Mineral nutrients in mediterranean ecosystems

J A Day (editor)

A report on a workshop meeting held at
Hermanus, South Africa, September 1980

SOUTH AFRICAN NATIONAL SCIENTIFIC PROGRAMMES REPORT NO

71

JUNE 1983

Issued by
Cooperative Scientific Programmes
Council for Scientific and Industrial Research
P O Box 395
PRETORIA
0001
from whom copies of this report are available on request.

Printed in 1983 in the Republic of South Africa
by the Graphic Arts Division of the CSIR

ISBN 0 7988 2693 2

Editor's address:

J.A. Day
Department of Zoology
University of Cape Town
Private Bag
RONDEBOSCH
7700

PREFACE

The notion of ecological convergence has influenced taxonomists and biogeographers since the development of ecology in the mid-nineteenth century. Our initial understanding of the ecosystems of the world resulted from plant geographers' classifications of plant forms and formations, categories implicitly based on their intuitive views of convergence. Because of the striking similarities in plant form among the small, widely-separated mediterranean ecosystems (Figure i), biogeographical concepts and early ideas on ecophysiology were strongly influenced by convergence in the sclerophyllous plant form and the inferred similarities in plant function. These views were controversial, however, and there has been no attempt at rigorous hypothesis testing until the second half of this century.

The question central to the hypothesis of evolutionary convergence is if "very similar physical environments, acting on phylogenetically dissimilar organisms in different parts of the world, will produce structurally and functionally similar ecosystems" (Cody and Mooney, 1978). This question is of crucial importance because its answer will determine the extent to which ecology is a generally applicable science. The answer is of immediate relevance to policy-makers and managers. To quote DiCastri and Mooney (1973), it ".... has major practical implications for the management of natural resources. In effect, in order to assess the transfer of technology, it is essential to know to what extent information acquired from studying one particular ecosystem is applicable to another ecosystem of the same type but situated in a different location."

Mediterranean ecosystems have become major testing grounds for the concept of ecological convergence. The very problem of generalizing from individual ecosystem studies led to a dual programme in the United States-International Biological Programme (US-IBP), where intensive site studies of ecosystem functioning were paralleled by intercontinental comparisons of the origin and structure of ecosystems. This included an investigation of convergent evolution in mediterranean Chile and California, the results of which provided substantial support for the convergence hypothesis. Subsequent work, however, has shown clear differences between the structure, and apparently the function, of mediterranean ecosystems of the Mediterranean Basin and the New World on the one hand, and those of Australia and South Africa on the other: differences which are ascribed partly to divergent evolutionary histories and partly to the marked differences in nutrient status.

The comparative studies in Chile and California were preceded by a symposium organized by the Universidad Austral de Chile in March 1971 at Valdivia, with the purpose of making a preliminary critical overview of the information available on mediterranean ecosystems. Published proceedings and many additional papers resulted from this symposium while work that arose as a consequence of the meeting has been summarized and synthesized in two volumes that appeared in 1977. Later, concern for acute management problems shared among countries with mediterranean-climate zones led to the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems at Stanford, California, in August 1977; this provided a review of the problem throughout the world and a belated opportunity for policy-makers, managers and research scientists to confer and look for common ground in a controversial field.

Fig. i Location of the mediterranean ecosystems

1. California
2. Chile
3. Mediterranean Basin
4. South-western Cape, South Africa
5. South-western and south-eastern Australia

The Third International Conference on Mediterranean-type Ecosystems was convened in South Africa by the National Programme for Environmental Sciences in September 1980. The meeting centred once more on the problem of evolutionary convergence by focusing on the extent to which nutrients, as opposed to climate, determine the structure and functioning of mediterranean ecosystems and the manner in which unusually large numbers of species are able to coexist in the face of environmental stress.

It was particularly fitting that the third international meeting should have been held in South Africa at that time. The particular environmental problems of the fynbos biome had prompted the initiation in 1977 of a cooperative programme of research aimed at developing the knowledge needed for the wise use of fynbos resources: the Fynbos Biome Project. The project is one of several national scientific programmes within the National Programme for Environmental Sciences administered by the CSIR. The National Programme is a cooperative undertaking of scientists and scientific institutions in South Africa concerned with research related to environmental problems. It includes research designed to meet local needs as well as projects being undertaken in South Africa as contributions to the international programme of SCOPE (Scientific Committee on Problems of the Environment), the body set up in 1970 by ICSU (International Council of Scientific Unions) to act as a focus of international non-governmental scientific effort in the environmental field.

The Third International Conference took the form of a symposium held at the University of Stellenbosch, from 22 to 23 September 1980, followed by a four-day workshop at Hermanus. This volume is the result of the workshop meeting, which addressed itself specifically to the topic of "nutrients as determinants of mediterranean-type ecosystems".

Each chapter is the result of close cooperation between small groups of biologists with expertise and experience in different fields and on different continents. The reports differ from those which appear in the Proceedings of the symposium, in that they not only consolidate ideas on nutrients as determinants of mediterranean ecosystems, but also suggest directions for future research. This volume is therefore intended to be of value to administrators concerned with the use and conservation of mediterranean ecosystems, which are characterized by high diversities of plants and animals and by large numbers of threatened species and habitats. It seems that these features are closely associated with the very low nutrient levels typical of soils of mediterreanean ecosystems. Thus an understanding of the impact, distribution and cycling of nutrients is of overwhelming importance in understanding the functioning of such systems. An understanding of their functioning will in turn enable enlightened planning and management in the face of agricultural expansion, invasion by exotic biota, soil erosion, and modification of natural water-bodies resulting from increased demands for water in these naturally-arid areas.

EXPLANATION OF TERMINOLOGY USED IN THIS VOLUME

1. Mediterranean ecosystems

Mediterranean ecosystems occur in very limited regions in six widely-separated areas of the world (the south-western and south-central parts Australia, the south-western tip of Africa, southern California, central Chile and around the Mediterranean Basin) and are best defined in climate terms. They occur in areas with rainfall of at least 500-700 mm yr^{-1} (although parts of California receive only 250 mm) and an extended dry summer period of two to six months, and correspond very closely with the winter-rainfall areas of the world. High summer temperatures occur during the driest part of the year. Mediterranean climates may further be defined by Koppen's climatic types Csb, Csa and BSk.

Koppen-type	Climate	Winter	Summer
Csb	warm	mild humid (at least one month below 18°)	dry and mild (hottest month below 22°)
Csa	warm	mild humid (at least one month below 18°)	dry and hot (hottest month below 22°)
BSk	semi-arid	mild sub-humid (at least one month below 18°)	dry and hot (hottest month above 22°)

The term "mediterranean" in this volume thus refers to mediterranean-climate systems in general and not only to the regions surrounding the Mediterranean Basin.

Mediterranean environments, occurring largely in winter-rainfall areas, have well-marked seasons. Rainfall may vary from as little as 250 to as much as 1200 mm yr^{-1}; although these values may be high, water is frequently a limiting factor during the hot, dry summers. Temperatures are seldom extreme, however. Mean monthly minima range from about 8 to 12°C; snow is uncommon except on mountain-tops, although frost may be a feature of some low-lying inland areas. Mean annual maxima vary from 18 to 30°C.

2. Mediterranean vegetation types

Although patches of sclerophyllous woodland or open forest, with heathy understorey, occur in mediterranean regions, the vegetation usually consists of low-growing shrubs and heaths.

Mediterranean heathlands comprise a complex mixture of evergreen, sclerophyllous plants arranged into three recognizable strata: a sclerophyllous ground stratum (<1 m tall), mid-height sclerophyllous shrubs (1 - 2 m tall) and low sclerophyllous trees (>2 m tall). Taller shrubs and trees may overtop the heathland.

Mediterranean shrublands comprise an overstorey of sclerophyllous shrubs with a seasonal ground stratum of herbaceous grasses and herbs. In dense shrublands, this herbaceous stratum may exist for only a few years of the pyric succession, reappearing after fire or other disturbances.

Many names have been given to the vegetation of the various mediterranean regions in different parts of the world. Some names are now used to refer to more than one type of community or, conversely, some communities are referred to by more than one name. The names are briefly explained below.

batha	dwarf Israeli mediterranean shrubland, often dominated by *Sarcopoterium spinosum* (= phrygana in Greece).
chaparral	Californian mediterranean shrubland; on soils moderately rich in nutrients.
coastal sage scrub	Californian shrublands dominated by drought-deciduous shrubs.
fynbos	South African mediterranean heathland; on nutrient-poor soils; sometimes termed "Cape macchia".
garrigue	low French and Italian mediterranean shrubland dominated by *Quercus coccifera*; on soils rich in Ca and with high pH.

kwongan	Western Australian aboriginal name for mediterranean heathlands north of Perth. (This term is not applicable in the rest of Australia, where over 300 aboriginal languages were once spoken).
macchia	(= maquis). An Italian term that has been applied to tall (>2 m) mediterranean shrubland dominated by *Quercus coccifera* and/or the taller *Q. calliprinos*. In Spain and Chile, similar regions are referred to as matorral.
mallee	Australian mediterranean shrubland dominated by mallee species of Eucalyptus; on soils moderately rich in nutrients and with high pH.
manzanita chaparral	Californian mediterranean shrubland dominated by *Arctostaphylos* (manzanita); on soils moderately rich in nutrients.
maquis	Corsican, Provencal and Cretian tall mediterranean heathlands of *Erica arborea* and *Arbutus unedo* (strawberry tree); on nutrient-poor soils; the term is often more widely used to denote mediterranean heathlands generally.
matorral	Spanish and Chilean mediterranean shrubland; on soils moderately rich in nutrients.
phrygana	dwarf mediterranean shrubland, often dominated by *Sarcopoterium spinosum* (= batha in Israel).
renosterveld	ecotonal, often degraded, South African mediterranean shrubland dominated by *Elytropappus rhinocerotis* (renosterbos); on soils moderately rich in nutrients.
strandveld	South African coastal shrubland with a succulent karroid component; on soils rich in Ca and with high pH.

3. *Nutrient levels*

Mediterranean regions are characterized not only by climatic similarities but also by soils with very low levels of mineral nutrients. But even within a single region the levels of nutrients can vary quite considerably. During the course of the workshop it became clear that there was no appropriate terminology for distinguishing these regions.

Pedologists classify soils according to various criteria but soil fertility is seldom considered, except indirectly as a consequence of the degree of leaching in the pedogenetic process. For the ecophysiologist, on the other hand, knowledge of soil fertility is necessary for understanding the morphological and physiological responses of plants to their environments. In this respect, a scale of soil fertility is usually constructed, based on responses of indicator species to nutrients applied to the soil (Specht 1981d). Since virtually all the available data concern levels of nitrogen and phosphorus, we have decided to base our definitions on assessments of the total amounts of N and P in surface soils, since the major rooting depth is about 30 cm.

Table i lists the terms which have been used to describe the nutrient status of soils, together with levels of N, P and total exchangeable cations characterizing each type of soil. The terms oligo-, meso- and eutrophic are to be avoided because of connotations of human interference in the word "eutrophic". Terms concerning leaching are valuable but do not take into account soils derived from rock which has always been low in N and P. Thus we have decided to use the terms "nutrient poor", "nutrient rich" and "agriculturally rich" to denote the three soil types.

It should be stressed that these definitions are not intended to be conclusive but are proposed so that reasonable approximations can be made. We realize that dividing soils into only three groups based on nutrient-content is a simplification and that soil depth, water regime and other factors may alter nutrient availability. Further, these total values cannot be used to predict the levels of nutrients available to plants. These levels may be affected by numerous factors and may therefore be considerably lower than the total levels determined chemically. Further, although only N and P are considered, this is no guarantee that there are no other minerals limiting plant or animal growth. In fynbos, for example, copper, manganese and fluorine are often indetectable and copper at least seems to be limiting to herbivorous mammals.

This generalized series of soil fertility classes (see also Figure 1.1) excludes soils where nutrients are imbalanced, or present in toxic levels, or where the pH is extreme. For example, serpentine rocks produce soils rich in Mg and poor in Ca, while saline soils show toxic levels of Na, and the availability of P, Fe, Cu and Co is reduced in alkaline soils rich in Ca.

Finally, these reports largely contrast the poorer and richer ends of the nutrient spectrum in mediterranean ecosystems but it should be borne in mind that all but the richest of these soils would be considered impoverished or deficient by world standards.

SPECIES DIVERSITY

It is not always easy to determine exactly what measures have been used in order to arrive at figures for diversity in the literature. Moreover, the term "species diversity" in the botanical literature is often used to denote the number of species per unit area while in the zoological literature a measure of relative abundance is often incorporated, resulting in a variety of diversity indices. Thus in these reports the term "species richness" is used, for both plants and animals, to denote the simplest measure of diversity - that of a number of species per unit area. This is often referred to in the botanical literature as "alpha diversity".

Table i Terms used to describe the nutrient status of soils, together with levels of N, P and total exchangeable cations characterizing each type of soil

	Nutrient-poor Strongly-leached Oligotrophic	Nutrient-rich Moderately-leached Mesotrophic	Agriculturally-rich Weakly-leached Eutrophic
Total P (%) HCl extraction	< 0,022	0,022 - 0,06	> 0,06
Total N (%) H_2SO_4 extraction	< 0,12	0,12 - 0,30	> 0,30
Total exchangeable cations (meq $100g^{-1}$)	5	10	23 - 44
Mediterranean regions with this soil type	South African south-western Australian	Chilean Californian Mediterranean south-central Australian	Small areas of south-central Australian and Californian

"Regional diversity" or "gamma diversity", is a measure of species richness of a broad geographical area such as an entire mediterranean ecosystem.

ACKNOWLEDGEMENTS

The following are acknowledged for their roles in seeing this report finalized: Dalene Coetzee, Lois Kloppers, Yvonne Smith, Martsie Olivier and Margaret Orton, all of the CSP, CSIR, who provided the secretarial back-up before, during and after the workshop meeting; Pam van Helsdingen, also of CSP, CSIR for typing undertaken during early stages of production; Pascal Chesselet of Cape Town, who drew all the figures in this report; Margie Jarman of CSP, CSIR for assistance in the latter stages of editing copy, and for her major role in the workshop organization; all chapter contributors, and chapter conveners, and in particular Ray Specht, for their assistance subsequent to the workshop in rewriting, editing etc; and Brian Huntley, CSP, CSIR for the ability to organize the undertaking which produced the first three drafts of this report during a four day meeting.

ABSTRACT

Consolidated ideas on the role of nutrients as determinants of the structure and function of mediterranean ecosystems are presented in eight concise chapters. The origins and characteristics of the biotic and abiotic features of these systems are reviewed in an introductory chapter. The second chapter discusses inputs, outputs and cycling of nutrients as well as approaches to simulation models of nutrient cycling processes. The third chapter examines the uptake of nutrients, storage of nutrients, nutrient metabolism in mediterranean plants and the physiological effects of nutrient and water limitations. The role of plant form and function in relation to nutrient gradients is then highlighted in the fourth chapter, as are the structure and dynamics of plant communities in the fifth. Chapters 6 and 7 deal with the diversity, density and dynamics of animal communities and with the interactions between plants and animals. The volume is concluded with a chapter on the origin and maintenance of plant species diversity, which looks specifically at patterns of species diversity encountered in mediterranean-type ecosystems, the maintenance of species richness and hypotheses concerning speciation, extinction and endemism. Each chapter highlights future research priorities in the particular field of application.

SAMEVATTING

Bevestigde idees oor die rol van voedingstowwe as bepalers van die struktuur en funksionering van mediterreense-tipe ekosisteme word in agt beknopte hoofstukke aangebied. Die oorsprong en kenmerke van mediterreense-tipe ekosisteme in terme van hul biotiese en abiotiese eienskappe word in oënskou geneem in 'n inleidende hoofstuk. In die tweede hoofstuk word voedingstoftoevoer en -lewering en voedingstofsiklusseringprosesse bespreek. Hierdie hoofstuk handel ook oor benaderingswyses tot simulasiemodelle van voedingstofsiklusseringprosesse. Die derde hoofstuk ondersoek die opneem van voedingstowwe, berging van voedingstowwe, voedingstofmetabolisme in mediterreense plante en die fisiologiese uitwerking van voedingstof- en waterbeperkings. Die rol van plantvorm en -funksionering met betrekking tot voedingstofgradiente word daarna in die vierde hoofstuk belig, soos ook die struktuur en dinamika van plantgemeenskappe in die vyfde hoofstuk. Hoofstukke 6 en 7 handel oor die verskeidenheid, digtheid en dinamika van diergemeenskappe aangetref in mediterreense-tipe ekosisteme en oor die wisselwerking tussen plante en diere in hierdie sisteme. Die boek word afgesluit met 'n hoofstuk oor die oorsprong en instandhouding van plantspesieverskeidenheid, wat spesifiek patrone van spesieverskeidenheid aangetref in mediterreense-tipe ekosisteme, die handhawing van spesierykheid en hipoteses vir spesiasie, uitsterwing en inheemsheid in oënskou neem. Elke hoofstuk belig toekomstige navorsingsprioriteite in die besondere toepassingsveld.

TABLE OF CONTENTS

1. INTRODUCTION: THE ORIGINS AND CHARACTERISTICS OF MEDITERRANEAN ECOSYSTEMS

R. H. Groves (convener), J. S. Beard, H. J. Deacon, J. J. N. Lambrechts,
A. Rabinovitch-Vin, R. L. Specht, W. D. Stock

The floras and faunas of present-day mediterranean ecosystems have been influenced through geological time by a number of factors, including climatic changes and pedogenesis as well as the nature and the genetic potential of the biotas. In this chapter we discuss first the interrelated abiotic factors that have most influenced these ecosystems, and then we look briefly at the characteristic features of mediterranean biotas.

1.1 ABIOTIC FEATURES

1.1.1 CLIMATE

Climate has a direct effect on weathering processes, on release of nutrients and on the structure and functioning of plants and yet the climatic type by which mediterranean regions are defined is geologically recent (Raven 1973), having developed only in the last three-and-a-half million years or so.

Major climatic fluctuations have been globally synchronous and have affected all mediterranean regions; the main trend through the Cenozoic (65-0 m.y.) has been towards cooler, drier and more seasonal climates, culminating in the pronounced glacial/interglacial fluctuations of the Pliocene and Pleistocene periods. Although some of the present-day mediterranean regions were located on "drifting continents" in higher latitudes during the early Cenozoic (Palaeocene and Eocene, 65-38 m.y.), warm, humid, non-seasonal climates extended to these latitudes at that time; thus present-day mediterranean regions experienced this climate no matter what their latitude (Deacon, in press). Evidence of these warmer climates is preserved for example in the mediterranean regions of Australia, where some of the latosols must have been formed by chemical weathering more intense than is possible under present climatic conditions.

The early Oligocene (38 m.y.) was marked by abrupt cooling and by the beginning of circulation of oceanic bottom water (Kennett & Shackleton 1976). The inception of more seasonal climates at this time has been suggested for California on geomorphological grounds (Peterson & Abbott 1979). According to palynological data, on the other hand, the climate of southern Australia was sufficiently humid to support rainforest, although evidence for reduced diversity in the microflora (Kemp 1978) may be a reflection of cooling in the Oligocene.

High temperatures, approaching those of the late Eocene, are indicated in the early Miocene (23-14 m.y.) and may have been associated with a further period of latosol development. The middle and late Miocene (14-4 m.y.) were marked by the growth of the Antarctic ice sheets and by the appearance of more open environments either in, or bordering on, mediterranean regions. Local factors such as the elevation of mountain ranges, in Mediterranean Europe for example, contributed to the scale of environmental changes recorded in the late Miocene. But these were overridden by changes in atmospheric and oceanic circulation brought about by the progression from an ice-free globe to one with a permanent ice sheet at the South Pole. This led to an increased temperature gradient from pole to equator, stronger atmospheric circulation and the greater production of cold bottom waters, which cooled the surface waters at lower latitudes. The resulting trend towards progressively cooler and drier climates, which began in the Miocene, reached a peak in the Pliocene and Pleistocene.

Summer-dry climates in the mediterranean regions appear to have followed the development of modern patterns of atmospheric circulation. The glaciation of Antarctica in the Miocene long preceded glaciation on other continents, which began some 3,5 million years ago in the mid-Pliocene, at a time when the mid-American seaway closed, cutting off circulation of surface water between the Atlantic and Pacific Oceans at low latitudes. The effect of high-latitude glaciation in the northern hemisphere was to restore the symmetry of climatic zonation and to balance the circulation patterns in the two hemispheres. It was from this time that there is evidence, from the Mediterranean littoral for example (Michaux *et al*. 1979), of the inception of summer-dry mediterranean climates.

Pleistocene climatic fluctuations, which affected pedogenesis and the distribution of plants and animals in all the mediterranean regions, are best understood for the last 125 000 years, that is the late Pleistocene and the Holocene. Records show cooler and drier conditions for the last glacial maximum, 18 000 years ago, in all regions with the possible exception of California, while *Artemisia* and grassy steppe vegetation was widespread on the northern Mediterranean littoral. The amelioration of the climate at the end of the Pleistocene (12 000 years ago in the northern hemisphere and somewhat earlier in the south) is marked by extinction of some large mammals, a pattern that affected mediterranean regions as well as the temperate grasslands. Modern vegetation patterns developed as a consequence of this amelioration of climate.

The warm interglacial Holocene (present-day) climate has not been the normal climate of the Pleistocene; climates have been cooler, and for the most part drier, during the longer glacial episodes. It is a feature of mediterranean climates that precipitation is caused by frontal systems originating in the belt of Westerlies, one of the most important and stable elements in atmospheric circulation. Thus, given estimated decreases in precipitation of as much as 20 per cent due to cooler ocean surface temperatures during glacial episodes, rainfall reliability would probably not have been affected in the more humid parts of the mediterranean regions. This has undoubtedly contributed to the maintenance of the higher species diversity shown by the floras of most of these regions relative to those of adjacent regions, which were affected to a greater degree by changes in precipitation or temperature in the Pleistocene.

1.1.2 LITHOLOGIES AND PEDOGENESIS

Mediterranean regions are commonly located on the western margins of continents but different geological processes have been involved in blocking out these margins. Rifting and shearing were the dominant processes in forming the relatively stable margins of Africa and Australia. Uplift, more pronounced in Africa due to the outward flexuring of the margins, has contributed to subsequent relief. The pre-Cenozoic rocks associated with the African and Australian regions are predominantly acid igneous rocks and quartzose sediments. By contrast the continental margins on which the Chilean, Californian and European mediterranean regions are located, as well as the mediterranean region of south-central Australia, have been associated with plate subduction and mountain-building in the Cenozoic. This has resulted in the creation of young landscapes through the geologically recent elevation of coastal ranges so that these landscapes are associated with varied lithologies, including basic igneous and calcareous rocks.

The climatic control of soil-forming processes has been the same in all mediterranean regions since they have all been subject to a similar range of climates in the Cenozoic; the variations in the soils result from climatic factors operating on the different lithologies or substrata (Thrower & Bradbury 1973). The main lithological formations of mediterranean regions are listed in Table 1.1 and the pedogenic processes in Table 1.2.

1.1.3 NUTRIENTS

Low levels of nutrients are characteristic of mediterranean soils (see Preface) but even within these soils the levels of nutrients vary considerably. Further, plants are affected more by the extent to which nutrients are available or accessible than by the total quantity of nutrients in a soil. Thus it is the availability of nutrients which determines some of the characteristics of the evolution, growth and reproduction of mediterranean plants. These influences are examined below and in more detail in Chapters 2-5.

1.1.3.1 QUANTITIES OF NUTRIENTS IN THE SOIL

Nutrient status varies considerably with the length of leaching over geological time and with the levels of each nutrient present in parent rocks. Thus soils representing six major nutritional types can be identified in mediterranean ecosystems. Data on the chemical properties of these soils are presented in Table 1.3. It must be stressed that the various nutritional groups of soils often intergrade, sharp discontinuities being rare or being masked by overlay of adjacent materials. The soils in the first group of three listed in Table 1.3 intergrade in fertility: Figure 1.1 demonstrates the relationship between total P and total N in surface soils; the soils in the second group in Table 1.3 show nutritional toxicities or imbalances. Naturally the type of soil will influence the vegetation which can grow in a particular area and the major vegetation types associated with the six soil nutritional groups are given in Table 1.4.

Table 1.5 lists some data on the sizes of pools P, N, Ca and Mg in heathlands on nutrient-poor soils and in shrublands on nutrient-rich soils. The data have been simplified to allow comparison of the relative proportions of nutrients in the various pools.

From these preliminary and fragmentary data we may conclude that

- whether the vegetation occurs on nutrient-poor or on nutrient-rich soils, the total soil nutrient pool is considerably in excess of the plant nutrient pool. The availability to plants of various nutrients in this nutrient pool may, however, depend on the soil exchange

Table 1.1 The main lithological formations of mediterranean regions. XXX = common; XX = less common; X = present but not widespread; trace = found in restricted localities; - = not recorded. (For details see Thrower & Bradbury 1973; Di Castri *et al*. 1981)

	South-central Australia	South-western Australia	South Africa	Chile	California	Mediterranean
Siliceous rocks (sands, sandstones, quartzites, acid igneous rocks etc)	XXX	XXX	XXX	-	X	X
Argillaceous rocks (shales, mafic igneous rocks etc)	XX	Trace	XX	XXX	XXX	Trace
Calcareous rocks (limestones, marls, calcarenites etc)	XXX	Trace	X	-	Trace	XXX
Ultramafic igneous rocks (serpentines etc)	-	-	-	-	X	Trace

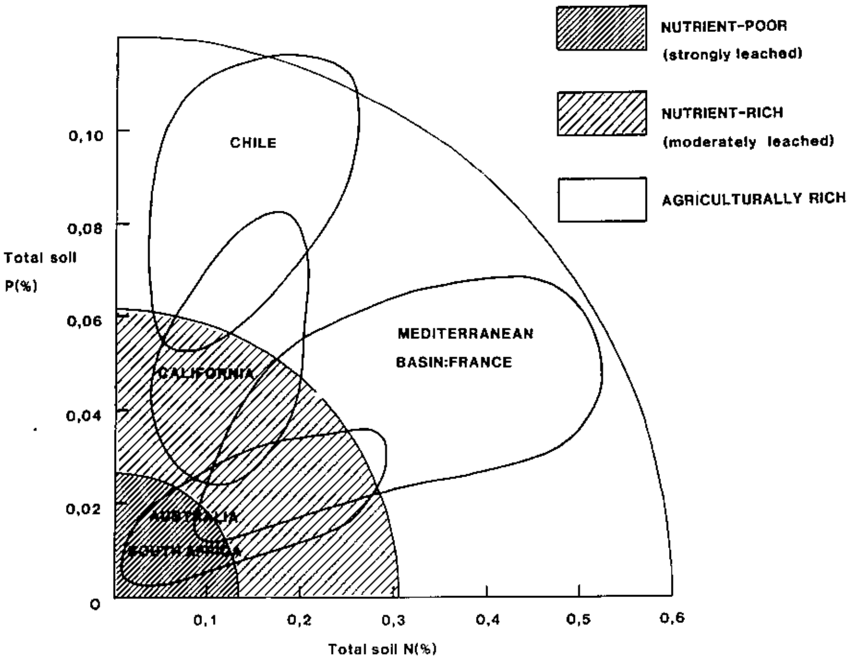


Fig. 1.1 Relative nutrient levels of surface soils in mediterranean regions, based on total soil nitrogen (H_2SO_4 extraction) and total soil phosphorus (HCl extraction) (after Di Castri 1981, Specht 1981b). Divisions between nutrient-poor, nutrient-rich and agriculturally-rich soils suggested by Specht (1981a)

Table 1.2 Pedogenesis of main substratum types in mediterranean regions

Substratum	Time			
	Early Cenozoic 65-23 m.y.	Miocene-Pliocene 23-3 m.y.	Pliocene-Pleistocene 3-0 m.y.	Today
Siliceous rocks	deep weathering, leaching and laterite formation	deep weathering and truncation through erosion	peat formation; erosion intensified; maintenance of skeletal soils and reworking of sands	strongly-leached nutrient-poor soils
Argillaceous rocks	leaching, deep weathering and laterite formation	truncation, deep weathering and truncation through erosion	leaching and shallow weathering	strongly-leached nutrient-poor and moderately-leached nutrient-rich soils
Calcareous rocks	deep weathering	deep weathering	erosion and truncation through natural or anthropogenic factors	moderately-leached nutrient-rich soils (eg Terra Rossa, Rendzina) and shallow, high pH soils
Ultramafic igneous rocks	deep weathering	deep weathering	deep weathering	Mg-rich, Ca-poor soils
Saline deposits and other evaporites	none recognized of this age	none recognized of this age	deposition of evaporites	saline gypseous soils

Table 1.3 Some chemical properties of surface soils from the six major soil-nutritional groups of the mediterranean regions of southern Australia (Data from Specht 1972; Stace *et al.* 1968)

Soil nutritional groups	pH	Total N (%)	Total P (%)	Total Exchangeable Cations (meq $100g^{-1}$)	Total Soluble Salts (%)
Strongly-leached nutrient-poor soils	5,7 ± 0,07[x]	0,07 ± 0,01	0,007 ± 0,001	5	0,016 ± 0,003
Moderately-leached nutrient-rich soils[xx]	6,5 ± 0,11	0,13 ± 0,01	0,026 ± 0,004	10	0,022 ± 0,004
Poorly-leached agriculturally-rich soils	5,0 to 7,7	0,17 to 0,61	0,04 to 0,18	23 to 44	0,02 to 0,13
High pH, Ca-rich soils	8,0 to 9,0	0,06 to 0,11	0,020	10 to 25	?
Mg-rich, Ca-poor soils	6,6	0,21	0,02 to 0,06	48 to 54	?
Saline and gypseous soils	6,7 to 7,5	0,03	0,035	25 to 38	2,0 to 2,5

[x] Standard error of mean

[xx] Black earths, chernozems, prairie soils, alluvial soils, etc.

Table 1.4 The major vegetation types associated with the six major soil nutritional groups of mediterranean regions

Soil nutritional groups	South-central Australia	South-western Australia	South Africa	Chile	California	Mediterranean
Strongly-leached nutrient-poor soils (extremely low availability of P,N,S and possibly of Cu, Zn, Mo)	sclerophyllous forest to heathland	sclerophyllous forest to heathland	sclerophyllous shrubland to fynbos heathland	none	manzanita chaparral to sclerophyllous forest	maquis to sclerophyllous forest (maquis arborée)
Moderately-leached nutrient-rich soils (marginal limitations due to lack of P)	savanna woodland	savanna woodland	renosterbos shrubland	matorral	chaparral to savanna woodland	sclerophyllous woodland and matorral to grassland
Poorly-leached agriculturally-rich soils (few if any deficiencies)	savanna woodland to grassland	none	none	matorral	chaparral to savanna woodland	original vegetation unknown
High pH, Ca-rich soils (low availability of P, Fe, Mn, Cu, Co)	mediterranean shrubland (mallee)	calcareous heathland	coastal fynbos, strandveld	none	none	garrigue, batha, phrygana
Mg-rich, Ca-poor soils (imbalance of Mg:Ca)	none	none	none	none	serpentine chaparral	none
Saline and gypseous soils (excessive levels of Na and/or Ca)	salt marsh	salt marsh	salt marsh	salt marsh	salt marsh	salt marsh

Table 1.5 Total levels of four elements in vegetation (kg ha^{-1}) and their relative proportions in soil, root, shoot and litter. The proportion of an element in litter is always 1 (from Lossaint 1973; Groves, in press)

Element	Australian heath (nutrient-poor, strongly-leached)	Californian chaparral (nutrient-rich, moderately-leached)	Mediterranean garrigue (Ca-rich, high pH)
Total P in vegetation	9,5	33	10,5
P in soil:root:shoot:litter	188:3:5:1		0,7:1,4:11:1*
Total N in vegetation	440	214	211
N in soil:root:shoot:litter	195:8:3:1	36:2:5:1	0,3:1:7:1*
Total Ca in vegetation	?	?	584
Ca in soil:root:shoot:litter	?	?	1:2:13:1*
Total Mg in vegetation	?	?	28
Mg in soil:root:shoot:litter	?	?	0,1:1,5:8:1*

*available, not total

capacity (see section 1.1.3.2.2).

- the absolute level of P in vegetation is low both on nutrient-poor and on nutrient-rich soils.
- the absolute level of N in vegetation is higher on nutrient-poor than on nutrient-rich and Ca-rich soils. This apparent anomaly possibly reflects a high proportion of legumes in Australian heath rather than the nutrient levels in the substratum itself.
- the proportion of P in roots of heath occurring on nutrient-poor soils is higher than that on nutrient-rich soils.
- the proportion of N in shoots of heaths occurring on nutrient-poor soils is lower than that on nutrient-rich soils.

1.1.3.2 AVAILABILITY OF NUTRIENTS IN THE SOIL

1.1.3.2.1 Quantification Available nutrients are here assumed to be those present in the soil complex, or in soil solution, which are readily exchangeable with the plant root. Quantification of available nutrients is a complex problem because we need to know which nutrients can be exchanged in the soil, the nutrient requirements of individual plants, and whether plants have different capacities to extract nutrients. The problem is exacerbated by the lack of standardization of analytical procedures. Techniques which have been used to determine availability in agricultural systems include chemical analyses and incubation studies of soils, bioassays, foliar analyses and analyses of xylem sap. All of these techniques have severe limitations. Problems of quantifying available nutrients will perhaps be solved using a combination of these different approaches.

1.1.3.2.2 Availability of nutrients in mediterranean ecosystems Availability of N and S, and of P to some extent, is regulated by biotic factors, whereas that of the other macro- and micronutrients is controlled by geochemical release (Figure 1.2). Both processes are seasonally variable, water availability and temperature being limiting factors. Microbially-released nutrients are thought to show seasonal flushes (Figure 1.3) of increased availability in both spring and autumn, when temperature and water are not limiting (Schaeffer 1973). Both nutrient-poor and nutrient-rich soils in mediterranean regions also show these flushes but the total quantities of nutrients released are thought to be correlated with the size of the pool of organics in the soil. Those other macro- and micronutrients (elements such as K, Mg, Na and Ca) which are largely independent of microbial release may have slightly different patterns of seasonal availability (Figure 1.4). The quantities of nutrients released geochemically show a close relationship with the elemental composition of the parent material and the rates of weathering (see Table 1.2) while the capacity of the soil to retain and store the nutrients released by biogeochemical processes is also of paramount importance.

The number of soil-exchange complexes is related to the quantity of clay and of humus in the soil, while the pH of soil affects nutrient retention by plants: the more acid the soil, the more saturated with H^+ ions is the exchange complex and hence the smaller the amount of nutrient which can be complexed.

Figure 1.5 indicates the traditional concept of the relationship between pH and nutrient availability. In soils of low pH, common in many mediterranean regions, nutrients such as Fe are readily available but as the pH of the soil increases, so does the availability of other nutrients, while that of Fe declines; at a pH of 6.5, uptake of nutrients is thought to be optimal for most plants (Truog 1946).

Finally, immobilization of nutrients, which is important in regulating their availability, may be biotic (due to microbial uptake), chemical (due to the formation of insoluble inorganic salts, as for example on high pH, calcareous soils) or physical (due to complexing by kaolinitic clays). Details are unknown.

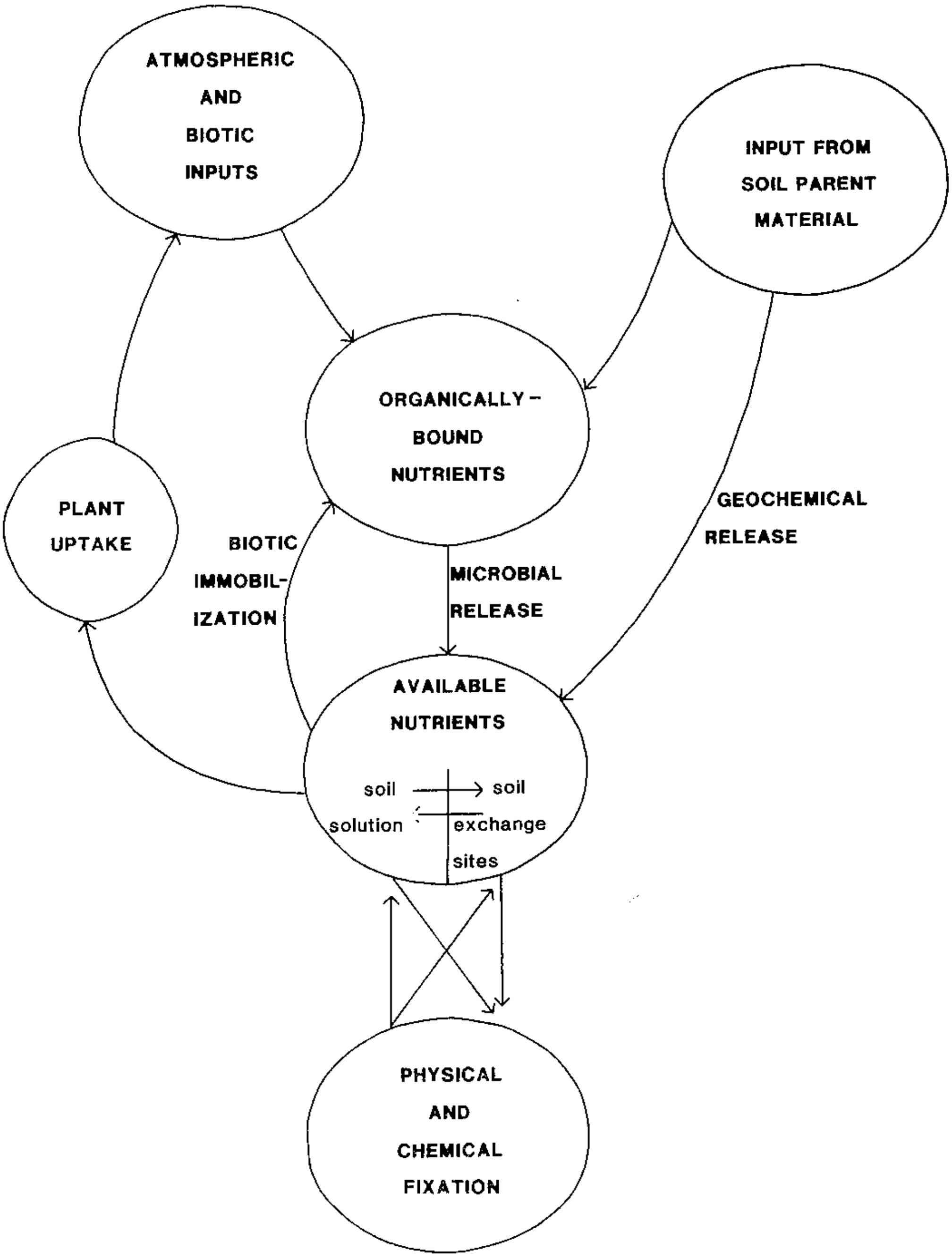


Fig. 1.2 Simplified biogeochemical cycle showing processes controlling nutrient availability

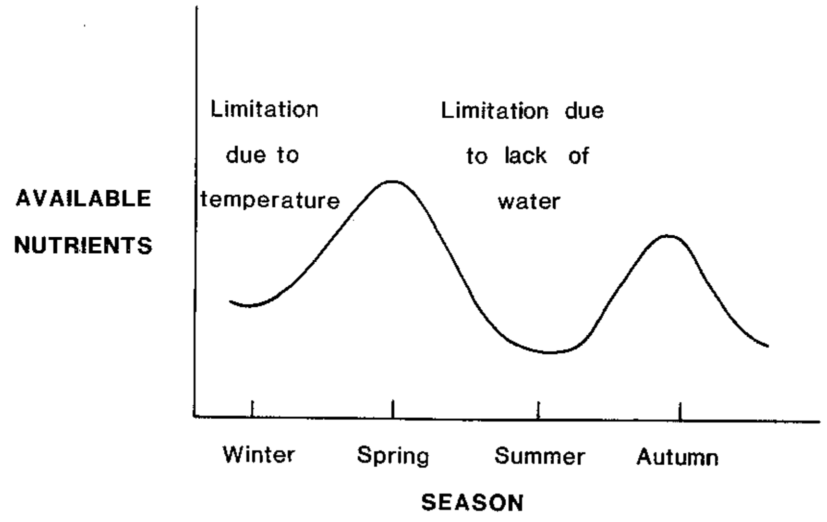


Fig. 1.3 Theoretical availability of microbially-released nutrients in mediterranean soils

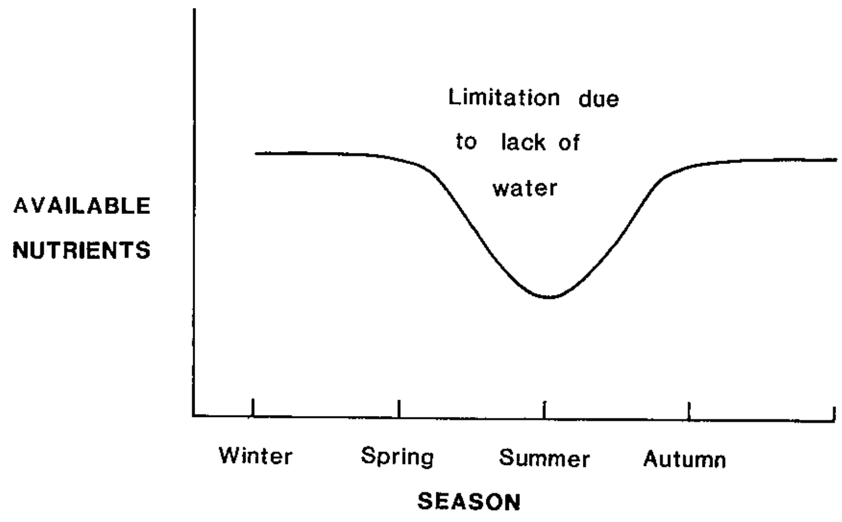


Fig. 1.4 Theoretical availability of geochemically-released nutrients in mediterranean soils

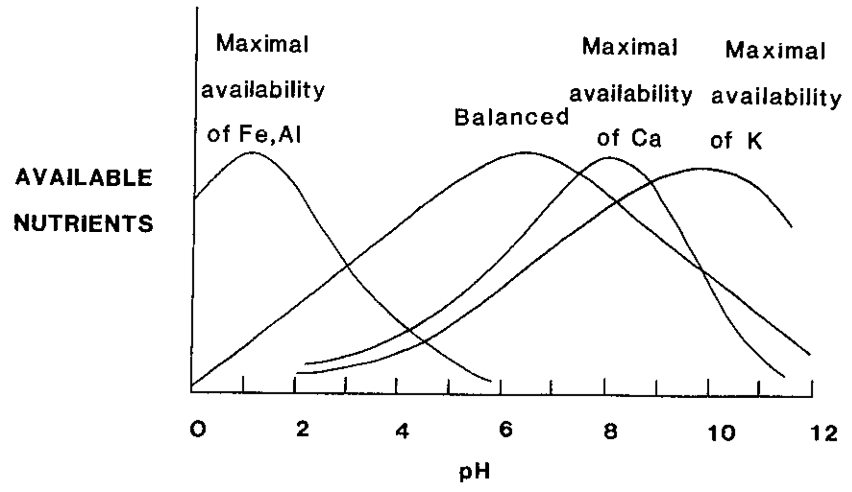


Fig. 1.5 Theoretical relationship between pH and nutrient-availability. (After Truog 1946)

1.1.3.3 ELEMENTS INFLUENCING PLANT GROWTH

Of all the elements known to be essential for plant growth, only P has been shown, in agronomic-type trials, to increase growth of Australian heath on nutrient-poor sites (Specht 1963) while Californian chaparral, occurring on a nutrient-rich soil, grows in response to additions of N rather than of P (Hellmers et al. 1955). On the other hand, addition of combinations of elements, such as P with N in $NaNO_3$ or in blood-and-bone fertilizer, also increase growth of Australian heath (Specht 1963; Jones 1968; Heddle & Specht 1975). Other elements, such as S, are known to be lost when Calluna heaths are burnt in Britain (Allen 1964), so that limits to the growth of mediterranean plants by lack of other elements cannot be dismissed if repeated burning tends to their depletion. As yet, however, we have no quantitative evidence for growth responses by mediterranean plants to elements other than P and N.

Annual herbaceous plants of Mediterranean origin, such as Trifolium subterraneum, are important for the agricultural use of heathland. In addition to N and P they require trace amounts of Cu and Zn and sometimes of other elements as well (Riceman 1948) while Pinus radiata from California also responds to addition of such trace elements when planted on heathland soils. Because some elements are required in trace amounts for symbiotic N-fixation as well as for other interactions with microorganisms, it is intriguing to speculate that the growth of heath plants may also be limited by a lack of such elements. A comparison of growth in sterile and non-sterile conditions may be one way of examining this possibility but experiments would need to be rigorously executed.

Imbalances of nutrients may also limit growth of mediterranean plants. For instance a high P:N ratio may limit growth of Proteaceae on nutrient-poor soils in Australia (Ozanne & Specht 1981) and South Africa, as may the form of N, be it ammonium or nitrate (Lewis & Stock 1978). On Californian serpentine soils the ratio of Mg:Ca influences plant growth and distribution. On the Cape Peninsula and on Ca-rich soils in some parts of Australia and in much of the Mediterranean Basin, high pH may interact with low levels of trace elements such as Fe, Co, Mn and Cu to limit both plant growth and animal production. Further, an excess of one nutrient relative to another, rather than an absolute deficiency, may influence the growth of plants in mediterranean regions. In spite of, or perhaps because of, nutrient deficiencies and imbalances, distinctive plant communities have evolved to occupy nutrient-poor soils (Specht 1981a). Special ecophysiological adaptations have developed which enable nutrients to be conserved during both internal and external cycling; some of these are examined in various chapters in Specht (1981b) but these studies form only the basis for the much more intensive research which is needed.

1.2 BIOTIC FEATURES

1.2.1 ORIGINS OF THE MEDITERRANEAN VEGETATIONS

Although mediterranean ecosystems are remarkably similar to each other in many respects, the biotas of the northern and southern mediterranean regions have had such separate starting points and have been physically apart for so long that there is a limit to the degree of convergence which can be generated by evolutionary processes. Further the Gondwanaland floras, because of their "primitive" make-up, seem to produce variations on the same theme rather than something new, despite their extreme isolation (Johnson 1973).

1.2.1.1 SOUTH AFRICA AND AUSTRALIA

As mediterranean climates are a relatively recent phenomenon, the origin of the evergreen sclerophyllous vegetation and its associated species must be sought in ancestral floras. In particular, the ecophysiological adaptations for drought-survival during the mediterranean summer must be derived from adaptations already present in ancestors that lived in the more equitable climates of the early Cenozoic. Thus the modern vegetation appears to have been derived from ancestral early Cenozoic rainforests and their peripheral communities. Rainforest containing Podocarpaceae and a wealth of tropical and sub-tropical woody angiosperms coexisting, in Australia, with Nothofagus-dominated vegetation, has shrunk to peripheral remnants in humid areas and is now azonal. Eucalyptus forests in Australia probably developed at the margins of the rainforests. "Heath forests" and wet heathlands, which occur on nutrient-poor substrata in the tropics today, are assumed also to have occurred in the early Cenozoic and to have been the source of the flora of modern nutrient-poor heathlands (Specht 1979a). Similarly, the "xeromorphic rainforests" and shrublands, now found on shallow soils in the tropics, are assumed to have existed in the early Cenozoic and to have been attenuated to the mediterranean shrublands of nutrient-rich and calcareous soils (Axelrod 1975). Grasses on forest margins furnished the grassy element in heathlands and expanded as the ground stratum in sclerophyllous shrublands and woodlands (Specht 1981a). Coastal halophytes in South Africa and karroid elements, provided the succulent and xeromorphic elements of saline and alkaline soils, speciating and extending on to the arid strandveld and coastal fynbos of South Africa and the semi-arid mallee of Australia (Specht 1981a).

1.2.1.2 CHILE

The Nothofagus and mixed evergreen forests of sub-tropical origin, widespread in the early Cenozoic, now survive as peripheral remnants in humid areas. The mixed evergreen forest has given rise to matorral by attenuation (Rundel 1981).

1.2.1.3 CALIFORNIA AND THE MEDITERRANEAN

On nutrient-rich argillaceous and calcareous soils, ancient laurophyllous forests seem to have given rise to sclerophyllous mixed evergreen forests, survivors of which still occur as peripheral elements in humid areas (Axelrod 1975). These sclerophyllous forests have in turn given rise, by attenuation, to oak woodland and savanna in areas of intermediate rainfall which, if eroded by man's intervention, may become Quercus coccifera garrigue. Further attenuation in dry areas has resulted in the formation of chaparral and matorral with the evolution of a herbaceous ground-stratum. On nutrient-poor soils an ancestral tall coniferous forest, which survives peripherally in humid areas, has become attenuated to form coniferous woodlands in mesic areas or to form maquis (sensu stricto) in dry areas.

There is thus a common pattern whereby ancestral early Cenozoic forests have become modified on the different continents. The forests were mostly mesomorphic, suggesting a humid, non-seasonal climate; they still survive as peripheral remnants in humid areas, although some species with coriaceous and sclerophyllous leaves may be found in restricted habitats including nutrient-poor soils, epiphytic niches and marginally xeric environments. Mostly, however, they have given rise to lower, more open and more specialized communities adapted to drier and more seasonal conditions (Axelrod 1975; Specht 1979a, 1981a).

1.2.2 SPECIES RICHNESS

The development and maintenance of species richness is considered in some detail in Chapter 8; of concern here is the wider perspective of the whole Cenozoic. Although species richness is associated with all mediterranean regions, it does not appear to be the direct result of the inception of summer-dry climates. There is evidence from south-western Australia of over thirty proteaceous species in the pollen flora of the late Eocene (c 40 m.y.) (Hoss 1975) and comparable diversity is found in the same time-range in the Gippsland Basin (Stover & Partridge 1973). This suggests that speciation is of considerable antiquity in some of the older families now found in the heathlands of the southern hemisphere. The palynological evidence from Australia also suggests some turnover of species; this serves as the basis for the recognition of biostratigraphic zones (Stover & Partridge 1973).

Species richness is not specifically associated with a mediterranean climate, which is a relatively recent development. Thus there is at present no satisfactory explanation for the origin, in the mediterranean regions, of floras very rich in numbers of species. However we believe, on fossil and biogeographical grounds, that species richness has developed *in situ* and not through large-scale intermingling of adjacent floras. The same environmental conditions that have enabled species richness to develop prior to the Miocene have allowed it to persist in the regions where mediterranean climates now exist. No single factor would seem sufficient to account for its origin and maintenance. The following abiotic and historical factors are probably involved:

- Temperature ranges have been relatively constant and have lacked extremes in present-day mediterranean regions since the beginning of the Cenozoic. Specht (1979b, Figure 6.6) indicates that colder climates north of 35° N and south of 35° S induce a reduction in species richness, as for example in the heathland flora of Australia, a fact first observed by Brown (1814).
- Precipitation levels have been maintained above a critical level of seasonal aridity.
- The regions show high topographic diversity, thus providing a mosaic of very diverse microhabitats.
- In some mediterranean regions, particularly those of Australia and South Africa, nutrient deprivation enables many species to form an open overstorey with minimal suppression of a large number of understorey species.

Furthermore, frequent fires or disturbance by natural or by biological agencies can increase the temporal or spatial "gaps" within communities so that speciation can proceed. Similarly, any factor which would lead to the suppression of overstorey shrubs and trees appears to increase species richness; for example waterlogged, anaerobic conditions, seasonal drought or too-frequent fires may destroy sensitive overstorey plants. Local species richness would be promoted under such conditions (Specht & Morgan 1981).

It must be stressed that many early Cenozoic taxa, even species, have remained relatively unchanged through the Tertiary and Quaternary periods. Rates of speciation are poorly understood at present and are unlikely to have remained constant through time even in a single taxon. However it would appear that speciation accelerated after the Miocene, adding to the species richness of already-rich floras.

1.2.3 INFLUENCE OF MAN ON MEDITERRANEAN ECOSYSTEMS

Table 1.6 summarizes the effects of man upon the vegetation of the six mediterranean regions. People have occupied the Mediterranean Basin and South Africa for equivalently long periods (Table 1.7) although in South Africa the impact of these earliest inhabitants may have been less marked because of their low densities. Late Pleistocene hunter-gatherers occupied all mediterranean ecosystems; ecosystem modification was achieved by such pre-agricultural peoples primarily by means of fire. The transition to more permanent settlement was very much earlier in the eastern Mediterranean than in the rest of the Mediterranean or elsewhere, and has had a corresponding greater impact on that ecosystem. Herders have occupied the mediterranean region in South Africa for the last 2000 years but agriculture dates only from the colonial period. In California and Chile, agriculture of any significance started with Spanish settlement, although indigenous agriculture was practised on a small scale prior to this. Although Australian aborgines have traditionally used fire, the Australian mediterranean regions have only recently come into intensive use, the rate of modification of the ecosystems being rapid due to the use of modern technology. Most of man's activities in all mediterranean regions are irreversible, but P-deficient landscapes are particularly susceptible to uncontrolled burning, overgrazing and other poor farming methods.

1.3 FURTHER RESEARCH

1.3.1 PALAEOECOLOGY

Much of the material discussed in section 1.1 is speculation. Further advances in the general areas of biogeography and palaeoecology will help to sort fact from fiction. In particular, collection of further palynological data, especially from South Africa, would provide a sounder basis for understanding the development of mediterranean ecosystems.

1.3.2 SPECIES RICHNESS

Although species richness is one of the most striking aspects of mediterranean ecosystems, explanations are still speculative. We need to know to what extent species richness is a product of the distinctive

Table 1.6 Effects of man on the principal soil types of mediterranean regions. A = agricultural clearing; P = pastoral use; 0 = no occupation; - = no such type

	South-western Australia	South-central Australia	South Africa	Chile	California	Mediterranean
Nutrient-poor	A,0	A,0	0 (P)	-	0	0
Nutrient-rich and agriculturally-rich	A	A,P	A,P	A,P	A,P,0	A,P
Calcareous	A,0	A,0	P (A)	-	-	A,P

Table 1.7 Timescale for human impact. Units are years before present

	Australia	South Africa	Chile	California	Mediterranean
First appearance of man - hunter-gatherers; management by fire	40 000	500 000	11 000	14 000	400 000
First appearance of domestic stock	150	20 000	400	400	10 000-6 000
First appearance of agriculture	150	300	?1 000	150	10 000-6 000
Intensive agriculture	50	300-200	400	50	2 000-1 000

present-day climates of the regions and to what extent it is a product of historical factors. Further, we do not know whether species richness is due to a single environmental factor or whether it arises from the interaction of many factors. These matters could best be tackled by palaeoecologists in collaboration with biogeographers. This topic is dealt with in detail in Chapter 8.

1.3.3 NUTRIENTS

It is necessary to quantify the pool sizes for at least N, P, Ca and Mg in all mediterranean regions, using internationally-accepted and standardized methods. The need for standardization of methods prior to the collection of data seems essential, especially in relation to the nutrient status of the soils involved.

International cooperation is necessary and urgent in comparative studies on the availability of nutrients to mediterranean plants.

Chemical analysis of soil as an indicator of nutrient availability implies a knowledge of plant requirements but these are still unknown for most mediterranean plants. A series of bioassays, using characteristic elements of mediterranean floras, is needed to investigate the correlation between nutrient levels determined chemically and the growth responses of plants. Comparisons between systems will require standardized methods of extraction and analysis. Further, since chemical analyses of soils do not reflect the dynamics of a system, incubation studies, bioassays, and chemical analyses of foliar and xylem sap are also needed; analyses of xylem sap are complicated, however, by the fact that data are required on the rate of water movement through the plant before results become meaningful.

Apparent discrepancies in data already published may be reconciled by a coordinated effort to grow a standard plant, such as *Avena*, on soils from each mediterranean region and to relate the level of nutrients taken up by that plant to the levels taken up by species such as *Banksia*, *Protea*, *Adenostoma* and *Quercus*, which are typical of mediterranean conditions.

1.4 CONCLUSIONS

We are beginning to understand the relationships between the origins, the histories and the characteristic features of mediterranean ecosystems.

Distinctive plants and plant communities have evolved to occupy each of the major types of mediterranean soil on each continent. Some of the communities have evolved ways of allowing uptake or exclusion of nutrients and have thus effectively overcome nutritional problems. Others have become only partly adapted to deficiencies or imbalances so that some of these communities, under nutritional stress, may respond by increased growth and reproduction when limiting nutrients are supplied.

This chapter attempts to synthesize some of the information, albeit imperfectly and within the limits of knowledge available to us in a four-day residential workshop. All the contributors hope that this initial effort will stimulate graduate students and research scientists in the various regions to refine our synthesis or even to refute it. If it also stimulates biogeographers and palaeoecologists to consider the origin of mediterranean ecosystems and the implications of these origins in the economy of nutrient movement in mediterranean regions, then our efforts will have been more than worthwhile.

2. NUTRIENT CYCLING PROCESSES

P. W. Rundel (convener), G. C. Bate, A. B. Low, P. C. Miller,
Patsy Miller, D. T. Mitchell

In this chapter we build upon the information presented in Chapter 1 to describe what is presently known about the origin and cycling of minerals in mediterranean ecosystems. While we have emphasized the importance of primary fluxes of nutrients, we have considered only briefly the differences in nutrient cycling in nutrient-poor and nutrient-rich soils because the major gaps in our knowledge lie in this field.

