VEGETATION PATTERNS
OF

EASTERN
SOUTH AUSTRALIA:

EDAPHIC CONTROL
&
EFFECTS OF HERBIVORY

by

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Frontispiece

The Olary Ranges in eastern South Australia. The long dark hill in the middle ground is the Grampus Range, and the tall peak in the right background is Tattawuppa Hill, near the town of Yunta. The photograph is taken from near Pualco Hill.

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ABSTRACT

The short time since European settlement and commencement of pastoralism in the Australian arid lands means that the vegetation is of significant heritage value. It also represents a unique opportunity to document the effects of domestic herbivores on arid vegetation. Methods for rapidly describing the vegetation, the variables controlling patterns within it, and the effects of domestic herbivores are therefore useful in other large, relatively unknown tracts of arid vegetation, and are important additions to the theory of rangeland management and vegetation science.

A 32 000 km^2 area including the Olary Ranges in eastern South Australia was selected as representing a range of arid land topography and vegetation, and surveyed using a nested sampling technique. The primary sampling strategy was a system of 8 north-south transects each 200 km long and 20 km apart, each with 20 100 ha strip-transects where floristic data for identification of vegetation alliances were collected by vehicle traverse. Traditional 0.1 ha plots were located at 10 km intervals along the transects at the mid-point of the strip-transects where floristic data for identification of vegetation associations were collected. The distribution of strip-transects and sites approximated a grid, permitting mapping.

These data were analysed using a range of complementary multivariate analysis techniques including Czekanowski/UPGMA clustering to produce a four-tiered hierarchical classification, and DCA ordination to examine the relationships between the groups produced. Eighteen vegetation associations were identified, mainly well associated with one or other of 10 alliances, although there was some degree of interchange, reflecting the different scale of sampling. A major floristic disjunction was encountered, corresponding to the previously mapped boundaries of the Euronotian and Eremian vegetation provinces, between a eucalypt-dominated mallee formation and a chenopod shrubland formation respectively. The Mallee Formation contained one alliance consisting of 2 major and 1 minor vegetation type. The Chenopod Formation contained a further floristic disjunction, between a *Maireana pyramidata* vegetation order common at higher elevation and rainfall, and a *Maireana astrotricha* order common on the plains at low rainfall.

A range of edaphic and topographic data was collected at each site, and the relationships between the distribution of vegetation associations and individual species analysed using a combination of pearson association analysis, DCCA canonical ordination and multiple regression. Edaphic variables were found to be the most important in determining vegetation distribution, supporting previous subjective observations of this and other arid vegetation.

A further survey was carried out to locate populations of perennial species at sites of various intensity of grazing by the most important vertebrate herbivores; sheep, rabbits, goats, and kangaroos. Sheep were found to be the most important herbivore in suppressing regeneration of perennial species, which is in conflict with previous literature reporting rabbits as the most important. Neither goats nor kangaroos were found to be important. Regeneration of some species was significantly reduced to such critical levels that it appears that these species will eventually become extinct in sheep-grazed areas.

Most plant species showed negative regeneration responses to sheep grazing, and none showed significant increases, suggesting that changes in vegetation composition are due to selectivity by sheep, with some species being more susceptible than others. No plants were found to significantly increase regeneration in response to modern levels of grazing. Hence the problem of "woody weeds" reported in other rangelands is a relative rather than an absolute response.

The results have significance to both vegetation theory and arid-zone ecology. The vegetation consists of both noda and continua, supporting theories that vegetation is neither fully continuous, nor fully discontinuous. The failure of some species to recruit even in sites free of grazing is taken as evidence that the vegetation is not fully in equilibrium with climate but is lagging behing geologically recent increases in aridity. Abrupt changes in vegetation composition in response to past heavy grazing provide objective support for the state-and-transition model of vegetation dynamics suggested by Westoby *et al.* (1989).

The significance of these results to conservation and vegetation management is discussed. The apparent increase in undesirable unpalatable shrubs or “woody weeds” is a relative effect of selective grazing on the whole vegetation. Attempts to control such species are therefore not likely to be successful, and may merely exacerbate the problem. Present levels of grazing do not appear to present a threat to most chenopod bush species, so it appears that pastoralism is sustainable for the forseeable future. However, a land-use system including a network of reserves ungrazed by sheep will be required to achieve ecological sustainability and conserve a range of grazing-susceptible trees and shrubs.

DECLARATION

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Fleur Tiver

30th March

Date

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ABBREVIATIONS & ACRONYMS

ABM	Australian Bureau of Meteorology
ACT	Australian Capital Territory
ANZAAS	Australian & New Zealand Association for the Advancement of Science
BP	before the present (geological time)
CA	correspondence analysis
CCA	canonical correspondence analysis
CCL	Commissioner of Crown Lands
CSIRO/CSIR	Commonwealth Scientific and Industrial Research Organisation
DCA	detrended correspondence analysis
DCCA	detrended canonical correspondence analysis
ENSO	El Niño/Southern Oscillation
GLIM	Generalized linear modelling
IBP	International Biome Program
IPGB	Imperial Parliament of Great Britain
mA	millions of years (geological time)
NATMAP	Division of National Mapping, Commonwealth of Australia
NCSSA	Nature Conservation Society of South Australia
NSW	New South Wales
NTP	Numerical Taxonomy Package
PCA	principal component analysis
PCoA	principal coordinate analysis
PNSW	Parliament of New South Wales
PO	Polar ordination
PSA	Parliament of South Australia
RA	Reciprocal averaging
RASC	Royal Australian Survey Corps
RDA	canonical form of PCA
SA	South Australia
SADENR	South Australian Department of Environment & Natural Resources
SADME	South Australian Department of Mines and Energy
UPGMA	unweighted pair-groups method using arithmetic averages
USDA	United States Department of Agriculture
WLC	Western Lands Commission of New South Wales

CHAPTER 1:
INTRODUCTION AND SCOPE OF THE STUDY

INTRODUCTION

The vegetation of eastern South Australia provides a set of characteristics, and poses a number of interesting patterns and problems, which are of relevance to the field of ecology known as vegetation science, and to scientific and human endeavour in general. A brief summary of some of the literature concerning vegetation particularly that of arid rangelands follows and reasons are given for the choice of study area. A framework of the study outlines a range of specific topics to be addressed in later chapters.

VEGETATION AS NATURAL HERITAGE

Vegetation is a fundamentally important part of the natural heritage of the Earth (Kent & Coker, 1992). Firstly, it is an integral part, and also the most obvious physical representation of an ecosystem. As a consequence of providing such a recognizable contribution to the landscape, vegetation can also be seen as contributing to the aesthetic and cultural heritage. Secondly, since plants carry out photosynthesis and therefore harvest the incoming energy of the sun, vegetation provides the base of the trophic pyramid. Thirdly, vegetation provides habitat for most other organisms. Therefore, the definition, description and study of vegetation is an important human endeavour.

Until about 140 years ago, the vegetation of eastern South Australia remained in relatively undisturbed condition because the original occupants, the Aboriginal people, were largely nomadic and did not practise any form of settled agriculture. Neither were there any large ungulate herbivores present (Osborn, 1926a; Platou & Tueller, 1988) until European settlement. The region is too dry for close settlement and the cultivation of crops, so the only form of agriculture practised since that time is extensive livestock grazing or pastoralism. Hence the vegetation of the region is in an unaltered state compared to that of other regions of Australia and the world, and represents a significant cultural heritage.

ARID VEGETATION

Hot arid lands occupy 13-14% of the earth, and occur on all the continents except Antarctica. (Evenari, 1985). Major hot deserts of the world include the Sahara and Sudan of North Africa, Namib, Karoo and Kalahari of South Africa, Sinai, Negev, Syrian, Iraqi and Arabian of the Middle East, the Thar of India, the Mojave, Sonoran and Chihuahuan of North America, Atacama of South America and the Simpson, Gibson and Sturt Deserts of Australia. These deserts have a range of features in common, including climate (low, unpredictable rainfall and high evaporation), geomorphology, hydrology, soils, vegetation and animal life, which are discussed in relation to the study area in Chapters 3 and 4.

Over 70% of the Australian continent is arid (Williams & Calaby, 1985), and over 80% of South Australia (Osborn, 1926a). Deserts are difficult to define (Cunningham, 1981), and there is some disagreement as to whether the Australian arid lands are deserts or semi-deserts. This is because the Australian arid lands are unique in that they contain more deep-rooted perennials (trees, shrubs and perennial grasses) for a given level of aridity than those elsewhere (Williams & Calaby, 1985; Stafford Smith & Morton, 1990). Several reasons are suggested for this. Firstly, the rainfall has a very high variability compared with regions of similar aridity elsewhere. Secondly, soils are highly weathered, sorted, and consequently low in nutrients, especially phosphorus and nitrogen, levels of which are commonly half that of other hot deserts (Stafford Smith & Morton, 1990). These two factors probably combine to produce an environment of sclerophyllous deep-rooted perennials (see Chapter 5). However, the Australian deserts do have a wide range of climatic and physical characteristics in common with other arid lands, and the Simpson, Great Sandy, Gibson, Great Victoria and Sturt Deserts are classified as true hot deserts according to Evenari (1985). As long as the above unique variables of soils and vegetation are taken into account, patterns and processes which can be identified in the Australian deserts may be usefully added to the theory of arid-land vegetation in general.

RANGELANDS

Native vegetation forms the immediate environment of humans and their domestic stock over large areas of the surface of the Earth (Mueller-Dombois & Ellenberg, 1974), including 60% of the Australian continent (Wilson, 1990). Because of the unpredictability of rainfall in arid lands usually no form of cultivated agriculture is possible (Lange, 1972; Belsky, 1989). Hence, the most common agricultural land-use in arid lands is that of extensive livestock grazing, or pastoralism, utilizing native vegetation (Osborn, 1926a; Osborn, 1926b). Within these grazed systems, or rangelands, landscape patterns are mostly influenced by natural variables, and grazing by domestic herbivores (Belsky, 1989). Herbivory is known to superimpose on a background of edaphic and climatic variables to cause changes in species composition and relative abundance through disruption of recruitment and survival of individuals (Hart & Norton, 1988; Archer, 1993). It can be seen from the above that any study of arid vegetation, and particularly one which examines the impact of humans and their livestock upon this vegetation, has world-wide application to vegetation theory, and also to global issues of management and conservation (Urban *et al.*, 1987).

Since the time of European settlement around 1850, eastern South Australia, like arid lands elsewhere, has been used for the grazing of domestic livestock, and has been subjected to other disturbing factors such as the introduction of rabbits and the invasion of a range of exotic plants. Most of the details of this land occupation are available in relatively detailed historical records held by various South Australian government departments. Thus, the region offers a unique opportunity to observe the effects of these disturbances upon arid lands, while still retaining enough of its original character that we can be reasonably certain of its pre-European nature (Lange, 1972; Wilson, 1990). It is therefore possible to observe these effects in progress, which is no longer possible in many other arid regions of the world.

THE STUDY AREA

A study area was chosen in the rangelands of eastern South Australia, against the border with New South Wales (Figure 1.1). It occupies an area of approximately 32 000 km^2 (200 km from north to south, and 180 km from east to west), with the south west corner approximately 300 km north-east of Adelaide, the capital of South Australia. The area lies on the southern fringes of the Sturt Desert (Evenari, 1985), which is classified as arid, with no marked season of preciptitation (Meigs, 1953). A large range of topography, soils, vegetation and grazing history are encountered within the study area (Chapters 4 and 5). This means that enough variation should be present to be able to deduce which variables are controlling the pattern and dynamics of vegetation, and hence to make more general conclusions about the effects of these variables.

A FRAMEWORK FOR THIS STUDY

The above observations present a number of questions. The following paragraphs explore these questions, and describe a framework for this thesis.

What is the vegetation of eastern South Australia? Chapters 4 and 5 deal with the scope, detail and information content of previous descriptions of the environment and vegetation of the study area. Chapters 6 and 7 present results of improved descriptions of the perennial vegetation using modern methods of survey and data analysis, in an original approach using two different scales of survey. Chapter 8 examines the environmental variables which control the distribution of the perennial vegetation.

What changes are occurring to the vegetation and what is its likely future? More particularly, what are the main causal agents? How many changes are attributable to human activities? Chapter 9 examines the relative effects of a range of domestic, feral and native herbivores on populations of perennial species.

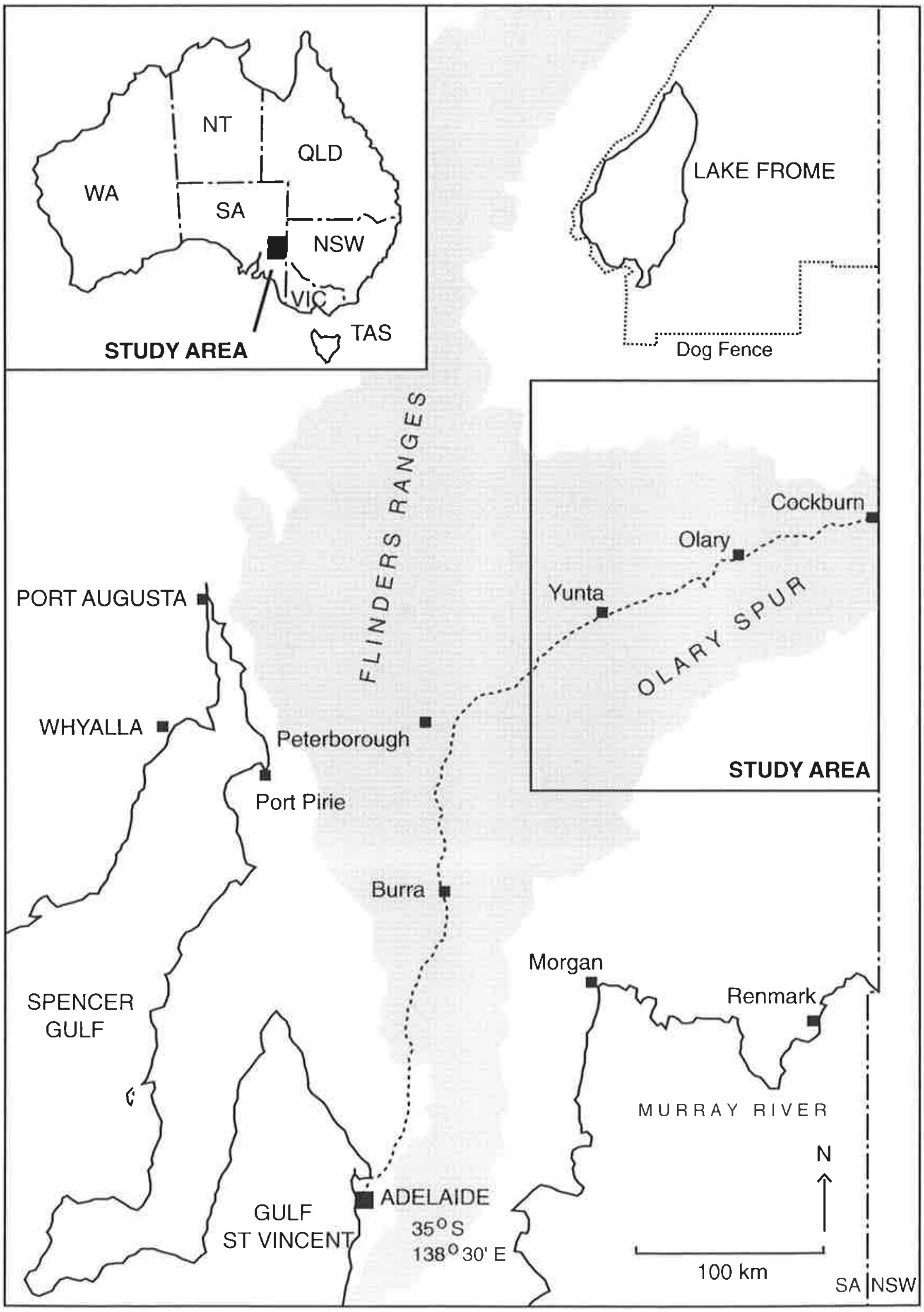


Figure 1.1

Location of the study area (32 000 sq. km) on the Australian continent (inset), and in South Australia (SA) against the border with New South Wales (NSW). The shaded area shows the principal topographic feature of SA, the Flinders Ranges.

What implications do these findings have in relation to conservation and land management of the study area? Which of the methodology and findings are relevant to the theory of ecology and vegetation science? Chapter 10 summarises these findings.

CONCLUSION

If we can ascertain what the vegetation is, what variables control its distribution, and what is happening to it under this relatively new grazing regime, it will be possible to assess some of the implications for management and conservation. An approach through a background of current methodology and theory in vegetation science will ensure that the findings will be relevant to conservation and management of other parts of Australia and the rest of the world, and will therefore be useful in planning for conservation and vegetation research elsewhere.

CHAPTER 2:
THE THEORY OF VEGETATION SCIENCE

INTRODUCTION

Ecology, the study of nature's house, the "oikos", (Redfield, 1988) is a notoriously ill-defined science other than that it is the study of the relationships of biological entities with each other and the environment (Anderson, 1971). Anderson concluded that any research providing a reasoned understanding of the biosphere and seeking to establish critical relationships can be called ecology, and that ecologists therefore "simultaneously handle an order of magnitude more parameters" than do physical scientists in any piece of problem-solving. The branch of ecology known as vegetation science is here broadly defined following Wiegleb (1989), as research concerning the description, explanation and prediction of distribution patterns of plant populations, species and vegetation units in space and time. Vegetation science is the European term for what would be called plant synecology in England and America (Mueller-Dombois & Ellenberg, 1974). The kinds of questions asked in the introduction (see Chapter 1) dictate that this thesis falls within the ecological field of vegetation science.

It is sometimes stated that there is a characteristic and general lack of conceptual unity within the field of ecology (Hagen, 1989), and particularly within vegetation science (Barbour *et al.*, 1987). This lack of a coherent conceptual basis has occasionally hindered communication (Acker, 1990) and means that it is difficult to place individual pieces of research into a general framework. It is consequently often difficult to decide which of the approaches available should be followed in any given piece of research. This chapter presents some of the major opposing points of view prevalent in vegetation science, shows where seemingly opposing points of view can be usefully reconciled (Wiegleb, 1989), and describes the emphasis which will be followed in this study.

INDUCTIVE, OBSERVATIONAL, HOLISTIC & SYNECOLOGICAL VERSUS DEDUCTIVE, EXPERIMENTAL, REDUCTIONIST & AUTECOLOGICAL RESEARCH METHODS

Philosophers such as Popper (1959) have defined science as a highly systematic and logical process whereby hypotheses are formed to explain existing problems or facts, and experiments carried out in order to falsify these hypotheses (Kent & Coker, 1992). Such methods involve the testing of significance and accompanying statements of probability of error (Greig-Smith, 1983). However, recent authors such as Feyerabend (1975), Fagerström (1987) and Taylor (1989) have argued that this definition is overly restrictive, that the importance of testability is often exaggerated, and that these notions do not accurately describe the way that scientists actually behave (Kuhn, 1962; Kuhn, 1970), especially biologists (Wiegleb, 1989). Kuhn (1962), after studying the history of scientific endeavour, stated that "science does not develop by the accumulation of individual discoveries and inventions". Feyerabend (1975) is even more emphatic, suggesting that science is essentially anarchistic, that there is no idea that cannot improve knowledge, and that these ideas may arise from seemingly irrelevant activities. By his definition, science is therefore much more creative than previously admitted, and to rely on the strict principle of falsification would "wipe out science as we know it".

Experimental science provides the most direct and convincing results (Noy-Meir, 1971). However, if this process of experimental science is to be productive, well-informed hypotheses must be made. This is a problem in the field of vegetation science, because basic descriptions of vegetation are often completely absent or, if in existence, extremely generalized (Kent & Coker, 1992). Deductive science includes such activities as systems analysis, modelling and theoretical ecology, but these methods all require a critical mass of basic and relevant information if realistic hypotheses and models are to result (Noy-Meir, 1971). In most cases, these data are not available. It is therefore often impossible to devise well-directed hypotheses (van der Maarel, 1989), so a total reliance on experimental methods would be very restrictive and selective (Noy-Meir, 1971). Investigations aimed at understanding and explaining observed phenomena are necessary before other goals of science - generalization (statement of theory and construction of models), testing (using statistics) and prediction (Pickett & Kolasa, 1989) - can take place. It is also true that the nature of the biological sciences means that it is not always possible to formulate deterministic laws, because stochastic processes are so important (Wiegleb, 1989). Hence understanding is the most general and primary goal of science, whereas theory, falsification and prediction can be seen as tools or specialized goals of the primary one, understanding (Pickett & Kolasa, 1989).

For these reasons, a lot of vegetation research is observational or descriptive in nature (Ludwig & Reynolds, 1988) and inductive (rather than deductive) in approach (Kent & Coker, 1992). These fall into the category of data exploration, erection of frameworks and generation of testable hypotheses, scientific methods which have no null hypothesis and require no significance testing (Greig-Smith, 1983). The fields of phytosociology, field ecology, and geobotany fall within this definition (Noy-Meir, 1971). Such research is by definition non-experimental, and usually multivariate in nature (Noy-Meir, 1971). Critics have suggested that this inductive approach is "messy" and fails to produce any advances to general ecological theory, but others suggest that an over-emphasis on deductive methods leads to more and more fragmentation of science, and that the real world demands a more holistic approach (Waldrop, 1992). One of the benefits of allowing inductive research a place in science, and vegetation science in particular, will be that more selective, directed and incisive hypotheses about the causes of observed patterns (Ludwig & Reynolds, 1988) can be formulated if there has been information input from exploratory research. These can then be experimentally tested (Ludwig & Reynolds, 1988), and statistically validated (Taylor, 1989) so that an overall greater advance of knowledge will result. Most vegetation scientists (Taylor, 1989; Kent & Coker, 1992) recognize that descriptive and experimental ecology have joint roles in the methodology of vegetation science.

This debate can also be seen as one separating the reductionist versus the holistic viewpoint (Anderson, 1971; Wiegert, 1988). A reductionist approach takes a whole system, breaking it down into smaller and smaller parts; followers of this approach expect that the system will ultimately be explained in terms of chemistry and physics. The problem with this approach is that totally deterministic relationships can usually only be identified in extremely simple ecological data (Legendre & Legendre, 1983). The holistic view is that real ecological systems have emergent qualities, unexpected complex interractions arising from the mutual dependence of organic parts, which cannot be explained in reductionist terms. Real ecological data are usually multi-dimensional (Legendre & Legendre, 1983) and ecological systems are usually much more complex than in the physical sciences (Wiegert, 1988). Almost by definition, ecology is holistic, rather than being isolated bits of biology (Redfield, 1988).

These different approaches to ecological research are probably a reflection of the fact that, although reductionist methods have occasionally proved useful, observational studies have led to the development of different intellectual perspectives. This is not usually taken to mean that experimental ecology using deductive methods should be abandoned, but rather that the role of exploratory, inductive research should be recognized. It is now accepted that there are three main approaches used in ecological science: experimental, observational and deductive (Noy-Meir, 1971). These different perspectives, rather than causing disunity, may be more usefully viewed as complementary approaches (Hagen, 1989). Wiegleb (1989) states that although a completely reductionist program leads to absurdity, so would a totally holistic one. He suggests that emergent materialism may have a place for refined forms of both methods. Predictions may not be possible at all in multivariate systems with non-linear dynamics, and are more likely to be made in future via stochastic models, with rather more limited domains of applicability (Wiegleb, 1989).

THE ORGANISMIC (ECOSYSTEM) AND INDIVIDUALISTIC (CONTINUUM) CONCEPTS OF VEGETATION

The nature of vegetation has historically been thought of in two quite distinct ways. The concept of orderly changes in vegetation over time, or succession, was first introduced into the literature by Cowles (1899), in studies of the vegetation of sand dunes at Lake Michigan. Building on Cowles' ideas of succession, Clements (1916; 1936) believed that vegetation could be divided into clearly recognizable entities which, like organisms (Wiegleb, 1989), repeat themselves regularly and exactly, a discrete, "organismic" concept of biotic communities (Ludwig & Reynolds, 1988). He believed that vegetation types were the inevitable outcomes of the effects of climatic and environmental factors, and that given sufficient time and stability, a given locality would reach equilibrium at a particular vegetation type by succession (Kent & Coker, 1992). Tansley (1935) developed this concept of the entity of the system (which he named the "ecosystem") still further, and led research into physiological investigations to examine the complex interactions between species which governed successional and equilibrium processes (Barbour *et al.*, 1987). Evans (1956) and Odum (1962; 1977) further ensured the predominance of this view-point by incorporating it into their articles and texts on the general structure of ecology. The views of Clements and Tansley dominated the English-speaking world for the first half of the twentieth century (Mueller-Dombois & Ellenberg, 1974). All components of the ecosystem were said to be functionally integrated through food chains, food webs and nutrient cycling (Odum, 1969), which tended to force the system to shift by succession, into a stable state, the climax, which is determined by the starting conditions (Wiegleb, 1989). These theories of succession and ecosystem theory underlie all methods of classification (Mueller-Dombois & Ellenberg, 1974), since it is not possible to classify a truly homogenous environment. Although Braun-Blanquet (1913; 1928) and his followers did not necessarily accept the organismic nature of vegetation *per se*, they did absorb this perspective of vegetation to the extreme whereby intermediate vegetation stands which did not fit the standard vegetation types were defined as "disclimax" (displaced from the climax by disturbance) or not yet reached their true climax vegetation type. These were ignored in their systems of phytosociology. However, although it is accepted that there is a certain amount of internal feedback (inhibition and facilitation) in associations, the totally organismic view of the community as a whole is no longer accepted (Wiegleb, 1989).

The opposing point of view is that of the continuum concept, attributed to Gleason (1926) and followed by Cain (1947), which states that each species responds independently to varying factors (Goodall, 1966), that these factors vary continuously in space and time, and that therefore the combination of species at any given point is unique. In fact, the Russian botanist Ramensky, (1910; Ruoff, 1926) had already clearly accepted that vegetation was sometimes continuous and sometimes discontinuous. Ramensky (1910), unknown to Gleason, had previously published work clearly based upon the concept of ordination (Sobolev & Utekhin, 1978), but because it was published in a non-western European language, it did not become widely known. The notion did however gain wide acceptance in Russia (Sukachev, 1928) and Poland (Paczoski, 1930). If species respond independently, this means that species do not form natural groupings (Harper, 1967). If taken to the extreme, and vegetation is completely continuous, never forming discrete communities, it is impossible to get meaningful results from classification techniques. Instead, communities intergrade continuously unless affected by disturbance or an environmental discontinuity (Curtis & McIntosh, 1951; Whittaker, 1978a). If this is so, then species can only arbitrarily be assigned to groups by similarity of distribution (Whittaker, 1978b). The concept of the continuum came to be the accepted point of view of the Wisconsin school of plant ecologists Bray, Curtis and McIntosh (1951, 1957 &1967), and of Whittaker (1956; 1960), who each contributed to the formulation of ordination techniques to describe vegetation in terms of its continuous nature. Austin (1989) further modified and developed the concept to explain Gaussian (bell-shaped) rather than linear responses to environment, and non-Gaussian (bi-modal and other) curves caused by species interaction, which are regularly observed in real vegetation data.

It is now felt that these two opposing views, community and continuum, have developed due to the type of environment and sampling methods used by the main proponents (Anderson, 1965; Kershaw & Looney, 1985), and that they are differences of emphasis and perspective (Westhoff & van der Maarel, 1978) rather than that one or the other is the true natural state of vegetation. Since plant communities of highly modified landscapes are often more clearly defined and demarcated (Kent & Coker, 1992), the European school (Zurich-Montpellier) has tended to emphasize this aspect of vegetation. In addition, the subjective selection of sites in the Braun-Blanquet system (Ludwig & Reynolds, 1988) meant that intermediates were deliberately ignored (Kershaw & Looney, 1985), so the results would always fall into distinct groups. Such well-defined clusters may not exist, being merely the result of inadequate sampling (Belbin & McDonald, 1993).

In contrast, the Americans, working in more continuous tracts of vegetation, have tended to emphasize ordination (Wiegleb, 1989). Their practice of deliberately sampling along a distinct environmental gradient also tends to emphasise the continuum nature of vegetation by amplifying the slope of variables controlling plant distributions. A more recent example of this tendency is provided by Auerbach and Shmida (1993), who sampled along a steep altitudinal gradient in Israel and found no evidence for discrete plant communities.

Most vegetation scientists now recognize that the real situation is somewhere between that of completely distinct communities and completely continuous gradients (Noy-Meir & Whittaker, 1978; Kershaw & Looney, 1985; Noy-Meir & van der Maarel, 1987; Kent & Coker, 1992). The concept of the nodum, relatively discrete communities separated by intergrading continua, was suggested by Goodall (1953) and Poore (1955a). Their nodum and continuum model represents vegetation as a complex mixture of continuity and discontinuity (Mueller-Dombois & Ellenberg, 1974; Whittaker, 1978b), and allows for the fact that the two veiws are not necessarily incompatible (Whittaker, 1953; Goodall, 1962; Lambert & Dale, 1964; Mirkin, 1987; West, 1988). Webb (1954) summarizes this viewpoint in his statement that "the pattern of vegetation hovers tantalizingly between the continuous and the discontinuous". If vegetation were completely continuous, traditional phytosociology would be impossible, but if entirely discontinuous, with sharp boundaries, a satisfactory taxonomy would have been found years ago, and there would be no further work possible. While similar species combinations do occur in similar habitats, even if geographically separated, no two species have exactly the same ecological amplitudes (Mueller-Dombois & Ellenberg, 1974). Therefore, although some species are so similar that they can be combined into groups of similar ecological requirements, no two relevés are exactly alike, and species assemblages change more or less continuously so that organismic character is lacking (Mueller-Dombois & Ellenberg, 1974). Because of this it is now felt by most researchers that it is best not to rely on clustering alone to explore the data, since classification of units is often artificial (Kershaw & Looney, 1985), and it is better to recognize vegetation types as foci within a range of variation (Noy-Meir & Whittaker, 1978). These foci are consistent with the nodum model of Poore (1956). A nodum is an abstract entity (Mueller-Dombois & Ellenberg, 1974) defined as a group of species in a group of samples, not necessarily discretely bounded from, nor hierarchically related to other groups and noda (Noy-Meir & Whittaker, 1978). These co-existing mixtures of plant individuals at a site as a result of migration and selection are known as communities (or phytocoenoses), and in integrated theory do have some function and identity because interactions among and between populations limit individualistic performance of species by restricting ecological amplitutes and shifting optima (Moravec, 1989). Hence, classification of such phytocoenoses is still possible, although they are usually interconnected by transition zones to form a continuum (Moravec, 1989). Indirect gradient analysis is usually used to identify noda and continua, and because it is derived from a floristic ordination, is very closely related to classification (Mueller-Dombois & Ellenberg, 1974). The concept of the nodum can be compared to the concept of the coenon of the Braun-Blanquet school, although the means of arriving at them are quite different (Noy-Meir & Whittaker, 1978).

EQUILIBRIUM AND NON-EQUILIBRIUM CONTROL OF VEGETATION PATTERNS

It is known that both climate and soil have a strong controlling influence over plant distributions; these effects are described in more detail in Chapter 4. If all plants were totally and immediately controlled in a linear fashion by edaphic and climatic variables, all that would remain is to determine these effects by pot experiments, derive the correct equations, and it would be possible to determine the exact vegetation of any point on the surface of the earth. Mueller-Dombois and Ellenberg (1974) describes how the ecological properties of the species such as life-form and physiology affect its ability to thrive at any given habitat which he defines as the sum total of environmental factors. Ecological amplitude and habitat are invoked as the sole controlling variables of plant distributions by believers of pure continuum theory. However, observations of real vegetation have suggested that there are further complicating factors. Mueller-Dombois (1974) stated that because it is the flora of a region which provides the basic material (phytogeography), accessibility, the ability of a given species to reach a particular habitat is an important factor in controlling plant distribution. Accessibility in turn depends on such factors as seed dispersal. Acker (1990) suggests that observed vegetation patterns are constrained not only by site factors, and the pool of species available, but also by interactions between species. He therefore divides into those which are non-labile, or unaffected by successional time (such as macro-climate and soil parent material), and those which are labile, or affected by the existing vegetation (such as available light, soil organic matter). Between-plant interactions may also determine vegetation patterns. Goodall (1962) has stated that the effect of environmental factors on plants can vary depending not only on inanimate features of the site, but also the effects of other organisms. For example, competition may mean that a plant cannot persist in a site which otherwise would provide all requirements for its growth.

Historical events may also be a variable controlling plant distributions (Herrera, 1992). Although climatic and edaphic variables may be thought of as strongly overriding attributes, it must be remembered that they do not necessarily remain constant within ecological time (Chesson & Case, 1986). Mueller-Dombois and Ellenberg (1974) also recognize a temporal factor in controlling plant distributions, especially the amount of time passed since major events such as plant invasions, environmental changes and disturbances. Acker (1990) also recognizes that there is a tendency of vegetation to remain on site once established. In other words, a long-lived plant may persist in a particular location, long after climatic or edaphic variables have changed so that its establishment there would theoretically no longer be favoured (Davis, 1986). This means that chance may play a role in the occupation of a site by a particular plant species (Goodall, 1966), through the timing of the opening of gaps to coincide with the timing of seed dispersal events and minor climatic and seasonal events. Greig-Smith (1983) also recognizes that chance events are important, and that a plant which establishes first of a number fitted to do so, will remain dominant at that location. Thus historical events are also known to have a strong complicating effect in explaining modern vegetation distribution (Greig-Smith, 1983; Chesson & Case, 1986).

These historical, local disturbance and chance effects have often been dismissed as "noise" (Gauch, 1982), random processes beyond explanation (Wiegleb, 1989). Their effects have usually only been detected in a negative fashion, following the failure of full explanation of plant distribution by present environmental variables (Greig-Smith, 1983). However Wiegleb (1989) suggests that this is an artificial definition and merely indicates the limitations of present models. Gauch (1982) stresses that historical and disturbance effects need to be identified and methods established for measuring them, and Pickett and Kolasa (1989) suggest that vegetation theories should include probability distributions at different temporal scales to explain such events. It seems logical that future models of vegetation distribution and dynamics should include both equilibrium and non-equilibrium variables.

EQUILIBRIUM VS STATE-AND-TRANSITION MODELS OF VEGETATION DYNAMICS

The concept of succession, leading inevitably to the development of pre-determined, stable (equilibrium) climax communities as developed by Cowles (1899) and Clements (1916) came to be widely accepted by the scientific and administrative world. Cooper (1926) early pointed out that the concepts of succession and climax had been over-emphasized and made too rigid. However, these ideas came to dominate the field of rangeland science (Walker, 1988), an applied branch of vegetation science which developed largely in North America. For example, authors of texts on range management such as Lewis (1969), Tueller (1973) and Heady (1975) believed that under an appropriate grazing regime, vegetation will be held in disclimax, an equilibrium state somewhere below climax (Smith, 1988). Removal of grazing should then automatically allow the vegetation to progress through to climax. However, it is now realised that although this model may be of some use, especially in grassland systems, it is no longer accepted as a general theory (Smith, 1988). Vegetation change can take multiple pathways and may be irreversible (Hart & Norton, 1988), such as in the case of invasion by shrubs and exotic species (Smith, 1988). In addition, the constantly changing abiotic envionment means that true equilibria are never reached, and that vegetation is always in a state of flux, sometimes dramatically so (Cooper, 1926). Westoby *et al.* (1989), suggest a formal "state-and-transition" model of rangeland vegetation, and list a number of cases in which vegetation may be irrevocably changed by certain combinations of climate and managment. For example, if land is badly overgrazed so that species composition is significantly altered, the vegetation may never regain its original composition. These transitions from one state to another may be unfavourable, representing hazards to be avoided, or favourable, representing opportunities to alter the state to a more advantageous one. Thus they believe that rangeland management may not necessarily mean finding a fixed form of management which achieves a productive equilibrium, but should be a matter of playing a continuing game of seizing opportunities and avoiding hazards. Westoby *et al.* (1989) recognize that successional changes and equilibrium dynamics do also occur within any given state, but that abrupt changes from one state to another are also possible. Hence both equilibrium and non-equilibrium models are of use in vegetation science, and Stafford Smith (1992) recommends that rangeland vegetation be viewed using a combination of both models.

CONCLUSIONS

It can be seen that the study of ecology is curiously divided into opposing points of view on almost every fundamental concept. Critics of ecology have cited this failure to reach consensus and any unified theory as a handicap. However, closer examination shows that these seeming dichotomies are often in fact merely different perspectives of the same subject. It is shown above that such views can usually be combined to form a more powerful approach to solving real world questions, an approach suggested by Mueller-Dombois and Ellenberg (1974). In line with this philosophy, many of these apparently opposing points of view are together called upon to answer the questions relevant to this study.

CHAPTER 3:
METHODS IN VEGETATION SCIENCE

INTRODUCTION

As a consequence of the tendency of ecological theory to be divided into opposing schools of thought on almost every important issue, there are correspondingly very different methods of research and analysis techniques available, each reflecting different theoretical viewpoints. Some of the more important methods and analysis techniques are discussed below, and reasons given for the methods selected for this study.

ASPECT AND SCALE OF VEGETATION STUDIES

Because of the controversy over the nature of vegetation, and science itself, there are a number of views about the aspects and scale at which vegetation should be studied. The aspect and scale chosen will depend on the viewpoint of the researcher and the kind of questions being asked.

Vegetation displays a number of aspects which are of interest to ecologists, each involving the study of the environmental variables which affect them (Noy-Meir & van der Maarel, 1987). These aspects include the following:

(1) structure, physiognomy, life-forms;
(2) diversity, dominance
(3) spatial variation in species composition, distribution patterns, and scale of patterns (phytosociology)
(4) temporal variation, stability.

The direction of this study is largely within the last three of these categories, since the main questions are about the composition of the vegetation and any changes which are occurring to it.

Anderson (1971) identifies three scales of investigation in ecology: micro-scales such as physico-chemical investigations; meso-scales of interactions between individual organisms and their environment, and macro-scales, the study of whole vegetation, or populations. Both landscape ecology and biogeography are therefore at the macro scale, with biogeography the broader scale of the two. Landscape ecology is a study of spatial patterns and the processes related to them, whereas biogeography is the study of large scale spatial distributions of species in relation to climate and soil (Jongman *et al.*, 1987). The size of the study area means that this work is primarily at the macro-scale of landscape ecology. However, as patterns become known and it is possible to generate more directed hypotheses, studies at meso and micro scales will add to the power of the study.

AUTECOLOGY (THE STUDY OF POPULATIONS) AND SYNECOLOGY (THE STUDY OF COMMUNITIES) - A QUESTION OF SCALE

Another aspect of scale is expressed in the holism versus reductionism debate. Harper (1982) argues that the holistic approach will never be successful in explaining the causes of present behaviour and distribution of organisms, and suggests that effort be concentrated at the individual plant level. Critics of the holistic approach cite how studies of animal populations involving a census of their numbers have occupied a central position in animal ecology for a considerable period of time, whereas plant ecology has been largely dominated by investigations into the spatial configurations of species in relation to their environment (Kershaw & Looney, 1985). Kershaw and Looney believe that this has led to neglect of the study of plant populations and the control of the numbers of individuals involved. They believe that the reasons for this partly stem from the pre-occupation with spatial configurations and partly from the difficulties inherent in studying changes in natural populations of plants. Barbour *et al.* (1987) cite this lack of directed, reductionist population studies as the reason why “depressingly few general concepts” have emerged within vegetation science. Kershaw and Looney (1985) complain that many vegetation studies are “relentlessly descriptive with very little attempt to relate the findings to potential mechanisms of change”, and call for more work aimed at identifying specific mechanisms involved in even a few selected cases. However, there are signs that the individualistic concept of vegetation as proposed by Ramensky, Gleason and their followers (see Chapter 2) has resulted in more attention being paid to the role of individuals and populations rather than species in determining overall vegetation pattern (Grubb, 1985). This has lead to further studies in the fields of plant species strategies and plant population biology as practised by Harper, Grime and Silvertown (Kent & Coker, 1992).

The scope of this study is predominantly large-scale and inductive (descriptive, with *a posteriori* explanations of probable causes of patterns found), which is the most useful approach in a very large region about which relatively little is known. This approach will answer the question of what vegetation occurs in the region. However, in order to answer questions regarding causes of patterns, and variables affecting changes to the vegetation, the research will also be directed into a more reductionist mode, including population dynamics, and physico-chemical explanations of pattern. This follows the recommendation of Redfield (1988) that an excellent strategy of science is to use both methods of analysis (reductionism) and synthesis (holism), moving to higher or lower levels of organization as necessary to solve problems.

AGE-CLASS & STAGE-CLASS DISTRIBUTIONS IN POPULATION STUDIES

Population data may be obtained from a vertical approach, where the life history of a particular cohort is followed for the life span of all the individuals, or from a horizontal approach, which uses data on all the ages within a given population at one time (Brower *et al.*, 1990). In long-lived species such as many woody plants, it is not possible to directly detect population changes during short-term studies. Therefore the horizontal approach of obtaining age and size structures of populations is frequently used to investigate changes occurring over time. The proportions of individuals belonging to certain age-groups are collectively referred to as age-structures, or age-distributions, and can be represented diagramatically as histograms (Brower *et al.*, 1990). A size-structure is a similar description using the relative numbers of large and small individuals, which is not necessarily the same as an age structure (Silvertown & Doust, 1993). A great deal of information can be accurately obtained from age-structures, concerning natality, mortality, and average life span.

In many perennial species it is not possible to assign ages to individuals with any accuracy. Hence, age must be inferred from the life-stage structure of the population. The resulting graphical summary is therefore more accurately referred to as a life-stage structure, or life-stage distribution. A stage-structure can only be only loosely correlated to age-structure (Harper, 1977), since many species show plastic responses to environment in moving from one stage to another, especially in forest plants, where transitions from one stage to another can be governed by availability of light (Silvertown & Doust, 1993). However, there is a broad correlation between the stage-structure and the age-structure of a population. Lange and Sparrow (1992), by measuring trunk-girths of *Acacia papyrocarpa* in the Australian arid zone for ten years, found previous estimates of life-span based on Lange and Purdie's (1976) life-stage structures to be a reasonably accurate indication of age. Neither may chronological age be the best descriptor of the present or predictor of the future in plant populations. This is because behaviours such as reproduction are more closely linked to size than to age in plants (Harper, 1977; Gatsuk *et al.*, 1980). For the above reasons, a life-stage distribution method can be very useful for describing plant populations and predicting their futures, and has been successfully used for this purpose by Rabotnov (1985), Roberts (1993) and others. Because the autecology of most Australian arid zone species is so little known it is not usually possible to assign precise ages to individuals and therefore the stage-class method was used in this study.

NUMERICAL (OBJECTIVE) VS DESCRIPTIVE (SUBJECTIVE) TECHNIQUES

As discussed, it is now recognized that most broadscale ecological studies are descriptive and based on field surveys, since the complex levels of communities, ecosystems and landscapes are not readily investigated by manipulative and experimental techniques. The result is that equally complex and large data sets are generally produced (Jongman *et al.*, 1987). The data are also usually multivariate, in that each sampling unit is characterized by many attributes (Gauch, 1982; Legendre & Legendre, 1983; Jongman *et al.*, 1987). For example, in this study each site is characterized by many species and a range of environmental variables. The data are not only complex, but they show noise (such as chance, historical events, local disturbances) and contain redundancies (many samples alike, repeating the same information), internal relations (such as factor complexes) and outliers (samples with low similarity to all other samples) (Gauch, 1982). Ecological data therefore usually contain information which is only indirectly interpretable. Hence multivariate analysis methods are the most useful in summarizing and interpreting such data, and were introduced from other areas of science into ecology from 1954 onwards (Noy-Meir & Whittaker, 1978). The numerical techniques have a high degree of mathematical sophistication, so their use has been greatly facilitated by the availability of computers (Noy-Meir & Whittaker, 1978). The present speed and capacity of computers means that it is now possible to consider large numbers of variables in a single calculation with a high degree of objectivity and repeatability (Goodall, 1978; Greig-Smith, 1983), and there is a consequent increasing trend towards use of multivariate numerical methods (Gauch, 1982).

Multivariate analysis includes techniques of direct gradient analysis (regression), indirect gradient analysis (ordination), and cluster analysis (classification) (Jongman *et al.*, 1987). Classification groups similar entities into clusters (Gauch, 1982) and closely replicates the natural cognitive tendency of humans to group objects. Ordination presents sample relationships in low-dimensional space with similar samples near one another and dissimilar ones apart (Gauch, 1982), so that relationships are identified and environmental interpretations can be made. Direct gradient analysis is a more simple technique that considers community responses to known gradients (Gauch, 1982), and is therefore a form of regression. Together, these facilitate analysis, description and interpretation of structure implicit in sites by species data matrices, which are not superficially obvious (Whittaker, 1978b), and it is stressed that their uses in summarizing and explaining complex data sets are complementary (Gauch, 1982).

PHYSIOGNOMIC & FLORISTIC METHODS OF VEGETATION CLASSIFICATION

A naturally human impulse, probably related to neural functioning, is a tendency to classify objects into groups. Hence, vegetation types such as prairie, forest and woodland are well-known concepts which pre-date modern science. There are several properties of vegetation on which classifications can be based (Goodall, 1953), the two most common being structural physiognomy and floristics. Physiognomic classifications take into account such criteria as the life-form (Raunkiaer, 1918), organization in space of the individuals within the vegetation type (Dansereau, 1951), and the overall appearance of the stand as a whole (woodland, prairie, savanna) (Greig-Smith, 1983). Floristic descriptions require an inventory of plant species present (Mueller-Dombois & Ellenberg, 1974), and vegetation types are determined on this basis. Neither of these methods has clear superiority (Whittaker, 1978a), and Dansereau (1951) admits that a combined approach is probably the most valuable. Physiognomic classifications are favoured by some people because floristics, being affected by historical events, do not necessarily coincide with major plant formations (Orlóci & Orlóci, 1985). Hence they are of diminished use in defining and describing landscapes (Dansereau, 1951), especially at the global scale, where floristic history and biogeography can play more important roles in plant distribution than environment. Examples of such large-scale physiognomic classifications are those of Schimper (1903), Warming (1909), Küchler (1947), Dansereau himself (1951), and Gillison (1988). However, it has been found that methods using full species composition are better for determining both the relationships between groups, and individual relationships with environmental variables (Westhoff & van der Maarel, 1978), so floristic classifications are more useful at smaller scales. Because of this, the majority of vegetation classifications have used information on the species present, whether presence/absence, or quantified (giving dominants) (Goodall, 1953). The most highly developed and well-known floristic technique is that of Braun-Blanquet and his associates of the "Zurich-Montpellier school" (Braun-Blanquet, 1928), known alternatively as "The Braun-Blanquet approach" or the "floristic-sociological approach". In this approach a hierarchical classification structure is determined by taking into account floristic composition only, rather than physiognomic characteristics (Westhoff & van der Maarel, 1978). The Braun-Blanquet floristic methods are easily adapted to a numerical approach (Greig-Smith, 1983), the advantages of which are discussed below. The existing vegetation maps of eastern South Australia (Specht, 1972), as shown in Chapter 5, are primarily structurally rather than floristically derived, which means it is not always possible to extract floristic information from them, or to extract species-environment relationships. These are both desirable characteristics of a classification system (Goodall, 1978) and correspond to one of the aims of this study, so a floristic classification was required.

The availability of powerful computing techniques has brought about a return to full floristic methods of classification. Multivariate analysis cannot be used when vegetation is described using the range of physiognomic and structural methods traditionally available (Dansereau, 1951; Küchler, 1951; Fosberg, 1961) since they are produced in tabular or graphic form, which are not able to be statistically analysed (Kent & Coker, 1992). Multivariate numerical techniques of structural and physiognomic classification are in the process of being developed (Orlóci & Orlóci, 1985; Gillison, 1988), but have not yet gained widespread acceptance. In the past, physiognomic methods were often preferred over floristic ones because data were only needed to be collected on life-forms, stratification, foliage density, coverage and plant dispersion of a few dominant species (Brower *et al.*, 1990). A classification could then be produced without having to sort and interpret massive amounts of floristic data by hand which, in pre-computing days, necessitated the use of cardboard strips, blocks or punched cards (Westhoff & van der Maarel, 1978). Physiognomic techniques usually also made the taxonomy much simpler, since only the dominant species had to be identified. In vegetation such as rainforest where the taxonomy is not well known, and where the structural component of the vegetation is considered to be ecologically highly important, physiognomic classifications are still preferred. However, advanced computer techniques are now available which can rapidly and effectively sort large floristic data sets. Full floristic numerical classifications have largely replaced physiognomic classifications because of their greater information content, objectivity and repeatability (Goodall, 1953; Sneath, 1957; Lambert & Dale, 1964; Westhoff & van der Maarel, 1978; Kent & Coker, 1992). This is especially so in regions where the flora is well enough known for most species to be identified. The floristic-numerical approach is also the one most suited to establishing links between vegetation and environmental patterns by ordination (Mueller-Dombois & Ellenberg, 1974). For these reasons a numerical, floristic classification was chosen to describe the vegetation of the study area.

SCALE OF CLASSIFICATION

Pattern exists at nested (hierarchical) scales within many natural systems, including vegetation (Palmer, 1988; Rahel, 1990; Sugihara & May, 1990; Reed *et al.*, 1993). Vegetation can therefore be classified at different scales, but there is some confusion in terminology (Beadle & Costin, 1952), since different researchers have occasionally used different terms for vegetation classes at the same scale, or used the same term for classes at different scales. There is also a tendency for definitions to have both a floristic and a physiognomic component, such as those suggested by Beadle and Costin (1952). A summary of classification terms most commonly used in the literature follows, with an explanation of the ones to be used in this study.

The basic unit of the Braun-Blanquet system is the association; "a plant community of definite floristic composition, presenting a uniform physiognomy and growing in uniform habitat conditions". This definition treats a community as a set of species, rather than a set of individuals, which is a consequence of the fact that botanists are dealing with sessile organisms (Goodall, 1966). This concept of the association was originally defined by Flahault and Schröter (1910) at the Third International Botanical Congress in Brussels. The term is interchangeable with vegetation type, as defined by Mueller-Dombois and Ellenberg (1974), a vegetation unit characterized by certain combinations of life-forms. It has since been agreed that floristically consistent units are not always physiognomically uniform (Westhoff & van der Maarel, 1978). A distinction is made between the plant community, which is a single real stand of vegetation, and the association, which is an abstract representation of groups of stands (Mueller-Dombois & Ellenberg, 1974). It has previously been found very difficult to map vegetation associations, because their distributions are governed by local topography and soil type, resulting in unmappable mosaics, especially in areas where the landscape is complex (Küchler, 1951). Existing classifications of South Australian vegetation have confirmed the difficulty of mapping such mosaic patterns (Tiver, 1987; Tiver *et al.*, 1989; Sparrow, 1991).

Although formal definitions for higher syntaxa are not well defined (Westhoff & van der Maarel, 1978), it is generally accepted that associations are combined into alliances, and so on into larger units such as orders and formations. Mueller-Dombois and Ellenberg (1974) define the alliance rather loosely as a large, easily identified vegetation unit, which is usually separated structurally as well as floristically, and is less narrowly defined than the overlapping associations within it. Moravec (1971) defines the alliance as a grouping of two or more related associations, a definition parallel to the structural alliances of Specht (1972). A community complex *sensu* Westhoff and van der Maarel (1978) is defined as a "set of contiguous or continuous communities forming a mosaic or pattern", and is therefore very close to the concept of an alliance as described above. This would be equivalent to the term edaphic complex, as defined by Crocker and Wood (1939 & 1947), a series of floristically related associations forming a closely-knit complex on allied soils, and forming the next natural grouping above the association. Very useful maps have been produced of South Australian vegetation based on the edaphic complex, for example those of Crocker (1946). Similarly, Specht (1972) found his structural versions of the alliance (same structure, related species as dominants, possibly different species in understorey) to be the smallest mappable units for South Australian vegetation. Floristic alliances have also proved useful in describing subalpine heathland in western Europe (Schaminée *et al.*, 1993).

The formation tends to be structurally rather than floristically defined (Beadle & Costin, 1952), combining all communities of the same structure, regardless of floristics (Beard & Webb, 1974). Hence formations such as tropical rain forests, mangrove swamps and cactus deserts are defined primarily on the structural characteristics of the dominant life-form (Mueller-Dombois & Ellenberg, 1974). Wood (1939) loosely defines the formation as having allied flora, soils, structure and life-form.

It is therefore proposed initially to classify the vegetation at the level of alliance *sensu* Mueller-Dombois and Ellenberg (1974). Classifying vegetation at this scale, and using numerical floristic data to do so has a number of advantages. Vegetation alliances can readily be mapped at relatively large scales of up to 1 : 5 000 000, such as those of Specht (1972) and, if combined with sub-groups such as associations, a large amount of floristic information should be able to be extracted from them. The floristic alliances produced should be readily comparable with the existing structural alliances already mapped by Specht (1972) for overlapping and nearby areas (see Chapter 5). This latter point is an important one if information on vegetation is not to become too fragmented, specialized and localized (Küchler, 1951). The method described here is preferable to creating a completely new classification system, which would be difficult to compare with existing descriptions (Whittaker, 1978a). Four levels of classification were found the most useful for the purposes of this study. The basic unit used is the association as defined by Flahault and Schröter (1910), which combines into floristically related groups called alliances (Moravec, 1971; Mueller-Dombois & Ellenberg, 1974). Groups of alliances with distinct floristic affinities will be classified at the level of order, *sensu* Westhoff and van der Maarel (1978), and at the next level, groups of alliances with both floristic and physiognomic affinities will be termed formations as defined by Mueller-Dombois and Ellenberg (1974).

TYPES OF ORDINATION

The use of ordination can be seen as a natural development from the belief that continuity is the natural state of vegetation cover, although there may be discontinuities where abrupt changes in environment occur. Ordination is an analysis method which uses floristic data to arrange vegetation samples in the best possible way along a continuum so that the points that are close together correspond to sites that are similar in species composition, and points which are far apart correspond to dissimilar sites (Jongman *et al.*, 1987; Ludwig & Reynolds, 1988). The technique was invented by the Russian geobotanist L.G. Ramensky and independently, but somewhat later, by the Americans R.H. Whittaker , J.T. Curtis and R.P.McIntosh during the 1950s (Sobolev & Utekhin, 1978). Techniques of ordination developed by them and others have proved to be extremely effective at simplifying and condensing massive data sets so that ecological relationships emerge (Ludwig & Reynolds, 1988). Ordinations can be used to study both noda (by defining systems of groups while allowing for continuous variation) and coenoclines (by non-linear, indirect ordination, or catenation) (Noy-Meir & Whittaker, 1978).

An ordination mirrors species data, although often with some distortion (Jongman *et al.*, 1987). In addition, none of the currently available ordination strategies is appropriate under all circumstances and degrees of species turnover (Kenkel & Orlóci, 1986). Therefore, although ordination is a very useful technique for recovering underlying data, which can then be related to environmental variables (Ludwig & Reynolds, 1988), some care must be taken to select an appropriate type of ordination. Belbin (1991), however, states that the determination of whether one ordination technique is better than another is subjective. Noy-Meir and Whittaker (1978) further comment that although several techniques have proved useful, no single method has emerged as a solution to all problems. The appropriate technique to use will vary depending upon the type of data, and the questions being asked.

COMBINATION OF CLASSIFICATION & ORDINATION (COMPLEMENTARY ANALYSIS)

One of the main uses of ordination is the identification and typing of groups of related samples, without necessarily creating boundaries between them (Noy-Meir & Whittaker, 1978). It is therefore appropriate to apply both ordination and classification to the same data, since ordinations provide important information on continuity and discontinuity within the data set (Goodall, 1978). A useful technique is to superimpose a known sites-by-species clustering onto an ordination (Legendre & Legendre, 1983). These diagrams can then be used to make decisions about the number of natural vegetation types which should be recognized from the cluster analysis (Goodall, 1978), and also to locate distinct floristic discontinuities. It is very limiting to rely on the "pigeon-hole" discrete, absolutely bounded groupings provided by a hierarchical classification system alone (Noy-Meir & Whittaker, 1978). The classifications produced by clustering provide a context for interpreting the ordination, so joint use of the two techniques increases the effectiveness of both, each increasing the information value of the other (Noy-Meir & Whittaker, 1978; Westhoff & van der Maarel, 1978; Bridgewater, 1981). For this reason, classification and ordination techniques are usually combined to explore a data set, a technique called complementary analysis (Kent & Ballard, 1988). Stands sampled for classification can be ordinated, and *vice versa* as long as the ordination data are floristically complete (Mueller-Dombois & Ellenberg, 1974). The most common type of complementary analysis is to plot the groups obtained by classification onto an ordination from the same data (Kershaw & Looney, 1985). In this way, the relevé analysis for classification supplies the first order of information, which is then ordinated to supply "fine structure" information within and among classes (Mueller-Dombois & Ellenberg, 1974). This technique gives information on the group structure of the data, the nature of the units and spectrum of species and the extent to which sites are distributed as continua, implying environmental gradients [coenoclines] (Kershaw & Looney, 1985), or as discrete clumps [noda, repeatable communities] (Kent & Coker, 1992).

CONCLUSIONS

The scale of this study was chosen so that it was large enough for climate to play a role in determining spatial pattern, but not large enough that local processes were negated. This study was thus largely at the macro-scale of landscape ecology and biogeography, verging onto the meso-scale in order to answer specific questions identified from the macro-scale investigations. The study was initially holistic, which is the best approach when dealing with large areas of relatively unknown vegetation, and was therefore mainly synecological rather than autecological. As the observation and description results became known, it was possible to formulate and refine hypotheses about causes of pattern. At this stage, the study moved into a more autecological, or deductive mode.

Numerical methods were preferred because of their greater objectivity, repeatability and power of summarising multivariate data, and were used wherever possible. This allowed full floristic data to be collected. It was recognised that vegetation is neither fully continuous, nor fully discontinuous, so a combination of methods incorporating both classification and ordination were used, to obtain a more rounded view of individual sets of data.

CHAPTER 4:
STUDY AREA - PHYSICAL & CLIMATIC CHARACTERISTICS

INTRODUCTION

This chapter presents a summary of the literature concerning the landforms, geology, soils and climate of the study area in eastern South Australia (Figure 1.1).

LANDFORMS

Prominent features of the landscape are shown in Figure 4.1. The most significant feature is the Olary Uplands or Olary Spur (Laut *et al.*, 1977), a series of low mountain ranges stretching from west to east across the middle of the study area. The Olary Spur is an eastern off-shoot of the mainly north-south trending Flinders Ranges (Alderman, 1973); see Figure 1.1. These ranges were originally formed by upfolding approximately 490 million years ago, as part of the episode known as the Cambrian-Ordovician Orogeny. They were subsequently eroded down through the Mesozoic, but later reactivated and uplifted during the Tertiary. The highest point in the Olary Spur, Oulnina Hill (750 m) is near the town of Manna Hill; see Figure 4.1. The plains to the south of the range, the South Olary Plains (Laut *et al.*, 1977), or "Murray Desert" of Tate (1880), stretch towards the River Murray; those to the north, the Lake Frome Plain (Laut *et al.*, 1977), extend towards Lake Frome. The watershed of the Olary Uplands (Figure 4.1) is conseqently both north and south; systems such as the Manunda and Olary Creeks draining south onto the Murray Plains, and Whey-Whey, Calico, Mingary and Eurinilla Creeks draining north to Lake Frome. Another prominent feature is the east-west parallel dune system of the Murray Plains (King, 1960), which extends onto the south-east corner of the study area. Other smaller dunes and sand-sheets occur to the north of the range approximately 75 km north of Olary (Figure 4.2). The landscape of rocky escarpments, dry, periodically

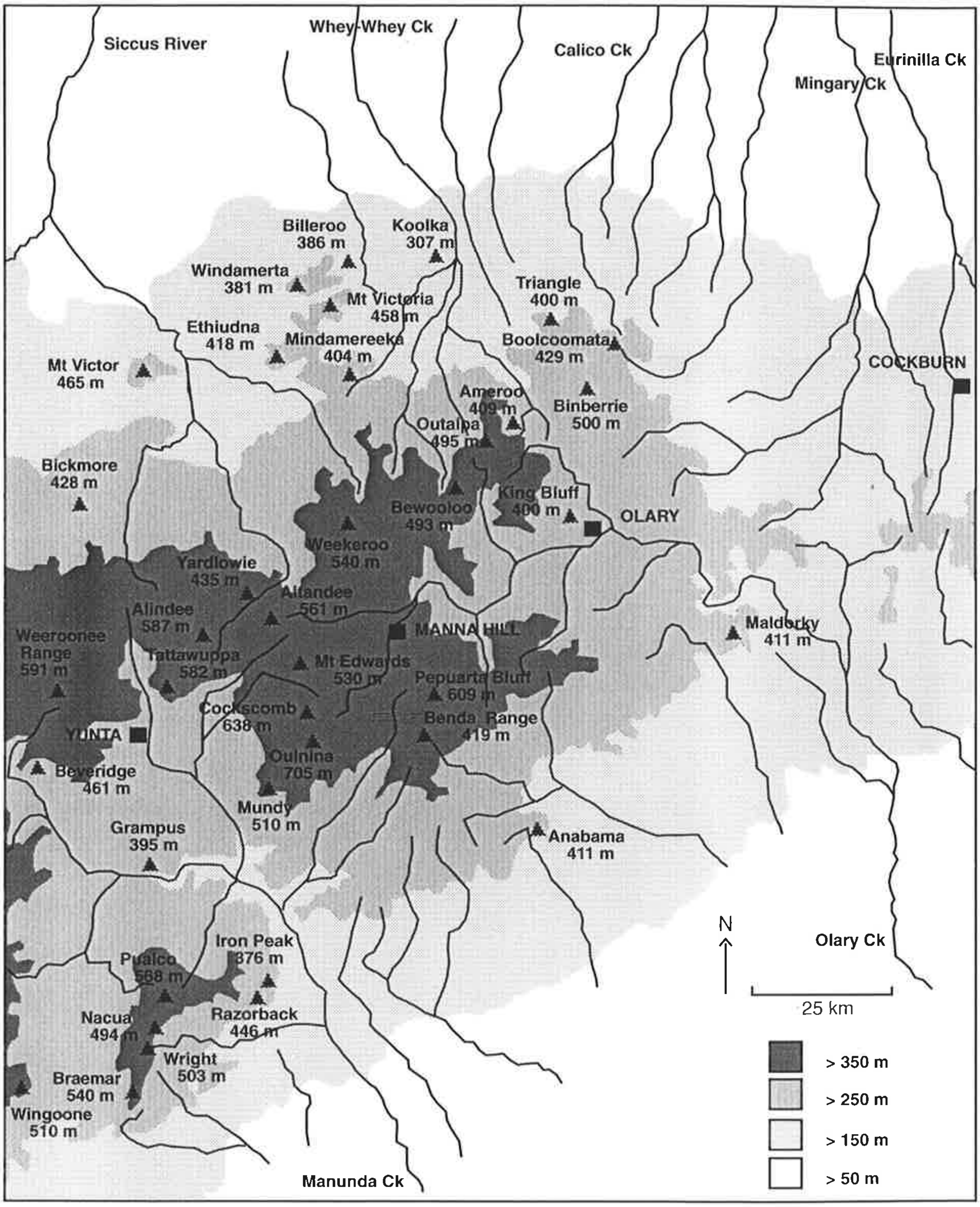


Figure 4.1

Topography and drainage system of the study area in eastern South Australia, showing significant peaks with their height above sea-level, and major creeks (after NATMAP 1984 - 1985, RASC 1987). The most important topographic feature is the Olary Spur, an eastern branch of the Flinders Ranges; see Fig 1.1.

