopes northeastwards from the west coast of Eyre Peninsula to the uplands of the Gawler Ranges and Cleve Hills, these being mainly volcanic and of Proterozoic origin (see topographic map, Figure 2.4). The Willyama Inlier to the northeast of the study area similarly originated in the Early Proterozoic.

The central portion of the study area is dominated by the Adelaide Geosyncline which originated during the Mid to Late Proterozoic from a Gondwanic sedimentation trough extending from Australia across eastern Antarctica. Together with the Early Palaeozoic Kanmantoo Group, these sandstones and quartzites were uplifted and folded during the Palaeozoic (Ordovician and Devonian) and the Early Cainozoic (Tertiary) to form Kangaroo Island, the Mt Lofty Ranges, the Flinders Ranges and the Olary Spur. These mountains are the most elevated parts of southern South Australia; Mt Brown in the southern Flinders Ranges is the highest peak in the study area (969 m above mean sealevel). The Stuart and Spencer Shelves to the west of the Adelaide Geosyncline are also derived from deposition during the Late Proterozoic, but have been subjected to minimal, uniform uplifting and little folding.

The remaining geological provinces (i.e. the Murray, Otway, St Vincent and Pirie-Torrens Basins) consist of marine limestone deposited during the Tertiary (Eocene to Miocene). These basins now form scarcely undulating plains, whose topography is relieved only by recent surficial deposits. The Eucla Basin lying immediately west of the Gawler Craton is likewise composed of Tertiary limestone and forms the Nullarbor Plain.

Surface geology (Figure 2.5) is more complex, and is a combination of exposed and outcropping older formations with more recent (Pliocene to Holocene) reworking and deposition of surface materials. Figure 2.6 is a map of soil types according to the Northcote classification. There is general correspondence between soils and surface geology, yet in many areas the latter probably acts as a better indicator of environmental conditions due to the rather simple primary division of the soil classification into uniform, gradational and duplex profiles.

The pre-Cainozoic structural features described above are exposed at the surface in several parts of the study area. On Eyre Peninsula this occurs in the Gawler Ranges, the Cleve Hills and the Koppio Hills, as well as along coastal cliffs. The Proterozoic rocks of the Adelaide Geosyncline are exposed in all the elevated regions from Kangaroo Island to the Flinders Ranges. In addition there are scattered island-like outcrops of Proterozoic and Palaeozoic granites in the Upper Southeast and across central and western Eyre Peninsula. Climate, in particular rainfall, seems to have a strong influence on the type of soil associated with these old formations. On southern Eyre Peninsula, Kangaroo Island and in the southern Mt Lofty Ranges, where rainfall is relatively high, the soils are duplexes with a mineral-deficient yellow clay subsoil, sometimes bearing ironstone gravel. At lower rainfall, there are duplexes with red clay subsoils, while shallow amorphous loams predominate in the Gawler and Flinders Ranges at the lowest rainfall.

Tertiary marine limestones approach the surface in parts of the coastal Lower Southeast and on Yorke Peninsula. Another Tertiary group, the Parilla and Loxton Sands, occur in the Murraylands and Upper Southeast. These formations are lacustrine and fluviatile and were deposited under deltaic conditions by the Murray River system during a Pliocene retreat of the sea. The Parilla Sand is associated with distinctive sandy duplex soils with mottled, yellow clay subsoils.

Three Quaternary (Pleistocene?) formations dominate the landscape of the study area: the Bridgewater, Woorinen and Molineaux Formations. The oldest of the three, the Bridgewater Formation, is aeolian calcarenite from coastal dunes in which massive calcrete has developed through dissolution and subsurface recrystalisation of the carbonates. As a result of erosion, the calcrete is usually close to the surface now and the covering sandy red soils are shallow. Some resemble terra rossa. On Eyre Peninsula, Yorke Peninsula and Kangaroo Island, the Bridgewater Formation occurs as a continuous sheet of calcrete extending inland as far as 80 km from the present coastline. Crocker (1946) believed that the aeolianite originated from the exposed continental shelf during a glacial period of low sealevel, but Short *et al.* (1986) have shown that the deposits could also arise from a high-energy coastline at high sealevel. In the Southeast, the Bridgewater Formation forms a series of consolidated dunes parallel to the present coastline (Figure 2.7). The dunes represent former coastal dunes which were stranded by the retreating sea through a combination of uplift and tilting of the Murray Basin, and glacial sealevel oscillations (Sprigg 1952; Blackburn 1966; Schwebel 1983). The formerly lagoonal interdune corridors are filled with sand and silt of the Padthaway Formation.

The Woorinen Formation, and its equivalents such as the Wiabuna Formation on western Eyre Peninsula, occurs inland of the Bridgewater Formation and consists of sand bearing fine carbonate. It is likely the result of weathering and surface reworking of the Tertiary marine limestone basins. The soils of the Woorinen Formation are loams to sandy loams and are commonly referred to as Loveday soils. Usually the carbonate has been washed down the profile and recrystalised as a layer of hard nodules (1–5 cm in diameter) loosely cemented together 20 cm to 1 m below the surface.

Dating from the late Pleistocene or early Holocene, the Molineaux Formation is of dunal, aeolian, siliceous sand, closely related to the dune systems of the Great Victoria, Simpson and Strzelecki Deserts in northern South Australia. The sands were probably blown westwards and southwards from central Australia in several stages. In Figure 2.8, modified from King (1960), the relationships between and orientation of these dunefields are shown. Orientation is thought to be related to the direction of the contemporaneous prevailing winds. The soils are typically deep acidic to neutral sands, white in colour or having a gradually increasing orange chroma with depth. Over much of the study area, the Molineaux sands have been blown over the Woorinen Formation, so that the interdune corridors are occupied by Loveday-type soils. In some districts the thickness and density of the dunefield entirely obscures the underlying formations.

Finally, some minor Holocene surface formations of restricted distribution need to be mentioned briefly. Most significant among these are:

- modern unconsolidated coastal dunes of deep, white calcareous sand, designated the Semaphore Formation;
- silty estuarine and subcoastal saltlake deposits, grouped under the St Kilda Formation;
- a number of sedimentary formations of valley and floodplain forming a narrow band along the River Murray; and
- a small area of surface basaltic volcanics near Mt Gambier in the Lower Southeast.

2.4 CLIMATE

There have been numerous classifications of the climate of Australia (Gentilli 1971, 1972). Rainfall (amount and/or seasonal distribution), average temperature (annual and/or monthly) and, occasionally, evaporation were the variables used to delineate climatic types. Rainfall and evaporation have sometimes been combined to indicate rainfall effectiveness, as in Prescott's (1949) index of hydric efficiency, $r/e^{0.7}$. The choice of delineating variables and the method of their combination have been influenced by the expected application of the classification.

Two climatic classifications are illustrated in Figure 2.9. Koeppen's (1936) system (adapted for Australia by Dick 1964) incorporates most of the elements listed above and is regarded as a worldwide benchmark. The climatic regions of Gentilli (1971) are based largely upon hydric efficiency and rainfall seasonality, and are considered to broadly correspond with the distribution of major vegetation formations.

Gentilli (1972) discusses in detail the climate of the various regions of the study area. The patterns can be summarised as follows. The climate of maritime, southern South Australia is frequently described as Mediterranean- temperate

(Koeppen types Csa and Csb; Gentilli's humid and subhumid regions, with $2.0 < r/e^{0.7} < 4.0$ and $1.0 < r/e^{0.7} < 2.0$ respectively)[3] meaning that there is a cool, moist winter and a mild to hot summer drought. Cool sea breezes moderate the severity of summer temperatures (Schwertfeger 1985). From the southern coast, there is a gradient of increasing aridity across the State, associated with decreasing annual rainfall and longer, hotter summers. Consequently the northern two-thirds of the study area are classed as semi-arid, still with winter rains predominating (Koeppen types BSfk and BSfh; $0.5 < r/e^{0.7} < 1.0$), and north of the study area lies the large expanse of arid-type climate (with seasonally uniform rainfall) that dominates the interior of the continent (Koeppen type BWh; $0.25 < r/e^{0.7} < 0.50$).

The north-south climatic gradient across South Australia can be clearly seen on the maps of mean annual rainfall, rainfall seasonality, mean January and July maximum temperatures, and mean annual pan evaporation (Figures 2.10 to 2.13). For each variable, there is a distortion of the north-south gradient in the central portion of the study area, caused by the high elevation of the Mt Lofty and Flinders Ranges block, which permits climatic conditions more mesic than would otherwise occur at such latitudes in this area. The dissection of southern South Australia by Spencer Gulf and Gulf St Vincent enhances this effect. The Mt Lofty Ranges also produce a rainshadow along their eastern flanks, since the winter rain-bearing winds prevail from the southwest and most of their moisture in dumped on the high parts of the ranges through orographic stimulus.

Mean annual rainfall in the study area ranges from about 225 mm across

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[3] Prescott (1949) proposed the index $r/e^{0.7}$ to indicate *monthly* hydric efficiency, based on mean monthly rainfall and pan evaporation, with the aim of quantifying the climatic suitability of any location for agricultural crop production. He showed empirically that the potential length of the growing season for cereals at any locality could be defined as the number of months per year in which $r/e^{0.7} > 0.5$.

Gentilli (1972) applies mean *annual* rainfall and evaporation to Prescott's index to give an indication of average hydric efficiency during the year, which can then be used to define climatic regions, as by the critical ranges included in the text here.

A further point to be made is that the critical levels delimiting climatic regimes are for rainfall and evaporation measured in *inches*, since both workers predate the introduction of the metric system into Australian meteorology. For modern values in millimetres, the index should be corrected as $0.38 \times r/e^{0.7}$ to maintain the earlier-defined critical levels.

the northern margins to 800 mm in parts of the Mt Lofty Ranges, Kangaroo Island and the Southeast, and peaks at 1100 mm at Mt Lofty (Figure 2.10). In the wettest regions, rainfall is highly seasonal and is concentrated during the winter months. With decreasing mean annual rainfall, the strength of the seasonal rainfall pattern decreases until it is barely discernible north of the 250 mm isohyet (Figure 2.11). Evaporation (Figure 2.13) is inverse to rainfall. Mean annual pan evaporation reaches ten times the mean annual rainfall along the 250 mm isohyet and nowhere in the State does annual rainfall exceed annual evaporation. Only in high rainfall areas does rainfall exceed evaporation during a few winter months, and thus permit saturation of the soil and surface water runoff in part of each year. The high evaporation to rainfall ratio and the dearth of free surface water lead to South Australia being regarded as the driest state of Australia.

In southern Australia, rainfall and its seasonal distribution are highly variable from year to year, particularly in the arid zone, and even in the mesic southern Mt Lofty Ranges (Gentilli 1972). Thus figures for mean annual rainfall need to be regarded with caution. Gentilli (1972) provides examples of right-skewed frequency distributions of annual rainfall at recording stations in the study area. Occasional years of exceptionally high rainfall bias the mean such that annual rainfall is below average in more than 50 % of years. However, data on *median* annual rainfall could not be obtained for most parts of the study area.

2.5 VEGETATION

Vegetation studies in South Australia were briefly reviewed from an historical perspective in Section 1.3. Although Groves (1981) includes some discussion of South Australia, the most recent comprehensive account of the State's vegetation, prior to this study, is that of Specht (1972) and it is this work which forms the basis of the following account. South Australia is divided into five land systems which, with the exception of the last, correspond with Diels' (1906) formations and whose broad distributions are discussed in terms of climate and soils. The five land systems are: sclerophyll, savannah, mallee, arid and coastal. All five occur in the study area (Figure 2.14; after Specht 1972).

The sclerophyll land system occurs chiefly in the humid zone of South Australia on acidic, podzolic, duplex soils and deep, leached sands, but extends into the subhumid zone on highly nutrient-deficient siliceous sands (Wood 1937; Specht 1972). There are examples of the sclerophyll land system in the Southeast, in the Northern and Southern Mt Lofty Ranges, on Kangaroo Island and on Eyre Peninsula. This system is unified by the ubiquity and diversity of sclerophyllous undershrubs, many of them in the families Epacridaceae, Fabaceae, Myrtaceae, Proteaceae and Xanthorrhoeaceae. The upperstorey is typically dominated by trees or tall shrubs of *Eucalyptus* (*E. baxteri, E. cosmophylla, E. fasciculosa, E. goniocalyx* and/or *E. obliqua*[4]) forming a woodland. The eucalypts are dwarfed or absent on subhumid sandy areas resulting in low heathland. Adamson & Osborn (1924), Coaldrake (1951), Crocker (1944, 1946), Martin (1961), Northcote & Tucker (1948) and Specht & Perry (1948) describe the various areas of sclerophyll vegetation in some detail. Specht (1979) discusses heathland ecology.

The savannah land system is distributed over the humid and subhumid zones on duplex soils which are more fertile than the soils supporting sclerophyll systems (Specht, 1972). Examples occur in the Southeast, in the Northern and Southern Mt Lofty Ranges, and on Yorke and Eyre Peninsulas. The savannahs are usually woodlands or open woodlands dominated by *Eucalyptus camaldulensis, E. leucoxylon, E. microcarpa, E. odorata, E. porosa, E. viminalis, Allocasuarina luehmannii, A. verticillata* or *Melaleuca lanceolata.* The understorey contains grasses (Poaceae: especially *Danthonia* spp., *Stipa* spp. and *Themeda triandra*), sedges (Cyperaceae), various herbs and scattered low, sometimes sclerophyllous shrubs. Again the understorey ("low and grassy") unifies the system. More detailed descriptions of savannah associations, their floristic composition and their distribution patterns are given in Adamson & Osborn (1924), Boomsma (1949),

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[4] Species nomenclature in this section follows Jessop & Toelken (1986). This standard has been used to update the differing nomenclature in the various vegetation studies mentioned here.

Crocker (1944), Specht & Perry (1948) and Todd (1965). Specht (1972) includes the treeless tussock grasslands and sedgelands of the Northern Mt Lofty Ranges and the Lower Southeast in this formation, even though their habitat requirements deviate from those usual for other savannah vegetation.

The term "mallee" describes a growth form peculiar to the genus *Eucalyptus*, consisting of a possibly clonal, multistemmed shrub or tall shrub, the stems arising from an underground body of lignified stem tissue called a lignotuber. The habit may be a response and adaptation to aridity, oligotrophic soils or high bushfire frequency. According to Specht (1981), 130 eucalypt species can assume the mallee habit, yet only a small proportion of them form mallee-dominated vegetation over wide areas.

In South Australia there is a broad belt of mallee vegetation across all of the semi-arid regions (annual rainfall 225 – 450 mm), occurring on a wide variety of soil types. The mallee belt extends into adjacent New South Wales, Victoria and Western Australia. There are also humid zone mallee types on very oligotrophic soils or on exposed coastal sites. The predominant mallee overstorey species are *Eucalyptus behriana, E. diversifolia, E. dumosa, E. foecunda, E. gracilis, E. incrassata, E. oleosa* and *E. socialis.* The understorey varies in response to climate and soils, and consists variously of sclerophyllous shrubs, grasses, *Melaleuca uncinata* (commonly called "broombush"), *Triodia irritans* (spinifex, a perennial tussock grass) or semi-succulent chenopod shrubs (Specht 1981). Some detail of mallee associations can be found in Barker (1970), Baldwin & Crocker (1941), Coaldrake (1951), Crocker (1946), Jessup (1948), Noy-Meir (1971), Parsons (1981), Smith (1963) and Wood (1929), but the information is sketchy for the drier mallee regions.

The arid land system contains a great variety of xeric vegetation types, as reviewed by Specht (1972) and Williams (1979). The mulga scrub and desert formations of Diels (1906) are combined in this land system. As the study area merely touches upon the southern limit of the arid zone, only the most southern of the arid associations need be mentioned here. Occurring on solonised brown soils with some calcrete development, the southern arid vegetation consists of chenopodiaceous low shrublands of *Atriplex vesicaria, Maireana pyramidata, M. sedifolia* or a combination of them. In all associations there is a well-developed ephemeral herb flora. Scattered low trees locally convert the chenopod shrublands into low open woodlands: *Casuarina cristata* over a *M. sedifolia* understorey, *Myoporum platycarpum* over *A. vesicaria* or grasses, and *Acacia aneura* (east of the Flinders Ranges) or *A. papyrocarpa* (west of the Flinders Ranges) over a variety of chenopod understoreys. There are more detailed descriptions of the southern South Australian arid associations and their ecology in Adamson & Osborn (1922), Carrodus *et al.* (1965), Jessup (1948, 1951) and Murray (1931).

Last of the five land systems, the coastal system forms the southern margin of much of the study area. It is divided into three subsystems by Specht (1972): coastal dunes, coastal cliffs and saltmarshes. Coastal dunes of unconsolidated sand show a gradation ("succession") of associations from the rhizomal grass *Spinifex hirsutus* on frontal dunes, to a heathy, coastal shrubland dominated by *Olearia axillaris* and *Leucopogon parviflorus*, and finally grading into savannah-like communities of *Allocasuarina verticillata* and/or *Melaleuca lanceolata.* Coastal cliffs typically bear heath dwarfed or prostrated according to the degree of exposure, and variously featuring *Atriplex paludosa, Beyeria lechenaultii, Melaleuca lanceolata, Olearia axillaris* and *Poa* spp. Saltmarshes on supratidal estuarine silt and clay usually include the samphires *Halosarcia halocnemoides* and *Sclerostegia arbuscula*, and the grass *Distichlis distichophylla.* Along low-energy coastlines, the saltmarshes are often fringed on the tidal side by mangrove communities of *Avicennia marina.*

The foregoing brief summary of South Australia's vegetation is merely intended to provide some indication of the high degree of floristic diversity within the study area and of the most important correlations between vegetation and abiotic environment. These factors have a bearing on the development of a sampling strategy for the study area, and on analysis and interpretation of the data. Consideration has not been given to Specht's (1972) classificatory hierarchy of structural formations, alliances and associations within the land systems. As pointed out in Section 1.3, the hierarchy's units are suspected to be of variable stature and thus unreliable.

2.6 LAND-USE

The influence of man on the South Australian environment probably began with the arrival of aboriginal cultures 40 000 – 50 000 years b.p. (Barker 1986). Aboriginals are thought to have used fire as a hunting aid and as a method of stimulating pasture growth for game (Martin 1973; Singh 1982). Fire used in this manner would likely induce selective pressure favouring fire-tolerant species, but the degree of change in vegetation composition wrought in this way is not clear. Aboriginal hunting resulted in the extinction of some large marsupial herbivores, and the dingo, later introduced to Australia by the Aboriginals, lead to the demise of smaller mammals (Barker 1986).

However, Aboriginal influence on vegetation is insignificant compared with the impact of permanent settlement of South Australia by Europeans which began in 1836; Adamson & Fox (1982) described European settlement (of Australia) as "apocalyptic". The environmental changes stemming from the colonisation and development of the State are reviewed by Meinig (1962), Williams (1974), Harris (1976, 1986) and Whitelock (1985).

Agricultural development was initially concentrated around Adelaide, in the adjacent southern Mt Lofty Ranges, and, to a lesser extent, in the Southeast. Savannah land systems were found to provide the most favourable environment for agriculture and these areas were rapidly cleared. The large eucalypts were a source of quality building and fencing timber, and the natural, grassy understoreys were suitable for stock grazing, although grazing soon lead to the native grasses being supplanted by introduced pasture species. Fertile savannah soils were also ideal for cereal farming and horticulture.

During the remainder of the nineteenth century, the colonial government supported development through programmes of land survey, foundation of numerous service townships and construction of railways (Fenner 1931; Meinig 1962). This permitted a northward expansion of vegetation clearance and cereal cropping into the drier savannahs of the Northern Mt Lofty Ranges, southern Flinders Ranges and onto Yorke Peninsula. Pastoral grazing of natural arid-zone shrublands in the far-north of the State began in this period. During a series of years of above-average rainfall, the northern front of agricultural expansion moved beyond the agroclimatic limit recommended by Surveyor-General G.M. Goyder in 1861 and into arid mallee and chenopod shrublands. Only droughts at the end of the century forced the permanent abandonment of these northern areas unable to sustain regular annual cropping. Natural vegetation types have not returned to most of these abandoned fields.

The first half of the twentieth century saw similar government-sponsored programmes of agricultural development necessitating clearance primarily of mallee vegetation in the Murraylands, on Eyre Peninsula, on Kangaroo Island and in the Upper Southeast. The programmes included schemes to resettle soldiers returning from active service in World Wars I and II. Farming on the low-fertility soils of these regions was made possible by improved understanding of the nature of the mineral deficiencies, by increased availability of fertilisers and by breeding of new hybrid strains of tolerant cereal crops. In the Lower Southeast, large areas of grazing land have been opened up by construction of a network of drains to prevent winter inundation of the seasonal swamps in the corridors between the calcarenite dune ridges. The swamp flora has been replaced by introduced pasture.

A number of other land-uses have appeared in this century:

- forestry, principally of the North American conifer *Pinus radiata*, in humid parts of the Southeast, Southern Mt Lofty Ranges and Flinders Ranges;
- irrigated citrus and stone-fruit orchards, and viticulture, in the Renmark-Waikerie and Mypolonga areas along the River Murray;
- water catchment and management in the Southern Mt Lofty Ranges;

- suburban sprawl on the Adelaide Plains and adjoining Mount Lofty Ranges; and
- mining, generally scattered and localised, although early mines denuded surrounding landscapes of vegetation to fuel smelters.

The rate of agricultural expansion has greatly slowed recently and patterns of land-use have become relatively stable, with the exception of continued rapid growth of suburban areas in the vicinity of Adelaide. Broad land-use patterns across southern South Australia are illustrated in Figure 2.15.

Remnant vegetation is claimed to cover 18.3 % of South Australia's Agricultural Districts (Native Vegetation Management Branch 1989). This optimistic figure includes some savannah woodlands lacking natural understorey. As shown in Figure 2.16, the remnant patches are not evenly distributed across these districts. The Southern Mt Lofty Ranges has only 5 % of its original vegetation cover while Kangaroo Island has 43 % (Harris 1986). The reasons stem from settlement patterns and are two-fold. Firstly, the districts that were first and most densely settled have of course been subjected to the highest level of clearance. Secondly, development has progressed from the most favourable lands to areas of poorest soils. Consequently remnant vegetation is most common in areas least suited to agriculture, such as coastal limestone formations and inland dunefields of highly leached sands, which themselves have well-defined regional distributions (Section 2.3). The vegetation types associated with extreme environments are the types least cleared and best preserved.

As a result of increasing public interest in conservation of the environment and the appearance of erosion and salinity problems due to clearance, government supports retention of the remaining natural vegetation in two ways. Under the National Parks and Wildlife Act 1972–74, approximately 37.2 % of the remnant vegetation in the State's Agricultural Districts is preserved on crown land in the form of 7 "national parks" and 185 "conservation parks"[5], the latter including 32

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[5] There are a further four conservation parks (Lake Gilles, Munyeroo, Pureba and Yumbarra; a

parks on offshore islets (as at 30 June 1990). Scattered across all regions, the parks range in size from 1 ha (Kapunda Island C.P. on the River Murray) to 207 941 ha (Ngarkat C.P. in the Murraylands). Retention and protection of natural vegetation by private landholders on their own properties is encouraged under the Native Vegetation Management Act 1985 which has the power to proscribe clearance and also to provide remunerative compensation to cover potential loss of land value or income.

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combined area of 530 000 ha) which lie immediately north of the Agricultural Districts and which contain significant areas of mallee vegetation relevant to this study. The southern fringes of these reserves are sampled as part of the survey in this study.

Chapter 3:
SURVEY METHODS AND DESCRIPTION OF THE DATA SET

3.1 INTRODUCTION

The design of a phytosociological survey is inextricably linked with the purpose of the study of which it is a part and with the nature of the analytic techniques to which the data are to be subjected (Noy-Meir 1971; Austin 1985, 1987b), leading to general tolerance by ecological workers of a great many approaches and methodologies. Whilst reviews such as those of Goodall (1952), Mueller-Dombois & Ellenberg (1974), Greig-Smith (1983), Kershaw & Looney (1985) and Jongman *et al.* (1987) provide guidelines for the selection of survey methods in relation to aims and analysis methods, the final choice of methods and survey design involves subjective input.

Studies of relatively small, undisturbed areas of vegetation permit surveys which approximate the mathematical / statistical ideal. However, as outlined in the previous chapter, southern South Australia presents an environment that is diverse and complex, and a landscape that is disturbed and disrupted. Any survey of the study area must therefore be subject to restrictions of a practical nature which force compromises of any ideal approach.

The dearth of broad-scale surveys involving multivariate analysis has resulted in little discussion of the practical constraints on survey design and implementation. Noy-Meir (1970), who wrote in depth about the evolution of his large area sampling program, provides a notable exception. In his case, the chief constraint was efficiency of field time. The Agricultural Districts of South Australia present the additional difficulty of extensive land clearance and the non-random distribution of remnant patches.

In this chapter the design of the survey will be considered in relation to aims and projected analysis methods, and also with regard to the practical compromises that were imposed by restricted field time and land clearance. Project aims, survey practice and data analysis methods are so highly interrelated in phytosociological studies that the survey design was arrived at by an almost iterative process, with the requirements of these aspects being balanced at each cycle until a satisfactory compromise was achieved. This chapter will also attempt to show these interrelationships.

3.2 DEFINITION OF THE SCOPE OF THE SURVEY

If the design of an ecological survey programme is considered to be an iterative process, starting conditions must be stipulated which, by continual refinement, lead to the final survey design. These conditions can be derived from the aims and are a preliminary, tentative statement of the scope of the survey in terms of the area to be covered, the time available, the data to be collected, and the analysis and interpretation for which the data are likely to be used (Jongman *et al.* 1987).

For this project, the preconceptions of the survey could be summarised as follows:

1. collection of floristic data;
2. survey to cover a large area of temperate South Australia;
3. study duration restricted to three years;
4. collection of data to permit definition and description of the major vegetation types in the study area using multivariate methods;
5. collection of data to permit correlation of vegetation with abiotic environment, particularly climate and soils;
6. collection of data suitable for assessment of the rarity and remnancy of species and vegetation types.

Of themselves, floristic data (the fundamental characteristic of the study) present no difficulty with respect to survey design. Difficulties arise only when floristics are applied to studies of large areas, but of limited duration. A large, highly heterogeneous survey area requires a large number of large-area sites to sample adequately the numerous vegetation types to be expected, although the precision of the data need not be as exact as for a study of a smaller, less variable area. In such areas of high Beta diversity, qualitative (presence/absence) or semi-quantitative floristic data describe most of the variation; full quantitative data are unnecessarily time-consuming (see Greig-Smith 1983; Jongman *et al.* 1987). The need for many sites is however counterbalanced by the rigid bounds on field time that restrict the number of sites possible during a study. Another consequence of these factors is that time is not available for repeated visits to sites to document the complete therophytic, geophytic and bryophytic floras as they vary in an annual cycle or in response to erratic environmental stimuli.

Given the above considerations, a data set of 500–1000 sites was thought appropriate for this study. The lower limit of this range was the minimum thought necessary to encompass the great perceived diversity of vegetation types in southern South Australia (as in Specht 1972); the upper limit was the maximum number of sites which might be visited during the study and which could be satisfactorily analysed and interpreted collectively. Data collection was restricted to native perennial angiosperms and gymnosperms, which are easily documented in single visits and which, in terms of both biomass and species numbers, dominate over native therophytes and geophytes in the study area. Vegetation data consisted of semi-quantitative cover estimates, amenable to multivariate analysis, for each species of the perennial flora.

Data collected along the above lines are suitable for all three of the survey's analytic objectives: definition of vegetation types and patterns, correlation of vegetation with environment, and assessment of conservation status. Interpretation of such analyses is limited only by the sampling strategy employed during the data collection. Although sampling strategies for definition of vegetation types and environmental correlation are usually compatible, sampling for assessment of rarity of vegetation types is in conflict with the first two analytic objectives and ideally requires a different strategy. The strategies appropriate for these objectives and the limits that they place upon interpretation of analysis results are discussed in the next section.

3.3 SURVEY STRATEGY

Goodall (1952) divided sampling procedures into three classes — random, restricted random and regular — and advocated the use of a restricted random approach for the majority of purposes. A further option available is the subjective placing of rélevés in typical examples of vegetation types, as practised by the earliest phytosociological schools (e.g. Braun-Blanquet 1932; Du Rietz 1930) and continued to the present time (e.g. Gagnon & Bradfield 1986).

For this survey of temperate South Australia, two of the above possibilities had to be rejected outright. There were few existing data to guide subjective sample location as the vegetation and its patterns of variation had not previously been examined sufficiently over much of the study area, viz. the uncertain hierarchical status of mallee "alliances" and "associations" in Specht (1972). For the same reason, restricted randomisation could not be employed, since insufficient information was available to permit preliminary stratification of the area into ecologically sensible units, particularly when the problem of fragmentation of the vegetation cover by clearance was taken into consideration.

Random sampling is the only method of obtaining a statistically unbiased estimate of mean and variance (Goodall 1952; Greig-Smith 1983). If random locations falling in cleared areas were ignored, random sampling would give an accurate, proportionate representation of remnant vegetation in South Australia and hence estimates of rarity of types. Yet the requirements of the project's aims dealing with environmental correlation would not be met. The contagious distribution of remnant vegetation is the result of differential clearing of vegetation types. Remnant patches are typically topographically or edaphically unsuitable for agriculture and occupied by vegetation indicative of such environments. Therefore the distribution is contagious not only geographically but also in abstract environmental space. Only a poor representation of vegetation-environment correlation could be obtained from a randomly-sampled data set. Likewise species response models would be inadequate.

The remaining option, a regular sampling pattern, seemed to offer the best prospects for overall success and was adopted with modifications to allow for clearance and efficiency of field time. Noy-Meir (1970) and Greig-Smith (1983) noted that systematic sampling results in expeditious data collection when the area being sampled is relatively large, and that serious non-random biases are not usually produced. The disadvantage of regular sampling for this survey was its inability to directly indicate remnancy/rarity of defined vegetation types and hence its limited usefulness in conservation status assessment, due to the irregular sizes, shapes and spatial distribution of remnant vegetation patches in such a survey grid. This difficulty could be overcome by obtaining an independent estimate of remnancy in the vicinity of each site (see Chapter 8). As these data were available from the South Australian Department of Environment and Planning, some assessment of rarity and conservation status was still possible from regular sampling. Thus all three analytic objectives could be met.

3.4 SAMPLING DENSITY

From practical viewpoint, sampling density is governed by the total survey area, the total available field time, and the time taken to collect the minimum data required per site.

Few published phytosociological studies or methodological texts give an indication of the time needed to measure a site. Whittaker (1978c) suggests 45 to 90 minutes for 2 people to sample a North American woodland site of 0.1 ha, including measurement of tree basal diameters and estimates of shrub and forb covers, provided the flora is well known. The 0.1 ha site has been found suitable for sampling Australian sclerophyllous systems (e.g. Outhred 1984; Margules & Nichols 1987) and so it was intended to use this size in this study. There was to be no regular field assistance, but as semi-quantitative data of perennials only were adequate and suitable, data collection at each site would be less intensive. Thus it was conservatively estimated that a sampling rate of six 0.1 ha semi-quantitative sites per day, including between-site travel, was feasible.

Although the study covered three years, field work was restricted to just 150 full days, to allow time for unforeseen difficulties in the field, identification of plant specimens after each field trip, collation and correction of data (including environmental data), and analysis and interpretation of the results. Given a sampling rate of six sites per day, 900 sites could be sampled i.e. a sampling density of one site per 173.3 km^2. For convenience, the density was rounded to one site per 200 km^2 for a projected data set size of 780 sites requiring 130 field days of sampling and falling within the initial requirement of 500 – 1000 sites.

3.5 DESIGN OF THE SAMPLING GRID

Regular sampling of sites along parallel transects, such that sites form a rectangular (rather than square) grid across the study area, reduces travelling time between sites and thus makes site location easier. For this reason, transect sampling was the method chosen for this study.

The main drawback of transects for vegetation sampling is their reduced ability to produce data that adequately describe patterns and gradients normal (perpendicular) to transects. This becomes significant when transects are placed arbitrarily, for example, parallel to a north-south axis. It follows that transects are ideally placed where they parallel major, ecologically significant, environmental gradients that are known *a priori* for a study area. This has the effect of maximising the information content about the vegetation gradient per unit data or field time. Helman (1983) and Gillison (1984) coined the term "gradsects" for transects along environmental gradients in this manner.

The complexity of edaphic and climatic gradients in the study area did not permit a single suitable orientation for all survey transects. Instead, the environmental patterns were examined within each of the seven floristic regions (Jessop & Toelken 1986) that make up the study area. The general correspondence between environmental factors and the biogeographic criteria on which the floristic regions are founded made this a legitimate subdivision of the study area. A suitable transect orientation was determined for each region, according to the known environmental gradients (Figure 3.1). Where adjacent regions had preferred transect orientations which were nearly compatible, the orientations were curved or otherwise modified such that the sampling grid was made continuous across the regional boundary (i.e. the South-East and Murray Mallee regions; and the Kangaroo Island, Northern and Southern Mt Lofty Ranges and Yorke Peninsula regions).

To satisfy the required 200 km^{-2} sampling density, transects were placed 25 km apart (Figure 3.2) and sampling grid points indicating site locations spaced at 8 km intervals along each transect, achieving approximately a 3:1 ratio of along-transect versus between-transect sampling intensity. A higher ratio than this was inappropriate since, in the most heavily cleared parts of southern South Australia, the resulting decrease in the distance along transects between the grid points would have critically decreased the probability of locating a patch of remnant vegetation near to each grid point. In each region, the position of the rectangular grid (with minor corrections made for curvature) was fixed from the site nearest the coastal or southern end of the lowest numbered transect in the region; this site was located 4 km along the transect from the coast. The sampling grid determined in this manner contained 784 points when completed.

3.6 LOCATION OF SITES

As 81.7 % of the survey area did not bear natural vegetation, the probability that any one of the interstices of the above-described grid would fall in a patch of vegetation was just 18.3 %. A further complication was that some of the grid locations which fell in vegetation patches would be accessible only by long cross-country hikes. This situation was an unacceptable compromise on the speed and efficiency of the field work. Noy-Meir (1970) faced similar difficulties with accessibility and chose to restrict his sampling to areas accessible by road.

Rules for the final location of the site corresponding to each grid point were developed specifically to overcome the problems of clearance and access, whilst maintaining as much objectivity in the sampling procedure as possible. The site was the accessible portion of the patch of remnant vegetation nearest the grid point and still within the 25 x 8 km cell of which the grid point was the centre. "Accessible" meant within a 15 minute hike of a road or track navigable by four-wheel-drive vehicle. A vegetation patch had a minimum area of 4 ha (200 x 200 m) except in some districts of very low vegetation remnancy, where the definition of a patch was allowed to include small patches (1–4 ha) and also wide, continuous corridors of vegetation on the reserves of minor country roads which were unlikely to have been subjected to heavy earthworks.

Site locations were pinpointed prior to fieldwork with the aid of Australian National Mapping Division 1:250 000 scale topographic maps, South Australian Department of Lands 1:50 000 aerial photo mosaics (dated 1972 to 1979) and more recent (1983) LANDSAT IV three band, false colour images, which clearly show remnant vegetation.

Preliminary tests of these sources revealed that selection of a single potential site location by this method was inadequate since (i) these sources provide information only about the upper vegetation stratum in most vegetation types and thus it is impossible to judge whether degradation of the understorey has occurred, and (ii) these sources are quickly outdated by continued clearance of remnant patches.

Consequently three potential sites were preselected and ranked in descending order according to their distance from the grid point. During field work, the three locations were visited according to their rank and the most highly ranked of the three which was neither cleared nor disturbed was the final site sampled. (See Section 3.9.1 for definition of "disturbed"). Where all three preselections were disturbed, the site was located in the least disturbed of the three, or, in some cases, on the immediately adjacent road reserve if this was less modified by grazing or ploughing and undamaged by earthworks. Where agricultural development has left few remnant patches, including suitable road reserve vegetation, three alternatives could not always be obtained and the above criteria were applied to the one or two locations available. In cases where no vegetation patches occurred in the 25 x 8 km cell around the grid point, no site was recorded for that area. This situation, readily detected from the aerial photographs and satellite images, was the case for 40 of the 784 grid points. Missing sites occurred in all regions except the South-East and Kangaroo Island, but were concentrated in the Northern Mt Lofty Ranges.

Site preselection and fieldwork were undertaken over two major periods: September 1985 - February 1986 (South-East and Southern Mt Lofty Ranges regions) and March - November 1987 (Murray Mallee, Eyre Peninsula, Yorke Peninsula, Northern Mt Lofty Ranges and Kangaroo Island regions, in that order).". niversal on of all the sites are given in Appendix 1.