The levels of nutrients in any system may be increased by hydrological input, by the products of weathering of rocks and by biological fixation, or may be decreased by leaching, by volatilization and by loss of particulate matter. Further, internal cycling may alter the levels of nutrients within different parts of the system (Groves, in press). These aspects are discussed separately below.

2.1 INPUTS

2.1.1 WEATHERING

Generally the mediterranean regions of California and Chile are dominated by granitic quartzdiorite with occasional outcrops of gabbro, basalt, andesite and granodiorite. A similar situation is found in south-western Australia where the common rock type is Archaean granite. South-central Australia is formed largely from pre-Cambrian and Cambrian rocks, including thick quartzites which may be locally conspicuous. Around the Mediterranean, Mesozoic sediments are interrupted by local occurrences of volcanic rock. Upper Ordovician sediments, chiefly quartzitic sandstones of the Table Mountain Group, occupy most of the landscape in the mediterranean region of South Africa (Rust 1967; Truswell 1970). Tertiary and Recent deposits are fairly widespread along the coastal areas of the Australian and South African mediterranean regions but do not appear to be as important as they are in California, in Chile and in the Mediterranean Basin (Wellington 1955; Thrower and Bradbury 1973).

Present climatic conditions in mediterranean regions do not favour rapid chemical or organic weathering (Paskoff 1973; Thrower & Bradbury 1973), due chiefly to low infiltration during summer droughts coupled with high runoff in the winter months. Hydrolysis and consequent formation of clay would therefore also be expected to be slow. Biogeochemical weathering may play some role where vegetation is dense, as is the case in forests. But it is unlikely that higher plants are of much consequence in the open vegetation of most mediterranean ecosystems, and the role of lichens in chemical weathering of rock may be much over-rated.

No extreme temperature variations are found in mediterranean regions and as a result there is minimal mechanical breakdown of rock by flaking, splitting or frost-shattering. On the other hand, earthquakes may play a role in the large-scale breaking up of landscapes; California, Chile and the Mediterranean all lie over major volcanic and/or seismic zones (Thrower & Bradbury 1973), while earthquakes are also known in the south-western Cape (Truswell 1970). Erosion is a major weathering process in the mountainous areas of mediterranean regions where rocks and soils are poorly consolidated. This effect is particularly pronounced in California and Chile, where the mountains are geologically very young, slopes are steep and precipitation may be very intense for short periods of time.

Non-metamorphic shales, and similarly fine-grained sedimentary rocks with low levels of SiO_2, decompose rapidly, producing deeply-weathered soils with a high clay content. Finer-grained metamorphics are fairly resistant to breakdown while sandstones, particularly quartzitic ones, show the slowest rates of weathering due to their highly siliceous nature (Twidale 1976). Further, since sandstones rarely form residual soils on slopes they are continually exposed, while granites and shales usually produce deep residual soils; obviously the depth of soil influences further weathering of the underlying parent material. Thus although rates of release of elements are probably highest in fine-grained sedimentary and igneous rocks during the initial stages of soil development, their rate of weathering will probably be slowed down by superimposed soil layers, especially since deep soils tend to be formed, while the slow weathering of sandstones is not retarded by the presence of deep overlying soils. High rates of weathering lead to correspondingly fast rates of release of the various elements, which may be held in clay-mineral complexes in the soil prior to being released and taken up by plants. Sandstones, having low concentration of elements other than Si and O, coupled with exceedingly slow rates of decomposition, probably contribute little in the way of nutrients to the soil.

P and the major plant cations form a small proportion of the total nutrient pool in these soils. Levels of important plant trace elements such as Zn, Cu and Mo are generally less than 2-4 ppm in Cape quartzites (Marchant and Moore 1978) and their rates of release from this material would also be extremely slow. On the whole, P-containing minerals form a small component of rocks (<1 per cent) (Turekian 1972) and the input of P into the soil nutrient pool is generally considered to be minor; this has been shown by Jones and Woodmansee (1979) for an annual grassland ecosystem in California.

Chemical weathering processes are favoured in soil owing to retention of moisture, low pH and other factors. Secondary weathering involves the alteration of primary clay minerals in the soil to secondary forms such as kaolinites and montmorillonites. The resulting fine-textured soils with a high clay content are of paramount importance in fixing and retaining nutrients, which may consequently be present in fairly high concentrations.

2.1.2 HYDROLOGICAL INPUTS

Nutrients entering a system via the hydrological cycle arrive in rain, snow, mist or fog. Input via fog and mist is believed to be extremely low except in areas very close to the sea. Precipitation, the major source, appears to supply more N than P, since levels of P in rainwater are frequently 0,001 ppm or less whereas those of N may be somewhat higher. For nutrient-poor South African and Australian soils, a mean annual rainfall of 400 mm would deliver only 0,0035 ppm P per metre depth of soil per 1000 years. Hence weathering rather than rain appears to be the major source of supply of P (Table 2.1). Clearly since the soil is so inherently low in P, selection should favour plants with strong P-retaining characteristics. In comparison, the input of N from rain has been shown to be 4 kg ha^{-1} y^{-1} or more in some ecosystems, but a rate of 1-2 kg ha^{-1} y^{-1} is probably a better guess for mediterranean regions.

It is easiest to consider nutrients moving in only one dimension, coming in from above with precipitation and out from below with leach-water. However the importance of lateral movement of N and P in ground- and soil-water is unknown; such movements are probably small for the same reasons which argue against large nutrient losses by leaching (see section 2.2.1). It is also important to consider lateral redistribution of nutrients via the faunal and floral components; this is discussed in section 2.4.2.

In the past century increased agricultural development of mediterranean regions has led to extensive use of artificial fertilizers. The effect of this input may be significant in many communities adjacent to agricultural areas, particularly in areas which are naturally deficient in nutrients, where the increased input would have greatest impact on the vegetation.

2.1.3 NITROGEN FIXATION

Although there is a significant body of literature describing the distribution of symbiotic N-fixing shrubs in mediterranean regions, their overall importance in N accretion is still very poorly understood. Rates of N-fixation by species of *Ceanothus* (Rhamnaceae) in coniferous forest ecosystems in the western United States may reach 60-100 kg ha^{-1} y^{-1} or more but these levels are much higher than those measured for *Ceanothus* in a more arid chaparral ecosystem, where fixation rates of only a fraction of a kg ha^{-1} y^{-1} have been reported (Kummerow *et al*. 1978). The low levels of fixation result from low densities of nodules with short periods of activity, rather than from reduced rates of nodular activity. Quantitative studies of symbiotic fixation rates have not been made for other mediterranean shrubs, but the characteristic patterns of climatic stress suggest that N-fixation may be similarly restricted in all mediterranean ecosystems. Despite apparently low rates of fixation, the significant appearance of N-fixing plants in many mediterranean communities, in particular in early successional sequences, suggests that even small inputs of N may be important.

The Australian and South African systems represent a major gap in our understanding of symbiotic N-fixation. This gap is particularly significant since the low-nutrient soils of these regions would be expected to provide strong selective pressures favouring increased N uptake by plants. The extremely low availability of P in these soils may, however, be of major importance in restricting N-fixation.

Very few data indicate the extent or the significance of N-fixation by free-living microorganisms within any of the mediterranean ecosystems, although current research on post-fire activity of such microorganisms is providing a better understanding of these processes (Dunn *et al*. 1979). Such microorganisms have been shown to have the potential for fixing up to 200 kg N ha^{-1} y^{-1} from agriculturally-rich soils in California and other areas, but levels of fixation in drought-stressed and energy-limited mediterranean soils are expected to be very low. Limited field data on microbial fixation rates in Chilean matorral suggest that allelochemical interactions in litter under plant canopies may provide an interspecies variable controlling rates of fixation (Rundel & Neel 1978).

Table 2.1 Relative importance of different types of weathering in mediterranean areas. (+++ = major; ++ = moderate; + = minor; 0 = no influence). Compiled from Thrower & Bradbury (1973) and Paskoff (1973)

	Past			Present				
	Volcanism, intrusion	Folding, faulting	Glaciation	Precipitation in winter only	Precipitation in winter and part of summer	Temperature variation	Stream erosion	Chemical
Mediterranean	+++	+++	+	++	+	++	+++	++
California	+++	+++	++	+++	0	++	+++	+
Chile	+++	+++	+	+++	0	++	+++	+
South Africa	++	+++	+	++	+	+	++	++
Australia	+++	+	+	++	+	+	+	++

Soil microorganisms in Californian chaparral show increased rates of N-fixation after fire (Christensen & Muller 1975; Dunn et al. 1979), as non-mediterranean ecosystems commonly do, suggesting that this will be true for the other mediterranean systems as well. Fire-induced increases in pH from acidic to more nearly neutral levels, together with breakdown of allelochemical inhibitors, probably allow these increased rates. This response is relatively short-term, however, lasting only a few years before pH begins a steady decline again.

2.2 OUTPUTS

2.2.1 LEACHING

Mediterranean soils dry down to very low water potentials during the summer. However, it is the volume of water retained in the soil, rather than lack of precipitation, which is the critical factor. Hence soil depth and texture play a vital role in determining the dynamics of leaching of an area.

Table 2.2 indicates that leaching through a soil profile is a function of rainfall, of water-holding capacity and of depth of soil. Thus at a level of precipitation of 400 mm y^{-1}, for example, 1000 mm-deep sand would hold 241 mm and allow 159 mm to leach through, while none would leach through an equivalent amount of clay soil. Such data represent maximal values; with rainfall spread throughout the year, evapotranspiration has to be taken into account so that actual leaching rates would be considerably lower than those indicated in the Table. Because precipitation in mediterranean regions occurs during the winter when transpiration and evaporation are low, the profile tends to remain relatively wet until spring temperatures raise rates of evapotranspiration. For this reason it is reasonable to assume that the soil profile is leached in the sense that water has passed through it, although it may not be well leached from the point of view of nutrient removal. On the contrary, many available data can be cited as evidence against significant loss of nutrients through leaching. Vitousek et al. (1979) have shown undisturbed ecosystems to have very low levels of nutrients leaching into rivers and streams, while eutrophication of lotic waters increases very markedly following disturbance. Bate & Du Preez (1978), working in savanna, have shown that only about 10 per cent of the measurable NO_3-N in soils is lost when reconstituted columns are leached with water equivalent to a rainfall of 1000 mm.

The leaching of nutrients out of vegetation by rain may also be important and comparative data between vegetation types might be particularly useful. If stem-flow and leaf-drip in forests are richer in nutrients than are their equivalents in mediterranean systems, then this feature may also be significant in explaining the sclerophyllous nature of leaves of mediterranean plants as a mechanism for reducing external cycling and so minimizing the loss by leaching of minerals in winter.

Overall, then, it appears that leaching does not result in a major output of nutrients from mediterranean soils, since the low background level of soil nutrients and the relatively low degree of precipitation limit the amount of leaching.

Table 2.2 Approximate water-holding capacity of sand and clay (mm rainfall) for a mediterranean region with precipitation of 400 mm y^{-1} leaching through a soil profile is a function of rainfall, water-holding capacity (i.e. sand about 16 per cent water m/mass; clay about 28 per cent water m/mass) and the depth of the soil. Hence, if the precipitation is 400 mm y^{-1}, then a sand 1000 mm deep would hold 241 mm of rainfall and 159 mm could leach through while none would leach through a clay soil. Obviously, these data represent maximum possible values. Real values, with rain spread over the year and with soil evaporation and transpiration, would indicate far lower rates of leaching

	WATER-HOLDING CAPACITY			
	Sand		Clay	
Soil depth (mm)	Held in profile (mm of total rainfall)	Leached (mm of total rainfall)	Held in profile (mm of total rainfall)	Leached (mm of total rainfall)
250	60	340	106	294
500	120	280	212	188
750	181	219	317	83
1000	241	159	400	Nil
1500	362	38	600	Nil
2000	400	Nil	400	Nil

2.2.2 RUNOFF AND EROSION

The obvious hydrological movement of nutrients out of mediterranean ecosystems following fire is an important feature which should be the subject of long-term modelling and should be brought to the attention of ecosystem managers. Clearly the long-term impact of nutrient losses following fire should be studied in greater detail in order to make suggestions as to whether or not these nutrients should be replaced.

Losses of nutrients by erosion following fires in chaparral have been investigated by DeBano & Conrad (1976). They found losses of both N and P to be large in comparison with those of unburnt control plots. Studies from some coniferous forest ecosystems have indicated however, that although losses of nutrients are increased following fire, these losses are still within the range of extreme seasonal losses recorded over a long period for unburnt controls. The impact of fire on erosion in Californian chaparral and in other ecosystems has recently been reviewed by Rundel (1981).

2.2.3 VOLATILIZATION

The volatilization of nitrogenous compounds during fires may be very important locally. In general, data on the quantitative effects of fire-temperature on N-volatilization are poor because of the artificial nature of most of the experiments. The best data relevant to mediterranean systems have been obtained by DeBano et al. (1979), using controlled fires over soil slabs. They found that in intense fires, reaching 700°C at the upper surface of the litter, the litter may lose up to 90 per cent of its N, while 50 per cent of the total N may be lost from the upper 20 mm of soil. The rate of loss drops linearly with fire temperature.

Field measurements of N-volatilization during fires in shrublands and heathlands yield highly variable results. DeBano & Conrad (1978) estimated a loss of 10 per cent of the total N in plant, litter and upper soil layers in a chaparral burn and large losses have been reported for fires in *Calluna* heaths (Allen 1964; Chapman 1967). Data on the rates of N-volatilization have been summarized by Rundel (1981).

The current state of knowledge of the volatilization of P compounds during fires is very poor and data in the literature are conflicting. Studies on shrubland and heathland fires have yielded figures for losses ranging from virtually zero (DeBano & Conrad 1978; Allen 1964) to very high values (Lloyd 1971). Similar data from other ecosystems are also variable (Rundel 1981).

Cations are generally considered to be meagrely volatile during fire. Here again, however, available data are highly variable. Most studies have reported losses of less than 25 per cent of the major cations in canopy and litter during fires, and some losses seem to be insignificant. DeBano & Conrad (1978), however, reported a loss of over 50 per cent of total K during a chaparral burn. The effect of temperature on volatilization rates of cations has not been investigated.

2.2.4 PARTICULATE LOSS

Particulate loss of nutrients through aeolian removal of soil appears to be restricted and local in mediterranean ecosystems. It may be important in the early days following fire, when ash beds are highly unconsolidated, but no data are available on the extent of such losses.

2.3 CYCLING BETWEEN PLANT AND ENVIRONMENT

2.3.1.1 LITTERFALL AND DECOMPOSITION

The release of nutrients during decomposition of litter is important in the maintenance of nutrient cycles. However, studies on litterfall and decomposition have been neglected in mediterranean ecosystems; it has been assumed that litterfall may not be significant in these ecosystems and that decomposition may be a slow process because of climatic restrictions and the chemical nature of the decaying tissues. Fire has traditionally been regarded as the most important agent in breaking down plant litter and thus increasing the availability of nutrients in the soil. Nevertheless recent studies by Schlesinger & Hasey (1981) have shown that decomposition in chaparral vegetation is important in providing soil nutrients for plant growth during the periods between fires.

Total litter production in mediterranean ecosystems varies from 900 kg ha^{-1} y^{-1} in an *Adenostoma* stand in California (Kittredge 1955) to 4900 kg ha^{-1} y^{-1} in an Australian coastal scrub-heath (Maggs & Pearson 1977). The quantities of litter produced may provide an indication of the potential availability of nutrients, but the quality of litter will be important in determining the rates of decomposition (Read & Mitchell, in press). Sixty-nine per cent of litter is leaf material in the scrub-heath of eastern Australia (Maggs & Pearson 1977) and 78 per cent in chaparral (Mooney et al. 1977) but the proportion of the different components in the litter may vary seasonally. Leaf-fall may occur at a different time from the fall of flowers and seeds. Dead roots, another component of the litter, has received some attention even though difficulties have been encountered in sampling and in distinguishing between dead and live roots (Kummerow et al. 1977, 1978; Edwards & Harris 1977). The production of ephemeral roots in mixed chaparral has been estimated to be 3000-10 000 kg ha^{-1} y^{-1} (Kummerow 1978, in press; Oechel & Lawrence 1981).

The leaf structure of mediterranean plants is an important factor in decomposition. Leaves of mediterranean plants are both sclerophyllous and evergreen (Kummerow 1973; Mooney et al. 1977, Mooney & Rundel 1979; Kruger 1979) and internal recycling occurs prior to leaf-fall. N and P compounds are exported from the leaf, greatly increasing the C:N and C:P ratios of the senescing leaves. Reabsorption of N, P and K has been found to be greater in the evergreen sclerophyll Ceanothus megacarpus than in the deciduous Salvia mellifera (Schlesinger & Hasey 1981).

The leaves of deciduous plants appear to decompose faster in litter than do those of evergreen ones (Schlesinger & Hasey 1981). Although the use of litter-bags in such decomposition studies has been criticised, bags with a mesh-size of about 1 mm appear to be widely used (Read & Mitchell, in press). Open as well as closed bags have been tested in fynbos; bags open at the sides allow ingress of large insects but at the same time restrict the entry of debris from above. Preliminary results using these two kinds of litter bag suggest that detritivores excluded by a mesh aperture greater than 1,5 mm may not be important in the decomposition of proteaceous leaves in fynbos (P. G. F. Coley, pers. obs.).

The rate of decomposition depends upon the quality of leaf litter and on environmental conditions; a number of models has been used to predict such rates (Table 2.3). Using Meentemeyer's (1978) formula, annual loss of litter from Ceanothus megacarpus and Salvia mellifera in Californian chaparral was predicted as 16,5% and 18% respectively (Schlesinger & Hasey 1981). Loss of litter from fynbos has been calculated as approximately 30 per cent per annum (Read & Mitchell, in press) but this figure was based on the assumption that the lignin content of the litter was similar to that of Ceanothus. Even though the content of C, N and lignin in the litter may be important in determining decomposition rates, other components such as its polyphenol composition and P content, and the pH of the soil, should not be overlooked. Specific polyphenols such as gallic acid, rather than total amount of polyphenol, are important in determining the palatability of litter (King & Heath 1967) while many potential decomposers are less active in soils with a pH below 5,0; litter with a high base content decomposes more rapidly than litter from which the bases have been removed (Mason 1977). The moisture content of soil and litter will also be important in the release of soluble constituents such as K, carbohydrates and phenolics.

The relative mobility of mineral nutrients is slightly different from one mediterranean region to another (Table 2.4), although in each case K is most mobile. Schlesinger & Hasey (1981) have demonstrated that there is no net N mineralization from chaparral litter during the first year; net N mineralization normally occurs at C:N ratios of 30:1 or less (Lutz & Chandler 1946) while at the time of leaf fall in chaparral vegetation the litter has a ratio as high as 80:1.

Table 2.3 Summary of models used to predict rates of litter decomposition

Model	Reference
Multiple linear regression analyses using lignin concentration of leaves and actual evapotranspiration	Meentemeyer (1978)
Lignin and nitrogen contents of leaves	Aber & Melillo (1980) Melillo _et al_. (1982)
C:N ratios of litter	Aber & Melillo (1980) Melillo _et al_. (1982)

Although litter production in mediterranean regions may be small compared with that of other ecosystems, the rate of decomposition may be fairly rapid; K and P may be released more quickly than N, which is retained in the litter for longer periods.

2.3.1.2 TRANSFORMATIONS OF NITROGEN

N transformations significant in nutrient cycling include ammonification, volatilization of NH_4+N, nitrification, immobilization and denitrification.

Levels of NH_4+N in mediterranean soils are generally low, which suggests that rates of ammonification may also be low. If indeed the rates are low, this is probably due to a combination of low levels of N in the soil and in plants, and inhibition of ammonification by the living plants (Rundel 1980). The low levels of NH_4+N in the soil may on the other hand be due simply to volatilization of gaseous ammonia.

Nitrification also appears to be very slow in fynbos (Lewis & Stock 1978), and this may be true in other mediterranean regions too, possibly due to low rates of formation of nitrate from NH_4+N. Further, low soil pH, which has an inhibitory effect on the activities of nitrifying bacteria, may be important (DeBano & Conrad 1976).

It seems likely that denitrification is of little importance in mediterranean systems since so little substrate is present and the soils are generally acidic, which inhibits the process. Further, when the soils are wettest, and therefore most likely to be exhibiting denitrification, they are also coldest and therefore relatively inactive biologically. More research should be encouraged, however, since substantial denitrification would force a closer examination of N inputs via fixation and other sources. In order to assess the importance of denitrification it may be necessary to examine the equilibrium values for the process since low levels of substrate may be indicative of fast turnover rates rather than merely reflecting small absolute amounts. Once these are known the process could be modelled using known levels of NO_3-N in the soil.

Table 2.4 Mobility of nutrients and of litter in mediterranean regions: a comparative series

Region	Mobility series	Reference
Californian chaparral	K>Mg>Ca>N P not consistent	Schlesinger & Hasey (1981)
French garrigue	K>P>Mg>N>Ca	Lossaint (1973)
Australian scrub heath	K>P>Ca>Mg>N	Maggs & Pearson (1977)

2.3.1.3 TRANSFORMATIONS OF PHOSPHORUS

There is little information on the mechanisms of transformation of P compounds in mediterranean soils. C:P ratios of the litter may determine the net mineralization of organic phosphates. The C:P ratios of Ceanothus and Salvia leaves were 1786:1 and 376:1 respectively (Schlesinger & Hasey 1981); these differences may reflect differences in the rate of loss of P from the litter of these two species. Phosphatase enzymes are involved in the release of orthophosphate from organic phosphates. There is no information on the levels of total soil phosphatase in mediterranean ecosystems but phosphatase activities have been studied in South African ericoid mycorrhizas (C. Straker & D. T. Mitchell, pers. obs.) and in the proteoid roots of Hakea sericea (P. Manders & D. T. Mitchell, pers. obs.).

The transformations of insoluble inorganic phosphates have received some attention. Clovelly soils from coastal fynbos contain iron-bound phosphates (G. Brown, S. M. Jongens-Roberts & D. T. Mitchell, pers. obs.). Rock phosphates known as "apatite" occur in Spain and southern France (Lossaint 1973; Barea et al. 1975); because these soils are neutral to alkaline, the release of P is due to the action of the bacteria Pseudomonas and Agrobacterium. Even though some of the phosphate will be retained by the bacteria, some may become available for uptake by plants (Azcon et al. 1976).

In conclusion, the biotic agents involved in the mineralization of organic phosphates and the release of phosphate from insoluble inorganic phosphates in the soil are bacteria, free-living soil fungi, mycorrhizas, non-mycorrhizal root-systems and proteoid roots. The rate of mineralization of organic phosphates in mediterranean soils will depend upon the activity of phosphatases. These in turn will largely be governed by the availability of moisture and the presence of suitable temperatures in the soil during autumn, winter and spring, when the soils are moist.

2.3.1.4 ASH DEPOSITION FOLLOWING FIRE

Nutrients contained in the above-ground biomass and in the litter may be rapidly cycled into the soil through ash deposition following fire. Nutrients not lost through volatilization during the combustion process (see section 2.1.2 (a) above) will be deposited in the ash. Thus the total quantity of nutrients deposited is a function of fire temperature and of the pre-fire biomass of litter and canopy.

The relatively high proportion of available forms of N and of other nutrients in ash is generally considered to be the major factor promoting rapid regrowth after a fire. In Californian chaparral, concentrations of ammonium-N in ash in the upper soil may be as much as 15 times those of pre-fire levels, while acid-soluble P may be more than 30 times as great (Rundel 1981).

Ash deposits may be subject to erosion through runoff or through particulate losses due to wind. The degree to which ash nutrients are lost from the system by these mechanisms is highly dependent on such factors as the seasonal and topographic position of the fire and the patterns of precipitation. Qualitative and quantitative data on soil changes following fire in chaparral suggest that mineralization of ash takes place very rapidly (P. W. Rundel, pers. obs.).

2.3.2 BIOLOGICAL UPTAKE OF NUTRIENTS

2.3.2.1 PLANTS

Annual budgets for uptake of nutrients by plants can be estimated by determining the net increase in nutrient standing crop (above- and below-ground) as well as the loss due to litterfall over a given period. There are considerable amounts of data on the net annual increase in the nutrient content of mediterranean plants but much less information is available on the litterfall component, which is necessary to calculate gross rates of uptake (see Gray & Schlesinger 1981). Figures available for California and France range between 29 and 65 kg ha^{-1} y^{-1}; temperate coniferous forests give very similar values, which are lower than most figures given for temperate deciduous forests (Gray & Schlesinger 1981).

Far fewer data are available on the uptake of P by plants. The small amount of data on Australian heathlands, and the lack of published data for fynbos, leave a major gap in our understanding of the dynamics of P in soils very poor in nutrients. Furthermore, our understanding of plant-soil-microbial interactions is scanty and much more information is required.

2.3.2.2 ANIMALS

Few data are available on nutrient fluxes through terrestrial animals. These pathways may be locally important for lateral movement of nutrients, particularly in Australia where rates of herbivory appear to be unusually high (see Chapter 7) or in South Africa where rodent moles and termites turn over the soil extensively. In coastal areas deposition of large quantities of guano by seabirds can be a major source of P.

2.4 APPROACHES TO A SIMULATION MODEL OF NUTRIENT CYCLING PROCESSES

Modelling has been used to coordinate the research efforts of several disciplines (Innis 1975) and to coordinate and standardize a common set of measurements made by various countries in the International Tundra Biome Programme (Bunnell & Dowding 1974). Modelling mediterranean ecosystems has been restricted to specific topics concerning vegetation and soil in Chile and California (Miller _et al_. 1978; Miller 1981); Table 2.3 provides a summary of models used to predict rates of litter decomposition. Models coordinating and standardizing a set of common measurements in all mediterranean regions would provide an interesting and important framework for more detailed studies on the unique aspects of each.

2.4.1 OBJECTIVES

Static budget models and dynamic models can both be used for simulating and comparing nutrient cycling. Static budget models can provide balance sheets and thus a basis for comparing functional characteristics of mediterranean ecosystems. The static cross-continent budget model is the fundamental basis for comparing nutrient cycling in mediterranean regions with that in other ecosystems (Bormann & Likens 1967; Woodmansee 1978). In the variable coefficient, process-based model and other dynamic models, the rates of processes are calculated in relation to controlling factors such as temperature and moisture. Such models can be used to determine a steady state, or by simulation to determine implications of perturbations such as fire or management practices, to suggest historic conditions and to perform experiments which are impossible or impracticable to carry out in nature. For example, the contribution of P to the ecosystem by weathering of the underlying rock is small, but viewed in the context of P losses over hundreds or thousands of years it may be important or insignificant. Similarly the role of fire, repeated periodically through long time-periods, on overall nutrient impoverishment of the ecosystem can be evaluated by projecting current information backwards or forwards through many simulated years. Specifically, modelling can provide a succinct statement of hypotheses being studied in different regions, can form a quantitative framework for regional comparisons, can evaluate the significance of variability due to natural sources or errors of measurement and can test hypotheses about the functional similarities of mediterranean or other ecosystems.

2.4.2 DEVELOPMENT OF A MODEL OF NUTRIENT CYCLING FOR COMPARING MEDITERRANEAN ECOSYSTEMS

In order to compare nutrient cycling, the basic compartments and fluxes should be agreed upon and measured in all mediterranean ecosystems. Then those controlling factors common to all systems can be elaborated on, both seasonally and annually. For example the temperature and moisture responses of mineralization processes, or the environmental control of N-fixation, might be established. Finally the unique features of each ecosystem, such as specialized uptake systems or the relationship between nutrient utilization and species diversity, can be quantified and elaborated upon. This stage requires the most detailed measurement, but is generally the most interesting scientifically, particularly if the unique features can be supported by a qualitative interpretation. Data are required for both construction and validation of a model. In dynamic simulation models, the precise measurement of the processes and their controls is more important than the precise measurement of the sizes of compartments, since the balance of the processes determines the final steady state more than do the initial values for compartment sizes. Thus measurement of compartment sizes is largely for validation rather than for construction, while measurements of processes are largely for model construction rather than for validation. For purposes of dynamic simulation and static budget models, the first priority is estimation of annual flux rates based on field measurement, the second is establishment of seasonal patterns of fluxes and the third is establishment of the controls of fluxes by means of field and laboratory experiments. The compartment sizes should be measured in the field for validating the overall flux rates. Measurements of compartment sizes and controls of the fluxes are of equal importance. When this background is established, the unique aspects of an ecosystem can be elaborated upon and their quantitative significance should become apparent.

The static budget models require information only on nutrient fluxes and on compartment sizes. The dynamic, variable-coefficient models require supplementary information on climate and abiotic processes since these aspects, especially temperature and moisture, control most fluxes. Among the climatic aspects, data on solar radiation, air temperature, humidity and wind should be available, together with data on physical characteristics of the soil, such as water-holding capacity. Information on soil moisture and temperatures and on plant water potentials is important for validating the abiotic aspects of such models. In addition, information on photosynthetic inputs, on respiration and on the allocation of carbon for the growth of different parts of the plant is important for calculating values for the uptake and storage of water and nutrients. Demographic characteristics of predominant species are necessary if the model is to simulate long-term changes in nutrient cycling associated with changing species composition, or changes in species composition related to changes in the cycling of nutrients.

The model should give a broad enough picture to simulate fluctuations over 50-year periods and a detailed enough picture to reflect seasonal changes. Data for four-weekly intervals should give a reasonable number of calculations; however it is more interesting ecologically to calculate processes and compartment sizes at one- to two-weekly intervals so as to obtain the resolution necessary for such aspects as the length of summer drought and the period favourable for growth (Miller, in press).

2.5 FUTURE RESEARCH

Although there has been a very great increase in publication of data on many aspects of nutrient cycling in mediterranean ecosystems in the last five years, information is still scanty, as reflected in Table 2.5, for example. Despite their significance, no published data are available for aspects such as rates of weathering and denitrification, and comparisons between regions are difficult because there are few data on nutrient cycling in areas such as Chile. None of the processes has been adequately studied even in California, where most research has been carried out. Because of the many and obvious gaps in the available data it is very difficult to produce an ordered list of research priorities. Nevertheless, there are several important areas where detailed studies of nutrient cycling processes are needed.

One important area for research is the broad question of comparative studies on nutrient cycling in the mediterranean regions. Do they have unifying characteristics which distinguish them from other major types of ecosystem? Can regional differences be attributed to differences in climate or substratum?

We also need to know the nature of the differences in nutrient cycling in nutrient-poor and nutrient-rich soils within a single region.

Simulation models, as discussed in section 2.4 above, may provide an important tool for assessing the ecological significance of such differences.

An intriguing area for study is the question of stability of nutrient cycling, particularly with respect to P. Outputs of P from local ecosystems through volatilization and hydrological shunts may be significant in the low-P regions of South Africa and Australia, yet available data suggest that inputs of P to these systems are close to zero. How then is balance maintained? Parallel questions can be asked concerning the N balance in all of the mediterranean regions.

As more data on cycling processes become available, it will be necessary to look at the relative importance of external and internal cycling in plant nutrition. Such comparisons should be made not only between the mediterranean ecosystems but also between nutrient-poor and nutrient-rich areas within a single ecosystem.

Few experimental studies have been carried out on transformations of soil nutrients in mediterranean regions. Standardized laboratory tests with incubated soils should provide a basis for comparison of these transformations both with and between ecosystems. Such studies would require careful validation of laboratory experiments by field measurements and require competent soil microbiologists to perform them.

Table 2.5 State of knowledge of nutrient-cycling processes in mediterranean ecosystems (++ = good data; + = very limited published data; - = no published data)

	South Africa	Australia	California	Chile	Mediterranean
<u>Inputs</u>					
Weathering	-	-	-	-	-
Hydrological	+	+	+	-	+
Nitrogen-fixation	+	+	+	+	+
<u>Outputs</u>					
Leaching	+	?	+	-	?
Denitrification	-	-	-	-	-
Hydrological	+	+	+	-	+
Volatilization by fire	-	+	++	-	+
Particulate losses	-	-	-	-	-
<u>Internal cycling</u>					
Litterfall and decomposition	+	+	++	-	+
Nitrogen transformations	+	+	+	-	+
Phosphorus transformations	+	+	+	-	-
Ash deposition following fire	-	+	++	-	+
Plant uptake	-	++	++	+	++
Importance of animals	+	+	+	+	+

3. PLANT NUTRITION AND ASSIMILATION

D. J. Read (convener), C. B. Field, S. Gulmon, S. M. Jongens-Roberts,
O. A. M. Lewis, D. T. Mitchell, W. Oechel

This chapter considers the nutritional adaptations of plants to mediterranean conditions. Certain features of nutrient absorption and storage appear to be peculiar to plants from these regions and related heathlands; some aspects of their physiology are discussed. The assimilation process is discussed in relation to the nutrient supply to leaves, to their nutrient content and to other potentially limiting factors. It should be mentioned in passing that assimilation pathways are almost exclusively of the C3 type, despite the seasonally high temperatures and the semi-aridity of the mediterranean environment.

3.1 UPTAKE OF NUTRIENTS

3.1.1 SPECIALIZED ROOT SYSTEMS IN RELATION TO NUTRIENT UPTAKE

Soils within each mediterranean region range from those in which major nutrients may be relatively abundant to those in which they are present in small enough quantities to be growth-limiting. Applications of nutrients to fynbos (E. J. Moll, pers. obs.) and to Australian heath (Specht 1963) have shown that on siliceous substrates these vegetation types suffer primarily from a deficiency of P. Because of the low mobility of the phosphate ion, P can quickly be exhausted from soils around active roots and the consequent formation of "depletion zones" leads to severe growth restrictions (Nye & Tinker 1977; Nye 1979). In any ecosystem evolving in circumstances of restricted nutrient availability there will be selection for rooting adaptations which allow maximal nutrient-uptake. Increases in surface area relative to volume provide the most effective mechanisms for increasing absorptive capacity; most efficient nutrient capture can be achieved by fine extensions of the root surface entering beyond the depletion zone and penetrating the smallest soil interstices. It appears that plants native to nutrient-poor habitats have evolved two major adaptations for enhanced nutrient capture. Both involve investment of fixed carbon for increasing absorptive capacity, but whereas one involves proliferation of plant structures such as fine roots or root hairs and is thus non-symbiotic, the other involves transfer of assimilates to a heterotrophic partner, which to a greater or lesser extent takes over the role of nutrient absorption in a symbiotic system. Mediterranean vegetations have particularly high proportions of plant species with one or other adaptation, and usually these are especially well developed in plants from the most extremely nutrient-poor areas.

3.1.1.1 NON-SYMBIOTIC SYSTEMS

Members of the Proteaceae are dominant representatives of fynbos and of Australian heath floras and great interest surrounds their success in soils which frequently have extremely low levels of available P and N. Practically all members of the family produce characteristic clusters of "proteoid rootlets," densely covered with root hairs that effectively increase the absorptive surface. While there is evidence that such roots are microbially induced (Lamont & McComb 1974; Malajczuk & Bowen 1974), there is no indication of mycorrhizal infection. Conservation of carbon resources is achieved by restriction of rootlet production to periods after rainfall, when microbial activity and hence nutrient release are maximal. The rootlets are formed most extensively in surface organic matter (Specht & Rayson 1957; Jeffrey 1967; Lamont 1973), which contains the greatest concentration of nutrient-rich material. It has been shown that proteoid rootlets allow enhanced uptake of inorganic P but that the amount taken up is not as great as that achieved by more productive mesophytic species when expressed per unit of root surface area. Improvement of P nutrition may therefore arise largely as a result of an increase in total root length. Since development of proteoid roots occurs primarily in organic horizons of the soil, the interesting probability arises that these structures may facilitate utilization of sources of organic P. Nothing is yet known of the microbial populations associated with these roots but they may be directly involved in the mobilization of organic phosphates. Preliminary observations by P. J. Manders and D. T. Mitchell (pers. obs.) indicate that proteoid rootlets show greater phosphatase activity than do normal roots or rootlets.

Best known of the other non-symbiotic root modifications are the dauciform roots of cyperaceous plants (Lamont 1974) and the restioid clusters of Restionaceae (Campbell 1980; Lamont 1980b). These structures also carry extensive proliferations of root hairs and may be assumed to improve nutrient capture; so far we have no experimental evidence to support such an assumption.

3.1.1.2 SYMBIOTIC SYSTEMS

3.1.1.2.1 Mycorrhizal roots Classical studies revealed that mycorrhizas of a sheathing, or "ecto-", type are a feature of most major forest trees through boreal, temperate and mediterranean regions. Thus pines, oaks, beeches and eucalypts are all essentially ectomycorrhizal. It was further revealed that the incidence of mycorrhizal infection increases markedly with reduced soil fertility in forest ecosystems (Hatch 1937). Since these early studies it has been established that ectomycorrhizal roots have an enhanced capacity for absorbing the major nutrients, N and P, and that infection significantly increases yields under nutrient-impoverished circumstances. A feature which characterizes the structure of these mycorrhizas is a very extensive external mycelium, often in the form of rhizomorphs, which can extend for distances of more than a metre from the parent root. Such structures provide extremely efficient exploitation of the soil and may be responsible for the superior competitive ability shown by pines when introduced into vegetation such as fynbos, which lacks ectomycorrhizal associations.

Trees become less important as nutrient status declines in mediterranean regions, and heathlands on very poor soil are dominated by proteoid or ericoid elements. Two types of mycorrhizal association are found in the Ericaceae, a family which dominates heathlands over wide latitudinal ranges. The "ecto-endo-" infection characteristic of *Arctostaphylos* in chaparral is intermediate in character between the sheathing types and the purely intracellular "endo-" types found in the major genera, *Erica* and *Calluna*. The "hair roots" of these genera are occupied by an ascomycete fungus which, in the terminal portions of the root system, occupies 80 per cent of the volume of the cortical cells and possesses in the region of 10^6 entry points per centimetre of root length (Read & Stribley 1975). Mature roots persisting through dry parts of the year retain a fragmentary infection which acts as a source of inoculum and provides re-infection of newly emerging roots during periods favourable for root growth and nutrient absorption. Recent experiments have shown that infection not only increases uptake of NH_4+N and phosphate but that it also allows the use of a range of simple organic N compounds which are unavailable to non-mycorrhizal plants (Stribley & Read, 1980). It appears from these observations that mycorrhizal infection provides access to the products of litter decomposition at an early stage in the breakdown process. Such access, apart from greatly improving the efficiency of nutrient capture, "tightens" the nutrient cycling process and improves the competitive ability of the host plant. Relatively little is known of the role of ericoid mycorrhizas in P nutrition, although active phosphatase systems have been isolated by Mitchell & Read (1980) and C. J. Straker (pers. obs.). The role of endophytes in storage of N and P compounds is discussed in section 3.2.2.

3.1.1.2.2 Nitrogen fixation in symbiotic associations While nodulated plants are present in all mediterranean ecosystems, they do not normally represent a significant component of the vegetation throughout the fire cycle. In Australian heath, *Casuarina* may be prominent in the early stages of pyric succession, as may *Aspalathus* in fynbos. The quantities of N fixed by these plants are thought to be small, but the rate is highest in early stages of plant colonization (Dunn *et al*. 1979). Kummerow *et al*. (1978) suggests a maximum of 1 kg ha^{-1} yr^{-1} in *Ceanothus*. A deficit in soil moisture or low availability of P may be responsible for slow fixation rates since the process is known to be sensitive to both factors (Specht *et al*., in press; Kummerow *et al*. 1978).

Levels of N are high in the leaves of those mediterranean plants which do fix N. Schlesinger & Hasey (1981) reported 1,6 per cent N for *Ceanothus* when levels in the non-fixing shrub *Salvia mellifera* were less than 1 per cent. Hannon (1956) showed a twofold difference in the N content of leaves of legumes and non-legumes in Australian heath. In view of the relationships between the N content of a leaf and its photosynthetic activity (see section 3.4.1), it is clear that fixation may play a significant part in the enhanced productivity shown by the early stages in post-fire succession; it may cease to be important when P becomes limiting.

3.1.3 ROOTING ADAPTATIONS OF SEEDERS AND RESPROUTERS

There is no evidence that the kinetics of nutrient uptake differ in resprouting and in seeding shrubs, nor is it likely that gross patterns of nutrient uptake would differ markedly. Resprouters may have higher root:shoot ratios due to the present of the lignotuber and because of accumulated growth through several fire cycles. However it is unlikely that the ratios of fine root area:leaf area differ in mature seeder and resprouter shrubs or that the additional weight of the root system in the mature resprouter is a major factor in the uptake of nutrient or of water.

It is true nevertheless that different constraints are placed on seedlings and on resprouts following fire. Seedlings must rapidly form root systems which are sufficiently deep to avoid summer drought but which are produced *de novo* from a limited carbon pool. So nutrient and energy constraints may initially preclude the development of surface roots for enhanced uptake of nutrients, which are in increased supply following burning. Seedlings are therefore not expected to be efficient at exploiting the nutrients available after fire.

Resprouters have large below-ground biomasses and extensive secondary root systems (Hellmers *et al*. 1955; Kummerow *et al*. 1978). A large proportion of this system probably survives most fires and forms at least the framework from which fine roots can rapidly be produced to exploit the nutrient flush which occurs after fire (Christensen & Muller 1975) while maintaining improved moisture status (Oechel & Hastings, in press).

The observation that nutrient uptake by resprouters is higher per unit area of soil after a fire than before attests to the efficiency of resprouter root systems (Rundel & Parsons 1980). The N content of tissues may actually be higher in seedlings than in resprouters (P. W. Rundel, pers. obs.) but because the biomass of seedlings will be smaller than will that of resprouters for several years after the fire, the actual amount of nutrients taken up by seeders is likely to be much smaller.

Although there may be substantial differences in nutrient uptake between mature sprouting and reseeding shrubs after fire, we have few experimental data so far.

3.2 STORAGE OF NUTRIENTS

3.2.1 STORAGE IN SEEDERS AND RESPROUTERS

Large below-ground organs have a substantial capacity for storing nutrients, an ability which should buffer the plant against variations in supply and demand of nutrients from season to season and after fire. Although lignotubers may have relatively low proportions of N and P, the storage of nutrients may be substantial because of their large biomass (Westman & Rogers 1977; Mullete & Bamber 1978). Of course it is possible that such storage also occurs in the root systems of seeding shrubs.

Mullete & Bamber (1978) have shown that the lignotuber of *Eucalyptus gummifera* contains substantial amounts of inorganic nutrients as well as starch reserves; thus they would be important when energy or nutrients were scarce, following defoliation or drought for example. A further advantage is conferred by these structures when nutrient supply is out of synchrony with growth and therefore with nutrient demand. The stored reserves would be of prime importance during resprouting after fire, when they would allow the rapid production of fine roots for exploiting the post-fire nutrient flush and for the production of shoots to maintain a competitive position in the canopy.

It is assumed that most nutrients are not stored in an altered form in storage organs and that they can be mobilized as needed. However, there are no data on the specific patterns of movement of N or P into or out of lignotubers or secondary roots or on the ways in which such movements are controlled. It is not known which tissues within the lignotuber are preferential sources of nutrients during periods of deficiency or sinks during periods of sufficiency. Nor do we know the proportion of the N or P in lignotubers which is potentially available for transport to the plant's active tissues.

3.2.2 STORAGE IN MYCORRHIZAL SYSTEMS

3.2.2.1 PHOSPHORUS

It is now believed that ectomycorrhizal systems, with their large external mycelial ramifications and thick sheaths, become important in regions of seasonal climate because the fungus stores nutrients as well as absorbing them. Phosphate ions absorbed at the sites of mineralization by the growing hyphal tips are translocated to the sheath, where they are polymerized in the fungal vacuoles to form polyphosphate (PP) granules. Where P is easily available, very high concentrations of PP granules accumulate in the sheath. Experiments have shown that the reserves of P can be mobilized at a later stage when the rate of mineralization in the soil is reduced. This type of uptake, storage and release is known to occur in *Eucalyptus* (Ashford *et al*. 1975).

Until recently it was not realized that extensive PP formation also occured in endomycorrhizal systems. It is now known that PP is synthesized in both vesicular-arbuscular (VA) and ericoid fungi but quantitative aspects and the ecological significances of these processes remains to be investigated.

3.2.2.2 NITROGEN

In endomycorrhizas of the ericoid type, nutrients contained in the intracellular hyphal coils are slowly released to the root as the association ages. Experiments have shown that certain N-containing compounds, amongst others, accumulate in the fungal coils during periods of active mineralization and are released during subsequent dry periods and transported to the shoot (Figure 3.1). This process is associated with degeneration of the whole root cortex in the distal regions of the root (Read 1978). Such a phenomenon may help to explain the capacity of some *Erica* species to grow, flower and set seed at the driest time of the year. It has been suggested that mycotrophy in ericaceous plants is thus functionally similar to the insectivory exhibited by members of the Droseraceae, a family which, with the Ericaceae, is commonly associated with N-deficient habitats. The fungal associate rather than the captured insect is the N source that permits successful exploitation of a nutritionally marginal habitat.

3.2.3 STORAGE IN NON-MYCORRHIZAL SYSTEMS

3.2.3.1 PHOSPHORUS

There have been reports of the presence of PP in proteoid and non-proteoid roots of Banksia (Jeffrey 1968), and in roots of *Casuarina* and *Leoptospermum* (R. L. Specht, pers. obs.). PP has also been reported to occur in leaves of heathland plants and of spinach. The extent to which PP storage occurs in plants, and the extent to which the formation of PP granules is dependent upon microorganisms, remains to be ascertained. Recent studies (Ashford *et al*. 1975; Callow *et al*. 1978) have suggested that previous reports of the formation of PP in the absence of microorganisms may be incorrect; this is an area of research which requires a good deal more attention.

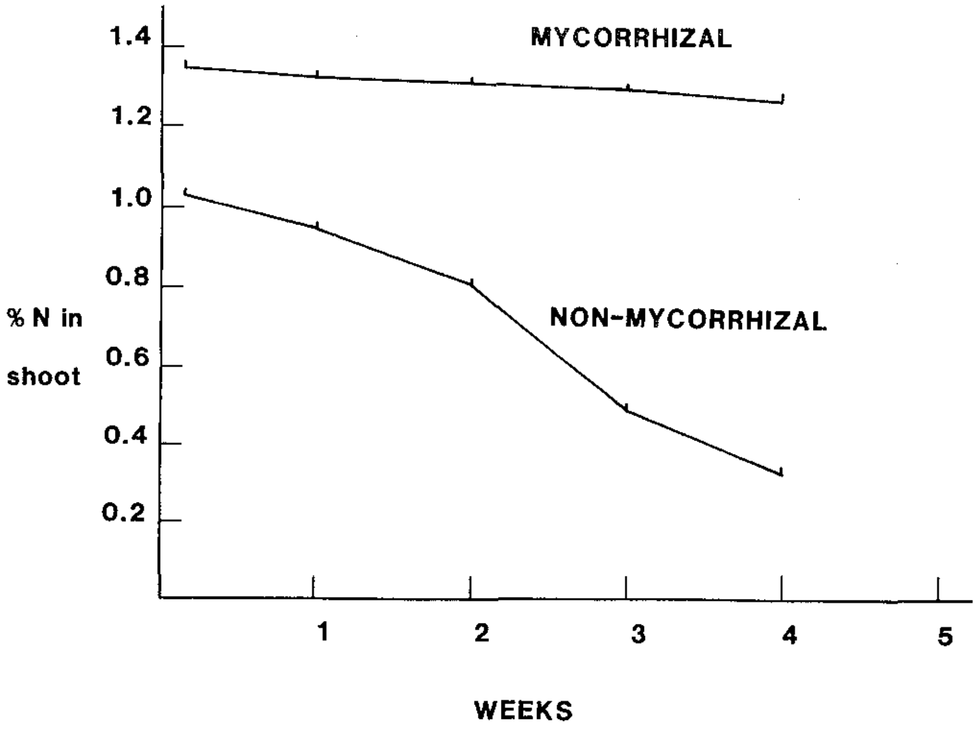


Fig. 3.1 Nitrogen content of shoots of mycorrhizal and non-mycorrhizal plants of Erica bauera when plants were transferred from soil to a stand containing no nitrogen (from Read 1978)

3.2.3.2 NITROGEN

During periods of high consumption of N, for example when higher-than-usual levels are available after fire, as in the Californian chaparral (Rundel & Parsons 1980), the ability to store this nutrient beyond immediate metabolic requirements may be an important adaptation of mediterranean plants, particularly of those growing on nutrient-poor soils. Unfortunately the mechanism, the locality and the form of nutrient storage have yet to be investigated. From studies on soil N by W. D. Stock and O. A. M. Lewis (pers. obs.), the period after fire would appear to be the only time when the available N supply might increase sufficiently to allow high consumption of N to occur and storage to take place at the same time.

3.3 NUTRIENT METABOLISM IN MEDITERRANEAN PLANTS

While many nutrients must support the various physiological functions of a plant, there is little information relevant to mediterranean plants. Despite the undoubted influence of these nutrients on growth and assimilation, as well as on other processes, knowledge of nutritional physiology is largely restricted to N.

A survey of the literature shows that the study even of N metabolism, which shows important nutritional adapatations in mediterranean plants, is severely neglected. It is generally acknowledged, however, that the amounts of N cycled annually through the soil-plant system are low (Groves, in press) and this fact should be particularly true for the nutrient-poor ecosystems such as that of the South African fynbos. Studies by Lewis & Stock (1978) have provided some understanding of the relationship between the uptake and distribution of nitrogenous compounds in the Proteaceae. Emphasis is placed on these features in the following discussion.

3.3.1 NITROGEN METABOLISM

It is reasonably certain that nitrogen assimilation in mediterranean plants follows the normal pathway now thought to exist in all higher plants. If nitrate is the N source it will be absorbed by the root and passed into root cortical cells, probably with the aid of permeases, to the enzyme nitrate reductase, which is thought to be localized on plastid membranes. After reduction, the nitrite so formed will enter root plastids where it is reduced to ammonium by nitrite reductase, a highly energy-consuming process involving the transfer of six electrons per nitrite molecule. The ammonium will then enter the glutamine synthetase - glutamate synthetase (GS-GOGAT) pathway (Lee & Miflin 1974) to form glutamine and glutamate. From glutamate, numerous amino acids will be formed by transamination and other reactions. Nitrate not reduced in the root will be loaded onto the xylem stream, as shown for Proteaceae by Lewis & Stock (1978) for reduction and assimilation by GS-GOGAT in the leaf chloroplasts. It is probable that ammonium, when it is the N source, directly enters the GS-GOGAT pathway or is loaded onto the xylem for transport to the leaf. In all species of Proteaceae so far studied by O. A. M. Lewis and W. D. Stock (pers. obs.), ammonium is the major form of reduced N translocated in the xylem. Glutamine, a product of root metabolism, is also a major translocated N-containing compound. It is possible that ureides, too, may be translocated in the xylem, but this fact still requires investigation.

Studies on the pools of free amino acids in the leaves of proteaceous species (Lewis & Stock 1978) confirm the low rate of metabolism of N thought to exist in mediterranean plants. These pools are minute and have a lower turnover rate when compared with those of non-mediterranean plants. *Leucodendrum xanthoconus* and *Protea lepidocarpodendron* have total leaf free amino acid pools of approximately 2,8 moles N g^{-1} fw compared with 16,0 moles N g^{-1} fw in *Datura stramontium*. Concentations of N in xylem sap also reflect the small N budget of these plants. While a cereal plant like barley may have an N load of 20 mM or more on its xylem stream, *Leucospermum parile*, *Protea laurifolia* and *Brabeium stellatifolium* growing in fynbos show an average N loading of only 0,3 mM. *L. xanthoconus* and *P. lepidocarpodendron*, growing in fynbos on somewhat richer soils on Table Mountain, show an average xylem stream loading of N of approximately 1,2 mM.

Mediterranean plants appear to be able to use both nitrate and ammonium as N sources, probably with a preference for ammonium. Recent studies on nitrate reductase activity in the leaves of *Protea repens*, in which polyvinylpyrrolidone (PVP) was incorporated in the extracting medium (W. D. Stock & O. A. M. Lewis, pers. obs.), have revealed *in vitro* nitrate reductase activity at a low level: 1 μmole NO_2 h^{-1} g^{-1} fw in plants fed nitrate at a level of 14 mM, compared to 8 μmole NO_2 h^{-1} g^{-1} fw normally found in barley fed nitrate at a level of 2 mM. In experiments on detatched shoots of *Leucadendron xanthoconus*, injection of 200 μg ml^{-1} $^{15}NO_3$ onto the xylem stream has produced ^{15}N enrichment of 6A%E (atom per cent excess) in glutamate, 5A%E in aspartate and 1,6A%E in threonine in the leaves after 24 hours (Lewis & Stock 1978). This represents a slow rate of incorporation of N but nevertheless indicates significant nitrate reductase activity. A more favourable response is indicated in experiments where ammonium rather than nitrate has been used. 200 μ g ml^{-1} nitrate- or ammonium-N were fed separately by xylem stream injection to shoots of L. xanthoconus. After 8 hours there was little perceptible change in the size of the free amino acid pool in the leaves of the nitrate-fed plants and a sevenfold increase in that of the ammonium-fed plants (Lewis & Stock 1978); most of the N accumulated in glutamine and serine. We do not yet know if increased availability of soil ammonium results in greater uptake of this ion by the plant and in increased delivery to sites of assimilation. This point is discussed further below.

The form in which N reaches the shoot from root and soil appears to depend largely on the amount and species of N in the soil. Leucadendron parile growing in soils low in N (1 μ g exchangeable NO_3-N g^{-1}, 2 μ g exchangeable NH_4-N g^{-1}) transports all of its nitrogen from the root in the reduced form, mainly as ammonium and glutamine. In L. xanthoconus and P. lepidocarpodendron growing in soils with a nitrate content of 6μ g NO_3-N g^{-1}, 80 per cent of the N translocated in the xylem was in the form of nitrate (Figure 3.2).

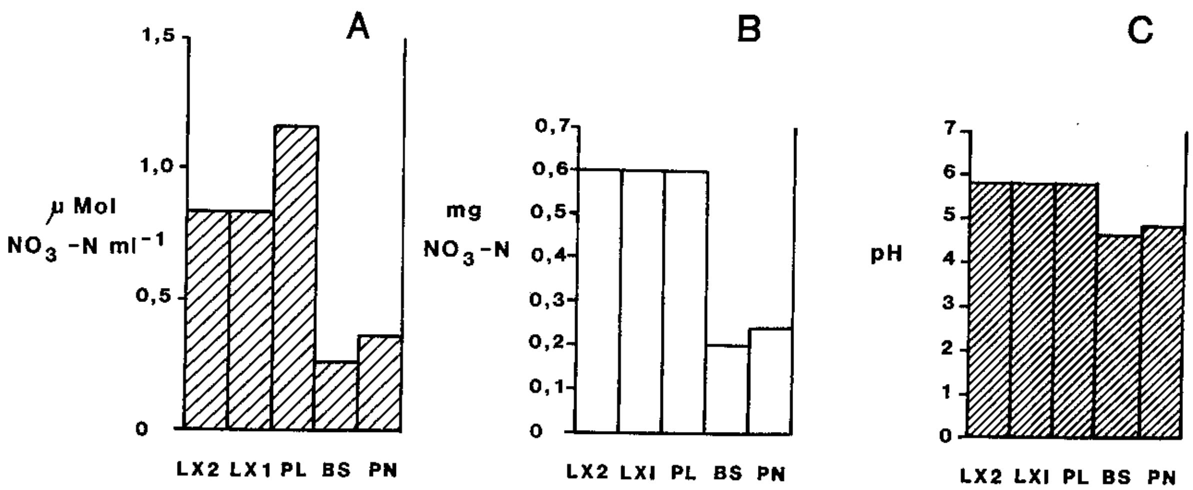


Fig. 3.2 a: Nitrate content of xylem sap of Leucadendron xanthoconus (LX) (two samples) Protea lepidocarpodendron (PL) Brabeium stellatifolium (BS) and Protea laurifolia (PN). b: Nitrate content of soils in which the plants were growing. c: pH of soils in which the plants were growing (from Lewis and Stock 1978)

Further work is necessary on the assimilation of nitrate in mediterranean plants living on low-nutrient soils, in view of their obvious ability to absorb nitrate but their apparently low capacity for reducing it.

Because of the dual use of ammonium and nitrate by mediterranean plants it is clear that assays for nitrate reductase activity cannot be used to predict the rate of N turnover, as has been done in the case of certain crop plants. Addition of ammonium or nitrate to the soil in which L. parile is growing has little effect on the N content of the xylem stream

(W. D. Stock & O. A. M. Lewis, pers. obs.). If the content of N in xylem sap can be used to indicate patterns of N uptake (Lewis et al. 1982) these results might show that, in contrast to their counterparts from nutrient-rich regions (Rundel & Parsons 1980), plants from nutrient-poor mediterranean regions are unable significantly to increase their rate of nutrient absorption. Groves & Keraitis (1976) have, in fact, shown that feeding high levels of N and P (250 μg N ml^{-1} nutrient solution) can prove fatal to Banksia serrata. The "nitrate-scavenging" effect which is so noticeable in many non-mediterranean plants, and which results in heavy nitrate loading of the xylem, is apparently absent in plants from low-nutrient mediterranean areas.

3.3.2 PHOSPHORUS METABOLISM

We know little of the P metabolism of mediterranean plants, though it is clear, from the fact that plants often show a growth response on addition of P, that internal P concentrations can limit growth. More information, both quantitative and qualitative, is required on virtually all aspects of P metabolism.