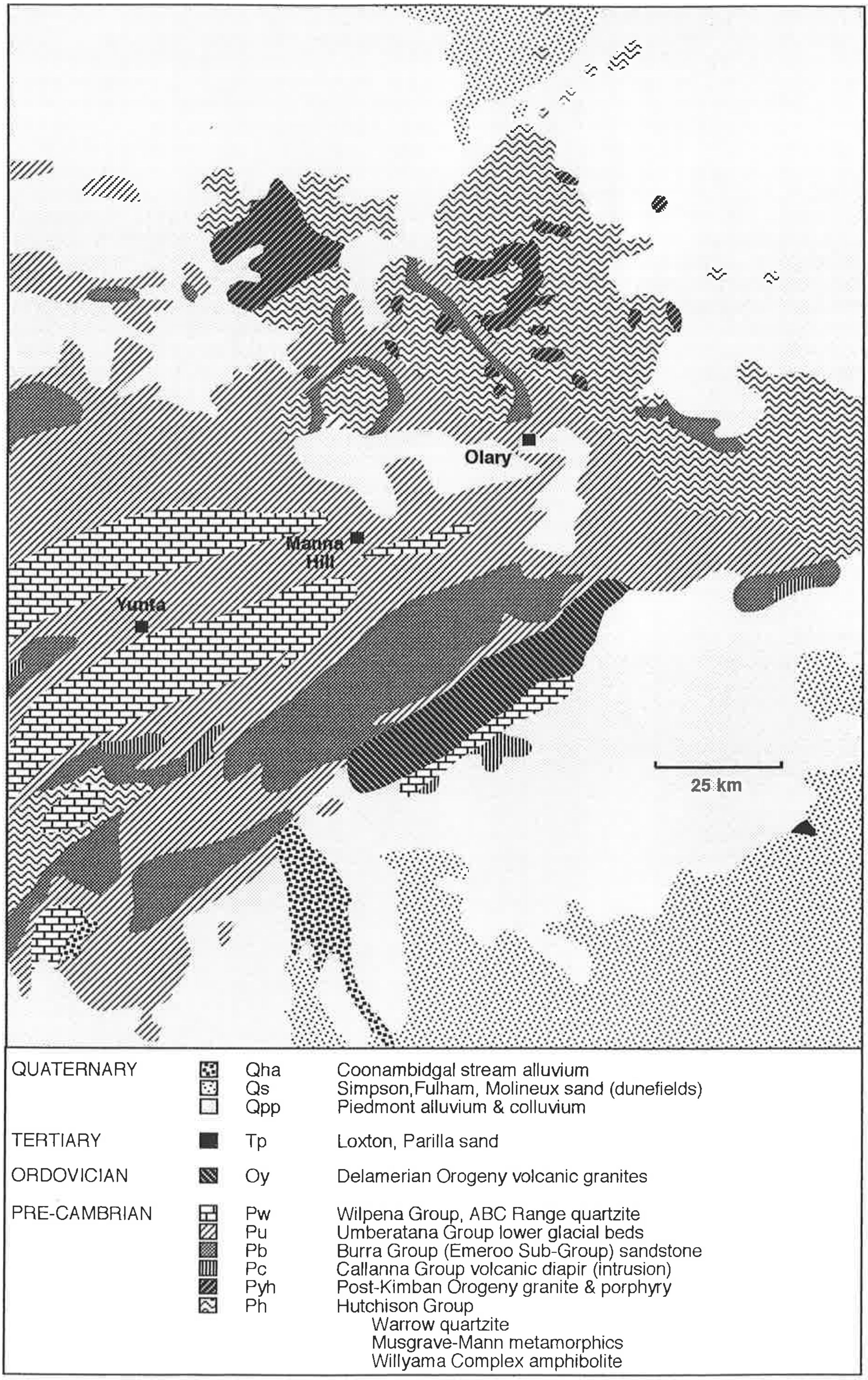


Figure 4.2

Geology of the study area in eastern South Australia (after SADME 1982) flooded rivers, alluvial plains and dune-fields are all characteristic of arid environments (Evenari, 1985).

GEOLOGY

The geology of the Olary Spur itself is highly complex (Figure 4.2), due to the folding and faulting which occurred during the Post-Kimban and Cambrian-Ordovician Orogenies. The oldest formation occurs in the north-eastern part of the range and consists of a basement of igneous and metamorphic crystalline rocks of older Pre-Cambrian (Archaean to mid-Proterozoic) age known as the Willyama Complex, part of the Hutchinson Group (Krieg *et al.*, 1990). Another very old formation is that of the Post-Kimban orogeny, igneous rocks which form volcanic diapir (intrusions) at Plumbago and Bimbowrie. The intense heat of the volcanics are part of the cause of the strongly metamorphosed formations of the Hutchinson Group, including the Musgrave-Mann metamorphics and Willyama Complex amphibolites, both well-known in South Australia for rare minerals and gemstones (Alderman, 1973). Equivalent formations on the NSW side of the border are well known for the silver, lead and zinc ore body at Broken Hill. The uranium deposits at Radium Hill near Olary are also part of this complex.

Younger Pre-Cambrian (late Proterozoic) formations are those of the Adelaide Geosyncline, on the western end of the Spur. These were originally laid down in shallow sea-water, and include the Umberatana glacial beds, which consist of unsorted sediments from boulders (drop-stones) to clay, Burra sandstones, and Wilpena (ABC Range) quartzites (SADME, 1982). Towards the end of the Cambrian and into the Ordovician (approximately 500 mA BP), these sediments became unstable and were compressed against the older Pre-Cambrian rocks, leaving folded or flat-lying unmetamorphosed formations (Krieg *et al.*, 1990). This was the most dramatic event in the geological history of South Australia and formed the original Flinders Ranges and the western part of the Olary Ranges. A younger set of volcanics (the Delamerian) are associated with the

Cambrian-Ordovician Orogeny itself, forming the granites at Anabama Range on the south of the Spur.

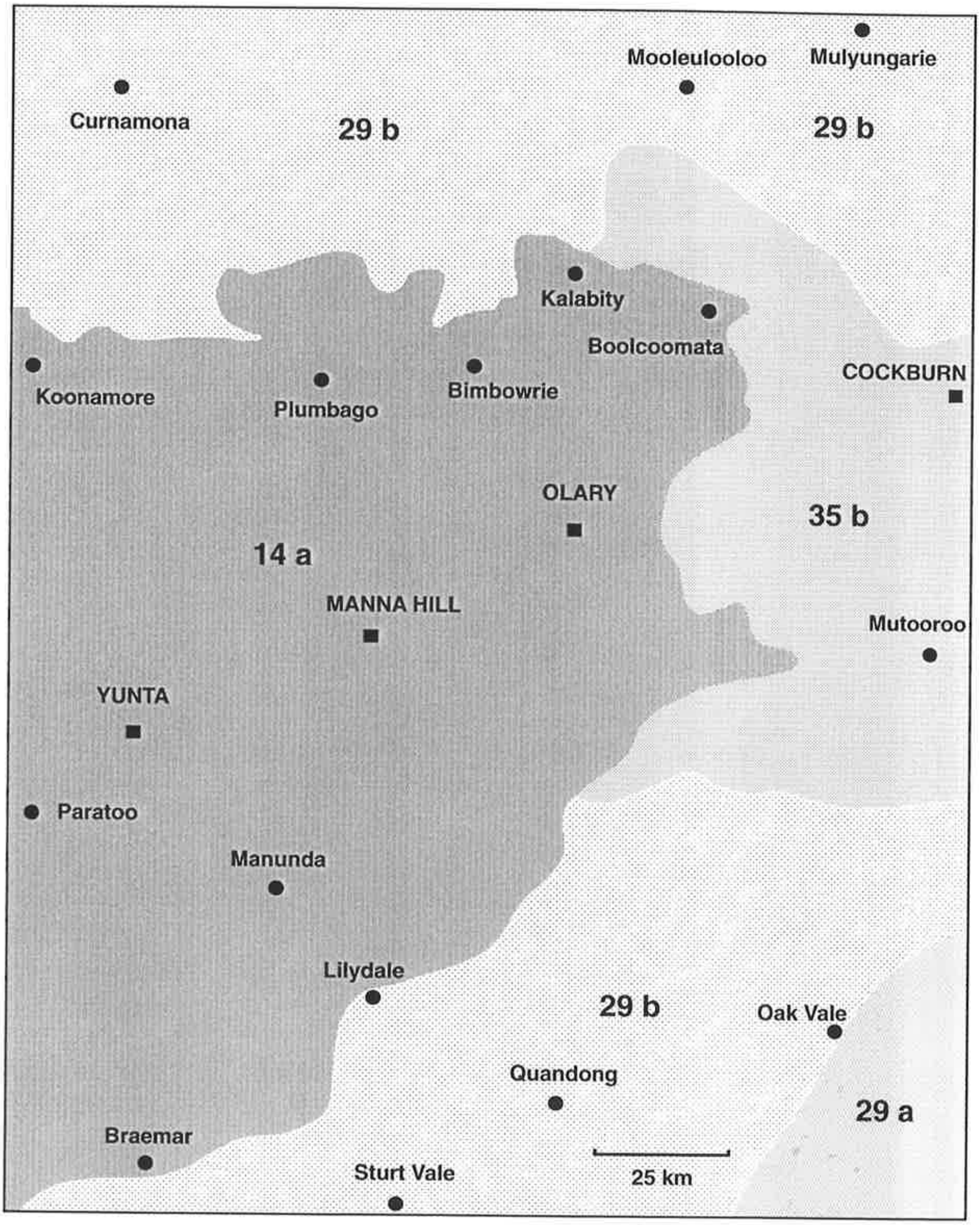
From the Ordovician to the beginning of the Tertiary (65 mA BP), the only geological event was the gradual erosion of these original ranges. Downwarping during the Tertiary allowed the formation of the shallow sea of the Murray Basin on what is now the Murray Plain, with further deposition of both marine and terrestrial sediments. Most of these are now hidden by younger Holocene deposits, but a small outcrop of Tertiary Parilla Sand in the south-east of the study area is evidence of this period. Towards the end of the Tertiary, the crustal movements changed in character from basin-forming depressions to movements causing uplift. At this time, the faults of the old mountain chain formed during the Cambrian-Ordovician Orogeny were reactivated, and blocks uplifted to form the modern Flinders and Olary Ranges. This movement also drained the Murray Basin (Alderman, 1973), and was the last geological episode of any significance in the area.

Holocene or Quaternary deposits (2.5 mA BP to present) form the other prominent feature of the landscape, the plains to the north and south of the ranges. These deposits are derived from the erosion of the ranges and are also found in the valleys throughout the ranges (Figure 4.2). The most common deposits occur at the region at the foot of the ranges (piedmont), and consist of sands and gravels deposited by water flow (alluvium) and weathered material transported by gravity, such as scree slopes (colluvium). Another widespread formation, the Simpson (also known as Fulham or Molineaux) Sand, consists of very recent aeolian deposits, which form dunefields in the centre far-north and south-west of the study area. These have probably formed since the onset of aridity, within the last 18 000 years (Bowler, 1980; Krieg *et al.*, 1990). The dunes in the south-east of the study area run parallel to one another in an east-west direction, reflecting the prevailing westerly winds during the Recent period (King, 1960).

SOILS

Soils (Figure 4.3) were described by Northcote (1968) and are obviously strongly influenced by the underlying geology. The soils within the highest, western part of the ranges are shallow calcareous loams, reflecting their origins in Pre-Cambrian marine sediments. The soils in the eastern part of the spur at lower elevation (around Cockburn and Mutooroo) are duplexes (soils with a lower clay horizon), reflecting a longer history of development in this older part of the range. These duplexes and clays are known to cause greater effective aridity than temperature and rainfall would suggest. For example, water able to be extracted from a normal wetted soil profile (maximum field capacity) at -15 bars is approximately 36 mm for red earthy sand, but only 14 mm from impermeable grey clays (Williams & Calaby, 1985). Brown calcareous earths occur on the plains to the north and south of the ranges, formed from the sediments washing down from the ranges. The more recent aeolian sands form a series of dunes, swales and plains in the south-east of the study area. The northern sand formation marked on the geological map (see Figure 4.2) does not apparently become extensive enough to rate a major soil type of its own. Field observations were that, in the north, this sand tends to form low dunes and thin sheets of limited distribution, leaving the underlying calcareous earths exposed in most places. However, in the south-east corner of the study area, the sand has formed a field of true dunes, with the underlying calcareous earths only occasionally still visible in the bottoms of the swales between the dunes. Overall, the soil environments are typical of the arid regions of Australia and elsewhere, skeletal soils of ranges and hills, limestone or stony gibber plains, sandhills, and dry watercourses and floodplains with silty soils (Wood, 1958).

Previous studies have shown that Australian soils in general are low in plant nutrients, due to the lack of recent volcanic or major tectonic events and the consequent long weathering history of most soil profiles (Williams & Calaby, 1985; Braithwaite, 1990). For example, average phosphorus content is 0.03%, compared with 0.06% in the US, and 0.04% in England (Braithwaite, 1990). This means that areas of high fertility are small and patchily distributed (Stafford Smith & Pickup, 1990). In addition, available nutrients from



LEGEND

14 a	Waukaringa Hills & Plains	Shallow calcareous loams
29 a	Loxton Dunes, Swales & Plains	Sand dunes calcareous earths
29 b	Quandong & Frome Plains	Brown calcareous earths
35 b	Mutooroo Undulating Plains	Crusty alkaline & neutral red duplexes

Figure 4.3

Soils of the study area in eastern South Australia (after Northcote, 1968). Towns are shown in upper-case type. Sheep stations on major routes are shown in normal type.

plant decomposition are usually concentrated in the top few centimetres of soil (Charley & Cowling, 1968). The periodic heavy floods typical of the arid Australian climate have a tendency to remove this topsoil with its nutrients and deposit it in areas of lower elevation as alluvium, so these run-on areas tend to have higher soil nutrition (Pickup, 1985; Stafford Smith & Pickup, 1990).

CLIMATE

Temperature

The Australian deserts exist because of the cells of high air pressure (subtropical anti-cyclones) which form with their cores 20 - 25° south of the equator (Shmida, 1985). The climate is warm, dry and seasonal, with short cool winters from May to September and hot summers from October to April (Wood, 1937; Laut *et al.*, 1977). Meteorological data from Yunta, in the centre of the study area, show that the mean maximum temperature for January is 32.5°C, and for July 15.3°C. Absolute maximum temperatures recorded at Yunta are 46.1°C (January 1960), within the range of 45 to 47°C expected for hot deserts (Evenari, 1985). Diurnal temperature ranges are high, reflecting continentality, with a mean minimum temperature for January of 15.5°C, and for July of 3.1°C (Laut *et al.*, 1977). Frosts are therefore common in winter, with a minimum of -7.7°C recorded at Yunta on 16th July, 1976 (ABM unpubl. data). However by world standards the winters are mild, and typical of the sub-tropical deserts (Walter, 1985). Humidity at Broken Hill (near the eastern side of the study area in NSW) is low, varying between 35% in January and 70% in June (Beadle, 1948). The combination of high temperatures and low humidity is reflected in high evaporation; Class A pan evaporation for the study area is between 2 000 and 3 200mm (Laut *et al.*, 1977), within the range of 2 000 - 4 000 expected for hot deserts (Evenari, 1985). Prevailing winds tend to be from the south-east in summer, and alternate between the south-west and north in winter (Laut *et al.*, 1977).

Rainfall

Rainfall is so low (median of 223 mm at Yunta) that evaporation exceeds the 90th percentile of monthly rainfall throughout the year (Laut *et al.*, 1977). This means that on average, only in one out of ten months will precipitation exceed evaporation. This much higher evaporation than precipitation is also indicative of desert environments (Walter, 1985).

A further feature reported for the Australian climate is an unusually variable rainfall for a comparable degree of aridity (Williams & Calaby, 1985), with longer and more unpredictable droughts interspersed with intense wet periods (Westoby, 1988). The rainfall at Yunta from 1888 to 1984 (Figure 4.4) illustrates this pattern, showing an extreme irregularity of rainfall between years. At Yunta it is reasonably common for rainfall to be double or half of the median (212mm) in any given year, resulting in a high standard deviation (mean = 238 mm; S.D. = 96 mm; 95% confidence limits = 47-429 mm). For this reason, mean figures are not particularly informative (Wood, 1937; Friedel *et al.*, 1990), and medians rather than means are used to express central tendency. Medians are calculated by ranks rather than values, so they are less affected by extremely high and low measurements, and therefore give a better expression of the central tendency of the data (Zar, 1984). Rainfall variability can be expressed as a fraction of maximum rainfall to minimum rainfall, which is 6.4 for Yunta. According to Evenari (1985) this fraction is usually over 6 in hot deserts, so the study area is within the most highly variable rainfall category by world standards.

Medians were also used to compare monthly rainfall (Figure 4.5); they show a lack of seasonality [or that rain is likely to fall in any month of the year]. This is a further characteristic of the hot deserts of the world (Evenari, 1985). The summer rains are a result of northern monsoonal trough activity, and the winter rains are a result of southerly Antarctic depressions and frontal activity (Wood, 1937; Williams & Calaby, 1985). The height of the 10-90 percentile error bars around the medians shows that all months have highly variable rainfall. This tendency is less marked during mid-winter, July and August, indicating a slightly higher reliability of rain during the winter months. The higher error

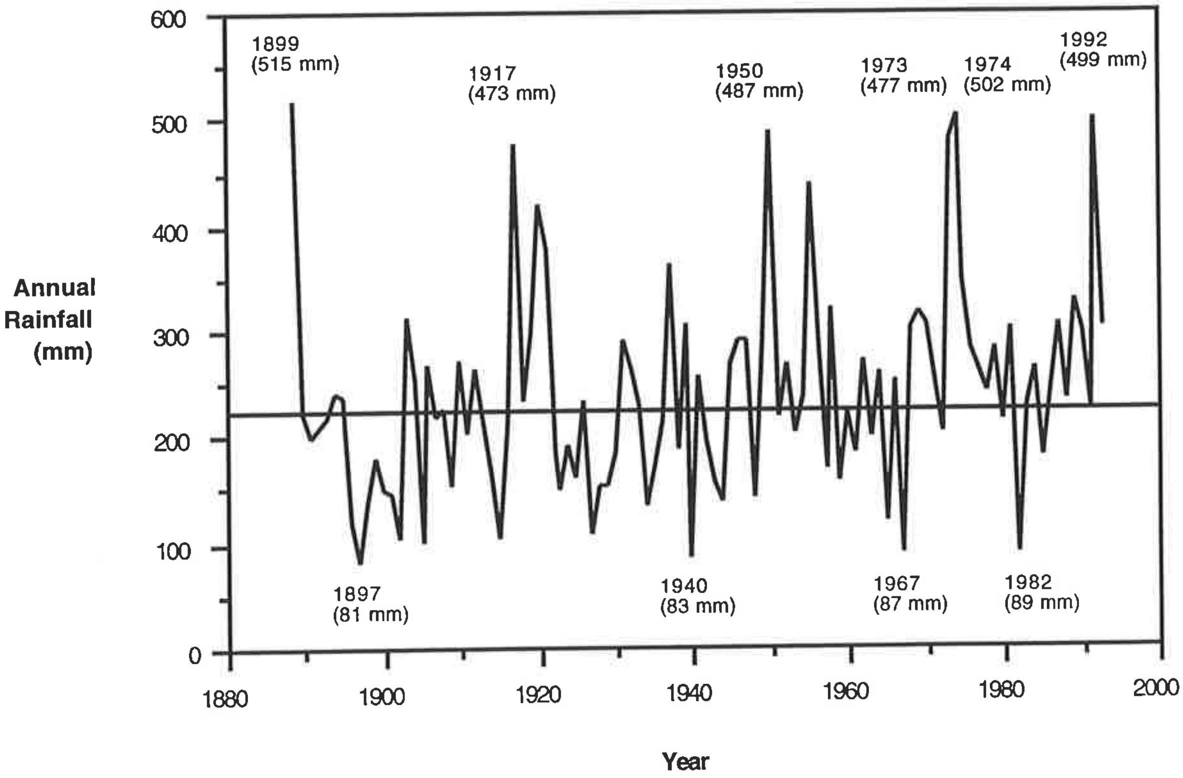


Figure 4.4

Annual rainfall for Yunta, South Australia, from 1888 - 1993 (ABM, 1984 & unpubl. data). The median (223 mm) is shown by the horizontal line. Mean = 238 mm. Standard deviation = 96 mm. 95% confidence limits = 47- 429 mm.

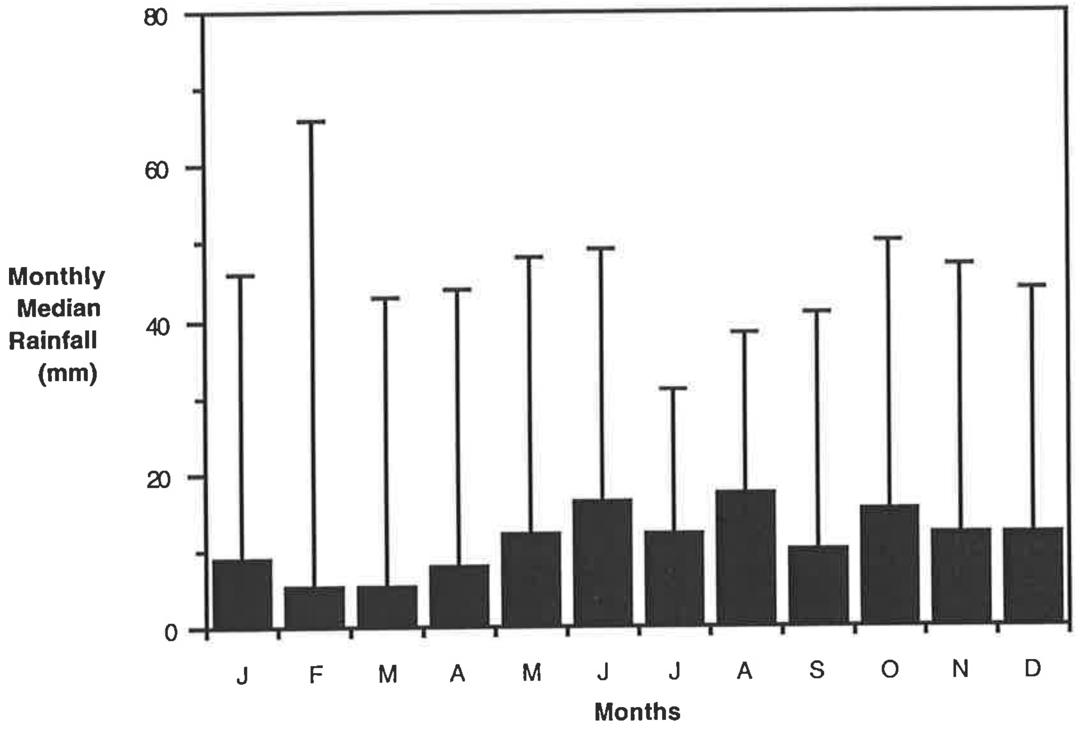


Figure 4.5

Monthly median (50th percentile) rainfall for Yunta, South Australia. Figures were derived from ABM (1984) and ABM unpublished data. Error bars show the difference between the 90th and 10th percentiles, giving an indication of the variability about the mean.

bars for the other months, September to June, indicate higher likelihood of heavy falls of rain. The month of February, although having a very low median rainfall of 5 mm, has the highest variability, indicating that the largest falls of rain are most likely in that month, the middle of the northern monsoon season.

Years of very high or very low rainfall also seem to occur in sequence, groups of high and groups of low rainfall occurring one after another. Periods of very high rainfall peak during 1889 (515 mm), 1917(473 mm), 1920 (418 mm), 1937 (361 mm), 1950 (487 mm), 1955 (435 mm), a long period from 1968 through to 1981, peaking during 1973 (477 mm)and 1974 (502 mm), and 1992 (499 mm) (Figure 4.4). Records have been kept at Paratoo Station, about 25 km south-west of Yunta, since 1869 and these show that the high rainfall of 1889 was at the end of another very long period of high rainfall from 1869 through to 1889.

These periods of very high rainfall also tend to be on a continental scale. For example, the 1982/83 drought affected about two thirds of the Australian continent (Nicholls, 1991b). It is now believed that these high rainfall periods correspond to the negative phase of the periodic El Niño/Southern Oscillation (ENSO) events (Allan, 1990). ENSO refers to the interconnected atmospheric and oceanic current patterns triggered by warm sea surface conditions in the eastern tropical Pacific (Cane *et al.*, 1986), which affect weather on the west coast of South and North America, New Zealand, Indonesia, Australia (Austin & Williams, 1988), India and South Africa (Nicholls, 1991b). Cool sea surface conditions set up atmospheric patterns which bring rain over Australia, often causing extensive flooding in the inland creeks and rivers, the only periods when Lakes Eyre and Frome are filled (Allan, 1990). Positive ENSO periods (warm sea surface in the eastern Pacific) cause drought over Australia as shown in Figure 4.4, most noticeably in 1897, 1902, 1915, 1927, 1940, 1967 and 1982. These droughts were also widespread, corresponding to periods when over 10% of the continent was affected (Heathcote, 1991). There is also evidence in the literature of other severe droughts pre-dating official records in the study area. A devastating drought occurred from 1859 to 1865 (Sinnett, 1862; 1865b; 1865c; PSA, 1865a), when large numbers of sheep and cattle congregated around the remaining

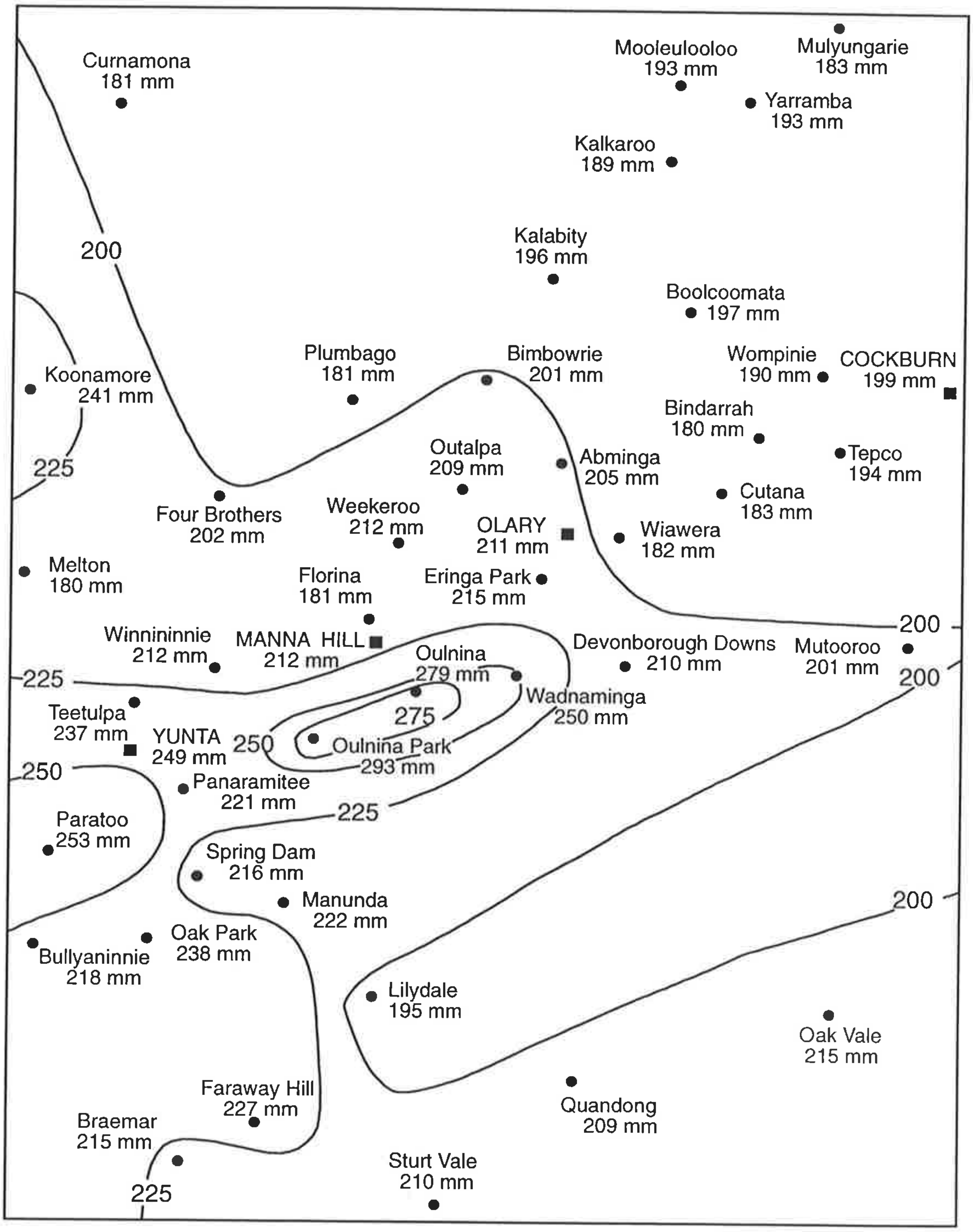


Figure 4.6

Median annual rainfall for the study area as recorded at sheep stations and official weather recording centres in eastern South Australia. These figures were used to calculate the rainfall isohyets shown.

water holes, and died, largely of starvation. Other severe droughts occurred in 1888 and 1896 - 1898 (PSA, 1898; Tunbridge, 1991). Obviously, periods of very severe drought, alternating with periods of much higher than average rainfall are a normal part of the environment.

This sequence of severe droughts (loss of vegetation and soil dessication) followed by heavy rain and flooding tends to create an environment very susceptible to wind and water erosion (Nicholls, 1991b). For example, during February 1983, following the 1982 drought, very serious dust-storms were experienced in Melbourne because of the loss of topsoil from the inland areas (Heathcote, 1991).

Figure 4.4 also shows that whereas droughts were much more frequent from 1897 through to 1950, there appears to be a marked increase in the frequency of negative ENSO rain events during the latter part of this century. This pattern is part of an Australia-wide trend towards greater influence of anti-ENSO events (Allan, 1990). Records have not been kept for long enough to determine if this is a long-term trend, or another amplitude of fluctuation.

There are only a few small towns in the area where official rainfall records are kept: Cockburn, Mannahill, Olary and Yunta (ABM, 1984). All of these towns are located on the Barrier Highway, alongside the east-west railway, so are distributed across the centre of the study area. In order to obtain a more even spread of data for the area, the Bureau also collect rainfall records from some of the stations (pastoral runs or sheep farms) in the district. Monthly rainfall data from 1955 to 1988 were obtained, either directly from station management, or from Bureau records, for 44 stations in the study area. This time-span was chosen as the one for which most complete records were available. Where records at a particular station were incomplete (missing more than five years of records) figures were included from the nearest run with complete records. These figures were firstly corrected by the long-term average difference in individual rain events between the two runs, following the technique of Brooks and Carruthers (1953). The 50th percentiles (medians) of total annual rainfall were calculated for each homestead, and used to construct a rainfall contour map (Figure 4.6) of the study area. As can be seen, there is a north-south gradient in rainfall, lowest in the north, and highest in the south. However, there is a strong overriding effect of topography, with an outlying tongue of higher values extending along the ranges. The highest rainfall recordings are at Oulnina Park (293 mm), which is also the highest point of elevation (705m). The lowest are at Plumbago and Curnamona (181 mm), both runs on the plains north of the ranges. Thus, if rainfall alone were considered, the southern portion of the study area and ranges would be considered semi-desert rather than true desert, according to Walter's (1985) rainfall criterion of 200 mm or less for deserts.

CLIMATIC & EDAPHIC CONTROL OF VEGETATION

The influences of climate and soil on plant distribution have always been observed (Linnaeus, 1750; Theophrastus, *c.* 300 BC), and early ecologists were aware that site factors have a strong controlling effect on vegetation. Warming (1909) suggested that climate, especially moisture and temperature, were important climatic factors, but also remarked that soil can have a strong overriding effect. He first put forward the terms halo-, hydro-, meso- and xerophyte, meaning plants of saline, wet, moist and dry habitats (Barbour *et al.*, 1987). Williams (1971) divides environmental attributes into three categories: major, macroscopic and microscopic. His major attributes include gross factors such as climate, topography and geology. Macroscopic features are usually those relating to easily observed soil characteristics such as the structure, colour and depth, which he states are easily measured, but not usually very useful. Microscopic attributes include those obtained from soil analysis, a range of chemical and physical qualities which can be accurately measured (Williams, 1971).

The term "edaphon" (soil) was introduced into plant ecology by Schimper in 1898 (Leonard *et al.*, 1988), in recognition of the importance of soil in determining vegetation cover. Soils, which in turn are governed by climate, topography, geology and time (Leonard *et al.*, 1988), have been shown to be important in arid plant community distributions (Bowers, 1988). Wood (1958) suggested that both edaphic and climatic variables are important in controlling the distribution of plants in arid South Australia. His observations led him to believe that the vegetation distributions were dominated by available water, which is in turn governed more by soil texture, through particle size, than rainfall. Soil morphological characteristics such as texture, depth, and stoniness are known to be important in controlling vegetation pattern through different moisture infiltration and retention characterisitics (Walter & Stadelmann, 1974; Leonard *et al.*, 1988). This hypothesis appears to be supported by the mosaic nature of vegetation, where neighbouring soil types carry quite different vegetation, even though climate must be more or less identical (Wood, 1937; Crocker, 1946). Walter and Stadelmann (1974; 1985) suggested two main reasons for this. Firstly, in arid areas such as eastern South Australia, evaporation is much higher than precipitation (as discussed earlier), so soils which allow deeper penetration of rainfall (sands and rocky ground with cracks) are slower to lose all their water through evaporation, and are consequently the more mesic habitats. Conversely, clay soils with fine particle size only allow shallow penetration of a similar amount of precipitation, which is then more rapidly able to be evaporated out (Walter, 1985). Thus, soils of fine texture (clays) are the driest habitat for plants in arid regions, while sandy soils provide better water supplies (Walter & Stadelmann, 1974; Hillel & van-Bauel, 1976; Greacen & Williams, 1983). This is the reverse of the situation in high rainfall areas, where sands are drier environments than clays. Secondly, sands, because they have a larger particle size than clays, have larger soil capillaries, and consequently lower matrix potential, the main controlling variable of water availability. For instance, a clay loam still holds 31 grams of water per 100 grams of dry soil at wilting point (-1.5 mPa), whereas a dune sand only holds 16 grams (Jeffrey, 1987). In other words, a sand can actually become twice as dry as a clay before plants growing in it will begin to wilt, because a higher proportion of soil water can be extracted by plants. Beadle (1948) observed plant species in western NSW which appeared to be indicators of soil texture. *Acacia aneura, Acacia tetragonophylla, Cassia nemophila, Codonocarpus cotiniifolius, Dodonaea viscosa angustissima, Duboisea hopwoodii, Eremophila longifolia E. sturtii,* *Eucalyptus dumosa, E. gracilis, E. oleosa, Hakea leucoptera, Myoporum platycarpum* and *Triodia irritans* were indicative of sandy soils. *Maireana aphylla* favoured clay soils.

Local topography can also have significant effects in determining vegetation patterns through water relations, largely because depressions intensify precipitation (Burke, 1989) through run-on. Drainage areas also tend to suffer high disturbance from periodic flooding and concentrated livestock grazing. Frequent flooding means that plant propagules are readily spread, and mechanical disturbance and augmented water supply mean that watercourses and drainage channels are particularly prone to exotic plant invasions (Humphries *et al.*, 1991).

Because of the marine inundation of most of the study area during the Tertiary discussed above, many of the soils are highly calcareous, containing calcium carbonate ($CaCO_3$) which was originally sequestered in the shells of marine organisms. As in many other arid zones where evaporation exceeds precipitation, calcium carbonate rises through the soil profile due to evaporation of soil solutions (Jeffrey, 1987). Evaporite calcium carbonate tends to form sub-round nodules or sheets of limestone in the topsoil; these are known as calcrete, kunkar or travertine (Alderman, 1973). Calcareous soils have special physical and chemical characteristics which can strongly influence the vegetation to be found on them. Calcium carbonate arising from evaporation of soil solutions (Jeffrey, 1987) is usually accompanied by gypsum and other salts. Together these cause high osmotic potential and also high pH. Negative effects caused by this combination of factors include low absolute quantities of major nutrients such as phosphate, potassium and nitrogen, and pH-dominated low availability of phosphate, iron, copper, zinc and manganese. Because of the nodular or platy structure of calcretes, calcareous soils also tend to have coarser texture (Jeffrey, 1987), which as described above, can mean better water availability to plants in arid areas by increasing soil permeability. Limestone content of soils has been shown to be important in controlling plant distributions in South Australia. Osborn (1926b) observed that both *Maireana sedifolia* and *Myoporum platycarpum* tend to be calcicolous, while, Wood (1937) and Wotton (1993) observed that although *Maireana sedifolia* grows preferentially in regions where limestone is close to the surface, the closely related *M. astrotricha* occurs in deeper soils. (Beadle, 1948) observed that *Casuarina cristata* grows on alkaline soils abundant in lime, and *Maireana astrotricha, Maireana pyramidata* and *Maireana sedifolia* also tend to occur on alkaline soils, but of light texture. He found *Eucalyptus intertexta* to prefer acid soils.

Arid and semi-arid soils tend to be low in organic matter. In addition, the lack of leaching by rainfall, and high evaporation rates in arid environments mean that saline soils are common (Belsky, 1989). Salinity affects plant growth by decreasing osmotic potentials thus interfering with water uptake, decreasing nutrient uptake, and by causing direct ion toxicity (Leonard *et al.*, 1988). However saline soils have previously been found to be restricted to areas of inland drainage in eastern South Australia (Osborn & Wood, 1923). These include soils of 3.52% NaCl supporting samphires such as *Pachycornia* and those of 0.22% supporting *Atriplex holocarpa* Osborne found that the upland soils were of relatively low salinity, between 0.02% with *Eucalyptus*, *Atriplex vesicarium* and *Myoporum platycarpum*) and 0.22%, supporting *Atriplex holocarpa.*

CONCLUSIONS

It can be seen that physically and climatically the study area is a transition zone between arid and semi-arid environments due to its location on the southern margin of Sturt's Desert (Evenari, 1985). The southern-most part of the study area would be classified semi-desert under some classification schemes. Both climatic and edaphic variables are known to exercise strong control over the distribution of vegetation, and edaphic variables are particularly important in arid environments. The broad range of topographic, geological, soil and rainfall environments contained within the study area means that vegetation responses to changes in these environments should be detectable, if present.

CHAPTER 5:
STUDY AREA - BIOTA

INTRODUCTION

The previous chapter dealt with the physical environment of the study area. This chapter summarises the available literature on the vegetation, animals, and human use of the area. For reasons of clarity and consistency, all plant species names have been updated to correspond with the nomenclature of Jessop and Toelken (1986).

EARLY ACCOUNTS OF THE PHYTOGEOGRAPHY OF SOUTH AUSTRALIA

Robert Brown produced the first written account of the vegetation of South Australia, based on plant specimens he collected while official naturalist on Matthew Flinders' voyage of exploration of the coast of southern Australia (Flinders, 1814; Maiden, 1907).

The voyage took place during the height of summer, and Flinders mentions excessive heat continually in his journal, suggesting that the voyage may have coincided with an anti-ENSO drought period. Brown found only 200 new species for the newly charted area, and recorded that the vegetation of the whole of South Australia was relatively depauperate. Although noting the less than favourable season, he considered the principal reason for this was the "greater sterility" of the region (Brown, 1814). Hooker (1847; 1859), citing Brown as his authority in his essay on the geography of the Australian vegetation, described the vegetation of South Australia around Spencer's Gulf as "apparently very poor in species". One of the earliest accounts of the vegetation following European settlement in 1836 is that of Behr (1851), who noted the sclerophyllous nature of the eucalypt scrub and the lack of herbaceous plants to be found there. Ferdinand von Müller spent four years in the colony of South Australia (Maiden, 1907) and prepared one of the first botanically detailed descriptions of the flora (von Müller, 1853). He divided the Australian flora into western, southern, eastern and Tasmanian, and noted the similarity of South Australia's flora to that of eastern Australia, while only bearing a sixteenth of the western flora. He gave beautiful descriptions of the vegetation of the known southern and eastern parts of the Colony, remarking on the dwarf forests of stunted eucalypts (later called "mallee") and the colourful variety of sclerophyll shrubs to be found there. George Bentham, at Kew Gardens, worked from specimens already in the collection, and others sent to him by von Müller, by then the government botanist in Victoria. Since he had no first hand knowledge of the vegetation, in his 'Flora Australiensis' he referred his readers to "the elaborate review contained in Dr. Hooker's above-mentioned essay" for a description of the phytogeography of South Australia (Bentham, 1863). It can be seen that very little phytogeography (a study precursive to ecology) had been carried out in South Australia until the arrival of Ralph Tate.

Ralph Tate came to South Australia in 1875, to take up the Elder Chair of Natural Science at the newly founded University of Adelaide (Maiden, 1907) and was subsequently the first to produce detailed, first-hand reports of the inland vegetation. He further developed the concept of vegetation provinces for Australia (1880; 1887; 1890), following those suggested by Hooker (1847; 1859). Two of these provinces, which he named the Eremian [*sic*, now spelt Eremaean] and the Euronotian occur in South Australia (Wood, 1958). The latter, the Euronotian (south-eastern) is distinguished by its dominance by *Eucalyptus* as both scrub and woodlands (Wood, 1958). Many species of *Eucalyptus* consistently form a coppice of multi-stemmed tall shrubs, known locally as "mallees", while other species form either trees or mallees, depending on location (Osborn, 1914), typically in arid, fire-prone or nutrient-poor environments (Lacey & Johnston, 1990). The plant communities dominated by these growth-forms are also collectively known as "mallee" (Wood, 1929). The second province, the Eremian (desert), lies further inland, in areas of 250 mm of rainfall or less, and is characterised by a marked absence of *Eucalyptus*. It is interesting to note that, of over 600 species of eucalypts which occur in Australia, only about a dozen occur in the Eremaean province (Wood, 1958). Instead of eucalypts, the upper storey species tend to be a wide range of phyllodineous

Acacias, with the Australian endemic genus *Eremophila* also common. Other woody taxa include *Atriplex, Sclerolaena, Maireana, Cassia, Eremophila, Myoporum* and *Triodia*. A number of chenopod genera including *Atriplex, Maireana* and *Sclerolaena* are the most common lower storey dominants. This flora is typical of world-wide desert vegetation (Shmida, 1985), where Chenopodiaceae and Zygophyllaceae are the most common chamaephytes (low shrubs), and Leguminosae the most common arboreal species. Tate, in describing the Eremaean, was referring to the region north of the River Murray that Osborn (1914) later referred to as "salt-steppe", chenopod shrublands with scattered low trees of *Acacia aneura, Cassia, Pittosporum* and *Myoporum*. He postulated that it had developed since Glacial times by adaption and radiation of certain floristic elements of the Euronotian and other vegetation. His first map of the vegetation of South Australia places the study area wholly within the Eremaean region (Tate, 1890). Tate's findings were reinforced by Diels, who was sent to Australia by Engler (Carolin, 1982) to carry out a detailed first-hand phytogeographic account of the Australian vegetation (Diels, 1906). In the Eremaean region, he observed a number of palaeotropic taxa such as *Zygophyllaceae, Atriplex* and *Cassia,* which are also found in other arid regions, a range of Australian endemic taxa including *Eucalyptus* and phyllodinous *Acacia* and Chenopodiaceae at greater diversity than in other arid regions, and a unique family of shrubs, the Myoporaceae (Carolin, 1982).

PALAEOBOTANICAL EVIDENCE OF PAST VEGETATION

During the Cretaceous and early Tertiary, Australia was a peneplain of mild climate largely covered by rainforest of *Nothofagus, Araucaria* and *Podocarpus* (Wood, 1958; Specht, 1981; Singh, 1982), but there is evidence that sandstone and granite soils of naturally poor fertility were vegetated by a specialized sclerophyllous vegetation called "heidewald" by Winkler (1914). Proteaceous macrofossils indicate *Banksia* as one of the dominants of this environment (Wood, 1958). The inland regions may have already had a drier, more seasonal climate. Eocene megafossils including a *Grevillea* -like taxon and *Brachychiton* are indicative of a less mesic climate (possibly monsoonal rainforest) at Nelly Creek near

Lake Eyre (Christophel *et al.*, 1992). Australia retained a warm, humid and pluvial climate until about 15 Ma BP (mid-Miocene), causing an extensive development of laterised (poor) soils over much of the continent. Specht (1981) suggests that during this time the heidewald vegetation was able to extend its range onto many of these soil types. During the Miocene the peneplain broke up, the major modern ranges were formed, and there were extensive marine inundations with accompanying limestone deposits over much of the southern part of the continent (Wood, 1958). The large areas of calciphobe heidewald retreated into three major disjunct areas in southern Western Australia, central South Australia, and south-eastern Australia (Victoria and New South Wales), and into isolated refugia within the newly created arid lands (Burbidge, 1960).

Climate changes have also had a profound effect on the Australian vegetation. From the mid-Miocene onwards, the climate became increasingly arid and more subject to fluctuation (Clark, 1990). Much of the existing rainforest and heidewald flora was destroyed (Wood, 1958), and taxa such as Gramineae, *Acacia*, and Chenopodiaceae become increasingly common in the pollen record. The chenopods had probably previously been restricted to coastal salt-marshes and calcareous, semi-saline coastal dunes (Burbidge, 1960), and were therefore pre-adapted to aridity, and able to invade the new calcareous soils exposed following marine inundation (Burbidge, 1960). From the middle to the end of the Pleistocene (50 000 to 30 000 mA BP), the climate was once again pluvial, the inland rivers were active (Horton, 1984), and there were correspondingly high lake and groundwater levels (Bowler, 1980). However, during the end of the Pleistocene, and beginning of the Recent (25 000 - 10 000 mA BP), conditions were drier than at present (Horton, 1984), and dominated by fluctuating climatic conditions. During this time pluvial episodes alternated with dry, windy periods and extensive aeolian erosion. This culminated in the most severe episode about 18 000 ma BP, coinciding with the height of the last ice age (Bowler, 1980; Krieg *et al.*, 1990). At this time the topsoil of many areas was removed and formed sheets and dunes elsewhere (Wood, 1958). Pollen analysis and carbon-dating of cores taken from the soft salt sediments of Lake Frome north of the study area (Figure 1.1) are convincing evidence of the development of an arid vegetation over the last 10 000 years (Singh, 1981). About 9 500 BP, the landscape was dominated by trees and tall shrubs, especially of the family Myrtaceae, and genera *Dodonaea* and *Codonocarpus,* with *Acacia* present in sporadic and low numbers. High numbers of Cyperaceae and Gramineae suggest a stable climate with dependable summer rainfall, so the summer monsoons probably extended further south with more reliability at that time (Singh, 1982). Since then, although a series of relatively minor climatic and vegetation fluctuations have taken place, there has been an overall trend of decrease in trees and shrubs and grasses, and an increase in Chenopodiaceae and Tubuliflorae, a group of herbaceous families including Scrophulariaceae, Solanaceae and Labiatae (Heywood, 1978). The changes in these taxa indicate increased overall aridity and decreasing summer rain. The pollen data give evidence of a substantial recovery period between 7 000 and 4 200 bp, and another slight recovery period around 2 200 bp. However, since about 2 200 bp the climate and vegetation have been more or less the same as at present. Crocker and Wood (1947) suggest that during the arid periods, the tree and shrub vegetation survived by retreating to more mesic relict areas such as rocky outcrops, which is where representatives of these taxa may still presently be found.

CHARACTERISTICS OF AUSTRALIAN ARID VEGETATION

The Australian and Kalahari deserts are unusual in that large numbers of shrubs and trees are present for equivalent levels of precipitation (Walter & Stadelmann, 1974). In most deserts, arboreal forms do not usually occur below 400 mm rainfall or, if they do occur, are restricted to the creek-beds or wadis (Shmida, 1985). So although the climatic variables of the study area are indicative of true desert, the presence of arboreal forms and the fact that the vegetation is often more than 25% total cover, is more indicative of a semi-desert environment (Walter, 1985). It has been postulated that the occurrence and periodicity of the ENSO events (Chapter 4) is the reason why the Australian deserts have more trees, shrubs and perennial grasses for a given level of aridity than other deserts (Williams & Calaby, 1985); deep rooted species being better able to survive irregular rainfall, since they remain active, and can respond quickly (Friedel *et al.*, 1990; Nicholls, 1991b). However, as stated above, the arid vegetation of Australia has developed from sclerophyllous taxa already adapted to low nutrients. It is possible that many of these sclerophyllous taxa were conveniently pre-adapted for aridity, enabling them to successfully persist in arid environments, so that the present high numbers of trees and shrubs may be explained by historical circumstances.

The irregularity of rainfall may be the reason why the Australian deserts have not developed the conspicuous stem-succulent species common in other deserts (Cactaceae in North America, Euphorbiaceae, Aizoaceae and Liliaceae of South Africa, and Bromeliaceae of South America) (Beard, 1981). Many of the Australian chenopods are leaf-succulents, but usually do not abandon their deep-rooted habit. Stem succulents require at least some rain at regular intervals to top up their storage. Neither are there as many taxa utilizing underground perennating organs (bulbs and corms) as in other deserts (Beard, 1981). This strategy probably also relies on a reasonably reliable, if low, annual rainfall. Also absent are the deciduous thorny trees common in other arid regions (Beard, 1981). Perhaps the cost of nutrient loss in fallen leaves does not compensate for the concomitant water-stress avoidance obtained, so Australian desert taxa have tended to reduce water-loss by other methods such as glaucescence, pubescence (Beard, 1981) and sunken stomata.

Trees and shrubs of arid Australia have two main modes of regeneration: by seedling recruitment, and by vegetative parts (Maconochie, 1982). It appears that large-scale events of regeneration occur at irregular intervals (Maconochie, 1982; Friedel *et al.*, 1990), probably associated with ENSO events of very high rainfall (see Chapter 3). Austin and Williams (1988) showed that anti-ENSO driven rainfall events in the Pilliga Scrub region of NSW were often associated with mass recruitment in a range of woody plant species. This rare establishment from seed is a common adaption of plants to environments in which droughts are common (Grubb, 1985). Spatial patterning of the vegetation may also be affected by ENSO events, since germination of many species is brought about by sheet-flooding following heavy rains (Walter, 1985).

Also in common with arid regions of other continents, a very large number of the plant species of arid Australia reproduce vegetatively, by sprouting of adventitious buds from the roots (Maconochie, 1982). Species within the study area which produce sprouts from sub-surface root laterals include *Acacia carnei* , *Casuarina crista*, *Pittosporum phylliraeoides* (Osborn, 1925) and *Cassia nemophila, Eremophila longifolia, Heterodendrum oleifolium, Santalum lanceolatum, Solanum ellipticum,* and *Eucalyptus socialis* (Maconochie, 1982); the latter from lignotubers. This ability appears to be a general feature of desert plants, the strategy probably being a means of drought-avoidance. A ramet (vegetative offspring) is still attached to its parent plant, and therefore has access to a greater volume of sub-surface water through the roots of its parent (Maconochie, 1982), whereas a genet (seedling) has to survive by quickly developing its own independent root system. Consequently young ramets have much lower mortality than young seedlings (Silvertown & Doust, 1993). In a highly variable environment such as that caused by aridity, vegetative regeneration is therefore a less risky strategy. By reproducing vegetatively, plant populations are able to persist during long periods of adverse conditions, possibly long enough to encounter windows of more favourable conditions, during which successful seedling recruitment and establishment can occur (Archer, 1993) The periodicity and severity of climate fluctuations in Australia from the Miocene onwards (Chapter 4) may have given a strong selective advantage to species with vegetative reproductive ability.

Low nutrient levels (see Chapter 4) may have favoured the radiation of certain woody plant families including the eucalypts, which use mycorrhizal symbiosis with soil fungi to fix phosphorus, and *Acacias*, which are able to fix nitrogen through mutualistic relations with bacteria housed in nodules on the roots (Braithwaite, 1990). The genus *Atriplex* is also known to use vesicular-arbuscular mycorrhizal (VAM) fungi to improve water absorption and uptake of nutrients, especially phosphorus. The poor nutritional status of Australian soils extends into the arid regions, especially in the siliceous soils, which tend to carry taxa similar to the sclerophyll woodlands, including the sclerophyllous grass *Triodia* (Beard, 1981). Bottom-land soils, although often calcareous and saline, are more base-rich than the sands, and tend to support vegetation of a more cosmopolitan Eremaean type, such as Chenopodiaceae. The concentration of nutrients and water into run-on areas (see Chapter 4) also means that plant production tends to be highly patterned, and concentrated along river channels, flood-plains, and other run-on areas (Stafford Smith & Morton, 1990).

VEGETATION MAPS

One of the earliest vegetation maps of South Australia is that of Prescott (1929), who compiled the records made by the early surveyors and official explorers, held at the then Lands and Survey Department. His map (Figure 5.1) shows two main vegetation formations for the study area, mallee (*Eucalyptus dumosa, E. oleosa* and allied species) in the south and along the ranges, and mulga (*Acacia aneura*) to the north. These correspond to the Euronotian and Eremaean provinces of Tate respectively. Figure 5.1 also shows Prescott's estimates of the southern limits of cottonbush (*Maireana aphylla*). His maps suggest that the mulga formations below this line have an understorey of bluebush (*Maireana sedifolia*) and saltbush (*Atriplex vesicaria*), with cottonbush being added to these in the north.

J.G.Wood, also a professor of Botany at the University of Adelaide, was a remarkably observant ecologist, and his handbook *TheVegetation of South Australia* (Wood, 1937) remains an authoritative treatment of South Australian vegetation. In this early work Wood attempts to place the vegetation associations in the context of the organismic community of Clements (1916) and Tansley (1935), the concept of vegetation which was fashionable at the time (see Chapter 2). However, it is clear from his descriptions and maps that he was able to observe distinct associations whose distributions are determined by soil type and topography, and his attempts to place them into climax and dis-climax relationships with one another are not convincing. Obviously in an attempt to place his observations on a better theoretical footing, Wood later abandoned successional theory in favour of his own system of edaphic control. He formally developed the concept of the edaphic complex, a series of floristically related plant associations united by similar soil and climatic

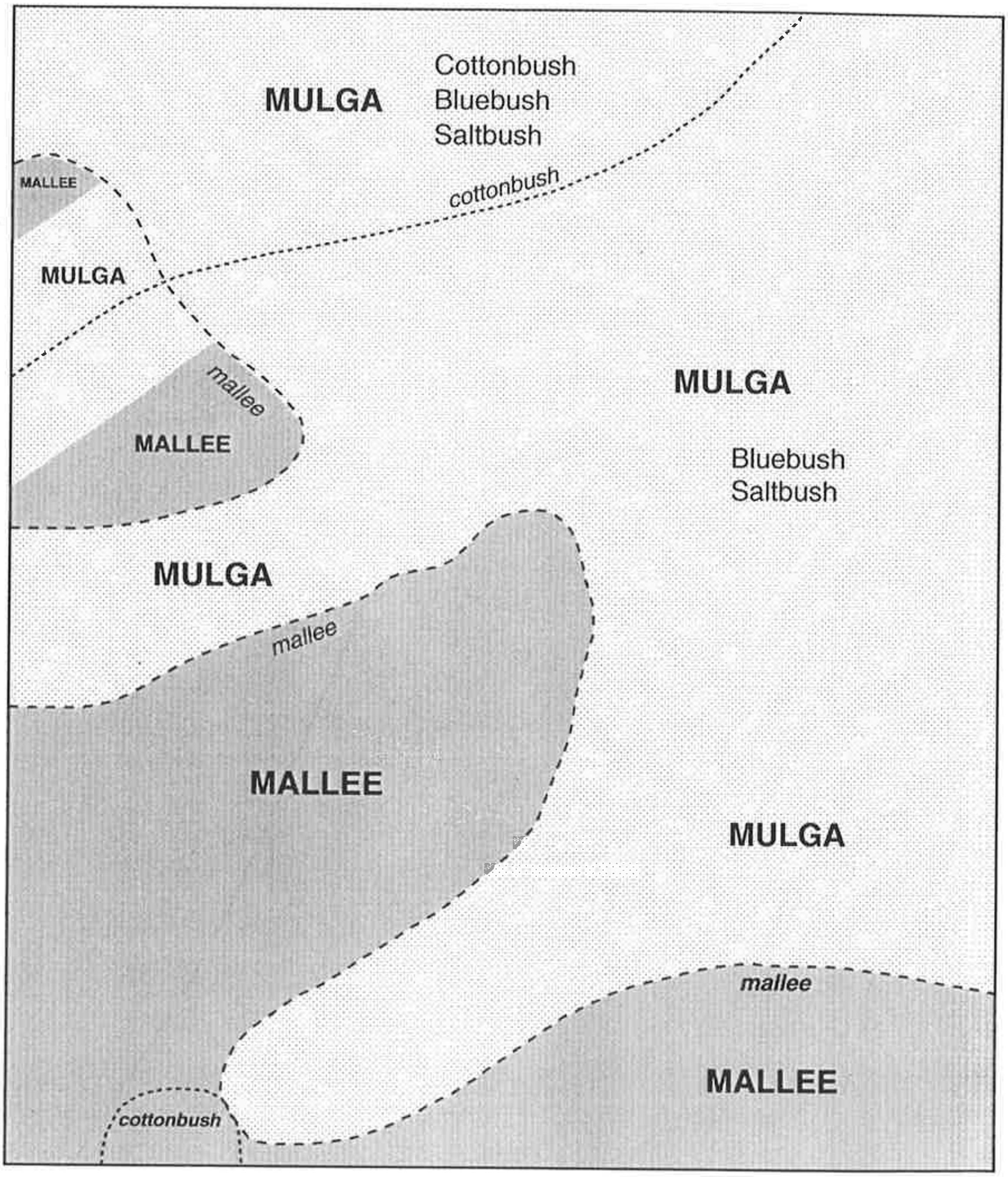


Figure 5.1

Vegetation of the study area in eastern South Australia (after Prescott 1929). Major vegetation zones are shown in block capitals. Important understorey species are shown in lower case type. Northern and southern limits of individual species are shown by dashed lines and italic type. Mulga = *Acacia aneura*, Mallee = *Eucalyptus* spp, Cottonbush = *Maireana aphylla*, Bluebush = *Maireana sedifolia*, Saltbush = *Atriplex vesicaria*.

requirements, which could be readily used as mapping units (Wood, 1939; Crocker & Wood, 1947). The portions of Wood's maps which are relevant to the study area are shown in Figures 5.2 and 5.3. Figure 5.2 shows the two main types of arid vegetation which he recognized; semi-desert scrub on rocky hills and sandhills, and shrub-steppe (mulga and saltbush) of the plains. The boundaries follow the topographic map and existing soil maps very closely, so Wood probably relied on these to extrapolate from his fieldwork. Figure 5.3 shows the distribution map of his soil and topography-related associations, which he later called edaphic complexes. It can be seen from this diagram that the associations he recognized form a complex mosaic over the main part of the range, with the plains dominated by chenopod shrubs. Wood followed Prescott (1929) in using the term "mallee" (Wood, 1929) to describe the Euronotian vegetation dominated by shrubby clump-forming eucalypts of 2-12 m height. He has marked a mallee association as present in the south, with outlying patches towards the ranges.

N.C.W. Beadle was stationed in western New South Wales (Soil Conservation Service), and his work on the soils and vegetation of that area is extremely comprehensive (Beadle, 1948). He describes five major plant associations for the region on the NSW side of the study area (Figure 5.4). Running from south to north these are: *Eucalyptus oleosa - E.dumosa* (mallee) on deep sands or clays over limestone, *Casuarina cristata-Heterodendrum oleifolium* over limestone, *Maireana pyramidata-M. sedifolia* (bluebush) over limestone, *Atriplex vesicaria* (saltbush) on loams and clays, and *Acacia-aneura* (mulga) on deep sands and loams (Beadle, 1945). He adopted the terminology of Wood in describing the saltbush and bluebush associations as forming an edaphic climax, but retained classic successional theory in describing the other three as climatic climaxes. His associations are floristically derived, and then united into structural formations, which means that floristic information can be more readily extracted from them than from purely structural classifications (see Chapter 3).