A regional summary of site numbers (Table 3.1) shows a strong correlation between area of region and number of survey points in the sampling grid, indicating that proportional sampling had been very nearly reached by the chosen sampling method of regularly-spaced and actively-oriented transects. In the breakdown of site numbers according to conservation and disturbance status, the Murray Mallee, Southern and Northern Mt Lofty Ranges, and Yorke Peninsula have above-average proportions of sites in disturbed patches and at least some grid points unsampled. These data confirm that these regions have been most widely cleared for agricultural development. The Northern Mt Lofty Ranges region is the most extensively cleared, with so many grid points lacking a site and sites generally so far from their respective grid points that the site distribution pattern appears random in comparison with those of other regions (Figure 3.3). Vegetation seems best conserved in N.P.W.S. reserves on Kangaroo Island and in the Southeast region.

3.7 POSITIONING OF QUADRATS AT SITES

At sites in large patches of homogeneous vegetation, a 50 x 20 m (0.1 ha) quadrat was positioned and oriented as in Figure 3.4. The long axis of the quadrat ran perpendicular to the access route at the predetermined site location. The end of the quadrat nearest the access route lay 50 m from the nearest edge of the road or track, except where the patch was bounded by a fence, firebreak or any other band of disturbance, when, to avoid edge effects, the quadrat was located 50 m from the margin of the disturbance. For sites at the corner of a remnant patch, the quadrat was located 50 m from both sections of the patch boundary.

In some situations, the size and shape of the quadrat, and the rules for its location had to be modified. In clearly patchy vegetation, the orientation and occasionally the shape of the quadrat were changed such that the quadrat fell entirely within what appeared to be uniform vegetation. In all such cases the changes were to place the quadrat in the vegetation type occurring at the point 50 m from the road, track or fenceline. In dunefields, for example, the long axis of the quadrat was placed along the dune crest, dune flank or interdune corridor, whichever occurred 50 m from the site location. In addition the quadrat was made narrower whenever a second of these units would have been otherwise encountered. Similarly when the site was in a road reserve corridor, the quadrat was made narrower and longer (e.g. 100 x 10 m) and oriented along the corridor.

3.8 VEGETATION DATA

Most of the vegetation data were directly collected in the field. Subsequent laboratory work consisted of identification of collected voucher specimens, correction or updating the data set for new identifications or taxonomic revisions, and collation of the vegetation data matrix on computer.

3.8.1 Measurements at the Sites

A preliminary description of the vegetation was made according to the physiognomic/floristic classification scheme of Specht (1972).

All native perennial angiosperm species in quadrats were listed. Introduced species, and native therophytes and geophytes present at the time of the site visit were also recorded for completeness, although not included in the data analysis. Voucher specimens were collected of all species which were newly-encountered, unable to be accurately identified in the field, or known to belong to taxonomically-difficult complexes and so demanding specialist attention.

Typical growth form at that site of all species (native or introduced, perennial or otherwise) was noted using the simple system in Table 3.2.

The vertically-projected foliage cover of each species was visually estimated according to the semi-quantitative cover-abundance scale in Table 3.3. Derived from the Hult-Sernander scale (Hult 1881; see Becking 1957), this simple, nearly logarithmic scale was easier to use in the field and more robust under repeated use than newer and more detailed cover-abundance scales such as those of Braun-Blanquet (1932), Domin-Krajina (Domin 1933; see Mueller-Dombois & Ellenberg 1974), Barkman *et al.* (1964) and van der Maarel (1979). The extra cover classes of these last scales at high percentage covers are very rarely reached by individual species in South Australian vegetation and hence were unnecessary in this survey.

3.8.2 Voucher Identification and Taxonomy

Jessop & Toelken (1986) was used as the primary source for identification of voucher specimens and for taxonomic nomenclature. Black (1943–56 and 1978), Boomsma (1981), Brooker & Kleinig (1983), Carrick & Chorney (1979), Cunningham *et al.* (1981) and Whibley (1980) were invaluable supplementary sources. All taxa were identified to the specific level, apart from the exceptions detailed in Tables 3.4 and 3.5. A total flora of 652 taxa was recorded and a full listing is given in Appendix 2.

Fourteen taxonomic groups, ten of them perennials, were not identified to species level (Table 3.4). In most cases the taxa were pairs of species which could not readily and consistently be distinguished in the field from the vegetative material usually available. Thus the data for the two species were combined and treated as a single taxon. The rather obscure distinction between *Xanthorrhoea australis* and *X. caespitosa* sp. nov. was published in late 1986, by which time survey work for the Southeast region (to which both species are restricted in South Australia) had been completed. These species were not clearly separable by their published distribution patterns and so the data could not be modified *a posteriori* to accommodate the change of taxonomy. The other noteworthy species complex, *Eucalyptus dumosa / E. calcareana*[6], is also the result of changing taxonomic nomenclature. These species could not be distinguished since the large amount of voucher material collected showed gradation of the characters which should have permitted their identification. Patterns of morphological variation in *Eucalyptus* sect. *Dumosae* are recognised by Lang (1983) to be highly continuous and thus the section was treated as a single species complex. Johnson (1976) pointed out that such complexes of species ("superspecies") are not uncommon in the genus *Eucalyptus*, although the *E. dumosa* complex is by far the most taxonomically problematic in southern South Australia.

The species in Table 3.5 were identified to subspecific level. For all these

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[6] This species complex also includes *Eucalyptus anceps, sensu* Chippendale (1988).

species, field observations indicated that each subspecies possibly showed a distinctive environmental response and hence had a different distribution pattern. For example, Jessop & Toelken (1986) noted that the two forms of *Zygophyllum billardieri* were almost certainly different species, with distinctive distribution patterns in coastal and arid areas respectively. However the two "species" had not been formally named or described as such at that time.

3.8.3 Data Collation

The vegetation data, including data for introduced and annual species, were collated as a two-dimensional matrix of single digit cover abundance scores, 744 sites by 652 taxa ("species").

3.9 ENVIRONMENTAL DATA

Collection of data concerning significant climatic and edaphic factors with which vegetation patterns could be correlated was the main interest. Only some of the environmental data were directly collected in the field: notes on topography, surface geology, soils and the nature and extent of vegetation disturbance. Field notes on soils consisted only of a general description of the profile, but representative soil samples were collected for later laboratory analysis. Climatic data could not be obtained in the field (since all sites were visited just once during the survey work); existing published and unpublished sources were used instead (see Section 3.9.3).

3.9.1 Measurements at the Sites

Topography at each site was identified as one of the eleven general units in Table 3.6 and, where appropriate, measurement made of the quadrat's average aspect (to the nearest 45° T) and slope (to the nearest 5°). In dunefields, estimates were made of the distance between dune ridges (dunefield "wavelength") and the height of dunes above the swales (dunefield "amplitude"). In addition, note was made of any evidence that the site was subject to regular flooding by daily tides, annual river flooding, or annual wetland basin filling.

Across the soil surface, the presence and estimated percent cover of rocks (diameter >2 cm), pebbles (diameter <2 cm), leaf litter, and soil-encrusting lichens, mosses and terrestrial algae were recorded.

At the centre of the 50 x 20 m quadrat, a soil core was dug. The core reached a depth of 1.0–1.2 m unless a layer of rock was struck above this level. The soil profile was described and the depth and nature of each horizon, including underlying rock, recorded. Representative 300–500 cm^3 samples were taken from the middle of each horizon. In gradational soils, samples were collected to encompass the range of variation present. In deep soils with uniform profiles, a single sample was taken from a standard depth of 30 cm.

A visual, subjective assessment was made of the degree of disturbance in the partially disturbed sites. Disturbance was assessed overall and in categories of particular disturbance types:

- wind and water erosion,
- grazing and development of stock tracks,
- clearing (vegetation chaining, brush cutting and tree felling),
- earthworks (road and track construction, and tilling),
- infestation by introduced weed species, and
- wild fire.

Assessment for each type was on a linear scale from 0 (no disturbance) to 4 (severe disturbance, 75–100 % estimated loss of understorey). The reason for recording even such a crude assessment of vegetation degradation was to permit identification of partially degraded sites during analyses. Degradation resulting in a decline in species number from that to be expected in the natural state influences calculation of between-site dissimilarity values and may bias clustering analyses. To allow for these possibilities, sites receiving an overall disturbance rating of 2 (mild, 25–50 % loss of understorey) or greater were defined as disturbed.

3.9.2 Soil Analyses

The following variables were determined in laboratory tests of all 878 soil samples collected.

- COLOUR (Moist): Using Munsell Soil Colour Charts.
- TEXTURE: Using the simple method of Northcote (1979). The nominal texture classes defined by this procedure were ranked on an ordinal scale from 1 to 9 according to percent clay content after the textural classification of Thompson (1952) (Table 3.7).
- SOIL WETTABILITY: Non-wetting soils, typically sands in the study area, do not readily absorb water. To test for this, drops of water were placed on a dry and lightly crushed sample of soil, and note made of whether the water was immediately absorbed or whether it formed surface beads. The character was treated as binary.
- pH: Measured in a continually stirred suspension of 1:5 v/v dry, crushed soil and distilled water using a Radiometer pH Meter 29.
- TOTAL SOLUBLE SALTS AND CARBONATES: Conductivity was measured concurrently with pH in the same 1:5 v/v soil suspension using a Hanna HI8033 Conductivitymeter and converted to concentration of total soluble salts (T.S.S.) with a standard curve for potassium chloride solution. Chloride concentration was not measured specifically. To distinguish calcium carbonate from other salts, presence of carbonates was tested by addition of 0.1 N HCl solution which has a rapid reaction with carbonates producing

gaseous CO_2. The acid reaction was rated on a three-point ordinal scale (absent, weak and strong).

3.9.3 Climatic Data

There are a large number of locations across southern South Australia at which rainfall records have been kept over periods of many years (>50 years). Mean annual rainfall data and the maps created from them are reliable and detailed enough to provide useful information at the scale of the study area. Records of other climatic variables such as evaporation, temperature and irradiance are held for far fewer stations and generally for much shorter periods. Maps of these variables are therefore highly generalised and accurate data are not possible at the scale of the survey. Consequently climatic data in this study were restricted to mean annual rainfall, with an implicit assumption that other aspects of the climate are correlated, as would appear to be the case (Section 2.3).

Mean annual rainfall was interpolated to the nearest 25 mm for all sites using a variety of data sources: Bureau of Meteorology, Adelaide (1984) 1:5 000 000 Rainfall Map of South Australia; Coaldrake (1951) and Penney (1983) in the Southeast region; Burrows (1979) on Kangaroo Island; and a set of unpublished (1986) 1:250 000 scale rainfall maps covering Eyre Peninsula by K. Burrows, Bureau of Meteorology, Adelaide. There was no satisfactory source of rainfall data in the Murray Mallee region. For this region, the Bureau of Meteorology's monthly rainfall records (1839–1983 inclusive) were examined, a mean calculated for every station in the region having more than 30 consecutive years of recordings, and a value determined for other stations by comparing their short-term records with records for the same period at another station nearby. Site estimates were made from the resulting map (Figure 3.5).

3.9.4 Data Collation

The environmental data set was completed by four variables obtained directly from National Mapping Division 1:250 000 topographic maps: Universal Map Grid longitudinal and latitudinal coordinates, elevation above mean sea level and distance from the coast. The grid coordinates were included as a possible way of detecting biogeographic and/or vicariance patterns should other environmental variables fail in correlative analyses or modelling, elevation as a potential mediator and modifier of climatic variables (especially temperature), and distance from the coast as an indicator of maritime moderation of climate and of wind-and-salt exposure.

The completed environmental data were collated as a matrix of 744 sites by 30 variables. A full listing of these variables is given in Table 3.8.

Chapter 4:
VEGETATION ANALYSIS I: SELECTION OF METHODS & PRELIMINARY STATISTICS.

4.1 INTRODUCTION

The following three chapters describe the analysis of the vegetation data to produce a floristic classification of the study area's remnant vegetation, an understanding of the relationships between the classification groups, and a description of the main compositional gradients and their environmental correlates; in short, an attempt to address the second, third and fourth aims of the project as set out in Section 1.5. The "geobotanic" interest of the project requires that these three aims be addressed together. A preliminary review of multivariate methods is given to explain the choice of vegetation analysis methods used.

4.2 MULTIVARIATE ANALYSIS: REVIEW AND CRITIQUE

There are a great many multivariate analysis methods (including numerous methodological variations and options) which might be used to examine a vegetation data matrix. The mathematical basis of all these numerical classification and ordination techniques, and their ecological applications, have been well reviewed in the recent past (Austin 1985; Beals 1984; Gauch 1982; Greig-Smith 1983; Jongman *et al.* 1987; Legendre & Legendre 1983; Orloci & Kenkel 1985; Pielou 1977). In view of this considerable literature, it is intended to give only a brief review of the topic here, from the perspective of a pragmatist.

Multivariate analysis can be divided into two broad categories: ordination or gradient analysis, and numerical classification or clustering. The boundaries between these categories are not as clear cut as they may at first seem, but this breakdown will suffice to structure the following discussion. The analysis of vegetation-environment correlations will also be examined.

4.2.1 Ordination

Ordination, in the most general sense of the term, has traditionally been divided into two types: direct gradient analysis, including "calibration" *sensu* ter Braak & Prentice (1988), and indirect ordination (Gauch 1982; Greig-Smith 1983). Direct gradient analysis stems from the work of Ramensky (1924) and Whittaker (1956) and involves simple representation of the positions of vegetation types or compositional dominants along axes of abiotic environmental variables, with the aim of correlating vegetation with environment. Despite efforts by the Wisconsinian School to introduce mathematical elegance, and thereby a semblance of "multivariateness", to the approach (e.g. Curtis & McIntosh 1951; Bray & Curtis 1957), the various forms of direct gradient analysis are not regarded as true multivariate techniques (Jongman *et al.* 1987) due to the low dimensionality of the results (Curtis & McIntosh 1951 — one gradient; Bray & Curtis 1957 — two gradients) and due to the degree of subjectivity in assignation of starting conditions in the former method (Greig-Smith 1983). The importance of direct gradient analysis lies in the use of its underlying philosophy to develop an important indirect multivariate method, reciprocal averaging, which is outlined below.

Indirect ordination is based in eigenanalysis of matrices. Goodall (1954b) demonstrated the ability of factor analysis (= principal components analysis or PCA; Hotelling 1933) to extract orthogonal axes (eigenvectors) describing the major sources of vegetation variation, the suitability of these axes for correlation with environment and hence the potential for regarding these axes as vegetation gradients. PCA became more widely appreciated in ecological circles through the examples of Dagnelie (1960, 1978), Orloci (1966) and Austin (1968). Noy-Meir (1973a) thoroughly examined and systematised the important effects of different combinations of data centring and standardisation on PCA efficiency and interpretation, making recommendations on the suitability of these for typical phytosociological data sets. However there is a serious problem with PCA: its requirement for linear (or at least monotonic) interspecific correlations i.e. linear environmental response models within the domain of the data set for the majority of species. As amply illustrated by Noy-Meir & Austin (1970) and Austin & Noy-Meir (1971), simple vegetation gradients that are sufficiently long for species to show Gaussian-style bell-shaped response curves are distorted by PCA into higher dimensions, appearing curved, folded or otherwise contorted. Thus PCA fails to extract adequate gradients from data sets of high β diversity.[7]

Hill (1973) produced a solution capable of dealing with unimodal species response curves: reciprocal averaging (RA). This method is based upon the single axis, weighted averages approach of Curtis & McIntosh (1951), but uses arbitrary initial species weightings rather than subjectively derived weightings, a simple iterative procedure to arrive at a unique stable solution for both species and sites, and a methodological extension that provides multidimensional ordination with orthogonal axes. RA is in fact a member of the PCA family, with double standardisation by totals, known as correspondence analysis (Greig-Smith 1983). It was soon observed that an RA second axis frequently tends to be a quadratic function of the first axis (Gauch *et al.* 1977) and that the extremities of the first axis are consequently compressed (Hill & Gauch 1980), much like the distortion produced by PCA of data sets with high β diversity. This led to the development of detrended correspondence analysis (Hill 1979a; Gauch 1982) in which detrending seeks to suppress arching of secondary axes and stretch axis ends. In this guise, correspondence analysis has been widely and successfully applied in ecological studies (e.g. Cooper 1984; Hughes & Huntley 1986; Lahti & Vaisanen 1987; Nilsson 1986; T. Ökland 1988; Woldu 1986) and canonical correspondence analysis (CCA)

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[7] β diversity here, and elsewhere in the text, refers to the sum of all types of floristic differences between locations, floristic variation within data sets and species turnover along multiple habitat gradients. Such convenient general usage may be equivalent to a loose combination of β, γ and δ diversity *sensu stricto* Whittaker (1977), but is not intended to offend these definitions.

and related forms have been devised to deal with simultaneous derivation and correlation of vegetation and environment gradients (ter Braak 1986, 1987a).

As with PCA, there are some problems with DCA. Firstly, there has been criticism of the crudeness of the original segmental detrending procedure (Pielou 1984; Minchin 1987a; Oksanen 1988; see Peet *et al.* 1988) which tends to make DCA over-conservative. More elegant polynomial detrending has recently been achieved by ter Braak (1987b), although Knox (1989) could find no significant improvement in solution stability or accuracy over detrending by segments. Secondly, as DCA performs better when dealing with unimodal species responses, it becomes less reliable when vegetation gradients are so short that species responses appear monotonic. Hence Jongman *et al.* (1987) recommended PCA over DCA for data sets with low β diversity and low levels of species turnover along gradients.

The third problem stems from the reliance of DCA on overlap of species responses. Using simulated data sets, it has been convincingly shown that DCA fails to reproduce a known gradient when sampling points are so widely dispersed along the gradient that they do not describe the full series of species replacements i.e. as the data set approaches complete discontinuity (Kenkel & Orloci 1986; Minchin 1987a). DCA ordination of a complete discontinuity results in a trivial first axis that simply separates the two discontinuous groups.

In both Kenkel & Orloci (1986) and Minchin (1987a), non-metric multidimensional scaling has been found superior to DCA, although its potential for ecological analysis has only recently been examined in depth. NMDS is an iterative eigenvector method distantly related to PCA that operates on a sites × sites dissimilarity matrix. NMDS accepts values for any dissimilarity metric and aims merely to rank-order sites along axes, thus it is not dependent on Euclidean linear geometry.

Despite its apparent mathematical superiority to all other indirect ordination methods, especially its simpler aim of rank-ordering sites, there are also problems with NMDS which do not seem to have been fully addressed in the literature. Firstly, the chosen dissimilarity metric must accurately represent vegetational dissimilarity. Although most metrics converge to a value of 1.0 at complete dissimilarity, their behaviour, especially with quantitative data, is complex at lower levels of vegetational dissimilarity (see Jongman *et al.* 1987). Thus NMDS is likely to be most accurate for analysis of data sets of very high β diversity approaching near discontinuous conditions, and least reliable at lower β diversity, where DCA or PCA may perform just as well. Bloom (1981) and Faith *et al.* (1987) have examined the problem of choosing a dissimilarity measure for any type of multivariate analysis and found the Bray-Curtis and Kulczynski metrics the best available, but the question of how much noise is introduced into NMDS by non-linear behaviour of dissimilarity measures is yet to be answered.[8]

Secondly, as NMDS solutions are not unique, but dependent upon user-defined starting conditions, the analysis must be run many times, each time with different starting conditions and either the ordination of minimum stress or some consensus ordination taken as the best solution (Jongman *et al.* 1987). Large amounts of computational time are expended during these multiple analyses, making NMDS much less efficient than DCA, PCA or related methods (Gauch *et al.* 1981).

Finally, if the superiority is only clear at high β diversity approaching compositional discontinuity, one may argue that NMDS is redundant by asking why one would want to ordinate a discontinuous vegetation data set. Classification would seem more appropriate and an observant ecologist could readily extract environmental correlations by simple direct gradient analysis.

4.2.2 Classification

Classification approaches are of two types: those devised or modified to their specific requirements by vegetation ecologists, and those acquired from numerical taxonomy.

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[8] DCA appears to avoid the whole issue with its intuitively appealing weighted-averages approach, but in fact this is equivalent to a detrended PCA using the Chi-square dissimilarity measure rather than simple Euclidean distance (Minchin 198~~7~~9).

Phytosociologists have favoured divisive approaches. This tendency stems from historical, philosophical and theoretical grounds related to the origins of their research in the Zurich-Montpellier and Scandinavian schools. The earliest methods included simple visual data matrix rearrangement (e.g. Braun-Blanquet 1932), which has now been formalised in computer programs such as TABORD (van der Maarel et al. 1978), and association analysis (Goodall 1953; Williams & Lambert 1959). However, association analysis on ecological data is flawed by the sensitivity of the χ^2 test of independence to the number of "double negatives" (quadrats in which any two species being tested for association are both absent) which may exaggerate or obscure the true nature of the species' relative distributions.

More recently, divisive classification based on ordination partitioning has been adopted (e.g. Noy-Meir 1973b; Hill 1979b). Such methods sequentially split groups of sites at their greatest ordinational discontinuities. Two-way indicator species analysis (TWINSPAN; Hill 1979b), based on DCA ordination and thus benefitting from DCA's features, has been widely used. Its popularity undoubtedly stems from its affinities to traditional table rearrangement techniques of earlier European schools of phytosociology. But a cautionary note should be made about composite methods such as these, because they must suffer the problems of each of their constituent parts. In the case of TWINSPAN, the ordination may be distorted if the vegetation gradients are either so short that species responses are monotonic or so long and sparsely sampled as to appear discontinuous; the crudeness of current DCA detrending may eliminate ecologically important information; and the divisive approach is appropriate only to the few-groups level in most cases before the probability of "misclassifications" becomes significant (see below).

Classification methods borrowed from numerical taxonomy are almost exclusively two-step processes: (i) calculation of a matrix of between-sites (dis)similarity and (ii) clustering of sites into groups by some algorithm that uses maximum similarity or minimum dissimilarity (see Sneath & Sokal 1973). Greig-Smith (1983, pp.194-5) lists numerous (dis)similarity measures for both qualitative and quantitative data. No (dis)similarity measure is consistently best and ideal for all studies. Selection of a measure from this wide array is a matter of personal judgment (Jongman *et al.* 1987) based on study objectives, data type and data complexity, since these factors are the criteria for assessing performance efficiency of multivariate classifications (Gauch 1982). Greig-Smith (1983), Jongman *et al.* (1987) and Faith *et al.* (1987) do however provide information about the behaviour of each metric in particular circumstances which may guide the choice.

The major choices in clustering algorithm are between hierarchical and non-hierarchical, and agglomerative and divisive approaches (Gauch 1982). Non-hierarchical methods have the disadvantage that an *a priori* decision must be made about the number of groups required. Hierarchical methods have the disadvantage that distortions of individual dissimilarities between site pairs are cumulative i.e. as the algorithm proceeds, the partial cophenetic correlation decreases and the level of "misclassifications" (in some purely ecological sense) increases. Thus the high level fusions of an agglomerative method are the least interpretable, as are the small groups of a divisive method. Choice of methodology clearly relates to preconceptions of the number of groups expected and how much information about group relationships is desired.

Numerical clustering has been discussed at length in phytosociological textbooks (e.g. Gauch 1982; Greig-Smith 1983). For example, the unweighted pair-group methods using arithmetic averages (UPGMA) is described as the superior agglomerative method since it maximises cophenetic correlation (Sneath & Sokal 1973) and the divisive approaches based on (dis)similarity matrices are regarded as unsatisfactory due to their very high computational requirements (Jongman *et al.* 1987). Despite this, practising phytosociologists have paid only cursory attention to these approaches, possibly in response to the debate about the theory and practice of numerical taxonomy during the 1960's (see Section 1.1) and possibly because no satisfactory divisive method compatible with traditional classification approaches was available. Thus little can be gained from the literature about the suitability of numerical clustering for investigation of vegetation survey data. There has been a renewal of interest as a result of (i) the research in NMDS (e.g. Austin 1987b) since NMDS computer programs manipulate precalculated distance matrices, and (ii) investigations into the use of fuzzy set theory as a basis for vegetation analysis (Equihua 1990). However, the dearth of published results means that an interested researcher must continue to experiment with classification methodology for himself.

4.2.3 Analysis of Vegetation-Environment Relationships

Most modern phytosociological studies are not merely concerned with producing a vegetation classification, but, as with this project, aim to gain some understanding of the (abiotic) environmental structure underlying observed vegetation patterns. Methodology is not yet well developed in this field, and Greig-Smith (1983) is critical of the frequent lack of depth and rigour shown in correlation of measured environmental variables with classifications and ordinations.

Due to the very nature of the philosophy which leads to the use of ordination in phytosociological studies (Curtis & McIntosh 1951; Whittaker 1967), the form of ordinations easily lend them to analyses of concomitant environmental patterns via correlation of environmental factors with the principal vegetation axes. This is frequently done by regression of individual environmental variables (e.g. Gagnon & Bradfield 1986; Whittaker 1987), multiple regression (e.g. Ezcurra *et al.* 1987; R.H. Ökland 1988) or by recently-developed CCA (e.g. ter Braak 1987a; Bouchard *et al.* 1987). These methods are subject to two drawbacks: vegetation gradients are distorted by imperfect ordination techniques, as discussed above, and linearity of relationships is assumed in regression and CCA. In both cases, environmental correlation will be underestimated. These problems may be overcome to some degree by the use of rank correlation or higher order regression such as trend-surface analysis (Gittins 1968; Neal & Kershaw 1973). The latter provides a method of examining analytical distortion at the vegetation-environmental interface by polynomial correlation of each environmental factor with two or more ordination axes.

Analysis of vegetation-environment relationships in classifications is more problematic and thus rarely undertaken. Since field survey does not approximate experimental design, traditional procedures such as single-factor analysis-of-variance (and its non-parametric equivalents) must be rejected in almost all cases, as sample size is usually highly variable between classification groups and heterogeneity of variances is correspondingly high. Intergradation of vegetation types along environmental gradients further complicates attempts to detect different environmental responses by vegetation types. Where vegetation types are relatively distinct, multiple logistic regression has been successfully used to model the responses of individual vegetation types with respect to classed data in the form of multidimensional contingency tables (e.g. Margules & Nicholls 1987). However this approach becomes cumbersome when applied to a large number of classification groups, and unsatisfactory for a data set displaying high compositional continuity. Batista (1988) has used multiple discriminant analysis (MDA; Legendre & Legendre 1983) as a non-rigorous exploratory tool to detect environmental separation and/or intergradation of vegetation types, and to determine the factors contributing most to their separation/intergradation. By placing vegetation types in the context of composite environmental gradients (the discriminant functions), MDA ordinates classification groups (as classification nodes) in the manner of a multidimensional environmental catenation (cf. Noy-Meir 1974a, 1974b). Although there may be minor reservations about the requirement of strict normality of data, the test results were encouragingly sensible and MDA appears to perform well as an exploratory tool for investigating vegetation-environment correlation.

4.2.4 Summary

The current state of multivariate analysis application to phytosociological studies may be summarised as follows. A combination of complementary classification and ordination methods is recommended for most circumstances (Gauch 1982). The most widely used and favoured combination in the recent past has been DCA and TWINSPAN, including the variant CCA which incorporates environmental data (Gauch 1982; Jongman *et al.* 1987). Most active use of DCA and TWINSPAN has been in countries and institutions where the methods originated or where there have been long traditions of quantitative phytosociological research. Growing interest in NMDS (Kenkel & Orloci 1986; Kenkel 1987; **Minchin 1987a**) has lead to the Bray-Curtis or Kulczynski distance metrics with UPGMA and NMDS being recommended as a classification-ordination combination (e.g. Austin 1987b). An unfortunate dilemma is that the two procedures in each of these pairs are not methodologically independent, making any attempt to cross-correlate them (e.g. plotting classification groups onto an ordination scattergram) merely tautological. Consequently, vegetation scientists continue to apply numerous different multivariate methods and take some sort of consensus result. There is also no uniformity in the choice of methods for analysis of vegetation-environmental relationships. The choice most strongly reflects the immediate aims of each study and the mathematical background of each researcher.

4.3 ANALYSIS METHODS

As pointed out in the previous chapter, prospective analysis methods must be considered when a sampling strategy is formulated. Thus the choice of analysis methods described below formed an integral part of the survey design process (and vice versa). During this process, two aspects of analysis of the vegetation data had to be addressed: selection of some appropriate mathematical techniques and determination of an effective way of dealing with the size and anticipated complexity of the data set.

4.3.1 Selection of Multivariate Methods

It was not the intention of this project to enter the realm of comparative studies to test the behaviour and performance of numerous multivariate techniques on an ecological data set, but to examine how these methods could be used to elucidate broad-scale patterns in Australian sclerophyllous vegetation and to apply them to the derivation of a floristic classification in southern South Australia. Consequently, multivariate methods were selected from the many available based on what theory and practical experience in the literature recommended as reasonably accurate and robust. Complementary classification and ordination methods were selected for a tandem analysis approach as advocated by Gauch (1982).

As apparent from the discussion in the previous section, choice of appropriate multivariate methods is strongly influenced by the level of β diversity in a data set. Existing literature on the vegetation of southern South Australia (e.g. Specht 1972) and preparatory field work before the start of this survey (subsequently corroborated by preliminary examination of the data set; see Section 4.4) indicated high β diversity in the study area (although without frequent discontinuity in the patterns) and thus the necessity of selecting methods suited to high diversity conditions.

Classification by Bray-Curtis distance metric with UPGMA fusion (Greig-Smith 1983) and ordination by DCA (Gauch 1982) were chosen as the basic analytic techniques. These complementary techniques are methodologically independent and hence can be cross-referenced without overt tautology. Classification by UPGMA fusion is agglomerative and hierarchical, and thus its use anticipated the need to identify many vegetation types and the need for flexibility of the level(s) at which vegetation types so defined might be most readily interpretable. DCA ordination was preferred over NMDS because the relative computational efficiency of DCA compared with NMDS seemed to outweigh disadvantages attributable to its relative crudeness or mathematical inelegance. The only condition on the ordinations was that compositional discontinuities or near discontinuities, with which DCA and most other ordination methods fail to cope (Hill & Gauch 1980), and which are readily detected from the classification, were removed by appropriate stratification of the data set.

Both classification and ordination analyses were performed using the "NTP" numerical taxonomy software package (Belbin *et al.* 1984)[9]. Beyond the logarithmic transformation of the cover score scale, the raw data were not subjected to any preliminary centring or standardisation, since both the Bray-Curtis metric and DCA have inherent standardisation properties (Greig-Smith 1983). Rare species were not downweighted during ordination and default detrending parameters were used.

Underlying abiotic environmental patterns were examined by three methods, either singly or in combination:

1. Kendall rank correlation of individual environmental variables with each of the principal ordination axes[10], using routine NONPAR CORR of the SPSS-X statistical software package (SPSS Inc. 1986);

2. trend-surface analysis (Gittins 1968) of selected environmental variables on two-dimensional ordinations. Surfaces were fitted by stepwise-additive, least-sums-of-squares regression using the GLIM package (Baker & Nelder 1978), up to a quartic function maximum. A "step" during these regressions consisted of a complete progression to a higher order of 2-D function including all possible interactions of lower order terms e.g. linear

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[9] These analyses, and all others, were executed using the Digital Corp. VAX 11/785 mainframe computers of the Computing Centre, University of Adelaide.

[10] It was accepted that there is uncertainty about the assumption that principal ordination axes should individually be correlated with environmental variables (hence the use of trend-surface analysis.) Despite their crudity and lack of subtlety, such axis correlations are, however, computationally efficient, and easily and concisely presented. Thus they have been used in this study whenever only a generalised picture, rather than a detailed examination, of underlying environmental pattern was required.

($a.x + b.y + k = 0$) to quadratic ($a.x^2 + b.y^2 + c.xy + d.x + e.y. + k = 0$). The stepping was continued until the increased order of the regression failed to significantly increase the model fit (decrease deviance); and

3. multiple discriminant analysis of classification groups by weighted linear combinations of measured environmental variables (as in Batista 1988) using the SPSS-X package routine DISCRIMINANT. Predictors were entered stepwise according to Wilks' method, and entry terminated when improvement of discrimination was not significant at the $P < 0.05$ level.

4.3.2 Approach for Dealing with a Large, Heterogeneous Data Set.

Studies in the past have accommodated large data sets collected over large survey areas by random subsampling of the data during the computationally more intensive aspects of analysis (e.g. Noy-Meir 1970, 1974) or by analysis of regional subsamples (e.g. Orloci & Stanek 1979; van der Maarel *et al.* 1987). In the case of regional analyses, some attempt at synthesis over the entire study area is desirable. Orloci & Stanek (1979) avoided the need for comparison of vegetation types between regions (and thus the need for synthesis) by defining regions on the basis of previous vegetation studies such that each of their vegetation types was restricted to a single region. In the study of van der Maarel *et al.* (1987), by contrast, it was apparent that vegetation types were not confined to regions and a subsequent synthesis over the whole area was achieved by secondary analysis of composite, synoptic "sites" representing each classification unit in each region.

As with the above-mentioned studies, analysis of the survey data in this study was initially conducted on a regional basis. However the synthesis approach of van der Maarel *et al.* (1987) was rejected outright, since multivariate analysis of synoptic data denies the internal variability of vegetation types, and consequently the location of natural discontinuities in abstract vegetational space, by which definition of classification units is most logical. The use of synoptic data can only succeed when all regional vegetation types are equally distinctive and when there is negligible regional variation within types. Since it seemed that these conditions were unlikely to be met in the present study, an alternate analysis pathway was used here, as outlined below.

A vegetation classification was produced for each region and the regional data set was ordinated to find the major vegetation gradients. As suggested by Peet (1980) and more recently by Bridgewater (1989), "partial ordinations" of the sites in individual (major) branches of the classificatory dendrogram were also undertaken where either (i) major disjunctions were demonstrated between dendrogram branches, or (ii) the full ordination had significant gradients along higher order (3rd or 4th) axes which distorted patterns when projected onto a two-dimensional scattergram. The latter condition was set because of doubts about the worth of higher order DCA axes as a consequence of both the iterative weighting and the detrending procedures (Pielou 1984) and because two-dimensional ordination plots are most easily interpreted. Principal axes of all full and partial ordinations were rank correlated with measured environmental variables.

Synthesis of vegetation patterns across the entire study area was achieved by a classification of all 744 sites, and by a series of full and partial ordinations according to the same guidelines as employed during regional analysis. As ordination scattergrams of several hundred data points were found difficult to assess, random subsamples of the largest ordination data sets were made, reducing them to fewer than 250 sites in any one analysis. Environmental variables were correlated with ordinations by Kendall rank correlation and trend surface analysis, and a multiple discriminant analysis of classification groups undertaken.

In addition to the above analyses of species-level data, analyses for the whole study area were carried out using generic and familial floristic data in order to examine the effectiveness of higher taxonomic levels for indicating major evolutionary and biogeographic patterns (see Dale & Clifford; del Moral & Denton 1977). Data sets for these analyses were constructed by converting species cover scores to the midpoint of the corresponding percent cover ranges, summing percent cover values across genera and families, and then reconverting the composite cover to a cover score according to the same semi-quantitative scale. Conversion of data in this manner overcame the logarithmic transformation of the cover score scale (see Currall 1987). One classification and one ordination were performed for each higher taxonomic level.

4.4 PRELIMINARY STATISTICS

Summary statistics describing the nature of the data set (Tables 4.1 to 4.3; Figure 4.1) confirm the anticipated high level of β diversity and give *a posteriori* support for the choice of analysis methods.

The full data matrix has a very high proportion of zero values (97.6 %; Table 4.1). Given that the total flora recorded is quite large (545 perennial taxa), it follows that the number of species per site (α diversity) must be low and that β diversity across the data set is high. Mean diversity **(viz. species richness)** of perennial species at sites was just 13.4, although species diversity encompassed the range 1–36 species. In addition, the median species cover score at a site was 1 (estimated projected foliage cover $\leq$ 2 %) and only 3.2 species per site on average had a cover score of 2 or greater. Species achieved 50–100 % cover at only nine sites; these were mostly seasonally- or tidally-flooded wetland monocultures. The low α diversity and low species cover together reflect the generally sparse perennial vegetation which predominates across the extensive semi-arid (mallee) portions of the study area combined with significant disturbance (loss) of woodland understorey in the more mesic parts; diversity of greater than 25 perennial species was attained in a few sites of sclerophyllous woodland and heathland in districts of relatively high annual rainfall.