3.3.3 INTERNAL NUTRIENT CYCLING: PHYSIOLOGICAL AND EVOLUTIONARY FACTORS

Internal cycling of nutrient, that is mobilization and removal of nutrients from leaves prior to abscission, may increase the efficiency of, and certainly does increase control over, a plant's nutrient balance. Little is known about the physiological costs of internal cycling but the available evidence suggests that this cycling is greater in plants adapted to nutrient-limited habitats (Specht & Groves 1966).

Internal nutrient cycling concerns both the total exports of nutrient prior to leaf abscission and the schedule of nutrient removal throughout the life of the leaf. Available evidence suggests that, by the time of leaf abscission, up to 90 per cent of the N and P may be translocated out of the leaves (Specht & Groves 1966; Schlesinger & Hasey 1980). N and P translocation may be under independent control (P. C. Miller, pers. obs.) but nothing is known about relative levels of N and P recovered as a result of variations in nutrient availability.

Since internal cycling is never 100 per cent efficient, leaf loss always represents nutrient loss. Intricately connected with the question of when and to what extent nutrients should be exported from a leaf is the question of selective pressures governing patterns of leaf duration and nutrient content. Although almost no information is available, it seems that at least three different processes may influence changes in the nutrient status of leaves well before abscission and may indirectly influence the timing and extent of nutrient export.

The first factor is light availability. Even in mediterranean regions, where leaf-area indices are around one, self-shading by leaves and stems may place old leaves in significantly shadier habitats than young leaves (Field 1981). Considerable evidence suggests that, in N-limited situations, returns in photosynthate are maximized when the N is invested in leaves exposed to the highest possible illumination (Gulmon & Chu 1981). Mediterranean plants generally appear to transport N from old to new leaves to maximize carbon gain. The relationship between P and photosynthesis is not well documented but testing parallel predictions for P translocation should prove very useful for understanding the adaptations of plants from mediterranean regions.

Competition between plants may result in the selection for patterns of N allocation similar to those due to self-shading. A plant experiencing competition for light may respond by concentrating leaves near the top of its canopy and by emphasizing vertical growth. Both processes create sinks for nutrients, which may be supplied from old leaves with low rates of photosynthesis.

A third factor encouraging nutrient export from ageing leaves is physiological regulation to achieve a balance between stomatal conductance and photosynthetic capacity (Wong et al. 1979). In many conifers, cuticular waxes progressively plug stomata as needles age (Jeffree et al. 1971). N and P may be exported from leaves with limited diffusion to sites where carbon dioxide exchange is less restricted. Though stomatal obstruction by resins has been noted in mediterranean plants, implications of these observations for exchange of CO_2 and water are unknown.

With these three factors, and perhaps others, exerting selective pressures for nutrient export well before leaf abscission, the timing of abscission may be controlled simply by the time at which nutrient concentrations fall so far that the leaf no longer constitutes a photosynthetic asset to the plant. This, however, seems unlikely in highly seasonal mediterranean environments.

Two principles probably determine the timing of abscission and the rapid internal cycling that precedes it. The first is that periods of growth are periods of nutrient demand. Whenever the nutrient demands of growing tissue are high, nutrients taken up by the roots may be supplemented both by mobilization of stored material and by transport from old leaves. Specht et al. (in press) describe cases in which the production of new leaves is very closely associated with the abscission of old leaves. Little is known about the possibility that in other cases leaf abscission coincides with flushes of root activity. The second principle influencing the timing of abscission and nutrient export is that, in mediterranean regions, not all seasons are equally suitable for photosynthesis. For fully- or partially-deciduous plants, the timing of unfavourable conditions (drought, low temperature, high temperature, high susceptibility to herbivores) dictates the timing of abscission and nutrient export. Evergreens may drop old leaves prior to a final season of adversity rather than suffer the consequences of maintaining those leaves simply as organs for nutrient storage. Transport costs and the inefficiency due to the introduction of intermediate storage sites are completely unknown.

Overall, three "trade-offs" probably determine the timing and the efficiency of internal cycling. The first is the energetic cost of producing roots for absorption versus the energetic cost of internal cycling and of loss of functional leaves. The second concerns the "trade-off" between the energetic cost to the individual of internal cycling as against the possible loss of nutrients and loss of control with external cycling. The third is the "trade-off" between the inefficiency in nutrient transport due to the insertion of one or more nutrient storage stages, and the energetic or other losses incurred from maintaining leaves, through unfavourable periods, as nothing more than stores of translocatable nutrient. None of these has been quantitatively evaluated in any mediterranean ecosystem but the following predictions could be tested.

1. As the environment becomes harsher (cold, dry, nutrient-limited), leaf abscission should increasingly coincide with periods of shoot, root, leaf or reproductive growth.

2. As the availability of nutrients for growth and maintenance increases, an increasing proportion of the plant's nutrients needs will be met by root uptake. In this case the rate of loss of nutrients from ageing leaves will be determined only secondarily by the nutrient and phenological status of the rest of the plant.

3.4 PHYSIOLOGICAL EFFECTS OF NUTRIENT AND WATER LIMITATIONS

Nearly all species in nearly all ecosystems are nutrient limited to some degree, in the sense that addition of one or more nutrient, major or minor, will enhance growth to some extent. In Californian mixed chaparral, the addition of 4 g m^{-2} of N has been shown to increase growth (J. Kummerow, pers. obs.). In Australian heath species, Specht et al. (in press) have demonstrated a response to added P but not to added N. In the case of South African fynbos, the addition of N, P or K results initially in increased growth, although the long-term effect on the community is negative, many plants soon dying (E. J. Moll, pers. obs.).

Availability of N should affect the rates of photosynthesis and of growth; this should be reflected in the structure and productivity of individual plants, and hence of communities. Such relationships appear to be general, so that when mediterranean communities vary chiefly in nutrient availability, observed differences in photosynthesis, growth and structure should be interpretable in terms of deficiency of nutrients.

Essential nutrients were originally identified by their effects on plant growth; obviously a deficiency of any nutrient relative to the plant's needs will inhibit growth. Nutrient deficiencies also adversely affect photosynthetic rates, either directly or as a long-term consequence of growth inhibition. However, deficiencies of particular nutrients do not, in general, affect both photosynthesis and growth to the same degree.

With these general considerations in mind, here we deal with the specific relationship between photosynthesis and the availability of N, and its consequent effects on plant growth. We have imposed this limitation because the most detailed data concern N and because we know more about the relationship between photosynthesis and N than we do about photosynthesis and any other nutrient.

Numerous studies (Medina 1971; Gordon et al. 1978; Bjorkman 1979; Wong 1979) have shown that, other factors being equal, the photosynthetic capacity of a leaf at light saturation is directly proportional to the amount of carboxylating enzyme present or, in some cases, to the amount of one of the other major enzymes in the pentose phosphate pathway. These enzymes constitute a major fraction of the soluble protein in the leaf, which in turn is directly correlated with the total amount of N in the leaf. Thus the relationships between photosynthesis and the content of N in the leaf can be understood in terms of chemical limitations on the rate of photosynthesis.

The availability of P and S may be expected to have a similar effect to that of N, partly because deficiencies in these elements reduce the capacity of the plant to accumulate N. Micronutrients would be expected to have more complex effects on photosynthesis and growth because of their involvement in catalysis.

3.4.1 THE EFFECT OF NUTRIENT LIMITATION ON PHOTOSYNTHESIS

Experiments on various species from Californian chaparral as well as from non-mediterranean systems (Takeda 1961; Yoshida & Coronel 1976; Mooney et al. 1978; Field 1981; Gulman & Chu 1981) have clearly indicated a direct relationship between leaf N content and photosynthetic rate. This relationship is most general where both quantities are considered on a basis of leaf dry weight but also appears to be true when leaf area is considered. It is important to point out that, for this relationship to hold, photosynthesis and N content must be expressed in comparable units; many published reports fail to do this.

There are published data which conflict with the above findings. However, when interpreting the available literature, it is necessary to be cognizant of several experimental constraints. Photosynthetic measurements must have been performed under standardized conditions of light intensity and internal CO_2 concentration; this is probably only truly attainable with single-leaf measurements. The relationship will not hold if there are nitrogenous secondary compounds such as cyanogenic glycosides in the leaf, unless the content of N in the secondary compounds is taken into account; mediterranean species are generally rich in such secondary compounds. In studies on photosynthesis relative to nutrient deficiencies it must be clear that the nutrient under consideration is truly limiting plant growth and is the primary limiting nutrient. Thus care must be taken when considering N-fixers. This methodological discussion is included here because the issue is controversial and because further research is urgently needed on plants from all mediterranean regions, especially on those from Australia and South Africa.

The effect of N availability on leaf N content has been the subject of far more research and yet has yielded a less clear result. In the most general sense, decades of agricultural research have shown that if N, or any other nutrient, is truly limiting total growth, then increased availability will result in higher foliar concentrations of that nutrient and usually of other nutrients as well. Though relatively little research has been done on mediterranean plants, that which is available suggests that these species should prove to be no different. The pattern has been confirmed for Mediterranean annual grasses (Bromis mollis, Avena fatua and Lolium multiflorum) (Gulmon 1979) and for a chaparral shrub (Gulmon & Chu 1981). It should be pointed out, however, that some species show little variation in foliar nutrient concentrations, and differences in growth are the plants' only response to nutrient availability (Warren-Wilson 1966 and others). Conversely, increases in foliar nutrient concentrations may occur without corresponding increases in growth rates (Shaver & Chapin 1980).

As in the case of photosynthesis, the caveats are largely methodological. First, the effect of nutrient availability on total plant growth must be kept in mind. This will be considered in more detail later but briefly, if increased nutrient availability stimulates canopy development, then increased self-shading or rates of leaf turnover may actually result in lower mean levels of leaf N. In this regard it would be important to consider N availability in relation both to leaf area and to leaf dry weight, as mentioned above. Second, the phrase "truly limiting" must be emphasized. It has been demonstrated that climax species in Australian heath show only a very modest growth response to applied P (Specht et al. in press). Presumably these plants have lost the capacity to absorb and use large quantities of P so that even at rather moderate levels of availability, P is simply not limiting their growth.

In summary, then, we expect a general correlation between nutrient availability, uptake of nutrients into foliage, and photosynthetic rates; these relationships should apply to species in all the mediterranean ecosystems. Plants which have evolved under conditions of chronically severe nutrient stress, as they have in Australia and South Africa, should generally have lower foliar concentrations of nutrients and lower rates of photosynthesis. Furthermore, species from these systems may show relatively small increases in foliar nutrient content in response to large increases in nutrient availability. This does not preclude a significant growth response, however. Further, mediterranean plants are sometimes limited by water as well as by nutrients. The interaction between availability of moisture and of nutrients, and their combined effects on photosynthesis, is open to research. However, available evidence suggests that, if stomatal conductance is reduced by low water availability over the long term, then the content of N in the leaves will usually be correspondingly low, so that there is still an overall correlation between photosynthesis and N content (Osmond *et al*. 1980). On the other hand, measurements made under field conditions often indicate that photosynthesis is more closely correlated with the water content of the plant than with its nutrient status. A possible example of this kind of interaction is found in the scrub oak, *Quercus dumosa*, which grows on N-rich soils in California, (P. C. Miller, pers. obs.) but which has one of the lowest photosynthetic rates known for chaparral plants (Mooney *et al*. 1977; Oechel *et al*. 1981).

3.4.2 THE EFFECT OF NUTRIENT LIMITATION ON PLANT GROWTH

Whereas the total rate of carbon gain of primary producers is related to available nutrients through photosynthesis, the structure of the vegetation is most directly affected by the growth response. In general a deficiency in any plant nutrient relative to the needs of the species will result in a reduction in rate of growth and the final size of its members. The important questions, in considering the effects of nutrients on the growth responses of mediterranean plants, concern the differential effects on different species and on systems with different degrees or types of chronic nutrient deficiency. It is to be emphasized that none of the questions posed in this section has been answered, and none of the statements is supported by a sufficient body of data from any of the mediterranean ecosystems.

The fact that growth rates of individual plants are also dependent on the allocation of carbon to, and the turnover rates of, leaves, stems, roots, and reproductive parts is discussed in detail in Chapter 4. Here we discuss specifically the effect of N availability on growth and on the N content of leaves. Growth is ultimately dependent on photosynthetic rate since photosynthesis is the source of fixed carbon. However, the effect of nutrient deficiencies on growth will not be the same as those on photosynthesis; different proportions of carbon and various nutrients are needed for the two processes. Furthermore, plants show differential sensitivity to other environmental factors such as water stress, temperature, and even light. For example in many sclerophyllous plants photosynthesis is relatively insensitive to leaf water potential over a fairly wide range, whereas cell expansion stops after only a slight reduction from full turgor (Hsaio 1973). In general, however, photosynthesis is more sensitive to N deficiency than is the relative growth rate (the increase in dry matter per unit of dry mass) (Gulmon 1979; Gulmon & Chu 1981).

Given a specified quantity of N, or of any other limiting nutrient, the number of leaves produced will depend on the quantity of N allocated to each leaf. The higher the N content of each, the lower will be the number of new leaves. Similarly, if N is being absorbed by the roots at a given rate, the rate of production of new leaves will also depend on the amount of N allocated per leaf. The fact that leaf production will also depend on N translocated from older leaves is discussed in section 3.3.3.

A second consideration is that N in the canopy can be spread thinly over a large area or concentrated over a smaller area. This will affect the rate of photosynthesis per unit area of leaf as well as the degree of shading within the canopy.

There are constraints to the distribution of N among leaves. If the N content of the leaves is too low, photosynthesis will be inhibited so that insufficient carbon will be fixed to produce new leaves. If the N content is too high, there will be a large supply of carbon but the rate at which N is translocated from the roots may be inadequate for additional growth. To some extent this excess carbon can be diverted to root growth to increase the uptake of nutrients. However in competitive environments this allocation to roots must eventually reach a point of diminishing returns, so that the excess carbon would have to be stored or the N content of leaves reduced. Experiments indicate that a decrease in the availability of N generally results in a reduction in N and in an increase in carbon per unit weight of leaf (Oxman et al. 1977; Longstreth & Nobel 1980; Gulmon & Chu 1981). The amount of N per unit area of leaf remains fairly constant.

The level of nutrients available from the environment imposes constraints on leaf longevity, on carbon allocation and on the ability to absorb nutrients, and will in turn affect the distribution of nutrients in leaves. Evergreen plants from mediterranean regions tend to have leaves low in N and high in carbon (Figure 3.3), or in other high specific weights. South African fynbos, generally considered to have smaller amounts of nutrients available than either Chilean matorral or Californian chaparral, also has lower levels of leaf N per unit weight. However, plants from all three areas have similar amounts of N per unit area of leaf. Australian heath, which also grows on soils deficient in nutrients compared to those of the mediterranean regions on the American continents, has a similar N content per unit weight of leaf and a higher N content per unit area of leaf than do leaves of plants from the other regions. This apparent anomaly may simply reflect the fact that P rather than N appears to be the primary limiting nutrient in the mediterranean regions of Australia. The P content of Australian heath plants is significantly lower than that of species from comparable areas in America or South Africa (Mooney, in press).

With regard to interpreting comparative data on foliar nutrient contents from plants of the different mediterranean regions, and to gathering new data, it is important to consider the way in which samples were taken for measurement, since nutrient contents differ among leaves of different ages (Woolhouse 1968; Gordon et al. 1978; Field 1981; Gulmon & Chu 1981) as well as in a single leaf over the course of a season (Gulmon, in press).

In summary, low availability of nutrients will result in reduced plant growth and in reduced community productivity. This is due both to reduced rates of carbon fixation and to reduced supplies of nutrients for construction of additional biomass. However, flexibility in the allocation of N to leaves provides a range of growth forms such that total community productivity may not directly reflect either photosynthetic rates or the total quantity of nutrients available.

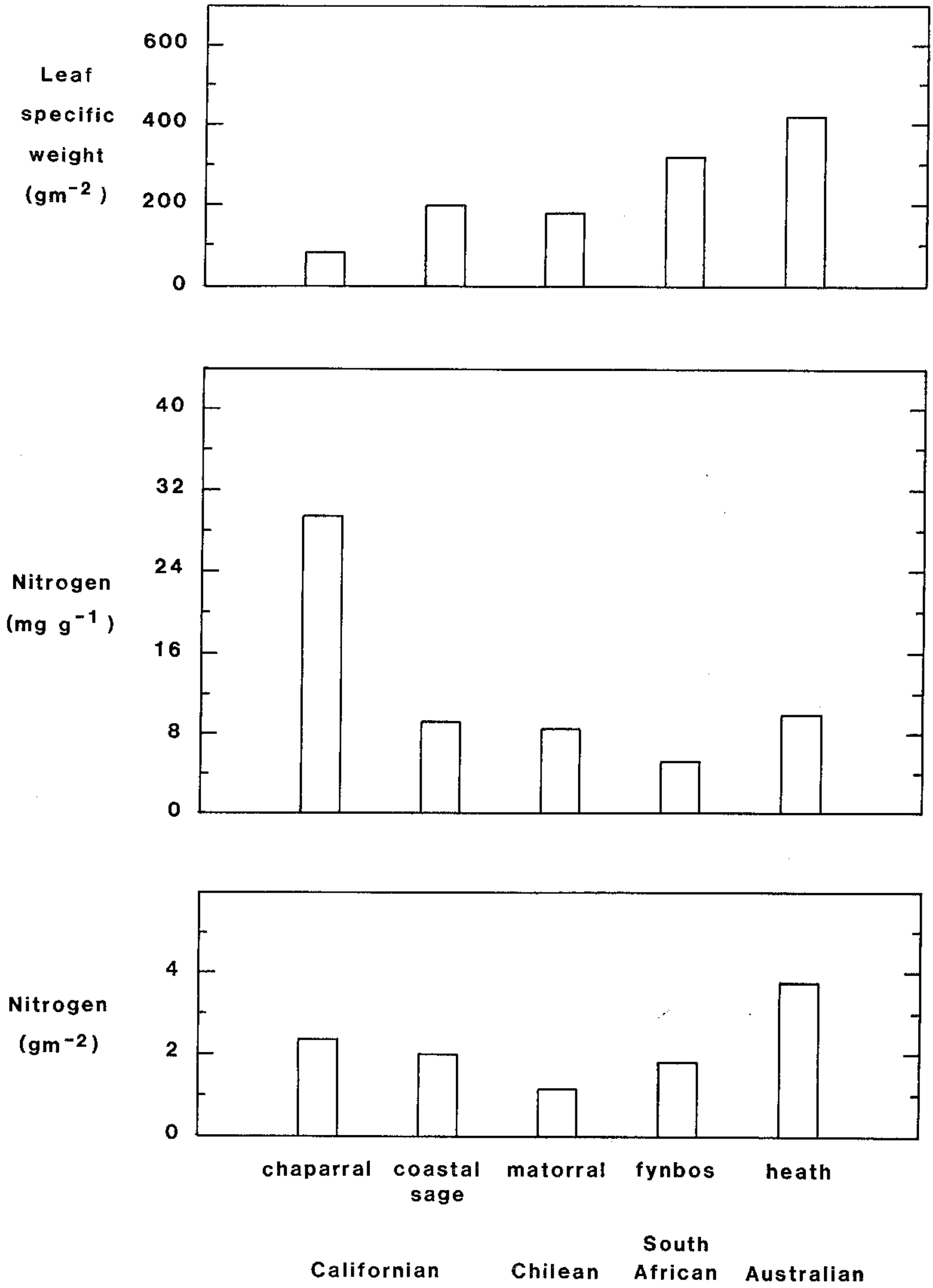


Fig. 3.3 Nitrogen content and leaf specific weight (carbon content) in evergreen species from four mediterranean ecosystems (after Mooney, in press)

3.4.3 THE RELATIONSHIP BETWEEN PHOTOSYNTHESIS AND WATER LOSS

The leaves of the evergreen sclerophylls charcteristic of mediterranean ecosystems operate in environments where both nutrients and water may be in limited supply. The interaction between photosynthetic carbon gain and transpirational water loss at the level of stomatal gas exchange makes it impossible to separate those structural features of the leaf which are related to water stress from those related to nutrient limitation.

The survival of evergreens in water-stressed habitats requires mechanisms to deal with three aspects of seasonally-limited water supply. Each mechanism may be modified by nutrient availability.

(1) Though some of the roots of evergreen sclerophylls may be deep enough to gain access to year-round water, all must be able to tolerate low water potentials. Those plants that can fix CO_2 under water stress should have an additional advantage.

(2) The leaf should be able to minimize water loss at times when photosynthesis is either not possible or is accompanied by an unacceptably high ratio of water lost to carbon gained.

(3) When water is available, the leaf should be able to fix a maximal amount of CO_2 per unit of water transpired. Modifications which improve performance with respect to one aspect of water limitation may decrease it with respect to others.

The ability of roots to tolerate low water potentials and to control water loss during photosynthesis are discussed in Chapter 4. Here, we consider those aspects of the leaves of evergreen sclerophylls that influence the ratio of CO_2 fixed to H_2O transpired. This is called the "water-use efficiency".

Modifications of water-use efficiency may be instantaneous or short-term, or may involve periods as long as the life of a plant. Short-term components are dependent on leaf structure and on the maximal stomatal conductances of CO_2 and H_2O. Long-term components depend on the interaction between stomatal conductance, leaf structure and photosynthetic capacity. In general, the photosynthetic capacity of evergreen sclerophylls is lower than that of mesophylls, whether photosynthesis is expressed on the basis of leaf area or leaf weight, or in the concentration of N in the leaf (Mooney, in press). The limitations on diffusion through stomata account for some, but not all, of the decreased photosynthesis in sclerophylls. The mechanism underlying the relatively low photosynthetic capacity and short-term water-use efficiency of sclerophylls is unknown.

Water-use efficiency is controlled by two sets of factors, neither of which is well understood. The first concerns changes in photosynthetic capacity during water stress. De Moraes _et al_. (1981) report that _Olea europa_ responds to water stress by increasing the water-use efficiency and by increasing net photosynthesis when highly stressed. The relationship between nutrient limitation and the ability of plants to modify photosynthetic characteristics in response to water stress are not known.

The second set of factors involves the modification of the leaf energy balance by changes in leaf size and in the temporal patterns of stomatal conductance. Several models have been designed in an attempt to identify the optimal size and shape of leaves for maximal water-use efficiency (Parkhurst & Loucks 1972; Givnish & Vermeij 1976). Although none has been well enough developed to be of predictive value for mediterranean plants, the theoretical framework is being developed for analyzing the patterns of stomatal conductance that maximize long-term water-use efficiency (Cowan & Farquhar 1977). Daily patterns of conductance for several evergreen sclerophylls are consistent with the hypothesis that it is long-term water-use efficiency which is being maximized.

3.4.4 PHYSIOLOGICAL RESPONSES TO CHANGES IN NUTRIENT AVAILABILITY AFTER FIRE

There are marked increases in nutrient availability after fire so that, for example, those soils which are normally nutrient limited may have a sufficiency of nutrients following a fire. In California there may be a 15-fold increase in ammonium as well as a lesser increase in nitrate (Christensen & Muller 1975), resulting in temporarily elevated levels of N in the tissues (Rundel & Parsons 1980). Ammonium is rapidly converted to nitrate so that the system tends to remain nitrate-dominated. These increases result in enhanced rates of growth (Christensen & Muller 1975) and of photosynthesis (Radosevich 1977; Oechel & Hastings, in press; Oechel *et al*. 1981).

In addition to N and P, other essential nutrients increase in availability, as does water, due to the decrease in leaf area resulting from the fire. However it has been shown that if the level of nutrients does not rise then an increase in soil moisture does not result in an increase in photosynthetic rate (Oechel & Hastings, in press). This implies that internal resistances are more important than stomatal resistances in limiting photosynthesis in the systems.

Figure 3.4 shows that, with the increased availability of nutrients and water following fire, photosynthesis may increase up to fivefold in resprouts of *Adenostoma fasciculatum* and may double in those of *Quercus dumosa* (Oechel & Hastings, in press). Elevated photosynthetic rates persist for at least ten months following fire, but the relative increase in rates may decline during this period.

Such field observations are largely uncontrolled and effects of single nutrients are not discernable. Laboratory studies with varying levels of nitrate availability show that in *Ceanothus crassifolius*, photosynthetic rates per unit area of leaf are depressed at higher levels of nitrate. However, because of increased leaf production under conditions of greater nitrate availability, total carbon fixed by the canopy increases despite these depressed photosynthetic rates. The reason for the apparent depression of photosynthesis with increasing N in these studies is not known. The plants used were not nodulated and therefore no additional N was added by fixation. When growth is increased at higher N levels, other nutrients may be diluted and may begin to limit photosynthetic rate. A second reason for the discrepancy in relation to data reported earlier in this chapter is that the earlier data concerned photosynthetic capacity, while these data concerned observed net photosynthetic rate under saturating light intensity, ambient CO_2 and observed stomatal conductance.

Another important consideration is that inorganic nutrients interact with.non-structural carbohydrates so that the levels of both will affect rates of growth and photosynthesis. These relationships are poorly understood. Decreased carbohydrate reserves may result from high growth rates and depressed ratios of photosynthetic to non-photosynthetic tissue (Oechel & Hastings, in press) and would be expected to depress respiratory rates while enhancing photosynthetic rates. Thus further information is needed to describe the relationships which exist between rates of carbon flux and storage carbohydrate levels in mediterranean plants following fire.

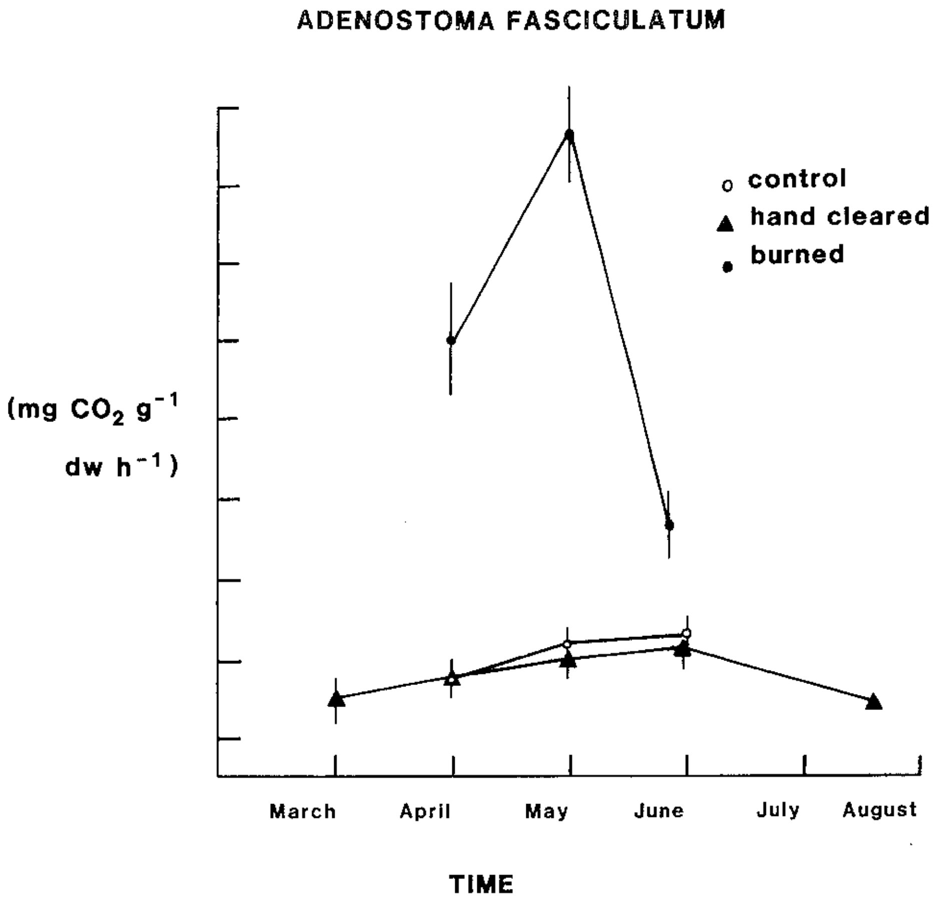


Fig. 3.4 Photosynthetic rate (mg CO_2 g^{-1} dw h^{-1}) of *Adenostoma fasciculatum* in control, hand-cleared, and burnt vegetation; vertical lines show standard errors (from Oechel & Hastings, in press)

3.5 FUTURE RESEARCH

The physiological mechanisms that allow plants to survive and grow under a series of environmental constraints are primary determinants of community diversity, structure and productivity. Most of the physiological processes important for plant nutrition and growth are understood in enough detail to allow investigations of alternative pathways and of plant responses to environmental limitations. We suggest that future work on the physiology of mediterranean plants be focused on these topics.

3.5.1 UPTAKE

Patterns of root activity should be assessed in relation to season and to fluctuations in the levels of nutrients in the soil. Emphasis should be placed on determination of effective root length in time and space. The physiological efficiency of the various types of specialized roots should be assessed in both detached roots and in intact root systems; these efficiencies should be related to growth and to the content of nutrients in the tissues of the whole plant.

The role of microorganisms in providing access to organically-bound nutrients requires further investigation, as does the mycorrhizal status of major plant species from P-deficient mediterranean ecosystems. Detailed analysis is required of the environmental factors controlling nodulation, and of nodular activity at different times of the year. Wherever possible, measurement of rates of N-fixation should be carried out on intact plants and not on detached nodules. Values obtained by means of acetylene reduction assays (ARA) should be confirmed using ^{15}N.

It is important that the patterns of nutrient uptake be quantified in seeders and resprouters over the fire cycle to determine their effects on nutrient budgets and on growth patterns. To this end, their relative capacities for nutrient uptake should be determined, as should the capacity of fine and secondary roots to survive following fires of differing intensities. Comparisions of the patterns of exploitation of the soil nutrient pool by each of these growth forms would be of value. Bulbs and tubers offer advantages to the plant similar to those of lignotubers (Pate & Dixon 1980; J. S. Pate & K. W. Dixon, pers. obs.); we need to understand the relative advantages of these organs for storage and for uptake of nutrients.

3.5.2 STORAGE

The dynamics of storage and mobilization of polyphosphates need to be further studied with special attention being paid to the many mediterranean plant groups for which P uptake and storage mechanisms have not yet been investigated.

The capacity of large below-ground structures to "buffer" nutrients should be evaluated along nutrient gradients in the seeders and resprouters of the various mediterranean regions, particularly in fynbos. Special emphasis should be placed on the importance of below-ground storage structures in the balance of water, carbon and nutrients through the fire cycle, comparing seeding and resprouting shrubs.

Experiments combining fertilization and shoot removal could effectively be used to determine the sites where N and P are stored and the magnitude of supply; radioactive tracers could also provide further details of the mechanisms and control of nutrient allocation. Apart from the material contained in the seed, obligate seeders possess no major capacity for nutrient storage following fire; however, it would be worthwhile examining the large below-ground root system as well as the stem, both of which may store some materials needed during periods of nutrient demand.

3.5.3 INTERNAL NUTRIENT CYCLING

Further research should concentrate on the efficiency of internal cycling along nutrient gradients in plants within and between the various mediterranean regions. We need to assess the extent to which cycling of N and P are independent of each other and are regulated by the nutrient status of both soil and plant. Export of nutrients from the leaves should be studied as a function of leaf age in plants with a broad range of leaf durations grown under a variety of nutrient regimes. Experiments that would be helpful in evaluating the overall significance of internal cycling in mediterranean plants are in situ comparisons of cycling efficiency in plants growing on soils of different nutrient availability on each continent, and fertilization experiments to determine the flexibility of the internal cycling response. Data from the first will provide insight into long-term responses to nutrient availability and phylogenetic constraints on cycling efficiency; data from the second will allow evaluations of the plasticity of the internal cycling response and would facilitate the construction of models comparing internal and external nutrient cycling.

3.5.4 NUTRIENT METABOLISM

Studies on the physiology and metabolism of N in mediterranean plants should focus on the following problems: differential responses to ammonium, nitrate and combined ammonium-nitrate nutrition; response to increased levels of soil N, particularly after fire, in plants from regions low in nutrients; partitioning of N-assimilatory activities between root and shoot; and the ways in which availability, metabolism and storage of N are linked.

Information on P metabolism is minimal. Levels at which internal concentrations of P become limiting should be determined for major plant groups of each mediterranean ecosystem so that tissue analyses could be used to assess the levels of P deficiency in a community. The relative sizes of organic and inorganic phosphate pools in leaves and in storage organs, at different stages of growth and under different nutritional circumstances, should also be measured.

3.5.5 RELATIONSHIP BETWEEN NUTRIENT AVAILABILITY, PHOTOSYNTHESIS AND PLANT PRODUCTIVITY

The relationship between photosynthesis and the contents of nutrients in the leaves needs further investigation, particularly in sclerophyllous plants and in plants growing on soils low in nutrients. These investigations should begin with carefully controlled laboratory measurements under specified growth conditions and be followed up with research in the field in order to determine the relationship between nutrient availability and plant productivity. In particular, the allocation of nutrients to leaves should be examined in order to determine the balance between the number of leaves produced and the nutrient content of each leaf. This in turn should help to explain the effect of nutrient content on photosynthetic capacity.

Photosynthetic rates of component species need to be related to overall community productivity. Such correlations could be achieved by modelling and should be a particularly fruitful area for comparative work. In particular we need to know if species from nutrient-poor mediterranean ecosystems have lower photosynthetic rates, as we predict, than those from richer mediterranean systems, and if they compensate for this in some way to attain productivities similar to those of less nutrient-impoverished ecosystems.

The effect of N:P ratios on photosynthesis and productivity should be examined, with emphasis on inter-ecosystem comparisons, since there is some evidence that species from different mediterranean regions have different N:P ratios, reflecting different availability of the nutrients in the soil (P. W. Rundel, pers. obs.).

3.5.6 WATER-USE EFFICIENCY

The mechanism underlying the low short-term water-use efficiency in evergreen sclerophylls should be studied in relation to nutrient content and sclerophylly. The relative importance of short- and long-term water-use efficiency should be evaluated in evergreen sclerophylls and other plants. The interactions between competition and pressures in selecting for water-use efficiency should be investigated in regions differing in the degree of drought and of nutrient stress.

3.5.7 PHYSIOLOGICAL RESPONSES FOLLOWING FIRE

The effect on photosynthesis and growth of the nutrient flush following fire needs further comparative study in seeders and resprouters. Comparisons of plants both from environments varying in nutrient status and from several mediterranean ecosystems would be helpful. This information is needed in the context of the varied water regimes which follow burning.

Neither the changes in respiratory rate nor the total plant respiratory loss following fire has been examined. Post-fire studies are needed to determine the carbon loss in resprouts and the length of time until the plant regains a positive carbon balance, as well as the maximal frequency of fire that can be tolerated by various species of resprouting plant. Nor are data available on the relative rates of growth and photosynthesis of seedlings in burnt areas compared with resprouts or seedlings in unburnt areas. The seedlings, having higher nutrient concentrations, must be expected to show higher rates of photosynthesis, respiration and growth than would the resprouters.

4. PLANT FORM AND FUNCTION IN RELATION TO NUTRIENT GRADIENTS

H. A. Mooney (convener), J. Kummerow, E. J. Moll,
G. Orshan, M. C. Rutherford, J. E. M. Sommerville

In this chapter we examine the ways in which both the structure and the seasonality of plants vary with the season and with the availability of nutrients. We consider the morphology of individual parts of plants such as leaves, stems, roots and reproductive organs and examine in particular how nutrients are important in selection not only for structure but also for seasonality. We also assess how other environmental factors, particularly water, play a role in determining plant structure and function, particularly in mediterranean ecosystems. From this assessment it is evident that many structural and functional features of plants play multiple roles in adaptation to complex environments.

4.1 LEAVES

4.1.1 SCLEROPHYLLY

Sclerophylly has been described in a variety of ways. Features such as the ratio of crude fibre to nitrogen, the thickness, the moisture content, the resistance to puncture or tearing and the leaf specific weight (weight per unit area) have all been used as measures of the degree of sclerophylly. Of these, leaf specific weight (LSW) is perhaps the easiest to measure although terete and ericoid leaves offer special problems. Since our knowledge of the multiplicity of factors which contribute to, and select for, sclerophylly is so inadequate, LSW is probably a sufficient measure for initial survey work. It should be recognized, however, that the thickness or density of cuticle, cell wall, epidermis, hypodermis, sclerenchyma and palisade can all contribute to a high LSW and that comparable LSW's may result from a balance of very different anatomical components.

It is important to separate the factors which select for leaf sclerophylly from those selecting for leaf size and duration. Often one automatically considers sclerophyllous leaves to be small and evergreen. Although size, duration and sclerophylly are often linked, particularly in mediterranean plants, this is not so in all ecosystems. Considering these features as a single syndrome hinders an analysis of the significance of each individual component.

. Nutrients have been suggested as a major force selecting for sclerophylly since sclerophyllous leaves are found in virtually all climatic types on particularly nutrient-deficient soils (Seddon 1974; Sabrado & Medina 1980). Sclerophyllous leaves (leaves with LSW's above about 150 g m^{-2}) are characteristic of the evergreen shrubs of all mediterranean ecosystems but there is a distinct increase in the average LSW of the dominant shrubs from Chile, through California and South Africa to Australia, which evidently also represents a gradient of decreasing nutrient availability (Mooney, in press). Figure 4.1 shows the

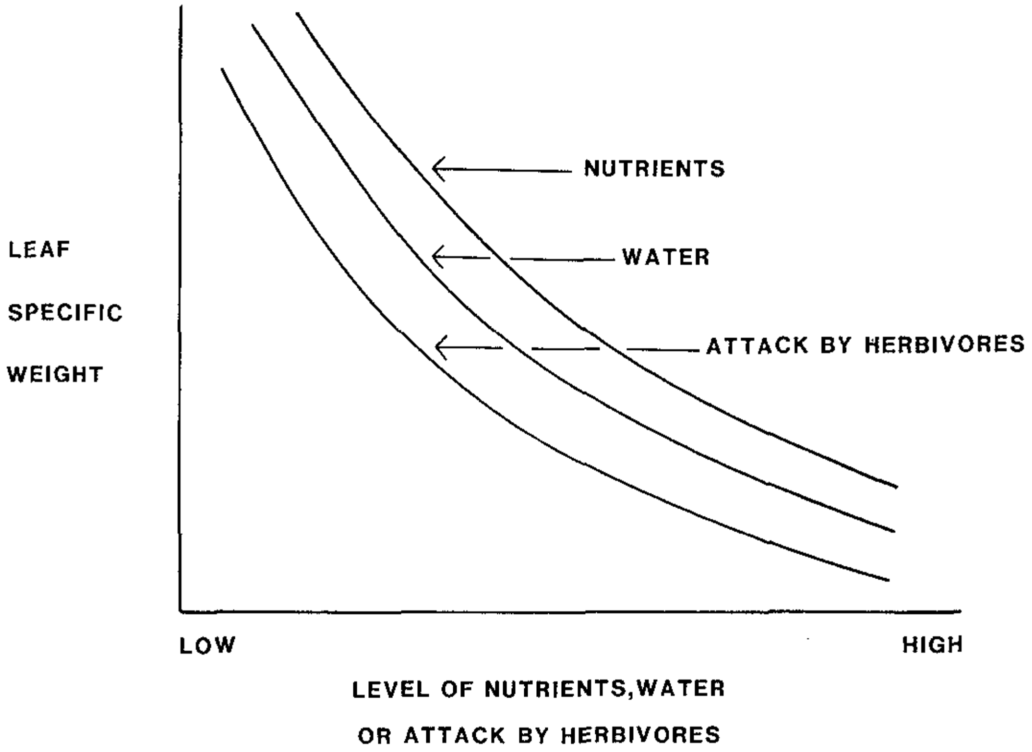


Fig. 4.1 Hypothetical relationship between leaf specific weight and availability of nutrients or water, or level of attack by herbivores

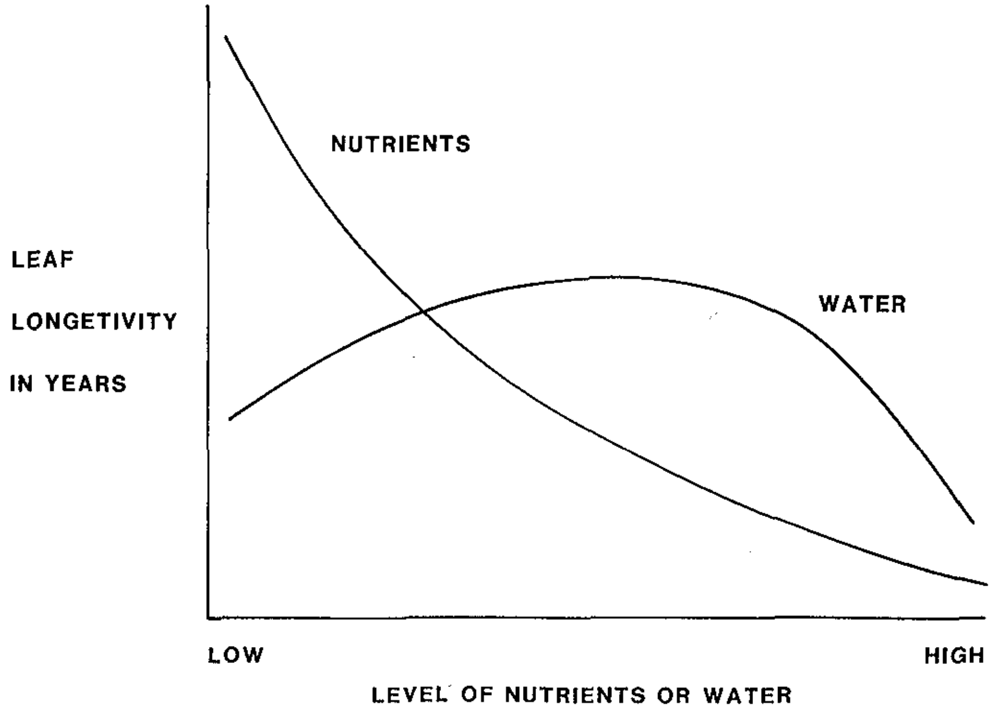


Fig. 4.2 Hypothetical relationship between leaf longevity and availability of water or nutrients. Where water is easily available, leaf longevity may decline because of competition for light

hypothetical relationship between LSW and availability of nutrients or water, or attack by herbivores. What is not fully understood is whether increasing sclerophylly with decreasing nutrients is simply a consequence of carbon accumulation due to the long lifespan of the leaves or whether there is active selection for this feature. The thick cuticles and high fibre contents of sclerophylls have been proposed as characteristics which would lead to slow leaching and decomposition of litter, which might be an advantage in nutrient-poor habitats (Monk 1966). Thickness per se could be important as a sink for nutrient storage in evergreen leaves (Mooney & Rundel 1979).

Lack of water is evidently also a strong selective agent for sclerophylly. Thick cuticles are important in survival during droughts, high fibre content is important in the maintenance of low water potentials, a well-developed hypodermis is important in water storage and leaf thickness per se is important in providing more favourable water-use efficiency.

Sclerophylly is probably also important in defence against herbivores (Feeny 1970). Thick cuticles can be important as a deterrent to fungi and herbivores. High fibre-content effectively dilutes nutrient contents and reduces palatability. Leaf thickness per se can be beneficial to herbivores, however, since the calorific intake is increased.

Thus it is apparent that sclerophylly is a complex phenomenon. Details of the distribution of this attribute in mediterranean plants are given in Chapter 5.

4.1.2 LEAF DURATION

Leaves of mediterranean plants vary in longevity from periods of weeks (or months in the case of annuals), to months for herbaceous perennials and drought-deciduous shrubs, to years in the case of certain evergreen shrubs. Surprisingly there are really very limited specific data available on leaf turnover in plants in general and in mediterranean plants in particular. It appears that longevity may vary even within a given season's leaf crop.

The benefit of leaf longevity has been viewed in terms of carbon gain in relation to resource availability (Mooney, in press; Gulmon, in press). Leaves with high N content will generally have a high photosynthetic capacity and N is continually shunted from old to new leaves for maximal capture of light or carbon per unit of N. In fast-growing plants this results in high N turnover as well as high leaf turnover (see Chapter 3 for a more detailed consideration). The overall efficiency with which a plant uses its resources of course increases with leaf age because the return on the investment of an element in a leaf increases with longevity as long as the leaf is not overtopped or stress limited.

We predict that in nutrient-poor habitats, which are usually not light limited, leaf longevity would be high (Figure 4.2); it has generally been found that where there is adequate water, leaves are held on plants only as long as there is sufficient light to maintain them above the compensation point. For example the leaves of evergreens in nutrient-poor and light-limited tropical rain forests tend to live for only one year (E. Medina, pers. obs.) whereas in more open, nutrient-poor and water-stressed mediterranean regions they may live a lot longer than this. In one of the most nutrient-impoverished regions, South Africa, some shrub species have leaves which may live for as long as six years (Kruger 1981). Leaves of Australian sclerophylls evidently do not live as long as this, however, although they occur on the most nutrient-poor soil of all.

Both water and nutrients can influence leaf longevity as well as the degree of sclerophylly. In severely water-limited habitats, leaves living over the drought period are costly to maintain; it may thus be more economical to shed than to maintain them (Miller & Mooney 1974). In an analysis of the significance of nutrients versus water as determinants of leaf longevity it is therefore important to separate these influences.

4.2 ROOTS

The surface of absorbing roots connects the soil solution with the plant, thus mediating water and ion uptake. The major roots, analogous to the above-ground branches, provide the framework for the absorbing rootlets. Any discussion of plant form and function has to consider the structure and the spatial distribution of root systems; here we consider the root systems of shrubs in particular.

4.2.1 HORIZONTAL AND VERTICAL ROOT EXTENSION

Substantial information has been accumulated on the horizontal and vertical extension of the root systems of mediterranean shrubs (Kummerow, in press), so that certain generalizations can now be made. The roots of these shrubs extend far beyond the crown radius and the bulk of the root biomass is virtually always in the upper 20-40 cm of the soil. The depth of root penetration depends largely on the substratum; deep sandy soils favour tap-root systems but do not exclude substantial masses of surface roots. Species are frequently found with deep rooting characteristics at one site but with shallow roots at another. Adenostoma fasciculatum was found by Hellmers et al. (1955) with roots 4-5 m deep, while Hanes (1965) found the same species with a rooting depth of 1,5-2,5 m and Kummerow et al. (1977) excavated vigorous Adenomstoma shrubs from a chaparral soil only 60 cm deep.

Some evidence has been reported for nutrient availability acting as a modifying influence on root extension. The positive chemotrophic reaction of root tips to nutrients is well known. Lamont (1973) has shown for Australian heath that the high density of roots beneath the canopy of shrubs is related to the higher nutrient availability under the litter layer. In general it can be stated that root systems are extremely plastic in regard to their spatial distribution in the soil.

4.2.2 ROOT ANATOMY

Very few data exist that relate root anatomy to nutrient availability. Experiments with seedling of chaparral shrubs demonstrated that low levels of N and P caused a significant reduction in root diameter as a result of a decrease in the size of root cortex cells (J. Kummerow, pers. obs.). The proteoid roots of Australian and South African Proteaceae have been interpreted as adaptations to low levels of P (Lamont 1980a). These root clusters are concentrated in the uppermost 10 cm of soil, especially in the region of actively-decomposing litter. The compound proteoid roots of Banksia and Dryandra form a dense mat at the soil surface. Lamont (1980a) reported that these specialized roots have a greater capacity to absorb nutrients than do "normal" roots. It seems significant that specialized root structures have only been observed in plants of the mediterranean regions of South Africa and Australia, both of which are characterized by very low concentrations of P. However, the Proteaceae are likewise most abundant in these two regions. The functional significance of many root structures is obvious. For example, enlargement of the root surface could well be the means for the more thorough exploitation of a soil volume for a growth-limiting mineral. But other structures such as succulent root cortices may serve multiple functions, including water-storage, as well as acting as a mineral reserve.

4.3 ALLOCATION

Allocation of carbon is influenced by the supply of nutrients in the soil although other important factors such as the availability of water may have additional effects on allocation.

4.3.1 ROOT:SHOOT RATIOS

The ratio of below-ground to above-ground plant biomass, the root:shoot ratio, is of great importance for understanding the resilience of resprouting plants to the adverse effects of factors such as fire. In areas where seeding species predominate, the proportion of root material that dies after fire is important in determining the extent of nutrient release within the soil.

Root:shoot ratios have been found to increase with decreasing nutrient supply in many different types of ecosystem; this relationship is expressed hypothetically in Figure 4.3. It is generally assumed that more extensive root systems develop to allow more effective nutrient uptake in nutrient-poor soils; data derived from mediterranean regions in Chile, California and Australia support this assumption (Hoffmann *et al*. 1977; Kummerow *et al*. 1978). Root:shoot ratios may vary from less than 1:1 on nutrient-rich soils to more than 3:1 on nutrient-poor soils. Experimental work in Australia confirms an increased root:shoot ratio in nutrient-poor soils, particularly when P is lacking. However, available data from South Africa are less clear and in fact are sometimes contradictory. It is clear that the age of the plant greatly influences root:shoot ratios and whether a plant is a seeder or a resprouter may also be significant. Root:shoot ratios of certain resprouting species in South Africa have been found to vary from 5:1 in plants a few years old to 1:1 in older plants, while the ratio for non-sprouting species appears to remain well below 1:1 for all plants of comparable ages (A. B. Low, D. T. Mitchell, pers. obs.). These data were all derived from plants growing on nutrient-poor South African soils, and may not support the generalization of an increase in root:shoot ratio with decreasing nutrient supply.

If, for other reasons, the incidence of fire is more frequent in nutrient-poor than in nutrient-rich areas, this would tend briefly to raise the root:shoot ratio in the nutrient-poor areas. In resprouting plants, successive fires may result in the below-ground parts being many times older than the above-ground parts, resulting in particularly high root:shoot ratios.

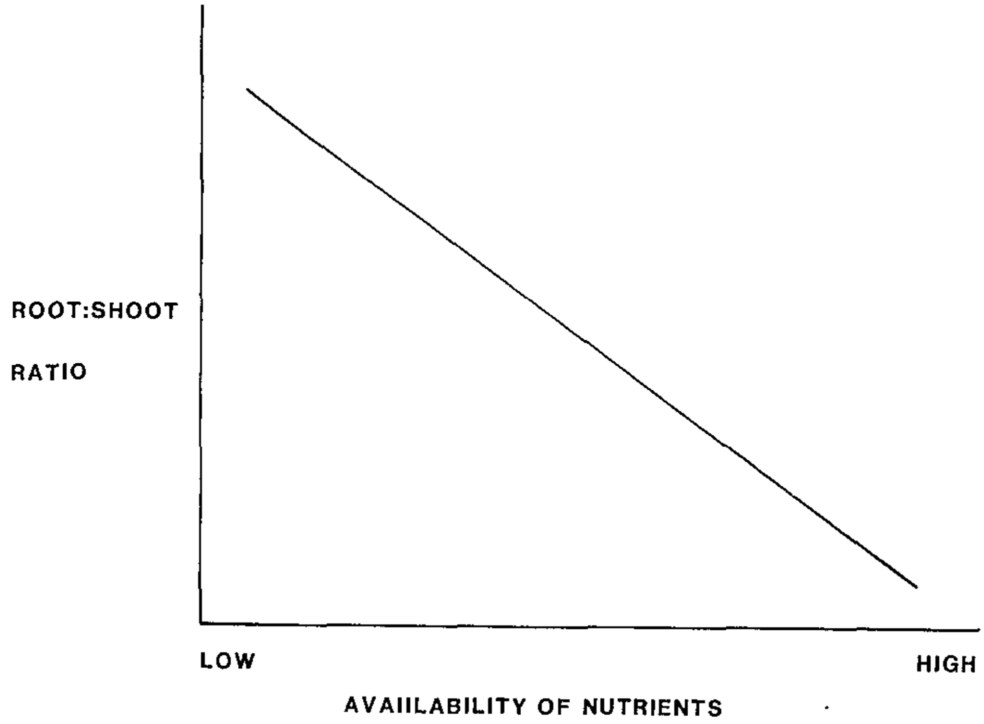


Fig. 4.3 Hypothetical relationship between availability of nutrients in the soil and the ratio of root biomass:shoot biomass

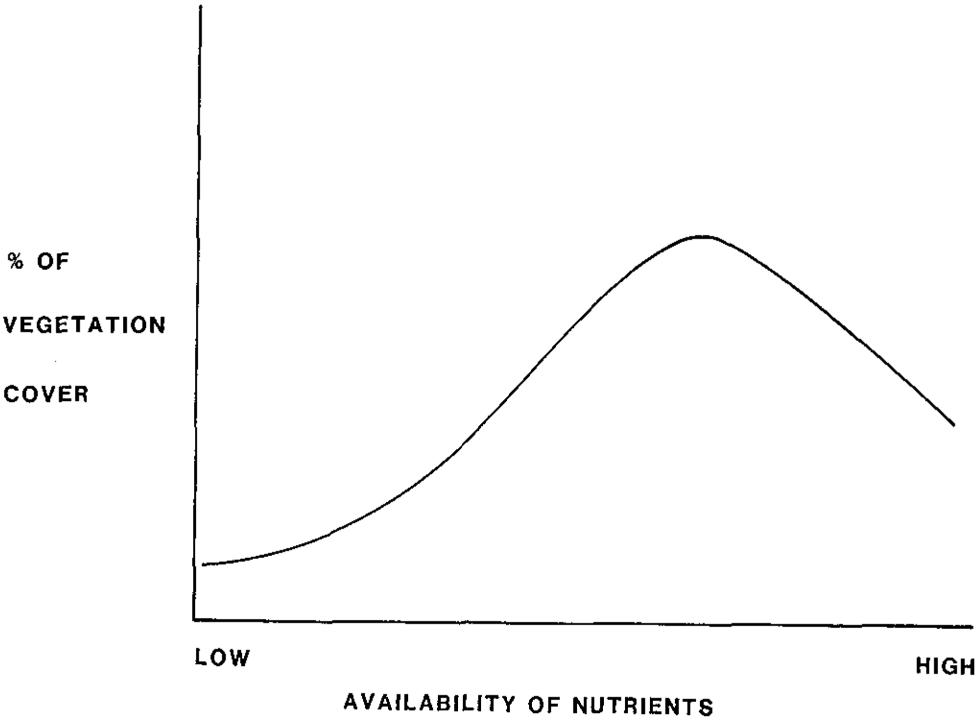


Fig. 4.4 Distribution of herbaceous plants with storage organs along a nutrient gradient, hypothesized from data collected in South African fynbos

4.3.2 VEGETATIVE:REPRODUCTIVE RATIOS

Vegetative:reproductive ratios indicate the efficiency of reproductive allocation. Since vegetative:reproductive ratios are generally low in annual plants and high in many woody plants, and since it appears that the proportion of annuals increases with nutrient-richness of soils in, for example, South Africa and California, lower vegetative:reproductive ratios may be expected to reflect increased nutrient-richness. On the other hand, certain Australian data indicate that such ratios remain constant despite differences in nutrient status (R. L. Specht, pers. obs.).

Vegetative:reproductive ratios also vary in the successional stages following fire; for example in California the ratios drop dramatically after a fire and gradually rise with succession. South African work (E. J. Moll, pers. obs.) has demonstrated that old fynbos plants in nutrient-poor situations increase flower production with application of nutrients and that this may result in a lower vegetative:reproductive ratio.

4.3.3 LEAF AREA RATIOS

The ratio of leaf area to mass of the whole plant (leaf area ratio - LAR) relates to the proportion of photosynthetically-active material in the plant. The LAR may be expected to increase with increasing nutrient-richness, but very few data are available. However if leaf duration increases on nutrient-poor soils, then possibly LAR's increase in soils of poor nutrient status. Data on such allocation patterns are at present wholly insufficient to allow definite conclusions, particularly regarding intercontinental comparisons.

4.4 STORAGE

A large number of herbaceous perennials and woody plants have underground organs from which annual, perennial or periodic shoots and inflorescences are produced. Here we review storage in general as a characteristic of mediterranean plants, as well as considering its competitive advantage.

We consider plant storage to be the accumulation of nutrients or carbohydrates in some perennial part of a plant for remobilization when required (Mullette & Bamber 1978; Pate & Dixon 1978). These tissues become swollen by their contents and can therefore be recognized as storage organs. Water may also be stored in such organs and it is often difficult to distinguish the main function of organs storing more than one product. At present there is no satisfactory acceptable term describing storage organs of woody plants (E. J. Moll, pers. obs.).

4.4.1 STRUCTURES

In general storage organs of mediterranean plants are below the ground and hence are partially protected from herbivores and fire. Herbaceous or sub-woody plants such as Asparagus, which have underground storage organs in the form of bulbs, corms, tubers or rhizomes, may have either seasonal or perennial above-ground parts. The storage organs of woody plants are usually less discrete than are those of herbaceous and sub-woody plants, and also contain a reservoir of adventitious buds from which the plant resprouts following a fire (Beadle 1968; White 1976; Mooney & Conrad 1977); these plants can thus be considered to be facultative phanerophytes or hemicryptophytes. The dominant growth form depends on the degree of perturbation; they may behave seasonally as phanerophytes but after fire as hemicryptophytes.