Because of the number of taxonomic revisions that had taken place during the following decades, it came to be felt that Wood's 1937 handbook needed expanding and up-dating. A second edition, by R.L. Specht (also of the University of Adelaide), was

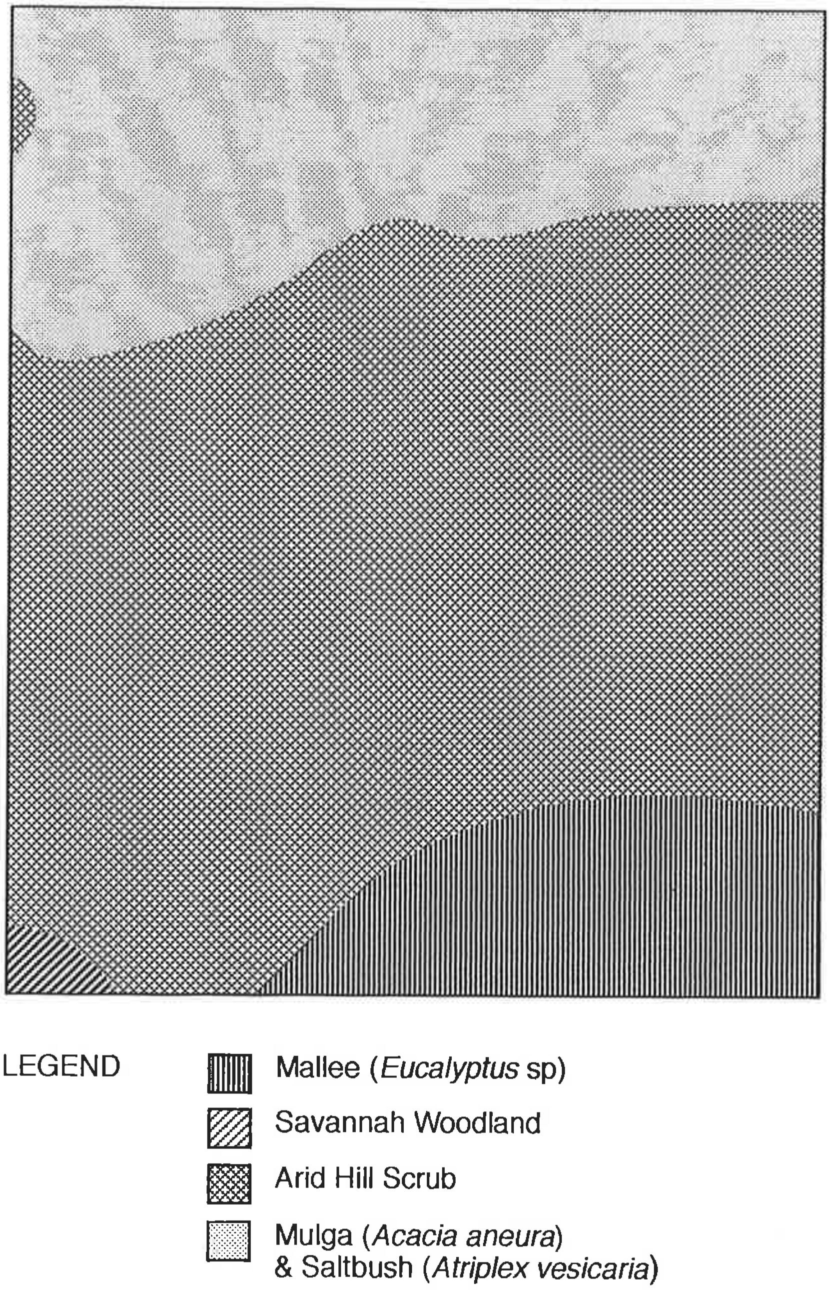


Figure 5.2

Vegetation regions of the study area in eastern South Australia (after Wood 1937).

Figure 5.3

Vegetation types of the study area in eastern South Australia (after Wood 1937).

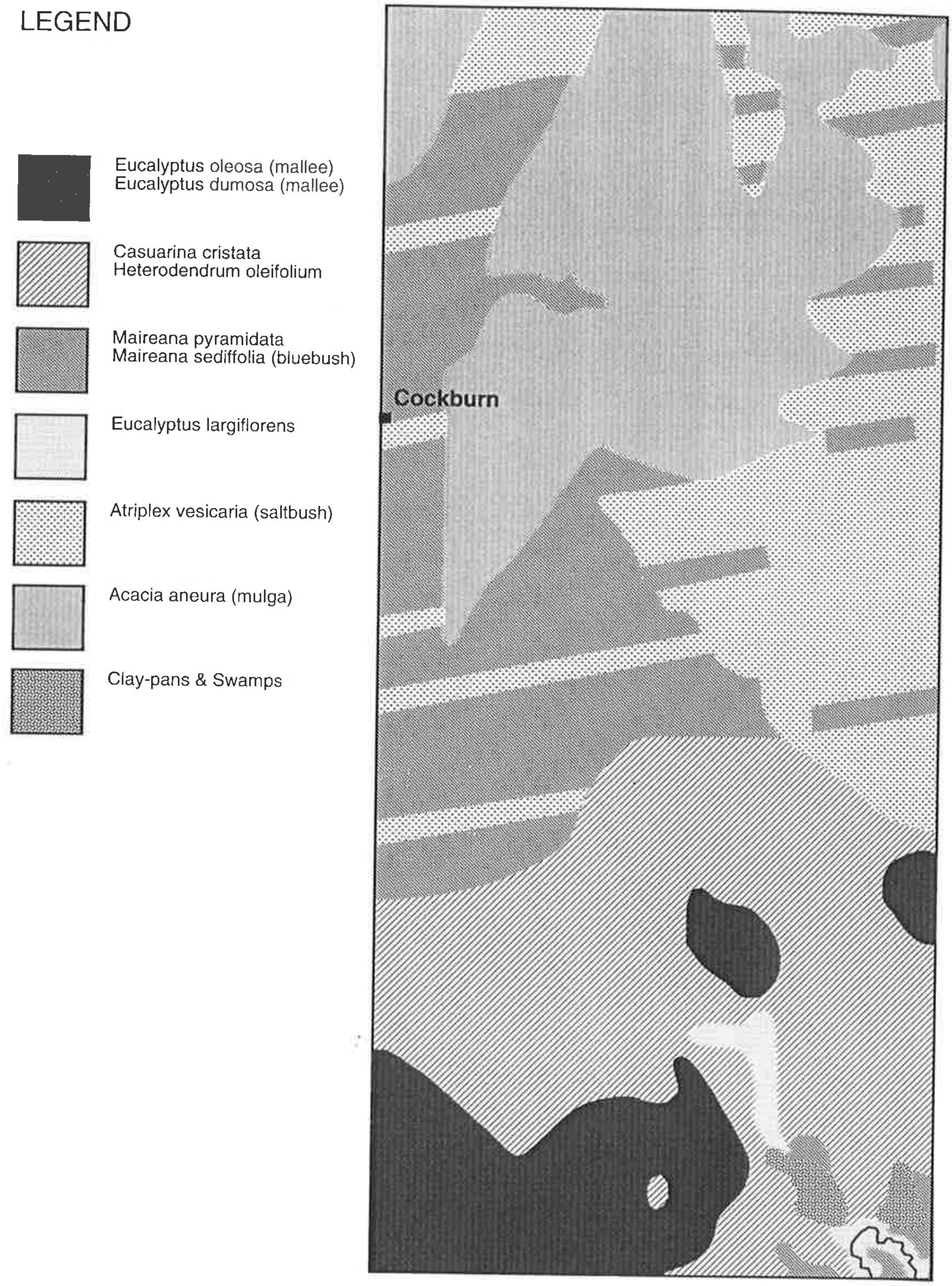


Figure 5.4

Vegetation of far-western New South Wales (after Beadle 1945). The area shown is that contiguous with the eastern side of the study area. The Darling River, a major tributary of the Murray River (see Fig 4.1), appears in the south-east corner of this map.

published in 1972 (Specht, 1972). The maps for the study area are summarized in Figure 5.5. The nomenclature of species is more up-to-date; however, the more remote areas of the State are still sketchily dealt with and the maps of the arid areas are not based on original fieldwork, but are a synthesis of existing soil maps, vegetation maps, and subjective vegetation descriptions from the literature. In the study area, the maps are entirely based upon the soil maps of Northcote (1968), with vegetation types described in the literature extrapolated onto them. Besides those of Wood and Beadle, previous descriptions used by Specht to prepare the maps covering the study area are those of Jessup (1948) (southern most part of the study area only), Carrodus *et al.* (1965) (of Koonamore Station only) and Barker (1970) (Quandong Station only). Four of the vegetation types shown on Specht's map were originally described by Jessup (1948), the *Eucalyptus socialis-E. gracilis*, the *Myoporum platycarpum-Maireana sedifolia*, the *Casuarina cristata*, and the *Eremophila-Dodonaea-Acacia* of the ranges. The eastern side of Specht's map obviously relies on Beadle (1945). It can be seen from these sources that there was very little new, first-hand information on the vegetation of the study area. The work is also flawed by its abandonment of Wood's very useful concept of the edaphic complex, and adoption of a structural classification to describe vegetation communities. The greatest disadvantage of such a classification is the failure to recognise that plastic responses of many species, with respect to height, density of stand, and relative importance in the community, can result in artificial divisions of essentially the same floristic associations into different structural entities. These problems had already been identified in the south east of the State by Crocker and Wood (1947). The basic mapping unit used is that of the structural formation, with groupings such as woodland or shrubland, even though the species in the upper stratum may be completely unrelated. Where possible this is broken down into alliances (which, in additon to having a similar structure, have the same or related major upper stratum or dominant species). In general, associations (same structure, same dominants in upper stratum) and societies (same structure, same species in both upper and lower strata) are not mapped, but are listed in an appendix. Because this structural classification, relying on upper-storey dominants, lumps quite different taxa together, it is

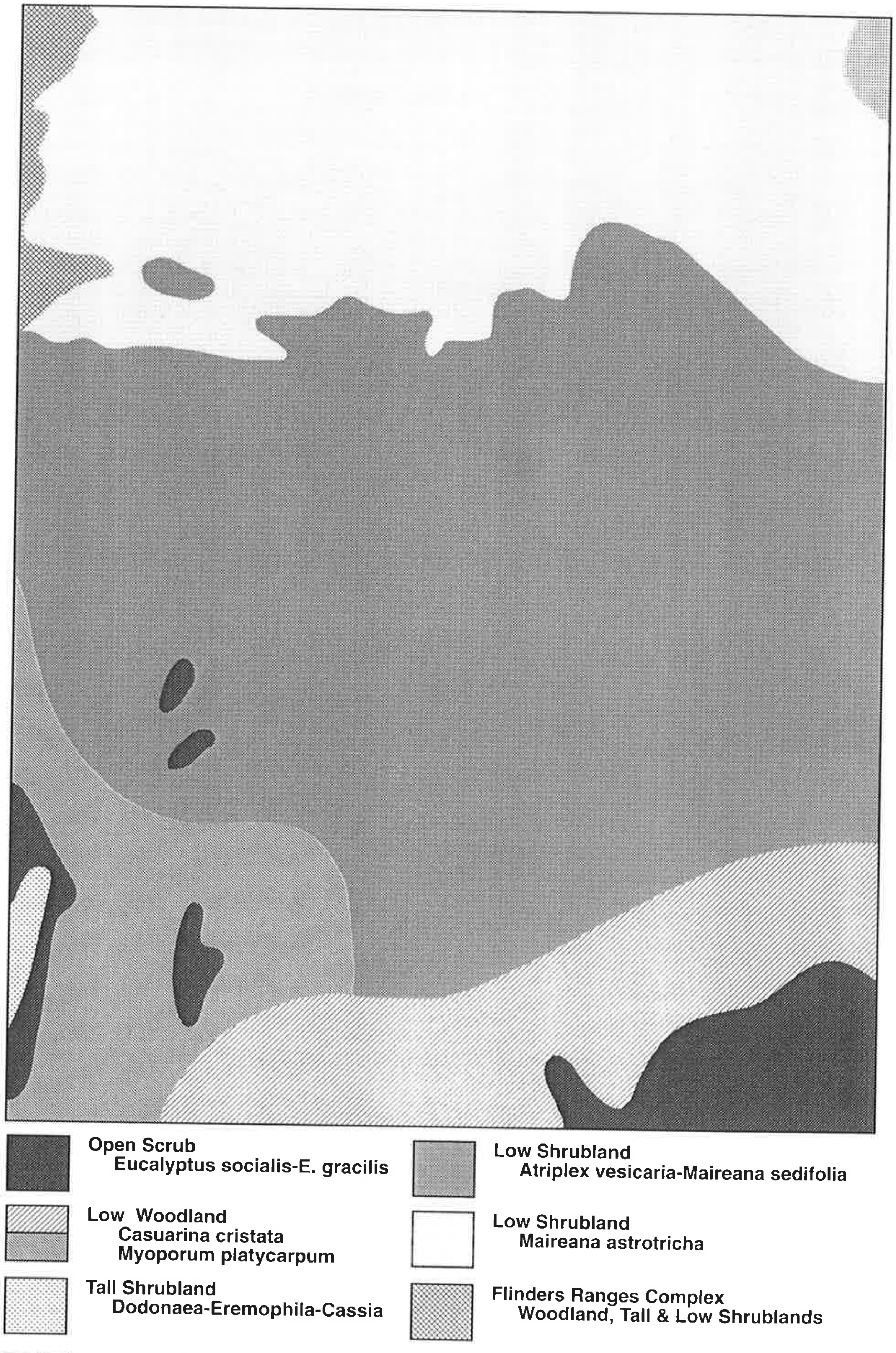


Figure 5.5

Vegetation of the study area in eastern South Australia (after Specht 1972).

very difficult to extract floristic information from the maps. In addition, Specht has ignored the composition of the lower strata on the basis that these are of less importance to the ecosystem, because they intercept less incoming light (Specht, 1972). In the northern parts of South Australia, where there tends to be a very sparse upper storey of scattered trees, the lower storey is much more dominant in terms of biomass, so a structural classification based on upperstore dominants is highly artificial. Notwithstanding these limitations, the work is still the most comprehensive treatment of the vegetation of South Australia available, and has greatly influenced the way the South Australian vegetation is perceived and studied.

NUMERICAL FLORISTIC STUDIES

Noy-Meir (1971) conducted a systematic survey of vegetation over 240 000 km^2 of semi-arid winter rainfall zone of south-eastern Australia. This study centred on an area overlapping north-eastern Victoria, south-western New South Wales, and across the border into eastern South Australia, thus overlapping approximately the southern half of the study area of this survey. This was one of the first attempts to apply a numerical technique, (in this case, component analysis) to floristic data collected in the area. Noy-Meir found one major floristic discontinuity between a southern temperate (mallee) flora and an Eremaean flora consisting of many discontinuous dominance units. These correspond to the vegetation formations described by Tate (1880; 1887; 1890), Diels (1906) and Prescott (1929). Noy-Meir concluded that the Eremaean vegetation did not fall readily into groups, and was best considered as a continuously integrating series of plant communities, the centres of which he refers to as "noda" or "foci", *sensu* Goodall (1953) and Poore (1955b; 1955c; 1955a).

NATIVE VERTEBRATE HERBIVORES

Animals known to occur in the eastern region of South Australia are listed in Watts (1990). The most frequently seen large animals are the macropods (kangaroos and wallabies), the most common being *Macropus fuliginosus melanops* (western grey kangaroo), found in scrubby regions, *Macropus robustus erubescens* (common wallaroo or euro) of the hilly regions and the red kangaroo (*M. rufus rufus*) of the plains. A lighter coloured variant of the red kangaroo (*M. rufus palidus*) inhabits the plains north of the ranges. Because of the provision of livestock watering points, kangaroo numbers are undoubtedly higher than in pre-European times (Adamson & Fox, 1982). Literature findings are that the diet of red kangaroos is almost entirely composed of grass, which is even more pronounced in grey kangaroos (Newsome & Corbett, 1972; Wilson, 1990). The proportion of browse in kangaroo diets is very low (Newsome & Corbett, 1972), and previous studies have shown that kangaroos have little effect on populations of woody perennial plants (Gardiner, 1986). Further studies show that kangaroos prefer to graze in areas which sheep do not visit (Andrew & Lange, 1986b). Other smaller native animals are present, but none in large enough numbers to have significant effects on the vegetation. Insect herbivores are widespread and abundant, and undoubtedly have a substantial background effect on the vegetation. However, the measurement of their effects was not one of the aims of the study, and was assumed to vary little from site to site.

LAND-USE

The Aboriginal People

Carbon dating of skeletal remains at Lake Mungo in western New South Wales shows that there has been human habitation of Australia for 40 000 years, and probably longer (Bowler, 1976). The Aborigines have bequeathed a rich legacy of language to the North-East. Such names as Nancatee, Boolcoomata, Weekeroo, Wye-Wye, Wooroonee and Tattawuppa (see Figure 4.1), are convincing evidence that the land was occupied by Aborigines at the time of European settlement, and that enough peaceful interchange occurred between them and the government surveyors and early settlers for these place-names to become gazetted. The tribe which inhabited the area between Lake Frome and the

Flinders Ranges were known as the Yadlhiauda (Tunbridge, 1991). This latter name is also sometimes spelt "Yadliyawara" (Hercus, 1990).

Little is written of the post-European history of the Aborigines of the North-East, but the little that has been recorded or comes down to us through hearsay is ominous. Aboriginal populations suffered badly from a very long and severe drought which began in 1859 and lasted until the end of 1865, with no effective rain at all for the last two years (PSA, 1865b). Both the Olary and Flinders ranges were closely settled by sheep-farmers by this time, and a run of good seasons meant that very high stock numbers had been built up. The terrible drought forced livestock, native animals and Aborigines alike back onto the only permanent water-holes, in fierce competition with one another. Many native animals, on which the Aborigines depended for food, became locally extinct at that time (Tunbridge, 1991), and from then onwards, the surviving Aborigines were dependent upon handouts. The shortage of native animals caused by the drought may have forced the Aborigines to kill domestic livestock for food. In 1865, Mr P. Levi, an early pioneer at what is now known as Oulnina Station, reported that livestock losses from "natives" were unusually heavy. Anecdotal evidence suggests that there may have been deliberate efforts by some pastoralists to rid the lands of the original occupants. The lessee of Boolcoomata Station in the earlier part of this century (which then covered hundreds of square miles in the north east; see Figure 5.7) was locally nicknamed "Four-in-Hand Tyndall" because of his habit of driving around the run at high speed in a buggy harnessed to four horses, shooting at any stray Aborigines he saw with a rifle (B. Treloar *pers. comm.*). Obviously, those who managed to avoid being shot vacated the area promptly. There are also reports of Aborigines being deliberately poisoned (Adamson & Fox, 1982). Basedow (1920) recorded that diseases such as influenza also took a heavy toll of the Aborigines of northern South Australia. No Aborigines occupy any part of the study area now; the nearest Aboriginal settlement is at Neppabunna in the northern Flinders (north-west of the study area), although there are significant urban populations of Aborigines in Port Augusta, (Figure 1.1), the largest township in the general vicinity of their original territories.

European Settlement and Pastoralism

British colonists arrived on mainland South Australia in 1836, and energetically set about exploring the interior and assessing the value of the land for agriculture. In the mallee areas to the south of the study area, large patches of unsuitable land were cleared and ploughed to grow cereal crops (Wood, 1937), which had to be abandoned later because of the unfavourable results (Jessup, 1948). However, the most promising land-use in the study area was seen as pastoralism, the grazing of domestic livestock, usually sheep and cattle. The earliest pastoralists in eastern South Australia were herding cattle (Dixon, 1892), but sheep were soon found to be more successful, and are now by far the most common domestic herbivore. Within 20 years, under a British Act of Parliament controlling "wastelands in the Australian Colonies" (IPGB, 1850; PSA, 1865d), a number of pastoral runs were established along the main part of the Olary Range (Figure 5.6), where the local topography and geological formations provided spring, creek and well-water (PSA, 1865b). These are described by Sinnett (1862) as "some of the best runs in the district". These waters did not extend any distance from the ranges (PSA, 1865b), and the plains to the south east of the ranges were not taken up for pastoral runs until after 1870, due to the paucity of water to be found there (Figure 5.7).

As stated above and in Chapter 1, the vegetation of eastern South Australia has only been subjected to close herbivory by large ungulates since about 1850. Hence the native vegetation is un-adapted to such effects as pruning and trampling of mature plants, and disruption of regeneration by the consumption of seed and seedlings (Osborn, 1926b). Seedlings are particularly susceptible to being killed by grazing, because one bite can remove not only all the leaves, but also all the shoot meristems (Harper, 1977), making recovery impossible.

In the early stages of the development of the pastoral industry very heavy sheep grazing was practised, because the newly arrived settlers were ignorant of the landscape and the stocking levels it could sustain (PSA, 1865b; Hobbs & Hopkins, 1990). Mobs of thousands of sheep completely removed the vegetation around dams and permanent waters (PSA, 1865b; Osborn, 1925), and in overstocked paddocks (Wood, 1937). The loss of

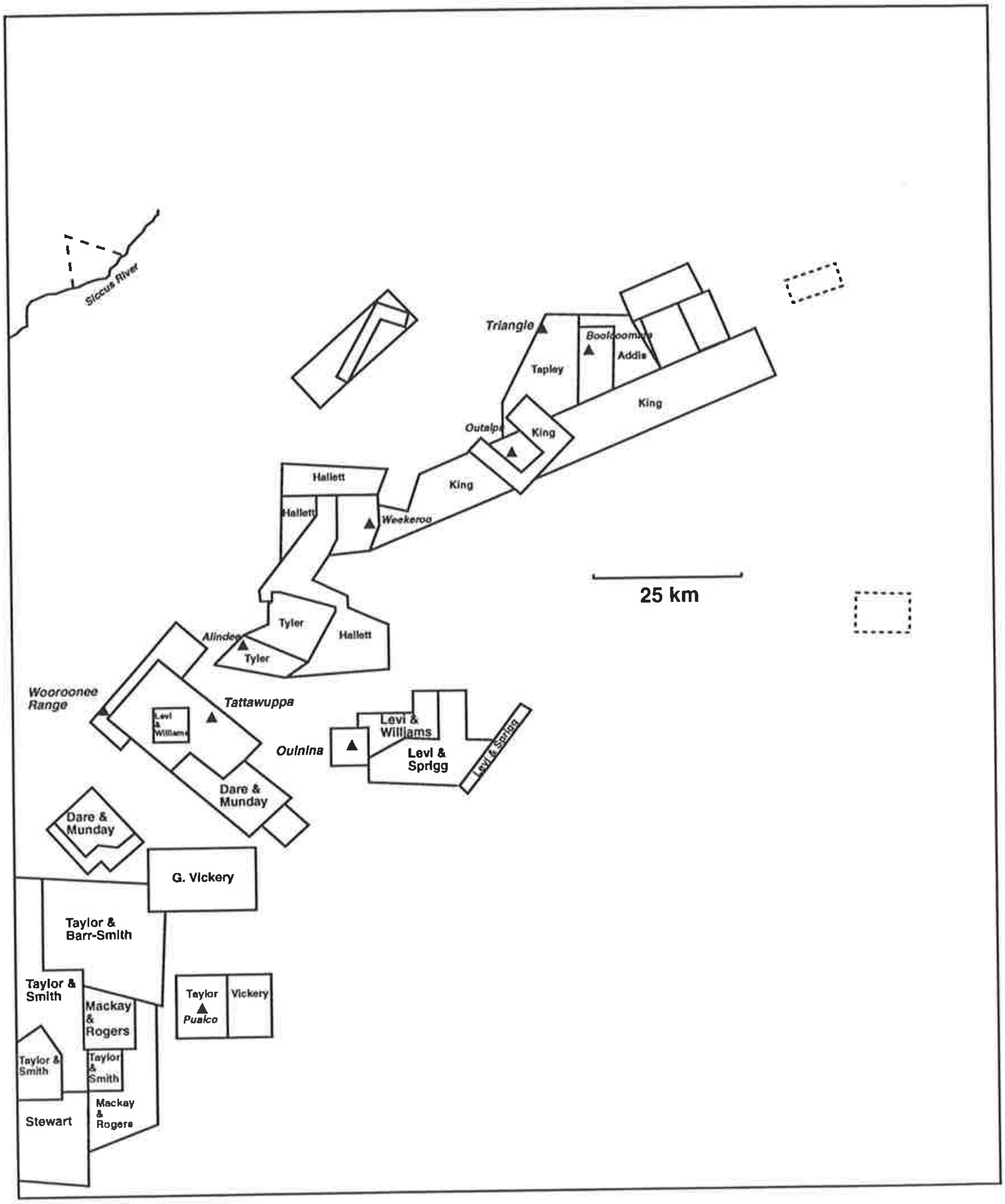


Figure 5.6

Pastoral leases of the study area in eastern South Australia *circa* 1860. (after CCL 1857-59). Lessees' names are in ordinary type. Dotted lines probably indicate unregistered pastoral runs. Significant peaks and landmarks are marked in italics.

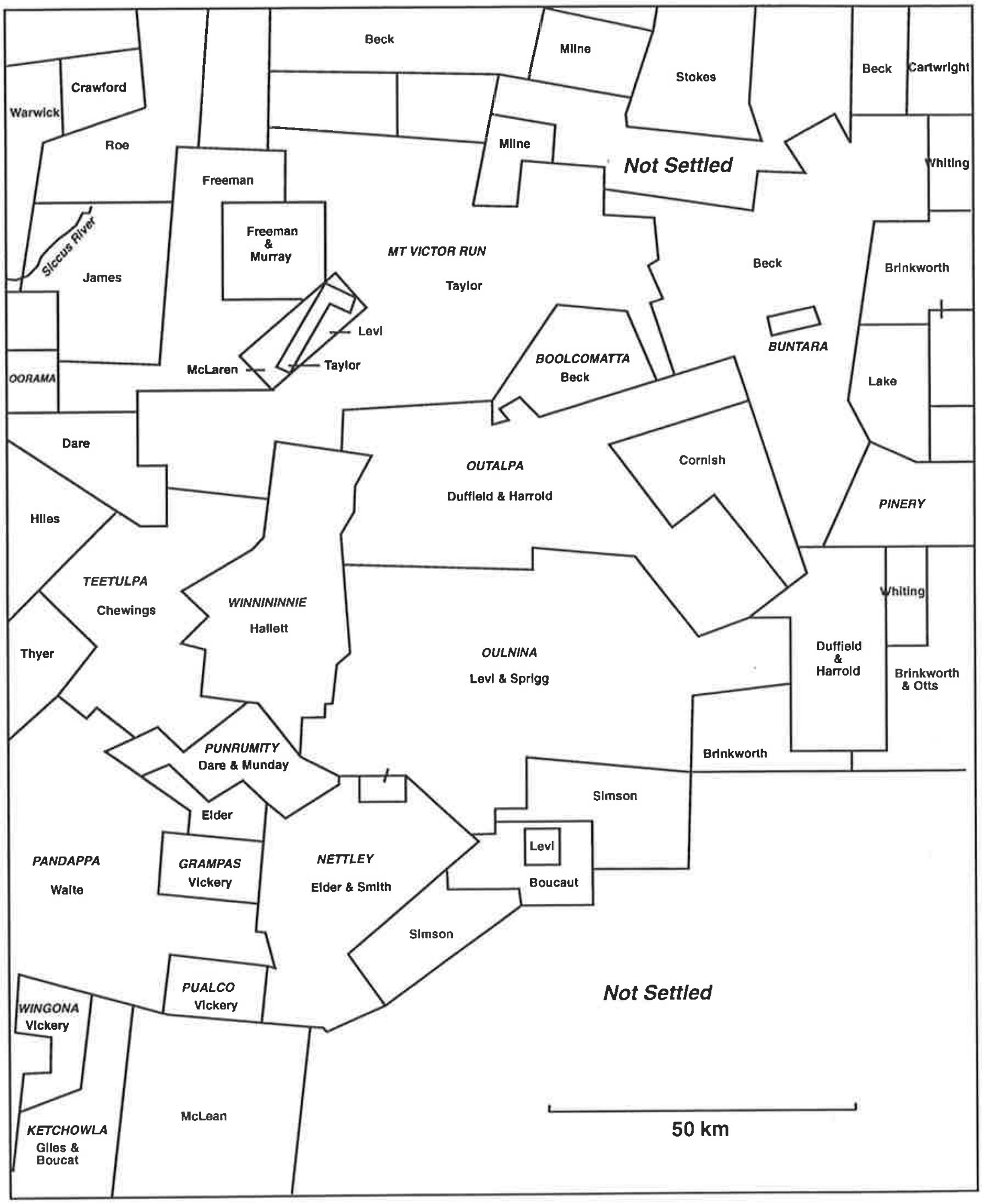


Figure 5.7

Pastoral leases of the study area in eastern South Australia *circa* 1867 (after CCL 1867). Station names are in capitals and lessees' names in lower case type. Spelling of station names follows the source map, and frequently differs from the modern spellings.

vegetation exposed the soil to the winds, and allowed severe loss of topsoil, often over considerable distances, and dust-storms were of such frequency and density as to "prevent a person seeing anything a few yards before him". Left behind were hamada (limestone) or serir (rocky) surfaces and adjacent accumulations of drifted silt (Wood, 1937). Most of these were localized around watering points (Ratcliffe, 1936), but one extensive system of drift was reported to run right across the study area from its source in the cleared agricultural lands near Peterborough to Broken Hill (Wood, 1937). This loss of topsoil is reflected in the fact that post-European sediment yield of the catchment area at Umberumberka Reservoir in the Barrier Ranges, just through the border into NSW, is 50 times higher than during pre-settlement (Wasson & Galloway, 1986). Such extensive damage to vegetation and soil was caused during the 1860s drought that the Parliament of South Australia ordered a commission of inquiry to look into the causes of the degradation (PSA, 1865a), and the surveyor-general, G.W.Goyder, was despatched to the pastoral lands to demarcate the country affected by the drought (PSA, 1865c; PSA, 1965). The report of the Commission (PSA, 1865b) stated that in some areas nearly all the vegetation fit for pasture, especially saltbush, was destroyed or dead. Hundreds of thousands of sheep and cattle died (over one quarter of the sheep, and half of the cattle and horses), and the rest were left in an emaciated condition. At the end of 1865, "not a live bullock or sheep" was left north of Peterborough (PSA, 1898). It appears that the losses were largely due to starvation, because the stock had eaten all the vegetation within reach of the watering points. The findings of the 1865 commission (PSA, 1865b) were that if the bush is removed, any herbage and grass which replaces it provides only temporary cover, and will rapidly die in a drought. Sheep numbers of 25 to 30 per square mile (10 to13 per km) were recommended as a safe stocking strategy by a number of pastoralists interviewed during the commission (PSA, 1865b).

Unfortunately, stock numbers were allowed to build up again during the good seasons which followed the drought, up to 100 sheep per square mile on some leases (PSA, 1898). This resulted in further devastation during the drought of 1894-1898 (PSA, 1898). Contemporary writers such as Dixon (1892) report widespread destruction of indigenous flora by grazing sheep in the pastoral country during this period. This pattern was repeated at Cobar in outback NSW, where similar devastation occurred during the drought of 1895. There, the saltbush communities and topsoil were completely lost from large areas, permanently lowering the productivity and carrying capacity (PNSW, 1901; Bean, 1925). Further damage was caused in the north-east during the drought of 1902, where for example, one station was forced to carry 60 000 sheep on half a dozen permanent waters (Ratcliffe, 1936). It is now widely accepted throughout the pastoral industry of South Australia that if pastoralism is to continue in a sustainable way, then much lower overall stocking levels, and lower numbers of around 250-350 sheep per watering point must be maintained in order to retain the cover of native perennial shrubs (Waite, 1896; Lange *et al.*, 1984). Otherwise, all bush within reach of watering points tends to be removed, the "ring round the water" first described by a pastoralist, P. Waite (PSA, 1898), and subsequently by Osborn *et al.* (1926a; 1932) and Ratcliffe (1936). This effect is due to the increased effective stocking-rate around watering points, since the sheep are obliged to congregate there once or twice a day (Squires, 1976). Squires' studies of sheep behaviour indicate that sheep can graze up to 4 km from a watering point. R.T. Lange named this phenomenon of increased grazing impact around watering points the "piosphere" (Lange, 1969; Barker & Lange, 1970; Barker, 1972; Andrew, 1978; Andrew & Lange, 1986a). In order to prevent bush destruction, it has now become an accepted goal to distribute grazing more evenly by careful placement of watering points, and subdivision of paddocks (Waite, 1896; Foran *et al.*, 1990; Friedel *et al.*, 1990). Although excessive damage events as described above are now less common, there are still piosphere-related effects on vegetation occurring under more conservative modern grazing regimes. The main initial effect observed is the mortaility of *Atriplex* , defoliation of *Maireana* , and an increase in density of small prickly perennials such as *Sclerolaena* (Andrew, 1978; Andrew & Lange, 1986a). However, Eldridge *et al.* (1990) has shown that grazing levels experienced in the outer piosphere (between 1 200 and 1 500m from water) at a sheep station in western NSW do not affect the population dynamics of three of the perennial bush species, *Atriplex vesicaria, Maireana astrotricha* and *M. pyramidata.* Barker and Lange (1970) noted that although heavy grazing causes high mortality of mature individuals, regeneration and population recovery can occur when grazing pressure is reduced. Thus there seems some indication that present grazing practices may be consistent with long-term shrub retention, a desirable goal if pastoralism is to continue and erosion avoided.

Very little is known of the autecology of individual tree and shrub species in arid South Australia (Lange & Sparrow, 1992), and correspondingly little is known as to what extent introduced herbivores are a perturbing influence on their populations. Sheep are known to suppress regeneration of a range of tree species. Lange and Purdie (1976) found recruitment of *Acacia papyrocarpa* was entirely suppressed in all sheep-stocked paddocks, but was able to occur in a paddock ungrazed by sheep for fifty years. Presumably rabbits were present in all paddocks, although this is not stated. Curiously, this paper is often cited as evidence for rabbit suppression of seedlings (Morton, 1990), though the results actually implicate sheep. Lange later conducted trials matching sheep flock movements in a large paddock with loss of simulated seedlings; sheep grazing levels typical of the district were sufficient to totally suppress recruitment in all parts of the paddock (Lange & Willcocks, 1980). There was a low, scattered, and fluctuating background of grazing due to other herbivores, which was negligible compared to the sheep effect. Harrington (1979) showed that sheep reduce regeneration of *Acacia aneura* and *Dodonaea viscosa,* but not *Cassia sp.* or *Eremophila sturtii.* Chesterfield and Parsons (1985) found sheep grazing levels to be threatening populations of *Casuarina* and *Heterodendrum* at sites 4km from water in south-western NSW. *Myoporum* appeared to be unaffected, with rabbits possibly suppressing recruitment at one site. Suppression may not necessarily occur at the recruitment stage; sheep showed a preference for adult foliage over seedlings in *Atriplex vesicaria* (Lange *et al.*, 1992).

FERAL & EXOTIC HERBIVORES & THEIR EFFECTS ON VEGETATION

Introduced herbivores are also present. *Capra hircus* (the goat) is common in scrubby and hilly areas of the Flinders and Olary Ranges (Tunbridge, 1991). Although little is known of the impact their browsing has on the native vegetation in Australia, it is assumed to be deleterious, and there have been many attempts to control their numbers (Tunbridge, 1991). Goats are browsers rather than grazers, and are known to eat seedlings, peel bark, and even climb trees to reach canopy leaves (Wilson *et al.*, 1976; Harrington, 1979; Daly, 1989). They can survive for much longer on a very woody diet than sheep can (Wilson *et al.*, 1976). Because of this, one would perhaps expect that they would have a much greater effect than other herbivores on perennial vegetation. Wilson *et al.* (1976) showed that goats kept at three times the normal sheep stocking-rate severely browsed *Casuarina cristata, Heterodendrum oleifolium* and *Templetonia egena,* and killed *Cassia nemophila platypoda, Cassia nemophila coriacea,* and *Dodonaea viscosa. Eremophila sturtii* was not browsed. Goats have been shown to suppress regeneration of *Acacia aneura, Cassia sp.* and *Dodonaea viscosa* (Harrington, 1979).

Another common pest herbivore is *Oryctolagus cuniculus* (the European rabbit). The invasion and impact of rabbits is summarized by Rolls (1984) and Stodart and Parer (1988). Wild-type rabbits were introduced into Australia at Barwon Park, Victoria, in 1859, and quickly spread, becoming a pest in the agricultural areas of western Victoria during the 1860s (Stodart & Parer, 1988). In 1870, rabbits (probably of the Barwon Park strain) were released at Kapunda, about 50 miles north east of Adelaide in South Australia, to the south-west of the study area. These also quickly spread, being recorded at Paratoo in the south-west corner of the study area by 1878. The South Australian rabbit populations merged with those spreading westwards from Victoria in about 1880, and spread northwards towards Central Australia, reaching Beltana in 1886, Callabonna in 1888 and Lake Eyre in 1891 (Stodart & Parer, 1988). They bred into enormous numbers during this initial wave of invasion (PSA, 1898), and it is estimated that the total population may have been as high as 750 million (Wilson, 1990). Factors aiding their rapid establishment were: the existing burrows of bettongs, bilbies and wombats; plentiful areas with sandy soil suitable for warrens; climate similar to their native range in southern Spain; and a reduced complement of parasites (Stodart & Parer, 1988). There is also some evidence that domestic stock had rendered the native pastures more suitable for rabbits by grazing out shrubs and native grasses, which were replaced by annual grasses and forbs, which are the favoured diet of rabbits (Stodart & Parer, 1988). Rabbit numbers fluctuate violently (Ratcliffe, 1936), from a few to several thousand per square km. This reflects the dependence of rabbits on green herbage, which means that rabbits are a pest of good seasons only. As soon as green feed dies back, populations crash, because they are unable to survive on dry bush (Ratcliffe, 1936; Reid, 1993). Drought was the only controlling variable of rabbit populations until the *Myxomatosis* virus was introduced in 1951 (Norris *et al.*, 1991). *Myxomatosis* was extremely effective in the short-term, causing a devastating fall in population numbers. However, the few surviving rabbits soon founded relatively immune populations, so eradication was not achieved. Post-*Myxomatosis* numbers are estimated at 200 million (Wilson, 1990), so the disease has suppressed population numbers. However, plagues are still occasionally reported in South Australia following periods of high rainfall, such as in 1975 and 1988 (Kemper, 1980).

Rabbits were cited as one of the major causes of failure of pastoral leases during the 1894-1898 drought, although individual pastoralists at the time disagreed on whether the bush losses were due to "swarms of rabbits" or overstocking with sheep (PSA, 1898). Beadle (1948) states that although rabbits cause damage by ringbarking stems and roots, they do not account for much of the total biomass destroyed. Dixon (1892), while stating that rabbits had more effect than "all the other causes put together" clearly identifies rabbits as a secondary influence on the vegetation: "and now the rabbit-plague comes to finish the devastation". Dixon noted the ability of rabbits to ringbark shrubs and trees, including *Myoporum platycarpum, Acacia aneura* and *Eremophila longifolia*. Osborn (1935) noted almost total loss of *Cassia nemophila* seedlings on the Koonamore Reserve during the rabbit plague of 1934. Ratcliffe (1936) concluded that the influence of rabbits has been overstated, that they do not seriously attack the perennial bushes, and that bush reductions are due to grazing by domestic livestock. However, he attributed the lack of regeneration in many species of trees and shrubs, including *Acacia aneura,* to rabbits.

A considerable amount of scientific work has been devoted to the impact of sheep and rabbits on shrub and tree populations, although replicated data allowing effective

1 Crisp and Lange maintain that "the period 1925 to 1970 included both droughts and wet periods as extreme as any experienced since settlement". This is inaccurate. The years 1973 and 1974 were unique in terms of the very high combined amount of rainfall received during that two-year period, over 979 mm (see Figure 4.4). Although the individual year total for 1950 was 487 mm, the previous year had been a drought and the following year was only only slightly above the median at about 275 mm. In addition, only 9 populations of Acacia burkitti were measured, 4 in the Reserve, 2 in nearby areas outside, and 2 at some distance from the Reserve. The sites within the Reserve are not separately enclosed, and cannot therefore be considered true replicates since a single random event (such as a fire) could affect all 3 sites. Crisp and Lange's method of calculating the ages of individuals is extremely elegant and frequently quoted in the literature. However, the coincidence of the rainfall event of 1973-74 with the removal of rabbits coupled with the lack of true replication means that there is no experimental control over the comparisons of grazed and ungrazed populations. Their conclusions about the effects of rabbits must therefore be viewed with caution.

comparisons are rare. Cochrane and Mc Donald (1966) recorded that rabbits ate the growing tips of juvenile *Callitris columellaris* at Hattah Lakes Conservation Park in western Victoria, killing 134 out of 350 individuals. However, they found that the principal effect of excluding rabbits was an increased diversity of native herbs. Crisp and Lange (1976), working at the Koonamore Reserve, concluded that although rabbits alone have some effect of reducing reproduction of *Acacia burkittii,* the combination of sheep and rabbits will totally prevent recruitment. Similar results were found for *Cassia nemophila* (Silander, 1983) and *Acacia aneura* (Crisp, 1978). Unfortunately, complicating factors of fire and rainfall mean that the results are not clear-cut, and the results are somewhat compromised by the fact that rabbits were only effectively controlled on the Koonamore Reserve in 1969, immediately preceding an anti-ENSO high rainfall period. High recruitment of shrub species in the years immediately following 1974 could just as well be attributed to the extreme rainfall of that time as to protection from rabbits.[1] Lange and Graham's (1983) exclosure experiments showed rabbits to be capable of effectively removing juveniles of *Acacia papyrocarpa* (western myall). The presence of ephemeral growth had a marked buffering effect, confirming that rabbits have a strong dietary preference for annual growth, and will tend not to take seedlings of woody species if the former is available. Similarly, Cooke (1987) found rabbit grazing caused damage to seedlings of *Allocasuarina verticillata* in Coorong National Park, the damage being less severe if other herbage was present. Lange and Graham (1983) state that their rabbit and sheep tree-guard experiment showed that even in the absence of sheep grazing, rabbits significantly pruned older juveniles of *Acacia papyrocarpa,* though no data are given. This paper is widely quoted as evidence that removal of livestock will not permit regeneration of trees and shrubs unless rabbits are controlled as well (Perry, 1972; Adamson & Fox, 1982). Austin and Williams (1988) demonstrate suppressed recruitment in *Callitris* at Pilliga Scrub in NSW from the 1880s, until the the 1950s, and cite rabbits as the most likely cause. Auld (1990) used tree-guards to show a rabbit-grazing effect on survival of suckers of *Acacia carnei*, although no such effect was found for *Acacia oswaldii*. A much slighter effect was observed for *Melaleuca halmaturorum*. Woodell (1990) recorded three recruiting and three non-recruiting populations of *Acacia burkittii* at Middleback. He gives a range of likely explanations including differences in local topography, and a reduction in rabbit grazing during the 1950s due to myxomatosis (mysteriously only affecting some populations), but presents no data to support this statement. Roberts (1993) demonstrated that although rabbits were present in large numbers at the Cooper Creek in the far north of South Australia, regeneration of *Eucalyptus coolabah* was only suppressed at the cattle-grazed sites .

The importance of rabbits is widely taken as an *a priori* assumption in designing research programmes, making decisions for pastoral management, and planning for conservation. A reappraisal of the literature presented above supports the views of Pickard (1990), who remarked that despite an abundant literature summarizing the invasion and impact of rabbits, there are surprisingly few data beyond anecdotal level. Often, the conclusions conflict with the somewhat equivocal data from these scientific studies, and it is clear that the authors are interpreting the results in a biased fashion. The result of this is that the deleterious effect of rabbits on wildlife and vegetation are frequently restated in review papers on the arid zone (Newsome & Corbett, 1972; Wilson, 1990), often without reference, and most authors seem to accept the theory that rabbits are the greatest problem. In spite of the equivocal nature of the evidence, it appears that the primary importance of the role of rabbits in causing vegetation damage has achieved the status of a paradigm. There is an urgent need for a more objective assessment of the relative effects of rabbits and other herbivores.

INCREASING POPULATIONS OF NATIVE SHRUBS ("WOODY WEEDS")

Rapidly regenerating populations of native shrubs which cause reduction of rangeland value has been well-documented in other arid rangelands, including those of North America (Hennessy *et al*., 1983; Jacoby, 1986; Brown & Archer, 1987; Archer *et al*., 1988; Archer, 1989; Brown & Archer, 1989) and southern Africa (Skarpe, 1990). The most important problem species in North America is honey mesquite, *Prosopis glandulosa,* which in pre-European times occupied scattered locations in drainage lines. Overgrazing, fire suppression and climate change have allowed *Prosopis* to invade the upland prairie grasslands (Archer, 1989). Similar phenomena with rapidly regenerating native species were first reported in Australia in western New South Wales, especially the Cobar district (WLC, 1969). Along with overgrazing and drought, such "woody weeds" were cited as a major cause of the depression in the pastoral industry there (PNSW, 1901; WLC, 1969; Hodgkinson & Harrington, 1985; Burgess, 1988). Species cited as a problem in the Australian rangelands include *Acacia aneura* (Harrington, 1979), *Dodonaea viscosa angustissima, Cassia artemisioides, Cassia nemophila platypoda, Eremophila duttonii, Eremophila sturtii* (Booth, 1987) and *Callitris columellaris* (Dixon, 1892). The increases in western NSW are attributed to the interacting effects of past overgrazing (Dowling, 1993) and the resulting changed fire regime, and to recruitment periods during ENSO-related periods of high rainfall. There is no evidence that fires were ever common in the chenopod shrublands of eastern South Australia, so this theory can be discounted for the study area, though fires were more common prior to European settlement in the grass-dominated rangelands of North America and western New South Wales. Numerous efforts have been made to control encroaching native shrubs by clearing, poisoning and heavy overstocking with goats (Green, 1983), which have proved unsuccessful and uneconomic (Harrington, 1979; Adamson & Fox, 1982). Similar experiences in North America caused Jacoby (1985) to express a need for holistic management practices which are more closely aligned to the ecology of the region.

CONSERVATION

The only conservation park officially gazetted within the study area is Danggali, in the far south-east corner of the study area (Figure 5.8). It is located entirely within the Holocene Molineaux Sand geological formation (Figure 4.3) and consists of mallee scrub vegetation (Figure 5.6). In 1925, the University of Adelaide fenced a square mile of previously overgrazed land on Koonamore Station (Osborn, 1925), now known as the T.G.B. Osborn Vegetation Reserve, where studies of shrub population dynamics are carried out

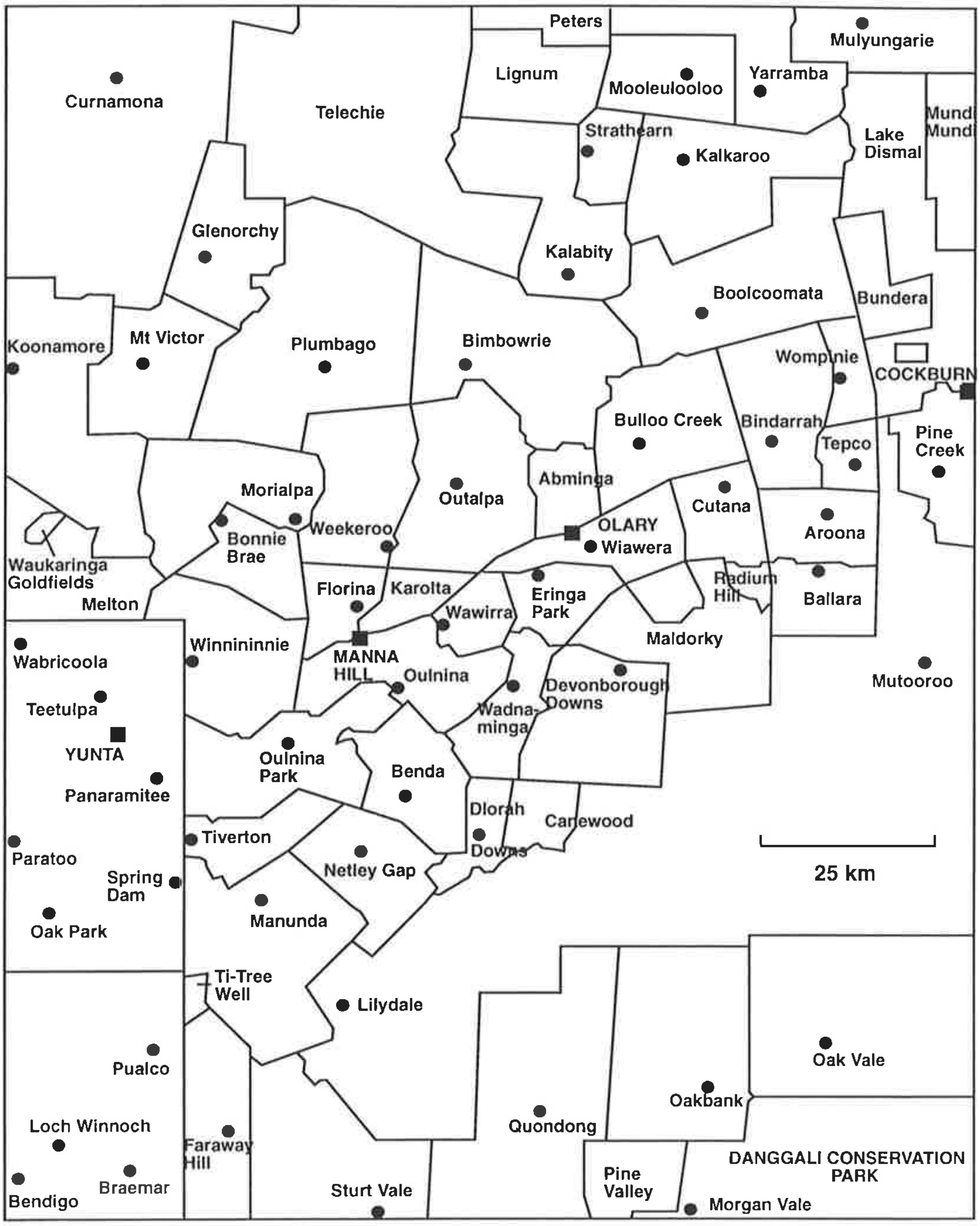


Figure 5.8

Pastoral leases of the study area in eastern South Australia (after SADENR, 1993). Station homesteads are marked by dots, and station names in lower-case type. Towns are marked by squares and upper-case type.

(Sinclair & Smith, 1983). Otherwise, all the land in the study area is subjected to livestock grazing of varying intensity (Figure 5.8).

DISCUSSION

Given the few official conservation measures carried out within the study area and the knowledge that livestock grazing has been known to cause severe land degradation in the past, it is of the utmost importance that the scanty knowledge of vegetation be improved upon. These facts do not make the study area unique: the same could be said of most of the semi-arid and arid grazing lands of Australia, and the rest of the world. Therefore, the objectives of this study will be not only to provide information about the vegetation of eastern South Australia, and any changes which are occurring to it, but also to develop techniques and increased knowledge of vegetation science which will be useful in answering similar questions in other parts of Australia and elsewhere.

CHAPTER 6:
PERENNIAL VEGETATION PATTERNS - ALLIANCES

INTRODUCTION

The type of data collected and analyses performed depends on the questions being asked, and the problems of method choice are at their most complex in studies of vegetation composition (Greig-Smith, 1983). It is generally accepted by vegetation scientists that a broad, qualitative analysis should precede any quantitative analyses. This is because preliminary investigation can often save a lot of time and effort by focusing attention on important factors, some of which may not be readily apparent without an exploratory analysis (Mueller-Dombois & Ellenberg, 1974). A technique which is often helpful in the exploratory stages of broadscale vegetation studies is to classify and generalize the field data into recognizable vegetation classes (Goodall, 1978; Greig-Smith, 1983; Belbin & McDonald, 1993) which can be mapped (Jongman *et al.*, 1987). Cartography tends to be a useful technique when dealing with sessile organisms such as plants (Goodall, 1966). This means that some kind of classification has to be produced. The preliminary investigation can then be used as a basis to identify discontinuities and detect correlations of composition and environment, and from these develop hypotheses about causality (Greig-Smith, 1983). Chapters 6 and 7 are concerned with this primary objective. As stated in Chapter 3, the initial stages of this study lie within the macro-scale of vegetation science, landscape ecology and biogeography, and are largely holistic and inductive in nature. Andersson (1988) has noted that, compared with phytosociology, descriptive phytogeography is methodologically underdeveloped, and few studies have applied multivariate techniques to data collected in large-scale surveys. The general objective is to use a floristic, numerical technique, combining methods of classification and ordination to achieve an understanding of vegetation patterns at the alliance level, which can be used to formulate more refined causal hypotheses.

The aims of this chapter are to:

Develop a rapid and efficient field technique for providing a numerical classification of the major floristic alliances in the form of a list of key species.

Compare this classification with existing descriptions of the vegetation of the area.

Present the results in mapped format, which will be readily accessible to others.

Ascertain if any major biogeographic patterns at the level of formation are encountered.

Formulate hypotheses about the causes of vegetation pattern.

METHODS

Survey & Sampling Strategy

In order to be able to identify alliances, representative information was required to summarise the range of environments and major plant species present over an area of several square kilometers at each location. Because different observational scales capture different aspects of the system being studied (Rahel, 1990; Sugihara & May, 1990), sampling decisions are dependent on the context of the study, the scale, and the spatial patterning of the sampling universe (Kenkel *et al.*, 1989). Sampling at too fine a scale though supplying more detail can result in sampling errors, whereas sampling at a broader scale reduces the detail, but means that generalizations are more likely to emerge (Wiens, 1989). It is therefore necessary to define the desired level of study, and match the scale of observation to this level (Noy-Meir & van der Maarel, 1987). When sampling extensive areas, it is usually recommended to sample a large number of samples relatively rapidly (Gauch, 1982). In regions of continuous vegetation, where it is impossible to record all of the vegetation present, it is necessary to impose restrictions on the sampling (Goodall, 1953). Decisions must be made about the style of sampling, whether it is to be random, regular or stratified (Kershaw & Looney, 1985; Kent & Ballard, 1988), and also the extent (size of area over which samples are distributed), intensity (total area sampled), and grain (size of the samples) (Reed *et al.*, 1993).

Random sampling is necessary if the resulting classification is to be truly representative of the vegetation in a statistical sense (Goodall, 1953), but this is not the main purpose of the study, and there are a number of advantages of regular over random sampling. The main problem of random sampling is that it is an inefficient method of encountering the range of variation because plant communities tend to have clumped rather than random distributions (Whittaker, 1978b; Rabotnov, 1984). Therefore more sites are required to provide even coverage of a surveyed area than would be required if using a regular sampling strategy of the same area (Williams, 1971; Mueller-Dombois & Ellenberg, 1974; Gauch, 1982). A regular arrangement of the same number of sites means that environmental space is more likely to be completely and uniformly sampled. This is important if numerical analysis techniques are to be used, because most of the multivariate ordination techniques available such as DCA and NMDS perform badly if this is not the case (Minchin, 1987). Uniform and regular (grid) sampling also have the advantage of allowing the construction of contour diagrams and maps (Gauch, 1982; Kent & Coker, 1992) which was another of the aims of the study as stated above.

Because of the low frequency and scattered distribution of the plants in the arid and semi-arid landscapes of the study area, initial reconnaissance work showed that the following technique was found to sample the vegetation in the most efficient manner. A system of transects placed close enough together that they form a rectangular grid as used by Williams and Lambert (1958) was found to retain the advantages of a grid, but provide some of the advantages of a transect. If placed across areas of major vegetation change, or marked environmental gradients (Kershaw & Looney, 1985), transects can obtain most of the information which would be obtained from a grid, but require less fieldwork (Kent & Coker, 1992). This concept has been further developed by Austin and Heyligers (1989) in developing the "gradsect", a method of placing transects across known environmental gradients to develop an efficient sampling strategy. This technique has previously been used to sample large areas of semi-arid southern Australian vegetation by Noy-Meir (1971) and Western Australian vegetation by Beard and Webb (1974) The major environmental gradient encountered in the study area was expected to be that presented by the Olary

Range, which runs east-west across the study area. For this reason a system of eight transects running north-south, spaced 20 km apart was used (Figure 6.1) to adequately sample the expected range of environments. Samples were taken at 10 km intervals along these transects, so that the highest sampling density was perpendicular to the greatest change in elevation. Each tradsect was 200 km long, allowing 20 samples, and since there were eight transects, a total of 160 samples were taken. Ramensky found that at least eight to ten sites should be included for each type of locality (Sobolev & Utekhin, 1978), and the grid frequency of 10 by 20 km used was found to sample localities at about that frequency or greater, except for the rarer vegetation types. The theoretical 10 x 20 km grid-points as described were not always accessible, so sampling was carried out at a point as near as possible to the grid points that was still accessible by an existing vehicle track. J.B. Cleland had previously used vehicle tracks as sampling routes, which he called "botanical traverses by motor car", in central Australia during the 1930s (Willis, 1981). Vehicle transects have also been used to sample other areas of sparse vegetation in the semi-arid rangelands of north-western South Australia (Lay, 1972), and the deserts of Egypt (Dargie & El Demerdash, 1991). The arrangement of samples approximated a true grid closely enough still to allow mapping of vegetation and other patterns.

Samples, equivalent to sampling units of statistics (Gauch, 1982), were taken by driving along the nearest accessible track in a north-south direction, keeping as close as possible to the line of one of the major transects, and recording all the perennial and woody species observed within a distance where species could be readily identified, approximately 200 m. Hence, the sampling units were examples of the strip-census or belt-transect, since they were elongated plots and had a defined area, rather than being line or intercept transects (Mueller-Dombois & Ellenberg, 1974; Brower *et al.*, 1990; Kent & Coker, 1992). Such elongated plot methods are preferred when estimating diversity, since they are more likely to represent it adequately, being more likely to cross through patches of species (Williams, 1971; Gauch, 1982; Kenkel *et al.*, 1989). The length of each strip-census was 5 km, giving a total area of 100 ha per sample, and each strip-census extended 2.5 km to the north and south of the theoretical grid intersections. Therefore, there was only a 5 km

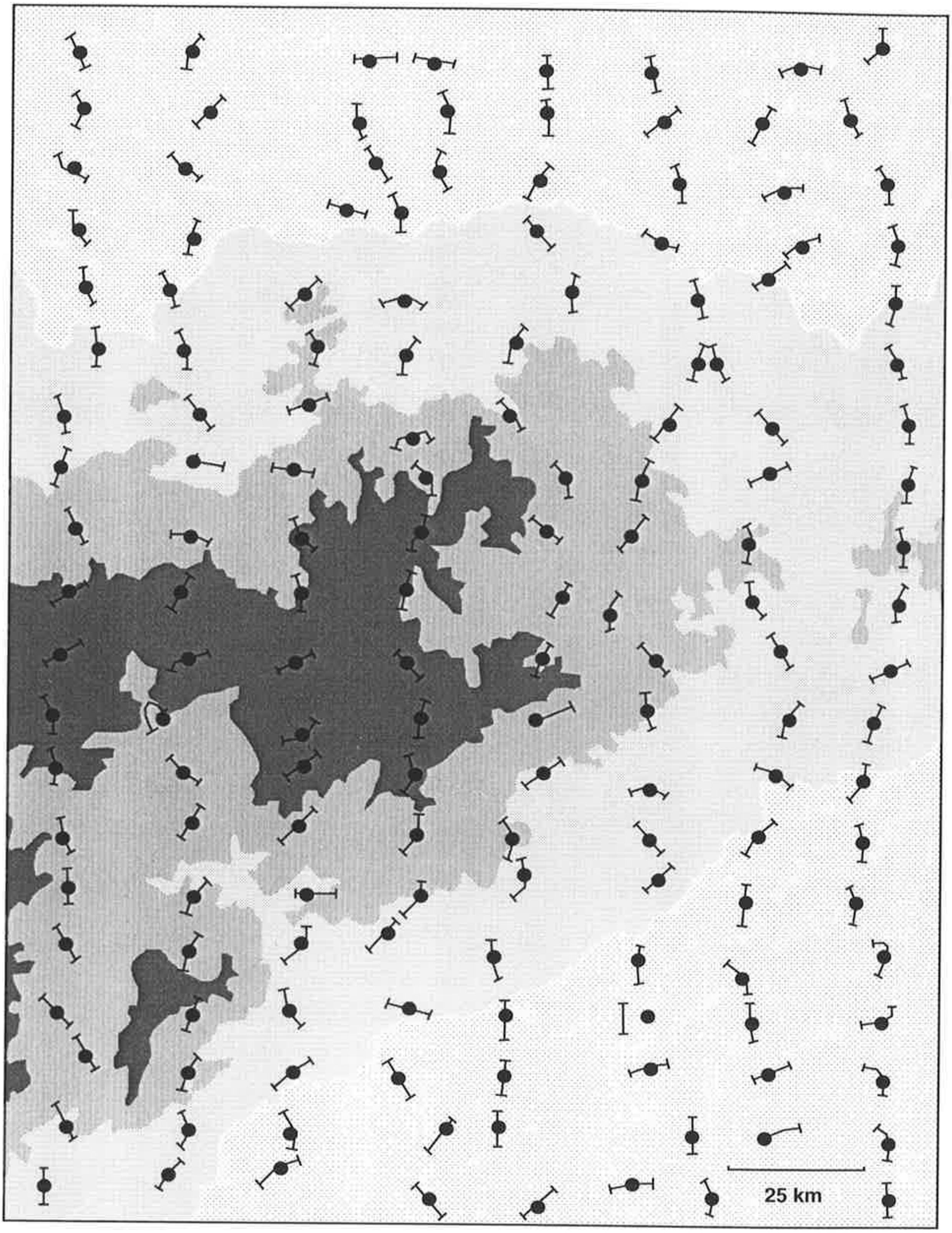


Figure 6.1

Sampling strategy for identifying vegetation alliances of the study area in eastern South Australia: a series of 160 5 km-long strip-censuses, arranged on a system of eight gradsects, the whole approximating a 20 x 10 km grid. The gradsects are arranged north-south across the main topographic feature of the region, the Olary Spur.

gap between the northern end of one strip-census, and the southern end of the next northerly one, giving semi-continuous information about the vegetation along each transect. Previous researchers such as Curtis (1955) had found similar large plots of six or more hectares useful in sampling prairie vegetation on a broad landscape scale, whilst recognizing that such data were heterogeneous, and could not be used to identify associations in the sense of Braun-Blanquet. In complex landscapes such as the Olary Ranges, the 5km belt-transects invariably crossed individual plant association boundaries, so species from several different communities or associations were recorded for each sample. Therefore individual associations could not be extracted from these data, and the resultant groupings from cluster analysis more closely approximate the level of alliance.