The mean and range of species diversity observed here are similar to those described by van der Moezel & Bell (1989) in a climatically comparable part of south-western Western Australia. They examined 16 mallee and woodland vegetation types and found that diversity of perennial species in 0.1 ha quadrats ranged from 4 to 40 with a mean of 18.1. By contrast, the diversity observed here is lower than that described by Whittaker *et al.* (1979) in mallee vegetation in western New South Wales. They recorded 35–46 perennial species in 0.1 ha quadrats, much higher than earlier studies had found in superficially similar Mediterranean-type shrublands in North America, and noted that this followed a general trend of greater species diversity in equivalent Australia vegetation. Allowing for the observed range of site diversity values, the mean level here is not significantly different from the North American communities with which Whittaker *et al.* (1979) made their comparisons.

The frequencies of occurrence of each species in the seven regions and in the study area as a whole are given in Appendix 2 as an annotation of the species list. Figure 4.1 is a histogram of these species frequencies over the whole area. The distribution of frequencies is Poisson-type and highly skewed to the right. Although the maximum frequency was 180 sites (*Melaleuca lanceolata*), the median was only 8 sites (or 1.1 % of sites). Clearly a majority of species are uncommon to rare. As α diversity is relatively low in all but a few sites, the occurrences of these uncommon species must be well dispersed amongst many sites in the data set. By corollary, the many uncommon species contribute significantly to the floristic differences between most sites, thereby generating much of the high β diversity of the vegetation in the study area.

A glimpse of the contribution of biogeographic patterns can be seen in Table 4.2. Individual regions contain only 25.3 % to 56.9 % of the total perennial flora recorded. Many regions do not share large portions of other regions floras (Table 4.3) and thus appear to be biogeographically distinctive. This distinctiveness of regional floras lends support to the proposed region-by-region approach to floristic analysis.

Chapter 5:
VEGETATION ANALYSIS II: REGIONAL ANALYSES — RESULTS AND DISCUSSION.

5.1 PREAMBLE

Regional analyses along the lines proposed in Section 4.3 produced a large quantity of results. Only the most significant aspects of these results are presented here, due to constraints of time and space, and the need for conciseness and minimal repetition. Innumerable subtleties of vegetation distribution patterns cannot be illustrated and discussed in detail. It is intended that a much more extensive exposition of the temperate vegetation of South Australia, including discussion of the lesser aspects of the classification only outlined here, will be published elsewhere in the near future.

The classification dendrograms and ordination scatterplots from the regional analyses are presented in Figures 5.1 to 5.17.

Dendrogram groupings at the 0.65 and 0.85 dissimilarity levels were used to create a two-tiered hierarchical classification. The groups at the 0.65 level are referred to as "types" and at the 0.85 level as "complexes". Groups at both levels are named after dominant, constant and/or characteristic species in the sense of Braun-Blanquet (1932), but, because of the numerical derivation of the groups, the nomenclature of traditional sociological classification (e.g. "associations") is not followed. Two-way data table rearrangement (NTP option TWAY; Belbin *et al.* 1984) was used to detect characteristic species composition for the vegetation types and complexes.

The two cut-off levels were selected subjectively on the basis of field experience and ease of comprehension, because there is still no satisfactory method of partitioning numerical vegetation classification, despite numerous attempts using statistical methods (e.g. Bock 1985; Hill 1980; Nemec & Brinkhurst 1988; Perruchet 1983; Popma *et al.* 1983; Ratliff & Pieper 1981), and no way of identifying "homogeneous" vegetation types from dendrograms. The primary difficulties with statistical dendrogram partitioning in vegetation studies are inadequate replication of some types in field data sets and the variability of α diversity between sites and between types, both of which tend to invalidate pair-wise tests of dendrogram branches by inflating variance within branches.

Ordinations were overplotted with the classification groups in order to indicate relationships and overlap of the groups in reduced dimensionality, and to illustrate the major vegetation gradients in terms of nameable units. Environmental correlates with ordination axes are indicated by accompanying vector diagrams, which show the net magnitude and direction in two dimensions of the Kendall rank correlations of all variables that have a correlation at the $P < 0.001$ significance level with at least one of the two principal axes.

5.2 SOUTH-EAST REGION

The classification dendrogram for the 169 sites of the South-East region (Figure 5.1) shows thirteen vegetation complexes representing a total of 39 types. Complexes range in size from just one site (EUCALYPTUS DUMOSA, E. MICROCARPA and MELALEUCA HALMATURORUM complexes) to 52 sites (BANKSIA ORNATA COMPLEX). There are no completely discontinuous complexes (i.e. with fusion at a dissimilarity level of 1.0).

Complexes are briefly characterised in Table 5.1. Seven of the complexes, encompassing "sclerophyll", "savannah" and "mallee" land systems *sensu* Specht (1972), are denoted by eucalypt dominants. All complexes correspond with an association or edaphic complex described in one or more studies in the literature. However, many types within complexes do not correspond with published association descriptions. In part, this reflects differences between classification based on total floristic composition (as in these analyses) and classification by structure and overstorey dominants (as in earlier studies). Thus, *Eucalyptus baxteri – Pteridium esculentum* and *E. baxteri – Banksia ornata – P. esculentum* are recognised here as distinct types (i.e. associations), although Specht (1972) regards the difference as merely an unspecified change of (understorey) "society"; and Specht would separate the *E. ovata – Leptospermum* aff. *juniperinum* and *E. viminalis – L.* aff. *juniperinum* types, which the dendrogram (Figure 5.1) groups together on the basis of understorey uniformity. The absence of equivalents for types also reflects a previous lack of intensive study of some complexes. Thus, due to the former preoccupation with overstorey, types within vegetation dominated by *E. diversifolia* and *E. incrassata* have not previously been recognised in the South-East region.

While the complexes appear to have equivalents in existing publications (Table 5.1), the relationships between some complexes are not in agreement with earlier thought (Figure 5.1). The EUCALYPTUS CAMALDULENSIS, E. LEUCOXYLON and E. MICROCARPA complexes are traditionally considered to be closely related within the savannah land system, forming open woodland or forest over an understorey of perennial grasses and low shrubs and herbs. On the dendrogram, these groups are the most dissimilar from one another and from all other complexes. The failure of the numerical approach (based on native perennial species only) to show closer relationships between the three complexes is a consequence of there no longer being a natural unifying perennial understorey in savannah communities in the South-East (Crocker 1944; Jessup 1946; Specht 1972). It has been replaced by introduced annual pasture grasses, clovers and medics which have been intentionally sown for stock grazing or have invaded through the agency of grazing, tilling and timber felling. Savannah woodland communities, such as those represented by the above three complexes, now appear most often as scattered clumps of trees over exotic pasture and close phytosociological examination of them as relatively inviolate communities is no longer possible.

The other major conflict with published accounts of South-East vegetation concerns the GAHNIA TRIFIDA/FILUM, MELALEUCA BREVIFOLIA and M. HALMATURORUM complexes which occur in seasonally-inundated interdune corridors of the Upper (northern) South-East. Crocker (1944) placed the "*M. gibbosa [M. brevifolia]* association" in a *Xanthorrhoea australis – Hakea rostrata* wet heathland complex and the "*Gahnia trifida – Cladium [Gahnia] filum* association" in an edaphic complex of its own. Likewise, Specht (1972) combined *M. brevifolia* communities with a wet heathland alliance in the Lower South-East, but he included *G. trifida/filum* tussock grasslands as an association in the savannah land systems for reasons of supposed structural similarity to savannah woodlands. Figure 5.1 denies the interpretations of both Crocker and Specht on the grounds of floristic composition and environmental pattern. The three complexes are floristically interrelated, but clearly distinct from heathlands and savannahs, and represent a single environmental gradient within interdune corridors. M. HALMATURORUM seems to predominate on highly saline soils in infrequently inundated areas, G. TRIFIDA/FILUM on less saline soils in the most often inundated areas where rainfall exceeds 600 mm p.a. and M. BREVIFOLIA on the same where rainfall is less than 600 mm p.a. This environmental relation is supported by the relative positions of the three complexes on the ordination (Figure 5.2; see below). Mosaic mixtures of all three complexes are common at around 550 – 600 mm rainfall.

A further minor point is the position on the dendrogram of the single site of the EUCALYPTUS DUMOSA COMPLEX amongst the seasonally-flooded lowland complexes. This placement is anomalous. It shares few species with these groups (or any others) and occurs neither on saline soils nor where there is seasonal flooding. The clustering can only be an artifact of the very low α diversity of all of these complexes.

The main vegetation gradients and the relative positions of the complexes along them are illustrated by the ordination of the full regional data set in Figure 5.2. The ordination in two dimensions presents a much better picture of the floristic relationships between groups (and their presumed environmental relationships) than does the dendrogram. The dendrogram is restricted to a single effective dimension in which to indicate relationships and, furthermore, the averaging algorithm of the fusion method employed (UPGMA) obscures important pair-wise interactions of lower level groupings when calculating fusions at high levels. For example, the dendrogram bifurcation between the branch comprising the EUCALYPTUS BAXTERI – PTERIDIUM ESCULENTUM and JUNCUS PALLIDUS complexes and the branch comprising the BANKSIA ORNATA – ALLOCASUARINA PUSILLA, E. INCRASSATA and E. DIVERSIFOLIA complexes does not indicate which cross-branch pair of complexes is most closely related. The ordination makes it plain that the gradation between the E. BAXTERI – P. ESCULENTUM and B. ORNATA – A. PUSILLA complexes links these two major branches. A more startling illustration is provided by the E. BAXTERI – P. ESCULENTUM and E. CAMALDULENSIS complexes, which are widely separated on the dendrogram (Figure 5.1) but shown by the ordination to be adjacent along a habitat gradient (Figure 5.2). It is because of these types of relationships revealed by ordination that a dissimilarity level of 0.85 was chosen to define complexes, rather than some higher level on the dendrogram.

There are few disjunctions or areas of reduced density of data points between complexes adjacent in the ordination space. In addition, a number of complex pairs overlap or interdigitate when projected from the multidimensional vegetation space onto the two-dimensional ordination. Both observations suggest that floristic composition is highly continuous from complex to complex and that the classification is probably subject to a degree of arbitrariness in its groupings i.e. types loosely bound to complexes are likely to be intermediary to other complexes. Thus the complexes are simply nodes of a multidimensional vegetation continuum (as in Noy-Meir 1971).

However continuity is artificially heightened by the low dimensionality of the ordination as presented. Distortion caused by the reduction of a data set of high β diversity is indicated by compression/elongation of the loci of some complexes into oblong or lunate shapes ("sausages") and by placement near one another of complexes which are only weakly related floristically. This distortion is most severe in complexes with low mean α diversity (1 – 5 perennial species at each site). The EUCALYPTUS CAMALDULENSIS and E. LEUCOXYLON complexes are examples of locus elongation. Both have low α diversity, although diversity is variable due to varying levels of understorey disturbance at sites. This variability of diversity is the most likely cause of the locus distortion. The relative position of the E. LEUCOXYLON and E. MICROCARPA complexes near the GAHNIA TRIFIDA/FILUM and MELALEUCA BREVIFOLIA complexes is an example of spurious complex placement. These pairs of complexes, not closely related according to the dendrogram (Figure 5.1), are in fact separated along the third DCA axis (not illustrated) which extends the approximately triangular array of sites in two dimensions into a tetrahedron in three dimensions, with the fourth vertex ("peak") of the tetrahedron in the upper centre of the ordination.

Because of their strong contribution to the definition of the principal axes, complexes at the bottom of the dendrogram (including the five mentioned immediately above) cause distortion and suppression of sensible gradational patterns between the more closely related complexes on the main branch at the top of the dendrogram. Partial ordination of the first six complexes (Figure 5.3) clarifies these patterns. Their interactions are fairly simple (i.e. there is minimal interdigitation of complexes and a third axis is not necessary to separate them) although still suggestive of continuity, even at the level of types.

Despite the limitations on interpretation imposed by gradient distortion, the ordinations still provide a clear picture of the environmental control of vegetation in the South-East. The significant environmental correlates with the full regional ordination (Figure 5.2 inset) form two approximately perpendicular sets which run diagonally across the ordination: (i) rainfall; and (ii) soils, along with annual flooding, altitude and distance from the coast (all autocorrelated). Mean annual rainfall increases from upper left to lower right, from the EUCALYPTUS INCRASSATA – MELALEUCA UNCINATA mallee broombush complex, via the E. BAXTERI – PTERIDIUM ESCULENTUM sclerophyll woodlands, to the

E. CAMALDULENSIS savannah woodland complex. The composite edaphic gradient forming the other diagonal runs from acidic, deep sandy soils typical of BANKSIA ORNATA – ALLOCASUARINA PUSILLA heathlands and E. BAXTERI – P. ESCULENTUM woodlands to the alkaline, usually calcareous and/or saline, heavy-textured soils of E. DUMOSA mallee, E. LEUCOXYLON savannah woodlands, and M. BREVIFOLIA and M. HALMATURORUM wetlands. The floristic continuity within and between complexes is thus derived from gradual changes in rainfall regime and soil type across the region.

Environmental correlation is similar for the partial ordination in Figure 5.3, with the omission of annual flooding which is characteristic of the excluded GAHNIA TRIFIDA/FILUM, MELALEUCA BREVIFOLIA and M. HALMATURORUM complexes only. The diagonal gradients of rainfall and soils are even more obviously perpendicular, possibly due to the reduced level of gradient distortion relative to the full ordination.

5.3 MURRAY MALLEE REGION

Classification of the 132 sites in the Murraylands produced 30 vegetation types in eight complexes (Figure 5.4). These complexes are characterised in Table 5.2 and range in size from one site (CALLITRIS PREISSII and EUCALYPTUS LARGIFLORENS) to 56 sites (E. OLEOSA – E. GRACILIS). The largest type, *E. oleosa – E. gracilis – Sclerolaena diacantha*, contains 34 sites or 25.8 % of the regional data set and, occurring on calcareous loams of the very widely distributed Woorinen Formation, can be considered to be the vegetation type most characteristic of the Murray Mallee region in its natural state.

β diversity, as measured in terms of the number of complexes present, is lower in this region than in the South-East, although the two regions are comparable in area. The almost uniform, scarcely undulating nature of the mostly aeolian landscape (see Figure 2.5), the small number of major soil types (Figure 2.6), and the short rainfall gradient across the region (Figure 2.10) account for the relatively low β diversity. By contrast, the numbers of types in the two regions are not so different. Internal diversity of complexes in response to more subtle habitat gradients is as high in the Murraylands as in the South-East, if not higher.

No complex arises on the dendrogram from a branch at the 100 % dissimilarity level and hence there is not complete discontinuity in the data set. However, the EUCALYPTUS CAMALDULENSIS, E. LARGIFLORENS and HALOSARCIA HALOCNEMOIDES complexes are separated from the other five complexes at a very high level ($d = 0.990$), indicating a disjunction between these two groups of complexes. This floristic disjunction is confirmed by ordination of the complete regional data set (Figure 5.5; see below) and corresponds with a primary division of the Murraylands environment. The E. CAMALDULENSIS, E. LARGIFLORENS and H. HALOCNEMOIDES complexes have distributions restricted to, or at least centred upon, the floodplain within the limestone gorge of the Murray River where soils are alluvial clays, often saline, and subject to periodic flooding (Table 5.2). The remaining complexes occur only on the aeolian plains outside of the Murray gorge, on well-drained, calcareous or siliceous sands and loams.

Until very recently, there had been no detailed study of the vegetation along the Murray River in South Australia and thus no equivalent association or alliance in the published literature for the EUCALYPTUS CAMALDULENSIS, E. LARGIFLORENS or HALOSARCIA HALOCNEMOIDES complexes. Specht (1972) made cursory reference to the eucalypt woodlands of the Murray floodplain (e.g. p.130 and p.202) and included them within the "savannah land systems". F. van der Sommen (in National Environmental Consultancy 1988) made some remarks on the distribution of four predominant species (including *E. camaldulensis* and *E. largiflorens*) in relation to flooding frequency and salinity tolerance, but refrained from definition of associations. However, as part of a larger ecological assessment of the River Murray, Margules & Partners *et al.* (1990) have defined 14 associations of Murray riparian vegetation in South Australia, loosely grouped into two ecological zones. The associations are of approximately the same hierarchical status as the types defined on the dendrogram, although the greater sampling density in the study of Margules & Partners *et al.* (1990) has lead to detection of more associations than the four types found here. Their zones (a Red Gum Zone, *E. camaldulensis*; and a Black Box Zone, *E. largiflorens*) are similar to the complexes defined here, with the exception that the H. HALOCNEMOIDES COMPLEX is incorporated into the Black Box Zone. The zonal combination of these two complexes is based on a habitat rationale of shared low frequency of annual flooding, similar depth to the (saline) water table, and mosaic distribution patterns.

As the broad-scale sampling strategy adopted for this survey resulted in only five sites within the Murray gorge[11], little information beyond the identification of the three complexes can be proffered here about the ecology of fluviatile vegetation along the Murray. There are too few data for any statistical treatment of the distribution of the complexes with respect to environmental correlates and so visual observations must suffice (see Table 5.2). Woodlands of the EUCALYPTUS CAMALDULENSIS COMPLEX occur on low salinity soils at, or just above, the seasonal mean water level of the river i.e. in areas regularly flooded every year. The duration of annual flooding appears to differentiate the environments of the two types in this complex: *Typha domingensis* in almost permanently inundated sites and *Muehlenbeckia cunninghamii* in sites flooded during spring only. E. LARGIFLORENS COMPLEX woodlands occur on soils of low-to-medium salinity, well above the mean water level and distant from the river i.e. in areas inundated only during years of exceptionally high flood levels. The HALOSARCIA HALOCNEMOIDES COMPLEX of chenopod samphire communities occurs on highly saline soils throughout the Murray floodplain regardless of flooding frequency, and also in saltpans beyond the river's gorge. Despite the new classification of Margules & Partners *et al.* (1990), further phytosociological studies of the Murray floodplain are needed to advance knowledge of these

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[11] Note that two sites classified in the HALOSARCIA HALOCNEMOIDES COMPLEX occurred on saltpans outside of the modern floodplain of the Murray River, although still within the general vicinity of the river.

complexes beyond the generalisations given here and to detail changing species composition along gradients of flooding frequency, depth to subterranean water table and soil salinity.

Four of the five complexes which encompass all other recorded vegetation outside of the Murray floodplain do not have unequivocal literature equivalents. For example, whilst the single site of the CALLITRIS PREISSII COMPLEX is dominated by *C. preissii, Eucalyptus odorata* is also present, giving to that location a character intermediate between the *C. preissii* and *E. odorata* savannah woodland associations described by Specht (1972) for areas east and west of this site respectively. As these areas are now largely cleared for agriculture, it is doubtful whether a more intensive sampling strategy (one with a greater theoretical probability of sampling these types) could lead to an improved determination of this site's affinities. The complex named here as "MAIREANA SEDIFOLIA – CASSIA NEMOPHILA" is a further example of difficulty in comparing the multivariate floristic analyses herein with established floristic-physiognomic classification. For purely geographic reasons, it should correspond with the chenopod shrubland communities mapped as *Myoporum platycarpum – Kochia [Maireana] sedifolia* by Jessup (1948). However, floristic composition in the complex is highly variable and there is no species common to all three sites, including *M. platycarpum* and *M. sedifolia.* The only unifying feature of these sites is the absence of overstorey eucalypts. Thus the group may be regarded as an anomaly or "artifact" of the numerical methods. The affinities of this group may be better elucidated by extension of the survey area to the north, thereby including more sites of arid chenopod shrubland communities to which the complex seems most similar.

The problems of finding literature equivalents for the EUCALYPTUS OLEOSA – E. GRACILIS and E. SOCIALIS – E. DUMOSA complexes stem from incorrect or misapplied nomenclature of dominant eucalypt species. Specht (1972), the only previous major study of all parts of the Murray Mallee consistently misnamed *E. oleosa* as *E. socialis*, thereby obscuring any differences of ecological response and distribution of the two species. The E. OLEOSA – E. GRACILIS COMPLEX would appear to correspond with his *E. socialis [E. oleosa] – E. dumosa – E. gracilis* alliance with "sclerophyll-semi-succulent" understorey, and the E. SOCIALIS – E. DUMOSA COMPLEX with his *E. conglobata – E. dumosa* alliance. However, as Specht combines the two alliances for mapping purposes, distinction of them by nature of their respective habitats or distributional areas is not possible. The classification in Figure 5.4 provides the first appreciation and resolution of the past confusion.

It should also be noted that almost all of the 22 types in the three large mallee complexes do not have any published equivalents simply due to the dearth of phytosociological studies sufficiently detailed to recognise associations at this level in the Murray Mallee. Detailed characterisation of these types will be covered elsewhere in the near future.

The main feature of the ordination of the full regional data set (Figure 5.5) is the separation of the three riverine complexes (EUCALYPTUS CAMALDULENSIS, E. LARGIFLORENS and HALOSARCIA HALOCNEMOIDES) from one another and from the other five complexes. These disjunctions dominate both axes 1 and 2, effecting severe compression of the five non-riverine complexes in two dimensions. Floristic patterns amongst the E. OLEOSA – E. GRACILIS, E. SOCIALIS – E. DUMOSA and E. INCRASSATA – MELALEUCA UNCINATA mallee complexes (121 sites) are reduced to a single, highly continuous and almost linear axis, along which types cannot be distinguished. A better picture of the relationships of these three complexes and their constituent types is given by the partial ordination in Figure 5.6. In marked contrast to the full ordination, partial ordination of these complexes is (with the exception of an outlier in the upper left corner) approximately diamond-shaped or toroidal. This form is correlated well with environmental variables (see below). Even in this partial ordination space, there is interdigitation of types (and complexes) and elongate distortion of many types which prevents clear presentation of their loci on the plot. This suggests that the floristics of the mallee complexes are not well represented by an ordination scattergram in just two dimensions, because of the presence of further, less significant gradients within each complex individually.

Due to the monoclinal nature of the full ordination, all significant environmental variables are correlated in approximately the same direction, nearly parallel to the first ordination axis (Figure 5.5 inset). There are, however, two distinct sets of correlates which should not be confused: (i) those correlated over the whole ordination, including the Murray floodplain complexes; and (ii) those strictly correlated over only that portion occupied by the mallee complexes, but which are statistically significant over the whole ordination due to the high proportion (and therefore weighting) of sites in these three complexes. Soil texture and soil salinity belong to the first group. The soils grade from sands in the EUCALYPTUS INCRASSATA – MELALEUCA UNCINATA COMPLEX, to loams in the E. OLEOSA – E. GRACILIS COMPLEX, and finally to heavy clays in the floodplain complexes. Salinity increases along the same gradient. One might expect frequency of flooding to follow this gradient, but it is prevented from attaining statistical significance by the very low proportion of sometimes inundated sites in the data set. Rainfall, altitude, longitude, soil depth, pH, carbonates and presence of calcrete nodules belong to the second group of variables relevant to the mallee complexes only. Their correlations with floristic gradients of the Murray Mallee region are better illustrated by the partial ordination (Figure 5.6 inset). There is a composite edaphic gradient running left to right, from calcareous alkaline loams with calcrete nodules in the E. OLEOSA – E. GRACILIS COMPLEX to acidic or neutral, carbonate-free siliceous sands in the E. INCRASSATA – M. UNCINATA COMPLEX. The other significant gradient, annual rainfall, is oblique to the soil gradient and increases from the E. OLEOSA – E. GRACILIS COMPLEX towards both the E. SOCIALIS – E. DUMOSA and E. INCRASSATA – M. UNCINATA complexes.

The toroidal shape of the partial ordination results from there being two floristic and environmental "bridges" between the EUCALYPTUS OLEOSA – E. GRACILIS and E. INCRASSATA – MELALEUCA UNCINATA complexes. The lower bridge indicates (from left to right) a simple gradient of gradually increasing depth of soil over calcrete nodules, decreasing soil carbonates and pH, and increasing sandiness of soils. This is the environmental sequence from interdune swales to dune crests in the most arid parts of the region. The overstorey changes from *E. oleosa* to *E. cyanophylla*, then to *E. socialis, E. foecunda* and *E. incrassata*, with a parallel understorey change of decreasing occurrence of chenopods (e.g. *Maireana erioclada* and *Sclerolaena diacantha*) and increasing density of *Triodia irritans.* The upper bridge, via the E. SOCIALIS – E. DUMOSA COMPLEX, indicates a two-step transition between geological formations in the relatively mesic parts of the region: first, increasing consolidation of limestone from nodular calcrete to sheet calcrete and decreasing depth of soil over calcrete, followed by increasing depth of siliceous sands on top of the calcareous formations. The parallel floristic changes are from *E. oleosa* and *E. gracilis* with a chenopod understorey; to *E. gracilis* and *E. socialis* with a barren understorey; then *E. socialis* and *E. dumosa* with scattered shrubs of *M. uncinata*; finally leading to *E. socialis, E. foecunda* and *E. incrassata* with dense *M. uncinata.* There are few intermediates between these bridges (hence the toroidal form of the ordination) due to the wide north-south geographical separation of the two gradients which they represent.

5.4 KANGAROO ISLAND REGION

Kangaroo Island is the smallest of the survey regions and has the smallest data set (24 sites). The classification (Figure 5.7) groups the sites into only three complexes and eight types, which are characterised in Table 5.3. Each complex is here named after one or two eucalypt species occurring frequently in its overstorey (*Eucalyptus baxteri* ± *E. remota, E. cneorifolia*, and *E. diversifolia*), although the complexes are unified primarily by understorey composition: calciphobic heathland species, broombush (*Melaleuca uncinata*) ± *Allocasuarina* spp., and calciphilic shrub species respectively. A number of regional endemic species are common in the complexes and contribute to their delineation (Table 5.3).

The three complexes correspond with the three groups of plant associations which Bauer (1959) identified with particular soil types on Kangaroo Island: EUCALYPTUS BAXTERI – E. REMOTA on podsolised soils; E. CNEORIFOLIA on solonised soils; and E. DIVERSIFOLIA on calcareous soils. However, as in the South-East region, the floristic types do not correspond closely with the individual associations defined by Bauer (1959) or by any other previous regional study (i.e. Baldwin & Crocker 1941; Northcote & Tucker 1948) due to the earlier emphasis on structural formation and/or dominant species of the overstorey rather than on total floristic composition. For example, the *Banksia ornata – Leptospermum myrsinoides* Type heathlands with scattered trees of *E. baxteri* or *E. remota* (occurring on western Kangaroo Island) are included within the *E. remota* sclerophyll mallee association of Bauer rather than as a heathland association in its own right. The problem of deciding the affinities of the *E. cosmophylla – Allocasuarina muelleriana* Type further illustrates the disparity of overstorey and understorey patterns on Kangaroo Island and the differences between classification by structural dominant versus that by overall floristics. Bauer (1959) placed this association in the podsolised soils group due to the dominance of *E. cosmophylla* (which occurs frequently on podsolised soils elsewhere), but notes that it may be an intermediate with the solonised soils groups due to the presence of *A. muelleriana* and *Melaleuca uncinata* in the understorey, and thus maps zones of admixture of the two soil groups. Based upon total floristic composition, the classification in Figure 5.7 places this type within the E. CNEORIFOLIA COMPLEX (= solonised soils group) because of understorey similarities, although the regional ordination (Figure 5.8; see below) shows that the type tends towards the E. BAXTERI – E. REMOTA COMPLEX. Both interpretations may be considered "correct", providing that the gradational effect is appreciated.

A full regional ordination (Figure 5.8) presents the main floristic patterns on Kangaroo Island as almost unidimensional. This monocline, from the EUCALYPTUS BAXTERI – E. REMOTA COMPLEX to the E. DIVERSIFOLIA COMPLEX is correlated with a combination climatic-edaphic gradient of decreasing rainfall, increasing soil pH, increasing presence of consolidated limestone and concomitant decreasing depth of soil (Figure 5.8 inset). As the E. BAXTERI – E. REMOTA COMPLEX occurs only on the western two-thirds of the island and the E. CNEORIFOLIA and E. DIVERSIFOLIA complexes occur chiefly on the eastern half, the cline runs (at a very broad scale) east-west along the length of Kangaroo Island and thus is positively correlated with longitude.

There is a noteworthy disjunction on the ordination which separates the E. DIVERSIFOLIA COMPLEX from the others. This disjunction corresponds with the primary split of the dendrogram (Figure 5.7) and is simply due to major differences of soil characteristics between the areas of Bridgewater Formation consolidated limestone (shallow calcareous terra rossa soils), on which the E. DIVERSIFOLIA COMPLEX occurs exclusively, and the remainder of the island (deep non-calcareous soils). By contrast, variation within and between the E. BAXTERI – E. REMOTA and E. CNEORIFOLIA complexes is continuous, reflecting the gradual changes of climatic and edaphic conditions over most of Kangaroo Island. The intermediary floristics of the *E. cosmophylla – Allocasuarina muelleriana* Type (see above) demonstrates an intermediary position between complexes in terms of location, rainfall and soil type.

5.5 SOUTHERN MOUNT LOFTY RANGES REGION

There are eleven complexes and a total of 30 vegetation types in the classification for the Southern Mt Lofty Ranges region (Figure 5.8; Table 5.4). This number of classificatory units implies that the level of β diversity per unit area is higher than in the South-East region, since the Southern Mt Lofty Ranges is less than half the area of the South-East and has less than half the number of sites in its data set. The diversity arises from the steep habitat gradients and environmental heterogeneity induced by the topography and geological patterns of the Mt Lofty Ranges.

With two exceptions, the floristic complexes have well-defined equivalents in existing literature. The two groups without close equivalents are the EUCALYPTUS OLEOSA – E. GRACILIS and E. SOCIALIS MALLEE complexes. Specht (1972), the only treatment of mallee vegetation throughout the region, included the latter in the former because of the taxonomic confusion surrounding *E. oleosa* and *E. socialis* at that time (as discussed above in Section 5.3).

There have been a number of earlier, excellent, non-quantitative phytosociological studies in the vicinity of the city of Adelaide, hence the high level of concordance of complexes with vegetation alliances or associations described in the literature. Notable among the earlier studies are the works of Adamson & Osborn (1924) and Specht & Perry (1948), which provide detailed classifications of the sclerophyll and savannah woodlands in the southern Mt Lofty Ranges and relate the distributions of types to rainfall, soils and parent materials. Indeed this study can scarcely provide an improvement upon these studies due to two factors:

1. the survey strategy adopted is not sufficiently dense to sample all vegetation forms adequately in an area of such β diversity; and
2. there has been extensive disruptive clearance of the native vegetation in the region since 1948.

At best, the analyses here will serve to link the preceding detailed classifications and habitat descriptions of Adelaide Hills woodlands into a more general classificatory framework for the entire study area.

The dendrogram (Figure 5.9) shows two discontinuities which separate the AVICENNIA MARINA mangrove complex and HALOSARCIA HALOCNEMOIDES samphire complex from one another and from all other groups. They have been excluded from the regional ordinations below, since they must produce trivial, binary first and second principal axes equivalent to the discontinuities in the classification. These two distinctive complexes occur on the very saline, coastal soils of the St Kilda Formation along the north-eastern shores of the Gulf St Vincent, below and above mean high tide mark respectively.

Specht (1972) considered that mangrove and samphire communities were merely socies of a "coastal succession". The analyses here elevate them to the higher status of complex. The implication is that the coastal cline of decreasing frequency of tidal inundation, decreasing duration of soil saturation and decreasing soil salinity should be interpreted as an environmental gradient like any other climatic or edaphic cline in South Australia, rather than as a temporal/spatial "succession" with some climax community sensu Clements (1916, 1920). All environmental conditions in the study area are believed to have changed in the past (Crocker & Wood 1947; Dodson 1974), and will continue to change in the future, due to fluctuating climate and evolving surface geology. Vegetation distribution patterns are modified accordingly. This point is made clearly by Cooper (1926), but the residues of the climax theory linger on. The "coastal succession" is nothing more than an environmental gradient and its suite of correlated vegetation types subject to (reversible) spatial displacement through climatic shifts.

There is also a disjunction in the classification between three mallee (and related) complexes (EUCALYPTUS GRACILIS – E. OLEOSA, E. SOCIALIS and CALLITRIS PREISSII) and the six sclerophyll and savannah woodland complexes. This split is strongly correlated with the major topographic division of the area: mallee on the plains to the east and west of the Mt Lofty Ranges block (rainfall < 500 mm p.a.); and woodlands on the ranges and hills (rainfall > 500 mm p.a.).

The mallee complexes each have a distinctive distribution pattern: E. GRACILIS – E. OLEOSA occurs chiefly to the east of the Mt Lofty Ranges and E. SOCIALIS to the west. It is unclear whether this geographical separation merely reflects a predominance of slightly sandier soils on the western plains. Certainly communities containing *E. socialis* were found more often on siliceous to weakly calcareous sands in the Murray Mallee, and *E. oleosa* - or *E. gracilis* - dominated communities on the calcareous loams of the Loveday soils there (see Section 5.3). However, not all *E. socialis*-dominated sites in the Southern Mt Lofty Ranges were on sandy soils (e.g. *E. socialis – E. dumosa – Heterodendrum oleifolium* Type) and it is possible that a historical / biogeographic factor (as in Crocker & Wood 1947; see also Burbidge 1960) is at least partly responsible for the effect. The pattern has not been reported before, no doubt due to the past taxonomic difficulties with *E. socialis* and *E. oleosa.*

As in the analyses for the South-East region, the savannah woodland land systems of Specht (1972), here comprising the EUCALYPTUS CAMALDULENSIS, E. LEUCOXYLON and E. ODORATA complexes, do not form a unified single-stemmed group on the dendrogram and most probably for the same reason as in the South-East i.e. lack in almost all relevant sites of most elements of a natural understorey dominated by perennial grasses by which savannah woodland affinities might be established.

The position of the MELALEUCA UNCINATA broombush complex in the dendrogram is also contrary to traditional treatments. "Broombush" and "mallee broombush" communities are usually placed with the main body of mallee vegetation (Wood 1929, 1937; Specht 1972). It is presumably because the M. UNCINATA COMPLEX shares a number of sclerophyllous undershrub species (e.g. *Astroloma conostephioides, A. humifusum, Correa reflexa, Hibbertia riparia*) with the EUCALYPTUS OBLIQUA – XANTHORRHOEA SEMIPLANA COMPLEX that the former complex is joined to the latter rather than to the E. GRACILIS – E. OLEOSA or E. SOCIALIS complexes with which it shares far fewer species.

Ordination of the regional data set (excepting the discontinuous mangrove and samphire complexes) in Figure 5.10 resolves relationships between complexes and shows the higher fusion levels on the dendrogram to be misleading, as was the case in the South-East analyses. Disjunction between the combined sclerophyll / savannah woodland complexes and the mallee complexes is supported, but the MELALEUCA UNCINATA COMPLEX occupies an intermediate position at the top of the disjunction. M. UNCINATA acts as an indirect floristic link between the two main groups of complexes and is loosely associated with both.

As in the classification, the savannah woodland complexes show only weak affinities with one another and instead are radially arrayed around the EUCALYPTUS OBLIQUA – XANTHORRHOEA SEMIPLANA COMPLEX along what appears to be a rainfall gradient: E. ODORATA to E. LEUCOXYLON to

E. CAMALDULENSIS with increasing mean annual rainfall. This sequence agrees with the habitat observations of these species by Adamson & Osborn (1924), Specht & Perry (1948) and Todd (1965).

The hitherto unmentioned "COMPLEX C" presents interpretational problems akin to those of the MAIREANA SEDIFOLIA – CASSIA NEMOPHILA COMPLEX in the Murray Mallee. COMPLEX C is dominated by either *Eucalyptus fasciculosa* or *Allocasuarina verticillata*, but is poorly characterised by total floristic composition. The ordination shows it to be part of a gradation between types of the E. OBLIQUA – XANTHORRHOEA SEMIPLANA and MELALEUCA UNCINATA complexes. The three complexes all contain at least one type with *E. fasciculosa* predominant and share a number of heathy undershrub species (see Table 5.4). The relationships of these complexes is at odds with earlier literature, since Jessup (1946) wrote of *E. fasciculosa* and *A. verticillata* occupying intermediate positions along rainfall and soils gradients between *E. obliqua* – *E. baxteri* sclerophyll woodlands and *E. leucoxylon* and *E. odorata* savannah woodlands. However, the question of the nature and affinities of COMPLEX C must now remain in an indeterminate state since localities in the south-eastern portions of the region which might permit elucidation of the gradation between all these complexes have been almost completely cleared.