4.4.2 DISTRIBUTION

4.4.2.1 HERBACEOUS STORAGE ORGANS

Plants able to store nutrients and water are not limited to mediterranean regions, although they are evidently more abundant in such ecosystems. The largest concentration of species and the highest density of such plants in South Africa are to be found in the mediterranean zones, where they tend to be most abundant on nutrient-rich sandy-clay loamy soils derived from granites and shales and less abundant on nutrient-rich shales and nutrient-poor sands. Figure 4.4 shows a hypothetical scheme for their distribution along nutrient gradients. However, most of the water in these soils is available in winter and they are severely water-stressed in summer, so that the relative importance of the availability of moisture and of nutrients in the soil is not clear. What is clear, though, is that the above-ground parts of these plants tend to be seasonal on nutrient-rich sites and perennial on nutrient-poor sites.

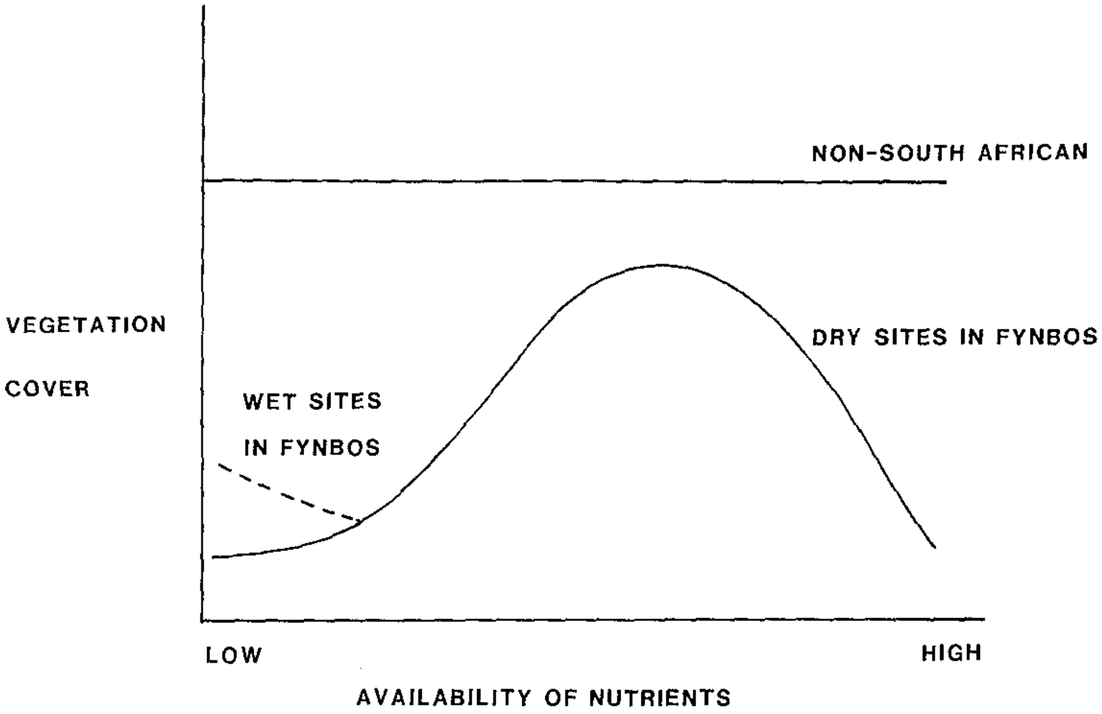
Data are not available on herbaceous plants with storage organs in the other mediterranean ecosystems but field experience indicates that the situation is similar.

4.4.2.2 WOODY STORAGE ORGANS

The distribution pattern of storage in woody plants (Figure 4.5) is more complicated than that of herbaceous plants (E. J. Moll, pers. obs.). Root-resprouters (such roots are assumed to be storage organs) are a feature of all mediterranean ecosystems except fynbos heaths. In mediterranean systems other than in South Africa there is apparently little change in the abundance of such organs along a nutrient gradient, except that the richest sites are possibly poorer in numbers of woody resprouters.

4.4.3 GENERAL

Whether plants with storage organs are a feature or even a characteristic of mediterranean regions is not yet clear. There is some observational evidence, notably from South Africa, to suggest that herbaceous plants with storage organs are characteristic of mediterranean regions but that woody resprouters are characteristic of nutrient-poor and fire-prone habitats in general, whether or not these are mediterranean (Specht 1970; Eiten 1972; White 1976).



Fiq. 4.5 Hypothetical distribution of woody resprouters alonq nutrient qradients in mediterranean ecosystems

4.5 SEASONALITY OF FLOWERS, FRUITS, LEAVES AND SHOOTS

Since leaf and shoot growth, flowering and fruiting require nutrients over and above those necessary for plant maintenance, it is obvious that the seasonality of these activities must be related to patterns of absolute and of seasonal availability of nutrients. Let us compare phenological relationships in mediterranean plants from soils low or high in nutrients, both between and within ecosystems.

4.5.1 SEASONALITY OF FLOWERING

There is a spring peak in community flowering in the mediterranean regions of Chile (Mooney & Kummerow 1977), California (Hoffman et al. 1977), southern Australia (Specht & Rayson 1957a), Palestine (Zohary 1962; Margaris 1976) and South Africa (Rycroft 1950; van der Merwe 1966; Kruger 1979; J. E. M. Sommerville, pers. obs.). There are no obvious differences in flowering patterns between communities from areas lower or higher in nutrients (Table 4.1), and this can perhaps be attributed to a predominance of insect-pollinated species in all of these regions. In contrast, many of the Proteaceae, characteristic of the mediterranean regions of Australia and South Africa, flower in winter; this may relate to pollination by birds or mammals rather than by insects.

4.5.2 SEASONALITY OF FRUITING

Fruiting in chaparral (Hoffman et al. 1977), renosterveld and fynbos (J. E. M. Sommerville, pers. obs.), and south-western Australian heath

(R. L. Specht, pers. obs.), is more protracted than is flowering (Table 4.2). But again there are no clear differences between communities from areas of differing nutrient status.

TABLE 4.1 Peak flowering season of mediterranean plants

NUTRIENTS HIGHER	Spring	Summer	Autumn	Winter
CHILEAN MATORRAL	X			
CALIFORNIAN CHAPARRAL	X			
SOUTH AFRICAN RENOSTERVELD	X			
PALESTINE	X			
NUTRIENTS LOWER				
SOUTH AFRICAN FYNBOS	X			
SOUTH-CENTRAL AUSTRALIAN HEATH UNDERSTOREY	X			
SOUTH-CENTRAL AUSTRALIAN HEATH OVERSTOREY		X	X	

TABLE 4.2 Peak fruiting season of mediterranean plants

NUTRIENTS HIGHER	Spring	Summer	Autumn	Winter
CHILEAN MATORRAL	X	X		
CALIFORNIAN CHAPARRAL	X	X		
SOUTH AFRICAN RENOSTERVELD		X	X	
NUTRIENTS LOWER				
SOUTH AFRICAN FYNBOS	X	X		
SOUTH-CENTRAL AUSTRALIAN HEATH UNDERSTOREY	X			
SOUTH-CENTRAL AUSTRALIAN HEATH OVERSTOREY			X	

4.5.3 SEASONALITY OF LEAF AND SHOOT GROWTH

Specht & Rayson (1957a) and Groves (1965) cite the summer shoot growth of the dominant overstorey species in south-western Australian sclerophyllous heath as a unique characteristic of heath vegetation. However, the less sclerophyllous understorey species exhibit growth in spring and/or autumn (Specht _et al._, in press). South-western Cape fynbos communities as a whole also exhibit a summer peak in leaf and shoot growth (Levyns 1964; Taylor 1978; J. E. M. Sommerville, pers. obs.). The dominant evergreen shrubs in Californian chaparral, Chilean matorral, the garrigue of southern France and the renosterveld and strandveld communities of the south-western Cape exhibit peaks of growth in spring and/or autumn (Specht 1969; Mooney & Parsons 1973; Mooney & Kummerow 1977; J. E. M. Sommerville, pers. obs.) (Table 4.3).

There are differences in the seasonality of above-ground vegetative growth between continents, between vegetation types in South Africa and between strata in southern Australia (Specht _et al._, in press). Data from fynbos in the non-seasonal rainfall area in South Africa show a similar difference between understorey ericoid shrubs and the Proteaceae of the overstorey but this area is not truly mediterranean (Bond 1980). Kruger

TABLE 4.3 Peak season of vegetative growth in mediterranean plants

NUTRIENTS HIGHER	Spring	Summer	Autumn	Winter
FRENCH GARRIGUE	X		X	
CHILEAN MATORRAL	X			
CALIFORNIAN CHAPARRAL	X			
SOUTH AFRICAN RENOSTERVELD	X		X	
NUTRIENTS LOWER				
SOUTH AFRICAN FYNBOS		X		
SOUTH-CENTRAL AUSTRALIAN HEATH UNDERSTOREY	X		X	
SOUTH-CENTRAL AUSTRALIAN HEATH OVERSTOREY		X		

(1979) showed that some mediterranean species of Proteaceae exhibit growth peaks in spring and others in summer.

Spring, and to a lesser extent autumn, appears to represent a period of optimal combinations of light, temperature and moisture for growth in mediterranean plants. But in the heath of south-western Australia and the fynbos of the south-western Cape, soil nutrients are comparatively low so that their seasonal availability in the soil and reallocation in the plant may be of overriding importance to seasonality of growth.

Summer growth of species in soils low in nutrients may be a result of the spring release of nutrients from the litter due to an increase in the activity of fungi and of insect decomposers when moisture and temperature conditions are optimal (Lossaint 1973; Schaefer 1973; A. B. Low, pers. obs.). Groves (1965) has also suggested that the growth of shrubs in summer represents a redistribution of metabolites within the plant rather than uptake from the soil; a summer increase in plant orthophosphate was assumed to be due to the hydrolysis of stored phosphate (Specht & Groves 1966). This, coupled with efficient redistribution of nutrients from senescing leaves before leaf fall in late summer or autumn, could account for summer growth.

Specht & Rayson (1957a) have stated that the summer growth rhythm is markedly out of phase with the present annual climatic cycle; they suggest that the apparent discrepancy may be related to the fact that wetter and warmer climatic conditions existed during the Pleistocene, when the Australian heath became widespread. This suggestion has been supported by Levyns (1964). It seems, then, that growth in the south-western Australian overstorey and in fynbos is governed by temperature rather than by nutrients. Specht et al. (in press) show a dichotomy in the season of growth in understorey and overstorey plants of Australian heath. Mooney (in press) (see Figure 4.6) for California, and Bond (1980) and Kruger (1979) for South Africa, also show dissimilar growth seasons in different growth forms. These results illustrate the need to consider the phenological responses of different growth forms and strata to the same macro-environment. Much of the work to date has been on dominant shrubs or communities and is therefore either very specific or very generalized.

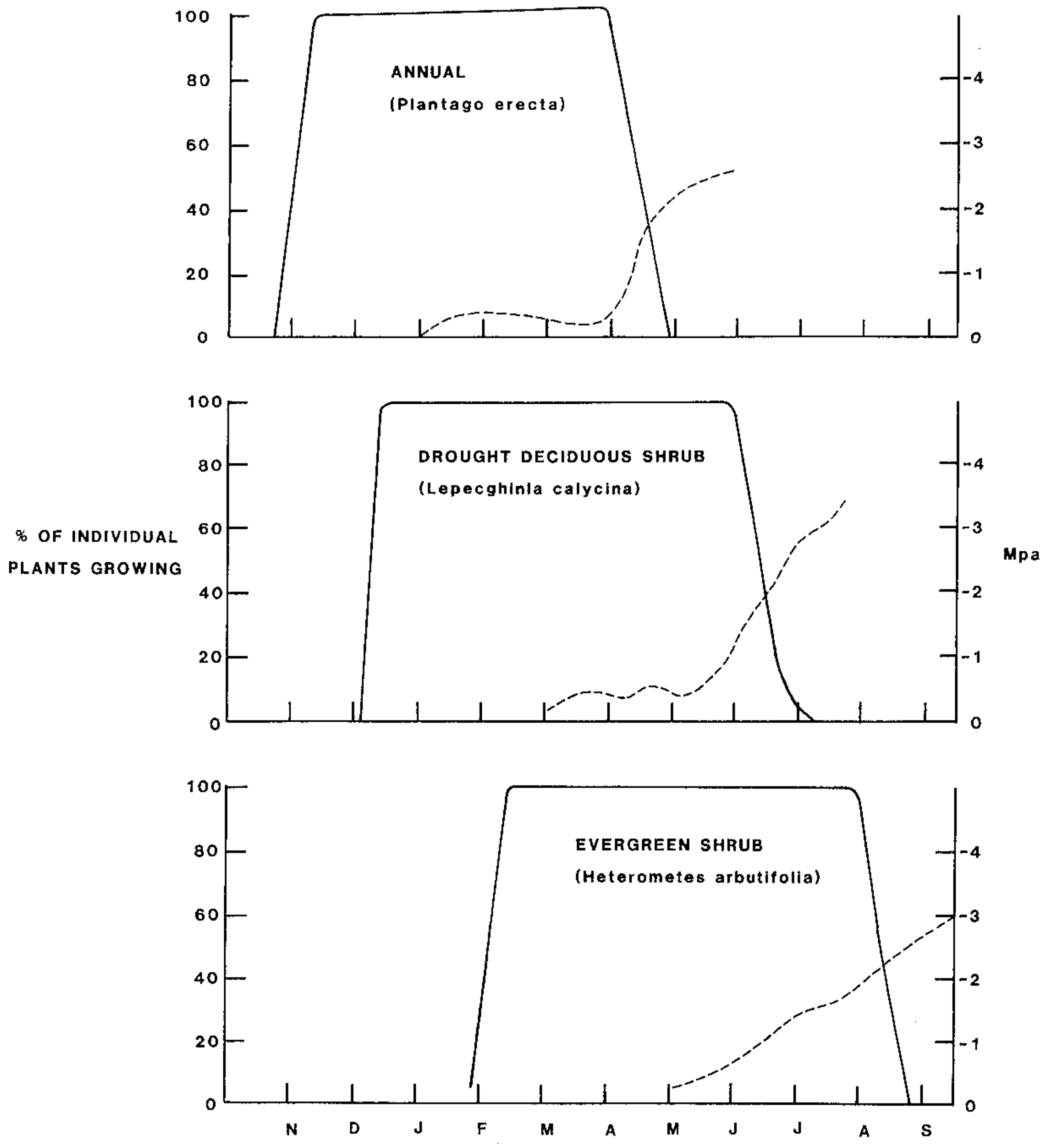


Fig. 4.6 Seasonality of growth in three species of plant from the Californian mediterranean region (——— = growth; - - - - = water potential) (after Mooney, in press)

4.5.4 SEASONALITY OF ROOT GROWTH

Abundant information has been recorded about the seasonality of leaf and stem growth of mediterranean plants (Mooney 1977; Thrower & Bradbury 1977) but only limited information is available on the seasonal periodicity of root growth. In root growth a distinction is made between the elongation of root tips, the growth of the vascular cambium of perennial roots (secondary root growth) and the seasonal growth of the ephemeral rootlets. Here we discuss whether growth rhythms of any of these are related to seasonal changes in the availability of nutrients and soil moisture.

Growth of the vascular cambium in the perennial roots of trees and shrubs of the Chilean mattoral closely follows the growth rhythm of the major branches. A bell-shaped growth curve for spring and summer is followed in most of the species by a complete cessation of cambial growth for the rest of the year. Since parallel observations on roots and shoots were made on two species only (Riveros de la Puente 1973), the vascular cambial activity of the stems of eight major species in the mattoral were used to extrapolate secondary growth in the roots of these shrubs. Analogous studies were reported for major chaparral shrubs in southern California (Avila et al. 1975), from the Greek phrygana (Margaris & Papadogianni 1978) and from the maquis of Israel (Fahn et al. 1968). The results indicate that vascular cambial activity in roots follows a generally fixed pattern of seasonality. Availability of nutrients and moisture modifies the quantity of new xylem formed but does not change the specific time-course of this process for each species.

Observations of seasonal changes in the density of the ephemeral rootlets in the Greek phrygana, on a relatively nutrient-rich, calcareous substrate 0,3 m deep, showed a maximal density of fine roots in April to May (600 g m^{-2}) and a minimal one in September to October (J. Kummerow, pers. obs.). In mixed southern Californian chaparral the rootlet biomass increased from an early spring value of about 300 g m^{-2} to 1300 g m^{-2} in late summer (Kummerow et al. 1978). N and P values were lower than those for the Greek site. Densities of fine roots in a fertilized Chilean matorral site (16 g N m^{-2}, 8 g P m^{-2}) were higher than those in California, although the seasonality of growth of fine roots was less pronounced (G. Avila, pers. obs.), in agreement with the general plant phenology of these two areas (Hoffman et al. 1977).

Studies in Victoria, south-eastern Australia, showed that root elongation in Leptospermum heathland began in September (spring) and continued until the end of May, although growth rates declined as soil moisture decreased (Haines 1967).

Substantial seasonal fluctuations have been shown in the biomass of fine roots of mediterranean plants, but no correlations have yet been revealed between nutrient status and root biomass. The availability of soil moisture seems to determine the patterns of root growth; more information is needed to test the effect of nutrient availability on the density of fine roots, although the results of an experiment in the Chilean matorral suggest that additional N and P might enhance the production of fine roots.

Observations in a cold desert area in Utah demonstrated convincingly that active root growth shifts during the year from the surface to deeper soil layers, strongly correlated with a gradual depletion of soil moisture from above during the growing period (Caldwell & Camp 1974).

4.6 LIFESPANS OF PLANTS

Lifespan is clearly defined for plants reproducing from seeds. It is more difficult to determine, however, for plants reproducing vegetatively because an individual plant is not always easy to define. For such plants one might define the lifespan as the length of time the mother plant can survive; it then becomes possible to distinguish for example between perennial geophytes with annual and with perennial bulbs or corms. Here we deal with the duration and lignification of above-ground stems but not of underground organs.

Rather little is known about plant lifespan as related to nutrient supply. One may suggest that, from the point of view of the nutrient economy of the plant, there is an advantage, in nutrient-poor systems, in accumulating and keeping as many nutrients in the plant for as long as possible. Thus there would appear to be an advantage in a longer life span both for the whole plant and for its organs.

4.6.1 LIFESPAN OF THE WHOLE PLANT

Since annuals form the most conspicuous group of short-lived plants, especially if one considers ratios on high-nutrient post-fire sites, we first consider variations in the ratio of annuals to perennials in relation to nutrient supply. The ratio generally seems to decrease with decreasing nutrient supply in the Mediterranean region (Berliner 1971; Rabinovitch-Vin 1979), in South Africa (E.J. Moll, pers. obs.), in California (Mooney & Parsons 1973) and in Australia (Lamont _et al_. 1977). In certain extreme cases where the supply of a certain element is limiting, there is a marked reduction in the percentage of annuals in the vegetation (Rabinovitch-Vin, in press); this relationship is shown hypothetically in Figure 4.7.

Little is known about the lifespans of perennial plants in relation to nutrient supply, nor is it easy to compare the distribution of types of lifespan in plant communities which differ in their nutrient supplies but where other environmental factors are more or less equal. Nevertheless qualitative observations suggest that the lifespans of individuals increase with decreasing nutrient supply up to a certain level, then drop again in the most nutrient-poor habitats (Figure 4.8). It has been found with _Staavia dodii_ in South Africa that the number of flowers per plant reaches a maximum after 10 years and the plant dies at an age of about 30 years (Figure 4.9). This may well be due not only to senescence but also to a continuous drop in the availability of nutrients around the plant (Moll & Gubb 1981); certainly a 45 year-old community of _Protea laurifolia_ produced significantly more flowers and longer shoots when fertilized (E. J. Moll, pers. obs.). The fact that additional nutrients supplied only once may cause the early death of plants (Specht 1963) may be due to a rapid increase in demand for nutrients by the plant.

The longer lifespan of chaparral shrubs in California seems to be related to the frequent fires which are followed by enormous increases in nutrient supply. There is evidence that natural fires were frequent even before the advent of primitive man (Mooney & Conrad 1977); reproduction by resprouting might be considered as an adaptation to a frequent fire regime on poor soils.

4.6.2 LONGEVITY OF ABOVE-GROUND STEMS

In order to determine whether stem longevity of perennial plants increases or decreases with decreasing nutrient supply, it is necessary to distinguish between perennial herbs and half-shrubs (axyles or semixyles) (Figure 4.10) on one hand, and trees and shrubs (holoxyles) on the other. The longevity of hemicryptophytes seems to increase with decreasing nutrient supply. Stems of plants of Restionaceae in South Africa persist for a number of years (J. E. M. Sommerville, pers. obs.) and it seems that other hemicryptophytes behave in the same way, while the stems of most of those in the Mediterranean Basin last no more than a few months (Orshan 1980). Less is known about stem longevity of geophytes, though some certainly have annual above-ground parts and others, mostly in South Africa, have perennial above-ground parts. Chamaephytes of the Mediterranean region tend to shed a greater part of their branches on nutrient-rich than on nutrient-poor soils (Orshan 1964; E. J. Moll pers. obs.). Stem longevity of trees and shrubs is apparently not directly related to nutrient supply, but to the lifespan of the whole plant.

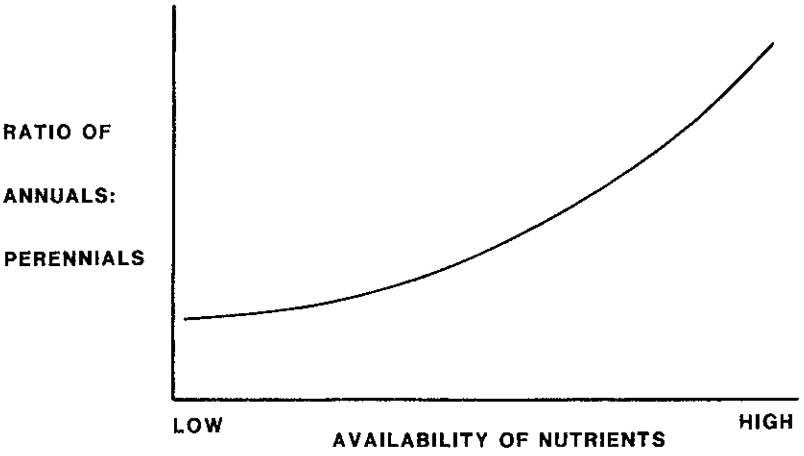


Fig. 4.7 Hypothetical relationship between availability of nutrients and the ratio of annuals:perennials

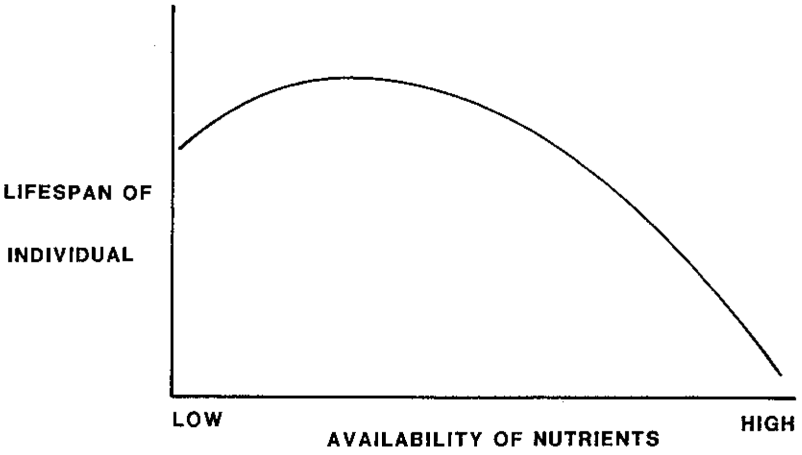


Fig. 4.8 Hypothetical relationship between availability of nutrients and the lifespans of plants

Fig. 4.9 Change with age in number of flowers per plant in Staavia dodii (from Moll & Gubb 1981)

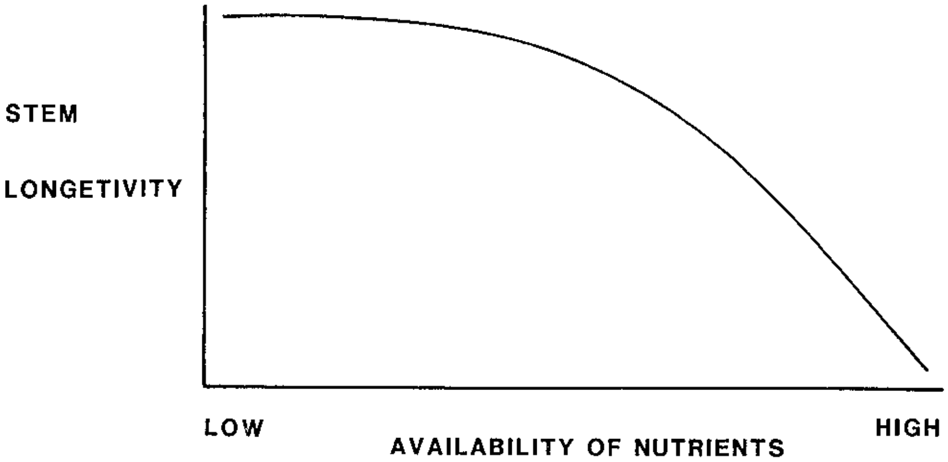


Fig. 4.10 Hypothetical relationship between availability of nutrients and the longevity of stems of herbaceous perennials and half-shrubs

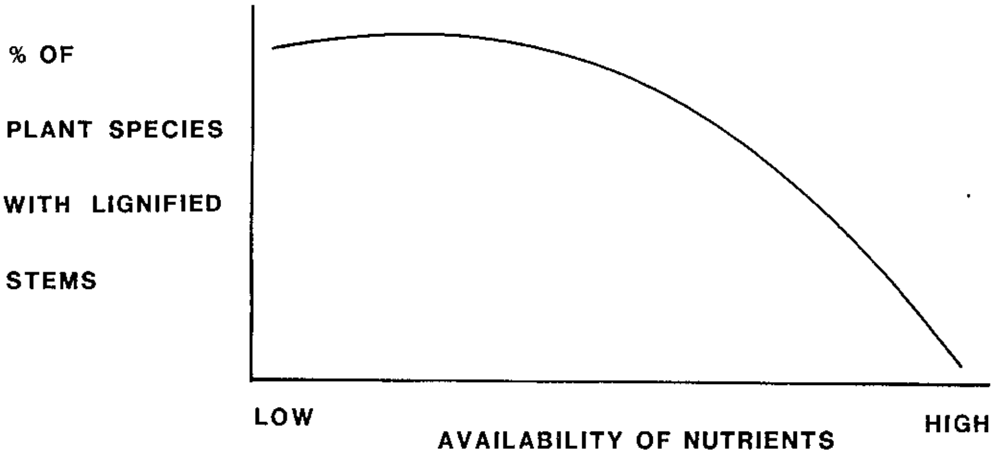


Fig. 4.11 Hypothetical relationship between availability of nutrients and the percentage of plants species with lignified stems

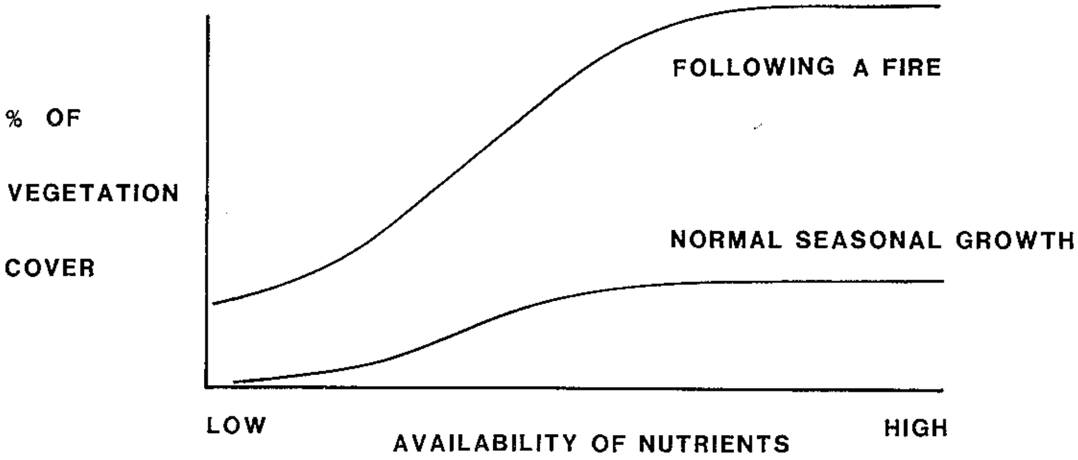


Fig. 4.12 Comparison between the hypothetical number of annuals after a fire and the number occurring in a normal season, along a nutrient gradient

4.6.3 LIGNIFICATION

Lignification is related to stem longevity in that non-lignified stems are generally, although not always, of short duration. There are some data on the correlation between nutrient availability and lignification. In Australia and Israel the percentage of herbaceous plants in the vegetation occurring on soils rich in P is higher than that on soils low in P (Specht 1973; Rabinovitch, in press). Ruderal vegetation developing on relatively N-rich soils is composed mainly of herbaceous plants. It is thus suggested (Figure 4.11) that the percentage of lignified stems increases with decreasing nutrient availability, although the supporting evidence is meagre.

4.7 REPRODUCTIVE ADAPTATIONS

Since mediterranean ecosystems occur in fire-prone environments (Cody & Mooney 1978), survival of the genotype and its reproduction after fire are critical. Plants may regrow from seeds, or from vegetative parts, or from some combination of these (Keeley 1977b).

4.7.1 REGENERATION FROM SEED

Annuals are a feature of mediterranean regions, though the number of species and their abundance varies considerably within and between ecosystems. Generally, annuals occur on nutrient-rich sites and are particularly common following fire rather than being common seasonally (Figure 4.12). This may relate to the post-fire nutrient flush (Rundel & Parsons 1980), which probably allows a greater abundance of annuals after a fire than during the normal seasonal flush.

Herbaceous perennials. These are generally uncommon in mediterranean regions except in South Africa where some Compositae and Restionaceae are perennial; they are most common on soils low in nutrients (Figure 4.13).

Woody species. Again the mediterranean region of South Africa is exceptional in that woody seed regenerators on nutrient-poor sites generally contribute more to the above-ground biomass than they do in other mediterranean ecosystems although exceptions such as *Leptospermum* and *Hakea* occur in Australia, and *Ceanothus* and *Salvia* in California.

4.7.2 REGENERATION OF RESPROUTERS

South Africa is unique in that, in many areas, communities growing on soils low in nutrients are dominated by herbaceous hemicryptophytes such as Restionaceae, Cyperaceae and Poaceae that resprout after fire. This resprouting of herbaceous hemicryptophytes after fire is not common in other mediterranean regions (Figure 4.14) except in some wet areas in Australia.

Woody resprouters are of two basic kinds, those such as *Eucalyptus* and *Protea nitida* that sprout epicormically from buds buried deeply under thick bark, and those such as *Banksia* and *Rhus* that sprout from some persistent underground tissue. The resprouting habit is characteristic not only of plants from all mediterranean regions, but also of those from low nutrient sites in general; fynbos heath may be an exception (Figure 4.15). It has been postulated that a prolonged history of herbivory and nutrient poverty

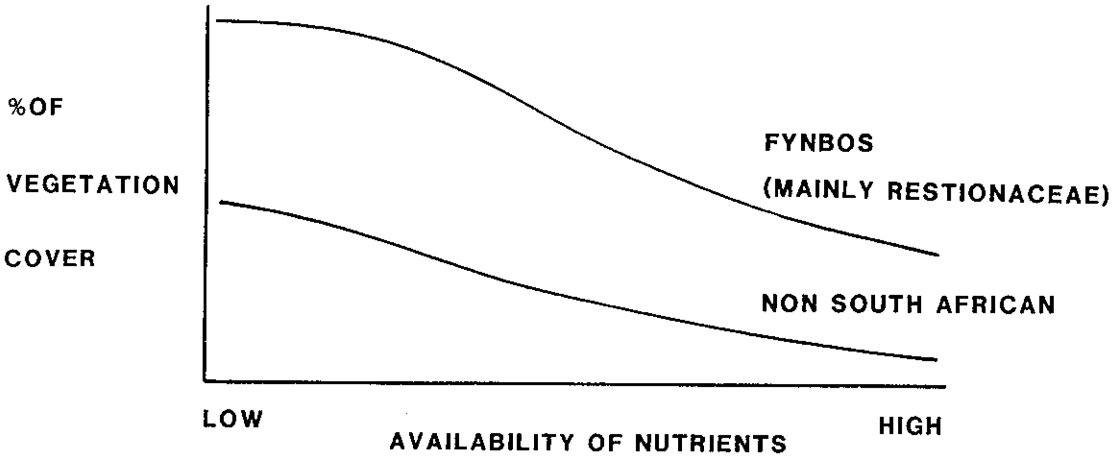


Fig. 4.13 Observed occurrence of herbaceous perennial re-seeders along nutrient gradients in mediterranean ecosystems. (E. J. Moll, pers. obs.)

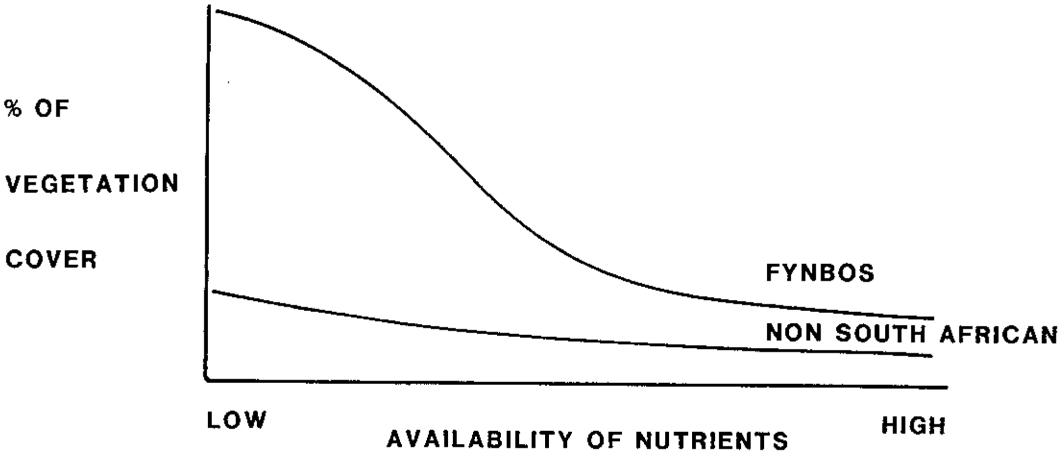


Fig. 4.14 Observed occurrence of herbaceous perennial resprouters along nutrient gradients in mediterranean ecosystems. (E.J. Moll, pers. obs.)

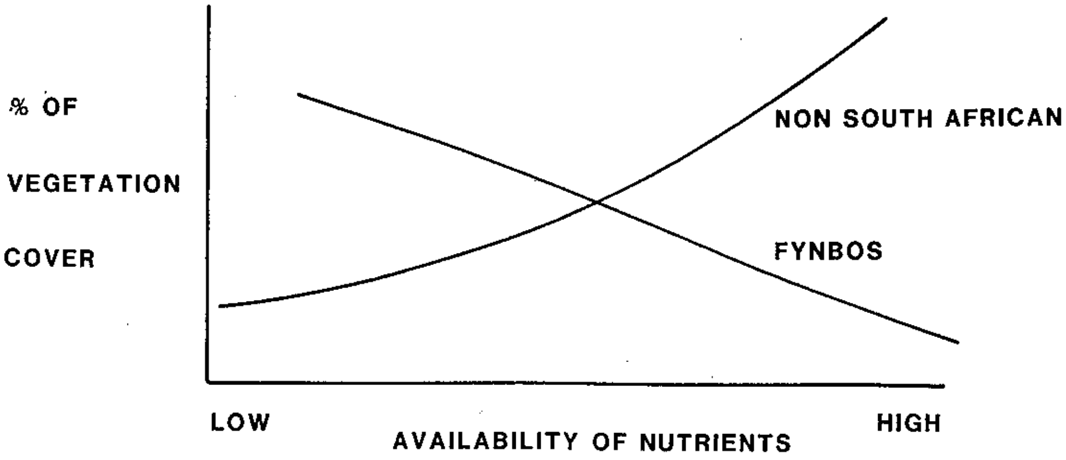


Fig. 4.15 Observed occurrence of woody resprouters along nutrient gradients in mediterranean ecosystems. (E. J. Moll, pers. obs.)

has led to this resprouting habit, which is pre-adaptive for survival after fire.

4.7.3 SPECIAL CASES

There are examples in the literature suggesting that fire, if not essential, certainly enhances reproduction. The best-documented case is the germination of *Acacia* seeds, which is normally episodic but is massive after fire. Other examples include the fact that plants such as *Staavia dodii*, *Haemanthus* spp., *Lanaria lanata* and *Xanthorrhoea* spp. do not flower unless burned. There is some evidence that flowering in *Xanthorrhoea* is ethylene induced (Gill & Ingwersen 1976). Although ethylene may be the environmental "cue" or trigger, the evolutionary advantage would be that more nutrients are available following a fire so that greater flower production is possible. Also at this time competition for pollinators is reduced. One could also argue that regrowth is slow in the year following a fire so that seeds would have less intraspecific competition and hence a greater chance of survival. In South Africa there is a suite of short-lived (5-7 y) species of *Euryops*, *Helichrysum*, *Aspalathus* and *Pelargonium* that grow immediately after fire in many areas (Kruger 1977a); it is possible that these species have evolved to occupy niche spaces created by fire, and are out-competed after some years of regrowth.

4.7.4 COLONIZATION

Plants that have a well-developed capacity for vegetative resprouting after a fire generally have low mobility of propagules. They have a competitive advantage though, especially on low-nutrient soils, in being able to absorb nutrients more readily after fire. Species that regenerate from seed can grow from seed stored in the soil (*Acacia*), from seed stored on the plant in serotinous fruits (*Hakea*) or from immigration of wind-blown seeds (*Euryops*). In low-nutrient regimes, seeds capable of withstanding competition for resources either have a high nutrient content (*Banksia*) or are produced in very large numbers (*Erica*). Since large seeds are a prime target of predators, woody protective capsules have evolved to protect them.

4.8 FUTURE STUDIES

4.8.1 PLANT TRAITS AND ENVIRONMENTAL RESOURCES

A number of approaches should be of value in establishing general patterns of distribution of particular plant traits and growth forms in relation to environment resources.

4.8.1.1 STUDIES ON GROWTH AND ANATOMY

We need a better understanding of those anatomical features leading to sclerophylly, we need to explore further the inducibility of various sclerophyllous components under experimental conditions where nutrients and water are independently manipulated, and we need a better view of the seasonality of sclerophylly. Such studies might help to distinguish between the influences of herbivores, of nutrients and of water. We most certainly need studies linking specific functional characteristics such as leaf duration with those specific anatomical features of the leaf which are related to sclerophylly.

The distribution and growth of roots and rootlets are poorly known. Root systems are important because they form the absorbing structures, mediating between the soil and the plant; their seasonal turnover in biomass may reach values twice as high as those of above-ground litter fall. There are virtually no data on the loss of minerals from the plant to the soil due to this turnover. Yet the root turnover represents a contribution of carbon to the soil and might assist in soil formation. In future work, fine-root density should be correlated with the nutrient status of the study sites and an effort should be made to separate the effects of moisture from that of nutrient in the soil.

Comparative studies on reproductive adaptations need careful investigation, both between and within mediterranean ecosystems. At present we know of rather few trends which are obviously related to gradients, but this may be a reflection merely of our very limited knowledge.

4.8.1.2 FIELD-CORRELATIVE APPROACHES

4.8.1.2.1 Environmental gradient analysis is a powerful approach for establishing the relationship between plant form and environment. In mediterranean regions this approach has already been used extensively to examine the relationship between growth form and environment along gradients of aridity (Parsons & Moldenke 1975; Cowling & Campbell 1980) and elevation (Mooney & Harrison 1972; Parsons 1976). Now comparable analyses are needed along gradients of nutrients or herbivory where aridity and elevation are held constant. In particular we need to establish the distribution of plants with storage organs relative to nutrient levels in the soil. So far, they seem to occur most commonly where nutrient levels are rather low. The role of water-stress in promoting storage organs needs investigation because both waterlogging and drought have been proposed as factors favouring pre-adaptation of storage organs for nutrient storage (Kerr 1925; Beadle 1968; Specht 1979).

Intercontinental comparisons should indicate how general are the relationships determined by such gradient analyses, which should be made not only between species but also between populations within single species along a gradient. These relationships need to be correlated with growth forms of the whole plant; such analyses may help to evolve more realistic classification systems for growth-forms than are now available.

4.8.1.2.2 Analyses of succession after fire is another approach which may be particularly valuable for examining the relationship between growth form and nutrients. It is well established that the nutrients in soil increase immediately after fire and decline through successional time (Rundel 1981); however, variations occur in microclimate, in levels of herbivory and in competitive relations at the same time.

4.8.1.2.3 Experimental manipulations of nutrient levels and subsequent long-term observations of the changes in growth forms which result should help in assessing the relationship between the resources needed by a community and the growth form of its constituent plants. Such experiments have been particularly revealing in Australian heath (Specht 1973).

4.8.1.3 RESPONSES TO A CONTROLLED ENVIRONMENT

Any trait in a plant may have arisen in response to climatic or biotic factors which are no longer selective. But where a trait is presently selected for, variation might occur within a given species along environmental gradients. Whether such variation is plastic or genetically fixed can be determined by cultivation of different populations of a species in a common garden, the approach pioneered by Clausen et al. (1940). By experimentation in controlled environments one can separate out, for example, the relative influences on leaf structure of nutrients and water (Radin & Parker 1979a) or of nutrients and light (Gulmon & Chu 1981).

Detailed quantified studies should look at the lives of individual leaves, their utilization of light and nutrients, and their carbon economy. These studies need to be done both under natural conditions and under conditions where the resource levels can be manipulated in the field and also in the laboratory.

4.8.2 ALLOCATION

The same approaches described above for unravelling the relationships between environmental factors such as nutrients, and plant traits such as growth forms, can be applied to examining the significance of differential allocation of carbon or of biomass between roots, stems and leaves. In the past, allocation of carbon to leaves has largely been inferred from work on net allocation. Far more data are required on the sources and sinks of carbon for each part of the plant, both short- and long-term, before satisfactory predictions of allocation can be made.

Since we are dealing here with entire functioning plants, we have the added opportunity of using models to aid in interpretations (Miller 1982). Thus, for example, as well as examining patterns along gradients or under various experimental treatments, we can simulate an infinite gradient of nutrient levels to determine their influence on patterns of allocation. Such an approach is only possible if considerable quantities of physiological and environmental data are available.

The significance of a given plant structure or product can be evaluated as cost and benefit in carbon units, as described for leaf duration by Miller (1979) and for a plant defensive compound. Although this approach is powerful and should be used more extensively, considerable biochemical and physiological information is needed to make this kind of assessment.

4.8.3 PLANT SEASONALITY AND RESOURCE ALLOCATION

In most cases it would appear that the seasonal patterns of carbon allocation in plants are related to fluctuations in the levels of resources available from the environment. There have been suggestions, however, that in certain cases plants are seasonally out of phase with the prevailing environmental conditions for historical reasons (Specht 1973). Further, it is known that plants can allocate large amounts of carbon during unfavourable non-growing periods by using stored reserves (Mooney & Bartholomew 1974). The first case is somewhat difficult to deal with and one can only look for clues from floristic relationships. The second is easily quantified by measuring seasonal stores of carbohydrates in stems and roots, and in some cases even leaves, since in evergreens these can store large amounts of carbohydrate.

More generally, though, particularly in the case of stem or root growth, resource availability is closely linked to patterns of carbon allocation. Thus maximal shoot growth, which demands large amounts of carbon and nutrients, should occur during the period of maximal availability of water and nutrients, when it also coincides with a period of favourable temperatures. The fact that there are differences in the seasonal growth cycles between various growth forms within a single mediterranean ecosystem, as well as differences within a single growth form in different ecosystems, suggests that there are different ways of acquiring resources in the first case (for example roots of different depths) and differential release of resources in the second. These relationships can readily be tested. As one of the highest priorities there should be a concerted effort to understand the basis of the patterns of summer growth in certain fynbos shrubs. A detailed study of seasonality in the relationships between water and nutrients among asynchronous but comparable growth forms should help to resolve this issue. Experimental laboratory or carefully-matched field studies are also needed in order to determine the effects of these factors in isolation.

5. THE STRUCTURE AND DYNAMICS OF PLANT COMMUNITIES

W. E. Westman (convener), C. Boucher, B. M. Campbell, R. M. Cowling,
B. Lamont, H. P. Linder, R. G. Noble, B. W. van Wilgen

The nutrient status of soils is clearly only one of the factors which influence the structure and functioning of vegetation, so that consideration of its influence on community structure in isolation is clearly an exercise in oversimplification. Despite this, a good deal can be learned from such an approach. This chapter starts by examining changes in the growth forms of plants along gradients of moisture availability in nutrient-poor and nutrient-rich communities, based on field experience and on information in the literature. The generalizations that have resulted, although inevitably subject to numerous exceptions in the field, are presented as hypotheses to be tested vigorously by future research workers. In addition, we discuss briefly some of the unusual or important trends in community structure that became apparent during this analysis.

5.1 STRUCTURE OF PLANT COMMUNITIES

In this section we graphically present hypothetical changes in growth forms within nutrient-rich and nutrient-poor mediterranean systems along a moisture gradient from xeric to mesic conditions. In order to relate our hypotheses roughly to conditions occurring in the field, we have used a rainfall gradient corresponding to 200 mm (xeric) to 1000 mm (mesic) per year or a moisture index value of 0,3 to 0,9 (see Table 5.1). We recognize that moisture availability is affected not only by precipitation but also by soil texture, radiation load and other factors. In choosing a single-factor gradient, we ignore the effects of such factors as altitude, temperature, aspect, rockiness and soil texture. Furthermore, only undisturbed climax communities are considered. Nevertheless these crude correspondences convert an otherwise vague presentation into a series of testable hypotheses.

Hypotheses are presented in the form of diagrams in Figures 5.1-5.5. The Y-axis in the figures refers to individual overlap foliar cover (absolute values). Some of the known divergences from these generalizations are indicated below the figures. Data on nutrient-rich and nutrient-poor community types within the five mediterranean systems are represented in Tables 5.1 and 5.2.

5.1.2 TRENDS IN THE STRUCTURE OF PLANT COMMUNITIES

Generally heathlands in Australia and South Africa are structurally more similar to each other than they are to adjacent shrublands on the same continent. This feature has been attributed to the lower levels of nutrients in heathland soils (Specht 1979; Cowling & Campbell 1980).

Below we discuss some of the features which distinguish the two vegetation types, mentioning where possible hypotheses concerning nutrient conservation which have been offered to explain their distribution.

Table 5.1 Types of vegetation in relation to soil nutrients and moisture availability[1]

Annual Moisture Index[2]	Poor in Nutrients		Rich in Nutrients		
	Australia[3]	South Africa	Australia	South Africa	California, Chile[4], Mediterranean Basin
0,9-0,8	open forest[5] with heath	scrub[6] with heath and/or forest	open forest[5] with grasses and/or herbs	forest[7]	forest
0,8-0,7	woodland and/or open scrub with heath	scrub with heath	open forest and/or woodland with grasses and/or herbs	forest[7] and/or thicket[8]	forest
0,7-0,6	woodland and/or open scrub with heath	scrub with heath	woodland with grasses and/or herbs	thicket[8] with grasses and/or herbs	woodland with grasses and/or herbs
0,6-0,5	open scrub with heath	open scrub with heath	woodland with grasses and/or herbs	closed scrub and/or scrub with grasses and/or renosterveld[9] with herbs	and/or herbs
0,5-0,3	open scrub with heath	open scrub with heath	open woodland and/or woodland with grasses, or with herbs and chenopods	renosterveld with or without succulent dwarf shrubs	semi-deciduous scrub with grasses and/or herbs (sage)
0,3	open scrub with *Triodea* or heath	open heath with succulent dwarf shrubs	open woodland with grasses and/or herbs with chenopods		deciduous scrub and/or succulents

1. Modified from Specht & Moll (in press)
2. Moisture Index (Ea/Eo) = ratio of plant community evapotranspiration to pan evaporation (Specht 1972)
3. Data from Specht (1972)
4. Data from Specht (1969), Harrison *et al.* (1971), Parsons & Moldenke (1975), Parsons (1976), Naveh & Whittaker (1979), Campbell (1980)
5. Forest woodland and scrub elements are *Eucalyptus* spp
6. South African nutrient-poor scrub elements are chiefly Proteaceae, occasionally with *Heeria*, *Maytenus* and *Diospiros* in moist areas
7. Afromontane forests (*Podocarpus*, *Cunonia*, *Rapanea* etc)
8. Thicket (scrub forest) is a dense shrubland, 5-10 m tall, of tropical affinity
9. Renosterveld is a putative disclimax, largely dominated by *Elytropappus rhinocerotis*, an evergreen cupressoid shrub, and presumably derived from an essentially tropical shrub and grass complex marginal to succulent dwarf shrubland in semi-desert. Suggested analogue in California is coastal sage (Axelrod 1975)

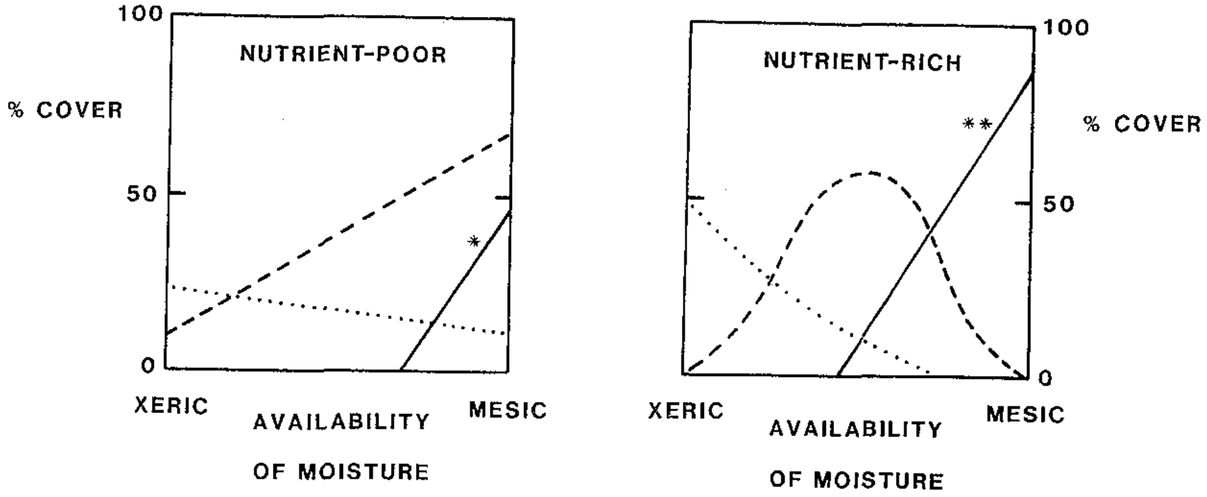


Fig. 5.1 Hypothetical changes in percentage cover of woody growth forms in relation to gradients in nutrients and in available moisture (mean annual precipitation between about 200 mm y^{-1} (xeric) and 1000 mm y^{-1} (mesic) or moisture index between 0,3 and 0,6)

——— = trees > 5,0 m
\- - - = tall shrubs 0,5-5,0 m
...... = low shrubs < 0,5 m

* Except in South Africa, where trees are rare (Campbell *et al.* 1979)
** In South Africa, renosterveld shrublands occur where trees would be found on other continents

5.1.2.1 THE LACK OF TREES IN FYNBOS

There are a number of alternative hypotheses to explain the absence in fynbos of trees taller than 5 m. Moll *et al.* (1980) suggest that the increased frequency of fires in the Pleistocene and Holocene has resulted in the elimination of the tree element. Milewski (1981) suggests that trees are abundant in Australia due to the deeply-penetrating cyclonic rain which is a feature of south-western Australia but which does not occur in the mediterranean regions of South Africa. Yet introduced trees are able to invade areas which normally support low fynbos only. Specht & Moll (in press) have suggested that a lack of mycorrhizas limits the occurrence of trees on dry sites (see also Lamont 1982) and that low pH causes stunting on wet sites. The relatively small size of trees adapted to nutrient-poor soils in the non-mediterranean climate area of South Africa may also mean that there has been a lack of a genetically appropriate source of invaders.

5.1.2.2 EVERGREENNESS

Evergreen plants, while not limited to nutrient-poor soils, are often associated with them. It has been suggested that deciduousness is disadvantageous on nutrient-poor sites since the costs of rebuilding tissue may place too great a burden on the plant's nutritional resources (Chapter 3, and Monk 1966). In mediterranean ecosystems on nutrient-poor soils, both woody and herbaceous components, such as non-seasonal graminoids and certain hemicryptophytes, are overwhelmingly green, while deciduous shrubs are lacking. Nutrient uptake may be equally costly for annuals, since

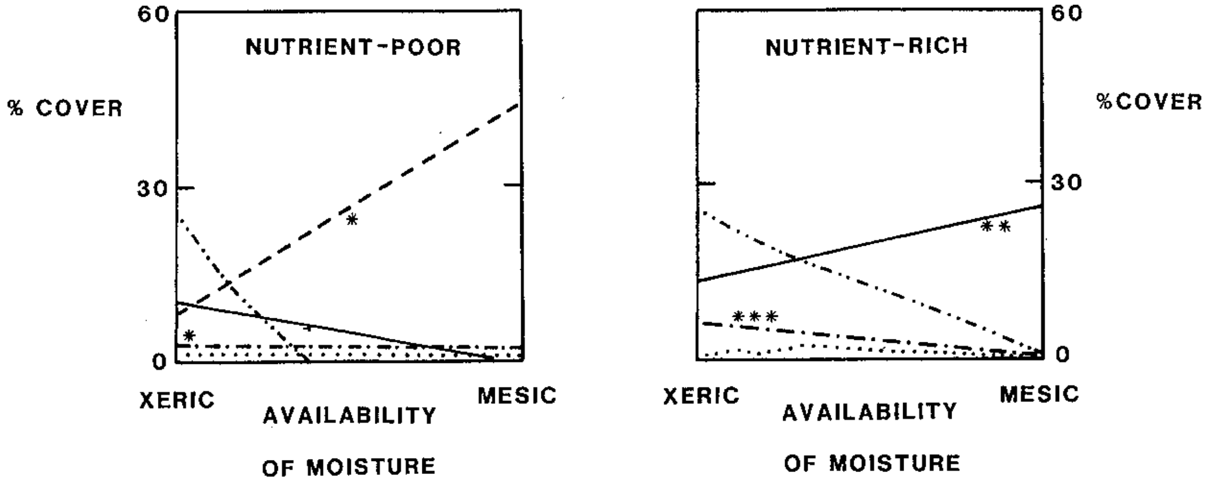


Fig. 5.2 Hypothetical changes in percentage cover of herbaceous growth forms in relation to gradients in nutrients and in available moisture (mean annual precipitation between about 200 mm y^{-1} (xeric) and 1000 mm y^{-1} (mesic) or moisture index between 0,3 and 0,6)

seasonal graminoids (eg grasses)	————————
non-seasonal graminoids (eg restios)	- - - - - - -
non-graminoid geophyte	— . — . — .
non-graminoid perennial herbs	....
non-graminoid annual herbs	-..-..-..-..-.

* In South Africa the incidence of non-seasonal graminoids and geophytes is higher than this (Kruger 1977)

** Patterns of grassiness are complex: in mature evergreen communities there is often very low cover of grasses

*** In South Africa geophyte cover is higher than this

these are virtually absent from South African fynbos and Australian heath. Since evergreenness is sometimes an adaption to stresses other than low fertility, it is not always possible to determine unequivocally its adaptive significance in mediterranean heathlands.

Drought-deciduous plants are relatively rare in the nutrient-rich mediterranean regions of Australia and South Africa, although Miller (1980) has suggested that summer droughts on these continents may be severe. However there are always some summer-deciduous plants in the drier, warmer areas of these mediterranean regions, where the warmer winters permit an early growing season advantageous to summer-deciduous plants.

Alternatively, even the richest sites on these continents are in fact poorer in nutrients than are those of California, Chile and the Mediterranean, so that their vegetations are unlikely to show "nutrient-rich" features; or perhaps a deciduous flora from which plants might be recruited is relatively abundant in California, Chile and the Mediterranean but absent in Australia and South Africa.