All woody perennial species visible within sight of the track were recorded. It is not always easy to distinguish annual, biennial and perennial species (Harper, 1977), especially in harsh environments where individuals may be capable of perennation if conditions are favourable (Silvertown & Doust, 1993). To be useful, maps should only contain information which is continuously present in the landscape, so it was decided only to record plant species capable of persisting in the landscape, even during dry seasons and droughts. Therefore, herbaceous plants, even if obviously capable of surviving for several years, were not included in the data set. Herbarium specimens were taken of previously unencountered species, but after some practice it was soon possible to identify most species on sight, even at quite a distance. Specimens taken were later identified with the assistance of staff of the State Herbarium of South Australia. Taxonomic nomenclature follows Jessop and Toelken (1986) for consistency, although there are a number of subsequently proposed alterations to some taxa (Jessop, *pers. comm.*). Perennial plant species included in the strip-census data set are marked "p" in the full species list of the study area (Appendix 1).

Relative Abundance

In highly heterogeneous vegetation, presence/absence data for plant species is often sufficient to characterize sampling units, but in more homogeneous environments, variables which express quantitative information are usually valuable (Goodall, 1978). Rankings of estimated percentage cover into ordinal scales were originally used for ease of computation, and have many advantages over more accurate measures of of cover because they can be assessed more rapidly and reliably (Goodall, 1978) and variability is less likely to be inflated due to sampling errors (Rahel, 1990). Being non-linear transformations of cover data, they tend to decrease emphasis on the dominant species (Currall, 1987). Although such ordinal scales are "weak" or lacking in power to provide information during statistical analysis (Jongman *et al.*, 1987), they require much less effort to collect than interval or ratio data, whilst still being "stronger", and not much more difficult to collect, than nominal (presence/absence) data. As long as they are strong enough for the analysis techniques proposed, it is therefore preferable to use as weak a scale as possible (Jongman *et al.*, 1987). However, the traditional Braun-Blanquet survey technique of estimating percentage cover and converting to an ordinal scale has serious short-comings when measuring vegetation cover in arid and semi-arid environments where the maximum perennial cover is less than 25% cover or less (McAuliffe, 1990). By assigning cover on a one to five Braun-Blanquet scale, only a very poor resolution of relative cover is obtained, as there is a tendency consistently to over-estimate the cover of species with very low contribution.

For the above reasons, the following technique of recording relative abundance was chosen. An estimate of the relative importance of each perennial species occurring in the strip-census was recorded by a ranking procedure, based on the ACFOR (abundant, common, frequent, occasional, rare) scale as described by Kent and Coker (1992); see Table 6.1. In this study, no distinction was made between occasional and rare, since it is not possible to make a judgement whether a plant is rare or not on observations at a single site. Thus, the scale chosen was still an ordinal one, since the classes are arranged in rank order (Kent & Coker, 1992), similar to those of Braun-Blanquet (1928), Domin (1923)

Table 6.1

Scale for estimating relative abundance of perennial species along the strip census; a rank-order procedure based on the ACFOR scale described by Kent & Coker (1992). Abundance here refers to the number of individuals encountered per strip census (5 km x 0.2 km).

SCORE	ABUNDANCE	DISTRIBUTION	ACFOR SCALE
4	> 200	dense stands	abundant
3	20-200	patches or common	common
2	5-20	clumps or scattered	frequent
1	1-5	uncommon	rare

and Krajina (1933) [as cited by Currall (1987)] and Ramensky, 1956 #407 (Table 7.1), but better adapted for broad-scale survey. The number of classes was kept to four, because if there are too many, it becomes difficult to distinguish between them, and the data will contain a large error in approximating relative importance (Kershaw & Looney, 1985). It is accepted that a species list with a subjective assessment of abundance such as this is the simplest and most rapid method of describing vegetation (Kershaw & Looney, 1985). Although relatively crude, such estimates of quantity have usually been found adequate for vegetation description (Mueller-Dombois & Ellenberg, 1974).

ANALYSIS METHODS

Cluster Analysis

Since the aim is to give information on co-occurrence of perennial species, and establish broadscale vegetation types (alliances) for mapping, it was necessary to perform a classification or cluster analysis, where sites are arranged into classes with characteristic species in common, (Küchler, 1951; Goodall, 1978; Greig-Smith, 1983). Similarity between sites was calculated using the Czekanowski distance measure, and sites were clustered using a polythetic, agglomerative, hierarchical, average linking method, flexible UPGMA (unweighted pair-groups method using arithmetic averages) for the reasons given below.

The dissimilarity measure used was the mean character difference of Czekanowski, which is also known as Bray-Curtis after Bray and Curtis (1957) who popularized its use. It has consistently performed well in a variety of simulated data sets and is therefore recommended for use with vegetation data (Bloom, 1981; Belbin & McDonald, 1993), particularly species abundance data (Legendre & Legendre, 1983). It has the advantage that it is sensitive to double positive occurrences of species (Greig-Smith, 1983), and is thus well-suited to vegetation studies which contain large numbers of similar sites. It is the most widely known and useful measure of dissimilarity for vegetation data (Kent & Coker, 1992). Monothetic (single attribute, in this case species) methods of clustering have been preferred in the past due to their ease of computation, but now that more sophisticated computer techniques are available, polythetic (many attributes) methods are preferred, because they produce more stable classifications, and provide more information (Lambert & Dale, 1964). Agglomerative methods are preferred over divisive methods for vegetation data because of their ability to separate groups arranged at near perpendicular angles to the first ordination axis, hence giving more reliable results (Belbin & McDonald, 1993). They are less likely to mis-classify stands than divisive techniques (Greig-Smith, 1983). Hierarchical clustering has the advantage that the output is displayed as a dendrogram (Kent & Coker, 1992)(Figure 6.2), which displays relationships between groups in a format which is readily interpretable ecologically and can be readily compared to environmental variables to develop hypotheses about causality (Greig-Smith, 1983). Flexible UPGMA is based on the original UPGMA developed by Sneath and Sokal (1973). Flexible UPGMA gives equal weight to objects [sites] (Legendre & Legendre, 1983) rather than groups, and weights the objects evenly throughout the fusion process (Belbin, 1992). Average linking methods are the most widely used in ecology, because they maximize the correlation between similarity and dissimilarity between samples. They therefore avoid as much as possible the problem of chaining (the formation of long straggly clusters) common with single linkage, or the formation of over-exaggerated groups common with complete linkage (Jongman *et al.*, 1987). The techniques used are available on the computer package NTP (Belbin *et al.*, 1984).

The determination of groups from a dendrogram is a somewhat arbitrary and subjective process unless there are distinct inherent discontinuities in the data (Goodall, 1978). In the absence of such discontinuities, it is best to avoid trying to divide too finely, since large numbers of fragmented clusters result (Ludwig & Reynolds, 1988). However, one of the aims of classification is predictiveness; it is desirable that the species composition of a sample can be predicted from its group membership (Gauch, 1982). This is more likely if groups are relatively compact. A decision was made to split the alliance dendrogram (Figure 6.2) at the 80% level, which gave a tractable number of natural groups with high predictive power. This subjective method of division has previously been shown to produce ecologically meaningul groups which can be predicted by environmental correlates (Burke, 1989).

Indirect Ordination

DCA (detrended correspondence analysis) was used to ordinate the data to show how the vegetation groupings relate to one another. The floristic data obtained from the gradsect and strip-census survey were highly continuous and of quite low overall beta-diversity. This is because there were a number of plant species such as *Enchylaena tomentosa* which occurred right across the study area. Since the aim was to identify noda and their relationships to one another, rather than individual species responses, the compression of axis centres (and subsequent stretching of axis ends) of metric ordination techniques was considered an advantage rather than a disadvantage, because it tends to accentuate floristic discontinuities. For this reason, it was not considered desirable to use a non-metric ordination technique, and the best metric technique, DCA with detrending by polynomials (Ter Braak, 1988b; 1988a) and available in the computer program CANOCO (Ter Braak, 1988b), was used.

DCA is an eigenvector technique (Ludwig & Reynolds, 1988),which was developed by Hill (1979) from its predecessor, CA (correspondence analysis). Both CA and DCA calculate simultaneous ordinations of both samples and species, approximately coordinated with one another; hence there is "correspondence" between samples and species (Noy-Meir & Whittaker, 1978; Ludwig & Reynolds, 1988). CA and DCA are the best of the metric strategies for recovering pattern (Kenkel & Orlóci, 1986), performing better than other types of ordination such as PO (polar ordination) and PCA (principal component analysis) when there is one long underlying gradient (Gauch, 1982; Ludwig & Reynolds, 1988). Therefore they have a better tolerance to high beta diversity (Noy-Meir & Whittaker, 1978; Jongman *et al.*, 1987). Beta diversity is the length of gradient in terms of the average width of species response curves, or the length of gradient over which sample similarity decreases by a factor of two (Noy-Meir & Whittaker, 1978), giving a measure of turnover in species composition. DCA has been widely and successfully used on data from broad-scale vegetation studies including: sage-brush steppe in North America (Jensen *et al.*, 1988); high mountain grasslands in the Caucasus (Pysek & Srutek, 1989); arid and semi-arid shrublands in Ethiopia (Woldu & Backéus, 1991); and mallee vegetation in South Australia (Tiver, 1987; Tiver *et al.*, 1989; Sparrow, 1991).

A characteristic of CA [still apparent in DCA] is that there is a tendency to compress the ends of axes relative to the middles (Kenkel & Orlóci, 1986; Kent & Coker, 1992). This compression occurs because currently available linear ecological resemblance metrics (distance and similarity coefficients) fail to adequately measure the true separation of sampling units at opposite ends of gradients (Ludwig & Reynolds, 1988). Thus differences in composition are not represented by equivalent differences in axis position (Greig-Smith, 1983). Therefore, metric methods such as CA and DCA give more emphasis to outliers (Kenkel & Orlóci, 1986), since the ordinal space in between them has to be estimated, which can cause distortion of the ordination diagram. If there is a significant proportion of under-estimated distances in the data set, non-linear structures tend to result from metric scaling techniques (Belbin, 1991). These can be corrected by variable scaling of the axes (Greig-Smith, 1983), but this approach is no longer recommended. If the aim is to summarize the overall interspecific relationships, a non-metric method would be preferable (Kenkel & Orlóci, 1986). However, if the main objective of the research is to recognise distinct noda within a vegetation continuum (which is the case in this instance), this may not be a disadvantage, since clusters and outliers tend to attract metric ordination axes (Kenkel & Orlóci, 1986).

Hill (1979) was prompted to develop DCA because of one of the major disadvantages of CA, a tendency to form "arches", curvilinear distortions , which make second and higher axes difficult to interpret (Noy-Meir & Whittaker, 1978; Jongman *et al.*, 1987; Ludwig & Reynolds, 1988) This "arch effect", also known as the "horseshoe" or "Guttmann effect" (Legendre & Legendre, 1983), is caused by the tendency of axes in CA to show quadratic relationships with previous axes (Kenkel & Orlóci, 1986; Kent & Coker, 1992). The DECORANA algorithm (Hill, 1979) straightens out arches in the data, segment by segment. Minchin (1987) has shown some lack of robustness of this form of DCA, where variations in response model and sampling pattern can lead to marked distortions in simulated data sets. This is because detrending acts by straightening out false non-linear components, but is equally effective in removing true non-linear distributions (Belbin, 1992). Consequently, DECORANA cannot distinguish "arch" distortions from real, non-linear environmental configurations, and will introduce distortions of its own to "correct" them (Minchin, 1987). Therefore, although the detrending was effective in dealing with the problem of false arches to give a more readily interpretable ordination (Kenkel & Orlóci, 1986), its action could also result in the loss of ecological meaningful information (Jongman *et al.*, 1987). Ter Braak (1988b; 1988a) has developed a more sophisticated form of detrending called polynomial detrending, which is preferable to previous methods.

RESULTS

Vegetation alliances & distribution maps

Ten vegetation alliances were identified by UPGMA clustering analysis of the broadscale vegetation data, as shown by the dendrogram (Figure 6.2). The dendrogram consists of three major branches, two of them occupied by a single alliance, and the other divided into two sub-branches of four relatively closely-related alliances. The DCA ordination (Figure 6.4) supports these groupings, and shows the close relationships between the alliances on the sub-branches. The structure of the clustering and ordination results is explained by examining the floristics of the groupings (Table 6.2), and the map of their distributions (Figure 6.3). Although the groups are determined by the full floristics, it is convenient to provide some kind of meaningful nomenclature for ease of reference. The terms dominant, indicator and character species are used here to conform with earlier subjective classifications based upon them, but for convenience only. The most important indicator species, which tend to occur together in groups, thus characterizing the associations (Westhoff & van der Maarel, 1978), are listed in a synoptic table (Table 6.2) of the type

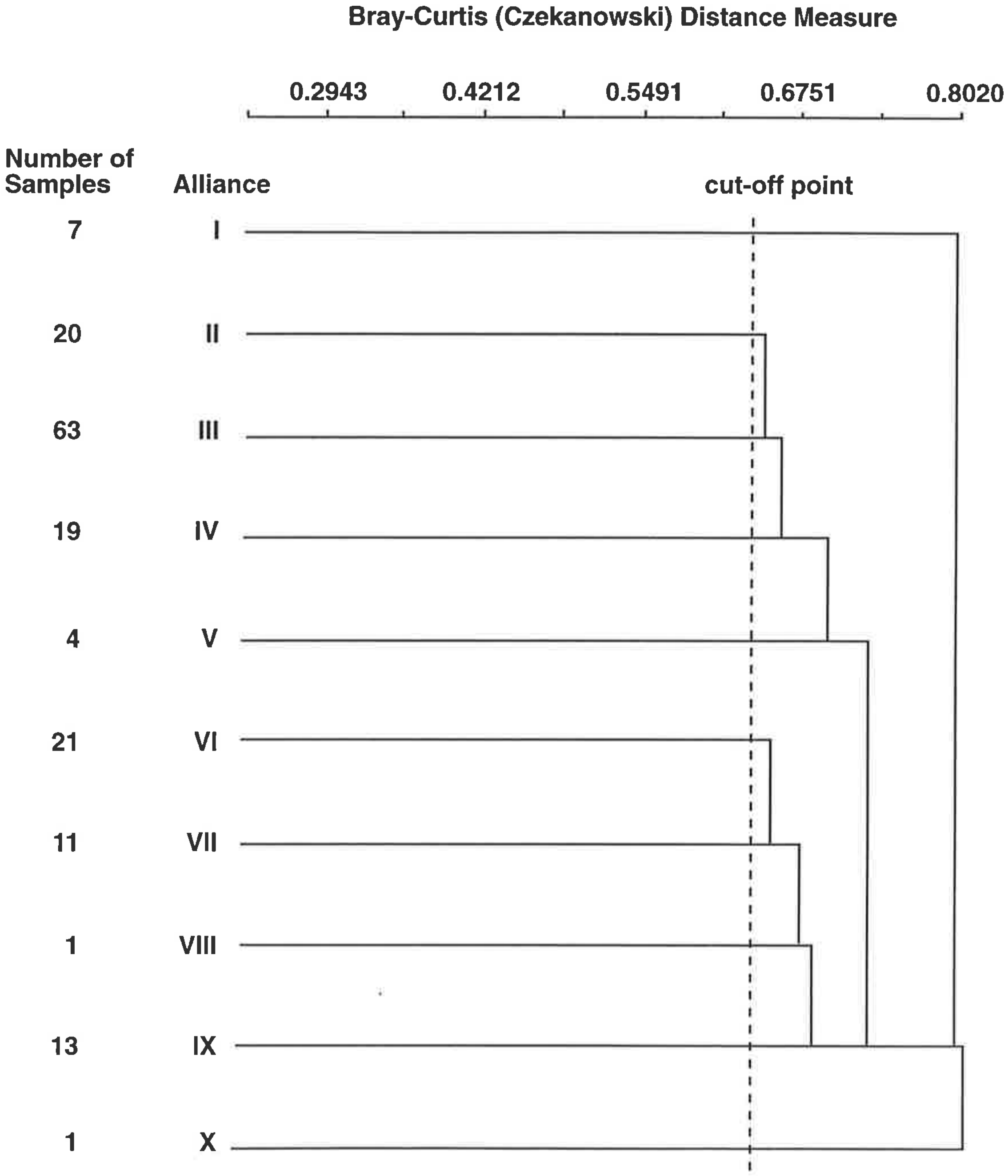


Figure 6.2

Summary dendrogram of floristic alliances of the study area in eastern South Australia. Clustering was performed by Bray-Curtis (Czekanowski) - UPGMA.

Table 6.2

Synoptic table of floristic alliances from survey data. Only species with constancy values of 75% (i.e. occur in 75% of line-transects of that alliance type) or more are shown. The figures in the table are importance values, derived from the mean score achieved for that species in that alliance and omitting the few line-transects from which it was absent.

VEGETATION ALLIANCE	I	II	III	IV	V	VI	VII	VIII	IX	X
Frequency (No of Line Transects)	7	20	63	19	4	21	11	1	13	1
Triodia irritans	3									3
Cassia nemophila platypoda		2.1				1.9				
Eremophila scoparia	2.7									
Eucalyptus socialis	2.5				2.5					
Casuarina cristata	2.4	3.3	2.8			2.8			2.6	
Eucalyptus gracilis	2.3									
Sclerolaena diacantha	2									
Cratystylis conocephala	2									
Codonocarpus cotinifolius	2									
Acacia colletioides	2									
Cassia nemophila coriacea	2	3								
Maireana sedifolia	2	4	2.8							
Myoporum platycarpum	2	2	2.4							
Eremophila glabra glabra	1.7									
Enchylaena tomentosa	1.7			1.1						
Dodonaea viscosa angustissima	1.7					2.3		3		3
Atriplex stipitata	1.6									
Grevillea huegelii	1.6									
Solanum esuriale	1.6									
Eucalyptus cyanophylla/dumosa	1.5									
Templetonia egena	1.3									
Ptilotus exaltatus	1	1.6								
Acacia oswaldii	1				1		1.4			
Eriochiton sclerolaenoides		2.3								
Exocarpos aphyllus		1.5								
Einadia nutans		1.3								
Heterodendrum oleifolium		2.1	2.3	1.9	1.8	1.9				
Eremophila sturtii		2	2	1.9		1.9	2.5	3		
Maireana pyramidata		1.8	3.3	3.2	3		3.2			
Rhagodia spinescens		1.4		1.3		1.9	1.9		1.6	
Atriplex vesicaria			3.5			3.8			3.5	
Sclerolaena obliquicuspis			2							
Lycium australe			1.8							
Sida calyxhymenia				2.3	2.8					
Acacia aneura				2.2		2.1	2.6			
Acacia victoriae				2.2	2		2.3		1.8	3
Sclerolaena lanicuspis				2.1						
Ptilotus obovatus				1.7						
Acacia tetragonophylla				1.6						
Nitraria billardieri					2.3					
Maireana brevifolia					2					
Maireana astrotricha						3.3	3.5	2	2.9	
Maireana aphylla						2.8			2.2	
Hakea leucoptera						2.2				
Eremophila duttonii						1.9	2.9			
Sclerolaena bicornis							1.9			
Eremophila longifolia							1.9			
Santalum lanceolatum							1.6			
Pittosporum phylliraeoides							1.1			
Atriplex nummularia								3		
Eucalyptus largiflorens								3		
Gunniopsis quadrifida								2		
Sclerochlamys brachyptera									2	
Sclerolaena divaricata									2	
Dissocarpus biflorus									1.5	
Rhagodia parabolica										3
Cassinia laevis										3
Callitris columnellaris										3
Eucalyptus intertexta										3

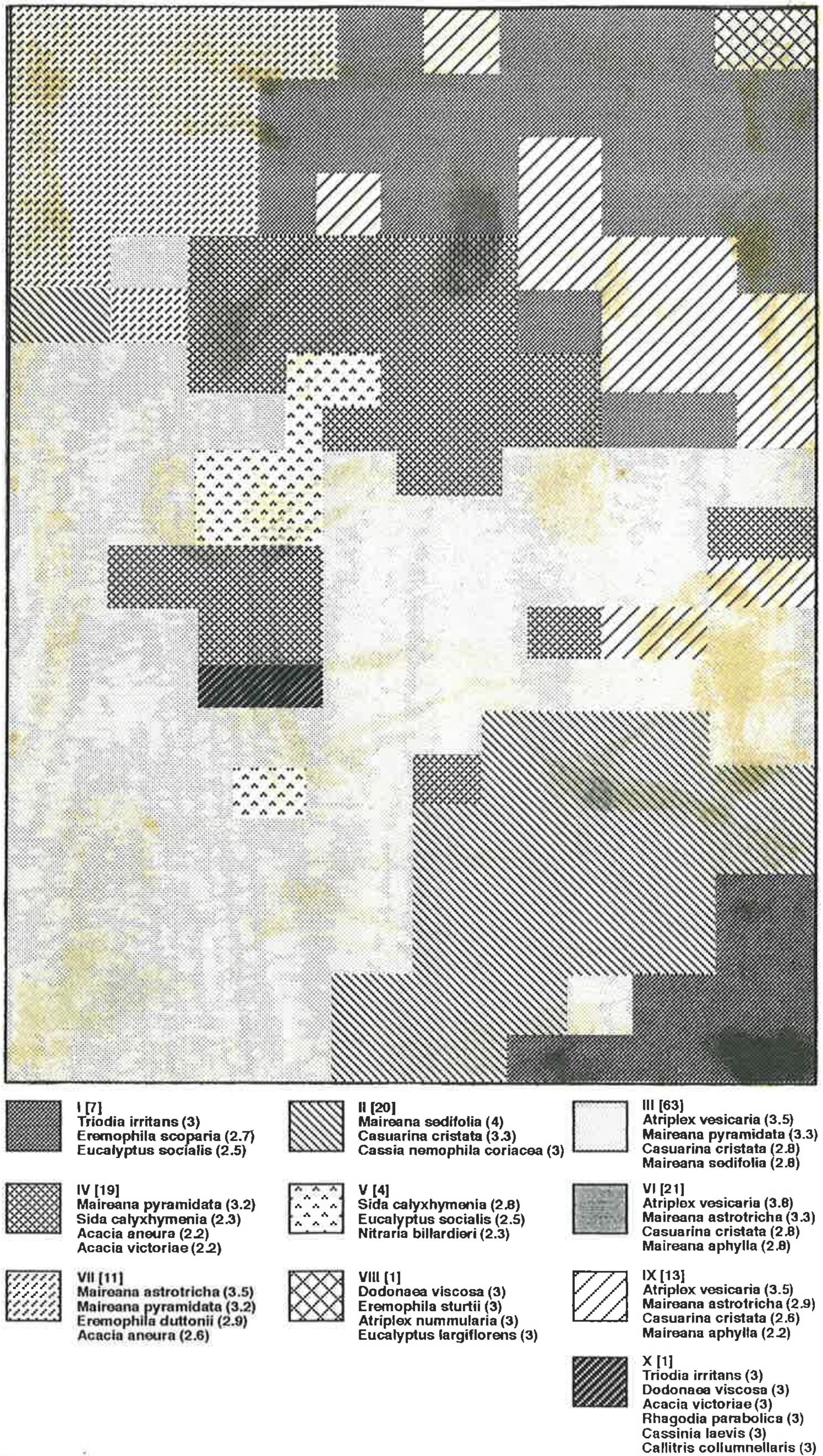


Figure 6.3

Floristic vegetation alliances of the study area in eastern South Australia, identified by Bray-Curtis (Czekanowski) -UPGMA clustering analysis. Figures in square brackets are the numbers of strip-transects assigned to each alliance. Figures in round brackets are the relative importance values of species, as shown in Table 6.2.

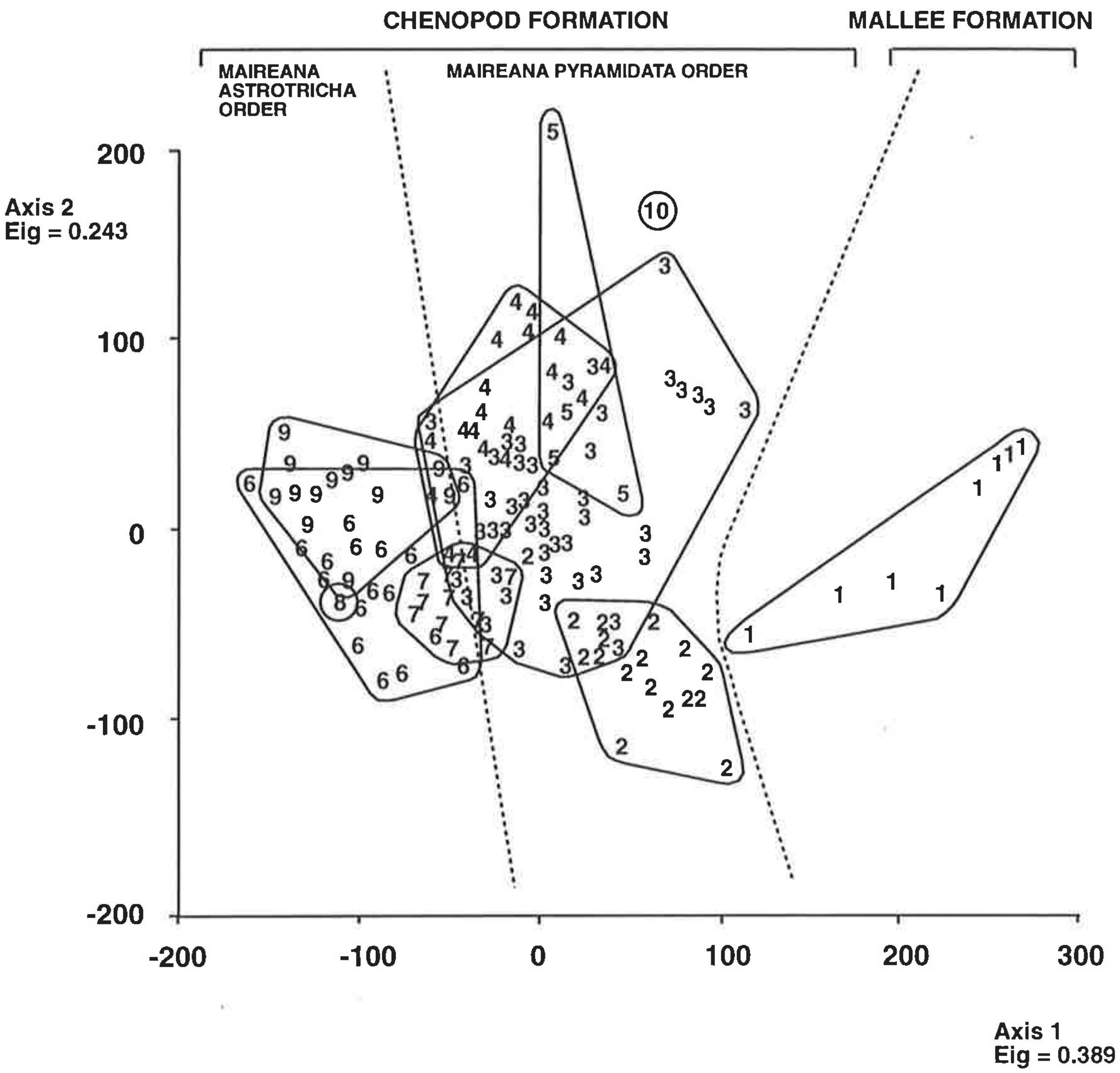


Figure 6.4

Detrended correspondence analysis (DCA) of full strip-census data, showing the degree of relationship between the 10 vegetation alliances identified by cluster analysis.

described by Kent and Coker (1992). Important indicator species were determined by using constancy values (Braun-Blanquet, 1928; Westhoff & van der Maarel, 1978), the percentage of samples of that particular alliance in which the species occurs. Only species with a constancy value of 75% or greater are included in the table. The average cover scores in the table are direct means of the raw cover scores for the species within the particular alliance. Although it is not strictly accurate to calculate mean cover in this way, since the cover scales are non-linear (Currall, 1987), the value obtained was considered indicative of the relative dominance of the species involved, which was the aim in this case. The species with high values in the table are the dominants of their particular alliance in the sense of Wood (1939); species which are constantly present, and occupy more cover on average than the others. These species which are important in defining the alliances (the ecological species group) are used to derive names for the alliances, which gives a precise, informative and adaptable nomenclature without implying any ranking (Mueller-Dombois & Ellenberg, 1974). Names were derived by using the indicator species with mean cover scores greater than 2. The only exception is the minor Alliance X, of only one site, with a number of species of equal importance. These names are listed with the mapped distributions of the vegetation alliances over the study area as shown in Figure 6.3.

As can be seen, Alliance I, containing a large number of unique species including *Eucalyptus cyanophylla/dumosa, Sclerolaena diacantha, Cratystylis conocephala, Codonocarpus cotinifolius, Acacia colletioides,* and *Grevillea huegelii* is floristically quite distinct from the remaining alliances (Table 6.2). This is reflected in its lone occupation of a major branch of the dendrogram (Figure 6.2). The eucalypts of Alliance I, *Eucalyptus socialis* and *E. gracilis*, (Table 6.2) display the "mallee" habit (see Chapter 5), which means that the alliance is not only floristically, but also physiognomically quite different to the rest, sufficient to rate ranking at the level of formation. It occupies the far south-east corner of the study area, so is also spatially separated from the remaining alliances. Two of the alliances, VIII and X, were both only represented by one site each, so are minor vegetation types. The first, VIII, is unique in containing significant populations of *Atriplex nummularia* and *Eucalyptus largiflorens* and occurs on Mulyungarie Station in the far north-east of the study area, where ephemeral lagoons are formed by the flooding out of the Olary Creek (Figure 4.2). However, it also contains *Maireana astrotricha*, which is why it appears on the same branch of the dendrogram as Alliances VI, VII and IX. The other minor alliance, X, occurs at the point of highest elevation, on Oulnina Park Station, and contains *Cassinia laevis*, *Callitris columnellaris* and *Eucalyptus intertexta,* none of which were encountered at other sampling points. It also contains *Triodia irritans*, which is why it is most closely linked to Alliance I on the dendrogram. The remaining alliances form a related group, dominated by various low shrubs of the family Chenopodiaceae, including *Maireana sedifolia*, *Atriplex vesicaria*, *M. pyramidata* and *M. astrotriicha* in various combinations. The above chenopod shrubs are physiognomically very similar, so these alliances have physiognomic affiliation and are consequently united at the rank of formation.

Following initial analysis, the outlying Alliance I, and minor Alliances VIII and X were removed and the remaining samples reanalysed as recommended by Austin (1979), Bridgewater (1989) and Dargie and El Demerdash (1991) (Figure 6.5). This takes into account the tendency of DCA to compress axes, and allows a reasonable scatter of the remaining samples. Figure 6.5 more clearly shows that DCA ordination tends to separate the chenopod formation into two groups, which is also evident from the cluster analysis (Figure 6.2) This split can be interpreted by referring to the dendrogram (Figure 6.2) and the floristic information in Table 6.2. Alliances VI, VII, VIII and IX share the same major branch of the dendrogram and are related to one another by all containing *Maireana astrotricha*. In fact, Alliances VI and IX share the same four species as dominants, in the same order, but less abundantly in Alliance IX. This is reflected by their close overlap on the DCA ordination (Figure 6.4). They must be separated by very minor edaphic changes, or possibly a grazing gradient. Rahel (1990) has observed that synchronous shifts in absolute abundances of species are difficult to detect when using abundance ranks, but the whole floristic approach and resolution of abundance in this study has obviously been sufficient to detect such shifts. Alliances II, III, IV and V are also grouped together, but by a different species in common, *Maireana pyramidata*. (Table 6.2) These two groups of

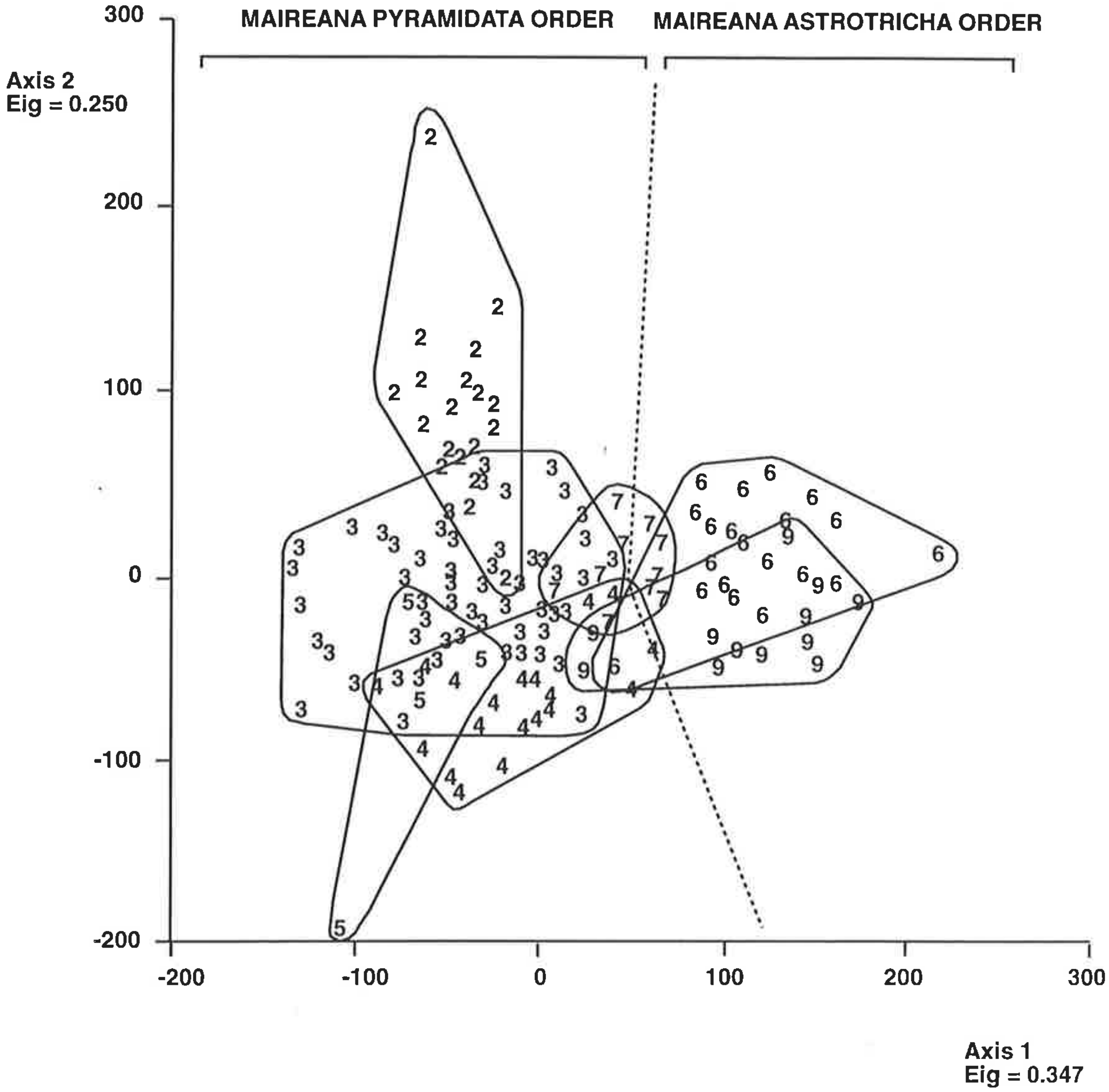


Figure 6.5

Detrended correspondence analysis (DCA) of strip-census data, with the mallee formation (Alliance I) and minor alliances VIII and X removed. Axis 1 separates the *Maireana astrotricha* order from the *Maireana pyramidata* order.

alliances, one dominated by *Maireana astrotricha* and one dominated by *M. pyramidata* occupy distinct regions, which can be seen by comparing the distribution map (Figure 6.3) with the topographic map (Figure 4.2). The *Maireana pyramidata* alliances occupy the western part of the Olary Range and the Murray Plains, while the the *M. astrotricha* alliances occupy the Frome Plains, with outliers in the eastern part of the ranges. These two groups of alliances are assigned the rank of order *sensu* (Westhoff & van der Maarel, 1978), which is somewhere above alliance, but below formation, since they are not physiognomically distinct, both forming low shrublands. Alliance VII forms an intermediate between the *M. astrotricha* and *M. pyramidata* orders, since it contains both species (see Table 6.2).

DISCUSSION

Mapping Techniques

The classification of alliances derived from strip-census survey proved to be at a suitable level of discrimination to allow useful broad-scale mapping. Most modern projects mapping broad-scale vegetation rely on the interpretation of aerial photographs (Beard & Webb, 1974), or satellite imagery (Laut *et al.*, 1977). This is followed by highly stratified ground-truthing to add floristic data to *a priori* -determined vegetation boundaries. The degree of resolution of these techniques is limited to separating vegetation types that can be identified remotely. It is therefore highly unlikely that vegetation types below the level of formation will be satisfactorily mapped by these techniques, because the differences are floristic rather than physiognomic. The advantage of the strip-census method of survey and mapping described here is that it combines the ability to survey very large areas rapidly, whilst retaining the accuracy and repeatability provided by the numerical methodology, and a high level of information content because of the floristic data collected. Finer detail can be inserted into the hierarchy at any other time, by conducting a more detailed site-based survey to determine individual vegetation associations (see Chapter 7). In fact, by using the pre-determined alliance boundaries to stratify the sampling technique, a much more efficient method of sampling for associations could be designed. It is therefore shown that multivariate techniques can be a very useful tool in the field of phytogeography which has remained methodologically underdeveloped in comparison to phytosociology (Andersson, 1988).

Comparison with Previous Vegetation Maps

The new vegetation map (Figure 6.3) shows some striking similarities with existing maps of broadscale vegetation (Chapter 2), and also some striking dissimilarities. The two major vegetation formations found, mallee woodlands and chenopod shrublands (Figure 6.3), correspond to the Euronotian and Eremian provinces of Tate (1880; 1887; 1890) and Diels (1906) described in Chapter 5. Their boundaries also agree reasonably well to those of the mallee and mulga of Prescott (1929). The appearance of *Acacia aneura* as a dominant in Prescott's classification is caused by the fact that he gave mulga more importance as a taller species. It is also possible that death and lack of recruitment have caused *Acacia aneura* to become less prominent in the landscape (see Chapter 9). This boundary also corresponds to the major floristic discontinuity identified by Noy-Meir (1971) between a southern temperate mallee formation (Euronotian), and an Eremaean formation for eastern South Australia, north-western Victoria and south-western New South Wales.

The maps of Wood (1937), Beadle (1948) and especially Specht (1972), as shown in Chapter 5, are much more accurate. They are based on the relevant topography and soil maps respectively. Specht's vegetation boundaries (Figure 5.5) are based on Northcote's soil maps (Northcote, 1968); as described in Chapter 4, so a strong resemblance to the new vegetation map (Figure 6.3) has probably occurred wherever a major change in soil type has been sufficient to cause a corresponding change in vegetation type. It is therefore likely that topographic and edaphic variables are the strongest influences on the vegetation of the area. These relationships are explored in Chapter 8. Similarly, Specht's Formation 7, a low shrubland of *Atriplex rhagodiodes* is equivalent to Alliance VIII, containing *Atriplex nummularia* among others. *Atriplex rhagodioides*~~s~~ is very closely related to *A.*

nummularia, and they are probably both variants of a polymorphic species complex (Jessop & Toelken, 1986)). Specht's *A. rhagodioides* is highly likely to be a misidentification of *A. nummularia*, since true *A. rhagodioides* only occurs along the River Murray (A. Sparrow pers. comm.).

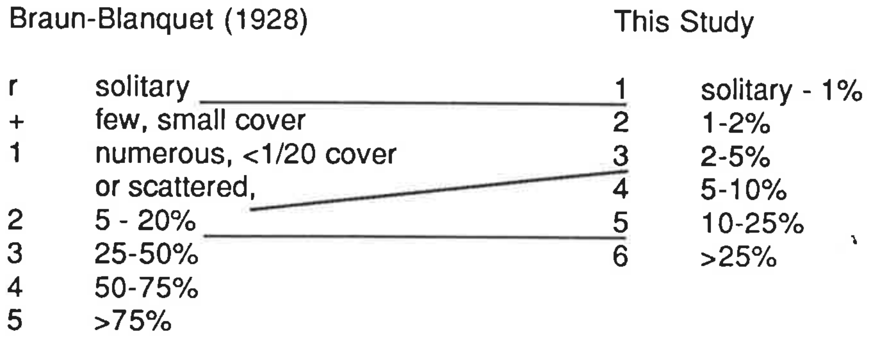
One of the limitations of a primarily physiognomic classification is that the habit of the structural dominant can be given too much emphasis, resulting in failure to delineate quite major floristic disjunctions. This is shown by the fact that each of Specht's major structural Formations shown in Figure 5.5, low shrubland of *Atriplex vesicaria* and *Maireana sedifolia*, and low shrubland of *Maireana astrotricha*, contain within themselves floristic entities worthy of distinguishing at the level of alliance. The former contains Alliances II, III, IV, V and X, and the latter VI, VIII and IX. As a further example, Specht's low woodland vegetation types,*Casuarina cristata* and *Myoporum platycarpum*, are united into one structural formation in Specht's classification because they both tend to form sparse low open woodlands, whereas they are actually floristically quite distinct, and fall into the separate Alliances II and III in this study. Conversely, Specht's formation of*Casuarina* or *Myoporum* low woodlands with chenopod understorey and chenopod shrubland formation actually have minimal floristic differences. Both types contain *Casuarina cristata*, *Atriplex vesicaria*, *Maireana pyramidata*, *M. sedifolia*, *Myoporum platycarpum* and *Heterodendrum oleifolium*, so are included within one Floristic Alliance III on the new map. This amalgamation illustrates how a minor change in abundance of one upper storey structural dominant species (in this case *Myoporum platycarpum*) can result in a rather artificial demarcation which has little floristic meaning. These examples show how a physiognomic classification not only creates artificial boundaries, but can also fail to detect real floristic differences.

CONCLUSIONS

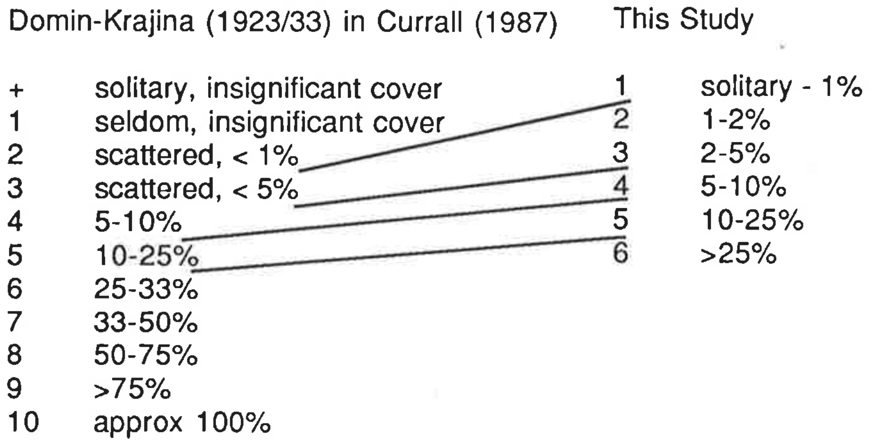
The broadscale survey method of strip-census sampling points arranged on a system of transects proved to be most rapid and efficient in producing a vegetation classification

Table 7.1

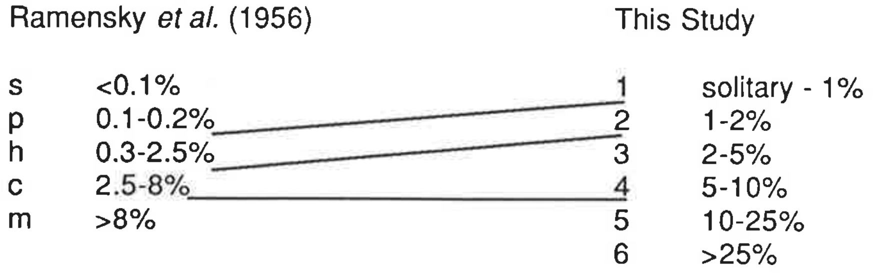
Comparison of the cover scale used in this study with other scales existing in the literature.



Braun-Blanquet (1928)		This Study	
r	solitary	1	solitary - 1%
+	few, small cover	2	1-2%
1	numerous, <1/20 cover	3	2-5%
	or scattered,	4	5-10%
2	5 - 20%	5	10-25%
3	25-50%	6	>25%
4	50-75%		
5	>75%		



Domin-Krajina (1923/33) in Currall (1987)		This Study	
+	solitary, insignificant cover	1	solitary - 1%
1	seldom, insignificant cover	2	1-2%
2	scattered, < 1%	3	2-5%
3	scattered, < 5%	4	5-10%
4	5-10%	5	10-25%
5	10-25%	6	>25%
6	25-33%		
7	33-50%		
8	50-75%		
9	>75%		
10	approx 100%		



Ramensky *et al.* (1956)		This Study	
s	<0.1%	1	solitary - 1%
p	0.1-0.2%	2	1-2%
h	0.3-2.5%	3	2-5%
c	2.5-8%	4	5-10%
m	>8%	5	10-25%
		6	>25%

which, while still using mapping units which could be compared to previous classifications, showed a much greater degree of floristic accuracy and information content compared with existing methods. The technique of broadscale survey and mapping of floristic alliances proved adequate for detecting a major phytogeographic boundary at the level of formation, the one dividing the mallee scrublands from the chenopod shrublands. Another relatively major discontinuity assigned the rank of vegetation order was detected separating the northern plains chenopod shrublands with *Maireana astrotricha* from the higher elevation and southern ones with *M. pyramidata*.

This technique would be very useful for describing vegetation in other arid and semi-arid regions of the world where very large areas of vegetation remain undescribed and large populations mean that the vegetation is under extreme pressure from the activities of humans and their livestock. In these regions capital for more expensive techniques of remote-sensing, mapping and monitoring are usually not available. This is particularly the case in East and Central Africa and the semi-arid and arid zones of Asia (Naveh, 1989; Woldu & Backéus, 1991).

CHAPTER 7:
PERENNIAL VEGETATION PATTERNS - ASSOCIATIONS

INTRODUCTION

In the previous chapter, vegetation was classified to the level of alliance, using a broadscale method of data collection by vehicle strip transects, which proved extremely useful for mapping. However, it is widely recognized that detection of patterns in communities is dependent on the scale of observation (Wiegleb, 1989; Reed *et al.*, 1993), and that patterns should be analyzed and interpreted at more than one scale (Rahel, 1990). If similar patterns are detected at different scales of exploration, the patterns can intuitively be accepted as robust (Wiegleb, 1989; Reed *et al.*, 1993). For this reason, a study at a smaller scale seemed appropriate, in order to verify the patterns already identified, and to detect patterns occurring at levels below alliance. Such groups (associations) are also more likely to correspond to environmental information to give an indication of the variables affecting vegetation distribution at a finer scale.

The aims of this chapter are to:

Develop a rapid and efficient field technique for providing a numerical classification of the major floristic associations in the form of a list of key species

To compare this classification with the classification of vegetation alliances produced in Chapter 4, and ascertain whether it is possible to link the two classifications for maximum content.of floristic information

METHODS

Sampling strategy

Sampling was carried out simultaneously with the transect survey described in Chapter 6,[1] and considerations of the overall design of the survey are discussed there. A nested sampling methodology as described below was found to be effective in combining data-

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[1] All transects and sites were surveyed between April and October of 1989.

collection at different scales. Ramensky found that at least 8 to 10 sites should be included for each type of locality (Sobolev & Utekhin, 1978) in order to be able to discriminate between vegetation associations. The grid frequency of 10 by 20 km described in Chapter 6 was found to sample localites at about that frequency or greater, except for the rarer vegetation types. Plots were objectively placed 50 m from the track (in order to avoid disturbance effects), at the point where the track came closest to the theoretical grid point.

It was observed in the field that plant communities tended to form mosaics in the landscape, depending on local topography and soil conditions. This phenomenon has been previously described as the "edaphic complex" by Crocker & Wood (, 1939; 1946). These edaphic complexes were commonly encountered within the Olary Range, where a wide variety of geology, topography and soils supported a correspondingly wide variety of vegetation types. For this reason, a multiple sampling technique was carried out. If the theoretical grid point fell within such an area of mosaic vegetation, extra samples were taken within each of the different vegetation types observed within short hiking distance (0.5 km) of the original sampling point. By this method, a regular sampling strategy was retained, although there was some subjectivity in selecting the extra sites.

The plots are based on the relevè system for sampling vegetation associations developed by Braun-Blanquet (1913; 1928) with the following exception. The traditional technique was to choose relevés carefully to represent stands, deliberately excluding "mixed, incomplete, or unstable" stands (Mueller-Dombois & Ellenberg, 1974; Westhoff & van der Maarel, 1978), since intermediates were not recognized as important (Whittaker, 1978b; Kent & Coker, 1992). However, this approach is usually no longer followed, because the recognition of distinct stands pre-supposes the occurrence of distinct discontinuities, and ignores the occurrence of gradients (Westhoff & van der Maarel, 1978). Since the data from this survey were to be subject to ordination as well as classification, intermediate types are essential in explaining the continuum aspects of vegetation. Therefore, there was no attempt to place the plots in homogeneous or representative areas. A regular or random sampling strategy is also important from the point of view of the proposed numerical analysis because many ordination procedures do not perform well unless the environmental continuum is regularly and evenly sampled (Minchin, 1987). Consequently it is now usually recommended that locations should be determined by a grid or other systematic method in order to minimize bias by purposely ignoring the nature of the vegetation and topography (Brower *et al.*, 1990).

When continuous vegetation is being sampled, an arbitrary sampling unit has to be chosen, bearing in mind that the results are influenced by the size and shape of the sampling unit chosen (Greig-Smith, 1983; Kershaw & Looney, 1985; Ludwig & Reynolds, 1988). Small plots are more likely to be useful in detecting small-scale vegetation patterns, but the size required to sample variation adequately within a vegetation type increases as the scale, heterogeneity of patches, and richness increases (Kenkel & Podani, 1991). Therefore, it is best to utilize the largest plot size possible, given the restraints of sampling time and effort (Kenkel & Podani, 1991). Large plots are used if the species are large and thinly scattered, and small if species are small and numerous, to make counting easier. Ramensky believed that 100 m^2 for meadows, 1000 m^2 for deserts and 2500 m^2 for forests were appropriate sizes (Sobolev & Utekhin, 1978). Followers of the Braun-Blanquet approach recommended a minimum size of 50 - 100 m^2 for steppe vegetation, although most of the methods were developed for mesic areas (Westhoff & van der Maarel, 1978).

Plot shapes were traditionally square (Brower *et al.*, 1990), but an advantage of rectangular plots is that they tend to level out small variances within the stand by intersecting patches within mosaic vegetation (Kershaw & Looney, 1985; Kenkel & Podani, 1991). Rectangular plots were often used by followers of Braun-Blanquet (Westhoff & van der Maarel, 1978), and Whittaker (1978b) found rectangular plots suitable for ordination analysis of a broad range of vegetation types, including forest, woodland, grassland and desert. Therefore, the plots used were rectangular. The size, 50 by 20 m (0.1 ha or 1000 m^2) was derived by performing preliminary species-area curves, as recommended by Braun-Blanquet (1928) and Mueller-Dombois and Ellenberg (1974). This gave the same size plot as independently recommended by Ramensky (Sobolev & Utekhin, 1978) and Whittaker (Whittaker, 1978b), indicating that the Russian and American vegetation must contain similar patterns of species distribution as that of South Australia. Although this minimum-area technique is inappropriate for probabilistic sampling, it is still recommended for phytosociology, when the data are to be subjected to classification and ordination (Kenkel *et al.*, 1989). Plots were temporarily marked out by laying two tapes, 50 m and 20 m long, at right angles across one another, and examining the area thus delineated.[1]

The determination of plant species within each plot was as complete and accurate as possible, following the recommendation of Ramensky (Sobolev & Utekhin, 1978) and Kent and Coker (1992). All vascular plants, including phanerogams or seed-plants (gymnosperms and angiosperms) and pteridophytes (ferns) were recorded as recommended by Westhoff and van der Maarel (1978) and Williams & Lambert (Williams & Lambert, 1958). This method also follows that of Whittaker (1978b), who found that the most commonly recorded plants from land communities were vascular plants. A complete species list was prepared at each site, and any plants which were unknown or could not be identified reliably in the field were taken as specimens and identified later at the State Herbarium of South Australia. A complete list of all plant species recorded is included in Appendix 1.

Estimation of percentage cover

Selection of a particular abundance measure (absolute abundance, abundance rankings or presence/absence) depends on the viewpoint and scale of observation (Rahel, 1990). Because of the finer scale of vegetation being examined, a more powerful estimate of relative abundance (such as absolute density, cover, or frequency (Greig-Smith, 1983)) than that used in the strip-census survey (Chapter 6) was required. This choice was largely governed by the size of the study area, and time available to carry out the sampling. Sampling must maximize the amount of information for the amount of effort and time expended (Greig-Smith, 1983). In a highly heterogeneous environment such as that of the

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[1] Each plot was searched in a set pattern by zigzagging first down side of the plot, then crossing the centre tape and zigzagging down the other side. This ensured that equal time and effort was spent in searching each plot.

Olary Ranges, it is better to measure a larger number of sites by estimate than a small number very accurately (Mueller-Dombois & Ellenberg, 1974).

An estimated determination of coverage, the proportion of ground occupied by perpendicular projection onto it of the aerial parts of individuals of the species under consideration (Greig-Smith, 1983; Kershaw & Looney, 1985; Brower *et al.*, 1990) was used, because it can be rapidly determined. Although estimation of cover by eye can result in bias towards conspicuous, species in flower, or species known to the observer (Greig-Smith, 1983), these problems may have been over-emphasized in the past (Kent & Coker, 1992), and consistent results can be obtained, especially if the estimations are carried out by one person experienced in vegetation work (Greig-Smith, 1983). These slight disadvantages are outweighed by the advantage of simplicity and resulting rapid determination (Pakarinen, 1984; Kent & Coker, 1992), an important consideration since there were often over 50 species per site. At the same time, the method is not so simple as to be superficial (Mueller-Dombois & Ellenberg, 1974). Estimation of cover was the method preferred by Ramensky (Sobolev & Utekhin, 1978), for the above reasons. Cover scores obtained in this fashion can be used as an indication of species dominance if dominant plants are defined as those with the highest grade of cover or density (Greig-Smith, 1983). This definition of dominance does not imply any degree of control by the dominants over the other species; nor does a dominant have to be the tallest, light-intercepting species (Greig-Smith, 1983.)

Raw estimates of percentage cover were converted to scores according to an ordinal cover-scale (Table 7.1), based on that of Braun-Blanquet (1928), with adjustments similar to those of Domin (1923) [as cited and used by Krajina (1933)] and Ramensky *et al.* (1956). The following modifications were made to the Braun-Blanquet scale. Because semi-arid and arid vegetation is so sparse, cover scores of 25% or greater rarely occur. Therefore the higher scores (3, 4 & 5) of the Braun-Blanquet scale were combined into one level, 6, for all cover over 25% which is similar to the Ramensky scale, which combines all cover over 8% into one ranking. The Braun-Blanquet ranking of 2 (5 - 25%) was split into two separate ranks, 4 (5 - 10%), and 5 (10 - 25%) in order to be able to better differentiate sparse vegetation. This resulted in the upper scores 4, 5, and 6 being exactly equivalent to the 4, 5 and 6 of the Domin-Krajina scale. The Braun-Blanquet ranks of + (few, small cover) and 1 (numerous, < 1/20 cover) were found to be too poorly defined to distinguish, and were combined into level 2. The r (solitary) rating became level 1. Species occurring outside the plot, but nearby in the same type of community were also included in level 1. This was done to minimise the chances of under-estimating the occurrence of very sparsely distributed species. The resulting scale has the greatest degree of discrimination at lower percentage cover, making it more suitable for arid and semi-arid envionrments with sparse vegetation. Species were listed first, whilst walking around the plot, then abundances were estimated and assigned all at once from a vantage point near the centre of the plot, as described by Mueller-Dombois and Ellenberg (1974).

ANALYSIS METHODS

Cluster analysis

Clustering analysis was performed by the same protocol as described in Chapter 6, using Czekanowski (Bray-Curtis) distance measure and flexible UPGMA linkage, both available on the computer package NTP (Belbin *et al.*, 1984). All available relevés were analysed together, as recommended by Braun-Blanquet (1928) and followed by Schaminée *et al.* (1993). A decision was made to split the association dendrogram Figure 3.2) at the 65% level of dissimilarity, which gave a tractable number of natural groups.

Indirect ordination

In order to obtain an alternative view of the floristic relationships between the associations, the data were ordinated by DCA, using detrending by second-order polynomials, (Ter Braak, 1988b) and available in the computer package CANOCO (Ter Braak, 1988a), also as described in Chapter 6. The dendrogram (Figure 7.1) and initial DCA (Figure 7.3) revealed two very distinct floristic discontinuities because two of the associations had very few species in common with the remaining associations. This caused extreme compression of the two main axes, and so, as recommended by Dargie and El Demerdash (1991) and Austin (1979), these two associations were removed from the data-set, and a further DCA analysis performed.

Chi-square comparisons of groupings

Since the groupings of associations were derived from a totally different data set to that used to derive the floristic alliances (Chapter 6), it was of interest to ascertain if there was any relationship between the two classifications. The groupings of alliances and associations can be sorted into a contingency table for testing, where the null hypothesis is that the frequencies of observations of association type are independent of the frequency of alliance type. The most appropriate procedure for testing this hypothesis is the chi-square statistic (Zar, 1984). Although chi-square analysis does not assign statistical significance to individual cells of a contingency table, it is possible to derive a post-hoc estimation of the relative contribution of individual cells to the final chi-square value (Feldman & Gagnon, 1988). Chi-square calculations and post-hoc estimations were carried out using the statistical package Statview (Feldman & Gagnon, 1988)..

RESULTS

Vegetation associations

As shown by the dendrogram (Figure 7.1) there are 4 major associations, each with more than 20 sites (D, E, H. and N), 9 less widespread associations with fewer than 10 sites each (A, B, C, F, I, L, M, O and Q), and 5 minor associations, each represented by only one site (G, J, K, P and R), giving 18 associations in total. The distributions of the associations over the study area are shown in Figure 7.2. The map of associations shows a much more complex mosaic pattern than the map of alliances (Figure 6.3). As expected, this is particularly obvious towards the centre of the study area, the area of high elevation

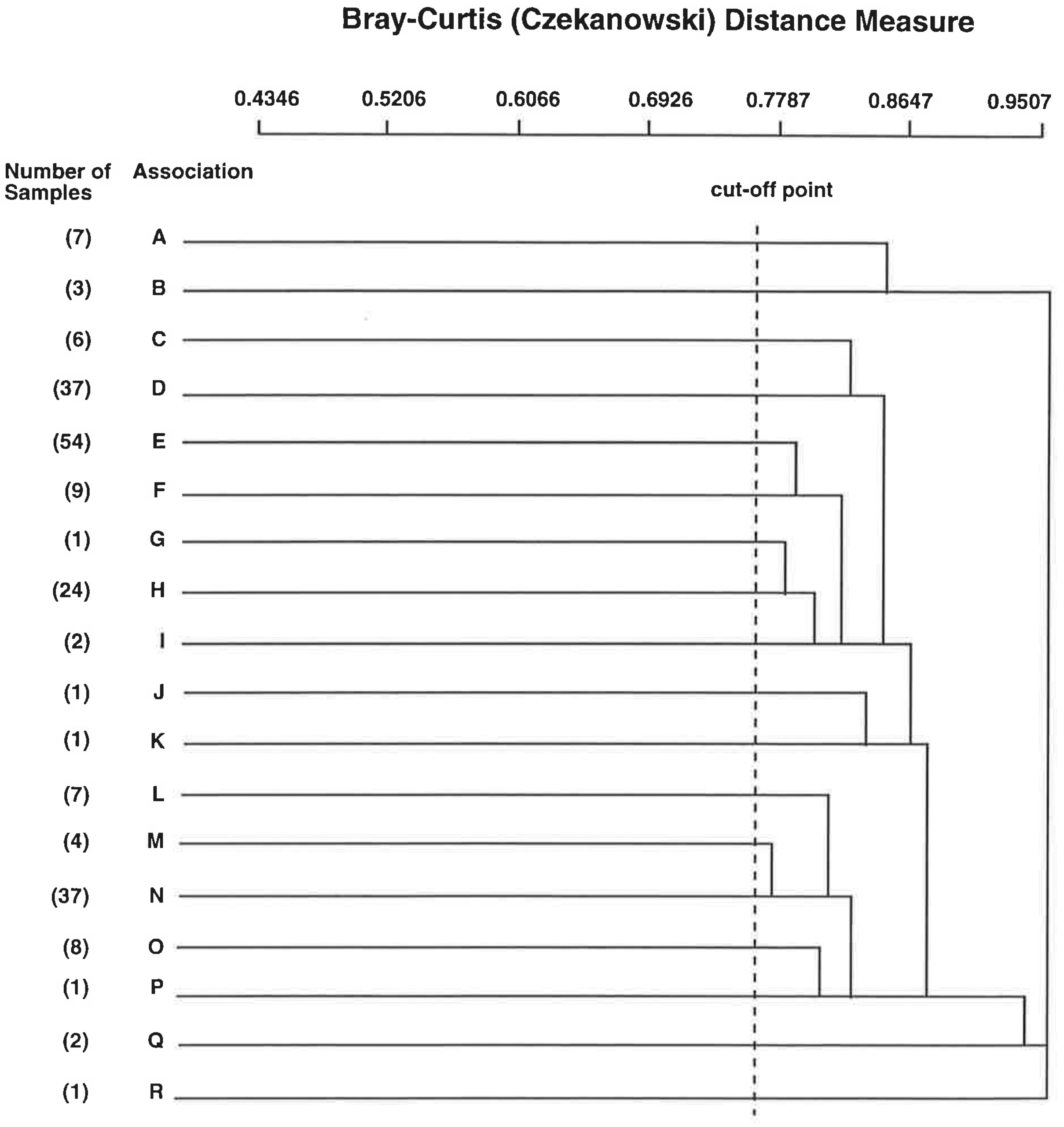


Figure 7.1

Summary dendrogram of floristic associations of the study area in eastern South Australia. Clustering was performed by Bray-Curtis (Czekanowski) - UPGMA.