The significant correlates with the ordination axes summarise the environmental control of the distribution of the complexes (Figure 5.10 inset). The first axis is strongly correlated with annual rainfall and a suite of soil variables describing pH and carbonate levels. The EUCALYPTUS CAMALDULENSIS and E. OBLIQUA – XANTHORRHOEA SEMIPLANA complexes on acidic clays in the wettest districts of the region and the E. GRACILIS – E. OLEOSA COMPLEX on calcareous loams represent the extremes of the gradient. The second axis is correlated with soil texture, calcrete and sandstone geologies. Sandy soils and calcrete distinguish the environments of the MELALEUCA UNCINATA and CALLITRIS PREISSII complexes from all others. Quartzitic sandstones with loamy soils are typical of areas of E. LEUCOXYLON and E. ODORATA complexes. An altitudinal gradient runs diagonally across the ordination and illustrates the topographic separation of the sclerophyll and savannah systems predominantly on the Mt Lofty Ranges block from the mallee and broombush groups on the surrounding plains.

5.6 NORTHERN MOUNT LOFTY RANGES REGION

The northern Mt Lofty Ranges and Yorke Peninsula (Section 5.7 below), are the most extensively cleared and disturbed parts of the study area. In the Northern Mt Lofty Ranges region, a number of the cells of the original survey grid were entirely devoid of vegetation remnants and were not sampled. The final positions of many other sites were so distant from their respective grid locations as to make the distribution of sites in the region highly irregular (see Figure 3.3), and to throw *a priori* doubt upon the likely worth of the analyses undertaken. However, high β diversity — higher than found in the Southern Mt Lofty Ranges and likewise due to great variation in topography, geology and soils — compensates for the deficiencies of sampling and leads to relatively clear and interpretable results.

Fourteen complexes and 31 types were defined by the classification (Figure 5.11). Not all complexes are equivalent to previously described alliances or associations (Table 5.5). What is here termed the MAIREANA PYRAMIDATA COMPLEX was subsumed under *Atriplex vesicaria* and *M. sedifolia* arid zone shrubland associations by Specht (1972). His "Flinders Ranges Complex", of almost entirely unspecified composition, probably included the XANTHORRHOEA QUADRANGULATA COMPLEX (nowhere recognised previously) and the CASSIA ARTEMISIOIDES COMPLEX (which is undoubtedly the same as the *Cassia* – *Dodonaea* association noted on hilly outcrops in the southern arid zone by Wood 1937) amongst a number of other vegetation types to be found beyond the northern limits of this region. For other complexes, equivalents could only be found by extrapolation of the literature for neighbouring regions. Savannah woodlands dominated by *Eucalyptus porosa* have not been recorded before in the

Northern Mt Lofty Ranges, but are mapped on Yorke Peninsula to the south-west by Specht (1972). The E. LEUCOXYLON and E. ODORATA complexes, as described by Boomsma (1946) and Todd (1965), are similar to their namesakes in the classification of the Southern Mt lofty Ranges above.

It is interesting to compare the EUCALYPTUS SOCIALIS – E. GRACILIS – E. OLEOSA COMPLEX with mallee groups of the Southern Mt Lofty Ranges (Section 5.5). In the Southern Mt Lofty Ranges these mallees were split into two groups with distinctive distribution patterns: an E. GRACILIS – E. OLEOSA COMPLEX mainly east of the ranges on Woorinen Formation loamy soils with nodular calcrete, and an E. SOCIALIS COMPLEX mainly west of the ranges on sandier soils with lower carbonate levels. These two groups are combined into a single group in the Northern Mt Lofty Ranges, but the distinction between species distributions remains. Types in which *E. oleosa* (or *E. brachycalyx*) dominates occur on Woorinen Formation soils east of the range or in the far south-west corner where the region abuts Yorke Peninsula. Types in which *E. socialis* dominates occurs on the various low carbonate soils on the ranges or immediately to their west. The habitat distinction is more clearly edaphic than in the Southern Mt Lofty Ranges, but some historical control is possible. *E. gracilis* is found in all types. Whether the classification identifies one or two such mallee complexes would seem to depend on the number of suitable intermediate types and their effect on weighting of group centroids during the fusion process.

Three complexes are entirely discontinuous from the rest of the classification and from one another: AVICENNIA MARINA, EUCALYPTUS CAMALDULENSIS and HALOSARCIA HALOCNEMOIDES (Figure 5.11). The A. MARINA and H. HALOCNEMOIDES complexes occupy the same coastal habitats as in the Southern Mt Lofty Ranges region. In contrast, the E. CAMALDULENSIS COMPLEX experiences a change of habitat from one region to the other. It is restricted to creeklines and floodplains in the Northern Mt Lofty Ranges, whereas it occurs as a generalist savannah woodland community on more fertile soils in the southern ranges and in the South-East region where annual rainfall is significantly higher.

Amongst the other eleven complexes there are no strong disjunctions. Ordination shows that their distributions are controlled largely by a single rainfall-soils gradient which nearly parallels the first axis (Figure 5.12). With decreasing rainfall, increasing soil pH and increasing soil carbonates, EUCALYPTUS CLADOCALYX and E. MACRORHYNCHA dry sclerophyll woodlands and E. LEUCOXYLON savannah woodlands are successively supplanted by: low savannah woodlands of E. ODORATA, E. POROSA or CALLITRIS COLUMELLARIS; E. SOCIALIS – E. GRACILIS – E. OLEOSA mallee; and finally CASUARINA CRISTATA – MAIREANA SEDIFOLIA and M. PYRAMIDATA chenopod shrublands at the southern limits of the arid land systems (Diels 1906; Specht 1972). The CASSIA ARTEMISIOIDES and XANTHORRHOEA QUADRANGULATA complexes appear not to fit this pattern. On the ordination they lie adjacent to the E. CLADOCALYX COMPLEX due to their many understorey species in common, yet they occur in areas of rather lower rainfall than does E. CLADOCALYX. It is very likely that all three complexes are relicts of a sclerophyllous vegetation type which was more widespread some time during the recent past when climatic conditions were more mesic (Crocker & Wood 1947), and whose component species have retreated to the ridgetops of outcropping sandstone in the southern Flinders Ranges in different combinations as the climate became more arid. Walter & Stadelmann (1974) have observed that rocky soils afford moderation of otherwise xeric soil water conditions and thus it is an easy step to envisage rocky outcrops as relict sites in arid areas. The other anomaly along the ordination's first axis is the outlying site of the E. SOCIALIS – GRACILIS – OLEOSA COMPLEX in the upper left corner. This site constitutes the *Atriplex vesicaria – Disphyma crassifolium* Type which differs from all other types in the complex by the absence of mallee eucalypts. It occurs on the plains of saline heavy clays around Pt Pirie, intermediate between the main body of mallee types with predominantly chenopod understoreys (e.g. *A. vesicaria* and *Maireana erioclada*) and the HALOSARCIA HALOCNEMOIDES samphires on the coastal flats (which are excluded from the ordination due to their discontinuity).

The second ordination axis achieves little more than the separation of the EUCALYPTUS POROSA COMPLEX from the E. ODORATA and CALLITRIS COLUMELLARIS complexes. There are no significant environmental correlates with this axis and it cannot be easily interpreted. It may be an irreconcilable artifact stemming from the absence of understorey by which to compare these savannah complexes (as discussed for other regions). Alternatively it may be a more subtle biogeographic pattern since *E. porosa* is confined to the north-west quadrant of the region, *C. columellaris* to the northern extremities and *E. odorata* to the south and west.

5.7 YORKE PENINSULA REGION

Yorke Peninsula is the second smallest of the regions examined and has a long history of agricultural development (see Meinig 1962). Its vegetation has been so extensively cleared for cropping and grazing that five cells of the region's sampling grid were unable to furnish suitable sites, and 10 sites of the 33 sampled were unmistakably disturbed and had reduced understorey diversity. Consequently the analyses of the vegetation of Yorke Peninsula proved to be the least satisfactory of all seven regions and presented the greatest interpretive difficulties. Interpretation was confounded by:

1. an insufficient sampling density to adequately delineate less common vegetation groups;
2. such a high degree of vegetation clearance that it was impossible even in the field to subjectively/visually deduce geobotanic relationships between some vegetation types; and
3. an inability to determine whether some sites retained a semblance of natural cover, albeit disturbed and species-poor, or whether they merely represented disturbance disclimax communities in which native perennials had become established.

Classification yielded nine complexes and 19 types (Figure 5.13). Complexes are characterised as nearly as possible in Table 5.6. As for the Northern and Southern Mt Lofty Ranges, the coastal AVICENNIA MARINA mangrove complex and HALOSARCIA HALOCNEMOIDES samphire complex are discontinuous from the rest of the data set. In addition, there is a disjunction at the 0.94 level between the EUCALYPTUS INCRASSATA – E. FOECUNDA – MELALEUCA UNCINATA mallee broombush complex and the other six complexes: E. GRACILIS – E. DUMOSA and M. LANCEOLATA – E. DIVERSIFOLIA mallee, E. POROSA savannah woodland, GAHNIA TRIFIDA/FILUM sedge wetland, and OLEARIA AXILLARIS and NITRARIA BILLARDIERI coastal foredune vegetation.

With a data set of just 33 sites, Yorke Peninsula has by far the highest ratio of the number of complexes and types to sites of any region, suggestive of very high β diversity. Not surprisingly, eleven types consist of a single site only. Consequently there is no measure of internal variability for these types, and a scant basis for examining the relationships and gradients between types. Combined with the problems of clearance and disturbance, this may explain some of the groupings in the top six complexes on the dendrogram which at first appear strange when compared with those of other regional analyses.

For example, the OLEARIA AXILLARIS COMPLEX, predominantly low scrub on coast-front dunes of coarse calcareous sand, includes one-site of *Callitris preissii* savannah woodland which occurred distant from the coast on a "red-earth" clay-loam. The disturbed and species-poor understorey of the *C. preissii* Type shared a few species with sites in both the O. AXILLARIS and EUCALYPTUS GRACILIS – E. DUMOSA complexes, but marginally more so with the former and hence the clustering observed. A similarly unexpected clustering is found in the MELALEUCA LANCEOLATA – E. DIVERSIFOLIA COMPLEX. This group includes mallee types of *E. diversifolia* and *E. brachycalyx* with *M. lanceolata* prominent in the understorey, a shrubland type of *M. lanceolata* and *Acacia calamifolia* on subcoastal dunes of calcareous sand, and two disturbed savannah woodland types of *M. lanceolata*, one with *E. porosa* as a codominant. Four of the types are represented by only one site each. Types dominated by *E. brachycalyx*, *E. diversifolia* and *E. porosa* were grouped together into one complex in no other region. Yet, despite subjectively seeming very different in terms of habitat and structure, they are united by the ubiquity of *M. lanceolata* across the southern half of Yorke Peninsula. The equally-puzzling affinity between the M. LANCEOLATA – E. DIVERSIFOLIA and E. GRACILIS – E. DUMOSA complexes is also due to the common occurrence of *M. lanceolata* in both.

Ordination (excluding discontinuous outliers) illustrates relationships between complexes and types marginally better (Figure 5.14). The single site of distinctive *Callitris preissii* woodland is shown as an outlier of the OLEARIA AXILLARIS COMPLEX. Within the MELALEUCA LANCEOLATA – EUCALYPTUS DIVERSIFOLIA COMPLEX, there is also separation of the *M. lanceolata* savannah woodlands from the *E. diversifolia* - dominated mallee type and the *E. brachycalyx* - dominated site is located nearer sites of the E. GRACILIS – DUMOSA COMPLEX, as would be expected from the analyses of the Murray Mallee and Northern Mt Lofty Ranges.

In two dimensions, the ordinated complexes form an inverted T-shape. The horizontal gradient runs from the EUCALYPTUS INCRASSATA – E. FOECUNDA – MELALEUCA UNCINATA COMPLEX on siliceous sands and acidic clays; via the *E. diversifolia – M. lanceolata – Beyeria lechenaultii* Type on shallow terra rossa loams, the *M. lanceolata* savannah woodland type on rendzina soils, and the E. GRACILIS – E. DUMOSA COMPLEX on Bakara calcrete and Woorinen Formation soils with nodular calcrete; to the OLEARIA AXILLARIS and NITRARIA BILLARDIERI complexes on calcareous coastal sands. Hence the first ordination axis is positively correlated with soil pH and soil carbonates. It is negatively correlated with distance from the coast and altitude. The vertical gradient runs from the mallees of the E. GRACILIS – E. DUMOSA COMPLEX, via the *M. lanceolata* woodland types and the E. POROSA savannah woodland complex, to the GAHNIA TRIFIDA/FILUM COMPLEX. Positive correlation of annual flooding with ordination axis 2 is due to the singular occurrence of G. TRIFIDA/FILUM in seasonally-inundated lowlands.

Negative correlation of calcrete nodules with axis 2 is due to the occurrence of the *E. gracilis – E. dumosa – Alyxia buxifolia* Type on Woorinen Formation soils.

Unlike all other regions, annual rainfall was not a significant environmental correlate with ordination axes. This might be used as evidence that edaphic factors override the effects of rainfall, but more likely it indicates the poor quality of rainfall data for Yorke Peninsula. There are few rainfall recording stations in the southern two-thirds of the region and the map from which the mean annual rainfall at each site was estimated was highly generalised. Thus rainfall estimates at sites may not reflect rainfall patterns to which vegetation is sensitive.

Many deficiencies in the results as presented above, especially those stemming from unexpectedly high β diversity, would theoretically be alleviated by an increased sampling density. In practice, the degree of vegetation clearance on Yorke Peninsula would make it impossible to locate additional sites throughout most of the region by any regular strategy, and thus impossible to significantly clarify the classification and the relationships between vegetation types. It must be concluded that patterns and affinities of what remains of Yorke Peninsula's natural vegetation would be better judged by analyses across the whole study area which would seek analogues of these vegetation types in other regions (see Chapter 6).

5.8 EYRE PENINSULA REGION

Analysis and interpretation of the vegetation patterns on Eyre Peninsula presented few of the problems posed by Yorke Peninsula. Eyre Peninsula is large, approximately 30 % of the total study area, and native vegetation remnancy is around 36 %, the second highest in the study area. As a result, the 239 sites in the Eyre Peninsula data set are distributed in a pattern closely following that of the original sampling grid (Figure 3.3). Just two grid cells, both in the pastorally grazed grasslands of the Polda Basin in the south-west of the region, could not be sampled and the degree of disturbance of remnants elsewhere was generally very low.

Ten complexes were defined by the classification (Figure 5.15) and they are briefly characterised in Table 5.7. There was no complete floristic discontinuity in the region, but there is a major division on the dendrogram at the 0.98 dissimilarity level which separates the three relatively uncommon wetland/fen complexes (JUNCUS KRAUSII, MELALEUCA DECUSSATA and M. HALMATURORUM – M. BREVIFOLIA) in seasonally-inundated lowlands on southern and south-western Eyre Peninsula from the large group of seven mallee, woodland and coastal shrubland complexes that typify the regional landscape.

The wetland complexes have been entirely ignored or overlooked in the regional studies of Crocker (1946) and Smith (1963). Neither classification even defined a vegetation grouping in which one might reasonably surmise that the three complexes are implicitly incorporated. Looking further afield, the MELALEUCA HALMATURORUM – M. BREVIFOLIA COMPLEX at least has analogues in the M. HALMATURORUM and M. BREVIFOLIA communities in the interdune corridors of the Upper South-East (Crocker 1944; Specht 1972; and the floristic classification in Section 5.2 above). Wetlands dominated by *Juncus kraussii* and *M. decussata* have not been recorded prior to this survey. From the data available, they appear to be endemic to south-western Eyre Peninsula.

By contrast, the mallee, woodland and coastal complexes all have close equivalents in the literature (Crocker 1946 and Smith 1963; see Table 5.7). The classification of Crocker (1946), based upon the concept of the "edaphic complex" (see Crocker & Wood 1947), most closely corresponds with that presented here. There are two significant exceptions to this correspondence: (i) Crocker failed to erect an edaphic complex of coastal dune and clifftop vegetation, although this omission was rectified by Smith (1963); and (ii) Crocker placed greater emphasis on vegetation dominated by *Eucalyptus cladocalyx* by dividing it amongst two edaphic / climatic complexes, whereas such a group merely assumes the status of a subcomplex of the E. INCRASSATA – E. SOCIALIS – E. DUMOSA COMPLEX in the quantitative analyses. The otherwise strong similarities between these two classifications which were reached by entirely independent processes leads one to conclude that

- the purely qualitative, pioneering work of Crocker (1946) on Eyre Peninsula is of a high standard capable of passing the tests of time and changing ecological methodology (Wright 1985 came to the same conclusion with regard Crocker's assessment of the soils);
- the edaphic complex of Crocker & Wood (1947) is a robust and ecologically sensible concept; and
- floristic complexes derived by the quantitative survey and analysis methods applied here can be equated with ecologically fundamental units such as edaphic complexes without injustice to classical ecological theory and thus the geobotanic outlook aspired to at the outset of the study has been achieved.

If the size of the region is taken into account, definition of ten complexes by the classification implies a low β diversity level on Eyre Peninsula, between the levels in the much smaller Murray Mallee and Southern Mt Lofty Ranges regions which contained 8 and 11 complexes respectively. The reasons for the low β diversity on Eyre Peninsula are the same as for the Murray Mallee i.e. short climatic gradients despite the large area involved and few important surface geological formations (or soil types) across the predominantly aeolian, mildly undulating landscape (see Section 5.3). In fact the two regions are climatically similar and share many aeolian surface geological formations (see Figures 2.5 and 2.10).

However, notwithstanding the seeming lack of environmental and biotic heterogeneity at a broad scale, the number of types defined by the Eyre Peninsula classification is the highest of all regions (55 types in total). Consequently, internal variability of the few defined complexes is high, especially in the EUCALYPTUS INCRASSATA – E. SOCIALIS – E. DUMOSA and E. OLEOSA – E. GRACILIS mallee complexes, which together account for over two-thirds of sites and types. There are 51 sites in 13 types in the E. OLEOSA – E. GRACILIS COMPLEX and the E. INCRASSATA – E. SOCIALIS – E. DUMOSA COMPLEX includes 22 types containing a total of 102 sites. The latter has sufficient internal variability for three subcomplexes of distinctive floristic composition to be recognised (E. CLADOCALYX, E. INCRASSATA – E. SOCIALIS, E. DUMOSA; see Figure 5.15 and Table 5.7). Although the different distributions of the three EUCALYPTUS INCRASSATA – E. SOCIALIS – E. DUMOSA subcomplexes can be attributed to associations with different surface geological features, much of the remaining variation in this and the other large mallee complexes is not overtly linked with edaphic and/or climatic factors.

Instead, chorological[12] pattern independent of habitat type appears to be a significant source of variability within complexes. A majority of mallee types are restricted to small portions of Eyre Peninsula (say, 10 000 to 20 000 km^2 overall range). In adjacent districts there are often clearly different, although floristically related, types in habitats which are indistinguishable by any of the measured environmental variables or by visual observation. For example, on the Great Victoria Desert dunefields across the northern and north-western parts of the region, the *Eucalyptus yumbarrana – E. incrassata – Triodia irritans – Melaleuca eleutherostachya* Type occurs on dune crests north-west of the town of Minnipa and the *E. incrassata – Triodia irritans – Melaleuca uncinata* Type occurs east of Minnipa in the same habitat. *E. yumbarrana* and *M. eleutherostachya* are both found in South Australia only as far east as Minnipa, and ***M. uncinata*** only to the east and south of the town. There are many other species in the rich Eyre Peninsula flora (310 perennial species recorded = 57 % of the study area total) which have restricted distributions (e.g. *Acacia merrallii, Eremophila behriana, Eucalyptus concinna, E. flocktoniae, Hakea cycloptera, Leptomeria preissiana, Maireana suaedifolia, Pultenaea elachista*, and *P. trichophylla*). They represent major and minor components of both overstorey and understorey in the mallee complexes. The combined effect of these numerous species of small but overlapping

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[12] Chorological = "pertaining to geographical distribution in regions".

distributions is to cause floristic classification to define many types of localised occurrence. By corollary, variability within any complex is roughly proportional to the area over which it is examined.

The recorded populations of some restricted species are small, disjunct outliers of larger populations in other parts of Australia, suggesting that they are relicts of former, more widespread and continuous populations e.g. *E. flocktoniae*, which occurs solely in the immediate vicinity of Tooligie and Ungarra on southern Eyre Peninsula, but is also found in Western Australia. Other species have populations that are almost continuous with populations in neighbouring regions and they are possibly in the process of expanding their ranges e.g. *E.yumbarrana* and *M. eleutherostachya*, which occur on the Great Victoria Desert dune systems from Western Australia to their current eastern distributional limit near Minnipa, following the line of purported Pleistocene / Holocene dunefield migration (see Twidale & Campbell 1985). Almost all of these species are elements of an east-west biogeographic cline across southern Australia as described by Burbidge (1960). The cline is essentially the summed distribution patterns of numerous discontinuous and vicarious southern temperate species whose distributions are believed to have been determined by a cycle of increasing aridity across Australia during climatic oscillations in the Pleistocene (Green 1965; Horton 1984). The chorological variation in complexes thus arises from the classification being a single, static impression of vegetation which is dynamic in a geological time frame through which a considerable proportion of the flora is subject to expansion or contraction of their individual, continuously overlapping, distributional ranges; and thus the distribution patterns of types have both abiotic environmental determinants and temporal - spatial determinants.

Ordination of the mallee, woodland and coastal complexes (excluding the single, loosely related site of ALLOCASUARINA VERTICILLATA COMPLEX savannah woodland) summarises all the important features of the dendrogram, the characterisation of the complexes and the degree of variability within complexes (Figure 5.16). The floristic patterns are highly continuous, with each complex grading into at least two other complexes via a series of intermediate types. The Olearia axillaris Complex grades into all five other complexes. Although clearly just nodes of a continuum, the six complexes and the subcomplexes of the Eucalyptus incrassata – E. socialis – E. dumosa group are each quite clearly defined since there is no severe elongation or interdigitation of their loci.

Rainfall and a large suite of soil variables are significant correlates with the ordination axes and thus appear to control the distribution of the complexes. Rainfall increases across the ordination from the Eucalyptus oleosa – E. gracilis Complex and the E. incrassata – E. socialis Subcomplex which dominate northern Eyre Peninsula towards the E. cladocalyx Subcomplex and the E. diversifolia Complex of the southern extremities of the region. The significant soils correlation do not indicate edaphic gradients across all complexes on the ordination. Rather they refer to the environmental distinction of one or two complexes from the remainder. Thus limestone, positively correlated with the second axis, indicates the E. diversifolia and E. porosa complexes; deep, sandy soils indicate the E. incrassata – E. socialis Subcomplex; and alkaline soils with nodular calcrete indicate the E. oleosa – E. gracilis and Casuarina cristata complexes. The relative clarity of the complexes on the ordination reflects the strong definition of the environmental gradients which separate each from the rest.

However, despite the clear environmental gradients, the numerous types in the complexes overlap and interdigitate, and thus have not been shown on the ordination plot. Each pair or triplet of overlapping types is a case of types differentiated by chorological factors independent of the main habitat gradients and whose separation is suppressed in two dimensions by the more broad-scale climatic and edaphic patterns.

Chapter 6:
VEGETATION ANALYSIS III: STUDY AREA SYNTHESIS — RESULTS AND DISCUSSION.

6.1 PREAMBLE

It was initially envisaged that a whole-area synthesis would simply achieve: (i) comparison and appropriate amalgamation of regionally-defined complexes and types, and (ii) a broad-scale summary of the major environmental gradients affecting vegetation in southern South Australia. It is apparent from the preceding sections that the synthesis was also needed as a remedy for the problems and inconsistencies in the results of the regional analyses. Almost all of the regional problems stemmed from the limited ability of numerical methods to discern nodes in a vegetation continuum (and also to map gradients between these nodes) under the following, commonly encountered set of conditions: high β diversity relative to the sampling density which could be afforded, low α diversity at sites, and highly variable levels of site disturbance. The Northern Mt Lofty Ranges and Yorke Peninsula are prime examples of these conditions. It was anticipated that the larger number of sites in an all-embracing analysis would lead to improved definition of unconvincing complexes and types in these regions in the same way that, in classical statistics, a larger sample size decreases the error associated with estimated population parameters. Consequently the analyses presented below are examined from dual perspectives: synthesis of regional patterns and rectification of perceived regional anomalies.

As with the regional investigations above, the methods selected in Section 4.3 as suitable for the types of data collected in this study have the potential to produce copious quantities of results from many analytic angles. Consequently, merely the more significant of the analysis approaches and the results from them, specifically those with universal implications beyond the study area, are presented below and many details are overlooked for the sake of brevity, as was the case in the regional investigations.

However, despite the aim of conciseness, a greater variety of methods were employed in order to cope with, and best display, the patterns of the large and highly diverse complete data set. More extensive use is made of partial ordination to examine floristic patterns in major dendrogram branches and to focus upon small portions of larger ordinations. Due to the high likelihood of gradient distortion induced when high diversity data sets are indirectly ordinated, trend surface analysis was used to map the most significant environmental factors onto almost all DCA scatterplots as two-dimensional, higher-order curve functions, rather than confining environmental interpretation to correlations of single variables with each of the principal axes in turn. In addition, multiple discriminant analysis of vegetation groupings by abiotic environmental data is put to the test as a form of indirect-cum-direct ordination, which simultaneously considers vegetation and habitat and is suited to data sets of high β diversity.

6.2 CLASSIFICATION

6.2.1 Definition of Complexes

Using the same interpretive approach to the dendrogram as in the preceding regional analyses, the clustering of all 744 sites in the data set defined 38 complexes containing a total of 164 types (Figure 6.1). The general nature and geographic distribution of each complex is informally characterised in Appendix 3, and a set of photographs in Appendix 4 illustrates the physiognomic structure of many of these complexes. The results of two additional analyses describe the species composition and abiotic environment of the complexes more formally.

Firstly, in Appendix 5, the floristic composition of each complex is specified by an analysis of the constancy and average cover-abundance score (dominance) of each species, producing a species × complexes table akin to the phytosociological summary tables of Mueller-Dombois & Ellenberg (1974, pp.198–201) and Ökland (1988). Only those species most characteristic (constancy ≥ 25 %) of at least one complex are tabulated, and they are arranged to produce a "leading diagonal" of their maximum constancies across the sequence of complexes (as ordered according to the dendrogram). Such tabular arrangement to form a leading diagonal highlights those species diagnostic of complexes i.e. the species after which complexes have been named. However, few of the 168 species are confined to only one complex and there are many occurrences of high constancy values away from the diagonal e.g. *Melaleuca uncinata* falls on the diagonal in Complex 6 (9 sites) with a constancy of 88 % and a mean cover score of 2, but is also common in Complex 11 (137 sites; constancy = 72 %; mean cover score = 2) and Complex 12 (33 sites; constancy = 51 %; mean cover score = 1). The extent of this scatter about the diagonal is indicative of the floristic gradation between complexes (inverse to their relative nodal distinctiveness). There is a trend of decreasing vertical scatter about the diagonal from left to right across the ordered complexes on the table, which corresponds with the structure of the dendrogram in which the intergrading sclerophyllous woodland, heathland and mallee complexes occur in the upper half, and the more distinctive (disjunct or outlying) complexes occur in the lower half (Figure 6.1).

Secondly, the abiotic environment of each complex is specified by the mean and standard deviation of the edaphic and climatic variables recorded at sites (Table 6.1). Some trends are apparent, most clearly those separating one distinctive complex or small group of complexes from the remainder e.g. tidal flooding in the AVICENNIA MARINA COMPLEX; annual flooding in the GAHNIA TRIFIDA/FILUM, MELALEUCA HALMATURORUM, M. BREVIFOLIA, JUNCUS KRAUSSII and EUCALYPTUS LARGIFLORENS complexes; high salinity in the M. HALMATURORUM, E. LARGIFLORENS, HALOSARCIA HALOCNEMOIDES, ATRIPLEX CINEREA and A. MARINA complexes; and high rainfall in the E. BAXTERI – PTERIDIUM ESCULENTUM, J. PALLIDUS and E. OBLIQUA –

E. FASCICULOSA complexes. For other variables and other comparisons of complexes, standard deviations are high relative to the observed range of the variables. This is not unexpected given the floristic gradation between complexes and the possibility of combinations of edaphic and/or climatic variables being the source of the gradation. Thus, these data can only be regarded as a guide to the habitat correlations of complexes (as noda) and thus no statistical tests of differences between complexes have been applied.

6.2.2 Regional Distribution of Complexes

A final classification of 38 complexes and 164 types does not represent a high level of amalgamation of the 68 complexes and 212 types defined by the seven regional analyses *in toto* (Table 6.2). This implies that there is chorological pattern across the entire study area comparable to that observed for types on Eyre Peninsula, although also applicable to the higher level of the classification hierarchy i.e. many complexes and the majority of types retain their exclusively regional character when compared with vegetation groups from other parts of the study area.

Some such "regionally endemic" complexes are small in number of sites, peculiar in floristic composition and/or abiotic habitat, and very localised e.g. ACACIA PYCNANTHA (SE), ATRIPLEX CINEREA (YP), EUCALYPTUS LARGIFLORENS (MU; riparian), E. MACRORHYNCHA (NL), E. MICROCARPA (SE), JUNCUS KRAUSSII (EP), J. PALLIDUS (SE), MUEHLENBECKIA CUNNINGHAMII (MU) and XANTHORRHOEA CAESPITOSA (SE). Other regionally endemic complexes are relatively common and typical of the vegetation in a region e.g. E. BAXTERI – PTERIDIUM ESCULENTUM (SE), E. CNEORIFOLIA (KI) and E. OBLIQUA – E.FASCICULOSA (SL). In both groups, the endemism reflects a combination of:

1. habitat specificity (either of very restricted distribution, even within the

region, or locally common), such that a near-continuous band of suitable habitat does not cross regional boundaries; and

2. some restrictive historical factor such as the climatic oscillations discussed by Green (1965) and Horton (1984) which have caused long, relictual confinement of vegetation types, leading to unique species combinations by different patterns of radiation, adaptation or local extinction.

Three small complexes which seem to be endemic to the Northern Mt lofty Ranges — ACACIA PAPYROCARPA, CALLITRIS COLUMELLARIS and DODONAEA LOBULATA — are Eremaean or Flinders Ranges vegetation groups whose southern limits are sparsely sampled by the survey grid. Northward extension of the bounds of the study area (Murray Mallee and Eyre Peninsula) would find these complexes much more widely distributed (see Wood 1937; Specht 1972). The CASUARINA CRISTATA and MAIREANA PYRAMIDATA complexes, each found in two regions, are also more common in the arid areas to the north.

By contrast, other complexes are simply the union of two to four regional namesakes e.g. AVICENNIA MARINA (SL, NL, YP), CASUARINA CRISTATA (NL, EP), EUCALYPTUS CAMALDULENSIS (SE,SL, NL, [EP]), E. DIVERSIFOLIA (SE, KI, YP, EP), E. LEUCOXYLON (SE, SL, NL), E. ODORATA (SL, NL, [EP]), E. POROSA (NL, YP, EP), GAHNIA TRIFIDA/FILUM (SE, YP), HALOSARCIA HALOCNEMOIDES (MU, SL, NL, YP), MELALEUCA BREVIFOLIA (SE, EP) and M. HALMATURORUM (SE, EP) (see Table 6.2). With the exception of C. CRISTATA and E. DIVERSIFOLIA, these complexes are of below-average species diversity and encompass savannah woodlands and saline, tidal or seasonally-inundated wetlands. In the case of the eucalypt-dominated savannah woodlands, uniformity of composition across the regions may be overestimated here since the natural grassy understoreys, almost everywhere now lost due to grazing disturbance, may have once indicated regional variation.

6.2.3 Mallee Complexes

Improved description and a better classification of vegetation pattern in mallee areas were important objectives during this stage of the study. The full classification delimits five mallee complexes: EUCALYPTUS DIVERSIFOLIA, E. DUMOSA, E. INCRASSATA – E. FOECUNDA, E. OLEOSA – E. GRACILIS and E. SOCIALIS. With the exception of the E. SOCIALIS COMPLEX which, as defined here, was recorded only twice on Eyre Peninsula, these complexes correspond broadly with mallee "edaphic complexes" identified on Eyre Peninsula by Crocker (1946) i.e. the edaphic complex seems to be a convenient and ecologically-sensible landscape unit for use in the mallee belt of southern South Australia, and its use could be extended into both more temperate and more arid parts of the State.

However, the correlation is floristic, not edaphic. The floristic units that Crocker associated with particular soil types on Eyre Peninsula occur throughout the mallee areas, but the soil type on which they occur varies, especially at extremes of rainfall regime. For example, the EUCALYPTUS OLEOSA – E. GRACILIS COMPLEX is most frequently associated with calcareous loams containing calcrete nodules (Woorinen Formation) in the annual rainfall range 225–350 mm; but at the lower rainfall limit, particular types also occur on weakly-calcareous sands (e.g. Moornaba Formation) and shaley skeletal soils, and, at the higher limit, other types occur on sheet calcrete (Bakara Formation) and non-calcareous clay-loams. The combinations of rainfall and soil type may indirectly indicate a correlation with soil water status or nutrient availability. Observation of these shifts suggests that "floristic complexes" is a more accurate term for the groups than "edaphic complexes".

The mallee complexes are also the most changed by the full classification due to "instability" of their outlying (intermediate) types. As noted in the previous section, the EUCALYPTUS DIVERSIFOLIA COMPLEX was formed from complete amalgamation of regional equivalents. In this sense it is a stable unit irrespective of sampling scale (whether in a regional or over the total area). The other four complexes are less stable. While core types of regional complexes, those clearly dominated by the one or two species after which the complexes are named, reappear as core types in the full classification, types which are intermediate between complex noda have been redistributed, and some regional complexes of variable dominants have been split amongst two new complexes. For example, the bulk of the E. INCRASSATA COMPLEX of the Murray Mallee is contained in the E. INCRASSATA – E. FOECUNDA Complex of the full classification, except for types dominated by *E. socialis* or *E. cyanophylla*, which fall into the new E. SOCIALIS COMPLEX. In addition, the E. DUMOSA – E. SOCIALIS COMPLEX of the Murray Mallee analysis has been divided almost equally between the new E. DUMOSA, E. OLEOSA – E. GRACILIS and E. SOCIALIS complexes.

The redistribution amongst complexes from the regional to full classification results from changes in the relative numbers (density) of sites in types and groups of similar types which alter the weighting of forming noda (centroids) during the agglomerative clustering procedure. Instability of groupings, especially of types between noda, is to be expected when classifying a highly continuous vegetation system (see also ordinations below; Sections 6.3 and 6.4). Although continuity and nodal instability hinder easy pigeonholing of vegetation, the classification of the mallee areas presented here is still a significant improvement over those of Specht (1972) and Davies (1982) because of uniform, quantified, hierarchical levels (fixed degrees of within-group variability) and corrected eucalypt taxonomy.

With respect to the instability of high level groups, it is interesting to note that groups of types which share the same overstorey *and* understorey dominants, and differ only in minor floristic components, remain together in both regional and full classifications, while groups of types sharing *either* overstorey *or* understorey dominants (but not both) are more frequently subject to subdivision and redistribution in the full classification. As complexes are most characterised by overstorey, this suggests that there might be, in some cases, a third comprehensible level of the classification hierarchy between mallee complexes and types, which identifies overstorey-understorey combinations which are more stable than the complexes as defined at a dissimilarity level of 0.85.

This leads to recognition of "subcomplexes" within the internally variable EUCALYPTUS INCRASSATA – E. FOECUNDA and E. SOCIALIS complexes (Figure 6.1; Appendix 3). In each of these complexes, there are three subcomplexes determined by understorey type and linked to particular climate-substrate combinations. The subcomplexes of E. INCRASSATA – E. FOECUNDA are dominated in the understorey by:

A. *Melaleuca uncinata* on siliceous sands and duplexes at 300–500 mm annual rainfall;

B. *Triodia irritans* on sands at <300 mm rainfall; and

C. *M. uncinata* with various calciphilic species common in the E. DIVERSIFOLIA COMPLEX (e.g. *Acroctriche patula, Gahnia lanigera* and *Lasiopetalum behrii*) on sheet calcrete of the Bridgewater Formation at >400 mm rainfall.

In the third, the mallee eucalypts are so sparse that *M. uncinata* is the single dominant species. These three subcomplexes are a modification of the major division noted in the E. INCRASSATA – E. SOCIALIS – E. DUMOSA COMPLEX on Eyre Peninsula during regional analysis. Pattern in the complex on Eyre Peninsula is strongly weighted in the full classification since 79 of the 137 sites in the E. INCRASSATA – E. FOECUNDA COMPLEX occur on Eyre Peninsula. In the EUCALYPTUS SOCIALIS COMPLEX, the equivalent understorey groupings are:

A. *Melaleuca uncinata* on various soils at >400 mm rainfall;

B. sparse *M. lanceolata* and small chenopods on Bakara calcrete or clay-loams at 300-400 mm rainfall; and

C. *Triodia irritans* on sand at <300 mm rainfall.

6.2.4 Northern Mt Lofty Ranges and Yorke Peninsula

A second important objective of the synthesis was clarification of interpretational difficulties in the Northern Mt Lofty Ranges and Yorke Peninsula regional analyses.