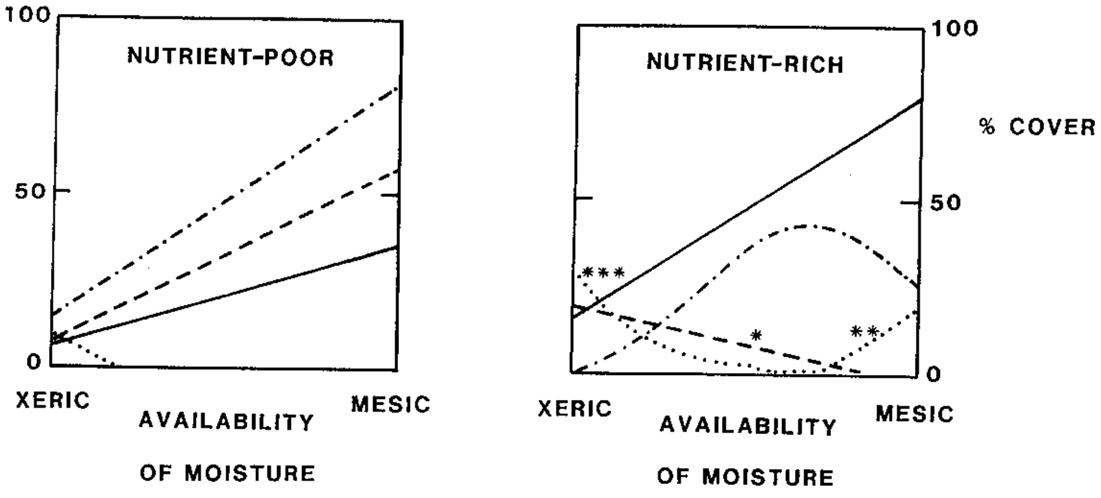


Fig. 5.3 Hypothetical changes in the percentage cover of narrow- or broad-leaved trees and shrubs, and of these with evergreen, deciduous or succulent leaves, in relation to gradients in nutrients and in available moisture (mean annual precipitation between about 200 mm y^{-1} (xeric) and 1000 mm y^{-1} (mesic) or moisture index between 0,3 and 0,6)

———————— = broad leaves
– – – – – – – = narrow leaves
— . — . — . = evergreen
.... = deciduous or succulent

* In South Africa and California there is a higher cover of narrow-leaved plants, chiefly Elytropappus rhinocerotis and Adenostoma fasciculatum towards the middle of the gradients

** Winter-deciduous elements are lacking in South Africa and Australia (Campbell 1980)

*** In Australia deciduous elements such as Atriplex and Maireana are poorly represented and deciduous elements in South Africa have lower cover than in Chile, California or the Mediterranean. In the Mediterranean, deciduous trees such as Quercus ithaturensis are common towards the xeric end of the gradient

5.1.2.3 HIGH INCIDENCE OF SMALL LEAVES (Fig. 5.3)

A high incidence of small leaves (leptophylly) has been correlate with low soil nutrients (Loveless 1962). On nutrient-poor soils in South African and Australian heaths, plants with small leaves tend to dominate over the entire moisture spectrum.

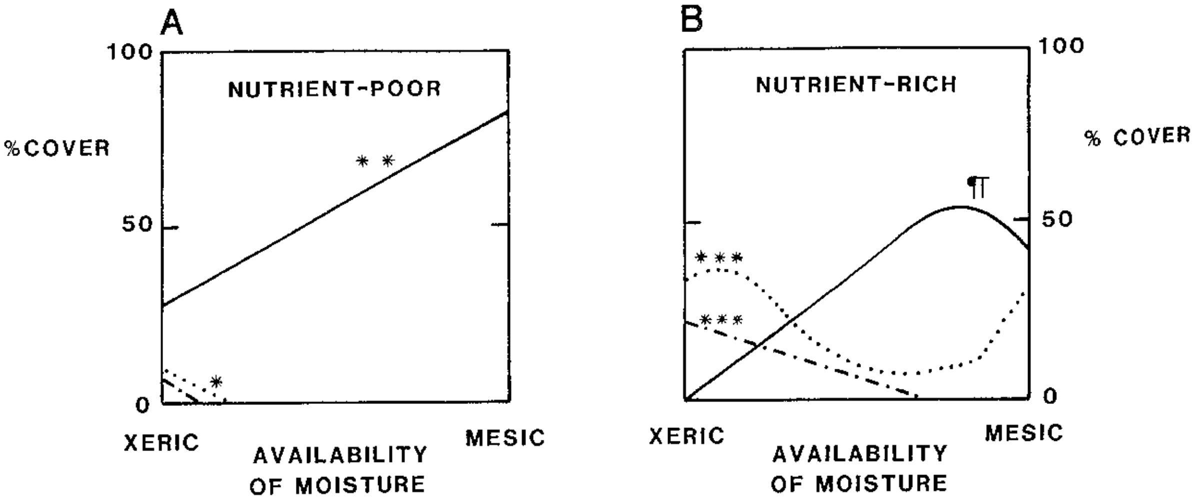


Fig. 5.4 Hypothetical changes in the percentage of shrubs and trees with sclerophyllous, mesophyllous or succulent leaves in relation to gradients in nutrients and in available moisture (mean annual precipitation between about 200 mm y^{-1} (xeric) and 1000 mm y^{-1} (mesic) or moisture index between 0,3 and 0,6)

———— = sclerophylls
.... = mesophylls
— . — . — = succulents

* Succulents and mesophylls have higher cover at the xeric end of the gradient in South Africa (Carlquist 1974)

** In Australia sclerophylly is highest at the xeric end, and is replaced by more flexible or coriaceous leaves on more mesic sites

*** Succulents and mesophylls are poorly represented in Australia

¶ Winter-deciduous mesophylls are lacking in Australia and South Africa at the mesic end of the gradient

5.1.2.4 SUCCULENCE

There are fewer succulents in south-western Australia than in South Africa, the Australian chenopod shrublands of drier reaches being an exception to the general pattern. Dismissing halophytes, which at best show osmotically-controlled semi-succulence, Carlquist (1974) noted that the only form of succulence in Australia was found in the underground storage organs of geophytes. Succulent parts, both below- and above-ground, form a greater proportion of the biomass in South Africa than they do in Australia, whether the soil is rich or poor in nutrients. But in order to explain the relative incidence of succulence we need to know its adaptive role in water storage, in providing a photosynthetic surface when leaves are absent and in vegetative reproduction; the extent of its phenotypic plasticity; those factors such as low levels of moisture, regularity of rainfall or the extent of pressure from herbivores, which favour its development; and the extent to which the special functions of succulence can be replaced by features such as non-succulent aphylly or deep rooting.

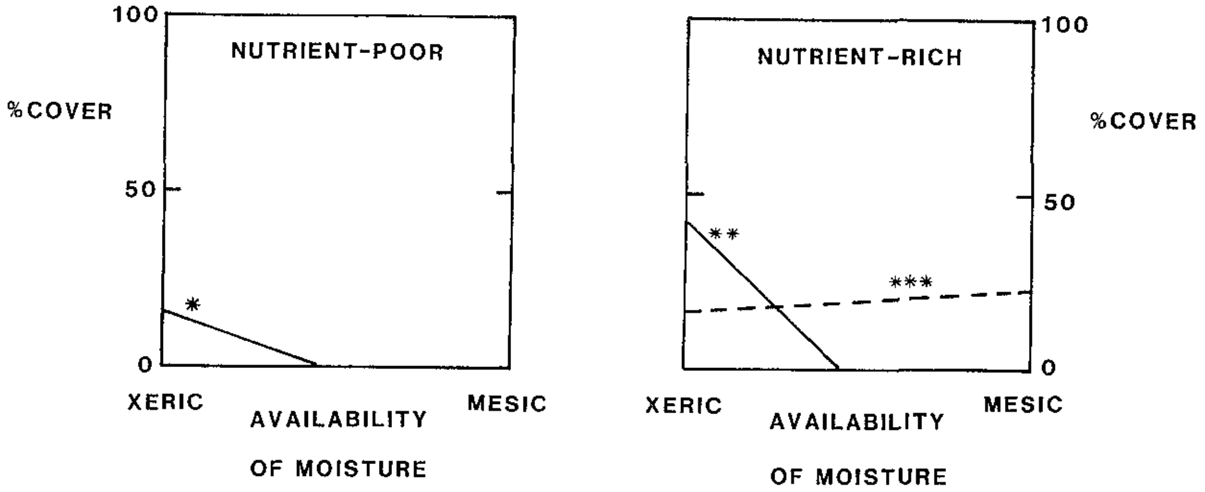


Fig. 5.5 Hypothetical changes in the percentage cover of vines and of spinescent plants in relation to gradients in nutrients and in available moisture (mean annual precipitation between about 200 mm y^{-1} (xeric) and 1000 mm y^{-1} (mesic) or moisture index between 0,3 and 0,6)

– – – – – = vines
———— = spines

* In Australia the incidence of spinescence is higher than this (Carlquist 1974)
** Spines are virtually absent in Australia
*** Vines are less common than this on mesic sites in California

Table 5.2 Vegetation types considered in Figs. 5.1-5.5

	Nutrient-poor	Nutrient-rich
California	-	Succulent coastal sage Coastal sage Chaparral Oak Woodland
Chile	-	Matorral (including coastal form)
Mediterranean Basin	-	Garrigue, Macchia Oak Woodland
Cape	Fynbos	Strandveld Renosterveld
Australia	Heath (Kwongan)	Mallee

5.1.2.5 SPINESCENCE

Spiny plants are generally present in the drier reaches of nutrient-rich mediterranean shrublands, although in Chile spinescence occurs on wetter sites as well. Spines are uncommon in the Australian mallee, except in the driest areas. The nutrient-poor South African heathlands are markedly less spiny than are Australian heaths, in which there is a high frequency of leaf-spines. In general, however, spinescence is less common on nutrient-poor soils than on nutrient-rich ones, where the foliage has a greater nutritional value and consequently suffers a higher level of herbivory.

5.1.3 ADDITIONAL FEATURES

5.1.3.1 PATTERNS OF INTERMINGLING OF SPECIES

As noted by Westman (in press), the degree of intermingling of different species is substantially greater in heathlands than in shrublands. This scale of pattern diversity may arise from such interrelated factors as the smaller size of plants and their slower growth rates (both of which are related in part to the low nutrient-status of the soils) and their stronger competitive abilities. Consequences of this pattern diversity include a greater evenness in the distribution of species, less canopy closure and greater species richness (Lamont *et al*. 1977). Westman (in press) has suggested that this pattern of intermingling could decrease herbivore pressure on a population of a species, thus reducing the need for spinescence, secondary substances and other defences against herbivores. Measures of pattern diversity and scales of patterning in heathlands and shrublands are scant, however, and more data are needed before this hypothesis can be adequately tested.

5.1.3.2 ALLELOPATHY

There may be a marked reduction in the growth of plants beneath certain shrubs and trees in Australia, California and Europe; conflicting ideas suggest that this is due to chemical inhibition by the dominant species (allelopathy) that it is simply due to differential grazing by native animals, or that it is due to reduced availability of moisture, light or nutrients (del Moraes *et al*. 1978; Newman 1978; Lamont 1981b; Westman, in press). Recent greenhouse experiments (Stowe & Osborne 1980) have shown that phenolics (likely candidates for allelopathic properties) are more likely to have a suppressive effect on target plants when the availability of nutrients is low.

5.1.3.3 EFFECT OF BIOGEOGRAPHIC HISTORY

Knowledge of the biogeographic history of the elements of mediterranean vegetation is vital to an understanding of the functioning, and ultimately the structure, of these ecosystems (Lamont 1982). For example the earlier origin of heath vegetation, compared with that of the eucalypt overstorey which sometimes accompanies it in Australia, has been used to explain the distinctive responsiveness of the heath to nutrients (Westman 1978). Sclerophylly as an adaption to lack of moisture, to

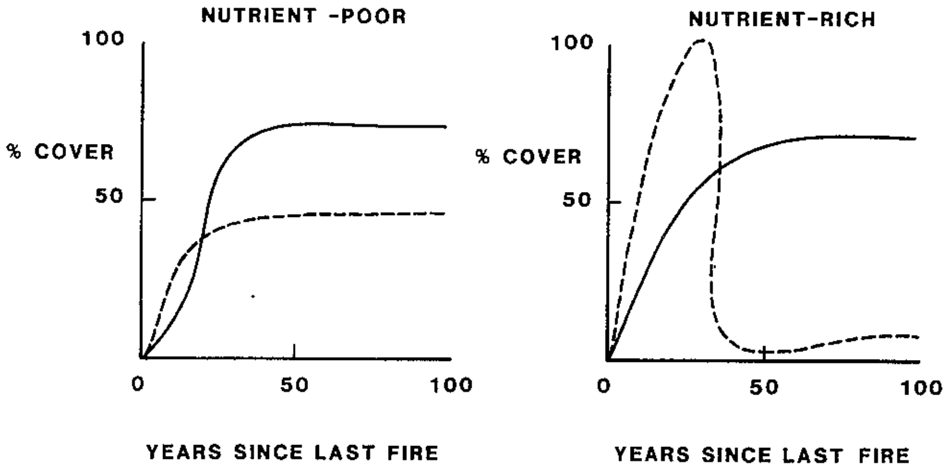


Fig. 5.6 Hypothetical changes in the percentage cover of herbs and shrubs following fire on soils poor and rich in nutrients (mean annual precipitation between about 200 mm y^{-1} (xeric) and 1000 mm y^{-1} (mesic) or moisture index between 0,3 and 0,6)

——— = shrubs
– – – = herbs

* In Israel, herbs will persist into the pyric climax community on P-rich soils where precipitation is less than 500 mm y^{-1}

nutrient stress or to both (Small 1973) has been discussed in Chapter 4. It is necessary to explore the extent to which differences in phenological behaviour between synusiae can be attributed to differences in rooting depth, shading and other micro-environmental features rather than, or in addition to, genetically encoded behaviour triggered by light or temperature. The same questions apply, for example, to the summer growth observed in certain fynbos species (Kruger 1981).

5.2 DYNAMICS

In this section we consider patterns of primary production and the secondary successional changes due to various forms of acute or chronic disturbance.

5.2.1 PATTERNS OF PRIMARY PRODUCTIVITY

The effect of the nutrient status of the soil is less evident than the effect of solar radiation and available water in limiting the primary productivity of mediterranean plants (Specht 1969). Thus Specht found that the mean annual increments in productivity in the first five years following fire in South Australian heath (640-1600 kg ha^{-1} yr^{-1}) was only slightly less than that for Californian chaparral (1000-2000 kg ha^{-1} yr^{-1}) and French garrigue (1500 kg ha^{-1} yr^{-1}). Kruger (1977b) reports values for South African fynbos of 1500-2500 kg ha^{-1} yr^{-1}, which are the highest values reported for any mediterranean region (Mooney, in press).

Nevertheless, productivity has been observed to decline with age after fire, a feature thought to be due to progressive accumulation of available soil nutrients by the standing vegetation (Hanes 1971). A second possible cause of this "senescence" is the rising ratio of sap wood to leaf in maturing shrubs, creating a respiratory drain that might eventually overwhelm photosynthetic capacity. Adequate data are not yet available to make useful comparisons between ecosystems within a region, for example between coastal sage scrub and chaparral in California. Nevertheless the standing biomass of chaparral is two to three times that of the sage scrub, suggesting higher net production for chaparral. If so, this occurs despite lower net photosynthetic rates for component shrub dominants (Mooney, in press). Drought-deciduous dominants from coastal sage scrub have been shown to have leaf photosynthetic rates at least twice those of chaparral species, attributed by Mooney (in press) both to the higher leaf conductances and to the higher levels of leaf N in the sage scrub. Nevertheless, the mesophytic nature of the leaves of these plants results in some of them being lost during summer drought, perhaps resulting in a lower net carbon gain over the year in these than in evergreen chaparral plants.

5.2.2 EFFECTS OF FIRE

Figure 5.6 shows typical successional changes in vegetation structure after fire in mediterranean ecosystems both on nutrient-poor and on nutrient-rich sites, given rainfall of 500 mm yr^{-1}. The main differences in the recovery of vegetation on these two types of substrate are firstly that graminoids, restioids and herbs which appear immediately after fire remain in the pyric climax community on nutrient-poor sites, whereas on nutrient-rich sites they disappear after a few years, and secondly that the herbs tend to be resprouters on nutrient-poor sites but reseeders on nutrient-rich sites. In all cases the vegetation contains both resprouting and reseeding elements, although the balance between the two differs between vegetation types. Because of resprouting, succession in the post-fire vegetation is strongly influenced by the composition of pre-fire vegetation. In some cases reception of seed from adjacent areas ("seed rains") influences post-fire succession as well, but seed shed from resprouted plants on the sites can be an even more important source of seedlings (Westman *et al.* 1981). The extent to which seeds retain viability in the soil between fires, which may be up to a hundred years apart, is unknown. Bond (1981) has attributed the low regeneration after fire of *Protea punctata* in senescent stands to degradation of seed in the soil, which also suggests that seed dispersal in fynbos is poor.

5.2.3 EFFECTS OF GRAZING BY DOMESTICATED HERBIVORES

As intensity of grazing increases, so annual herbs usually increase in abundance and in number of species (Naveh & Whittaker 1980), and shrub cover decreases. This is not true of South African renosterveld, where an increase in density of the unpalatable shrub *Elytropappus rhinocerotis* often occurs as a response to overgrazing of palatable species. In general, we could expect a more rapid decline in vegetative cover under intense grazing pressure on nutrient-poor sites than on nutrient-rich sites. In practice, however, the nutrient-poor sites are unlikely to receive a continuously high pressure of grazing because the nutrient poverty of the vegetation does not provide an adequate diet for herbivores. Historically the highest degree of herbivory by domestic animals has occurred in the Mediterranean Basin (see Chapter 1), which therefore shows the influence of this selective pressure. Chile experiences a lower level of such herbivory, followed by Australia (nutrient-rich), South Africa (nutrient-rich), California, Australia (nutrient-poor) and South Africa (nutrient-poor) in descending order of intensity.

5.2.4 MODELLING OF SUCCESSION

A number of models of succession, especially in forests, have been constructed in the past decade. Among models of mediterranean ecosystems, that of Kessel & Cattelino (1978) attempts to predict the recovery of Californian chaparral from fire on the basis of field sampling of stands of different ages along major environmental gradients. Noble & Slatyer (1977) attempted a population approach by examining life-history attributes, including requirements for germination, mode of reproduction and longevity of component dominants in a Callitris woodland in Australia. Currently the "population-type" of model is being combined with those which predict the fire intensity of stands of different age and fuel load, again to predict patterns of recovery of Californian coastal sage scrub after fire (G. Malason pers. obs., W. Westman, pers. obs.). Work of this kind is presently impeded by ignorance of the requirements for germination, the extent of seed dispersal and dormancy, and the fire tolerance of the root crowns of dominant mediterranean species.

5.3 EXAMPLES OF CHRONIC DISTURBANCES

Mediterranean climates are particularly favourable for human settlement and most of these regions have consequently been subject to a high degree of human disturbance, so that the structure and dynamics of their communities have been chronically disturbed. The invasion of natural communities by introduced exotics, and the effects of grazing, fire and erosion on South African renosterveld, are given as examples of such changes.

5.3.1 INVASION OF NATURAL PLANT COMMUNITIES BY EXOTIC WEEDS

The problem of invasion by exotic weeds in mediterranean ecosystems is most marked in the nutrient-poor environments of South Africa and Australia. In the South African mediterranean regions, where trees are lacking, invasive weeds are mainly large woody Australian trees and shrubs capable of utilizing environmental resources more effectively than can the indigenous flora. In Australia, on the other hand, only a small proportion of the flora consists of geophytes and herbs, and most invading weeds fall into this category; many are South African. Further, while woody weeds invade undisturbed fynbos, weeds colonize Australian heath only after disturbance and enhancement of the nutrient status of the soil through fire or agricultural practices. The lack of natural controls such as parasites or diseases in a new environment will increase the competitive advantage of invaders (Milton 1979). In the nutrient-rich environments of Chile, California and Europe the invasion of exotic weeds is far less of a problem. Plant invaders in these areas are mainly herbaceous and were introduced from similar nutrient-rich environments.

In California and Chile woody weeds have not, as yet, become important, possibly due to the superior competitive ability of native species of the same growth form. The Mediterranean Basin has a long history of human influence which makes it almost impossible to determine which plant species are natural and which are imported; for this reason the extent of invasion cannot be quantified.

5.3.2 DEVELOPMENT AND MAINTENANCE OF RENOSTERVELD IN SOUTH AFRICA

Renosterveld occurs on nutrient-rich substrates between mountain fynbos on the one side and karroid vegetation on the other (Boucher & Moll, 1981). It is typically dominated by relatively few species over most of its range. The structural dominants are divaricate shrubs and small trees with sub-sclerophyllous leaves, while geophytes are common.

It is unclear whether retrogressive changes due to erosion would allow persistence of the dominant renosterbos, Elytropappus rhinocerotis, or whether it would eventually be replaced by more arid-adapted karroid species. The occurrence of patches of broad-leaved shrubs of tropical origin (Olea, Rhus, Euclea) within renosterveld has led to speculation that prehistorically these sites were covered by shrubland in which the cover of these tropical species was much more extensive. Clearing, grazing or burning of renosterveld at present results in the return of renosterbos rather than in an increase in broad-leaved tall shrubs (Levyns 1935). It has been suggested that reproduction of such shrubs or low trees is limited by the lack of a suitable microclimate, or by the lack of perching sites for dispersal agents in the areas between the patches of tall shrubs. Of course we should not overlook the possibility that certain pioneer species might arrest succession for fifty or a hundred years or more when once they have reached dominance.

5.4 FUTURE RESEARCH

Further research is needed into most aspects of mediterranean communities.

As far as community structure is concerned, it is still uncertain which of the hypotheses explaining the lack of trees in fynbos is correct. Nor do we know the relative value of succulence for water storage, for vegetative reproduction, for nutrient storage or for protection against excessive heat or light. In order to understand patterns of deciduousness, it is necessary to distinguish between seasonal dimorphism, wilting and true deciduousness of leaves, particularly on drier sites. Carefully-controlled field and laboratory experiments are needed to determine the conditions controlling the effectiveness of allelopathic substances. We do not yet know if allelopathy is more common in individual plants or in species when nutrients are in short supply, or if there is a link between sclerophylly, secondary compounds and allelopathy. Are secondary compounds produced by plants for allelopathy rather than for resistance to drought or against herbivores? The influence of the nutrient-status of soils on the potential effectiveness of allelopathy needs to be thoroughly explored.

Studies on community dynamics should address academic questions concerning primary productivity at the level of whole communities, or even of ecosystems, in relation to availability of water and nutrients, as well as more practical questions.

As yet there are no studies on the extent and manner of colonization of mediterranean regions by exotic plants. Such studies could provide clues to the control of exotics, as well as to the identification of potentially dangerous invaders.

Critical experiments could test the hypotheses concerning the origin and status of renosterveld. Such experiments might involve fencing an area of renosterveld from domesticated grazers, fertilizing to reverse the effect of nutrient losses from erosion, providing perching sites for birds, and observing successional changes that result. The apparent association of the patches of tall shrubs with present or ancient termitaria, which may locally enrich the soil, might also be examined.

5.5 CONCLUSIONS

While Figures 5.1-5.5 indicate similar trends in community structure in the different mediterranean regions, the exceptions due to biogeographic history, to differences in land use, in topographic diversity and in other features, impress upon us the distinctive features of the vegetation patterns of each continent. While we found the distinction between shrublands on nutrient-rich soils and heathlands on nutrient-poor ones to be useful, we are keenly aware that some shrublands are to be found on soils of striking infertility, while some species of heath extend on to nutrient-rich soils. Indeed, while the contrasts in vegetation structure on the two broad classes of soils are often impressive, field experiments showing the primary role of nutrients as determinants of these structural differences are scanty (see, for example, Specht *et al*. 1977), especially for South Africa. One of the difficulties in explaining the occurrence of structural features observed in the field is that a feature such as sclerophylly or root crowns, which appears to serve as an adaption to nutrient stress on one site, may be seen as an adaptation to moisture stress on another, or indeed may be serving both functions simultaneously. In such situations the formulation of experiments to unravel the functional significance of morphological features becomes a difficult and sometimes an impossible task.

Gaps in our knowledge are particularly conspicuous in such areas as the role of biogeographic history in modern floristic patterns, the effect of nutrient status on the primary productivity of the communities on each continent, the overall resilience of mediterranean ecosystems to disturbances such as grazing and air pollution, and the mechanisms involved in such resilience.

Nevertheless, our present knowledge already provides some insights of practical value. Nutrient-poor sites in South Africa are particularly vulnerable to invasion by exotic woody shrubs or trees while in Australia, invasion by exotic herbs and geophytes may occur after disturbance or nutrient-enrichment. Mesophyllous, summer-deciduous shrubs are more likely to be vulnerable to air pollution, especially due to sulphur dioxide, than are evergreens. Clearing of broad-leaved shrublands on nutrient-rich sites, especially when followed by repeated fire or grazing, may lead to replacement of the vegetation by more xeric or weedy pioneer species. With increasing pressures for human use of mediterranean regions, the need for an understanding of the environmental factor determining change in vegetation structure has become a matter of concern both for resource managers and for the public they serve.

6. ANIMAL COMMUNITIES: DIVERSITY, DENSITY AND DYNAMICS

M. L. Cody (convener), G. J. Breytenbach, B. Fox, A. E. Newsome,
R. D. Quinn, W. R. Siegfried

In this chapter we consider the terrestrial faunas of the mediterranean regions of Australia, California, Chile, the Mediterranean Basin and South Africa. Within the limits of the available data, we examine the extent to which the nutrient status of the soil influences the communities of consumers in each region. Although we have confined our discussion largely to the vertebrates, even here we have been hampered by lack of information on amphibians and to a lesser extent on reptiles.

6.1 MAMMALS

6.1.1 AUSTRALIA

6.1.1.1 ENDEMISM AND SPECIES RICHNESS

With the exception of the endemic honey-possum (Tarsipes rostratus, = T. spenceri) with its brush-tipped tongue, mammals occurring in the mediterranean regions of Australia do not show any particular morphological adaptions, and indeed few species are confined to such regions. It has thus been suggested (Newsome & Catling 1979, in press) that there is no specifically mediterranean mammalian fauna in Australia, most species transcending boundaries of climate, vegetation and nutrient status.

Some of the small mammals confined to mediterranean heathlands include the dasyurids Antechinus apicalis (the dibbler) and Sminthopsis granulipes (the white-tailed dunnart), as well as the rodents Pseudomys albocinereus (the ash-grey mouse) and P. apodemoides (the silky mouse). The dibbler mates in autumn, an interesting reproductive adaptation not found in other, non-mediterranean, species of Antechinus, which mate in late winter or early spring (Woolley 1971). Other small mammals such as Pseudomys shortridgei (the heath mouse), P. gracilicaudatus (the eastern chestnut mouse), P. novaehollandiae (the New Holland mouse), P. fumeus (the smoky mouse), Sminthopsis crassicaudata (the fat-tailed dunnart), S. murina (the common dunnart), Phascogale calura (the red-tailed phascogale), Isoodon obesulus (the southern brown bandicoot) and Perameles bougainville (the western barred bandicoot) are important components not only of mediterranean regions but of nutrient-poor heathlands in general. This association in the case of some species of Pseudomys, Sminthopsis and Isoodon seems to be related to their ability to occupy early and mid-seral stages after fire (Cockburn 1978; Stoddart & Braithwaite 1979; Fox 1980, 1982, in press; Fox & McKay 1981), thus reflecting the high frequency of fire in the mediterranean regions. Habitat diversity plays a much more important role in determining species richness than does nutrient status (Fox, in press): no more than three or four species of small mammal normally occur in a single uniform area of south-western Australian heathland, irrespective of the nutrient status of the soil (Baynes 1979).

In one study, on comparable soils, a structurally-complex dry heath habitat contained up to six species whereas a structurally-simple wet heath habitat contained only three. The small mammals of this wet heath, which had a high restioid component, were herbivorous or insectivorous, whereas those on dry heath, which had a greater component of shrubs, were insectivorous, granivorous or omnivorous (Fox 1980).

Most of the larger mammals found in Australian heathlands are temporary visitors from adjacent forests and woodlands, and range in size from Isoodon obesulus (the bandicoot) (0,75 kg) and Potorous tridactylus (the rat-kangaroo) (1-1,5 kg), through Wallabia bicolor, Macropus rufogriseus, M. irma and Setonix brachyurus (wallabies) (4-25 kg) to Macropus giganteus and M. fuliginosus (the eastern and western grey kangaroos) (30-75 kg).

In their biogeographic interpretation of all vertebrates associated with Australian heathlands, Kikkawa et al. (1979) have concluded that heathlands, which are now restricted to coastal areas, were widespread in the early Tertiary. In the intervening period the herbivorous macropodids radiated, so that there are now about 50 species. This radiation may have resulted at least partly from an increase in the areas covered by grasslands as the heathlands and rainforests contracted and became discontinuous. Of course this hypothesis is not testable. But it is supported by the fact that there are no large herbivorous mammals endemic to any mediterranean region, with the possible exception of Damaliscus dorcas dorcas (the bontebok) in the south-western Cape. This suggests that conditions in mediterranean regions are not conducive to radiation in large herbivores. Perhaps this in turn is due to the unsuitability of the small leaves and secondary compounds of heathland shrubs and the infrequent occurrence of natural fires. Grasses and herbs predominate for only a year or two after fire (Specht et al. 1958), a fact well known to cattlemen, who frequently burn heathlands to promote the growth of pasture.

The lack of suitable shelter would discourage the presence of medium-sized mammals; Trichosurus vulpecula (the possum) nests in hollow boughs and tree trunks, while Pseudocheirus peregrinus (the ring-tailed phalanger) makes external twig-nests (dreys) in trees and in tall thicket-like shrubs. Thus only small mammals might be expected to find suitable habitats in mediterranean vegetation.

6.1.1.2 DENSITY

With numbers ranging from two to ten per hectare, the density of small mammals is extremely low in the nutrient-poor regions in comparison with those of sclerophyllous forests on richer soils, but comparable with those of sclerophyllous forests on similarly deficient substrata (Fox & McKay 1981).

The occasional presence of large grazing marsupials in heathlands is ecotonal. Hypothetical curves (Figure 6.1) show that grazing is most apparent during the time that grasses and herbs sprout, soon after fire. The three marsupials making most use of heathlands are, the herbivorous Macropus irma and Setonix brachyurus in mediterranean south-western Australia and the omnivorous Isoodon obesulus in coastal south-eastern Australia. Even so, the frequency of grazing in these habitats is low, probably due to the meagre unpalatable browse of heathy shrubs relative to that of adjacent forests and woodlands.

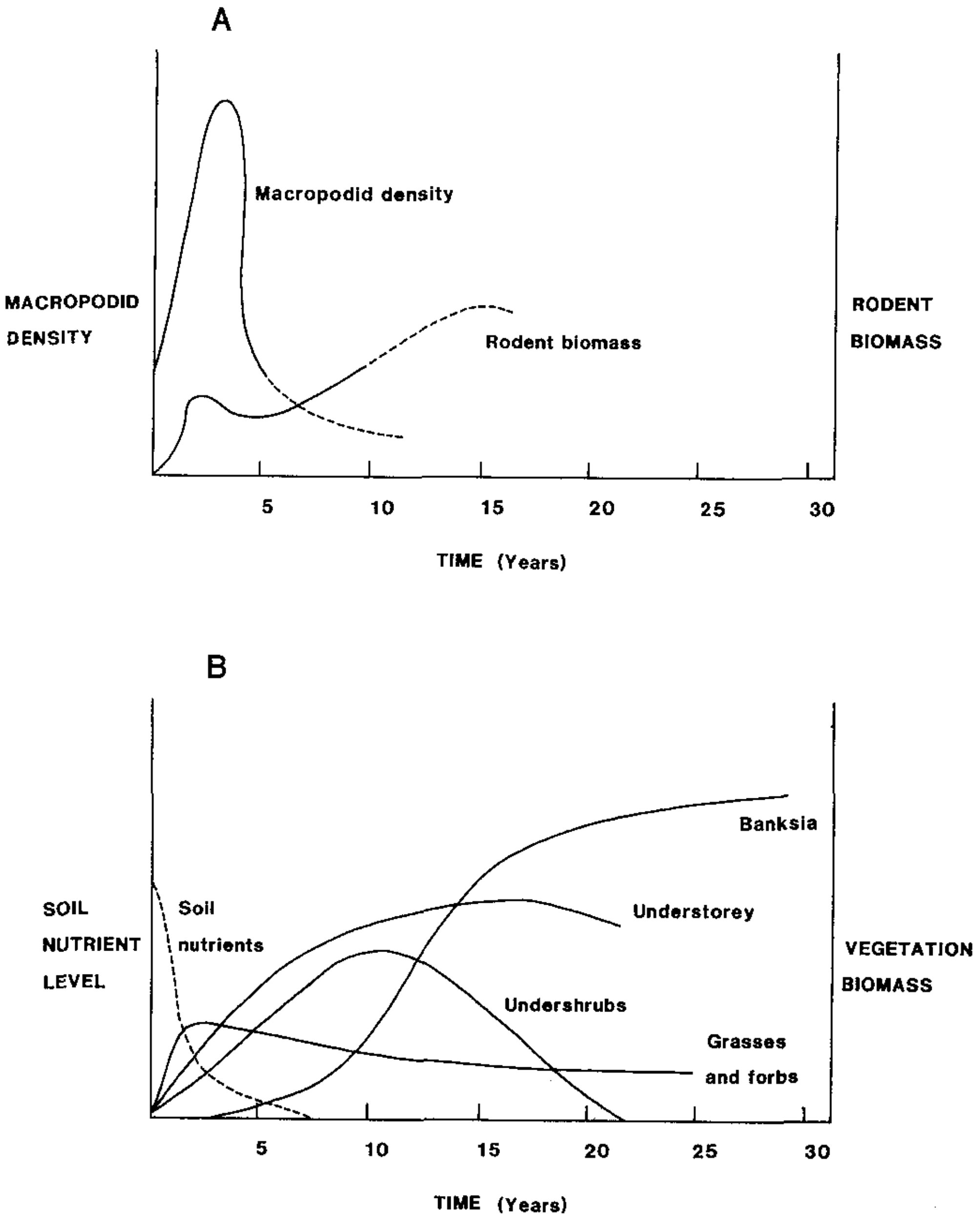


Fig. 6.1 Hypothetical illustration of successional relationships in Australia as a function of time since fire - A) Macropod density and rodent biomass (different scales) in the absence of predators, B) Vegetation biomass in terms of grasses and forbs, undershrubs, understorey and Banksia (same scale) together with soil nutrient levels (different scale). (Vegetation biomass from Specht et al. 1958)

6.1.1.3 DYNAMICS

All species of small mammals inhabiting Australian heathlands exhibit seasonal fluctuations in population density. Fire however is by far the most important factor in the dynamics both of populations and of communities in heathlands. Wild fires completely alter the vegetation structure by removing much of the plant cover. Mammals also disappear, returning as the vegetation recovers (Fox 1980, 1982; Catling et al. in press).

Species of Pseudomys, Sminthopsis and Isoodon, which occur early in succession, may be completely replaced as the structure of the vegetation changes during the pyric succession. On the other hand, the early successional species may persist in low numbers rather than being replaced entirely, so that the succession is one of changes in abundance or dominance. No data exist for changes in the mammalian communities in senescing tall heath vegetation, but from limited information gained from the understorey of mature heathland in open eucalypt forests, it appears that species richness increases as cover is reduced in the lowest strata (Fox & McKay 1981). In addition to changes in species richness in post-fire succession, marked effects over much longer periods, linked with the fire regime, can have important consequences for the maintenance of species diversity (Fox, in press; Newsome & Catling, in press).

Two species of marsupial endemic to mediterranean regions have been studied in some detail. Setonix brachyurus, (the quokka), is common on Rottnest Island off the south-western coast of Australia, and Macropus eugenii, (the tammar wallaby), on Flinders Island off South Australia.

There is comprehensive information on Setonix, data on population dynamics, reproduction, mortality, age-structure, physiology and diet having been collected over a number of years. Quokkas are remarkably sedentary on Rottnest Island (Tyndale-Biscoe 1973); Holsworth (1967) concluded that home-ranges averaged about 2,4 ha with groups of 10-25 adults occupying group territories. There is no free water in the study-area, yet no marked wallaby was ever re-caught at the other end of the island where freshwater seepages are available and where the local wallabies drink in great numbers in summer (Dunnett 1962). Most water must come from the food (Storr 1964) since the quokka cannot subsist on sea-water (Bentley 1965).

Populations decline in summer when food is depleted (Storr 1964) and the animals become anaemic (11 g per cent haemoglobin compared to 16g per cent in well-fed animals) (Barker 1961). The soils of Rottnest Island are sufficiently low in cobalt for sheep to develop symptoms of deficiency, since cobalt is necessary for the microbial synthesis of vitamin B_{12} in the rumen. However, despite declines in the levels of cobalt in the liver, the pseudo-ruminant quokkas do not develop symptoms of deficiency (Barker 1961).

A post-partum oestrus and prolonged delay implantation occur in both the quokka and the tammar (Sharman 1955; Sadleir & Shield 1960). Both become reproductive in mid-summer, a time when pastures are at their worst. The tammar's response in the seasonally harsh environment is photoperiodically induced and timed on the summer solstice (Sadleir & Tyndale-Biscoe 1977) since breeding in mid-summer allows young to leave the pouch when pastures are at their best after the winter rains. This pattern contrasts with that seen in the desert kangaroos Macropus robustus and M. rufus and in the tropical M. agilis, which are opportunistic even though they have the same reproductive pattern (Ealey 1963; Newsome 1965, in press; Sadleir 1965).

Predators are lacking on the islands, since *Canis familiaris dingo* (the dingo) has not yet reached them. In the few mediterranean areas where they do still survive, dingoes hunt across heathlands as part of their general feeding activities (Newsome & Catling 1979). Studies in south-eastern Australia indicated that small mammals were reduced to rarity or even to extinction over large areas after a severe summer fire (Newsome *et al.* 1975; Newsome & Catling, in press) and as a result, *Wallabia bicolor*, *Macropus rufogriseus* and *M. giganteus* were severely preyed upon (A. E. Newsome, pers. obs.). Feral European foxes, *Vulpes vulpes*, are now found in all mainland mediterranean regions. They are known to have contributed to the decimation of a small colony of *Bettongia penicillata* (the rare rat-kangroo), in fire-opened *Casuarina* thickets in south-western Australia (Christensen 1977). Feral domestic cats, *Felis catus*, may have a significant effect on populations of small mamamls, and more particularly of birds (Jones 1977; Merton 1977, Jones & Coman 1981).

6.1.2 SOUTH AFRICA

6.1.2.1 ENDEMISM AND SPECIES RICHNESS

Endemism of mammals is not considered to be a significant feature of the South African mediterranean region (Bigalke 1979). Only one rodent, *Aconmys subspinosus*, can be considered to be limited to fynbos while all other species are more widespread and are found in non-fynbos mediterraean regions as well. They are *Chrysochloris asiatica*, (the golden mole) *Myosorex longicaudatus* (the Knysna forest shrew), *Myotis lesueure* and *Eptesicus siullus* (bats), *Praomys vereuxi* and *Tatera afra* (rodents), *Hippotragus leucophaeus* (the bloubok, now extinct), and *Damaliscus dorcas dorcas* (bontebok). However, of the 106 species of mammal which have been recorded from the South African mediterranean region during historical times, only 60 per cent have been recorded from nutrient-poor fynbos areas.

The low levels of nutrients in the fynbos soils are reflected in the plants (Louw 1969), so that one is not surprised to find that of the antelope, only the small, selectively-feeding *Oreotragus oreotragus* (klipspringer), *Raphicerus melanotis* (grysbok) and *Pelea capreolus* (vaal rhebok) occur in fynbos. It seems that such antelopes usually obtain sufficient nutrients from herbage, although the klipspringer may resort to eating soil, dung and bones (Norton 1980). The larger herbivores such as the bontebok and the black rhinoceros prefer vegetation such as renosterveld, on richer soils, which are now primarily agricultural areas.

The relatively low species richness of small mammals has to be explained on other grounds: lack of suitable substrata for the *Otomys unisulcatus* (vlei rat), lack of fleshy fruits and nesting sites for *Graphiurus murinus* (the dormouse), and scarcity of sleeping sites under bark for bats, may contribute to their scarcity. Moreover, there is only a quarter as much food in the form of insects in fynbos as there is in woodlands (Cody, in press).

Given similar rainfall, species richness is not influenced by differences in nutrient levels in the soil (G. J. Breytenbach, pers. obs.). Within fynbos itself, species diversity increases along a rainfall gradient; this could be attributed to an increase in productivity, structural complexity, predation or a combination of these. Highest species turnover rates (beta diversities) occur at the interfaces of nutrient-rich and nutrient-poor areas (Bond *et al.* 1981).

The South African fauna is unique in including a large number of species of fossorial mammals. Although there are six species of insectivorous mole in the south-western Cape, it is the rodent moles which play a major role by turning and aerating the soil and by feeding on underground plant storage-organs. Bathyergus suillus, a large mole-rat, is limited to the coastal dunes of the south-eastern and south-western Cape, whereas Georychus capensis and Cryptomys hottentottus are more widespread. These three species feed on roots and bulbs: it is suggested (A. E. Milewski, pers. obs.) that the rich geophytic flora of the south-western Cape might be due in part to their activities.

Carnivores tend to be rather widespread and none is confined to the mediterranean regions.

6.1.2.2 DENSITY

Densities of small mammals increase with decreasing aridity and are similar to, or higher than, densities recorded from other African biomes, varying from 30 to 130 animals per hectare at sites receiving an average of at least 700 mm of rain per annum. Some evidence suggests that densities increase along a gradient from regions of winter to regions of summer rainfall, possibly due to increasing nutrient levels and grass cover (G. J. Breytenbach, pers. obs.). No data are available on the density of larger mammals; it is known that the density of the klipspringer increases with increasing rainfall but no comparative data are available for areas with similar rainfall but differing nutrient status.

6.1.2.3 DYNAMICS

Seven species of small mammal commonly occur in stands of fynbos about fifteen years old. Two of these species disappear directly after fire and a further three disappear after the post-fire glut of seeds is depleted. Only one rodent, Dendromus melanotis, can be considered to be successional during the post-fire period, since it first appears some two months after fire and disappears two to three years later. Most species have recolonized the burned areas after some eight to fifteen years (Figure 6.2). In areas left unburned, many of the obligate seed reproducing plants will senesce and die, eventually leading to a decrease in the diversity of small mammals as a result of reduced diversity in the vegetation.

6.1.3 CALIFORNIA, CHILE AND THE MEDITERRANEAN BASIN

6.1.3.1 ENDEMISM, SPECIES RICHNESS AND DENSITY

Approximately 33 species of terrestrial mammal and 12 species of bat regularly occur in the Californian chaparral (Quinn, in press). Ten of these are endemic to chaparral, another four are confined to chaparral and adjacent mediterranean areas and the remaining 19 are widespread. Of the ten endemic species, nine are rodents belonging to the genera Eutamias and Dipodomys; a single chaparral habitat usually contains only one species each. Both genera, having a limited ability to disperse, are easily isolated by relatively weak geographical barriers and have apparently speciated in the chaparral. The greater mobility of larger mammals, and their relatively large ranges when compared to the extent of chaparral, have probably prevented the evolution of endemic species.

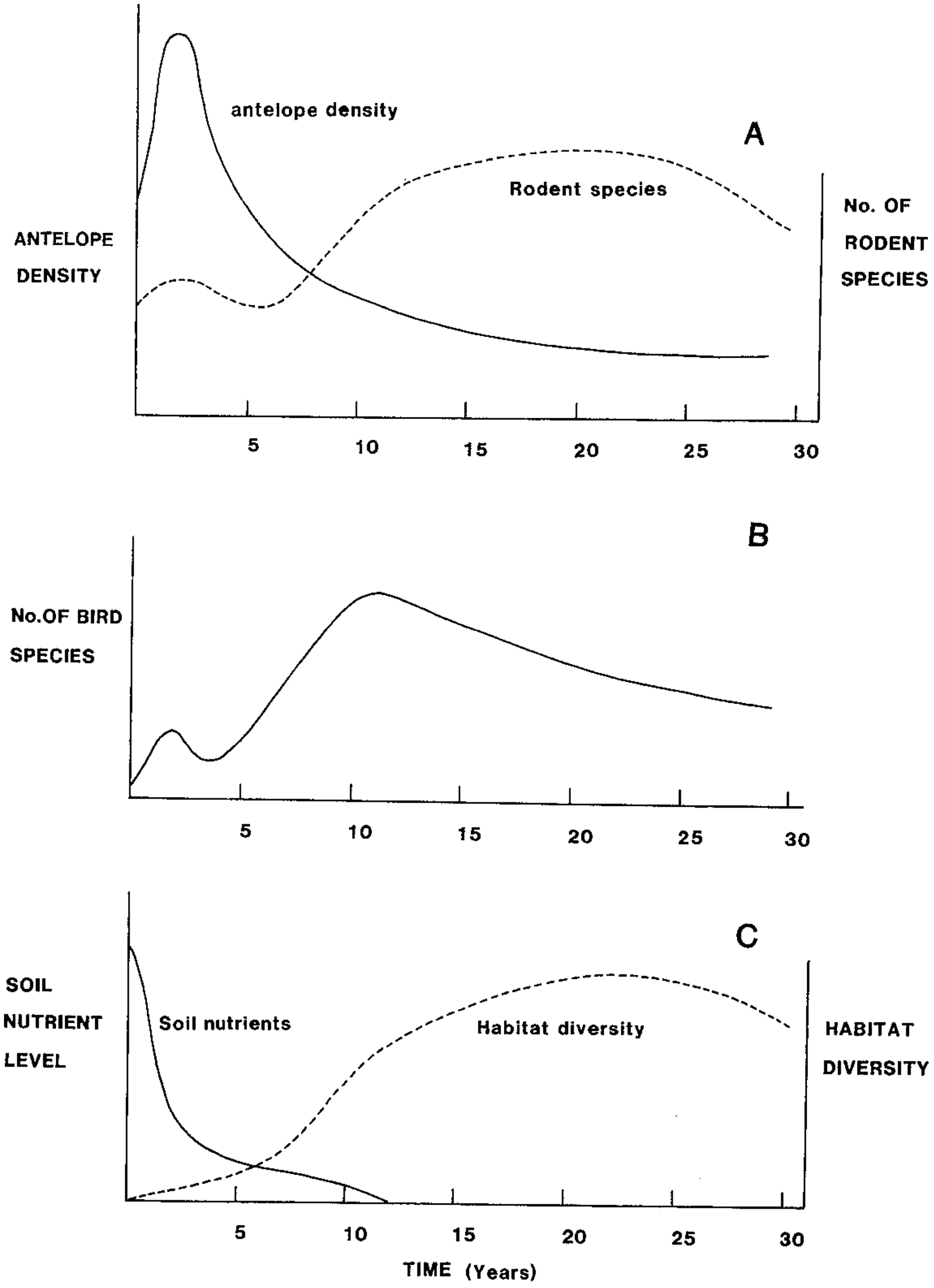


Fig. 6.2 Hypothetical illustration of successional relationships in South Africa as a function of time since fire - A) Bird diversity in fynbos, B) Antelope density and rodent diversity (different scales), C) Soil nutrient levels and habitat diversity (different scales)

The mediterranean regions of Europe and Chile have fewer species of small mammals than does that of California (Cody et al. 1977). In Chile both species richness and beta diversity are lower, but population densities are higher than in California (Fulk 1975). Excluding introduced species and fossorial insectivores in Chile, there are four species of small mammal in open shrublands and four preferring thick shrubs (Glanz 1977). From this one would predict that fire and other habitat disturbances might cause shifts in species composition, but not necessarily in species richness or total abundance. The communities of small mammals of two semi-arid shrublands at different latitudes in Chile were found to differ in species richness, total abundance and evenness (Fulk 1975).

A comparison of the small mammals of relatively mesic and xeric habitats in northern Israel showed few species and relatively low population densities in dense, open or grazed maquis. Much higher population densities were recorded in grassland sparsely covered with shrubs (Warburg et al. 1978). The high levels of disturbance in the Mediterranean might tend to support a higher diversity than that of other, less intensively-used, mediterranean regions. The effects of intensive land use and changes in habitat over many thousands of years on the small mammals of the Mediterranean Basin are not known. Further research is needed on habitat requirements and on distribution patterns of existing species.

6.1.3.2 DYNAMICS

In Californian chaparral, fire is the most important factor affecting the density, diversity and dynamics of mammalian populations (Figure 6.3). Since fire eliminates all edible vegetation, food is limited to invertebrates and buried seeds until the following spring. Under these conditions the community of small mammals is confined to one heteromyid gramnivore, Dipodomys sp., and one or two species of the omnivorous cricetids, Peromyscus spp. The nutrients that become available to resprouting plants and to seedlings after the fire contribute to the rapid regeneration of the plant community in the following spring; this soon provides small mammals with a large variety and quantity of food and of microhabitats. At this stage other cricetid rodents, two species of the lagamorph genus Sylvilagus, a browsing ungulate Odocoileus hemionus (the mule deer) and three large carnivores are added to the community. Species richness and overall densities of small mammals reach maxima in the fourth and fifth years after fire, declining thereafter. This decline is correlated with a decrease in the structural diversity, net primary productivity and species richness of the plant community. Chaparral older than about 15 years supports high population densities of only four species of small mammal and of one large predator (Longhurst 1978). More than 30 years after fire, openings appear in the canopy due to the death of shrubs so that small numbers of a few species of small mammal that prefer less dense cover may once again appear.

Since wildfires in chaparral vary in size, intensity and frequency, the resulting vegetation consists of a mosaic of patches differing spatially and temporally in structure and productivity. Most mammals prefer only a portion of this mosaic and many tend to concentrate around the boundaries between patches. The distributions and densities of mammalian populations shift constantly against this background of changing vegetation. Comparisons across a gradient of moisture and altitude in California showed that chaparral has the same total number of species of small mammals as does a more xeric community, but that fewer species were common (Cody et

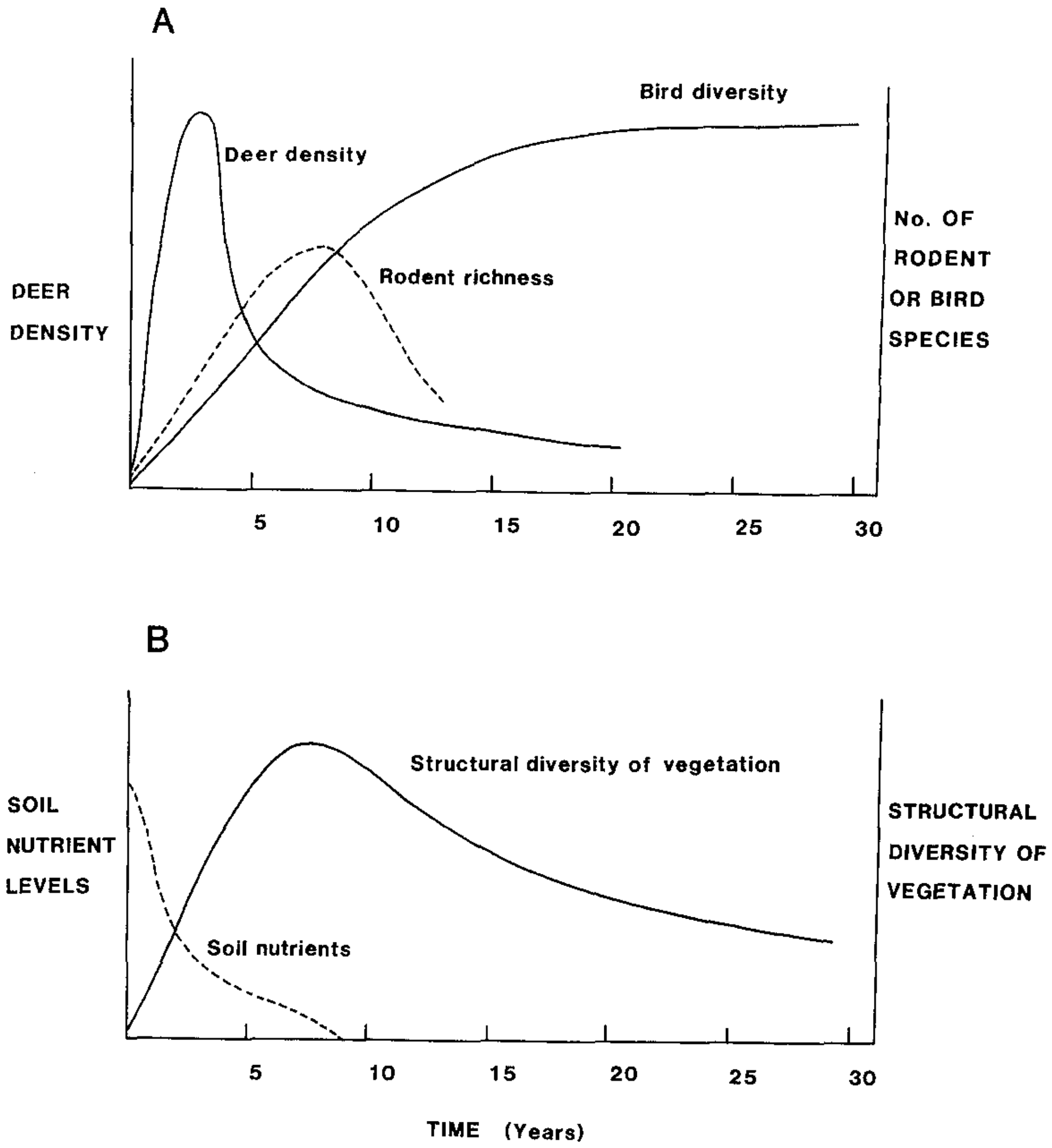


Fig. 6.3 Hypothetical illustration of successional relationships in California as a function of time since fire - A) Deer density and rodent diversity (different scales), B) Soil nutrients and vegetation structural diversity

al. 1977). Mesic sites at higher elevations had fewer species than did chaparral, and of these, fewer were abundant.

6.1.4 COMPARISONS OF MAMMALIAN FAUNAS

6.1.4.1 ENDEMISM AND SPECIES RICHNESS

Mammalian species richness is by far the highest in South Africa, especially when its small area is considered, and lowest in Australia. Despite this, the heathlands of South Africa, North America and Australia contain 6, 10 and 22 per cent respectively of the total rodent fauna of each continent (Lee et al. 1981); the level of endemism in South Africa and Australia is markedly lower than that in California, however. A comparison of the number of species and genera found in the mediterranean regions of Australia, South Africa and California is shown in Table 6.1. The low numbers are accentuated if one considers the proportion of endemic species in the total mammalian fauna of each mediterranean region. The low level of endemism in south-eastern Australia may reflect the lack of any of those marked geographical or climatic barriers which are present in south-western Australia and are a most important feature of the south-western Cape Province of South Africa. The high level of endemism in California appears, however, to be related to speciation in Dipodomys and Eutamias, where species replace one another geographically. Both genera also exhibit similar levels of relatively recent speciation outside the mediterranean region, for example in Dipodomys in the seed-rich habitats of the adjacent deserts.

A different picture emerges when one considers the numbers of genera. There are three times as many genera in the South African mediterranean region as there are in the equivalent regions of California and Australia, although endemic genera are known only from the south-western Australian region. Both of these are monotypic and show reproductive adaptations: opportunism in Tarsipes and seasonal anoestrus in Setonix. The number of species per genus is comparably low in South Africa and Australia but is much higher in California, again reflecting the apparently high rate of speciation.

The trophic structure of the communities of small mammal present on comparable sites in chaparral, mountain fynbos, matorral and heathland (Figure 6.4) shows a marked increase in the proportion of granivores with increasing nutrient content of the soil, although the number of species of herbivores generally decreases. This pattern seems to reflect a greater variation in the availability of specific trophic resources such as seeds and insects rather than reflecting differences in nutrient levels in the plants themselves.

The differences in species richness and endemism in mammals in general, and in the community structures in small mammals, suggest that nutrient levels do not have a serious impact on the composition of the fauna since nutrient levels do not correlate with richness either of species or of genera. On the other hand, the degree of endemism of species does show some correlation with nutrient levels although that of genera does not. If nutrient levels were important, we might expect the low-nutrient ecosystems to have evolved a higher proportion of endemic species in response to the limited availability of nutrients in the diet, and yet in fact quite the opposite trend is seen. Perhaps the nutrient levels can be so low that heathlands are then only used opportunistically by mammals from adjacent forests, as is the case in south-eastern Australia.