LEGEND

≋ **A [7]**
Triodia irritans (3)
Eucalyptus socialis (2.4)
Eucalyptus cyanophylla (2)

▦ **B [3]**
Enchylaena tomentosa (1.3)
Ptilotus exaltatus (1)
Rhagodia parabolica (1)

▩ **C [6]**
Enchylaena tomentosa (1)
Ptilotus exaltatus (1)
Sclerolaena diacantha (1)
Cassia nemophila platypoda (1)
Eremophila sturtii (1)

▨ **D [37]**
Maireana sedifolia (3)
Casuarina cristata (2.7)
Sclerolaena obliquicuspis (1.1)

▒ **E [54]**
Maireana pyramidata (2.2)
Sclerolaena obliquicuspis (1.8)

░ **F [9]**
Maireana pyramidata (2)

▤ **G [1]**
Atriplex vesicaria (2)
Casuarina cristata (1)
Maireana pyramidata (1)
Callitris columnellaris (1)

▤ **H [24]**
Sida calyxhymenia (2)
Ptilotus obovatus (1.8)
Solanum ellipticum (1)
Enchylaena tomentosa (1)

⁘ **I [2]**
Sida calyxhymenia (1.5)

⁘ **J [1]**
Rhagodia spinescens (2)
Sida intricata (2)
Pimelea microphylla (1)
Santalum lanceolatum (1)

▨ **K [1]**
Eucalyptus socialis (1)
Atriplex vesicaria (1)
Eucalyptus gracilis (1)
Eucalyptus porosa (1)

▩ **L [7]**
Maireana astrotricha (1.5)
Rhagodia spinescens (1)

▨ **M [4]**
Atriplex vesicaria (2.3)
Cassia nemophila coriacea (1)
Eremophila longifolia (1)
Eremophila sturtii (1)

▨ **N [37]**
Atriplex vesicaria (2.8)
Maireana astrotricha (2.5)

▤ **O [8]**
Schlerochlamys brachyptera (1)
Sclerolaena ventricosa (1)

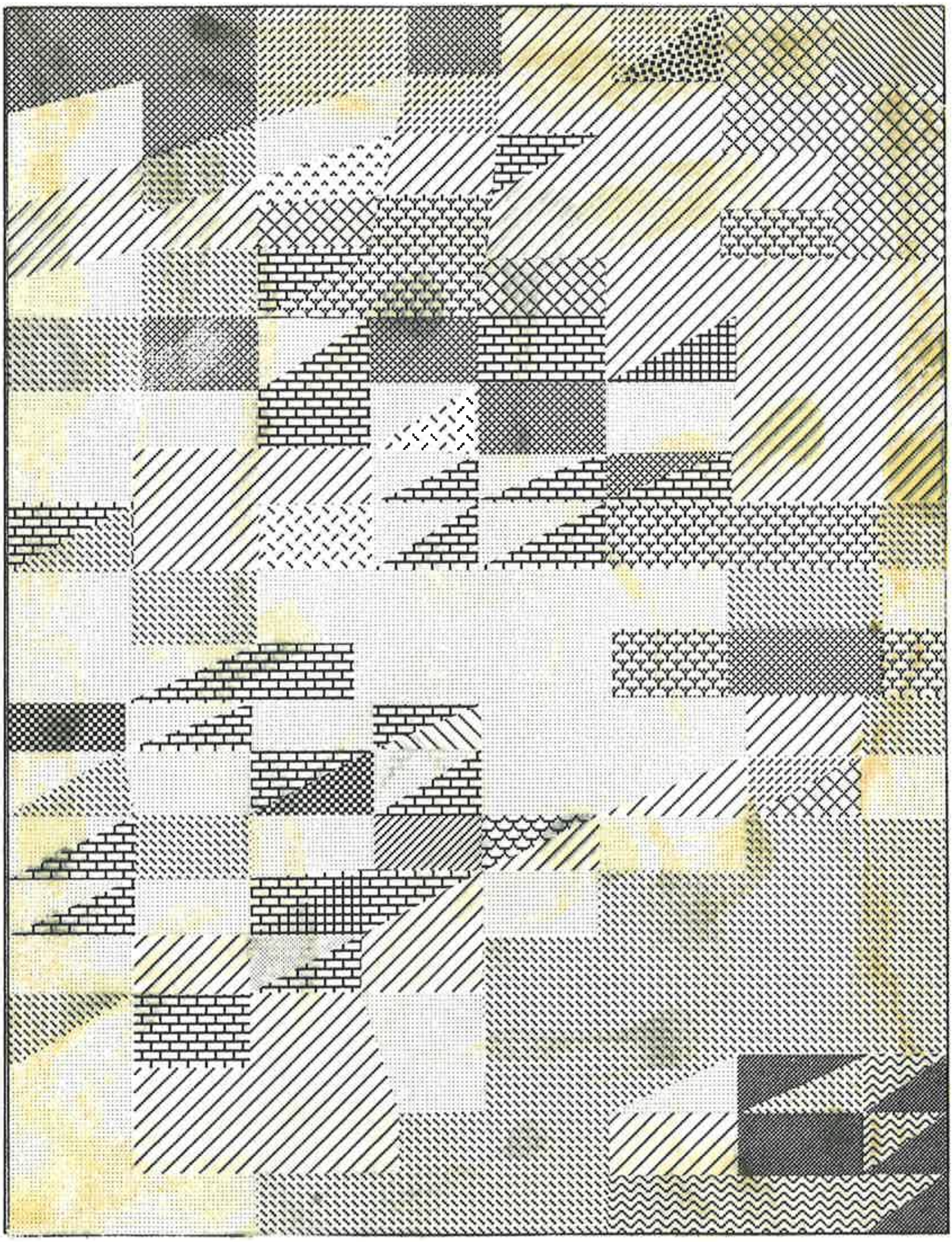
▧ **P [1]**
Dodonaea viscosa angustissima (5)
Heterodendrum oleifolium (1)

▦ **Q [1]**
Eucalyptus camaldulensis (3)
Lycium ferocissimum (1)

▒ **R [1]**
Eragrostis australasica (3)
Eragrostis leptocarpa (2)

Figure 7.2 (facing page)

Floristic vegetation associations of the study area, identified by Bray-Curtis (Czekanowski) - UPGMA clustering analysis. Figures in square brackets are the numbers of sites assigned to each association. Figures in round brackets are the relative importance values of species, as shown in Table 7.2.



associated with the Olary Range, because of the increased local variation in topography and soils.

Several associations are floristically quite distinct, as shown by the dendrogram (Figure 7.1), and synoptic table of indicator species (Table 7.2). Association A (*Triodia irritans - Eucalyptus socialis - E. cyanophylla*) is highly correlated with Alliance I, the mallee formation (Table 7.3). Association B occurs at very high elevation in the ranges, and is floristically most similar to A, although they are spatially quite disjunct from one another. Association B appears to be an outlying refuge of sclerophyllous Euronotian vegetation as postulated by Crocker and Wood (1947). Association R is a minor (single site) type, dominated by *Eragrostis australasica*, and found in ephemeral swamps where water floods down from the ranges and ponds after rain for months at a time. Q is another distinctive minor vegetation type, occurring in the creeks draining the ranges. It is characterized by *Eucalyptus camaldulensis* and *Lycium ferocissimum*, an exotic woody species.

The remaining associations form two sub-branches of the remaining major branch. The Chi-square analysis (Table 7.3) shows that these two sub-branches are correlated to the two orders within the chenopod formation identified in Chapter 6. Associations C to K occur within the Alliances II to V of the *Maireana pyramidata* order, while Associations L to P occur largely within Alliances VI to IX of the *Maireana astrotricha* order, though N and O overlap somewhat into the *Maireana pyramidata* order. It is interesting to note that only Associations E, F and G contain *M. pyramidata* as an indicator species, and Associations L and N *M. astrotricha*, because the classifications are based on the whole floristics, not just the cover dominants. The synoptic table is much more discontinuous than that produced for alliances (Table 6.2). This is because the sampling area was much smaller and edaphic and local topographic variables play a much greater role in determining species distributions at this level.

The results of the DCA ordination are displayed in Figures 7.3 and 7.4. As can be seen from the initial ordination (Figure 7.3), Associations A (mallee) and R (swamp) are completely discontinuous floristically from the remaining 16 types. The compression thus

Table 7.2

Synoptic table of indicator species of floristic associations from site-based survey data. Only species with constancy values of 75% (occur in 75% of sites of that association type) or more are shown. The figures in the table are importance values, derived from the means score achieved for that species in that alliance and omitting the few sites from which it was absent. Asterisks indicate introduced species.

VEG ASSOCIATION	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
Frequency (No of Sites)	7	3	6	37	54	9	1	24	2	1	1	7	4	37	8	1	2	1
Triodia irritans	3.4																	
Eucalyptus cyanophylla	2.4																	
Eucalyptus socialis	2.4										1							
Acacia burkittii	1.2																	
Halgania cyanea	1.2																	
Sclerolaena parviflora	1																	
Enchylaena tomentosa		1.3	1				1	1										
Ptilotus exaltatus		1	1															
Rhagodia parabolica		1																
Sclerolaena diacantha			1.5															
Cassia nemophila platypoda			1.3															
Eremophila sturtii			1															
Maireana sedifolia				3.1														
Casuarina cristata				2.7			1											
Sclerolaena obliquicuspis				1.1	1.8													
Maireana pyramidata					2.2	2	1											
Callitris collumellaris							1											
Heterodendrum oleifolium							1			1						1		
Pittosporum phylliraeoides							1											
Maireana brevifolia							1											
Cassinia laevis							1											
Ptilotus obovatus							1	1.8										
Einadia nutans							1											
Cheilanthes tenuifolia							1											
Cheilanthes lasiophylla							1											
*Marrubium vulgare							1											
Atriplex vesicaria							2				1		2.3	2.8				
Sida calyxhymenia							1	2	1.5									
Solanum ellipticum								1										
Rhagodia spinescens										2		1						
Sida intricata										2								
Pimelea microcephala										1								
Santalum lanceolatum										1								
Eucalyptus gracilis											1							
Eucalyptus porosa											1							
Maireana astrotricha												1.5		2.5				
Cassia nemophila coriacea													1					
Eremophila longifolia													1					
Eremophila sturtii													1					1
Sclerochlamys brachyptera															1.7			
Sclerolaena ventricosa															1.5			
Dodonaea viscosa angustissima																5		
Eucalyptus camaldulensis																	3	
*Lycium ferocissimum																	1.5	
Eragrostis australasica																		3
Maireana aphylla																		1
Eragrostis leptocarpa																		2
Eleocharis pallens																		1
Fimbristylis dichotoma																		1

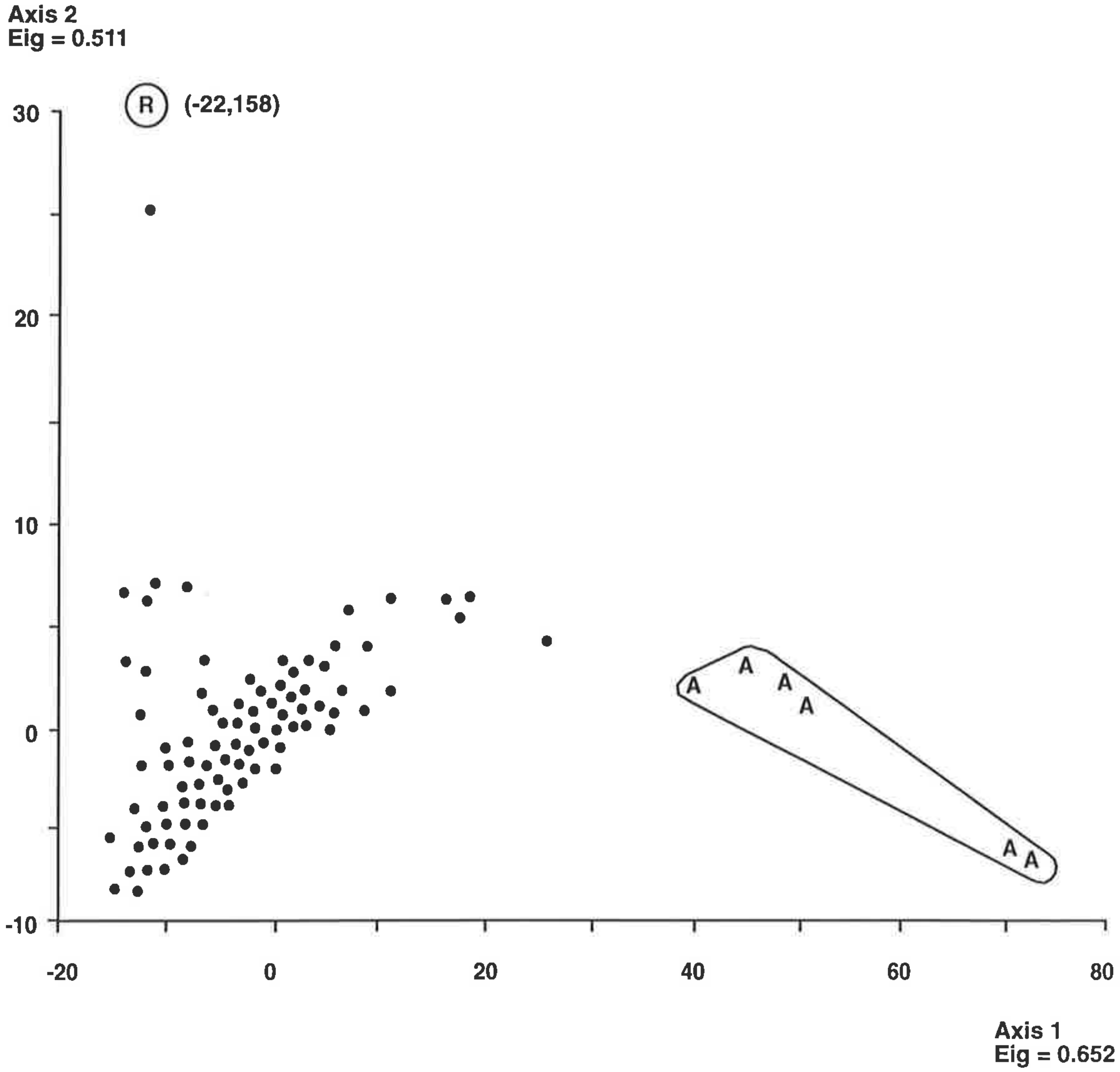


Figure 7.3

Detrended correspondence analysis (DCA) of floristic data from all 205 sites.

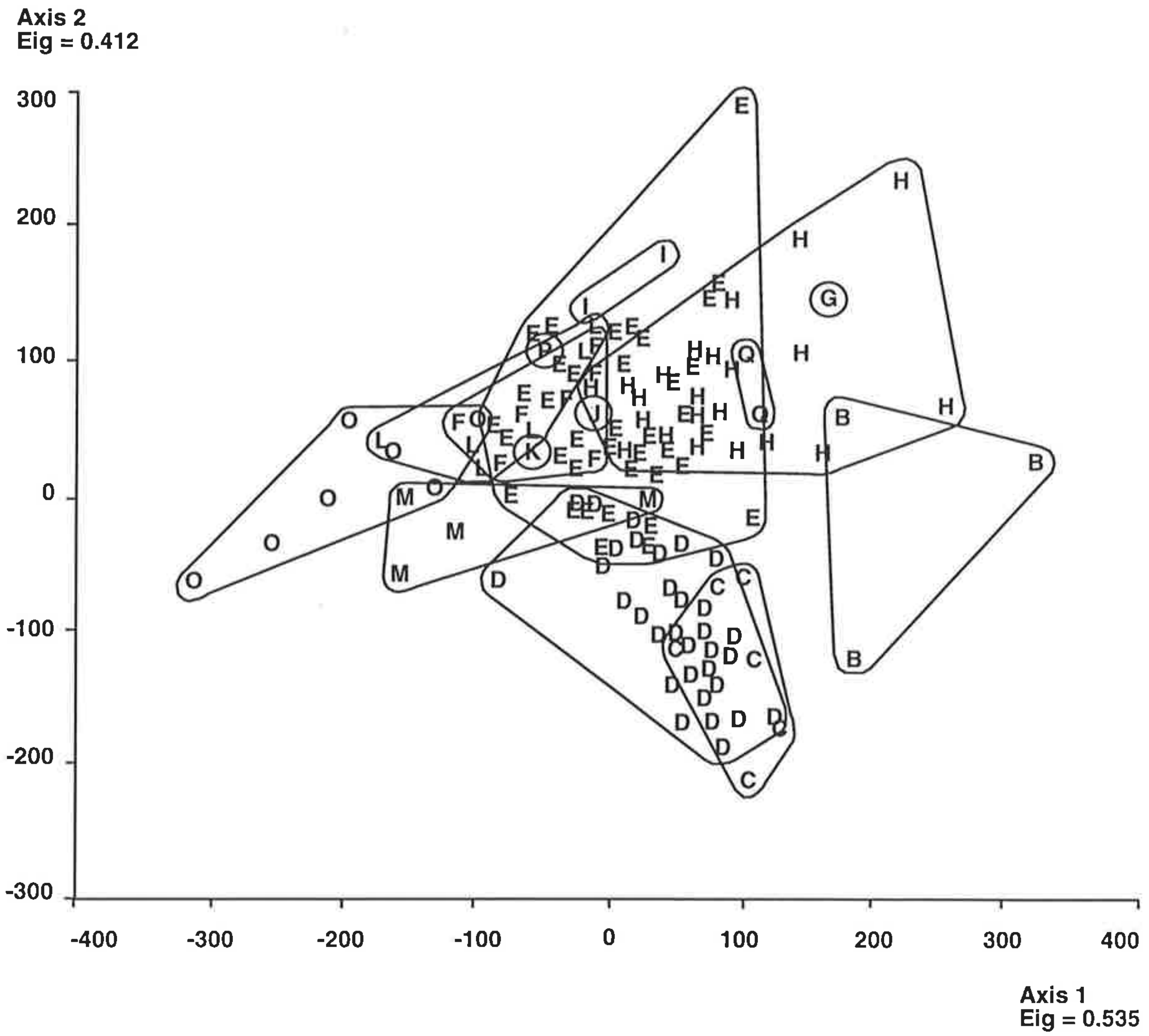


Figure 7.4

Detrended correspondence analysis (DCA) of floristic data, omitting sites of Vegetation Associations A and R.

Table 7.3

Chi-square contingency table ($X^2 = 768.339$, df = 153, $p = 0.0001$), of the distribution of vegetation associations (A - R) across vegetation alliances (I - X). Matches with post-hoc cell contributions ≥ 2 indicating a high level of contribution to the final chi-square are shown in bold type.

VEGETATION ALLIANCE	I	II	III	IV	V	VI	VII	VIII	IX	X
VEGETATION ASSOCIATION										
A	**7**	0	0	0	0	0	0	0	0	0
B	0	0	2	0	0	0	0	0	0	**1**
C	**5**	1	0	0	0	0	0	0	0	0
D	2	**23**	11	0	0	0	1	0	0	0
E	0	3	**32**	12	3	1	3	0	0	0
F	0	0	1	3	0	1	**4**	0	0	0
G	0	**1**	0	0	0	0	0	0	0	0
H	0	0	9	13	0	1	0	0	0	1
I	0	0	0	0	**2**	0	0	0	0	0
J	0	0	0	0	0	**1**	0	0	0	0
K	0	0	1	0	0	0	0	0	0	0
L	0	0	1	1	0	**5**	0	0	0	0
M	0	0	1	0	0	**2**	1	0	0	0
N	0	0	14	0	0	**10**	2	0	**11**	0
O	0	0	3	2	0	1	0	0	**2**	0
P	0	0	0	0	0	0	0	**1**	0	0
Q	0	0	0	0	**1**	1	0	0	0	0
R	0	0	0	0	0	**1**	0	0	0	0

caused in the major axes was relieved by dropping these two types from further analysis (Figure 7.4), leaving the remaining 16 associations, which are floristically quite continuous. The first axis of the second ordination (Figure 7.4) ranges from Association B (*Enchylaena tomentosa - Ptilotus obovatus - Rhagodia spinescens),* a high elevation type (Figure 7.2), to O (*Sclerochlamys brachyptera - Sclerolaena ventricosa*), a low elevation, clay-pan type common on the alluvial soils of the plains (Figure 7.2). It is therefore expected that Axis 1 corresponds to an elevation or run-on/run-off gradient. Axis 2 has Association E, (*Maireana pyramidata - Sclerolaena obliquicuspis*) at one end and C (*Enchylaena tomentosa - Ptilotus exaltatus - Sclerolaena diacantha* etc) at the other. Axis 2 probably reflects a biogeographic change in floristics, since C is another of the associations found within Alliance I, the sole member of the mallee formation (Table 7.3).

The chi-square analysis was highly significant (Table 7.3), indicating that there is a strong degree of unique correlation between individual alliances and associations. Hence the site-based data are reflecting similar patterns to those detected by the transect-based data collected as described in Chapter 6.

DISCUSSION

Significance to theory & methodology of vegetation science

Although some strongly discontinuous and discrete vegetation associations were found, the majority of the vegetation could more accurately be described as noda interconnected to one another by intergrading continua as suggested by (Goodall, 1953) and (Poore, 1955a). These findings confirm the views of Webb (1954) and Whittaker (1978b), that vegetation is neither fully continuous, nor fully discontinuous. The use of numerical floristic techniques, coupled with the "complementary approach" (Kent & Ballard, 1988) of subjecting the same data set to both classification and ordination proved extremely useful in identifying both noda and continua within the data. This supports the views of Goodall (1978), Noy-Meir and Whittaker (1978), Legendre and Legendre (1983) and others (Chapter 3).

The occurrence of associations is clearly responding to local topographic and edaphic variables rather than broad-scale climatic ones. This confirms the observations of Warming (1909) who had early observed the strong overriding effect of edaphic conditions on climate (Chapter 4). Walter and Stadelmann (1974) suggested that the main reason for this is the control that soil type exerts on water relations, and this effect has therefore been predicted to be particularly important in arid regions (Leonard *et al.*, 1988). Each alliance, though tending to be represented by one or two major associations, usually also contains other minor associations (often ones more common in other alliances). Mosaic patterns of associations are thus formed, corresponding to the edaphic complex as defined by Crocker and Wood (1939; 1946). A summary of the edaphic complexes occurring within each vegetation alliance is included in Appendix 2. These complexes largely reflect local soil and topographic conditions, the causes of which will be investigated in Chapter 8. These results confirm previous literature suggesting the difficulty of mapping vegetation at the scale of association. The alliance classification (Chapter 4) remains superior in this respect, and appears to be able to summarise much of the information obtained in the smaller scale study. However, the additional information value of adopting a hierarchical, multi-scale approach to classify vegetation as suggested by Beadle and Costin (1952) and others (Chapter 3) is demonstrated. The alliances are extremely useful for summarising and mapping vegetation patterns at a large scale, while the nested descriptions of associations contained within each alliance (as set out in Appendix 3) provides a useful descriptive guide to finer floristic patterns. This was the approach adopted by Wood (1937) and Specht (1972) who mapped vegetation at broad scales only, with accompanying descriptions of small scale patterns.

The results of this largely inductive survey can thus be used to formulate and test much more directed hypotheses concerning the degree of edaphic control over plant distributions in the approach suggested by Ludwig and Reynolds (1988), Kent and Coker (1992) and others (Chapter 2).

Relationship to previous classifications

Many of the associations found by this survey correspond to those described in previous vegetation maps (Chapter 5). For example, Wood's (1937) *Atriplex-Maireana* Association (Figure 5.3) becomes a combination of the following floristically related associations of the *Maireana astrotricha* order described in Chapter 6: L(*Maireana astrotricha -Rhagodia spinescens*); M (*Atriplex vesicaria -Cassia nemophila coriacea - Eremophila longifolia - Eremophila sturtii*); and N (*Atriplex vesicaria -Maireana astrotricha*); see Figure 7.2. Wood had observed these three associations, which he described as part of the edaphic complex of the *Atriplex-Maireana* association, but did not attempt to map them separately. However, Wood may have extrapolated his *Cassia-Dodonaea-Eremophila* association (Figure 5.3) too far eastwards along the ranges. Although this association is confirmed to be present in the ranges near Dawson (to the south-west of the study area) by Sparrow (1991) it appears to be replaced by Association H (*Sida calyxhymenia - Ptilotus obovatus - Solanum ellipticum - Enchylaena tomentosa*) in the ranges within the study area.

The associations mapped (Figure 7.2) show strong similarity to the boundaries mapped by Beadle (1945); Figure 5.4, especially those of the mallee and black oak in the south. Neither Beadle nor Wood (1937) have distinguished *Maireana sedifolia* from *Maireana astrotricha*, which is perhaps not surprising. The two species are highly similar in appearance as shown in the photographs of Appendix 3D and 3N. *Maireana sedifolia* has leaves which narrow down into a distinct petiole, whereas those of *Maireana astrotricha* do not. Leaves of *M. astrotricha* bear stellate hairs, and *M. sedifolia* simple ones (Jessop & Toelken, 1986). *Maireana sedifolia* also grows slightly taller, up to 1m or more, and is a bright "sky" blue in overall appearance, whereas *M. astrotricha* is shorter and more compact, rarely over 0.5m, and is a duller, greyish blue. The division of Wood's and Beadle's *Maireana-Atriplex* association into two quite distinct associations on total floristics supports the taxonomic division between *M. astrotricha* and *M. sedifolia,* which probably have different edaphic or climatic requirements. Yet *M. astrotricha* and *M. sedifolia* are obviously very close genetically. I postulate that *M. sedifolia* is the older taxon, evolved to conditions prior to the onset of aridity (see Chapter 5). This would explain its modern day restriction to the ranges, where rocky soils provide a more mesic environment (Walter & Stadelmann, 1974; Leonard *et al.*, 1988); see Chapter 4. *M. astrotricha* is probably an arid-adapted variant of *M. sedifolia*, which developed and spread onto the newly available arid areas during the onset of aridity over the last 18 000 years. Such features as the stellate hairs support this hypothesis, which will be investigated in Chapter 8.

Specht's (1976) *Atriplex nummularia* association (Figure 5.5) is not supported by the present classification. Although *A. nummularia* is present within the alliance for the area (see Figure 6.3), the association present is now dominated by *Dodonaea viscosa angustissima* and *Heterodendrum oleifolium*. This could be a reflection of increasing and spreading populations of *Dodonaea viscosa*, a plant often cited as an increasing woody weed (Chapter 5). Nonetheless, it is however likely that Specht over-emphasized the importance of *Atriplex nummularia,* which is a conspicuous tall species of chenopod with silvery-white leaves. Both Wood (1937) and Beadle (1945) show an *Acacia aneura* association for the far north-east corner of the study area, and all four previous maps show a distinct association in this area. It is unlikely that climate would cause such an abrupt change in floristics, and it is here postulated that the causes are also likely to be edaphic. Specht's other mapped vegetation types are obviously derived from those of Wood and Beadle, and are therefore not discussed here.

Relationship of associations to alliances

The high degee of unique correlation between the alliances and associations (Table 7.3) indicates the overall floristic unity of the alliances. Association N (*Atriplex vesicaria-Maireana astrotricha*), one of the most common associations, is the only exception, being shared almost equally between two alliances (VI and IX), which in any case both fall within the *Maireana astrotricha* floristic order.

Alternatively, associations H and K are the only ones not highly correlated with a particular alliance. These are associations strongly correlated with local edaphic and topographic features, influences so powerful that they override the more general trends able to be detected in the strip-transect samples used in the classification of alliances. This result confirms the importance of scale in designing a sampling strategy, particularly in relation to plot-size (Greig-Smith, 1983; Kershaw & Looney, 1985; Ludwig & Reynolds, 1988) as discussed in the methodology of this chapter. Association H is one of the high elevation vegetation types, containing *Sida calyxhymenia* and *Ptilotus obovatus,* and occurs within both Alliances III and IV, two of the important alliances in the *Maireana pyramidata* order, reflecting the close affiliation of these two alliances. Association H is probably strongly influenced by the edaphic conditions of the high ridges of the range, which tend to confound the boundaries of the Alliances (Figure 7.2). Association K is a minor dryland mallee type, represented by only one site containing *Eucalyptus socialis, E. gracilis, E. porosa,* and *Atriplex vesicaria.* Lacey and Johnston (1990) have observed that many of the mallee eucalypts can persist for hundreds of years, long after changing environmental conditions prevent further recruitment by seedlings. Such clumps can form relict communities. Association K is an example of one of these, an outlier of the mallee formation now stranded within the Eremaean chenopod formation.

CONCLUSIONS

The results support the nodum-continuum model of vegetation as suggested by Goodall (1953) and Poore (1955a), and demonstrate the usefulness of complementary analysis in identifying both of these aspects of vegetation. The overriding importance of edaphic variables in controlling arid vegetation is also confirmed. The associations were able to be mapped, but the classification at the level of alliance (Chapter 4) remains superior for broad-scale mapping. However, the association groupings provide a very close match with the alliance classification, whilst providing a much greater degree of information than the alliance classification alone, so this scaled approach provides an extremely useful adjunct to mapping. Since information provided by association classification is much more closely tied to local edaphic conditions, the association classification was the one used to relate vegetation distribution to environment (see Chapter 8).

CHAPTER 8:

VARIABLES CONTROLLING PERENNIAL VEGETATION DISTRIBUTION

INTRODUCTION

The emphasis in vegetation science, especially in Europe, has traditionally been on vegetation systematics, the classification of typical communities (repeating groups of associated plants), although this is no longer considered an end in itself (Mueller-Dombois & Ellenberg, 1974). It is now generally accepted that although classification and inventory are valuable for management, one of the most interesting theoretical applications of a classification is that it allows the generation of more directed hypotheses about the causes of stand composition, and provides a basis for comparison of vegetation composition with environmental and other variables. (Greig-Smith, 1983). An initial exploration of vegetation pattern followed by an exploration of the environmental explanations has become a tradition in vegetation science (Mueller-Dombois & Ellenberg, 1974).

The results of Chapter 7, although largely descriptive and inductive, suggest that a range of edaphic variables play a major role in plant distributions. Previous studies of arid-zone vegetation both in South Australia and elsewhere support the view that both edaphic and climatic variables have a controlling effect on vegetation distribution (Chapter 4). Non-equilibrium variables such as timing and chance may also have some controlling effects on vegetation (Chapter 2). What is known of the recent geological and vegetation history of the study area is summarized in Chapters 4 and 5, and shows that vegetation type has fluctuated markedly in response to climate changes in recent geological and ecological time, giving plenty of scope for these kinds of effects. Grazing history is another non-equilibrium variable known to have an influence on vegetation pattern, particularly in arid regions (Skarpe, 1986). Further investigations of a more powerfully deductive nature are therefore necessary to explain the patterns observed in the vegetation.

The main aims of this part of the thesis are as follows:

> To measure a range of climatic, edaphic and other variables likely to be important in influencing plant distributions within the study area.
>
> To analyse whether a combination of these environmental factors can be used to formally explain the patterns observed in the vegetation distribution.
>
> To determine whether non-equilibrium variables such as historical events have some role in controlling vegetation distributions.

METHODS

Major Environmental Variables

Median annual rainfall at each site was interpolated from the median rainfall contour map prepared from Bureau of Meteorology and station records (Figure 4.6). Because a contour map was used, rainfall could not be determined reliably as a continuous variable, and was assigned to ordinal classes according to the scale shown in Table 8.1. Elevation was similarly determined for each site from the topographical maps of the study area (Figure 4.1) and classed (Table 8.1). Local topography was recorded in the field, in values corresponding to the degree of run-on or run-off of surface water, and classed in a similar fashion (Table 8.1). Degree of past grazing by domestic livestock was estimated by referring to the historical pastoral maps from 1857 to 1867 (summarized in Figures 5.6 and 5.7). These estimates of nineteenth century grazing intensity were expressed in classes as shown in Table 8.1.

Macro and Micro-Scale Edaphic Variables

Environmental data ~~was~~ were collected at each of the 205 sites visited during the during the survey described in Chapters 6 and 7. A soil core was dug in the centre of each quadrat as recommended by Reed *et al.* (1993) and Woldu & Backéus (1991). Soils usually consist of an O horizon (decomposing organic matter), A horizon (topsoil), and B horizon (subsoil) (Brower *et al.*, 1990). In the study area, the O horizon was usually very thin, often only a few centimetres, and occasionally appeared to be absent altogether. In areas

Table 8.1

Ordinal scaling of environmental variables used for DCCA analysis.

Rainfall	1	=	175-199 mm/annum
	2	=	200-224 mm/annum
	3	=	225-249 mm/annum
	4	=	250-274 mm/annum
	5	=	275-299 mm/annum
Elevation	1	=	100-149 m
	2	=	150-249 m
	3	=	250-349 m
	4	=	350-449 m
Water Runoff	1	=	creeks, watercourses, flood-plains
	2	=	plains
	3	=	slopes, rises, hills, dunes, ridges
Pebbles	0	=	fragments ≥ 2 cm diameter absent
	1	=	fragments ≥2 cm diameter present
1900 Grazing	0	=	nil (land not taken up)
	1	=	light, intermittent (stock routes etc.)
	2	=	moderate (taken up)
	3	=	heavy (within 20 km of water)
	4	=	severe (within 5 km of water)

where a lot of soil erosion had occurred in the past, the A horizon was also very thin or absent. In practice, most of the soils were typical desert loams (Northcote, 1968), and very gradational in nature, so it was often not possible to distinguish clear horizons. Initial testing of separate horizons within profiles showed that samples taken at varying depths did not differ markedly in any of the physical or chemical characteristics measured, and subsequently only one sample was taken, at a standard depth of 20cm.

Soil samples were analysed under supervision at the Analytical Services Section, Division of Soils, CSIRO, Adelaide, as described below:

> Conductivity in dSm^{-1} on an air-dry basis was determined at 25°C by the method set out in Rhoades (1982).
>
> pH was also determined at 25°C in a 1:5 soil:water extract, according to Blackemore *et al.* (1987).
>
> The exchangeable basic cations (calcium, magnesium, sodium and potassium) and cation exchange capacity of the soil were determined by mechanical leaching (Holmgren *et al.*, 1977) followed by auto-analysis of the leaching product. These were expressed as meq%, or mg kg^{-1}.
>
> Total nitrogen content was not determined for the following reasons. Nitrogen is present in soils as ammonia, as nitrates, or in organic form, but ammonia and nitrates vaporize rapidly at temperatures above 25° C (Brower *et al.*, 1990). Because of the remoteness of the study area, soil samples had been kept unsealed and unrefrigerated. Thus, only the nitrogen present in organic form was still present with certainty. This value is directly proportional to the organic carbon content of the soil, so organic carbon content was calculated instead of nitrogen content because it is a much less labour-intensive analytical technique. The method used was that of Heanes (1984), using wet oxidation in dichromate-sulphuric acid mixture, with an external heating step to ensure complete oxidation of organic carbon. The method requires correction for the positive interference from chlorine ions in saline soils, which were separately determined by automatic colorimetry based on the reaction of chlorine ions with ferric nitrate and mercuric thiocyanate, the automated ferricyanide method) (APHA, 1985). Total organic carbon was expressed as a percentage of dry weight of soil.
>
> Inorganic carbon content was measured as an estimate of limestone content. This was calculated by deducting organic carbon, as determined above, from total combustible carbon, as determined by the dry combusion method using a LECO furnace (LECO, 1988).
>
> Soil texture fractions of sand, silt and clay were determined by taking aliquots from a soil-water suspension as described by Hutton (1955), and expressed as a percentage of dry weight. These values were determined from the fine fraction of the soil only, that portion which passed through a 2mm sieve. The coarse tail (or fraction with a grain-size greater than 2mm (Jeffrey, 1987), and therefore remaining in the sieve), was also recorded as a fraction of total weight of the sample. It is therefore possible for this fraction to be greater than 100% (Jeffrey, 1987). The presence of pebbles of greater than 0.5 cm diameter was also

recorded, as a presence/absence ordered variable. Presence/absence data were converted to binary scores of one or zero for analysis.

Soluble phosphorus was determined by extraction in $NaHCO_3$ as described by Olsen (1954),expressed in mg kg^{-1}, and taken to be equivalent to the phosphorus available for plant growth.

The complete list of variables measured at each site (Table 8.2) shows the means and ranges of each variable. The environmental data was kept separate from the floristic data, as advised by Williams (1971). Rather than combining the sets, where information will either be duplicated or swamped, it is preferable to analyse the two data sets in programs which compare the two (Williams, 1971). Some soil samples were lost before returning from the field, so that no physical or chemical analyses could be performed. It was not considered useful to substitute mean values as recommended by Ter Braak (1988a), so these fourteen sites were omitted, leaving a total of 191 sites for analysis.

ANALYSIS METHODS

Canonical correspondence analysis

The relationships of environmental variables to the vegetation association data described in Chapter 7 were analysed by DCCA, the detrended version of canonical correspondence analysis (CCA), a form of multivariate direct gradient analysis available on the computer package CANOCO (Ter Braak, 1988a). The use of direct gradient analysis by canonical ordination in combination with classification and indirect ordination techniques has previously proved useful in revealing multivariate relationships between vegetation and environmental variables (Retuerto & Carballeira, 1991). Canonical ordination has been used by: Bergeron *et al.*, (1985) to compare ordinations of vegetation and edaphic data in Canada; Skarpe (1986) in the Kalahari desert; Oksanen & Huttunen (1989) to compare community data with chemical data from a lake in Finland; and Johnston, (1992) in forest communities of Puerto Rico.

Ordination is a valuable tool for gradient analysis, i.e. the identification and definition of sequences of community compositional variation which can be directly related to gradients of environmental factors (Noy-Meir & Whittaker, 1978; Greig-Smith, 1983; Kent

Table 8.2

Summary of climatic and edaphic variables used in DCCA analysis. Means and standard deviations are not calculated for classed variables.

Variable	Abbreviation	Units	Mean	SDEV	Lowest	Highest
Conductivity	COND	dSm^{-1}	0.469	0.04	0.03	10
pH	-	pH Scale	7.906	4.3	4.9	9
Calcium	CA	mg/kg	91.85	37.4041	23.4	182
Magnesium	MG	mg/kg	34.21	22.6889	2.88	119.2
Sodium	NA	mg/kg	19.59	29.1286	0	177.33
Potassium	K	mg/kg	11.2	6.6036	1.8	40.55
Cation Exchange Capacity	CEC	mg/kg	155.6	80.2364	16.4	572.7
Organic Carbon	OC	% dry wt	0.5075	0.5413	0.07	4.97
Inorganic Carbon	IC	% dry wt	0.5953	0.8039	0	3.66
Sand	-	% dry wt	59.73	17.4031	20.37	93.67
Silt	-	% 10.8344	10.32	12.1396	0	83.6
Clay	-	% dry wt	22.6	16.4872	3	183
Soluble Phosphorus	PHOS	mg/kg	11.98	14.8695	0	93
Median Rainfall	RAIN	classed	-	-	1	4
Elevation	ELEV	classed	-	-	100	650
Water Runoff	RUN	classed	-	-	1	3
Pebbles	PEBB	classed	-	-	0	1
Coarse Tail	CT	% dry wt	26.12	47.4504	0	476.17
Grazing 1850 to 1870	1900	classed	-	-	0	4

& Coker, 1992); see Chapter 3. The DCA ordinations of Chapters 6 and 7 were useful in this respect. Since plant species data from surveys usually show non-linear, non-monotonic responses to environmental variables, it was previously necessary to use such indirect techniques to analyse species-environment relationships (Ter Braak, 1987).

Direct ordination as first practised by L.G. Ramensky involves the arrangement of stands in relation to specified environmental gradients (Greig-Smith, 1983), therefore directly inferring relationships between vegetation and environment, so is actually a form of regression. Regression and direct ordination are more powerful methods of detecting correlations of variables with vegetation composition than indirect ordination (Ter Braak, 1988b), and allow development of hypotheses about causality (Greig-Smith, 1983). However, both regression and direct ordination introduce a need to assess the relevance of variables to be included (Greig-Smith, 1983). Problems with regression and traditional forms of indirect ordination are that they will not cope with strongly non-linear data, and are unable to separate the effects of strongly correlated variables or "factor-complexes" (Greig-Smith, 1983). Jongman and Ter Braak therefore developed a form of multivariate direct gradient analysis, called canonical ordination, which is available on the computer package CANOCO (Ter Braak, 1988b). Canonical ordination is an ordination which constructs a multiple regression from a set of environmental variables, along which distributions of species in a matching data-set are dispersed as far as possible (Ter Braak, 1987; Kent & Coker, 1992). Because it incorporates environmental gradient interpretation, it combines aspects of ordination with aspects of regression (Jongman *et al.*, 1987; Kent & Coker, 1992) and is effective in detecting species-environment relationships (Ter Braak, 1987; Reed *et al.*, 1993). The length of the arrows indicating the direction of environmental gradients is proportional to their correlation with ordination axes, and therefore to the pattern of community variation (Ter Braak, 1987).

CCA (canonical correspondence analysis) is the canonical and therefore restricted form of correspondence analysis (CA), although the restrictions become less strict as more environmental variables are included in the analysis (Ter Braak, 1987). If enough variables are included, the amount of restriction is neglibible, and CCA will closely approximate CA

(Ter Braak, 1987). CCA is also prone to the "arch effect" of CA (Kent & Coker, 1992) as described in Chapter 3, so Ter Braak (1988b; 1988a) developed DCCA, the detrended version of CCA. CCA does not perform well when highly correlated variables are included, and it is recommended that they be removed prior to analysis (Ter Braak, 1988b; 1988a). However, when there is more than one characteristic, and especially if these characteristics interact with one another, it is desirable that they be analysed together using multivariate methods (Gauch, 1982). The aim of the analysis was to summarise the data and refine further hypotheses, so although the arch effect of CCA can be dealt with by dropping superfluous multicollinear environmental variables, usually the ones strongly correlated with the second, arching, axis (Ter Braak, 1987), it was considered desirable to analyse the full set of variables. None of the variables was so strongly correlated with another as to cause an inflation factor which would strongly recommend its removal (Ter Braak, 1988a). For this reason, DCCA, the detrended version of CCA (Jongman *et al.*, 1987) was used rather than CCA.

Because of the large number of vegetation types, and the complex environmental gradients between them, it was not possible to summarize these effects in one diagram. Individual gradients and the positions of the vegetation associations on them were clarified by successively subdividing the data-set, a method recommended by Dargie (1991) and Austin (1979) for other ordination methods. This was done by removing associations with strong environmental associations, identified by their corresponding positions at the extreme ends of environmental axes. Their removal tended to decompress the ordination, making the remaining environmental and vegetation relationships easier to assess.

Direct correlations (pearson correlation coefficients)

It is rarely possible in ecology to isolate one variable at a time (Greig-Smith, 1983). Environmental factors tend to form highly correlated groups (Gauch, 1982), and it is therefore difficult to distinguish individual effects. One variable, though not strictly effective itself, can consequently act as a surrogate for a complex array of intercorrelated environmental variables (Reed *et al.*, 1993). Extreme values of one environmental gradient can also mask the importance of other variables (Reed *et al.*, 1993). For example, it is common for altitude to be correlated with temperature, humidity, rainfall and soil (Gauch, 1982). In order to clarify the relationships of variables with one another, pearson correlation coefficients were calculated between all variables in the environmental data-set using the statistical program Statview (Feldman & Gagnon, 1988).

Multiple Regressions

Although CCA is more powerful than other methods of indirect ordination, it is still by definition an exploratory analysis, and its resolution is limited by the multivariate nature of the explained variable, the vegetation data set. Therefore, it was decided to use an even more powerfully deductive form of true regression, multiple regression, as recommended by Crosbie and Hinch (1985), and available on the computer package GENSTAT (1987), to further test the effects of the environmental variables on individual plant species. Multiple regression has the advantage that the response-variable being modelled, in this case, the cover score of a plant species, is univariate. However, this means that each species has to be modelled separately, which is very time-consuming. The value of the indirect and direct ordinations in summarising the very large data set, refining the hypotheses and narrowing down the set of species to be tested, is therefore apparent.

Twenty-six species were selected for multiple regression analysis, including all species which had an importance value of greater than 1 in the classification of vegetation associations (Table 7.2). Several other species were included because they had been mentioned as dominants in other vegetation classifications: *Acacia aneura*, *Heterodendrum oleifolium*, *Maireana aphylla*, and *Myoporum platycarpum* (see Chapter 5). One of the disadvantages of direct ordination [applicable to CCA], and particularly regression, is that important factors may not be evident in the data collection phase and therefore not be available for inclusion in the analysis (Gauch, 1982; Palmer, 1993). If there is pattern in the data, but no relationship between sites and variables supplied, one explanation is that there is a missing environmental variable (Jongman *et al.*, 1987).

The multiple regression available on GENSTAT (1987) allows the fitting of a sequence of models (Lane *et al.*, 1987). In this case modelling was performed by the additive method, starting with a null model (no variables), and in step-wise fashion adding variables which significantly improve the model as recommended by Nicholls (1991a). Therefore, biologically important variables may be left out of the model if other correlated variables can successfully code for them. The results must therefore be viewed in the light of the limitations of the technique, familiarity with the vegetation, and a knowledge of processes affecting plants (Greig-Smith, 1983).

RESULTS

Overview

An initial correlation matrix (Table 8.3) of the variables used in this data set reveals a high level of multicollinearity. A plexus diagram of the configuration of the correlations (Figure 8.1), as used by Okland (1988), shows that the variables are divided into several different groups. Although correlations between variables are very frequent within groups, there is usually negative or no correlation at all between groups. For example, clay, cation exchange capacity, conductivity, pH, magnesium, sodium, calcium and potassium are highly interconnected. This would be expected, since clay soils contain colloids, molecules with a high degree of negative charge, which provide many sites for cation exchange and therefore tend to retain higher levels of cations. The high amount of salts thus present causes the high conductivity and high pH. Clay soils are obviously therefore coding for a range of other variables. The variables elevation, topography, rainfall, phosphorus and silt, are also in a closely related group, and highly diassociated with the clay group first described, with the exception of a correlation between potassium and phosphorus. Elevation is the most likely cause of higher rainfall (Figures 4.1 & 4.6). There is also an obvious correlation between topography and elevation, strong enough to

Table 8.3

Association matrix showing pearson correlation coefficients between 18 climatic and edaphic variables. Significant correlations (r>0.236, df = 191, p = 0.001) are marked in bold.

	cond	pH	ca	mg	na	k	cec	OC	IC	sand	silt	clay	phos	rain	elev	runoff	pebb	coarse
pH	0.1356																	
ca	0.2207	**0.2898**																
mg	**0.3783**	**0.3449**	**0.5023**															
na	**0.6451**	**0.3719**	**0.2785**	**0.6481**														
k	-0.0026	-0.0274	**0.3128**	**0.2842**	0.0103													
cec	**0.3283**	0.1684	**0.7037**	**0.7744**	**0.5943**	**0.3393**												
oc	-0.0443	**-0.5260**	0.0882	-0.0699	-0.1613	0.2227	0.1750											
IC	0.0973	0.1261	0.1470	0.0168	0.0008	-0.1366	0.0659	**0.2453**										
sand	**-0.3695**	**-0.2818**	**-0.6338**	**-0.6272**	**-0.4723**	**-0.2564**	**-0.6223**	-0.0602	**-0.3063**									
silt	-0.0425	**-0.3209**	0.1185	-0.0798	-0.1075	0.1067	0.1222	**0.5997**	0.1585	**-0.4005**								
clay	**0.2752**	0.2201	**0.4919**	**0.6030**	**0.4294**	**0.2469**	**0.5851**	-0.1217	-0.0484	**-0.5123**	0.0433							
phos	-0.0210	**-0.2984**	-0.0393	-0.1206	-0.1444	**0.4681**	-0.0281	**0.5565**	-0.0798	0.0735	**0.2587**	-0.1474						
rain	-0.0143	-0.1610	-0.0653	-0.0711	-0.0642	-0.0142	-0.0846	0.2344	-0.0124	**-0.3311**	**0.5715**	-0.1019	0.1552					
elev	-0.0120	**-0.3567**	0.0602	-0.1187	-0.1795	0.1999	-0.0364	**0.4914**	-0.0317	-0.0015	**0.2661**	-0.1596	**0.4718**	**0.2763**				
runoff	-0.0262	-0.1344	-0.0889	-0.0860	-0.0027	-0.0378	-0.0791	0.0095	-0.0881	**-0.3664**	**0.4406**	0.0050	0.0216	**0.6044**	-0.1858			
pebb	-0.0137	0.0239	-0.0143	0.1166	0.0240	0.0229	0.0352	0.0211	-0.0432	-0.0190	0.0127	0.0210	-0.0218	0.0010	0.0555	-0.0064		
coarse	0.0265	-0.1072	-0.0347	-0.0807	-0.1360	0.0292	-0.1052	**0.2507**	0.1110	0.0028	0.1292	-0.1471	0.1966	0.1347	**0.3912**	-0.0503	**0.5835**	
1900	-0.0086	-0.2204	0.0576	-0.0943	-0.0515	0.0636	0.0023	0.1695	-0.0658	**-0.3444**	**0.4545**	-0.0083	0.1983	**0.4924**	**0.2976**	**0.7120**	0.0382	-0.0536

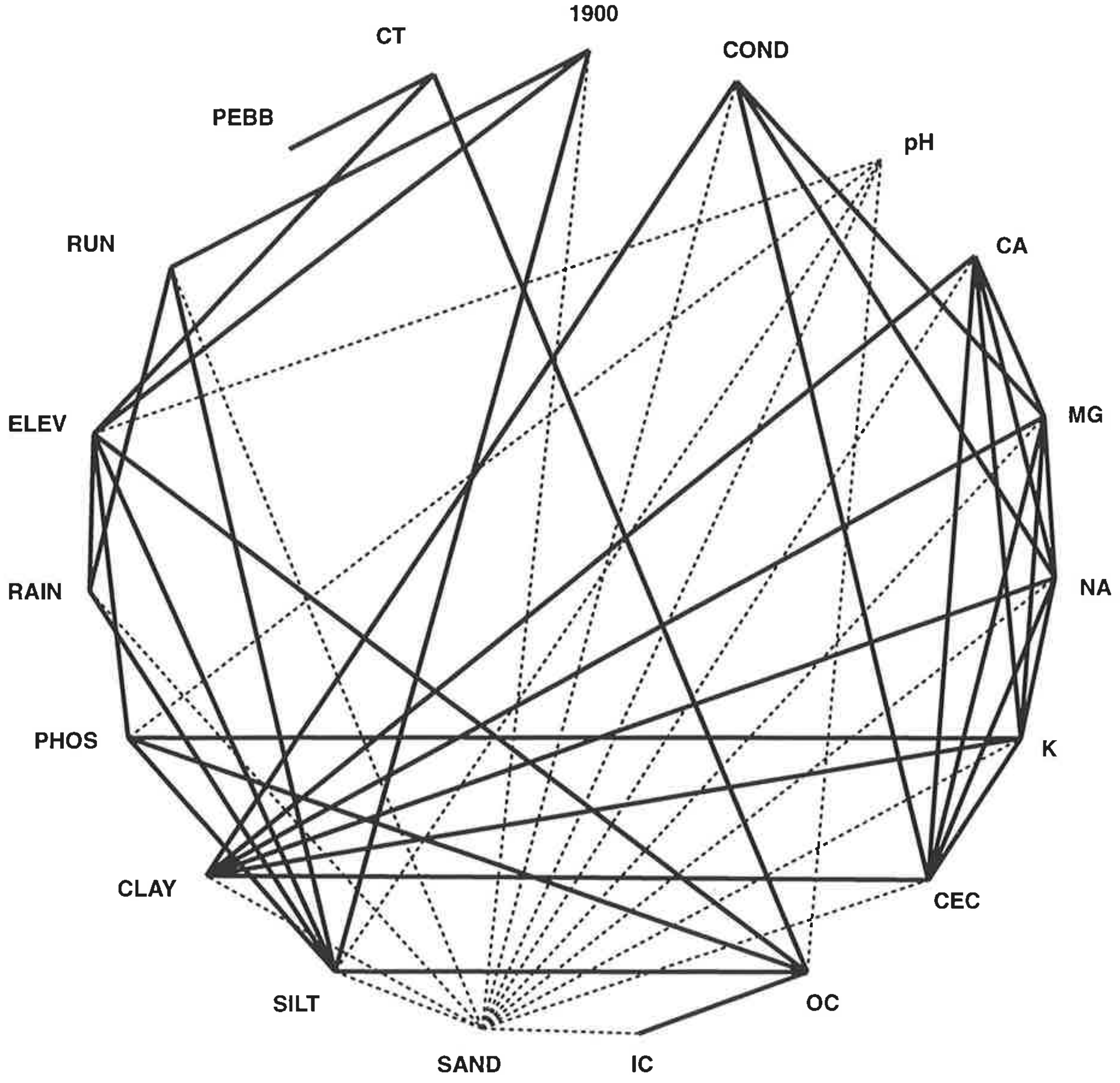


Figure 8.1

Plexus diagram showing degree of multicollinearity of variables used in DCCA analysis. Solid lines indicate positive correlations and dotted lines indicate negative correlations, as indicated in Table 8.3. Abbreviations of variables are set out in full in Table 8.2.

override the heterogeneity of run-on and run-off patterns present within the ranges. The soils within the ranges tend to be siltier and of lower pH, and contain higher levels of phosphorus and organic carbon. Thus, elevation, although itself not necessarily a causative factor, codes for a number of other variables.

The results of the DCCA are shown in Figures 8.2a, 8.2b and 8.2c. Figure 8.2a shows the full set of vegetation associations as previously determined by cluster analysis (Chapter 7). The greatest vegetation sequences are related to elevation and phosphorus, pH, sand and calcium. Association A is present on sand at low elevation, and Associations B,G, H and I at high elevation. A,B, G, H and I, the most prominent outliers, were removed from subsequent ordinations as described in the methodology. The second ordination (Figure 8.2b) still shows an elevation gradient, with E and D at high elevation and C at low elevation. This trend can actually be observed on closer examination of Figure 8.2a, so the decompressing action of removing A is clear. C is not as sandy as A, and G and I are at about the same elevation as B and H. R then occupied a position at the lowest end of the inorganic and organic carbon gradients, so was removed from further analysis. Figure 8.2c still had an elevation gradient along the first axis, but a sodium and phosphorus gradient were also prominent.

The major environmental variables produced by the DCCA analysis and the relative positions of the vegetation associations along them were used to produce descriptive environmental profiles of all 18 vegetation associations, which are included as part of Appendix 2.

The results of the multiple regressions are shown in Table 8.4. It can be seen that a range of climatic and edaphic variables were significant in explaining the distribution of the 24 species. *Eragrostis australasica* could not be modelled because it only occurred at one site. *Sida intricata* was the only species for which no variables were significantly correlated with the model. Most species models include more than one variable, indicating that the variables tend to interact with one another. Variables important in modelling individual species cover as determined by multiple regression are also included in Appendix 2.

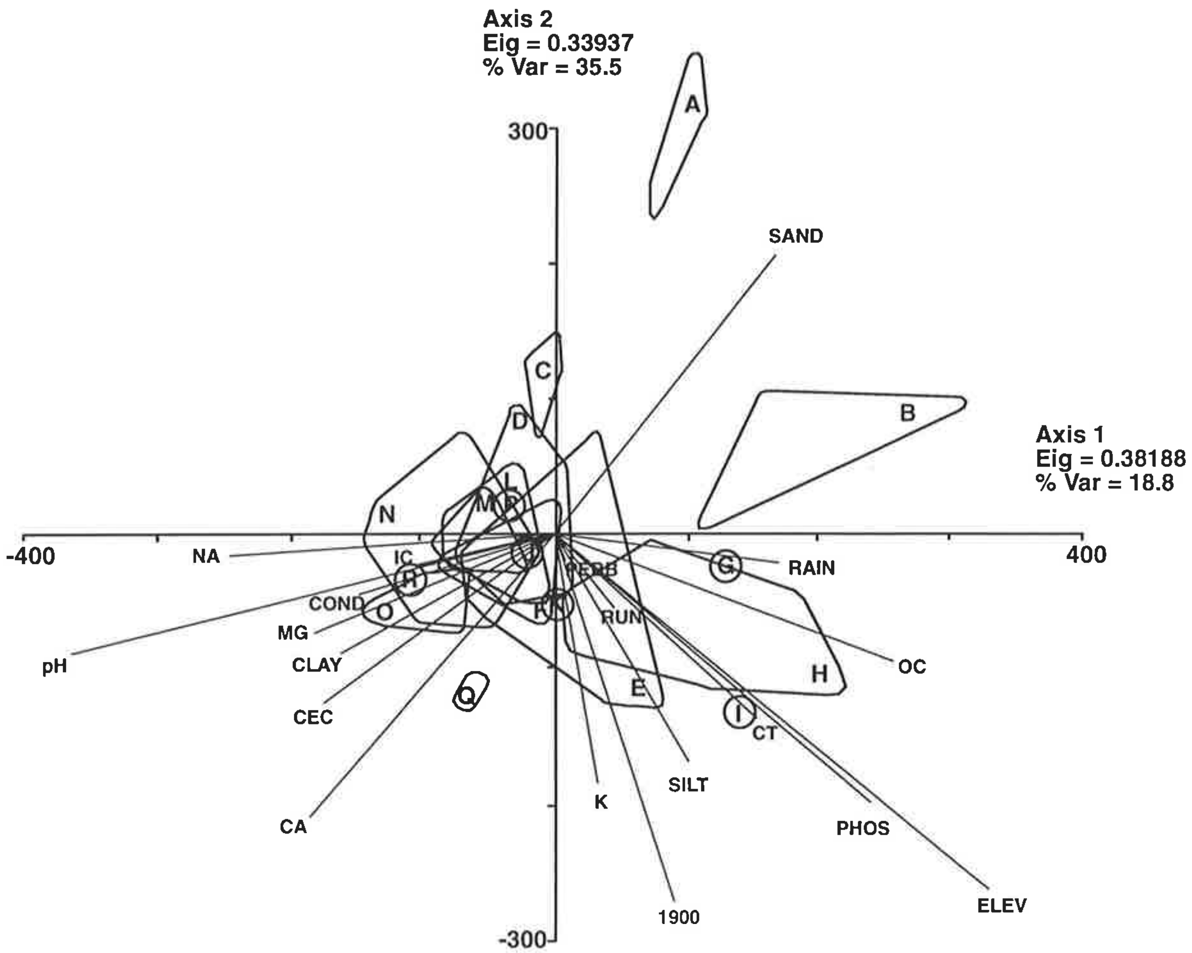


Figure 8.2a

DCCA (detrended canonical correspondence analysis) of association data; all sites and all variables. Minimum area polygons delineate the ordination space of the vegetation associations A - R. Full names of abbreviated variables are given in Table 8.2.

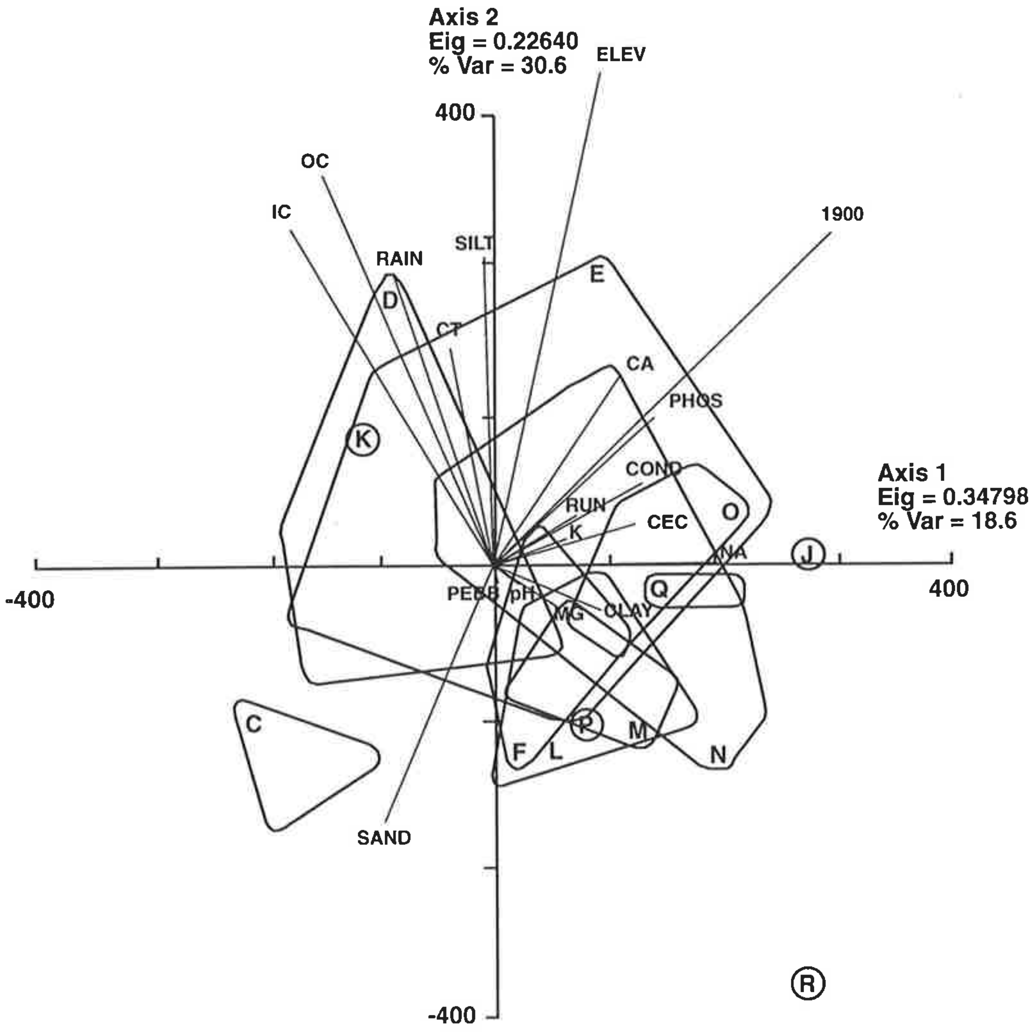


Figure 8.2b

DCCA (detrended canonical correspondence analysis) of association data with Associations A, B, G, H and I removed. Minimum area polygons delineate the ordination space of the vegetation associations. Full names of abbreviated variables are given in Table 8.2.