Sites in the Northern Mt Lofty Ranges were classified in much the same way as before. Most of the endemic complexes remain highly distinctive when placed in the wider context, i.e. ACACIA PAPYROCARPA, CALLITRIS COLUMELLARIS, DODONAEA LOBULATA and EUCALYPTUS MACRORHYNCHA, although the E. CLADOCALYX and XANTHORRHOEA QUADRANGULATA complexes were merged into a new CASSINIA LAEVIS – X. QUADRANGULATA complex by common elements in their understoreys. The non-endemic complexes are chiefly savannah woodlands and arid chenopod shrubland groups which have become part of equally distinctive namesake complexes in the full classification. Thus only the gradients between these complexes, as in the ordinations below, may be better elucidated by the synthesis.

Stability of well-defined complexes in the Northern Mt Lofty Ranges contrasts with the redistribution of the majority of Yorke Peninsula sites (Table 6.2). The former EUCALYPTUS GRACILIS – E. DUMOSA COMPLEX has been redistributed between CALLITRIS PREISSII, E. DUMOSA and E. OLEOSA – E. GRACILIS. GAHNIA TRIFIDA/FILUM has been split between the G. TRIFIDA/FILUM and MELALEUCA HALMATURORUM swamp complexes. The variable M. LANCEOLATA – E. DIVERSIFOLIA COMPLEX is separated into E. DIVERSIFOLIA mallee, E. POROSA savannah woodland and M. LANCEOLATA – OLEARIA AXILLARIS clifftop coastal scrub. The coastal site of the NITRARIA BILLARDIERI COMPLEX has become the unique ATRIPLEX CINEREA COMPLEX, while the other, mallee-dominated site falls into the E. OLEOSA – E. GRACILIS COMPLEX. Lastly, the inland *Callitris preissii* - dominated site in the O. AXILLARIS COMPLEX has been removed to become part of the C. PREISSII COMPLEX. In all cases, the new assignment of sites into complexes clearly reflects dominant tree or shrub species such that a field botanist could recognise complexes; this was not true of the regional classification. The redistribution supports the hypothesis, suggested during presentation of the Yorke Peninsula classification, that the sampling density was inadequate to encompass the regional β diversity, further hampered by extensive land clearance and remnant disturbance i.e. sample density in species space was below the critical threshold at which recognisable noda can be delimited. Synthesis has remedied the problem.

6.2.5 Relationships Between Complexes

Above the level of complexes, the structure of the dendrogram (Figure 6.1) is a consensus of patterns shown by the regional dendrograms. The hypersaline AVICENNIA MARINA and HALOSARCIA HALOCNEMOIDES complexes are completely disjunct (as before), the latter joined by the single site of the ATRIPLEX CINEREA COMPLEX from coastal Yorke Peninsula. A group formed by the EUCALYPTUS CAMALDULENSIS and E. MICROCARPA savannah woodlands and the MUEHLENBECKIA CUNNINGHAMII riparian complex is also disjunct. As in the regional analyses, most of the remaining savannah woodland complexes (ALLOCASUARINA VERTICILLATA, E. LEUCOXYLON, E. MACRORHYNCHA, E. ODORATA and related Flinders Ranges complexes; but excluding E. POROSA) are only weakly associated with the main body of sites on the dendrogram. However, they are linked with one another at lower levels of dissimilarity than in the regional analyses, indicating that the larger data set has detected an increase in the number of understorey species shared by them, even though, due to disturbance losses, the frequency of occurrence of these species in each complex is low. Shared taxa include *Acacia pycnantha, Allocasuarina verticillata, Danthonia* spp., *Hibbertia exutiaces, Lepidosperma laterale, Pultenaea largiflorens* and *Stipa* spp.

The sclerophyllous woodland and heathland complexes form a large group with the EUCALYPTUS CNEORIFOLIA "mallee" at the top of the dendrogram. All six complexes occur on acidic soils at relatively high rainfall (>400 mm annually). Two other groups of complexes are loosely related: (i) the E. DIVERSIFOLIA mallee with the three coastal dune and clifftop complexes, which together signify coastal calcareous soils at high rainfall (>400 mm); and (ii) the E. INCRASSATA – E. FOECUNDA and E. DUMOSA mallee complexes, respectively on acidic soils at low rainfall (<400 mm) and inland calcareous soils at high rainfall (>400 mm). The remaining mallee complexes, E OLEOSA – E. GRACILIS and E. SOCIALIS, are grouped with the chenopod shrublands, CALLITRIS COLUMELLARIS, C. PREISSII and E. POROSA, all of which occur on calcareous or skeletal soils at low rainfall (<400 mm). The last group contains the four complexes which are found in seasonally-inundated areas on semi-saline soils (rainfall >400 mm). Even such a brief summary indicates that the large groups of complexes on the dendrogram correspond with simple divisions of rainfall, soil and inundation gradients. Furthermore, the divisions are independent of chorological factors (which *are* important at the level of complexes). The larger groups are roughly comparable to formations in the sense of Diels (1906).

However, although ordinations of the Murray Mallee and Eyre Peninsula data sets have shown that the five mallee complexes intergrade, they are not adjacent (immediately related) on the dendrogram. As with the unresolvable instability of outlying mallee types with respect to mallee noda, this artifact arises from variable weighting of centroids during agglomerative clustering of sites showing high floristic continuity. The final stages of fusion found the weighted centroid of the group of temperate sclerophyll-mallee complexes (Complexes 1–12) to be marginally more similar to the centroid of the group of wetland complexes than to the centroid of the semi-arid mallee and arid shrubland complexes. The two clustering steps involved correspond with fusion of large groups along two binary environmental "gradients" which are equally important in terms of species turnover: free-draining / seasonally-inundated and temperate / semi-arid. The order in which the fusions have occurred is meaningless from an ecological perspective. Thus little importance can be attached to the split of mallee complexes, nor to the highest structural level of the dendrogram, beyond the indication of complete floristic disjunctions (which are stable).

6.3 ORDINATION

The complete data set of 744 sites proved to be too large for satisfactory overall ordination of floristic gradients in the study area due to high data point density on the ordination plots. Thus an unbiased subsample of sites for ordination was made by random selection of approximately one third of sites (235 sites). The two ordinations presented in this section were derived from this subsample.

The subsample included representatives of 28 of the 38 complexes. Nine of the omitted complexes are small: six contain only one site (Atriplex cinerea, Dodonaea lobulata, Eucalyptus largiflorens, E. macrorhyncha, E. microcarpa and Juncus kraussii); two contain two sites (Callitris columellaris and Juncus pallidus); and one contains three sites ("Complex 23"). The tenth was the Gahnia trifida/filum Complex, which contains seven sites.

With the single site of the Avicennia marina Complex excluded because of its disjunction, ordination of the random subsample shows two groups of complexes outlying the main body of more closely related complexes (Figure 6.2). The outliers in the upper right are the Eucalyptus camaldulensis Complex and the Muehlenbeckia cunninghamii Complex (in which *E. camaldulensis* also occurs). These two complexes form a disjunct branch of the dendrogram because of the lack of natural understorey by which *E. camaldulensis* could be shown to grade into other savannah woodland complexes (according to Specht 1972). The lower group of outliers is characterised by the dominance of chenopods: samphires, arid-zone shrublands and the E. largiflorens Complex in which *Atriplex rhagodioides* and †***Pachycornia*** *triandra* form the understorey. These complexes occur on three different major branches of the dendrogram, two of which are disjunct.

The lower group of outliers is an example of the "tongue effect", a distortion in DCA ordination by which a few sites from a small portion of a floristic gradient are well-spaced at one end of a principal ordination axis, but compressed in all other dimensions, while the majority of sites are clustered together at the other end without being compressed in other dimensions (Minchin 1987a; R.H. Ökland 1990). The effect has been attributed to imperfections of chi-squared dissimilarity and the detrending procedure used in DCA. In the case of Figure 6.2, it is mostly the result of a systematic change in α diversity along the major floristic gradient (Figure 6.3). Species diversity grades from an average of 28 perennial species per site at the left end of DCA axis 1 to only 4 species per site at the lower right. The effect is then enhanced by a combination of high β diversity amongst these arid complexes (despite their low average α diversity) and the relatively low numbers of sites in the data set which fall into this portion of the gradient. It is doubtful whether other ordination methods could better resolve this set of conditions.

If allowance is made for the distortion associated with the outlier complexes, the ordination provides a summary of the major vegetation gradients (and the relative positions of complexes along the gradients) which is superior to any such information available from the literature. In addition, "ecological – neighbour" relationships between complexes are more apparent than on the dendrogram (Figure 6.1).

The main floristic gradient in the study area runs diagonally across the lower (left) two-thirds of the ordination: from the EUCALYPTUS BAXTERI – PTERIDIUM ESCULENTUM and E. OBLIQUA – E. FASCICULOSA sclerophyll woodland complexes; via, successively, BANKSIA ORNATA – ALLOCASUARINA PUSILLA heathland; E. DIVERSIFOLIA and E. INCRASSATA – E. FOECUNDA mallee; E. DUMOSA mallee and the related CALLITRIS PREISSII and E. POROSA semi-arid savannah woodlands; E. OLEOSA – E. GRACILIS and E. SOCIALIS mallee; ACACIA PAPYROCARPA, CASUARINA CRISTATA and MAIREANA PYRAMIDATA arid shrublands; to the HALOSARCIA HALOCNEMOIDES samphires. The gradient is negatively correlated with annual rainfall and positively correlated with soil pH, T.S.S., carbonates and calcrete nodules. South-to-north transects in eastern South-East / Murray Mallee and central Eyre Peninsula follow this sequence of habitat conditions.[13]

The upper (right) third of the ordination contains a mixture of three types of complexes (coastal , wetland and savannah woodland) which are weakly related by floristic composition and fall on different major branches of the dendrogram. The three groups of complexes are known to occur in different habitats, especially with respect to inundation, soil texture[14], pH and T.S.S. (Appendix 3 and Table 6.1). Their separation is shown by the third and fourth DCA axes. The third axis separates the savannah woodland complexes (high scores) from the coastal and wetland complexes (low scores). [The main rainfall-determined floristic gradient runs diagonal to this axis: at high values, EUCALYPTUS BAXTERI – PTERIDIUM ESCULENTUM, adjacent to the savannah woodlands; at low values, HALOSARCIA HALOCNEMOIDES, adjacent to the coastal complexes]. The fourth axis separates the wetland complexes (high scores) from the coastal complexes (low scores). Two-dimensional plots of the third or fourth axis against either of the first two axes do not clarify these patterns (and thus are not presented), as the failure to plot either of the principal axes causes mixing of the complexes separated by the main rainfall-soils gradient. Such mixing is more difficult to interpret than the mix of complexes in the upper part of Figure 6.2. Only a four-dimensional space fully represents the four major gradients.

More detailed analysis of environmental correlations was permitted by

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[13] In the Mt Lofty Ranges, the sequence also includes savannah woodland complexes which the ordination is unable to place due to their floristic disjunction.

[14] Despite their known differences of soil texture, soil texture is a significant environmental correlate with the first two DCA axes and it implies uniformly heavy-textured soils (clays and clay-loams) for complexes in the upper right of the ordination, as opposed to the BANKSIA ORNATA – ALLOCASUARINA PUSILLA and EUCALYPTUS INCRASSATA – E. FOECUNDA complexes on siliceous sand. While heavy-textured soils are the norm in the wetland and savannah woodland complexes, this generalisation about soil texture cannot be extended to the other component of the upper right of the ordination, the coastal complexes, which occur on sands and sandy loams (calcareous, not siliceous). This edaphic difference results in soil texture also being a significant correlate with the fourth DCA axis, which separates the coastal complexes from the wetlands and savannah woodlands.

ordination of a reduced data set from which the outlying chenopod shrublands, samphire and (all) savannah woodlands had been removed (Figure 6.4). The ordination is similar to the left side of Figure 6.2 (with the Allocasuarina verticillata, Cassinia laevis – Xanthorrhoea quadrangulata, Eucalyptus leucoxylon and E. odorata complexes removed), although there have been some relative placement changes by the Leucopogon parviflorus – Olearia axillaris and Melaleuca lanceolata – O. axillaris coastal complexes, and the principal axes are slightly rotated with respect to the complexes (as indicated by the +45° rotation of the environmental correlation vectors). There is still a systematic change in α diversity (Figure 6.5) from a maximum in the Banksia ornata – Allocasuarina pusilla Complex to two minima, one in the M. halmaturorum Complex at the top of the ordination, and a second on the far right at the most arid and disturbed parts of the E. oleosa – E. gracilis and E. socialis complexes. However, there is no "tongue" distortion associated with either low diversity extreme.

Annual rainfall, soil texture, pH, T.S.S. and carbonates were the environmental variables most significant as linear correlates with the first two ordination axes. The two-dimensional trend surfaces of the first three variables show significant non-linear trends (Figure 6.6). Although four of these five variables *are* predominantly left to right trending along the first axis despite non-linearity (soil texture is the exception), their differences in curvature allow a more subtle pattern of climatic and edaphic gradation with which to correlate the floristic gradients.

While the linear correlation vector for rainfall is almost parallel to the first axis (Figure 6.4), the isotels of the annual rainfall trend curve, from a maximum of 850 mm in the Eucalyptus baxteri – Pteridium esculentum Complex at the centre left, to a minimum of 280 mm in the E. socialis Complex at the lower right (Figure 6.6a). The trend of soil pH curves in the opposite direction, from a minimum in the E. baxteri – P. esculentum Complex, to two local maxima, one in the Melaleuca brevifolia Complex and one in the

E. OLEOSA – E. GRACILIS COMPLEX (Figure 6.6b). Consequently pH aids habitat discrimination at medium and low annual rainfall. Soil T.S.S. and carbonates are linear functions only (Figures 6.6d and e), running along a diagonal between the two axes which is also the main direction of the pH trend.

The soil texture trend is less clearly patterned (Figure 6.6c). Loam or sandy loam occurs over much of the ordination, but there are a number of local maxima/minima, such as sand and loamy sand in the E. INCRASSATA – E. FOECUNDA and BANKSIA ORNATA – ALLOCASUARINA PUSILLA complexes respectively, and heavy clay in the M. BREVIFOLIA COMPLEX. Thus there is a tendency for particular complexes to occur on soils of particular texture extremes unrelated to the more broad-scale gradients of rainfall, pH and T.S.S., thereby explaining the low linear correlation of soil texture with DCA axes. When the irregular soil texture surface is superimposed on the more regular rainfall, pH and T.S.S./carbonates trends, most complexes are found to occur in a unique climatic-edaphic combination, as are the correlations along the gradients between complexes. This same conclusion might be reached from the habitat summary of complexes in Table 6.1, but the trend surfaces of environmental variables in the ordination space also provides information on the nature (direction and magnitude) of the habitat gradients linking floristically-related complexes.

6.4 PARTIAL ORDINATIONS

Partial ordinations were used to examine in more detail the floristic and environmental gradients between small groups of complexes. Chosen groups consisted of the complexes on major branches of the dendrogram (Figure 6.1), and an additional partial ordination of the five mallee complexes was undertaken even though they were split between three dendrogram branches (see Section 6.2.3). In each case, all member sites of the complexes in the group were included in the analysis i.e. there was no random subsampling to reduce the size of data sets.

6.4.1 Sclerophyllous Woodlands and Heathlands

Ordination of the sclerophyllous woodlands and heathlands (Complexes 1–6) is given in Figure 6.7. The first axis separates the woodlands (Eucalyptus baxteri – Pteridium esculentum and E. obliqua – E. fasciculosa) from the heathlands and heathy mallees (Banksia ornata – Allocasuarina pusilla, Xanthorrhoea caespitosa and E. cneorifolia), and it is most strongly correlated with annual rainfall (positive correlation) and pH (negative). The woodland complexes occur where annual rainfall exceeds 600 mm and pH is in the range 4–6, and the heathlands occur in the rainfall range 400–600 mm annually, with pH 5-7. Trend surface analysis of rainfall shows a more subtle pattern (Figure 6.8a) with a maximum in the E. obliqua – E. fasciculosa Complex, which is found on the highest elevation parts of the Southern Mt lofty Ranges (Figure 6.8b), and minima in the B. ornata – A. pusilla and E. cneorifolia complexes.

The second axis separates those complexes occurring in the South-East region (Eucalyptus baxteri – Pteridium esculentum, Juncus pallidus and Xanthorrhoea caespitosa) from those occurring in the Southern Mt Lofty Ranges and on Kangaroo Island (E. obliqua – E. fasciculosa and E. cneorifolia). Hence the second axis is inversely correlated with longitude. The locus of the Banksia ornata – Allocasuarina pusilla Complex, which occurs in both areas, is elongated along the second axis, its South-East components in the lower half where they intergrade with the E. baxteri – P. esculentum Complex, and its Kangaroo Island and Mt Lofty Ranges components in the upper half where they grade into the E. cneorifolia Complex. This regional split of sclerophyllous woodland and heathland complexes may have a chorological / geohistorical cause due to the presence of endemic species of sclerophyllous undershrub in each region, especially on Kangaroo Island. However, it is also correlated with major differences of geology in the two areas which are most obviously manifested as a difference in soil texture (Figure 6.8c). The Lower

South-East is dominated by aeolian, siliceous sands, while the high rainfall districts of the Mt Lofty Ranges and Kangaroo Island occur mostly on uplifted sedimentary rocks which give rise to heavy-textured duplex soils, and often contain laterite.

The two large complexes in the sclerophyll group demonstrate perpendicular internal floristic gradients which follow the habitat gradients between complexes. The span of the Eucalyptus baxteri – Pteridium esculentum Complex along the first DCA axis is correlated with changing annual rainfall. From right to left with decreasing annual rainfall, the sequence of types is: *E. obliqua* or *E. viminalis* – *E. ovata* with a dense *P. esculentum*, to *E. baxteri* – *P. esculentum*, thence to *E. baxteri* with an understorey less dense in *P. esculentum* and more diverse in heathland subshrub species (including *Banksia ornata*); which finally grades into the B. ornata – Allocasuarina pusilla heathlands. For the B. ornata – A. pusilla Complex, the main internal gradient is from the South-East regional types in the lower half, to the Kangaroo Island types (characterised by regionally endemic species) in the upper half, which grade into those types of the E. cneorifolia Complex which are dominated by *E. cosmophylla* rather than by *E. cneorifolia* itself.

These gradients of sclerophyllous woodlands and heathlands can be placed into the wider perspective of the full classification by predicting the position of related complexes in this partial ordination space. Crocker (1944) showed that *E. camaldulensis* woodland in the South-East is similar in habitat and understorey flora to *E. ovata* and *E. viminalis* woodlands. Thus the E. camaldulensis Complex should lie adjacent to the E. baxteri – Pteridium esculentum and Juncus pallidus complexes (the latter also includes *E. viminalis*) in the lower right corner of the ordination. Similarly, the full ordinations of complexes (Figures 6.2 and 6.4) indicate that the E. diversifolia Complex lies beyond the upper left corner, next to the E. cneorifolia Complex, and the E. incrassata – E. foecunda Complex lies immediately to the left of the Banksia ornata – Allocasuarina pusilla Complex.

6.4.2 Coastal Foredune Scrub and Subcoastal Mallee

Floristic gradients among the coastal complexes are primarily correlated with outcropping calcrete and rainfall (Figure 6.9). The first axis is a composite edaphic gradient describing the transition from shallow, loamy soils on outcropping calcrete, on which the Acacia pycnantha and Eucalyptus diversifolia complexes most commonly occur, to the deep, highly calcareous soils of coast-front dunes or clifftops, where the Leucopogon parviflorus – Olearia axillaris and Melaleuca lanceolata – O. axillaris complexes are found. The transition is inversely correlated with distance from the coast and altitude, because of the confinement of the latter pair of complexes to dunes immediately fronting the sea.

The second axis is correlated with annual rainfall. Thus Acacia pycnantha replaces Eucalyptus diversifolia on calcrete where annual rainfall is above 600 mm (South-East region only) and Leucopogon parviflorus – Olearia axillaris replaces Melaleuca lanceolata – O. axillaris on foredunes where rainfall is above 500 mm. But longitude is as strongly correlated with the second axis as rainfall, since the L. parviflorus – O. axillaris and M. lanceolata – O. axillaris complexes form an east-west biogeographic cline along the South Australian coastline. L. parviflorus – O. axillaris occurs along the entire coast of the South-East region and on the southern tip of Eyre Peninsula (Coffin Bay). The upper half of the M. lanceolata – O. axillaris Complex on the ordination occurs on Yorke Peninsula and on the Spencer Gulf (eastern) coastline of Eyre Peninsula. The lower half contains sites from the west coast of Eyre Peninsula. The Spencer Gulf types are dominated by *O. axillaris* and *Callitris preissii*, and the West Coast types are dominated by *M. lanceolata* and *Templetonia retusa*; the rest of their floras are similar.

The distributions of the two dune complexes may be attributed to different rainfall regimes (>500 mm annually in the South-East; <500 mm on Yorke and Eyre Peninsulas; see Figure 6.10a for trend). Soil pH and T.S.S. show a similar, but inverse trend (Figure 6.10b) and therefore may be an expression of rainfall regime on the coastal dune formations. The gradient within the Melaleuca lanceolata – Olearia axillaris Complex could be attributed speculatively to "exposure"; the western Eyre Peninsula coastline faces directly onto the Indian Ocean, while the eastern Eyre Peninsula and Yorke Peninsula coasts lie on Spencer Gulf and Gulf St Vincent, where they are protected from the Indian Ocean by Kangaroo Island and the southern tip of Eyre Peninsula. "Exposure" *per se* is difficult to quantify.

6.4.3 Mallee Complexes

Partial ordination of the five mallee complexes produced a triangular array of sites (Figure 6.11). The three vertices are: (i) upper left, Eucalyptus diversifolia (on Bridgewater Formation calcrete); (ii) lower left, E. incrassata – E. foecunda (mainly on Molineaux Formation siliceous sand, or duplex sand-over-clay e.g. Parilla Formation); and (iii) right, E. oleosa – E. gracilis (on Woorinen Formation calcareous loams). The E. dumosa and E. socialis complexes occupy intermediate positions. E. dumosa falls between E. diversifolia and E. oleosa – E. gracilis, on Bridgewater limestone. E. socialis falls between three other complexes (E. dumosa, E. incrassata – E. foecunda and E. oleosa – E. gracilis), its three subcomplexes occurring on the three geological formations / soil types on which its neighbours predominate respectively.

The floristic gradients between the complexes are correlated with three sets of habitat variables: (i) rainfall; (ii) sheet calcrete, calcrete nodules and soil depth; and (iii) soil texture, pH, carbonates and T.S.S. (Figure 6.11 inset). The correlation vector for rainfall is almost parallel to DCA axis 1 and shows a gradient from Eucalyptus oleosa – E. gracilis to E. diversifolia. The non-linear trend is more informative (Figure 6.12a). There are maxima in the E. diversifolia and E. incrassata – E. foecunda complexes and the isotels curve to a minimum along the lower right side of the array of sites. Although divergent, the correlation vectors for sheet calcrete (E. DIVERSIFOLIA and E. DUMOSA) and calcrete nodules (E. OLEOSA – E. GRACILIS) are related by the soil depth vector; both geologies are associated with shallow soils (Figure 6.12b), so that the depth correlation is inverse to the geometric sum of the sheet calcrete and calcrete nodules vectors. The third set of correlates describes the siliceous sand to calcareous loam gradient between the E. INCRASSATA – E. FOECUNDA and E. OLEOSA – E. GRACILIS complexes. While the trends for soil pH, carbonates and T.S.S. are monotonic (e.g. Figure 6.12c), the texture gradient is more irregular (Figure 6.12d) as has been found with texture correlations on earlier ordinations. Thus there is a clay maximum in the E. INCRASSATA – E. FOECUNDA COMPLEX where it occurs on lateritic and duplex soils on southern Eyre Peninsula.

In response to the gently-sloping habitat gradients, the floristic pattern is highly continuous. Each complex, except EUCALYPTUS OLEOSA – E. GRACILIS, does not have a cluster of sites at its centre which might be considered the "nodum" of the complex. Instead sites are evenly scattered across the loci of the complexes and site density is not reduced along the boundaries with adjacent complexes. The exception, E. OLEOSA – E. GRACILIS, is more tightly clustered, suggesting relatively uniform floristic composition with few outlying sites.

The most interesting aspect of the continuity is the "independence" of overstorey and understorey components of mallee vegetation. While both respond to the same habitat gradients, the transitions between overstorey forms and the transitions between understorey forms take place at different locations along the gradients. Thus one overstorey form spans more than one understorey form and vice versa. This is illustrated well by the relative placement of the subcomplexes of the EUCALYPTUS INCRASSATA – E. FOECUNDA and E. SOCIALIS complexes on the ordination (Figure 6.11). An understorey including calciphilic subshrubs is found in E. DIVERSIFOLIA and E. INCRASSATA – E. FOECUNDA SUBCOMPLEX C (which are adjacent). *Melaleuca uncinata* predominates in the understorey of E. DUMOSA, E. INCRASSATA – E. FOECUNDA subcomplexes A and C, and E. SOCIALIS

SUBCOMPLEX A. Likewise, *Triodia irritans* is the understorey of E. INCRASSATA – E. FOECUNDA SUBCOMPLEX B and E. SOCIALIS SUBCOMPLEX C, and chenopod subshrubs are the understorey for E. OLEOSA – E. GRACILIS and E. SOCIALIS SUBCOMPLEX B. Noy-Meir (1971, 1974a) has remarked on the independence of overstorey and understorey in mallee systems in eastern Australia, but the demonstration provided by Figure 6.11 is even more convincing. The overlap also accounts for the instability of the mallee complexes, as characterised by mallee species, versus the relative stability of the subcomplexes identified by overstorey-understorey combination (Section 6.2.3)

6.4.4 Semi-Arid Mallee and Arid Shrublands

A triangular array of sites is also produced by partial ordination of the semi-arid mallee and arid shrubland complexes (Complexes 17–23; Figure 6.13). The first axis separates the CALLITRIS PREISSII COMPLEX from the four Eremaean complexes with the EUCALYPTUS OLEOSA – E. GRACILIS and E. SOCIALIS mallee complexes occupying the intermediate position. The second axis chiefly distinguishes between the two mallee complexes. The ordination is subject to some distortion as projected in two dimensions because the loci of the chenopod shrubland complexes are elongated to form a "tongue" *sensu* R.H. Ökland (1990).

The environmental correlation vector diagram for the ordination indicates few significant correlations and the correlation coefficients are low (Kendall $\tau < 0.4$) even though significant. These correlations fail to reflect clear trends, apparently because of the small range of variability of the habitat factors and their non-linear trends in the ordination space. For example, although DCA axis 1 clearly separates the semi-arid mallees from the more arid shrublands, annual rainfall was not found to be significantly correlated with the ordination axes. However, a non-linear trend surface of rainfall is able to show the left-to-right decrease in rainfall (Figure 6.14a).

The significant axis correlates concern soil type. EUCALYPTUS OLEOSA –

E. GRACILIS and arid shrubland complexes show higher pH, T.S.S. and carbonates. Soils over sheet calcrete are typical of some of the CALLITRIS PREISSII and E. SOCIALIS complexes, as opposed to the soils with nodular calcrete typical of E. OLEOSA – E. GRACILIS and the arid shrublands. Texture is also included as a significant soil factor, but its weak correlation almost parallel to the first DCA axis is misleading. Over much of the ordination, soils are loams or sandy loams, but there is a trend from sand in the lower left of the E. SOCIALIS COMPLEX to three different clay-loam maxima/minima in the C. PREISSII, E. OLEOSA – E. GRACILIS and MAIREANA PYRAMIDATA complexes at the top and right of the ordination (Figure 6.14b). According to this surface, the main trend of soil texture is almost perpendicular to that indicated by the vector diagram of axis correlations.

6.4.5 Savannah Woodlands

As measured by the length of the first DCA axis (10.6 half-change units), β diversity is high between the savannah woodlands and related complexes (Figure 6.15). Despite this, the partial ordination presents more cohesive gradients between complexes than is apparent from ordination of the full data set (e.g. Figure 6.2), and, in doing so, resolves all the difficulties of interpreting the floristic / habitat gradients which arose during the Northern Mt Lofty Ranges regional analysis (Section 5.6).

The main gradient is the diagonal sequence of complexes, EUCALYPTUS CAMALDULENSIS to E. LEUCOXYLON to E. ODORATA. This sequence has been described in detail by Adamson & Osborn (1924) and Specht & Perry (1948), and is correlated with annual rainfall. However, the rainfall trend is not perfectly linear (Figure 6.16a) because of the variety of rainfall regimes under which E. CAMALDULENSIS woodland occurs. It is more frequently found where rainfall exceed 500 mm annually, but can occur at lower rainfall where surface water increases soil water availability. Thus, in the lower left of the ordination, there are sites of E. CAMALDULENSIS from creeklines in the Northern Mt Lofty Ranges where rainfall is <400 mm, and at the upper left is the unique site of the *E. camaldulensis – Melaleuca decussata* Type which occurred on south-western Eyre Peninsula in a limestone catchment basin at approximately 400 mm rainfall.

The EUCALYPTUS CAMALDULENSIS to E. ODORATA gradient is also correlated, but less closely, with longitude. For these savannah woodlands, longitude indirectly measures rainfall since the highest rainfall examples of savannah woodland were in the South-East and the lowest were in the Northern Mt Lofty Ranges. It is not suggestive of chorological pattern in the sense of a geohistorical cause.

At the lower rainfall of the main gradient, there is a perpendicular gradient separating the semi-sclerophyllous complexes which are restricted to steep ridgetop environments in the Northern Mt Lofty Ranges and southern Flinders Ranges (ALLOCASUARINA VERTILLATA, CASSINIA LAEVIS – XANTHORRHOEA QUADRANGULATA and EUCALYPTUS MACRORHYNCHA) from the more widely distributed E. LEUCOXYLON and E. ODORATA savannah woodlands. Weakly discontinuous with the others, DODONAEA LOBULATA is also part of the ridgetop vegetation system; it is its arid-most component. Like E. LEUCOXYLON and E. ODORATA, the ridgetop complexes are arrayed along the rainfall gradient (Figure 6.16a), but there is no significant correlation of measured habitat variables with the gradient separating ridgetops from E. LEUCOXYLON and E. ODORATA. A purely historical cause which led to relictual confinement to ridgetops during a period of increased aridity is most plausible.

The single site of the EUCALYPTUS LARGIFLORENS COMPLEX belongs to neither of the above gradients. It is both floristically distinctive (hence its outlying position at the end of DCA axis 1) and environmentally distinctive, occurring on the floodplain of the River Murray.

It is interesting to note that, unlike any other partial ordination, no edaphic variables were significantly correlated with the ordination axes, and only soil pH showed a weak non-linear trend from slightly acidic soils at the centre of the ordination to alkaline soils at each of the four extremes (Figure 6.16b). Thus soil type seems to be a poor predictor of the distribution of the savannah woodland complexes. Todd (1965) also reported a lack of edaphic determination of savannah woodland types and this has been the cause of some perplexity for South Australian ecobotanists.

6.5 MULTIPLE DISCRIMINANT ANALYSIS

Environmental catenation of the 38 complexes by multiple discriminant analysis found seasonal flooding and tidal flooding to be the most significant habitat discriminators (Table 6.3). On a scatterplot of the first two linear discriminating functions (Figure 6.17), the combination of the two flood variables separates the centroids (noda) of the eight complexes typical of inundated localities from the 30 complexes found in well-drained sites. The 30 complexes not subject to flooding form a dense, oval locus, the long axis of which runs perpendicular to the inundation gradient. This axis is primarily a gradient of rainfall and soil pH, the third and fourth most significant discriminating variables (Table 6.3). Although the MDA extends into 16 dimensions (equal to the number of selected predictors), the first two axes account for 50.5 % of the environmental variation (28.0 % and 22.5 % respectively). Using all 16 linear discriminant functions, group membership of 43.0 % of the 744 sites can be predicted "correctly" i.e. in the habitat space defined by MDA, only 43.0 % of sites fall closer to the centroid of the floristic complex of which they are a member, than to any other complex. The low percentage of correctly assigned sites is a function of the floristic continuity and habitat overlap between complexes.

Just as partial ordination was used to improve detail of ordination patterns distorted by floristic discontinuity, MDA of a reduced data set, excluding the eight wetland complexes which were "environmentally discontinuous", clarified habitat gradients between the 30 complexes not subject to inundation (Figure 6.18). Annual rainfall was the most significant discriminating habitat variable, followed by soil pH, soil texture, sheet calcrete and distance from the coast (Table 6.4).

Rainfall is the chief component of the first discriminant function. Consequently, the MDA recreates along its first axis the sequence of complexes (EUCALYPTUS BAXTERI – PTERIDIUM ESCULENTUM sclerophyllous woodland to arid shrublands via the mallee complexes) which DCA ordination of the full data set extracted along its first axis (see Figure 6.2). However, the second MDA axis is able to segregate the coastal complexes from the savannah woodlands and from one another (and from the main rainfall gradient), which only a combination of the second and third DCA axes was able to achieve[15]. This axis is correlated with soil texture, sheet calcrete, altitude and distance from the coast. The first two axes accounted for 66.8 % of the environmental variation in the data set (54.2 % and 12.6 % respectively), although only 42.5 % of sites were correctly assigned to complexes.

As applied here, MDA is an effective technique of vegetation analysis for concurrent use with indirect ordination. It is able to clarify major, ordinated floristic / environmental gradients in lower dimensionality. Its only drawbacks are: (i) the assumption that the available (measured) environmental variables are the best predictors of the vegetation patterns at the scale of interest; and (ii) its inability to fully account for and display the extent of gradation between complex noda. With regard to the latter drawback, the scatter of sites in each complex around the centroid is high, as is the overlap between complexes, hence the low percentages of "correct" assignment of sites to noda.

6.6 SUPRASPECIFIC ANALYSES

The efficacy of applying multivariate classification and ordination methods to matrices of generic and familial data was tested using the random subsample of 235 sites selected for full ordination.

Classification using generic data produced 31 groups at an arbitrarily

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[15] The separation of wetland complexes from those not inundated, as achieved by the previous "full" MDA, took place along the fourth DCA axis.

chosen dissimilarity level of 0.625 (Figure 6.19). There is poor correspondence between the 31 generic groups and the 39 complexes defined by species data. Generic classification group no. 11 contains sites from 9 complexes, and the EUCALYPTUS INCRASSATA – E. FOECUNDA COMPLEX is spread across 9 generic groups. However, there is a better, coarser-scale correlation between generic groups defined at a dissimilarity level of 0.80 (i.e. the groups marked A – F) and the groupings of complexes discussed in Section 6.2.5: group A ≡ coastal dune and clifftop shrublands (Complexes 7–9); group B ≡ sclerophyllous woodlands and heathlands (Complexes 1–6); group D ≡ River Murray riparian vegetation (Complexes 31 and 34); group E ≡ arid chenopod shrublands (Complexes 20–22); and group F ≡ samphire (Complex 36). Generic group C is very large, encompassing all savannah woodland, mallee and seasonally-inundated wetland complexes. Three factors account for this grouping: (i) the dominance of *Eucalyptus* in all savannah woodland and mallee; (ii) the dominance of *Melaleuca* in the wetlands complexes (Complexes 14 and 15) and half of the sites in mallee complexes (Complexes 10–12 and 18a); and (iii) the low diversity of other genera in any of these complexes. The effect of low diversity is enhanced by disturbance such that generic group no. 11 consists of disturbed sites in which the understorey is so sparse that only a half-dozen taxa are present and *Eucalyptus* (savannah tree or mallee) is the only taxon present with a cover score > 1. The overriding influence of *Eucalyptus*, and related problems of low species diversity and disturbance, contrast with the successful use of classification by supraspecific data by Dale & Clifford (1979) and Elsol (1986) in Queensland, and del Moral & Denton (1977) in Washington State, U.S.A.