TABLE 6.1 Richness and endemism of mammals in the mediterranean regions of Australia, southern Africa and California

	Area ($X10^3km^2$)	Total number of species	Endemic Species		Total number of Genera	Endemic Genera		Number of species per genus
			No.	%		No.	%	
South-eastern Australia	376	35	2	6	26	0	0	1.3
South-western Australia	293	37	4	11	28	2	7	1.3
South Africa	89	106	9	9	90	0	0	1.2
California	324	50	14	28	25	0	0	2.0

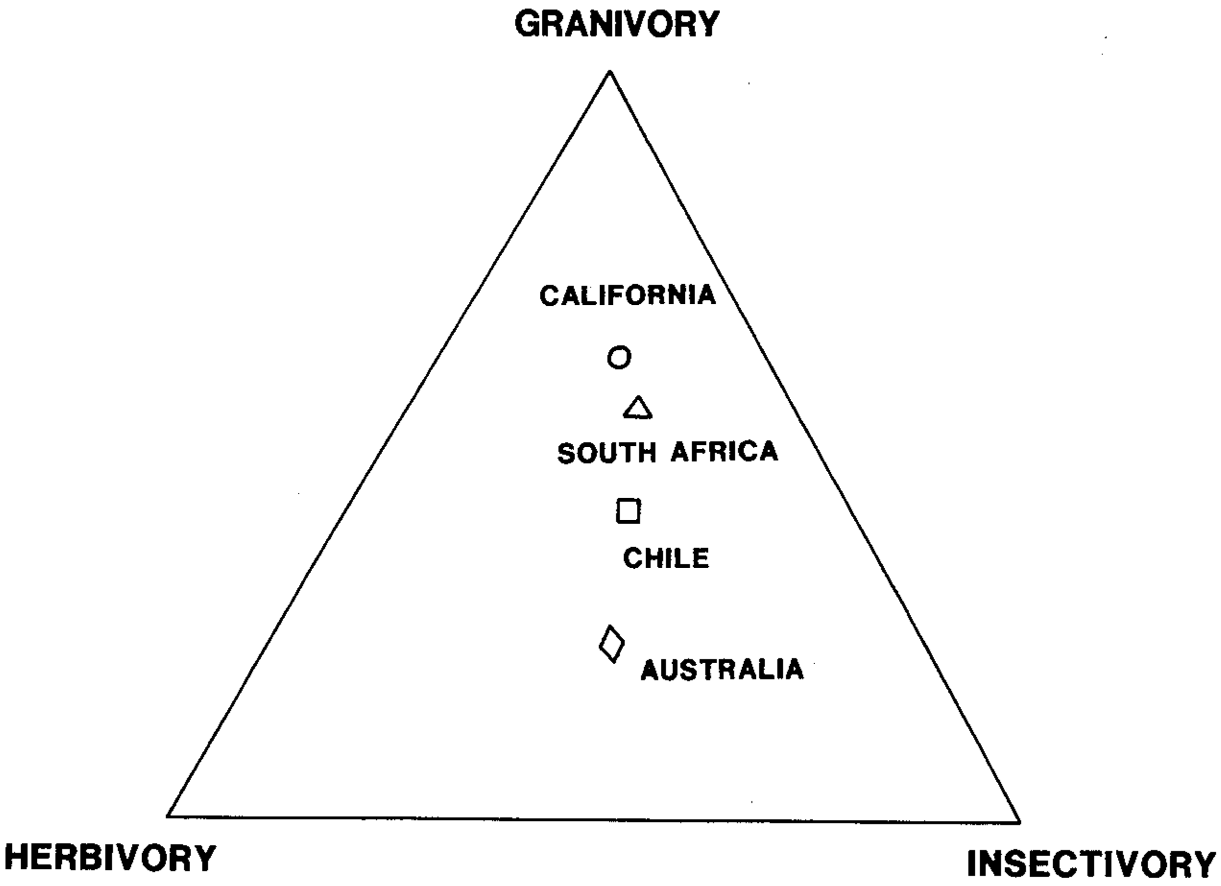


Fig. 6.4 The trophic community structure of small mammals in structurally similar study sites in mediterranean regions. Within each community, species were allocated to a specific trophic category according to the proportional contributions of herbage, seeds or insects to the diet

6.1.4.2 RESPONSES OF MAMMALIAN COMMUNITIES TO FIRE

Intense fires directly affect communities of small mammals both in California and in Australia (Newsome et al. 1975; Fox 1980, 1982), where populations of most species decline or disappear for the first year or two after fire. Soon after this decline, the number of species and the total abundance of individuals increases. Changes in community structure may continue for at least five years, the observed pattern being related to the response of individual species to the changing vegetation (Catling et al., in press; Fox 1982, in press; Quinn, in press). Broadly similar patterns may apply in fynbos. Toes (1974) and De Hoogh (1968) (reported in Bigalke 1979) found population densities of small mammals to be almost twice as high in three year-old as in 31 year-old fynbos.

6.2 BIRDS

6.2.1 AUSTRALIA

6.2.1.1 ENDEMISM AND SPECIES RICHNESS

The level of endemism in Australian mediterranean regions is not high, at least partly because many forest and woodland birds make use of the heathlands at times. Data in Catling & Newsome (1981) indicate that about 20% of the birds of the mediterranean south-west are endemic; the figure for the mediterranean south-central region is about half of this.

Species richness is low, being about half of that estimated for California or South Africa in nutrient-poor areas and not a great deal higher in nutrient-rich areas. Beta diversity is similar on soils of similar types and is generally less than elsewhere. The greatest turnover of species occurs between one heath region and another, rather than between different types of habitat within a single region.

6.2.1.2 DENSITY

In nutrient-poor areas the density of birds is comparable to that in the South African mediterranean area but the increased number of birds on richer sites is not as great in Australia.

Exclusively insectivorous birds are extremely rare, especially in heathlands on poor soils, although insects may form an important component of the diet of honeyeaters (Pyke 1980). Nectarivores are extremely common. Half of 13 species in nutrient-poor woodland are nectarivorous while of about 18 species from mallee, on better soil, five are nectarivorous and seven insectivorous.

While more detailed studies from Australia await publication, enough is understood to dramatize the influence of soils on the reproductive and vegetative adaptations of plants, which in turn probably influence the bird communities which are so divergent on this continent.

6.2.1.3 DYNAMICS

Unlike reports for avian species richness in relation to fire in other areas, the admittedly limited Australian data indicate that successional changes may be quantitative rather than qualitative (Catling & Newsome

1981). Comprehensive data are available on fire in a forest habitat. In this study, only one of nine species which forage on the ground and in heathy shrubs were shown to decline in numbers. The numbers of three species increased while the rest showed no significant change. After a severe heathland fire, the numbers of the endemic ground parrot, Pezoporus wallicus, fell from 0,43 km^{-1} of transect to 0,01 km^{-1} two years later; after five years the numbers had increased again to 0,46. On the other hand, Roberts (1970) reported a drop from nine species to one after a fire had destroyed the understorey of heathy vegetation in eastern Australia. Three species moved to adjacent non-heath vegetation while the three species normally associated with ground cover did not reappear for more than two years.

6.2.2 SOUTH AFRICA

6.2.2.1 ENDEMISM AND SPECIES RICHNESS

Due to the nutrient impoverishment of some areas, habitats are variable within the South African mediterranean region. In general, species richness of birds is high in mountain fynbos, intermediate in low coastal scrub and low in woodland, which is very scarce. There is no simple relation between species richness and vegetation structure, marked discontinuities occurring in habitats of comparable structure on soils of different productivity. In particular, the species richness of the birds of coastal strandveld, coastal fynbos and renosterveld is higher than it is in habitats of comparable vegetation structure in mountain fynbos or in renosterveld of lower productivity. It remains to be seen (cf. Siegfried & Crowe, in press) if structural indices, taking account of resource variability and availability, can be constructed to reflect these differences.

Total numbers of bird species are high for the South African mediterranean region in general, reflecting its wide accessibility to the rich faunas to the north and the east but those species found in fynbos itself form a surprisingly small part of the total. Beta diversity is very high compared with that of other mediterranean regions, and is highest in vegetation structurally typical of areas of low or high productivity.

There are fewer species of small insectivorous birds and more nectarivores than in structurally comparable habitats in Chile, California or Sardinia.

Unlike its demonstrated lack of importance in California, the floristic diversity of the South African mediterranean region plays a role in maintaining species richness (Figure 6.2b,c) by providing more specific types of resources and more foraging opportunities in the heterogeneous fynbos and strandveld. This aspect has not specifically been investigated.

6.2.2.2 DENSITY

Trapping has revealed a lower biomass of insects in fynbos than in other regions of macchia-like vegetation. This is reflected in lower densities of birds, especially of foliage insectivores (Cody & Mooney 1978). In general the relationship between estimates of plant productivity and bird counts is such that a tenfold increase in productivity corresponds to a twofold increase in bird numbers (Cody 1981). The differential availability of food in Chile, California and Sardinia, and on poor and rich soils within South Africa, is reflected in differences in the composition of bird communities. Further, there are striking differences between continents in the availability of resources such as nectar. Proteas, which produce abundant nectar, occur as isolated bushes rather than as a part of the monospecifically-monopolized patchwork in chaparral, for example. Thus the nectar may be used less by bees, favouring increased use by birds.

In South African mediterranean areas where soils are deficient in N and P, the biomasses of nectarivores are higher than those of insectivores, which in turn are higher than those of granivores; frugivores are virtually absent. Ground-foragers are present in low densities, although litter is common enough; presumably its decomposition rate is slow due to the biochemical properties of the proteoid leaves. In vegetation on richer soils nectarivores are scarcer and granivores more common, although abundances of insectivores are still not as high as they are in California and Sardinia. Again this is presumably a reflection of vegetation structure: where the vegetation canopy is continuous it becomes energetically feasible for more birds to eat insects, since gaps in the canopy are economically detrimental, especially to small birds. Overall there is a fourfold increase in bird density between sites of low and high productivity (Siegfried & Crowe, in press).

6.2.2.3 DYNAMICS

There are virtually no palaearctic or intra-African migrants at any time of the year. However, presumably as a consequence of the low levels of insect food and the highly seasonal nature of nectar production, there is a high turnover of bird species between seasons because of local movements of resident populations. Many of the birds appear to use nectar and fruit opportunistically, seeking out areas where they are abundant at a particular time of year. This is reflected in the colonial habits of large, wide-ranging birds such as Onychognathus morio (a starling), the almost social nature of Promerops cafer (the sugarbird), and the movement of both to higher elevations as the season progresses. In some seasons a single species of nectarivore, Anthobaphes violacea (a sunbird), numerically dominates low mountain fynbos. As is true in some Mediterranean habitats, bird densities are at least as high in the winter, when many proteas are flowering, as in summer.

Although some of the flycatchers of the south-western Cape are migrants, as are flycatchers elsewhere, the resident insectivores appear to be hard-pressed in some seasons by the reduced abundance of insects. Zosterops pallidus (the white-eye), the dominant species of the few which occur, incorporates considerable quantities of fruit into its diet. But since plants may flower, fruit or set seed at all times of the year, local shifts in the density and diversity of birds tend to take the place of long-distance migration.

6.2.3 CHILE, CALIFORNIA AND THE MEDITERRANEAN BASIN

6.2.3.1 SPECIES RICHNESS

Census data are available over a range of habitat types in the mediterranean regions of Chile, California and Sardinia. Comparisons of species richness between the three regions were made by Cody (1973,

1975) and Cody & Mooney (1978); other data are available (for example, Blondel 1969). Fewer than five per cent of the species are restricted to mediterranean habitats, and most of the birds are also found in adjacent temperature zones or in drier scrub. Despite differences between continents in the total number of species in each system (California > Sardinia > Chile), there is good correspondence in species richness in different habitats. Simple indices of vegetation structure are closely related to the species richness of tall chaparral, matorral and macchia, each of which has 25 abundant species. Taller vegetation in more mesic sites or in richer soils provides more distinctively different types of foraging site and more different opportunities for foraging, thus supporting more bird species. Estimates suggest that the numbers of insects available for insectivorous birds do not vary much; nor do they appear to affect the species richness of the birds. The areal extent of a particular habitat may influence species richness, which in California is higher in taller shrubs for example, since they happen to cover a greater area than do low-growing shrubs. This may also explain the species richness of lower and more open habitats in Chile.

Species turnover between habitats (beta diversity) is highest in California and lowest in Chile, where the value is only 10 per cent of that for California. Both the position on the habitat gradient where beta diversity peaks, and its values in general, are related to the extent or accessibility of various habitat types. In Chile, where the mediterranean region is a small area locked between the Andes and the coast, the total number of bird species is low; each species has a wider habitat tolerance and thus beta diversity is low. In California, habitats are accessible to a much larger fauna and beta diversity is higher, especially between the extensive taller chaparral and woodland habitats.

6.2.3.2 DENSITY

Plant productivity in California, Chile and Sardinia is uniformly high and results in uniformly high bird densities. Chaparral supports about 14 pairs of birds per hectare, a total which is intermediate between the lower densities (about 10 pairs per hectare) in short, dry and more open habitats and the 20 or so pairs per hectare in evergreen woodlands. Accurate measurements of food resources have yet to be made, but qualitatively the availability of insects is very similar in the three regions, as are the densities of insectivorous birds. Ground-foraging species are more common and more diverse in Chile, where there is more herbaceous vegetation at ground-level. Seed-eaters are comparably represented everywhere. Sardinia, and the rest of the Mediterranean, lacks nectarivores but has rather more small insectivores. Bird densities are expected to be comparable only between sites where food availability is comparable; for granivores, frugivores and nectarivores resource availability is far less readily correlated with vegetation structure. Although the covariance between vegetation and insect density is high, as in the covariance between insects and their consumers, in non-insectivores covariance is reduced by the co-evolutionary aspects of food specialists and their food supplies.

Although biomass values have not yet been analysed, those for California and Sardinia appear to be comparable and somewhat lower than those for Chile. Birds in Chile, especially the tyrannids, furnariids and rhinocryptids, may be somewhat larger than their counterparts elsewhere. Higher productivity of the vegetation and especially its more open aspect may account for this.

6.2.3.3 DYNAMICS

In these three mediterranean regions the majority of endemic insectivorous birds is resident, since insect availability is high all year round. Breeding communities are augmented by non-breeding summer visitors, especially flycatchers, taking advantage of the spring peaks in food. In autumn and winter the residents are augmented by overwintering species, mainly seed- and fruit-eaters. But this augmentation is least in the more stable woodlands and greatest in the lower open habitats, where seeds of annual plants boost the food supply.

The Sardinian macchia and the French garrigue support higher diversities, and higher densities, of birds in winter than in summer. The enormous production of seed and particularly of fruit by *Arbutus unedo*, for example, supports a big influx of north-temperate thrushes and other frugivores and seed-eaters. Year-round studies on resources and consumers are becoming more prevalent and the seasonal dynamics of bird communities will soon be better understood.

6.2.4 RESPONSES OF BIRD COMMUNITIES TO FIRE

Fire affects bird communities by changing vegetation structure and food resources and is particularly important in South Africa now that prescribed burning has become an integral part of management programmes. Unlike the dominant shrubs of mediterranean regions elsewhere, many proteas become markedly senescent within 25 years of germination so that species richness in older fynbos stands is lower than in younger ones (Figure 6.3B). Nothing of this sort has been reported elsewhere; in California both diversity and density of birds increase for at least 50 years after a fire. Nonetheless birds such as *Erythropygia coryphaeus* (the scrub robin) in fynbos, *Amphispiza belli* (the sage sparrow), and *Passerina ciris* (the lazuli bunting) in chaparral, occur soon after a fire and drop out as the succession progresses.

6.3 REPTILES

There are about twice as many species of reptiles in the Australian and South African mediterranean regions (about 55 and 40 species respectively) as in the Mediterranean Basin, California or Chile (with about 20, 25 and 20 species respectively). However, the area of each region would need to be taken into account in a more refined comparison of species richness.

The South African region is unique in having at least four species of terrestrial tortoise, two of which are endemic. The only terrapin in south-western Australia is also endemic, while that in the south-east is widespread.

In the Australian mediterranean regions, lizards constitute about 69 per cent of the species of reptiles (Cogger & Heatwole 1981). The figure is about 55 per cent for South Africa. Snakes predominate in California, where they represent 60 per cent of the total, while they form only 10 per cent in Chile. Apparently the species richness of lizards is similar (3-5 species) in Chile, California and the Mediterranean Basin. With the exception of a single species of herbivore in California and another in Chile, the lizards are primarily insectivorous. Although plant-eating lizards are apparently absent from the south-western Cape, the tortoises are herbivorous.

It appears that both species richness and density of reptiles increase along a gradient from relatively closed-canopy vegetation, excluding forest, to open arid habitats on all five continents. This might in part be a function of enhanced insolation in arid environments. Dense, woody vegetation coupled with high insect productivity apparently correlates with an increased incidence of arboreal lizards, independent of increases in avian species richness or density. This implies a relatively low level of competition between birds and lizards for food.

The amphibians of the south-western Cape show a high degree of endemism (Bigalke 1979), as do the fish, and there is some evidence that the endemics are mostly of Gondwana origin.

6.4 INVERTEBRATES

Data on invertebrates are grossly inadequate and no comparisons are possible. In south-western Australia, millipedes preferred the litter of Bossiaea, which has high contents of N, P and K, to the litter of Eucalyptus and Banksia, which are low in nutrients (Springett 1978). In a forest of jarrah, Eucalyptus marginata, the heavy leaf-fall that followed an intense fire resulted in a fourfold increase in the concentrations of P and N on the forest floor; concentrations remained 50 per cent higher than those in an unburnt forest even after two years (O'Connell et al. 1979). Equally, a hot summer fire may reduce the number of soil micro-arthropods by 40-75 per cent (Springett 1978). In forests, fires of low intensity have little effect on the litter fauna (Campbell & Tainton 1981) while heathland fires generally destroy all the litter and its fauna.

The Chilean and Californian ecosystems compared by Mooney (1977) chiefly provide information on pollinating insects and on ants. As might be expected from coevolutionary considerations, the bee faunas corresponded at only the most superficial levels, the discrepancies being aggravated by major differences in the number of species: 365 in California and 150 in Chile.

Endemic insects in the South African fynbos seem to be relicts with a Gondwana origin (Endrody-Younga 1978; Bigalke 1979) or belong to groups that are not herbivorous during at least some part of their life cycle. In the Lepidoptera, for example, the only endemics are species with larvae that live in ants' nests and are fed by them (Cottrell 1980). Anthophilous flies have also speciated actively in the fynbos (Bowden 1978). Thus the relatively low levels of endemism may be related to the poor nutrient status of the soils.

In Australia, leaf-eating insects have coevolved with the sclerophyllous plant communities by maintaining high pH levels in their guts, effectively inhibiting the toxic action of the secondary compounds. Insect larvae living in Banksia trees and shrubs in heathlands are sometimes heavily preyed upon by black cockatoos, Calyptrorhynchus spp., which rip open boughs with their massive sharp bills (Morrow 1980).

6.5 DIRECTIONS FOR THE FUTURE

At the most fundamental level, there is no understanding of the relationships between soil nutrient status, plant nutrition and the invertebrate and vertebrate faunas of any of the mediterranean ecosystems, let alone an understanding of the partitioning of actual resources of food and shelter between the animals. For some areas there are insufficient check-lists even of the insects, reptiles, birds and mammals that may compete for resources. This makes comparisons difficult. Some data exist on the nutrition of soil arthropods in relation to leaf litter and fire, on endemism in vertebrates, on successional responses of small mammals and birds after fire, and on their responses, in numbers and in species, to the structure and diversity of their habitat. Most data concern species diversity of birds relative to structural variation in their habitats. Even here there is insufficient knowledge for intercontinental comparisons, and we are little further advanced than general steady-state models relating the fauna to supplies of resources, to their partitioning, and to temporal pulses due to seasons and to fire.

It is clear that the understanding of faunal components relative to those of the flora of mediterranean regions has far to go. It is particularly important to rectify the imbalance in understanding of the various invertebrate and vertebrate taxa. Clearly a great deal more research is needed on insect taxa, especially since they have such potential as herbivores, as pollinators and as food for insectivorous birds and lizards.

The following questions should be particularly considered in order to compare and contrast the mediterranean ecosystems of the five continents.

- Do mediterranean plants, especially on poor soils, "safeguard" their supplies of nutrients by being unpalatable to consumers, both vertebrate and invertebrate?

- What are the relationships between the nutrient status of the soils, plant diversity and the production and dispersion of nectar? Why does this result in some systems in pollination by birds and in others by bees? Why are animals not involved in pollination in some systems?

- Do herbivorous and sucking insects on plants, and ants and reptiles on the ground, commandeer the nutrients available to mediterranean plants? Does this affect the abundance and richness of birds and mammals?

- What effects do large predators have on the degree of utilization of mediterranean ecosystems by birds and mammals?

- Does seasonal aridity on poor soils limit the utilization of vegetation by animals? Does it favour some, such as insects and reptiles, over others, such as birds and mammals?

- Are the opportunities for herbivory limited by the episodic nature of nutrients made available by fire?

- Does density compensation operate at both inter- and intra-taxonomic levels of species diversity? To what extent does it contribute to the maintenance of species diversity and community structure?

- Is the diversity of invertebrate consumer groups more closely related to plant diversity than is the diversity of most vertebrate groups?

- What causes the anomalies in faunal structure and diversity in different mediterranean ecosystems?

6.5 CONCLUSIONS

It appears that the low nutrient status of the mediterranean regions is reflected in the generally low densities and diversities of all vertebrate taxa, which nevertheless seem to respond more to structure and diversity of habitat than to the levels of nutrients themselves.

The greatest change-over (beta diversity) of small mammal species occurs in Australia at the boundary between the structurally very different wet and dry coastal heathlands whereas in fynbos the greatest change-over occurs at the junction between soils of low and medium nutrient status. If nutrient status were the main determinant, then the South African and Australian regions, with their greatly-impoverished soils, might be expected to have similar degrees of species richness and similar proportions of small granivorous, herbivorous and insectivorous mammals; they do not do so (Table 6.1, Fig. 6.4). Animals presumably overcome problems of nutrient limitations through flexibility in behaviour, such as selection of food and shelter, and in physiology, such as reproduction. The effects of habitat structure have been analysed best for the birds (Cody in press). But workers on small mammals in Australia, California and South Africa have independently demonstrated the predictive power of structural components of habitats for both abundance and richness of species (Newsome & Catling 1979; Quinn, in press; Fox 1980, 1982, in press; Bond et al. 1981; G. J. Breytenbach, pers. obs). This effect extends beyond heathlands, to heathy shrub understoreys growing beneath tree canopies (Fox & McKay 1981). The presence of litter, logs, rocks and moisture in any habitat also enhances abundance and richness (Newsome & Catling 1979).

No adequate syntheses relate the availability of resources such as food and shelter to spatial and dynamic patterns in the fauna and vegetation. This omission needs rectifying. We regard studies to this end as more feasible and relevant than studies which try to determine directly the relationship between soil nutrients and the fauna.

The relationship between areal extent, distribution and patchiness of habitat on the one hand and the components of diversity (alpha, beta etc.) on the other have as yet been poorly investigated; a coherent theory of continental species diversity has yet to emerge. Diversity figures may reflect the effects of past climates as well as the present distribution of a habitat. In turn the continuing changes in landscapes, in areal extent and in contiguity of habitat, are expected to have major implications for species richness in habitats increasingly restricted in area, dissected by barriers and reduced to isolated patches due to the actions of man.

Lack of historical information, and especially lack of both plant and animal fossils, greatly hinders understanding of present-day mediterranean regions. Kikkawa et al. (1979) have proposed, for Australian heathlands in all climatic zones, that many species specially adapted for heathlands have become extinct while others, such as present-day frogs, lizards with large eggs, and birds feeding on nectar, continue to evolve. They propose that this continuous process is tied to the changing patterns of distribution of heathlands, which are now generally contracting. In South Africa, fossils show evidence of fluctuations during the Holocene, with the coastal areas becoming more grassy and the alcelaphines (the bontebok and its allies) increasing correspondingly during certain periods (Avery 1979).

In nutrient-poor ecosystems, and especially in those with temporal fluctuations in primary productivity and thus in numbers of primary consumers, there will be alternating periods of abundance and shortage of food for secondary and tertiary consumers. Under such conditions, natural selection will favour those consumers which are best equipped, physiologically and behaviourally, to survive periods of temporary food shortage. Ectothermic vertebrates such as reptiles are potentially better adapted to surviving periods of temporary food shortage than are endotherms, given that both are equally restricted in mobility. From this we predict that reptiles should be relatively well represented in the mediterranean ecosystems of Australia and South Africa. This prediction is borne out in a comparison of total species richness of reptiles, birds and mammals, which shows that reptiles are relatively better represented in Australia and South Africa, than in the Mediterranean Basin, California and Chile. The higher proportion of reptiles to birds in an Australian desert than in the Kalahari or Chihuhuan deserts (Pianka 1969) should further be tested for mediterranean systems by comparing the density as well as the biomass of reptiles, birds and mammals.

A better understanding of the effects of fire would assist in completing the picture. The spectacular nature of brush fires, the dramatic responses of the biota and the importance of fire to man's management policies have resulted in some information becoming available, but this is inadequate. Fire plays an important role in the creation of a mosaic of vegetation of varying ages. If this variation were to be lost, then successional species might disappear from the system. Mammalian species diversity and density increases as large herbivores congregate on newly-burned areas. As structural diversity of the vegetation increases with time, so species diversity of small mammals increases to a peak, before beginning to decline (Figure 6.3). This suggests that the flush of nutrients after a fire may be the first factor influencing mammalian density and species richness but that the effect of nutrients is over-ridden by changes in the structural diversity of the habitat, both horizontally and vertically. Thus both fire and habitat diversity appear to be important in the maintenance of species diversity in these systems.

The succession of large herbivores and also of small mammals shows marked similarities in the three mediterranean regions illustrated in Figures 6.1-6.3 (the response curve for macropodids represents conditions in the absence of predators). We know too little about invertebrates in mediterranean ecosystems to be able to draw any conclusions about them. The rapid influx of large herbivores appears to be a response to new growth of herbs and particularly of grasses in response to the increased availability of nutrients in the soil. Rodent diversities show somewhat similar trends but the time-scales differ. After an initial response, changes in rodent diversity follow changes in habitat diversity, perhaps related to the flush of nutrients.

We know too little about invertebrates in mediterranean ecosystems to be able to draw any conclusions about them.

7. INTERACTION BETWEEN PLANTS AND ANIMALS

P. A. Morrow (convener), J. A. Day, M. D. Fox, P. G. H. Frost,
J. U. M. Jarvis, A. V. Milewski, P. M. Norton

In this chapter we discuss the observed patterns of interaction between plants and animals in the various mediterranean regions, how these are modified within systems differing in the fertility of their substrata, and what accounts for these patterns. In particular we try to answer the questions, "What roles do animals play in determining the morphological characteristics of mediterranean vegetation?" and "What is the extent of convergence in the structure and functioning of animal communities in mediterranean ecosystems?".

7.1 MAJOR ANIMAL TAXA

Although the very similar environments in the mediterranean regions of each continent have resulted in fairly similar floras, the faunas vary quite profoundly even between systems of similar nutrient status. Therefore before discussing the major types of interactions between plants and animals, it is necessary to mention the major faunal components associated with the flora of each continent, since in each the roles that different animal groups play as pollinators, herbivores, predators and dispersers, are quite different.

Where it has been possible to do so, the following accounts have been drawn from published data but, since these are few, we have had to rely largely on our own observations and on discussions with other workers in mediterranean ecosystems. The major deficiency in our combined experience is a lack of familiarity with the Mediterranean Basin.

7.1.1 AUSTRALIA

Mediterranean Australia supports a diverse array of herbivorous insects, with many closely-related species present in groups such as chrysomelid leaf-beetles, psyllid bugs, pergid sawflies and scarab beetles (CSIRO 1970). Herbivorous vertebrates apear to be relatively unimportant. A wide variety of honeyeaters (Aves: Meliphagidae), as well as certain insects, feed on pollen and nectar. Birds of the parrot family (Psittacidae) are common and diverse, feeding on seeds and in some cases on pollen and nectar as well (Kikkawa et al. 1979). Although certain mammals are notable in feeding on nectar, mammals in general are poorly represented.

The Australian ant fauna is one of the richest in the world. With at least 2500 species, compared to approximately 500 in North America, the ants are an important and conspicuous element in most Australian ecosystems. Ants feed on a wide variety of items and many species take nectar and seeds, or the food bodies attached to them. Termites, too, are common and diverse in the Australian mediterranean region.

7.1.2 SOUTH AFRICA

Mediterranean South Africa supports a diverse array of mammals of various sizes and of birds, particularly frugivores and nectarivores. Although the species richness of insects, particularly of herbivores, seems to be rather less than that in other mediterranean regions, ants and termites are abundant and are important components of this system (Ruelle 1978).

Fossorial mammals, particularly mole-rats and golden moles, are a feature of the South African mediterranean region. Mole-rats are rodents, feeding mainly on underground bulbs and tubers, while golden moles are insectivores. Although similar mammals occur in all the other mediterranean regions, except in Australia, mole-rats are particularly diverse and common in South Africa.

7.1.3 CALIFORNIA

Mediterranean California is notable in supporting a diverse array of small- and medium-sized mammals, mainly rodents. The frequency of occurrence of ants, of large herbivorous mammals, and of birds feeding on fleshy fruits, is intermediate between that of Australia and of South Africa. Insects such as bees are important pollinators, while the density of herbivorous insects is low compared to that of Australia. Rodents such as mice, wood-rats and squirrels feed largely on seeds, including large ones such as acorns, while other mammals such as skunks and raccoons include fleshy fruits in their diets. Termites, ants and nectarivorous birds are less diverse and less common here than they are in the mediterranean regions of either Australia or South Africa.

7.1.4 CHILE

Mediterranean Chile shows few distinctive faunistic features. The variety of mammals is low, exceeding only that of Australia. Mammals are generally small to medium in size, with a mixed diet of foliage, insects and seeds. The occurrence of herbivorous insects appears to be similar to that in California and South Africa, while the occurrence of insects, birds and mammals feeding on nectar and pollen is similar to that in California; bees are the major pollinators (Moldenke 1976). As in Australia, there are few frugivores and termites, while ant diversity seems to be very low (E. R. Fuentes, pers. obs.). Birds are the major seed-eaters and form a diverse array compared to that of Australia, where such birds are virtually absent, or even of California, where densities of birds are similar to those in Chile (Cody 1974).

7.2 PLANT-ANIMAL INTERACTIONS AND THEIR CONSEQUENCES IN MEDITERRANEAN COMMUNITIES

The relative abundance as well as the relative importance of major animal taxa varies not only between the mediterranean regions but also to some extent within those of Australia and South Africa, where the fertility of the substratum varies. Although it is not always obvious, animal communities may greatly influence the patterns of plant spacing, the relative abundance and physical structure of plants, the rate and direction of succession and the rate of turnover of nutrients.

7.2.1 HERBIVORY

Janzen (1974) suggests that, in vegetation growing on impoverished soils, the cycling of nutrients is so critical to the plant that it is worthwhile, from an evolutionary point of view, for a large proportion of available energy to be used in defense against herbivory, even if the actual level of herbivory is very low. Herbivory is generally inconspicuous in mediterranean ecosystems but there is some evidence that defensive mechanisms such as spines and secondary compounds play a role in the selection of food by herbivores. As yet, there is no evidence as to whether energy is invested specifically in physical or chemical deterrents.

There are two basic types of chemical deterrents. "Quantitative" defensive compounds are thought to reduce digestibility, and thus the nutritive value of plant tissues, in a dose-dependent fashion. "Qualitative" defensive compounds, which tend to be toxic, are generally present in low concentrations and act by poisoning rather than starving herbivores (Feeny 1976). Plant toxins are apparently rare in mediterranean regions, where the vegetation is characterized by high concentrations of quantitative defensive compounds, mainly phenolics and terpenes. This appears to be particularly true where the soil is poor in nutrients (P. A. Morrow, pers. obs.). Janzen (1974) and Feeny (1976) hypothesize the abundance of quantitative chemical compounds to be negatively correlated with levels of herbivory, although this hypothesis does not hold true for insects feeding on Eucalyptus in Australia (Fox & Macauley 1977; Morrow & Fox 1980). Studies in South Africa have shown that plants with high concentrations of phenolics, or with structural defences such as leaf- and stem-spines, are less palatable to small antelopes than are plants lacking these defences (Norton 1980, Puttick & Glyphis 1980), although plants in this mediterranean region are generally not spinescent. The defensive role of quantitative compounds in sclerophyllous vegetation is reviewed by Morrow (in press).

In discussing herbivory we distinguish between invertebrate and vertebrate herbivores because of differences in the ways in which they interact with plants and in the conspicuousness of their impact. Insect attack is often easier to observe because insects generally eat only part of a leaf, the rest usually remaining on the plant, while large animals usually eat whole leaves and shoots, making it difficult to assess the amount of tissue removed. Further, the destruction of young expanding shoots, flowers or fruits, particularly by bud-boring and sap-sucking insects, may have a much more significant impact on plant functioning than does the more conspicuous consumption of mature expanded leaves. In addition to affecting growth rates, the destruction of buds and shoots may also alter canopy structure (Jacobs 1955).

By virtue of their small body sizes and narrow biochemical specializations, insects, individually or as a species, generally include fewer plant species in their diets than do large herbivores. This often leads to apparent local specializations (Fox & Morrow 1981) that will differentially affect the plant species within a community and in turn may influence the outcome of inter- and intraspecific competition between plants.

Very little information is available on the total quantities of plant material consumed by different types of herbivores. Some work has been done on leaf area reduction by insects, but it is more difficult to gather quantitative data when whole leaves or shoots are eaten; indirect methods such as control plots using insecticides, or animal exclosures, need to be used. We consider that such quantitative experiments will show losses due to herbivores to be more extensive than is generally apparent.

There are substantial differences in the apparent levels of damage by herbivores in different mediterranean regions. Losses of foliage to herbivorous insects are generally less than 10 per cent and less than 2 per cent on nutrient-poor sites (A. V. Milewski, pers. obs., F. J. Kruger, pers. obs.). In Australia, however, a diverse and abundant insect fauna removes between 9 and 22 per cent of the leaf area from the dominant mallee Eucalyptus trees (Fox & Morrow 1981) and more than 50 per cent of the foliar biomass of heath in south-eastern Australia (Jones 1968). These insects generally have very specific diets and therefore exert a differential impact on the productivity of different species of plant in the community (Burdon & Chilvers 1974; Morrow & La Marche 1978; Fox & Morrow 1981). In the richer strandveld vegetation of South Africa, Puttick & Glyphis (1980) recorded figures for leaf area reduction of only 15 g m^{-2} on the dominant broad-leaved deciduous plants. In spite of these low figures, this study showed an interesting inverse relationship between the losses due to herbivory and the presence of secondary plant compounds.

Studies in parts of Australia outside the mediterranean climate region, comparing plants on different soils, suggest that attack by insects is low on plants growing in exceptionally impoverished sites. This is apparently because the protein content of expanding leaf tissue is below six per cent of leaf dry weight, which is about the level necessary to support insect growth (Morrow & Fox 1980). Particularly in early developmental stages, insects normally feed only on expanding leaves, which are softer, contain more water and protein, and have lower concentrations of defensive compounds than do mature leaves.

The biomass of vertebrate herbivores appears to be roughly equivalent in all mediterranean regions. Except in Australia, consumption of foliage by vertebrates is apparently of the same degree as that by invertebrates. The main vertebrate herbivores in mediterranean regions are browsing mammals. Small- and medium-sized herbivorous mammals, such as rodents, lagomorphs and ungulates, are found in all regions except Australia, where marsupials replace lagomorphs and ungulates. Here browsing terrestrial kangaroos and wallabies and the arboreal phalanger, Pseudocheirus peregrinus, may add to the damage caused by the herbivorous insects.

The impact of large herbivorous mammals differs from region to region. California and Chile have very few large browsers and, perhaps as a result, the shrubs are generally not spinescent. In Chile the single large native browser, the guanaco Lama guanicoe is extinct in the matorral. The only large herbivore in California, the white-tailed deer Oedocoileus virginianus, appears to browse mainly on shrubs resprouting after fire. Several studies suggest that these deer feed so extensively on resprouting vegetation that they slow down plant succession and may even alter its course (P. Jordan, pers. obs.).

The small mammals of California and Chile are known to restrict their foraging to a narrow band surrounding their shrubby refuges, resulting in a bare zone around the shrubs in California (Bartholomew 1970) and bare zones or an alteration in the species composition of herbs. In Chile, for example, this results from the activities of mountain viscachas, Ligidium spp. (Fuentes & Etchegaray, in press).

In South Africa, small antelope are important browsers, selecting the protein-rich buds and flowers of many plants. Many plants appear to have evolved defence mechanisms to deter herbivory by these antelope: Norton (1980) records leaf- and stem-spines on several species of typical fynbos plants while Puttick & Glyphis (1980) showed that the high concentrations of polyphenols in strandveld plants appear to reduce herbivory by small antelope. Small browsing antelope are common in both nutrient-rich and nutrient-poor areas, while the larger grazing and browsing ungulates such as eland, bontebok and mountain zebra, are mostly restricted to vegetation growing on richer soils. Among the smaller mammals, two rodents that feed on foliage have been known to exterminate whole populations of some species of shrub (G. J. Breytenbach, pers. obs.). In areas where rocky shelters are available, the rock hyrax Procavia capensis may browse extensively on the surrounding vegetation (Norton 1980). Two species of mousebird feed primarily on the buds and young leaves of shrubs in nutrient-rich areas but are rare on poorer sites (P. Frost, pers. obs.). Three species of tortoise typical of fynbos (Greig 1976) feed on the lower strata of vegetation, but their importance as consumers is unknown. Generally, then, this array of herbivorous vertebrates is much larger and more varied than is that in any of the other mediterranean ecosystems, despite the fact that a number of very large mammals, including elephant, rhinoceros, hippopotamus, eland and kudu, no longer occur in fynbos.

7.2.2 POLLINATION

Insects act as pollinators in all mediterranean regions, a function also of nectarivorous birds in South Africa and Australia. Such birds are present, but appear to be less important, in California and Chile, where bees are the major pollinating agents. Certain plants in the nutrient-poor heathlands of Australia and South Africa are pollinated by small mammals.

Many South African plants exhibit characteristics suggesting coadaptation with avian and mammalian pollinators but very little is known about insects as pollinators. Pollination of Protea spp. by scarabaeid beetles and other coleopterans is inferred from the numbers and diversity of the beetles as well as from specializations enabling them to live on inflorescences, although no data are available.

More information is available on the role of vertebrate nectarivores as pollinators. Wiens & Rourke (1978) have described certain geoflorous proteas adapted to pollination by rodents; in all about 35 species of Protea are similarly geoflorous and may therefore be pollinated by rodents.

Although only four species of specialized nectarivorous birds occur in the South African fynbos, two of these are endemic to, and three are largely confined to, the fynbos heathlands on nutrient-poor soils; the fourth occurs only in the shrublands. Mostert et al. (1980) show that the energy requirements of the endemic Cape sugarbird, Promerops cafer, require each bird to visit a large number of flower heads daily, thus fulfilling an important requirement of any pollinator. The white eye Zosterops pallidus, a fifth species, is a generalized feeder wich takes nectar and may pollinate incidentally. However, the degree of coadaptation between Zosterops and the plant which it visits appears to be limited (P. Frost, pers. obs.). The diversity of bird-pollinated plants and the numerical abundance of nectarivores in fynbos heathlands contrasts with their paucity in shrublands on more fertile soils; in contrast to this, seed dispersal by birds, which is common in shrublands, is virtually non-existent in heathlands (P. Frost, pers. obs.).

In the fynbos heathlands the main plants that appear to be bird-pollinated are species of Erica, Protea and various geophytes such as Watsonia and Antholiza. Since very few studies have been carried out, pollination by birds must be inferred from morphological characteristics such as a tubular corolla and a bright colour, usually red or orange. W. R. Siegfried (pers. obs.) has studied the distribution and flowering phenology of various suites of species of Erica along altitudinal gradients in the fynbos and has correlated these with the altitudinal migrations of sunbirds. During the winter months the birds are limited by low temperatures to low altitudes, although during summer they can migrate to higher altitudes. There is a strong positive correlation between the flowering of tubular-flowered ericas thought to be pollinated by birds and these seasonal movements, but an inverse correlation between the flowering of ericas with globular flowers, which may be wind- or insect-pollinated, and bird movements. Thus globular-flowered ericas bloom during the winter at higher altitudes and during the summer at lower altitudes, so that flowering occurs during the most windy seasons at these altitudes.

Where neighbouring plants are distantly related genetically, as might be expected when animals disperse seeds some distance from the parent plant, the necessity for distant transport of pollen diminishes. This suggests that there is little need for elaborate out-crossing systems in fynbos shrublands, where wide dispersal of seeds occurs, while in heath communities, where such dispersal may be localized, efficient out-crossing becomes necessary for many plants. Plants like some of the ericas, which combine limited dispersal of seed with short-distance dispersal of pollen by insects or by wind, may be adapted to particular micro-sites or to soils with particular nutrient conditions; this may in turn favour partial inbreeding for the maintenance of specific adaptive gene complexes.

Nectar- and pollen-feeding birds are widespread in Australia, where pollination by birds and mammals is even more a feature of the mediterranean regions than it is in South Africa. Nectar- and pollen-feeding birds and mammals are particularly common on areas where the soils are poor in nutrients, although they also occur on richer soils, where species of Eucalyptus are the main plants visited (Milewski, in press). Honeyeaters (Meliphagidae), which are common throughout Australia, fill the same niche as the sunbirds and sugarbirds of South Africa, while several other species of birds have no counterparts in South Africa. These include lorikeets (Psittacidae), large honeyeaters and climbing marsupials (Christensen 1971; Ford & Paton 1976, 1977; Paton & Ford 1977; Burbridge et al. 1979; Kikkawa et al. 1979) such as the honey possum Tarsipes spencerae, which has a tubular mouth and a brush-tipped tongue and feeds entirely on nectar and pollen (Ride 1970). This marsupial is endemic to the south-western heath vegetation on nutrient-poor soils (Vose 1973; Hopper 1980). The honey possum is not merely an ecological counterpart of the pollinating rodents found in South Africa; mediterranean Australia also has several rodents and ground-living marsupials that take nectar as an incidental part of their diet (Carpenter 1978; Hopper 1980; Recher 1981) and that presumably aid in plant pollination as do the South African rodents.

7.2.3 PREDATION AND SEED DISPERSAL

Seed-dispersal by animals is of two main types. In the one, predominant in systems richer in nutrients, plants attract dispersers by producing fleshy fruits or by producing seeds bearing an attached eliaosome, a food-body rich in lipids and proteins. Fleshy fruits are dispersed by frugivorous birds and rodents while eliaosome-bearing seeds are principally dispersed by ants, many of which are highly specialized for doing this. In the other type, common in nutrient-poor systems, dispersal is a secondary consequence of the consumption or storage of seeds.

We first consider the individual aspects of predation and dispersal and then discuss the situations pertaining to both in different mediterranean ecosystems.

7.2.3.1 PREDATION

Mediterranean regions differ greatly in the types of seed present, in the length of time for which they are held on the plant and in their distribution on the ground. Not all of these differences can be correlated with differences in nutrient status. The types of seed-eating animals will obviously vary according to the types and availability of seeds. For example, although doves (Columbidae) and small finch-like birds (Fringillidae and Proceidae) take seed from the ground in all regions, parrots are the main seed-eaters in Australia, while mammals seem to be unimportant in this regard.

Patterns of predation are affected not only by the type of seed and the timing of dehiscence but also by fire and by the behaviour of animals. For example, the sudden flush of seeds released from woody fruits during or immediately after a fire may locally satiate seed predators so that some seeds escape and may germinate (Jacobs 1955). Ants feeding on eliaosomes attached to seeds may move seeds into the open, where rodents are reluctant to forage (O'Dowd & Hay 1980). Birds and mammals feeding on fleshy fruits defaecate intact seeds over a wide area so that concentrated supplies are not available to seed predators; other mammals may bury their faeces, incidentally interring the seeds they contain.

It appears that ants do not have the same significance in the other mediterranean regions that they do in Australia. Neither South Africa nor Chile (Hunt 1977) has a high density of ants, although seed predation may prove to be more important in South Africa than was previously estimated, just as myrmecochory is (see 7.2.3.2). North America has a rich ant fauna in its desert areas (Brown & Davidson 1977) so that presumably the ant richness in adjacent mediterranean regions is commensurately larger than it is in South Africa or Chile, although it still does not approach that of Australia.

Seedlings are presumably taken by small mammals and ground-foraging omnivorous birds in all the mediterranean regions, although little is known of seedling predation in any of these areas.

Underground plant propagules such as bulbs, corms and stem tubers occur in all mediterranean regions, although they are extremely rare in Australia and extremely common in South Africa, where they occur more frequently on nutrient-rich than on nutrient-poor soils. Many such propagules are consumed and must contribute to the overall level of loss to predators.

7.2.3.2 SEED DISPERSAL

The degree of correspondence between suitable germination sites and the density of seeds depends largely on the patterns of seed distribution generated by dispersal agents. Abiotic dispersal of seeds usually results either in localized, uniform seed shadows or in highly-undirectional and less uniform distributions. The patterns formed when dispersal is due to animals depend largely on the behaviour of the animal concerned. Distribution is often patchy, tending to be localized around middens or perch sites, and may often extend some distance from the parent plant.

Seeds dispersed by birds are usually concentrated around bushes whose fleshy fruits attract birds or around elevated perching sites such as dead trees. This localized dispersal gives rise to bush clumps which in turn serve as a focus for further bird activity and thus for further seed deposition. The size and complexity of.these clumps increases with age and with the number of plant species involved (P. Frost, pers. obs.).

Coevolution can be expected between plants and those seed-dispersal agents generating appropriate seed shadows, so that we would expect to find some agents being favoured over others. For example birds should be favoured over mammals in circumstances where long-distance, directional dispersal of seeds is advantageous. Ants may be favoured in systems where the establishment of propagules close to the parent plant is advantageous but where localized seed predation limits recruitment. Short-distance dispersal by ants can remove seeds from areas where seed predators are active (O'Dowd & Hay 1980).

Predators of seeds and seedlings modify seed-shadows, the impact depending on the abundance, diversity and food preference of the predators (see for example Keeley & Hays 1976). The probability of a seed or seedling surviving is inversely related to the abundance of predators, which in turn is related to the availability and proximity of appropriate cover (Jansen 1970; see also Hubbel (1980) for a discussion on the consequences for a community of the patterns of seed predation). Much more attention needs to be paid to the interplay of these factors and to their effects on the patterning of plants in mediterranean ecosystems.

7.2.3.3 PREDATION AND DISPERSAL IN MEDITERRANEAN ECOSYSTEMS

7.2.3.3.1 Australia Seeds of the common plants in mediterranean Australia are of two main types. Those produced by the Proteaceae, for example, grow on nutrient-poor soils and may be held in large woody fruits, remaining on the plant for up to ten years or until fire causes shedding. Many other plants, however, produce seeds in woody or leathery fruits (capsules in the Myrtaceae or pods in the Leguminosae) that usually dehisce soon after maturity. Members of the Myrtaceae generally produce numerous small seeds in woody capsules, irrespective of whether the soil is rich or poor in nutrients.

Parrots are the main seed-eating vertebrates, extracting seeds of Proteaceae and Myrtaceae while the woody capsules are still in the plant canopy (Kikkawa et al. 1979). Mammalian granivores are rare.

Insects as seed predators are apparently most common on nutrient-poor soils, although few data are available. In particular we need information on predation, as opposed to dispersal, by ants on similar soil in Australia and South Africa. The seeds of Proteaceae remaining on the plant are known to be heavily attacked by stem-boring insects in Australia (M. Specht, R. Black, pers. obs.) and the same may be true in South Africa. Insects other than ants feeding on fallen seeds include beetles and heteropteran bugs.

In Australia there is a large guild of seed-harvesting ants that are undoubtedly very important predators, particularly on the seeds of members of the Myrtaceae. The ants collect seed from beneath the shrubs or, to a limited extent, from the plants themselves. Ashton (1979), working outside the mediterranean region, has estimated that ants consume 90 per cent of seed produced by Eucalyptus regnans, the mountain ash.

Few plants in mediterranean Australia produce fleshy fruits attractive to vertebrates, even on the richest soils. On the other hand, the Australian continental ant fauna, with at least 2500 species, is one of the richest in the world; apparently in consequence, the flora has the highest known incidence of seed dispersal by ants (myrmecochory).

There are some 1500 species of myrmecochorous plants in Australia compared to about 300 known species of ant-dispersed plants in the rest of the world (Berg 1975; Matthews 1976), excluding the newly-discovered myrmecochorous plants in South Africa. Australian myrmecochorous plants invest considerable quantities of nutrients in the rich lipo-protein eliaosome attached to the seed. Foraging ants carry the seed, with its eliaosome, back to the nest, sometimes a distance of 200 m or more. Here specialized workers remove the food body and discard the seed on the ground above the nest. It has been suggested by Berg (1975) that the main advantage of myrmecochory is the protection from fire of seed located in subterranean ant galleries, although dispersal away from the parent plant may be equally important (O'Dowd & Hay 1980).

Although the occurrence of plants with food bodies attached to their seeds has not been compared on nutrient-rich and nutrient-poor soils, patterns of plant dispersal by animals do not appear to differ much on different soils in mediterranean Australia, in which case the situation is quite different from that in South Africa. The high level of species richness and the even distribution of plant species, characteristic of the nutrient-poor mediterranean regions of Australia, may in part be the result of the transport of seed by ants. Ants forage over wide distances and those collecting seed, either directly for the food in the attached eliaosome or incidentally as general scavengers, may drop individual seeds en route to the nest (M. Fox, pers. obs).

7.2.3.3.2 South Africa Seed types vary markedly according to soil conditions and this in turn affects the sorts of animals preying on seeds. On nutrient-rich soils the seeds of the common plants are relatively large and are borne in fleshy berries that reach the ground intact or in the faeces of fruit-eating vertebrates. Seeds of plants from nutrient-poor areas are small and seldom fleshy and are probably not attractive to vertebrates.

Consumption and boring of seeds by invertebrates must occur but no data are available on the taxa concerned or on their significance to plant communities.

Bulbs, corms and tubers, very common on richer soils, are taken mainly by fossorial rodents such as Cryptomys and Georychus. Cryptomys in particular feeds on little else (J. U. M. Jarvis, pers. obs.). Geophytes are also taken as in incidental part of the diet by francolins, baboons and porcupines, as well as by several other species of bird and rodent.

Many aspects of plant dispersal vary with the nutrient status of the soils in mediterranean South Africa. Until recently, seeds of virtually all plants on nutrient-poor soils were assumed to be dispersed passively by wind, gravity or water. Reliance on abiotic mechanisms was considered to be related to variations in topography or soil chemistry that would favour the establishment of seedlings on the site at which their parent was successful and to the fact that sites suitable for establishment of seedlings are generally unavailable in established vegetation. However, we are now becoming aware of the fact that myrmecochory is probably as important in South Africa as it is in Australia (Slingsby & Bond 1981). It appears that several hundreds of species of fynbos plants produce eliaosomes to encourage myrmecochory.

Seeds on nutrient-rich soils in South Africa are dispersed mainly by seven species of frugivorous birds. These include bulbuls (Pycnonotidae), mousebirds (Coliidae), doves (Columbidae), white-eyes (Zosteropidae) and thrushes (Turdidae), all of which disperse the seeds of most of the taller shrubs and trees in their faeces. The most specialized dispersers, the mousebirds, feed entirely on soft plant parts such as fleshy fruits and buds; dispersal distances are short owing to the behavioural and digestive characteristics of the birds. Other species such as the Rameron Pigeon *Columba arquatrix* may cover large distances when visiting widely scattered fruit-bearing trees such as *Olea*.

Some dispersal of seeds over longer distances is achieved in the faeces of mammals such as small antelopes, baboons and rock hyraxes (P. M. Norton, pers. obs.) and of a few species of fruit-eating birds but this type of dispersal is hardly more common than it is on similarly nutrient-poor soils in Australia. Other mammals also play some part in plant dispersal on nutrient-rich soils in South Africa. Small carnivorous viverrids and canids are known to eat fleshy fruits and thus presumably disperse some intact seeds. The significance of the fruit bat *Rousettus* sp. in seed dispersal is unknown.

By contrast, seed-eating mammals, birds and ants seem to play a very small role in dispersal. Only one species of rodent, *Saccostomus* sp., stores seeds, although incidental dispersal by other rodents, as well as by small birds, may occur while they are gathering nesting material. The fluffy pappus attached to the seeds of shrubby composites such as *Chrysocome*, *Eriocephalus* and *Elytropappus* are well adapted for dispersal in this way. Mole-rats are thought to disperse geophytic plants on both nutrient-rich and nutrient-poor soils in South Africa. These rodents may move bulbs, corms and stem tubers by as much as 200 m for storage in underground chambers close to their nests. Decomposition of nesting material may raise the nutrient status of the surrounding soils so that bulbs overlooked by the mole-rats would be able to resprout and might additionally benefit from the elevated levels of nutrients (K. C. Davies & M. Beviss-Chalinor, pers. obs.).

7.2.3.3.3 California and Chile Small birds and mammals are important seed-eaters in California and in Chile (Keeley 1977a; R. D. Quinn, pers. obs.) but birds are thought to have a relatively greater impact in Chile, where they are more diverse and where there are fewer seed-eating mammals than in California, where the reverse is true (Cody & Mooney, 1978). No single type of seed appears to dominate in Chile, where several of the common shrubs produce fairly large seeds dehiscing from leathery capsules held only briefly on the plant. While still green, small, windblown achenes, common on nutrient-rich soils in California and South Africa as well as in Chile, are eaten, mainly by small finch-like birds.

The impact of small seed-eating rodents seems to be greater in California than in any other mediterranean region. Here squirrels and other small rodents eat bulbs and seedlings, although their most important role stems from their propensity for burying caches of nuts, acorns and other seeds. A proportion of these seeds may subsequently escape the attention of predators, eventually germinating and becoming established *in situ*. This in turn results in the clumping of shrubs. Further, many of these rodents have cheek pouches in which they accumulate seeds, some of which may be dropped on the way to the store or nest. Chilean rodents do not have this facility, resulting in a lesser impact on the vegetation. Fossorial rodents, *Thomomys* spp. in California and *Spalacopus cyanus* in Chile, feed on the few bulbs, corms and tubers available.

Seeds are dispersed abiotically and by birds and mammals in mediterranean California. Large, fleshy fruits containing numerous small seeds are dispersed mainly by birds. Rodents are important due to their habit of burying caches of bulbs, acorns and other seeds, although dispersal may also result from the propagules being dropped en route to storage places. Seeds may be dispersed in this way both above the ground by seed-eating rodents and below the ground by burrowing rodents similar to South African mole-rats.

The role of ants is poorly known here and, as in other mediterranean regions, warrants further investigation.

Mechanisms of seed-dispersal are poorly known in mediterranean Chile and few animals seem to be specialized for this task. Few rodents feed mainly on seeds; squirrels are absent and the others do not have cheek-pouches; caching of seeds has not been recorded. Presumably some seed is dispersed accidentally or in the faeces of animals such as the fox Disicyon sp., which takes fruits as an incidental part of its diet (E. R. Fuentes, pers. obs.). The fossorial rodent Spalacopus cyanus probably disperses bulbous plants, as mole-rats do on other continents.

7.3 BROAD ECOLOGICAL CONSEQUENCES OF ANIMAL ACTIVITY

7.3.1 DETRITIVORY AND SOIL MOVEMENT

As well as interactions between animals and the plants themselves, the activity of detritivores and burrowers may have a major impact on ecosystems. They are particularly significant in the nutrient-poor mediterranean regions of Australia and South Africa.

7.3.1.1 TERMITES IN AUSTRALIA AND SOUTH AFRICA

Termites have been called "the earthworms of the southern hemisphere" (Drummond 1886). The analogy is not exact but they are nevertheless very important in resorting soil horizons, aerating soil, comminuting organic matter and accelerating nutrient cycling.

Termites are numerous in most Australian and many South African ecosystems. But since termites prefer heavy soils, mound-building forms are uncommon in mediterranean regions. Where they do occur, they tend to have subterranean colonies or to inhabit living plants, either in arboreal nests or within the boles of trees and shrubs.

Wood-eating termites feed either on dead heart-wood or on the woody component of litter, both of which are particularly low in protein. Recent investigations (French et al. 1978) have shown that symbiotic gut bacteria fix N in all the Australian species studied so far. Nonetheless chemical analyses (Lee & Wood 1971) have failed to show a significant increase in the N content of the soil in the nest in comparison with that of surrounding areas. On the other hand, analyses in a very nutrient-deficient area have shown significantly higher N:P ratios in structures made by termites than in those of their main food source (M. Fox, pers. obs.). Where woody litter accumulates slowly and is prone to fire, very large quantities of N may be volatilized and thus lost from the system (Rundel, in press). Thus the rate at which this litter is decomposed, and particularly the rate at which it is removed from the surface of the soil and taken underground, will determine the amount which is lost in fires. Obviously the more impoverished the soil, the more significant this becomes. Termites feeding on wood or litter, and sometimes those feeding on grass, are the main agents influencing the rate of return of nutrients to the soil.

7.3.1.2 THE IMPACT OF FOSSORIAL MAMMALS

Fossorial rodents (mole-rats, gophers and coruros) occur in the mediterranean regions of South Africa, Europe, California and Chile but not of Australia; burrowing animals were once abundant in mediterranean south-western Australia but have been greatly reduced by clearing and by introduced predators. Burrows can be extensive, reaching a length of 250 m or more and running 15-30 cm below the surface, with nesting areas at a deeper level. Excavated soil is pushed onto the surface and plant material for food and nesting is carried underground. Subterranean rodents profoundly influence microtopography, which in turn affects water runoff, as well as influencing the physical and chemical structure of soil. Data are not available for the rates at which these animals turn over soil in most mediterranean regions but some idea of their impact can be gained from work on Spalax sp., a Mediterranean mole-rat, which moves earth at a rate of 13-15 m^3 km^{-2} yr^{-1}. Such turnover of soil by vertebrates is of greatest significance in ecosystems lacking deep-rooted plants and those in which soils are low in nutrients. Available evidence suggests that plant productivity, soil hardness and the rate of nutrient cycling, as well as the resulting degree of sclerophylly, may all be influenced by the presence or absence of subterranean rodents (Milewski, in press).

7.3.2 PATTERNING

In most mediterranean ecosystems, germination and the establishment of seedlings are largely dependent on the availability of soil moisture, of nutrients and of light, since most seeds are small and therefore cannot be independent of external conditions for long after germinating. Thus patterning in mediterranean communities is largely the consequence of the temporal and spatial distribution of suitable germination sites, as well as of the method of seed dispersal (and consequently of the shape of seed shadows), of the modification of these patterns by seed predators and of the competitive pressures exerted on seedlings by established plants. Thus, for example, shrubs whose seeds are dispersed by birds tend to form clumps; wind-dispersed shrubs become established in these protected areas after the bird-dispersed ones have become large enough to form a wind-shadow (E. R. Fuentes, pers. obs.).