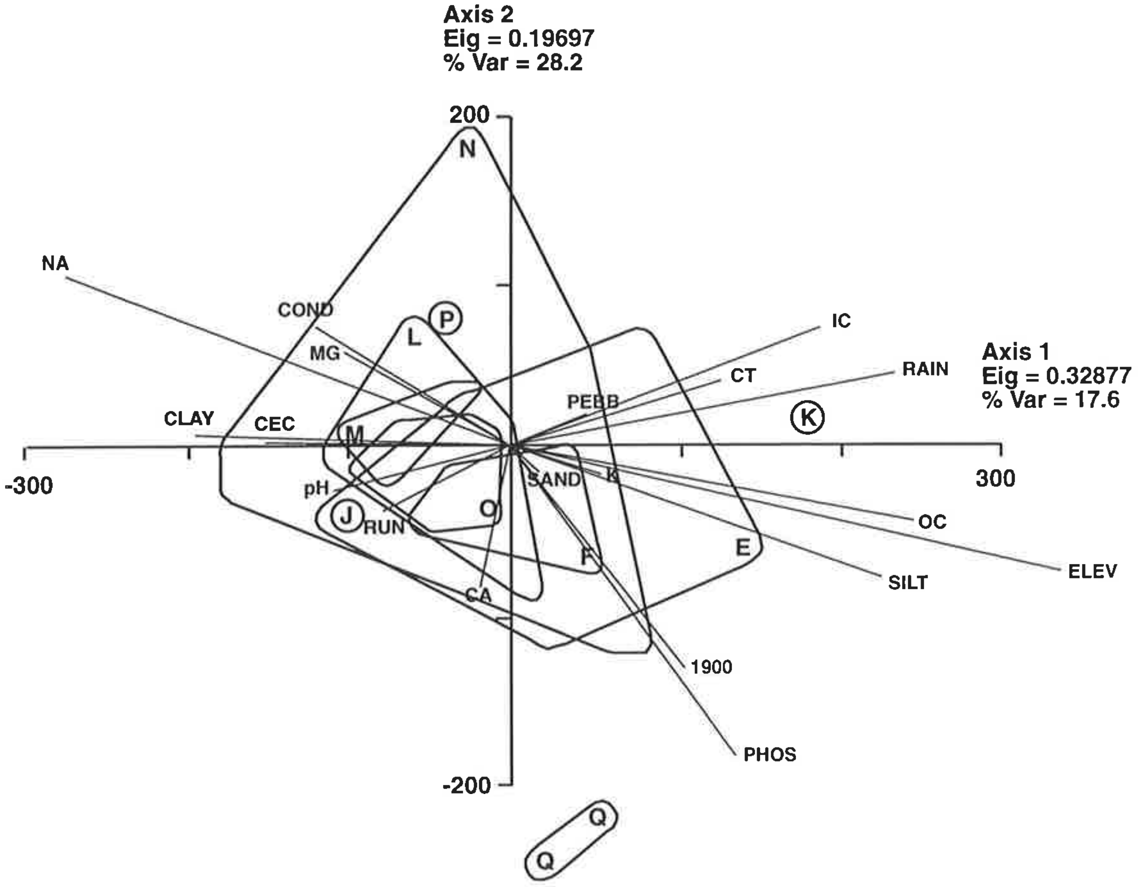


Figure 8.2c

DCCA (detrended canonical correspondence analysis) of association data with Associations A, B, G, H, I, D, C and R removed. Minimum area polygons delineate the ordination space of the vegetation associations. Full names of abbreviated variables are given in Table 8.2.

Table 8.4

Results of multiple regressions, showing variables significant in the final regressions (F = 5.11, df = 1,190, p = 0.05). Only the significant t-values (t = 1.973, df = 190, p = 0.05) are shown, the signs of which indicate whether the correlation is positive or negative. The total value for F indicates the significance of the whole regression model, with degrees of freedom depending on the number of significant variables. For p = 0.05, total F = 5.11 (df = 1,190), F = 3.77 (df = 2,189), 3.19 (df = 3,188), F = 2.85 (df = 4,187). *Eragrostis australasica* only occurred at one site, so could not be modelled by regression, denoted nm. None of the variables were significantly correlated with the *Sida intricata* model. 19HD = 1900.

	COND	pH	CA	MG	NA	K	CEC	OC	IC	SAND	SILT	CLAY	PHOS	RAIN	ELEV	RUN	PEBB	CT	19HD	TOT F
Acacia aneura	-	-3.20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.24
Atriplex vesicaria	-	-	-	-	2.70	-	-	-	-	-	-	-	-	-	-	2.32	-	-	2.34	6.31
Callitris columellaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.57	-	-	-	-	6.62
Cassia nemophila platypoda	-	-	-2.95	-	-	-	-	-	-	-	-	-	-	-	-2.93	-	-	-	-3.81	21.70
Casuarina cristata	-	-	-	3.62	-	-	-	-	4.39	-	-	-	-	2.82	-	-	-	-	-6.92	62.69
Dodonaea viscosa angustissima	-	-	-	-	-	-	-	-	-	2.91	-	-	-	-	-	-	3.73	-	-	3.73
Enchylaena tomentosa	-	-	-	-	-	-	-	-	-	-	-	-	-	6.63	-	-	-	-	-3.83	24.97
Eragrostis australasica	nm	nm	nm	nm	nm	nm	nm	nm	nm	nm	nm	nm	nm	nm	nm	nm	nm	nm	nm	nm
Eragrostis leptocarpa/parviflora	-	-	-	-	4.20	-	-	-	-	2.81	-	-	-	-	-	-	-	-	-	9.18
Eremophila sturtii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-4.65	-	-	-	21.62
Eucalyptus camaldulensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-2.26	-	-	-	5.11
Eucalyptus cyanophylla	-	-	-	-	-	-	-	-	-	4.08	-	-	-2.29	-	-	2.72	-	-	-2.45	10.50
Eucalyptus socialis	-	-	-	-	-	-	-	-	-	4.24	-	-	-	5.80	-3.92	-	-	-	-	13.52
Heterodendrum oleifolium	-	-	-	-	-2.29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.22
Maireana aphylla	-	-	2.98	-	-	-	-	-	-	-	-	-	-	-2.34	-	-	-	-	-	7.55
Maireana astrotricha	-	-	-	-	4.35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.51
Maireana pyramidata	-	-	-	-	-	-	-	-	-	-	-	-	-	3.03	-	-	-	-	-	9.16
Maireana sedifolia	-	-	-	-	-	-	-	-	4.25	-	-	-	-	-	-	3.19	-	-	-4.52	15.91
Myoporum platycarpum	-	-	-	-	-	-	-	-	3.02	-	-	-	-	-	-	-	-	-	-	14.62
Ptilotus obovatus	-	-2.98	-	-	-	-	-	-	-	-	-	-	2.99	-	2.42	-	-	-	-	18.00
Rhagodia spinescens	-	-	-	-	-	-	-	-	-	-	-	-	2.92	-	-	-2.66	-	-	-	8.76
Sclerochlamys brachyptera	-	-	-	-	8.16	-	-	-	-	-	-	-	-	-	-	-	-	-	2.42	17.28
Sclerolaena obliquicuspis	-	-	-	-	-	-	-	-	3.98	-	-	-	-	3.45	-	-	-	-	-	15.22
Sida calyxhymenia	-	-	-	-	-	-	-	-	-2.46	-	-	-	3.69	-	5.29	3.00	-	-	-	26.77
Sida intricata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Triodia irritans	-	-	-	-	-	-	-	-	-	3.21	-	-	-	-	-	-	-	-	-	31.84

Variables associated with major floristic differences

Of all the variables, elevation above sea level has the strongest explanation of the full data set (Figure 8.2a). Elevation is a variable which codes for a number of other variables including organic carbon, silt, phosphorus, grazing history, percentage of coarse tail in the soil, and rainfall (see Table 8.3). The inclusion of elevation results in a very short arrow for rainfall, indicating that it is either not important, or that it is satisfactorily explained by another variable. The latter is suspected, since the other variables mentioned have considerable influence of their own (Figure 8.2a). It is possible that elevation is better at accounting for local orographic influences which rainfall contours, based on data collected at homesteads (generally located in low-lying areas) cannot. Elevation may also be coding for soil water availability, through high levels of coarse tail, a characteristic which tends to increase percolation and increase water storage as discussed in Chapter 4. Thus, the ranges are mesic environments because of increased rainfall, and better storage of that rain. Appendix 2 shows the mallee formation of Alliance I occurs at low elevation, on sands of low pH, and in areas with low intensity of past grazing. Although rain does not show as a major trend from DCCA analysis, the individual models for many of the dominant species show rainfall as an important variable. Alliance X, of the highest elevation and rainfall, is the most floristically related to Alliance I, supporting the view that water relations explain the greatest variation in the vegetation.

The Chenopod Formation (Alliances II - X) is too large to be easily characterised (Appendix 2), but differs from the mallee formation in occurring on silty or clay soils, and therefore in being more xeric, even if rainfall is higher. The soils of the chenopod formation also tend to a higher content of both organic and inorganic carbon. A major division within the chenopod formation is determined by a combination of climatic and edaphic variables. The *Maireana pyramidata* order occurs at high elevation and high rainfall, on the ranges and south of them. Soils tend to be lower in sodium and have lower pH, possibly due to increased downward leaching caused by the additional rainfall. There is also better availability of magnesium and phosphorus, perhaps controlled by the lower pH. The *Maireana astrotricha* order occurs at low elevation and low rainfall on the plains, mostly to the north and east of the ranges, on soils which are high in pH and sodium. This order therefore occupies the zone of harshest water and nutrient status. Mean sodium levels for the whole study area were 19.59 mg/kg, or 0.0196%, with a minimum of zero and a maximum of 177.33 mg/kg or 0.17733% (Table 8.2), corresponding to the overall low levels observed by Osborn *et al.* (1923). Relatively small changes in soil sodium content are therefore having substantial effects on the vegetation.

The divisions of vegetation into alliances are also jointly controlled by climate and soil (Appendix 2). For instance, Alliance X is distinguished from the remainder of the *Maireana pyramidata* order by high elevation and low pH. Alliance II occurs at medium elevation and pH, whereas Alliance V occurs at high elevation and low pH, but with high organic and inorganic carbon. These three alliances are restricted to the highest part of the ranges. The very large Alliance III, which occurs over most of the ranges, and onto the Murray Plains, occurs at medium elevation, with medium pH, and high organic and inorganic carbon. Alliances IV and VII, which were floristically intermediate between the two chenopod orders also tended to occupy central positions on the environmental axes, so are characterised by medium values of most environmental variables. Within the *Maireana astrotricha* order, the alliances are also divided on a combination of climatic and soil characteristics. The very large Alliance VI is characterised by low-medium elevation (and, by inference, rainfall), medium pH and high sodium. The closely related Alliance IX, a sparser version of VI, tends to occur on soils of higher pH. Alliance VIII occurs at low elevation and rainfall, on sandier soils of high sodium and low phosphorus, in the far north-east corner of the study area. The sandier soils of this alliance means that it is therefore slightly more mesic than the rest of the *Maireana astrotricha* order, supporting taller shrubs such as *Dodonaea viscosa angustissima*, *Heterodendrum oleifolium*, and *Atriplex nummularia*. *Eucalyptus largiflorens* may be a relict of the last pluvial period, lining the creek-beds and lagoons where water floods northwards towards Lake Frome.

Two major associations of the *Maireana pyramidata* order of the chenopod formation, D and E, are separated by the presence of limestone and degree of run-off. *Maireana* *sedifolia*, the dominant of D, prefers high inorganic carbon, and high run-off. *Maireana pyramidata*, the dominant of E, does not appear to respond to edaphic variables, but only to rainfall. It is obviously tolerant to a wider range of edaphic variables than *Maireana sedifolia* . Association N also occurs occasionally in complex with D and E, although it is more characteristic of the *Maireana astrotricha* order. Its dominants, *Maireana astrotricha* and *Atriplex vesicaria*, are characterised by high soil sodium.

Local topography also plays a part in causing vegetation mosaics (Appendix 2). For example, Associations L and J occur on the Frome Plains in areas of run-on (Figure 7.2). This supports anecdotal reports that *Rhagodia spinescens*, one of the dominants, prefers occasional flooding. In run-on areas with high sodium soils, this association may be replaced by Association M, which includes *Atriplex vesicaria, Cassia nemophila coriacea, Eremophila longifolia* and *Eremophila sturtii*. Association Q, dominated by *Eucalyptus camaldulensis* and the exotic woody plant *Lycium ferocissiumum*, also occurs in areas of local run-on, but with lower sodium and higher phosphorus. This confirms the view of Humphries *et al.* (1991), that drainage areas are more prone to exotic invasions.

Association O, dominated by *Sclerochlamys brachyptera* and *Sclerolaena ventricosa* is characterised by a history of heavy grazing. It is possible that these species are well-adapted to survival on the clay-pans and scalds caused by bush removal and erosion. It is interesting to note that *Atriplex vesicaria* is present in areas subject to past grazing. This supports the findings of Eldridge (1990), that *Atriplex* can recover population levels after heavy grazing. *Cassia nemophila platypoda, Casuarina cristata, Enchylaena tomentosa, Eucalyptus cyanophylla* and *Maireana sedifolia* also had denser populations in areas which had not been heavily grazed in the past, but this could be an effect of multicollinearity. All of these species occur more commonly in the south-east corner of the study area, which was not settled for pastoralism until much later than other areas, and therefore has a history of low grazing intensity.

DISCUSSION

The importance of various moisture-related variables such as elevation (which controls rainfall) and coarse fraction of the soil supports Wood's (1937) theory that both climate and edaphic variables control the vegetation of arid South Australia. It also lends support to the theory that ranges of hills in the Australian arid zone represent refugia of mesic-adapted vegetation, which is all that remains from past pluvial periods (Crocker & Wood, 1947); see Chapters 4 and 5. The plains, with lower rainfall and clay soils of recent origin are harsher environments for plants (see Chapter 4). These soils bear the more recently-developed xeric vegetation, demonstrating how recent geological events can be an important factor in governing vegetation distribution. The geology and subsequent landforms also control rainfall, which has further refining effects on the vegetation. The predominance of landscape variables in controlling vegetation distribution is similar to that observed in the Kalahari desert (Belsky, 1989). These results are a demonstration that edaphic control is largely exercised through soil texture, which in turn controls water availability to plants. In deserts, where water is supplied only very erratically by rainfall, soil factors are therefore able to override climate, supporting the theories of Walter and Stadelmann (1974).

Within alliances, associations are divided primarily on soil and other micro-characteristics, in line with Wood's view of the edaphic complex (Wood, 1939). For instance, within Alliance I, Associations A and C occur on sand-dunes and swales respectively, A on deeper sands of low pH, and low phosphorus. Being deeper sands, the dunes support a more mesic vegetation of *Eucalyptus* and *Triodia*. Both of these species are sclerophyllous, supporting the theory that sclerophylly is an adaption to low nutrients (see Chapter 5). Within the mallee formation, where limestone occurs near the surface, can be found inliers of Association D, dominated by *Maireana sedifolia* and *Casuarina cristata*. Since the sand-dunes have been formed in very recent geological time, the importance of such non-equilibrium events as the movement of sand-dunes in determining vegetation distribution is demonstrated.

These results support the possibility of speciation of the closely related taxa *Maireana sedifolia* and *M. astrotricha* by adaptation to separate edaphic habitats as postulated in the discussion section of Chapter 7. As predicted, *M. sedifolia* and *M. astrotricha* are ecologically quite distinct, *M.astrotricha* being much more xeric-adapted than *M. sedifolia.*

Past grazing events are another non-equilibrium variable which has affected vegetation. The increased density of the small prickly shrubs *Sclerochlamys brachyptera* and *Sclerolaena ventricosa* support the results of Andrew and Lange (Andrew, 1978; 1986a), who found that the proliferation of *Sclerolaena* was one of the earliest events in the development of a piosphere (Chapter 5).

CONCLUSIONS

Environmental data analysed by a combination of association, canonical correlation and multiple regression was found to be highly effective in explaining quite complex vegetation patterns. DCCA was useful in an initial exploration of the data, by summarising the effects of environmental variables on the vegetation associations, whereas multiple regression was useful in deducing explanations of individual species distributions. It was found very valuable to interpret the results of the environmental analyses by adding them to the framework of classification and ordination analyses already performed on the vegetation data, since a high level of explanation was achieved. The combination of various methods, both exploratory and reductionist, as discussed in Chapters 2 and 3, was once again found to be a very efficient method of summarizing and explaining ecological information.

Geological history, by controlling landform, rainfall and soils, has an important effect in determining vegetation pattern in eastern South Australia. These patterns confirm similar findings in the Kalahari (Belsky, 1989), and confirm Wood's (1937) belief that soil variables are responsible for the mosaic patterns observed between vegetation associations. Edaphic variables are capable of over-riding climatic variables, which is illustrated by the occurrence of *Eucalyptus* and *Triodia irritans* on sands at low rainfall, and again on siltier soils in the ranges at high rainfall.

This study is unusual in demonstrating that a more recent non-equilibrium variable, grazing history, also has effects in controlling vegetation pattern. The effects of grazing and associated variables are examined more fully in Chapter 9.

CHAPTER 9:
PERENNIAL POPULATION DYNAMICS

INTRODUCTION

The emergence of woody weeds as a problem (Chapter 5) indicates that population dynamics of perennial plant species are an important area of research in the rangelands of eastern South Australia and elsewhere. This reflects a general trend towards increased emphasis on autecology and population dynamics, since it is now recognized that studies which merely describe vegetation patterns are lacking the important dimension of time (see Chapter 3).

Variables which can cause disruption of age and stage structures are very important, because quite small perturbations can have dramatic effects on the long-term survival of plant populations (Harper, 1977). The events surrounding the entry of new individuals into populations represent a critical phase in the maintenance of those populations. The effects of habitat and other species may operate mainly through modification of conditions for establishment, rather than through resource availability to adult plants (Grubb, 1977). Two terms used to describe the process of entry are recruitment, when seedlings are established from seed, and regeneration, the overall successful entry of new individuals into populations (Harper, 1977). An explanation of these events may shed considerable light on the success or otherwise of the population, and is a focus of this part of the study. Some of the variables affecting recruitment and regeneration are discussed below.

Because plant species have relative palatability to polyphagous herbivores (animals which include many different plant species in their diet), herbivory can be extremely important in determining the relative abundance of different species in a habitat (Harper, 1977). The effects of the four main vertebrate herbivores present in the study area - sheep, rabbits, goats and kangaroos - on vegetation is discussed in detail in Chapter 5, and can be summarised as follows. The impact of sheep grazing upon native chenopod vegetation has been well documented, particularly the development of high levels of change associated with heavy grazing impact close to watering points. Sheep are polyphages, and are known to be highly selective in their dietary preferences (Harper, 1977; Maywald, 1993). Rabbits are often cited as the most important herbivore affecting regeneration of native trees and shrubs, in spite of the somewhat equivocal evidence for this. Little is known about the effects goats have on native shrubs, though once again the deleterious effects of browsing by goats on populations of woody species is usually taken as an *a priori* assumption. It has been shown in the past that kangaroo diets are comprised largely of grasses, so it has always been assumed that kangaroos do not have a major impact on shrub and tree populations. A study comparing the effects of these herbivores on regeneration of woody perennial plants should provide very valuable information for rangeland management in the chenopod shrublands of South Australia.

It is known that climatic variability has important effects on community structure, but it has usually been assumed that climatic variables are distributed evenly around a mean, and that there is no directional change. However, there has always been directional change in climatic variables (Davis, 1986), such as the increase in rainfall in the second half of this century (see Chapter 4). There are also concerns that recently elevated levels of CO_2 may have effects on vegetation composition and distribution (Steffen *et al.*, 1992). It is known that although animal populations are able to track climate closely, communites of long-lived sessile organisms such as trees and shrubs react much more slowly to changes in climate, and may take thousands of years to reach equilibrium with the new environment. Biotic factors such as seed dispersal, establishment and competition from established vegetation are factors which limit the speed at which plant populations can track climate (Davis, 1986). Consequently, in a continually changing climate, plant populations may always be at disequilibrium, and mature populations may be persisting in conditions which no longer favour recruitment and regeneration. An examination of the correlation of edaphic and climatic variables with regeneration success are also important variables in population dynamics.

The aims of this part of the study were:

> By studying the present population structures, to determine the level of recruitment success in a range of woody perennial plant species, and hence to determine which species are likely to be increasing in the landscape, and which may be decreasing.
>
> To identify woody species which are susceptible to grazing by introduced herbivores
>
> To identify species which are unaffected by grazing, or even promoted by it, and thereby having the potential to increase in the grazed landscape, and possibly to be seen as "woody weeds".
>
> To ascertain if other historic and edaphic variables affect recruitment in these plant species.

METHODS

The following section outlines a stratified method of sampling populations of a range of perennial species at sites subjected to varying grazing levels of the four main vertebrate herbivores: sheep, rabbits, goats and kangaroos. Additional data were collected of a range of edaphic and climatic variables so that the interactions of these variables with grazing could be ascertained.

Stratification of grazing levels

Effects of herbivory have not often been studied quantitatively, because browsing and grazing effects are often very subtle and difficult to recognize (Mueller-Dombois & Ellenberg, 1974). Watkinson (1986) states that only by experimentally perturbing natural populations can the role of herbivores be fully understood. The use of exclosures, areas fenced and protected from grazing to act as controls, as used by Lange & Graham (1983), is a widely accepted manipulative technique recommended for studying the role of predators on plants (Mueller-Dombois & Ellenberg, 1974; Harper, 1977). However, given the very long life-spans of many of the perennial species under study, such experiments have to be run for many years before they can be read and meaningful information obtained. Fortunately, there exist within the past and present management regime of eastern South Australia, discrete areas which have for various reasons been exposed to consistently different levels of grazing by various herbivores. Most pastoral leases contain paddocks or other areas which have been lightly grazed or ungrazed, usually because of lack of available stock water, or distance from the station headquarters, which creates difficulty in management of livestock. In addition, Osborn *et al.* (1932) describe virtually ungrazed areas of paddocks which lie beyond the piosphere, where the vegetation is in a more or less virgin state. The use of grazing gradients around watering points has been previously used to design experiments requiring different levels of grazing by Graetz (1978), and is a stratified technique (Kent & Coker, 1992) of experimental design recommended by Andrew (1988) and Stafford Smith & Pickup (1990). These can be treated as a set of "natural" exclosure experiments, and the results "read" by comparing the age-stage structures of perennial plant populations within and without them as described in Chapter 3. In this way, the effect of grazing can be separated from that due to other ecological factors such as herbivory by native, exotic and feral animals and edaphic variables (Mueller-Dombois & Ellenberg, 1974). This technique has previously been used in the rangelands of Western Australia by Hacker (1987). Sites which were ungrazed by domestic herbivores were selected by a combination of consultation with pastoral managers, and searching topographic maps for areas in paddocks beyond the piospheres generated by watering points. Ungrazed populations of each species located by this method were paired with the closest possible grazed population whenever possible in an attempt to minimise confounding environmental effects, following a procedure developedby the author and associates on the Jornada Experimental Range at Las Cruces in New Mexico (Kerley *et al.*, 1993). The above technique was efficient in locating sufficient numbers of ungrazed or little grazed sites, which occur at low frequency in the landscape. A random sampling procedure would have been a much less efficient method of obtaining a large enough sample size.

Collection of population data

At each site, and within a population of each species present, individuals were scored into one of 9 possible stage-classes (Figure 9.1). This method of developing a stage-structure for each population is closely related to the phenological condition classes described by Mueller-Dombois and Ellenberg (1974), where annual plants were divided into 11 classes depending on their stage in the life-cycle. The method had to be adapted to suit a range of long-lived perennial plants, so the number of phenological condition classes were reduced to nine, which could be readily used for a range of perennial species. These stage-classes closely resembled the ten-state classification of Gatsuk *et al.* (1980), which was designed to be used for over 100 species of perennial and annual plants The major difference is the inclusion of a class of deadfall (lying dead) individuals in this study. These were included because even decaying remnants of woody plants can give a good indication of past history of the population (Ogden, 1985). Stage-class distributions have previously been used to study long-lived perennials in South Australia by Lange & Purdie (1976) and Ireland (1992).

Populations were sampled by a modified "random walk" method (Kent & Coker, 1992) as outlined by Ireland (1992). At each site, the walked route left the vehicular access track at an angle and described a loop of several hundred metres back to the starting point. Individuals were recorded within a field of view in which seedlings and juveniles could be reliably observed (about 20 m to either side of the route). The arc described was as large as required to encounter at least 10, but preferably about 50 individuals, which was a sufficient number for stable population statistics to be calculated. Care was taken to avoid sampling adjacent areas with different topography or soil type, so that the population statistics collected could be attributed to the effects of the variables at the site. Exceptions to the rule that 10 to 50 individuals should be scored were the 17 species listed in Table 9.1, which occasionally occurred in the landscape at a very low frequency, particularly at ungrazed sites. Even by extending the searched area to the maximum size possible without overlapping adjacent and very different environments, only 3 to 9 individuals could be

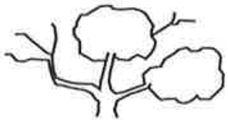
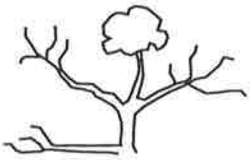
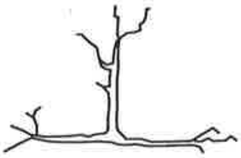
LIFE-STAGE	DESCRIPTION	APPEARANCE
I SEEDLING/SUCKER	≤ 20 cm high single stem often with juvenile foliage	
II BUSHY JUVENILE	branching apparent often multi-stemmed rounded shape	
III OLDER JUVENILE	one stem gaining dominance	
IV YOUNG MATURE	crown not fully formed reproductive full size not reached	
V MATURE	full size crown fully developed fully reproductive growth vigourous	
VI OLD MATURE	canopy spreading dead branches appearing growth vigour decreased	
VII SENESCENT	many dead branches some fallen branches pronounced canopy spread	
VIII STANDING DEAD	completely dead still standing many branches fallen	
IX LYING DEAD	whole tree fallen over many branches rotting	

Figure 9.1

Nine life-stage classes recognizable in woody perennial plant species, the rules for assigning individuals to classes, and a theoretical diagram of each stage. Adapted from the phenological condition classes of Mueller-Dombois (1974). Mueller-Dombois and Ellenberg (1974).

Table 9.1

Woody perennial species which occasionally occur in the landscape at very low frequency. Within these species, populations with low numbers of individuals (3 - 10) were not discarded from the data set.

LOW FREQUENCY SPECIES
Acacia oswaldii
Cassia artemisioides
Dodonaea viscosa
Eremophila longifolia
Eremophila scoparia
Eremophila sturtii
Eucalyptus dumosa
Eucalyptus oleosa
Exocarpos aphyllus
Grevillea huegelii
Hakea leucoptera
Heterodendrum oleifolium
Lycium australe
Lycium ferocissimum
Pittosporum phylliraeoides
Santalum lanceolatum
Schinus molle

found in a given locality. Field observations indicated that many of these species are capable of becoming more frequent in the landscape following severe grazing. Therefore, to ignore these low number sites may have resulted in loss of important information. Consequently, populations with low numbers of individuals were included in the results for these 17 species.

Plant recruitment tends to occur episodically, and following the occurrence of a certain set of conditions for each species, the "regeneration niche" of Grubb (1977). This means that there is both spatial and temporal patchiness in regeneration patterns, causing high background variability of the stage-structure profiles between sites (Clark, 1991). This background variability tends to mask the effects of herbivores, the investigation of which was the aim of the study. Therefore, enough individual populations had to be measured for each species to ensure that the final data were representative of the metapopulation (the sum of all the populations for most species) and indicative of its response to herbivory. Preferably, at least 10 sites (with a minimum of 6) were located for each species, with roughly equal representation of heavily and lightly grazed areas, (with a minimum of 3 each). Where this minimum number of sites could not be located for certain species (*Acacia colletioides, Codonocarpus cotinifolius, Cratystylis conocephala, Eremophila glabra glabra, Eucalyptus intertexta, Pimelea microcephala, Sida calyxhymenia* and *Triodia irritans*), summary statistics only were calculated and the results must be interpreted with caution.

At some sites, standing dead individuals which had been killed after successful regeneration were present . Individuals of stages 4 and 5 had often been cut for fence-posts in species such as *Acacia aneura*, *Callitris columellaris* and *Casuarina cristata.* In *Acacia aneura* this was also occasionally due to ring-barking by rabbits, especially affecting individuals of stages 2 or 3. Such individuals were omitted from the data for analysis, because their inclusion in the age class at which they died would tend to make that class disproportionately large. Distortion of results would also occur if these individuals were included in the standing dead category (stage 8), which otherwise contains only individuals which have senesced and died after progressing through the intervening life-stages.

However, the overall effects of ring-barking by rabbits and wood-cutting are still present in the data, because of the resulting lowered proportions of individuals in the older stages.

Individuals of some species are of a small enough size to be completely removed by grazing if sufficiently palatable as adults. Total loss of populations following higher levels of past sheep grazing (detected from station records and historical maps as described below) was observed by cross-fence comparisons in *Atriplex vesicaria, Cassia nemophila coriacea,* and *C. artemisioides*. Consequently, there is a strong bias against grazed sites in the raw data for these species, and difficulty was experienced in locating sufficient grazed sites with persistent populations. In order to counteract this effect, "zero" sites (showing a value of zero for all age classes) were included wherever it could be stated with certainty that populations would have once been present on cross-fence grazed sites. Criteria were that other site conditions such as soil texture, and topography had to be the same at the zero site as for its matching pair, and there was to be no other apparent reason why the species would not be present at both sites.

Individuals were easy to identify in species which reproduce solely by seed, each individual having arisen from a seedling and thus being a genetically distinct individual or genet as defined by Silvertown (1993), usually spatially well separated from its parent. However, many Australian arid zone perennial plants regenerate largely or completely by vegetative means (Chapter 5). Exploratory excavations revealed that this was the case for several species in the study area including: *Grevillea huegelli; Myoporum insulare; Casuarina cristata; Eremophila longifolia; Lycium australe* and *Heterodendrum oleifolium*. These species appeared to be reproducing almost exclusively vegetatively, by root suckers. This means that the resulting populations are really only clones of one or relatively few genetically discrete individuals, or ramets following the definition of Silvertown and Doust (1993). Within these clonal species, clonally produced parts with their own roots, and independent existence, or ramets (Silvertown & Doust, 1993), were treated as individuals. Regeneration was also vegetative in the mallee-forming species of *Eucalyptus*, where suckering usually occurs at or above ground level from a well-developed ligno-tuber

(Lacey & Johnston, 1990). In this case ramets are not capable of independent existence, so clumps of *Eucalyptus* were therefore treated as single, multi-branched individuals.

Values for recruitment and regeneration were calculated as follows. The presence of juveniles (life-stages 1, 2 & 3), can be used as an indication of recruitment success. However, individuals of this size cannot yet be said to have successfully entered the population, since they are still in a size range where they can easily be destroyed by grazing or lost through density-dependent competition. Hence their presence does not necessarily indicate that present and recent conditions have been adequate for long-term successful regeneration. Observations in the field were that grazing by domestic and other herbivores on any given population tended to be very episodic. It is therefore quite possible for juvenile individuals of life-stages 1, 2 or 3 to be present for several years before being removed by grazing, competition, or unfavourable seasonal conditions. It is possible that ENSO-driven recruitment events are infrequent enough, and that juvenile mortality is frequent enough to ensure that few if any of these individuals ever reach maturity, giving a Type III survivorship curve with high juvenile mortality and much lower mature mortality as described by Begon *et al.* (1990). Consequently the numbers of juveniles were not considered to be a useful indication of the overall level of regeneration. Regeneration success in each population was therefore calculated by dividing the total number of successful entrants into the population (young mature individuals; stage 4) by the total of all the non-juvenile individuals (young mature, mature, old mature, senescent, standing dead, and lying dead; stages 5 - 9). A regeneration percentage value of 17 was considered sufficient to allow survival of a population, on the following basis. Type III survivorship as described above was assumed, so that once an individual had gained the young mature stage, it was expected to have a very low likelihood of mortality. It was also assumed that the stage-structure approximates the age-structure, and that individuals move at a reasonably constant rate through subsequent stages. Thus, at any given time, there should be one young mature individual for every individual of young mature through to lying dead (six stages). A ratio of 1:6 for sufficient recruitment can therefore be expressed as 16.67%, rounded to 17%. Although these assumptions are never likely to be met in real

1 Although rabbit populations fluctuate markedly between years (see Chapter 5), it is possible to identify areas where past rabbit populations have been high. Low rainfall in the study area means that such evidence of high rabbit populations as scratchings, empty burrows and dung-heaps remain in place for many years. It is obvious from the localized distribution of these signs that such areas are prone to recurring rabbit plagues, whereas other areas are not.

plant populations (Harper, 1977), this value gives some indication of whether regeneration is at sufficient levels to ensure population maintenance.

Collection of environmental data

Twelve environmental variables were recorded at each site, and coded as shown in Table 9.2. A brief description of the methods for measuring each variable and the reasons for measuring it follows.

Sheep grazing intensity was estimated from station records, or by calculating the distance to the nearest watering point using survey maps (NATMAP, 1984c; NATMAP, 1984b; NATMAP, 1984a; NATMAP, 1985a; NATMAP, 1985b; RASC, 1987). This was based on the assumption that sheep grazing intensity is highest near watering points, the "piosphere effect" of Lange (1969; 1985). Grazing intensity of the other three herbivores, rabbits, goats and kangaroos, was estimated by observation at the site, mainly according to the presence of recent spoor (tracks and dung).[1] Sheep grazing history for the late nineteenth and early twentieth centuries was determined by referring to historical maps housed by the South Australian Department of Environment and Natural Resources (SADENR) (CCL, 1857 - 59; 1867; 1868; 1880; 1893; 1898; 1901; 1913; 1923; 1931; c. 1880). When estimating grazing history, particular attention was paid to the location of wells, yards, shepherds' huts, stock routes and homesteads. Location of old wells was particularly important, because of the grazing practices prevalent at the time, as recorded by Wilkinson (1849). Before wire fences and galvanized water-pipe came into use, thus enabling the subdivision of paddocks, and before the dingo-proof fence was built, sheep had to be kept together in flocks and shepherded between the few watering-points and pasture. These practices tended to result in severe devastation to vegetation around watering-points (Waite, 1896), so location of these old watering-points is usually correlated with the most severe grazing pressure on the vegetation in the past.

Bush density was estimated in the field as a percentage cover score, and converted to an approximately logarithmic scale in order to minimise errors of estimation as described in

Table 9.2

The following twelve environmental variables were recorded at each site, and assigned ordinal classes, coded as shown. The abbreviations for the variables as used in subsequent results tables are also shown.

(1) SHEEP GRAZING, PRESENT, 1950 - 1990 (From Station Records & Topographic Maps) (SHEEP)

0 = nil (ungrazed)
1 = light or intermittent (>5km from water, or rarely stocked, old spoor only)
2 = moderate (within 5km of watering point, fresh spoor)
3 = heavy (within 1km of watering point, frequent fresh spoor)
4 = severe (within 500m of watering point/heavy fresh spoor)

(2) RABBIT GRAZING, PRESENT (RBTS)

0 = nil (dung, soil scratchings absent)
1 = light or intermittent (old dung, soil scratchings infrequent)
2 = moderate (fresh dung and scratchings present, more frequent)
3 = heavy (100 m - 500 m from warren)
4 = severe (within 100 m of warren)

(3 & 4) GOAT & KANGAROO GRAZING (GTS & KROOS)

0 = nil (dung, tracks absent)
1 = light or intermittent (old dung, tracks infrequent)
2 = moderate (fresh dung and tracks present)
3 = heavy (frequent fresh dung and tracks, animals may be seen)
4 = severe (heavy fresh dung and tracks, animals usually seen)

(5) BUSH DENSITY (Estimated Percentage Projected Cover) (BDEN)
0 = absent
1 = 0 - 1%
2 = 1 - 2%
3 = 2 - 5%
4 = 5 - 10%
5 = 10 - 100%

(6) TOPOGRAPHY (TOP)
1 = creeks, watercourses, swamps, floodplains
2 = plains, plateaux
3 = rises, hill flanks
4 = low hills, sand-dunes
5 = hilltops, ridges

(7) SOIL TEXTURE (TEX)
1 = clay
2 = silt, loam
3 = sand

(8) CHEMICAL CRUSTING (observed on the soil surface) (CHEM)
0 = zero (no chemical crust present)
1 = mild (chemical crust cover present <2%)
2 = moderate (chemical crust cover ≥ 2 %)
3 = severe (chemical crust cover ≥ 20%)

(9) SHEEP GRAZING, 1860 - 1900 (From Maps) (18HD/1800)
0 = nil (land not taken up)
1 = light or intermittent (stock routes etc)
2 = moderate (available for pastoral use)
3 = heavy (within 20 km of wells)
4 = severe (within 5 km of wells)

(10) SHEEP GRAZING,1900 - 1950 (From Station Records & Maps) (19HD/1900)
0 = nil (ungrazed)
1 = light or intermittent (>5km from watering point, or rarely grazed)
2 = moderate (within 5km of watering point)
3 = heavy (within 1km of watering point)
4 = severe (within 500 m of watering point)

(11) WIND EROSION (WIND)
0 = zero (topsoil intact)
1 = mild (slight topsoil lost)
2 = moderate (topsoil > 5% lost)
3 = severe (> 50% topsoil lost)

(12) SOIL DISTURBANCE (Degree of mechanical disruption to the soil profile) (DIST)
0 = zero (no apparent disturbance)
1 = mild (e.g. fence-post holes)
2 = moderate (e.g. road grading)
3 = severe (e.g. road cuttings)

Chapter 7. Competitive advantage of established individuals can result in density-dependent decreases in fecundity and increases in mortality (Harper, 1977; Silvertown & Doust, 1993). This in turn means that competition may have some effect in suppressing recruitment and regeneration both within and between species.

A number of edaphic (soil) variables have been suggested as important in controlling recruitment and regeneration processes. Osborn (1935) noticed that seedlings were more abundant amongst fallen bushes and on soil mounds, suggesting that texture variables may be important for seedling establishment. Woodell (1990) suggested that either or both of topography and soil texture may have some effect on recruitment success in *Acacia burkitti* in the chenopod shrublands of South Australia. An important effect of topography is to vary the amount of extra water available through run-on. Areas of low topography also tend to retain pools of water after rain, and support richer growth of ephemerals. Herbivores tend to concentrate their grazing activities in these areas (Roberts, 1993). For this reason, topography was scored on a scale ranking sites prone to flooding with low scores and non flood-prone sites high scores. Soil texture also affects water availability, with sandy soils providing more available water than clays (as described in Chapter 4). Consequently soils with large particles can get much drier before wilting point is reached than soils with fine particles (Jeffrey, 1987). Soil texture was graded according to particle size; sand (having large particles) had the highest score, and clay, with fine particles, the lowest. Soils at some low-lying sites were observed to have a chemical crust at the surface. Since this may have an effect on germination and survival of seedlings, the severity of chemical cursting was also scaled and recorded. Wind erosion, as observed by loss of topsoil, results in reduced depth of seed-bed which may affect recruitment, so severity was recorded using a similar scale. Any event which disturbs the soil may damage roots and bury, expose, or damage seed in the seed-bank, and was included as a variable likely to affect recruitment. Soil disturbance was most often encountered on roadside sites and near fences due to the use of heavy machinery for construction and repair, and was also recorded in classed order of severity.

Rainfall was not considered as a variable, since rainfall records (Chapter 4) show that rainfall events of a magnitude necessary for germination and survival of perennial species tend to be widespread ENSO events, affecting all of the study area and beyond. As such, they were considered to have a consistent effect over the study area, and were therefore unlikely to play a role in differences between populations within a species.

ANALYSIS METHODS

Pearson correlation coefficients were calculated for the environmental data to ascertain the degree of multicollinearity between variables since the correlation between variables is important in interpreting the results of multivariate studies. The relationships of these variables to both recruitment and regeneration success were also tested using direct pearson correlation coefficients. The percentage recruitment data were arcsin transformed prior to calculation of the correlations, a procedure recommended by Zar (1984). This was done because percentage data form a binomial rather than a normal distribution, with the greatest deviation from normal at large and small percentages. Such a distribution would invalidate any parametric statistical test (such as pearson correlation), which includes assumptions of normality and homogeneity of variance. Although some distortion occurs as a result of the arcsin transformation, the only alternative would have been to use a non-parametric equivalent. Non-parametric tests are usually more conservative and consequently less powerful (Kent & Coker, 1992). Such tests have a lower likelihood of rejecting a true null hypothesis (Type I error), but a correspondingly higher likelihood of accepting a false null hypothesis (Type II error) (Zar, 1984). Since my aim was to detect patterns within the data, it was considered undesirable to sacrifice power for a lower likelihood of Type I error in this case. Pearson Correlation Coefficients were performed using the computer program Statview (Feldman & Gagnon, 1988).

Simple correlations do not give any indication of the complex nature of environment-environment and consequently, environment-plant interactions. Multivariate regression (as described in Chapter 8) was used to give an indication of the variables most important in determining recruitment and regeneration of the 59 species for which population data were collected. Multiple linear regression was performed using the analysis package GENSTAT (1987). A linear model was constructed, by adding variables step-wise, in order of their individual power of improving the null model, as recommended by Nicholls (1991a). The environmental data are in the form of classed variables, which would normally require their treatment as factors in GENSTAT and an analysis of variance performed rather than multiple linear regression. However, each factor level results in a loss of one degree of freedom, so that for the number of factors and levels required, there would be very little likelihood of developing significant models. For this reason, and because the variables were originally continuous ones which had been classed for convenience, the classed levels were treated as continuous variables.

Because one of the main aims was to ascertain if grazing by domestic herbivores has an effect on regeneration, the difference in mean regeneration between nil and very lightly grazed (present sheep-grazing intensity classes 0 and 1) and moderate to heavily grazed (sheep grazing classes 2, 3 and 4) was calculated, and expressed as absolute values. The decreasing or increasing status of the metapopulations was determined by noting whether these absolute differences were positive or negative respectively. Significance of the differences in means was calculated by t-test using Statview (Feldman & Gagnon, 1988) and performed on arcsin transformed data for the reasons given above.

RESULTS

Multicollinearity of variables

The correlation table of environmental variables indicates a very high level of multicollinearity within the environmental data, and the variables measured form a complex web of interactions (Table 9.3 and Figure 9.2). Both present and past sheep-grazing are key variables, being negatively or positively correlated with almost every other variable. Current sheep grazing is highly correlated to 19th century and early 20th century grazing, both rabbit and kangaroo grazing, and wind erosion. It is negatively correlated to goat

Table 9.3

Pearson correlation coefficients of variables suspected of affecting recruitment and regeneration in woody perennial plants. Sample size is 239 sites. Significant r-values ($r \geq 0.128$, df = 238, $p = 0.05$) are marked in bold italics. Full names of abbreviated variables are listed in Table 9.~~3~~.
2

	SHEEP	RBTS	GOATS	KROOS	BDEN	TOP	TEX	CHEM	EIGHT	NINE	WIND	DIST
SHEEP	1.000											
RBTS	***0.285***	1.000										
GOATS	***-.0.146***	***-0.394***	1.000									
KROOS	***0.245***	0.093	0.084	1.000								
BDEN	***-0.312***	***-0.133***	-0.070	0.051	1.000							
TOP	***-0.164***	***-0.142***	0.100	0.040	***0.133***	1.000						
TEX	-0.070	0.011	0.007	***0.141***	***-0.139***	***0.129***	1.000					
CHEM	0.100	***0.142***	***-0.134***	-0.112	-0.089	***-0.239***	-0.024	1.000				
18HD	***0.169***	***0.388***	***-0.520***	***-0.160***	-0.026	-0.025	-0.122	***0.288***	1.000			
19HD	***0.482***	***0.377***	***-0.145***	0.100	***-0.380***	***-0.141***	-0.083	***0.197***	***0.309***	1.000		
WIND	***0.464***	***0.288***	***-0.180***	0.108	***-0.559***	-0.048	0.080	***0.227***	***0.289***	***0.543***	1.000	
DIST	***-0.372***	0.144	***-0.171***	***-0.342***	0.048	***-0.134***	-0.059	0.012	0.126	0.011	-0.048	1.000

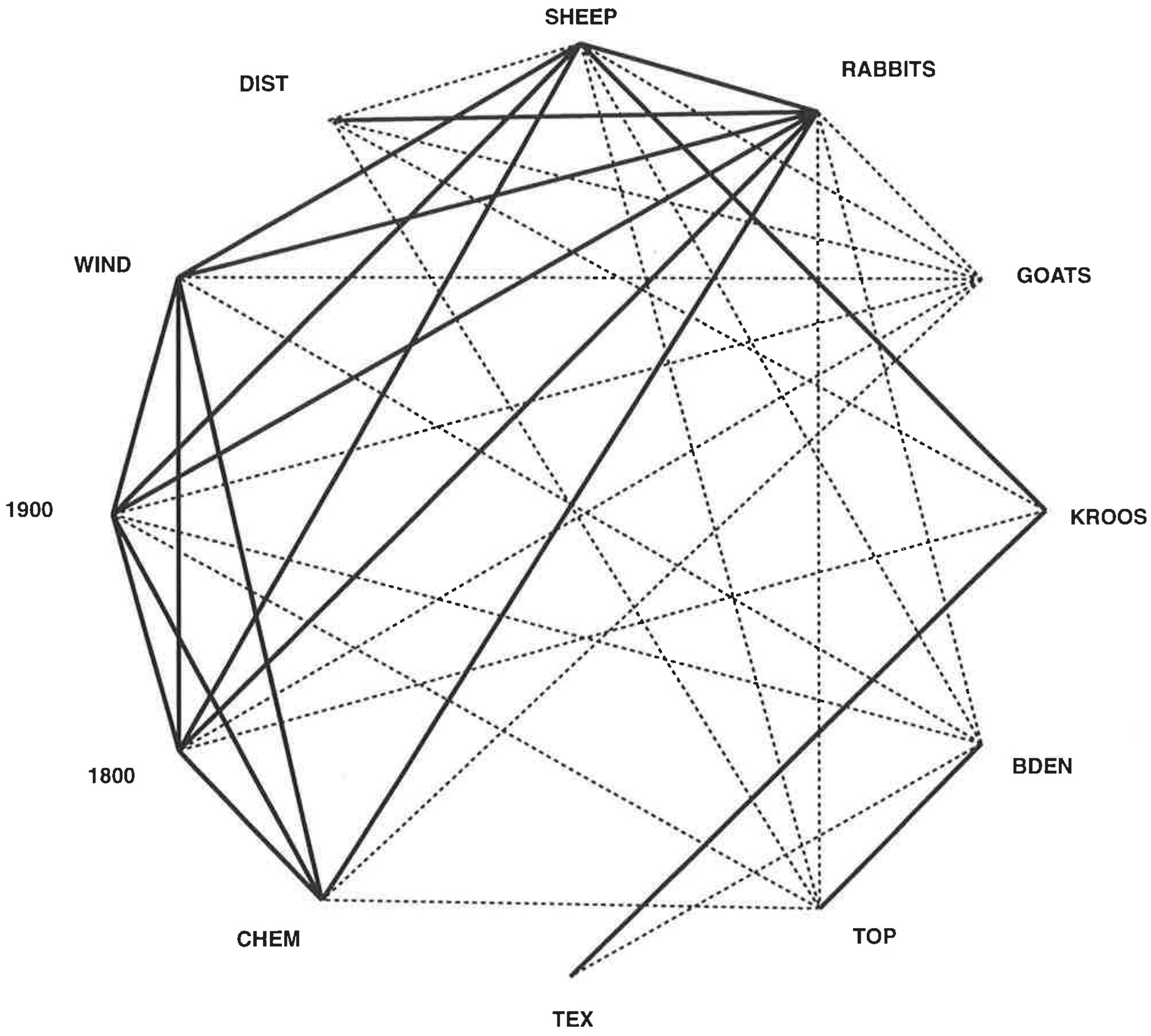


Figure 9.2

Plexus diagram showing relationships of variables suspected of affecting recruitment and regeneration. Solid lines indicate positive correlations and dotted lines indicate negative correlations. R values are given in Table 9.2.

grazing, topography, bush density, and soil disturbance. Although chemical crusting is not directly related to sheep grazing, it is related to past grazing history. Soil texture shows least correlation with other variables, but it is still positively correlated with kangaroo grazing and negatively correlated with bush density.

Correlation of recruitment and regeneration with grazing and environmental variables

Results of the pearson correlations of environmental variables with recruitment and regeneration are shown in Tables 9.4 and 9.5. The results of the multiple regressions are shown in Tables 9.6 and 9.7, including t-values for the individual variables (indicating the direction and degree of contribution to the final model), and F-values for the final model (indicating the degree of improvement of the final model over the initial null model). In some species, the null model could not be improved by addition of any variable, indicating that none of the measured variables had any power in explaining the degree of recruitment. In such cases, no F-value was obtained. Mean regeneration values at sites grazed and ungrazed by domestic herbivores are shown in Table 9.8, with absolute differences between the means marked as decreases or increases. Although only 8 of the 59 species show significant decreases in regeneration in response to grazing, 41 showed absolute decreases, intuitively more than would be expected by chance. Only 9 species showed an increase, none of which was significant. The results of Tables 9.4 - 9.8 showed that many of the variables with explanatory power in recruitment and regeneration were those of herbivore-grazing, or correlated to herbivore-grazing. These results are combined and summarised in Tables 9.9 and 9.10, Table 9.9 showing the species negatively affected by grazing and grazing-related variables, and Table 9.10 showing the species for which grazing had positive or no effect, together with those species for which insufficient sites were located to perform any more than summary statistics. Important features of these results are discussed in the following paragraphs.

Table 9.4

Pearson correlation coefficients showing the relationship of a range of grazing and environmental variables to percentage recruitment of juveniles. Percentage juveniles = classes 1 2 3 / 1-9. Significant values ($p \leq 0.05$) at the relevant degrees of freedom (df) and critical r-values for each species are underlined. nc = not calculated, values all equal for that variable. nj = no juveniles found in any population. - = too few sites (1 or 2) to perform correlations. Full names of abbreviated variables are shown in Table 9.3.2

SPECIES	SHEEP	RBTS	GOATS	KROOS	BDEN	TOP	TEX	CHEM	18HD	19HD	WIND	DIST	df	R VAL
Acacia aneura	-0.427	-0.015	-0.298	-0.034	0.258	0.053	-0.015	0.040	0.306	-0.321	-0.288	0.529	41	0.301
Acacia burkittii	-0.521	-0.385	0.199	0.044	0.302	0.232	0.217	nc	-0.153	-0.310	-0.273	0.517	14	0.497
Acacia carnei	-0.350	-0.083	nc	-0.349	-0.039	0.290	0.069	-0.053	-0.209	-0.050	0.382	0.499	13	0.514
Acacia colletioides	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acacia loderi	-0.768	-0.358	0.247	-0.557	0.800	0.698	0.698	-0.557	0.039	-0.776	-0.843	-0.538	7	0.666
Acacia nyssophylla	-0.271	0.029	0.030	-0.269	-0.101	-0.267	0.883	-0.049	0.034	-0.401	-0.245	0.276	14	0.497
Acacia oswaldii	-0.553	-0.127	0.348	-0.223	0.274	0.720	0.632	-0.283	-0.041	0.180	-0.241	-0.121	10	0.576
Acacia tetragonophylla	-0.193	0.478	0.144	-0.083	0.421	0.848	-0.201	nc	-0.085	-0.378	-0.373	0.078	8	0.362
Acacia victoriae	-0.355	-0.266	-0.269	-0.107	-0.119	0.238	-0.149	-0.083	-0.027	-0.254	-0.176	0.359	28	0.361
Atriplex nummularia	-0.900	-0.743	nc	-0.452	-0.137	-0.207	0.307	0.100	-0.567	-0.847	-0.415	-0.534	6	0.707
Atriplex stipitata	0.230	-0.180	0.079	0.131	-0.050	0.240	-0.045	0.011	-0.070	-0.017	0.029	-0.031	14	0.497
Atriplex vesicaria	-0.186	-0.248	0.056	0.074	0.253	-0.114	-0.015	-0.159	-0.067	0.009	-0.116	0.093	46	0.285
Callitris collumnellaris	-0.793	-0.305	0.034	-0.166	0.229	0.243	0.042	nc	-0.373	-0.010	-0.007	0.782	13	0.514
Cassia artemisioides	-0.384	-0.428	0.202	0.291	0.395	0.691	0.156	nc	0.148	nc	-0.045	0.392	9	0.602
Cassia nemophila coriacea	-0.407	-0.108	0.225	0.351	0.222	-0.054	0.303	nc	-0.178	-0.089	0.057	-0.025	39	0.308
Cassia nemophila platypoda	-0.384	-0.499	0.376	0.234	0.233	0.074	0.016	-0.066	-0.635	-0.430	-0.249	-0.038	44	0.291
Cassinia laevis	nc	-0.657	nc	nc	nc	0.324	nc	nc	-0.657	-0.981	nc	nc	2	0.950
Casuarina cristata	-0.779	0.088	-0.362	-0.153	0.163	-0.029	0.076	nc	0.271	0.038	-0.131	0.245	39	0.308
Chenopodium nitrariaceum	0.590	-0.033	0.419	0.066	-0.045	-0.338	0.238	-0.070	0.068	0.431	0.126	-0.266	20	0.423
Codonocarpus cotinifolius	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cratystylis conocephala	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dodonaea viscosa	-0.247	-0.552	0.182	0.073	0.067	0.388	0.230	nc	-0.165	-0.492	-0.452	-0.177	25	0.381
Eremophila alternifolia	-0.340	0.049	0.486	-0.287	0.033	0.423	0.345	nc	-0.473	-0.314	-0.603	-0.228	13	0.514
Eremophila duttonii	-0.571	-0.067	-0.516	-0.310	-0.074	-0.358	0.501	nc	0.332	-0.749	-0.335	0.442	11	0.553
Eremophila glabra glabra	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eremophila longifolia	-0.327	-0.025	-0.102	0.262	0.309	0.006	0.186	0.051	0.007	-0.285	-0.012	-0.012	20	0.423
Eremophila oppositifolia	-0.406	0.304	-0.611	-0.013	-0.110	0.948	0.052	-0.321	0.724	0.352	0.119	-0.321	7	0.666
Eremophila scoparia	-0.270	-0.416	0.566	0.596	-0.305	0.510	0.269	-0.510	-0.215	-0.064	-0.150	-0.510	10	0.576
Eremophila sturtii	-0.246	-0.131	0.331	0.260	-0.134	0.115	0.310	0.055	-0.207	0.337	0.113	-0.003	45	0.288
Eucalyptus camaldulensis	-0.023	0.224	0.381	0.144	0.185	nc	-0.154	-0.379	-0.275	0.156	-0.185	0.420	15	0.482
Eucalyptus dumosa	nj													
Eucalyptus gracilis	nj												8	0.632
Eucalyptus intertexta	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eucalyptus largiflorens	-0.152	0.708	-0.585	0.830	0.200	nc	nc	nc	0.221	-0.152	nc	nc	4	0.811
Eucalyptus porosa	0.042	0.167	0.146	0.116	0.063	-0.252	0.085	0.138	-0.147	0.609	0.167	-0.023	10	0.576
Eucalyptus socialis	-0.178	-0.220	0.285	0.069	0.185	0.323	0.202	0.218	-0.158	-0.056	0.187	-0.263	13	0.514
Exocarpos aphyllus	-0.742	0.678	0.420	-0.332	-0.092	-0.331	0.455	0.319	-0.220	-0.014	0.654	0.401	11	0.553
Grevillea huegelii	-0.391	0.205	-0.399	0.470	0.217	-0.071	-0.060	nc	0.567	0.097	0.278	nc	6	0.707
Hakea leucoptera	-0.128	0.166	-0.296	0.451	0.272	-0.176	-0.055	nc	-0.017	-0.442	-0.266	-0.282	16	0.468
Heterodendrum oleifolium	-0.521	0.125	-0.183	-0.359	0.217	-0.041	0.067	nc	0.061	-0.148	-0.201	0.815	48	0.279
Lycium australe	0.102	0.354	-0.349	-0.296	-0.263	0.052	0.049	-0.148	0.453	0.037	-0.014	-0.155	18	0.444
Lycium ferocissimum	-0.206	-0.380	nc	0.081	-0.044	-0.065	0.070	0.442	0.520	0.204	0.239	-0.338	19	0.433
Maireana aphylla	0.230	-0.232	nc	-0.261	-0.194	-0.130	-0.213	nc	-0.255	0.247	0.036	-0.210	19	0.433
Maireana astrotricha	-0.040	-0.179	0.000	0.123	0.128	0.130	-0.079	-0.041	0.038	0.070	-0.091	-0.169	28	0.361
Maireana brevifolia	-0.476	-0.254	nc	-0.738	-0.473	-0.030	0.441	-0.419	0.399	-0.372	0.732	-0.269	4	0.811
Maireana pyramidata	0.112	0.078	-0.096	0.010	-0.234	0.195	0.091	-0.072	0.146	0.200	0.235	-0.045	44	0.291
Maireana sedifolia	-0.131	0.125	0.160	-0.130	-0.295	0.288	0.003	-0.123	-0.053	0.155	-0.098	0.003	34	0.329
Myoporum insulare	-0.521	-0.892	0.808	0.447	-0.654	nc	0.222	-0.447	-0.118	-0.739	0.292	0.222	3	0.878
Myoporum platycarpum	-0.537	-0.097	-0.003	-0.027	0.397	0.040	0.488	-0.424	0.079	-0.326	-0.340	0.192	38	0.312
Nitraria billardieri	0.182	0.161	0.110	-0.308	0.205	-0.004	0.079	0.172	-0.308	0.167	-0.721	0.002	14	0.497
Pimelea microcephala	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pittosporum phylliraeoides	-0.060	0.064	0.172	-0.106	-0.370	-0.308	-0.025	0.503	0.360	-0.168	0.465	-0.005	19	0.433
Rhagodia parabolica	0.604	-0.375	0.475	-0.030	-0.193	0.053	-0.024	0.168	-0.028	0.438	0.001	-0.630	8	0.632
Rhagodia spinescens	-0.491	-0.247	nc	0.300	0.741	-0.119	-0.077	-0.340	-0.773	-0.453	-0.699	-0.189	28	0.361
Santalum lanceolatum	-0.409	0.207	nc	0.461	0.362	-0.029	-0.340	0.728	0.163	-0.119	0.403	0.041	16	0.468
Schinus molle	-0.355	0.294	nc	-0.523	-0.420	nc	0.502	0.806	0.376	0.348	0.255	-0.005	10	0.576
Sida calyxhymenia	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Templetonia egena	-0.129	-0.568	0.352	-0.206	0.102	-0.188	0.241	-0.519	-0.394	-0.575	-0.665	-0.224	11	0.553
Triodia irritans	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 9.5

Pearson correlation coefficients showing the relationship of a range of grazing and environmental variables to percentage regeneration. Regeneration = life-stage 4 / 4-9. Significant values ($p \leq 0.05$) are underlined. nc = variable not calculated, values all equal. - = insufficient sites for correlation analysis (1 or 2 sites). Full names of abbreviated variables are shown in Table 9.~~3~~.2

SPECIES	SHEEP	RBTS	GOATS	KROOS	BDEN	TOP	TEX	CHEM	18HD	19HD	WIND	DIST	df	R VAL
Acacia aneura	-0.346	-0.300	0.136	0.139	-0.191	-0.331	0.167	0.066	-0.352	-0.378	-0.382	-0.150	41	0.301
Acacia burkittii	-0.406	-0.443	0.459	-0.193	0.092	-0.062	0.181	nc	-0.440	-0.323	-0.369	0.451	14	0.497
Acacia carnei	0.124	-0.186	nc	0.021	0.329	0.262	0.076	nc	-0.183	-0.129	-0.418	-0.036	13	0.514
Acacia colletioides	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acacia loderi	-0.431	-0.610	0.175	-0.317	0.506	0.981	0.981	-0.317	-0.218	-0.661	-0.548	-0.408	7	0.666
Acacia nyssophylla	-0.534	-0.005	-0.178	-0.506	0.390	-0.013	0.604	0.029	0.133	-0.159	-0.185	0.747	14	0.497
Acacia oswaldii	0.318	0.440	-0.408	0.084	-0.002	-0.383	-0.374	-0.122	0.326	-0.067	-0.047	0.454	10	0.576
Acacia tetragonophylla	-0.449	0.385	-0.265	-0.024	0.648	0.583	-0.163	nc	0.132	-0.431	-0.283	0.536	8	0.632
Acacia victoriae	-0.304	-0.145	-0.294	-0.137	0.318	0.189	-0.322	-0.012	-0.004	-0.100	-0.252	0.353	28	0.361
Atriplex nummularia	-0.599	-0.047	nc	0.357	-0.131	0.427	-0.140	-0.286	-0.094	-0.527	-0.164	-0.183	6	0.707
Atriplex stipitata	0.157	-0.120	0.438	-0.023	-0.150	0.107	-0.482	0.215	-0.261	0.225	0.152	-0.094	14	0.497
Atriplex vesicaria	-0.079	-0.179	-0.074	0.091	0.230	-0.213	-0.108	-0.192	-0.364	-0.020	-0.000	0.106	46	0.285
Callitris collumnellaris	-0.544	-0.051	-0.110	-0.543	0.253	0.377	-0.182	nc	0.159	-0.355	-0.545	0.312	13	0.514
Cassia artemisioides	-0.384	-0.428	0.202	0.291	0.395	0.691	0.156	nc	0.148	nc	-0.045	0.392	9	0.602
Cassia nemophila coriacea	-0.548	-0.172	0.363	0.290	0.380	-0.241	0.020	nc	-0.237	0.043	-0.142	0.278	39	0.308
Cassia nemophila platypoda	-0.188	-0.376	0.348	0.120	0.176	0.095	0.336	-0.102	-0.594	-0.521	-0.346	-0.154	44	0.291
Cassinia laevis	nc	-0.842	nc	nc	nc	0.047	nc	nc	-0.842	-0.889	nc	nc	2	0.95
Casuarina cristata	-0.257	0.070	-0.340	-0.064	0.077	-0.201	0.150	nc	0.009	-0.284	-0.098	0.436	39	0.308
Chenopodium nitrariaceum	0.429	0.098	0.506	0.251	-0.173	-0.269	0.075	-0.103	-0.159	0.430	0.152	-0.066	20	0.423
Codonocarpus cotinifolius	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cratystylis conocephala	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dodonaea viscosa	0.025	0.072	-0.350	0.052	0.204	0.161	-0.020	nc	0.110	-0.004	-0.093	-0.037	25	0.381
Eremophila alternifolia	-0.381	0.304	0.565	-0.154	-0.084	0.799	0.014	nc	-0.753	-0.297	-0.512	-0.050	13	0.514
Eremophila duttonii	-0.069	-0.169	-0.378	0.280	0.286	0.419	0.247	nc	-0.104	-0.383	-0.484	-0.216	11	0.553
Eremophila glabra glabra	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eremophila longifolia	-0.268	-0.117	0.129	0.233	0.297	0.209	0.141	-0.010	-0.163	-0.170	-0.249	0.003	20	0.423
Eremophila oppositifolia	-0.468	-0.310	-0.046	-0.127	0.175	0.776	-0.055	-0.145	0.329	-0.194	-0.494	-0.502	7	0.666
Eremophila scoparia	-0.241	-0.625	0.389	0.200	0.198	0.404	0.175	-0.361	-0.118	-0.489	-0.394	-0.287	10	0.576
Eremophila sturtii	-0.056	0.204	0.163	-0.072	-0.350	0.008	0.133	0.051	-0.054	0.197	0.128	0.117	45	0.288
Eucalyptus camaldulensis	0.432	0.292	-0.113	0.259	-0.210	nc	-0.156	-0.218	-0.173	-0.158	0.119	0.643	15	0.482
Eucalyptus dumosa	-0.340	-0.073	0.304	0.648	0.037	0.237	0.445	nc	-0.513	0.193	0.652	0.820	5	0.755
Eucalyptus gracilis	0.049	-0.169	0.775	0.663	-0.129	-0.383	0.762	nc	-0.678	0.488	0.086	0.269	8	0.632
Eucalyptus intertexta	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eucalyptus largiflorens	0.163	0.468	-0.213	0.428	0.129	nc	nc	nc	0.316	0.163	nc	nc	4	0.811
Eucalyptus porosa	-0.415	-0.105	0.116	-0.184	0.575	0.123	-0.203	0.565	-0.400	0.204	-0.167	0.344	10	0.576
Eucalyptus socialis	0.169	0.269	-0.131	0.043	-0.146	-0.368	-0.130	0.304	0.374	0.124	0.368	0.185	13	0.514
Exocarpos aphyllus	-0.234	0.324	-0.575	-0.287	-0.005	0.239	0.159	nc	0.287	-0.112	-0.036	0.612	11	0.553
Grevillea huegelii	-0.290	0.329	-0.843	0.152	0.162	-0.516	-0.807	nc	0.750	0.066	0.232	nc	6	0.707
Hakea leucoptera	0.293	0.145	-0.287	-0.036	-0.627	-0.038	0.020	nc	0.252	0.312	0.481	0.182	16	0.468
Heterodendrum oleifolium	-0.509	0.043	0.003	-0.374	0.140	-0.036	0.178	nc	-0.008	-0.124	-0.233	0.689	48	0.279
Lycium australe	-0.027	-0.017	-0.291	0.378	0.271	-0.207	-0.024	0.172	0.025	-0.319	0.080	-0.006	18	0.444
Lycium ferocissimum	-0.414	-0.246	nc	-0.150	0.294	0.619	0.588	-0.025	0.309	0.339	-0.165	-0.139	19	0.433
Maireana aphylla	0.028	-0.071	nc	-0.125	-0.239	-0.389	-0.271	nc	-0.110	0.231	0.159	-0.017	19	0.433
Maireana astrotricha	-0.425	-0.151	0.079	-0.459	0.231	-0.155	-0.261	-0.205	0.224	-0.467	-0.331	0.040	28	0.361
Maireana brevifolia	-0.241	-0.735	nc	-0.057	-0.513	0.942	0.821	-0.246	0.191	0.173	0.192	-0.866	4	0.811
Maireana pyramidata	0.149	0.096	-0.148	0.130	-0.258	0.225	0.195	0.095	0.261	0.198	0.322	-0.141	44	0.291
Maireana sedifolia	-0.062	0.051	-0.054	-0.009	-0.095	0.218	-0.038	-0.117	0.162	0.105	-0.053	-0.057	34	0.329
Myoporum insulare	-0.552	0.008	-0.795	-0.862	-0.405	nc	0.785	0.862	0.625	0.210	0.704	0.785	3	0.878
Myoporum platycarpum	-0.471	-0.160	0.295	-0.277	0.138	-0.295	0.371	-0.256	-0.288	-0.320	-0.513	0.369	38	0.312
Nitraria billardieri	0.022	-0.365	0.647	0.409	-0.482	0.011	0.026	-0.127	-0.421	-0.240	-0.005	0.118	14	0.497
Pimelea microcephala	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pittosporum phylliraeoides	-0.206	-0.309	-0.371	-0.213	-0.229	0.525	0.457	-0.338	-0.262	-0.561	-0.169	0.225	19	0.433
Rhagodia parabolica	0.297	0.099	-0.356	0.063	0.202	-0.477	-0.235	0.700	0.367	0.227	0.436	-0.313	8	0.632
Rhagodia spinescens	-0.339	-0.298	nc	0.246	0.423	0.162	0.431	-0.310	-0.612	-0.521	-0.450	-0.259	28	0.361
Santalum lanceolatum	-0.145	-0.430	nc	-0.253	-0.015	0.179	0.391	-0.406	-0.338	-0.562	-0.339	-0.007	16	0.468
Schinus molle	-0.500	-0.216	nc	-0.559	-0.474	nc	0.605	0.795	0.371	0.471	0.444	-0.322	10	0.576
Sida calyxhymenia	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Templetonia egena	-0.564	-0.344	0.124	-0.414	-0.044	0.281	0.228	-0.260	0.030	0.045	0.067	0.559	11	0.553
Triodia irritans	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 9.6

Variables contributing to the species models of percentage recruitment of juveniles. Only variables with significant t-values are shown in the table. Final value of F indicates the degree of explanation of the whole model. The sign of the t-value indicates the positive or negative directions of the relationship. nm = species not modelled (only 1 or 2 sites). nv = no variables had significant explanatory value over the null regression model. Full names of abbreviated variables are shown in Table 9.3.