Along its first axis, DCA ordination of the sites from generic groups A–C recovered, in very general terms, the rainfall-correlated gradient from BANKSIA ORNATA – ALLOCASUARINA PUSILLA heathland to EUCALYPTUS OLEOSA – E. GRACILIS mallee via E. INCRASSATA – E. FOECUNDA (Figure 6.20). These three complexes each have a consistent understorey: diverse sclerophyllous subshrubs, *Melaleuca uncinata / Triodia irritans* and chenopods respectively. Sites from E. DIVERSIFOLIA, E. DUMOSA and E. SOCIALIS, which have been shown to have more variable understorey floras, have been scattered over the loci of the E. INCRASSATA – E. FOECUNDA and E. OLEOSA – E. GRACILIS complexes, as have sites from the species-poor savannah woodlands. The second DCA axis functions only to segregate the sclerophyllous woodland and heathland complexes, largely according to generic diversity (Figure 6.21). The third axis (not illustrated) separates the coastal complexes from the sclerophyllous woodland and mallee complexes through which they appear scattered in the two-dimensional ordination plot.

Classification and ordination using familial data are not presented here. They showed further breakdown of pattern, being unable even to recover the general rainfall gradient between the proteaceous / epacridaceous (temperate) and chenopodiaceous (Eremaean) understorey extremes. This poor recovery of pattern is again a function of low diversity, since there are many fewer families than genera. By cover or incidence, most of the perennial vegetation of southern South Australia is made up by only six families: Myrtaceae, plus Casuarinaceae, Chenopodiaceae, Fabaceae, Mimosaceae and Proteaceae. Furthermore, each of the six families occurs throughout the study area in a variety of habitats. For example, chenopods occur in complexes associated with coastal dunes, samphires, seasonally-inundated wetlands, riparian woodlands, semi-arid mallee and arid shrublands.

6.7 DISCUSSION

6.7.1 Appraisal of Analysis Methods

For multivariate analysis of a vegetation data set of which the "true" structure is not known *a priori* (cf. tests of analysis methods with a synthetic, "simulated" data set), assessment of the facility and suitability of the analysis procedures must be made by subjective criteria e.g. the extent and nature of interpretable vegetation patterns which are extracted, the degree to which patterns correlate with habitat, the degree to which patterns correspond with field observation, and, most importantly, the degree to which the revealed patterns extend understanding beyond that gained in the field. By these criteria, the approach adopted for this study has been successful.

Preceding analysis of the complete data set by smaller, regional analyses promoted easy interpretation of classification and ordination patterns across the entire study area by permitting reference to analogues from the simpler regional analyses. Furthermore, this approach highlighted the importance of chorological/geohistorical factors (independent of climatic and edaphic gradients) in the determination of the modern vegetation cover of South Australia (see Section 6.7.2).

The application of Bray-Curtis dissimilarity and UPGMA fusion to unstandardised species cover-abundance data produced two-tiered (rarely three-tiered) classification hierarchies, the units of which are concomitant with field observation and, in most instances, with descriptions in the earlier literature. The distinctiveness of the 38 complexes so defined by the final classification is a function of the high β diversity of the vegetation of southern South Australia. However, high β diversity was also the cause of one of the shortcomings of the analysis, the unsatisfactory classification of the vegetation of Yorke Peninsula. In this region, low sampling density relative to high β diversity, and very extensive land clearance and disturbance (such that few intermediates between vegetation complexes remained), lead to the definition of groupings which did not correspond with field observation and which were redistributed when placed in the context of the full classification. The second shortcoming of the classifications was the unstable affiliations of types intermediate between noda of complexes displaying high floristic continuity. The clearest case of instability occurred in the five mallee complexes, largely due to the asynchronicity of their overstorey and understorey floras along habitat gradients.

While Pielou (1984), Minchin (1987a) and Oksanen (1988) have raised doubts about DCA as a mathematical technique, in practice DCA proved to be an adequate method for indirect ordination such that floristic gradients could be clearly displayed and correlated with measured environmental variables. Its shortcomings largely stemmed from the manner in which it deals with particular combinations of species diversity, especially high β diversity and low α diversity. The data sets of highest β diversity (the full data set, and the Southeast and Murray Mallee regional data sets) produced ordinations for which presentation of all major floristic gradients required display in as many as four dimensions, unattainable on the printed page. In addition, these ordinations showed individual complexes or small groups of complexes outlying along the principal axes. The complexes were, for the most part, also outlying according to the high level structure of the corresponding dendrogram and usually of low average α diversity. Partial ordination of reduced data set provided satisfactory resolution of the problems and gave greater insight into habitat gradients, including more subtle gradients masked by distortion in full ordinations.

It is significant that the distortion of gradients by outliers and examples of the "tongue effect" during ordination was associated with complexes or particular sites of low α diversity at the extremities of principal axes. Often this was symptomatic of systematic changes in α diversity along the axes. For example, species diversity was inversely correlated with DCA axis 1 score in Figures 6.2 and 6.4, due to a correlation between diversity and mean annual rainfall, the main environmental gradient along the axis. In other examples, diversity is influenced by inundation or disturbance. Austin (1987b) and Margules *et al.* (1987) have also recorded diversity gradients. However, the effect of systematic changes of species diversity along floristic gradients (i.e. the interaction of α and β diversities) on the behaviour of ordination techniques has not been addressed by simulation studies of ordination robustness in the literature (e.g. Kenkel & Orloci 1986; Minchin 1987a). Thus this would be a worthy topic of investigation for workers involved in mathematical development and testing of multivariate techniques.

Correlation of measured habitat factors with DCA ordination axes by rank correlation and trend surface analysis gives a modest level of understanding of environmental control of vegetation patterns. Partial ordination of the savannah woodland complexes is the only example of an ordination on which the floristic gradients could not be related to a combination of at least two of rainfall, soil types and inundation. For some correlations, the rank correlation vectors corresponded well with the environmental pattern described by trend surface analysis. However, the vectors were often a gross simplification of curved trends, including trends displaying numerous local maxima and/or minima at different locations on the ordination. Only some non-linearity could be attributed to gradient distortion by the ordination. In other cases, the non-linearity had biological meaning. Soil texture is the most extreme example. Although clearly an important controlling variable, texture was rarely one of the most significant correlation vectors, because its response was rarely monotonic in any direction across an ordination. Instead, local maxima/minima of texture were dispersed irregularly across the ordination, each confined to the loci of one or two complexes. Its multimodal response in two dimensions made texture independent of ordination axes and other correlated habitat factors.

A further point must be made about the correlation vectors. There is a tendency for the most significant correlation vectors to lie diagonal to both of the two principal ordination axes (e.g. Figures 5.2 and 5.16). Intuitively this might be expected. If two independent habitat variables control vegetation distribution, and if sites occur in all parts of the habitat space that the two habitat variables delineate, then the longest floristic gradient (i.e. the principal axis of an ordination) lies diagonally across the habitat space between opposite vertices. The second axis, perpendicular to the first, must also form a diagonal. Consequently, the original habitat variables themselves appear diagonal to both axes on the plotted ordination. The frequency with which diagonal habitat gradients occur is not fully appreciated in the literature. By simply tabulating correlation coefficients of environmental variables against individual ordination axes, some ecologists have underestimated the extent and nature of habitat correlations (e.g. Gagnon & Bradfield 1987; T. Ökland 1988).

A more succinct and satisfying picture of habitat correlations was produced by the multiple discriminant analysis catenation. The two MDA's undertaken relate the abiotic environment of all 38 complexes to a three-dimensional space whose principal axes are chiefly determined by flood inundation, mean annual rainfall and soil type (texture and T.S.S.) in order of significance. The clarity of the catenation again reflects the high β diversity of the data set, which made for easy definition of complexes, the *a priori* groupings for the MDA. However, unlike DCA or other indirect ordination methods, MDA does not suffer from floristic disjunctions between complexes nor from the gradient distortion that discontinuities induce, while still achieving a gradational presentation of vegetation/habitat relationships. Consequently, the method is recommended as a descriptive tool for similar studies in the future.

The only methodological failure was the use of supraspecific data in classification and ordination. Contrary to interstate and overseas findings, most pattern is obscured by the overwhelming, near-uniform dominance of a few supraspecific taxa (especially *Eucalyptus* and Myrtaceae) and the low diversity of other taxa. At the familial level, even the north-south rainfall-related gradient could not be recovered.

In summary, it can be concluded that the combination of selected, quantitative classification, ordination and catenation methods has provided an extensive description of noda and gradients from which to improve understanding of vegetation pattern in the temperate and semi-arid parts of southern South Australia (see below). There were no unique problems associated with the large expanse of the study area, beyond the need to be wary of the effects of the many, long floristic gradients on analysis performance.

6.7.2 Comparisons with Earlier Studies

The results compare well with the many earlier works in the literature which deal with smaller areas of South Australia (see Section 1.3 and Tables 5.1

to 5.7). This leads to general concurrence with Wood (1937) and Specht (1972), the two previous treatments of a similar scope, although the series of classifications and ordinations also contains several improvements over both these earlier syntheses.

Of the two previous works, agreement is greatest with Wood (1937). The primary level of Wood's classification hierarchy, "formations" (after Diels 1906), corresponds to the supergroups of complexes identified on the dendrogram (Section 6.2.5) e.g. sclerophyllous woodlands and heathlands, and savannah woodlands. The only deviation is the inability of the numerical approach to link all mallee complexes in one supergroup. However, the observed division of mallee complexes does correspond with the temperate – semi-arid split described by Noy-Meir (1971, 1974a). Thus it may be inappropriate to consider all mallee as being part of just one "formation".

Wood's "associations" and "associes" are of the same magnitude and composition as complexes defined here. The cases of complexes for which Wood provides the only satisfactory equivalent in the literature make the correlation particularly convincing (e.g. the DODONAEA LOBULATA COMPLEX), as do the resemblances between his "succession diagrams" (actually pioneering direct ordinations) and the DCA ordinations and MDA catenations herein. The close correpondence may be the result of Wood beginning to formulate the concept of the "edaphic complex" (Wood 1939; Crocker 1946). The Eyre Peninsula regional classification showed the similarities between complexes from multivariate floristic analysis and Crocker's edaphic complexes based on Wood's concept (Section 5.8), and analysis of the full data set suggested that the idea may be extrapolated throughout the study area, if allowance is made for some regional shifts of soil type. Clearly Wood had a detailed understanding of vegetation patterning which was ahead of his time, a fact not always appreciated by his present-day ecologist counterparts.

There are deficiencies in Wood's treatment:

1. Poor coverage of semi-arid mallee. Only one association was defined, *Eucalyptus dumosa – E. oleosa*, which is an amalgam of E. DUMOSA, E. OLEOSA – E. GRACILIS and E. SOCIALIS;
2. No associations of seasonally-inundated wetland vegetation in the Upper Southeast e.g. GAHNIA TRIFIDA/FILUM, MELALEUCA BREVIFOLIA and M. HALMATURORUM; and
3. Little definition of "societies" and "socies" (equivalent to types) within associations, except those occurring in the well-studied districts surrounding Adelaide.

However, all three aspects simply result from the small number of vegetation surveys up to 1937, and do not detract from Wood's perceptive acuity.

As a revision of Wood (1937), Specht (1972) had the advantage of 35 years of additional ecological survey work, but agreement with the classification here is reduced. Wood's formations were renamed "systems", and Specht adopted and applied rigorously a rigid hierarchy of structural formations, and floristic alliances, associations and societies. He thereby suppressed some floristic groups which were found to be significant in both Wood (1937) and the current classification, and also grouped together, within one system, associations which are floristically dissimilar e.g. the GAHNIA TRIFIDA/FILUM and River Murray riparian sedgelands in the savannah woodlands system.

Specht provided a detailed breakdown of the sclerophyllous woodlands and heathlands to the level of societies (i.e. types) based on quality regional surveys of the highest rainfall districts (Baldwin & Crocker 1941; Crocker 1944, 1946; Northcote & Tucker 1948; Specht & Perry 1948). Classification detail for these areas cannot be improved here because of the relatively coarse scale of sampling. However this detail contrasts with the lack thereof for mallee and arid-zone communities, for which tentatively designated alliances and associations do not seem to be of the same hierarchical stature (in terms of internal floristic variability) as the same units in the well-studied areas. The other important point to be made about the Specht classification is that, at the scale of this study, the structural "formation" does not provide any information which is not conveyed by complex or supergroup (alliance and system). Formations in this sense can be sidestepped completely without loss of clarity or detail.

Beyond the similarities to Wood (1937) and Specht (1972), the quantitative sampling and analysis approach used here has produced two major improvements. Firstly, the minimal bias of the data collection during the survey itself (most of the remaining bias is due to non-random vegetation clearance patterns) and the numerical treatment of the data produced a classification which is nearly unbiased. All parts of the study area are equally-well represented. Furthermore, there is no downweighting of sites or types which are intermediate between more clearly defined types or complexes. Although the classification then becomes implicitly "fuzzy" *sensu* fuzzy set theory (see Novak 1989; Equihua 1990) , floristic gradients and their environmental correlates are fully appreciated. The classification also has quantified within-group variability and between-group similarity. All types and complexes exhibit or, where naturally more uniform in composition, have the potential to exhibit the same degree of species constancy and fidelity. Thus the analyses have produced a *regularly-structured* classification framework to which all previous and future detailed studies of smaller areas can be related.

The classification does omit some uncommon vegetation types due to the coarse scale of survey sampling e.g. *Allocasuarina luehmannii* woodland (Specht 1951), *Baumea juncea – B. rubiginosa* sedge wetland and *Eucalyptus behriana* . mallee (Specht *et al.* 1974; Davies 1982), *E. nitida [E. willisii]* woodland (Crocker 1944) and *Lomandra dura – L. effusa* tussock "grassland" (Wood 1937; Jessup 1948; Specht 1972). However, these vegetation types could be readily incorporated using additional site-based cover-abundance data.

The second improvement is the greater and better representation of mallee vegetation. Past taxonomic difficulties, especially of the *Eucalyptus oleosa /*

E. socialis / E. transcontinentalis group, have been resolved to allow definition of five complexes by overstorey dominants. Two complexes may be further subdivided into subcomplexes according to dominant species of their understorey floras. For the first time, numerous types are recognised in complexes. The large number of types reflects highly continuous floristic gradients which can be attributed to three factors, the first two of which are plainly illustrated by the classification and ordinations:

1. The independence of overstorey and understorey. Although local dune – swale patterns are purported to be well-developed in mallee systems, with each species associated with dune crest, slope or swale (Parsons & Rowan 1968; Alston 1982), their local habitat associations shift, especially along the rainfall gradient (Parsons & Rowan 1968). Different species show different shifts. Consequently, at the broad scale, mallee overstorey and understorey are not in phase. Each overstorey form occurs with different understorey dominants over a range of annual rainfall and vice versa, resulting in many permutations.

2. Geohistorical factors. The east-west biogeographical cline across southern Australia results in the occurrence of species with eastern Australian affinities only in the Murray Mallee region and species of Western Australian affinities only on western Eyre Peninsula (Sparrow 1990). Neither species type occurs on Yorke Peninsula and eastern Eyre Peninsula. Thus there are pairs of types, each type in a different region, which share eucalypts and dominant undershrub species, but have different minor floristic components.

   Historical effects may also admit of past occasions of vegetation types breaking up into a number of dispersed relicts for extended periods of time during climatic fluctuations such that allopatric speciation took place. Likely examples of this phenomenon in mallee complexes are the restricted distributions of *Eucalyptus cyanophylla* to northeastern Murray Mallee and *E. flocktoniae* to south-central Eyre Peninsula, each isolated from their respective, more widely distributed sister species *E. dumosa* and *E. socialis*.

3. Disturbance. Floristic composition may be sufficiently different during the early and middle stages of post-fire regeneration, or after prolonged grazing, for sites to be assigned to different types. The effect would not necessarily be noticeable in the field if a disturbance has only caused a decrease in α diversity, rather than species replacement as in a sere or disclimax.

The importance of historical factors was also emphasised for the most mesic parts of the study area viz. the regional endemicity of the EUCALYPTUS BAXTERI – PTERIDIUM ESCULENTUM, E. OBLIQUA – E. FASCICULOSA and E. CNEORIFOLIA complexes. For their floristic compositions to have diverged so greatly, these complexes must have long been isolated in climatic refugia. The semisclerophyllous complexes endemic to the Northern Mt Lofty Ranges (southern Flinders Ranges) must also be explained by past confinement to refugia, as neither rainfall nor any measured edaphic variable accounted for their differentiation from related savannah woodland complexes.

6.7.3 Summary of Habitat Gradients

The environmental variables most often correlated with the floristic gradients between complexes were mean annual rainfall, and soil depth, texture, pH, T.S.S. and carbonates. All except soil texture showed simple linear or curved trends with respects to floristic gradients. Soil texture frequently showed more involuted trend surfaces with many local maxima/minima. The localisation of the texture response relative to the more generalised correlations of, say, rainfall suggests that texture is important in its interaction with the broad-scale gradients i.e. it is able to locally modify other responses such as rainfall.

These correlated variables and the locally modifying influence of soil texture point to plant-soil water relations and soil nutrient availability (including salinity) as the prime causal factors of vegetation distribution in southern South

Australia. In practice, such a hypothesis could only be confirmed by laboratory and field manipulative experimentation beyond the scope of this study. However, detailed analyses of individual species field responses to habitat factors can help to further elucidate correlations and permit refinement of causal hypotheses prior to experimentation. Thus analyses of the habitat responses of selected species are presented in the following chapter.

Chapter 7:
DIRECT GRADIENT ANALYSIS: RESPONSE MODELS OF PREDOMINANT SPECIES

7.1 INTRODUCTION

As demonstrated in the previous chapter, multivariate classification and ordination are efficient and effective methods for defining floristic vegetation groups, for determining the degree of variability within groups, and for examining the patterns of gradation between such groups. Greig-Smith (1983) envisaged the joint analysis of vegetation and environmental data as the next step towards a more general, informative and unified approach to phytosociology. However, correlation of abiotic environmental parameters with ordinations (or classifications) provides an imperfect picture of the environmental control of observed vegetation patterns. Imperfections arise from distortion of vegetation gradients by all ordination methods and from assumptions of linear (or even monotonic) correlations between measured variables and ordination axes. Although current research into analytic methods such as CCA addresses these problems (see ter Braak 1987a; ter Braak & Prentice 1988), there are still more fundamental concerns about the use of such methods to produce environmental understanding, especially in a highly diverse and heterogeneous data set such as under consideration here. An ordination to two or three dimensions cannot adequately represent vegetation responding to an environment that is multidimensional in the sense of containing many independent or poorly correlated abiotic influences on plant distribution. Correlation analyses of complex data sets can only be a superficial summary of the manner in which vegetation responds to environment, with more subtle information (that not highly correlated over the entire data set) lost or suppressed. The inability of this approach to yield much beyond the obvious has lead Austin (1987b) to conclude that traditional phytosociological methods will not result in significant contributions to vegetation theory, and that a change in approach and methodology is needed. Austin calls for a more reductionistic attitude to the study of plant communities, in line with current trends in animal ecology.

Although considered by Greig-Smith (1983) to be the simplest form of vegetation-environment correlation, direct gradient analysis in the guise of modelling environmental responses of individual species has been, and continues to be, successfully used to examine the nature and causes of vegetation gradation / continuity (Brown & Curtis 1952; Whittaker 1967; Austin *et al.* 1983; Feoli & Orloci 1985;Ökland 1986a-c). The use of species response models in phytosociology stems from Eltonian and Gaussian theories of niche and competition, for which yield or abundance of a species is plotted against an appropriate environmental variable, thus producing a bell-shaped curve (see Harper 1977). Brown & Curtis (1952) and Whittaker (1967) used such plots to support Wisconsinian ideas of vegetation continuity by demonstrating gradual turnover of species and the succession of dominants along environmental gradients, and loosely ascribed the relative positions of species to facets of their respective niches. As most phytosociological surveys do not furnish accurate abundance data, more recent direct gradient analysis has concentrated on modelling the probability of occurrence of a species under given conditions. Probability responses have been modelled by a number of methods, most notable of which is (multiple) logistic regression from the family of regression procedures known as "generalised linear models" (McCullagh & Nelder 1983; Dobson 1983). Logistic regression has been used to produce predictive species models from both classed environmental data in the form of contingency tables (e.g. Austin *et al.* 1983) and continuous data to which species exhibit linear or bell-shaped responses (e.g. Austin *et al.* 1983; ter Braak & Looman 1986), and there is no theoretical or practical reason to bar regression of a combination of data types (see McCullagh & Nelder 1983).

In this chapter, the environmental responses of twenty species, selected as being characteristic of a wide variety of vegetation complexes, are examined in detail using logistic regression as a generalised linear model. The species models are not seen as alternative to, but rather as complementary to the multivariate analyses in the previous chapter i.e. the two approaches should provide a balance of holism and reductionism by which understanding of vegetation patterns might be furthered (see Wiegert 1988).

7.2 METHODS

Due to the high computational demands of logistic regression, the responses of all 545 species of native perennials recorded could not be modelled. Furthermore half of the species occurred in less than 1 % of sites and it is unlikely that a statistically significant response model could be produced for any of these species. Hence twenty species only were selected for detailed investigation. Each selected species was characteristic of a vegetation complex or an important type in a large complex, and in most cases the species was dominant or codominant (cover score ≥ 2) in a majority of sites where it occurred. Each selected species also occurred in at least 20 sites (2.5 % of total) to ensure satisfactory confidence in the models. Emphasis was placed on species from mallee complexes due to the wide spread of the complexes, and as their floristic patterns have been poorly documented. A summary of the twenty species selected for modelling is given in Table 7.1 and their geographic distributions are mapped in Figure 7.1. Twelve species are eucalypts, of which eight frequently assume the mallee habit.

The environmental responses of each species was defined as the probability of its occurrence (presence) only. Responses were modelled by logistic regression with stepwise removal of variables according to the maximum likelihood criterion using routine "LR" in the BMDP software package (Dixon 1981). Due to the large size of the data set, regressions were undertaken in two stages. In the first stage, all thirty environmental variables listed in Table 3.10 were used as main effects. Interactions were omitted. Linear and square terms were included for all continuous variables at this stage of the modelling. Westman (1980), Austin *et al.* (1984) and ter Braak & Looman (1986) describe the use of square terms in the regression of approximate Gaussian-type bell-shaped responses. The stepwise removal of variables was constrained so that linear predictors could only be removed after removal of their respective square terms. The second stage of modelling consisted of testing the interactions of the variables found to be significant in the first stage. The same stepwise reduction procedure was used. Only first order interactions were fully tested. Preliminary trials had found no second order interactions significant at the 5 % level.

Nominal or ordinal classed variables were treated as factors in the manner of a contingency table. Some variables were presented to the regression in a form different from that by which they were measured. The geological substrate variables (originally continuous e.g. depth to sheet calcrete) were converted to factors, each of three ordinal classes ($<$25 cm, 25–75 cm and $>$75 cm). Soil texture, although really an ordinal classed variable, was treated as continuous for the purposes of regression.[16]

7.3 RESULTS

The final models from the stepwise regressions are presented in Tables 7.2 to 7.21. A more readily assimilable summary of the significance of each variable in the models and of the models themselves is given in Table 7.22.

7.3.1 Significant Environmental Variables as Predictors

All ecological modelling is a search for a set of variables by which to enhance prediction of an event, in this case the occurrence of a particular species,

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[16] Nominal or ordinal variables of many classes, especially when included in interaction terms, result in the loss of numerous degress of freedom in the regression and rapid near-saturation of response models (cf. Austin *et al.* 1983). Although saturated models may be statistically sound, the ecological value of their interaction terms is equivocal.

with a known degree of confidence. The summary of column significance at the bottom of Table 7.22 give a crude indication of the value of each environmental variable as a predictor of species composition over temperate South Australia. Annual rainfall is clearly the best of all variables measured, followed in a group by altitude, texture of soil (horizon A), pH of same and longitude.

7.3.1.1 Rainfall, Soil Texture and Soil pH

The importance of rainfall, soil texture and pH is not surprising since they were highly significant correlates with the axes of most ordinations in the previous chapter. It is generally accepted by ecologists that these variables influence, and hence indicate, water relations and mineral nutrient aspects of plant environment (Braun-Blanquet 1932; Daubenmire 1974; Barbour *et al.* 1987). Results pertaining to them warrant closer examination.

A preliminary demonstration of the import of these variables for species distributions and the way in which they control the major vegetational gradients in terms of predominant tree and shrub species is given by the histograms of observed response patterns to each variable separately (Figures 7.2 to 7.4). The effects of the combination and interaction of rainfall, soil texture and soil pH are shown in Figure 7.5 for the eucalypts and Figure 7.6 for the shrub species; modelled rainfall × texture surfaces are displayed for three pH levels representative of the observed range.

Almost all responses to individual variables are approximately bell-shaped, although some are skewed in the way observed by Austin (1987a) in eucalypts of the forests of south-eastern Australia. There are a number of bimodalities: rainfall — *Eucalyptus socialis*; texture — *E. baxteri*, *E. incrassata* and *E. leucoxylon*; pH — *E. dumosa* and *E. socialis*. Such patterns in observed responses are often seen as a reflection of the difference between the "physiological" and "ecological" responses of species (Minchin 1987a) or their "fundamental" and "realised" niches (Austin 1985). However most of the skewed and bimodal responses here can be attributed to sampling error, as could those found by Austin (1987a) i.e. the aberrations do not reflect environmental "behaviour" of a species, merely the natural scarcity or absence of particular combinations of environmental factors in which the species would occur. For example, the bimodal texture response of *E. incrassata* (Figure 7.3) might be thought to be the result of an intolerance of loamy soils, but is in fact an intolerance of alkaline, calcareous soils (Figure 7.4). The saddle in the *E. incrassata* texture response is simply due to the small percentage of sites in the data set with loamy soils which have acid or neutral pH and are low in carbonates.

With two exceptions, **(*Eucalyptus leucoxylon* and *E. odorata*),** the order of species optima along the rainfall gradient (Figure 7.2) mirrors the order of vegetation complexes along the first axis of the ordination of the random subsample of the full data set in Figure 6.4. This axis is highly correlated with annual rainfall. Along with *Eucalyptus camaldulensis, E. porosa* and *Callitris columellaris*, the two exceptions are dominants of complexes in the savannah land systems which form a species series with respect to rainfall seemingly independent of the sclerophyllous woodland to mallee to chenopod shrubland series (e.g. the MDA catenation, Figure 6.18). Specht & Perry (1948) showed that the distinction between sclerophyllous and savannah woodlands, was due to the nutrient levels of the soils with which they are respectively associated.

The combination of rainfall, soil texture and soil pH accounts for most of the overlap of species responses along any one of the three gradients alone (Figures 7.5 and 7.6). Thus *Eucalyptus baxteri* and *E. obliqua* have similar rainfall and pH responses, but are distinctive with respect to soil texture and are consequently dissociated (modified Sorenson coefficient of correlation/association[17] d_s = -0.73). Overlap of species responses in three dimensions can be ascribed to either differentiation by a fourth environmental variable, as in the case of *E. dumosa* and *E. socialis* which have differential response to calcrete, or a tendency for coexistence, as with *E. oleosa* and *E. gracilis* which are upper stratum codominants over about two-thirds of their respective ranges ($d_s = 0.19$).

The high degree of overlap of species response surfaces can be taken as

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[17] See Greig-Smith 1983.

establishing the cause, at least at this supraphysiological level of understanding, of the continuity of floristic compositional patterns in the survey area. While it is true to a certain extent, this conclusion must be qualified. The overlap of mapped responses has been exaggerated by the manner in which other variables, important for fewer species, have been incorporated. Values for those variables were set at the observed median for each species, effectively optimising the model for the species and maximising its response to rainfall, texture and pH. It is impractical to map responses with a fourth (and even a fifth) variable which would remove much overlap, but other edaphic and geological predictors which notably enhance habitat definition are noted on Figures 7.5 and 7.6. These variables are discussed in following sections.

The mathematical process of regression by stepwise deletion of variables also confounds interpretation of response overlaps. As it simply uses parsimony to select a subset of available variables that best predicts occurrence of a species, the regression model attaches no ecological or physiological significance to selected variables. Thus when two variables are correlated within the environmental range of the modelled species, the choice of which variable to retain and which variable to remove may be marginal and quasi-arbitrary, based on minor statistical differences. Soil pH and total soluble salts illustrate the problem. In the mallee regions, both are related to the degree of leaching of soils and so are correlated. (They are less well correlated over the entire study area which includes extreme cases of each). pH, not T.S.S., is a component of the model for *Maireana erioclada*, while the reverse is true for *Triodia irritans*. Although they are rarely found together (d_s = -0.78), the absence of pH in the ***T. irritans*** model gives the impression of habitat overlap in the rainfall × texture × pH surface maps. In this case, as in others, the need for additional environmental variables to distinguish responses merely stems from imperfections of the modelling approach. There is no better approach save cumbersome models which include all variables for all species.

Although the response surfaces provide insight into niche separation and overlap of chief species in southern South Australia, a more interesting aspect of the models is that the interaction of rainfall and soil texture is significant for three mallee species: *Eucalyptus incrassata, E. foecunda* and *E. socialis.* This is discernible as a rotation of the long axis of the response such that it runs diagonally across the diagram **(Figures 7.5g, e and l)".** As rainfall decreases across their ranges, these species occur on sandier soils. This interaction is expressed in the field by a retreat from sandy clays or calcareous loams in interdune corridors onto siliceous sand dunes as one progresses northwards through the mallee regions through the rainfall gradient.

Significant interaction between rainfall and soil texture has been recorded in semi-arid Australia previously. Parsons & Rowan (1968) noted that, under different rainfall regimes, mallee eucalypt species showed shifts between soil types of differing textures. However, in successive papers on the topic, their observations were explained as an effect not of soil texture, but of soil nutrient status; drought susceptibility was correlated with soil fertility, which was only indirectly related to texture (Parsons 1968, 1969a). Shortly afterwards, Noy-Meir (1970,1974a) found that depth of soil wetting by 10 % winter rainfall and available soil water were highly correlated with the primary vegetation patterns in arid south-eastern Australia, and that this effect was perceivable as an interaction of soil texture with rainfall. Even so, Noy-Meir did not demonstrate the interaction for individual species nor which species show the response most clearly.

The influence of soil texture on availability of soil water is discussed by Walter & Stadelmann (1974) and Kramer (1983). The larger size of particles and interstitial pores of sands compared with soils of higher clay content results in lower runoff and deeper penetration of rainfall, lower proportional loss through surface evaporation, and lower potential for extraction of stored water by roots. The interaction of rainfall and soil texture must act to maintain constant water relations i.e. water availability at a given pressure potential is similar on clays or loams at high rainfall and on sandy soils at low rainfall. By retreating to sand dunes under more arid conditions, *Eucalyptus incrassata, E. foecunda* and *E. socialis* maintain their water balance.

In much the same way, the response models of *Eucalyptus incrassata* and *Banksia ornata* include the interaction of rainfall and depth of soil over underlying rock or subsoil. Both species retreat to deeper soils with decreasing rainfall. Increasing soil depth effects greater storage of extractable water per unit ground surface area i.e. per plant. This interaction occurs with constant soil texture (coarse sand) in *B. ornata*, but parallels, and so compounds, the rainfall-soil texture interaction in *E. incrassata*. Soil becomes both coarser and deeper as *E. incrassata* retreats onto sand dunes towards its lower rainfall limit. This is consistent with the top-to-bottom drying of soil profiles during drought, as investigated by Crombie *et al.* (1988).

7.3.1.2 Altitude and Longitude

Altitude and longitude do not have a direct influence on plant physiology and some comments need to be made about their significance in the species models.

As is evident from the Chapter 2 descriptions of the geomorphology and topography of the study area (also Figure 2.4), the major elevational feature of southern South Australia is the uplifted Adelaide Geosyncline which bisects the region north-south as the Mt Lofty and Flinders Ranges. East and west of the ranges lie undulating plains, largely of more recent sedimentary origin and rarely attaining altitudes greater than 150 m above sea level. In all models where it is a significant predictor, altitude is simply indicating this topographic division of the area.

It is not clear why the division is important. Altitude mediates Mediterranean climates, especially precipitation and temperature. However, the models are supplied with independent rainfall values and there does not appear to be a strong temperature gradient associated with the Mt Lofty-Flinders Ranges block (Figure 2.12), although detailed data are not available. There are geomorphological and edaphic differences between the ranges and elsewhere. The ranges are predominately hills and valleys of acid to neutral loams and clays, with outcropping granites and sandstones; the Tertiary basins are blanketed by a mosaic of siliceous sand dunes, calcareous alkaline loams and various forms of calcrete. Other measured edaphic (and geological) variables included in the models should account for these differences. However, it is possible that altitude may be correlated with a combination of variables which better represent the factors eliciting physiological responses, resulting in selection of altitude over other variables in the stepwise regression.

A third feasible explanation is that altitude indirectly points out some historical factor influencing vegetation distribution. The Mt Lofty and Flinders Ranges, along with other ranges systems in southern Australia, are seen by biogeographers as refugia to which plant species have been forced to retreat during past periods of aridification (Crocker & Wood 1947; Burbidge 1960). There have been many warm arid periods during Pleistocene and Holocene times (Burbidge 1960), most recently between 12 000 and 17 000 years b.p. (Beard 1982; Bowler 1982). There is some evidence to support such a historical influence for two species. *Eucalyptus oleosa* is uncommon in the vicinity of the Mt Lofty Ranges and foothills (Figure 7.1k). Instead, *E. socialis* (Figure 7.1l) and *E. brachycalyx* (Figure 7.1b) occur in habitats whose climatic and edaphic conditions would favour *E. oleosa* elsewhere. This species replacement frequently takes place without a change of associated mallee (*E. gracilis*) or understorey species. In the absence of palynological data - semiarid South Australia has few pollen deposit sites - it can only be speculated whether *E. socialis* and *E. oleosa* have survived an arid period in different refugia, and are yet to readjust and reattain their potential (equilibrial) distributional ranges.

A fourth reason for the significance of altitude is that it is an artifact of analysis caused by the skew of the altitude frequency distribution, with the infrequent high values having a disproportionate weighting upon the regression calculation. For a number of species, this is the most plausible explanation, but since correction of this fault should scarcely change the significance of other environmental variables, the models have not been reconstructed without altitudinal data.

Longitude, even more so than altitude, cannot reflect a direct physiological pressure on plant growth. It reflects instead biogeographic pattern, either east-west restriction of distributional area or different environmental responses from region to region. Of the ten species with longitude in their final models, *Melaleuca lanceolata, M. pauperiflora, M. uncinata* and *Triodia irritans* have a negative regression coefficient for longitude indicating highest probability of occurrence in the west of the study area. The remainder have positive coefficients and maxima in the east.

For *Eucalyptus leucoxylon, E. obliqua* and *Melaleuca pauperiflora*, longitude in the model indicates restricted geographic range. *M. pauperiflora* occurs on Eyre Peninsula and Yorke Peninsula, but is most common in the far west of the study area. Its distribution extends into Western Australia (Jessop & Toelken 1986) and thus this species is a transitional component of the southern Australian biogeographic cline of Burbidge (1960). *E. leucoxylon* and *E. obliqua* are confined to the eastern half of the study area. Their absence on Eyre Peninsula results from the lack of suitably mesic climatic-edaphic conditions more than from a biogeographic pattern *per se.*

The seven other species do not have clearly restricted distributions. Instead, longitude indicates a difference in their "performance" between Eyre Peninsula and the Murraylands. *Eucalyptus incrassata* and *E. socialis* are less likely to occur on Eyre Peninsula in habitats optimal according to the models (e.g. on sand dune systems) because they are locally supplanted by *E. flocktoniae, E. yumbarrana* (both closely related to *E. socialis*) and *E. striaticalyx*, the three of which have Western Australian affinities and ranges broadly paralleling those of *Melaleuca pauperiflora.* Like *M. pauperiflora*, these five species of mallee eucalypt are still components of the east-west cline, but their more subtle distributions reflect competitive interaction at a smaller scale (in specific habitats) in the zone of their overlapping general distributions such that they coexist at the regional scale on Eyre Peninsula. In a similar way, *Callitris preissii* ssp. *verrucosa* and

M. acuminata also seem to be supplanted at their western limits by other shrub species (e.g. *Hakea francissiana* and *M. eleutherostachya*), the bulk of whose distributions lie further west.

The last two species for which longitude is a significant predictor, *Melaleuca uncinata* and *Triodia irritans*, are also typical of siliceous sand dunes, but are both more likely to occur in the west than in the east. Given that the two species are widely distributed in the Murray Mallee and Eyre Peninsula regions (Figures 7.1s and t), it is unlikely that their modified performance is directly attributable to a biogeographic cause. To further elucidate the effect, their environmental responses were modelled in the two regions separately. For this purpose, the northern half of the South-East region was annexed to the Murray Mallee so that east and west spanned the same rainfall range (250–600 mm). The regional models are given in Tables 7.23 and 7.24, and the rainfall × soil texture × soil pH responses mapped in Figures 7.7 and 7.8.