Termitaria in tropical Africa reach impressive proportions and may contribute to, or be a major determinant of, patterning of shrub communities: the sites even of old termitaria in tropical savannas are characterized by unique floras (Malaisse 1978). Large mounds, thought to be the remains of old termitaria, are strongly associated with patterned plant distribution in mountain fynbos, even though present-day termitaria are small and do not appear to influence the distribution of plants to any great extent.

Several species of mammal deposit their dung at special midden sites, producing nutrient-rich patches that are often associated with particular plants. In mountain fynbos, for example, Carpobrotus and Solanum are nearly always found in association with dung heaps used by small antelope to mark their territories, suggesting that such plants require nutrient-enriched soils (P. M. Norton, pers. obs.). Rock hyraxes also accumulate dung near their shelters, providing enriched conditions, as well as a means of dispersal for their seeds, for Solanum and Diospyros. Many other species of shrubs are usually associated with rocky outcrops. Dispersal of their seeds may be dependent on animals that use these sites as refuges.

7.3.3 INTRODUCED SPECIES

The introduction of exotic animals into mediterranean regions has generally not had the same disastrous consequences as has the introduction of exotic plants. Nonetheless there are a number of examples of the detrimental consequences of such introductions.

It seems that bees introduced into Australian heathlands might have a effect on the reproductive performance of some plants: the bees cut through the base of the corolla to get at the nectar, rather than passing the anthers and stigma as native bees do. This would lower the reward available to native pollinators and might therefore change the pattern and frequency of visits, lowering the likelihood of pollination and thereby reducing seed-set.

Introduced rabbits in mediterranean regions of Australia and Chile cause patterning in populations of annual herbs and perennial shrubs. Selective feeding, usually localized around suitable cover, together with nutrient enrichment of warren areas and around dung piles, leads to alterations in the nutrient status of the soil. This might produce conditions suitable for the establishment and persistence of plants requiring high levels of nutrients (Fuentes & Etchegaray, in press).

The dispersal of exotic plants can also be enhanced by the native fauna. In South Africa the seeds of introduced acacias, particularly of *Acacia cyclops*, are extensively dispersed by birds (Glyphis *et al*. 1981) and mammals, especially baboons (Davidge 1977). These vertebrates might then be particularly important in the spread of such alien plants.

In South Africa, millipedes and snails fom the Mediterranean Basin are very common, although the impact of these exotic invertebrates has yet to be documented. Preliminary investigations suggest that the exotic Argentine ant may be critically important in fynbos, in that they outcompete local myrmecochorous ants and may therefore have a marked impact on seed dispersal, germination and protection from fire (P. Slingsby, pers. obs.).

7.4 FURTHER WORK

There is perhaps no reason to expect that climatically similar areas on continents with very different histories should have a similar number or biomass of, say, birds, insects or berries. It might be more fruitful to ask if organisms filling similar niches, such as pollinators, frugivores or herbivores, occur in comparable numbers or biomass, regardless of the taxonomic groups to which they belong. If the biomass of frugivores is less in some systems, is there a concomittant increase in the biomass of non-frugivorous seed dispersers or predators? These and related questions can be addressed when comparing any ecosystems, but the answers would be especially informative from mediterranean regions, the vegetations of which are similar but the evolutionary histories of which are quite dissimilar.

Much more work is required to verify and clarify the patterns we have outlined here. Comparisons between mediterranean ecosystems require quantitative data which do not yet exist. We know a good deal about the numbers of species in most communities but the impact of any one species, or guild of species, may depend on its abundance relative to that of another which produces or uses the same resources, or fills similar niches. Valuable quantitative data could fairly easily be obtained on the abundance and biomass of seeds, fruits, nectar and bulbs. Data would be more difficult to obtain on the densities of various groups of animals such as seed harvesters, frugivores, herbivores, fossorial mammals and termites, and on the quantities of soil turned over, of litter produced or of detritus consumed by fossorial animals of various sorts; however these data are essential for any comparative analyses.

The importance of animals in the nutrient cycles of mediterranean ecosystems has not been examined. Further, although studies suggest that physiognomic characters such as spinescence and high concentrations of secondary compounds are adaptations to pressure from herbivores, we do not know the extent to which herbivory affects the composition of mediterranean plant communities. Comparative data on nutrient levels and on levels of secondary compounds in the soil, in plants and in litter should go at least part of the way towards quantifying and clarifying these relationships, as should experiments designed to determine the nutritive value to animals of plants growing on soils of different nutrient status. Only when such data are available will it be possible to understand the influence of the nutrient status of soils on the interactions between plants and the animals living with them.

7.5 CONCLUSIONS

1. Convergence at a taxonomic level is not apparent in the faunas or in the frequency of occurrence of the different plant-animal interactions in the various mediterranean ecosystems. In fact we question whether we should expect the details of such interactions to be similar in systems with entirely different histories. We suggest instead that convergence is more likely to occur at a functional level and expect to find similar proportions of animals acting for example as dispersal agents or pollinators, regardless of taxon, and in the proportions of resources allocated by plants to defence against herbivory, or for attraction of pollinators or of dispersal agents.

2. Climate and the nutrient status of the soils seem to determine plant-animal interactions within broad limits only, since such interactions differ even on soils of similar nutrient status. On the other hand, animals seem to determine the more specific characters of the plant communities in that different animal taxa form the major herbivores, predators, pollinators and dispersal agents in mediterranean ecosystems.

8. ORIGIN AND MAINTENANCE OF PLANT SPECIES DIVERSITY

D. Tilman (convenor), W. J. Bond, B. M. Campbell, F. J. Kruger,
H. P. Linder, A. Scholtz, H. C. Taylor, M. Witter.

This chapter considers the features of mediterranean ecosystems that may be important in the origin and maintenance of high plant diversity. In particular, we consider local species richness (alpha diversity in the botanical sense) and the composition of the entire flora of the different ecosystems (regional diversity). We then explore the possible causes of these patterns by considering the mechanisms whereby local species diversity is maintained, the geographical factors correlated with high regional diversity, and the factors influencing rates of speciation and extinction in mediterranean ecosystems. We suggest that soil nutrients and other limited resources, such as moisture and available open sites, may be important variables in the origin and maintenance of plant species diversity.

The concept of species diversity, as used in this chapter, needs some discussion. Although we use the term "diversity" in the title, we often measure diversity in terms of the numbers of species (i.e. species richness) and we define the species richness of an area as the number of species living in that area. Since the term "diversity" has slightly different meanings in the botanical and zoological literature (see the preface for a brief discussion), we use the common term "species richness" to avoid ambiguity.

We consider vascular plants only, and ignore plants whose seeds or bulbs alone are present. Although this restriction is necessary for easy comparison of patterns of species richness, it largely ignores the problem of the "regeneration niche" (Grubb 1977) as is seen, for example, in the short-lived "fire herbs" of chaparral (Christensen & Muller 1975).

8.1 PATTERNS OF SPECIES DIVERSITY IN MEDITERRANEAN REGIONS

8.1.1 SPECIES RICHNESS (ALPHA DIVERSITY)

Naveh & Whittaker (1980) have suggested that plant communities in the heathlands of the southern hemisphere have higher levels of species richness than do any other temperate communities with the exception of certain heavily-grazed Israeli woodlands and shrublands, which are particularly rich in annuals. This assertion can be explored at least partially using data presented in Table 8.1, which lists species richness for 0,1 ha sites in various mediterranean and other ecosystems. The data are not always entirely comparable, since at least one study excludes geophytes and annuals. Moreover some of the data may reflect a tendency for research on, or preferential reporting of, data from unusually diverse habitats. Thus although these data are suggestive of possible trends, much further descriptive work is needed before any firm conclusions can be reached.

TABLE 8.1 Species richness in mediterranean and other ecosystems on plots of 0,1 ha.
+ = nutrient-rich, - = nutrient-poor.
From Werger (1972), Peet (1978), Whittaker (1977), George *et al*. (1979), Whittaker *et al*. (1979), Naveh & Whittaker (1980), Bond (in press)

MEDITERRANEAN ECOSYSTEMS	Nutrient Status	Number of species			No. of plots
		Average	Minimum	Maximum	
South Africa					
Fynbos heathland *	-	68	31	128	52
Renosterveld shrubland	+	66	28+	105	2
Karoo shrubland & succulents *	+	43	23	62	9
South-western Australia**					
Heath	-	61(69)	37(43)	92(104)	32
Mallee	+	51(64)	39(44)	68(77)	16
California					
Chaparral*	+	28	16	34	10
Israel					
Maquis	+	65			2
Open shrublands	+	139	118	179	3
OTHER ECOSYSTEMS					
Arizona shrublands	+	37	33	41	2
Sonoran desert scrublands	+	63			1
New South Wales grasslands	+	55			1
British grasslands	+	89			1
Tenessee heathlands	-	21	20	23	2
North Carolina woodlands	+	97	85	115	4

* Seasonal plants excluded. Not all authors are clear on this point.

** 0,05 ha plots. Species numbers increase on average by 12,5 per cent between 0,05 and 0,1 ha plots in a study in Cape fynbos (Bond, in press).
Assuming alpha diversity of Australian heath responds similarly, figures in brackets give equivalents for 0,1 ha plots

Comparisons (Table 8.1) show considerable variations in species richness even within a single mediterranean ecosystem. For instance within the South African fynbos, on 0,1 ha plots, the average species richness is 68, with the least diverse of 52 plots having 31 species and the most diverse having 128. Figures for south-western Australian heathlands range from 42 to 104 with an average of 68. The reasons for such large variations within an ecosystem are poorly understood and deserve much further research; they are discussed in section 8.3 below.

The large variations in species richness make comparisons between mediterranean ecosystems difficult when there is no information on the way in which study sites were chosen. The data in Table 8.1 nevertheless indicate some patterns. The heathland floras of the Cape and south-western Australian are very similar, with averages of roughly 60-70 species. That of one Israeli site falls within this range, while that of another is approximately double and that of Californian chaparral is apparently about half; note, however, that the data for California exclude post-fire herbs, which may represent 40-80 per cent of the flora of a large chaparral stand (Vogl & Schorr 1972; Christensen & Muller 1975). If annuals also were considered, then the species richness of chaparral would probably be more comparable to that of the other mediterraneran ecosystems. Thus the available data suggest that, for plots 0,1 ha, these regions do not differ greatly in species richness.

A number of authors have suggested that species richness increases on nutrient-poor soils. Others have found it to be lower, for example on heathlands in comparison with limestone grasslands in Britain. The nutrient-poor heaths and mallee heaths in the Barrens, south-western Australia, have 95 and 58 species respectively, whereas adjoining mallee open-scrub and closed forest on richer sites have averages of 35 and 21 species (Newbey 1979). Similar tendencies for plants on nutrient-poor soils to be rich in species have been reported by Huston (1979, 1980) and Tilman (in press) for other ecosystems.

The null hypothesis, suggesting comparable species richness in communities on nutrient-rich and nutrient-poor soils in mediterranean and in other temperate communities, is not disproved in every case. The evidence from fynbos and from other South African vegetation types is equivocal because of some fynbos stands that are exceptionally rich and others that are poorer than Knysna Forest, Valley Bushveld, Karroid Shrublands or Grassveld, for example (Bond, in press). There is no unanimous agreement on what constitutes a "nutrient-poor" soil. The Australians use values of P and N. Soil scientists would probably use S-values (the sum of exchangeable Ca, Mg, Na, K). Older literature may use "per cent base saturation": Kruger (1979) suggests that this is low for fynbos soils but work in preparation shows that fynbos occurs on highly-leached and base-satured soils (W. J. Bond, pers. obs.). Bond (in press) has found no relationship between species richness in 0,1 ha plots and any of the usual nutrient measures. In smaller areas (1-5 m^2) the number of species increases with increasing plant biomass but decreases again in dense, high-biomass vegetation. Most of the variation in biomass and in numbers is associated with rainfall but does not correlate with low levels of P or of N. S-values are related to rainfall, with lower S-values in high-rainfall areas due to leaching. There is a weak relationship between S-value, biomass and numbers on small plots but Bond believes this to be secondary. In other words, it seems that species richness in small areas is related to productivity, which is controlled primarily by rainfall in the southern Cape fynbos. This view is closer to the hypotheses of Huston (1979) and Grime (1973) than to Tilman's (in press) deterministic, mechanistic equilibrial model of resource competition.

Bond (in press) has further questioned the value of 0,1 ha plots in comparing species richness of different communities. Although he was able to demonstrate environmental control of species numbers in small plots ($1-5m^2$) in fynbos by correlation methods (see above), no significant relationship with environmental variables could be detected in larger plots. He suggested that the number of species in larger plots is a compound of the number of species coexisting in small areas and of habitat heterogeneity (patchiness), both of which may vary independently and for different reasons. Diversity studies should then consider both the numbers of species in small plots and the rates of change in numbers with increasing plot size: 0,1 ha plots include components of both species richness and species turnover (beta diversity).

8.1.2 REGIONAL DIVERSITY

The data available for comparing the total number of species of the different mediterranean regions are difficult to interpret. The floristic regions have not been defined using comparable climatic boundaries and their surface-areas differ considerably. The data shown in Table 8.2 suggest that the regional diversities of California and of south-western Australia are approximately equal in the number of species, and are about half that of the South African mediterranean region, although this covers a much smaller area. This twofold difference in diversity between the South African and the other mediterranean ecosystems cannot be explained by differences in species richness alone but may be explicable in terms of differences in topography and age, or of other factors discussed in section 8.3 below.

8.2 MAINTENANCE OF SPECIES RICHNESS

The data given in Tables 8.1 and 8.2 provide an intriguing challenge to current ecological theory. No rigorously-tested theories are available that could explain the stable coexistence of 30-120 species in an area of 0,1 ha or the occurrence of 2000-8000 species in an area of about 300 km^2. It would seem that the causes of differences in regional diversity will only be understood when we know the mechanisms that allow the local coexistence of numerous species. For this reason, let us explore the factors influencing the maintenance of species richness.

High levels of species richness may reflect a state of equilibrium resulting from interspecific interactions such as competition, predation and herbivory, or it may result from stochastic, non-eqilibrial processes such as immigration, extinction and incomplete competitive displacement. It is thus necessary to determine the relative importance of these factors.

Species richness may be maintained because of competitive interactions between species for various limiting resources such as nutrients, light, water and space. Assuming that the availability of all possible limiting resources is spatially uniform, and assuming that species respond to these resources in a linear manner, then theory predicts a simple relationship between species richness and availability of resources. There can be no more species coexisting at equilibrium than there are limiting resources. Of the coexisting species, each should be limited by a different resource (MacArthur 1972).

Fertilization experiments by Specht (1975) in Australian heath showed that of all the minerals, only P and N were limiting to any of the 40 or

TABLE 8.2 Regional diversity in mediterranean regions. From Goldblatt (1978), Taylor (1979), Lamont (in press)

	Area (10^3 km^2)	Number of genera	Number of species
Cape Floristic Region	89	957	8550
Cape Peninsula	0,67	533	2256
South-western Australia	320	287	3600
California	324	795	4452

TABLE 8.3 Endemism in mediterranean and other regions. From Stebbins & Major (1965), Goldblatt (1978), Hopper (1979)

	Area (10^3 m^2)	Per cent endemic genera	Per cent endemic species	Species/ genus
Africa excluding Cape	2573	21	70	7.7
Cape Floristic Region	89	21	73	8.9
South-western Australia	320	25	68	8.0
California	324	6.3	48	5/6

more species coexisting in experimental plots, thus quickly eliminating the hypothesis based on spatial homogeneity of the habitat and simple responses of species to their resources.

A modification of the hypothesis of nutrient competition (Tilman 1980, in press), which considers small-scale spatial diferences in nutrient supply rates, makes quite a different prediction. It suggests that the physiology of each plant allows it to grow optimally when limiting nutrients are available in specific proportions. Where nutrients are limiting, coexistence can occur when each species differs in the optimal ratio of nutrients it requires, if such ratios differ in different microsites within the habitat. As long as the spatial heterogeneity of a habitat includes areas where the nutrient ratio is optimal for a particular species, that species will be able to occur. Thus any factor which increases the range of availability of limiting nutrients, and of other resources, should increase the number of species that coexist in a particular locality. If the ratios are most variable in low-nutrient environments, then species richness should be highest in habitats moderately poor in nutrients and having just enough nutrients for the survival of most species, assuming that competition is minimal. Thus the hypothesis predicts that a graph of local species richness against the resource-richness of the soil would give a "peaked" or "humped" curve with maximal species richness in habitats moderately poor in nutrient resources (Figure 8.1). This hypothesis can be tested in several ways. Firstly, the relationship between species richness and nutrient availability should give a humped curve. Secondly, application of mineral fertilizers should lead to decreases in species richness if nutrients are naturally limiting. Thirdly, a different group of species should tend to dominate after fertilization of the soil, depending on the ratio of nutrients in the fertilizer. Some studies have already been performed in mediterrranean ecosystems but none has been of sufficient duration or completeness to clarify the role of nutrients in determining species richness.

An alternative hypothesis for explaining species richness emphasizes the non-equilibrial nature of plant interactions and the importance of disturbance in preventing competitive displacement (Connell 1978; Huston 1979). Any resource which limits extremes of growth rates will limit the rate of competitive displacement. Displacement rates would thus be slower on nutrient-poor than on nutrient-rich sites and the number of coexisting species would be greater on the poorer soils. The theory incorporates observations on the significance of disturbances such as fire and herbivory in maintaining species richness (Harper 1969; Grubb 1977). Long periods without disturbance would lead to a reduction in the numbers of species through competitive displacement; similarly, only a few species could survive very short disturbance cycles. Intermediate levels of disturbance would allow the maximal number of species to coexist.

Tilman's view differs in that he considers space to be a limiting resource, and suggests that disturbance would lead to a humped diversity curve as would supply rates for any other limiting resource.

Fire is a major cause of disturbance in mediterranean ecosystems, where a successional sequence of species follows fires. The "intermediate disturbance" hypotheses of Connell, Grubb, Huston and Tilman suggest that studies on the role of fire in mediterranean regions must include data on the frequency and extent of fire. An adequate test of this hypothesis would require controlled burning of various sites over a prescribed range of time periods. Because fire also affects the availability of nutrients, these would have to be monitored and various nutrient treatments included within the burn schedule.

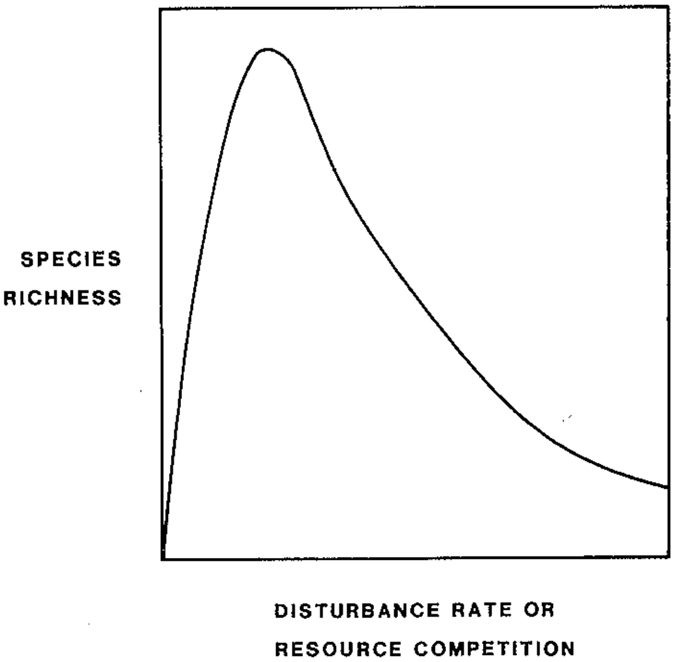


Fig. 8.1 A peaked or humped curve for species richness, as illustrated above, is predicted by numerous theories such as that of resource competition in spatially heterogeneous habitats (Tilman, in press), the intermediate disturbance hypothesis (Connell 1978) and the theories of disturbance proposed by Huston (1979) and Tilman (in press)

Predictions suggest that disturbance and fertilization should have similar effects because both processes increase the supply of limited resources. Similarly, on theoretical grounds we can predict that the level of species richness could depend on the availability of any resource, be it a nutrient, space, light or water. This suggests that experimental studies are to be preferred to correlational studies in the field, since the availabilities of various resources are apt to be interrelated, making it almost impossible to distinguish the effects of any one in particular. Using a combination of correlational and experimental studies it should then be possible to determine whether competition for limiting resources is important in allowing the local coexistence of numerous species. It should be mentioned that other hypotheses using quite different mechanisms might similarly predict that species richness is dependent on nutrients; these are discussed in section 8.3.

The hypotheses of Tilman (in press), Connell (1978) and Huston (1979) suggest that high levels of species richness may result not only from differences in the requirements of species for nutrients, light, water and other limiting resources, but that differences in response time after disturbance may also allow coexistence. These, then, are hypotheses concerning niche-partitioning by plants. There are many other ways in which plants may partition their environment. For example, rooting systems may differ in such a way that plants exploit different soil masses. Microsites may differ sufficiently in pH, aspect, soil texture and so on, as well as in levels of available nutrients, that species may be separated accordingly. Such alternative hypotheses of niche partitioning must also be explored in any study of the maintenance of species richness.

Two other biotic processes deserve investigation because they are possibly important in allowing local coexistence of species. These factors are species-specific mortality, such as the "seed predation" hypothesis of Janzen (1970), and preferential herbivory on the species which are the superior competitors (Lubchenco 1978). Lubchenco has presented experimental support for her hypothesis: her data show that maximal species richness occurs at intermediate rates of herbivory, giving a humped curve of species richness against grazing rate. As herbivory is a form of natural disturbance, Lubchenco's result can perhaps be considered to support the "disturbance" hypothesis.

Finally, the null hypothesis for explaining species richness is that the number of species is a function (or sample) of the size of the source flora. In any sample (community) of a very rich flora, one would assume a larger number of species than in a poor flora (Connell 1978). The size of a flora may, of course, have nothing to do with species interactions at the community level.

The various views of the processes that can maintain species richness often make similar predictions. However, since they embody different assumptions and postulate different mechanisms, they must be tested experimentally before they can be used to form a theory of the causes of species richness. A predictive theory is of some importance, not only for scientific reasons, but also for any management scheme which has as one of its goals the maintenance of species richness and the preservation of natural flora. Intensive studies of the factors determining species richness are needed in a variety of areas both low and high in diversity. Such studies must examine the importance of nutrients, light and water and also the significance of competition, of disturbance and of local immigration and extinction.

8.3 SPECIATION, EXTINCTION AND ENDEMISM

Diversity in mediterranean ecosystems has both a quantitative aspect, the number of species, and a qualitative one, the number of species unique or endemic to each. Endemic species may have two origins: they are either relictual (refugial) or represent relatively recent speciation. Thus one component of the differences between mediterranean ecosystems may be differences in intrinsic rates or modes of speciation and extinction, or of migration from points of speciation. These processes of speciation, extinction and so on can best be studied by comparing the proportion of relictual and recent species in the different mediterranean ecosystems, because such species represent unique products of each.

Data on endemism in mediterranean ecosystems are compiled in Table 8.3. Considering its relatively small area, the Cape Floristic Region has a very high percentage of endemic plants (73 per cent) in comparison to that of other areas for which data are available, and is comparable with highly isolated floras such as those of Hawaii (85 per cent) and New Zealand (73,1 per cent) (Goldblatt 1978). Generic endemism is high in the Cape (21 per cent) and south-western Australia (25 per cent), and approximately twice that of other areas of notably high specific endemism (12,3 per cent in Hawaii and 9,9 per cent in New Zealand). Because the area surrounding the Cape region also has an unusually large number of endemics, the high specific and generic endemism of the Cape may be a function of its biogeographic history and not necessarily a function of its mediterranean climate.

8.3.1 HYPOTHESES CONCERNING ENDEMISM AND SPECIES RICHNESS

A number of hypotheses, several of which are mutually exclusive, have been suggested for explaining the high levels of endemism and the large numbers of species in each mediterranean region. These are summarized below.

8.3.1.1 AGE

Elements of the Cape and Australian heathland floras have Gondwana derivations and their great age is invoked as a explanation of their high levels of species richness (Levyns 1964; Goldblatt 1978; Naveh & Whittaker 1980). This does not however, explain the high diversity in the younger mediterranean regions.

8.3.1.2 ENVIRONMENTAL STABILITY

Competitive interactions over evolutionary time may lead to specialization resulting in narrow niches, dense packing of species and survival of relics. This is a variation of the "age hypotheses" and suffers from the same drawback.

8.3.1.3 ENVIRONMENTAL INSTABILITY

Hopper (1979) has argued that erosional dynamics would produce a mosaic of landforms and soils. He observed that the highest speciation rate in south-western Australia was in areas with a history of active erosion and that relics on ancient land surfaces contributed little to the total flora. Thus he suggested that environmental instability would promote bursts of speciation. Emergence of new landforms along the coast and, more distantly, continental uplift in the middle and late Cenozoic might have had similar effects in the Cape (Axelrod & Raven 1978; H. C. Taylor 1978). In addition, Stebbins (1952) suggested that transitional climates such as mediterranean ones have high rates of speciation with high population turnover and more frequent rates of isolation, migration, extinction, confluence and possibly of hybridization than in more stable climatic zones. Climatic changes in the Pleistocene have been widely invoked as providing a mechanism for the isolation and subsequent speciation of populations (Axelrod & Raven 1978; Goldblatt 1978; Hopper & Martin 1978; H. C. Taylor 1978; Hopper 1979).

8.3.1.4 TOPOGRAPHIC DIVERSITY

The topographic complexity of the Cape has been postulated as a major reason for the high floristic richness of the region; variation in the soils and geological formations (shale, sandstone, granite) would contribute to this diversity (Levyns 1964; Goldblatt 1978). This hypothesis also offers an explanation for differences in floristic richness between the Cape and south-western Australia, the Cape having steep altitudinal gradients and south-western Australia generally being rather flat. This is a difficult hypothesis to test, but it is possible to obtain some information by comparing floristic richness in landscapes of comparable topography and of comparably uniform substrates and precipitation gradients in the various mediterranean regions. Geomorphological indices incorporating variability in altitude, relief and rainfall have been developed and might be used as a first approximation of habitat heterogeneity (see, for example, Holland 1978). Alternatively, floras on landscapes of low relief might be compared in south-western Australia and in the Cape (Milewski 1979).

8.3.1.5 NUTRIENT POVERTY

This hypothesis suggests that the heathland floras on nutrient-poor soils were pre-adapted to increasing aridity and to the onset of a mediterranean climate by features, such as long leaf duration and small leaf size, originally adapted to the poor soils (Small 1973; Hopper 1979; Cowling & Campbell 1980). This may explain the greater persistence of ancient taxa in Australia and in the Cape and hence the more diverse genetic stock able to radiate in the Pliocene and Pleistocene.

8.3.1.6 OVERSATURATION - FYNBOS AS AN ISLAND

Levyns (1964) and Axelrod & Raven (1978) have suggested that in previous pluvials the Cape flora extended far into what are presently arid biomes to the north. With increasing aridity the flora, leaving scattered outliers, has retreated into the island-like sandstone mountains of the south. Kruger & Taylor (1979) reported species-area curves in fynbos which are unusually steep and comparable to biotas of islands rather than of continents. The richness of the Cape flora may thus be due to lower rates of extinction rather than to the more rapid rates of speciation.

8.3.2 DISCUSSION OF THE HYPOTHESES

Central to these six hypotheses is the question of the mode of origin of species in mediterranean ecosystems. In order to choose between these hypotheses it will be necessary to know the answers to a number of questions.

1. Do relictual and migrating species contribute differentially to the modern floras of different mediterranean ecosystems?

2. Have the environmental stresses peculiar to mediterranean regions (summer drought and relatively low levels of nutrients) resulted in the evolution of numerous highly-localized species which narrowly subdivide the available habitat?

3. Did the dissected topography of some mediterranean regions, and possibly the associated climatic fluctuations in the Pleistocene, result in the evolution of species occupying similar niches but isolated by geographic barriers?

8.4 FURTHER RESEARCH

The review and discussions on mediterranean ecosystems that led to this chapter have raised numerous questions which we believe should be considered.

1. To what extent do the differing species compositions of small areas (1-5 m^2) depend on the differing ratios of their limiting resources?

2. How much of the variation in species richness within a local habitat can be explained by equilibrial processes and deterministic competitive exclusion models and how much of it can only be explained as the result of stochastic, non-equilibrial processes such as local immigration or extinction?

3. How are species composition, dominance, and diversity affected by the period, intensity and spatial extent of fires?

4. What are the rates and specificities of herbivory and predation and what role do these play in structuring plant communities?

5. To what extent do the observed patterns of species richness depend on the taxonomic or functional groups which have been included in the available estimates of diversity? How different would patterns be if all plant species, including soil algae as well as mosses and lichens, were to be considered?

6. If there is a desire to increase the productivity of a managed site, must such an increase necessarily lead to decreased plant species richness, or would it be possible to impose regimes of fire, grazing and fertilization which would maintain plant species richness?

Hypotheses explaining the floristic richness of an entire mediterranean region are not easily tested. However, local extinction and speciation, both of which contributed to differences between mediterraean ecosystems, must also be investigated. Such studies might best start by investigating demographic patterns in the life-histories of plants, both rare and common, on sites differing in nutrient status.

In order to answer these questions it is going to be necessary to study patterns of diversity in some detail. It is highly desirable that other information be obtained at the same time. Data should thus include measures of total, available and mineralizable nutrients (for at least N and P), together with the pH and size fractions of the soil, as well as estimates of total local standing crop, productivity, herbivory and fire history. In at least some cases this additional information should be collected for numerous adjacent microsites (1-5 m^2) so that small-scale patchiness can be quantified. Such descriptive data are essential to an understanding of the mechanisms controlling diversity at all levels and it is only when such mechanisms are understood that intelligent management schemes can be devised.

Hypotheses concerning the control of species richness may make predictions that are similar but that are based on entirely different assumptions and that involve entirely different mechanisms. Correlational information alone will not be sufffficient to distinguish between them or to explain the mechanisms controlling local species richness and the processes influencing extinction of rare or endangered species. Only carefully-controlled experiments, using fertilization or burning for example, and replicated at several points along major environmental gradients such as altitude, nutrients and moisture, will provide this information. Such studies should include experimental manipulations of the levels and ratios of nutrients, of water availability, of the timing, intensity and extent of disturbance and of the rate of seed immigration, predation and herbivory.

8.5 CONCLUSIONS

Available data (Tables 8.1 and 8.2) suggest that mediterranean regions are generally similar in species richness, values for which are not very different from those for richer communities in other ecosystems. Data for mediterranean ecosystems are sketchy, however, and diversity patterns on many spatial scales need to be thoroughly and systematically studied.

It is not yet possible to distinguish the most appropriate of the many hypotheses concerning the origin and maintenance of species richness or regional diversity in mediterranean ecosystems.

REFERENCES CITED

ABER, J.D., & MELLILO, J.M. 1980. Litter decomposition: measuring relative contributions of organic matter and nitrogen to forest soils. Can. J. Bot. 58: 416-421

ALLEN, S.E. 1964. Chemical aspects of heather burning. J. appl. Ecol. 1: 347-367

ASHFORD, A.E., LING-LEE, M., & CHILVERS, G.A. 1975. Polyphosphate in eucalypt mycorrhizas - a cytochemical demonstration. New Phytol. 74: 447-460

ASHTON, D.H. 1979. Seed harvesting by ants in forests of Eucalyptus regnans F. Muell. in central Victoria. Aust. J. Ecol. 4: 265-78

AVERY, D.M. 1979. Upper Pleistocene and Holocene Palaeoenvironments in the southern Cape: the micromammalian evidence from archaeological sites. Unpublished Ph.D. Thesis, University of Stellenbosch, Stellenbosch

AVILA, G., ALJARO, M.E., ARAYA, S., MONTENEGRO, G.A., & KUMMEROW, J. 1975. The seasonal cambium activity of Chilean and Californian shrubs. Am. J. Bot. 62: 473-478

AXELROD, D.I. 1975. Evolution and biogeography of Madr.-Tethyan sclerophyll vegetation. Ann. Mo. bot. Gdn. 62: 280-334

AXELROD, D.I., & RAVEN, P.H. 1978. Late Cretaceous and Tertiary vegetation history of Africa. Pp 77-130 in: WERGER, M.J.A. (ed.) Biogeography and ecology of southern Africa. Dr. W. Junk, The Hague

AZCON, R., BAREA, J.M., & HAYMAN, D.S. 1976. Utilization of rock phosphate in alkaline soils by plants innoculated with mycorrhizal fungi and phosphate-solubilizing bacteria. Soil Biol. Biochem. 8: 135-138

BAREA, J.M., AZCON, R., & HAYMAN, D.S. 1975. Possible synergistic interactions between Endogone and phosphate-solubilizing bacteria in low phosphate soils. Pp 409-417 in: SANDERS, F.E., MOSS, B., & TINKER, P.B. (eds) Endomycorrhizas. Academic Press, New York

BARKER, S. 1961. Studies on marsupial nutrition. 3. The copper - molybdenum - inorganic sulphate interactions in the Rottnest Quokka, Setonix brachyurus (Quoy & Gamard). Aust. J. biol. Sci. 14: 646-658

BATE, G.C., & DU PREEZ, P. 1978. Preliminary investigations into a nitrogen budget for the Burkea savanna. 41 pp. Unpublished report to the National Programme for Environmental Sciences, CSIR, Republic of South Africa

BARTHOLOMEW, B. 1970. Bare zone between California shrub and grassland communities: the role of animals. Science, N.Y. 170: 1210-1212

BAYNES, A. 1979. The analysis of a late Quaternary mammal fauna from Hastings Cave, Jurien, Western Australia. Unpublished Ph.D. Thesis, University of Western Australia

BEADLE, N.C.W. 1968. Some aspects of the ecology and physiology of Australian xeromorphic plants. Aust. J. Sci. 30: 348-355

BENTLEY, P.J. 1965. Some aspects of the water metabolism of an Australian marsupial Setonix brachyurus. J. Physiol., Lond. 127: 1-10

BERG, R.Y. 1975. Myrmecochorous plants in Australia and their dispersal by ants. Aust. J. Bot. 23: 475-508

BERLINER, R. 1971. The vegetation of the Cusalt soils in the upper Jordan Valley. Unpublished M.Sc. Thesis, the Hebrew University of Jerusalem

BIGALKE, R.C. 1979. Aspects of vertebrate life in fynbos, South Africa. Pp. 81-95 in: SPECHT, R.C. (ed.) Ecosystems of the world. Vol. 9a. Heathlands and related shrublands: descriptive studies. Elsevier, Amsterdam

BJÖRKMAN, O. 1979. The response of photosynthesis to temperature. Pp 273-301 in: JARVIS, P.G., & GRACE, J. (eds) Plants and their atmospheric environment. Blackwells Scientific Publications, Oxford. Proceedings of the British Ecological Society, March 1979

BLONDEL, J. 1969. Synecologie des Passercaux Residents et Migrateurs dans le Midi Méditerraneén Francais. Centre Regionale de Documentation Pedagogique, Marseilles

BOND, W.J. 1980. Periodicity in fynbos of the non-seasonal rainfall belt. J. S. Afr. Bot. 46(4): 343-354

BOND, W.J. 1981. Fire and senescent fynbos in the Swartberg, southern Cape. S. Afr. For. J. 114: 68-71

BOND, W.J. (in press). On alpha diversity and the richness of the Cape flora: a study in southern Cape fynbos. in: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

BOND, W.J., FERGUSON, M., & FORSYTH, G. 1981. Small mammals in habitat structure along altitudinal gradients in the southern Cape mountains. S. Afr. J. Zool. 15: 34-43

BORMAN, F.H., & LIKENS, G.E. 1967. Nutrient cycling. Science, N.Y. 155: 424-429

BOWDEN, J. 1978. Diptera. in: WERGER, M.J.A. (ed.) Biogeography and ecology of southern Africa. Dr. W. Junk, The Hague

BROWN, J.H., & DAVIDSON, D.W. 1977. Competition between seed-eating rodents and ants in desert ecosystems. Science N.Y. 196: 880-882

BROWN, R. 1814. General remarks, geographical and systematical, on the botany of Terra Australis. Pp 535-613 in: FLINDERS, M. (ed.) A voyage to Terra Australis. Vol. II. Mat. G. & W. Nicol, Publisher, London

BOUCHER, C., & MOLL, E.J. 1981. South African mediterranean shrublands. Pp 233-248 in: DI CASTRI, E., GOODALL, D W. & SPECHT, R. L. (eds) Ecosystems of the world. Vol. 11. Mediterranean-type shrublands. Elsevier, Amsterdam

BUNNELL, F.L., & DOWDING, P. 1974. ABISKO - a generalized model for comparisons between sites. Pp 227-247 in: HOLDING, A.J., HEAL, O.W., MACLEAN, S.F. Jr., & FLANAGAN, P.W. (eds) Soil organisms and decomposition in tundra. IBP Tundra Biome Steering Committee, Stockholm

BURBIDGE, A.H., HOPPER, S.D., & COATES, D.J. 197. Pollen loads on New Holland honeyeaters at Qualup, Western Australia. W. Aust. Nat. 14: 116-128

BURDON, J.J., & CHILVERS, G.A. 1974. Fungal and insect parasites contributing to niche differentiation in mixed species stands of eucalypt saplings. Aust. J. Bot. 22: 103-114

CALDWELL, M., & CAMP, D. 1974. Belowground productivity of two cool desert communities. Oecologia 17: 123-130

CALLOW, J.A., CAPACCIO, L.C.M, PARISH, G., & TINKER, P.B. 1978. Detection and estimation of polyphosphate in vesicular-arbuscular mycorrhizas. New Phytol. 80: 125-134

CAMPBELL, A.J., & TAINTON, M.T. 1981. Effects of fire on the invertebrate fauna of soil and litter of a eucalypt forest. Pp 215-242 in: GILL, A.M., NOBLE, I.R., & GROVES, R.H. (eds) Fire and the Australian biota. Australian Academy of Sciences, Canberra

CAMPBELL, B.M. 1980. Some mixed hardwood forest communities of the coastal ranges of southern California. Phytocoenologia 8: 297-320

CAMPBELL, B.M., MACKENZIE, B., & MOLL, E.J. 1979. Should there be more tree vegetation in the mediterranean climate region of South Africa? J. S. Afr. Bot. 45: 543-457

CAMPBELL, J.A. 1980. Oxygen flux measured in organic soil. Can. J. Soil Sci. 60: 641-650

CARLQUIST, S. 1974. *Island biology*. Columbia University Press, N.Y.

CARPENTER, F.L. 1978. Hooks for animal pollination? *Oecologia* 35: 123-132

CATLING, P.C., & NEWSOME, A.E. 1981. Responses of the Australian vertebrate fauna to fire: an evolutionary approach. Pp 272-310 *in*: GILL, A.M., NOBLE, I.R., & GROVES, R.H. (eds) *Fire and the Australian biota*. Australian Academy of Sciences, Canberra

CATLING, P.C., NEWSOME, A.E., & DUDZINSKI, M.L. 1981. Small mammals, habitat components and fire in south eastern Australia. *in*: *Proceedings on the dynamics and management of mediterranean-type ecosystems*. San Diego, California, June 1981

CHAPMAN, S.B. 1967. Nutrient budgets for a dry heath ecosystem in the south of England. *J. Ecol.* 55: 677-689

CHRISTENSEN, N.L., & MULLER, C.H. 1975a. Relative importance of factors controlling germination and seedling survival in *Adenostoma* chaparral. *Am. Midl. Nat.* 93: 71-78

CHRISTENSEN, N.L., & MULLER, C.H. 1975b. Effects of fire on factors controlling plant growth in *Adenostoma* chapparal. *Ecol. Monogr.* 45: 29-55

CHRISTENSEN, P. 1971. The purple-crowned lorikeet and eucalypt pollination. *Aust. For.* 35: 263-270

CHRISTENSEN, P.E. 1977. *The biology of BETTONGIA PENCILLATA (Gray 1837), and MACROPUS EUGENII (Desm. 1817), in relation to fire*. Unpublished Ph.D. Thesis, University of Western Australia, Nedlands

CLAUSEN, J., KECK, D., & HIESEY, W. 1940. 452 pp. *Experimental studies on the nature of species*. Carnegie Inst., Washington. Publ. No. 520

COCKBURN, A. 1978. The distribution of *Pseudomys shortridgei* (Muridae: Rodentia) and its relevance to that of other heathland *Pseudomys*. *Aust. Widl. Res.* 5: 213-220

CODY, M.L. 1973. Parallel evolution and bird niches. Pp 307-338 *in*: DI CASTRI, F., & MOONEY, H.A. (eds) *Ecological studies, analysis and synthesis*. Springer-Verlag, Berlin

CODY, M.L. 1974. *Competition and the structure of bird communities*. 317 pp. Princeton University Press, Princeton

CODY, M.L. 1975. Towards a theory of continental species diversities: bird distribution over mediterranean habitat gradients. Pp 214-257 *in*: CODY, M.L., & DIAMOND, J.M. (eds) *Ecology and evolution of communities*. Belknap Press, Harvard University, Cambridge, Mass.

CODY, M.L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors and productivity. *Bioscience* 31: 107-113

CODY, M.L. (in press). Continental diversity patterns and convergent evolution in bird communities. *in*: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) *Mediterranean-type ecosystems: the role of nutrients*. Springer-Verlag, Berlin

CODY, M.L., FUENTES, E.R., GLANTZ, W., HUNT, J.H., & MOLDENKE, A. 1977. Convergent evolution in the consumer organisms of mediterranean Chile and California. Pp 144-199 *in*: MOONEY, H.A. (ed.) *Convergent evolution in Chile and California*. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa.

CODY, M.L., & MOONEY, H.A. 1978. Convergence versus nonconvergence in mediterranean-climate ecosystems. *A. Rev. Ecol. Syst.* 9: 265-321

COGGER, H.G., & HEATWOLE, H. 1981. The Australian reptiles: origins, biogeography, distribution patterns and island evolution. Pp 1331-1374 *in*: HEAST, A. (ed.) *Ecological biogeography of Australia. Vol. II. Part Five: Poikilothermic vertebrates*. Dr. W. Junk, The Hague

CONNELL, J.H. 1978. Diversity in tropical rainforests and coral reefs. Science, N.Y. 199: 1302-1310

COWAN, I.R., & FARQUHAR, G.D. 1977. Stomatal function in relation to leaf metabolism and environment. Symp. Soc. exp. Biol. 31: 471-505

COWLING, R.M., & CAMPBELL, B.M. 1980. Convergence in vegetation structure in the mediterranean communities of California, Chile and South Africa. Vegetatio 43: 191-198

CSIRO, DIVISION OF ENTOMOLOGY 1970. The insects of Australia. Vol. 1. 1029 pp. Melbourne University Press, Carleton, Victoria

DAVIDGE, C. 1977. Baboons as dispersal agents for Acacia cyclops. Zool. Afr. 12: 249-250

DEACON, H.J. (in press). The comparative evolution of mediterranean-type ecosystems: a southern perspective. in: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

DEBANO, L.F., & CONRAD, C.E. 1976. Nutrients lost in debris and runoff water from a burned chapparal watershed. Pp 3-13 to 3-27 in: Proceedings of the Third Federal Interagency Sedimentation Conference, March 1976, Denver, Colorado

DEBANO, L.F., & CONRAD, C.E. 1978. The effect of fire on nutrients in a chaparral ecosystem. Ecology 59: 489-497

DEBANO, L. F., EBERLEIN, G. E., & DUNN, P. H. 1979. Effects of burning on chaparral soils. I. Soil nitrogen. Proc. Soil Sci. Soc. Am. 43: 504-509

DE HOOGH, R.J. 1968. Report of practical work in South Africa. Unpublished Ph.D. Thesis, University of Wageningen, Wageningen

DEL MORAL, R., WILLIS, R.J., & ASHTON, D.H. 1978. Suppression of coastal heath vegetation by Eucalyptus baxteri. Aust. J. Bot. 26: 203-219

DE MORAES, J.A.P.V., BOUER, H., & LAICHEN, W. 1981. CO_2 gas exchange, water-use efficiency and adaptive responses of Olea europa during drying and rewatering. in: MARGARIS, N.S., & MOONEY, H.A. (eds) Components of productivity of mediterranean regions - basic and applied aspects. Dr. W. Junk, The Hague

DI CASTRI, F. 1981. Mediterranean-type shrublands of the world. Pp 1-52 in: DI CASTRI, F., GOODALL, D.W., & SPECHT, R.L. (eds) Ecosystems of the world. Vol. 11. Mediterranean-type shrublands. Elsevier, Amsterdam

DI CASTRI, F., & MOONEY, H.A. 1973. (eds) Mediterranean-type ecosystems: origin and structure. 405 pp. Springer-Verlag, Berlin

DRUMMOND, H. 1886. On the termite as the tropical analogue of the earth-worm. Proc. R. Soc. Edinb. 13: 137-196

DUNN, P.H., DEBANO, L.F., & EBERLEIN, G.E. 1979. Effects of burning on chaparral soils. II. Soil microbes and nitrogen mineralization. Proc. Soil Sci. Soc. Am. 43: 509-514

DUNNETT, G.M. 1962. A population study of the quokka, Setonix brachyurus (Quoy & Gaimard) (Marsupialia). 2. Habitat, movements, breeding and growth. CSIRO Wildl. Res. 7: 13-32

EALEY, E.H.M. 1963. The ecological significance of delayed implantation in a population of the hill kangaroo (Macropus robustus). Pp 33-48 in: ENDERS, A.C. (ed.) Delayed implantation. University of Chicago Press, Chicago

ENDRÖDY-YOUNGA, S. 1978. Coleoptera. Pp. 797-822 in: WERGER, M.J.A. (ed.) Biogeography and ecology in southern Africa. Dr. W. Junk, The Hague

EDWARDS, N.T., & HARRIS, W.F. 1977. Carbon cycling in a mixed deciduous forest floor. Ecology 58: 431-437

EITEN, G. 1972. The Cerrado vegetation in Brazil. *Bot. Rev. 38*: 201-341

FAHN, A., WAISEL, G.A., & BENJAMINI, L. 1968. Cambial activity in *Acacia raddiana* Savi. *Ann. Bot. 32*: 677-686

FEENY, P.P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology 51*: 565-581

FEENY, P. 1976. Plant apparency and chemical defence. *Rec. Adv. Phytochem. 10*: 1-40

FIELD, C. 1981. Leaf age effects on the carbon gain of individual leaves in relation to microsite. *in*: MARGARIS, N.S., & MOONEY, H.A. (eds) *Components of productivity of mediterranean regions: basic and applied aspects*. Dr. W. Junk, The Hague

FORD, H.A., & PATON, D.C. 1976. Resource partitioning and competition in honeyeaters of the genus *Meliphaga*. *Aust. J. Ecol. 1*: 281-287

FORD, H.A., & PATON, D.C. 1977. The comparative ecology of ten species of honeyeaters in Southern Australia. *Aust. J. Ecol. 2*: 399-408

FOX, B.J. 1980. *The ecology of a small mammal community: secondary succession, niche dynamics, habitat partitioning, community structure and species diversity*. Unpublished Ph.D. Thesis, Macquarie University, Sydney, Australia

FOX, B.J. 1982. Fire and mammal secondary succession in an Australian coastal heath. *Ecology 63*

FOX, B.J. (in press). Mammal species diversity in Australian heathlands: the importance of pyric succession and habitat diversity. *in*: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) *Mediterranean-type ecosystems: the role of nutrients*. Springer-Verlag, Berlin

FOX, B.J., & McKAY, G.M. 1981. Small mammal responses to pyric successional changes in eucalypt forest. *Aust. J. Ecol. 6*(1): 29-41

FOX, L.R., & MACAULEY, B.J. 1977. Insect grazing on *Eucalyptus* in response to variation in leaf tannins and nitrogen. *Oecologia 29*: 145-162

FOX, L.R., & MORROW, P.A. 1981. Specialization: species property or local phenomena? *Science N.Y. 211*: 887-893

FRENCH, J.R.J., TURNER, G.L., & BRADBURY, J.F. 1978. Nitrogen fixation by bacteria from the hindgut of termites. *J. gen. Microbiol. 95*: 202-6

FUENTES, E.R., & ETCHEGARAY, J. (in press). Defoliation patterns in matorral ecosystems. *in*: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) *Mediterranean-type ecosystems: the role of nutrients*. Springer-Verlag, Berlin

FULK, G.W. 1975. Population ecology of rodents in the semiarid shrublands of Chile. *Occ. Pap. Mus. Tex. Tech. Univ. 33*:1-40

GEORGE, A.S., HOPKINS, A.J.M., & MARCHANT, N.G. 1979. The heathlands of western Australia. Pp 211-230. *in*: SPECHT, R.L. (ed.) *Ecosystems of the world. Vol. 9A. Heathlands and related shrublands: descriptive studies*. Elsevier, Amsterdam

GILL, A.M., & INGWEISEN, F. 1976. Growth of *Xanthorrhoea australis* R. Dr. in relation to fire. *J. appl. Ecol. 13*: 195-203

GIVNISH, T.J., & VERMEIJ, G.J. 1976. The sizes and shapes of liane leaves. *Am. Nat. 110*: 773-778

GLANZ, W. 1977. Small mammals. Pp 232-237. *in*: THROWER, N.J.W., & BRADBURY, D.E. (eds) *Chile-California mediterranean scrub atlas*. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa.

GOLDBLATT, P. 1978. An analysis of the flora of southern Africa: its characteristics, relationship and origins. *Ann. Mo. bot. Gdn. 65*: 369-436

GORDON, K.H.J., PEOPLES, M.B., & MURRAY, D.R. 1978. Age-linked changes in photosynthetic capacity fractionation. I. Protein content of the first leaf of *Pisum sativum*. L. *New Phytol*. *81*: 35-42

GRAY, J.T., & SCHLESINGER, W.H. 1981. Nutrient cycling in mediterranean-type ecosystems. Pp 259-285 *in*: MILLER, P.C. (ed.) *Resource use in chapparal and matorral: a comparison of vegetation function in two mediterranean-type ecosystems*. Springer-Verlag, Berlin

GREIG, J.C. 1976. *Herpetology in southern Cape fynbos*. 7pp. Unpublished report to the Cape Department of Nature and Environmental Conservation, Cape Town

GRIME, J. 1973. Control of species diversity in herbaceous vegetation. *J. Env. Manag*. *1*: 151-167

GROVES, R.H. 1965. Growth of heath vegetation. II. The seasonal growth of a heath on a ground-water podzol at Wilson's Promontory, Victoria. *Aust. J. Bot*. *13*: 281-289

GROVES, R.H., & KERAITIS, K. 1976. Survival and growth of seedlings of three sclerophyll species at high levels of phosphorus and nitrogen. *Aust. J. Bot*. *24*: 681-690

GROVES, R.H. (in press). Nutrient cycling in Australian heath and South African fynbos. *in*: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) *Mediterranean-type ecosystems: the role of nutrients*. Springer-verlag, Berlin

GRUBB, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev*. *52*: 107-145

GULMON, S.L. 1979. Competition and coexistence. Three annual grass species. *Am. Midl. Nat*. *101*: 403-416

GULMON, S.L. (in press). Carbon and nitrogen economy of *Diplacus aurantiacus*, a Californian mediterranean-climate drought-deciduous shrub. *in*: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) *Mediterranean-type ecosystems: the role of nutrients*. Springer-Verlag, Berlin

GULMON, S.L., & CHU, C.C. 1981. The effects of light and nitrogen on photosynthesis, leaf characteristics and dry matter allocation in the chaparral shrub, *Diplacus aurantiacus*. *Oecologia* *49*: 207-212

HAINES, W.M. 1967. *Experimental approaches to the study of seasonal root activity and phosphorus nutrition of Australian heath plants*. 83 pp. Unpublished Ph.D. Thesis, University of Melbourne, Victoria, Australia

HANES, T.L. 1965. Ecological studies on two closely related chaparral shrubs in southern California. *Ecol. Monogr*. *35*: 213-235

HANES, T.L. 1971. Succession after fire in the chaparral of southern California. *Ecol. Monogr*. *41*: 27-52

HANNON, N.J. 1956. The status of nitrogen in the Hawkesbury Sandstone soils and their plant communities in the Sydney district. I. The significance and level of nitrogen. *Proceedings of the Linnean Society of New South Wales* *81*: 118-143

HARPER, J.L. 1969. The role of predation in vegetational diversity. *in*: Diversity and stability in ecological systems, Brookhaven Symposium. *Biology* *22*: 48-62

HARRISON, A.T., SMALL, E., & MOONEY, H.A. 1971. Drought relationships and distribution of two Mediterranean-climate Californian plant communities. *Ecology* *52*: 869-875

HATCH, A.B. 1937. The physical basis of mycotrophy in the genus *Pinus*. *Black Rock Forest Bulletin* *6*: 1-168

HEDDLE, E.M., & SPECHT, R.L. 1975. Dark Island heath (Ninety-Mile Plain, South Australia). VIII. The effect of fertilizers on composition and growth, 1950-72. Aust. J. Bot. 23: 151-164

HELLMERS, H., BONNER, J.F., & KELLEHER, J.M. 1955. Soil fertility: a watershed management problem in the San Gabriel mountains of southern California. Soil Sci. 80: 189-197

HELLMERS, H., HORTON, J.S., JUHREN, G., & O'KEEFE, J. 1955. Root systems of some plants in southern California. Ecology 36: 667-678

HOFFMAN, A., MOONEY, H.A., & KUMMEROW, J. 1977. Qualitative phenology. Pp 102-120 in: THROWER, N.J.W., & BRADBURY, D.E. (eds) Chile-California mediterranean scrub atlas. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa.

HOLLAND, P.G. 1978. An evolutionary biogeography of the genus Aloe. J. Biogeog. 5: 213-216

HOLSWORTH, W.N. 1967. Population dynamics of the quokka, Setonix brachyurus, on the west end of Rottnest Island, Western Australia. I. Habitat and distribution of the quokka. Aust. J. Zool. 15: 29-46

HOPPER, S.D. 1979. Biogeographical aspects of speciation in the south west Australian flora. A. Rev. Ecol. Syst. 10: 399-422

HOPPER, S.D. 1980. Bird and mammal pollen vectors in Banksia communities at Cheyne Beach, Western Australia. Aust. J. Bot.

HOPPER, S.D., & MASLIN, B.R. 1978. Phytogeography of Acacia in Western Australia. Aust. J. Bot. 26: 63-78

HORTON, J.S., & WRIGHT, J.T. 1944. The wood rat as an ecological factor in southern California watersheds. Ecology 25: 341-351

HOSS, D. 1975. Preliminary investigation of the palynology of the upper Eocene Werillup Formation, Western Australia. Jl. R. Soc. W. Aust. 58: 1-13

HSAIO, T.C. 1973. Plant responses to water stress. A. Rev. Pl. Physiol. 24: 519-70

HUBBELL, S.P. 1980. Seed predation and the co-existence of tree species in tropical forests. Oikos 35: 214-229

HUNT, J. 1977. Ants. in: THROWER, N., & BRADBURY, D. (eds) Chile-California mediterranean scrub atlas. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa.