SPECIES	SHEEP	RBTS	GOATS	KROOS	BDEN	TOP	TEX	CHEM	EIGHT	NINE	WIND	DIST	df	F VAL
Acacia aneura	-	-	-	-	-	-	-	-	-	-2.340	-	3.840	2 39	11.76
Acacia burkittii	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Acacia carnei	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Acacia colletioides	-	-	-	-	-	-	-	-	-	-	-	-	nm	nm
Acacia loderi	-	-	-	-	-	-	-	-	-	-	-3.840	-	1 6	14.74
Acacia nyssophylla	-	-	-	-	-	-	6.790	-	-	-	-	-	1 13	46.07
Acacia oswaldii	-	-	-	-	-	3.120	-	-	-	-	-	-	1 9	9.71
Acacia tetragonophylla	-	-	-	-	-	7.950	-3.770	-	-	-	-	-	2 6	33.03
Acacia victoriae	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Atriplex nummularia	-7.990	-	-	-	-	-	-	-	-3.880	-	-	-	2 4	48.04
Atriplex stipitata	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Atriplex vesicaria	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Callitris collumnellaris	-4.500	-	-	-	-	-	-	-	-	-	-	-	1 12	20.28
Cassia artemisioides	-	-	-	-	-	2.700	-	-	-	-	-	-	1 8	7.29
Cassia nemophila coriacea	-3.100	-	-	-	-	-	2.390	-	-	-	-	-	2 38	9.43
Cassia nemophila platypoda	-2.680	-	-	-	-	-	-	-	-	-0.285	-	-	3 41	19.82
Cassinia laevis	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Casuarina cristata	-2.400	-	-2.900	-	-	-	-	-	-	-	-	-	2 37	6.11
Chenopodium nitrariaceum	3.180	-	-	-	-	-	-	-	-	-	-	-	1 19	10.12
Codonocarpus cotinifolius	-	-	-	-	-	-	-	-	-	-	-	-	nm	nm
Cratystylis conocephala	-	-	-	-	-	-	-	-	-	-	-	-	nm	nm
Dodonaea viscosa	-	-3.240	-	-	-	-	-	-	-	-	-	-	1 24	10.5
Eremophila alternifolia	-	-	-	-	-	-	-	-	-	-	-0.262	-	1 12	6.85
Eremophila duttonii	-	-	-	-4.150	-	-	-	-	-	-6.700	-	-	2 9	25.31
Eremophila glabra glabra	-	-	-	-	-	-	-	-	-	-	-	-	nm	nm
Eremophila longifolia	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eremophila oppositifolia	-	-	-	-	-	7.330	-	-	-	-	-	-	1 6	53.67
Eremophila scoparia	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eremophila sturtii	-3.560	-	-	-	-	-	-	-	-	4.000	-	-	2 43	9.92
Eucalyptus camaldulensis	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eucalyptus dumosa	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eucalyptus gracilis	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eucalyptus intertexta	-	-	-	-	-	-	-	-	-	-	-	-	nm	nm
Eucalyptus largiflorens	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eucalyptus porosa	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eucalyptus socialis	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Exocarpos aphyllus	-7.210	6.440	-	3.850	-	-	-	-	-	-	-	-	3 8	34.44
Grevillea huegelii	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Hakea leucoptera	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Heterodendrum oleifolium	-	-	-	-	-	-	-	-	-	-	-	9.640	1 47	92.87
Lycium australe	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Lycium ferocissimum	-	-	-	-	-	-	-	-	2.510	-	-	-	1 17	6.31
Maireana aphylla	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Maireana astrotricha	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Maireana brevifolia	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Maireana pyramidata	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Maireana sedifolia	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Myoporum insulare	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Myoporum platycarpum	-0.342	-	-	-	-	-	2.930	-	-	-	-	-	2 36	13.29
Nitraria billardieri	-	-	-	-	-	-	-	-	-	-	-3.750	-	1 13	14.04
Pimelea microcephala	-	-	-	-	-	-	-	-	-	-	-	-	nm	nm
Pittosporum phylliraeoides	-	-	-	-	-	-	-	2.470	-	-	-	-	1 18	6.11
Rhagodia parabolica	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Rhagodia spinescens	-	-	-	-	6.290	-	-	-	-5.430	-5.370	-	-2.590	4 25	52.23
Santalum lanceolatum	-	-	-	-	-	-	-	4.110	-	-	-	-	1 9	16.88
Schinus molle	-	-	-	-	-	-	-	4.080	-	-	-	-	1 9	16.67
Sida calyxhymenia	-	-	-	-	-	-	-	-	-	-	-	-	nm	nm
Templetonia egena	-	-	-	-	-	-	-	-	-	-	-2.810	-	1 10	7.92
Triodia irritans	-	-	-	-	-	-	-	-	-	-	-	-	nm	nm

Table 9.7

Variables contributing to the species models of percentage regeneration. Only variables with significant t-values are included in the models. Final value of F indicates the degree of explanation of the whole model. The sign of the t-value indicates the positive or negative direction of the relationship. nm = species not modelled (only 1 or 2 sites). nv = no variables had explanatory value over the null regression model. Full names of abbreviated variables are shown in Table 9.3.

SPECIES	SHEEP	RBTS	GOATS	KROOS	BDEN	TOP	TEX	CHEM	EIGHT	NINE	WIND	DIST	df	F VAL
Acacia aneura	-	-	-	-	-2.96	-	-	-	-	-	-3.86	-	2 39	8.47
Acacia burkittii	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Acacia carnei	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Acacia colletioides	-	-	-	-	-	-	-	-	-	-	-	-	nm	nm
Acacia loderi	-	-	-	-	-	12.23	-	-	-	-	-	-	1 6	149.47
Acacia nyssophylla	-	-	-	-	-	-	-	-	-	-		4.05	1 13	16.37
Acacia oswaldii	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Acacia tetragonophylla	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Acacia victoriae	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Atriplex nummularia	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Atriplex stipitata	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Atriplex vesicaria	-	-	-	-	-	-	-	-	-2.62	-	-	-	1 45	6.88
Callitris collumnellaris	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Cassia artemisioides	-	-	-	-	-	-	3.42	-	-	-	-	-	1 8	11.67
Cassia nemophila coriacea	-4.09	-	-	-	-	-	-	-	-	-	-	-	1 39	16.73
Cassia nemophila platypoda	-	-	-	-	-	-	2.89	-	-5.18	-4.58	-	-	3 41	19.82
Cassinia laevis	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Casuarina cristata	-	-	-	-	-	-	-	-	-	-	-	2.99	1 38	8.93
Chenopodium nitrariaceum	-	-	2.56	-	-	-	-	-	-	-	-	-	1 19	6.55
Codonocarpus cotinifolius	-	-	-	-	-	-	-	-	-	-	-	-	nm	nv
Cratystylis conocephala	-	-	-	-	-	-	-	-	-	-	-	-	nm	nv
Dodonaea viscosa	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eremophila alternifolia	-	-	-	-	-	4.6	-	-	-	-	-	-	1 12	21.18
Eremophila duttonii	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eremophila glabra glabra	-	-	-	-	-	-	-	-	-	-	-	-	nm	nm
Eremophila longifolia	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eremophila oppositifolia	-4.36	-	-	-	-	14.01	-	-	-	-	-12.66	-	3 4	144.31
Eremophila scoparia	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eremophila sturtii	-	-	-	-	-2.48	-	-	-	-	-	-	-	1 44	6.13
Eucalyptus camaldulensis	5.84	-	-	-	-	-	-	-	-	-	-	7.22	2 15	67.17
Eucalyptus dumosa	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eucalyptus gracilis	-	-	3.25	-	-	-	-	-	-	-	-	-	1 7	10.54
Eucalyptus intertexta	-	-	-	-	-	-	-	-	-	-	-	-	nm	-
Eucalyptus largiflorens	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eucalyptus porosa	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Eucalyptus socialis	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Exocarpos aphyllus	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Grevillea huegelii	-	-	-3.5	-	-	-	-	-	-	-	-	-	1 5	12.24
Hakea leucoptera	-	-	-	-	-3.12	-	-	-	-	-	-	-	1 15	9.71
Heterodendrum oleifolium	-	-	-	-	-	-	-	-	-	-	-	6.52	1 47	42.53
Lycium australe	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Lycium ferocissimum	-	-	-	-	-	4.41	-	-	2.87	-	-	-	2 16	11.61
Maireana aphylla	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Maireana astrotricha	-	-	-	-2.44	-	-	-	-	-	-2.5	-	-	2 27	7.43
Maireana brevifolia	-	-	-	-	-	4.86	-	-	-	-	-	-	1 3	23.57
Maireana pyramidata	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Maireana sedifolia	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Myoporum insulare	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Myoporum platycarpum	-	-	-	-	-	-	-	-	-	-	-3.64	-	1 37	13.22
Nitraria billardieri	-	-	3.06	-	-	-	-	-	-	-	-	-	1 13	9.37
Pimelea microcephala	-	-	-	-	-	-	-	-	-	-	-	-	nm	nv
Pittosporum phylliraeoides	-	-	-	-	-	-	-	-	-	-2.87	-	-	1 18	8.25
Rhagodia parabolica	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Rhagodia spinescens	-	-	-	-	-	-	4.38	-	-5.49	-4.44	-	-	3 25	25.63
Santalum lanceolatum	-	-	-	-	-	-	-	-	-	-2.63	-	-	1 15	6.91
Schinus molle	-11.68	-6.49	-	-	-3.68	-	-	11.01	8.53	-	-	-	5 5	48.35
Sida calyxhymenia	-	-	-	-	-	-	-	-	-	-	-	-	nm	nm
Templetonia egena	-	-	-	-	-	-	-	-	-	-	-	-	nv	nv
Triodia irritans	-	-	-	-	-	-	-	-	-	-	-	-	nm	nm

Table 9.8

Comparison of average regeneration for each species between grazed (S=234) and non or very lightly grazed sites (S=01). Where mean recruitment is less than 17%, means are marked in bold italics. t-values and associated probability (p) indicate where grazed and ungrazed means are significantly different, and are also marked in bold italics. The status column indicates whether there is an absolute decrease or increase in mean regeneration at grazed versus ungrazed sites. Full names of abbreviated variables are shown in Table 9.3.

SPECIES	NO OF SITES	NO OF 0 1 SITES	NO OF 2 3 4 SITES	0 1 REGEN	2 3 4 REGEN	DF	T VALUE	P VALUE	STATUS
Acacia aneura	42	22	20	39.1	***15.1***	40	2.624	***0.0122***	***dec***
Acacia burkittii	15	9	6	19.8	***6.5***	13	1.431	0.1762	dec
Acacia carnei	14	10	4	25.9	32.2	12	-0.336	0.743	inc
Acacia colletioides	2	2	-	***0***	-	nc	nc	nc	nc
Acacia loderi	8	6	2	54.2	***13.5***	6	1.237	0.2623	dec
Acacia nyssophylla	15	7	8	47	21.3	13	1.916	0.0776	dec
Acacia oswaldii	11	7	4	23.6	49	9	-0.701	0.501	inc
Acacia tetragonophylla	9	5	4	20.6	***6.8***	7	1.26	0.248	dec
Acacia victoriae	29	15	14	27.3	***8.2***	27	0.434	0.6678	dec
Atriplex nummularia	7	4	3	36.5	***8***	5	2.411	0.0608	dec
Atriplex stipitata	15	10	5	28.7	26	13	0.328	0.748	dec
Atriplex vesicaria	47	27	20	18.3	***14***	45	1.037	0.3055	dec
Callitris collumnellaris	14	8	6	38.1	***8.2***	12	2.159	***0.0518***	***dec***
Cassia artemisioides	8	7	1	***15.5***	***7***	8	1.151	0.2829	dec
Cassia nemophila coriacea	41	26	15	41.4	***7.7***	39	4.449	***0.0001***	***dec***
Cassia nemophila platypoda	45	26	19	35.5	***13***	43	3.333	***0.0018***	***dec***
Cassinia laevis	3	3	-	21.3	-	nc	nc	nc	nc
Casuarina cristata	40	24	16	37.9	25	38	1.798	0.0801	dec
Chenopodium nitrariaceum	21	9	12	37	55.5	19	-1.739	0.0982	inc
Codonocarpus cotinifolius	1	1	-	89	-	-	nc	nc	nc
Cratystylis conocephala	2	2	-	17.5	-	-	nc	nc	nc
Dodonaea viscosa	26	17	9	51.4	41.4	24	0.948	0.3526	dec
Eremophila alternifolia	14	9	5	50	***4.8***	12	2.097	0.0579	dec
Eremophila duttonii	12	5	7	46	35.1	10	0.791	0.4475	dec
Eremophila glabra glabra	1	1	-	38	-	-	nc	nc	nc
Eremophila longifolia	21	15	6	61.3	36.5	19	1.142	0.2677	dec
Eremophila oppositifolia	8	5	3	63.8	23.3	6	1.829	0.1171	dec
Eremophila scoparia	11	9	2	44.8	34	9	0.53	0.6089	dec
Eremophila sturtii	46	17	29	36.8	32.8	44	0.578	0.5622	dec
Eucalyptus camaldulensis	16	7	9	20.7	29.9	14	-0.946	0.36	inc
Eucalyptus dumosa	6	4	2	***6.5***	***0***	4	1.097	0.3342	dec
Eucalyptus gracilis	9	6	3	***2.8***	***2.7***	7	0.01	0.9926	dec
Eucalyptus intertexta	2	2	-	***7.5***	-	-	nc	nc	nc
Eucalyptus largiflorens	5	3	2	39.7	48.5	3	-0.286	0.7936	inc
Eucalyptus porosa	11	6	5	32.8	***15.4***	9	1.405	0.1936	dec
Eucalyptus socialis	14	8	6	32	34.2	12	-0.29	0.7769	inc
Exocarpos aphyllus	12	9	3	29	17.3	10	1.064	0.3122	dec
Grevillea huegelii	7	6	1	33.3	***7***	5	1.505	0.1926	dec
Hakea leucoptera	17	10	7	46	63.7	15	-0.754	0.4623	inc
Heterodendrum oleifolium	49	24	25	***16.1***	***1.2***	47	2.588	***0.0128***	***dec***
Lycium australe	19	7	12	37.4	36.6	17	0.114	0.9107	dec
Lycium ferocissimum	20	9	11	67.4	43.7	18	2.379	***0.0286***	***dec***
Maireana aphylla	20	8	12	30.5	26.6	18	0.452	0.6565	dec
Maireana astrotricha	29	17	12	21.1	***11.8***	27	1.878	0.0712	dec
Maireana brevifolia	5	1	4	22	***17.7***	3	0.337	0.7582	dec
Maireana pyramidata	45	22	23	26.2	30.4	43	-1.018	0.3144	inc
Maireana sedifolia	35	22	13	19.6	***16.1***	33	0.793	0.4335	dec
Myoporum insulare	4	1	3	73	26.7	2	1.795	0.2145	dec
Myoporum platycarpum	39	24	15	50.3	19.1	37	3.013	***0.0046***	***dec***
Nitraria billardieri	15	4	11	36.8	31.7	13	0.07	0.9456	dec
Pimelea microcephala	1	1	-	30	-	-	nc	nc	nc
Pittosporum phylliraeoides	20	12	8	71.8	60	18	0.83	0.4175	dec
Rhagodia parabolica	9	5	4	34.8	40.2	7	-0.912	0.3921	inc
Rhagodia spinescens	29	12	17	25.5	***16.1***	27	2.128	***0.0426***	***dec***
Santalum lanceolatum	17	9	8	45.4	39	15	0.601	0.5569	dec
Schinus molle	11	4	7	59.8	38	9	1.443	0.1828	dec
Sida calyxhymenia	1	1	-	***8***	-	-	nc	nc	nc
Templetonia egena	12	8	4	48.6	23.5	10	1.71	11.81	dec
Triodia irritans	1	1	-	62	-	-	nc	nc	nc

Table 9.9

Summary of species significantly and negatively affected by grazing-related variables. Unbracketed plus or minus indicate significant pearson correlations between recruitment, regeneration and variables (Tables 9.5 & 9.6). Bracketed plus or minus represent variables with both significant Pearson Correlation r-values significant t-values in multiple regression models of recruitment and regeneration (Tables 9.7 & 9.8), whereas (+) and (-) indicate significant t-values only. The status column indicates absolute increase or decrease in mean recruitment of grazed populations compared to ungrazed populations, with significant differences as detected by t-tests in italics (Table 9.9). * indicates where mean recruitment of either ungrazed or grazed is critically low (less than 17% of the population). nj = no juveniles located in any population for that species.

SPECIES		SHEEP	19HD	18HD	RBTS	GOATS	KROOS	WIND	BDEN	CHEM	TOP	TEX	DIST	STATUS	REG<17 S=01	REG<17 S=234
Acacia aneura	REC	minus	(minus)	plus	-	-	-	-	-	-	-	-	plus			
	REGEN	(minus)	minus	minus	-	-	-	minus	(-)	-	minus	-	-	***DEC***	-	*
Acacia burkittii	REC	minus	-	-	-	-	-	-	-	-	-	-	plus			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	DEC	-	•
Acacia loderi	REC	minus	minus	-	-	-	-	(minus)	plus	-	plus	plus	-			
	REGEN	-	-	-	-	-	-	-	-	-	(plus)	plus	-	DEC	-	•
Acacia nyssophylla	REC	-	-	-	-	-	-	-	-	-	-	(plus)	-			
	REGEN	minus	-	-	-	-	minus	-	-	-	-	plus	(plus)	DEC	-	-
Acacia tetragonophylla	REC	-	minus	-	plus	-	-	minus	-	-	(plus)	(minus)	-			
	REGEN	-	-	-	-	-	-	-	plus	-	-	-	-	DEC	-	•
Atriplex nummularia	REC	(minus)	minus	(-)	minus	-	-	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	DEC	-	•
Atriplex vesicaria	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	-	(-)	(minus)	-	-	-	-	-	-	-	-	-	DEC	-	•
Callitris columellaris	REC	(minus)	-	-	-	-	-	-	-	-	-	-	plus			
	REGEN	minus	-	-	minus	-	minus	minus	-	-	-	-	-	***DEC***	-	•
Cassia artemisioides	REC	-	-	-	(-)	(+)	-	minus	-	-	-	-	-			
	REGEN	(-)	-	-	-	(+)	-	-	-	-	plus	(+)	-	DEC	•	•
Cassia nemophila coriacea	REC	(minus)	-	-	-	-	plus	-	-	-	-	(plus)	-			
	REGEN	(minus)	-	-	-	plus	-	-	plus	-	-	-	-	***DEC***	-	*
Cassia nemophila platypoda	REC	(minus)	(minus)	(minus)	minus	plus	-	-	-	-	-	-	-			
	REGEN		(minus)	(minus)	minus	plus	-	minus	-	-	-	(plus)	-	***DEC***	-	-
Casuarina cristata	REC	(-)	-	-	-	(minus)	-	-	-	-	-	-	-			
	REGEN	-	-	-	-	minus	-	-	-	-	-	-	(plus)	DEC	-	-
Dodonaea viscosa	REC	-	minus	-	(minus)	-	-	minus	-	-	plus	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	DEC	-	-
Eremophila alternifolia	REC	-	-	-	-	(plus)	-	(minus)	-	-	-	-	-			
	REGEN	-	minus	minus	-	plus	-	minus	-	-	plus	-	-	DEC	-	•
Eremophila duttonii	REC	minus	(minus)	-	-	minus	(minus)	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	DEC	-	-
Eremophila oppositifolia	REC	-	-	plus	-	-	-	-	-	-	(plus)	-	-			
	REGEN	(-)	-	-	-	-	-	(minus)	-	-	(plus)	-	-	DEC	-	-
Eremophila scoparia	REC	-	-	-	-	plus	plus	-	-	-	-	-	-			
	REGEN	-	-	-	minus	-	-	-	-	-	-	-	-	DEC	-	-
Eremophila sturtii	REC	(-)	(plus)	-	-	plus	-	-	-	-	-	-	-			
	REGEN	(-)	(+)	-	-	-	-	-	(-)	-	-	-	-	DEC	-	-
Eucalyptus gracilis	REC	nj	nj	nj	nj	nj	nj	nj	nj	nj	nj	nj	nj			
	REGEN	-	-	minus	-	(plus)	plus	-		-	-	plus	-	DEC	•	*
Exocarpos aphyllus	REC	(minus)	-	-	(plus)	-	(+)	plus	-	-	-	-	-			
	REGEN	(-)	-	-	plus	minus	(+)	-	-	-	-	-	plus	DEC	-	•
Grevillia huegelii	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	-	-	plus	-	(minus)	-	-	-	-	-	minus	-	DEC	-	-
Heterodendrum oleifolium	REC	minus	-	-	-	-	minus	-	-	-	-	-	(plus)			
	REGEN	minus	-	-	-	-	minus	-	-	-	-	-	(plus)	***DEC***	*	•
Maireana astrotricha	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	minus	(minus)	-	-	-	(minus)	-	-	-	-	-	-	DEC	-	•
Myoporum insulare	REC	-	-	-	minus	-	-	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-		-	-	-	-	-	DEC	-	-
Myoporum platycarpum	REC	(minus)	minus	-	-	-	-	-	plus	minus	-	plus	-			
	REGEN	minus	-	-	-	-	-	(minus)	-	-	-	plus	plus	***DEC***	-	-
Pittosporum phylliraeoides	REC	-	-	-	-	-	-	plus	-	(plus)	-	-	-			
	REGEN	-	minus	-	-	-	-	-	-	(plus)	plus	plus	-	DEC	-	-
Rhagodia parabolica	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	-	(-)	-	-	-	-	-	-	-	-	-	-	INC	-	-
Rhagodia spinescens	REC	minus	(minus)	(minus)	-	-	-	minus	(plus)	-	-	-	(minus)			
	REGEN	-	(minus)	(minus)	-	-	-	-	plus	-	-	(plus)	-	***DEC***	-	•
Santalum lanceolatum	REC	-	-	-	-	-	-	-	-	(plus)	-	-	-			
	REGEN	-	(minus)	-	-	-	-	-	-	-	-	-	-	DEC	-	-
Schinus molle	REC	-	-	-	-	-	-	-	-	(plus)	-	-	-			
	REGEN	(-)	(+)	-	(-)	-	-	-	(-)	(plus)	-	plus	-	DEC	-	-
Templetonia egena	REC	-	minus	-	minus	-	-	(minus)	-	minus	-	-	-			
	REGEN	minus	-	-	-	-	-	-	-	-	-	-	minus	DEC	-	-

Table 9.10

Summary of species unaffected by or positively related to grazing-related variables, or for which there were not enough sites to perform analyses. Unbracketed plus or minus indicate significant Pearson Correlations between regeneration, recruitment and non grazing-related variables (Tables 9.5 & 9.6). Bracketed plus or minus represent variables with significant t-values in multiple regression models of recruitment and regeneration (Tables 9.7 & 9.8), whereas (+) and (-) indicate significant t-values only. The status column indicates absolute increase or decrease in mean recruitment of grazed populations compared to ungrazed populations, with significant differences as detected by tminustests in italics (Table 9.9). * = mean regeneration of either ungrazed or grazed is critically low, less than 17% of the population (Table 9.9). nc = insufficient sites available for correlation or multiple regression analysis. nj = no juveniles located in any population for that species.

SPECIES		SHEEP	1900	1800	RBTS	GOATS	KROOS	WIND	BDEN	CHEM	TOP	TEX	DIST	STATUS	REG<17 S=01	GEN<17 S=234
Acacia carnei	REC	-	-	-	-	-	-	-	-	-	-	-	-			
		-	-	-	-	-	-	-	-	-	-	-	-	INC	-	-
Acacia colletioides	REC	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc		*	
	REGEN	nc	nc	nc	nc	nc	nc	REGEN	nc	nc	nc	nc	nc	nc		nc
Acacia oswaldii	REC	-	-	-	-	-	-	-	-	-	(+)	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	INC	-	-
Acacia victoriae	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	DEC	-	-
Atriplex stipitata	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	DEC	-	-
Chenopodium nitrariaceum	REC	(plus)	plus	-	-	-	-	-	-	-	-	-	-			
	REGEN	plus	-	-	-	(plus)	-	-	-	-	-	-	-	INC	-	-
Codonocarpus cotinifolius	REC	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc			
	REGEN	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	-	nc
Cratystylis conocephala	REC	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc			
	REGEN	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	-	nc
Eremophila glabra glabra	REC	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc			
	REGEN	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	-	nc
Eremophila longifolia	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	DEC	-	-
Eucalyptus camaldulensis	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	(+)	-	-	-	-	-	-	-	-	-	-	(+)	INC	-	-
Eucalyptus dumosa	REC	nj	nj	nj	nj	nj	nj	nj	nj	nj	nj	nj	nj		*	*
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	DEC		
Eucalyptus intertexta	REC	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc		*	
	REGEN	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc		nc
Eucalyptus largiflorens	REC	-	-	-	-	-	plus	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	INC	-	-
Eucalyptus porosa	REC	-	-	-	-	-	-	-	-	-	-	-	-			*
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	DEC	-	
Eucalyptus socialis	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	INC	-	-
Hakea leucoptera	REC	-	-	-	-	-	-	(+)	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	-	(-)	-	-	-	-	INC	-	-
Lycium australe	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	DEC	-	-
Lycium ferocissimum	REC	-	-	(+)	-	-	-	-	-	plus	-	-	-			
	REGEN	-	-	(plus)	-	-	-	-	-	-	(+)	-	-	***DEC***	-	-
Maireana aphylla	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	DEC	-	-
Maireana brevifolia	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	(plus)	plus	minus	DEC	-	-
Maireana pyramidata	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	plus	-	-	-	-	-	INC	-	-
Maireana sedifolia	REC	-	-	-	-	-	-	-	-	-	-	-	-			*
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	DEC	-	
Nitraria billardieri	REC	-	-	-	-	-	-	(-)	-	-	-	-	-			
	REGEN	-	-	-	-	(+)	-	-	-	-	-	-	-	DEC	-	-
Pimelea microcephala	REC	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc			
	REGEN	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	-	nc
Rhagodia parabolica	REC	-	-	-	-	-	-	-	-	-	-	-	-			
	REGEN	-	-	-	-	-	-	-	-	-	-	-	-	INC	-	-
Sida calyxhymenia	REC	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc			
	REGEN	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	-	nc
Triodia irritans	REC	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc			
	REGEN	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	-	nc

Grazing by herbivores

Thirty one species show significant negative correlation of either recruitment or regeneration with present or past grazing by herbivores (Table 9.9). Past and present sheep-grazing is the most consistently appearing variable, and all of these species but one, *Rhagodia parabolica*, show absolute decreases in mean regeneration between sites ungrazed and grazed by sheep. These absolute differences are significant in 7 species, *Acacia aneura, Callitris columellaris, Cassia nemophila coriacea, Cassia nemophila platypoda, Heterodendrum oleifolium, Myoporum platycarpum* and *Rhagodia spinescens.* Regeneration of all 7 of these species is negatively correlated to past or present sheep grazing. Multiple regression shows that the most important variables are present sheep grazing in *Cassia nemophila coriacea* and *Callitris collumellaris,* and past sheep grazing in *Cassia nemophila platypoda* and *Rhagodia spinescens.* In *Heterodendrum oleifolium*, the presence of soil disturbance appears to be the principal factor encouraging regeneration (see edaphic variables below), although sheep grazing is correlated with poor regeneration. In *Callitris*, no one factor was more important, but in *Myoporum platycarpum,* wind erosion was the most important, possibly coding for 19th and early 20th century grazing in the regression models. In all 7 of these species but *Myoporum platycarpum*, regeneration at grazed sites is below the estimated critical level for population maintenance. A further 10 species in which recruitment or regeneration are related to herbivore grazing have regeneration percentages at grazed sites below the estimated critical level: *Acacia burkittii; A. loderi; A. tetragonophylla; Atriplex nummularia; Atriplex vesicaria; Cassia artemisiodes; Eremophila alternifolia; Eucalyptus gracilis; Exocarpos aphyllus*; and *Maireana astrotricha.* In addition, four species in which herbivore grazing appears to have no effect, but which have critically low levels of regeneration are *Acacia colletioides*, *Eucalyptus dumosa*, *E. intertexta,* and *Maireana sedifolia.* These results agree to some extent with those of Harrington (1979) in western New South Wales, who demonstrated that sheep grazing reduces regeneration of *Acacia aneura* and *Dodonaea viscosa.* However, Harrington found that sheep did not reduce regeneration of *Cassia sp.*, or *Eremophila sturtii*, both of which were negatively affected in this study.

Rabbit grazing is also correlated with decreased regeneration in *Callitris columellaris,* and *Cassia nemophila platypoda*, but is not the sole or most important explanatory grazing variable for either of these, and is not a factor with any of the other five significantly affected species. This supports the findings of Cochrane & McDonald (1966), who found that rabbits ate the growing tips of *Callitris columellaris*, but only killed 134 out of 350 seedlings over a period of nearly two years. However, although population decreases are not significant, or causing regeneration to drop below critical levels, rabbits appear to have more of a role than sheep in suppressing regeneration of *Eremophila scoparia.*

Goat grazing was negatively correlated with regeneration of *Casuarina cristata, Grevillea huegellii*, and *Exocarpos aphyllus*, and is the most important variable in *Exocarpos aphyllus* (Table 9.10). Wilson et al.(1976) reported that *Casuarina cristata* was browsed by goats. However, goat grazing is negatively correlated to sheep grazing (Table 9.3), and none of these species is below critical levels in the non sheep-grazed sites where goats tend to be more prevalent, so it would appear that goats in normal numbers are not capable of reducing regeneration to the point of extinction. In addition, the *Grevillea huegelii* results are based on few sites. This is further illustrated by a number of species which show positive correlation between goat grazing and regeneration, in which closer examination reveals that these species are usually negatively affected by sheep grazing (*Cassia nemophila coriacea, Cassia nemophila platypoda, Eremophila alternifolia*) or edaphic variables (*Eucalyptus gracilis, Nitraria billardieri*). Goat grazing therefore appears as a positive variable, only because of its negative association with other variables.

Kangaroo grazing is correlated with lack of regeneration in *Acacia nyssophylla, Callitris columellaris, Maireana astrotricha* and *Heterodendrum oleifolium.* However, multiple regressions of all but *Maireana astrotricha* show that kangaroo grazing is not the main explanatory variable, low regeneration of both of these species being more correlated with sheep grazing. The apparent correlation of kangaroos with lack of regeneration is therefore an artifact of collinearity with sheep grazing (Table 9.3). This correlation of sheep and kangaroo grazing confirms the findings of Landsberg *et al.* (1992), but contradicts those of Andrew & Lange (1986b), who found dissociation between sheep and kangaroo grazing. The survey of perennial populations was carried out in a dry winter, so possibly both kangaroos and sheep were tending to congregate around watering points.

Species unaffected or promoted by grazing

Some species appear to be unaffected by grazing, or grazing-related variables (Table 9.10). However, although some of these (*Acacia carnei, A. oswaldii, Chenopodium nitrariaceum, Eucalyptus camaldulensis, E. largiflorens, E. socialis, Hakea leucoptera, Maireana pyramidata* and *Rhagodia parabolica*) show absolute increases under grazing, none showed significant increases. In addition, a number of species, some of which have a reputation as "woody weeds", *Acacia nyssophylla, A. victoriae, Atriplex stipitata, Cassia nemophila platypoda, Casuarina cristata, Chenopodium nitrariaceum, Dodonaea viscosa, Eremophila duttonii, E. longifolia, E. oppositifolia, E. scoparia, E. sturtii, Grevillea huegelii, Lycium australe, L. ferocissimum, Maireana aphylla, Myoporum insulare, M. platycarpum, Nitraria billardieri, Pittosporum phylliraeoides, Santalum lanceolatum, Schinus molle* and *Templetonia egena* were able to maintain sufficient levels of recruitment for population survival, regardless of whether overall recruitment was affected by grazing (Table 9.9).

Lycium ferocissimum, Chenopodium nitrariaceum and *Eremophila oppositifolia* show increased regeneration in response to heavy grazing in the past, so are exhibiting "weedy" characteristics. *Acacia aneura, Eremophila sturtii* and *Schinus molle* also show increased regeneration following heavy 19th century grazing, but coupled with decreased regeneration in response to modern grazing, and correlation with low bush density, perhaps indicating an ability to invade areas cleared of bush by past heavy grazing. *Grevillea huegelii* also shows increased regeneration following 19th century grazing, but this is probably explained by a correlation with low goat grazing (Table 9.3), the only herbivore shown to affect its recruitment (Table 9.5). Several other species show increased regeneration on soil with a chemical crust (*Pittosporum phylliraeoides, Lycium ferocissimum, Santalum lanceolatum* and *Schinus molle*); Tables 9.9 & 9.10.

Edaphic variables affecting recruitment & regeneration

Non-grazing related variables of topography, soil texture and soil disturbance also appear to affect recruitment and regeneration. Many species show a recruitment or regeneration response to sandier soils (*Acacia loderi, A. nyssophylla, Cassia artemisioides, C. nemophila coriaceaea, C. nemophila platypoda, Eucalyptus gracilis, Lycium ferocissimum, Maireana brevifolia, Myoporum platycarpum, Maireana brevifolia, Rhagodia spinescens* and *Schinus molle*); Tables 9.9 & 9.10. However, *Acacia tetragonophylla* and *Grevillea huegelii* have increased regeneration on clay soils. Once again, most species affected by local topography, *Acacia loderi, A. tetragonophylla, Dodonaea viscosa, Eremophila alternifolia,* and *Pittosporum phylliraeoides* prefer rising ground for regeneration; the only species showing a reverse trend is *Acacia aneura.* Soil disturbance also contributes to regeneration in *Acacia aneura, A. nyssophyllla, Callitris columellaris, Casuarina cristata, Exocarpos aphyllus, Eucalyptus camaldulensis, Heterodendrum oleifolium* and *Myoporum platycarpum.* Disturbance has a negative influence for *Maireana brevifolia, Rhagodia spinescens,*and *Templetonia egena*, although this is based on a low number of sites for *Maireana brevifolia.*

Lack of correlation between recruitment & regeneration

The data show little connection between suppression of recruitment, and suppression of regeneration. Although both recruitment and regeneration are suppressed by sheep in *Acacia aneura, Callitris columellaris, Cassia nemophila platypoda, Eremophila sturtii, Heterodendrum oleifolium* and *Myoporum platycarpum*, recruitment, but not regeneration is affected in *Acacia burkittii, A. loderi, Atriplex nummularia, Eremophila duttonii* and *Rhagodia spinescens.* Additionally, regeneration but not recruitment is affected by current sheep grazing in *Acacia nyssophylla, Maireana astrotricha, Schinus molle* and *Templetonia* *egenaa*. Similarly, rabbit grazing reduces recruitment, but not regeneration, in *Ariplex nummularia, Dodonaea viscosa angustissima, Myoporum insulare* and *Templetonia egena;* and regeneration but not recruitment in *Eremophila scoparia* and *Schinus molle.*

Lack of regeneration not attributable to grazing

A number of species do not appear to be achieving critical levels of regeneration, even at ungrazed sites, assuming that the minimum level for population maintenance is 17% as calculated (Table 9.8). Such species include *Acacia colletioides, Cassia artemisioides, Eucalyptus dumosa, Eucalyptus gracilis, Eucalyptus intertexta* and *Heterodendrum oleifolium.* A further species, *Maireana sedifolia,* has regeneration at grazed sites below critical levels, even though there appear to be no direct effects of grazing. No juveniles at all were observed in any population of either *Eucalyptus dumosa* or *E. gracilis* both of which appeared to rely totally on vegetative reproduction.

DISCUSSION

Relative effects of domestic & non-domestic vertebrate herbivores

The above results show clearly that sheep are the most significant vertebrate herbivore affecting present levels of regeneration in the chenopod shrublands of eastern South Australia, possibly with some species also being affected by rabbits or goats. Kangaroo grazing is comparatively unimportant, as would be expected from a co-evolved herbivore. This finding tends to support earlier reports that kangaroos subsist mainly on a diet of grasses (Chapter 5). Thirty one of the 59 species studied are affected in some way by sheep grazing, 7 significantly and to critical levels. In 4 of these (*Acacia aneura, Callitris columellaris, Cassia nemophila coriacea* and *Heterodendrum oleifolium*) this can be directly attributed to current levels of sheep grazing. These species appear to be able to regenerate at sites with intermittent or very light grazing, such as those found beyond the limits of the piosphere. It is interesting to note that the recommended pastoral management

1 This finding is in direct contradiction to some of the literature on rabbits, particularly that of Crisp and Lange (1976), see page 61. However, the conclusions of their paper are based on only 9 sites with very limited spatial distribution, of which 4 are within the same enclosure (Koonamore Reserve). There is also the complication that rabbit control at Koonamore unfortunately coincided with a unique two year period of extremely high rainfall. The results presented in this thesis are based on data from over 900 spatially separated populations of 59 different woody species with varying histories of grazing by sheep and other herbivores.

technique of locating additional watering points and reducing paddock sizes to spread stock more evenly (as described in Chapter 5), while being a better strategy for bush retention, may actually be detrimental to these highly grazing-sensitive species. A network of ungrazed reserves, such as that recommended by Stafford Smith & Morton (1992) is required to conserve species such as these. This could be achieved by fencing and retaining the ungrazed portions of paddocks which lie beyond the piosphere.

Grazing by the three major non-domestic herbivores - rabbits, goats and kangaroos - is much less important compared to that of sheep. Although often negatively correlated to recruitment, they were rarely important in the multiple regressions, indicating that it is highly likely that this is an artifact of association between sheep, kangaroo and rabbit grazing and dissociation between sheep and goat grazing.[1] A possible reason for the lesser effects of these herbivores are the different dynamics of domestic livestock and feral and exotic animals such as goats and rabbits. When seasonal conditions deteriorate, both sheep and rabbits are forced to switch from ephemeral to shrubby species. Rabbits tend to cause spectacular and devastating damage to shrubs and trees at the end of good seasons, but they are largely unable to cope with a woody diet, and populations invariably crash in dry seasons (Ratcliffe, 1936); see Chapter 5. These episodes appear to have a low overall effect on regeneration. On the other hand, sheep are restrained by the fencing system and management aims of the pastoralist, and numbers can artificially be kept high under deteriorating conditions as long as water is available, and long after rabbits have ceased to have any impact (Reid, 1993). Under this regime sheep represent a greater threat to regeneration. Neither is goat grazing correlated to population structure of most of the species recorded. Perhaps their browsing habit means that they are not a threat to recruiting seedlings, and canopy browsing by ordinary numbers of unrestrained goats is not sufficiently harmful to cause death of individuals, thereby affecting the population structure. These results indicate that kangaroos have no effect on recruitment at all, even at the post-European settlement high numbers, supporting early findings that kangaroos are largely grass-eaters (Chapter 5).

There are several contributing factors causing rabbits to be so often cited as the major herbivore causing suppression of regeneration. The strong relationship of rabbit grazing with both present and past levels of sheep grazing suggests that rabbits are most successful in invading areas where sheep have already severely reduced the bush cover, which confirms contemporary reports such as those of Ratcliffe (1936). Thus, rabbits are coincidentally present in areas where regeneration is being affected by sheep. The rabbit effect of ring-barking larger individuals is also much more noticeable than a steady and complete disappearance of juveniles caused by sheep. However, the most persuasive argument has undoubtedly been the literature surrounding the pre-*Myxomatosis* rabbit plagues (Chapter 5). It is possible that the populations of rabbits present and frequency of plagues before 1950 were sufficient for rabbits to have a greater effect than they do now, as suggested by the data on *Callitris* from Pilliga Scrub in New South Wales (Norris *et al.*, 1991).

"Woody weeds"

These data suggest that the perceived increase in numbers of "woody weeds" is a relative rather than an absolute effect, since the regeneration of nearly all species is negatively affected by sheep grazing, and no species show significantly increased regeneration under sheep grazing. Similarly, the predominance of absolute decreases in mean regeneration between ungrazed and grazed sites for nearly all species seems to suggest that there could be an overall reduction in total numbers of woody perennial individuals in the landscape. This supports Silvertown & Doust (1993) who state that although the theoretical carrying capacity of the landscape is resource-based, herbivory may mean that not all possible locations are filled within a grazed landscape. This reduction in shrub numbers occurs in spite of the fact that all but a few species theoretically seem able to recruit more than sufficient numbers for population maintenance. It is possible that the 17% minimum regeneration level suggested earlier is too conservative, and that critical levels for recruitment are higher than that for most species. Even if there is an overall reduction in occupied locations, it is still possible that species in which regeneration is relatively less affected by grazing may therefore come to occupy a higher relative proportion of locations than previously, giving the false impression that they are increasing in absolute terms. So presumably the main effect of the introduction of sheep has been to alter the competetive dominance relationships of the species, allowing some species such as *Dodonaea viscosa* to increase at the expense, but not [yet at least] to the total exclusion of others. The changes in relative numbers of different species depends on there being grazing susceptible species, and not quite so grazing susceptible species. If there are relative rather than absolute effects on the vegetation composition in grazed landscapes, this means that the phenomenon of woody weeds must be viewed synecologically rather than autecologically. It is also important to note that "woody weediness" is not an absolute characteristic of a plant species, since the changes seen over a whole landscape are due to the relative susceptibility to grazing of the species and varieties present. This explains why plants such as *Cassia nemophila* and *Acacia aneura* have been cited as woody weeds in western New South Wales, but were found to have absolute reduced regeneration in the study area. Sheep from different breeding stock are also known to show different dietary preferences (Maywald, 1993) which could also change the proportions of different species present in response to grazing, and cause different perceptions of which species are "woody weeds".

Another explanation for the perception that woody weeds are rapidly encroaching is that past severe grazing pressure may have caused transition changes *sensu* Westoby *et al.* (1989) which are still apparent in the landscape. Relatively non-susceptible species have been able to preferentially invade areas where populations of highly susceptible species such as *Atriplex vesicaria* and *Cassia nemophila coriacea* were destroyed by over-grazing during the droughts of last century documented in Chapters 4 and 5. This is reflected in the positive regeneration responses of *Eremophila sturtii, Schinus molle,* and *Chenopodium nitrariaceum* to 19th century grazing and is further supported by the fact that low bush density permits high recruitment in *Eremophila sturtii*. This indicates that there is a competitive effect in woody weed invasions, in that removal of an existing individual by herbivory may allow another plant to invade, even though it is less competitive under ungrazed conditions. This would explain why many woody weed species had more restricted distributions prior to European settlement as described by Austin and Williams (1988). Plants which previously had localized distributions on ridges and areas of run-on are probably adapted to higher soil-water relations, and may benefit markedly from removal of more drought-tolerant competitors due to overgrazing.

It is also interesting to note that two very closely related taxa are behaving quite differently. *Cassia nemophila platypoda* is able to maintain regeneration under grazing, whereas *Cassia nemophila coriacea* is not. Workers dealing with woody weeds will need to define carefully which taxa they are dealing with, since not only species, but varietal differences are here shown to be significant. This finding supports that of Pearson *et al.* (1990) who have previously shown varietal differences in palatability of *Atriplex vesicaria.*

Several woody species have increased regeneration in areas of chemical crusting on the soil surface. It is interesting that the two most successful exotic species in the study area, *Lycium ferocissimum* and *Schinus molle,* are in this category. Chemical crusting is correlated with both past grazing history and wind erosion, so it is likely that it has been caused by increased evaporation from bare, eroded soil surfaces. Presumably increased salinity may decrease the competetive ability of many native species, creating niches for salt-tolerant exotics.

Differences between recruitment and regeneration

These results show that the presence of seedling recruits does not necessarily mean that there will be successful regeneration in the long-term. Ten of the species with reduced regeneration showed no recruitment response to grazing. Where this is the case herbivores appear to avoid juveniles, which may contain compounds which make them less palatable as a survival mechanism. Another possibility is that seedlings are too small to attract large herbivores, but are able to grow rapidly to maturity. This supports the findings of Lange and Coleman (1992), who found that sheep avoided seedlings of *Atriplex vesicaria.* In cases where rabbits are correlated with post-juvenile mortality, this is may be by ring-barking older individuals.

On the other hand recruitment can be negatively affected by herbivores without necessarily affecting overall regeneration. This confirms the findings of Watkinson (1986) who concluded that the effects of grazing have to be sufficient to reduce regeneration below those due to competition or microsite limitation for there to be a danger of extinction through grazing. Where recruitment but not regeneration is affected, recruitment must naturally be at higher levels than actually required for minimum levels of regeneration, perhaps as an insurance measure against higher mortality of juveniles. Such a strategy may be effective, simply because higher recruitment levels mean there is a higher chance of successfully occupying an available site, supporting the stochastic models of vegetation pattern suggested by Chesson and Case (1986) and Greig-Smith (1983).

Edaphic variables & regeneration

Many of the environmental variables measured such as wind erosion (positive) and bush density (negative) were associated with sheep grazing, especially historical grazing, further emphasizing the importance of sheep grazing as the main influence on population dynamics. Many species prefer soils of sandy texture, and sites on rising ground (either sand-hills, slopes, or rocky outcrops) for recruitment and regeneration. It is likely that this response is a soil-moisture one. Soil disturbance also tends to promote recruitment and regeneration in many species. This may be a combination of direct mechanical effects, such as seed scarification in seed-regenerating species such as *Acacia* and damage-response shooting of buds from roots in vegetatively regenerating species such as *Heterodendrum oleifolium*. There may also be increased water infiltration and consequently better water relations in disturbed soil, creating regeneration niches (Grubb, 1977) for species which are in disequilibrium with the newly arid environment. If the disturbances have also removed existing individuals, there may be additional advantages due to decreased competition for water, an effect which Wotton (1993) has previously demonstrated for *Maireana sedifolia.*

Importance of historical events

This study is one of the few to quantify and include historical effects in a model explaining vegetation dynamics. Considering the intense grazing history of the area, it is not surprising to find that grazing practices of over 100 years ago had significant effects on the vegetation. The lack of regeneration of *Atriplex vesicaria* at sites with heavy 19th century grazing confirms contemporary reports of bush removal by heavy grazing. Many of these sites have been invaded by the species less susceptible to grazing such as *Eremophila sturtii* and *Chenopodium nitrariaceum* (see above).

Many species are failing to regenerate even at ungrazed sites, or for reasons which appear to be unattributable to grazing. This may be due to historical factors. Because of the lag-factor in long-lived species (Davis, 1986) conditions may have become less favourable for recruitment of these species since the present individuals entered the population. The complete absence of juveniles in populations of *Eucalyptus dumosa* and *E. gracilis* indicate that regeneration by seed is a very rare event in these species. These species as well as *Heterodendrum* have probably switched to vegetative reproduction as a more certain method of regeneration in response to the increased aridity described in Chapters 4 and 5. Low levels of recruitment have been previously recorded for *Maireana sedifolia* (Ratcliffe, 1936; Wood, 1936; Wotton, 1993), and it is likely that this species has survived by being very long-lived (Wood, 1936). For some species such as *Heterodendrum*, the addition of domestic livestock and exotic and feral herbivores to the landscape may have exacerbated an already disequilibrium species-environment relationship to one which is very rapidly approaching a complete transition to another state, extinction. This confirms the existence of transition changes as predicted by the state and transition model of Westoby (1989).

CONCLUSIONS

This study shows that "woody weeds" are a symptom of overall changes to vegetation composition, supporting the view of Harper (1977) that differential grazing pressure by herbivores is an important variable in vegetation composition. The problem of "woody weeds" must therefore be dealt with using synecological rather than autecological models. If a real need is felt to attempt to alter the vegetation composition to a more productive one for pastoral management, then more holistic management practices which take the whole of the vegetation into account such as those recommended by Jacoby (1985) for Texas rangelands should be adopted. Managment practices such as grubbing, burning, and mass-grazing with goats (Green, 1983) to remove "woody weeds" are quite mis-directed, and in fact more likely to exacerbate rather than improve the situation.

Sheep are clearly the most important vertebrate herbivore affecting the regeneration of trees and shrubs in eastern South Australia. These results indicate that the emphasis on rabbit control as the most important objective in conservation of native perennial species in the chenopod shrublands of South Australia must be re-examined. Rabbits and, to a lesser extent, goats, have been widely cited as the most important factor in preventing regeneration of woody perennial species (see Chapter 5). This assumption is so widely stated as fact in literature concerning research and management that it has achieved the status of a paradigm. In this sense, the word paradigm is used following Kuhn (1970), denoting that which is "rejected and replaced during scientific revolutions". For example, it is often stated that adjustments to sheep grazing practices will have little effect in changing the projected survival of woody species in the Australian rangelands unless good rabbit control is also achieved, as stated by Perry (1972). These results show that if grazing susceptible perennial species are to be retained in the landscape, then it will be necessary to alter existing management practices. Such alterations must occur at both the small scale (individual property and paddock plans) and the broad scale (provision of a regional network of ungrazed reserves). It is also essential that more research be carried out to ascertain if these findings hold true in other land systems.

On the other hand, many of the chenopod bush species such as *Atriplex vesicaria, Maireana pyramidata* and *M. astrotricha* do appear to be able to regenerate successfully under the present grazing regime. It seems, then, that conservative grazing management will permit the maintenance of present bush cover and even allow some bush regeneration on previously overgrazed land. So economically sustainable pastoralism should be an achievable goal (Friedel *et al.*, 1990), as long as the deleterious transition events *sensu* Westoby *et al.* (1989) which were common during the last century are not permitted to recur.

Many species showed a positive response to a range of edaphic variables, especially those which affect soil-water relations. Mature, non-regenerating populations of many species are probably remnants of the last pluvial period (Crocker & Wood, 1947) which are unable to successfully regenerate there under the drier climate of the present. This supports Grubb's (1977) view that the requirements for recruitment and regeneration may be different for those required by mature individuals. In summary, as suggested by Davis (1986) and Clark (1990), it appears that many species are in disequilibrium with the present climate; their regeneration continuing only at isolated favourable sites, by switching to vegetative methods, or that they persist fortuitously by longevity. This would also explain why recruitment and regeneration in many Australian arid zone plants is restricted to the abnormal rainfall events experienced during anti-ENSO years (Chapters 4 & 5). The addition of domestic livestock to this landscape may have further competitively disadvantaged these species to the point where some species such as *Heterodendrum* will eventually become locally extinct.

The demonstration that high levels of recruitment are not necessarily matched by high levels of regeneration tends to support the stochastic niche models of vegetation pattern as posed by Greig-Smith (1983) and Chesson and Case (1986). This reinforces the finding that although much can be learned about plant population dynamics through autecological studies, synecological studies are necessary to understand the pattern of populations and species in the landscape.

CHAPTER 10:
GENERAL DISCUSSION

INTRODUCTION

As discussed in the general introduction (Chapter 1), arid lands occupy a significant proportion of the surface of the earth. Eastern South Australia was only settled for pastoralism in about 1850, so the vegetation there retains enough of its original character to be important as heritage. The most significant human activity in arid lands is pastoralism, so it is vital to understand how domestic livestock affect existing vegetation patterns. Because of the relatively short time since European settlement it is possible to determine the main effects pastoralism has had on the vegetation. In this sense, the pastoral use of the arid lands of Australia can be considered as a broad-scale unreplicated experiment. Knowledge which can be gained from research into these effects is therefore relevant, not only for the conservation and management of the arid lands of Australia, but also for other arid regions of the world where pastoralism is a major influence on the environment. Insights into vegetation patterns, the factors controlling them, and the effects of herbivory are also of importance to general vegetation theory.

The results of this study are discussed below and include a number of findings which have relevance to:

The theory of arid and rangeland ecology, and general vegetation science.

Conservation and management of the Australian chenopod shrublands.

IMPORTANCE OF RESULTS TO ARID-ZONE ECOLOGY & VEGETATION SCIENCE

Methods in Vegetation Science

Phytogeography remains a methodologically immature science in comparison to phytosociology, where objective numerical methods have become commonplace. The mapping and description of vegetation at the level of alliance (Chapter 6) demonstrated the value to be gained by applying modern methods of classification and ordination to phytogeographical data. This application of modern analysis methods to broadscale vegetation survey data has only been performed previously in a few studies, usually from herbarium data. The results demonstrate that the methodology of numerical floristic data collection followed by multivariate analysis is an extremely efficient and effective technique for rapidly describing very large areas of relatively unknown vegetation. Such methods should therefore be very useful in arid lands elsewhere, particularly where available capital does not permit the use of high-technology remote methods of data collection. Compared to structural classifications, floristic methods were found to be a more reliable method of summarizing vegetation information, and a much greater level of information can be extracted from them. A number of seeming errors of description of the previous treatments of the vegetation can be assigned to problems inherent in using structural methods of vegetation description. Structural classifications appear to be particularly weak in arid regions where the vegetation is sparse, and structure is a less important characteristic than in more dense vegetation such as closed forests.

Scale is a very important issue in vegetation science. The results of Chapters 6 and 7 demonstrate that although useful information can be gathered at two widely different scales, 100 ha strip-transects, and 0.1 ha plots, a much better degree of floristic information was obtained by carrying out data collection at two scales within the same vegetation. The broadscale survey of strip-transects was more useful in producing vegetation maps at the level of alliance (Chapter 6), since the vegetation of small plots is dominated by local topographic and edaphic effects, producing mosaic patterns of associations which are difficult to map (Chapter 7). A map of alliances accompanied by written descriptions of the associations within them (Appendix 2) was found to be the most effective method of vegetation description, supporting the similarly constructed but subjective systems of Wood (1937), Beadle (1945) and Specht (1972).

Holistic, synecological studies which are largely observational and inductive by nature (Chapter 2) were therefore extremely valuable in providing initial descriptions of relatively unknown vegetation, but another important value is their ability to generate increasingly directed hypotheses (Chapters 6 & 7). The best methods of testing these hypotheses were found to be the more deductive, reductionist methods such as those developed in experimental autecology and population ecology (Chapter 9). This confirms the value of combining both holistic and reductionist approaches in research as suggested by Noy-Meir (1971), Hagen (1989) and Wiegleb (1989); see Chapter 2.

The nature of vegetation

Chapter 7 confirms the tendency of vegetation to be neither continuous nor discontinuous, instead forming noda separated by continua as suggested by Goodall (1953) and Poore (1955a). The results are therefore an important contribution to the current models of vegetation science (Chapter 2), and demonstrate the need to use a range of research approaches and techniques in collecting and interpreting vegetation data (Chapter 3). Complementary analysis, the practice of clustering vegetation data to identify noda, followed by ordination to detect continua, was shown to be an extremely effective technique in assessing the relative importance of continuity and discontinuity in vegetation data sets (Chapters 6 & 7).