The regional models for *Triodia irritans* differ only in a greater tolerance of finer-textured soils on Eyre Peninsula. This may be explained by the occurrence of *T. irritans* on such soils on outcropping calcrete formations on western Eyre Peninsula and outcropping granitic and quartzitic formation on eastern Eyre Peninsula. These substrates are absent from areas of the Murray Mallee which fall within the rainfall tolerance of *T. irritans.* Walter & Stadelmann (1974) describe how rocky outcrops enhance availability of soil water in arid areas in much the same way as do deep sands.

There is a significant difference between the regional responses of *Melaleuca uncinata.* Its rainfall × soil texture × soil pH response in the Murray Mallee is similar to that of *Eucalyptus incrassata*, including the presence of a rainfall-texture interaction (cf. Figure 7.5g). On Eyre Peninsula, the response is broader and omits soil texture. The omission of texture is probably due to the occurrence of *M. uncinata* on the same geological formations as mentioned above for *Triodia irritans.* The broadening of the response, particularly the shift towards higher rainfall, most likely reflects the dearth of habitats suitable for BANKSIA

ORNATA – ALLOCASUARINA PUSILLA COMPLEX heathlands and all savannah woodlands on Eyre Peninsula i.e. deep siliceous sands at >475 mm annual rainfall, and carbonate free (clay) loams at >400 mm rainfall respectively. In the eastern half of the State, *M. uncinata* is outcompeted in these habitats. Thus the inclusion of longitude in the models of *M. uncinata* and *T. irritans* arises indirectly from regional variation in availability of suitable habitat, as noted previously for *E. leucoxylon* and *E. odorata.*

7.3.1.3 Other Variables

Other environmental variables included in the models were significant for fewer species, generally indicating specific habitat requirements not embraced by the variables discussed above. Thus, for example, *Eucalyptus diversifolia, E. dumosa, Melaleuca acuminata* and *M. lanceolata* are associated with sheet calcrete of the Bridgewater and Bakara formations, although not exclusively so. The interaction of calcrete with rainfall is significant for *E. dumosa*, pointing to it favouring shallow soils over calcrete at relatively low rainfall and deeper soils at higher rainfall. *E. diversifolia* replaces *E. dumosa* on exposed calcrete at higher rainfall. This is possibly an indirect indication of a water relations interaction within the calciphilic flora. Outcropping calcrete may mediate greater water availability than an equivalent alkaline loam at the lower rainfall limit of a species distribution, as do other outcropping rock formations (Walter & Stadelmann 1974).

Of the other species, *Melaleuca pauperiflora* is associated with high levels of total soluble salt, a feature of the calcareous sands of marine origin recently deposited on far-western Eyre Peninsula; *Triodia irritans* is associated with low T.S.S., as discussed above, probably indicating the same nutrient effects as low pH; and *Eucalyptus baxteri, E. incrassata* and *Banksia ornata* are associated with deep soil, specifically siliceous sand. The inclusion of texture of the B horizon in the model for *M. uncinata* reflects its occurrence in parts of the mallee belt on "duplex" soils consisting of up to 1 m of siliceous sand, neutral in reaction, over alkaline orange-brown sandy clay. These soils are in fact intermediate between the shallow loams and deep sands at the extremes of the rainfall-soil texture interaction that *M. uncinata* exhibits in the Murray Mallee region.

The ecological significance of the inclusion of other interactions of these variables is difficult to assess, and further investigation of their physiological meaning in specific cases is needed. For example, there is a negative interaction of soil pH and carbonates in the *Melaleuca uncinata* model, indicating decreasing carbonate levels with increasing pH, even though the two are highly positively correlated over the whole data set (Pearson rank correlation $r = 0.69$, d.f. = 743, $P < 0.001$). pH, carbonates and calcium (the anion usually accompanying unconsolidated carbonate) are all known to influence the nutrient status of soils, particularly by controlling (i) the equilibria of cation exchanges onto clay and humus particles, and (ii) anion solubilities (Jeffrey 1987; Russell 1973). Their regression interaction may be describing either a chemical interaction between soil pH and the buffering of the CO_3^{2-}/HCO_3^- carbonate equilibrium as they effect cation exchange and anion solubility, or an antagonistic interaction between the effect of pH on cation exchange and the competitive binding of Ca^{2+} ions versus other cations onto soil particles (see Nye & Tinker 1977).

7.3.2 Significance of Models

All models are highly significant ($P < 0.001$), partly by dint of the size of the data set. However, there is no uniformity of the proportion of the variation explained by the modelled responses (Table 7.22); r^2 ranges from 0.21 to 0.70, with a median of 0.42.

As is to be expected, the best-fitting models are for species with responses at environmental extremes and geographically restricted distributions: *Eucalyptus baxteri, E. obliqua* and *M. pauperiflora*. *E. baxteri* and *E. obliqua* have extreme rainfall and pH responses (Figures 7.2 and 7.4) and occur only in the high rainfall areas of the southern Mt Lofty Ranges, Kangaroo Island and the South-East.

M. pauperiflora is restricted to far western Eyre Peninsula. Responses of species occupying positions at the ends of environmental axes are easily modelled since their responses are monotonic and overlap the responses of other species only on the side away from the axis end. Species with medial positions on axes have bell-shaped responses and have overlapping responses with species of both higher and lower optima.

Three of the four species with the poorest-fitting models present a dilemma caused by the interface of taxonomy and ecology: *Eucalyptus brachycalyx, E. dumosa* and *E. socialis.* These species are members of hybrid swarms of close vicariads (Lang 1983; also P. Lang pers. comm.) and they exhibit extensive intraspecific morphological variation. Some problems of the *E. socialis* group were described in Section 7.3.1.2 in relation to the presence of altitude and longitude in the response model of *E. socialis.* There appear to be two forms of *E. socialis*: a narrow-leaved small-fruited variety occurring on the alkaline loams on the northern Mt Lofty and Flinders Ranges and on similar ranges on eastern Eyre Peninsula; and a large- and blue-leaved larger-fruited variety on northern sandhills and southern calcrete ridges across the mallee plains elsewhere. To what extent they represent distinct ecotypes cannot be judged from the data presented here. The bimodal response of *E. socialis* to annual rainfall (Figure 7.2) and soil pH (Figure 7.4) could be used to support a hypothesis of ecotypic variation, although this might equally well be attributable to sampling error and the rainfall-soil texture interaction. Further to the ecotypic variation is the existence of two closely related species, *E. flocktoniae* and *E. yumbarrana*, the latter being almost certainly a vicariad originating in the Great Victoria Desert dune system. These species occur on south-eastern and far western Eyre Peninsula respectively in habitats where *E. socialis* might otherwise be expected to occur, leading to the inclusion of longitude in the *E. socialis* model.

An evolutionary/historical scenario beyond current eucalypt taxonomy is required to account for these subtleties. To explain some modern distribution patterns, Crocker & Wood (1947) and Burbidge (1960) postulated retreat of species to more mesic refugia during arid Pleistocene and Holocene periods followed by recolonisation of former distributional areas during more mesic periods. Under current genetic theories, different types of refugia, different sizes of remnant populations in refugia, and different times and distances of isolation could result in varying levels of morphological differentiation and reproductive isolation (Grant 1981), and hence complexes of species, subspecies and ecotypes. It seems that this complexity has not been previously recognised in *Eucalyptus socialis* and so there have been no genetic-taxonomic analyses which might support this postulate.

The case of *Eucalyptus brachycalyx* is similar. There appear to be two ecotypes with distributions paralleling those of the *E. socialis* ecotypes. In addition, *E. brachycalyx* grades into the species most closely related to it in South Australia, *E. rugosa*, along a rainfall gradient that roughly separates the two. Confusing intermediates can be assigned to either species (P. Lang, pers. comm.).

Unlike the instance above, morphological and taxonomic variation in *Eucalyptus dumosa* and related species in *Eucalyptus* Sect. *Dumosae* have been examined (Lang 1983). However the full implications do not seem to have been realised in the taxonomic treatment of Jessop & Toelken (1986). From field observation during the current survey, as many as four forms of *E. dumosa* may be recognised. One form corresponds with *E. calcareana* which proved difficult to consistently identify (see Section 3.8.2) and was consequently united with *E. dumosa* for the purposes of analysis. A second form resembles what was previously named *E. anceps* (based on an incorrect type specimen) but which is no longer recognised by Jessop & Toelken (1986) as a separate species. The appearance of *E. dumosa* as dominant or co-dominant in vegetation types of five classification complexes seems to stem from the existence of these four or so (ecotypic) variants. There are also closely related sibling species (*E. calcareana, E. conglobata, E. cyanophylla, E. striaticalyx*) which locally supplant *E. dumosa.* Again modelling of the environmental response of "*E. dumosa*" might be enhanced by appreciation of ecotypic variation and sibling relationships.

Melaleuca lanceolata is the fourth species having a poorly-fitting response model. *M. lanceolata* is the most frequently found of the 20 species and is present in 12 of the 39 vegetation complexes. Of the twenty species whose responses were modelled, it has the widest range of tolerance with respect to annual rainfall and pH. Size of individual plants varies with rainfall and substrate, from a 5 m tall arboriform shrub of savannah woodland communities near its upper rainfall limit to a 0.5 m high undershrub in semi-arid coastal communities. However no overt variation ascribable to potential ecotypic variation was observed in the field. With respect to the environmental data gathered, the distribution of *M. lanceolata* is enigmatic and no plausible explanation for it can be proffered here. Its elucidation requires a more detailed autecological approach.

The remaining thirteen species, whose models gave r^2 in the range 0.30–0.55, are floristic elements which are taxonomically sound and readily identified, and which do not occur in restricted environmental extremes. Their responses to continuous variables are bell-shaped or skewed or truncated bell-shaped for the most part. While not very high, this degree of fit in models can be regarded as the norm for the scale of the survey undertaken. Disturbance, more subtle biogeographic patterns and natural stochastic elements contribute to this level of unexplained variation.

7.4 DISCUSSION

The three outstanding results of the environmental response models are the interaction of soil texture with rainfall as an indicator of water availability in the root zone, longitude as an indicator of east-west biogeographic gradation, and the influence of taxonomic instability on single-species ecological modelling.

The importance of the rainfall-soil texture interaction accounts for the individual correlations of annual rainfall and texture with ordinations in the previous chapters. Where soil texture showed a monotonic trend, the correlation vectors of rainfall and texture were perpendicular (e.g. Figure 5.2, the Southeast regional ordination). There, the principal ordination axis was a direct representation of the soil water status gradient described by the rainfall-texture interaction. Where soil texture showed a complex trend on the ordination plot, the interaction shown above reinforces the hypothesis that texture acts to locally modify the rainfall regime, thereby more accurately reflecting soil water availability.

Of the twenty species examined, the rainfall-soil texture interaction was demonstrated to be significant for *Eucalyptus incrassata, E. foecunda, E. socialis* and in the Murray Mallee region for *Melaleuca uncinata.* An equivalent rainfall-soil depth interaction for *Banksia ornata* was recorded. There is additional external evidence to suggest that this water relations effect is more general.

Throughout temperate South Australia, *Eucalyptus oleosa* occurs on a variety of calcareous loams and sandy loams (Figure 7.3). However, Barker (1972) records that *E. oleosa* is strictly associated with *Triodia irritans* on siliceous sand dunes on Quandong Station, which lies about 100 km north of the northern boundary of the Murray Mallee region (as defined here) at an average rainfall of 200 mm. Adamson & Osborn (1922) also noted *E. oleosa* as a sand dune species near Ooldea on the north-east flanks of the Nullarbor Plain in a similar rainfall regime. Hence *E. oleosa*, too, retreats to sand dunes under decreasing rainfall and displays a rainfall-soil texture interactive response, but does so beyond the northern limits of the survey, thus preventing its detection by the model. *Eucalyptus baxteri* can also be shown to respond to the interaction, although its response was undetected due to truncation of the rainfall gradient by the location of the South Australian coast. It was recorded chiefly on coarse sands in the South-East region, but at higher rainfall in confined areas of the southern Mt Lofty Ranges and Kangaroo Island and over much wider areas of neighbouring Victoria, *E. baxteri* occurs on fine-textured duplex clays (see, for example, Boomsma 1981), as predicted by a water relations interaction.

Consequently a generalised water relations model is proposed (Figure 7.9). Each species is represented by a line describing the diagonal ridge of its most probable occurrence under the given climatic and edaphic conditions. Probabilities taper off to either side of the diagonals. Lines parallel to the axes summarise the floristic gradients along edaphic gradients at constant rainfall or along rainfall gradients on particular soil types.

Some points need to be made about the generalised model. Firstly, the model refers to only the continuum of semi-arid and temperate sclerophyllous communities, and omits species of savannah woodlands. Savannah woodland species do not extend onto sand dune systems, and they represent a distinct water relations series restricted to soils uncommonly fertile for South Australia (Specht & Perry 1948; see also Figures 6.15 and 6.18). (Note however that Todd (1965) found potential water relations control within the savannah woodlands series obscure and impossible to measure in the field). By contrast, for most species shown on Figure 7.9, the rainfall-soil texture interaction entails shifts in other environmental variables, particularly soil pH, total soluble salts and carbonates. It must be inferred that these species' requirements for maintenance of water balance override any changes to nutritional status that result.

Secondly, the slopes of the interactions *are not all the same.* Other variables, different for each species, must slightly modify the water relations response by appeal to different physiological functions. Some species such as *Maireana sedifolia* and *Triodia irritans*, show none or a very weak interactive response. They must maintain water balance by alternative means. Thus the model based on water availability does not apply universally to all species to the same degree. The net result of the different slopes, or absence thereof, is the myriad of potential species combinations (vegetation types) and the high level of compositional continuity displayed in the previous chapter, even when variation of purely biogeographic origins is excluded.

This model of water relations as the prime controller of vegetation in south-eastern Australia is not a new idea. Noy-Meir (1974a) discussed the interaction of rainfall and soil texture for distribution of vegetation types, and is to be credited with the initial demonstrations. Here, however, by taking an individual species approach, as Noy-Meir did not do, the rainfall-soil texture interaction is shown to be widespread in the flora, but with sufficient *individuality* of responses to account for more subtle and "continuous" compositional patterns, extending along the whole climatic gradient from chenopod shrubland to temperate sclerophyllous woodland.

There have been a number of relevant studies by Australian ecophysiologists who have compared the water potential responses of dominant eucalypt species during summer drought (e.g. Sinclair 1980; Crombie *et al.* 1988; Davidson & Reid 1989). These studies have shown interspecific differences of water balance and suggested that, within their area, the boundaries between communities dominated by different eucalypts might be related to the advantages conferred by higher (or lower) tolerance of water stress. However, while this work indicates that the general distribution patterns of species are correlated with soil water availability patterns in summer, the data are insufficient to permit extrapolation over a large area of varying climate and soils.

Thirdly, the model describes realised niche in an all-embracing way, but does not provide an ecological mechanism by which it is achieved. Competition is seen by current theory as the mechanism by which potential or fundamental niche is converted into realised niche (Harper 1977; Silvertown 1982). A lower limit of soil water availability beyond which the anatomy and physiology of mature, and more especially, seedling plants of a species cannot maintain competitive ability during summer dry periods and prolonged droughts, is intuitively straightforward. In this case, the lower limit of fundamental and realised niches nearly coincide. An upper limit is more problematic. Horticulturists commonly grow species under more mesic conditions than those under which the species are naturally found. Thus the upper limit of the realised niche is significantly lower than that of the fundamental niche. If competition is the mechanism by which upper limits are determined, leading to species replacement along a soil moisture gradient, then either the innate competitive ability of species must increase along the moisture gradient or a second, negatively-correlated factor must modify competitive ability. Soil pH is the most likely candidate for a second factor negatively correlated with water relations in the study area. Mineral nutrient availability may be controlled by pH. Testing this hypothesis would require intensive manipulative experimentation.

The significance of longitude to the models and, by inference, the east-west biogeographic cline cannot be overestimated. Burbidge (1960) examined the well-defined biogeographic differentiation east-west across southern Australia and proposed a historical sequence of speciation and migration to account for it. Green (1965), Parsons (1969b, 1970) and Horton (1984) provided corroborative evidence. The mallee belt in South Australia (and adjoining parts of Western Australia) provide the most continuous manifestation of the cline. Perhaps half of the species in the mallee floras of eastern and central South Australia are replaced by species with Western Australian affinities as one progresses westwards across the study area within one soil group (see Sparrow 1990). Some species with western affinities occur as remnant populations on Eyre Peninsula, separated from the main body of their species by the Nullarbor Plain e.g. *Eucalyptus flocktoniae.* Some have more recently intruded as the Great Victoria Desert dunefield was blown eastwards 10 000-20 000 years ago (see Twidale & Campbell 1985) e.g. *E. yumbarrana.* The east and west variants of most mallee complex vegetation types that result from the cline are apparent from the synecological analyses of Chapter 6. The response models in this chapter are affected such that species have extensively overlapping responses without anywhere coexisting. An unmeasurable historical factor rather than any physical or chemical characteristic of their habitats differentiates their distributions.

The difficulties experienced with inadequate taxonomic treatments also stem from the temporal disequilibrium of vegetation along the biogeographic cline. With the exception of successional concepts, phytosociology ignores time and evolutionary change. Vegetation and environment are correlated at a single instant, or at best with regard to the past century or two. As illustrated here, at any instant some species are apparently in a state of evolutionary equilibrium while other species, even higher taxonomic groups, are in the process of change and divergence. *Eucalyptus dumosa* and *E. socialis* are examples of species groups in change. They seem to represent collections of ecotypes and vicariant (?) species correlated with the east-west biogeographic cline and possibly arising from isolation on different refugia during recent arid periods (see Crocker & Wood 1947).

Hereditable ecotypic variation in plant species has been demonstrated in Europe and North America (Turesson 1922, 1925; Clausen *et al.* 1948). There have been no comparable demonstrations with plant ecotypes in Australia. Moran & Hopper (1987) and Sampson *et al.* (1988) have examined the purely genetic consequences of isolation in small populations of mallee-form eucalypts, but did not observe ecotypic differentiation. However, in a zoological example, Williams *et al.* (1988) and Schwaner (1990a, 1990b) described molecular *and morphological* variation in small isolated island populations of tiger snake in South Australia. Molecular variation was related to the duration and degree of their genetic bottleneck (a function of maximum isolation distance and minimum population size whilst isolated), while morphological variation was related to the size of available prey and burrows, and to molecular divergence (see also Grant 1981 for a discussion of the genetic bottlenecks as a divergence mechanism).

When expressed as ecotypic variation, genetic variation in plants leads to bimodality (multimodality) of the environmental responses of species. Poor fit of a Gaussian logistic regression environmental model is but one manifestation of high genetic variability. It must also affect ordination and classification in phytosociological analysis. Austin (1985, 1987a) expressed concern about distortion of ordinations induced by bimodal responses. Species of high genetic/ecotypic variation need to be identified and allowance made for them during interpretative stages of phytosociological studies. Some attempt at initial recognition of ecologically distinct subspecies was made in this study (see Section 3.8.2). Ultimately such variation ought to be accommodated in a general approach to vegetation studies at scales beyond the purely local. Furthermore, the additional evidence of ecotypic and vicariant pattern detailed here should prompt eucalypt taxonomists to reconsider taxa and their relationships in a more flexible manner, concordant with the field situation.

Chapter 8: IMPLICATIONS OF THE STUDY FOR ENVIRONMENTAL MANAGEMENT AND CONSERVATION

For many miles about
There's scarce a bush.

William Shakespeare: King Lear, II, iv, 296–7.
(From "The Complete Works", Viking, New York, 1979).

— As treeless as Portugal we'll be soon, says John Wyse, or Heligoland with its one tree if something is not done to reafforest the land.

James Joyce: Ulysses.
(Penguin, London, 1985).

8.1 INTRODUCTION

Surveys of the kind undertaken as part of this project provide data suitable to guide the development of policy for environmental management. The native vegetation of southern South Australia is not managed for traditional economic activity. Its sclerophyllous, depauperate and largely semi-arid nature renders it unconducive to profitable forestry, stock grazing of native grasslands or other agricultural pursuits. Instead, the natural vegetation cover of the temperate parts of the State has been extensively cleared by European settlers to make way for forestry, agriculture and pastoralism based on exotic species, mostly imported from the Northern Hemisphere (see Section 2.6). However, rising interest by the general community for conservation of the environment has lead to a desire to preserve at least part of the area's remnant vegetation on philosophical, aesthetic and practical grounds, the last relating to problems of soil erosion and dryland salinisation (Whitelock 1985; Harris 1986). This wish is recognised at the governmental level and is embodied in State legislation such as the National Parks and Wildlife Act, 1972–1974, and the Native Vegetation Management Act, 1985. Conservation in this sense is now the major environmental management issue.

Selection of patches of vegetation for preservation is governed by principles of rarity, diversity, representation and size (Usher 1986). There is worldwide interest in the identification and documentation of rare plant species (e.g. Ayensu & DeFilipps 1978; Goldsmith 1974; Gomez-Campo 1985 and all papers therein; Hall & Veldhuis 1985; Kelly 1988; Leigh *et al.* 1981; Lucas & Synge 1978) with the aim of encouraging their culture in research institutions and their preservation in natural ecosystems (Ruiz de la Torre 1985). Conservation of rare species can be seen as maintenance of world stores of genetic variation. In addition, rare species often act as indicators of high α diversity (Nilsson *et al.* 1988). There is no less interest in rare species in South Australia and there are a number of local sources of information on rarities (Specht & Cleland 1963; Specht *et al.* 1974; Jessop 1977; Leigh *et al.* 1981, 1984; Davies 1986; Lang & Kraehenbuehl 1987; Briggs & Leigh 1988), all based upon herbarium collections and undocumented field experience. Concern for rarity in South Australia has been extended to rare vegetation types and their role in conservation assessment (e.g. Specht & Cleland 1961; Specht *et al.* 1974; Davies 1982; Moore 1985). In practice, rarity is the most effective reason for retention of vegetation under the State's Native Vegetation Management Act.

The aim of a representation principle is to conserve the full range of ecosystems in any one area and thereby both α and β diversity (Austin 1984). Hence conservation by representation can be allied with conservation by rare vegetation types if "rare" equates with "rare in designated preserves". Purdie *et al.* (1986), Purdie (1987), Margules & Nicholls (1987), Nilsson (1986), Nilsson *et al.* (1988) and Cocks & Baird (1989) illustrate the spectrum of studies in which survey data sets have been used to examine the question of representation and to optimise a conservation strategy based on this by algorithms which find minimum areas for maximum representation.

Patch size derives its significance to conservation from two sources: the tenets of the island biogeography theory (MacArthur & Wilson 1967), much of which is now somewhat discredited, and from genetics (see Drury 1974; Main 1982). The latter concerns the minimum population size (thus area) required to sustain a viable population in the face of natural stochastic events. Schonewald-Cox & Bayless (1986) and Soulé & Simberloff (1986) summarise approaches to the patch size problem, which is usually referred to as the "single large versus several small" question. Little has been done in this field in Australia, especially with plants, and so its application is largely speculative. Some relevant examples are the recent studies of Moran & Hopper (1987) and Sampson *et al.* (1988) which provide data on genetic variation of some rare eucalypts in Western Australia, and reflect on the implications for the conservation of the species and their variation.

Austin (1984) stressed the link between management application and sampling strategy in the design of conservation-oriented surveys. His comments are highly pertinent to survey scale. The scale of the survey described over the preceding chapters means that it cannot address questions of remnant patch size nor representation of vegetation associations within individual patches. It can, however, contribute to questions of species rarity, vegetation type rarity and representation of vegetation types in the existing network of State reserves. These factors are examined below. In addition, a method to measure relative remnancy along major vegetation gradients as described by indirect ordination axes is proposed and tested.

8.2 METHODS

8.2.1 Rarity of Species

One consequence of the differential patterns of vegetation clearance in the study area is that the number of sites at which a perennial species occurred does not necessarily indicate its remnant population size nor the area of its present-day range.

However, a probabilistic approach to assessment of remnancy using the survey data is possible on two conditions: firstly, local remnancy in the vicinity of each site is known, and, secondly, it is assumed that each site is randomly located with respect to the vegetation types in its corresponding 200 km^2 sampling cell. Figures for percent remnance of each hundred in the Agricultural Districts were available from the records of the Native Vegetation Management Branch, South Australian Department of Environment and Planning. The assumption of local randomisation was acceptable given patchy clearance patterns and the difficulties of access that determined site placement (see Chapter 3), and in the absence of any better survey data of this kind.

Thus the remnant range of habitat in which each recorded native perennial species occurred was estimated by correcting its frequency by the local remnancies of each site, using the following formula:

$$A_k = \sum_{i=1}^{n}(p_{ki}.\frac{R_i}{100}.200)$$

where:

- A_k = estimated range area of species k;
- n = total number of sites;
- p_{ki} = presence or absence of species k at site i; if present, $p_{ki} = 1$; if absent, $p_{ki} = 0$; and
- R_i = local remnancy at site i, as a percentage.

Local remnancy was the remaining cover for the hundred in which the site fell. For sites occurring within 2 km of hundred boundaries and thus whose 200 km^2 sampling cells extended into two hundreds, the mean of the two hundreds' remnancies was used. Percent remnancy was halved for Transect 8 sites along the South Australian – Victorian border, since half of the sampling cells which these represented fell in the neighbouring state.

Variation in local clearance made calculation of a binomial error term on the remnancy areas impossible. Instead the confidence of species remnancy values was set at the simple probability of ± 1 site and converted to an area by taking the mean cell remnancy for those sites at which the species was present.

8.2.2 Remnancy of Vegetation Types

Remnancies of the vegetation complexes and types of the full classification were estimated by the method devised in the previous section for species rarity. For each complex and type, total remnancy was partitioned into three estimates covering sites in N.P.W.S. reserves, other undisturbed sites, and disturbed sites, thereby aiding assessment of relative conservation status.

Remnancy of vegetation types relies on an adequate vegetation classification and does not take into account the gradation (or otherwise) between types nor the variability within types. As ordinations provide information on patterns of gradation and internal variation, a method was proposed to determine relative remnancy in the context of vegetation gradients by making point estimates of remnancy across an ordination scattergram of few dimensions by means of a moving averages technique. The remnancy index was calculated as follows.

A square grid of sampling points spaced at regular 0.125 half-change unit intervals was superimposed on the ordination. An estimate of remnancy was made at each vertex by summing the local remnancy of all sites falling within a radius of 0.25 hc units. The choice of a radius of 0.25 hc was rather arbitrary; it was found to be sufficiently large to produce a smooth moving averages plot and small enough to avoid an oversmoothed, trivial curve. A radius of 0.25 hc is equivalent to all vegetation which shares at least 87.5 % of the floristic composition (in terms of the ordination space) at the grid point.[17] Remnancies were standardised to the units $\mathrm{km}^2/\mathrm{hc}^n$ where n is the number of ordination dimensions examined. The gridded estimates were then contoured to produce a continuous mapping of remnancy in relation to the species turnover patterns described by the ordination axes.

The method was applied only to full and partial DCA analyses of the complete data set which exhibited no near discontinuities (as analysed in Chapter 6) and only to two-dimensional ordinations.

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[17] See Gauch (1982) for interpretation of half-change units as compositional dissimilarity.

8.3 RESULTS

8.3.1 Species Rarity

Estimated remnant ranges of the perennial species are presented in Table 8.1, along with the conservation status ratings of each according to Leigh *et al.* (1981; updated as Briggs & Leigh 1988) and Lang & Kraehenbuehl (1987). In order to exclude species whose rarity is entirely attributable to the position of the bounds of the study area, species with an estimated range of less than 1000 km^2 have been omitted where Jessop & Toelken (1986) centres their known ranges in the arid northern portions of South Australia.

The remnancy estimates cover the range 0–10 600 km^2, but, as for species frequencies, the distribution of species remnant areas approximates a Poisson-type or truncated log-normal distribution (Figure 8.1; cf. Figure 3.5), with a median of just 450 km^2. *Triodia irritans* (10 600 km^2) and *Hibbertia riparia* (10 500 km^2) are the most widespread, occurring in approximately 30 % of the total area of remnant vegetation (35 500 km^2; see Table 8.1), although rarely together. *T. irritans* occurs across the northern, drier half of the study area and *H. riparia* across the southern, wetter half. *Melaleuca lanceolata* and the sedge *Lepidosperma laterale* are almost as widespread, the former being the most frequently encountered species of all (Appendix 2).

The lowest recorded remnancy is that of *Spyridium nitidum* (0.6 km^2), present at a single site in a heavily cleared portion of the Murray Mallee region. Sixty-five species have remnancies less than 50 km^2 and a further 38 have estimated remnancy in the range 50–100 km^2. Almost all these species were found at only one site in extensively cleared districts. Given the assumptions of the calculations of remnancies and the lack of confidence which can be placed on remnancies based upon a single record, the rankings amongst these least common species is subject to doubt and in practice all should be assigned an equivalent status of “rare” or similar.

Unrecorded perennial species (with distributions known to be concentrated in the study area) can be considered "very rare". Leigh *et al.* (1981) listed 84 perennial species of the temperate zone which they considered to have conservation significance in southern South Australia, but only 31 of them were recorded during this survey (Table 8.2). The absence of the remainder from this data set provides implicit support for their high conservation ranking.

The species rankings derived from estimates of remnant habitat areas do not correspond well with the conservation status codes from the two main published sources for South Australia. The 35 species to which Leigh *et al.* (1981) attached some significance are seemingly randomly dispersed over the estimated remnancy range 0–2400 km^2. The much larger number of species noted by Lang & Kraehenbuehl (1987) to be worthy of concern occur over the same range of remnancies, but, in contrast with Leigh *et al.* (1981), are concentrated among the species calculated to have lowest remnancy. However, Lang & Kraehenbuehl's categories "uncommon", "rare" and "vulnerable" (here listed in order of increasing significance) are not correlated with habitat area estimates as might be expected. The remnancies of species rated "rare" and "vulnerable" cover overlapping ranges of 1–231 km^2 and 15–373 km^2 respectively (Table 8.3). Many unrated species also fall into these ranges. "Endangered" is reserved by Lang & Kraehenbuehl (1987) to describe species at highest risk. This category is perhaps the most reliable as only one recorded species had been given this rating.

In Briggs & Leigh (1988), a conservative revision of Leigh *et al.* (1981), only 16 perennial species which occur in the study area are given a conservation status code (13 of the original list, plus three additional species). Despite the more restricted definition of rarity, these species are still irregularly dispersed over a wide remnancy range (0–1000 km^2). This small number of significant species renders Briggs & Leigh (1988) unsuitable for most applications within Australia (and thus is not considered in detail here). Their Australia-wide study focusses more on the diverse floras of Queensland, the Northern Territory (e.g. the Arnhem Land tablelands) and Western Australia, where newly-discovered species have recently attracted the attention of taxonomists.

The lack of correspondence between published rankings and estimated remnant areas stems from three possible sources: (i) inaccuracies in the calculations above, (ii) insufficient information on the parts of Leigh *et al.* (1981), Lang & Kraehenbuehl (1987) and Briggs & Leigh (1988), and (iii) differences in interpretation of "rarity". There is no reason to suspect that rare perennial species have been often misidentified or overlooked at sites in this survey. The inaccuracies associated with the estimations of infrequently recorded species and the difficulty of determining confidence in these estimates were described above. The remnancies of some more common species with unusual distributions may have been underestimated and the distributions of rarer species overestimated through purely random factors.

Such inaccuracies do not however account for species previously given the same significance rating having remnant areas of four orders of magnitude difference. *Acacia dodonaeifolia* and *Phyllota remota* are both rated rare (3R) by Leigh *et al.* (1981) and uncommon (U) by Lang & Kraehenbuehl (1987), yet their remnant areas are respectively 0.8 km^2 and 2420 km^2. Although the common *P. remota* is not listed by Briggs & Leigh (1988), conservation significance has instead been assigned to *Grammosolen truncatus* for which the estimated range is 890 km^2. Thus the three published studies must suffer from bias attributable to herbarium collections and/or a lack of relevant regional ecological survey data. Lang & Kraehenbuehl (1987) admitted these limitations and also the impossibility of overcoming them with the data then available. Limitations are also acknowledged implicitly by the conservatism of Briggs & Leigh (1988) relative to Leigh *et al.* (1981).

Some differences are undoubtedly due to differences of interpretation of rarity. Leigh *et al.* (1981) and Briggs & Leigh (1988) were national studies, despite their regional breakdowns, while Lang & Kraehenbuehl (1987) was confined to South Australia, leading to divergent perspectives on the significance of some species. Numerous species having restricted distributions in South Australia are a common feature in parts of other states. For example, *Eucalyptus macrorhyncha* is widespread in Victoria, but is found in South Australia in only one mesic refuge in the Northern Mt Lofty Ranges. Consequently it was listed by Lang & Kraehenbuehl (1987). Alternatively some species are relatively common at a State level but attain national significance as they occur only in South Australia. Since Kangaroo Island is the least extensively cleared region in the State (43 % remnant cover) and has many nature reserves, the latter group includes Kangaroo Island endemics and other species with distributions concentrated there, such as *E. cneorifolia, E. remota, Micrantheum demissum, Petrophile multisecta* and *Spyridium halmaturinum.* These species were listed by Leigh *et al.* (1981), but were omitted by Briggs & Leigh (1988) probably due to their representation in reserves.

In contrast with other methods which, although it is not explicitly stated, presumably assess remnant population size, assessment by remnancy area determines the extent of suitable habitat for each species. For a species to be recorded at a site i.e. for the site to be included as "suitable habitat", there had to be one plant in the 0.1 ha quadrat and therefore a local population density in the order of 10 individuals per hectare or greater. Thus remnancy area conservatively indicates just a minimum population size for each species and does not attempt to measure the exact size of a remnant population. Remnant area is an index of conservation status of species in natural ecosystems at natural (sustainable) densities. Furthermore, the calculations are of a probabilistic (speculative) nature, in the sense that the likelihood of encountering a species is measured, and thus suffer from sampling uncertainties described by McArdle (1990). The combination of these mathematical features accounts for a large proportion of the differences between conservation ranking of species by area of remnant habitat and by previous published lists.

For the most part, the discrepancies are for species which have a low estimated remnant area, but lack acknowledged conservation requirements. These species tend to be common over restricted areas, but whose habitat is being depleted. A number of species with distributions confined to or centred upon the southern parts of the Mt Lofty Ranges fit this description: *Billardiera bignoniacea, Daviesia leptophylla, Hakea carinata* and *Pultenaea involucrata*, as well as *Acrotriche fasciculiflora* rated "uncommon" by Lang & Kraehenbuehl (1987). All these species feature in the sclerophyllous woodlands at high rainfall along the spine of the ranges, and distinguish the vegetation there from related sclerophyllous types in other regions of the State. Their low estimated remnancies are entirely the product of extensive clearance of their woodland habitat to make way for dairying, intensive horticulture and expanding outer suburbs of the Adelaide metropolitan area (see Harris 1986). Overall remnancy in the region is merely 5 %. In view of the threat to their natural habitat, reappraisal of the conservation status of at least some of the flora in this region is suggested.

The number of rare species present at a site cannot be accurately predicted from the total number of species present (Figure 8.2). Although a linear regression of the relationship is statistically significant ($r = 0.34$, d.f. = 743, $P < 0.001$), its biological significance must be questioned as only 12 % of the variance is explained by the regression. This result contrasts with the findings of Nilsson *et al.* (1988) that diversity predicts occurrence of rare species and vice versa. Two differences in the data may account for the differing results. Firstly, and more importantly, Nilsson *et al.* (1988) dealt with a single complex of ecosystems, namely river banks in northern Sweden, while the present study encompasses a great variety of complexes. A number of different environmental gradients such as rainfall, soil micronutrient levels and salinity influence average species diversity in these complexes and so confound a simple rarity-diversity relationship over all complexes. For example, a linear regression of this relationship within the EUCALYPTUS INCRASSATA – E. FOECUNDA COMPLEX is more significant than for the whole data set ($r = 0.53$, d.f. = 136, $P < 0.001$; 28 % variance explained). Secondly, there is much variability across the study area in the level of degradation of sites and therefore a tendency to underestimate natural diversity of some sites in heavily cleared districts where rare species occur. Thus no generalisations can be made about the distribution of rare species with respect to total α diversity.

8.3.2 Vegetation Type Rarity

As with the species remnancy figures, the estimates of remnant areas of vegetation classification groups (Table 8.4) cover a wide range: complexes, 0–7500 km^2 and types, 0–2900 km^2. Again, distributions have a strong right skew and least confidence can be placed on the smallest remnancy values; all figures under 50 km^2 (or even 100 km^2) should be regarded as equivalent and assigned the same preliminary conservation status.