INNIS, F.A. 1975. The role of total systems models in the grassland biome study. Pp 14-46 in: PATTEN, B.C. (ed.) Systems analysis and simulation ecology. Academic Press, New York

JACOBS, M.R. 1955. Growth habits of the eucalypts. 262 pp. Canberra Forest & Timber Bureau, Dept. of Interior. Commonwealth Government Printer, Canberra

JANZEN, D.H. 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104: 501-528

JANZEN, D.H. 1974. Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. Biotropica 6: 69-103

JEFFREE, G.E., JOHNSON, R.P.C., & JARVIS, P.G. 1971. Epicuticular wax in the stomatal antechamber of Sitka spruce and its effects on the diffusion of water vapour and carbon dioxide. Plant 98: 1-10

JEFFREY, D.W. 1967. Phosphate nutrition of Australian heath plants. I. The importance of proteoid roots in Banksia (Proteaceae). Austr. J. Bot. 15: 403-411

JEFFREY, D.W. 1968. The formation of polyphosphate in Banksia ornata, an Australian heath plant. Aust. J. biol. Sci. 17: 845-853

JOHNSON, A.W. 1973. Historical view of the concept of ecosystem convergence. Pp 3-7 in: DI CASTRI, F., & MOONEY, H.A. (eds) Mediterranean-type ecosystems: origin and structure. Springer-Verlag, Berlin

JONES, E. 1977. Ecology of the feral cat, Felis catus (L.), (Carnivora: Felidae) on Macquarie Island. Aust. Wildl. Res. 4: 249-62

JONES, E., & COMAN, B.J. 1981. Ecology of the feral cat Felis catus (L.) in south eastern Australia. I. Diet. Aust. Wildl. Res. 8: 537-47

JONES, M.B., & WOODMANSEE, R.G. 1979. Biogeochemical cycling in annual grassland ecosystems. Bot. Rev. 45: 111-144

JONES, R. 1968a. Productivity studies on heath vegetation in southern Australia. The use of fertilizers in studies of production processes. Folio Geobot. Phytotax. (Praha) 3: 355-362

JONES, R. 1968b. Estimating productivity and apparent photosynthesis from differences in consecutive measurements of living plant parts of an Australian heathland. Aust. J. Bot. 16: 589-602

KEELEY, J.E. 1977a. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and non-sprouting chaparral shrubs. Ecology 58: 820-829

KEELEY, J.E. 1977b. Fire-dependent reproductive strategies in Arctostaphylos and Ceanothus. Pp 391-396 in: MOONEY, H.A., & CONRAD, C.E. (eds) Proceedings of the symposium on environmental consequences of fire and fuel management in mediterranean ecosystems. U.S.D.A. For. Serv. Gen. Tech. Rep. WO-3

KEELEY, J.E., & HAYS, R.L. 1976. Differential seed predation on two species of Arctostaphylos (Ericaceae). Oecologia 24: 71-81

KEMP, E.M. 1978. Tertiary climatic evolution and vegetation history in the south-east Indian Ocean region. Palaeogeog. Palaeoclimatol. Palaeoecol. 24: 169-208

KENNETT, J.P., & SHACKLETON, N.J. 1976. Oxygen isotopic evidence for the development of the psychrosphere 38 m.y. ago. Nature, Lond. 260: 513-515

KERR, L.R. 1925. The lignotubers of eucalyptus seedlings. Proc. R. Soc. Vict. 37: 79-97

KESSELL, S.R., & CATTELINO, P.J. 1978. Evaluation of a fire behaviour information integration system for southern Californian chaparral wildlands. J. Env. Manag. 2: 135-159

KIKKAWA, J., INGRAM, G.J., & DWYER, P.D. 1979. The vertebrate fauna of Australian heathlands - an evolutionary perspective. Pp 231-275. in: SPECHT, R.L. (ed.) Ecosystems of the world. Vol. 9A. Heathlands and related shrublands. Elsevier, Amsterdam

KING, H.G.C., & HEATH, G.W. 1967. The chemical analysis of small samples of leaf material and the relationship between the disappearance and composition of leaves. Pedobiologia 7: 192-197

KITTREDGE, J. 1955. Litter and forest floor of the chaparral in parts of the San Dimas Experimental Forest, California. Hilgardia 23: 563-596

KRUGER, F.J. 1977a. Ecology of Cape fynbos in relation to fire. Pp 230-244 in: MOONEY, H.A., & CONRAD, C.E. (eds) Proceedings of the symposium on environmental consequences of fire and fuel management in mediterranean ecosystems. U.S.D.A. For. Serv. Gen. Tech. Rep. WO-3

KRUGER, F.J. 1977b. A preliminary account of aerial plant biomass in fynbos communities of the mediterranean-type climate zone of the Cape Province. Bothalia 12: 301-309

KRUGER, F.J. 1979. South African heathlands. Pp 19-80 in: SPECHT, R.L. (ed.) Ecosystems of the world. Vol. 9A. Heathlands and related shrublands: descriptive studies. Elsevier, Amsterdam

KRUGER, F.J. 1981. Seasonal growth and flowering rhythms: South African heathlands. in: SPECHT, R.L. (ed.) Ecosystems of the world. Vol 9B. Heathlands and related shrublands: analytical studies. Elsevier, Amsterdam

KRUGER, F.J., & TAYLOR, H.C. 1979. Plant species diversity in Cape fynbos: gamma and delta diversity. Vegetatio 41: 85-93

KUMMEROW, J. 1973. Comparative anatomy of sclerophylls of mediterranean climatic areas. Pp 157-167 in: DI CASTRI, F., & MOONEY, H.A. (eds) Mediterranean-type ecosystems: origin and structure. Springer-Verlag, Berlin

KUMMEROW, J. (in press). Comparative phenology of mediterranean-type plant communities. in: KRUGER, F.J.,MITCHELL, D.T., & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

KUMMEROW, J., ALEXANDER, J.V., NEEL, J.W., & FISHBECK, K. 1978. Symbiotic nitrogen fixation in Ceanothus roots. Am. J. Bot. 65: 63-69

KUMMEROW, J., KRAUSE, D., & JOW, W. 1977. Root systems of chaparral shrubs. Oecologia 29: 163-177

KUMMEROW, J., KRAUSE, D., & JOW, W. 1978. Seasonal changes of fine root density in southern Californian chaparral. Oecologia 37: 201-212

LAMONT, B.B. 1973. Factors affecting the distribution of proteoid roots within the root systems of two Hakea species. Aust. J. Bot. 21: 165-187

LAMONT, B.B. 1974. The biology of dauciform roots in the sedge Cyathochaete avenacea. New Phytol. 73: 985-996

LAMONT, B.B. 1980b. Proteoid roots in the South African Proteaceae. Unpublished report to the National Programme for Environmental Sciences, CSIR, Republic of South Africa

LAMONT, B.B. 1981a. Specialized roots of non-symbiotic origin in heathlands. in: SPECHT, R L. (ed.) Ecosystems of the world. Vol. 9B. Heathlands and related shrublands: analytical studies. Elsevier, Amsterdam

LAMONT, B.B. 1981b. Understorey suppression by Eucalpytus wandoo. Conference on the biology of Eucalyptus. Aust. Syst. Bot. Soc., King's Park and Botanic Garden

LAMONT, B.B. (in press). Strategies for maximizing nutrient uptake in two mediterranean ecosystems of low nutrient status. in: KRUGER, F.J., MITCHELL, D.T. & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

LAMONT, B.B., DOWNES, S., & FOX, J.E.D. 1977. Importance value curves and diversity indices applied to a species-rich heathland in western Australia. Nature, Lond. 265: 438-441

LAMONT, B., & McCOMB, A. 1974. Soil micro-organisms and the formation of proteoid roots. Aust. J. Bot. 22: 681-688

LEE, A.K., BAVERSTOCK, P.R., & WATTS, C.H.S. 1981. Rodents - the late invaders. Pp 1523-1553 in: HEAST, A. (ed.) Ecological biogeography in Australia. Dr. W. Junk, The Hague

LEE, K.E., & WOOD, T.G. 1971. Physical and chemical effects on soils of Australian termites, and their pedological significance. Pedobiologia 11: 376-409

LEE, P.J., & MIFLIN, B.J. 1974. An alternative route for nitrogen assimilation in higher plants. Nature, Lond. 251: 614-616

LEVYNS, M.L. 1935. Veld burning experiments at Oakdale, Riversdale. Trans. R. Soc. S. Afr. 23: 231-243

LEVYNS, M.L. 1964. Migration and origin of the Cape Flora. Trans. R. Soc. S. Afr. 37: 85-107

LEWIS, O.A.M., JAMES, D., & HEWITT, E.J. 1982. Nitrogen assimilation in barley in the response to nitrate and ammonium nutrition. Analyt. Bot. 49: 39-50

LEWIS, O.A.M., & STOCK, W.D. 1978. A preliminary study of the nitrogen nutritional status of members of the South African Proteaceae. *J. S. Afr. Bot. 44*: 143-151

LONGHURST, W.M. 1978. Responses of bird and mammal populations to fire in chaparral. *Calif. Agric. 32*(10): 9-12

LONGSTRETH, D.J., & NOBEL, P.S. 1980. Nutrient influences on leaf photosynthesis: effects of nitrogen, phosphorus and potassium on *Gossypium hirsutum* L. *Pl. Physiol., Lancaster 65*: 541-543

LOUW, G.N. 1969. The nutritive value of natural grazings in South Africa. *Proc. S. Afr. Soc. Anim. Prod. 8*: 57-61

LOVELESS, A.R. 1962. Further evidence to support a nutritional interpretation of sclerophylly. *Ann. Bot. 26*: 551-561

LLOYD, P.S. 1971. Effects of fire on the chemical status of herbaceous communities of the Derbyshire Dales. *J. Ecol. 59*: 261-273

LOISSANT, P. 1973. Soil-vegetation relationships in mediterranean ecosystems of southern France. Pp 199-210 *in*: DI CASTRI, F., & MOONEY, H.A. (eds) *Mediterranean-type ecosystems: origin and structure*. Springer-Verlag, Berlin

LUBCHENCO, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive ability. *Am. Nat. 112*: 23-39

LUTZ, H.J., & CHANDLER, R.F. 1946. *Forest soils*. 150 pp. John Wiley & Sons, New York

MACARTHUR, R.H. 1972. *Geographical ecology*. 269 pp. Harper & Row, New York

MAGGS, J., & PEARSON, C.J. 1977. Litterfall and litter layer decay in coastal scrub at Sydney, Australia. *Oecologia 31*: 239-250

MALAISSE, F. 1978. High termitaria. Pp 1279-1300. *in*: WERGER, M.J.A. (ed.) *Biogeography and ecology of southern Africa*. Dr. W. Junk, The Hague

MALAJCZUK, N., & BOWEN, G.D. 1974. Proteoid roots are microbially induced. *Nature, Lond. 251*: 316-317

MARCHANT, J.W., & MOORE, A.E. 1978. Geochemistry of the Table Mountain Group. II. Analysis of two suites of western Graafwater rocks. *Trans. Geol. Soc. S. Afr. 81*: 353-357

MARGARIS, N.W. 1976. Structure and dynamics in a phryganic (east Mediterranean) ecosystem. *J. Biogeog. 3*: 249-259

MARGARIS, N.W., & PAPADOGIANNI, P. 1978. Cambial activity in some plants dominating phryganic formations in Greece. *Phyton, B. Aires 36*: 1-5

MASON, C.F. 1977. *Decomposition*. Studies in biology, no 74. Institute of Biology. Edward Arnold, London

MATTHEWS, E.G. 1976. *Insect ecology*. University of Queensland Press, St. Lucia, Queensland

MEDINA, E., 1971. Effect of nitrogen supply and light intensity during growth on the photosynthetic capacity and carboxydismutase activity of leaves of *Atriplex patula* ssp. *hastata*. *Year Book 70*: 551-559, Carnegie Inst., Washington

MEENTEMEYER, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology 59*: 465-472

MELLILO, J.M., ABER, J.D., & MURATORE, J.F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* (in press)

MERTON, D.V. 1977. Controlling introduced predators and competitors on an island. Pp 121-8. *in*: TEMPLE, S.A. (ed.) *Endangered birds: management techniques for rescuing threatened species*. University of Wisconsin Press, Wisconsin

MICHAUX, J., SUE, J-P., & VERNET, J-L. 1979. Climatic inferences from the history of the Taxodiaceae during the Pliocene and the early Pleistocene in western Europe. Rev. Palaeobot. Palynol. 27: 185-191

MILEWSKI, A.V. 1978. Diet of Serinus species in the south western Cape, with special reference to the Protea Seedeater. Ostrich 49: 174-184

MILEWSKI, A.V. 1979. A climatic basis for the study of convergence of vegetation structure in mediterranean Australia and southern Africa. J. Biogeog. 6: 293-299

MILEWSKI, A.V. 1981. A comparison of vegetation height in relation to the effectiveness of rainfall in the mediterranean and adjacent arid parts of Australia and South Africa. J. Biogeog. 8: 107-116

MILEWSKI, A.V. (in press). A new approach to intercontinental comparisons: the role of co-adaptation between plants and animals in explaining differences between communities in mediterranean Australia and South Africa. in: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

MILEWSKI, A.V. (in press). A comparison of reptile communities in relation to soil fertility in the mediterranean and adjacent arid parts of Australia and South Africa. J. Biogeog.

MILLER, P.C. 1979. Quantitative plant ecology. Pp 179-232 in: HORN, D.J., STAIRS, G.R., & MITCHELL, R.D. (eds) Analysis of ecological systems. Ohio State University Press, Columbus, Ohio

MILLER, P.C. (ed.) 1981. Resource use by chaparral and matorral: a comparison of vegetation function in two mediterranean-type ecosystems. 455 pp. Springer-Verlag, Berlin

MILLER, P.C. (in press). Canopy structure of mediterranean-type shrubs in relation to heat and moisture. in: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

MILLER, P.C., & MOONEY, H.A. 1974. The origin and structure of American arid-zone ecosystems. The producers: interactions between environment, form and function. Pp 201-209. Proceedings of the first international congress of ecology. The Hague, Netherlands

MILLER, P.C., STONER, W.A., & RICHARDS, S.P. 1978. MEDECS, a simulator for mediterranean ecosystems. Simulation 30: 173-190

MILTON, S.J. 1979. Australian acacias in the south western Cape: preadaption, predation and success. Pp 69-78. Proc. 3rd Nat. Weeds Conf. S. Afr.

MITCHELL, D.T. 1980. The status of nutrient relation studies in the Fynbos Biome Project. Terrestrial Ecosystems Newsletter, National Programme for Environmental Sciences, CSIR, Republic of South Africa

MITCHELL, D.T. & READ, D.J. 1981. Utilization of inorganic and organic phosphates by the mycorrhizal endophytes of Vaccinium macrocarpon and Rhododendron ponticum. Trans. Br. mycol. Soc.

MOLL, E.J., & GUBB, A.A. 1981. Aspects of the ecology of Staavia dodii in the south western Cape of South Africa. Pp 331-342 in: SYNGE, H. (ed.) The biological aspects of rare plant conservation. John Wiley & Sons, New York

MOLL, E.J., MACKENZIE, B., & MCLACHLAN, D. 1980. A possible explanation for the lack of trees in the fynbos, Cape Province, South Africa. Biol. Cons. 17: 221-228

MONK, C.D. 1966. An ecological significance of evergreenness. Ecology 47: 504-505

MOONEY, H.A. (ed.) 1977. Convergent evolution in Chile and California: mediterranean-climate ecosystems. 224 pp. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa.

MOONEY, H.A., (in press). Carbon-gaining capacity and allocation patterns of mediterranean-climate plants. *in*: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) *Mediterranean-type ecosystems: the role of nutrients*. Springer-Verlag, Berlin

MOONEY, H.A., & BARTHOLOMEW, B. 1974. Comparative carbon balance and reproductive modes of two Californian *Aesculus* species. *Bot. Gaz. 135*: 306-313

MOONEY, H.A., & CONRAD, C.E. (technical coordinators) 1977. *Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems*. 498 pp. U.S.D.A. For. Serv. Gen. Tech. Rep. WO-3

MOONEY, H.A., FERRAR, P.J., & SLATYER, R.O. 1978. Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. *Oecologia 36*: 103-111

MOONEY, H.A., & HARRISON, A.T. 1972. The vegetational gradient on the lower slopes of the Sierra San Pedro Martin in north west Baja California. *Madrono 21*: 439-445

MOONEY, H.A., & KUMMEROW, J. 1977. Quantitative phenology. Pp 121-125 *in*: THROWER, N.J.W., & BRADBURY, D.E. (eds) *Chile-California mediterranean scrub atlas*. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa.

MOONEY, H.A., KUMMEROW, J., JOHNSON, A.W., PARSONS, D.J., KEELEY, S., HOFFMANN, A., HAYS, R.I., GILIBERTO, J, & CHU, C. 1977. The producers - their resources and adaptive responses. Pp 85-143 *in*: MOONEY, H.A. (ed.) *Convergent evolution in Chile and California: mediterranean-climate ecosystems*. Dowden, Hutchinson & Ross, Inc., Stroudsberg, Pa.

MOONEY, H.A. & PARSONS, D.J. 1973. Structure and function of the Californian chaparral. Pp 83-112 *in*: DI CASTRI, F., & MOONEY, H.A. (eds) *Mediterranean-type ecosystems: origin and structure*. Springer-Verlag, Berlin

MOONEY, H.A., & RUNDEL, P.W. 1979. Nutrient relations of the evergreen shrub, *Adenostoma fasciculatum*, in the Californian chaparral. *Bot. Gaz. 140*: 107-113

MORROW, P.A. (in press). The role of sclerophyllous leaves in determining insect grazing damage. *in*: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) *Mediterranean-type ecosystems: the role of nutrients*. Springer-Verlag, Berlin

MORROW, P.A., & FOX, L.R. 1980. Effects of variation in *Eucalyptus* essential oil yield on insect growth and grazing damage. *Oecologia 45*: 209-219

MORROW, P.A., & LAMARCHE, V.C. 1978. Tree ring evidence for chronic insect suppression of productivity in subalpine *Eucalyptus*. *Science 201*: 1244-1245

MOSTERT, D.P., SIEGFRIED, W.R., & LOUW, G.N. 1980. Protea nectar and satellite fauna in relation to the food requirements and pollinating role of the Cape sugarbird. *S. Afr. J. Sci. 76*: 409-412

MULLETE, K.J., & BAMBER, R.K. 1978. Studies of the lignotubers of *Eucalyptus gummifera* (Gaertn. & Hochr.). III. Inheritance and chemical composition. *Aust. J. Bot. 26*: 23-28

NAVEH, Z., & WHITTAKER, R.H. 1980. Structural and floristic diversity of shrublands and woodlands on northern Israel and other mediterranean areas. *Vegetatio 41*: 171-190

NEWMAN, E.I. 1978. Allelopathy: adaptation or accident? Pp 327-342. in: HARBORNE, J.B. (ed.) Biochemical aspects of plant and animal co-evolution. Academic Press, London

NEWSOME, A.E. 1965. Reproduction in natural populations of the red kangaroo, Megaleia rufa, in central Australia. Aust. J. Zool. 13: 735-759

NEWSOME, A.E. (in press). Grazing mammals of tropical savannas of Australia. in: BOURLIERE, F. (ed.) Tropical savannas of the world. Elsevier, Amsterdam

NEWSOME, A.E., & CATLING, P.C. 1979. Habitat preferences of vertebrates inhabiting heathlands of coastal, montane and alpine regions of south eastern Australia. Pp 301-315 in: SPECHT, R.L. (ed.) Ecosystems of the world. Vol. 9A. Heathlands and related shrublands: descriptive studies. Elsevier, Amsterdam

NEWSOME, A.E., & CATLING, P.C. (in press). Animal demography in relation to fire and shortage of food: some indicative models. in: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

NEWSOME, A.E., McGILROY, J., & CATLING, P.C. 1975. The effects of an extensive wildfire on populations of twenty ground vertebrates in south east Australia. Proc. Ecol. Soc. Aust. 9: 107-123

NOBLE, I., & SLATYER, R.O. 1977. Post-fire succession of plants in mediterranean ecosystems. Pp 27-36. in: MOONEY, H.A., & CONRAD, C.E. (eds) Proceedings of a symposium on the consequences of fire and fuel management in mediterranean ecosystems. U.S.D.A. For. Serv. Gen. Tech. Rep. WO-3

NORTON, P.M. 1980. The habitat and feeding ecology of the Klipspringer, OREOTRAGUS OREOTRAGUS (Zimmermann, 1783) in two areas of the Cape Province. Unpublished M.Sc. Thesis, University of Pretoria

NYE, P.H. 1979. Soil properties controlling the supply of nutrients to the root surface. Pp 39-49 in: HARLEY, J.L., & RUSSEL, R.S. (eds) The soil-root interface. Academic Press, London

NYE, P.H., & TINKER, P.B. 1977. Solute movement in the soil-root system. Blackwell Scientific Publications, Oxford

O'CONNELL, A.M., GROVE, T.S., & DIMMOCK, G.M. 1979. The effects of a high-intensity fire on nutrient cycling in jarrah forest. Aust. J. Ecol. 4: 331-337

O'DOWD, D.J., & HAY, M.E. 1980. Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. Ecology 61: 531-540

OECHEL, W.C., & HASTINGS, S.J. (in press). The effects of periodic fire on photosynthesis in chaparral resprouts. in: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

OECHEL, W.C., & LAWRENCE, W.T. 1981. Carbon allocation and utilization. Pp 185-235 in: MILLER, P.C. (ed.) Resource use by chaparral and matorral. A comparison of vegetation function in two mediterranean-type ecosystems. Springer-Verlag, Berlin

ORSHAN, G. 1964. Seasonal dimorphism of desert and mediterranean chamaephytes and their significance as a factor in their water economy. Pp 206-222 in: RUTTER, A.J., & WHITEHEAD, F.H. (eds) The water relations of plants. Blackwell Scientific Publications, Oxford

ORSHAN, G. (in press). Approaches to the definition of mediterranean growth forms. in: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

OSMOND, C.B., BJÖRKMAN, O., ANDERSON D.J. (eds) 1980. Photosynthesis. Pp 291-378 *in*: *Physiological processes in plant ecology - toward a synthesis with Atriplex*. Springer-Verlag, Berlin

OXMAN, A.M., GOODMAN, P.J., COOPER, J.P. 1977. The effects of nitrogen, phosphorus and potassium on rates of growth and photosynthesis of wheat. *Photosynthetics* *11*: 66-75

OZANNE, P.G., & SPECHT, R.L. 1981. Mineral nutrition of heathlands. Phosphorus toxicity. Pp 209-213 *in*: SPECHT, R.L. (ed.) *Ecosystems of the world. Vol. 9B. Heathlands and related shrublands: analytical studies*. Elsevier, Amsterdam

PARKHURST, D.F., & LOUCKS, O.L. 1972. Optimal leaf size in relation to environment

PARSONS, D.J. 1976. Vegetation structure in the mediterranean scrub communities of California and Chile. *J*. *Ecol*. *64*: 435-447

PARSONS, D.J., & MOLDENKE, A. 1975. Convergence in vegetation structure along analogous climatic gradients in the mediterranean climate ecosystems of Chile and California. *Ecology* *56*: 950-957

PASKOFF, R.P. 1973. Geomorphological processes and characteristic landforms in the mediterranean regions of the world. Pp 53-60 *in*: DI CASTRI, F., & MOONEY, H.A. (eds) *Mediterranean-type ecosystems: origin and structure*. Springer-Verlag, Berlin

PATE, J.S., & DIXON, K.W. 1978. Mineral nutrition of *Drosera* *erythrorhiza* Lindl. with special reference to its tuberous habit. *Aust*. *J*. *Bot*. *26*: 455-464

PATE, J.S., & DIXON, K.W. 1980. Plants with fleshy underground storage organs - a western Australian survey. *in*: PATE, J.S., & McCOMB, A.J. (eds) *Biology of native Australian plants*. University of Australia Press, Perth

PATON, D.C., & FORD, H.A. 1977. Pollination by birds of native plants in South Australia. *Emu* *77*: 73-85

PEET, R.K. 1978. Forest vegetation of the Colorado Front Range: patterns of species diversity. *Vegetatio* *37*: 65-78

PETERSON, G.L., & ABBOTT, P.L. 1979. Mid-Eocene climatic change, south-western California and northwestern Baja California. *Palaeogeog*. *Palaeoclimatol*. *Palaeoecol*. 26: 73-87

PIANKA, E.R. 1969. Habitat specificity, speciation, and species density in Australian desert lizards. *Ecology* *50*: 498-502

PUTTICK, G., & GLYPHIS, J. 1980. *Herbivory studies in a Strandveld community*. 188 pp, Typescript. Unpublished report to the National Programme for Environmental Sciences, CSIR, Republic of South Africa

PYKE, G.H. 1980. The foraging behaviour of Australian honeyeaters: a review and some comparisons with hummingbirds. *Aust*. *J*. *Ecol*. *5*: 343-69

QUINN, R.D. (in press). Habitat preferences and distribution of mammals in Californian chaparral. *in*: QUINN, R.D., & CONRAD, C.E. (eds) *Proceedings of the symposium on the classification and distribution of Californian chaparral ecosystems*. U.S.D.A. For. Serv. Washington, D.C.

RABINOVITCH-VIN, A. 1979. *Influence of present rock on soil properties & composition of vegetation in the Galilee*. Unpublished Ph.D. Thesis, the Hebrew University of Jerusalem (Hebrew with English summary)

RABINOVITCH-VIN, A. (in press). Influence of nutrients on the composition and distribution of plant communities in mediterranean-type ecosystems of the Upper Galilee, Israel. in: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) *Mediterranean-type ecosystems: The role of nutrients*

RADIN, J.W., & PARKER, L.L. 1979a. Water relations of cotton plants under nitrogen deficiency I. Dependence on leaf structure. *Plant* *Physiol*. *64*: 495-498

RADOSEVICH, S.R., CONRAD, S.G., & ADAMS, D.R. 1977. Regrowth responses of chamise following fire. Pp 378-382 *in*: MOONEY H.A., & CONRAD, C.E. (eds) *Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems*. U.S.D.A. For. Serv. Gen. Tech. Rep. WO-3

RAVEN, P.H. 1973. The evolution of mediterranean floras. Pp 213-224 *in*: DI CASTRI, F., & MOONEY, H.A. (eds) *Mediterranean-type ecosystems: origin and structure*. Springer-Verlag, Berlin

READ, D.J., 1978. The biology of mycorrhiza in the heathland ecosystem with special reference to the nitrogen nutrition of the Ericaceae. Pp 324-328 *in*: LONTIK, M.W., & MILES, J.A.R. (eds) *Microbial ecology*. Springer-Verlag, Berlin

READ, D.J., & MITCHELL, D.T. (in press). Decomposition and mineralization processes in mediterranean-type ecosystems and in heathlands of similar structure. *in*: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) *Mediterranean-type ecosystems: the role of nutrients*. Springer-Verlag, Berlin

READ, D.J., & STRIBLEY, D.P. 1975. Some mycological aspects of the biology of mycorrhiza and the Ericaceae. Pp 105-117 *in*: SANDER, F.E., MORESE, B., INKER, P.B. (eds) *Endomycorrhizas*. Academic Press, London

RECHER, H.F. 1981. Nectar feeding and its evolution among Australian vertebrates. *in*: KEAST, A. (ed.) *Ecological biogeography of Australia*. Dr. W. Junk, The Hague

RICEMAN, D.S. 1948. Mineral deficiency in plants on the soils of the Ninety-Mile Plain in South Australia. II. Effect of zinc, copper and phosphate on subterranean clover and lucerne grown on Laffer Sand near Keith. *CSIRO Bull. No. 234*, Canberra, Australia

RIDE, W.D.L. 1970. *A guide to the native mammals of Australia*. 249 pp. Oxford University Press, London

ROBERTS, P.E. 1970. Some effects of a bush fire on heathland bird life. *Proc. Zool. Soc. New South Wales*, 1968-69: 4-43

RUELLE, J.E. 1978. Isoptera. Pp 747-762 *in*: WERGER, M.J.A. (ed.) *Biogeography and ecology of Southern Africa*. Dr. W. Junk, The Hague

RUNDEL, P.W. 1981. The matorral zone of central Chile. Pp 175-202 *in*: DI CASTRI, F., GOODALL, D.W., & SPECHT, R.L. (eds) *Ecosystems of the world. Vol 11. Mediterranean-type shrublands*. Elsevier, Amsterdam

RUNDEL, P.W. (in press). Impact of fire on nutrient cycles in mediterranean-type ecosystems with reference to chaparral. *in*: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) *Mediterranean-type ecosystems: the role of nutrients*. Springer-Verlag, Berlin

RUNDEL, P.W., & NEEL, J.W. 1978. Nitrogen fixation by *Trevoa trinervis* (Rhamnaceae) in the Chilean matorral. *Flora, Jena 167*: 127-132

RUNDEL, P.W., & PARSONS, D.J. 1980. Nutrient changes in two chaparral shrubs along a fire-induced age-gradient. *Am. J. Bot. 67*: 51-58

RUST, I.C. 1967. *On the sedimentation of the Table Mountain group in the western Cape Province*. Unpublished D.Sc. Thesis, University of Stellenbosch

RYCROFT, H.B. 1950. *A quantitative ecological study of the vegetation of Biesiesvlei, Jonkershoek*. Unpublished Ph.D. Thesis, University of Cape Town

SABRADO, M.A., & MEDINA, E. 1980. General morphology, anatomical structure and nutrient content of sclerophyllous leaves of the "bana" vegetation of the Amazons. *Oecologia 45*: 341-345

SADLEIR, R.M.F.S. 1965. Reproduction in two species of kangaroo (*Macropus robustus* and *Megaleia rufa*) in the arid Pilbara region of western Australia. *Proc. zool. Soc. Lond. 145*: 239-61

SADLEIR, R.M.F.S., & SHIELD, J.W. 1960. Delayed birth in marsupial macropods - the euro, the tammar and the marloo. Nature, Lond. 183: 335

SADLIER, R.M.F.S., & TYNDALE-BISCOE, C.H. 1977. Photoperiod and termination of diapause in the marsupial, Macropus eugenii. Biol. Reprod. 16: 605-8

SCHAEFFER, R. 1973. Microbial activity under seasonal conditions of drought in mediterranean climates. Pp 191-198 in: DI CASTRI, F. & MOONEY, H.A. (eds) Mediterranean-type ecosystems: origin and structure. Springer-Verlag, Berlin

SCHLESINGER, W.H., & HASEY, M.M. 1980. The nutrient content of precipitation, dry fall-out and intercepted aerosols in the chaparral of southern California. Am. Midl. Natur. 103: 114-122

SCHLESINGER, W.H., & HASEY, M.M. 1981. Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. Ecology 62: 762-774

SEDDON, G. 1974. Xerophytes, xeromorphs and sclerophylls: the history of some concepts in ecology. Biol. J. Linn. Soc. 6: 65-87

SHARMAN, G.B. 1955. Studies on marsupial reproduction. III. Normal delayed pregnancy in Setonix brachyurus. Aust. J. Zool. 3: 56-70

SIEGFRIED, W.R., & CROWE, T.C. (in press). Distribution and species diversity of birds and plants in fynbos vegetation of the mediterranean climate-zone, South Africa. in: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

SLINGSBY, P., & BOND, W.J. 1981. Ants - friends of the fynbos. Veld & Flora 67(2): 39-45

SMALL, F. 1973. Xeromorphy in plants as a possible basis for migration between arid and nutritionally-deficient environments. Bot. Notiser. 126: 534-539

SPECHT, R.L. 1963. Dark Island Heath (Ninety-Mile Plain, South Australia). VII. The effect of fertilizers on composition and growth, 1950-60. Aust. J. Bot. 11: 67-94

SPECHT, R.L. 1969. A comparison of the sclerophyllous vegetation characteristic of mediterranean-type climates in France, California and Southern Australia. II. Dry matter, energy and nutrient accumulation. Aust. J. Bot. 17: 293-308

SPECHT, R.L. 1970. Vegetation. Pp. 44-67 in: LEEPER, G.W. (ed.) The Australian environment. CSIRO and Melbourne University Press, Melbourne

SPECHT, R.L. 1972. The vegetation of South Australia. 328 pp. 2nd ed. Government Printer, Adelaide, South Australia

SPECHT, R.L. 1973. Structure and functional response of ecosystems in the mediterranean climate of Australia. Pp 113-120 in: DI CASTRI, F., & MOONEY, H.A. (eds) Mediterranean-type ecosystems: origin and structure. Springer-Verlag, Berlin

SPECHT, R.L. 1975. The effect of fertilizers on sclerophyll (heath) vegetation - the problems of regeneration after sand mining of high dunes. Search 6: 459-461

SPECHT, R.L. 1979a. Heathlands and related shrublands of the world. Pp 1-18 in: SPECHT, R.L. (ed.) Ecosystems of the world. Vol 9A. Heathlands and related shrublands: descriptive studies. Elsevier, Amsterdam

SPECHT, R.L. 1979b. The sclerophyllous (heath) vegetation of Australia: the eastern and central states. Pp 125-210 in: SPECHT, R.L. (ed.) Ecosystems of the world. Vol 9A. Heathlands and related shrublands: descriptive studies. Elsevier, Amsterdam

SPECHT, R.L. 1981a. Evolution of the Australian flora: some generalizations. Pp 783-806 in: KEAST, A. (ed.) Ecological biogeography of Australia. Dr. W. Junk, The Hague

SPECHT, R.L. 1981b. Primary production in mediterranean-climate ecosystems regenerating after fire. Pp 257-267 in: DI CASTRI, F., GOODALL, D.W., & SPECHT, R.L. (eds) Ecosystems of the world. Vol. 11. Mediteranean-type shrublands. Elsevier, Amsterdam

SPECHT, R.L. 1981c. Growth indices - their role in understanding the growth, structure and distribution of Australian vegetation. Oecologia 50: 347-356

SPECHT, R.L., CONNER, D.J. & CLIFFORD, H.T. 1977. The heath-savannah problem: the effect of fertilizer on sand-heath vegetation on North Stradbroke Island, Queensland. Aust. J. Ecol. 2: 179-186

SPECHT, R.L., & GROVES, R.H. 1966. A comparison of the phosphate nutrition of Australian heath plants and introduced economic plants. Austr. J. Bot. 14: 201-221

SPECHT, R.L., & MOLL, E.J. (in press). Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. in: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

SPECHT, R.L., MOLL, E.J., PRESSINGER, F., & SOMMERVILLE, J.E.M. (in press). Moisture regime and nutrient control of seasonal growth in mediterranean ecosystems. in: KRUGER, F.J., MITCHELL D.T., & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

SPECHT, R.L., & MORGAN, D.G. 1981. The balance between the foliage projective covers of overstorey and understorey strata in Australian vegetation. Aust. J. Ecol. 6: 193-202

SPECHT, R.L., & RAYSON, P. 1957a. Dark Island Heath (Ninety-mile Plain, South Australia). I. Definition of the ecosystem. Aust. J. Bot. 5: 52-85

SPECHT, R.L., & RAYSON, P. 1957b. Dark Island Heath (Ninety-mile Plain, South Australia). III. The root systems. Aust. J. Bot. 5: 103-114

SPECHT, R.L., RAYSON, P., & JACKMAN, M.E. 1958. Dark Island Heath (Ninety-mile Plain, South Australia). VI. Pyric succession: changes in composition, coverage, dry weight and mineral nutrient status. Aust. J. Bot. 6: 59-88

SPRINGETT, J.A. 1978. The effects of a single hot summer fire on soil fauna and on litter decomposition in jarrah (Eucalyptus marginata) forest in Western Australia. Aust. J. Ecol. 4: 279-291

STACE, H.C.T., HUBBLE, G.D., BREWER, R., NORTHCOTE, K.H., SLEEMAN, J.R., MULCAHY, M.J., & HALLSWORTH, E.G. 1968. 435 pp. A handbook of Australian soils. Rellim Technical Publishers, Glenside, South Australia

STEBBINS, G.L., & MAJOR, J. 1965. Endemism and speciation in the Californian flora. Ecol. Monogr. 35: 1-35

STODDART, D.M., & BRAITHWAITE, R.W. 1979. A strategy for utilization of regenerating heathland habitat by the brown bandicoot (Isodoon obesulus: Marsupialia, Peramelidae). J. Anim. Ecol. 48: 165-179

STORR, G.M. 1964. Studies on marsupial nutrition. IV. Diet of the quokka, Setonix brachyurus (Quoy & Gaimard), on Rottnest Island, Western Australia. Aust. J. Biol. Sci. 17: 469-481

STOWE, L.G., & OSBORNE, A. 1980. The influence of nitrogen and phosphorus levels in the phytotoxicity of phenolic compounds. Can. J. Bot. 58: 1149-1153

STOVER, L.E., & PARTRIDGE, A.G. 1973. Tertiary and late Cretaceous spores and pollens from Gippsland Basin, south-eastern Australia. *Proc. R. Soc. Vict. 85*: 237-286

STRIBLEY, D.P., & READ, D.J. 1980. The biology of mycorrhiza in the Ericaceae. VII. The relationship between mycorrhizal infection and the capacity to utilize simple and complex organic nitrogen sources. *New Phytol. 86*: 365-371

TAKEDA, T. 1961. Studies on the photosynthesis and production of dry matter in the community of rice plants. *Jap. J. Bot. 17*: 403-437

TAYLOR, H.C. 1978. Capensis. Pp 171-229 *in*: WERGER, M.J.A. (ed.) *The biogeography and ecology of southern Africa*. Dr. W. Junk, The Hague

TAYLOR, W. 1979. Overlap among cohabiting ciliates in their growth responses to various prey bacteria. *Can. J. Zool. 57*: 949-951

THROWER, N.J.W., & BRADBURY, D.E. 1973. The physiography of the mediterranean lands with special emphasis on California and Chile. Pp 37-52 *in*: DI CASTRI, F., & MOONEY, H.A. (eds) *Mediterranean-type ecosystems: origin and structure*. Springer-Verlag, Berlin

THROWER, N.J.W., & BRADBURY, D.E. (eds) 1977. *Chile-California mediterranean scrub atlas: a comparative analysis*. 237 pp. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa.

TILMAN, D. 1980. Resources: a graphical mechanistic approach to competition and predation. *Am. Natur. 116*: 362-393

TILMAN, D. (in press). Some thoughts on resource competition and diversity of plant communities. *in*: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) *Mediterranean-type ecosystems: the role of nutrients*. Springer-Verlag, Berlin

TOES, E. 1974. *Tellingen van kleine zoogdieren en vogels in de Jonkershoek vallei, Zuid Afrika, 1972*. 65 pp. Landbouwhogeskool, afd. Natuurbeheer en -behoud, Wageningen. Verslag no. 171.

TRUOG, E. 1946. Soil reaction influence on availability of plant nutrients. *Soil Sci. Am. Proc. 11*: 305-308

TRUSWELL, J.F. 1970. *An introduction to the historical geology of South Africa*. Purnell, Cape Town

TUREKIAN, K.K. 1972. *Chemistry of the earth*. Holt, Rinehart & Winston, New York

TWIDALE, C.R. 1976. *Analysis of landforms*. John Wiley & Sons, New York

TYNDALE-BRISCOE, H. 1975. *Life of marsupials*. 254 pp. Edward Arnold, London

VAN DER MERWE, P. 1966. Die flora van Swartboskloof, Stellenbosch, en die herstel van die soorte na 'n brand. *Ann. Univ. Stellenbosch*: *42* series A (14)

VITOUSEK, P.M., GOSZ, J.R., GRIER, C.C., MELILLO, J.M., REINERS, W.A., & TODD, R.L. 1979. Nitrate losses from disturbed ecosystems. *Science, N.Y. 204*: 469-619

VOGL, R.J., & SCHORR, P.K. 1972. Fire and manzanita chaparral in the San Jacinto Mountains, California. *Ecology 53*: 1179-1188

VOSE, H. 1973. Feeding habits of the Western Australian honey possum, *Tarsipes spencerae*. *J. Mammal. 54*: 245-247

WARBURG, M.R. , BEN-HORIN, A., & RANKEVITCH, D. 1978. Rodent species diversity in mesic and xeric habitats in the mediterranean region of northern Israel. *J. Arid Env. 1*: 63-69

WARREN-WILSON, J. 1966. Analysis of plant growth and its control in arctic environments. *Ann. Bot. 30*: 383-402

WELLINGTON, J.H.C. 1955. *Southern Africa, a geological study. Part I. Physical geography*. Cambridge University Press, Cambridge

WERGER, M.J.A. 1972. Species-area relationship and plot size: with some examples from South African vegetation. Bothalia 10: 583-594

WESTMAN, W.E. 1978. Evidence for the distinct evolutionary histories of canopy and understorey of the Eucalyptus forest-heath alliance of Australia. J. Biogeog. 5: 365-376

WESTMAN, W.E. 1979. Oxidant effects on Californian coastal sage scrub. Science 205: 1001-1003

WESTMAN, W.E. (in press). Plant community structure - spatial partitioning of resources. in: KRUGER, F.J., MITCHELL, D.T., & JARVIS, J.U.M. (eds) Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin

WESTMAN, W.E., & O'LEARY, J.F., & MALANSON, G.P. 1981. The effects of fire intensity, aspect and substrate on post-fire growth of Californian coastal sage scrub. in: MARGARIS, N.S., & MOONEY, H.A. (eds) Components of productivity of mediterranean regions - basic and applied aspects. Dr.W. Junk, The Hague

WESTMAN, W.E., & ROGERS, R.W. 1977. Nutrient stocks in a subtropical eucalypt forest, North Stradbroke Island. Aust. J. Ecol. 2: 447-460

WHITTAKER, R.H. 1977. Evolution of species diversity in land communities. Evolutionary Biology 10: 583-594

WHITTAKER, R.H., NIERING, W.A., & CRISP, M.D. 1979. Structure, pattern and diversity of a mallee community in New South Wales. Vegetatio 39: 65-76

WHITE, F. 1976. The underground forests of Africa: a preliminary review. Gdns' Bull. Singapore 29: 57-71

WIENS, D. & ROURKE, J.P. 1978. Rodent pollination in southern African Protea spp. Nature, Lond. 276: 71-73

WONG, S.C. 1979. Elevated atmospheric partial pressure of CO_2 and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C_3 and C_4 plants. Oecologia 44; 68-44

WONG, S.C., COWAN, I.R., & FARQUHAR, G.D. 1979. Stomatal conductance correlates with photosynthetic capacity. Nature, Lond. 2828: 424-426

WOODMANSEE, R.G. 1978. Additions and losses of nitrogen in grassland ecosystems. Bioscience 28: 448-453

WOOLHOUSE, H.W. 1968. Leaf age and mesophyll resistance as factors in the rate of photosynthesis. Hilger J. 11: 424-426

WOOLLEY, P. 1971. Observations on the reproductive biology of the dibbler, (Antechinus apicalis) (Marsupialia: Dasyuridae). J. R. Soc. W. Aust. 54: 99-102

YOSHIDA, S., & CORONEL, V. 1976. Nitrogen nutrition, leaf resistance and leaf photosynthetic rate of the rice plant. Soil Sci. Plant Nutr. 22: 207-211

ZOHARY, M. 1962. Plant life of Palestine. Pp 262. The Ronald Press Co., New York

APPENDIX 1. NAMES AND ADDRESSES OF INVITED WORKSHOP PARTICIPANTS

HUNTLEY B.J. (Mr), CSP: CSIR, P.O.Box 395, Pretoria 0001, SA (Workshop Chairman)

BATE G.C. (Prof), Department of Botany, University of Port Elizabeth, P.O. Box 1600, Port Elizabeth 6000, SA

BEARD J.S. (Dr), 6 Fraser Road, Applecross, Western Australia, 6153, Australia

BOND W.J. (Mr), Saasveld Forestry Research Station, Department of Environment Affairs, Private Bag X6531, George 6530, SA

BOUCHER C. (Mr), Botanical Research Unit, Department of Agriculture, P.O. Box 471, Stellenbosch 7600, SA

BREYTENBACH G.J. (Mr), Saasveld Forestry Research Station, Department of Environment Affairs, Private Bag X6531, George 6530, SA

CAMPBELL B.M. (Mr), Division of Biological Sciences, University of Zimbabwe, Box M.P. 167, Mount Pleasant, Harare, Zimbabwe

CODY M.L. (Prof), Department of Biology, University of California, Los Angeles, California 90024, USA

COWLING R.M. (Mr), Department of Botany, University of Cape Town, Private Bag, Rondebosch 7700, SA

DAY J. (Dr), Department of Zoology, University of Cape Town, Private Bag, Rondebosch 7700, SA

DEACON H.J. (Prof), Department of Archaeology, University of Stellenbosch, Stellenbosch 7600, SA

FIELD C.B. (Dr), Department of Biological Sciences, Stanford University, Stanford, California 94305, USA

FOX B. (Dr), School of Zoology, University of New South Wales, P.O.Box 1, Kensington 2033, Australia

FOX M. (Dr), Royal Botanical Gardens, Sydney 2000, Australia

FROST P.G.H. (Mr), Savanna Ecosystem Project, P.O. Boekenhout 0561, SA

FUENTES E.A. (Dr), Laboratoria de Ecologia, Instituto de Ciencias Biologicas, Universidad Catolica de Chile, Cassilla 114-D, Santiago, Chile

*GLYPHIS, J. (Mr), c/o Department of Zoology, University of Cape Town, Private Bag, Rondebosch 7700, SA

GROVES R.H. (Dr), CSIRO Division of Plant Industry, P.O.Box 1600, Canberra City, ACT 2601, Australia

GULMON S. (Dr), Department of Biological Sciences, Stanford University, Stanford, California 94305, USA

JARVIS J.U.M. (Dr), Department of Zoology, University of Cape Town, Private Bag, Rondebosch 7700, SA

KRUGER F.J. (Mr), South African Forestry Research Institute, Department of Environment Affairs, P.O.Box 727, Pretoria 0001, SA

*JONGENS-ROBERTS, S.M. (Dr), c/o Department of Botany, University of Cape Town, Private Bag, Rondebosch 7700, SA

KUMMEROW J. (Dr), Botany Department, San Diego State University, San Diego, California 92182, USA

*LAMBRECHTS, J.J.N. (Mr), Department of Soil Science, University of Stellenbosch, Stellenbosch 7600, SA

LAMONT B. (Dr), School of Biology, Western Australian Institute of Technology, Kent Street, Bentley, Western Australia 6102, Australia

LEWIS, O.A.M. (Prof), Department of Botany, University of Cape Town, Private Bag, Rondebosch 7700, SA

LINDER H.P. (Mr), Botanical Research Institute, Department of Agriculture, Private Bag X101, Pretoria 0001, SA
LOW A.B. (Mr), Curator: Cape Flats Nature Reserve, Department of Botany, University of the Western Cape, Private Bag X17, Bellville 7530, SA
MILEWSKI A.V. (Mr), Environmental & Life Sciences, Murdoch University, Murdoch 6160, Western Australia, Australia
MILLER P.C. (Prof), Systems Ecology Research Group, Department of Biology, College of Sciences, San Diego State University, San Diego, California 92182, USA
MILLER P (Mrs), Systems Ecology Research Group, Department of Biology, College of Sciences, San Diego State University, San Diego, California 92182, USA
MITCHELL D.T. (Prof), Department of Botany, University of Cape Town, Private Bag, Rondebosch 7700, SA
MOLL E.J. (Prof), Department of Botany, University of Cape Town, Private Bag, Rondebosch 7700, SA
MOONEY H.A. (Prof), Department of Biological Sciences, Stanford University, Stanford, California 94305, USA
MORROW P.A. (Dr), Department of Ecology, Univerity of Minnesota, Minneapolis, Minnesota 55401, USA
NEWSOME A.E. (Dr), Division of Wildlife Research, CSIRO, P.O.Box 84, Lyneham, Canberra ACT 2602, Australia
NOBLE R.G. (Dr), CSP: CSIR, P.O.Box 395, Pretoria 0001, SA
NORTON P.M. (Mr), Department of Nature and Environmental Conservation, Cape Provincial Administration, Private Bag X5014, Stellenbosch 7600, SA
OECHEL W.C. (Prof), Systems Ecology Research Group, Department of Biology, San Diego State University, San Diego, California 92182, USA
ORSHAN G (Prof), Department of Botany, The Hebrew University of Jerusalem, Jerusalem, Israel
*PUTTICK, G. (Dr), c/o Department of Zoology, University of Cape Town, Private Bag, Rondebosch 7700, SA
QUINN R.D. (Dr), Department of Biology, California State Polytechnic University, Pomona, California 91768, USA
RABINOVITCH A. (Dr), Chief Biologist, Nature Reserves Authority, 16 Hanatziv Street, Israel
READ D. (Dr), Department of Botany, University of Sheffield, Sheffield, S10 2TN, United Kingdom
RUNDEL P.W. (Prof), Department of Population and Environmental Biology, University of California, Irvine, California 92664, USA
RUTHERFORD M.C. (Dr), Botanical Research Institute, Department of Agriculture, Private Bag X101, Pretoria 0001, SA
SCHOLTZ, A. (Mr), Department of Archaeology, University of Stellenbosch, Crozier Street, Stellenbosch 7600, SA
SCHUTTE, K. (Dr), Department of Botany, University of Cape Town, Private Bag, Rondebosch 7700, SA
SIEGFRIED, W.R. (Prof), Percy FitzPatrick Institute for African Ornithology, University of Cape Town, Private Bag, Rondebosch 7700, SA
SOMMERVILLE, J.E.M. (Ms), Department of Botany, University of Cape Town, Private Bag, Rondebosch 7700, SA
SPECHT, R.L. (Prof), Department of Botany, University of Queensland, St Lucia, Queensland 4067, Australia
STOCK, W.D. (Mr), Department of Botany, University of Cape Town, Private Bag, Rondebosch 7700, SA
TAYLOR, H.C. (Mr), Botanical Research Unit, Department of Agriculture, P.O.Box 471, Stellenbosch, 7600, SA

TILMAN, D. (Dr), Department of Ecology, University of Minnesota. Minneapolis, Minnesota 55401, USA

VAN WILGEN, B.W. (Mr), Jonkershoek Forestry Research Station, Department of Environment Affairs, Private Bag X5011, Stellenbosch 7600, SA

WESTMAN, W.E. (Dr), Department of Geography, University of California, Los Angeles, California 90024, USA

WITTE, M. (Ms), c/o Department of Population and Environmental Biology, University of California, Irvine, California 92664, USA

---

* These individuals were unable to participate in the workshop, but contributed material to two preliminary planning sessions held during the first half of 1980, within the Fynbos Biome Project, SA.

TITLES IN THIS SERIES

1. *A description of the Savanna Ecosystem Project, Nylsvley, South Africa. December 1975. 24 pp.
2. *Sensitivity analysis of a simple linear model of a savanna ecosystem at Nylsvley. W M Getz and A M Starfield. December 1975. 18 pp.
3. *Savanna Ecosystem Project - Progress report 1974/1975. S M Hirst. December 1975. 27 pp.
4. Solid wastes research in South Africa. R G Noble. June 1976. 13 pp.
5. *Bibliography on marine pollution in South Africa. D A Darracott and C E Cloete. June 1976. 131 pp.
6. *Recycling and disposal of plastics waste in South Africa. R H Nurse, N C Symington, G R de V Brooks and L J Heyl. June 1976. 35 pp.
7. *South African Red Data Book - Aves. W R Siegfried, P G H Frost, J Cooper and A C Kemp. June 1976. 108 pp.
8. South African marine pollution survey report 1974-1975. C E Cloete and W D Oliff (editors). September 1976. 60 pp.
9. Modelling of the flow of stable air over a complex region. M T Scholtz and C J Brouckaert. September 1976. 42 pp.
10. Methods and machinery for pulverising solid wastes. M J Simpkins. October 1976. 29 pp.
11. *South African Red Data Book - Small mammals. J A J Meester. November 1976. 59 pp.
12. Savanna Ecosystem Project - Progress report 1975/1976. B J Huntley. March 1977. 41 pp.
13. Disposal and recovery of waste paper in South Africa. G R de V Brooks. April 1977. 35 pp.
14. South African Red Data Book - Fishes. P H Skelton. July 1977. 39 pp.
15. *A checklist of the birds of the Nylsvley Nature Reserve. W R Tarboton. September 1977. 14 pp.
16. *Grondsoorte van die Nylsvley-natuurreservaat. H J von M Harmse. September 1977. 64 pp.
17. Description and manual for the use of DRIVER - an interactive modelling aid. P R Furniss. September 1977. 23 pp.

18. South African Red Data Book - Large mammals. J D Skinner, N Fairall and J du P Bothma. November 1977. 29 pp.

19. Introducing you to satellite operated Data Collection Platforms (DCP's). C C Stavropoulos. September 1977. 9 pp.

20. A phytosociological classification of the Nylsvley Nature Reserve. B J Coetzee, F van der Meulen, S Zwanziger, P Gonsalves and P J Weisser. December 1977. 31 pp.

21. An annotated checklist of the amphibians, reptiles and mammals of the Nylsvley Nature Reserve. N H G Jacobsen. December 1977. 65 pp.

22. *Cooperative National Oceanographic Programme. SANCOR. January 1978. 19 pp.

23. *South African Red Data Book - Reptiles and amphibians. G R McLachlan. February 1978. 53 pp.

24. *Guidelines for the disposal of dangerous and toxic wastes so as to minimize or prevent environmental and water pollution. R T Rudd. January 1978. 12 pp.

25. Richards Bay mesometeorological data. Vertical profiles of air temperature and wind velocity and surface wind statistics. M T Scholtz, E T Woodburn, C J Brouckaert and M Mulholland. March 1978. 104 pp.

26. *Studies of mineralization in South African rivers. G C Hall and A H M Gorgens (editors). March 1978. 24 pp.

27. Nylsvley - A South African Savanna Ecosystem Project: objectives, organization and research programme. March 1978. 37 pp.

28. *A description of the Fynbos Biome Project. June 1978. 25 pp.

29. *Savanna Ecosystem Project - Phase I summary and Phase II progress. B J Huntley and J W Morris. July 1978. 52 pp.

30. *Review of Coastal Currents in Southern African Waters. T F W Harris. August 1978. 106 pp.

31. *Report of the Task Group on Fermentation Technology. R J Andrews, J A de Villiers, P M Lategan, F G Neytzell-de Wilde, J P van der Walt and Professor D R Woods. September 1978. 16 pp.

32. South African programme for the SCOPE mid-term project on the ecological effects of fire. September 1978. 36 pp.

33. Fire in South African ecosystems: an annotated bibliography. G U Schirge and A H Penderis. October 1978. 114 pp.

34. Inland water ecosystems in South Africa : a review of research needs. R G Noble and J Hemens. November 1978. 150 pp.

35. *South African Antarctic Research Programme, 1978-1982. SASCAR. December 1978. 39 pp. Out of print but partially replaced by No 50.

36. *Aboveground biomass subdivisions in woody species of the Savanna Ecosystem Project Study Area, Nylsvley. M C Rutherford. January 1979. 33 pp.

37. *Marine Line Fish Research Programme. SANCOR. April 1979. 17 pp.

38. *The Southern Ocean - South African Cooperative Research Programme. SANCOR. May 1979. 26 pp.

39. The Transfer of Pollutants in Two Southern Hemispheric Oceanic Systems. Proceedings of a workshop held at Plettenberg Bay, South Africa, 23-26 April 1979. October 1979. 188 pp.

40. Fynbos ecology : a preliminary synthesis. J Day, W R Siegfried, G N Louw and M L Jarman. December 1979. 166 pp.

41. *Bibliography of Marine Biology in South Africa. D A Darracott and A C Brown. February 1980. 250 pp.

42. Advances in understanding phosphorus cycling in inland waters - their significance for South African limnology. A J Twinch and C M Breen. March 1980. 22 pp.

43. Terrestrial ecology in South Africa - project abstracts for 1978. February 1980. 92 pp.

44. A manual of methods for use in the South African Marine Pollution Monitoring Programme. R J Watling. July 1981. 82 pp.

45. Threatened plants of Southern Africa. A V Hall, M de Winter, B de Winter and S A M van Oosterhout. May 1980. 244 pp.

46. South African legislation with respect to the control of pollution of the sea. André Rabie. January 1981. 73 pp.

47. Terrestrial ecology in South Africa and South West Africa - project abstracts for 1979. May 1981. 107 pp.

48. A bibliography of seabirds in the waters of southern Africa, the Prince Edward and Tristan Groups. J Cooper and R K Brooke. December 1981. 297 pp.

49. National Geoscience Programme. The Evolution of Earth Resource Systems. SACUGS. June 1981. 42 pp.

50. South African Antarctic Biological Research Programme. SASCAR. July 1981. 54 pp.

51. South African Marine Pollution Monitoring Programme 1979-1982. R J Watling and C E Cloete (editors). July 1981. 52 pp.

52. Structural characterization of vegetation in the Fynbos Biome. B M Campbell, R M Cowling, W J Bond and F J Kruger in collaboration with D P Bands, C Boucher, E J Moll, H C Taylor and B W van Wilgen. August 1981. 19 pp.

53. A bibliography of fynbos ecology. M L Jarman, R M Cowling, R Haynes, F J Kruger, S M Price and G Moll. August 1981. 73 pp.

54. A description of the Benguela Ecology Programme 1982-1986. SANCOR: (W R Siegfried and J G Field editors). March 1982. 39 pp.

55. Trophic Ecology of Lepidoptera Larvae associated with woody vegetation in a Savanna Ecosystem. C H Scholtz. June 1982. 29 pp.

56. Man and the Pongolo floodplain. J Heeg and C M Breen. June 1982. 117 pp.

57. An inventory of plant communities recorded in the western, southern and eastern Cape Province, South Africa up to the end of 1980. C Boucher and A E McDonald. September 1982. 58 pp.

58. A bibliography of African inland water invertebrates (to 1980). B R Davies, T Davies, J Frazer and F M Chutter. September 1982. 418 pp.

59. An annotated checklist of dung-associated beetles of the Savanna Ecosystem Project study area, Nylsvley. S Endrödy-Younga. September 1982. 34 pp.

60. The termites of the Savanna Ecosystem Project study area, Nylsvley. P Ferrar. September 1982. 42 pp.

61. Conservation of Ecosystems: Theory and Practice. A report on a workshop meeting held at Tsitsikama, South Africa, September 1980. Edited by W R Siegfried and B R Davies. September 1982. 97 pp.

62. A description of the Grassland Biome Project. Edited by M T Mentis and B J Huntley. October 1982. 29 pp.

63. Description of a fire and its effects in the Nylsvley Nature Reserve: A Synthesis Report. M V Gandar. October 1982. 39 pp.

64. Terrestrial ecology in South Africa - project abstracts for 1980-1981. December 1982. 148 pp.

65. Alien invasive vascular plants in South African natural and semi-natural environments: bibliography from 1830. V C Moran and P M Moran. December 1982. 42 pp.

66. Environmental Research Perspectives in South Africa. December 1982. 39 pp.

67. The Sancor Estuaries Programme 1982-1986. February 1983. 43 pp.

68. The Sancor Programme on Coastal Processes. April 1982 - March 1988. Edited by D H Swart. February 1983. 29 pp.

69. Guidelines for the management of large mammals in African conservation areas. The proceedings of an international workshop held at Olifants Camp, Kruger National Park, South Africa. Edited by A A Ferrar. May 1983. 95 pp.

70. Marine Linefish Programme Priority Species List. Sancor. Edited by J H Wallace and R P van der Elst. May 1983. 113 pp.

71. Mineral nutrients in mediterranean ecosystems. Edited by J A Day. June 1983. 165 pp.

*Out of print.