The tendency of vegetation associations to form complex mosaics in the landscape is strongly suggestive that edaphic, rather than climatic variables exercise the most powerful degree of control over the vegetation at this scale (Chapter 7). The results of Chapter 8 confirm this hypothesis, since a range of edaphic variables are significantly correlated to the distributions of both vegetation associations and individual species. This also confirms the writings of Wood (1939), Walter & Stadelmann (1974), Skarpe (1986) and Belsky (1989), who suggest that edaphic and topographic variables are more important determinants of arid zone vegetation than climate. This is because edaphic and topographic variables have more influence over water availability to the plant than the low erratic rainfall. These findings are therefore important additions to the theory of arid zone ecology.

The climax theory of vegetation

Edaphic variables are in turn largely controlled by geology and landforms (Chapter 4), both of which have undergone relatively recent changes. Vegetation patterns have already shown a response to some of these more recent changes, as shown by the mosaic pattern of vegetation in response to the deposition of sand-dunes of Recent age (10 000 mA BP); Chapters 7 and 8. However, the longevity of many of the species involved suggests that the vegetation could hardly be said to be in full equilibrium with the changed environment, in the sense of the traditional concept of climax. Some woody perennial species are failing to recruit, even at un-grazed sites (Chapter 9), which suggests that the vegetation has not reached equilibrium in response to climate changes which have occurred over the last 18 000 years (Chapters 4 & 5). This supports the views of Chesson and Case (1986) and Davis (1986) who postulate that this may be a widespread occurrence, and that climate and edaphic changes are occurring continually everywhere, so that vegetation is always in lag-phase. Models of vegetation which assume that it is always at equilibrium with the environment must therefore be false.

Evidence for the state-and-transition model of vegetation dynamics

These results are unique in that they provide objective evidence of control of vegetation pattern explained by non-equilibrium as well as equilibrium models. An historical event, heavy grazing by sheep during the 19th century, was shown to be a very important variable in controlling the relative numbers of woody perennial plant species (Chapter 9). Most changes to populations of woody perennials are negative in response to grazing, indicating that apparent relative increases in some species are due to the fact that some species are less susceptible to grazing than others. This demonstrates that sheep grazing is an equilibrium variable to some extent, in that changes to the vegetation cover are due to interference in the competetive relationships between species. However, there is evidence that sheep grazing negatively affects the regeneration of some species to the point where it is highly unlikely that these species will be able to persist in the long term in a grazed landscape. These results therefore provide some of the first objective evidence of shifts between equilibrium states or transitions, consistent with the model suggested by Westoby *et al.* (1989). This confirms the importance of visualizing rangeland vegetation in terms of the state-and-transition model as suggested by [illegible] Smith(1988) in conjunction with the more traditional equilibrium models (Stafford Smith, 1992).

IMPORTANCE OF RESULTS TO CONSERVATION AND MANAGEMENT

Representativeness of areas conserved

It is generally recognized that a good reserve system should contain samples of all major ecosystems (Purdie, 1987). However, there is very little land set aside for conservation purposes within the study area, which reflects the situation over most of Australia. There is a strong tendency in Australia for conservation parks to be located in areas for which no economic use has yet been found (Margules, 1989). Danggali Conservation Park is such an example, located in waterless, inaccessible mallee scrub and sand-dune country, which is of no use for pastoralism. However, the edaphic control of vegetation demonstrated in Chapter 8 means that while vegetation types common in such environments are well-conserved, some vegetation types are not conserved at all. These are the vegetation types which have economic value for pastoralism, including most of the vegetation associations found within the Chenopod Formation. The importance of this issue is underlined by the findings of Chapter 9, which demonstrate that sheep grazing has a very powerful impact on vegetation composition, by differentially reducing the regeneration success of the woody perennial species present. While most species are negatively affected to some extent, some are so severely affected that their populations are already significantly reduced. It seems likely that these species will become extinct, particularly if current management practices of spreading sheep grazing more evenly become more general. These findings support those of Crisp and Lange (1976; 1978). It is therefore very important that this be taken into account when planning for conservation in the arid regions of Australia. A network of small ungrazed reserves as suggested by Stafford Smith &

Morton (1992) may be a more appropriate means of conservation for these and similar species.

Sheep were found to be by far the most important vertebrate herbivore in affecting regeneration of woody perennials. The remaining vertebrates, rabbits, goats and kangaroos had much less, if any effect. This is in direct contradiction to much of the literature citing rabbits are the most important herbivore in suppressing regeneration of trees and shrubs in the Australian arid zone. Several reasons are suggested for this contradiction. Rabbits cannot survive unless they have a diet of green herbaceous material, so their populations tend to fluctuate in response to ENSO-related rainfall events, building up to high numbers after rain, and dropping rapidly during dry periods. On the other hand, sheep numbers remain relatively stable as long as stock watering points are maintained, since they can survive on a much more woody diet. At the beginning of droughts, when herbaceous vegetation becomes scarce, rabbits are known to ring-bark trees and shrubs, probably for the moisture contained in the bark. However, these events are very episodic, both temporally and spatially, and although there are visible signs of injury by rabbits to the vegetation, the effects are neither widespread nor continuing. Because the sheep effects are more widespread and continuous, they are more insidious, and tend to be ignored. It is also possible that rabbits caused much more conspicuous and widespread damage prior to 1950, when *Myxomatosis* was introduced.

The rabbit paradigm is particularly dangerous for conservation, because the mistaken importance of rabbits in comparison to livestock then becomes an *a priori* assumption in designing research programmes, making decisions for pastoral management and designing reserve systems. For instance, the rabbit argument is widely used in opposition to the setting up of traditional stock-exclusion national parks, since it can therefore be assumed that there will be no benefit unless rabbits are excluded as well. In combination with economic forces it has been a major factor leading to the development of the so-called "multiple-use" regional reserve concept. The regional reserves (such as Innamincka) are a special form of tenure allowing other forms of land-use besides conservation (Cohen, 1990). They are very attractive to government because they are cheap to establish because no compensation is required since existing land-uses continue, albeit supposedly with some restrictions to meet conservation needs. These results show that at least some stock-free reserves will be necessary for adequate conservation of many woody species.

"Woody weeds"

The imbalance caused by the addition of domestic livestock to the landscape has resulted in another phenomenon, that known as "woody weeds". These are loosely defined as undesirable species capable of rapidly increasing in response to grazing. The results of this study show that this is not a current phenomenon in eastern South Australia, since no species showed significant increases in regeneration at sheep-grazed sites (Chapter 9). Most species showed absolute decreases in regeneration, indicating that apparent increases in populations of certain species, including many cited as "woody weeds" are merely relative. These are probably due to changes in competitive ability, brought about by the addition of a herbivore which grazes preferentially. Since the changes are relative, synecological and holistic approaches as suggested by Jacoby (1985) are essential in managing rangeland vegetation. Eradication programs aimed at individual undesirable species are unlikely to be successful and may even exacerbate the problem.

Sustainability of pastoralism

These results show that carefully managed pastoralism will not damage populations of chenopod shrubs (Chapter 9), which indicates that economically sustainable pastoralism should be an achievable goal as suggested by Friedel *et al.* (1990). It will be necessary to ensure that the overgrazing events of last century are not permitted to recur, since the results show that these can lead to abrupt transitions resulting in erosion, salination, increasing numbers of unpalatable shubs, and a range of other undesirable outcomes, many of which may be irreversible. However, if the diversity of vegetation is to be maintained, and ecological sustainability achieved, a regional management plan which recognises the special conservation needs of a range of grazing susceptible species is required. The multiple-use plan of a network of reserves and pastoral land as suggested by Stafford Smith & Morton (1992) is likely to be a useful approach. Such a plan may also be more useful in other arid lands where the pressure of human needs tends to preclude the establishment of the traditional large reserve.

Vegetation description

There is a very urgent need for basic description of vegetation in Australia, where vast land areas and a small population have meant that a great deal still needs to be carried out. The results of Chapters 6 and 7 provide an objectively derived series of classifications and maps of eastern South Australia, which has only been mapped by subjective methods previously. Since a good data-base is essential for conservation management (Hopkins & Saunders, 1987; Margules, 1989), these maps are an important management tool. The techniques used were rapid and cost-effective, which means that they would be very useful in preparing basic inventories in other arid areas of Australia and elsewhere where large tracts of vegetation remain undescribed.

CONCLUSIONS

This study demonstrates the value of a broadscale, inductive approach to large areas in which vegetation is relatively little known, coupled with a shift to more reductionist methods once more directed hypotheses had been formed. Multivariate methods were found to be very efficient in summarizing such data, especially when different analysis techniques were used to complement one another. The collection of data at nested scales was found to provide more information than could be provided by surveys at a single scale, and modern analysis techniques already widely used in phytosociology at small scales were found be very useful when applied to larger-scale phytogeographical problems. The results show a strong edaphic control of vegetation patterns, which is capable of overriding climatic control at small scales, explaining the tendency of vegetation associations to form complex mosaics. For this reason, vegetation classifications at the broader scale of alliance were more useful for vegetation mapping of large areas, whereas classifications at the scale of association were more useful for determining the effects of edaphic and other variables. Grazing by sheep was found to be the strongest variable in suppressing regeneration of trees and shrubs, although rabbit grazing, being episodic, may be more immediately apparent. Goats and kangaroos had little effect on regeneration. The lack of conservation within the chenopod shrublands is therefore a serious problem, and represents a threat to the maintenance of heritage vegetation, and to ecological sustainability. A solution may be a network of small and large stock-free reserves, permitting multiple use of arid rangelands.

Appendix 1

Plant species found within the study area in eastern South Australia. Species names and common names are those used by Jessop and Toelken (1986), except where other citations are given. Asterisks denote introduced species. Perennial species, here defined as plants capable of living for longer than two years, are marked (p). Plants found within the study area, but not within the vegetation association sites are marked +.

SCIENTIFIC NAME	COMMON NAMES	PLANT ASSOCIATIONS
ADIANTACEAE		
Cheilanthes lasiophylla (p)	Woolly Cloak-Fern	B D G H
C. sieberi subsp. _sieberi_ (p)	Mulga Fern	A G H
AGAVACEAE		
*_Agave americana_ (p)	Century Plant, American Aloe	+
AIZOACEAE		
Carpobrotus rossii (p)	Angular Pigface, Karkalla	D N
Gunniopsis quadrifida (p) (syn. _Aizoon sturtii_)	Sturt's Pigface	M N P
*_Mesembryanthemum crystallinum_	Common Iceplant	E D
Tetragonia eremaea	Native Spinach	B C D E F G H I J L M N Q
Trianthema triquetra	Red Spinach, Small Hogweed	+
AMARANTHACEAE		
Ptilotus exaltatus var. _exaltatus_ (p)	Pink Mulla Mulla	A B C D F H
P. gaudichaudii var. _parviflorus_ (p)	Paper Fox Tail	H
P. obovatus (p)	Silver Mulla Mulla	B D E F G H N
P. polystachyus (p)		+
AMARYLLIDACEAE		
Crinum flaccidum (p)	Darling Lily	N
ANACARDIACEAE		
*_Schinus areira_ (p)	Pepper Tree	+
ASCLEPIADACEAE		
Leichhardtia australis (p)	Native Pear, Austral Doubah	B D
Sarcostemma australe (p)	Caustic Bush/Vine	H
BORAGINACEAE		
*_Buglossoides arvensis_	Sheepweed, Corn Gromwell	+
*_Echium plantagineum_	Salvation Jane, Paterson's Curse	D E F H I L N Q
Halgania cyanea		
*_Heliotropium amplexicaule_	Blue Heliotrope	D
*_H. europaeum_	PotatoWeed, CommonHeliotrope	D E
*_Neatostema apulum_	Hairy Sheepweed, Blackweed	D E
Omphalolappula concava	Burr Stickseed	B D E F H I M N
CAMPANULACEAE		
Isotoma petraea (p)	Rock Isotome	G H
Wahlenbergia communis	Tufted Bluebell	H
W. gracilenta	Annual Bluebell	D E F H N
W. luteola		
W. stricta	Tall/Austral Bluebell	B C D E H I L N O
W. tumidifructa	Native Bluebell	E L O
CARYOPHYLLACEAE		
*_Herniaria hirsuta_	Rupture-Wort, Dense Mat-Plant	D E K
*_Polycarpon tetraphyllum_	Allseed, Four-leaf Allseed	H
Scleranthus pungens (p)	Prickly Knawel	B E H
*_Silene gallica_	French Catchfly	H
*_Silene nocturna_	Mediterranean Catchfly	H
*_Spergularia diandra_	Lesser Sand-Spurrey	B H L N O
CASUARINACEAE		
Casuarina cristata (p)	Black Oak, Belah	B E F G H N O
CHARACEAE		
Chara corallina		+
CHENOPODIACEAE		
Atriplex acutibractea		B E F H N O
A. angulata	Fan Saltbush	E J L N O R
A. eardleyi	Small Saltbush	O
A. fissivalvis (p)	Gibber Saltbush	N O
A. limbata (p)	Spreading Saltbush	E F L M P
A. lindleyi subsp. _conduplicata_	Baldoo, Annual Saltbush	H N O
A. lindleyi subsp. _inflata_	Baldoo, Annual Saltbush	E F G H L N O
A. nummularia (p)	Old Man Saltbush	+
A. holocarpa (syn. _A. spongiosa_ var _holocarpa_)	Pop Saltbush	E F L N O

A. stipitata (p)	Bitter/Mallee/Kidney Saltbush	C D E J M
A. suberecta/velutinella (p)	Lagoon/Sandhill Saltbush	+
A. vesicaria (p)	Bladder Saltbush	D E F G H L M N O
Chenopodium cristatum	Crested Goosefoot	F L
C. curvispicatum		
C. desertorum subsp. *anidophyllum* (p)	Mallee Goosefoot	A B G
C. desertorum subsp. *desertorum* (p)	Desert/Frosted Goosefoot	A E F
C. melanocarpum	Black Crumbweed	B
**C. murale*	Nettle-leaved Goosefoot, Green Fat Hen	+
C. nitrariaceum (p)	Nitre Goosefoot	+
C. pumilio	Clammy Goosefoot, SmallCrumbweed	D G L
Dissocarpus biflorus	Twin-horned Copperburr	B E J K L M N O P R
D. paradoxus	Cannonball, Ball Bindyii	B C D E F K L M N O
Einadia nutans (p)	Climbing/Nodding Saltbush	B C D E G N Q
Enchylaena tomentosa (p)	Ruby/Barrier Saltbush	A B C D E G H L N Q
Eriochiton sclerolaenoides	Woolly-fruit Copperburr	B D E F H K
Maireana aphylla (p)	Cottonbush, Leafless Bluebush	D H M N R
M. appressa (p)		D
M. astrotricha (p)	Low Bluebush	D E F H L M N O
M. brevifolia (p)	Greenbush, Short-leaved Bluebush	E G L O Q
M. erioclada (p)	Rosy Bluebush	C E H N
M. integra (p)		C D E F H L N O
M. pyramidata (p)	Black Bluebush, Sago-Bush	D E F G H I L N O P Q
M. sedifolia (p)	Bluebush, Pearl/Hoary Bluebush	B C D E H N
M. trichoptera		B C D E H
M. triptera (p)	Three-wing Bluebush	A C D N
M. turbinata or *georgei* (p)		C D E F H N O
Osteocarpum acropterum var. *deminutum* (p)	Water-Weed, Babbagia	D E F L O
Rhagodia parabolica (p)	Fragrant/Mealy/Old Man Saltbush	B D E H M
R. spinescens (p)	Spiny/Thorny/Hedge/Creeping Saltbush	B D E H M
R. ulicina (p)	Spiny Goosefoot	D F H
Salsola kali	Buckbush, Roly-Poly, Russian Thistle	D E H K L M N O P
Sclerochlamys brachyptera (p)	Short-winged Copperburr, Hairy Bassia	D L N O P
Sclerolaena bicornis (p)	Goathead Burr	D F
S. convexula (p)	Tall Copperburr	H
S. cuneata (p)		
S. decurrens (p)	Green Copperburr	D E F H N
S. diacantha/holtiana/uniflora complex (p)	Grey Copperburr/Bassia	A B C D E F H M N O R
S. divaricata (p)	Poverty Bush, Tangled Copperburr/Bassia	+
S. intricata (p)	Poverty Bush, Tangled Poverty Bush	
S. lanicuspis (p)	Woolly Copperburr, Spinach Burr	D E F H J N O P
S. obliquicuspis (p)	Limestone Copperburr	C D E F H K M
S. parviflora (p)	Mallee Copperburr, Small-flowered Bassia	A
S. patenticuspis (p)	Spear-fruit Copperburr/Bassia	D
S. ventricosa (p)	Salt Copperburr	L M N O
Sclerostegia tenuis (p)	Slender Glasswort	D
COMPOSITAE		
Actinobole uliginosum	Flannel Cudweed, Camel Dung, Cotton Weed	A B C D E F H L M N O
Angianthus tomentosus	Hairy Cup-Flower	F L N O
**Aster subulatus*	Wild Aster, Aster Weed, Bushy Starwort	E
Brachycome ciliaris var. *ciliaris*	Variable Daisy	B C D E F H L M N O
B. ciliaris var. *brachyglossa*		
B. ciliaris var. *languinosa*		
B. eriogona		
B. lineariloba	Hard-headed Daisy	B D E F H I J L M N O P R
B. trachycarpa	Smooth Daisy	+
**Calendula arvensis*	Field Marigold	L O
Calotis cymbacantha	Showy Burr Daisy	C E F M
C. erinacea	Tangled Burr Daisy	L N P
C. hispidula	Bogan Flea, Hairy Burr Daisy, Bindyii	B C D E F G H
C. lappulacea	Yellow Burr Daisy	N R
C. plumulifera	Woolly-headed Burr Daisy	L O
C. multicaulis	Woolly-headed Burr Daisy	J L M N R
**Carthamus lanatus*	Saffron Thistle, Woolly Star Thistle	B G H
Cassinia laevis (p)	Cough Bush, Curry Bush, Rosemary Bush	B G H
**Centaurea melitensis*	Cockspur Thistle, Malta Thistle	C D E F H J O Q
Centipeda thespidioides	Desert Sneezeweed	L N R
**Cirsium vulgare*	Spear Thistle	F
Conyza bonariensis		
Craspedia pleiocephala	Soft Billybuttons	D E F H L M N O
Cratystylis conocepha (p)	Bluebush Daisy	C
**Dimorphocoma minutula*		
Eriochlamys behrii	Woolly Mantle	N
Erodiophyllum elderi	Koonamore Daisy	D E F
Gnaphalium involucratum	Star Cudweed, Common Cudweed	+
Gnephosis arachnoidea (syn *G. foliata*)	Erect Yellow-Heads	D E F H J M N O
G. burkittii	Wires-and-Wool	B C D E H K N O
Gnephosis pusilla (syn. *Chrysocoryne pusilla*)	Dwarf Cup-Flower, Dwarf Angianthus	F L M O P

G. skirrophora (syn. _Trichanthodium skirrophurum_)	Woolly Yellow-Heads, Woolly Gnephosis	D E H L M N
Haeckeria punctulata (p)		E H
Hedypnois rhagodioides	Cretan Weed, Cretan Hedypnois	+
*_Helianthus annuus_	Sunflower, Common Sunflower	D E N
Helichrysum ambiguum subsp. _ambiguum_	Hill Everlasting	B G H
H. apiculatum	Common Everlasting, Yellow Buttons	L N
H. bracteatum	Golden Everlasting, Straw Flower	+
H. leucopsideum	Satin/Coast Everlasting	A
H. monochaetum		E L
H. pterochaetum	Perennial Sunray	+
H. semipapposum	Clustered Everlasting	B H N
Helipterum corymbiflorum	Grey/Small White Sunray	E F H L N O
H. floribundum	Common White/Large White Sunray	D F I L M N O
H. jessenii	Orange Sunray	D E N
H. microglossum	Clustered Sunray	D E F H I L M N O P
H. moschatum	Musk Sunray	B D E F H N
H. polygalifolium	Brilliant Sunray	A B D E F H J K L M N O
H. pygmaeum	Pigmy Sunray	C F H L M R
H. strictum	Slender Sunray, Urn Paper Daisy	D N
H. troedelii		
H. uniflorum	Woolly Sunray	F N
*_Hypochoeris glabra_	Smooth/Glabrous Catsear	B C D E F G H K M N O
Isoetopsis graminifolia	Grass Cushion, Grass Buttons	B C D E F H N
Ixiochlamys nana	Small Fuzzweed	D F
Ixiolaena chloroleuca		
I. leptolepis	Stalked Ixiolaena/Plover Daisy	E O P Q R
I. tomentosa	Woolly Ixiolaena/Plover Daisy	B E F L N
*_Lactuca serriola_	Prickly Lettuce, Compass Plant, Milk Thistle	D E F H O
Leptorhynchos baileyi		
Millotia greevesii	Creeping Millotia	E N Q
M. myosotidifolia	Broad-leaved Millotia	E N
Minuria cunninghamii	Bush Minuria	C F H M N
M. denticulata	Woolly Minuria	H
M. leptophylla	Minnie Daisy	D E F H L N O P
Myriocephalus stuartii	Poached-egg/Ham-and-Eggs Daisy	E L N O Q R
Olearia calcarea (p)		
O. decurrens (p)	Clammy Daisy-Bush	D F L M N
O. muelleri (p)	Mueller's Daisy Bush	L M
O. pimelioides (p)	Daisy Bush, Burrbunga	B E
O. rudis (p)	Azure Daisy Bush	+
O. subspicata (p)	Shrubby Daisy Bush	A B C D H
*_Onopordum acanthium_	Scotch/Cotton/Heraldic Thistle	C D F H
*_O. acaulon_	Stemless/Horse Thistle, Stemless Onopordum	C D E H
Podolepis canescens	Large Copperwire Daisy, Bright/Grey Podolepis	F
P. capillaris	Wiry/Bright Podolepis, Invisible Plant	A C E F H L M N O P
Pogonolepis muelleriana (syn. _Angianthus strictus_)	Stiff Cup-Flower/Angianthus	D E N
Pseudognaphalium luteo-album	Cudweed, Jersey/Japanese Cudweed	L
Pterocaulon sphacelatum	Apple-Bush, Fruit Salad Plant	+
*_Reichardia tingitana_	False Sow-Thistle, Reichardia	C D E F H N Q
Rutidosis helichrysoides	Grey Wrinklewort	L
Senecio anethifolius	Feathery Groundsel	E H
S. cunninghamii var. _serratus_	Shrubby Groundsel	M
S. glossanthus	Slender Groundsel	B D E F H I J L O Q
S. gregorii (syn. _Othonna gregorii_)		D
S. lautus	Variable Groundsel, Fireweed	B D E F H L M N O
S. magnificus	Tall Yellow-Top, Showy Groundsel	D E H
S. runcinifolius	Tall Groundsel	C D E
S. quadridentatis	Cotton Fireweed, Fireweed	D E G H
Sigesbeckia microcephala	Pale Indian Weed	H
*_Sonchus oleraceus_	Common Sow-Thistle, Milk Thistle	B D E F G H I K N Q
Toxanthes perpusillus (now _Millotia perpusillus_, Martin O'Leary pers. comm.)	Tiny Bow-Flower	F
*_Urospermum picrioides_	False Hawkbit, Urospermum	H
Vittadinia cervicularis	Vittadinia	A D H
V. dissecta		B C D E F H J M N O
V. eremaea		D E F H L M N
V. gracilis	Woolly New-Holland Daisy	D E H
V. pterochaeta	Rough Fuzzweed	H N
V. sulcata		N
Waitzia acuminata	Orange Immortelle	B D
*_Xanthium spinosum_	Bathurst Burr	L Q
CONVOLVULACEAE		
Convolvulus erubescens	Australian/Pink Bindweed	E F J L M N O
C. remotus	Australian Bindweed	B D E F H L M N O P
CRASSULACEAE		
Crassula colorata var. _colorata_	Dense Crassula, Dense Stonecrop	B C D E F H I J K M N O
C. sieberana subsp. _tetramera_	Sieber Crassula, Australian Stonecrop	B F G
CRUCIFERAE		
*_Alyssum linifolium_	Flax-leaved Alyssum	C D E F H J K L N O

Arabidella trisecta	Shrubby Cress	DEFHLM
**Brassica tournefortii*	Long-fruited Wild/Mediterranean/Wild Turnip	EFHJLMP
**Carrichtera annua*	Wards Weed	BDEFHKLNOQ
**Diplotaxis tenuifolia*	Lincoln Weed, Sand Rocket	+
Harmsiodoxa blenodiodioides	Hairypod Cress, May Smocks	+
**Lepidium africanum*	Common/Rubble Peppercress	+
L. fasciculatum	Bundled/Fascicled Peppercress	D
L. leptopetalum	Shrubby Peppercress	L
L. oxytrichum	Green Peppercress	BHELNO
L. phlebopetalum	Veined Peppercress	CDFHELMNOP
L. sagittulatum	Fine-leaved Peppercress	F
Phlegmatospermum cochlearinum	Oval-podded/Downy Cress	FELMNOP
**Sisymbrium erysimoides*	Smooth Mustard	BDFGHELNQR
**S. orientale*	Wild/Indian Hedge Mustard	FHJE
Stenopetalum lineare	Narrow Thread-Petal	+
S. velutinum	Downy/Velvet Thread-Petal	BDFHKELNO
CUCURBITACEAE		
**Cucumis myriocarpus*	Paddy Melon, Gooseberry Cucumber	D
**C. lanatus*	Bitter/Wild/Camel/Paddy Melon	GHE
CUPRESSACEAE		
Callitris columellaris (p)	Northern/White/Flinders Range Cypress-Pine	BGHE
C. verrucosa (p)	Mallee Cypress-Pine, Mallee Pine	+
CYPERACEAE		
Cyperus gymnocaulos (p)	Spiny Flat-Sedge/Sedge	+
C. squarrosus	Bearded Flat-Sedge	MR
Eleocharis pallens (p)	Pale Spike-Rush	A
Fimbristylis dichotoma (p)	Common Fringe-Rush, Eight-Day Grass	AB
Schoenus subaphyllus (p)	Desert Bog-Rush	A
EUPHORBIACEAE		
Beyeria lechenaultii (p)	Pale Turpentine Bush, Felted Wallaby Bush	AB
B. opaca (p)	Dark Turpentine Bush, Smooth Wallaby Bush	AB
Euphorbia australis	Hairy Caustic Weed	H
E. drummondii	Caustic Weed/Creeper, Flat/Mat Spurge, Milkweed	BCDRIHELMNO
E. tannensis subsp. eremophila	Desert Spurge, Caustic Bush/Plant, Spurgewort, Bottletree Caustic	DHMN
**Ricinus communis* (p)	Castor Oil Plant	+
FRANKENIACEAE		
Frankenia serpyllifolia (p)	Bristly/Clustered/Dainty/Downy/Hairy Sea-Heath	LN
GENTIANACEAE		
**Centaurium spicatum*	Spike Centaury	DO
GERANIACEAE		
Erodium angustilobium		BGHR
**E. aureum*		
**E. cicutarium*	Common Storksbill/Heronsbill/Crowfoot, Cutleaf Erodium	DGHLMNO
E. crinitum (common small blue)	Blue Storksbill/Heronsbill/Crowfoot	CDGHELMNO
E. cygnorum subsp. *glandulosum*	Blue Storksbil/Geranium	DFHIEMNO
GOODENIACEAE		
Goodenia fascicularis	Silky/Mallee Goodenia	CDFHELMN
G. pinnatifida	Scrambled Eggs, Mother Ducks, Cut-leaved Goodenia	BHEN
G. pusilliflora	Small-flowered Goodenia	BHELMNO
Scaevola depauperata	Skeleton Fan-Flower	H
S. parvibarbata		
S. spinescens (p)	Spiny/Prickly Fan-Flower, Currant Bush, Poontoo	ADH
Velleia arguta	Spur Velleia	BN
GRAMINEAE		
Aristida contorta	Mulga Grass, Sand Wire-Grass/Spear-Grass, Bunched Kerosene Grass	FHIELMN
A. arida/nitidula	Flat-awned Threeawn	AHEL
Arundo donax (p)	Bamboo, Spanish/Giant/Danubian Reed	+
Astrebla lappacea	Curly Mitchell Grass, Wheat Mitchell	N
**Avena barbata*	Bearded Oat	+
Bromus arenarius	Sand Brome	DHELNO
**B. catharticus*	Prairie/Rescue Grass	Q
**B. madritensis*	Madrid Brome, Lesser Brome	BDFHENOQ
**B. rubens*	Red Brome	B
Chloris pectinata	Comb Windmill Grass/Chloris	ELNOQ
Cymbopogon ambiguus (p)	Scented Grass/Oil-Grass, Lemon-scented Grass	HE
Dactyloctenium radulans	Button/Finger Grass	FLM
Danthonia caespitosa	White Top, Common Wallaby-Grass	BDFHKENO
Dichanthium sericeum	Silky/Queensland Blue-Grass	MNO
Digitaria brownii	Cotton Grass/Panic Grass	GH
Elymus scabrus	Rough/Common Wheat-Grass	BH

Enneapogon avenaceus	Common Bottlewashers	D F H I J E L M N O P
E. caerulescens		D F H I E M N O
E. cylindricus	Jointed Nine-Awn/Bottlewashers	+
E. nigricans	Black-Heads, Nigger-Heads	+
Enteropogon acicularis	Umbrella/Spider/Curly Windmill Grass	D H L M N
Eragrostis australasica (p)	Cane-Grass, Bamboo Grass	R
E. barrelieri	Pitted Lovegrass	E
E. dielsii	Mulka Grass, Mulka, Mallee Lovegrass	F E L M N O
E. eriopoda	Woollybutt, Naked Woollybutt, Neverfail	D F E L M N P
E. falcata	Sickle Lovegrass	F
E. lacunaria	Purple Lovegrass	H
E. leptocarpa	Drooping Lovegrass	C F J N O R
E. parviflora	Weeping Lovegrass	+
E. setifolia	Narrow-leaved Neverfail, Bristly Lovegrass	+
Eriochloa australiensis	Australian Cupgrass	R
**Hordeum glaucum/leporinum*	Barley Grass	D H E L N O Q
**Lamarckia aurea*	Golden Top, Comb Grass	C H E Q
**Lophochloa pumila*	Tiny Bristle Grass	B D F H K E L M N O
Panicum decompositum	Native Millet, Windmill Grass	C F M N R
Paspalidium basicladum		
**Schismus barbatus*	Arabian/Kelch/Mulga Grass	B C D F G H J K E L M N O
Sporobolus actinocladus	Ray Grass, Katoora	+
Stipa acrociliata (p)	Graceful Spear Grass	B C D E N
S. drummondii	Cottony Spear Grass	B D G H E
S. elegantissima	Elegant/Feather Spear Grass	B E N
S. eremophila	Desert Spear Grass	C D F H K E N
S. nitida	Balcarra Grass	B C D F H K E M N O P
S. nodosa		
S. platychaeta	Flat-awned Spear Grass	D E N
S. scabra		
Tragus australianus	Burr/Small Burr Grass	F J L N O
Triodia irritans (p)	Porcupine Grass, Desert Spinifex	A B C H E
Tripogon loliiformis	Five Minute Grass, Rye Beetle Grass	F H J E M N O
Triraphis mollis	Purple Heads, Purple Plume Grass, Needle Grass	H E L M N
**Vulpia muralis*	Wall Fescue, Silver Grass	D E O
**V. myuros*	Rat's Tail Fescue, Silver Grass	+
GYROSTEMONACEAE		
Codonocarpus cotinifolius (p)	Camel Poison, Bell Fruit	A
HALORAGACEAE		
Haloragis aspera	Rough Raspwort	J E M Q
Myriophyllum verrucosum	Red Water Milfoil	+
LABIATAE		
Ajuga australis	Austral/Australian Bugle	+
**Marrubium vulgare* (p)	Horehound	G E
Prostanthera striatiflora (p)	Jockeys Cap, Striated/Striped Mintbush	B D H
**Salvia verbenaca*	Wild Sage	D K E N O Q
Teucrium racemosum	Grey Germander	C D F L M Q
Westringia rigida (p)	Stiff Westringia/Western Rosemary	A B D
LEGUMINOSAE		
Acacia aneura (p)	Mulga	D H E L M N
A. argyrophylla (p)	Silver Mulga	+
A. beckleri (p)	Barrier Range Wattle	H
A. brachybotrya (p)	Grey Mulga/Wattle	+
A. burkittii (p)	Sandhill Wattle/Pinbush, Burkitt's Wattle	A B C D E H
A. calamifolia (p)	Wallowa	
A. carnei (p)	Needle Wattle, Dead Finish, Purplewood Wattle	E H
A. colletioides (p)	Wait-a-While, Spine Bush	A C D
A. continua (p)	Thorn/Thorny Wattle	+
A. ligulata (p)	Umbrella Bush, Small Cooba, Sandhill Wattle	A
A. loderi (p)	Nealie, Nealia	+
A. nyssophylla (p)		
A. oswaldii (p)	Umbrella Wattle, Miljee	A C D E L N
A. pendula (p) (new record for S. Aust.)	Myall, Boree, Balaar, Nilyah, True/Weeping Myall	+
A. rigens (p)	Nealie, Needle Wattle, Needle Bush	A
A. salicina (p)	Broughton/Native Willow, Willow Wattle, Cooba	+
A. spinescens (p)	Spiny Wattle	+
A. tetragonophylla (p)	Dead Finish, Kurara	E H
A. victoriae (p)	Elegant/Bramble/Prickly Wattle	E F H N O Q
**Astragalus sesameus* (p)	Purple Milk-Vetch	E Q
Cassia artemisioides (p) (now *Senna artemisioides* subsp. *artemisioides*, B. Randell pers. comm.)	Silver Cassia	E H
C. nemophila var. *coriacea* (p) (now *S. artemisioides* subsp. *coriacea*, B. Randell pers. comm.)	Punty Bush, Desert Cassia	C D E F M

C. desolata var. *planipes* (p) (now S. *artemisioides* subsp. *petiolaris*, B. Randell pers. comm.)	Grey Cassia	+
C. nemophila var. *platypoda* (p) (now S. *artemisioides* subsp. *petiolaris*, B. Randell pers. comm.)	Punty Bush, Desert Cassia, Y-Bush	A C D E F L M
C. nemophila var. *zygophylla* (p) (now S. *artemisioides* subsp. *zygophylla*, B. Randell pers. comm.)	Punty Bush, Desert Cassia	+
C. phyllodinea (p) (now *S. artemisioides* subsp. *petiolaris*, B. Randell pers. comm.)	Woody/Silver Cassia	L M
C. sturtii (p) (now S. *artemisioides* subsp. *sturtii*, B. Randell pers. comm.)	Sturt's/Grey/Dense Cassia	+
Clianthus formosus	Sturt's Desert Pea, Marlu Pedi, Blood Flower	D E
Glycine clandestina var. *sericea*	Twining Glycine	D
Indigofera australis (p)	Austral/Native/Hill Indigo	+
Lotus cruentus	Red-flower Lotus, Red Birdsfoot/Red Trefoil	B D E F H I J K L M N O
**Medicago littoralis*	Strand/Harbinger Medic	+
**M. minima*	Woolly/Small Burr-Medic, Little Medic	B D E F H M N O Q
**M. polymorpha*	Burr/Toothed Medic	D E N O
**M. truncatula*	Barrel/Snail/Caltrop Medic	E N
**Melilotus officinalis*	Common Melilot, Yellow Sweet Clover	F
**Prosopis juliflora* (p)	Mesquite	+
Psoralea cinerea	Annual Verbine	E H J M N O
Swainsona fissimontana	Broken Hill Pea	D
S. microcalyx	Wild Violet	E
S. microphylla subsp. *affinis* (syn. *S. affinis*)	Small-leaved Swainson-Pea	N
S. murrayana	Slender Darling-Pea, Murray Swainson-Pea	E
S. oroboides	Variable Swainson-Pea/Swainsona, Darling-Pea	E F N
S. phacoides	Dwarf Swainsona, Dwarf Swainson-Pea, Lilac Darling-Pea	+
S. stipularis	Orange Darling-Pea	N
S. swainsonioides	Downy Swainsona/Darling-Pea	N
S. viridis	Creeping Darling-Pea	E N O
Templetonia egena (p)	Desert/Round Broom-Bush	C
Trigonella suavissima	Sweet Fenugreek, Cooper/Channel Clover	D
**Vicia monantha*	Spurred/Square-stemmed/One-flower Vetch	+
LILIACEAE		
**Asphodelus fistulosus*	Onion Weed, Wild Onion	E H N O
Bulbine semibarbata	Leek Lily	A B C D E F G H L M N O P
Lomandra effusa (p)	Scented Mat-Rush	+
Lomandra leucocephala (p)	Woolly/Woolly-head Mat-Rush	A
Thysanotus baueri	Mallee Fringe-Lily	B D E F H L M N
Wurmbea centralis		
Wurmbea dioica subsp. *dioica*	Early Nancy	D E H N
Xanthorrhoea quadrangulata (p)	Mount Lofty Grass Tree, Yacca, Black Boy	B
LIMONIACEAE		
**Limonium lobatum*	Winged Sea-Lavendar	E
LORANTHACEAE		
Amyema maidenii (p)	Pale-leaved Mistletoe	E
A. miquelii (p)	Box Mistletoe	A
A. preissii (p)	Wire-leaved Mistletoe	+
Lysiana exocarpi (p)	Harlequin Mistletoe	+
MALVACEAE		
Abutilon fraseri (p)	Dwarf Lantern-Flower	E H
A. halophilum (p)	Plain Lantern-Flower	N
A. leucopetalum (p)	Desert Chinese Lantern	P
A. otocarpum (p)	Desert Chinese/Desert Lantern	D E F N
Lavatera plebeia (p)	Australian/Native Hollyhock	D E F N O
Lawrencia glomerata	Clustered Lawrencia, Small Golden-Spike	+
L. squamata (p)	Thorny/Fan-leaved Lawrencia	+
**Malva parviflora*	Small-flowered Marshmallow	Q
**Malvastrum americanum*	Malvastrum, Spiked Malvastrum	N
Radyera farragei (p)	Desert Rose-Mallow, Bush/Knobby Hibiscus	+
Sida calyxhymenia (p) (syn. *S. petrophila*)	Tall/Rock Sida	B D E H I
S. corrugata var. *A* (p)	Limestone Sida	D E F K L

S. corrugata var. *corrugata* (p)	Corrugated/Variable Sida	B N
S. fibulifera (p)	Pin Sida	C D E F H I M N P
S. intricata (p)	Twiggy Sida	D E L M N O
S. trichopoda (p)	High/Narrow-leaved Sida	E F N P
MARSILEACEAE		
Marsilea drummondii	Common Nardoo	J L Q R
MYOPORACEAE		
Eremophila alternifolia (p)	Narrow-leaved Fuchsia, Native Honeysuckle	+
E. deserti (p)	Turkey Bush	A C D E L N
E. duttonii (p)	Budda, Harlequin Fuchsia Bush	
E. freelingii (p)	Limestone Fuchsia, Rock Fuchsia Bush	
E. glabra subsp. *glabra* (p)	Tar Bush, Common Emu Bush, Fuchsia Bush	D F L M O
E. glabra subsp. *murrayana* (p)		+
E. longifolia (p)	Weeping Emu Bush, Berrigan, Long-leaved Eremophila	A C E F L N
E. maculata (p)	Spotted Emu Bush, Fuchsia Bush, Spotted/Native Fuchsia	A E
E. oppositifolia (p)	Weeooka, Twin-leaved Emu Bush	B
E. scoparia (p)	Broom/Silver Emu Bush, Scotia Bush	A C D E
E. serrulata (p)	Green Fuchsia Bush	+
E. sturtii (p)	Turpentine Bush, Narrow-leaved Emu Bush	C D E F L M O R
Myoporum acuminatum (p) (now *M. montanum*)	Native Myrtle, Western Boobialla, Water-Bush	+
Myoporum platycarpum (p)	False Sandalwood, Sugarwood	A C D E F
MYRTACEAE		
Eucalyptus brachycalyx (p)	Gilja	+
E. camaldulensis (p)	River/Murray Red Gum, Red Gum	D Q
E. cyanophylla/dumosa (p)	White/Dumosa/Cong or Murraylands/Blue Mallee	A C
E. flindersii (p)	Grey/Flinders Mallee, Mallee Red Gum	B E
E. gillii (p)	Curly Mallee	+
E. gracilis (p)	Yorrell, White Mallee	A C E K
E. incrassata (p)	Ridge-fruited/Yellow/Lerp/Rib-fruited Mallee	A
E. intertexta (p)	Gum-barked/Gum/Bastard Coolibah, Red Box	B
E. largiflorens (p)	River/Black Box	C
E. oleosa (p)	Red/Giant/Acorn Mallee	B C
E. porosa (p)	Mallee/Swamp Box, Black/S.A. Mallee Box, Water/Quorn/Lerp Mallee	K
E. socialis (p)	Red/Summer Red/Grey/Pointed Mallee	A B C D E K
Melaleuca lanceolata (p)	Dryland/Black Tea-Tree, Moonah, Moonah Honey-Myrtle	+
NYCTAGINACEAE		
Boerhavia dominii/schomburgkiana	Tar Vine, Tah Vine, Geotcho	B E H N
OLEACEAE		
Jasminum didymum subsp. lineare (p)	Native/Desert Jasmine	B D
ORCHIDACEAE		
Pterostylis excelsa	Dryland Greenhood	B
OROBANCHACEAE		
Orobanche australiana	Australian Broomrape	H
OXALIDACEAE		
Oxalis perennans	Oxalis	C D E H N Q
PAPAVERACEAE		
**Argemone subfusiformis*	Mexican/Prickly Poppy	H
**Glaucium corniculatum*	Red/Bristly Horned Poppy	H
PITTOSPORACEAE		
Pittosporum phylliraeoides (p)	Native Apricot/Willow, Weeping Pittosporum, Poisonberry, Berrigan	D E F G H N
PLANTAGINACEAE		
Plantago cunninghamii	Sago Weed	H
**P. drummondii*	Sago Weed, Dark Sago Weed	A B C D E F H I J L M N O
**P. scabra*		B Q
POLYGONACEAE		
**Emex australis*	Three-cornered Jack, Spiny Emex, Goat Heads, Double Gee, Cape Spinach	D Q
Muehlenbeckia cunninghamii (p)	Lignum, Tangled Lignum	C
**Polygonum aviculare*	Wireweed, Hogweed, Prostrate Knotweed	Q
**Rumex crispus*	Curled Dock	Q

*_R. vesicarius_	Rosy/Bladder/Pink Dock, Wild Hop	E F H
PORTULACACEAE		
Calandrinia eremaea	Small Purslane	A B C D E F G H M N O
Portulaca oleracea	Munyeroo, Common Purslane/Pigweed	H J N
PRIMULACEAE		
*_Anagallis arvensis_	Scarlet/Blue Pimpernel	E G H O
PROTEACEAE		
Grevillea huegelii (p)	Comb Spider-Flower/Grevillea	A C D
Hakea leucoptera (p)	Needlebush/Needlewood, Silver Needlewood, Pinbush, Water Tree, Kulua	A C L M
RANUNCULACEAE		
Ranunculus pumilio	Ferny/Small-flowered Buttercup	+
RESEDACEAE		
*_Reseda luteola_	Weld, Dyers Mignonette	E N
RHAMNACEAE		
Spyridium phlebophyllum (p)		+
RUBIACEAE		
Galium migrans	Bedstraw	H
Synaptantha tillaeacea		N
RUTACEAE		
Eriostemon linearis (p)	Narrow-leaved Wax-Flower	B H
Geijera parviflora (p)	Wilga	+
		+
SANTALACEAE		
Exocarpos aphyllus (p)	Leafless Ballart, Stiff Cherry, Currant Bush	C D E F H
Santalum acuminatum (p)	Quandong, Native Peach, Sweet Quandong, Katunga, Burn Burn	C D
S. lanceolatum (p)	Plumbush, Native Plumbush, Cherrybush, Northern Sandalwood	E H J
S. murrayanum (p)	Bitter Quandong, Ming	A
SAPINDACEAE		
Dodonaea baueri (p)	Crinkled Hop-Bush	+
D. bursariifolia (p)	Small Hop-Bush	+
D. lobulata (p)	Lobe-leaved/Lobed Hop-Bush	B D E H
D. microzyga (p)	Brilliant Hop-Bush	D F M
D. viscosa subsp. _angustissima_ (p)	Narrow/Slender-leaved Hop-Bush, Slender Hop-bush	A B C D H L P
Heterodendrum oleifolium (p)	Bullock Bush, Rosewood, Boonaree, Cattle Bush	B C D E F G H J L M N
SCROPHULARIACEAE		
Limosella curdieana	Large Mudwort	E R
SOLANACEAE		
*?_Datura leichardtii_	Native Thornapple	+
Duboisea hopwoodii (p)	Pituri, Pitchuri Thornapple, Pitcheri	A
Lycium australe (p)	Australian Boxthorn	D E H N
*_L. ferocissimum_ (p)	African Boxthorn	E N Q
*_Nicotiana glauca_ (p)	Tree Tobacco, Tobacco Bush	+
N. goodspeedii	Small-flowered Tobacco	C D E H
N. occidentalis		H
N. velutina	Velvet Tobacco	B G H
Solanum ellipticum (p)	Velvet Potato Bush	E F H
S. esuriale	Quena	A C M O
*_S. nigrum_	Blackberry/Black/Deadly Nightshade	E G H Q
S. petrophilum (p)	Rock Nightshade	E H
S. sturtianum	Sturt's Nightshade	E
TAMARICACEAE		
Tamarix aphylla (p)	Athel Pine, Athel Tamarix, Athel Tree	+
THYMELEACEAE		
Pimelea curviflora subsp. _micrantha_	Silky Rice-Flower	D E H N
P. microcephala (p)	Mallee Rice-Flower	+
P. simplex	Desert Rice-Flower	D E F H I N O P
TYPHACEAE		
Typha domingensis (p)	Bulrush, Cumbungi	+
UMBELLIFERAE		
*_Conium maculatum_	Hemlock	+
Daucus glochidiatus	Native/Australian/Austral Carrot	B C D E F H K M N O
URTICACEAE		
Parietaria debilis	Shade/Forest Pellitory	B G H

VERBENACEAE		
* *Verbena officinalis*	Common Verbena	+
ZYGOPHYLLACEAE		
Nitraria billardierei (p)	Nitre/Dillon Bush	D E N
* *Tribulus terrestris*	Caltrop, Cat-Head	D E M
Zygophyllum ammophilum spp complex	Sand Twinleaf	C D E N
Z. ammophilum complex (twining type)		D E N
Z. apiculatum	Gallweed, Pointed/Common Twinleaf, Squash Bush	B C D E H N
Z. aurantiacum/eremaeum	Shrubby/Climbing Twinleaf, Native Hop	A B C D E F
Z. crenatum	Lobed/Notched Twinleaf	E L
Z. glaucum	Pale/Annual Twinleaf	+
Z. idiocarpum	Violet Twinleaf	D E N O
Z. ovatum	Dwarf Twinleaf	D E
Z. prismatothecum	Square-fruit Twinleaf	E F

Appendix 2

Summary of the vegetation alliances and associations identified for the study area in eastern South Australia and the variables controlling their distributions. Alliances are listed in the order of the main gradient on the Alliance DCA ordination (Figure 6.4). Associations with marked affinity for particular alliances are shown in bold type. Number of samples of each alliance and association are listed in brackets. Note that the sum of samples within an alliance is greater than the sum of alliance samples, because of the dual sampling strategy (see Chapter 5). Environmental trends are derived from the DCCA analysis of Chapter 8. Alliance trends are a summary of association trends which occur within the alliance. Individual species environmental trends are for the whole study area, and derived from the multiple regressions in Chapter 8. Dashes for species environment trends indicate that no regressions were carried out for that species.

MALLEE FORMATION

ALLIANCE	ALLIANCE TRENDS	ASSOCIATION TRENDS	ASSOCIATION	SPECIES ENVIRONMENTAL TRENDS
I (7) ***Triodia irritans*** ***Eremophila scoparia*** ***Eucalyptus socialis***	SE Murray Plains high rainfall low 1900 grazing low elevation	low elevation low pH high % sand	**A (7)** ***Triodia irritans*** ***Eucalyptus socialis*** ***Eucalyptus cyanophylla***	+sand +sand, +rain, -elevation +sand, +run-off, -phosphorus
		low elevation low 1900 grazing medium % sand	**C (5)** ***Enchylaena tomentosa*** ***Ptilotus exaltatus*** ***Sclerolaena diacantha*** ***Cassia nemophila platypoda*** ***Eremophila sturtii***	+rain, -1900 grazing - - -Ca, -elevation -run-off
		medium elevation medium pH	D (2) *Maireana sedifolia* *Casuarina cristata* *Sclerolaena obliquicuspis*	+inorganic C, +run-off +Mg, +inorganic C, +rain, -1900 grazing +Inorganic C, +rain

CHENOPOD FORMATION

Maireana pyramidata Order

X (1) ***Triodia irritans*** ***Dodonaea viscosa*** ***Acacia victoriae*** ***Rhagodia parabolica*** ***Cassinia laevis*** ***Callitris columnellaris*** ***Eucalyptus intertexta***	high ranges high elevation low pH	high % sand medium-high elevation low pH	B (1) *Enchylaena tomentosa* *Ptilotus exaltatus* *Rhagodia parabolica*	+rain, -1900 grazing - -
		high elevation medium-low pH	H (1) *Sida calyxhymenia* *Ptilotus obovatus* *Solanum ellipticum*	-IC, +P, +elev, +run-
V (4) ***Sida calyxhymenia*** ***Eucalyptus socialis*** ***Nitraria billardiera***	high elevation high OC/IC	high elevation low pH high OC/IC medium Na medium P	**I (2)** ***Sida calyxhymenia***	-inorganic C, +P, +elevation, +run-off

			medium-high elevation medium pH medium-high IC/OC medium-low Na medium-high P	E (3)	*Maireana pyramidata* *Sclerolaena obliquicuspis*	+rain +inorganic C, +rain
			medium elevation medium-high pH medium OC/IC low Na high P	Q (1)	*Eucalyptus camaldulensis* *Lycium ferocissimum*	-run-off -
II (20)	***Maireana sedifolia*** ***Casuarina cristata*** ***Cassia nemophila coriacea***	Murray Plains medium-high elev medium-low pH	medium elevation medium pH	**D** **(23)**	***Maireana sedifolia*** ***Casuarina cristata*** ***Sclerolaena obliquicuspis***	+inorganic C, +run-off +Mg, +inorganic C, +rain, -1900 grazing +inorganic C, +rain
			high elevation low pH	**G** **(1)**	***Atriplex vesicaria*** ***Casuarina cristata*** ***Maireana pyramidata*** ***Callitris columnellaris* etc**	+Na, +run-off, +1900 grazing +Mg, +inorganic C, +rain, -1900 grazing +rain +elevation
			medium-high elevation medium pH medium-high IC medium-low Na medium-high P	E (3)	*Maireana pyramidata* *Sclerolaena obliquicuspis*	+rain +inorganic C, +rain
			low elevation low 1900 grazing medium % sand	C (1)	*Enchylaena tomentosa* *Ptilotus exaltatus* *Sclerolaena diacantha* *Cassia nemophila platypoda* *Eremophila sturtii*	+rain, -1900 grazing - - -Ca, -elevation -run-off
III (63)	***Atriplex vesicaria*** ***Maireana pyramidata*** ***Casuarina cristata*** ***Maireana sedifolia***	medium-high elev medium pH high IC/OC	medium-high elevation medium pH medium-high IC medium-low Na medium-high P	**E** **(32)**	***Maireana pyramidata*** ***Sclerolaena obliquicuspis***	+rain +inorganic C, +rain
			medium elevation medium pH	**D** **(11)**	***Maireana sedifolia*** ***Casuarina cristata*** ***Sclerolaena obliquicuspis***	+inorganic C, +run-off +Mg, +inorganic C, +rain, -1900 grazing +inorganic C, +rain
			medium-low elevation high pH range of organic C range of Na	N (14)	*Atriplex vesicaria* *Maireana astrotricha*	+Na, +run-off +Na

			high elevation	H	*Sida calyxhymenia*	-inorganic C, +P, +elevation +run-off
			medium-low pH	(9)	*Ptilotus obovatus*	-pH, +P, +elevation
					Solanum ellipticum	-
					Enchylaena tomentosa	+rain, -1900 grazing
			medium-low elevation	O	*Sclerochlamys brachyptera*	+Na, +1900 grazing
			high pH	(3)	*Sclerolaena ventricosa*	-
			medium organic C			
			medium Na			
			high %sand	B	*Enchylaena tomentosa*	+rain, -1900 grazing
			medium-high elevation	(2)	*Ptilotus exaltatus*	-
			low pH		*Rhagodia parabolica*	-
			medium elevation	M	*Atriplex vesicaria*	+Na
			medium pH	(1)	*Cassia nemophila coriacea*	-
			medium-low OC/IC		*Eremophila longifolia*	-
			high Na		*Eremophila sturtii*	-run-off
			medium-low elevation	F	*Maireana pyramidata*	+rain
			medium pH	(1)		
			medium IC/OC			
			medium Na			
			medium P			
			medium elevation	K	*Eucalyptus socialis*	+sand, +rain
			medium pH	(1)	*Atriplex vesicaria*	+Na, +run-off
			high OC/IC		*Eucalyptus gracilis*	-
			low Na		*Eucalyptus porosa*	-
			medium-high P			
			medium elevation	L	*Maireana astrotricha*	+Na
			medium-low pH	(1)	*Rhagodia spinescens*	+P, -run-off
			medium-low IC/OC			
			medium-high Na			

Intermediate Alliances

IV	***Maireana pyramidata***	middle &north	high elevation	H	*Sida calyxhymenia*	-inorganic C,+P,+elevation, +run-off
(19)	***Sida calyxhymenia***	ranges	medium-low pH	(13)	*Ptilotus obovatus*	-pH, +P, +elevation
	Acacia aneura	medium - high			*Solanum ellipticum*	-
	Acacia victoriae	elevation			*Enchylaena tomentosa*	+rain, -1900 grazing
			medium-high elevation	E	*Maireana pyramidata*	+rain
			medium pH	(12)	*Sclerolaena obliquicuspis*	+inorganic C, +rain
			medium-high IC/OC			
			medium-low Na			
			medium-high P			

			medium-low elevation medium pH medium IC/OC medium Na medium P	F (3)	*Maireana pyramidata*	+rain
			medium-low elevation high pH mediumOC/IC medium Na	O (2)	*Sclerochlamys brachyptera* *Sclerolaena ventricosa*	Na, +1900 grazing
			medium elevation medium-low pH medium-low OC/IC medium Na	L (1)	*Maireana astrotricha* *Rhagodia spinescens*	+Na +P, -run-off
VII **(11)**	**Maireana astrotricha** ***Maireana pyramidata*** ***Eremophila duttonii*** ***Acacia aneura***	western Frome Plains med-low elevation	medium-low elevation medium pH medium IC/OC medium Na medium P	**F** **(4)**	***Maireana pyramidata***	+rain
			medium-high elevation medium pH medium-high inorganic C medium-low Na medium-high P	E (3)	*Maireana pyramidata* *Sclerolaena obliquicuspis*	+rain +inorganic C, +rain
			medium-low elevation high pH range of OC/IC range of Na	N (2)	*Atriplex vesicaria* *Maireana astrotricha*	+Na, +run-off +Na
			medium elevation medium pH	D (1)	*Maireana sedifolia* *Casuarina cristata* *Sclerolaena obliquicuspis*	+inorganic C, +run-off +Mg, +inorganic C, +rain, -1900 grazing +inorganic C, +rain
			medium elevation medium pH medium-low OC/IIC high Na	M (1)	*Atriplex vesicaria* *Cassia nemophila coriacea* *Eremophila longifolia* *Eremophila sturtii*	+Na - - -run-off

Maireana astrotricha Order

VI **(21)**	***Atriplex vesicaria*** ***Maireana astrotricha*** ***Casuarina cristata*** ***Maireana aphylla***	SE Frome Plains & S ranges med-low elevation medium pH med-high Na	medium-low elevation high pH range of OC/IC range of Na	**N** **(10)**	***Atriplex vesicaria*** ***Maireana astrotricha***	+Na, +run-off +Na

medium elevation medium-low pH medium-low IC/IC medium-high Na	**L** **(5)**	***Maireana astrotricha*** ***Rhagodia spinescens***	+Na +P, -run-off
medium elevation medium pH medium-low OC/IC high Na	**M** **(2)**	***Atriplex vesicaria*** ***Cassia nemophila coriacea*** ***Eremophila longifolia*** ***Eremophila sturtii***	+Na - - -run-off
medium-high elevation medium pH medium-high IC/OC medium-low Na medium-high P	E (1)	*Maireana pyramidata* *Sclerolaena obliquicuspis*	+rain +inorganic C, +rain
low-medium elevation medium pH medium IC/OC medium Na medium P	F (1)	*Maireana pyramidata*	+rain
high elevation medium-low pH	H (1)	*Sida calyxhymenia* *Ptilotus obovatus* *Solanum ellipticum* *Enchylaena tomentosa*	-inorganic C, +P, +elevation, +run-off -pH, +P, +elevation - +rain, -1900 grazing
medium elevation medium pH medium OC/IC high Na	J (1)	*Rhagodia spinescens* *Sida intricata* *Pimelea microcephala* *Santalum lanceolatum*	+P, -run-off - - -
medium-low elevation high pH medium OC/IC medium Na	O (1)	*Sclerochlamys brachyptera* *Sclerolaena ventricosa*	+Na, +1900 grazing
medium elevation medium-high pH medium OC/IC low Na high P	Q (1)	*Eucalyptus camaldulensis* *Lycium ferocissimum*	-run-off
low elevation high pH very low IC/OC medium-high Na	R (1)	*Eragrostis australasica* *Eragrostis leptocarpa/parviflora*	- +Na, +sand

VIII **(1)**	***Dodonaea viscosa angustissima*** ***Eremophila sturtii*** ***Atriplex nummularia*** ***Eucalyptus largiflorens***	far NE plains low elevation med-high Na low P sand	low elevation medium pH low OC/IC med-high Na low P	P (1)	*Dodonaea viscosa angustissima* *Heterodendrum oleifolium*	+sand, +pebbles -Na
IX **(13)**	***Atriplex vesicaria*** ***Maireana astrotricha*** ***Casuarina cristata*** ***Maireana aphylla***	E & N plains med-low elevation high pH medium Na	medium-low elevation high pH range of OC/IC range of Na	**N** **(11)**	***Atriplex vesicaria*** ***Maireana astrotricha***	+Na, +run-off +Na
			medium-low elevation high pH medium OC/IC medium Na	**O** **(2)**	***Sclerochlamys brachyptera*** ***Sclerolaena ventricosa***	+Na, +1900 grazing

Appendix III - A

Vegetation Association A in Danggali Conservation Park. The association occurs on sandy soils of low pH and low phosphorus. The mallee-forming habit of *Eucalyptus dumosa* is apparent. The tussock-forming sclerophyllous grass in the foreground is *Triodia irritans*.

Appendix III - B

Vegetation Association B at Oulnina Park Station. The foreground plant is *Rhagodia parabolica.*

Appendix III - C

Vegetation association C at Bullyaninnie Station. The round green bushes in the right foreground are stage 2 and 3 *Cassia nemophila platypoda.*

Appendix III - D

Vegetation Association D at Spring Dam Station. The tree is *Casuarina cristata* about 8 m tall as indicated by the 20 cm gradations on the measuring standard. The light blue bushes in the low foreground are *Maireana sedifolia*. Pualco Hill is partially obscured by the tree.

Appendix III - E

Vegetation Association E near Winninninnie Station. The bush is *Maireana pyramidata*, and the greyish ground cover is partially *Sclerolaena obliquicuspis*.

Appendix III - F

Vegetation Association F near Grampus Hill. The dominant species is *Maireana pyramidata*, the dark green bush. The dryland mallee Association K appears in the distance closer to the foot of the hill.

Appendix III - G

Vegetation Association G at Oulnina Park Station. The foreground trees are *Callitris columnellaris*, and those on the opposite hillside are *Casuarina cristata.*

Appendix III - H & I

Sida calyxymenia, representing Vegetation Associations H and I, near Bulloo Creek Station. It is the sole dominant of Association I, but occurs with other species in Association H. Gradations on the measuring standard are 20 cm.

Appendix III - J

Vegetation Association J at Pine Creek Station. *Rhagodia spinescens* is one of the dominants of this association, which tends to occur in run-on areas with clay soils.

Appendix III - K

Vegetation Association K near Winnininnie Station. *Eucalyptus socialis* in the foreground is tending to show a tree rather than a mallee habit. The greenish grey bushes in the low foreground are *Atriplex vesicaria.*

Appendix III - L

Vegetation Association L at Wompinie Station. The low shrubs are mainly *Maireana astrotricha* with some *Rhagodia spinescens*. The foreground shrub is *Eremophila longifolia*.

Appendix III - M

Vegetation Association M at Mulyungarie Station. Foreground shrubs are *Eremophila sturtii* and tall background shrubs are *Eremophila longifolia.*

Appendix III - N

Vegetation Association N at Boolcoomata Station. The dark blue-grey shrubs are *Maireana astrotricha*, and the lighter grey-green shrubs are *Atriplex vesicaria*.

Appendix III - O

Vegetation Association O at Netley Gap Station. The low almost herbaceous plants in the foreground include *Sclerolaena ventricosa* and *Schlerochlamys brachyptera.* Feral goats are common in the central and southern part of the study area.

Appendix III - P

Vegetation Association P at Bulloo Creek Station. The shrubs are *Dodonaea viscosa.*

Appendix III - Q

Vegetation Association Q at Manunda Station. The large trees are *Eucalyptus camaldulensis*, and the two dark-green rounded shrubs in the middle distance are an introduced species, *Lycium ferocissimum*.

Appendix III -R

Vegetation Association R at Lake Dismal Station. *Eragrostis australasica* occurs in ephemeral swamps on clay soils.

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