The two most widely occurring complexes are the EUCALYPTUS OLEOSA – E. GRACILIS and E. INCRASSATA – E. FOECUNDA complexes, with approximately 7500 km^2 and 7200 km^2 remnant respectively. They are the predominant types of vegetation in the study area at lower rainfall regimes (<400 mm annually) and together constitute just over 40 % of all remnant vegetation. Despite these similarities, the two complexes have contrasting representation in designated conservation areas: 7 % of remnant E. OLEOSA – E. GRACILIS occurs in N.P.W.S. reserves, incorporating 4 of its 21 recorded types; whereas there is 28 % of remnant E. INCRASSATA – E. FOECUNDA in reserves, including 10 of the 25 types. The disparity of protection levels stems from the suitability of their habitats for agriculture. The calcareous loams on which E. OLEOSA – E. GRACILIS types occur form the basis of dryland cereal farming in South Australia. Consequently this country has been extensively settled and cleared, and most of the land has been purchased from the Crown by private individuals. Reacquisition by the State for conservation purposes is infrequently possible. In comparison, the sand dune systems of the E. INCRASSATA – E. FOECUNDA COMPLEX were early recognised as unsuitable for agricultural purposes. As a result of the absence of private interest, these lands have been retained by the Crown estate so that their transfer to the N.P.W.S. is easy and many reserves have been created in large areas of sand dunes. The third most widespread complex, BANKSIA ORNATA – ALLOCASUARINA

PUSILLA, likewise occurs exclusively on siliceous dunefields noted for mineral nutrient deficiencies and sand drift which renders its habitat unpracticable for agriculture (see Riceman 1945, 1948), with the result that 73 % of its remnant area is contained in N.P.W.S. reserves.

Seventeen of the 38 described complexes have remnancy estimated at 200 km^2 or less. Some are merely the most southern extensions of the arid zone land systems and from this data set cannot be judged to be under threat in South Australia, e.g. the ACACIA PAPYROCARPA, CALLITRIS COLUMELLARIS and DODONAEA LOBULATA complexes (see Section 6.2.2). Some are strictly coastal and, under current coastal protection laws, are similarly not at risk, e.g. the ATRIPLEX CINEREA, AVICENNIA MARITIMA and JUNCUS KRAUSSII complexes. The ACACIA PYCNANTHA and JUNCUS PALLIDUS complexes appear to be disclimaxes of the EUCALYPTUS BAXTERI – PTERIDIUM ESCULENTUM COMPLEX (or possibly E. LEUCOXYLON) and do not warrant individual attention. The other nine complexes with remnancy <200 km^2 are those on which a representative conservation strategy should focus. They are all savannah woodland, riverine and swamp communities:

- XANTHORRHOEA CAESPITOSA: savannah woodland/heathland intermediate
- MELALEUCA HALMATURORUM: saline swamp shrubland
- GAHNIA TRIFIDA/FILUM: tussock grassland swamp
- CALLITRIS PREISSII: savannah woodland
- ALLOCASUARINA VERTICILLATA: savannah woodland
- EUCALYPTUS MACRORHYNCHA: savannah/sclerophyllous woodland intermediate (recorded in N.P.W.S. reserve)
- EUCALYPTUS LARGIFLORENS: Murray River floodplain
- MUEHLENBECKIA CUNNINGHAMII: Murray River floodplain

- EUCALYPTUS MICROCARPA: savannah woodland.

In addition, two further savannah woodland complexes, E. CAMALDULENSIS and E. ODORATA, have remnancy <200 km^2 when degraded sites are excluded and E. LEUCOXYLON follows closely with an area of 233 km^2 undisturbed. In terms of rarity, these complexes appear to require secondary conservation priority.

Space does not permit a full examination of the remnancy data for all the minor vegetation types and the extent to which they are represented in N.P.W.S. reserves or are degraded. However it must be pointed out that the very low frequency with which the majority were found (median = 2) renders the estimates of most of their remnancies imprecise. At best the presented data should be interpreted by simplification to, say, a scale of few classes ranging from "very rare" (remnancy <50 km^2) to "very common" (remnancy >1000 km^2).

Just 43 (26 %) of the 164 types were recorded in N.P.W.S. reserves. As approximately 26 % of all estimated remnant area (including disturbed areas) is contained in reserves, it appears that the N.P.W.S. network does not conserve a significantly greater "density of diversity/variation" than the average for southern South Australia i.e. in terms of the overall area, there is no evidence to suggest that the existing reserve network reflects selective conservation aimed at maximising representation of vegetation types per unit area reserved, nor is there any serious deficiency, but rather that the reserve network contains a random sample of all remnant vegetation. This assessment might be criticised by claiming that the adopted survey sampling density does not have the potential to detect all vegetation types occurring in conservation parks. But equally well there are other vegetation types which were not detected due to the same limitations of sampling, e.g. *Baumea juncea – B. rubiginosa, Phragmites australis* and *Potamogeton pectinatus* wetland associations; *Eucalyptus behriana* mallee and *Lomandra effusa – L. dura* savannah sedgelands (see Specht 1972).

In Table 8.5, the 28 associations of conservation priority listed by Davies (1982) are compared with the estimated remnancy figures. Floristic types equivalent to 13 of those associations were not recorded by the survey and their absence implicitly confirms their rarity. Two associations do not have direct floristic analogues. The *Eucalyptus odorata – E. leucoxylon +/- E. fasciculosa* low woodland is probably an intermediate between the E. LEUCOXYLON and E. ODORATA complexes and included in the latter. In terms of the floristic analyses described in Chapters 5 & 6, *E. oleosa – E. socialis – E. gracilis – E. dumosa* low open-forest can only be described as an ill-defined association which is a structural variant in the E. OLEOSA – E. GRACILIS COMPLEX. Barker (1988) demonstrated that eucalypt community structure largely reflects disturbance history over as much as the previous 300 years. In a conservation strategy that admits and accommodates dynamic vegetation change, the value of structural variants is doubtful. A floristic equivalent of the other listed associations was recorded and, with three exceptions, they had low undegraded remnancies of less than 100 km^2. Two exceptions (*E. cneorifolia* and *E. cosmophylla – Melaleuca uncinata*) occur over much of eastern Kangaroo Island, but no conservation park contains a significant sample of either, thus accounting for the priority ranking assigned by Davies (1982). The third exception (*E. porosa*) is almost entirely cleared from the Northern Mt Lofty Ranges and Yorke Peninsula, and is poorly protected on western Eyre Peninsula where the remainder is concentrated.

One of the major outcomes of the phytosociological analyses in Chapter 6 is an improved classification of mallee vegetation and better appreciation of the underlying gradational patterns. There are 73 types in the five mallee complexes of the full classification, many more than have been recognised in the past by Specht (1972), Davies (1982) or any of the regional sources on which they are based. Davies included in his priority listing four associations that fall into the mallee complexes. (*Eucalyptus cneorifolia* and *E. cosmophylla* types are excluded as they are floristically more allied to the sclerophyllous woodlands). However only 22 of the 73 types in the new classification were recorded in reserves during the survey work, i.e. a large proportion of the diversity of mallee land systems in South Australia is unconserved. Many of the seemingly newly described types which were not recorded in conservation parks can not be considered either infrequent or of very low remnancy, and so are simply mallee diversity that has been overlooked in the past. These types require some conservation priority. A large data base would be needed to fully assess the remnancies of the least frequent types, about which there is least confidence. These numerous mallee types can all be described as relatively uncommon and their conservation status is much lower than might be inferred from Davies (1982) or Moore (1985).

8.3.3 Ordination Overplots of Remnancy

Contoured point estimates of remnant area are presented for two partial ordinations: Figure 8.3, the six temperate sclerophyllous woodland and heathland complexes (cf. Figure 6.7); and Figure 8.4, the four semi-arid mallee complexes (cf. Figure 6.11). These examples illustrate the philosophy, application, advantages and disadvantages of the remnancy overplot technique.

The remnancy surface for the ordination of the temperate sclerophyllous complexes has two prominent peaks (Figure 8.3), the lower one associated with the BANKSIA ORNATA – ALLOCASUARINA PUSILLA heathlands in the South-East region, and the other one associated with the interface of the B. ORNATA – A. PUSILLA heathlands and EUCALYPTUS CNEORIFOLIA temperate mallees on Kangaroo Island. The peaks indicate a combination of two factors: the relatively high remnancy of these vegetation forms in these areas and their relatively low variation in total floristic composition. The strongly gradational floristic patterns on Kangaroo Island (Chapter 4) and the comparatively low overall clearance there are responsible for the upper peak straddling the boundary between two complexes as plotted on the ordination scattergram.

Over the right two-thirds of the diagram, the remnancy index is low. This area corresponds with the EUCALYPTUS BAXTERI – PTERIDIUM ESCULENTUM and E. OBLIQUA – E. FASCICULOSA complexes. As axis 1 is positively correlated with annual rainfall, these are the most mesic of the sclerophyllous groups. These complexes have relatively high variation of floristic composition and occupy relatively small remnant areas. Any of six *Eucalyptus* species may be dominant or codominant in the former, and occur in many combinations. By contrast, *Banksia ornata* and/or *Allocasuarina pusilla* are consistently (co-)dominant in Upper South-East heathland vegetation.

Of the 24 conserved sites in the temperate sclerophyll ordination, 22 are in close proximity to the two prominent peaks of remnancy. This is not surprising as the breakdown of remnancy of vegetation types in Section 8.3.2 found that an approximately random sample of total observed floristic diversity was contained in the N.P.W.S. reserve network and thus that the most common types are most likely to occur in reserves. The continuous index of remnancy merely serves to reinforce this observation. Representation of the diverse EUCALYPTUS BAXTERI – PTERIDIUM ESCULENTUM, XANTHORRHOEA CAESPITOSA and E. OBLIQUA – E. FASCICULOSA complexes is low. From the stance of maximising representation of temperate sclerophyllous systems within conserved areas, the remnancy plot illustrates that emphasis is needed on these three complexes in future reserve selection. The JUNCUS PALLIDUS COMPLEX is omitted from consideration here due to suspicions of its disclimax nature.

Overall remnancy is higher across the ordination of mallee complexes (Figure 8.4) than across the sclerophyllous woodlands and heathlands. Remnancy patterns are also more irregular with a number of local maxima of various magnitudes. The largest peak is centred in the EUCALYPTUS OLEOSA – E. GRACILIS COMPLEX. Remnancy is low in the peripheral areas of this complex. Although floristic composition of E. OLEOSA – E. GRACILIS appears to be more uniform than that of other mallee complexes (Section 6.4.3), the magnitude of its peak remnancy may simply be due to compression of its variation in two dimensions by the more important rainfall and soil gradients which result from analysis with other mallee complexes.

The other features of Figure 8.4 are:

1. the large area occupied by the EUCALYPTUS INCRASSATA – E. FOECUNDA COMPLEX, suggesting that it has the greatest inherent variation of the five complexes;

2. the lower average remnancy index in the upper (left) half of the E. INCRASSATA – E. FOECUNDA COMPLEX than in its lower (right) half. The upper half embraces types which occur at higher rainfall and have an understorey of *Melaleuca uncinata.* The lower half includes types dominated by *Triodia irritans* (see Figure 6.11), of which a large uncleared tract crosses northern Eyre Peninsula;

3. the low remnancy and apparent rarity of types in the E. SOCIALIS COMPLEX which serves as a floristic bridge between the E. OLEOSA – E. GRACILIS COMPLEX and the drier types of the E. INCRASSATA – E. FOECUNDA COMPLEX. Further examples of these intermediates occur to the north of the study area, such as in the Danggali Conservation Park beyond the northeast corner (pers. obs.), where the reduced rainfall finds most mallee species restricted to siliceous dunes in order to maintain water relations within tolerance ranges, as outlined in the previous chapter; and

4. the low level of remnancy in the lower left corner. These *E. cladocalyx* woodlands were found on the hills of southern Eyre Peninsula, where few examples have survived clearance.

Sites in conservation areas are widespread across the ordination and are not concentrated about the peaks of remnancy. Thus, unlike the temperate woodlands, conserved mallee is not a random sample of total remnant mallee. There is bias in favour of less common types, particularly those of distinctive floristic composition. A wide selection of the variable EUCALYPTUS INCRASSATA – E. FOECUNDA and E. DUMOSA types are conserved. Sand dune mallee types on north-western Eyre Peninsula and, more notably, nearly all types in the E. OLEOSA – E. GRACILIS COMPLEX are underrepresented compared with the mean for all mallee ecosystems. The low conservation status of the latter, but not of the former, was apparent from the classificatory analysis of remnancies in Section 8.3.2.

8.4 DISCUSSION

The presented data on species rarity have several implications for the way in which rarity is used as a criterion for assessment of conservation value and management of remnant vegetation patches. The most significant implications stem from the right skew on the distribution of both species frequencies and species estimated remnant habitat areas.

Skewed distributions of species frequencies have been demonstrated at various sampling scales in the past (e.g. Raunkiaer 1918; Gleason 1920, 1929; Preston 1948) such that Preston (1962) affirmed that species frequencies in any vegetation sample would describe a truncated log-normal distribution. Thus every plant community or ecosystem has few common species and many uncommon species, a phenomenon appreciated by Main (1982) and McArdle (1990) when discussing species rarity as a concept, but apparently not considered by those undertaking conservation inventories.

However, the skews in the frequency and remnancy data collected in this study are stronger than any in the literature. The median species frequencies and estimated remnant ranges are respectively just 1.1 % and 1.3 % of the maximum possible. Hence, a very large part (the majority) of the native perennial flora could be considered uncommon or rare to some degree. In light of the similarity to earlier findings, there is no reason to expect that the same is not true of native perennials in the arid north of South Australia, of native annuals and geophytes across the State, and indeed the floras of other parts of Australia. This "commonness of rarity" in floras is a view with which Lang & Kraehenbuehl (1987) seem to agree, as they rate 523 species as significant throughout South Australia's temperate districts and a further 350 as regionally threatened, from a total flora which is estimated to be about 2000 species.

The second effect of the skewed remnancy distribution is to render delineation of rareness categories arbitrary and difficult. There are no natural bounds besides the absolute lower limit: extinction. Furthermore the assessment of species status and their accurate assignment to a defined portion of the rareness gradient is only possible with either an intimate knowledge of all of the remnant population or a very large data bank, far larger than the one provided here. The difficulties of assessing a species' status without adequate data is apparent from the intermixture of the categories "vulnerable", "rare", "uncommon" and "not threatened" in the lower ranges of estimated remnancy (Table 8.1). Subjective and objective methods tend to agree only on the "endangered" category of most threatened species, in which remnancy nearly approaches zero by all definitions. Most species endangered in South Australia are already sufficiently well-studied that it is believed the location and size of all remaining populations are known. The same cannot be said of species under lesser threat.

Besides the problems associated with determination of rank among species thought rare, there are more fundamental objections to too great an emphasis upon rarity in a conservation strategy. The overall rareness of any one species may be wholly or partially determined by a number of factors (after Sparrow 1986):

1. rarity due to naturally restricted geographic range and/or specific habitat requirements;
2. rarity due to recent speciation or impending natural extinction;
3. apparent rarity due to natural restriction to a short-lived subclimactic successional sere;
4. apparent rarity due to lack of collected specimens or taxonomic interest, or due to taxonomic confusion and misidentification of specimens;
5. rarity due to widespread clearance of native habitat or selective grazing by stock.

Walters (1976) has discussed the significance of specific and/or transient habitats for rare species and their distributions. Lang & Kraehenbuehl (1987) recognised the problem of biased herbarium collections and continually changing taxonomy, and attempted to redress obviously misleading records. However there is still an overwhelming ignorance of the importance of the rarity factors pertinent to every species. The dearth of data to assess rarity of most species and to appreciate the reason for the rarity is the chief obstacle to a conservation strategy based upon rarity. Another is whether the definition of rarity is based upon total population size or extent of native habitat. This vexation is indirectly linked to the question whether one large or several small populations represents the better long-term guarantee of survival, which again tends to be different for each species.

Given the above reservations, it is probably more rational to conserve representative ecosystems likely to embrace combinations of the first four types of (apparent) rarity and to supplement this with additional measures for individual, most threatened species for which an ecosystems approach is seriously deficient i.e. reduce reliance on species rarity as the criterion for native vegetation retention in South Australia and elsewhere.

Conservation by rarity of vegetation types (i.e. an ecosystems approach) is confounded primarily by the gradational nature of compositional variation and the definition of an adequate classification. The assessment of Davies (1982) suffers from the classificatory inconsistencies of Specht (1972), on which the former is based, with its detail of vegetation in the sclerophyll and savannah land systems, but superficial coverage of mallee and arid areas. In addition, Davies presents a binary outlook on rarity, dividing associations into those rare and poorly conserved in N.P.W.S. parks and all others, thus suppressing satisfactory gradation from very abundant to very rare.

The floristic classifications and ordinations from Chapter 4 and the analyses of corresponding remnancy data above provide two improvements on existing sources. Firstly, there is even coverage of all parts of the study area. The most obvious manifestation of this improvement is that floristic patterns in the mallee regions (which constitute 55 % of the study area) are presented in greater detail, thus concomitantly permitting a more detailed assessment of the conservation status of mallee types. The second improvement is that estimates of remnancy and conservation status are based on numerical analysis of survey data, and not just on subjective perceptions of the compiler.

Despite these improvements, the remnancy data are neither ideal nor definitive. The serious reservation is the size of the data set. A sample of 744 sites may give a satisfactory appraisal of 39 complexes, but are inadequate for the 164 types. The median number of sites per type is two[18] and thus the proportional error of most remnancy estimates is high. For reduced error, a larger data set is needed, preferably from a survey based on random sampling which would avert the need to correct frequencies of occurrence by local remnancies. The reason for the choice of sampling strategy and the compromises thereby induced were discussed in Chapter 3.

This reservation does not invalidate the important results and the implications they have for conservation management. For example, total remnancy (and representation in reserves) is very low in all savannah woodland, riverine, and swamp complexes, and representation of the EUCALYPTUS BAXTERI – PTERIDIUM ESCULENTUM and E. OLEOSA – E. GRACILIS complexes is below the average in temperate South Australia.

A more important result pertains to overall representation of types. N.P.W.S. reserves contain a random selection of total floristic variation and no selective representation is evident; about 25 % of all remnant area and the same proportion of all recorded types occur in parks. A significant increase in the total area protected would be needed to enhance representation of vegetation types (β diversity) in conservation reserves. It must be concluded that optimal representative conservation requires retention of a large proportion of vegetation in an area. This conclusion has been reached elsewhere by Margules & Nicholls

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[18] The distribution of vegetation type remnancies is right skewed, but less so than the distribution of species remnancies. Thus the "commonness of rarity" observed in the flora applies to vegetation types as well, albeit to a less well marked degree.

(1987) and Nilsson (1986) for representative conservation of rare species and high α diversity, as well as for vegetation associations. Selection of conservation areas becomes a compromise of the desirability of retaining most remnant patches by the wishes of private landowners, the pressure for agricultural and mineral development and the problems of reserve maintenance with respect to fire, vermin, etc. In essence, a practical conservation strategy is determined by mundane matters rather than by theoretical principles which of necessity are unattainable.

Finally some comments need to be made on the technique of overplotting smoothed remnancy data on ordinations. As indirect ordination is used to simplify a vegetation data set by reducing its dimensionality, remnancy assessed from an ordination plot presents a simpler picture than assessment from a detailed classification. Minor vegetation types which are slight variants of other types are not individually expressed and remnancies for groups of variants are summed. (More dissimilar types should either contribute to the axes, occur as outliers or be treated as disjunct; in the last case assessment via a classification is preferable). Instead, remnancy is presented along the two predominant habitat gradients characterising the group of complexes under analysis, with the advantage over classificatory assessment that internal variation of types and gradation between types is accommodated. The result is a broad overview of remnancy and representation of the major sources of β diversity.

The method is successful for ordinations which lack near discontinuous gaps and whose first two axes represent strong habitat gradients accounting for a high proportion of the total variance. The overplots of Figures 8.3 and 8.4 illustrate such conditions. Poorly conserved portions of major floristic gradients are readily detected. However, remnancy overplotting has limited value when vegetation is controlled by many gradients of equal magnitude which require ordination in more than two dimensions (e.g. the full data set ordination Figure 6.2 or 6.4). Although it can in principle be extended to higher dimensionality, the continuous remnancy function cannot be graphically presented on three or more axes. In this case, the method would be at its practical limits and remnancy by vegetation types would be conceptually simpler.

A continuous remnancy index has two potential applications. Firstly it is a simple tool for judging the merit of any patch of vegetation for conservation. The position of any site along a DCA axis is the dot product of the site's species vector and the axis' species vector. Thus the position on a DCA ordination of additional sites from a vegetation patch under assessment is readily calculable and its remnancy index, inversely proportional to conservation value, can be read directly from the diagram. Such a tool could be used to aid detection of additional vegetation representative of poorly conserved compositional combinations and thus worthy of retention.

The second possible application is for assessment of habitat for species of fauna. If the range of habitats suitable for an animal species can be circumscribed on an ordination, relative remnancy of habitat can be determined and portions of the range under greatest threat identified. The use of an ordinational approach frees faunal habitat assessment from correlation with vegetation types which may be distinguished by plant species or other features that are of no significance to the distribution of the particular animal species. It also caters for the possibility that the favoured habitat of an animal species is the transitional zone between complexes or types.

Chapter 9:
CONCLUDING DISCUSSION.

9.1 REVIEW OF THE STUDY

In the preceding chapters, the significance of the various individual aspects of the methodology and results has been discussed in some detail. Their contributions to improved understanding of the native vegetation of temperate and semi-arid South Australia have been highlighted. Consequently, by way of conclusion, the project needs to be reviewed only briefly here. This task can be achieved most effectively by referring to the five aims set out in Section 1.5, although some allowance must be made for the interdependence of sampling strategy and data analysis, and hence of the aims dealing with these components.

9.1.1 Sampling Strategy

Two factors distinguish the survey developed in Chapter 3 from the type of study usually undertaken by European phytosociologists: low sampling density over a large area (one site per 200 km^2 over 151 000 km^2), and lack of stratification based on preconceptions of vegetation or habitat patterns.

In scale the study falls between Noy-Meir (1970, 1971) in Australia and Orloci & Stanek (1979) in Canada. In terms of areal coverage, it is of the same order of magnitude as the larger survey of Noy-Meir; in terms of sampling density, it is nearer the more intensive survey of Orloci & Stanek. This combination of scale and intensity produced a larger data set than either of these studies (744 sites here versus 383 and 323 respectively in the others).

As in this study, Noy-Meir (1970, 1971) and Orloci & Stanek (1979) used an explicitly unstratified sampling approach to cover large, poorly-studied areas. The advantage of such an approach is to allow description of vegetation variation and distribution in which representation of vegetation types and gradients is unbiased. In the present case, bias is restricted to that attributable to agricultural development e.g. selective clearance of vegetation types according to soil fertility. This constrasts with traditional European approaches which sample only typical stands (e.g. Braun-Blanquet 1932; Becking 1957; Gagnon & Bradfield 1986, 1987), effectively avoiding gradation of composition, or which sample along predetermined habitat gradients, thereby testing a single, specific distributional hypothesis.

There are no objective, numerical criteria for assessing the sampling strategy of a vegetation survey; one can only ask *a posteriori* whether all analysis aims have been met or whether another approach might allow better elucidation of pattern. The strategy adopted here can be judged a success as it permitted fulfilment of all four analytical aims. The data were sufficient for classification and ordination analysis to compare all previous regional studies within a unifying, quantitative framework superior to all other works of similar coverage. Representation of mallee vegetation was greater than in earlier work, thereby revealing its variation, gradation and relationships with temperate and arid systems. From a less holistic perspective, analysis of the responses of common species to habitat gradients could be approached in an unbiased, multivariate manner. In addition, for the first time in South Australia, there are data by which quantitative definition and assessment of rarity in plant species can be examined.

There were negative aspects to the study, especially the lack of rare species and vegetation types. From the perspective of assessing conservation status, this is not necessarily problematic, as lack of occurrence implies rarity. However, some vegetation types were not incorporated into the classification. As a general increase in sampling density is impractical for reasons of reward-per-unit-effort, additional, purposely-located sites are needed. These sites could be incorporated into the data set to discern the affinities of omitted types without greatly influencing the overall results of classifications and ordinations.

Furthermore, a cautionary note must be sounded about the inadequacy of the chosen sampling density to describe the vegetation of Yorke Peninsula, due to the region's small area, high β diversity and extensive clearance. Regional analysis was unsuccessful under these circumstances, although the patterns were recovered in the context of the full data set analysis. This behaviour was unforeseen at the time of survey design.

The use of "gradsects" in the survey strategy appeared to be neutral with respect to analyses. The 3:1 ratio of between-transect spacing to along-transect spacing of sites was not high enough to lead naturally into analyses examining pattern along gradsects. In fact, given the high observed level of natural, stochastic variation of vegetation types, the gradsect approach did not bias classifications, ordination or calibrations significantly. However, the use of systematic sampling along transects was very efficacious in terms of keeping fieldwork time within available limits.

9.1.2 Multivariate Analysis of Floristic Data

The tandem analysis approach using classification by Bray-Curtis dissimilarity / UPGMA fusion and ordination by DCA provides a clear "node-and-gradient" description of the vegetation in the study area. The patterns so revealed are compatible with field observations and with almost all previous literature, but these patterns are presented in a much more cohesive and lucid manner than ever before. The clarity is a function of the high β diversity and the well-defined climatic, edaphic and inundation gradients. Thus a multivariate survey and analysis approach as applied in this study can be endorsed for use in Australian sclerophyllous vegetation systems, at least at the scale examined here.

There is one overriding problem: high β diversity combined with large variation in α diversity, such as led to the "tongue" distortion on the ordination of the full data set (Figure 6.2) and contributed to the instability of mallee complexes.

Estimation of between-site dissimilarity from the data using any standard metric is greatly influenced by the presence or absence of one species when α diversity is low. An example calculation is given in Figure 9.1. When species diversity is less than 10 species per site, a compositional difference of just one species leads to a significant dissimilarity value. Thus "stochastic" factors must affect low diversity types (and the calculation of their affinities) much more than high diversity types. Therefore compositional "noise" is higher among low diversity vegetation and it is more likely to be mistaken for a true habitat gradient.

In southern South Australia, diversity is generally low. The average was 13.4 native perennial species per site. In addition, diversity is positively correlated with annual rainfall (if saline extremes are excluded). Thus stochastic factors have a greater influence on analysis behaviour in the low rainfall districts of the study area. Confounding this further, disturbance by grazing (which may cause apparently "random" loss of understorey species) is also higher in complexes occurring at low rainfall, due to the presence of palatable, semi-succulent subshrub species. This explains the distortion of chenopod shrubland complexes into a tongue on Figure 6.2 and the instability of semi-arid mallee noda. The latter would be more unstable if presence/absence data were used instead of cover-abundance data, since cover scores describe the dominance of eucalypts and some understorey species by which the mallee complexes are held together.

Thus, for the data set collected during this study, the subtle mathematical arguments for NMDS versus DCA, or Bray-Curtis metric versus other metrics, are subordinate to the important, problematic influences of diversity systematically related to habitat gradients. Austin (1987b), Margules *et al.* (1987) and Minchin (1987a) have demonstrated similar, systematic patterns of species diversity. However, the implications of such trends on multivariate methods have not been examined by simulation studies (e.g. Faith *et al.* 1987). They must also affect the stability of dendrogram partitioning, such as by the Monte Carlo method of Nemec & Brinkhurst (1988). The problems warrant further serious study.

9.1.3 A New, Floristic Classification

As desired at the outset of the project, the classification derived from the multivariate analyses provides a framework with a quantified structure within which can be placed all earlier work on a smaller, regional scale. Associations and alliances described previously can be assigned to complexes and types. However, the units of the new classification have consistent, defined levels of internal variability such that there are no doubts about the relative hierarchical status of complexes and types. There are cases where affinities of groupings do not agree with earlier interpretations e.g. the GAHNIA TRIFIDA/FILUM COMPLEX was found to belong to a group of wetlands complexes rather than to the savannah lands system as suggested by Specht (1972). In all such cases, the groupings in the new classification are more readily correlated with similarities of habitat.

The classification most closely parallels Wood (1937) and, in particular, the concept of the "edaphic complex" (Wood 1939) as applied by Crocker (1946) and Bauer (1959). The major improvement is with mallee vegetation, for which five complexes, six subcomplexes and numerous types are delineated.

Agreement is lower with Specht (1972). The area of divergence stems from Specht's use of a structural *schema*. The structurally-defined land systems include groupings which cannot be justified on floristic affinity nor habitat similarity. In fact, the structural element is usually superfluous, since overstorey height and spacing can be deduced from knowledge of the species dominant at a site. Furthermore, the *schema* ignores substrata altogether. At the local scale, physiognomic nomenclature is most useful for providing a layman's image of the form of the vegetation and in this role it has the potential to be greatly simplified e.g. "woodland" rather than "low open woodland" and "forest" rather than "tall closed forest". Another improvement would be to use the term "mallee scrub" instead of the more generic "tall shrubland". A detailed structural *schema* only has true merit in cases for which floristic data are inappropriate e.g. mapping at a continental scale or comparing vegetation pattern between continents.

9.1.4 Description of Environmental Gradients

Despite the distortion induced by low species diversity in low rainfall complexes, indirect ordination by DCA disclosed major floristic gradients which could be related to measured environmental variables such as annual rainfall, soils (physical and chemical characteristics) and inundation patterns. In the full data set, adequate presentation of the main gradients required simultaneous display of at least four dimensions. Ordination of data subsets clarified this complexity in lower dimensionality. For most ordinations, higher-order trend-surfaces gave a more realistic indication of habitat gradients between complexes than did vectors of rank correlation with ordination axes.

From a practical point of view, if not from that of a statistical purist, catenation by MDA gave a more satisfactory summary of the major gradients. The catenation required a total of only three dimensions (presented as two "nested" 2-D scatterplots) to relate all complexes to significant habitat variables, in a way which is intuitively appealing and undistorted by ordinational imperfection. MDA shows much potential as a catenation tool in cases for which it has been demonstrated previously (say, by indirect ordination) that the major floristic gradients can be accounted for by the available environmental data.

Logistic regression response models provided a more refined and detailed description of habitat correlation for more common species. These regressions demonstrated the uniqueness of each species' response with respect to interacting climatic and edaphic variables. This individuality of reponse is the source of compositional continuity along habitat gradients, particularly the independence of overstorey and understorey components in the mallee complexes.

9.1.5 Relevence to Conservation Assessment

The analyses presented in Chapter 8 are the first attempt to quantify rarity of species and vegetation types in South Australia. The analyses might be criticised for attempting too much with too little data (i.e. determining the conservation status of an estimated 2000 native species in the study area with data from just 744 sites). However, the *principles* demonstrated can be expected to withstand future analysis of a much larger data set.

Many doubts were raised about the definition of categories of rarity in past conservation status studies.

The distribution of species frequencies and estimated remnant habitat areas were found to be strongly right-skewed and continuous. The extremes of rareness and commonness may be obvious, but most members of the flora (and most vegetation types) lie on the continuum between very rare and very common, with a distinct tendency to uncommonness. An important component of this tendency is attributable to small-scale, infraregional chorological pattern. Selection of a boundary below which a species or vegetation type is considered rare is quite arbitrary. There are no discontinuities in frequency or habitat area distributions by which to define categories of rareness. Consequently there is poor agreement between conservation ranks from earlier studies and relative frequencies or remnant habitat areas. Thus might one ask: "What is a rare species (or vegetation type) ?".

From the distributional skew toward uncommonness, the lack of discontinuity in the distribution, and the significant contribution of localised chorological pattern (see Sparrow 1990), it can be concluded that, in order to achieve long-term conservation of representative populations of all species and areas of all vegetation types, almost all remnant vegetation in southern South Australia must be preserved. This conclusion is supported by the results of other studies which have quantitatively assessed representation of vegetation systems e.g. Nilsson (1986) and Margules & Nicholls (1987).

9.2 CONTRIBUTION TO VEGETATION THEORY

Austin (1987a) exhorted phytosociologists to tackle theoretical aspects of vegetation rather than simply continuing descriptive work. On the basis of this study, it is hard to envisage how this could be achieved using multivariate analysis of field survey data.

Multivariate analysis, as undertaken here, is a flexible tool for description of vegetation pattern. It provides a vocabulary and syntax by which to communicate ideas about vegetation distribution (and its control by habitat) in a thought-provoking manner. Evidence confirming concepts of vegetation theory can be proferred, for example, concerning the individuality of species reponses to environmental gradients and continuity of composition along such gradients. In addition, many hypotheses were generated during the course of the analysis, particularly with respect to the control of species distributions by the abiotic environment.

However, despite the best intentions of Austin (1987a), the data are ultimately insufficient to test hypotheses convincingly. Sampling "errors" (in the statistical sense) of the unstratified survey lead to large confidence intervals around parameter estimates and there is a lack of homogeneity of variances, viz. the standard deviations around means of measured habitat variables for complexes (Table 6.1) and the low fit of logistic regression models for species (Table 8.22). Furthermore, there is limited scope for manipulation of data such that many hypotheses could be statistically tested simultaneously i.e. a purpose-designed sample is needed for each hypothesis individually. Related to both these points is the problem of autocorrelation of predictor habitat variables and the overlap of physiological and competitive effects in determining observed distributions of species in the field. Even theoretical assessment of niche width and skewness using ordination spaces, as attempted by R.H. Ökland (1986c), must be queried given the distortions induced in ordinations by systematic diversity changes along habitat gradients.

9.3 AVENUES FOR FURTHER RESEARCH

Given limited contribution to theory possible with the holistic approach of multivariate phytosociological analysis, complementary work along more reductionist lines is warranted in an effort to further broaden understanding of vegetation pattern in southern South Australia, and to allow contribution at a more theoretical level. In previous chapters, hypotheses have been proposed dealing with ecophysiological, genetic, taxonomic and palaeological aspects of plant distribution. These hypotheses beg further investigation and could serve as a basis for a programme of future vegetation research in South Australia.

The control of species distributions by soil water availability (as indexed by the annual rainfall – soil texture interaction in ordination spaces and logistic regression models; Chapters 5 to 7) could be examined by a combination of: (i) field measurements of seasonal plant water status cycles, using the methods of Sinclair (1980); (ii) field manipulations of soil water availability by watering or rain diversion treatments, during which effects on the water responses of plants are monitored; and (iii) glasshouse trials to test the influence of soil moisture on seed germination and seedling survivorship. Such a multifaceted approach should provide a considerable advance over the conclusions of Parsons (1969a) regarding water relations of semi-arid mallee species. It would also give insight into the degree of differentiation of realised niche from potential niche by competition, and the stage(s) of lifecycles at which the selective pressure is experienced (Harper 1977; Silvertown 1982).

A similar approach involving field and glasshouse manipulations could be used to examine the influence of mineral nutrients (including salinity) on species distributions. Analysis would be enhanced by data on the availability of particular nutrients in field soils.

Attention should also be focused on evolutionary, taxonomic and historical influences on vegetation distribution patterns by standard phytosociological procedures. The study revealed examples of complexes of vicariant species, such as the *Eucalyptus dumosa* and *E. socialis* groups. Logistic regression models of the environmental responses of these species showed poor fit. Their habitats overlap with those of sibling species which are differentiated morphologically and (bio-)geographically, but not ecologically. There are also examples of suspected ecotypic variation within species leading to poor environmental correlations e.g. *E.socialis* and *Melaleuca lanceolata.* When it is taxonomically "fuzzy", the value of the species as the fundamental unit for phytosociological analysis must be questioned. Methods are needed for measuring taxonomic fuzziness and incorporating it into multivariate analyses in a suitable way. An initial approach might be to compare ecotypes or species in a complex using genetic techniques such as analyses of enzyme polymorphism (Brown 1978; Moran *et al.* 1989) or DNA restriction fragment polymorphism (Palmer *et al.* 1985, 1988). Such a measure of evolutionary dissimilarity could then be correlated with dissimilarities of response to environmental gradients, as was attempted in Chapter 8 by the separate regional analyses of *M. uncinata* and *Triodia irritans* in the Murray Mallee and on Eyre Peninsula.

A final point worth considering is the importance of historical factors. Any study of modern vegetation pattern is a "snap-shot" of a continuum of migrations, extinctions and speciations in a context of climatic change. In Europe and North America, research on pollen deposits in wetland soils has allowed reconstruction of Holocene climate change and vegetation migration such that modern relicts can be accounted for (e.g. Davis 1983; Huntley 1990; Webb *et al.* 1983). Equivalent data are sparse in South Australia due to the drier climate (see Dodson 1974; Singh 1981), thus making reconstruction of local Holocene changes difficult. Additional data would greatly aid interpretation of current landscapes.

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